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Integrating dispersal and social learning in wild vervet monkeys (Chlorocebus pygerythrus)

Dongre Pooja

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et de médecine

Département de Ecology and Evolution

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Thèse de doctorat ès sciences de la vie (PhD)

présentée à la

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par

Pooja DONGRE

Psychologue diplômée ou Master de l'Université de St. Andrews.

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pour le Doyen
de la Faculté de biologie et de médecine

Prof. Liliane Michalik

Contents

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Abstract (English)

Research attention on dispersers is lacking, due to the additional challenges of following them in the wild. In particular, research may have overlooked the impact of social learning on dispersers, and the contributions of dispersers to behavioural adaptation and social transmission of novel behaviours, due to a major focus on philopatric individuals. The studies within this thesis combined the methods of experimental and observational research in the field, and literature review to address this gap.

Chapter 1 presents field experimental evidence that dispersing males may contribute to the generation and spread of novel behaviours in a population. Chapter 2 explores patterns of correlation between maternally inherited rank in the natal group and grooming and rank acquisition post-dispersal. This chapter explores the possibility that social learning experiences as a juvenile, related to maternal rank, influence development of social competence in dispersing males, with potential fitness consequences. Finally, Chapter 3 makes the case that social benefits of social learning in animals, such as increased affiliation, may have been prematurely dismissed, due to a focus the value of information transmitted. We propose novel research questions, including whether conforming to group typical behaviour may be a strategy for dispersers to integrate into new groups.

Together, these results suggest that dispersing animals might operate with different social learning biases to philopatric individuals, due to the different selective pressures set up by the process of dispersal. Moreover, they may be more important in the generation and spread of behavioural adaptations than previously acknowledged. This has important implications for population fitness, as it suggests dispersers could facilitate behavioural adaptation to rapid environmental change, at a faster rate than genetic adaptation. Our results open up new questions that should inspire future work. For example, if immigrants are important for generating and transmitting information around a population, whilst also learning socially from residents, how does the social or ecological context influence the social learning biases they use? Furthermore, if maternal rank contributes to variation in the development of social competence, which impacts future fitness, what mechanisms govern this? These studies provide new bases upon which future work can build, and incorporation of technological aides, such as biologging to follow dispersers outside of studied groups will be beneficial. The perspectives developed here should be interesting and informative to empirical and theoretical scholars of behavioural ecology and evolutionary biology as well as primatology and comparative and evolutionary psychology.

Abstract (Français)

Les migrants ne font pas l'objet d'une attention particulière de la part de la recherche, en raison des défis supplémentaires que représente leur suivi dans la nature. En particulier, la recherche peut avoir négligé l'impact de l'apprentissage social sur les migrants, et les contributions des migrants à l'adaptation comportementale et à la transmission sociale de nouveaux comportements, en raison de l'accent mis sur les individus philopatriques. Les études menées dans le cadre de cette thèse ont combiné des méthodes de recherche expérimentale et d'observation sur le terrain, ainsi qu'une revue de la littérature pour combler cette lacune.

Le chapitre 1 présente les preuves expérimentales sur le terrain que les mâles migrants peuvent contribuer à la génération et à la propagation de comportements nouveaux dans une population. Le chapitre 2 explore des modèles de corrélation entre le rang hérité de la mère dans le groupe natal et le toilettage et l'acquisition du rang après la migration. Ce chapitre explore la possibilité que les expériences d'apprentissage social à l'âge juvénile, liées au rang maternel, influencent le développement de la compétence sociale chez les mâles migrant, avec des conséquences potentielles sur leur fitness. Enfin, le chapitre 3 montre que les avantages sociaux de l'apprentissage social chez les animaux, tels que l'augmentation de l'affiliation, peuvent avoir été prématurément écartés, en raison d'une focalisation sur la valeur des informations transmises. Nous proposons de nouvelles questions de recherche, notamment si le fait de se conformer au comportement typique du groupe peut être une stratégie pour les migrants afin de s'intégrer dans de nouveaux groupes.

Ensemble, ces résultats suggèrent que les animaux migrants pourraient fonctionner avec des biais d'apprentissage social différents de ceux des individus philopatriques, en raison des pressions sélectives différentes mises en place par le processus de migration. De plus, ces biais pourraient être plus importants dans la génération et la propagation des adaptations comportementales que ce qui a été reconnu jusqu'à présent. Cela a des implications importantes pour l'aptitude des populations, car cela suggère que les migrants pourraient faciliter l'adaptation comportementale aux changements environnementaux rapides, à un rythme plus rapide que l'adaptation génétique. Nos résultats ouvrent de nouvelles questions qui devraient inspirer les travaux futurs. Par exemple, si les immigrants sont importants pour générer et transmettre des informations autour d'une population, tout en apprenant socialement des résidents, comment le contexte social ou écologique influence-t-il les biais d'apprentissage social qu'ils utilisent ? En outre, si le rang maternel contribue à la variation du développement de la compétence sociale, qui a un impact sur la condition physique future, quels sont les mécanismes qui régissent cette variation ? Ces études fournissent de nouvelles bases sur lesquelles les travaux futurs pourront s'appuyer, et l'incorporation d'aides technologiques, comme la bio-localisation pour suivre les migrants en dehors des groupes étudiés, sera bénéfique. Les perspectives développées ici devraient être intéressantes et instructives pour les chercheurs empiriques et théoriques en écologie comportementale et en biologie évolutive, ainsi qu'en primatologie et en psychologie comparative et évolutive.

General Introduction

This thesis presents a project that aimed to study the causes and consequences of social learning in dispersing male vervet monkeys (*Chlorocebus pygerythrus*) in the wild. In what follows I aim to introduce relevant concepts, beginning with why animals live in groups, and two important mechanisms – dominance hierarchies and dispersal – that have evolved to deal with the challenges of group living. The dispersal of animals between groups around a population is well understood to facilitate gene flow, with consequences for population fitness and dynamics. Importantly, recent work has suggested that in species that learn socially, and potentially have group-level and population-level traditions, dispersers are likely to influence cultural evolution too. Therefore, I end the introduction with a background to social learning and culture, in which researchers have gained deeper insights into social learning biases of the philopatric sex. With this, I aim to set the scene for this thesis, in which my colleagues and I explored some important aspects of how the dispersing sex in vervet monkeys may influence and be influenced by the residents in groups that they join, via social learning, and their potential impact on cultural change.

Evolution of social groups

Through the process of natural selection (Darwin, 1859), where the evolutionary benefits of living together in groups outweigh the costs, selection pressures shape animals to live socially (Alexander, 1974). Benefits of sociality include predator avoidance, foraging efficiency through information transmission and intragroup defence of resources, while costs include intragroup competition for resources and disease transmission (Krause & Ruxton, 2002). Social life is extremely diverse, and social systems have evolved in insects (Wilson, 1971), reptiles (Halliwell, Uller, Holland, & While, 2017), birds (Beauchamp, 2010) and mammals (Clutton-Brock, 2021). Animal groups are diverse on various dimensions, such as average or maximum group size, group stability, social structure, breeding systems and mating systems (Clutton-Brock, 2021; Taborsky, Cant, & Komdeur, 2021). Diversity among social systems arises because once groups form, self-reinforcing social mechanisms evolve within them, which further enhance the benefits and decrease the costs of sociality, giving rise to the emergence of various social phenomena (Alexander, 1974; Hemelrijk, 2005). Dominance hierarchies are an example of self-organised emergent phenomena that arise due to competition for resources, which causes intragroup aggression. Due to new selective pressure emerging from this aggression, further mechanisms emerge whereby individuals generalise the outcomes of conflicts over resources – whether they win or lose – to other group members, and stable hierarchies emerge (Hobson & DeDeo, 2015; Leimar, 2021). The rate of aggression decreases, as subordinate individuals avoid conflicts by deferring resources to more dominant individuals, and generally positioning themselves further away. Targets of direct aggression thus become restricted to those close in rank, probably due to lower deference of resources and closer proximity. Overall levels of costly aggression are therefore reduced, and limited resources are distributed. The benefits of these outcomes outweigh the costs of both, not living in a group, and the initial aggression itself. This process demonstrates how novel circumstances, here, a formed group that brings about conflict over resources, can set up selective pressures that shape novel traits and give rise to emergent phenomena. The novel trait shaped here is the future deference by the conflict loser, and the emergent property is the eventual stable dominance hierarchy. Properties of the emergent feature are dependent on variable circumstances, such as the level of competition imposed by the environment or individual differences in the behaviour of actors in the system. This can produce great emergent diversity. Macaques (genus *Macaca*) provide evidence of diverse dominance hierarchy dynamics among closely related species (Sueur et al., 2011; Thierry, 2008). The steepness of species' dominance hierarchies range from highly despotic (very steep hierarchy with high intolerance of subordinates by dominants, e.g. *M. mulatta* & *M. fuscata*) to highly tolerant (relatively flat with greater tolerance of subordinates, e.g. *M. tonkeana* & *M. nigra* ; see Table 1 in Thierry, 2008). Interestingly, the more despotic species show lower frequencies and intensities of aggression, but the more tolerant species, which show aggression more frequently, engage in a greater diversity of reconciliatory behaviours (Thierry, 2008).

An experiment in captive monk parakeets (*Myiopsitta monachus*) investigated the dynamics of dominance hierarchy establishment by mimicking natural group formation (Hobson & DeDeo, 2015). The fundamental social units of this species are pairs, or sometimes trios, which flock together with other pairs/trios, following fission-fusion dynamics, with moderately linear dominance hierarchies (Hobson, Avery, & Wright, 2014). By experimentally separating and re-mixing captive groups into new groups with low overlap of previously co-habiting pairs/trios, Hobson & DeDeo (2015) created a situation in which they could observe dynamics of hierarchy formation. Their results concur with the results of modelled self-organising hierarchies (Hemelrijk, 1999, 2002). Hobson & DeDeo's (2015) study is an excellent example of how the flexibility of controlled experiments in captivity can contribute to some aspects of our understanding of the evolution of sociality. This study worked because dominance hierarchies will arise whenever researchers place social animals together, making it possible to study their dynamics in captivity. However, there may still be limitations to captive studies of dominance, for example, a confined captive environment may induce artificial pressure on the expression of aggression, as individuals will not have the freedom to move away and avoid a conflict as they would if unconfined in the wild. Moreover, some aspects of social phenomena that occur in the wild may simply not be amenable to study in captivity, if researchers cannot accurately replicate the pressures that influence particular behaviours. One example is the process of dispersal, a central theme to this thesis.

Dispersal

Dispersal is the widespread phenomenon whereby animals leave (emigrate from) one group (or area) and join (immigrate into) another in order to mate with unrelated individuals (Greenwood, 1980). This movement can occur from the group/area where the individual was born (*natal dispersal*), or between subsequent breeding groups/areas (*secondary dispersal*) (Pusey & Packer, 1987). Dispersal is a highly risky process as dispersers temporarily forgo all the benefits of living in a group, becoming more conspicuous to predators, and/or move through unknown areas where their knowledge of resources and predators is limited. Nonetheless, the overall benefits of inbreeding avoidance, and potentially improved access to mates, outweigh these costs, and dispersal persists, facilitating gene flow around populations (Greenwood, 1980; Howard, 1960; Pusey & Packer, 1987). Given the intense risks associated with dispersing, adaptive mechanisms govern when and by whom emigration takes place to optimise fitness. Insights into these mechanisms have come from field studies, as captive environments cannot provide realistic scenarios in which to recreate the pressures acting on behaviour in this context.

Species vary according to which individuals disperse. Due to the function in inbreeding avoidance, sex-biased dispersal arises due to differential investment in offspring production and care, particularly in birds and mammals, and the biases vary according to species' mating systems. In birds, which are mostly monogamous, females are most likely to disperse because the cost of inbreeding is higher due to the energy invested in producing an egg. In polygynous and polygynandrous mammals, males tend to disperse due to increased competition for mates between males relative to females and female choice shaped by kin-recognition (and therefore a preference to mate with unfamiliar males). Among the few monogamous mammals, there is no strong sex-bias in dispersal (Greenwood, 1980; Lehmann & Perrin, 2003). These patterns generally appear to hold across the diverse primate mating systems (which include monogamy, polygyny, polyandry and polygynandry; Kappeler & van Schaik, 2002). In some instances, additional female dispersal occurs alongside male dispersal in some polygynandrous species. This usually corresponds with other proximate triggers such as infanticide by immigrant males or degradation of local resource availability (Jack & Isbell, 2009). Furthermore, it demonstrates flexibility among primate social systems at the level of individual behaviour (Henzi et al., 2013). Primate social systems are also diverse in terms of group structure, including from solitary, pair-bonded, multi-male multi-female, male harems (single male with multiple females), and multi-level societies made up of smaller male harems which associate together in larger groups or aggregations (Kappeler & van Schaik, 2002). Due to the complexity and diversity of their social systems, primates have held considerable research attention from long-term observational field studies. These studies have attempted to understand details of species-specific dispersal patterns (e.g. Alberts & Altmann, 1995; Cheney & Seyfarth, 1983; Romano, Martins, & Ruiz-Miranda, 2019; and reviewed in Jack & Isbell, 2009). Researchers have explored the proximate mechanisms triggering dispersal in primates, with some indications that hormonal levels (e.g. Akinyi et al., 2017; Toda et al., 2022), aggression from residents (e.g. van Blerk, 2021) and relative reproductive opportunity (Wikberg et al., 2022) may trigger dispersal. In addition, the availability of co-dispersers that may help mitigate the risk of dispersal may also influence dispersal timing. Nonetheless, variation in individual dispersal strategies is expected depending on the specific combinations of circumstances for each disperser (Jack & Isbell, 2009).

Cercopithecine primates, tend to live in multi-male multi-female groups, with male-biased dispersal. Research on captive populations has been valuable in examining, in particular, how resident females and groups’ social structures respond to introductions of new males (Balasubramaniam, Beisner, Mccowan, & Bloomsmith, 2021; Rox, 2020; Rox, van Vliet, Sterck, Langermans, & Louwerse, 2019; Rox, Vries, Louwerse, & Sterck, 2018). These studies created conditions resembling male dispersal between captive groups of rhesus and long-tailed macaques (*Macaca mulatta* and *fascicularis*, respectively) by utilising routine between-group transfers of males by animal carers that are carried out to allow expression of natural behaviour by captive animals (Balasubramaniam et al., 2021; Rox, 2020). For the contexts of these studies, this procedure worked well, facilitating collection of large, reliable datasets with high levels of observability of the animals (Rox, 2020; Rox et al., 2019, 2018). This demonstrates the usefulness of the experimental and observational control possible in captive studies of post-immigration social interactions. However, this method is not suitable to study other aspects of dispersal, such as the triggers of dispersal nor how males decide which groups to join. In addition, whilst these studies are of great use for animal welfare, the captive setting may influence social interactions between residents and immigrants, and whether results can be generalised beyond captivity is not clear.

Technological methods of analysing genetic data, which can be collected from the field instantaneously and analysed in a laboratory, have facilitated a detailed understanding of the role of dispersers in gene flow and their contribution to the genetic structure of populations. In contrast, practical difficulties in following dispersers in the field when they leave long-term study groups have considerably hindered behavioural research on them (De Moor, Roos, Ostner, & Schülke, 2020; Jack & Isbell, 2009; Kajokaite, Whalen, Koster, & Perry, 2022; Sugiyama, 1976). One aspect that has received some attention is the possibility that dispersers bring novel behaviours or information into groups, from which group-mates can learn (Barrett, McElreath, & Perry, 2017; McDougall, Forshaw, Barrett, & Henzi, 2010; Samuni, Mundry, Terkel, Zuberbühler, & Hobaiter, 2014). Information transmitted by dispersers can influence change faster than genetic adaptations, thus influencing population fitness. Consequently, understanding disperser induced behavioural changes in social groups and their potential fitness consequences deserves more attention.

Social learning and culture

Social learning is “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products” (Heyes, 1994). It has been found to influence a range of behavioural contexts across diverse taxa, from mate choice in fruit flies, vocal dialects in songbirds to hunting techniques in whales (recently reviewed in: Kendal et al., 2018; Whiten, 2021). Unlike transmission via genes, social learning can lead to the spread of novel behaviours along multiple axes – vertically from parents to offspring (as in genetic adaptation) and reverse-vertically from offspring to parents, as well as horizontally among related or unrelated members of the same generation, or obliquely between unrelated members of different generations. This can happen rapidly, and, if learned behaviours persist throughout different generations of a group, can generate group-level traditions (Whiten, 2005). Social learning may seem inherently adaptive, because it saves individuals the costs of directly acquiring information from the environment, which can be risky, for example through exposure to unknown toxins in novel foods or exposure to unknown predators in a new environment. However, social learning can also lead to the spread of costly behaviours based on outdated information, and as the number of individuals that learn socially in a group increases, the direct relevance of the information to the current environment is predicted to decrease (Barrett, Zepeda, Pollack, Munson, & Sih, 2019; Laland, 2004). Therefore, researchers initially hypothesised heuristic rules governing what, when and from whom social learning takes place (Laland, 2004) to optimise fitness benefits of social learning and mitigate the associated risks. Research has since discovered that whilst social learning is often biased, there is great variation and flexibility between which kinds of biases occur and when (Kendal et al., 2018).

Social learning can be biased in relation to the either the content or the context of the learned behaviour, and biases are found across taxa including insects, fish and mammals (Kendal et al., 2018). For example, content-biases relate to characteristics of the behaviour itself, such as the relative payoff of two alternatives. Context-biases relate to other contextual features, for example, of the behaviour to be learned (e.g. its frequency in the population), traits of the demonstrator (e.g. adult or juvenile), or the learner’s own state (e.g. level of uncertainty or lack of information; Kendal et al., 2018). Among primates, context-biases identified include age- and rank-biases, whereby social information is used more by younger individuals in tufted capuchins (*Sapajus apella*) and humans (*Homo sapiens*; Bolhuis, Okanoya, & Scharff, 2010; Coelho et al., 2015), and lower ranked vervet monkeys and chimpanzees (*Pan troglodytes*; Canteloup, Cera, Barrett, & van de Waal, 2021; Canteloup, Hoppitt, & van de Waal, 2020; Kendal et al., 2015). Chimpanzees also preferred higher ranked demonstrators (Kendal et al., 2015). Similarly, older and higher ranked demonstrators were preferred by capuchins (Coelho et al., 2015). In vervet monkeys a sex-bias was found, with individuals preferentially learning from philopatric females (van de Waal, Renevey, Favre, & Bshary, 2010), and a bias to copy when uncertain has been identified in humans (Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012; Toelch, Bruce, Newson, Richerson, & Reader, 2014) and chimpanzees (Kendal et al., 2015). Frequency-biased social learning (another contextual bias) has been identified in two ways – a bias to copy the behaviour of most numerous individuals or to copy the most frequently observed behaviour, which may or may not coincide. Evidence has been found of the former in human children and chimpanzees (Haun, Rekers, & Tomasello, 2012), and a weak effect of the latter in vervet monkeys (Canteloup et al., 2021). Furthermore, a bias to preferentially learn behaviours that obtain a higher payoff (payoff-bias), has been identified in vervet monkeys (Bono et al., 2018; Canteloup et al., 2021), white-faced capuchins (*Cebus capucinus* ; Barrett et al., 2017) and chimpanzees (Vale et al., 2017; Van Leeuwen, Cronin, Schütte, Call, & Haun, 2013). It is clear from this list that multiple biases exist within species, and the combinations of contexts and contents of behaviour are likely to affect individuals’ biases in a complex manner that can be difficult to tease apart. Furthermore, social learning biases can constrain the flow of information within groups, as well as the potential for dispersers to transmit information between groups.

Group-level traditions, or cultures, are socially learned behaviours that are common in a group, and can be identified through observations of intergroup behavioural variation that is not attributable to genetic or ecological differences (Boesch & Tomasello, 1998; Whiten, 2017; Whiten et al., 1999). Since early observations of probable group-level traditions among chimpanzees (Boesch & Tomasello, 1998; Whiten et al., 1999), cultural behaviour has been identified in a wide range of animal taxa (reviewed in: Whiten, Ayala, Feldman, & Laland, 2017). In addition, as early as the mid-20th century, researchers observed the spontaneous, emergence and spread of novel traditions in groups of titmice of opening milk bottles (Fisher & Hinde, 1949), and in groups of Japanese macaques of washing sweet potatoes in salty sea water (Kawai, 1965). Moreover, tentative evidence for the intergroup transmission of cultural behaviour by dispersers exists in Japanese macaques (Leca, Gunst, & Huffman, 2007) where inter-group comparisons of variation in stone-handling behaviour strongly suggest that immigrants have transmitted behavioural variants around a population. Similarly, in chimpanzees, the emergence and spread of complex tool use appeared to be linked to immigrants that possessed prior skills with them, suggesting that they already knew these methods from their prior groups (Biro et al., 2003; O'Malley, Wallauer, Murray, & Goodall, 2012). An immigrant chimpanzee also appears to have socially influenced her new group during researcher habituation (Samuni et al., 2014). Similar observations have been made in capuchins in both foraging and social behavioural domains (Barrett et al., 2017; Perry et al., 2003). Direct observations of intergroup transmission by dispersers are, however, difficult to obtain in the wild, where real-world pressures are likely to influence social learning biases in ways that could promote or inhibit this mode of transfer. On the other hand, if dispersers immigrate into groups with different traditions, how might they respond? Experiments in wild vervet monkeys and great tits (*Parus major*), in which groups were trained with alternative food preferences (thus establishing group-level traditions), found that upon arrival in new groups, immigrants switched their preferences to match their new groups' preferences (Aplin et al., 2015; van de Waal, Borgeaud, & Whiten, 2013). Further evidence from chimpanzees also suggests that in some cases, immigrants abandon their own behavioural preferences for group preferences (Luncz & Boesch, 2014). It is clear that social learning surrounding dispersers can operate in various ways, with information transmitted from them to their new groups and from their new groups to them, each with opposing effects. One results in the maintenance of group-level cultures and the other spreads group-level culture to the population-level. With evidence of both, further research is required to understand what influences which occurs.

Whilst dispersal, on the one hand, is a relatively well-understood phenomenon, social learning and culture are relatively new fields of research with much left to uncover. The intersection of the two is, in particular, an area of great interest. As described earlier, dispersal is a period of intense risk. Alongside what we understand about social learning biases, this raises potentially conflicting expectations for how these conditions might affect dispersers' behaviour. On the one hand, they may be inherently more prone to risk-taking and therefore exploring and obtaining novel information directly from the environment, which can lead to innovation (see Chapter 1). On the other hand, they may be highly susceptible to social information, when available, which might be due to uncertainty, or due to the potential for social learning to facilitate similarity-based social bonding (see Chapter 3). Indeed, evidence of a similar contrast has been found in children, who are more likely to learn socially when uncertain, but have also been found to innovate more when uncertain (Carr, Kendal, & Flynn, 2015).

Study site and species

Vervet monkeys are a Cercopithecine primate that live in multi-male multi-female groups. Females are philopatric and males disperse multiple times throughout their lives, usually to neighbouring groups (Cheney & Seyfarth, 1983). They are geographically distributed widely throughout Southern-Eastern parts of the African continent (Fig. 1A) and inhabit a wide range of habitats, including the savannah biome, coastal areas and urban areas (Thatcher, Downs & Koyama, 2019). The home ranges of the groups studied in the research presented here are situated within the Mawana Game Reserve, KwaZulu Natal, South Africa – a 12,000 hectare private game reserve (Fig. 1A). The Inkawu Vervet Project (IVP) research site is a smaller area within this reserve (Fig. 1B). The home ranges of the vervet monkey study population contain areas of mosaic savannah biome with open grassland and clumped bushveld, dense acacia thickets (in areas previously used for agriculture), and riparian woodland. Some human artefacts and old structural ruins remain within the area, but are disused, except for one house in which a ranger of the reserve resides (within the BD home range). Parts of the reserve outside of the research area are used for hunting. The IVP researchers' quarters are on the edge of one group's home range (NH) but the group has never entered the grounds of the building.

Researchers at IVP regularly follow three to six habituated groups of vervet monkeys (home ranges shown in Fig. 1B). Habituation began in 2010 in four groups: AK, BD, LH and NH, and two more, KB and CR were added to the study population in 2013 and 2014 respectively. The relatively open habitat and semi-terrestrial semi-arboreal nature of vervet monkeys allows good visibility conditions for observational behavioural research. Highly overlapping territories (Fig. 1B) and frequent male dispersal make them a good model species in which to study dispersal. Furthermore, their wide distribution among diverse habitats suggests the species are highly adaptable to novel environmental affordances (also see Forss et al., 2022). Alongside a great deal of previous work on social learning research within groups of this species (e.g. Botting et al., 2018; Bono et al., 2018; Canteloup et al., 2020, 2021; van de Waal et al., 2010; van de Waal et al., 2013), there is a good existing baseline for further work on social learning, particularly switching the focus to dispersers, and studies of intergroup transmission of behavioural adaptations.

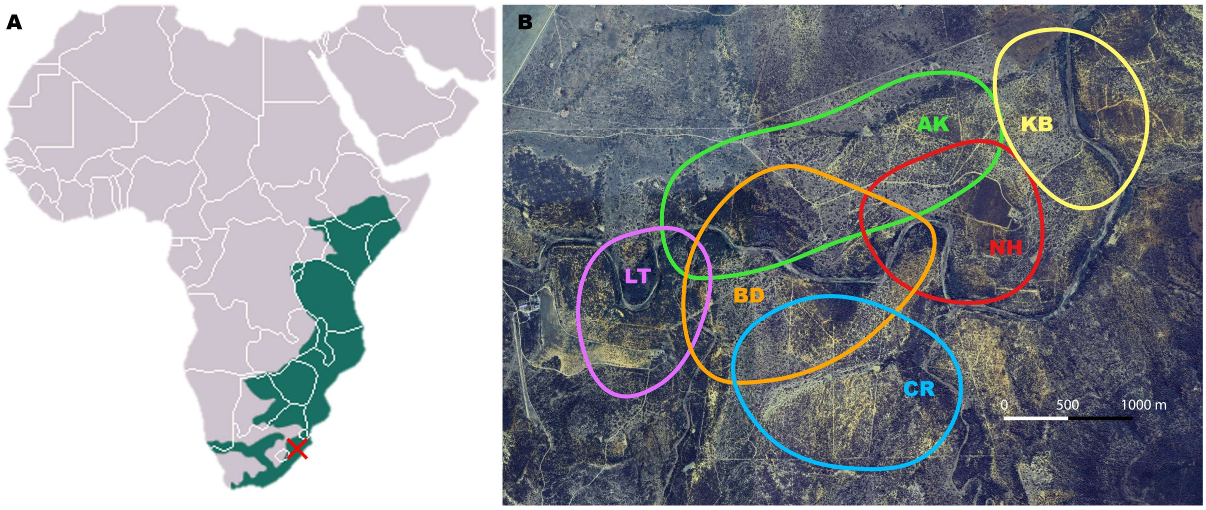

Figure 1. A: Geographical distribution of vervet monkeys (Chlorocebus pygerythrus; image by *Chermundy*, with distribution data from IUCN Red List, licenced under CC BY-SA 3.0; accessed via Wikimedia). The red 'X' marks the location of the Inkawu Vervet Project (IVP) field site. B: Aerial view of IVP and the six habituated groups' home ranges.

Summary of results

Chapter 1. Role of immigrant males and muzzle contacts in the uptake of a novel food by wild vervet monkeys. (*Under review*, eLife. Joint first author)

Exploiting novel resources, particularly potential foods, is a risky endeavour if individuals have not encountered them before, as unknown items may contain toxins. We presented a novel food, peanuts, to five groups of vervet monkeys. We found evidence that recently immigrated males might be more prone to eating novel foods, which we interpret in light of heightened risk proclivity surrounding the dispersal period. Furthermore, we observed that males could transfer knowledge of the novel food between groups. Finally, our results suggest that, whilst an infant also innovated, and began extracting and eating peanuts, their group members did not follow them in doing so. This study provides evidence that immigrant males may facilitate innovation to exploit novel resources and their spread in populations via intergroup transfer.

Chapter 2. Does maternal rank predict rank acquired and grooming patterns of wild male vervet monkeys after their natal dispersal? (First author)

Long-term field research on the fitness consequences of social behaviour has historically focussed on philopatric individuals out of convenience. Understanding the links between social behaviour and fitness in dispersers is important too. Utilising a long-term database, spanning eleven years, we investigated whether maternally inherited dominance rank of ten juvenile males predicted their social outcomes during the first year in their immigration groups, following dispersal from the natal group. We found significant negative correlations between maternal rank and frequencies of grooming given and received. We also find a potential a negative association between maternal rank and rank acquired in the new group. We propose that low rank during juvenescence may provide more opportunities to learn social competence, which influences males' grooming behaviour post-dispersal. This in turn may influence their rank acquisition, which suggests that their early social learning experiences can influence later fitness-related outcomes.

Chapter 3. A natural history of conformity. (Joint first author)

In this review, we combine evidence from literatures rarely considered alongside one another that suggests that when immigrants conform to their new groups' traditions, forgoing their own knowledge of alternative behavioural variants, this may serve a social function – to socially integrate. Previous research efforts social learning biases have attempted to study these processes analogously to biological or genetic evolution, viewing the most important feature of social learning to be the adaptive value of the information transmitted. This field has therefore neglected the potential social benefits of learning socially. We review literature suggesting that: alike animals associate more; in primates, imitating others leads to increased affiliation; and, that an unconscious form of imitation (rapid facial mimicry) is linked to longer social interactions, potentially facilitating stronger social bonds. Given the proliferation of research driven by the perspective that social learning biases are governed primarily by optimal information acquisition, the evidence that we review suggests greater attention is required to social motivations for social learning.

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Chapter 1. Role of immigrant males and muzzle contacts in the uptake of a novel food by wild vervet monkeys

(in review)

Pooja Dongre [#, 1, 2], Charlotte Canteloup [#, 1, 2], Gaëlle Lanté [1, 3], Mathieu Cantat [2], Erica van de Waal [1, 2, *]

[1] Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

[2] Inkawu Vervet Project, Mawana Game Reserve, KwaZulu Natal, 3115, South Africa

[3] University of Poitiers, France

[#] These authors contributed equally

*Correspondence to: erica.vandewaal@unil.ch

ABSTRACT

The entry into and uptake of information in social groups is critical for behavioural adaptation by long-lived species in rapidly changing environments. We exposed five groups of wild vervet monkeys to a novel food to investigate innovation of processing and consuming it. We report that immigrant males innovated in two groups, and an infant innovated in one group. In two other groups, immigrant males imported the innovation from their previous groups. We compared uptake between groups according to the innovator to examine the extent to which dispersing males could introduce an innovation into groups. Uptake of the novel food was faster in groups where immigrant males ate first rather than the infant. Younger individuals were more likely overall, and faster, to subsequently acquire the novel food. We also investigated the role of muzzle contact behaviour in information seeking around the novel food. Muzzle contacts decreased in frequency over repeated exposures to the novel food when many individuals were eating. Muzzle contacts were initiated the most by naïve individuals, high rankers and juveniles; and were targeted most towards knowledgeable individuals and high rankers, and the least towards infants. Finally, knowledge influenced females and juveniles less than males and adults in becoming more likely targets than initiators. We highlight the potential importance of dispersers in rapidly exploiting novel resources among populations.

INTRODUCTION

To thrive in rapidly changing environments, including those induced by humans, animals must respond quickly to relevant information about their surroundings [1]. Climate change or human induced invasions, as well as the introduction of human artefacts into the environment can affect different species in myriad ways, for example, bringing new threats, disruptions, competition, or novel resource opportunities. Adaptive behavioural responses to such changes can include effectively avoiding new predators, maintaining high competitive ability and exploiting novel resources [1–4]. For long-lived species, fast, learned behavioural adaptations are crucial for survival when circumstances change too rapidly for genetic adaption to suffice. Whilst transmission mechanisms of genetic adaptation are well-understood, our understanding of how behavioural adaptations arise and spread is murky, and the role of individual heterogeneity in a group in this remains underexplored [5].

Research has identified two main classes of behavioural response to novel stimuli in animals. These are neophobia and exploration [6,7]. Neophobia refers to the avoidance of potentially risky novelty, which could include new predators or unknown toxins, and is common in response to potential novel foods [8]. Exploration, on the other hand, involves behaviours that seek information about novel stimuli. Obtaining novel information directly from the environment requires overcoming neophobia and engaging in exploration, tendencies for which may vary between individuals [5], and which produces information or knowledge, potentially facilitating innovation. Kummer & Goodall [9] defined innovation as, “a solution to a novel problem, or a novel solution to an old one”, and “a new ecological discovery such as a food item not previously part of the group”. Behavioural innovations can therefore allow species with slow generational turnover to adapt their behaviour quickly to changing circumstances, for example to exploit a novel resource introduced into the current habitat (e.g. [10]). To innovate, however, it is necessary to go beyond obtaining information through exploration. Individuals must enact novel behavioural patterns in interaction with known or novel aspects of the environment, which additionally requires behavioural plasticity [11]. This can also be highly variable, both between individuals of a species, and within individuals across time [8]. Given the risks associated with novelty and innovation, it is likely only beneficial to innovate when necessary; and motivation based on internal states is likely important in variation in innovation within species [11,12]. Moreover, within individuals, reduced neophobia and motivation to innovate may be plastically driven, triggered by environmental uncertainty [8], which may depend on current needs and developmental status [12]. For example, innovation might be more common in juveniles who need to learn a lot about their environment before adulthood, or dispersing individuals who need to find a new home territory. Greater behavioural flexibility, an important requisite for innovation, is apparent in both juvenile [13] and dispersing male [14] vervet monkeys.

Nonetheless, if innovative conspecifics or individuals that uniquely possess particular knowledge are present, individuals can save energy and avoid risks by learning socially from them. Indeed, many studies of diverse species in captivity have found that observing a conspecific eating a novel food reduces neophobic responses [6,8]. A study on wild jackdaws found the same [15], and similarly, wild baboons handled a novel food for longer after seeing a demonstrator do so, though this was dependent on their personality [16]. Further investigation is required in the wild, since the risk for foraging animals to ingest toxins via unknown foods can be high, whilst this risk is diminished in captivity. In addition, individual differences, such as age or sex, of the observed conspecifics may be important. Moreover, in wild groups of chimpanzees, dispersing individuals have been hypothesized to import information or behavioural innovations, upon immigration, into new groups [17–21]; and one study reports an immigrant vervet monkey providing spatial knowledge to his new group of a remaining water hole, during a drought, in a neighbouring territory [22]. Detailed work in capuchins suggests the involvement of immigrants in both creating and spreading innovations in social and foraging domains [19,20]. Male Japanese macaques have been suspected to transfer stone handling patterns between troops [23]. Dispersing individuals might thus facilitate the spread of information at the population level, but experimental evidence focusing on multiple groups is sparse. Within wild groups, animals can use social information to guide foraging decisions. Many social learning studies in primates have focused on visual access to information (e.g. [14,16,19,24–26], and see review in [27]). However, for Cercopithecoid monkeys, detailed olfactory information, in a foraging context, may also be acquired through muzzle contact behaviour – the act of one individual bringing their muzzle into very close proximity with another's [28–31]. Indeed, previous studies found that, whilst foraging, muzzle contacts were most commonly initiated by infants and juveniles towards adults [31,32], which supports their function in information acquisition as young animals are still learning about their dietary repertoire, and adults are likely the most reliable sources of information. Nord et al. [31] also suggest that, due to the necessary close proximity, social tolerance may constrain information transmission in this modality. In the presence of novel resources, muzzle contacts may be useful to adults as well as youngsters.

Experimental research into this mode of information transmission in the presence of a novel resource is now required.

Vervet monkeys (*Chlorocebus pygerythrus*) are a species that thrive in natural, urban and agricultural habitats, and are widely distributed throughout eastern sub-Saharan Africa [33]. This makes them ideal species in which to investigate adaptation to novel environmental conditions. They live in multi-male multi-female troops, with philopatric females, and males dispersing multiple times during their lives. Furthermore, frequently dispersing males could serve not only as vectors of information between groups, but also as innovators in novel environments [12], potentially facilitating behavioural adaptation to diverse habitats across their geographical range [33]. In a previous study by our team [24], two groups (NH, KB) of wild vervet monkeys were provided in 2018 with a novel food that required extraction (peanuts in shells) before consumption. The aim of this initial study was to test whether vervet monkeys socially learned how to extract peanuts from their shells, and from whom they did learn. The results supported social transmission of the opening techniques used to extract peanuts, based on visual attention to demonstrators and that vervet monkeys socially learned the technique that yielded the highest observed payoff and demonstrated by higher-ranked individuals [24]. Here, we replicated the same experimental paradigm in 2019 and 2020 in three more groups (AK, BD, LT) after some males from the initial studied groups dispersed to other studied groups with another aim: investigating whether dispersing males could trigger the uptake of an innovation in their new groups. Specifically, we took advantage of natural dispersals of males from groups already accustomed to extracting and eating peanuts [24] into groups that never had. This endeavour afforded us the opportunity to also observe innovation, which subsequently inspired hypotheses about the potential role of dispersal in innovation, building upon the work of others [11,12]. Our observations of innovation are limited in number, but further testing of the hypotheses we propose, may aid our understanding of animal innovation.

The present study addressed the following questions: First, 1a) Who innovated and how did it affect the extent to which the innovation was adopted by the group? We expected uptake of the novel food to be faster and more widespread when the innovators or initiators (in case of immigrant males importing the innovation) were adults rather than juveniles or infants. Next, to further our understanding of the uptake of innovations, we assessed 1b) which socio-demographic characteristics (age, sex, rank) of group members predicted their adoption of the innovation at the first exposure, and over all four exposures. We expected this to be more likely in younger monkeys, during both the first exposure, and over four exposures, due to previous findings that juveniles take more risks [34], are less neophobic [35–38] and generally tend to learn faster [13] than adults. We also expected higher-rankers to adopt the novel food earlier and in a bigger extent than lower-rankers as previous studies suggested it [24,39].

Second, we experimentally investigated the function of muzzle contact behaviour in novel food information acquisition. Specifically, we tested 2a) the effects of the amount of exposure to the food (and therefore familiarity with it) and the number of monkeys eating it on the rate of muzzle contacts. We expected that the rate of muzzle contacts would decrease the more exposures to peanuts monkeys had, if there were many monkeys eating. This would show that muzzle contact's function is obtaining novel food information. We also analysed 2b) whether individuals' knowledge of the food, and their age, sex and rank predicted initiating and being targets of muzzle contacts. We expected an effect of knowledge, specifically for naïve monkeys to initiate more, and knowledgeable monkeys to be targeted more, with muzzle contact being the media used to acquire information about what conspecifics are eating. We also expected effects of age, with juveniles more likely initiators and adults more likely targets, as these are the theoretically predicted directions of social information transfer [40], under the rationale that adults should have the most reliable information. Given the close proximity required to initiate muzzle contacts, we also expected low rank individuals to be less likely to initiate muzzle contacts, as they are tolerated by fewer group members [31].

Finally, we analysed 2c) variation in the influence of knowledge on the likelihood of initiating vs. being targeted *within* the different age- / sex-classes. Given that we did not expect individuals to seek information from juveniles [40], we expected knowledge to push the tendencies of adults towards being targeted rather than initiating, whereas we expected juveniles to still initiate more than they are targeted, even when they are knowledgeable. Whilst tolerance is an important factor constraining muzzle contact behaviour [31], we did not expect it to shape this pattern because even though juveniles are likely to be tolerated more in general than adults, this should not be related to whether they are knowledgeable or not. Lastly, we returned to consider dispersing males. Due to the different experiences of novelty arising from the life history trajectories of the philopatric vs. dispersing sex, we expected differences in how gaining knowledge of a novel resource might affect their muzzle contact behaviour. We did not expect differences in naïve adults' likelihoods of initiating vs. being targets of muzzle contacts. However, if this behaviour functions to acquire information, we expected that knowledgeable females, for whom encountering novelty is rare, might still initiate some muzzle contacts even when they have eaten the novel food. On the other hand, as encountering novelty is not so rare for males, once knowledgeable, their likelihood of initiating vs. being targeted might be more heavily swayed towards being targeted due to them no longer initiating. Again, we did not expect such a pattern to be driven by tolerance, because tolerance is required from the target towards the initiator, and there is no reason for naive adult males to be any more tolerated than knowledgeable males - if anything this would be expected in the opposite direction.

RESULTS

Across the experiment, a total of 81/164 vervet monkeys in all five groups, learned to successfully extract and eat peanuts during four exposures from each group's first eating event (Table 1).

We refer to the group AK differentially as AK_{19} and AK_{20}, representing their status in 2019 and 2020, respectively, as 40% of the group composition changed between years due to dispersals, deaths and changes in age categories (see Appendix 1 – Table 1 and detailed description in Materials and Methods).

When presented with the novel food, multiple individuals (2-16 individuals) in all groups (except BD where the knowledgeable immigrant approached the box first and immediately started eating) approached the box, looked at the peanuts, and retreated without touching any (visual inspection; Table 2); and at least one group member (1-7 individuals) approached and handled, sniffed or nibbled the peanuts before rejecting them and retreating from the box (contact inspection; Table 2).

Table 1. Cumulative numbers of monkeys eating at each exposure in each group, with a total of 81 (of a possible 164) monkeys eating across the whole experiment.

		Exposure number						
Group	Group size	1	2	3	4	5	6	**Total**
AK	~20	0*	5**	13**	17**	19**	-	**19**
BD	65	19	25	29	32	-	-	**32**
KB	19	0	0	1	3	3	3	**3**
LT	25	5	13	16	21	-	-	**21**
NH	35	3	3	3	6	-	-	**6**
						Grand total =		**81**

NB. *AK in 2019; **AK in 2020

Table 2. *Number of individuals in each group that showed each type of response to the peanuts before the innovator or knowledgeable immigrant started eating.*

Group	Approach box and leave	Contact exploration and rejection
AK19	12	5
AK20	3	1
BD	0	0
KB	15	4
LT	16	7
NH	2	1

1a) Who innovated and how did it affect the extent to which the innovation was adopted by the group?

When tested in 2018, in NH, an immigrant male, *Avo*, was the third monkey to approach the box, and innovated extracting and eating peanuts during the group's first exposure to the novel food. In KB an infant male, *Aar*, was the 16th monkey to approach the box (across all the exposures) and innovated at the group's third exposure.

In 2019, in BD, a knowledgeable immigrant male, *Pro* (who emigrated from NH, Fig. 1B), was the first to approach the box and started extracting and eating immediately. In LT, an immigrant male, *Bab*, was the 17th monkey to approach the box and innovated during the groups' first exposure. In AK no monkeys innovated in 2019 (AK_{19}), but in 2020 (AK_{20}), at the group's second exposure (but the first with a knowledgeable immigrant), *Yan* (also emigrating from NH; Fig. 1B), was the fourth to approach the box and the first to extract and eat peanuts (Appendix 1 – Table 1).

During the first exposures to peanuts in BD, LT and NH, when new immigrant males initiated eating peanuts, we observed that the following percentages of these groups started to extract and eat peanuts during that exposure: BD: 31% (total n = 65); LT: 20% (total n = 25); NH: 9% (total n = 35; Fig. 2A). In the first exposures in AK_{19} and KB, no monkeys started to extract and eat peanuts. After an immigrant male ate in AK_{20}, at the second exposure in that group, 30% (total n = 20) of the group followed during that exposure (Fig. 2A). When an infant innovated at the third exposure in KB, no other group members followed during that exposure (Fig. 2A). The immigrant who innovated in NH left the group after their first exposure, leaving just two juveniles who had also started eating at the first exposure. After four exposures from the first eating event in all groups, the percentages of each group extracting and eating peanuts were: 95% in AK_{20}; 66% in BD; 21% in KB; 84% in LT; and 20% in NH (Fig. 2B).

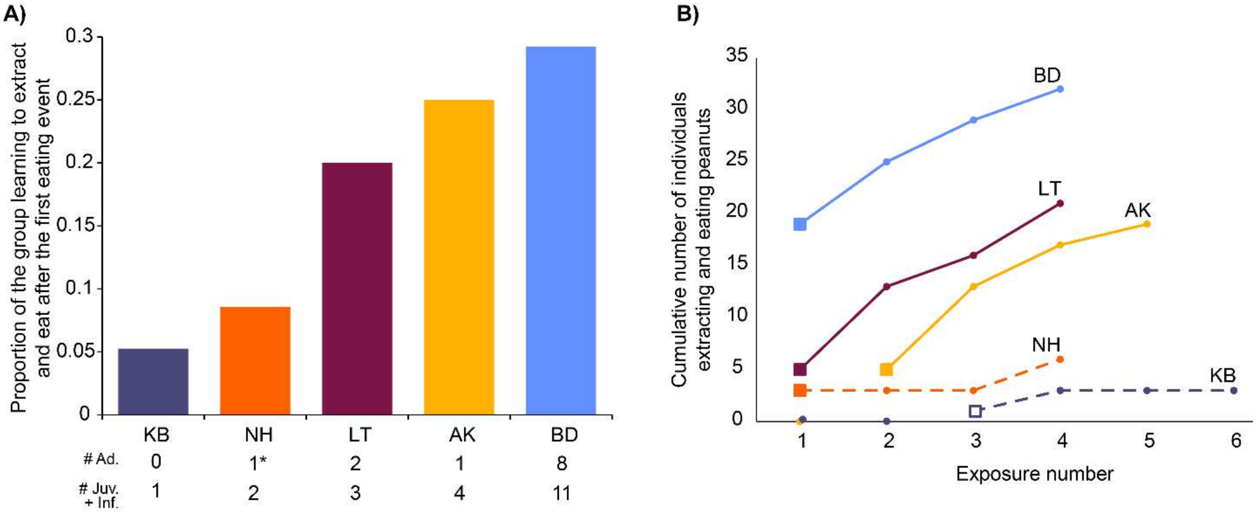

Figure 2. Uptake of extracting and eating peanuts in each group. A) Shows the proportion of each group that started eating when the first eating event took place. Total numbers of individuals, split by age, are shown below the x-axis. In NH the asterisk highlights the one adult which was the innovator male that left after their first exposure, and was only followed by juveniles learning to extract and eat. B) Shows the progression in each group over four exposures from the first eating event. Solid squares represent when immigrant males were the first to eat, and the open square shows when the infant was first to eat. Solid lines show when there were adults present who had started to eat, whereas dashed lines show when there were only juveniles and infants present that had already started to eat. Males who were knowledgeable and imported innovations from other groups (*Pro* in BD and *Yan* in AK) are excluded from totals in both panels (visualised in Microsoft Excel).

1b) Socio-demographic variation in uptake of the innovation

Here we examined whether age, sex and rank predicted successfully extracting and eating peanuts in the first exposure and over the course of four exposures. During the first exposure, we found a significant main effect of age, with juveniles 4.17 times (417%) more likely to extract and eat peanuts than adults, and 5.43 times (543%) more likely than infants, but there was no significant difference between infants and adults (Model 1, Table 3).

Over four exposures, we found a significant main effect of age, with juveniles 5.39 times (539%) more likely to extract and eat peanuts than adults, and 6.77 times (677%) more likely than infants, but no significant difference between infants and adults (Model 2, Table 3). We also found a significant main effect of rank, whereby higher ranked individuals were more likely to extract and eat peanuts. Specifically, low ranked individuals were 93% less likely, per unit of standardised rank, than higher rank individuals to eat. Again, we found no significant effect of sex (Model 2, Table 3).

2a) Muzzle contact rate across repeated exposure to novel food

We recorded a total of 498 muzzle contacts initiated by 64 different individuals in all four study groups during the first four exposures from the first eating event.

Regarding the rate of muzzle contacts across exposures, we found a significant interaction between the number of monkeys eating and exposure number (Model 3, Table 3). The main effects of exposure number and the number of monkeys eating were also significant.). The significant interaction shows that effect of exposure number depends on the number of monkeys eating (Figure 3). In Fig. 3A and 3B we can see that whilst muzzle contact rate decreases across the exposures, this decrease is less extreme when more monkeys are eating.

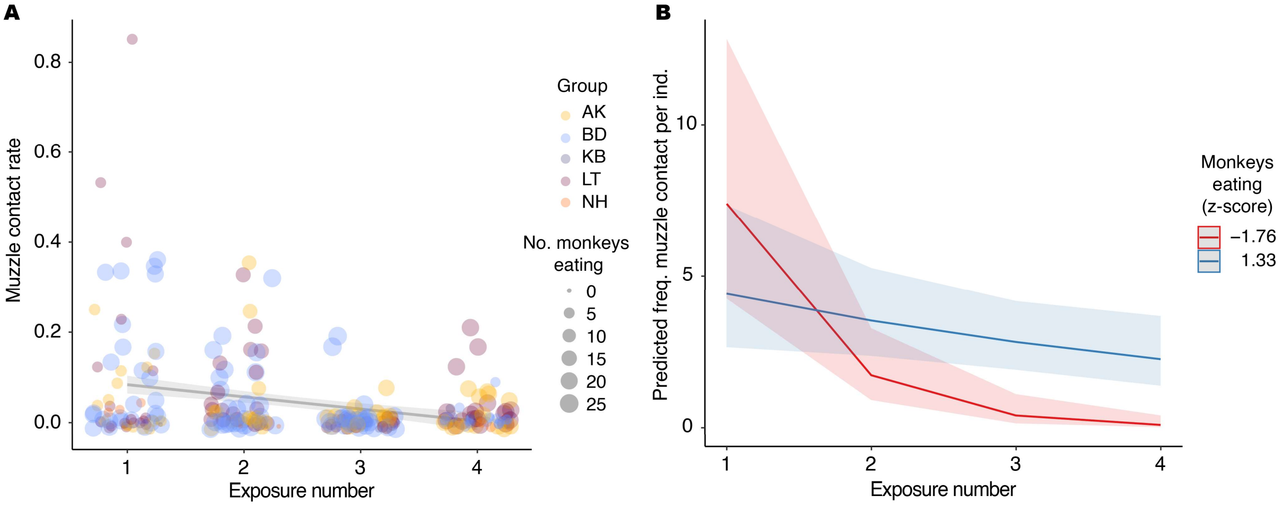

Figure 3. A. Variation in muzzle contact rate according to the number of monkeys eating and exposure number. Shading shows 95% CI. B. Model predictions based on the significant interaction between exposure number and number of monkeys eating. When greater numbers of monkeys are eating (blue) the effect of exposure number is less extreme than when fewer monkeys are eating (red).

2b) Influence of knowledge of novel food and socio-demographic variation on muzzle contact behaviour

For all individuals present in groups during the experiment, across the four exposures from the first eating event, the mean (s.d.; range) number of muzzle contacts each naïve individual initiated was 2.30 (4.79; 0-26) and they were targeted 0.91 (3.21; 0-22) times; and each knowledgeable initiated 2.20 (4.01; 0-26) muzzle contacts and they were targeted 4.81 (11.18; 0-79) times (Fig. 4D).

We found significant main effects of prior knowledge, age and rank on frequency of initiating muzzle contacts (Model 4, Table 3). The number of muzzle contacts initiated by knowledgeable individuals, who had already extracted and eaten peanuts, was reduced by

37% compared to the number initiated by naïve individuals. The odds of lower rank individuals initiating muzzle contacts were 92% lower than higher rank individuals, per unit of standardised rank. Post-hoc multiple comparisons between age categories showed that juveniles initiated 6 times (600%) as much as adults did, and 4.07 times (407%) as much as infants did.

Regarding being targets of muzzle contacts, we found significant main effects of knowledge and age, and trends for effects of sex and rank (Model 5, Table 3). Here, knowledgeable individuals that had succeeded to extract and eat peanuts were targeted 3.13 times (313%) more than naïve individuals were; juveniles were targeted 37.9 times (3790%) more than infants were, the odds of infants being targeted were 98% less than adults, and there was no significant difference between juveniles and adults (Model 5, Table 3). With marginal significance, males were targeted 2.41 times (241%) more than females were, and there was a non-significant trend for lower rank individuals to be targeted less than higher rank individuals were (Model 5, Table 3).

2c) Differential effects of knowledge on muzzle contact behaviour within age / sex classes

We did not find a significant three-way interaction between knowledge, age and sex, and we did not include the three-way interaction, nor group as a random effect in the final model because the model was too complex to converge properly (Appendix 1 – Table 2). Our final model included interactions between knowledge and age, and between knowledge and sex. Main effects of knowledge and age were significant, as were both interactions (Model 6, Table 3). Knowledge had a significant effect on both adults and juveniles, but the effect was stronger in adults (Model 6 post-hoc, Table 3, Fig. 4A). Post-hoc comparisons revealed that naive adults' odds of being targets rather than initiators were 94% less than knowledgeable adults, whereas naive juveniles' odds were 69% less than knowledgeable juveniles. Similarly, knowledge had a significant effect on both males and females but was stronger in males: the odds of being targets rather than initiators in naïve females was 69% less than knowledgeable females, whereas naive males' odds were 94% less than knowledgeable males (Model 6 post-hoc, Table 3; Fig. 4B). Figure 4C shows the model predictions based on these two significant interactions, separated by both age and sex.

Table 3. Models outputs for binomial and Poisson generalised linear mixed models.

Model no.	Outcome	Predictors [1]	Coefficient	Odds ratio	SE	z- value	*p*-value [2]
1	Eat at first exposure with eating event: yes/ no (binomial)	Age: Infant – Adult*	-0.27	-	0.65	-0.41	0.912
		Juvenile – Adult*	1.43	4.17	0.52	2.74	***0.017***
		Juvenile – Infant*	1.69	5.43	0.67	2.51	***0.032***
		Sex (M)	0.57	-	0.42	1.36	0.175
		Standardised rank	-1.52	-	0.81	-1.89	0.058
2	Eat over four exposures from first eating event: yes / no (binomial)	Age: Infant – Adult*	-0.23	-	0.55	-0.42	0.908
		Juvenile – Adult*	1.68	5.39	0.55	3.09	***0.006***
		Juvenile – Infant*	1.91	6.77	0.63	3.01	***0.007***
		Sex (M)	0.18	-	0.41	0.45	0.656
		Standardised rank	-2.69	0.07	0.81	-3.34	***<0.001***
3	Freq. muzzle contact per individual per exposure (Zero-Inflated Poisson)	Exposure no.	-0.75	-	0.10	-7.20	***<0.001***
		No. eating (std.)	-0.56	-	0.21	-2.70	***0.007***
		Exposure no. X no. eating	0.40	-	0.10	3.92	***<0.001***
4	Frequency of muzzle contacts initiated (Poisson)	Prior knowledge (K)		0.63	0.09	-5.035	***<0.001***
		Sex (M)		0.97	0.29	-0.11	0.910
		Standardised rank		0.08	0.57	-4.42	***<0.001***
		Age: Infant – Adult*		1.47	0.43	0.90	0.636
		Juvenile – Adult*		6.00	0.36	5.02	***<0.001***
		Juvenile – Infant*		4.07	0.45	3.09	***0.006***
5	Frequency targeted by muzzle contacts (Poisson)	Prior knowledge (K)		3.13	0.10	11.67	***<0.001***
		Sex (M)		2.41	0.45	1.95	***0.051***
		Standardised rank		0.21	0.85	-1.84	***0.066***
		Age: Infant – Adult*		0.02	1.03	-3.98	***<0.001***
		Juvenile – Adult*		0.62	0.51	-0.94	0.603
		Juvenile – Infant*		37.9	1.07	3.37	***0.002***
6	Status: initiator / target (binomial)	Prior knowledge (K)		7.54	0.40	5.07	***<0.001***
		Age (juv.)		0.15	0.70	-2.76	***0.006***
		Sex		1.05	0.71	0.07	0.941
		Knowledge X Age*: N-K Adult*		0.06	0.42	-6.95	***<0.001***

	N-K Juveniles*	0.31	0.34	-3.37	***<0.001***
	Knowledge X Sex*:				
	N-K Females*	0.31	0.30	-3.83	***<0.001***
	N-K Males*	0.06	0.47	-6.13	***<0.001***

NB. [1] Reference categories are Adult, Female and Naïve for categorical predictors: age, sex and knowledge, respectively; abbr.: N = naïve; K = knowledgeable; M = male. [2] Bold italics show significant p-values at 0.05 level. *Indicates post-hoc multiple comparisons (with Tukey correction).

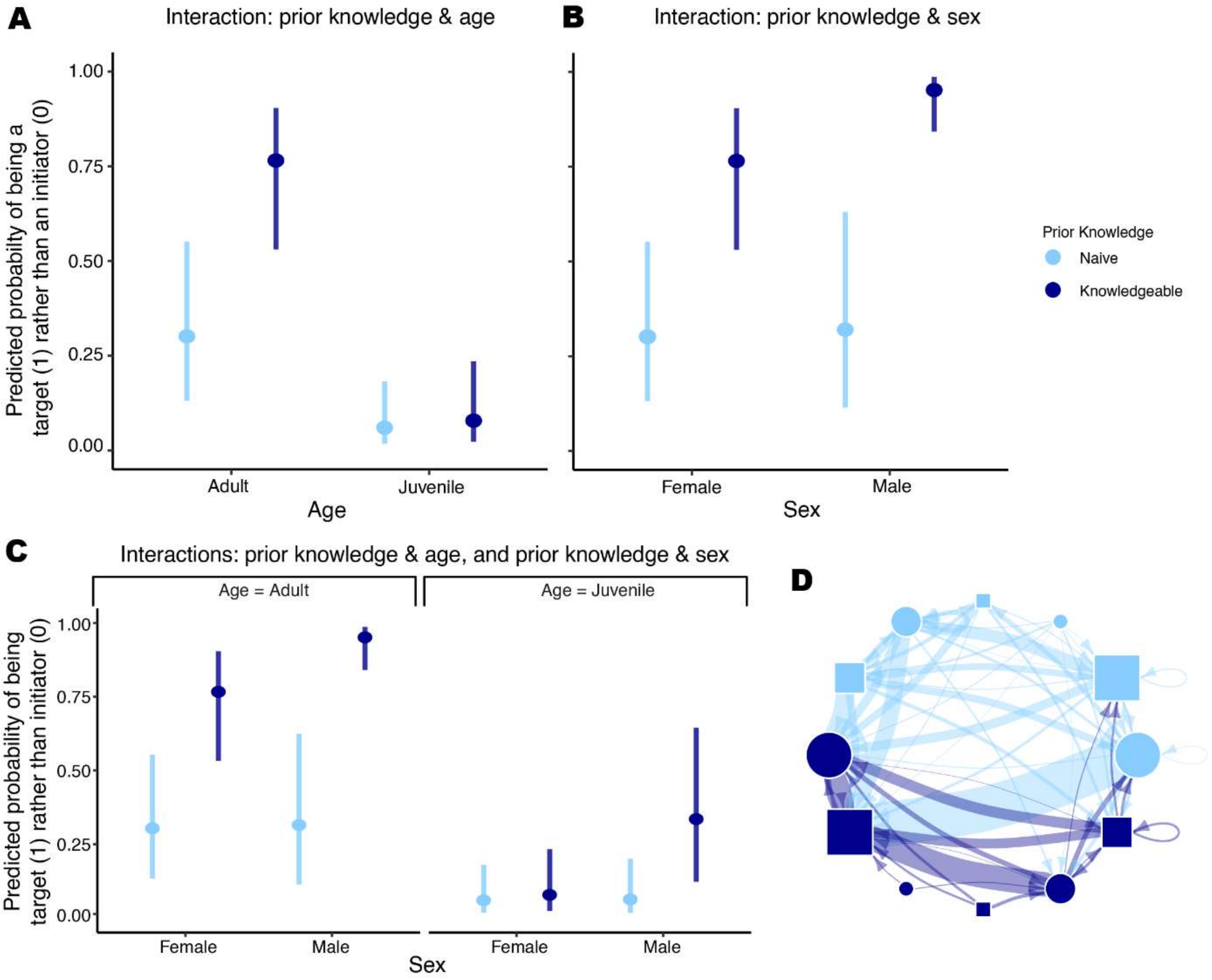

Figure 4. Plots illustrating significant interactions between the effects of A) knowledge and age, and B) knowledge and sex on the likelihood of individuals being initiators rather than targets of muzzle contact; and C) illustrates both interactions from the same model, but separated by age and sex. Solid circles show predicted probabilities, and extending bars show 95% confidence intervals (visualised using ‘cat_plot’ function from R package ‘interactions’ [59]). D) Sociogram summarising muzzle contacts between different age/sex/knowledge-classes, across all groups. Knowledge is indicated by colour of nodes: dark = knowledgeable, light = naïve; age is indicated by size of nodes: large = adult, medium = juveniles, small = infants; and sex is indicated by shape: square = male, circle = female. Edge size indicates the frequency of muzzle contacts. Edge colour matches the origin node. (NB. D includes infants, which are excluded from A, B and C due to statistical constraints; see Materials and Methods).

DISCUSSION

By exposing five groups of wild vervet monkeys to a novel extractive foraging problem, we created conditions under which to 1) observe innovation by individuals, and the uptake of transmission of knowledge within and between groups, and 2) assess the function and patterns of muzzle contact behaviour in the context of encountering a novel food. We found evidence of immigrant males as fast innovators, and as vectors of information between groups. We observed faster uptake of the innovation in groups when new immigrant males, rather than infants or juveniles, ate first. We found effects of age and rank on uptake of the food, both during the first exposure, and over four exposures, with juveniles and high-rankers eating the novel food more readily than adults and low-rankers. Furthermore, as groups had more exposures to the food, if many monkeys had started to eat peanuts, the rate of muzzle contacts decreased. Initiating muzzle contacts was influenced by prior knowledge of the food, age and rank, and being targeted by muzzle contacts was influenced by knowledge and age. Finally, we found different effects across age-/sex-classes linked to knowledge of the novel food on whether individuals initiated or were targets of muzzle contacts more. Below we discuss the contributions of these results to perspectives on the potential value of dispersing individuals in the innovation and transmission of behavioural adaptations to novel circumstances around populations.

1a) Who innovated and how did it affect the extent to which the innovation was adopted by the group?

In the two groups where innovation occurred at the first exposure to peanuts (LT and NH), immigrant males, each with less than three months tenure in the group, were the innovators. In KB, an infant innovated, but only at their group's third exposure to the novel food. Fast innovation (i.e. at the first exposure) to exploit a novel resource by new immigrants could be linked to a physiological state related to dispersal. In the first exposure in AK_{19} there was a relatively new male, *Boc* (Appendix 1 – Table 1), who had immigrated within four months, but he was very old (> 12 years old), having held an alpha position in one of our study groups for two years, had dispersed between three different study groups, and had recently become very inactive. *Boc* disappeared, presumably due to natural death, two months after AK_{19}'s exposure to peanuts. Such characteristics may counteract any effects of recent dispersal on exploratory tendencies. Indeed, very old age has been found to be related to declining boldness – a personality trait related to exploration – in big horn ewes [Reale et al., 2000]. In addition, the group started travelling away from the experiment area within five minutes from the start of the experiment, limiting the time available for any individuals of the group to innovate. Dispersal has previously been associated with exploration and boldness (i.e. low neophobia) in several taxa, with associated neurochemical variation, both within (ontogenetically) and between individuals [41]. Moreover, evidence links lower serotonergic activity with: earlier dispersal in rhesus macaques [42], greater social impulsivity in vervet monkeys [43], and reduced harm avoidance in humans [44]; all of which together relate low neophobia, or novelty seeking, with dispersal. Evidence does not however suggest that the dispersing sex in wild vervet monkeys are more bold or explorative overall [45], and in the present study long-term resident males did not show increased interest in the novel food. In another population, long-term resident males also showed reduced responses to novel foods compared to other age-sex classes [46]. We suggest rather that the unique individual, social and environmental factors that prompt a male to disperse [47] may trigger a transitory exploratory behavioural syndrome [48] that may subside again once males acquire more secure residency in a group. Since dispersal inherently involves heightened risk, periods of long-term residency would be well-served by a state characterised by reduced exploration and increased neophobia to balance costs of risk-taking over the lifetime. The large variation in risky predator inspection by adult male vervet monkeys, compared to adult females found in [45] also supports this. Future work focusing on the behaviour of dispersing individuals at multiple time points, both proximal and distal to dispersal events, in this species, and others, will help to more conclusively address this hypothesis. We highlight the need for researchers to consider the nuances of life-history characteristics beyond simply splitting by broad age-sex categories.

We found that when immigrant males were first to extract and eat a novel food in their new groups, during the first exposure to it in BD, LT and NH, and during the second exposure in AK_{20}, other monkeys quickly followed them in doing so. As discussed above, two of these cases (LT, NH) involved innovation by the immigrant males, and in BD and AK_{20}, the males had learned to extract and eat the food in their previous groups. In contrast, following innovation by the infant in KB at their third exposure, no other individuals followed in extracting and eating peanuts during that exposure. Over the three subsequent exposures that followed these initial eating events, very few monkeys started to extract and eat peanuts in KB, whereas in BD, LT and AK, where new immigrants ate first, large proportions of these groups learned to extract and eat peanuts. In NH however, this was not the case and is of great interest because though a new immigrant male innovated at the first exposure, he left the group before the second exposure. Closer inspection of our data revealed that only juveniles had started extracting and eating peanuts after the male in the first exposure and were thus the only knowledgeable individuals at the second exposure. Similarly, in KB, only juveniles ate after the infant. Our interpretation of these results is that immigrant males were more effective in facilitating group members to overcome neophobia towards a novel food than infants or juveniles, which is in line with studies reporting age-biased social learning

[19,24]. Nonetheless, in NH, more individuals did eventually start to eat during their fourth exposure, including a high-ranked adult female (after which it spread rapidly, resulting in the data presented in [24]). In NH, the juveniles eating at the beginning were older than the infants and one year old who started eating in KB. It is possible that age-bias is less strong for older juveniles since they should have more reliable knowledge than their very young counterparts. Alternatively, this difference between NH and KB could be because the juveniles eating earlier in NH were of high rank, whereas the infants and juveniles who began to eat in KB were of low rank. Indeed, rank-biased social learning has also been found in previous work in two groups (KB and NH) of this study population [24,39]. It is nonetheless likely that various interactions of socioecological factors affect the influence of juveniles in overcoming food neophobia in the wild, and it still took repeated exposures before groupmates of the NH juveniles began eating.

Alternative explanations for these patterns of uptake, such as group size or the different experimental histories of each group (see STRANGE framework: [49]), can be ruled out. Contrary to predictions based on group size or experimental history, innovation took longest in the smallest group (KB) relative to larger groups where it occurred at the first exposure (LT, NH, BD). In addition, uptake of the innovation was fastest in the largest group (BD), and slowest in the smallest group (KB). In the same vein, in two groups with extensive experimental history (NH, AK), few individuals ate the novel food at their first exposure, whilst in the least habituated group (LT), with the most minimal experimental history [50], a great proportion of individuals adopted the novel food at the first exposure. We find the most likely explanation to be that observing new immigrants eat the novel food triggered groupmates to try it.

Moreover, whilst previous experiments suggested that high-ranked adult philopatric females are preferred over high-ranked adult males as models to learn from [25], in the context of exploiting a novel resource, risk dynamics come into play. Adult females are likely to be the most risk averse age-sex category, due to great potential negative impact of risks on their inclusive fitness, especially when young dependent offspring are present or whilst pregnant. This might limit their potential to discover new information that others can exploit. Under these conditions, adult males that are either in an exploratory dispersal state, or that enter a group with knowledge of resources previously unknown to the group (as in [22]) may play important roles in generating and/or facilitating the spread of behavioural adaptations to exploit novel resources and face rapid environmental changes.

1b) Socio-demographic variation in the uptake of the novel food

Both, in the first exposure, and over four exposures, juveniles were more likely to eat than adults and infants. These results suggest that juveniles overcome neophobia faster, corresponding closely with results regarding risk-taking in another population of vervet monkeys [34]. Furthermore, juvenile vervets have been found to learn faster [13], and work on other species suggests that juveniles are overall more exploratory and less neophobic [35–38]. Taken together we propose that juveniles are, in general, more prone to taking risks around novelty, particularly when conspecifics provide social information. Moreover, alongside the results of section 1a, we propose that it could be adaptive that groups do not follow novel foraging information from juveniles as readily as adults (i.e. in NH), as this may limit the spread of potentially dangerous information acquired by exploratory but inexperienced juveniles. We also expect that infants were not more likely than adults to eat due to still being at least partly reliant on their mothers to learn their foraging repertoire [40] in contrast to juveniles who explore more independently.

Over four exposures, higher ranked individuals were significantly more likely to eat than lower ranked individuals (with a non-significant tendency in the same direction in the first exposure), probably due to preferential access to the resource as it became more familiar and sought-after.

2a) Muzzle contact frequency in groups

Muzzle contact rates decreased over repeated exposure to the novel food, providing some support for our hypothesis that the less muzzle contacts would occur when the food had become more familiar in each group. However, we expected this effect to be greatest when many monkeys were eating. Contrary to this, muzzle contact rates decreased more slowly when more monkeys were eating. This also make sense, because more monkeys eating means more monkeys were in the area of the novel food, and therefore there were more opportunities to engage in muzzle contact. The steeper decrease in muzzle contact rate when fewer monkeys were eating also likely reflects that there were more muzzle contacts at the very beginning, when very few monkeys were eating, and the later exposures where very few monkeys were eating also gave rise to fewer opportunities for muzzle contacts. Cases where very few monkeys were eating in later exposures were due to KB and NH, where very few individuals started to eat over the four exposure time frame examined here, and the two exposures in BD (Expo. 4) and LT (Expo. 3) with only small portions of the group present. Nonetheless, the overall decrease in muzzle contact rate demonstrates the relevance of the behaviour in the context of an unknown foraging item, because as the monkeys became more familiar with it by eating it, they sought olfactory information from their conspecifics less frequently. This result concurs with findings from a similar study in wild olive baboons [28]. It could be argued that our conclusion regarding muzzle contact serving to acquire information is premature in absence of evidence that muzzle contact directly led to individuals eating. However, unlike in the context of observing and learning to use novel tools (e.g. [51]), we do not expect muzzle contact to be a pre-requisite to learning to extract and eat peanuts. We argue that muzzle contacts need not be correlated with extracting peanuts in such a manner in order to support that they serve to acquire information. We provide further evidence to support this function below (section 2b).

That there were more muzzle contacts when more monkeys were eating could be interpreted that muzzle contacts are provoked by seeing conspecifics consume any food, regardless of its novelty. We have, however, used provisions of corn kernels in experiments for 10 years with this study population, and when presenting monkeys with this now familiar resource, we do not see rates of muzzle contact anywhere close to those observed during the early exposures in this experiment [52]. This is supported by the significant main effect of exposure number (Fig. 3).

2b) Influence of knowledge of novel food and socio-demographic variation on muzzle contact behaviour

Muzzle contacts were initiated the most by individuals that had not yet extracted and eaten peanuts (hereafter, naïve individuals; opposite: knowledgeable), higher ranked individuals and juveniles. Contrastingly, muzzle contacts were targeted the most towards knowledgeable individuals, and the least towards infants. There were also non-significant trends for males and higher ranked individuals to be targeted more. We find the most compelling evidence for our hypothesis of the function of muzzle contact in information acquisition in that naïve individuals initiated the most and knowledgeable individuals were targeted the most. We do not make claims related to knowing what others know, but rather we assume that seeing a group member eating an unknown resource prompts the initiation of muzzle contact towards that individual. Moreover, this result corroborates the finding in 2a) of decreasing muzzle contact frequency with increased exposure to and familiarity with the resource, and the overall function of muzzle contact in soliciting foraging information.

The effect of age on initiating muzzle contacts falls in line with the expected direction of information transfer from older to younger individuals [40], with juveniles initiating the most (as also found in [29 and 30]). It also corroborates general findings regarding juveniles' novelty seeking and faster learning (e.g. [13,35–38]) as discussed above. However, that adults were not targeted significantly more than juveniles in this study (as in [29 and 30]) is probably because juveniles were more likely to become knowledgeable of the novel food in this experiment (section 1b), and were therefore targeted more. This may seem contradictory to our assertion above, that individuals would adaptively not follow information from juveniles, however it is also possible that there is a critical mass effect, whereby when many individuals are already consuming a novel resource, juveniles may become valid sources of information. This is, however, beyond the scope of the present study, but requires further investigation.

Furthermore, that infants were targeted the least does follow the direction of information transfer from older to younger individuals, and complements our finding that when an infant innovated, the innovation was not taken up widely in the group.

That high ranked individuals were more likely to be both initiators and targets is likely because, first, like juveniles they were far more likely to become knowledgeable, and second, because a high degree of tolerance is required by the target towards the initiator due to the close proximity in which this behaviour occurs (as described in [31]). Lower ranked individuals are not tolerated at the close proximity required to initiate muzzle contacts, especially around food resources; and they were much less likely to become knowledgeable, likely reducing their salience as targets.

The almost significant trend ($p = 0.051$) towards males being targeted the most is likely due to the fact that males were most often the first individual to eat, which we observed to trigger a high level of muzzle contacts (Fig. 4D).

2c) Differential effects of knowledge on muzzle contact behaviour within age / sex classes

The significant interactions between knowledge and age and knowledge and sex on the likelihood of being targets rather than initiators of muzzle contacts require careful interpretation. With this modelling approach we did not test for the most likely initiators or preferred targets (this is the focus of the previous section, 2b). Here, we take a more nuanced view, of how knowledge affects these different demographic groups (adults vs. juveniles and males vs. females) in their likelihood to switch to being targeted more than initiating, in light of the effects of knowledge on initiating and targeting in 2b. Building on the evidence above (in 2a and 2b), that muzzle contact plays a role in information acquisition, we suggest nuanced insights from the interaction of knowledge with age and sex into how information acquisition may differ under different life history pressures.

First, concerning age, becoming knowledgeable shifted adults' likelihood significantly more towards being targets rather than initiators than it did for juveniles. Inspection of Figures 4A and 4D suggests that juveniles, relative to adults, still initiate more than they are targeted even when knowledgeable. In addition, the main effect of age in this model suggests that all adults were already more likely to be targets than initiators relative to all juveniles (Fig. 4A). Taken together, these age-related results suggest that adults generally provide more information than they seek from others, and information is only sought from juveniles if they evidently possess valuable knowledge (Fig. 4C and 4D). However, knowledgeable juveniles still seek information from others more than others seek it from them.

Whilst there was a significant interaction between knowledge and sex, there was no significant main effect of sex. Figure 4C displays that both adult and juvenile males show greater shifts, relative to adult and juvenile females, towards being targets rather than initiators when they become knowledgeable. For adult males, this shift is striking, as they become almost exclusively targets and no longer initiate when knowledgeable (Fig. 4C and 4D). Knowledgeable adult females, on the other hand, did still initiate muzzle contacts, as seen by their more intermediate likelihood of being targets or initiators (Fig. 4C and 4D). For juveniles, the difference between males and females is in the same direction, but modest, and knowledgeable juvenile males still initiate with a similar ratio to being targeted as naïve adults of both sexes. One explanation for these sex-differences, especially in adults, could be due to adult females imparting information towards their known offspring in the group. This possibility, however, does not hold up as in figure 4D we can see that most initiations by knowledgeable adult females are towards knowledgeable adult males. We rather interpret these results as reflecting the need for males to more readily rely on their own knowledge than females, due to their status as the dispersing sex in this species. That adult females still initiate muzzle contacts, even when knowledgeable, suggests that they still seek social information from knowledgeable groupmates even when they have first-hand experience (and the same is true for juveniles of both sexes, though more for juvenile females relative to males). This is in line with the assertion that adult females are the most risk-averse age-sex category, given the dramatic effects of risk-taking on their inclusive fitness, particularly with dependent offspring around or if pregnant. Moreover, given that they are philopatric, their social environment is likely to be a dependable and consistent source of reliable information. Contrastingly, it seems that adult males, once acquiring their own knowledge of a resource, will rely on this alone without initiating more muzzle contacts, which arguably reflects boldness or low neophobia. This may be related to their status as dispersers (as discussed in section 1a), given that during dispersal they have no group-mates to rely on and must fend for themselves. Regarding juvenile males, the slight shift in the same direction may represent a tendency present in juvenile males too, as they develop towards their adult roles.

Another explanation for the sex-differences could be related to tolerance, as dispersing males may be expected to be tolerated less than philopatric females, which could be demonstrated in a lower ratio of muzzle contacts initiated by males. We do not find this explanation compelling, however, as any sex-related tolerance effects should be the same regardless of whether individuals were naïve or knowledgeable. Nonetheless, a different potentially sex-related effect of tolerance may be revealed in Figure 4D, by comparing the muzzle contacts initiated by female and male juveniles (both knowledgeable and naïve), and targeted toward adults of each sex. Here we can see a general pattern of greater initiation by juveniles towards adults of the opposite sex. It is possible that adults tolerate juveniles of the same and opposite sex differently, particularly adult males, for whom juvenile females may be future mates, and juvenile males may be future competitors.

Overall, alongside results from our group's previous study [24], where males were more likely to be observed by others when extracting and eating peanuts, as well as our observations of immigrant males innovating (section 1a of this study), results from this section show support for the potential role of dispersing male vervet monkeys in generating and transmitting novel information within groups, and transferring it between groups. However, given that we could not include group as a random effect, due to the complexity of the model, these results and subsequent discussion should be treated with caution until further evidence can be provided.

Conclusion

We add to the literature an experimental example of exploitation of a novel resource by multiple groups, facilitated here by dispersers. Our results provide evidence that dispersing individuals may promote the generation of new, environmentally relevant information and its spread around populations – a factor that has been largely overlooked, despite the known role of dispersal in gene flow [53]. We urge future research to investigate what physiological mechanisms might exist underpinning a transitory dispersal syndrome characterised by heightened exploration and reduced neophobia that is triggered during, or triggers, dispersal. We studied a species with sex-biased dispersal and we open up the question of whether similar dynamics as suggested here might be at play in species where both sexes disperse, and whether dispersing females and males show similar levels of boldness during dispersal or not, due to different life-time risk mitigation strategies. Finally, we suggest further research, in diverse species, into whether dispersers transmit valuable information between groups, which can have major implications for population fitness, especially in the context of the rapid anthropogenic change that most animal populations now face. This study contributes novel insights into the roles of dispersers in wider behavioural ecology, which we hope will inspire and inform future work, spanning the disciplines of behavioural ecology and cultural evolution.

MATERIALS AND METHODS

Experimental model and subject details

The study was conducted at the ‘Inkawu Vervet Project’ (IVP) in a 12000-hectares private game reserve: Mawana (28°00.327S, 031°12.348E) in KwaZulu Natal province, South Africa. The biome of the study site is described in [14].

Five groups of habituated wild vervet monkeys (*Chlorocebus pygerythrus*) took part in the study: ‘Ankhase’ (AK), ‘Baie Dankie’ (BD), ‘Kubu’ (KB), ‘Lemon Tree’ (LT) and ‘Noha’ (NH). Habituation began in 2010 in AK, BD, LT and NH, and in 2013 in KB. All observers in the field were trained to identify individuals by individual bodily and facial features (eye-rings, scars, colour, shape etc.). During the study period, these stable groups comprised between 19 and 65 individuals including infants (Table 1). We refer to the group AK differentially as AK_{19} and AK_{20}, representing their status in 2019 and 2020, respectively, as 40% of the group composition changed between years due to dispersals, deaths and changes in age categories (infants that became juveniles; see Appendix 1 – Table 1).

Ethical statement: Our study was approved by the relevant local wildlife authority, Ezemvelo KZN Wildlife, South Africa (though no reference number was provided by them). The University of Lausanne, Switzerland, did not have an ethics committee for the study of animals in other countries, however, we ensured our research adhered to the “Guidelines for the use of animals in research” of the Association for the Study of Animal Behaviour (available here: doi:10.1016/j.anbehav.2019.11.002).

Dominance rank calculations

Agonistic interactions (aggressor behaviour: stare, chase, attack, hit, bite, take place; victim behaviour: retreat, flee, leave, avoid, jump aside) were collected *ad libitum* [54] on all adults and juveniles of each group. These data were collected for a duration of one year, up until the date of each group’s first exposure, during all behavioural observation hours and during experiments involving food provisions. Data were collected by CC, PD and different trained observers from the IVP team. Before beginning data collection, observers had to pass an inter-observer reliability test with Cohen’s kappa > .80 [55] for each data category between two observers. Data were collected on handheld computers (Palm Zire 22) using Pendragon software version 5.1 and, from the end of August 2017, on tablets (Vodacom Smart Tab 2) and smartphones (Runbo F1) equipped with the Pendragon version 8.

Individual ranks were calculated using the I&SI method [56], based on win / lose outcomes of dyadic agonistic interactions, using Socprog software version 2.7. Linearity of hierarchies are reported in Appendix 1 – Table 3. Ranks were standardised to represent the proportion of the group that outranks each individual, falling between 0 (highest) and 1 (lowest) in each group (rank – 1 / group size). Agonistic data on adults and juveniles were included, and we assigned infants with the rank just below their mother, based on the youngest offspring ascendency in this species [57].

Peanut exposures

We provided each group with a highly nutritious novel food that required extraction before consumption – unshelled peanuts (Fig. 1A) – in large quantities to avoid monopolisation by single individuals. Experiments took place after sunrise when the monkeys were located at their sleeping site during the dry, food-scarce South African winter, to maximise both the motivation to engage in food-rewarded experiments and the number of group members in the vicinity.

CC ran field experiments during May-June 2018 in KB and NH, and PD led the experiments during August-September 2019 in AK (AK_{19}), BD and LT, and May-June 2020 in AK (AK_{20}; Appendix 1 – Table 1). Figure 1B illustrates the relevant male immigrations into and emigrations out of these groups. *Avo* left his natal group KB to immigrate into NH two weeks before their first experiment in 2018. *Avo* never ate peanuts before the first exposure in NH. KB had no new males since 2017. *Pro* originated from NH and learned to eat peanuts during their experiment in 2018. He immigrated into BD three weeks before their first experiment in 2019. *Bab* immigrated into LT six weeks before their first experiment in 2019, from an unhabituated group, though he was habituated to humans due to previous residence in two habituated study groups. *Bab* never ate peanuts before LT's first exposure. In 2020, two males, *Twe* and *Yan*, who were present in NH during peanut exposures in 2018, immigrated into AK, six and ten weeks, respectively, before their experiment in 2020. *Twe* ate peanuts in NH during peanut exposures that continued beyond the four presented here in a previous study [24], and *Yan* had observed many others eating peanuts. *Yan* was the first to eat in AK in 2020 (Fig. 1B).

Peanuts were presented to all groups in clear rectangular plastic boxes (34 x 14 x 12 cm), containing 1 – 2.5 kg of unshelled peanuts. We considered the beginning of an exposure when the experimenters placed the box on the ground, removed the lid, and stepped away, giving access to the monkeys. Exposures ended when the monkeys were clearly travelling away from the experiment site. Sites were chosen opportunistically depending on where the monkeys were found, though in all but BD, this was always at the sleeping site of the group to ensure most of the group would be present (in BD it was after one hour of a focal follow of *Pro*, due to previous aims of the study, which was not always at the sleeping site anymore). The boxes were placed visible to as many group members as possible, with the exception of the first exposure in BD where we placed the box close to the knowledgeable male, *Pro,* due to our initial aim to investigate intergroup transmission. One box of peanuts was offered per exposure in AK_{20}, BD and LT, all of which lasted up to one hour. In AK_{19}, the exposure of one box of peanuts lasted approximately five minutes. In KB and NH, two boxes were offered during each exposure, and were topped up when they were empty, for a maximum duration of 2 hrs 45 minutes. KB and NH had 10 exposures on 10 different days; AK_{20}, BD, and LT had four exposures on four different days; and AK_{19} had a single exposure (Appendix 1 – Table 1). The groups tested by PD (AK, BD, LT) had fewer exposures overall due to time constraints. Here we present results for each group from the first four exposures *from the first eating event* in each group. Whilst AK, NH and KB had more than four exposures in total, BD and LT had only four, meaning that taking four exposures from the first eating event is the most reasonable way to compare these groups. In addition, after four exposures from the first eating event, over 90% of AK and LT had learned to eat peanuts, limiting the reasons to run further exposures with them.

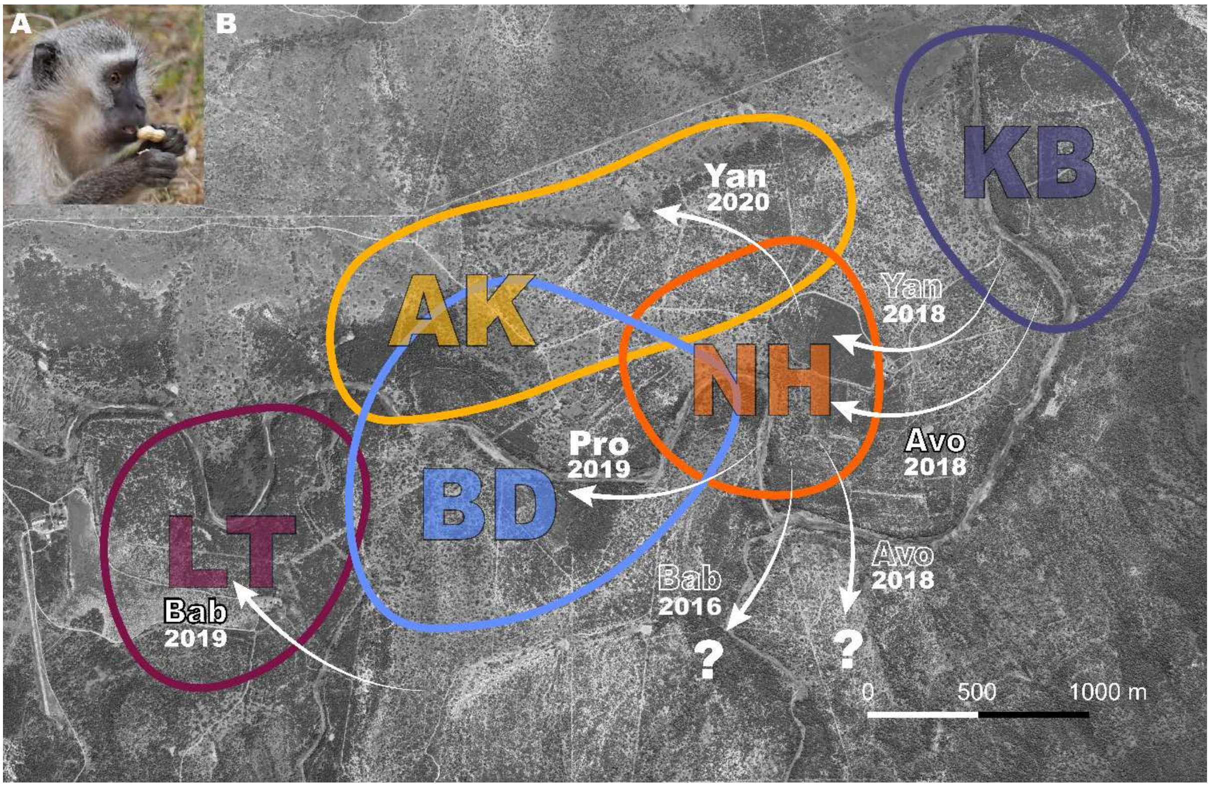

Figure 1. A) A vervet monkey holding unshelled peanut, about to open it. B) Aerial view of study area with coloured shapes showing a rough estimate of group home-ranges for study groups AK, BD, KB, LT and NH. White arrows with annotations represent relevant dispersals. Names of males and year of dispersal are shown. Black outlined text indicates the immigrant innovators who were naïve to peanuts, solid white text shows the immigrants that imported innovations, and white outlined text shows: parallel dispersal with innovator (*Yan* 2018); that the innovator was habituated in a study group prior to participation in this experiment (*Bab* 2016); or that the innovator left the study group (*Avo* 2018). Question mark shows that males dispersed to an unstudied group.

Reactions to and interactions with peanuts were recorded by three to five observers using handheld JVC video cameras (EverioR Quad Proof GZ-R430BE) and cameras mounted on a tripod. Observers narrated identities of monkeys interacting with peanuts for later video coding.

Quantification and statistical analysis

Video coding

To extract the identities of individuals who successfully extracted and ate peanuts from their shells during each exposure, PD coded videos of AK$_{19-20}$, BD and LT with the Windows 10 default video software, and CC coded videos of KB and NH with Media Player Classic Home Cinema software version 1.7.11. Having extensive experience working in the field with these groups, PD and CC were proficient in recognising individuals from the videos, and often the identities were narrated live in the audio of the video recordings which provided additional assurance of accuracy.

For analyses of muzzle contacts, GL and PD counted the frequency of muzzle contacts in videos of AK$_{20}$, BD, KB, LT and NH. MC assigned identities of individuals involved in these muzzle contacts using data provided by PD in the form of scan samples of the identities of all monkeys on the screen from left to right at every minute of each video.

To test interobserver reliability, PD recoded 15% of all videos in the study that were originally coded by CC, to verify agreement on what each coded as “successful extracting and eating”, and achieved a Cohen’s kappa of 0.96. PD also recoded 10% of the videos of the study that were originally coded by GL to verify agreement on what constituted muzzle contact interactions, and achieved a Cohen’s kappa of 0.98.

Data analysis

1a) Who innovated and how did it affect the extent to which the innovation was adopted by the group?

We did not formally analyse these data, we only described who innovated and which individuals began to consume the novel food in each group.

1b) Demographic variation in the uptake of the novel food

We used two generalised linear mixed models (GLMMs) for data following a binomial distribution to investigate demographic variation in whether or not individuals extracted and ate peanuts (question 2b). The first model investigated i) the first exposure with an eating event (AK$_{20}$, BD, KB, LT & NH; Model 1), and the second model investigated ii) four exposures from the first eating event (AK$_{-20}$, BD, KB, LT & NH; Model 2). In each model, the outcome was a binomial yes/no variable (did the individual eat), we considered age, sex and rank (standardised rank) as fixed effects and group was included as random effect. Males that dispersed between groups were only considered in their first group in this analysis, so all individuals were only considered once in these models. Effect sizes are reported as odds ratios. Inspection of Q-Q plots and residual deviation plots from the DHARMa R package helped to assess model suitability.

2a) Rate of muzzle contact over repeated exposure to the novel food

To investigate the effect of exposure to the novel food on muzzle contact rate, we looked at four exposures from the first eating event for each group, as this event marks when at least one member of the group had recognised the novel food as a viable food. We also wanted to account for the number of individuals eating during each exposure, as it was inherent in our hypothesis that muzzle contacts around the novel food would be related to individuals eating it. Specifically, we expected muzzle contact rate to decrease across exposures when there were many monkeys eating it and therefore developing their own knowledge of it, but not if only very few were eating. To test this, we fitted a Zero-Inflated Poisson GLMM (using the glmmTMB function from R package 'glmmTMB' [ref]) with frequency of muzzle contacts initiated by each individual as the outcome variable, exposure number and number of monkeys eating during the exposure (z-transformed) as fixed effects, with an interaction between the two, and group and individual as random effects (Model 3). We included an offset of the duration of the experiment (log) in order to model the rate of muzzle contacts per minute per individual. Effect sizes are reported as odds ratios. We used the DHARMa R package [60] to assess model suitability via Q-Q plots and residual deviation plots, to test for overdispersion, and to test zero-inflation in an initial Poisson GLMM.

2b) Influence of knowledge of novel food and socio-demographic variation in muzzle contact behaviour

We wanted to assess which factors influenced individuals' involvement in muzzle contact interactions. Specifically, we wanted to test hypotheses regarding the function of this behaviour in information acquisition, so whether individuals' prior knowledge of the food was an important factor or not. We expected individuals who had not yet successfully extracted and eaten peanuts to initiate more muzzle contacts, and those who had already successfully extracted and eaten peanuts to be targeted more. In addition, if muzzle contact is involved in information acquisition, as we predicted, we would also expect variation between different age, sex and rank classes in whether they initiated more or were targeted more in line with our current state of understanding of social learning in this species. To investigate this, we counted how many muzzle contacts each individual of each group were involved in, first separated by whether they were the initiator or target, and further, by whether they were naïve or knowledgeable to the novel food. We then used two generalised linear mixed effect models (GLMMs) to analyse i) what factors influenced *initiating* muzzle contacts (Model 4), and ii) what factors influenced *being targeted* by muzzle contacts (Model 5). Model 4 had frequency of initiating as the outcome variable, with prior knowledge, age, sex and standardised rank as predictors, and individual and group as random effects. Model 5 had frequency of being targeted as the outcome variable, with prior knowledge, age, sex and standardised rank as predictors, and individual and group as random effects. Effect sizes for both of these models were assessed as odds ratios.

We ran post-hoc multiple comparisons (with Tukey correction) between the age categories (adult / juvenile / infant) using estimated marginal means comparisons from the 'emmeans' R package [58].

2c) Differential effects of knowledge on muzzle contact behaviour within age / sex classes

Here, we were interested in variation in how knowledge affected individuals' propensities to initiate or be targets of muzzle contacts *within* different age and sex classes, and how that might relate to either information-seeking or other factors at play in this type of close-contact social interaction. We therefore focussed only on individuals that were involved in muzzle contacts at least once, as either an initiator or a target. There were very few infants in this dataset, which caused abnormally high standard errors in the model. For this reason, we removed them and restricted our focus in this analysis to adults and juveniles. Since we were concerned with the effects of knowledge within the age-classes, we do not believe this decision caused bias in the results, and we found mostly similar results when including infants, only with much greater error which distorted some of the results (see annotated R script for details).

The outcome variable in this binomial GLMM was each individuals' status as either initiator or target in each muzzle contact. Fixed effects were whether each individual was naïve or knowledgeable to the novel food at the time of each muzzle contact, and their age and sex. We did not include rank here, as in the analyses described above (section 2b) the effect of rank on initiating and being targeted was in the same direction, and we did not expect knowledge to influence individuals of different ranks differentially. Based on the differences in life history trajectories between philopatric females and dispersing males, and the likely differences in information acquisition between adults and juveniles, we initially included a three-way interaction between prior knowledge, age and sex. We included individual as a random effect, but we did not include group as a random effect in the final model because the model fit was singular, indicating likely overfitting when including this random effect. In the final model (Model 6) we removed the three-way interaction, as it was not significant (Appendix 1 – Table 2), and tested for separate interactions between knowledge and age, and knowledge and sex, with fixed and random effects as described above (Model 6). Effect sizes were calculated as odd ratios.

In all analyses described above, we probed interactions using post-hoc multiple comparisons (with Tukey correction) of estimated marginal means using the R package ‘emmeans’ [58], and plotted the interactions using the R package ‘interactions’ [59]. All model diagnostics were analysed using the ‘DHARMa’ R package [60], and multicollinearity was assessed using variance inflation factors (VIFs). Model assumptions were satisfied unless otherwise reported and adjustments made. Statistics were computed in R Studio (R version 4.0.3), and linear regression was done with the base R stats package [61]. GLMMs were done using the ‘lmerTest’ package [62].

All data and R scripts are made available at: https://doi.org/10.5281/zenodo.5767598.

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Appendix

Appendix 1 – Table 1. Table showing details of group membership. Bold text indicates the first to eat in each group. Bold-italic text indicates the first individual to follow the immigrant innovator in extracting and eating peanuts.

Group	Individual	Age	Sex	Immigration date	Notes	Exposure when first extracting peanuts
AK$_{19}$	Ati	Adult	M	03/03/2016		n/a
AK$_{19}$	Boc	Adult	M	15/05/2019		n/a
AK$_{19}$	Ghi	Infant	M	n/a		n/a
AK$_{19}$	Ghid	Adult	F	n/a		n/a
AK$_{19}$	Gil	Infant	M	n/a		n/a
AK$_{19}$	Ginq	Adult	F	n/a		n/a
AK$_{19}$	Godu	Juvenile	F	n/a		n/a
AK$_{19}$	Guba	Infant	F	n/a		n/a
AK$_{19}$	Gubh	Adult	F	n/a		n/a
AK$_{19}$	Gugu	Adult	F	n/a		n/a
AK$_{19}$	Guny	Juvenile	F	n/a		n/a
AK$_{19}$	Guz	Infant	M	n/a		n/a
AK$_{19}$	Hlu	Juvenile	M	n/a		n/a
AK$_{19}$	Kek	Adult	M	31/05/2019	Unhabituated	n/a
AK$_{19}$	Mat	Juvenile	M	n/a		n/a
AK$_{19}$	Mbil	Infant	F	n/a		n/a
AK$_{19}$	Moya	Juvenile	F	n/a		n/a
AK$_{19}$	Nak	Juvenile	M	n/a		n/a
AK$_{19}$	Ncok	Infant	F	n/a		n/a
AK$_{19}$	Nda	Infant	M	n/a		n/a
AK$_{19}$	Ndaw	Juvenile	F	n/a		n/a
AK$_{19}$	Ndi	Juvenile	M	n/a		n/a
AK$_{19}$	Ndik	Juvenile	F	n/a		n/a
AK$_{19}$	Ndon	Adult	F	n/a		n/a
AK$_{19}$	Nge	Juvenile	M	n/a		n/a
AK$_{19}$	Nkos	Adult	F	n/a		n/a

AK$_{19}$	Nyan	Adult	F	n/a	n/a
AK$_{20}$	Ghi	Juvenile	M	n/a	1
AK$_{20}$	Ghid	Adult	F	n/a	2
AK$_{20}$	Gil	Juvenile	M	n/a	2
AK$_{20}$	Ginq	Adult	F	n/a	3
AK$_{20}$	Godu	Juvenile	F	n/a	2
AK$_{20}$	Guba	Juvenile	F	n/a	3
AK$_{20}$	***Gubh***	***Adult***	***F***	n/a	1
AK$_{20}$	Gugu	Adult	F	n/a	2
AK$_{20}$	Guz	Juvenile	M	n/a	1
AK$_{20}$	Nak	Juvenile	M	n/a	2
AK$_{20}$	Ncok	Juvenile	F	n/a	1
AK$_{20}$	Nda	Juvenile	M	n/a	4
AK$_{20}$	Ndaw	Juvenile	F	n/a	3
AK$_{20}$	Ndik	Juvenile	F	n/a	2
AK$_{20}$	Ndon	Adult	F	n/a	2
AK$_{20}$	Nge	Juvenile	M	n/a	2
AK$_{20}$	Nkos	Adult	F	n/a	n/a
AK$_{20}$	Nyan	Adult	F	n/a	4
AK$_{20}$	Twe	Adult	M	02/04/2020	2
AK$_{20}$	**Yan**	**Adult**	**M**	**04/03/2020**	1
BD	Aal	Infant	M	n/a	n/a
BD	Aan	Juvenile	M	n/a	1
BD	Aapi	Adult	F	n/a	n/a
BD	Add	Juvenile	M	n/a	1
BD	Alc	Adult	M	23/05/2019	n/a
BD	Ard	Infant	M	n/a	n/a
BD	Asis	Adult	F	n/a	3
BD	Bas	Adult	M	05/05/2017	n/a
BD	Dok	Adult	M	21/05/2019	n/a
BD	Eina	Adult	F	n/a	n/a
BD	Enge	Adult	F	n/a	4
BD	Fen	Adult	M	01/09/2017	3
BD	Flu	Adult	M	30/04/2019	n/a
BD	Gese	Adult	F	n/a	n/a
BD	Goe	Infant	M	n/a	n/a
BD	Han	Adult	M	06/05/2017	n/a
BD	Hee	Juvenile	M	n/a	3
BD	Heer	Adult	F	n/a	4
BD	Hia	Infant	M	n/a	n/a
BD	Hibi	Juvenile	F	n/a	n/a
BD	***Hipp***	***Adult***	***F***	n/a	1
BD	Hlo	Adult	M	16/05/2017	1

BD	Hond	Juvenile	F	n/a		1
BD	Kom	Adult	M	2017	Exact date unknown	n/a
BD	Lblind	Adult	F	n/a		1
BD	Lewe	Infant	F	n/a		n/a
BD	Miel	Adult	F	n/a		n/a
BD	Mimi	Infant	F	n/a		n/a
BD	Naal	Infant	F	n/a		n/a
BD	Neu	Adult	M	09/06/2014		1
BD	Non	Infant	M	n/a		n/a
BD	Nooi	Adult	F	n/a		n/a
BD	Numb	Adult	F	n/a		n/a
BD	Nurk	Adult	F	n/a		n/a
BD	Nuu	Juvenile	M	n/a		n/a
BD	Obse	Juvenile	F	n/a		1
BD	Oerw	Infant	F	n/a		n/a
BD	Oort	Juvenile	F	n/a		1
BD	Ouli	Adult	F	n/a		2
BD	Pal	Adult	M	07/12/2016		n/a
BD	Pann	Adult	F	n/a		n/a
BD	Piep	Adult	F	n/a		n/a
BD	Pix	Infant	M	n/a		n/a
BD	Poff	Infant	F	n/a		n/a
BD	Pom	Juvenile	M	n/a		1
BD	Potj	Adult	F	n/a		3
BD	**Pro**	**Adult**	**M**	**13/07/2019**		1
BD	Puol	Juvenile	F	n/a		1
BD	Rat	Juvenile	M	n/a		1
BD	Rede	Adult	F	n/a		n/a
BD	Reen	Infant	F	n/a		n/a
BD	Rhe	Adult	M	05/12/2017		n/a
BD	Rid	Infant	M	n/a		n/a
BD	Riss	Adult	F	n/a		n/a
BD	Sari	Juvenile	F	n/a		n/a
BD	Sey	Adult	M	21/05/2019		1
BD	Siel	Adult	F	n/a		n/a
BD	Sig	Infant	M	n/a		n/a
BD	Sirk	Juvenile	F	n/a		n/a
BD	Skem	Infant	F	n/a		n/a
BD	Snor	Adult	F	n/a		n/a
BD	Spam	Infant	F	n/a		n/a
BD	Ted	Adult	M	25/05/2019		1
BD	Ubu	Adult	M	28/05/2019		3
BD	Van	Adult	M	29/05/2018		4

KB	Aar	Infant	M	n/a	3
KB	Aara	Juvenile	F	n/a	n/a
KB	Aare	Adult	F	n/a	n/a
KB	Amg	Infant	M	n/a	n/a
KB	Amur	Adult	F	n/a	n/a
KB	Arn	Juvenile	M	n/a	n/a
KB	Lif	Adult	M	28/04/2015	n/a
KB	Mal	Juvenile	M	n/a	n/a
KB	Mara	Adult	F	n/a	n/a
KB	Mhao	Juvenile	F	n/a	4
KB	Mokc	Infant	F	n/a	n/a
KB	Nah	Juvenile	M	n/a	n/a
KB	Ness	Adult	F	n/a	n/a
KB	Yalu	Adult	F	n/a	n/a
KB	Yamu	Juvenile	F	n/a	n/a
KB	Yara	Infant	F	n/a	n/a
KB	Yeni	Adult	F	n/a	n/a
KB	Yuko	Juvenile	F	n/a	4
KB	Yze	Infant	M	n/a	n/a
LT	**Bab**	**Adult**	**M**	**24/06/2019**	1
LT	Ben	Adult	M	08/06/2018	4
LT	Daa	Juvenile	M	n/a	2
LT	Daen	Adult	F	n/a	2
LT	Dais	Adult	F	n/a	2
LT	Dal	Infant	M	n/a	3
LT	Deli	Adult	F	n/a	2
LT	Dewe	Juvenile	F	n/a	2
LT	Dext	Juvenile	F	n/a	3
LT	Dian	Adult	F	n/a	1
LT	Digb	Adult	F	n/a	2
LT	Dil	Juvenile	M	n/a	4
LT	Dio	Juvenile	M	n/a	1
LT	Dix	Infant	M	n/a	1
LT	Dore	Juvenile	F	n/a	2
LT	Geo	Adult	M	18/03/2019	2
LT	Lail	Infant	F	n/a	n/a
LT	Lanc	Adult	F	n/a	4
LT	Lar	Infant	M	n/a	n/a
LT	Laur	Adult	F	n/a	3
LT	Lava	Juvenile	F	n/a	n/a
LT	***Lill***	***Juvenile***	***F***	n/a	1
LT	Lizz	Adult	F	n/a	n/a
LT	Loui	Juvenile	F	n/a	4

LT	Rob	Juvenile	M	n/a	n/a
NH	**Avo**	**Adult**	**M**	**14/05/2018**	1
NH	Bela	Juvenile	F	n/a	n/a
NH	Can	Adult	M	30/05/2017	n/a
NH	Cus	Adult	M	21/05/2018	n/a
NH	Gabi	Infant	F	n/a	n/a
NH	Gan	Infant	M	n/a	n/a
NH	Gaya	Adult	F	n/a	n/a
NH	Gene	Adult	F	n/a	n/a
NH	***Gran***	***Juvenile***	***F***	n/a	1
NH	Guat	Juvenile	F	n/a	n/a
NH	Jixi	Juvenile	M	n/a	n/a
NH	Lima	Juvenile	F	n/a	4
NH	Prai	Juvenile	F	n/a	n/a
NH	Pret	Adult	F	n/a	n/a
NH	Pro	Juvenile	M	n/a	n/a
NH	Pru	Juvenile	M	n/a	n/a
NH	Pye	Infant	M	n/a	n/a
NH	Raba	Juvenile	F	n/a	n/a
NH	Renn	Adult	F	n/a	n/a
NH	Rev	Infant	M	n/a	n/a
NH	Reva	Adult	F	n/a	n/a
NH	Rey	Juvenile	M	n/a	n/a
NH	Rioj	Infant	F	n/a	n/a
NH	Roma	Adult	F	n/a	n/a
NH	Rosl	Juvenile	F	n/a	n/a
NH	Twe	Adult	M	24/05/2014	n/a
NH	Ula	Juvenile	M	n/a	n/a
NH	Umt	Juvenile	M	n/a	n/a
NH	Upps	Adult	F	n/a	4
NH	Ura	Infant	M	n/a	n/a
NH	Wol	Adult	M	29/05/2018	n/a
NH	Xal	Infant	M	n/a	4
NH	Xala	Adult	F	n/a	n/a
NH	Xia	Juvenile	M	n/a	1
NH	Xin	Infant	M	n/a	n/a
NH	Xian	Adult	F	n/a	n/a
NH	Yan	Adult	M	14/05/2019	n/a

Appendix 1 – Table 2. Model including three-way interaction effects between knowledge, age and sex on muzzle contact behaviour

	estimate	odds ratio	st. error	z-value	p-value
(Intercept)	-0.83	0.44	0.54	-1.53	0.126
knowledgeable	1.65	5.22	0.40	4.09	***<0.001***
age (juvenile)	-1.17	0.31	0.81	-1.44	0.149
sex (male)	0.19	1.21	0.95	0.20	0.839
knowledgeable X age (juvenile)	-1.17	0.31	0.58	-2.02	***0.044***
knowledgeable X sex (male)	2.71	15.05	1.02	2.67	***0.008***
age (juvenile) X sex (male)	-0.79	0.45	1.35	-0.59	0.558
knowledge X age X sex	-1.65	0.19	1.21	-1.37	0.171

NB. Reference categories: age = adult; sex = female; knowledgeable = naïve. Bold italics indicate significant p-values at < 0.05.

Appendix 1 – Table 3. Dominance hierarchies for all groups were significantly linear.

Group	AK19	AK20	BD	KB	LT	NH
h’	0.45	0.26	0.21	0.53	0.22	0.33
p-value	<0.001	<0.001	<0.001	<0.001	0.017	<0.001

Chapter 2. Does maternal rank predict rank acquired and grooming patterns of wild male vervet monkeys after their natal dispersal?

Pooja Dongre[1, 2], Varun Manavazhi[2, 3], Erica van de Waal[1, 2]

[1] Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

[2] Inkawu Vervet Project, Mawana Game Reserve, KwaZulu Natal, 3115, South Africa

[3] Indian Institute of Science Education and Research, Pune, India

ABSTRACT

Dispersing primates have received much less attention in long-term field research than their philopatric counterparts due to the considerable challenges in following them throughout multiple life-stages when they emigrate from habituated study groups. Dominance ranks have pervasive influence on the lives of group-living primates, and juveniles ‘inherit’ their mothers’ ranks. Whilst philopatric female cercophithecines keep their inherited rank throughout life, with lasting impacts on their fitness, how dispersing males acquire rank and form social bonds after dispersal, and the influence of social skills developed during juvenescence on this remain under-explored. We utilised a long-term database, spanning ten years, to follow ten dispersing male vervet monkeys across their natal dispersal. We calculated males’ average maternal ranks between their ages of one to three years in the natal group; and, during their first year post-dispersal in their immigration groups, we calculated the ranks males acquired, their number of grooming partners and frequency of grooming interactions. We found a trend for males of higher maternal rank to acquire lower ranks in the first year in their immigration groups than those of lower maternal rank. We also found inverse relationships between maternal rank and frequency of grooming given and received, but no relationship between rank acquired by males and their grooming frequencies. Number of grooming partners to whom grooming was given may be related to male rank acquired in a larger sample. Our results suggest that an individual’s dominance rank during juvenescence, which heavily shapes the social environment, may have impacts on development of social competence, lasting into adulthood. We propose future avenues of research into mechanisms such as inhibitory control and behavioural flexibility, which might be influenced by juveniles’ experience of dominance rank, and subsequently affect social outcomes post-dispersal. We urge that overcoming the challenges of studying dispersers can be valuable in our understanding of how animals develop skills to deal with changing environments that can benefit the fields of primate behavioural ecology and conservation.

INTRODUCTION

Most early research into primate social behaviour emerged from the study of a few female philopatric Cercopithecoid primates, largely due to easy observational conditions in the field, usually outside of dense forests for these species (Kapsalis, 2004; Strier, 1994). Similarly, within these species, philopatric females have been afforded considerably more research attention than their dispersing male counterparts, due to lifelong group membership (Pusey & Packer, 1987), which has facilitated long-term field studies of distinguishable individuals. This has given rise to decades' worth of refined understanding of female social strategies which underlie the matrilineal group dynamics in these species, such as such as fitness-enhancing social bonds, particularly within matrilines, and dominance rank inheritance (e.g. Borgeaud, van de Waal, & Bshary, 2013; Brent, Ruiz-Lambides, & Platt, 2017; Kapsalis, 2004; Silk, Alberts, & Altmann, 2003). Males, however, disperse upon reaching sexual maturity, and join new groups as adults, which makes long-term studies of them challenging, particularly in the wild. Whilst some recent field studies have focussed on male social bonding (e.g. Kalbitz, Ostner, & Schülke, 2016; Marty, Hodges, Agil, & Engelhardt, 2017; Patzelt et al., 2014; Young, Majolo, Schülke, & Ostner, 2014), studies following them across dispersals or through different life stages are lacking (but see: van Noordwijk & van Schaik, 1985; 2001). Furthermore, though captive studies can make reasonable approximations at socio-ecologically relevant housing conditions for philopatric females, simply by housing related females together, for males, natural dispersal and subsequent social integration is much harder to imitate. There are captive studies into social challenges faced by males, in which males are transferred between groups to mimic dispersal (e.g. Raleigh, Mcguire, Brammer, Deborah, & Yuwiler, 1991; Rox, Van Vliet, Sterck, Langermans, & Louwerse, 2019) but many variables may be at play in the wild (e.g. timing of dispersal, choice of immigration group etc.) that cannot be replicated. Moreover, relative to females who can rely on social bonds with kin and lifelong group mates, males arguably face greater complexity in the socioecological challenges of adult life, due to their need to travel between groups and integrate socially into new groups. In the wild, males' natural movement into and out of known study groups has been a challenge for long-term observational field studies of them (De Moor, Roos, Ostner, & Schülke, 2020; Kajokaite, Whalen, Koster, & Perry, 2022; Sugiyama, 1976). Studying multiple neighbouring groups in the long-term can help to overcome these hurdles by providing more opportunities for natural dispersals between studied groups, and can further our understanding of how animals deal with the additional difficulties of dispersal.

Dominance hierarchies are fundamental aspects of primate groups, facilitating cooperative inter-group defence of resources, whilst simultaneously distributing intra-group access to those resources. Whilst the outcomes of intra-group conflicts for resources underlie hierarchy formation, the majority of contests are based on aggressive signals, and severe harmful aggression in the group is reduced. Stable hierarchies form and are maintained by the psychological effects of winning or losing conflicts. Individuals generalise these outcomes towards other group members, influencing subsequent conflict outcomes in the same direction (Hemelrijk, Wantia, & Isler, 2008; Leimar, 2021). Consistent winners become dominant over consistent losers through this learning process, and high dominance ranks are largely associated with fitness benefits across many primate species (Majolo, Lehmann, De Bortoli Vizioli, & Schino, 2012). In primates with female philopatry, both male and female offspring inherit their mothers' ranks. Dominant females show aggression towards infants of females lower in rank than them, which begins the rank-learning process described above early in life, and leads to maternal rank inheritance (Holekamp & Smale, 1991; Horrocks & Hunte, 1983; Hemelrijk et al., 2008; Leimar, 2021). For philopatric females, their maternally inherited rank will most likely remain with them throughout their lives. Adult males, however, must compete for rank in the groups into which they immigrate. Later life outcomes of males (i.e. post-dispersal) may be influenced by their mothers' ranks due to rank-related learning experiences, shaping their development of social skills. For example, learning to defer resources to higher ranked individuals as a low ranked juvenile might have lasting effects on social cognition and behaviour that persist into adulthood. Maternal rank can also have direct and long-lasting consequences on egg or foetal development, with effects lasting into later life. For example, in yellow baboons (*Papio cynocephalus*), maternal rank at the time of conception of male offspring predicted chronic levels of a stress-related hormone (glucocorticoid) in these males when they became subadults (approx. 5 years later; Onyango, Gesquiere, Wango, Alberts, & Altmann, 2008). High maternal rank was also associated with faster growth rate in male and female yellow baboons (Altmann & Alberts, 2005) and earlier age of sexual maturity in males (Alberts & Altmann, 1995). Furthermore, in long-tailed macaques (*Macaca fascicularis*), sons of high ranked females were more likely to achieve top dominance rank in groups they dispersed to as adults (van Noordwijk & van Schaik, 2001), whereas a study investigating whether maternal rank predicted male post-dispersal rank acquisition in captive vervet monkeys (Fairbanks et al., 2004) found no link. On the one hand, research in the wild, however, is required to validate the finding in vervet monkeys. Whilst captive settings allow greater experimental control, this study may not have yielded an ecologically valid outcome in this context due to confounding factors such as unnatural spatial constraints on social interactions, artificial dispersal timing, and an intermediate period in an all-male group with novel learning experiences (Fairbanks et al., 2004). On the other hand, rank acquisition by adult males may be subject to different social forces in vervet monkeys and macaque species related to the nuanced differences in adult intersexual relationships between the species. For example, in vervet monkeys, the dominance hierarchy is interdigitated between the sexes with alpha female positions and alpha male positions arising under different conditions (Hemelrijk et al., 2020). In addition, infanticide by adult males is rare in vervet monkeys relative to macaque species, suggesting that male vervets may be more appeasing towards females (Soltis et al., 2000). Indeed, links between affiliative social skills, particularly regarding male-female relationships, and male rank acquisition have been found in vervet monkeys (Raleigh & McGuire, 1989; Young, McFarland, Barrett, & Henzi, 2017). Therefore, research into the effects of maternal rank on post-dispersal rank acquisition in wild vervet monkeys is timely.

Taborsky & Oliveira (2012) define social competence as "…the ability of an individual to optimise its social behaviour depending on available social information". Research suggests that, across many taxa, including primates (Taborsky, Arnold, Junker, & Tschopp, 2012; Waters & Sroufe, 1983; Taborsky et al., 2012; White, Gersick, Freed-Brown, & Snyder-Mackler, 2010; Wooddell, Kaburu, & Dettmer, 2020), social competence is predicted by developmental social complexity i.e. the diversity of potential social partners and appropriate suites of interaction patterns available to use with them (Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017). Greater social complexity during development can offer more diverse learning experiences, preparing individuals for a wider range of unexpected situations in the future. Inhibitory control and behavioural flexibility are likely to be important components of social competence, particularly when contexts change and previous strategies must be inhibited according to newly available social information (Amici, Call, Watzek, Brosnan, & Aureli, 2018). In wild spotted hyenas (*Crocutta crocutta*), a female philopatric carnivore species with remarkably similar social dynamics to many Cercopithecine primates, greater inhibitory control was associated with low dominance rank, specifically for individuals living in larger groups (Johnson-Ulrich & Holekamp, 2020). Arguably, in large groups, individuals of lower rank face more social complexity than their higher ranked counterparts. With the greatest proportion of individuals outranking them, they have a larger number of individuals to observe cautiously and defer resources to, whilst also learning who is more tolerant and can be approached safely and interacted with. Given Taborsky and Oliveira's (2012) definition (above) we can see how low maternally inherited rank could afford development of greater social competence. Furthermore, upon joining a new group, an individual that had low rank as a juvenile would be more adept at avoiding conflicts against established dominant residents (which would most likely be lost) by inhibiting its own desires for sought after resources. In contrast, having grown up with high rank might lead to challenging the established dominants in the new group and therefore losing conflicts early on in a new group. These early losses might be hard to recover from, given that effects of losing on future conflicts outcomes are likely to be stronger than the effects of winning (Leimar, 2021). Specific cognitive mechanisms, however, can be complicated to test in the wild, but by establishing whether links exist between maternal rank and social outcomes such as rank acquisition and social bond development post-dispersal, we can lay foundations to inform targeted in-depth studies in the future. Moreover, research in this area can afford greater insight, more generally, into the development of mechanisms that underlie flexible social skills and cognition in adulthood.

Vervet monkeys are a female philopatric Cercopithecine primate species, ideally suited to behavioural observation studies due to their semi-terrestrial nature and non-endangered status (Mertz, Surreault, van de Waal, & Botting, 2019). Their life history, with males dispersing multiple times during their adult lives, usually to neighbouring groups (Cheney & Seyfarth, 1983), makes them particularly suitable for studies of dispersers. Grooming socially central females and spending time in close proximity to them appears to influence male vervet monkeys' ability to improve their rank (Young et al., 2017), implicating social competence in their rank acquisition process. In this study, we aimed to assess whether maternal rank influenced the rank males achieved a year after their natal dispersal into their first immigration group. We defined maternal rank as the mother's rank during the male's juvenile ages of one to three years because juveniles spend more time in proximity to their mothers during this period of their lives (Fairbanks & McGuire, 1985). We focus on the natal dispersal, since this limits the males' prior social experience to that related to their maternally inherited rank in the natal group. Utilising a long-term database spanning almost a decade, we followed the natal dispersals of ten males between four of our habituated study groups. Given the winner and loser effects that support the formation of hierarchies, we might expect males of high, rather than low, maternal rank to gain rank more quickly after joining a new group, due to their confidence and dominating behaviour. This would result in positive correlation between maternal rank and male rank acquired after a year in the new group. Other factors, such as larger body size in high maternal rank males, due to greater developmental access to resources, could influence their competitive ability in this way. Contrastingly, if the potential links exist between greater development of inhibitory control and social competence in males of low maternal rank, as outlined above, this would give rise to an inverse relationship between maternal rank and male rank acquired. We assessed whether our data support either hypothesis by testing the correlation between maternal rank and male rank acquired.

Next, we attempted to examine whether any patterns of association exist between males’ involvement in grooming interactions and, both, maternal rank and male rank acquired, and whether these associations would better support either hypothesis. We measured males’ numbers of grooming partners, to whom grooming was given, and from whom it was received (*out-degree* and *in-degree*, respectively). We also measured the frequency of their grooming interactions both given and received (*out-strength* and *in-strength*, respectively) during their first year in their new groups. To establish for which hypotheses our results provide better support, we measured correlation between in-/out-degree and in-/out-strength with, both, maternal rank and male rank attained in the immigration group. We distinguish between what degree and strength measures can each reveal, and our corresponding predictions for associations of each with maternal rank or male rank acquired. Degree shows the number of other monkeys that each male interacted with, across the whole first year in the immigration group, which is likely to reflect their access to social partners. Access to more partners is likely related to current rank, as social partners are a limited and contested resource. Degree, however, can easily reflect numerous superficial connections and does not reveal anything about the quality of relationships. Therefore, under either hypothesis, we would more likely expect associations between in- or out-degree with male rank acquired, than with maternal rank. Strength, on the other hand, shows the relative level of investment in social relationships of each male. Whilst it does not show investment per partner, and it does not distinguish between investing heavily in a few relationships or lightly across many relationships, it does nonetheless reflect overall investment in socialising. Therefore, if grooming many partners facilitates males to gain rank, and if maternal rank and male rank acquired correlate positively, we would expect positive correlations between out-strength and both, maternal rank and male rank acquired. Since grooming is often reciprocal, we would make similar predictions for in-strength, though perhaps for weaker associations, if male behaviour drives these effects. On the other hand, if low maternal rank results in greater development of social competence, we would expect out-strength to correlate inversely with maternal rank. If grooming others frequently also contributes to their increase in rank in the new group, we would expect a positive correlation between out-strength and male rank acquired. Again, we make similar, though weaker predictions regarding in-strength.

METHODS

Ethical considerations

All data were collected following ASAB/ABS guidelines for the care and use of animals (doi:10.1016/j.anbehav.2019.11.002). All the behavioural observations of wild vervet monkeys in our study were in accordance with the ethical standards of the institution at which the studies were conducted and have been approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa.

Study site and population

The project was carried out at the Inkawu Vervet Project (IVP), located in the Mawana Game Reserve in the province of KwaZulu-Natal, South Africa (28°00’ S, 31°12’ E). The vegetation of the area is typical of the savannah biome, consisting of mainly thickets and bushveld. Two distinct seasons occur in a year: a hot, wet season from November to April; and a cold, dry season from May to October. We focused on four groups of wild vervet monkeys – Ankhase (AK), Baie Dankie (BD), Noha (NH), and Kubu (KB) – that have overlapping home ranges, and had group sizes ranging between 20 to 68 individuals during the study period. Habituation of AK, BD and NH started in 2010, and of KB in 2013.

Data collection

We collected behavioural data for this study at IVP between January 2011 and February 2020 according to established protocols. A team comprising both researchers and field assistants (hereafter, observers) followed the four groups for up to six days per week, for a minimum of eight hours up to a full day, according to daylight hours. To locate the monkeys efficiently each day, one adult female in each group was fitted with an active VHF telemetry collar. All observers were trained and tested to identify monkeys using unique facial and bodily features and natural markings, as well as to collect behavioural data according to IVP’s established protocols, and had to pass an inter-observer reliability test with an experienced researcher (minimum 0.80 Cohen’s kappa; McHugh, 2012). Researchers keep a file consistently up to date, containing information on all monkeys’ births, deaths, dispersals, matrilineal membership, group membership and permanent group fissions, at the field site (the IVP Life History file).

Observers recorded all agonistic (conflict) and grooming interactions *ad-libitum* (Altmann, 1974) using IVP’s ethogram (Table S2). Specifically, we recorded grooming on a basis of frequency, with no durations, to allow observers to distribute attention to a maximum number of individuals during *ad libitum* data collection. This method reduces the bias that might be introduced by increased observer attention towards more socially central individuals and observers made a conscious effort to move throughout the group during data collection. Our team has previously found comparable results when analysing data collecting using both focal animal sampling and *ad libitum* sampling (Canteloup, Puga-Gonzalez, Sueur, & van de Waal, 2020). We recorded all social interactions (conflicts and grooming) that we could observe from beginning to end, and recorded the sequence of each according to our ethogram. We counted grooming frequency in bouts, with one bout determined from the onset of one individual grooming another, until they stop and the other takes over, or until they stop for a minimum of ten seconds before starting again. We used the behavioural sequences of agonistic interactions to construct dominance hierarchies, and grooming data to calculate social network metrics. Researchers collected and entered all data, in the field, using mobile devices with Pendragon Forms® software.

From the IVP Life History file, ranging from 2011 to February 2020, we shortlisted all males that were born into one of the study groups and whose natal dispersal was into another study group. We looked only at natal dispersal events (and not subsequent secondary dispersals) as our hypothesis concerns the effects of social experience in the natal group due to their maternally inherited rank. Learning experiences in secondary groups might influence male behaviour surrounding dispersals subsequent to the natal one. We considered a male to have completed a dispersal after they slept among the new group regularly for at least two months. We selected only males whose maternal identity was known, and whose mothers were present until at least the third year of their juvenile period. Ten males met these criteria (Table 1). After dispersal, we chose a study period of one full year of residence in the new group to allow comparisons between individuals despite potential variation in their total length of residence.

Table 1. *List of study subjects*

Study subject	Mother	Natal Group	Immigration Group	Birth Year	Date of Immigration	Date of Departure
Hlokoloza	Hleka	AK	BD	2012	16/05/2017	20/11/2019
Hwahwaza	Hamba	AK	BD	2011	08/06/2016	11/12/2017
Mvula	Mamoobi	AK	BD	2010	13/06/2015	17/12/2016
Nyoni	Nkosikasi	AK	BD	2013	16/05/2017	19/11/2018
Rheban	Roma	NH	BD	2012	05/12/2017	27/09/2021
Toronto	Troia	NH	BD	2009	16/06/2014	13/02/2016
Ububhibhi	Ulaka	AK	BD	2011	28/05/2016	06/06/2020

Wolfie	Wietnie	BD	AK	2010	20/07/2015	24/05/2018
Yangtze	Yenissei	KB	NH	2013	14/05/2018	27/01/2020
Zurich	Zara	NH	BD	2009	03/06/2014	15/02/2016

AK= Ankhase, BD= Baie Dankie, NH= Noha, KB= Kubu

Dominance hierarchy calculations

We constructed dominance hierarchies using the R package “Elo Rating” (Neumann & Kulik, 2020). An individual’s Elo rating reflects their dominance rank because it increases or decreases based on the outcome (win or lose) of the conflicts that they take part in. We used only dyadic interactions with a clear ‘winner’ and ‘loser’ to construct the dominance hierarchy. We determined a ‘winner’ and ‘loser’ for an interaction only when the interaction ended with one individual performing an aggressive behaviour and the other responded with a submissive behaviour (Table S2). We excluded all other undecided conflicts.

In order to calculate the maternal ranks for the study males, we constructed adult female dominance hierarchies in the study males’ natal groups. We used data spanning from the beginning of the project (2011) for this, as adult female group membership and dominance ranks are relatively stable. We calculated adult female-female only hierarchies for this, as they are most relevant given the relative instability of adult male rank and group membership over the study subjects' juvenile periods. In addition, it is the behaviour of adult females towards juveniles, dependent on female ranks relative to one another, from which juveniles learn their ranks. We did not calculate exact ranks for the males as juveniles themselves because priority is given to data collection from adults to allow adequate sample sizes. Since juveniles inherit maternal rank, we used the mothers’ ranks as proxies for the study subjects’ juvenile ranks.

Using a long duration of up to nine years of data gave ample time for the Elo ratings of adult females to stabilise and the adult female hierarchy to be distinct. We extracted the mothers’ standardised ELO scores (using ‘scale_elo’ from the ‘EloRating’ R package; Neumann & Kulik, 2020), averaged from the males’ date of birth until their third birthday. The ‘scale_elo’ command gives scores that fall between 0 and 1, which are proportional to their absolute ELO scores, allowing comparisons of dominance rank between individuals from groups of varying size.

To calculate the rank attained by each study male one year after dispersal, we first used one year of conflict data from the immigration groups *prior to* each males’ immigration. This allowed a stable group hierarchy to be obtained before introducing the new immigrants into it. Then, from each male's date of immigration, we added a further year of conflict data for the group, including the study males, to establish their ranks achieved after the first year. Since vervet monkeys display linear dominance hierarchies in which females and males are co-dominant (our population: Hemelrijk, Wubs, Gort, Botting, & van de Waal, 2020; another population: Young et al., 2017), a single, interdigitated adult dominance hierarchy was constructed to study immigrant male ranks in their new group. This contrasts with our treatment of maternal ranks above, because the instability of adult male ranks, and the relationships of adult males' and adult females' ranks are relevant to our interest, here, in the ranks attained by the study males in their new groups. Again, we calculated standardised ELO ratings (using 'scale_elo'), as above, this time as a single rating (not averaged) on the date that marked one year of tenure in the immigration group of each male.

Social network analyses

To calculate social network metrics for males during their first year in their immigration groups, we considered all grooming interactions during the year following each male's immigration into each group. The ten study males immigrated into three different groups (AK, BD and NH) during different years (see Table 1). Due to some males immigrating in pairs (within two weeks of one another), this resulted in seven unique annual group compositions among the three groups. We therefore created seven directional grooming matrices for all individuals in each annual group, with grooming given by each individual in rows, and grooming received in columns. From these matrices, we removed all individuals that were not present for the full year, due to new births, deaths, disappearances, immigrations and emigrations, to ensure equal sampling duration for every individual in the matrix. We then used these matrices to calculate the social network metrics: *degree* and *strength*. Degree is the total number of partners of an individual, and strength is the total number of interactions of an individual. We also calculated the directional counterparts of these metrics, *in-degree, out-degree, in-strength* and *out-strength*, which differentiate grooming received (in-) and grooming given (out-). All metrics were calculated using the R package 'igraph' (Csardi & Nepusz, 2006).

Finally, we standardised each of our metrics: in-degree, out-degree, in-strength and out-strength, for each annual group by calculating the deviation from the mean for each individual of the group. We used this method of standardisation to allow comparisons of our ten study males with one another across different groups, because it maintains potential variation in grooming frequencies among group members that could differ between groups, whilst accounting for group differences in overall grooming behaviour that could arise due to seasonal variation, annual resource availability, group habits and observer effort. We could then compare the ten study males with one another, with regard to how far they deviated from their own group's mean.

Excluded data

Whilst we used all available data to explore the patterns of association in our dataset, four males that were present during the earliest years of the study (Mvu, Wol, Tor and Zur) had five or fewer conflicts that informed the ELO ratings of their ranks acquired in the first year in their new groups. Whilst we did run analyses with these males included (due to the already small sample size), whenever we analysed male rank acquired, we repeated the analysis with them excluded. We did this to establish whether or not the patterns we expected were strengthened when potentially unreliable data points were excluded. In one further case, we repeated an analysis excluding a single extreme outlier (Rhe; more details below), in order to establish the extent to which this data point influenced the result.

Statistical analyses

We used linear regression using the function "lm" from the base R "stats" package (R Core Team, 2020) to test our hypothesis regarding the effect of maternal rank on male rank acquired. After removing potentially unreliable data points (see *Excluded data*), we also ran a Pearson's correlation test ("cor.test" function in base R "stats" package; R Core Team, 2020), due to the smaller sample size, between maternal rank and male rank acquired. We then used eight Pearson's correlation tests to compare relationships between both, maternal rank and male rank acquired, with each of: a) in-degree, b) out-degree, c) in-strength and d) out-strength. In all statistical tests involving male rank, we repeated the analysis after having removed the four unreliable males (see *Excluded data*, above). When analysing the correlation between maternal rank and out-strength, we repeated the analysis removing the single extreme outlier, Rhe, to establish how strong an effect he had on the result. All variables analysed were standardised to allow us to compare males dispersing from and immigrating into different groups, as described above. We ran all statistical analyses in R version 4.0.3 (R Core Team, 2020). All significance levels were set to α two-tailed = 0.05. All plots were made with the 'ggplot2' R package (Wickham, 2016).

RESULTS

Maternal rank and male rank attained

Maternal rank did not predict male rank attained significantly (Est. = -0.26, df = 0.22, SE = 7.43, t = -1.18, p = 0.276; Figure 1). However, after removing Wol, Mvu, Tor and Zur, due to their unreliable ELO ratings, we found a marginally significant inverse correlation (r = -0.80, df = 4, p = 0.054). Males of higher maternal rank tended to acquire lower ranks in the first year in their immigration groups than those of lower maternal rank.

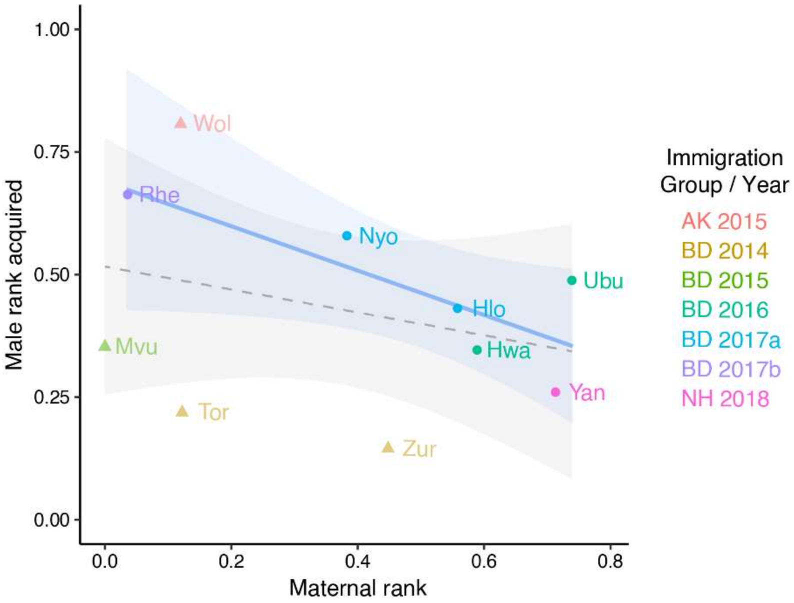

Figure 1. Relationship between maternal rank and male rank acquired in the new group of ten study males (three letter codes of their names). Ranks on both axes are ELO scores, proportionally scaled between 0 (lowest) and 1 (highest) within each group. Dashed line and grey shaded area refer to all ten data points, and indicate linear model prediction (p = 0.276) and 95% confidence interval. Blue shaded area and solid line refer to relationship with four potentially unreliable (triangular) data points removed (r = -0.80; p = 0.054; see Excluded Data in Methods for further details).

Number of grooming partners

In-degree was not significantly correlated with maternal rank (Pearson’s r = -0.27, df = 8, t = -0.79, p = 0.450; Fig. 2A), indicating no relationship between the number of partners that groomed each male and their maternal rank. In-degree was also not correlated with male rank attained, whether the unreliable male data were used (r = 0.17, df = 8, t = 0.48, p = 0.646; Fig. 2B) or not (r = -0.30, df = 4, t = -0.63, p = 0.563). This indicates no relationship between the number of partners that groomed each male and the rank they acquired during a year in their immigration group.

Out-degree was not correlated with maternal rank (r = -0.08, df = 8, t = 0.24, p = 0.814; Fig 2C), indicating no relationship between the number of partners that each male groomed and their maternal rank. Out-degree was not correlated with male rank attained, whether the unreliable male data were used (r = -0.07, df = 8, t = -0.19, p = 0.853 Fig. 2D) or not (r = -0.65, df = 4, t = -1.70, p = 0.164), though the negative correlation coefficient became stronger and the probability of incorrectly rejecting the null hypothesis decreased dramatically in the latter. The latter suggests that including more reliable data points may reveal an inverse association between ranks acquired by males in their immigration groups and the number of partners they groomed

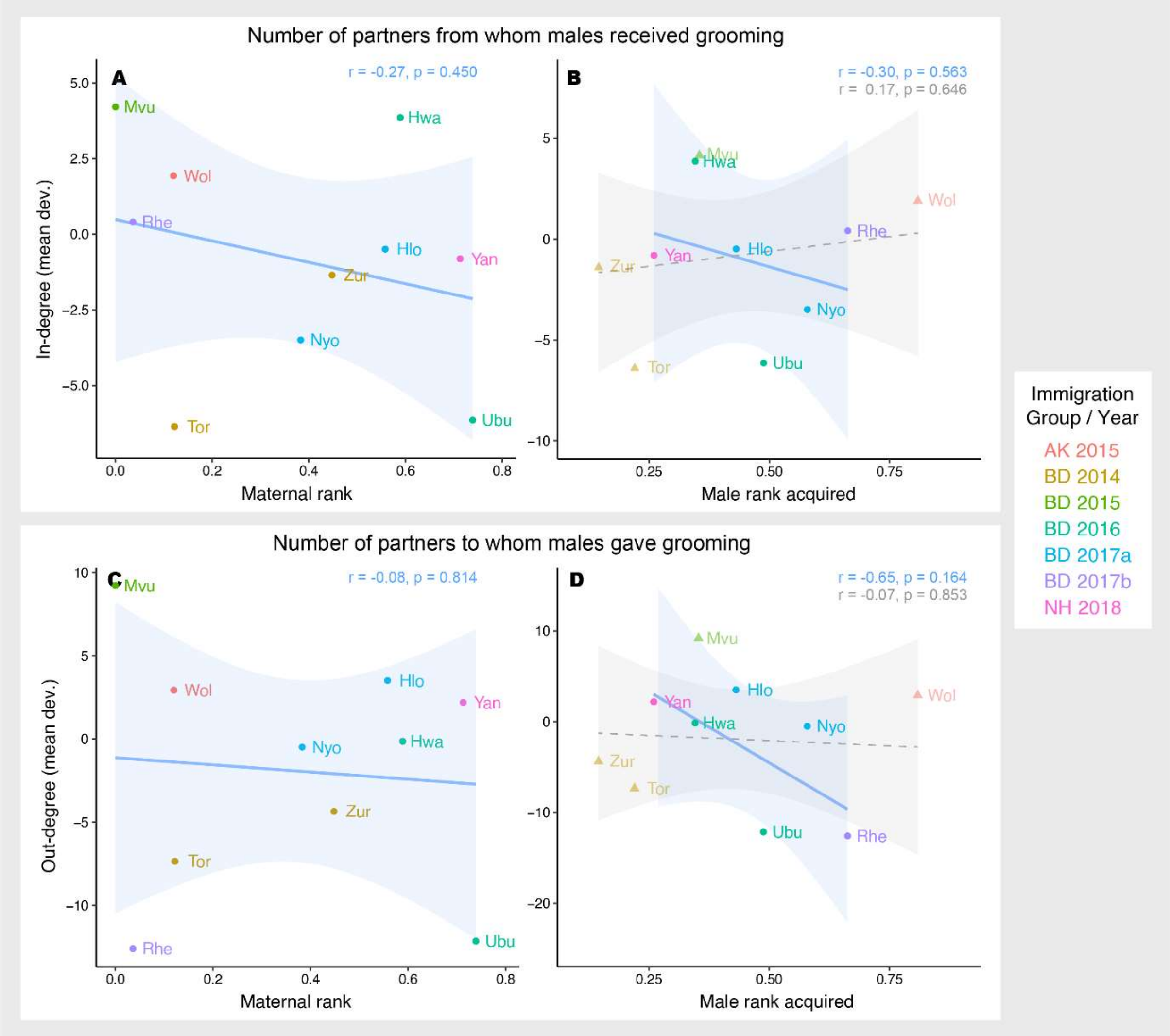

Figure 2. Relationships between A) maternal rank and in-degree, and B) male rank acquired and in-degree, C) maternal rank and out-degree, and D) male rank acquired and out-degree. Ranks on the x-axes are ELO scores, proportionally scaled between 0 (lowest) and 1 (highest) in each group. Maternal ranks are the males' mothers' ranks in the natal group, and male rank acquired are males' ranks after one year in the immigration group. On the y-axes, in- and out-degree (mean dev.) are the number of grooming partners of each male during the first year in their immigration groups from whom grooming was received and to whom grooming was given, respectively. These values are standardised across the groups into which each male immigrated (immigration group / year) by subtracting the mean of their immigration group from each males' value (positive values are high relative to their own group, negative values are low relative to their own group). Blue lines and shading show relationships when only reliable data only are included. Grey shading and dashed lines (in B and D) show relationships when four potentially unreliable (triangular) data points are included (see Excluded Data in Methods for further details).

Frequency of grooming interactions

In-strength was significantly inversely correlated with maternal rank (r = -0.68, df = 8, t = -2.63, p = 0.030 = ; Fig. 3A) It was not correlated with male rank attained whether the unreliable male data were used (r = -0.02, df = 8, t = -0.07, p = 0.950; Fig. 3B) or not (r = -0.04, df = 4, t = -0.08, p = 0.938). These results suggest a relationship between the frequency of grooming received by males and their maternal rank, but not the rank they acquired in their immigration groups.

Out-strength was not significantly correlated with maternal rank (r = -0.55, df = 8, t = -1.87, p = 0.098; Fig 3C), though there is a trend, and there is clearly a single strong outlier (Rhe). When this outlier is removed, this correlation becomes highly significant (r = -0.93, df = 7, t = -6.77, p < 0.001). Out-strength was not correlated with male rank attained, whether the unreliable male ranks were used (r = -0.04, df = 8, t = -0.12, p = 0.907; Fig. 3D) or not (r = -0.19, df = 4, t = -0.40, p = 0.712). These results suggest that, among most males, there is a strong inverse relationship between the frequency of grooming they give and their maternal ranks, but not the rank they acquired in their immigration groups.

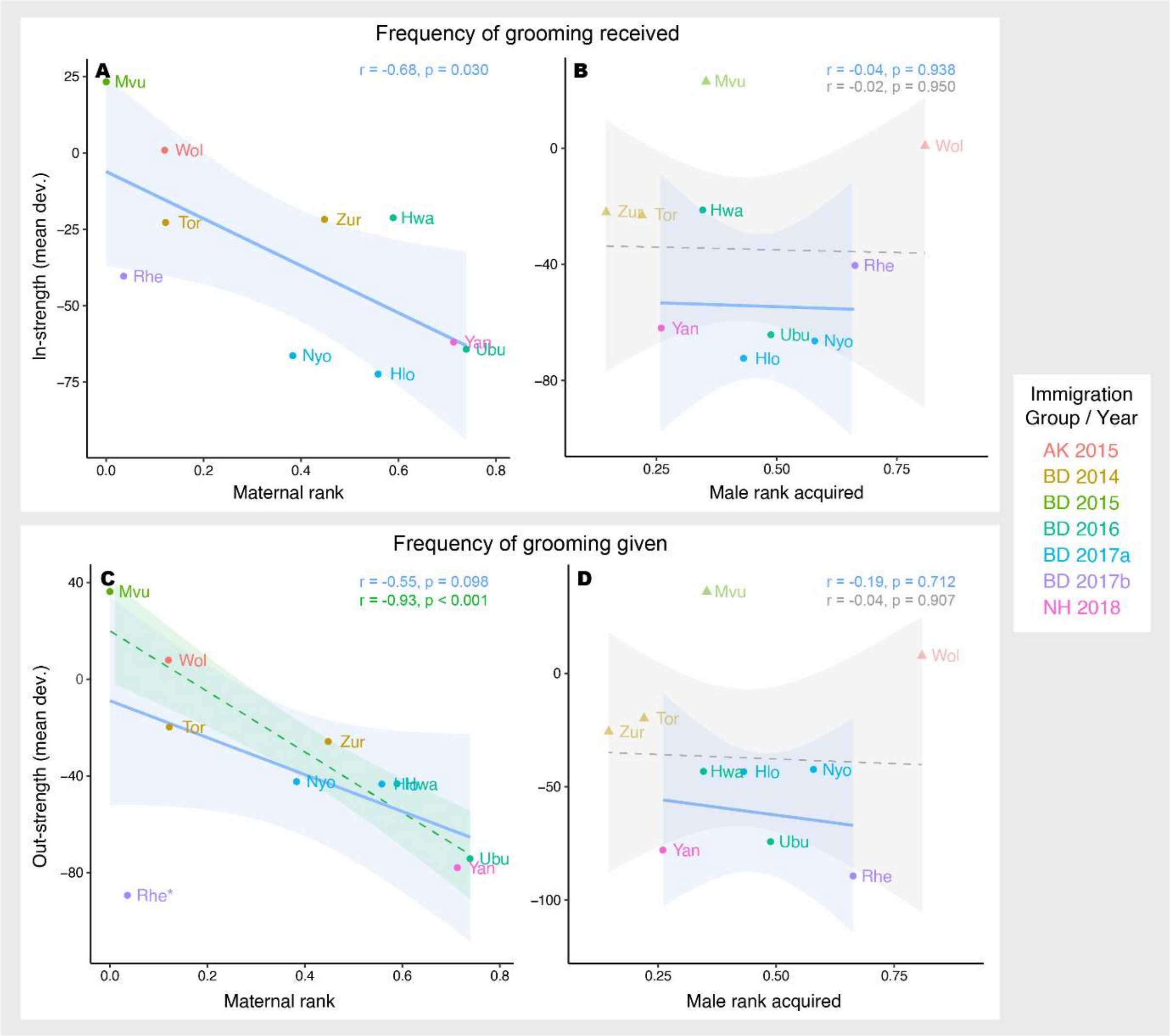

Figure 3. Relationships between A) maternal rank and in-strength, B) male rank acquired and in-strength, C) maternal rank and out-strength, and D) male rank acquired and out-strength. Ranks on the x-axes are ELO scores, proportionally scaled between 0 (lowest) and 1 (highest) in each group. Maternal ranks are the males' mothers' ranks in the natal group, and male rank acquired are males' ranks after one year in the immigration group. On the y-axes, in- and out-strength (mean dev.) are the frequency of grooming received and given, respectively, of each male during the first year in their immigration groups. These values are standardised across the groups into which each male immigrated (immigration group / year) by subtracting the mean of their immigration group from each males' value (positive values are high relative to their own group, negative values are low relative to their own group). Blue lines and shading show relationships when reliable data only are included. Grey shading and dashed lines (in B and D) show relationships when four potentially unreliable data points are included, which are identified as triangular points. Green shading and dashed line in C shows relationship with extreme outlier* removed (see Excluded Data in Methods for further details).

DISCUSSION

We aimed to further our understanding of whether maternally inherited rank influenced later life outcomes in the dispersing sex of vervet monkeys. Our results suggest there may be an inverse relationship between maternal rank and the dominance rank that males attained during the first year in new groups following their natal dispersal. We also explored whether patterns of association existed between male involvement in grooming in their new groups and, both, maternal rank and male rank acquired, to further examine whether low maternal rank might be related to the development of social competence during juvenescence. Maternal rank was not correlated with either the number of partners a male was groomed by (in-degree) or that he groomed (out-degree) during the first year in the immigration group, but did correlate inversely with the frequency of grooming received (in-strength) and tended to do so with grooming given (out-strength). On the other hand, male rank acquired did not correlate with in-strength or out-strength, nor in-degree, or out-degree, but our analyses suggest that the addition of more reliable data may reveal an inverse relationship between male rank acquired and out-degree (number of partners that the male groomed). Whilst we refrain from drawing strong conclusions from a small sample size, we explain below how the pattern of results we have obtained shows most likely support for the hypothesis that low maternal rank supports the development of greater social competence, possibly via inhibitory control. More data are however required to establish whether the patterns we found are robust in a large, reliable dataset.

Whilst we did not initially find that maternal rank significantly predicted the ranks that males acquired in their new groups, when we removed the data points for *Mvu*, *Wol*, *Zur* and *Tor* (due to their ranks acquired being based on fewer than five conflicts), there was a strong inverse correlation that bordered on significance ($r = -0.80$, $p = 0.054$). This indicates that males of lower maternal rank tended to acquire a higher rank during their first year in a new group. As we are dealing with a relatively small sample, it is not immediately clear in which direction (if any) a larger sample would affect this relationship. However, the other results obtained after removing these potentially unreliable data points support the same hypothesis, which suggests that this borderline result is indicative of a pattern that would exist in a larger sample. We found a similar pattern in the correlational analysis of male rank acquired and out-degree, whereby, initially we found no relationship at all ($r = -0.07$, $p = 0.853$). However, when we removed *Mvu*, *Wol*, *Tor* and *Zur*, there was a stronger correlation with much lesser likelihood of rejecting the null hypothesis ($r = -0.65$, $p = 0.164$). Whilst this did not come as close to significance, the large shift towards a smaller p-value and stronger correlation coefficient suggest that a larger, more reliable sample might show a pattern of significant negative correlation. This would suggest that males that acquired a higher rank over the year had groomed fewer partners during that year. That the same was not found in the correlation between in-degree and male rank acquired implies that not every monkey groomed by a study male groomed them back. This result is, nonetheless, surprising, as we expected degree measures to reflect access to social partners – a limited resource – that should be greater with higher dominance rank acquired. However, a picture emerges when we further compare this to the strong inverse correlations that we found between maternal rank and frequency of grooming (with the exception of one male's frequency of grooming given; *Rhe*). Taken together, should these patterns of association hold with the addition of more reliable data, they suggest that males of lower maternal rank went on to acquire higher ranks, and gave and received grooming more frequently; and that those who acquired higher ranks (coming from lower maternal ranks) may have groomed a smaller sub-set of the group. Grooming frequently but towards a smaller set of partners suggests heavy investment in targeted relationships, which may reflect social competence in the context of establishing new, beneficial social bonds in a new group. These results would also concur with the finding of Young et al. (2017), where males that groomed socially central females were more likely to gain rank. Inhibitory control, which is associated with low dominance rank in large groups of hyenas (Johnson-Ulrich & Holekamp, 2020), may also be implicated in this process, in avoiding contests with resident dominants, thus avoiding the likely outcome of losing fights, and perhaps taking time to identify which individuals might be the most beneficial social partners with whom to interact. Nonetheless, our sample size is small, so before strong conclusions can be drawn, additional data should be added, when available, and re-analysed in order to confirm whether these patterns are strengthened or not.

Whilst we cannot draw strong conclusions here, further evidence supports our expectation that the patterns we found would be strengthened in a larger sample. For example, low dominance rank has been associated with adopting alternative behavioural strategies, both, theoretically (Barta & Giraldeau, 1998) and empirically in wild brown bears (*Ursus arctos*; Gill & Helfield, 2012) and chimpanzees (*Pan troglodytes*; Reader & Laland, 2001). Low ranked individuals maintain optimal fitness by finding behavioural alternatives (e.g. different locations to forage in) to those used by dominant individuals, thus avoiding aggression from them, whilst still meeting their needs. This suggests that low ranked individuals need greater behavioural flexibility, and supports the association with inhibitory control. Furthermore, constantly observing others in order to avoid them might increase opportunities to learn the dominance relationships between others, which, in addition to identifying beneficial grooming partners (e.g. Young et al., 2017), could optimise spontaneous coalition formation against higher ranked opponents (as was the most frequently observed coalition type among vervets; Freeman, Young, Barrett, & Henzi, 2016) should opportunities arise. Considering the winner and loser effects inherent in dominance hierarchy formation (Hemelrijk et al., 2008; Leimar, 2021), coalescing against higher ranked individuals may help in rank acquisition by increasing the likelihood of the higher ranked individual losing, therefore increasing the chances of everyone else lower in rank than them of winning subsequently, thereby gaining rank. The associations described above, between dominance rank and a) inhibitory control and b) behavioural flexibility require further research across multiple primate species, as different levels of socioecological complexity might enforce different constraints. Moreover, research is needed to test directly whether greater juvenile development of these capacities can facilitate more competent social decisions that optimise fitness later in adulthood.

In this study, we only assessed male rank acquired within one year after the natal dispersal, and it has not been established whether the potential effects in our data would be maintained for longer, or whether they are predictive of rank acquisition in subsequent immigration groups or not. It is possible that males who had lower maternal rank, even if achieving a higher rank after one year, might not maintain their new-found position for long, due to a lack of experience enacting behaviours needed to maintain a high rank position. In vervet monkeys, higher maternally ranked males might take longer to achieve a high rank as an adult, due to initial over-confidence leading to early rank losses, but they might be better at maintaining positions once acquired. In long-tailed macaques, van Noordwijk & van Schaik (2001) found that sons of high ranked females were the most likely to achieve alpha dominance status in their adult groups, but these analyses were not restricted to one year after natal dispersal. It is possible that maternal rank will have different effects over the full adult lifetime in vervet monkeys than those described in this study. We restricted our analyses to one year after dispersal to maintain a sample size of ten males who fit our other criteria, which included staying in their first immigration group for one year, whereas the majority disperse again within one year. In addition, unfortunately, *ad hoc*, we still removed four of these males from analyses involving the rank they acquired due to fewer-than-satisfactory conflicts informing their ELO ratings. Data collected more recently were adequate, most likely due to larger teams at the field site facilitating denser data collection across our study groups. It is important to highlight also that three of the four unreliable data points that we removed corresponded to males with relatively low maternal rank (see Fig. 1), leaving only one reliable data point in that area, which adds to the uncertainty of what a more representative sample might reveal. This line of research will benefit greatly if future studies can obtain large enough samples following adult male dominance rank acquisition beyond one year, and across multiple dispersals, as well as investigation of whether maternal rank and/or male rank acquired predict tenure in the group when large enough samples of conflicts per individual can be obtained.

Furthermore, relative to other species (e.g. long-tailed macaques; van Noordwijk & van Schaik, 2001), even if analyses are not restricted to one year after the natal dispersal, we might still expect different results due to species-specific intersexual social dynamics. For example, in vervet monkeys, adult dominance hierarchies are interdigitated with groups exhibiting female alpha individuals as well as male alphas (Hemelrijk et al., 2020). In addition, males have been found to benefit in rank acquisition by socialising with females (Young et al., 2017), and males that support females in conflicts obtain higher mating success (Arsenau et al., 2015). Furthermore, male vervet monkey coalitions are opportunistic (Freeman et al., 2016) rather than long-term, as in macaque species (Berghänel, Ostner, Schröder, & Schülke, 2011; Berman, Ionica, & Li, 2007; Young, Majolo, Schülke, & Ostner, 2014), and male macaque dispersal decisions are influenced by the presence of other males in groups (van Noordwijk & van Schaik, 2001). Together, these lines of evidence suggest different pressures may shape male sociality in species that otherwise appear to have similar social systems, with greater social influence of females on males in vervet monkeys than macaques. We propose future work around the questions investigated here, incorporating comparisons between natal and secondary dispersals, and between different species.

We return now to the inverse correlations between maternal rank and, both, the frequency of grooming received and given. Due to constraints on field data collection from a large number of monkeys, we did not measure durations of grooming in our data collection. We expect that if durations are measured, there may be inequalities between grooming given and received by immigrant males and their new groupmates during their integration. Furthermore, whilst our initial analyses suggested a stronger (inverse) correlation between in-strength and maternal rank, when we re-ran the out-strength correlation without the very clear outlier (*Rhe*), this correlation was even stronger and highly significant (Fig. 3C). This relationship is also clear from visual inspection of the plots in Figures 3A and 3C, and supports our hypothesis that males that grew up with lower maternal ranks invested more in grooming relationships in their new groups than those of higher maternal rank, except for *Rhe*. Regardless of the differences caused by including or excluding *Rhe*, it can be argued that receiving grooming nonetheless represents investment in a relationship, as does giving grooming, because it still requires time invested with a specific partner. *Rhe* may have also initiated grooming interactions by presenting himself to be groomed by selected partners (without reciprocating the grooming he received). Moreover, that these were our strongest results may indicate that this could be a mechanism upon which other effects are built i.e. that low maternal rank influences males to invest more in grooming relationships, which could subsequently influence their rank acquisition. Young et al. (2017) indeed found that males that groomed and associated particularly with socially central females were more likely to gain rank. This suggests that males use social skills besides brute force and competition in order to gain rank. However, whilst removing *Rhe* strengthened this result in the direction of our hypothesis, we note that his presence as an outlier is important. Whilst he did gain high rank in his new group (Fig. 1), he cannot have achieved this by grooming others frequently, whether other individuals did or not. According to researchers who worked extensively in the field with *Rhe* (E. van de Waal, *personal communication*), upon immigrating into BD, he played with the juveniles of the group a lot more than was typical of other adult males, especially recently immigrated ones. It is possible, therefore, that he used a different social strategy to other males that may have helped him gain rank. Whilst we only measured grooming here, Young et al. (2017) found that both, being in close proximity to influential females, as well as grooming them, were instrumental in gaining rank. Given that juveniles are likely to spend time with their matrilines, especially their mothers, (Borgeaud, Sosa, Sueur, & Bshary, 2017), by attempting to play with them, *Rhe* may have been afforded similar benefits that other males gained by grooming and staying close to highly central females. He did nonetheless receive grooming at a frequency in line with our other predictions based on maternal rank and social competence. Multiple social measures (e.g. grooming, proximity, play) can be of benefit to multi-level network analyses, which could elucidate more nuanced variation in social strategies used by individuals. Future work should investigate the contribution of adult male play to their development of social bonds, receipt of grooming and rank acquisition in new groups.

A limitation in our study is that we do not look into details of the identities of males' grooming partners, precluding conclusions as detailed as those of Young et al. (2017). We do however provide a broad foundation, across several groups and spanning ten years of data, upon which to base future, more detailed studies. We draw attention to remaining difficulties in long-term observational field studies of dispersing individuals. Despite having a ten-year database, some data from earlier years were still deemed unreliable (male ranks of Mvu, Wol, Tor and Zur, in 2014-15), probably due to reduced observability of individuals because of a) less habituated individuals and b) a smaller sized team of observers. Moreover, due to the sampling criteria for this study, only ten males were suitable, despite 38 having been born into and making natal dispersals into another of these study groups over the years (unpublished data). The exclusion of 28 males was necessary, for example, because their mothers died within the appropriate time period for calculating maternal rank, or the males did not remain in their immigration groups for one full year. We had to exclude many more because they dispersed into surrounding unhabituated groups other than our study groups. With ever-increasing technological advancement, we propose future incorporation of tracking technologies into long-term studies of dispersing individuals, in combination with remote sensing of data in unhabituated groups, which might afford similar studies with much larger samples when dispersers leave regularly followed study groups.

Finally, we open two related questions: 1) Do dispersers continue to develop their social competence during adulthood by learning new social skills in new groups and applying them in subsequent dispersals (Cheney & Seyfarth, 1983), after the natal dispersal? Following this: 2) Whilst reproductive skew does not appear to be strong in vervet monkeys (Minkner et al., 2018), there are likely some fitness benefits of high dominance rank (Majolo et al., 2012). If maternal rank influences male lifetime reproductive success at all (e.g. via social skills in the natal group, dominance ranks post-dispersal, or other pre-birth physiological maternal effects), investigating birth-sex ratio in philopatric females would elucidate whether females of low rank might ultimately improve their inclusive fitness by having more male offspring.

CONCLUSION

In a long-term field study, we observed patterns of social interaction in wild dispersing male vervet monkeys, following them from their natal groups to their first immigration groups, which link maternal rank with later social outcomes. We propose that social development associated with dominance rank in the natal group can affect social bonding and dominance rank acquisition post-dispersal via development of mechanisms such as inhibitory control and behavioural flexibility. We suggest future research into the development of these mechanisms in the wild, particularly, whether they are influenced by juvenile dominance rank, and whether they continue to develop during adult life. Finally, building on the foundations laid here, research into how these mechanisms and social competences develop and influence fitness in primates and other taxa would benefit the fields of sociobiology and behavioural ecology.

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Chapter 3. The Forgotten Social Benefits of Social Learning

Pooja Dongre[1]*, Rachel Harrison[1]*, Carel van Schaik[2], Erica van de Waal[1]

[1] Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

[2] Department of Anthropology, University of Zurich, Switzerland

*Joint first authors

ABSTRACT

Theoretical and empirical scholars of cultural evolution have traditionally studied social learning strategies, such as conformity, as adaptive strategies to obtain accurate information about the environment, whilst within social psychology there has been a greater focus upon the social function of such strategies. Although these two approaches are often used in concert when studying human social learning, we believe the potential social functions of conformity, and social learning more broadly, have been overlooked in studies of non-humans. We review evidence from studies of homophily, imitation, and rapid facial mimicry that suggests that behaving like others affords social benefits to non-human animals and that behavioural matching may be deployed strategically to increase affiliation. Furthermore, we review studies of conformity in dispersers, and suggest that forgoing personal information or preferences in favour of those of the new group during immigration might thus be a strategy to facilitate social integration. We propose the delineation of two functions of conformity: informational and social. We highlight the need for research attention towards the potential social benefits of conformity, and social learning in general, in animals. We use this perspective to generate several interesting research questions to inspire work in this field. For example, under what conditions do animals use informational or social conformity? What role does uncertainty play in social learning in immigrant individuals?

INTRODUCTION

In recent decades, the study of social learning and animal cultures has been a fruitful area of research, greatly increasing our understanding of the strategies driving social learning in both humans and non-human animals (Kendal et al., 2018). Social learning has been studied from two main perspectives:: cultural evolution, and social psychology. Cultural evolutionary theory (Boyd & Richerson, 2005; Mesoudi, Whiten & Laland, 2006; Mesoudi, 2009), posits that the transmission of information can be studied in a way analogous to genetic evolution. Theoretical models predict that individuals should be selective in terms of when they learn, what they learn, and who they learn from; the heuristics or biases guiding this are called 'social learning strategies' (Laland, 2004). Much focus has been placed upon the adaptive value of the information transmitted during social learning. Research on social learning strategies has thus explored questions such as how individual uncertainty impacts the likelihood of learning socially (e.g. Kendal et al., 2015; Williamson & Meltzoff, 2011) or whether individuals are more likely to copy older group members who may have more knowledge to transmit (e.g. Wood et al., 2012). This approach assumes that the most important function of social learning is the quality of information being transmitted between individuals.

Social psychology has equally focused on social learning processes, though from a different perspective. Bandura (1977) argued for the importance of social learning in human behaviour, and conducted a series of classic studies on when and from whom children learn (e.g. Bandura, Ross and Ross, 1961; Bandura, Ross and Ross 1963). Social psychology, perhaps more so than cultural evolutionary approaches, has also explored the social, rather than informational, benefits of social learning (Deutsch & Gerard, 1955; Uzgiris, 1981). However, social psychology has tended not to focus on long-term, multi-transmission or multi-generational effects of social learning (see Mesoudi, 2009, for a review of the contrasts and connections between social psychology and cultural evolution approaches). We are not the first to suggest that the two fields could work in concert more effectively to study social learning (Mesoudi, 2009; Over and Carpenter, 2011). However, while both cultural evolution and social psychology have been applied to questions related to social learning in humans, we argue that an approach influenced by social psychology is missing in the non-human literature on social learning. Studies of social learning in non-humans most often follow a cultural evolutionary approach, placing emphasis on informational benefits of social learning, which has led to a neglect of the social benefits of social learning. In this paper, we will argue that these social benefits are equally fitness-relevant, and will focus on one social learning strategy in particular, in regards to which the non-human research might benefit from blending these dichotomous approaches: conformity.

The study of conformity has its roots in social psychology, with perhaps one of the most influential studies being Asch's seminal work (1956), in which undergraduate students tasked with matching images of lines to a target were significantly more likely to make an error if faced with a unanimous group of peers who gave the incorrect answer. Conformity has since been defined in variety of ways within the cultural evolution literature (see Whiten, 2019, for review), with perhaps the simplest being "copy the majority" (Laland, 2004, also termed 'linear conformity': Claidière & Whiten, 2012), while other definitions refer to disproportionate copying of majority behaviours ('conformist transmission': Boyd & Richerson, 1985). These definitions are verbal descriptions of formal models, which make specific predictions regarding the population-level effects of such a learning strategy and are often not explicitly tested in social psychology approaches to conformity (Mesoudi, 2009). Drawing more on social psychology, some definitions have also included the overriding of personal knowledge in deference to group behaviour (also termed 'strong conformity': Haun & Tomasello, 2011). Studies of conformity in humans have additionally often delineated two types of conformity, defined by the underlying motivation: 'informational' conformity, employed in order to access the best information available about reality, and 'normative' conformity, which is used to manage social interactions (Deutsch & Gerard, 1955; Claidière & Whiten, 2012). Experimentally, normative conformity is usually identified by a control condition allowing participants to make their choice in private (arguably thus removing any social pressure to conform). If conformity to the group behaviour is reduced in private, it can be argued that any observed conformity in a group context is motivated by social integration rather than accessing information. In humans, this method has demonstrated that, at least for perceptual tasks in the style of Asch, conformity appears to be normatively motivated, with participants conforming to the group opinion more often if their own answer is made publicly rather than privately (Haun & Tomasello, 2011; Zhang et al., 2017; Sibilsky et al., 2021).

It has been argued that normativity evolved uniquely in the human lineage (e.g. Schmidt & Rakoczy, 2016), and generally definitions of normativity require the imposition of sanctions for transgressions against group norms (e.g. Schlingloff & Moore, 2017, though see also Westra & Andrews, 2022), for which evidence is limited in non-humans (Riedl et al., 2012; Rudolf von Rohr et al., 2011). Therefore, while some authors have suggested that experimental observations of apparently conformist behaviour in non-humans may be consistent with normative motivations (Hopper et al., 2011, though see also van Leeuwen et al., 2013, for alternative interpretation of these results), we suggest for clarity instead distinguishing normative conformity (conforming to behaviours when there may be sanctions against non-conformity) from social conformity (as defined in van de Waal et al. 2017: 'by social conformity we mean that individuals act like others not to achieve an informational function, but instead to achieve a social function that derives from simply "being like others"').

Both of these types of conformity explicitly relate to social rather than informational functions. We note here that throughout this paper, we are primarily interested in the potential social *functions* of conformity in non-human animals, and that this should be distinguished from discussion of the proximate mechanisms of conformity.

In this paper, we will argue that a social function of conformity plays a larger role than previously thought, and that incorporating approaches from the social psychology literature could prove useful in exploring this. Studies across taxa, including in humans, have demonstrated that social integration has fitness and survival impacts (Gerber et al., 2022; Kajokaite et al., 2022; Archie et al., 2022; Yang et al., 2016; see Snyder-Mackler et al., 2020, for review), indicating that there is likely selective pressure favouring the emergence of strategies to increase integration. In order for conformity to have plausibly evolved for a social function, then a) similarity should promote affiliation, and b) the likelihood of learning socially should increase when trying to integrate socially. To explore whether these two criteria are met, we will use examples from both the human and non-human literature.

Homophilic assortment

Social grouping, whether in temporary aggregations or stable groups, comes with many evolutionary benefits, such as increased predator detection and avoidance, and foraging efficiency (Krause & Ruxton, 2002), but there are also costs. Alongside increased competition for resources such as food and mates, individuals must coordinate their behaviour to remain together as a group and maintain the benefits that this brings. Group coordination requires individuals to behave similarly and simultaneously, which is inherently a cooperative operation, as individuals must forgo, at least sometimes, their own needs in order to remain as a group (Conradt & Roper, 2003; Franz, Schülke, & Ostner, 2013). By associating with similar others, however, the cost to individuals may be reduced, as their needs may align more closely, thereby minimising the costs of coordination. Therefore, homophily – the widespread phenomenon whereby similar individuals associate preferentially (Fu, Nowak, Christakis, & Fowler, 2012; Haun & Over, 2015; McPherson, Smith-Lovin, & Cook, 2001) – may be an important proximate mechanism underlying group formation, coordination and cooperation (Franz et al., 2013). Indeed, within groups, social interactions are rarely random, and across diverse taxa, patterns of interaction and association are often shaped by homophily according to physical traits such as sex (Dey & Quinn, 2014; Hirsch, Stanton, & Maldonado, 2012; Lusseau & Newman, 2004; Weiss et al., 2021), age (Lusseau & Newman, 2004; Ozella et al., 2020; Weiss et al., 2021), (Konik horses: Bouskila et al., 2015; van den Bos & de Vries, 1996), size (Croft et al., 2005; Eifler,

Eifler, Malela, & Childers, 2016; and see review of fish shoals: Krause, Butlin, Peuhkuri, & Pritchard, 2000), and breed (Boyland, Mlynski, James, Brent, & Croft, 2016). Physical traits such as these are likely to reflect similar underlying physiological states and therefore energetic demands (Ruckstuhl, 1999), demonstrating the role of homophily in reducing the costs of group coordination. Furthermore, for animals that form social bonds, homophily should promote affiliation between individuals that are similar, as affiliation and social bonding are necessarily facilitated by spatial proximity.

In addition to physical traits, homophily can shape social networks of diverse taxa according to repeatable behavioural tendencies (Kovacs, Perrtree, & Cox, 2017), or personality traits (Croft et al., 2005, 2009; Briard, Dorn, & Petit, 2015; Ebenau, von Borell, Penke, Ostner, & Schülke, 2019; Morton, Weiss, Buchanan-Smith, & Lee, 2015; Massen & Koski, 2014), which may provide increased opportunities to affiliate between the most behaviourally similar individuals. Notably, when homophily is based on personality, traits related to sociality are often involved, and importantly, homophily according to sociable traits occurs across the whole spectrum of sociability, not only in highly sociable individuals (Ebenau et al., 2019; Massen & Koski, 2014; Morton et al., 2015). Whilst this could be related to energetic budget allocation, as with the physical traits above, social tendencies may instead be an honest signal of cooperation to maintain group cohesion. Furthermore, for species that live in stable groups and form differentiated, long-lasting social bonds with group members, forming and maintaining bonds requires investment of time and energy, and partners that seem reliable or reciprocative in interactions might therefore be preferred (Massen & Koski, 2014). Likewise, other observable behavioural similarities could reflect honest signals of synergetic potential, thereby facilitating homophilic social bonding. In humans, homophily is well documented according to a wide range of factors, from demographic traits such as sex, age, and ethnicity, to behaviour and personality, and even attitudes and beliefs (DellaPosta, Shi, & Macy, 2015; Haun & Over, 2015; McPherson et al., 2001). Human infants less than a year old already demonstrate an affinity for others that share their preferences (Mahajan & Wynn, 2012), and 14-month-old infants expect others that share preferences to affiliate with one another (Liberman, Kinzler, & Woodward, 2021).

Imitation, mimicry, and social affiliation

One means of assessing the potential function of conformity is to look at the impact of the mechanisms underlying it: social learning mechanisms. For conformity to have evolved for primarily social purposes, learning socially from others should increase affiliation with them, and this should be a strategy used when trying to integrate socially. In both human and non-human primates, imitation has been shown to have an impact upon social affiliation. Capuchin monkeys (*Cebus apella*) preferred to look at humans who imitated their manipulations of a plastic ball, rather than humans who performed contingent, non-imitative, actions. Beyond this, the capuchins also preferentially spent time in proximity to, and were more likely to engage in token exchange with, the imitator rather than the non-imitator (Paukner et al., 2009). In juvenile rhesus macaques (*Macaca mulatta*), individuals who ‘mimicked’ group members (interacting with the same object, foraging in the same location, or moving in the same direction as a group member) more frequently received more play overtures than those who mimicked less often (Anderson & Kinally, 2021). These studies demonstrate that in non-human primates, imitation of behaviours, or similarity in behaviour likely driven by local enhancement, has the potential to increase affiliative behaviours between individuals. In humans, it has already been suggested that imitation serves an affiliative function, with Uzgiris (1981) arguing that alongside an informational function, imitation in infants serves to communicate “mutuality” (the connection between individuals). Experimental studies support this view: young infants (~4.5 months) preferentially attend to imitators, and older infants (~12 months) preferentially reach for imitators rather than non-imitators, after observing third party interactions (Powell & Spelke, 2018). This indicates that a preference for imitators emerges early in development in humans and extends beyond a preference for individuals who imitate *us* to a preference for those who imitate others. This means that a preference for imitators could have effects on affiliation outside of the dyadic interaction in which imitation occurred, with bystanders also choosing to affiliate with an imitative individual. Together, these studies suggest that imitative interactions carry social meaning for both human and non-human primates and thus can impact affiliation. Crucially, many of these studies demonstrate a causal relationship between imitation and affiliation with imitation increasing affiliation, rather than close associates happening to learn more from one another. While the studies discussed here largely focus on imitation (high-fidelity action copying), we suggest that any form of social learning which leads to behavioural matching between two individuals would have the same effect (i.e., the important aspect is the resulting similarity in behaviour, not the social learning mechanism it results from). Therefore, even if, as has been suggested, non-human species do not engage in high-fidelity action copying (Tennie et al., 2009; Tennie et al., 2012), other social learning mechanisms which result in behavioural matching between individuals would be sufficient to drive increased affiliation. Imitation recognition (the ability to recognise when one is being imitated) has been demonstrated throughout the primate lineage, in both monkeys and great apes (Paukner et al., 2005; Paukner et al., 2009; Haun & Call, 2008). Therefore, it is possible that sensitivity to behavioural matching by others predates the ability to engage in high-fidelity copying.

Imitation is also used by humans as a strategy to mitigate ostracism. Over and Carpenter (2009) found that children primed with ostracism copied more components of a series of demonstrated unnecessary actions than those in a control group. Increased social learning following ostracism has been found repeatedly, both in cases of direct (Hopkins & Branigan, 2020; Watson-Jones et al., 2016) and third-party (Watson-Jones et al., 2014) ostracism, and has been shown in adults as well as children (Williams et al., 2000, though see Stengelin et al., 2021). Williams et al. (2000) found adults primed with ostracism in an online game were more likely to conform to incorrect answers given by confederates in an Asch-style perceptual judgement task. Children also explicitly identify conformity as a potential strategy to achieve social integration. Cordonier and colleagues (2018) showed children a group of puppets, which looked inside a box and whispered to the child what they each saw, the last puppet giving a different answer to the others. When asked what the last puppet should do to make friends, five-year-old children (but not three-year-olds) stated that the puppet should conform to the majority opinion, contrary to its own, thus showing strong conformity. The authors link this understanding of strategic strong conformity to children's development of theory of mind, and indeed, making this judgement about third party interactions indicates an understanding that others are engaged in social image management. Taken together, these studies indicate that in human adults and children, social learning, including strong conformity, is used either consciously or subconsciously to increase affiliation with others following direct or even indirect experience of ostracism.

It has been suggested that, in the studies cited above, individuals who experienced ostracism may have been simply more likely to attend to and reproduce *any* behaviours (not only social information, but also information presented asocially in a proposed 'ghost' control, Heyes, 2017). There is, however, evidence suggesting that ostracism primes humans to specifically attend to social information. Gardner and colleagues (2000) found that after experiencing ostracism in a simulated chat room, participants showed selective memory for social events rather than individual events. The valence of the events had no effect – both positive and negative interpersonal events were recalled more than individual events. This finding hints at a deeper mechanism – not only are we more likely to learn socially when trying to gain social acceptance, but we are biased towards encoding social information, potentially better allowing us to learn socially.

Research into rapid behavioural mimicry also points towards social payoffs driving social learning. This unconscious form of mimicry (also referred to as 'automatic imitation' and 'simple imitation', Heyes, 2012) is observed in both human and non-human primates (Davila-Ross et al., 2008; Mancini et al., 2013a; Davila-Ross et al., 2011) as well as non-primate mammals (Taylor et al., 2019; Palagi et al., 2015; Palagi et al., 2019). This process is often not discussed in the context of social learning, as novel behaviours are generally not learned this way (Heyes, 2012) and mimicking results in action-only copying (as opposed to action+goal or action+goal+result copying, Carpenter & Call, 2002), making mimicry of limited interest to those focused on cultural evolution as a process of information transfer. Nonetheless, this simple automatic form of social learning can give us a critical insight into the function of social learning more broadly. Mimicry is used by humans to increase affiliation, both when affiliation is a conscious goal and when it is primed unconsciously (Lakin & Chartrand, 2003). As with instrumental imitation, discussed above, increased rates of behavioural mimicry are observed in humans following ostracism (Lakin et al., 2008). Rapid facial mimicry has been shown to be linked to longer play bouts in multiple primate and non-primate species (Mancini et al., 2013b; Scopa & Palagi, 2016; Palagi et al., 2019), and while the causal direction of this relationship has not yet been elucidated, it is possible that engaging in rapid facial mimicry leads to increased affiliation within play dyads. Unlike instrumental imitation or conformity, which may be at least partially consciously controlled in humans, mimicry is spontaneous and generally not thought to be under conscious control (with evidence that automatic imitation occurs even when participants are incentivised not to copy: Belot et al., 2013). Its use as a response to ostracism therefore points towards this being a deep-rooted impulse rather than a conscious strategy. Interestingly, some of the most compelling evidence for a capacity for high-fidelity imitation in non-human primates comes from ‘do-as-I-do’ paradigms, in which subjects imitate the posture or gestures of human experimenters following training (Custance, Bard & Whiten, 1995; Hribar et al., 2014), and from observations of individuals performing unusual and arbitrary body movements or manipulations (e.g. Goldsborough et al., 2021; van Leeuwen, Cronin & Haun, 2014). If social learning serves a social function, it is possible that this is why non-human animals appear to apply social learning more readily when matching postures or arbitrary behaviours in the social domain in comparison to ecological problem solving.

Conformity during social integration

We have presented evidence, from animals and humans, that behaving similarly to others may have important social underpinnings. At the most basic level, it can facilitate group coordination, and at least in some cases, can lead to increased affiliation. Based on this, we propose that socially motivated conformity may be more common in animals than previously acknowledged and may play a role in social integration.

Evidence from humans shows that they not only associate with similar others, but also learn new preferences from similar others (DellaPosta et al., 2015), which increases similarity between individuals within networks, which may further increase affiliation between associates. Research suggests that a similar process involving homophily and conformity occurs during vocalisation pattern (coda) learning by sperm whales (Cantor et al., 2015). Individuals appear, first, to preferentially associate with others with similar codas, and subsequently, modify their codas to be more like those most frequently encountered among their associates. Importantly, this demonstrates that a bidirectional process, whereby individuals associate with similar others *and* modify their behaviour to be more like that of their associates, is not unique to humans. Moreover, becoming more similar to others might be important when individuals have little control over with whom they associate, to promote social cohesion. In addition, behaving like others might facilitate the formation of new social ties when needed. For example, when experimentally grouped together, individuals of several other species have been found to modify their own behaviour to be more similar to their new group mates (Herbert-Read et al., 2013; King, Williams, & Mettke-Hofmann, 2015; Schuett & Dall, 2009; Zürcher, Willems, & Burkart, 2019). Furthermore, vocal convergence occurs in humans and other primates, in both the short and the long term (reviewed in: Ruch, Zürcher, & Burkart, 2018). In most cases, individuals introduced into a group modify their vocalisations to be more similar to the group that they join. This suggests that when socially integrating, or establishing connections with others is important, there may be deeply social evolutionary drives to behave more similarly to others. This view is bolstered by evidence from dispersing primates, attesting that their conformity is socially motivated (Luncz, Sirianni, Mundry, & Boesch, 2018; Luncz, Wittig, & Boesch, 2015; Luncz & Boesch, 2014; van de Waal, Borgeaud, & Whiten, 2013). In these examples, individuals either had prior knowledge of alternative behaviours, with equal or improved value, which implies that the motivation to conform was not informational; or the adopted behaviour was highly arbitrary with no intrinsic functional value. We also offer our insights into why studies in captivity might not have found conformity, due to challenges in eliciting the potentially underlying social motivations that are present in the wild (Haun, Rekers, & Tomasello, 2014; Vale et al., 2017; see also Harrison & van de Waal, 2022). Finally, we turn to a complementary line of evidence from wild animals, which shows that individuals in groups regularly modify their behaviour according to that displayed by a majority, or plurality (cf. Hastie & Kameda, 2005), with the function of facilitating the possibility of group life by maintaining group cohesion.

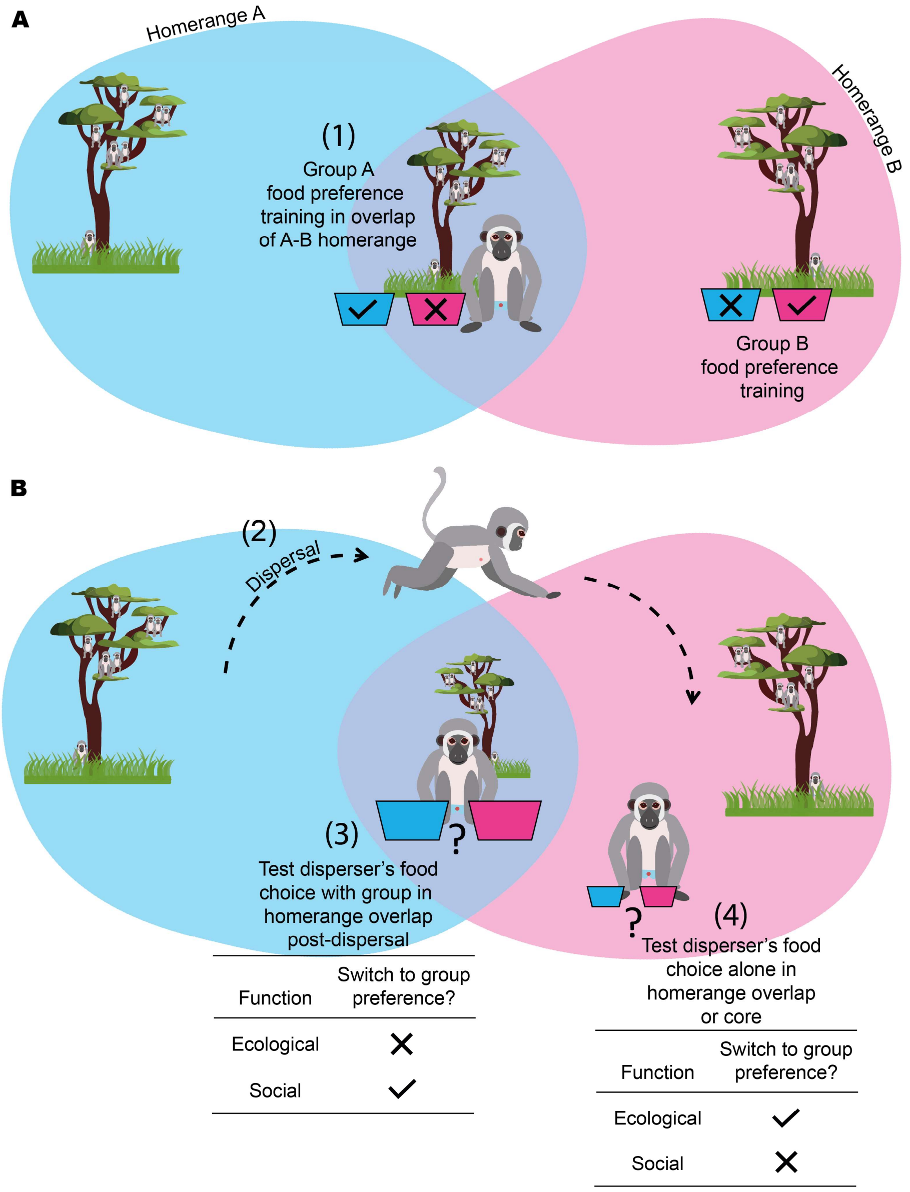
If we want to examine the possibility of a social function of conformity, it is important that our tests are capable of eliciting that motivation. Studies in the wild are ideal for this, as the pressures that would have shaped these phenomena should be present. Experimental evidence from a wild population of great tits (*Parus major*) found that when joining a new flock, individuals switched from using their own trained foraging strategy to match that which had been experimentally seeded in their new flock, despite both options being equally difficult and equally rewarded (Aplin et al., 2015). They preferred to use available social information, displayed by the majority in their new group, despite already having accurate personal information. Dispersing individuals provide an apt opportunity to examine whether conformity, or behavioural modifications to become more similar to new group-mates, might function to facilitate the formation of social bonds, and thus social integration. Evidence from wild dispersing primates also suggests that immigrants adopt local behavioural variants preferred by their new groups, even when these conflict with their own preferences. For example, new immigrant male vervet monkeys switched from eating their own previously trained food preferences to eating those of their new groups, which they had been trained to avoid in their old groups (van de Waal et al., 2013). Additionally, evidence suggests that wild immigrant female chimpanzees adopt their new groups' preferences for particular tools, despite availability of tools that they used in previous groups, which were potentially more efficient (Luncz et al., 2018, 2015; Luncz & Boesch, 2014). Whilst none of these studies formally assessed a link between conformity to group preferences and social integration, it was reported anecdotally that the single male vervet monkey that did not switch his food preference after immigrating, was aggressively forced out of the group soon after (van de Waal et al., 2013). This anecdote is to be treated with some caution, as there is no data provided on the integration success of the conforming males. There is, however, a more convincing (though also anecdotal) study linking social integration and behaviour matching in captive chimpanzees (Goldsborough, Webb, de Waal, & van Leeuwen, 2021). In this study, two female chimpanzees were introduced into a group that traditionally performed a unique and apparently arbitrary behaviour – the "cross-arm walk". The authors report that one immigrant female, Moni, immediately adopted the cross-arm walk on immigration, and the other, Erika, did not (Goldsborough et al., 2021). Subsequent analyses revealed that Moni became better socially integrated into the network of the group than Erika did. Moni performed the behaviour after observing it in only one other individual, and there is no way to know whether her maintenance of it was related to other group members performing it or not. Whilst this suggests that conformity *per se* was not operating, the result was the performance of a group tradition and subsequent improved social integration.

Two controlled experiments compared rates of conformity in chimpanzees, human children, and orangutans. The first found majority-biased transmission of a new behaviour in chimpanzees and children, but not orangutans (Haun, Rekers, & Tomasello, 2012). The second found conformity, involving switching from a previously learned behaviour to an alternative (“strong conformity”), in children, but not chimpanzees or orangutans (Haun et al., 2014). This led the authors to conclude that strong conformity is restricted to humans. They also tested whether children continued to conform in private, and found they did not, concluding further that social conformity is restricted to humans. Whilst these studies were carefully designed to target specific social learning strategies, the second (Haun et al., 2014) may have failed to elicit underlying social motivations for strong conformity in the chimpanzees. Importantly, this experiment did not involve any overt social pressure on individuals to conform, as the participants were already members of the group. Therefore, similar experiments involving individuals that are new to a group are required to test for social conformity in non-humans. Humans, on the other hand, may respond to social (or normative) pressure more readily and in more diverse situations than non-human primates, due the numerousness and diversity of social groups that they can participate in. In contrast, social pressure may be more situationally constrained in animals, such as when immigrating into a new group, when forming new social bonds is necessary. In a study of captive chimpanzees (Vale et al., 2017), designed to replicate the vervet monkey study discussed above (van de Waal et al., 2013), captive chimpanzee minorities (one or two individuals) were introduced into resident groups of relative majorities (ranging from two to nine individuals). Immigrating minorities and resident majorities had been trained to prefer alternatively coloured food. This study did not find conformity of immigrants to the resident majorities’ food preferences, but rather that both the residents and the immigrants sampled the food that they previously learned to dislike when observing their new group mates eat it (before reverting to their original preferences; Vale et al., 2017). However, in many cases, the majority was not very large: in four of the nine groups, the majority was two residents to one immigrant; and in one case, four residents received two immigrants. Therefore, more than half of the “majorities” in this experiment were not at the threshold for human sensitivity to conform to a majority (of three; Bond & Smith, 1996). While this was used as a benchmark for a majority size by Haun et al. (2012; 2014), it may still not represent an ecologically valid majority that a wild chimpanzee would observe exhibiting a group tradition. A majority of three might be enough for chimpanzees to learn a new behaviour (as in Haun et al., 2012), but not to override a behaviour they already know. On the other hand, whether conformity in the wild actually relies on frequencies of behaviours in a group, sampled by the learner, is yet to be determined.

The question has been the subject of extensive debate (van Leeuwen & Haun, 2014; van Leeuwen et al., 2015; van Leeuwen et al., 2016; Whiten & van de Waal, 2016), which is heavily influenced by a cultural evolutionist view of conformity. It is based upon models that generally assume animals have access to complete information about the behaviour of their group with which to ascertain which behaviours are exhibited by a majority of group members (see Morgan, Acerbi & van Leeuwen, 2019, for exploration of the impact of this assumption; this issue is also discussed in Nobel et al., 2022). The debate focuses largely upon the value of conformity in terms of accessing information about the environment. It is possible that individuals produce behaviours that are typical to the group after observing just a few individuals (as in Goldsborough et al., 2021; Watson et al., 2018). This could appear to be a majority bias (Acerbi et al., 2016), and nonetheless result in social benefits such as increased affiliation from many group members, thus facilitating social integration. As Morgan et al. (2019) point out, individuals in social groups are not equally likely to be observed, with well-connected individuals potentially being disproportionately influential, potentially causing a "majority illusion" (Lerman, Yan & Wu, 2016), in which the behaviour of well-connected individuals is assumed to be the typical behaviour in a group. In terms of a social function of conformity, however, falling prey to such a majority illusion would potentially be beneficial, as behaving like well-connected individuals would increase an individual's chance of positive affiliative interactions with these core group members. These mechanistic questions are crucial to our understanding of the population-level effects of conformist social transmission but a focus on them rather than the social function of conformity to group-typical behaviours may leave us with an incomplete picture. Considering potential social functions may open up potential insights regarding mechanism; alternative frameworks such as affective social learning (Gruber & Sievers, 2019; Gruber et al., 2021) may be usefully applied in concert with this approach. Equally, a focus on social functions could change our perspective on group behaviours; if being socially integrated is key, and group members are all feeding in the same patch, we would expect new arrivals to join them purely to maximise group cohesion. These new arrivals might then acquire information socially thanks to their proximity to group members. Both their choice of food patch and potential information acquisition could be seen "conforming", but would arise as a by-product of other social behaviour.

Whilst controlled captive experiments have many benefits, it can be extremely hard to replicate the evolutionary pressures that may influence the behaviour of wild animals (for review, see Harrison & van de Waal, 2022). Further experiments are needed to determine under what circumstances individuals conform (Figure 1 and 'Outstanding Questions'). One field study already hinted at a social motivation for conformity in wild non-human animals (van de Waal et al., 2017), and is based upon long-term observation of wild vervet monkeys following the experiment conducted by van de Waal and colleagues (2013), which found conformity to food choices in dispersing males. In the 2013 study, groups of monkeys acquired a preference for one colour of dyed maize (blue or pink) via training sessions in which one colour was rendered unpalatable. Following these training sessions, the maize was presented repeatedly, but without any bitter taste. Low ranking females tended to eat both the groups’ preferred (trained) colour and the previously unpalatable colour due to monopolisation of the former by more dominant group members (van de Waal et al., 2017). Later, group fissions occurred, with six of these low ranking females permanently leaving their home groups to form new groups. They were tested again in their fission groups, and under these conditions universally returned to their originally trained group preference colour. This was despite direct individual experience that both colours of maize were equally palatable, and the fact that only one of the six adult females tested had ever directly tasted the maize when it was unpalatable (van de Waal et al., 2017). This loyalty to the trained group preference therefore does not seem explicable via purely informational motivations, as all individuals had personal experience that both colours of maize were equally palatable. Rather, this finding suggests an ongoing social motivation to behave like the parent group (or perhaps to behave like high-ranking members of the parent group).

Finally, it is more difficult in the wild than in captivity to test conclusively the degree to which an individual attends to a majority, a single influential individual or simply the first individual observed (e.g. Goldsborough et al., 2021) before deciding whether to modify their behaviour. Indeed, mechanisms such as imitation and rapid facial mimicry, as discussed above, do work at the dyadic level, so it may appear that dyadic level processes are sufficient to result in ‘conformity’. However, in several species, evidence does suggest that individuals frequently make decisions regarding to where and when to move, and modify their behaviour, potentially in conflict with their individual needs, in accordance with the behaviour of a decisive majority (e.g. Lee & Teichroeb, 2016; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015; Sueur, Deneubourg, & Petit, 2010; Walker, King, McNutt, & Jordan, 2017; and see Conradt & Roper, 2003). Whilst the cognitive mechanisms involved in coordinating movement and learning (socially) a new behaviour may be different (though see Heyes & Pearce, 2015), this does suggest that animals attend to and track the behaviour of multiple group mates, and respond to majority influences during day-to-day behaviours, with inherently social motivations related to being part of a group.



Function	Switch to group preference?
Ecological	✗
Social	✓

Function	Switch to group preference?
Ecological	✓
Social	✗

Figure 1. Schematic of a proposed experiment, based on van de Waal et al. (2013), to delineate informational and social conformity. A) Groups with males that can disperse are trained to eat either pink or blue corn in overlapping homerange areas. B) After dispersal into a group with the opposite trained food preference, when the whole group is present, testing takes place in the same overlapping homerange area (3); tests also take place of the immigrant male when alone, in the absence of the rest of the group (4). Predictions are that if social learning is serving a social function, immigrants would follow the new group's preference at stage (3) when tested in a familiar area that is also part of their old group's homerange, but not if social learning is serving an informational function. At stage (4), informational social learning would be suggested if the immigrant maintains the new group's preference when tested alone, despite no observers present.

CONCLUSION

In this paper, we have discussed evidence that a) behaving similarly to others can have general social benefits, from facilitating group cohesion to social bonding, and b) new immigrants may use conformity and/or social learning when forming new social bonds is important. We propose that future research should further probe the potential social functions of conformity in non-human animals. The distinction between informational and normative conformity arose within human psychology literature, with these alternatives seen as goals of the actor. This may have excluded serious considerations of possible alternative functions of conformity in non-human animals resulting in the assumption regarding the adaptiveness of information. This may also have lead evolutionary theorists to concentrate on majority-biased transmission as a central theme of conformity. Rather than taking a goal-oriented anthropocentric view of social learning, we propose to view informational or social functions of social learning via the potential immediate social benefits. This offers more scope to pursue investigations into the potential social functions of conformity and social learning more generally. Moreover, informational and social functions need not be mutually exclusive, and further research into the conditions that produce either will be beneficial. Finally, it remains unclear whether conformity that appears to be majority-biased social learning truly is, or whether this appearance emerges through the copying of a few individuals that exhibit group-typical behaviour. Similar social benefits would arise in either situation. We outline our suggestions for future work in the ‘Outstanding Questions’ section. This topic will likely benefit from interdisciplinary approaches combining expertise from social psychologists, behavioural ecologists and cultural evolutionists, in both the theoretical and empirical stages of research.

Outstanding questions

To what extent does conformity serve social or informational functions in non-humans? Do informational and social motivations drive social learning in different contexts? What is the contribution of uncertainty to social learning in dispersing individuals? If social learning from or conformity to the new group is primarily socially motivated, any uncertainty about the payoff of specific behaviours in the environment should have little impact – the potential social benefit will promote social learning even if the individual is highly certain that their existing knowledge is functional. Conversely, if informational motivations power social learning when integrating into a new group, relative uncertainty regarding payoff should influence the likelihood of social learning. Experiments could provide dispersing individuals with opportunities to learn socially from new groups members and subsequently track their social integration. One could test immigrants' proclivity to conform in home range overlaps with their previous group versus non-overlapping areas to manipulate their uncertainty. Detailed studies of splinter groups could identify to what extent they maintain behaviours from the parent group in a new territory where alternative behaviours might be more effective.

To what extent is conformity majority-biased? Do dyadic social learning processes give rise to what appears as conformity; and, if learned behaviours are already typical in a group, will there be any detectable difference in a) the speed of transmission, and b) affiliative outcomes? Careful planning of field, captive and modelling studies can target specific mechanisms of the social learning and conformity.

What physiological mechanisms underlie social learning in immigrating individuals? Are there hormonal or other physiological changes during dispersal that render an individual more prone to learn socially, or to attend to social information, during this phase of their lifespan in comparison to at other points? Whilst dispersal might be characterised by exploration, with physiological mechanisms potentially promoting asocial learning, the social isolation could elicit similar responses to ostracism in humans. Furthermore, the immigration process might involve socially triggered stress that could promote social learning.

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General Discussion

The aim of this thesis was to address gaps in the literature surrounding dispersers, particularly in the context of social learning and culture. Particular aims were to deepen our understanding of a) the contributions of dispersers to cultural transmission, and b) the influence of social learning and culture on dispersers. In what follows, I first outline the results of each chapter separately, and situate them within these aims. I then integrate the results according to the different topics, discuss the insights we can gain by considering them together where relevant, and elaborate on the novel perspectives raised and how these can inform future research. Furthermore, I discuss the advantages and limitations of the work presented, and suggest solutions that may facilitate research into similar questions in the future.

Summary of findings

The experimental study presented in Chapter 1 provides evidence that immigrant male vervet monkeys (dispersers) can bring information into groups regarding novel resources, which can then spread rapidly within the group. This is an important finding, because previous studies in this species had found conflicting results regarding the extent of social attention and social learning towards males (Canteloup, Cera, Barrett, & van de Waal, 2021; van de Waal, Renevey, Favre, & Bshary, 2010). That both female and juvenile residents sought information, via muzzle contacts, from adult males, and that in these groups, large proportions of each group began eating the novel resource suggests that in vervet monkeys, male dispersers can facilitate behavioural transmission between groups. Moreover, we also found evidence that innovation might be more likely in dispersing males than philopatric females, particularly around the time of their dispersal or immigration. Whilst we also observed innovation by an infant, this did not spread far in the group, further emphasising the potential importance of dispersers in the generation and spread of novel information. We propose further research, first, to establish whether the patterns we observed here can be confirmed with a larger sample size, and second, to investigate whether social learning biases, and even a bias to learn socially versus asocially (the latter including innovation), vary across the lifetime of dispersers, and at times of varying proximity to their dispersal.

The study presented in Chapter 2 used an observational approach, and found evidence that the socially learned and inherited maternal rank of male juveniles might influence the dominance ranks they achieve in their first immigration group, and further that it influenced how frequently they were involved in grooming interactions. As the frequency of their involvement in grooming is more under their own control, and indeed showed a tighter relationship with maternal rank than their acquired ranks in the new group did, we propose that different social experiences in the natal group according to their maternal rank may shape the development of social competence. This social competence can then go on to affect how they form relationships in the new group, which in turn can affect the rank they achieve within the first year after immigration. We discuss this further below in relation to group-level traditions, particularly in relation to social learning of juvenile rank, which also has implications for philopatric females, and could contribute to the maintenance of cultural hierarchy characteristics (e.g. Sapolsky & Share, 2004; van de Waal et al., 2010). This in turn could influence male immigration success in groups they attempt to join, which would have further implications on gene flow and behavioural transmission within a population.

In Chapter 3, we review and combine evidence from literatures rarely compared that suggests that when immigrants conform to their new groups' traditions (Aplin et al., 2015; Luncz & Boesch, 2014; van de Waal, Borgeaud, & Whiten, 2013), forgoing their own knowledge of alternatives, this may primarily serve a social function – to socially integrate. In biology, research into any form of social learning and its role in cultural evolution have attempted to study these processes analogously to biological or genetic evolution. From this perspective, the most important feature of social learning is the adaptive value of the information transmitted. This field has therefore neglected the potential adaptive function of the process of learning socially itself. We present diverse literature that shows, for animals that live in groups, that there may be inherently adaptive qualities to simply being like other group members that have important functions in facilitating social life, from group coordination to social bonding. Importantly, we provide evidence that animals that are alike associate more, that in primates, imitating others leads to affiliation, and that an unconscious form of imitation (rapid facial mimicry) is linked to longer social interactions. Moreover, we propose that to investigate this further, studies of dispersers during the immigration process would be valuable to assess whether those that adopt group-specific behavioural variants socially integrate better than those that do not. The question of social motivations for social learning is of great importance given the proliferation of research driven by the perspective that social learning biases are governed primarily by optimal information acquisition.

Novel perspectives on social learning biases

Social learning biases (heuristic rules proposed to guide whether, when, what and from whom individuals learn) have been studied in a wide variety of species (Kendal et al., 2018). Previous experiments in vervet monkeys have found different biases under different experimental conditions. For example, in groups with either a trained dominant female or dominant male demonstrator, group members observed the behaviour of and learned socially from the females, but not from the males, with no sex differences in aggression towards bystanders that could have deterred them (van de Waal et al., 2010). Later, a similar study found that when given a choice of a dominant male or dominant female demonstrator obtaining the same payoff, group members still preferred to copy females (Bono et al., 2018). However, when male demonstrators obtained a five times higher payoff, male group members switched to preferentially copy them, whereas females maintained an overall preference to copy the female model, despite the lower payoff. This highlighted a level of conservatism among the philopatric sex and relative flexibility in the dispersing sex regarding their learning biases. In addition, the results of both studies together suggested that social learning biases towards demonstrators of the philopatric sex might constrain intergroup transmission of information by dispersers and its subsequent spread within groups. We show in Chapter 1, however, that this is not the case, and despite the learning biases towards female demonstrators found in these two previous studies, we showed that new immigrant (usually low ranked) males could import information about a novel food source into groups. We provide evidence of social information being sought from knowledgeable males (and females), via muzzle contacts, by adult females and juveniles. A potential difference could appear to be that in Chapter 1 there was only one male demonstrator available, to begin with, however in van de Waal et al.'s (2010) study, each group had only one model, either a female or a male (not a choice of the two). The tasks were, to some degree, of a similar nature: either opening a box containing food (also known as an 'artificial fruit' task), or learning to open peanuts shells to eat the food inside. However, a major difference may arise from the salience of the stimulus and its abundance to the potential learners. In the 2010 study, only one piece of apple was available in the box, whereas in Chapter 1 there were several kilograms of peanuts on display, which, in such abundance, may have altered the likelihood of potential learners to use information provided by the male. Other differences include the rewards used and the tasks: in the previous studies (Bono et al., 2018; van de Waal et al., 2010), rewards were high value and familiar, the learning task was which side to open a box, and the reward was obtained from a box. In contrast, in Chapter 1, the reward was completely novel, and individuals learned to eat a novel food during food-scarce winter. One explanation for the variation in our results is that when learning an arbitrary preference (i.e. which side to open, whilst obtaining a reward anyway), philopatric females maintain their preference to copy other females regardless of reward quantity, which would be a potent force to maintain group traditions. Contrastingly, when adaptation is required in the form of novel information provided by exploratory dispersing males, all group members may learn from them.

Another previous study of social learning biases in vervet monkeys used a different experimental design, with no pre-selected, trained demonstrators, but rather free access to multiple boxes that visibly contained a familiar food for any group members to innovate one of two simple solutions to access it (Canteloup, Hoppitt, & van de Waal, 2020). Studying the subsequent diffusion of the innovation in the two groups tested via a carefully collected observation network, the researchers found only a bias to copy higher ranked individuals, and no sex, age or kin related biases. This contrast with the two studies described above (Bono et al., 2018; van de Waal et al., 2010), which precluded rank-bias by using only high ranked demonstrators, further highlights the circumstantial nature of learning biases. The Canteloup et al. (2020) experiment used a very different design with more variation in potential demonstrators. In relation to the results of Bono et al. (2018) and van de Waal et al. (2010), this implied that demonstrator rank has a greater influence on learning bias than sex, which the previous studies could not detect when all models were highly dominant. Rank could be a signal of proficiency, perhaps due to the immediacy with which they access resources, which could reflect a bias guiding ‘adaptive information’ acquisition. However, the previous preferences for female over male models when demonstrator ranks were equal (and high) remain (Bono et al., 2018; van de Waal et al., 2010), and in particular, the persistent preference in female learners for female demonstrators that obtained lower payoffs remains striking. This is in direct conflict with a bias in the philopatric sex to learn based on information quality as they had direct access to this, and raises the points made in Chapter 3, that social motivations may underlie social learning in some cases, rather than ‘adaptive information’ motivations. Canteloup et al. (2020) also found that females socially learned faster than males, which emphasises the need to dig a little deeper into the sex differences of learners, beyond the previous conclusions that learning from philopatric models should provide the most accurate information about the local environment (an information-based motivation). The results of Chapter 1 also suggest that dispersers might be more likely to innovate – a result of asocial learning, or exploration – which they need to rely on during the dispersal process (Debeffe et al., 2013). Importantly, whilst Canteloup et al. (2020) saw both an alpha female and an alpha male innovate, they had visual access to a highly desirable familiar food, which contrasts with the innovation in Chapter 1, of exploiting an unknown, novel food resource. This is an obvious difference in risk, and further supports the idea that individuals might experience a greater proclivity towards risk in the time around dispersal. Therefore, taken together these results emphasise that the life history trajectories of philopatric and dispersing individuals may shape their learning biases in ways reflecting their social and ecological differences.

Moreover, we contrast the results of Chapter 1 of new immigrants as innovators with those of van de Waal et al. (2013) of immigrants as conformers. van de Waal et al. (2013) found that, upon immigrating into a new group, males switched from food preferences they had learned in their previous groups, to match those of their new groups. This further highlights the variable nature of social learning biases that are influenced heavily by context. In Chapter 1, despite other group members investigating the novel food and dismissing it, the immigrants persisted and innovated by starting to extract peanuts from the shells and eating them. These immigrants had dispersed within the last three months. In the cases of immigrant conformity (van de Waal, et al., 2013), males had immigrated within, at most, six months (based on the one year duration of the study, and a four to six month lag from ending the training phase and beginning the test phase; supplementary material: van de Waal, Borgeaud, et al., 2013). This is a similar explanation to the one given above, regarding Bono et al.'s (2018) payoff-bias study. There, and in van de Waal et al. (2010), a baseline of copying philopatric females existed in males. When a potential high payoff was available, males switched to copy other males that obtained it (Bono et al., 2018). In the case of innovation, it is possible that the opportunity to obtain a highly abundant novel resource motivated them, whilst already in a relatively exploratory state just after dispersal (Debeffe et al., 2013), to persist in exploring. A cue was available to them, as the food was presented in a box that they previously received familiar food in. This cue was also available to females (and juveniles), which prompted their brief inspections, but the adult males, and an infant, were the ones that were curious enough to innovate in this circumstance. In the case of conformity (van de Waal et al., 2013), it could be that their recent immigration heightened their motivation to conform for social reasons, though this remains to be directly tested, as uncertainty in a novel habitat might also have driven this. Furthermore, as discussed in Chapter 1, further examination is required as to whether the dispersal period is specifically a period of higher risk proclivity in males, with greater exploratory tendencies than during periods of long-term residence. This could be a beneficial mechanism to optimise their level of risk during their lifetime. The precise conditions under which males learn socially and when they innovate still need to be tested.

As alluded to previously, the perspective provided in Chapter 3 regarding social motivations for social learning as opposed to informational motivations, can provide a useful perspective to guide future research into the apparent sex differences in social learning biases. Specifically, from the studies discussed above I draw attention to the following sex differences: females copied other females despite a lower payoff whilst males switched to a high payoff strategy (Bono et al., 2018); and females learned socially faster than males (Canteloup et al., 2020). As discussed in Chapter 3, a major social motivation to learn socially, other than the adaptiveness of the information acquired, might be to create or strengthen social bonds. In support of this, we highlight various evidence in Chapter 3 suggesting that in many species, behaving similarly to other individuals is associated with affiliation (Chapter 3, Homophilic Assortment). Moreover, two specific studies in non-human primates showed that individuals preferentially affiliated with others that enacted similar behaviours as (or 'mimicked') them (Anderson & Kinnally, 2021; Paukner, Suomi, Visalberghi, & Ferrari, 2009). Therefore, a greater tendency for the philopatric sex to learn socially, especially from other philopatric – and therefore lifelong group members – despite observing lower payoffs (a direct indication of information quality), offers further evidence for this. Furthermore, dispersing males switching to a high payoff strategy may reflect that the payoff itself is more salient to them than the need to form lifelong social bonds. That males were slower to learn socially than females might equally reflect a lesser tendency to rely on social information for two reasons: a) during dispersal they are forced to rely on information they gather independently, and b) forming lifelong social bonds is less important to them. Nonetheless, upon immigration into groups trained to have conflicting food preferences to their own, immigrant males conformed to their groups' preferences (van de Waal, Borgeaud, et al., 2013). From the perspective of social motivations, this may reflect that social integration is a priority for them at that particular moment in life. Furthermore, regarding rank-biased social learning (Canteloup et al., 2020), a similar argument can be applied – that individuals in general might attempt to bond more with higher ranked individuals than with low ranked individuals (as also suggested by grooming up the hierarchy to gain tolerance, reviewed in (Wubs, Bshary, & Lehmann, 2018). There is also evidence that higher ranked individuals tend to be more central in social networks (Borgeaud, Sosa, Sueur, & Bshary, 2017), and male vervet monkeys that associate with central females were more likely to gain rank, providing a further avenue of social motivation for males to socially learn from females (Young & Mcfarland, 2017). This may even be a more parsimonious explanation than rank-biased social learning based on informational motivation, which assumes that higher ranked individuals have better information. By comparing the results from Chapter 1, where we placed experimental focus on the role of dispersing individuals in social learning with previous research in this species, the arguments discussed above arise, providing further support for the perspective provided in Chapter 3. However, we also found in Chapter 1 that muzzle contacts were directed more towards adults than juveniles, suggesting an age-related social learning bias surrounding a novel unknown resource. Muzzle contacts indicate acquisition of information, not necessarily the use of information, nor subsequent modification of behaviour. Age-biased learning about novel foods could be highly adaptive with respect to the quality of the information, given that juveniles tend to show heightened curiosity (Bergman & Kitchen, 2009; Debeffe et al., 2013; Thornton & Samson, 2012) whilst lacking experience. We emphasise that the point of our arguments regarding social motivations to learn socially is not to replace the idea of ‘adaptive information’ biases completely, but rather to complement them. Perhaps in high-risk situations, learning is biased according to the most adaptive information source, whereas in low-risk situations social motivations might be more important. Further research is required to understand these contingencies. Experiments could manipulate payoffs between differently ranked females, or between adults and juveniles to explore this further, or could compare different model biases directly with alternate food rewards that are either familiar or novel to the potential learners (though familiarised to the demonstrators).

Effects of social learning on male social competence

In Chapter 2, we present evidence that males’ maternally inherited rank, which reflects their dominance rank as juveniles, influenced their involvement in grooming interactions, and potentially their rank acquisition, during the first year in their first immigration group. Within the broader context of this thesis, it is important to recognise that, since maternally inherited juvenile rank is an outcome of aggression directed at juveniles by adult females higher in rank than their mothers (Holekamp & Smale, 1991; Horrocks & Hunte, 1983; Leimar, 2021), it is a socially learned trait. Juveniles learn, via the interactions they have with group members, how to interact with their group mates, i.e. who to defer resources to, who they can supplant and take resources from, and with whom it might be safe to socialise without receiving aggression. Chapter 2 provides evidence that these learning experiences may shape their development of social competence (Arnold & Taborsky, 2010; Taborsky, Arnold, Junker, & Tschopp, 2012; Wooddell, Kaburu, & Dettmer, 2020), which could explain the link between maternal rank and the ranks males acquired, as well as their involvement in grooming. Moreover, the results of Chapter 2 show that measuring the mothers’ rank does give valuable insights into the social experience of the juvenile, as indicated by the correlation with males’ grooming frequencies post-dispersal. Furthermore, as male rank is related to reproductive success in vervet monkeys (Minkner et al., 2018), this shows that socially learned behavioural tendencies during juvenescence can impact their fitness later in life. However, from a database spanning 11 years (at the time of analysis), only ten males out of 38 leaving their natal groups (natal dispersal) into another study group remained in their first group for at least one year. Indeed, in our study population, for both natal and secondary dispersal (between subsequent groups), there is vast variation in the duration of residence in immigration groups, ranging from a few days to over six years, with an average of one year (similar to another population of vervet monkeys (Young et al., 2019). The factors that influence whether males stay up to one year or not are extremely difficult to assess with current methodology, due to the time-consuming nature of data collection that obtains very little data from males that spend very short durations within a group.

The negative correlations between mothers' dominance ranks and males' grooming frequencies (given and received) in their new groups that we found in Chapter 2, has two implications. First, it suggests that measuring mothers' ranks does give valuable insight into the social experience of juvenile males; and second, it suggests that they learn how to socialise in accordance with their mothers' behaviour. Male juveniles have been found to give less grooming to others than female juveniles (Jarrett, Bonnell, Young, Barrett, & Henzi, 2018), which follows the general trend of males being less sociable than females (Borgeaud et al., 2017). However, they still appear to learn to groom others at a rate equivalent to their mother, with low maternal rank males giving and receiving grooming more. Alongside the evidence that low ranked females groom higher ranked females more than they receive grooming from them (Borgeaud & Bshary, 2015), this suggests that these patterns are driven by males' grooming investments, as learned via their mothers. Since dominance hierarchies have important socioecological functions in mitigating competition for limited resources, it might be assumed that relative resource abundance is the most important factor affecting dominance dynamics. However, research comparing two populations in relative resource scarcity found that female relationships in the two populations responded in different ways to harsh conditions (Peter Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013). These researchers concluded that variability in vervet social systems occurs at the individual level rather than the population level, in which case social learning may play a major role in intergroup variation in social behaviour. Philopatric females are likely to maintain their socially learned juvenile ranks lifelong. This provides each group with a stable hierarchy, into which males' dominance ranks become interdigitated (Hemelrijk, Wubs, Gort, Botting, & van de Waal, 2020). Therefore, any variation in social dynamics within groups will shape the social strategies that males attempt to use when joining the group. It would be interesting to investigate whether males that stay in groups for a very short duration have more success in entering groups with more similar social dynamics to their natal group. Furthermore, evidence that males integrate and acquire rank more quickly after secondary dispersals (Young et al., 2019) suggests that they develop greater social competence via learning experiences in subsequent immigration groups. Whilst research into social learning, and social bonding in particular, has focussed on philopatric individuals due to the importance of lifelong social bonds for them, I emphasise here the importance of social learning for the social competence of males, which may have important fitness consequences for them as well.

As discussed earlier, philopatric female vervet monkeys show biases towards learning socially from other philopatric females and/or high-ranked individuals (Bono et al., 2018; Canteloup et al., 2020; van de Waal et al., 2010). Therefore, if any variation is present in how individuals use aggression, social learning of rank and rank-related behaviour may lead to persistent variation between groups in the social domain. Whilst grooming and dominance behaviours are used in different contexts, they are also used in conjunction with one another, for example grooming up the hierarchy (Wubs et al., 2018). In addition, dominance behaviours such as supplanting subordinates occurs from high ranked individuals to lower ranked individuals in order to obtain social partners (personal observation), suggesting that dominance constrains affiliation. Therefore, intergroup differences in one social domain, e.g. dominance behaviour, are likely to affect the dynamics of others, e.g. affiliative behaviour, as well. Moreover, where variation in rank-related behaviours cannot be explained by ecological or genetic means, this variation may reflect social traditions. By social traditions, I refer to cultural variation in social behaviours, and emphasise them in contrast to foraging traditions, which often take the spotlight in studies and discussions of intergroup variation, perhaps due to the ease with which they are observed. Social traditions have been observed in capuchins (Perry, 2011), chimpanzees (e.g. (McGrew, Marchant, Scott, & Tutin, 2017), and potentially baboons (Sapolsky & Share, 2004), whilst in meerkats, researchers found non-foraging traditions of being ‘late sleepers’ or ‘early risers’ (Thornton, Samson, & Clutton-Brock, 2010). Non-foraging traditions may sometimes be more difficult to identify, if not expressed as overt behaviours such as the hand-clasp grooming tradition in chimpanzees (McGrew et al., 2017) or social games in capuchins (Perry, 2011; Perry et al., 2003). The sleeping patterns of meerkats (Thornton et al., 2010) and the potential dominance related traditions in baboons (Sapolsky & Share, 2004) involve different patterns of behaviours that are expressed ubiquitously, i.e. sleep-wake cycles and dominance hierarchies, thus requiring careful attention to detail to identify. Similarly, variation could exist within socially learned dominance hierarchies, example in conflict management behaviours, the steepness of the hierarchy, or in how individuals of different ranks interact.

Some of the variation in social dynamics identified among vervet monkey groups can potentially be explained by differences in group composition, or in the groups’ overall relatedness (Borgeaud et al., 2016). For example, groups BD and NH associated significantly more within matrilines, whereas AK did not. The authors identify that AK may have greater relatedness across the group (unpublished results), meaning their matrilines are probably more related than those of BD and NH. In addition, in AK and NH, individuals preferentially associated with the same sex, whereas BD did not. The authors suggest this could be due to a few adult males in BD that had very long tenure, potentially allowing them to develop close bonds with adult females. This study shows how social dynamics can be explained in ways besides cultural variation. Another study (van de Waal, 2018) found that ‘lip-smacking’, a communicative behaviour used in highly stressful situations (van de Waal, Spinelli, Bshary, Ros, & Noë, 2013), was used differently in two groups. In one it was directed from high to low rank individuals, probably as a sign of appeasement, and in another from low to high rank individuals, probably as a request for tolerance (van de Waal, 2018). This implies the two groups use this communicative gesture differently with respect to rank. Further research is needed to ascertain whether use of this signal is socially learned, though this is highly likely regarding the specificities of which contexts it is used in, and to rule out genetic or ecological explanations. Furthermore, van de Waal (2018) also found differences in conflict management among six neighbouring groups. The causes are not identified in that study, but evidence suggests that post-conflict behaviours are socially learned in primates (de Waal & Johanowicz, 1993). Together, the variation found in conflict or dominance-related behaviours suggest that, whether these differences represent traditions or not, it is highly likely that the early social learning of social competence in juvenile males will take place under different social dynamics than those of the groups into which they disperse. Therefore, when males immigrate and attempt to socialise with their new groupmates, they may fare better in groups with similar social dynamics to their natal group. The ability of males to integrate quickly into a group, rather than leave after only a short stay, is likely to affect their fitness, because of the risks they face when dispersing between groups alone (e.g. exposure to predators). From the dataset in Chapter 2, it does not appear that males of low maternal rank (and therefore potentially with better-developed social competence) are more likely to stay in a group up to one year, though a larger dataset would be beneficial to form a more solid conclusion. From this dataset, it appears that males’ socially learned social tendencies contribute to their behaviour within the group, potentially influencing their rank acquisition. Network analyses of intergroup dispersal, with groups as nodes and dispersing males as links, where groups are characterised by variation in their social dynamics and dominance related behaviours might help to understand whether intergroup variation affects the ability of males to integrate based on the similarity to their natal group.

Advantages and disadvantages of the methodology

A major advantage of the empirical work carried out in this thesis is the contribution of novel perspectives on dispersers, afforded by the long-term field setting in which it has been carried out, alongside much previous work on vervet monkeys both in this study population and others. Natural settings are particularly important for the fundamental nature of the questions addressed here, regarding the involvement of the dispersing sex in social learning surrounding their dispersal and immigration into new groups. For this type of research it is imperative for study animals to be subject to natural motivations and free of the constraints of captivity, which can impose artificial pressures on behaviour. Specifically, the motivations, whether physiological, social or environmental, to disperse, to immigrate, to socialise or to enter conflicts are representative of those under which they have evolved (or as close as possible), and all components of the social system are operating in a natural system. Our results conflict with previous results from captive work, for example Fairbanks et al. (2004) which did not find any effect of maternal rank on rank acquisition in a new group. The Fairbanks et al. study may have several points of artificial pressure that precluded finding the results that we found in the wild. For example, the timing of dispersal in the wild and choice of immigration groups might affect the individuals' behaviour and the responses of residents to them, particularly since dispersers prospect groups before attempting to join (Cheney & Seyfarth, 1983). A similar comparison of methodology can be made between the van de Waal et al. (2013) study in which immigrants conformed to group preferences, whereas no such effect was found in attempts to replicate this study in captive chimpanzees (Vale et al., 2017). This is discussed in more detail in Chapter 3, but demonstrates that natural dispersal and immigration is subject to many nuanced pressures that cannot easily be recreated in captivity.

Despite the benefits of field studies, there are of course limitations. Particularly, having focussed on dispersers, the empirical work in this thesis is based on small sample sizes, meaning that the studies need to be repeated, either in the same or in other study populations, in order to test more conclusively whether the patterns we found can be generalised. A major problem leading researchers to focus on philopatric individuals, as has been found in the past, is that dispersers often leave study groups and move to other non-studied groups in the area, or in some years may not disperse at all if the environmental conditions are too harsh. This can lead to a whole year(s) with no study subjects available, which is problematic for research that needs to be completed within time limits of funding availability. Furthermore, when unhabituated males join study groups, it takes some time before reliable data can be collected from them, which is problematic for research on how they integrate into social groups. Cases such as these also contributed to the small sample size in the datasets presented here. While these sources of unpredictability make it extremely challenging to study dispersers, this makes the results of this thesis highly valuable in providing initial samples for future work to build upon. Ultimately, the challenge of embarking on such a study has led to novel perspectives that I hope will be explored further in future work.

Future perspectives

As discussed above, the results of this thesis open novel perspectives, and aside from the need for replicating studies to gain larger sample sizes, several new questions are generated. For example, following the results of Chapter 1, it would be interesting to explore whether bringing valuable novel information into a group might lead to better social integration. Previous work in vervet monkeys found that low ranked females that could ‘provide’ food to others received increased amounts of grooming (Fruteau, Voelkl, Damme, & Noe, 2009). This could be investigated by experimentally providing males the opportunity to import novel food information whilst tracking changes in their social networks, and comparing these changes with the networks of control males. In Chapter 2, we have interpreted our results regarding the development of social competence based on work in other species (Johnson-Ulrich & Holekamp, 2020; Taborsky et al., 2012; Wooddell et al., 2020). It will be important to test directly whether juvenile rank is associated with mechanisms such as inhibitory control, and general social competence in vervet monkeys. Comparisons between male and female juveniles would also be interesting, as males may be freer to interact flexibly with other group members than females since they focus less on forming strong bonds within the natal group. Furthermore, experiments with spotted hyenas used ‘puzzle boxes’ to study inhibitory control (Johnson-Ulrich & Holekamp, 2020), the design of which could be adapted for use in vervet monkeys. This would also provide an opportunity to compare this aspect of cognition in these species by replicating their experimental design. Finally, Chapter 3 urges for an overall increased focus of research attention towards the social benefits of social learning. Studies comparing the social integration trajectories of immigrants with their social learning from new group members will be invaluable to explore this.

Furthermore, due to the practical issues of studying dispersers, future work would benefit greatly from the incorporation of remote data collection technology such as biologging. Global Positioning System (GPS), proximity sensing and accelerometer technologies will allow researchers to follow dispersers from study groups wherever they go, and collect remote data regarding their behaviour. Whilst the level of detail into social interactions obtained by human observers might be challenging to achieve remotely, we would regardless build up a greater picture of what happens to them. Currently, it is very difficult to ascertain the true level of additional predation on males when they are alone during dispersal, and we have no way of knowing how many groups they attempt to join before actually immigrating, nor where they go, or how far they travel.

Whilst this thesis focussed on the social transmission of information-related foraging and social skills, spatial information is another important domain of information for dispersers. An interesting hypothesis arises from preliminary data (Brun & Dongre, unpublished data), where annual home range usage in one group varied in concurrence with the immigration of several males from a group that previously occupied the area into which their new group shifted. It would be interesting to explore, during a longer time frame and with more groups, whether patterns of home range shifts are a cause or consequence of male immigration. If home range shifts are a consequence of male immigration, this would provide observational evidence, in complement of the experimental evidence in Chapter 1, that males bring information regarding resources beyond the group home range boundary into the group. This area of study in particular would benefit from GPS tracking of group home range usage, which is relatively easy for observers to collect whilst with the study group. However, remote tracking of dispersing males would be highly beneficial, as they may acquire additional spatial information when moving between groups, which could not be recorded by human observers following the groups. Moreover, if one or two adult females of unhabituated groups surrounding the study groups could also be tracked, this question could be addressed with data spanning a larger number of groups over time.

Other recent studies in our study population provide complementary avenues of research, in which our results regarding dispersers can inform novel hypotheses. For example, a study comparing curiosity in captive, wild-habituated, and wild-unhabituated vervet monkey groups found that habituation to humans and exposure to human artefacts increases curiosity (Annexe 3: Forss, Motes-Rodrigo, Dongre, Mohr, & van de Waal, 2021). Another study analysed environmental DNA (eDNA) from faecal samples to infer seasonal variation in the monkeys' diet composition (Annexe 2: Brun & Schneider et al., 2022). This study found comparable results to those from direct observations of the monkeys foraging, but with much greater resolution and greatly improved identification of more cryptic food species that observers cannot identify easily in the field. Future studies comparing intergroup variation in diet with this level of detail will be immensely useful in identify whether group variation exists, and if so corresponds to resource abundance in each home range, or whether they it may reflect group foraging traditions.

Conclusion

Besides the social transmission of information, innovation is an important aspect of culture as it gives rise to cultural diversity. From the evidence discussed here, it is possible that philopatric individuals learn socially from their lifelong group mates for social benefits, which can maintain cultural diversity between groups. Social benefits, i.e. outcomes that strengthen bonds between lifelong group members, are likely to be highly adaptive for philopatric individuals that must defend their territory against neighbouring groups together. Dispersers might therefore aid the ability of this species to adapt to changes in the environment, thanks to their frequent dispersal around groups, and their potential to be more exploratory. Whilst the philopatric females prefer to learn from ‘their own’, evidence presented here suggests they will utilise the opportunity to adapt when novel information provided by dispersers is highly adaptive, e.g. a novel food source during food scarcity. Understanding the complexities of such dynamics might be important in the broader perspective of predicting how different species will respond to the rapid environmental changes imposed by human activities.

The studies contained within this thesis contribute to a growing body of literature on the dispersing sex in primate species. These studies extend the literature through the study of several life stages of male vervet monkeys, and the relevance of social learning throughout them. We also draw attention to the potential impacts of social learning on male fitness, and of dispersing males on cultural transmission. Furthermore, we show that explorations of variation between groups, and between philopatric and dispersing sexes within groups can shed light onto adaptive learning biases that otherwise remain undetected, whilst generating further hypotheses that can be tested in order to identify them. This thesis further highlights how interdisciplinary approaches, including fields such as primatology, evolutionary and comparative psychology, and behavioural ecology can contribute to broader perspectives in evolutionary biology.

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Annexe 1. Focal vs. faecal: seasonal variation in the diet of wild vervet monkeys from observational and DNA metabarcoding data

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Loïc Brun[1,§], Judith Schneider[1,§], Eduard Mas Carrió[1], Pooja Dongre[2,3], Pierre Taberlet[4,5], Erica van de Waal[2,3,‡] and Luca Fumagalli[1,6,‡*]

[§] joint first authors

[‡] joint last authors

[1]Laboratory for Conservation Biology, Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland.

[2]Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland.

[3]Inkawu Vervet Project, Mawana Game Reserve, Swart Mfolozi, KwaZulu Natal, South Africa.

[4]Université Grenoble Alpes, CNRS, Laboratoire d'Ecologie Alpine, 38000 Grenoble, France.

[5]UiT – The Arctic University of Norway, Tromsø Museum, Tromsø, Norway.

[6]Swiss Human Institute of Forensic Taphonomy, University Centre of Legal Medicine Lausanne-Geneva, Lausanne University Hospital and University of Lausanne, Ch. de la Vulliette 4, 1000 Lausanne 25, Switzerland.

*corresponding author: Luca Fumagalli, Laboratory for Conservation Biology, Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland; luca.fumagalli@unil.ch

Abstract

1. Assessing the diet of wild animals reveals valuable information about their ecology and trophic relationships that may help elucidate dynamic interactions in ecosystems and forecast responses to environmental changes.
2. Advances in molecular biology provide valuable research tools in this field. However, comparative empirical research is still required to highlight strengths and potential biases of different approaches. Therefore, this study compares environmental DNA and observational methods for the same study population and sampling duration.
3. We employed DNA metabarcoding assays targeting plant and arthropod diet items in 823 faecal samples collected over 12 months in a wild population of an omnivorous primate, the vervet monkey (*Chlorocebus pygerythrus*). DNA metabarcoding data were subsequently compared to direct observations.
4. We observed the same seasonal patterns of plant consumption with both methods, however, DNA metabarcoding showed considerably greater taxonomic coverage and resolution compared to observations, mostly due to the construction of a local plant DNA database. We found a strong effect of season on variation in plant consumption largely shaped by the dry and wet seasons. The seasonal effect on arthropod consumption was weaker but feeding on arthropods was more frequent in spring and summer, showing overall that vervets adapt their diet according to available resources. The DNA metabarcoding assay outperformed also direct observations of arthropod consumption in both taxonomic coverage and resolution.
5. Combining traditional techniques and DNA metabarcoding data can therefore not only provide enhanced assessments of complex diets or reveal trophic interactions to the benefit of wildlife conservationists and managers, but also opens new perspectives for behavioural ecologists studying whether diet variation in social species is induced by environmental differences or might reflect selective foraging behaviours.

Keywords: diet estimation; DNA metabarcoding; environmental DNA; method comparison; primates; seasonal variation

1. Introduction

Assessing a wild organism's diet is key to understanding its ecology and to highlight dynamics of communities and ecosystems through species' trophic interactions (Duffy et al., 2007). Traditionally employed methods, e.g. direct observations, microhistology of faeces or gut contents, fatty acid and stable isotope analysis, encounter certain limits when analysing the diet of generalist and omnivorous species, or attempting to disentangle the structure of complex food webs (Nielsen, Clare, Hayden, Brett, & Kratina, 2018; Pompanon et al., 2012). The advent of DNA metabarcoding (Taberlet, Coissac, Pompanon, Brochmann, & Willerslev, 2012) and the simultaneous assessment of heterogeneous species mixes provides a valuable technique to open new perspectives in ecological network analysis (Clare, 2014). DNA metabarcoding studies using faeces cover a range of different aims, such as diet characterization (Burgar et al., 2014; De Barba et al., 2014; Shehzad et al., 2012), parallel prey and predator identification (Galan et al., 2018; Gillet et al., 2015) or biodiversity assessment (Nørgaard et al., 2021; Shao et al., 2021). Some studies include different variables such as endoparasites and sex ratios along with the diet (Swift et al., 2018), or the predator's population structure (Bohmann et al., 2018). For many research questions in ecology, robust estimations of biomass or abundances are necessary for meaningful results going beyond simple detection or non-detection (Pimm et al., 2014). Therefore, a number of studies show the method's potential for assessing complex correlations relying on its semi-quantitative explanatory power when studying for example, niche partitioning (Arrizabalaga-Escudero et al., 2018; Kartzinel et al., 2015; Pansu et al., 2019; Vesterinen, Puisto, Blomberg, & Lilley, 2018) or intergroup variation (Voelker, Schwarz, Thomas, Nelson, & Acevedo-Gutiérrez, 2020).

In many cases, reliable abundance data can be obtained by observation, however, there is an ongoing debate about the quantification potential of eDNA-based methods (Deagle et al., 2019; Zinger et al., 2019). For example, PCR primer-induced biases, i.e. the preferential amplification of certain taxa and the under- or non-representation of others, are considered a main source of biases in DNA metabarcoding (Jusino et al., 2019; Piñol, Mir, Gomez-Polo, & Agustí, 2015; Piñol, Senar, & Symondson, 2019). Data treatment also influences the outcome (Calderón-Sanou, Münkemüller, Boyer, Zinger, & Thuiller, 2019); occurrence data supposedly inflate rare taxa but are less sensitive to PCR-introduced biases whereas the use of relative read abundances (RRA) may better account for variations in biomass (Deagle et al., 2019). RRA correspond to the number of reads of a sequence in a sample divided by the total number of reads of the same sample. Relative data do not only account for the presence of taxa in a sample but are expected to correlate to some extent (as discussed above) with the amount of DNA present in the sample, therefore representing a semi-quantitative approach. In this study, we used RRA data, maintaining identical experimental conditions for all samples to minimise biases and to allow for comparisons.

The DNA metabarcoding approach has been used only recently for diet studies in primatology, as the research field has traditionally relied on various observational methods for behavioural studies (but see (Lyke, Di Fiore, Fierer, Madden, & Lambert, 2018; Mallott, Garber, & Malhi, 2017, 2018; Mallott, Malhi, & Garber, 2015; Osman et al., 2020; Quéméré et al., 2013; Rowe et al., 2021)). Inter-method comparisons are useful to test different methods' reliabilities and congruencies to assess consistency of results. However, the aim is not only to compare performances, but also to determine under which circumstance the complementary use of these methods is advisable to allow their optimal application in future studies. Since in many cases observational feeding data are available, but with weak taxonomic resolution and/or with a limitation due to feeding habits that are difficult to observe, complementing these data by a DNA metabarcoding approach would beneficial.

To this aim, we compare dietary variation inferred from DNA metabarcoding to direct observations, in an opportunistic and generalist primate, the vervet monkey (*Chlorocebus pygerythrus*, Fig. 1). Vervet monkeys are omnivorous and previous observational studies found that they feed mainly on trees, invertebrates and occasionally small vertebrates (Barrett, 2009; Tournier et al., 2014). We analysed 823 faecal samples of 130 individuals from four neighbouring wild groups collected over one year, with two DNA metabarcoding assays targeting plant and arthropod components of the diet. The study of omnivorous species represents certain challenges (Tercel, Symondson, & Cuff, 2021) that will be addressed in the discussion. The aim of the present study was threefold: a) compare taxonomic coverage and resolution between observational and DNA metabarcoding data, b) establish the most complete dietary profile in a wild vervet monkeys' population and c) assess resource use by vervet monkeys across seasons.

2. Materials and Methods

2.1 Study site and subjects

The study was conducted between 09/2017 and 02/2019 as part of the Inkawu Vervet Project (IVP) in the Mawana game reserve (28°00.327S, 031°12.348E), KwaZulu Natal, South Africa. IVP was founded in 2010 and research has been conducted ever since on wild vervet monkeys mainly in the field of behavioural ecology, demonstrating the high social learning capacity of this species (Whiten & van de Waal, 2018). Our study includes four neighbouring groups that are routinely followed by researchers. All individuals were identified using specific bodily and facial features (e.g. scars, colours, shape). The vegetation of the study site is classed as Savannah biome, characterized by areas of grasslands with dispersed singular or clusters of trees forming a mosaic with the typical savannah thornveld, bushveld and thicket patches (Mucina & Rutherford, 2006). Each dataset, observational and DNA metabarcoding data, covers a period of 12 months, but they overlap for six months only due to temporary constraints on focal sampling activities. Meteorological data assessed for the whole sampling period does not show major variation between the two sampled years for rainfall and temperature (Appendix S1: Fig. S1). Therefore, we expected season to have a greater impact in terms of vegetation variation than the year of sampling and we consequently compared the data per month/season regardless of the year. Seasons were defined as follows, with the middle of a month as the seasonal delimitation (van Wyk & van Wyk, 2013): August – November (spring), November – March (summer), March – May (autumn), May – August (winter).

2.2 Observational data

The observational data used for this study was obtained by instantaneous focal animal sampling methods on 101 adult group members between 09/2017 and 08/2018. In focal samplings, the focal individual is followed for a defined period and occurrences of (inter)actions are recorded, but parameters can vary according to specific study designs (Altmann, 1974). Here, each focal sample lasted 20 minutes and the focal animal's behaviour was recorded instantaneously every two minutes resulting in ten data points per focal sample (6,176 focal screenings in total). Observers chose focal animals opportunistically, with the aim to collect one full focal sample per individual across three different time windows (morning, midday, afternoon), every ten days. Total length of the data collection periods per day varied throughout the year according to sunrise and sunset times, while being equally distributed between the three daily time windows covering all daylight hours. Prior to data collection, all IVP observers had to pass an inter-observer reliability test with a minimum Cohen's kappa value of 0.8 for each data category with an experienced researcher. Data were collected on tablets (Vodacom Smart Tab 2, equipped with Pendragon Forms version 8). From the complete dataset, we extracted all feeding observations and created separate datasets for plant and arthropod items. The focal-dataset for plants contained 19,406 observations, of which 12,315 identified plant genera or species (63.46 %). The arthropod dataset contained 1,359 observations (of which 15.82 % indicated broad insect categories, i.e. termites or grasshoppers). Plant and arthropod observations that only occurred once were omitted from the final dataset.

2.3 Local plant database

In the field, 54 plant species were morphologically identified and collected (van Wyk & van Wyk, 2013). These include all species confirmed by previous observation of feeding behaviour in the area and other frequently occurring plants that could potentially be consumed. Sampled material from each species was stored in silica gel until DNA extraction using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) with a final elution in 100 µL AE buffer. To construct a local database, the whole chloroplast *trn*L (UAA) intron, which comprises the P6 loop targeted in the DNA metabarcoding assay described below, was amplified with primers c/d (Taberlet et al., 2007). The PCR reactions were performed in 25 µL. The mixture contained 1x PCR Gold Buffer (Thermo Fisher Scientific, USA), 2 mM $MgCl_2$, 0.2 mM of dNTPs, 0.04 µg of bovine serum albumin (Roche Diagnostics, Basel, Switzerland), 0.5 µM of forward and reverse primers, 1 U of AmpliTaq Gold (Thermo Fischer Scientific, USA) and 2 µL of template DNA. PCR cycling conditions were 10 min denaturation at 95 °C, followed by 35 cycles of 30 s at 95 °C, 30 s at 50 °C and 1 min at 72 °C, with a final elongation step of 5 min at 72 °C. PCR products were purified using the QIAquick PCR Purification Kit (Qiagen, Hilden, Germany) before Sanger sequencing in both directions at Microsynth AG (Balgach, Switzerland). The obtained P6 loop sequences were used for our reference database. The final database consisted of 48 sequences matching 54 species (i.e. 43 unique sequences, four sequences shared between two species and one sequence shared between three species, Appendix S1: Table S1).

2.4 Faecal sample collection

A total of 823 faecal samples of 130 known individuals were collected during a 12-month period (03/2018 to 02/2019, Fig. 2). Whenever a specific individual was observed defecating, the inner part of the scat was immediately collected unless it had already been sampled the same day or if an experiment involving food rewards had been conducted with the group in the 48 preceding hours. Approximately 0.5 cm^3 were collected with gloves and a disposable plastic spoon from inside the scat into 20 mL HDPE scintillation vials (Carl Roth GmbH, Karlsruhe, Germany) and covered with 10 mL absolute ethanol. After 24 – 36 hours, the ethanol was replaced by silica gel beads and samples stored until DNA extraction.

2.5 DNA metabarcoding

2.5.1 DNA extraction

DNA extraction of scat samples was performed using a phosphate buffer-based approach (Taberlet, Bonin, Zinger, & Coissac, 2018) following a modified protocol of the NucleoSpin Soil Kit (Macherey-Nagel, Düren, Germany). Scats were directly transferred from the scintillation vials into 2 mL Eppendorf tubes with 1.3 mL of saturated phosphate buffer. For a better absorption of the DNA, the samples were homogenized by vortexing before spinning on a tube rotator for 15 minutes. The suite of the protocol was as recommended using the QIAvac technology (Qiagen, Hilden, Germany), with a final elution in 100 µL of SE buffer. Extractions were performed in a pre-PCR laboratory exclusively dedicated to low DNA-content analyses (Laboratory for Conservation Biology, University of Lausanne, Switzerland). A subset of the extractions was tested for inhibitors with real-time quantitative PCR (qPCR) applying different dilutions in triplicates. qPCR reagents and conditions were the same as in DNA metabarcoding PCR (see below), but for 45 cycles and with the addition of SybrGreen (Thermo Fischer Scientific, USA). Following these analyses, all samples were diluted 5-fold.

2.5.2 DNA metabarcoding assay

DNA extracts were amplified in triplicates with two sets of primers. The first one targets the plant components of the diet amplifying the P6 loop of the *trn*L intron (UAA) of chloroplast DNA (10-220 bp, Sper01 (Taberlet et al., 2018) corresponding to g/h (Taberlet et al., 2007)). The second primer pair amplifies a fragment of 16S mitochondrial rDNA within the phylum Arthropoda (76-168 bp, Arth02 (Taberlet et al., 2018)). For the latter, one blocking oligonucleotide (5’-AGGGATAACAGCGCAATYCTATTCTAGAGTC-C3-3’) was added, designed specifically for this study to limit the amplification of both human and vervet monkey DNA (for specifications see Appendix S1: Fig. S2 and Taberlet et al., 2018). PCR reactions were performed in a final volume of 20 µL in 384-well plates. The mixture contained 1 U AmpliTaq Gold 360 mix (Thermo Fischer Scientific, USA), 0.04 µg of bovine serum albumin (Roche Diagnostics, Basel, Switzerland), 2 µM of human-blocking primer (coupled with Arth02 primers only), 0.2 µM of tagged forward and reverse primers (i.e. primers with eight variable nucleotides added to their 5’-end, allowing sample identification) and 2 µL of template DNA. PCR cycling conditions were 10 min at 95 °C, followed by 40 cycles of 30 s at 95 °C, 30 s at 49 °C or 52 °C for Arth02 and Sper01, respectively, and 1 min at 72 °C, with a final elongation step of 7 min at 72 °C. For each assay, extraction negative, PCR negative (H_2O) and positive controls as well as blanks were included. The positive controls of DNA mixtures of known concentrations were added in order to control for amplification success and were composed of species not expected in the study site (Appendix S1: Table S2), sequences were added to the respective databases. The inclusion of blanks, i.e. completely empty wells, allows to detect artifactual sequences after tag switches during the sequencing process (Schnell, Bohmann, & Gilbert, 2015). Amplification success was verified for a subset of samples, using the QIAxel technology (Qiagen, Hilden, Germany). All PCRs were performed at the Laboratoire d'Ecologie Alpine (LECA, Grenoble, France).

PCR reactions were pooled per replicate before library preparation, i.e. resulting in six separate libraries (i.e. three per metabarcode) each containing 823 samples plus controls. Amplicon pools were purified using the MinElute PCR Purification Kit (Qiagen, Hilden, Germany) and quantified using a Qubit 2.0 Fluorometer (Life Technology Corporation, USA). Library preparation was performed using the TruSeq DNA PCR-Free Library Prep Kit (Illumina, San Diego, CA, USA) starting at the repair ends and library size selection step with an adjusted beads ratio of 1.8 to remove small fragments. After adapter ligation, libraries were validated on a fragment analyser (Advanced Analytical Technologies, USA). Final libraries were quantified by qPCR, normalized and pooled before 150 paired-end sequencing on the Illumina Miniseq Sequencing System with a High-Output Kit, yielding up to 25 million reads (Illumina, San Diego, CA, USA).

2.5.3 Bioinformatic data treatment

Bioinformatic processing of raw sequences was conducted separately for each library using the *OBITools* package (Boyer et al., 2016). Forward and reverse reads were assembled with a minimum quality score of 40 and assigned to samples based on unique tag and primer combinations, allowing two mismatches with primer, and identical sequences were clustered. All sequences with less than ten reads per library were discarded as well as those not corresponding to primer specific barcode lengths, i.e., 10-220 bp for Sper01 and 76-168 bp for Arth02 (Taberlet et al., 2018). This was followed by two different clustering methods. First, pairwise dissimilarities between reads were computed and lesser abundant sequences were clustered into the most abundant ones. Second, we reduced remaining clusters based on a sequence similarity of 97 % using the *sumaclust* algorithm (Mercier, Boyer, Bonin, & Coissac, 2013). For taxonomic assignment of sequences, three different reference databases were used. The *local* database for Sper01 was based on the local plant collection (see 2.3). Furthermore, to construct *global* databases, both primer sets were used to simulate *in silico* PCRs on GenBank using the *ecoPCR* software (Ficetola et al., 2010) to select all sequences corresponding to our primers (restrained to three mismatches, the targeted barcode lengths and to Metazoa and Viridiplantae, respectively). Sper01 sequences were first assigned to the local database and non-assigned sequences were subsequently run against the global Sper01 database, both with 97 % thresholds. In addition, in order to test the effect of the local database, we did the taxonomic assignment of Sper01 sequences with only the global database and assessed the ratio of assigned sequences. Arthropod sequences were directly run against the global Arth02 database with a 97 % similarity threshold.

Additional filtering of sequences and subsequent data analyses were performed in R (version 4.0.2). Sequences that were more abundant in extraction and PCR controls than in samples were considered as contaminants and removed. To account for tag switching, we considered the leaking of a sequence to be directly linked to its abundance. To test this, we performed Wilcoxon signed-rank tests to assess the relationship between samples and blanks and a ratio was defined independently for each library to remove likely leaked sequences, as implemented in the R package *metabar* (Zinger et al., 2021). Replicates per sample were compared and the mean number of reads was retained if a sequence was present in at least two out of three replicates, in line with (Ficetola et al., 2015) and a minimum of five reads. All plant species-level assignments were manually verified and re-assigned to genus level if the known geographic species range did not match but the genus was known to occur in South Africa, else to family. For Arth02, we retained only the family level to avoid any taxonomic ambiguities (Meiklejohn, Damaso, & Robertson, 2019) and all sequences assigned to vervets and humans were discarded.

2.6 Data analyses

Analyses on the sequence data were conducted using RRA if not stated otherwise. In order to treat the observational data similarly, the sum of observations of each consumed item per day was divided by the total number of focal screenings conducted that day. Sample numbers varied between months/seasons and methods, hence for subsequent analyses mean values were taken per temporal unit. Since data was not normally distributed (according to Shapiro-Wilk's tests), we employed non-parametric tests. The impact of seasons on dietary variation was determined Principal Coordinates Analyses (PCoA) using the ade4 package (Dray & Dufour, 2007). To account for pseudo-replication, the same weight was given here to all individuals, i.e. replicate samples sum up to 1 per specific individual, while observational data were aggregated per focal individual/season and transformed to relative abundances. We identified plant indicators for seasons using *Indicator value analyses* (Indval) (Dufrêne &

Legendre, 1997). Shannon-Wiener diversity indices were calculated per season (genera/species for plants, family level for arthropods) and Hutcheson t-tests performed to test for significant differences between seasons (Hutcheson, 1970). We performed Mantel's tests (Mantel, 1967) implemented in the *vegan* package with 9999 permutations to compare the correlation between datasets with data aggregated per month and transformed to Bray-Curtis dissimilarity matrices. Spearman rank correlations were calculated for all plant species present in both datasets and with a minimum count of 350 in the focal-dataset (with the exception of *V. nilotica*/*C. decapetala* and *E. crispa*/*E. undulata*/*D. dichrophylla* since sequence data matched two different species in the focal-dataset).

3. Results

The final dataset for Sper01 contained 5,275,361 reads assigned to 22 orders, 43 families, 61 genera and 35 species. Of these 4,599,838 reads were assigned to 31 items with the local database, including 25 identifications at species-level. Most of the plant genera and species consumed by this species are trees and shrubs, but also cactuses, herbs and grasses (Appendix S1: Table S3). Taxonomic assignment with solely the global database resulted in 330,612 reads assigned to 15 different species, however, only 10 species were reliable (Appendix S1: Fig. S3). The taxonomic resolution was hence greatly increased with the local database allowing for more detailed analyses.

During focal follows, vervet monkeys were observed feeding on 27 different plant species and two plant genera. Mean observations per month of the eight most frequent plant species in the focal dataset show similar temporal patterns as the DNA metabarcoding data (Fig. 4A) and a Mantel's test of Bray-Curtis dissimilarity matrices of data aggregated per month shows a high correlation between methods ($r = 0.62$, $p = 1e-04$). There was no positive correlation between methods for numbers of different diet items detected/observed per month (Appendix S1: Fig. S4). However, positive Spearman rank correlations were observed when comparing single plant species, among which the most consumed ones (Appendix S1: Fig. S5). In addition to the plant genera and species that were identified by both methods, DNA metabarcoding revealed 41 supplementary dietary items at this taxonomic level of which 21 at species level (Figs. 3A and 5, Appendix S1: Table S3). The Shannon diversity does not differ significantly between both methods for plant genera and species observations/detections (Hutcheson t-tests not significant) despite the variable total numbers, i.e. richness (Fig. 4C). Seasonal shifts are most pronounced between the wet and the dry season for *B. zeyheri* and *Z. mucronata* indicating that one substitutes the other as principal food resource (Fig. 4A). Season explains a lot of the variation in both datasets as illustrated by PCoAs (Fig. 6A, 6B) and confirmed by *ANOSIM* with R = 0.51 and R = 0.57, both p = 1e-04, for eDNA and observational data respectively. Figure S6 shows observations and RRA over 12 months for seven plant species that are season indicators based on observational data. All except one, *C. jamacaru,* were indicator species in the metabarcoding dataset as well. The latter revealed several additional season indicator species (Appendix S1: Table S3).

Over 12 months of observational focal sampling there were in total 1,359 foraging events for arthropods (1,142 undetermined insects, 191 termites, 24 grasshoppers; Fig. 3B). We investigated in particular the temporal dimension of the "termites" category since vervets feed on termites extensively during swarming periods, which can be easily observed. Figure 4B shows percentages of the occurrences of these categories together with the combined RRA data for the families Hodotermitidae and Termitidae ("termites") as well as all taxa of the order Orthoptera ("grasshoppers"), and all other sequences combined ("others"). While a consistent trend was observed between methods, observations and DNA sequence data are not significantly correlated (Appendix S1: Fig. S7).

Without relying on a reference database for taxonomic assignments, the Arth02 assay resulted in 1,698,439 sequences in total whereof, however, 961,542 belonged to vervets, leaving 736,897 reads clustered to 404 presumed arthropod operational taxonomic units (OTUs) (Appendix S1: Fig. S3). By relying on the global database, the number of DNA sequences after final data filtering were 360,040 assigned to 11 orders and 35 families (Appendix S1: Table S4), i.e. 48.86 % of reads were taxonomically assigned (not considering those of *C. pygerythrus*). The most abundant arthropod orders in terms of read counts and frequencies were Coleoptera, Blattodea and Lepidoptera. We detected arthropod sequences in 96 % of the samples in spring, 89.15 % in summer, 58.59 % in autumn and 82.72 % in winter, whereas the highest number of different orders and families was detected in summer, also showing the highest Shannon-diversity (Fig. 4C). While we observed monthly variation for certain taxa (Fig. 7), there was overall a significant yet weak seasonal effect (Appendix S1: Fig. S8).

4. Discussion

The present study of vervet monkeys' diet over a twelve-months period highlights strong seasonal variation in consumed plants and less pronounced variation in arthropod consumption across seasons. The comparison of DNA metabarcoding data of plant diet components with field observational data shows similar patterns, in particular regarding relative abundances and seasonal variation. However, whilst observations do capture the main plant diet components well, DNA sequencing data showed improved taxonomic coverage and resolution. With respect to arthropod consumption, DNA metabarcoding outperformed observations, allowing for a considerable expansion of the range of dietary items identified and demonstrating the clear advantages of this method to describe cryptic feeding behaviour. Both methods have certain advantages and shortcomings as further discussed below, and genetic data are increasingly merged for network analyses with data from different sources to be used in a complementary way. For example, observational data provide in many cases more information regarding state and life stage of consumed items. While this may lead to more complete datasets, it implies also specific challenges as discussed by Cuff et al. (Cuff, Windsor, Tercel, Kitson, & Evans, 2022).

For plants items, our DNA metabarcoding assay detected many additional species and genera that had not been observed or identified to this level, as well as most of the species observed during focal follows. The taxonomic resolution was excellent for the plant assay due to the use of the local database (see also (Quéméré et al., 2013)). The increased detection by metabarcoding is likely due to observational difficulties in recording certain food items that are hard to identify or to observe, e.g. taking place in inaccessible or dense terrain (Matthews, Ridley, Kaplin, & Grueter, 2020; Su & Lee, 2001). In our study DNA metabarcoding further revealed consumption of otherwise well-documented species in periods when they were missed during observations, likely due to the consumption of less visible parts, e.g. tree sap, or dried seeds or fruits collected from the ground.

All new information made available by DNA metabarcoding could imply important trophic relations that have been overlooked so far. This is particularly relevant for arthropod items, a food type rich in proteins and lipids (Rothman, Raubenheimer, Bryer, Takahashi, & Gilbert, 2014), for which feeding habits are poorly studied in primatology. Previous observational studies indicate feeding of vervets on arthropods with varying degrees of precision (Barrett, 2005; Struhsaker, 1967; Tournier et al., 2014) but detailed records have so far been missing. Here, with DNA metabarcoding, 35 different families representing 11 orders were identified and demonstrate increased diversity of arthropod consumption in vervets' diets compared to the three broad taxonomic categories grouping termites, orthopterans and others as identified with observations (Figs. 3B and 7 and Appendix S1: Table S4). For arthropods, dietary diversity and richness are hence markedly higher when relying on DNA metabarcoding (Fig. 4C). Accordingly, we found no correlation between observational and genetic data (Appendix S1: Fig. S7), indicating the aptitude of the latter to unmask new trophic interactions and to shed light on cryptic feeding behaviour. A good example illustrated by our dataset is that of the twiceyearly termite swarming, a major ecological event in South-Africa (Lesnik, 2014), which was adequately captured by both our methods (Fig. 4B). Although showing a similar trend, the observations and DNA sequence data are not significantly correlated. This is because during swarming, the large number of flying termites emerging from the nest makes them highly visible to observers. However, during the rest of the year, when monkeys forage directly on the ground or in dead wood and in lesser quantities, most of these foraging events are cryptic or difficult to identify and thus missed by observers but documented by genetics. In general, observation of feeding on arthropods is particularly challenging (Pickett, Bergey, & Di Fiore, 2012) and this is the likely cause of the minimal detail available from our observational data and previous observational studies on vervets. A comparison between observations and DNA metabarcoding yielded similar results for white-faced capuchins (*Cebus capucinus*), with eight arthropod orders observed against 29 orders detected (Mallott et al., 2017). Furthermore, recent genetic studies on other primate species have similarly contributed to a better representation of arthropod diet components, either by using a cloning approach (Pickett et al., 2012), DNA metabarcoding (Lyke et al., 2018; Mallott et al., 2017, 2015; Rowe et al., 2021) or metagenomic sequencing (Srivathsan, Sha, Vogler, & Meier, 2015). This study demonstrates the advantages of using DNA metabarcoding alongside observations, adding to previous findings for the part of plants and arthropods of the diet of wild vervets.

This is in line with previous work showing that movements of vervets were mostly driven by plant resource availability, and therefore seasonality (Barrett, 2009). This is in line with our study as we found significant seasonal variation in plant consumption, largely shaped by the dry and wet seasons (Fig. 6). For the plant genera and plant species that have been recorded with both methods, we find comparable abundances, similar seasonal patterns and season indicator species (Appendix S1: Fig. S6, Table S3). Our inter-method comparison illustrates for certain plant species very clear temporal correlations (Fig. 4A, Appendix S1: Fig. S5). Regarding plants, both methods indicated similar Shannon-indices per season but the genetic approach resulted in higher dietary richness (Fig. 4C). While some plants are consumed continuously (different parts may be eaten over the year), the consumption of others was associated with particular seasons (e.g. strong association of *Z. mucronata* with winter). Previous studies on vervets found that they spend more time foraging in the dry season because of resource scarcity (Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017; Canteloup, Borgeaud, Wubs, & van de Waal, 2019). They can hence be expected to be more opportunistic feeders in the dry season than when food is abundant in the wet season and the opportunity to engage in selective foraging behaviours arises. During wet, food-abundant summer, we detected a higher diversity of consumed items in the scat samples. This shows that vervets adapt their diet according to available resources.

Concerning arthropod consumption, although the statistical effect of season on arthropod consumption was weak, the highest percentage of samples containing arthropod sequences was found in spring and summer, as well as the highest (family) richness and Shannon diversity (Fig. 4C). Given the very different numbers of arthropod items detected per method, the comparable diversity might surprise but can be explained by the dominance of few abundant families/categories; this may be different in other study contexts. Overall, our results show that season is an important variable for diet choice, therefore sampling designs should take it into account when relevant for the research question. Here, selective behaviours are most likely in the wet season when differences are the most accentuated and resources are not limiting, hence future sampling could focus on that season to capture most efficiently any behavioural differences that are not driven by resource availability, as discussed below.

DNA metabarcoding approaches do nonetheless entail their own limitations, some marker-specific and some methodological. Primer-induced biases may have led to under- or non-representation of certain arthropod taxa in this study. The study of omnivorous species is often neglected and thus highly necessary but requires in most cases the combination of different primer sets, which increases study cost and introduces new challenges (Tercel et al., 2021). Plants and arthropods were considered the most important targets based on observational data, however, our marker choice excluded the detection of other dietary items (i.e. feeding on birds, eggs and mushrooms was occasionally observed). Some plant species shared identical sequences in the metabarcode we amplified, making it impossible to differentiate genetically between them (Taberlet et al., 2007). For plants observed only in small numbers and not detected (false negatives), this may be due to stochastic reasons and the fact that observations and scat samplings were not conducted at the same time. For the observed but not detected *V. karroo* and *Z. capense* there is no sequence available in our databases. While this can be overcome by including further sequences, it points to the issue of incomplete databases in metabarcoding studies (Furlan, Davis, & Duncan, 2020; Taberlet et al., 2012). A local database would certainly increase the taxonomic coverage and resolution as well for the Arth02 assay and would have allowed the attribution of some abundantly represented OTUs, in particular since our research is pursued in a geographic region underrepresented in genetic databases (Kvist, 2013; Marques et al., 2021). In addition, unlike observational data, genetic data cannot detail which part and state of the plant or which life stage of an arthropod has been consumed (Pompanon et al., 2012; Rees, Maddison, Middleditch, Patmore, & Gough, 2014). Parts of the sequences may be due to secondary ingestion, accidental consumption or of parasitic origin and not represent (intentionally) consumed items (Tercel et al., 2021), therefore interdisciplinary studies with parasitology may be fruitful. Arthropods may have ingested plant DNA that we thus falsely detected as part of vervet diet, and at the other end of the spectrum unintentional feeding of arthropods is possible, e.g. of small Thripidae. The feeding on termites and grasshoppers is confirmed by observations, and also active foraging (i.e. vervets searching for insects), showing once more the benefit of complementary use of methods.

Choices made during the processing of DNA metabarcoding data may influence the outcome of these studies (Calderón-Sanou et al., 2019). In this study, we applied a stringent filtering of the data to avoid spurious DNA, using percentual and absolute thresholds. It has been argued that arbitrary minimum copy thresholds might omit true sequences (Littleford-Colquhoun et al., 2022) and that percentual thresholds were more suitable in case of uneven sequencing depths (Drake et al., 2022). To avoid the generation of supplementary biases, it is recommended to normalize PCR amplicons before pooling. Here we accepted the risk of missing some true detections by omitting items with very small read counts, which may also affect samples with uneven sequencing depths differently. Another point is the transformation of read counts; while most studies traditionally rely on occurrence data, a number of studies showed that RRA data might better capture ecological signals (Deagle et al., 2019; Kartzinel et al., 2015; Voelker et al., 2020). Here, we chose RRA for this study and although it may entail biases, the comparison to observational data validates this choice. For example, two of the most consumed plants throughout the year, *B. zeyheri* and *Z. mucronata*, represent very variable proportions of the diet depending on the season. Categorical data would not show any variation here, however, we observed strong seasonal patterns with both RRA and observational data (Fig. S6). A recent diet study targeting the same genetic region found positive correlations between the RRA of plant families in faecal samples and the observed duration spent feeding on those (Mallott et al., 2018).

The taxonomic coverage and resolution as well as the methodological standardization (including no inter-observer variability) point to the benefits of environmental DNA (eDNA)-based surveys. Depending on the species studied, DNA metabarcoding represents cost- and labour-effective alternatives or complements to traditional methods (Mena et al., 2021) and sequencing costs are likely to further decrease in the near future. The sensitivity, taxonomic resolution and non-invasiveness of the method are major advantages in conservation research (Thomsen & Willerslev, 2015). There is great potential to learn more about, for example, nocturnal, arboreal and other elusive species and/or the adaptive potential of fragmented populations (Quéméré et al., 2013). Many primates are threatened and of high conservation concern (IUCN, 2020; Schwitzer et al., 2017). There is thus a need for robust data to inform empirically-based conservation strategies (Pimm et al., 2014), where diet studies are undoubtedly of primary interest. Although it remains challenging to properly assess to what extent the final data represents the biomass of food items initially ingested, controls incorporated throughout the study and appropriate knowledge of the ecology enable valuable insights going beyond traditional approaches. DNA metabarcoding has thus great potential to bring new insights on foraging behaviours and ultimately, on the underlying mechanisms shaping such behaviours.

Our study demonstrates benefits of an interdisciplinary approach. Moreover, this study being the first validating the use of eDNA to assess diet in our system, future analyses may investigate whether variation in individual or group diet is induced by environmental differences or if it might reflect selective foraging behaviours. Therefore, the application of a DNA metabarcoding approach can be useful not only for conservation studies aimed at disentangling complex diets or reveal trophic interactions, but also opens new perspectives for behavioural ecologists and cultural evolutionists studying social species in the wild.

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Conflict of Interest

The authors note that PT is co-inventor of a patent related to the Sper01 primers and the use of the P6 loop of the chloroplast trn*L* (UAA) intron for plant identification using degraded template DNA. This patent only restricts commercial applications and have no impact on the use of this loci by academic researchers.

Authors’ Contributions

EW and LF conceived and designed the study; LB and PD collected the data; EM-C, JS, LB and PT performed laboratory analyses; JS and LB analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

The DNA metabarcoding data generated for this study is available on DRYAD (availability upon acceptance of the manuscript). Sanger sequences for the local database have been deposited in GenBank under accession numbers OL898555-OL898608.

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Figures

Figure 1. Juvenile vervet monkey (*Chlorocebus pygerythrus*) feeding on fruits of *Ziziphus mucronata*. © Michael Henshall.

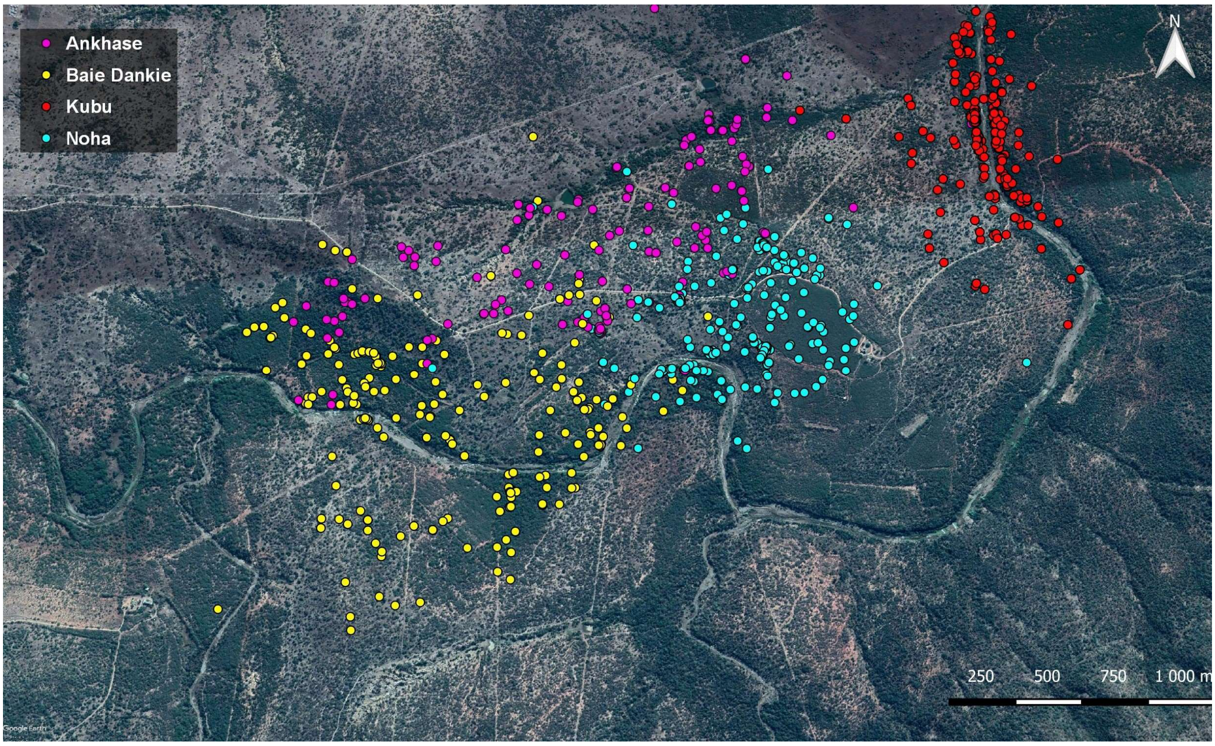

Figure 2. The map indicates the sampling locations of the 823 faecal samples of 130 individuals in the Inkawu Vervet Project, South Africa. The different groups are represented by different coloured dots: Ankhase: purple (n=146), Baie Dankie: yellow (n=212), Kubu: red (n=224), Noha: blue (n=241).

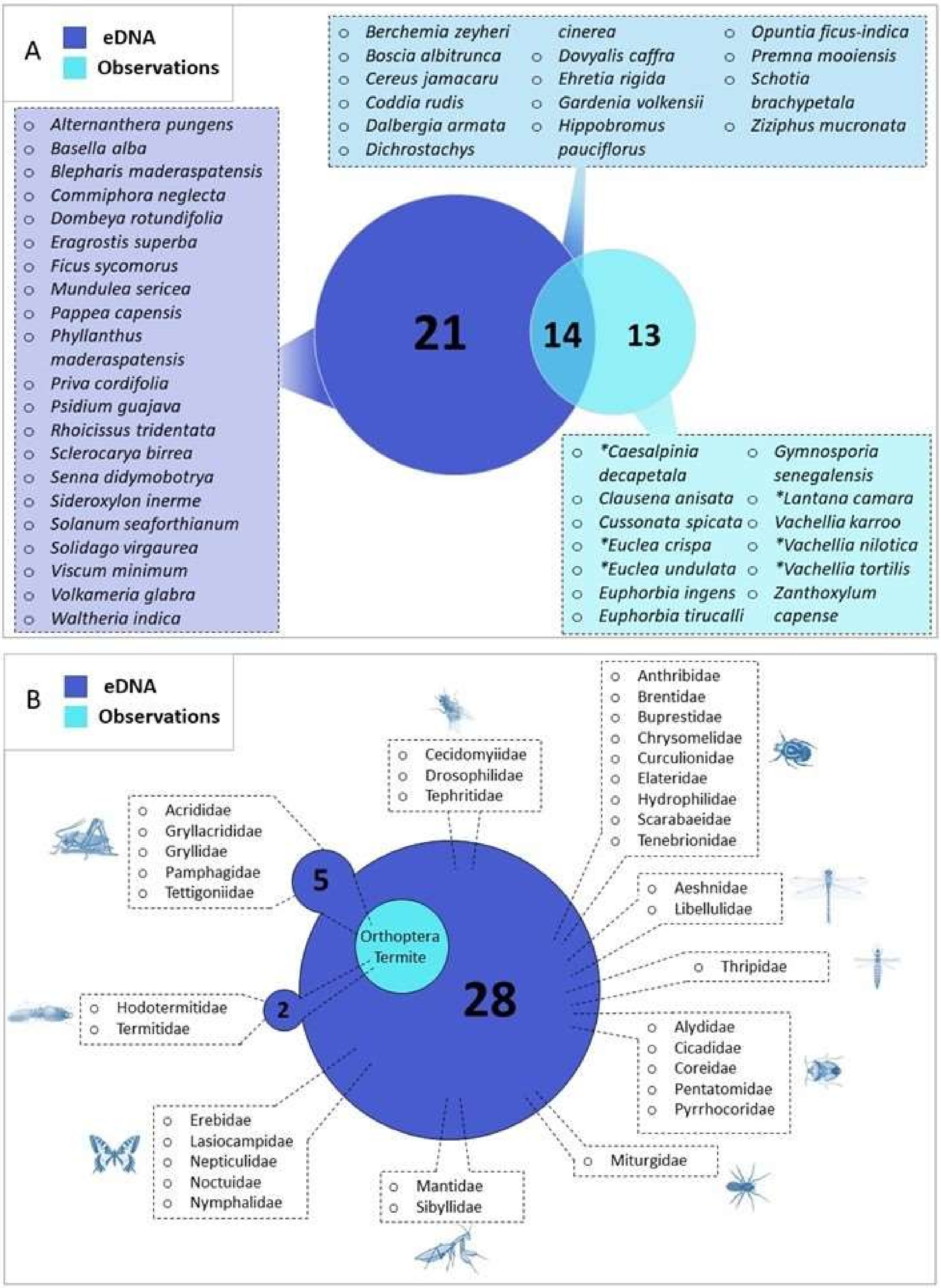

Figure 3: Venn diagrams **A.** between consumed plant items at the taxonomic level of species detected by observation and eDNA. Plant species beginning with an asterisk (*) correspond to species for which the sequences amplified by the Sper01 metabarcode were identical between

species as shown in Table S1. And **B.** between arthropods detected by observation and eDNA. For eDNA data the family level is included, whereas observations were limited to the order level for orthopterans and the infraorder level for termites. The two bubbles on the left side of the diagram indicate the families detected by eDNA that compose these two taxonomic groups. The category “undetermined insects” is not included for observations (see text). Rectangles separate the different orders illustrated by icons.

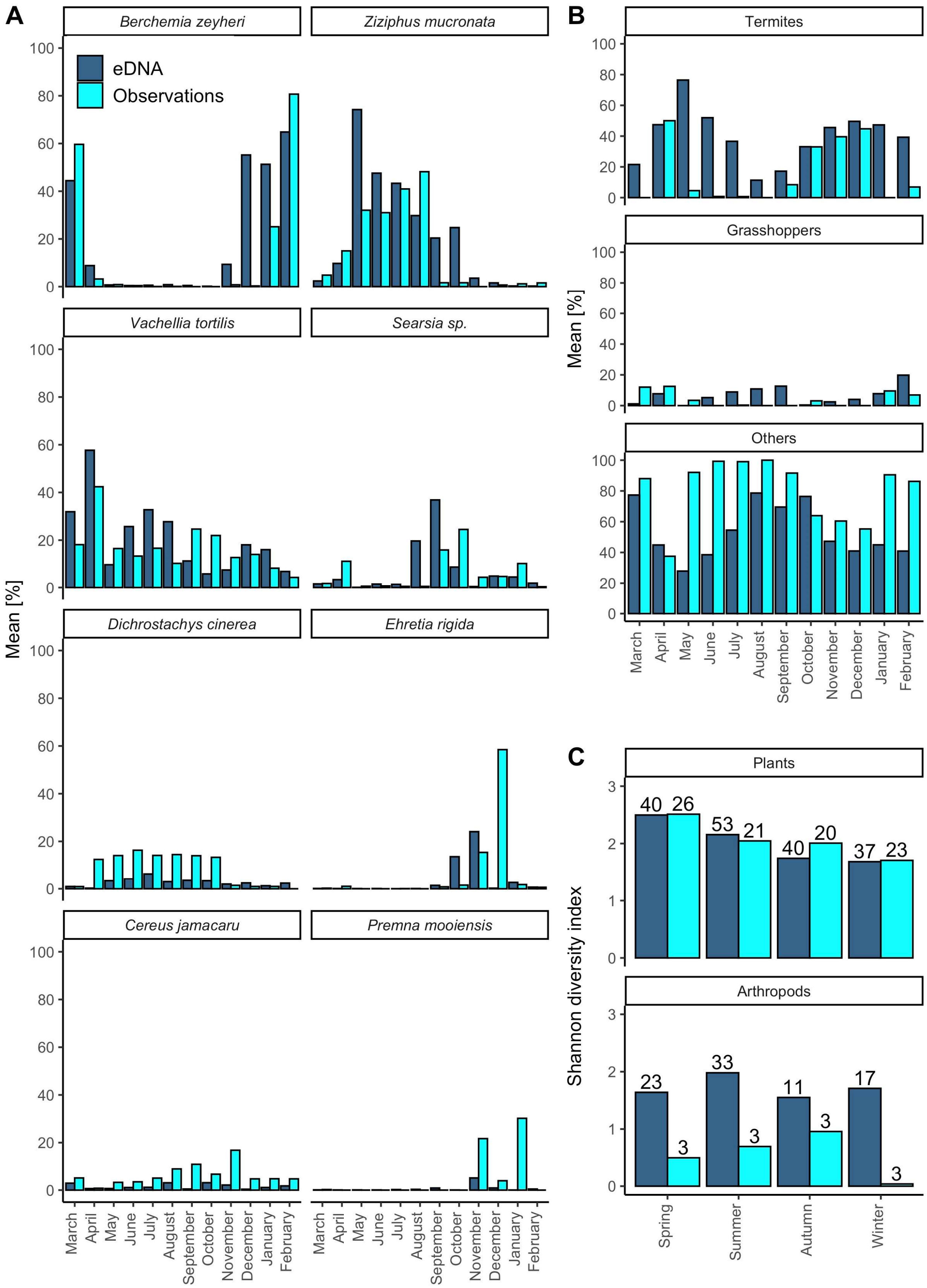

Figure 4. A. Monthly comparison of DNA metabarcoding and observational data for the most frequent species in the focal dataset (> 350 observations), with the exception of those that had

identical metabarcodes and matched several species in the focal dataset. The observed plant *V. tortilis* corresponds to *V. tortilis/sieberiana* in the DNA metabarcoding dataset. Metabarcoding data are represented by the mean RRA and observational data by the mean count, both in percent. **B.** Monthly comparison of DNA metabarcoding and observational data for “termites" (RRA of Hodotermitidae and Termitidae combined), “grasshoppers” (RRA of all detected families belonging to the order Orthoptera) and “others” (RRA of all remaining items). Metabarcoding data are represented by the mean RRA and observational data by the mean count, both in percent. **C.** Shannon diversity index per season for observations and eDNA. There was no significant differences in diversity between methods (Hutcheson t-test). Number on the bars indicate numbers of different observed/detected items per season. For plants the included items are all observed/detected species and genera. For arthropods the Shannon diversity was measured at family level for the metabarcoding data and for observational data based on the three categories (see Fig. 4B).

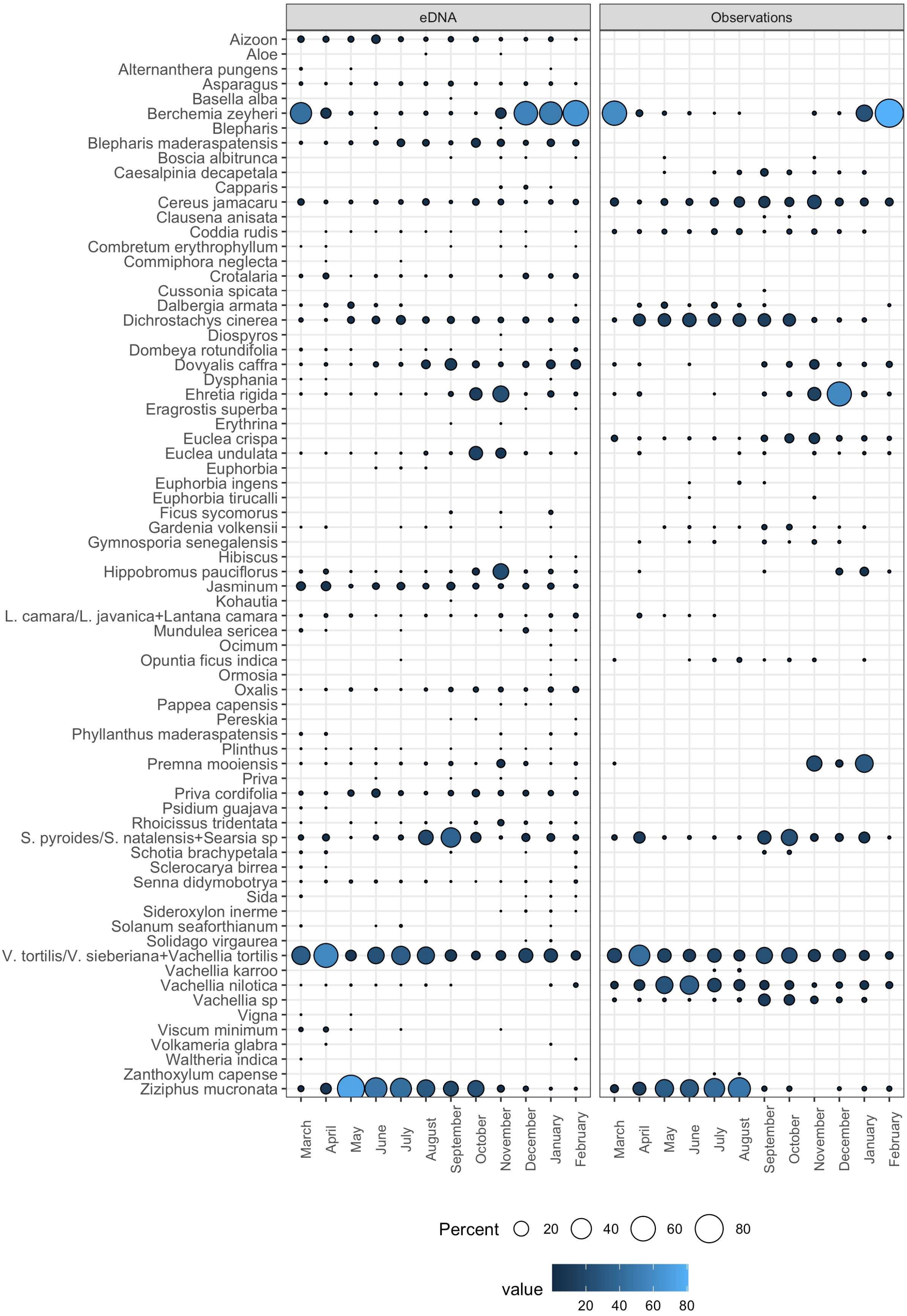

Figure 5. Mean RRA of plants genera and species in faecal samples per month (left) and mean of observations in focal follows per month (right). Note that the obtained sequence for

Euphorbia is different from *E. ingens* and *E. tirucalli*. Also *E. crispa*, *E. undulata* were identified to species level in the field but have identical sequences, the same is true for *V. nilotica* and *C. decapetala*, therefore both entries for observations were kept but only one for eDNA. Several names in one line indicate identical sequences as well (on the left), but only one observed genus/species (on the right).

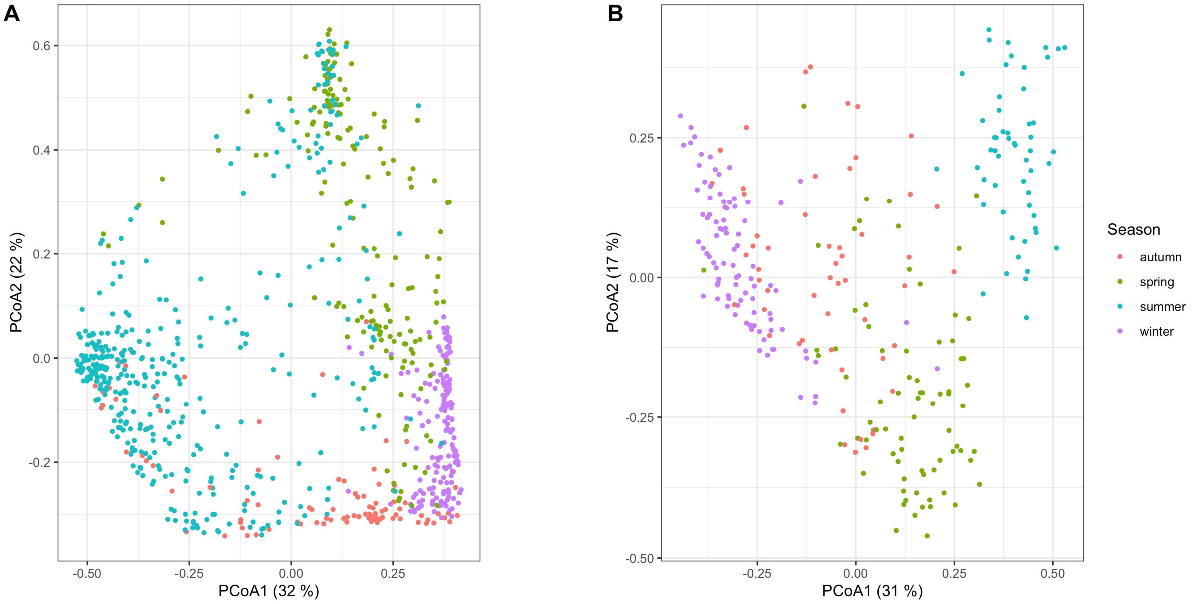

Figure 6. Principal Coordinates Analyses (PCoA) based on **A.** relative read abundances (RRA) of consumed plants detected in faecal samples per sampling day (n=823) and **B.** observational plant data of focal follows transformed to relative abundances per individual/season (n=279). In brackets the relative Eigenvalues in percent.

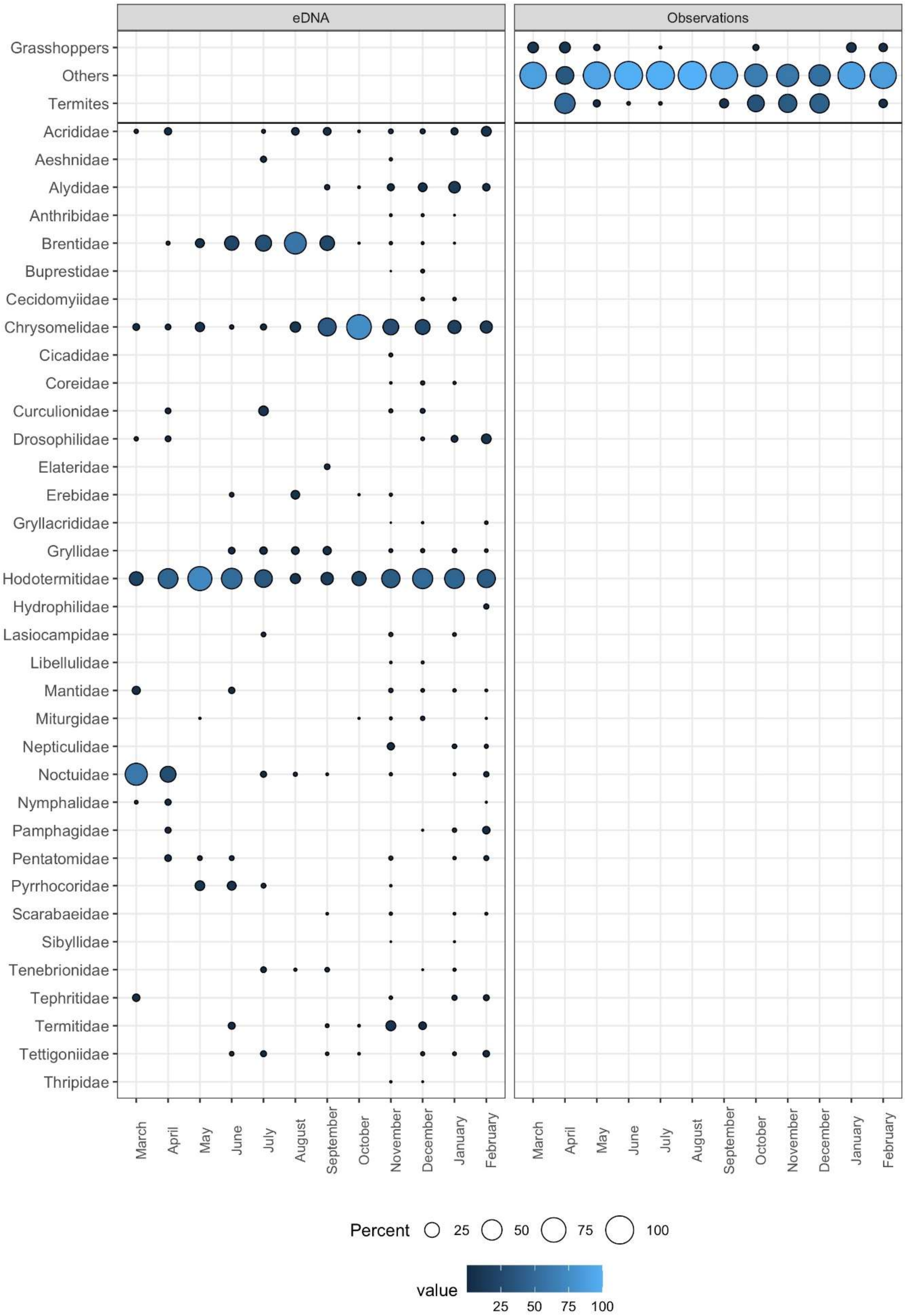

Figure 7. Mean RRA of arthropods families in faecal samples per month (left) and mean of observations in focal follows per month (right). The category "others" includes all insect

observations that were neither identified as grasshoppers nor as termites. The families in the order Orthoptera ("grasshoppers") are: Acrididae, Gryllacrididae, Gryllidae, Pamphagidae, Tettigoniidae. The families in the order Blattodea (equivalent to "termites") are: Hodotermitidae and Termitidae.

Appendix S1

Focal vs. faecal: seasonal variation in the diet of wild vervet monkeys from observational and DNA metabarcoding data

Loïc Brun, Judith Schneider, Eduard Mas Carrió, Pooja Dongre, Pierre Taberlet, Erica van de Waal and Luca Fumagalli

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Appendix S1: Table S1: Species of local database, in bold species with identical sequences.

Family	Species
Anacardiaceae	***Searsia pyroides, Searsia natalensis***
Anacardiaceae	*Sclerocarya birrea*
Araliaceae	*Cussonia spicata*
Arecaceae	*Phoenix reclinata*
Bignoniaceae	*Jacaranda mimosifolia*
Boraginaceae	*Ehretia rigida*

Burseraceae	*Commiphora neglecta*
Cactaceae	*Cereus jamacaru*
Cactaceae	*Opuntia ficus-indica*
Caesalpiniaceae	*Schotia brachypetala*
Capparaceae	*Boscia albitrunca*
Celastraceae	*Gymnosporia senegalensis*
Celtidaceae	*Celtis africana*
Combretaceae	*Combretum erythrophyllum*
Combretaceae	*Combretum apiculatum*
Ebenaceae	***Euclea crispa, Euclea undulata, Diospyros dichrophylla***
Euphorbiaceae	*Euphorbia ingens*
Euphorbiaceae	*Euphorbia tirucalli*
Fabaceae	*Dalbergia armata*
Fabaceae	*Dalbergia obovata*
Fabaceae	*Senna didymobotrya*
Fabaceae	*Sesbania punicea*
Fabaceae	*Mundulea sericea*
Flacourtiaceae	*Dovyalis caffra*
Lamiaceae	*Premna mooiensis*
Lamiaceae	*Volkameria glabra*
Meliaceae	*Melia azedarach*

Mimosaceae	***Vachellia tortilis, Vachellia sieberiana***
Mimosaceae	*Dichrostachys cinerea*
Mimosaceae, Caesalpiniaceae	***Vachellia nilotica, Caesalpinia decapetala***
Moraceae	*Ficus sycomorus*
Myrtaceae	*Psidium guajava*
Myrtaceae	*Eucalyptus camaldulensis*
Olacaceae	*Ximenia caffra*
Oleaceae	*Olea europaea*
Pentapetaceae	*Dombeya rotundifolia*
Rhamnaceae	*Berchemia zeyheri*
Rhamnaceae	*Ziziphus mucronata*
Rubiaceae	*Gardenia volkensii*
Rubiaceae	*Coddia rudis*
Rutaceae	*Citrus limon*
Sapindaceae	*Hippobromus pauciflorus*
Sapindaceae	*Pappea capensis*
Sapotaceae	*Sideroxylon inerme*
Solanaceae	*Solanum seaforthianum*
Solanaceae	*Solanum aculeastrum*
Verbenaceae	***Lantana camara, Lippia javanica***
Vitaceae	*Rhoicissus tridentata*

Appendix S1: Table S2 Species included in positive controls for Sper01 and Arth02 assays, in the order of 2-fold dilutions.

Metabarcode	Species
Sper01	*Taxus baccata, Salvia pratensis, Populus tremula, Rumex acetosa, Carpinus betulus, Fraxinus excelsior, Picea abies, Lonicera xylosteum, Abies alba, Acer campestre, Briza media, Rosa canina, Capsella bursa-pastoris, Geranium robertianum, Rhododendron ferrugineum, Lotus corniculatus*
Arth02	*Acheta domesticus, Timema douglasi, Harmonia axyridis, Galleria mellonella, Pyrrhocoris apterus, Blaptica dubia, Isoperla rivulorum, Silo pallipes*

Appendix S1: Table S3 Plant genus and species in observational focal follows and detected in faecal samples. Plant indicators for seasons were identified using *Indicator value analyses* (Indval; Dufrêne & Legendre, 1997). For database assignments: L = assigned with local database, G = assigned with global database, NA = no sequence available for the used metabarcode.

Observational Data			**DNA metabarcoding data**					
Genus/species observed	**Frequency/12315**	**Season indicator > 0.2, *****	**Genus/species detected**	**Frequency/823**	**Total read counts**	**Season indicator RRA > 0.2, *****	**Data-base**	**Plant category**
Berchemia zeyheri	704	summer+autumn, 0.397	*Berchemia zeyheri*	811	1285128	summer+autumn, 0.460	L	tree
Boscia albitrunca	2		*Boscia albitrunca*	15	417		L	tree
Caesalpinia decapetala	84	spring, 0.255	*V. nilotica/C. decapetala*	82	4621		L	tree/shrub
Cereus jamacaru	752	spring, 0.324	*Cereus jamacaru*	365	53092		L	cactus
Clausena anisata	2		*Clausena anisata*	0	0		G	shrub
Coddia rudis	145	autumn, 0.236	*Coddia rudis*	31	324		L	shrub
Cussonia spicata	2		*Cussonia spicata*	0	0		L	tree
Dalbergia armata	92		*Dalbergia armata*	80	8113	autumn+winter, 0.235	L	liane

Dichrostachys cinerea	1346		*Dichrostachys cinerea*	685	95218	winter, 0.295	L	small tree/shrub
Dovyalis caffra	132	spring, 0.340	*Dovyalis caffra*	559	163527		L	small tree/shrub
Ehretia rigida	785	spring, 0.233	*Ehretia rigida*	523	236935	spring, 0.585	L	small tree/shrub
Euclea crispa	249	spring, 0.332	*E. crispa/E. undulata/ D. dichrophylla*	321	98890	spring, 0.446	L	tree
Euclea undulata	16		*E. crispa/E. undulata/ D. dichrophylla*	321	98890	spring, 0.446	L	small tree/shrub
Euphorbia ingens	6		*Euphorbia ingens*	0	0		L	cactus
Euphorbia tirucalli	3		*Euphorbia tirucalli*	0	0		L	shrub
Gardenia volkensii	51		*Gardenia volkensii*	23	483		L	small tree/shrub
Gymnosporia senegalensis	29		*Gymnosporia senegalensis*	0	0		L	small tree/shrub
Hippobromus pauciflorus	68	summer, 0.244	*Hippobromus pauciflorus*	444	225809	spring, 0.345	L	tree
Lantana camara	15	autumn, 0.216	*L. camara/Lippia javanica*	202	14426	autumn, 0.238	L	shrub

Opuntia ficus-indica	37		*Opuntia ficus-indica*	3	34		L	cactus
Premna mooiensis	391	spring+summer, 0.276	*Premna mooiensis*	309	48541	spring+summer, 0.223	L	tree
Schotia brachypetala	15		*Schotia brachypetala*	18	2490		L	tree
Searsia sp	688	autumn+spring, 0.278	*S. pyroides/S. natalensis*	638	256910	spring, 0.339	L	tree/shrub
Vachellia karroo	7		*NA*	0	0		NA	tree
Vachellia nilotica	1763	autumn+winter, 0.400	*V. nilotica/C. decapetala*	82	4621		L	tree/shrub
Vachellia sp	323	spring, 0.464	*NA*	0	0		NA	tree
Vachellia tortilis	2109	autumn, 0.423	*V. tortilis/V. sieberiana*	817	772456	autumn, 0.768	L	tree
Zanthoxylum capense	2		*NA*	0	0		NA	tree
Ziziphus mucronata	2497	autumn+winter, 0.490	*Ziziphus mucronata*	765	511273	winter, 0.681	L	tree
NA	0		*Aizoon*	467	50557	autumn+winter, 0.203	G	herb/shrub

NA	0	*Aloe*	3	37	G	various
NA	0	*Alternanthera pungens*	4	208	G	herb/shrub
NA	0	*Asparagus*	309	18695	G	herb/shrub
NA	0	*Basella alba*	4	26	G	climbing plant
NA	0	*Blepharis*	3	41	G	herb/shrub
NA	0	*Blepharis maderaspatensis*	447	87987	G	herb
NA	0	*Capparis*	45	7161	G	herb/shrub
NA	0	*Combretum*	9	190	G	shrub
NA	0	*Commiphora neglecta*	2	17	G	small tree/shrub
NA	0	*Crotalaria*	205	38455	G	herb/shrub
NA	0	*Diospyros*	4	30	G	tree
NA	0	*Dombeya rotundifolia*	31	2112	L	tree
NA	0	*Dysphania*	5	65	G	herb
NA	0	*Eragrostis superba*	2	51	G	grass
NA	0	*Erythrina*	2	104	G	tree

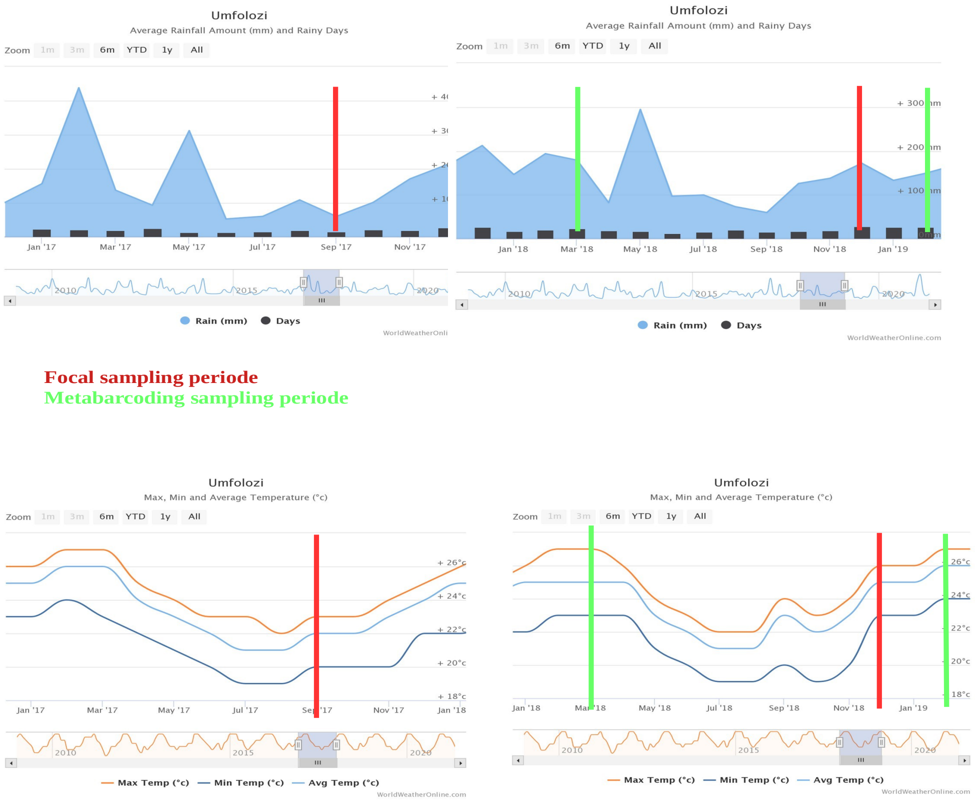
NA	0	*Euphorbia*	9	343		L	various
NA	0	*Ficus sycomorus*	21	6481		L	tree
NA	0	*Hibiscus*	4	197		G	shrub
NA	0	*Jasminum*	699	114664	autumn, 0.452	G	shrub
NA	0	*Kohautia*	2	16		G	herb/shrub
NA	0	*Mundulea sericea*	43	12193		L	shrub
NA	0	*Ocimum*	2	128		G	herb/shrub
NA	0	*Ormosia*	2	11		G	small tree/shrub
NA	0	*Oxalis*	325	36621	spring, 0.218	G	herb/shrub
NA	0	*Pappea capensis*	6	144		L	tree
NA	0	*Pereskia*	4	24		G	cactus
NA	0	*Phyllanthus maderaspatensis*	19	2943		G	herb
NA	0	*Plinthus*	17	141		G	herb/shrub
NA	0	*Priva*	7	109		G	herb/shrub
NA	0	*Priva cordifolia*	555	69468	winter+spring, 0.245	G	herb/shrub

NA	0	*Psidium guajava*	5	272		L	shrub
NA	0	*Rhoicissus tridentata*	212	31942		L	shrub
NA	0	*Sclerocarya birrea*	7	586		L	tree
NA	0	*Senna didymobotrya*	225	4949	autumn+winter, 0.324	L	herb/shrub
NA	0	*Sida*	6	1040		G	herb/shrub
NA	0	*Sideroxylon inerme*	11	1098		L	tree
NA	0	*Solanum seaforthianum*	5	696		L	shrub
NA	0	*Solidago virgaurea*	3	524		G	herb/shrub
NA	0	*Viscum minimum*	37	6829	autumn, 0.242	G	hemi-parasite
NA	0	*Volkameria glabra*	7	431		L	tree
NA	0	*Vigna*	2	47		G	herb/shrub
NA	0	*Waltheria indica*	6	217		G	herb/shrub

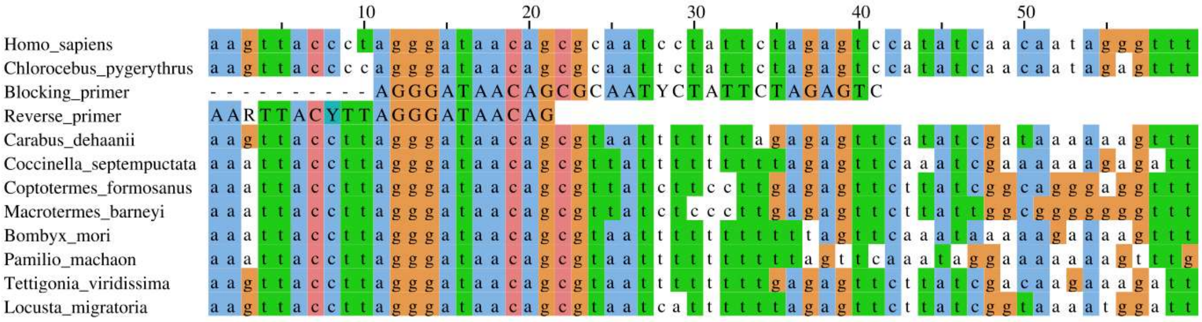
Appendix S1: Table S4 Taxonomy of detected arthropod items in 823 faecal samples, total read counts over all samples.

Order	**Family**	**Count**	**Frequency**
Araneae	Miturgidae	3734	7
Blattodea	Hodotermitidae	98835	438
	Termitidae	21619	46
Coleoptera	NA	59596	265
	Anthribidae	297	3
	Brentidae	12321	77
	Buprestidae	295	4
	Chrysomelidae	38345	300
	Curculionidae	8126	18
	Elateridae	321	2
	Hydrophilidae	212	3
	Scarabaeidae	572	6
	Tenebrionidae	1076	8
Diptera	NA	3069	7
	Cecidomyiidae	408	6
	Drosophilidae	2702	20
	Tephritidae	1645	9
Hemiptera	Alydidae	9594	131
	Cicadidae	1286	2
	Coreidae	250	7

	Pentatomidae	1012	26
	Pyrrhocoridae	197	7
Lepidoptera	NA	71362	372
	Erebidae	464	5
	Lasiocampidae	458	6
	Nepticulidae	1446	24
	Noctuidae	4724	52
	Nymphalidae	248	5
Mantodea	NA	178	2
	Mantidae	927	19
	Sibyllidae	69	2
Neuroptera	NA	180	5
Odonata	NA	283	2
	Aeshnidae	247	2
	Libellulidae	149	2
Orthoptera	NA	611	6
	Acrididae	7196	81
	Gryllacrididae	170	4
	Gryllidae	3636	29
	Pamphagidae	783	11
	Tettigoniidae	1368	19
Thysanoptera	Thripidae	29	2



Appendix S1: Figure S1: Meteorological conditions have been assessed for the entire sampling period in terms of rainfall (at the top; https://www.weathersa.co.za/home/historicalrain) and temperature (at the bottom; https://www.worldweatheronline.com/umfolozi-weather-averages/kwazulu-natal/za.aspx). The period when focal screenings have been conducted is indicated in red, the one for eDNA sampling in green.



```
                          10        20        30        40        50
Homo_sapiens              aagttaccctagggataacagcgcaatcctattctagagtccatatcaacaatagggttt
Chlorocebus_pygerythrus   aagttaccccagggataacagcgcaattctattctagagtccatatcaacaatagagttt
Blocking_primer           ----------AGGGATAACAGCGCAATYCTATTCTAGAGTC
Reverse_primer            AARTTACYTTAGGGATAACAG
Carabus_dehaanii          aagttaccttagggataacagcgtaattttttttagagagttcatatcgataaaaaagttt
Coccinella_septempuctata  aaattaccttagggataacagcgttattttttttagagttcaaatcgaaaaaagagatt
Coptotermes_formosanus    aaattaccttagggataacagcgttatcttccttgagagttcttatcggcagggaggttt
Macrotermes_barneyi       aaattaccttagggataacagcgttatctcccttgagagttcttattggcgggggggttt
Bombyx_mori               aaattaccttagggataacagcgtaatttttttttagttcaaataaaaagaaaagttt
Pamilio_machaon           aaattaccttagggataacagcgtaattttttttagttcaaataggaaaaaagtttg
Tettigonia_viridissima    aagttaccttagggataacagcgtaattttttttgagagttcttatcgacaagaaagatt
Locusta_migratoria        aagttaccttagggataacagcgtaatcattttttagagttcttatcggtaaaatggatt
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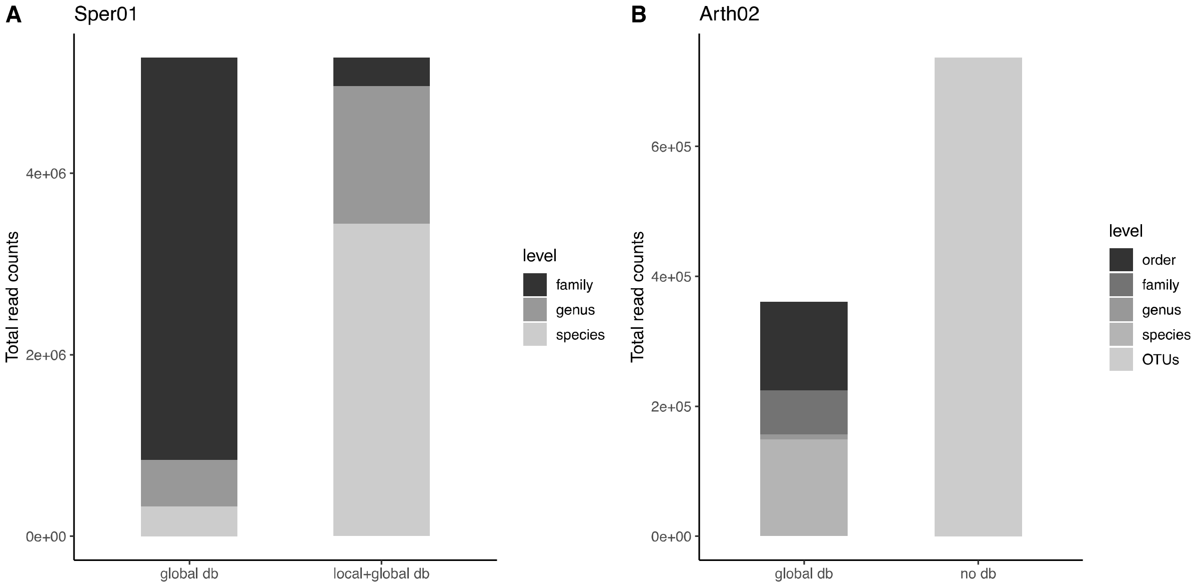
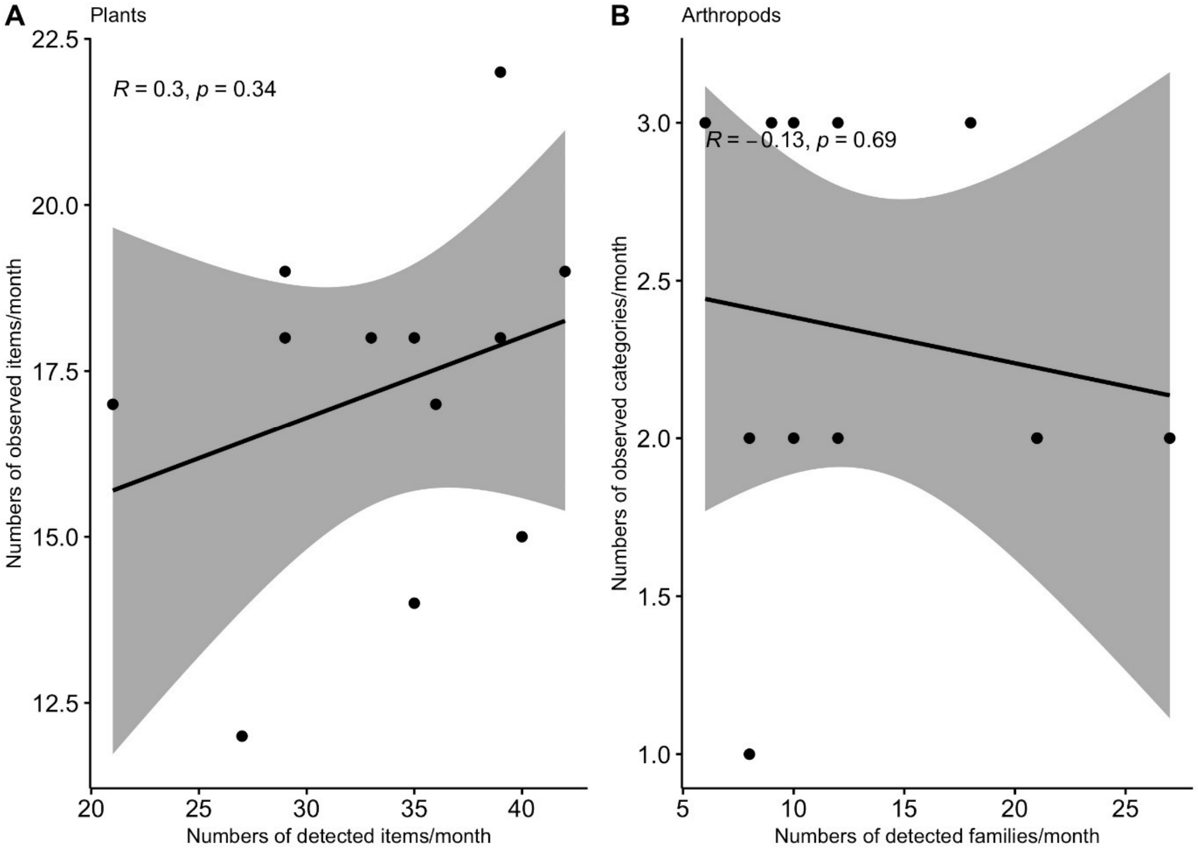
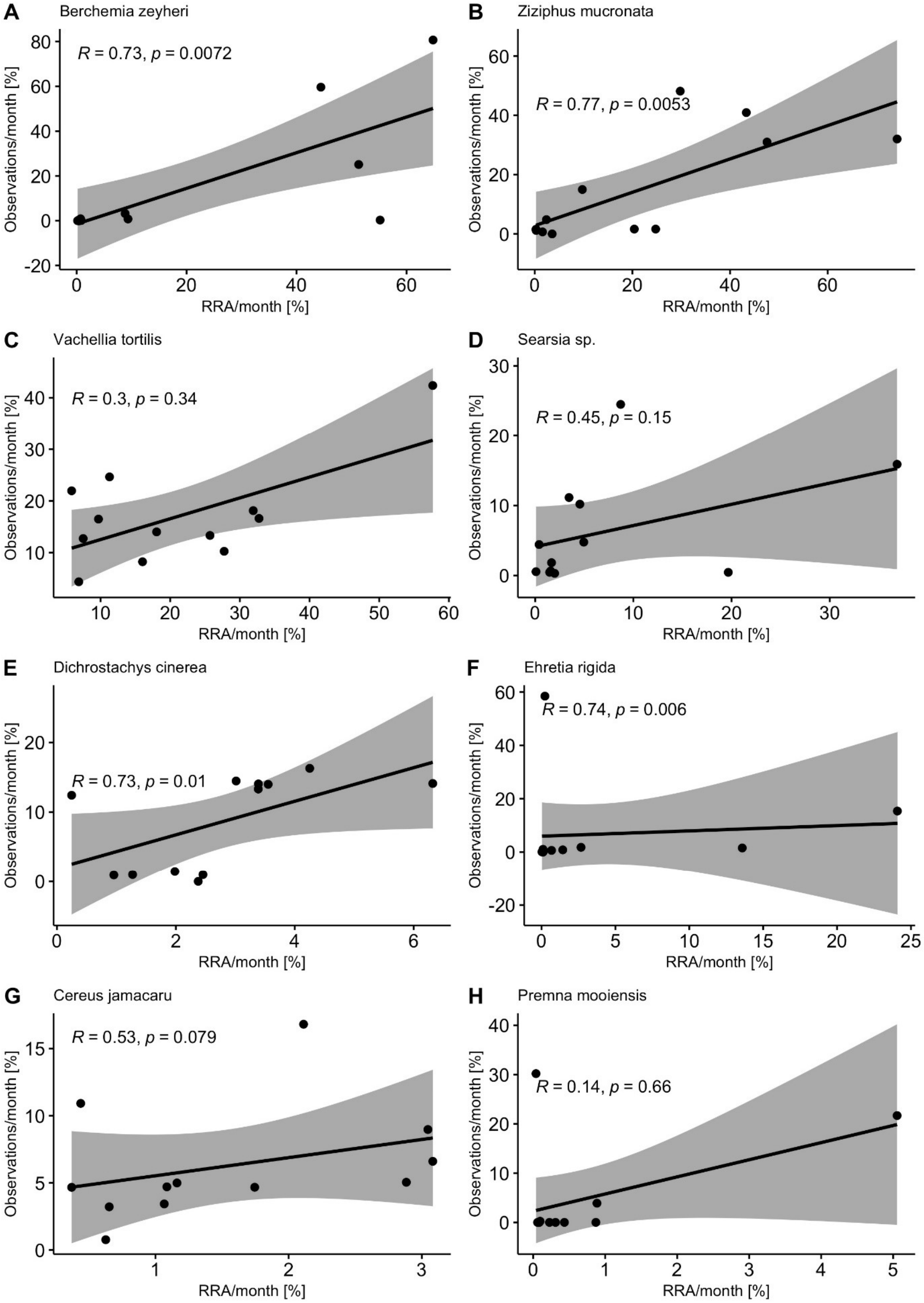
Appendix S1: Figure S2. Design of a blocking primer for vervet and human DNA for the Arth02 primer pair, allowing the amplification of target arthropod species. In this case, the 5'end of the blocking primer overlaps eleven nucleotides of the 3'-end of the reverse Arth02 amplification primer (Reverse_primer). The ideal position for the blocking primer is at the end of the PCR fragment where the variation between the sequence of the species to be blocked and the sequences of the target species is highest (Taberlet, Bonin, Zinger, & Coissac, 2018). A C3 carbon spacer must be added on the 3'-end of the blocking primer to prevent its 3'-extension (Vestheim & Jarman, 2008). In addition of human, vervet, blocking primer and Arth02 reverse primer, representative arthropod sequences are also shown in the alignment.



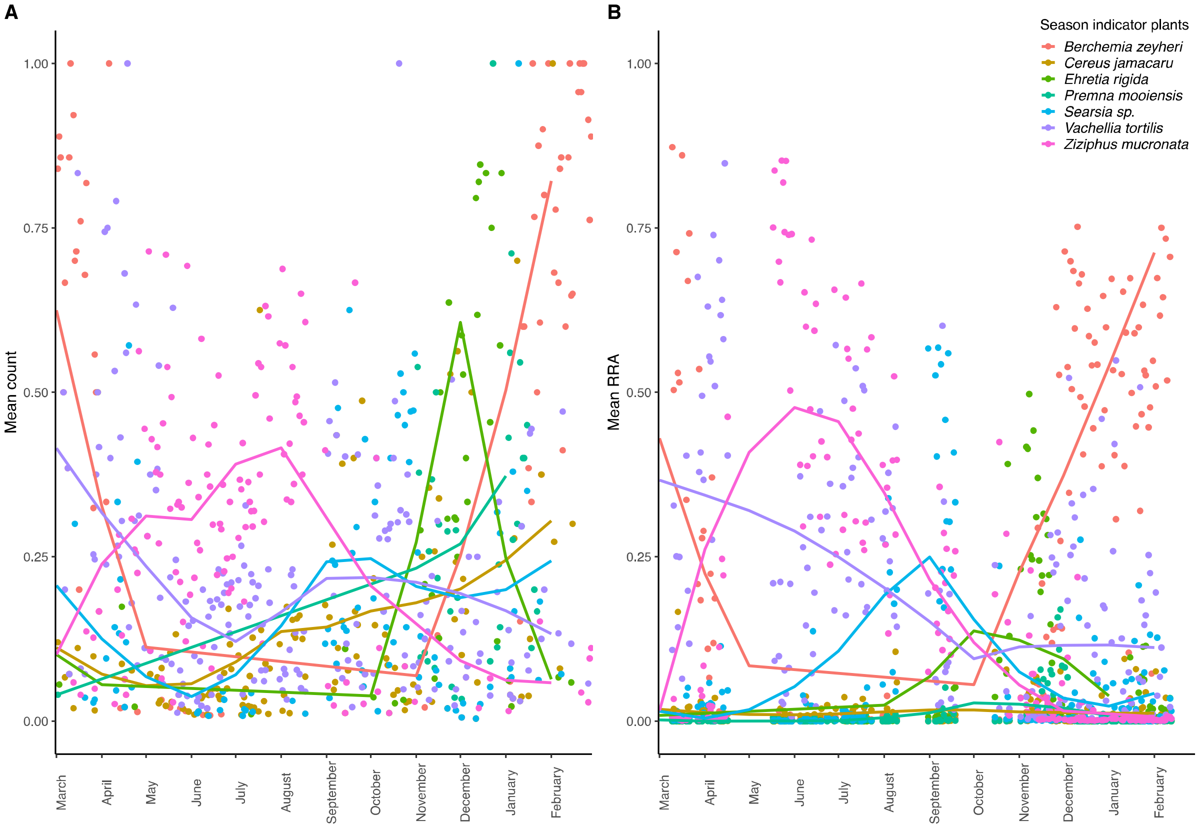
Appendix S1: Figure S3. Stacked bar plots resuming the proportion of read counts assigned to different taxonomic levels by using particular database options for **A.** the Sper01 assay and **B.** the Arth02 assay.



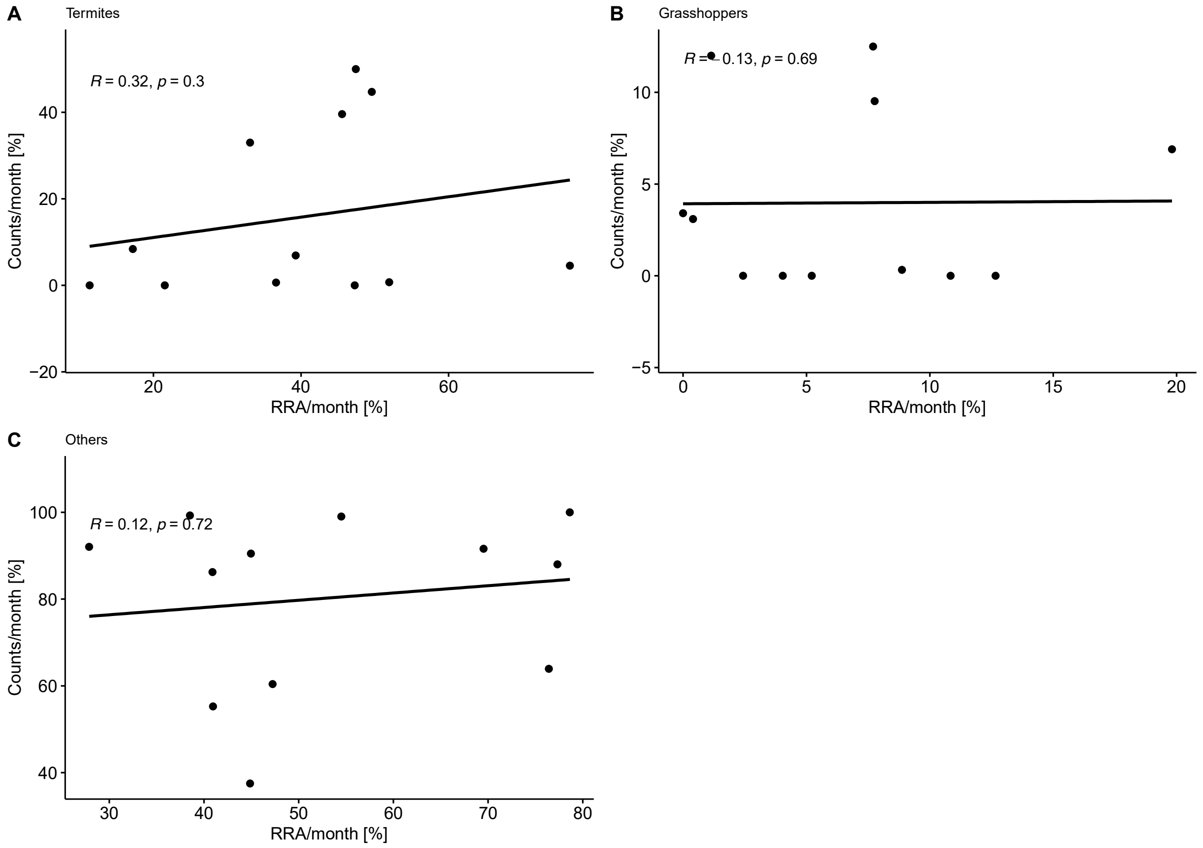
Appendix S1: Figure S4: Spearman rank correlations and coefficients based on total numbers per month of different dietary items as observed during focal follows and detected in faecal samples for **A.** plant data and **B.** arthropod data.



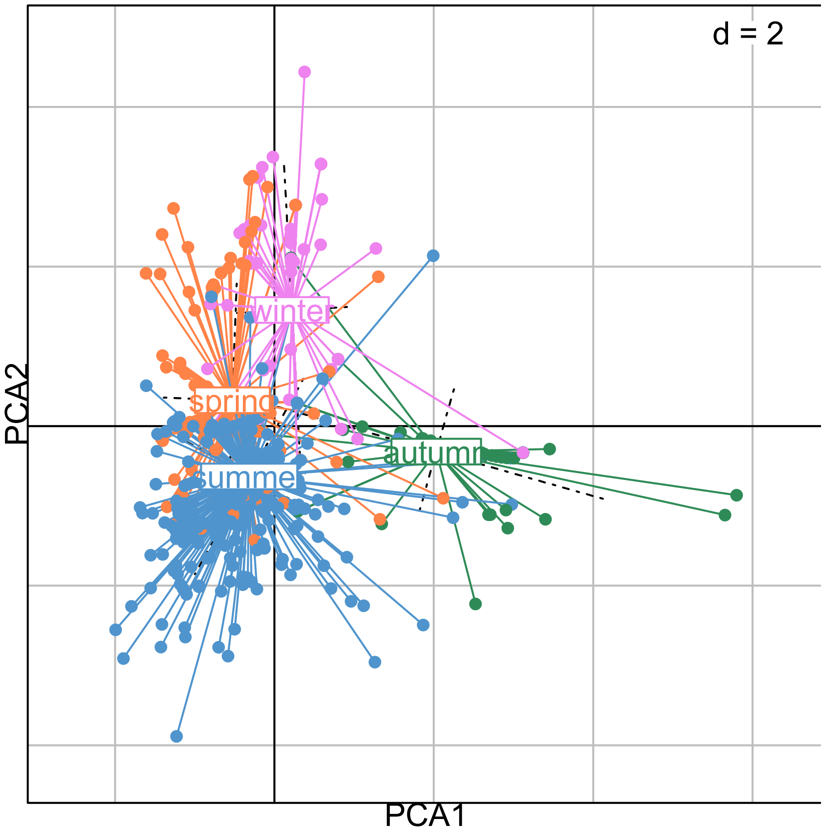
Appendix S1: Figure S5: Spearman rank correlations and coefficients based on mean count and RRA per month for all plant species present in both datasets and with a minimum of 350 observations, with the exception of those that had identical metabarcodes and matched several species in the focal dataset (i.e. *E. crispa*/*E. undulata*/*D. dichrophylla* and *V. nilotica*/*C. decapetala*). The observed plant *V. tortilis* corresponds to *V. tortilis/sieberiana* in the eDNA dataset.



Appendix S1: Figure S6. A. Mean counts per date of seven consumed plant species observed during focal screenings that are indicators for seasons (shown are those plants with Indval value > 0.2, which were observed > 350 times and which do not share sequences with other observed species, Appendix S1: Table S3). **B.** Mean RRA per date of the same seven consumed plant species in faecal samples, only included RRA > 0.001. All species, except *C. jamacaru*, are also season indicator species (> 0.2) in the RRA dataset (Appendix S1: Table S3). The observed plant *V. tortilis* corresponds to *V. tortilis/sieberiana* in the eDNA dataset. Note that this representation serves to compare methods and that there are a number of additional indicator species and genus in the metabarcoding dataset not included here (Appendix S1: Table S3).



Appendix S1: Figure S7: Spearman rank correlations and coefficients based on mean count and RRA per month for all arthropod categories as shown in Fig. 2B.



Appendix S1: Figure S8: Principal component analysis (PCA), based on relative read abundances (RRA) of consumed arthropod families detected in faecal samples (R2 = 3.6 %). The four seasons are represented by different colours and the texts represent the centroids.

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Vestheim, H., & Jarman, S. N. (2008). Blocking primers to enhance PCR amplification of rare sequences in mixed samples - A case study on prey DNA in Antarctic krill stomachs. Frontiers in Zoology, 5, 1–11. https://doi.org/10.1186/1742-9994-5-12

Annexe 2. Captivity and habituation to humans raise curiosity in vervet monkeys

Sofia Ingrid Fredrika Forss[1,2,3], Alba Motes-Rodrigo[1,4], Pooja Dongre[1,2], Tecla Mohr[1,2] & Erica van de Waal[1,2]

[1]*Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland*

[2]*Inkawu Vervet Project, Mawana Game Reserve, KwaZulu Natal, 3115, South Africa*

[3]*Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland*

[4]*Department of Early Prehistory and Quaternary Ecology, Eberhard-Karls-Universität Tübingen, Tübingen, Germany*

Corresponding author:

Sofia Forss: sofia.forss@ieu.uzh.ch
ORCID: 0000-0002-6551-1907

Abstract

The cognitive mechanisms causing intraspecific behavioural differences between wild and captive animals remain poorly understood. Although diminished neophobia, resulting from a safer environment and more "*free*" time, has been proposed to underlie these differences among settings, less is known about how captivity influences exploration tendency. Here we refer to the combination of reduced neophobia and increased interest in exploring novelty as "*curiosity*", which we systematically compared across seven groups of captive and wild vervet monkeys (*Chlorocebus pygerythrus*) by exposing them to a test battery of eight novel stimuli. In the wild sample, we included both monkeys habituated to human presence and unhabituated individuals filmed using motion triggered cameras. Results revealed clear differences in number of approaches to novel stimuli among captive, wild habituated and wild unhabituated monkeys. As foraging pressure and predation risks are assumed to be equal for all wild monkeys, our results do not support a relationship between curiosity and safety or free time. Instead, we propose "*the habituation hypothesis*" as an explanation of why well-habituated and captive monkeys both approached and explored novelty more than unhabituated individuals. We conclude that varying levels of human and/or human artefact habituation, rather than the risks present in natural environments, better explain variation in curiosity in our sample of vervet monkeys.

Keywords: curiosity, novelty response, neophobia, exploration, captivity effect, captivity bias, human habituation

Declarations:

Funding:

SF: the Wenner-Gren Foundation, USA and the Waldemar von Frenckell Foundation, Finland

EvdW: the Swiss National Science Foundation (PP00P3_170624), Switzerland

Conflicts of interest:

The authors declare no conflict of interests

Availability of data and material:

All data for these analyses can be found in the Open Science Framework with the link: https://osf.io/2cahn/?view_only=e1d66702bc544363b5ced2ae51d97af5.

Code availability:

The code employed in these analyses can be found in the Open Science Framework with the link: https://osf.io/2cahn/?view_only=e1d66702bc544363b5ced2ae51d97af5.

Authors' contributions:

SF: Conceptualization of the study, acquired funding, designing experiments, collected the data and main writer of the manuscript.

AM-R: Statistical analyses, text editing and manuscript writing.

PD: Assistance by data collection and text editing.

TM: Assistance by data collection.

EvdW: Supervisor, provided resources and funding for the study to take place at the IVP, manuscript editing.

Ethics approval:

We declare that all experiments performed for this study were conducted on sole observational basis. This research adhered to the "Guidelines for the use of animals in research" of Association for Study of Animal Behaviour and was approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa.

Consent to participate: Not applicable

Consent for publication: Not applicable

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Introduction

Due to both feasibility and logistics, most experimental work on animal cognition is performed in captivity. Nevertheless, cognitive experiments are increasingly being carried out with wild populations in ecologically relevant field settings (Morand-Ferron et al. 2011; van de Waal and Bshary 2011; Thornton and Samson 2012; Benson-Amram et al. 2013; Cauchard et al. 2013; Shaw et al. 2015; Rasolofoniaina et al. 2021). Field experiments usually present wild animals with novel problems in the form of puzzle-boxes or devices made of anthropogenic materials. Despite habituation to the apparatuses over time, many studies point to individual differences in neophobia and motivation to participate rather than to differences in cognitive capacities between wild and captive individuals (Overington et al. 2011; Benson-Amram and Holekamp 2012; van Horik et al. 2017; Rössler et al. 2020; Martina et al. 2021). These results suggest that, in order to successfully implement comparisons of further cognitive skills among settings, we need to improve our understanding of how the motivation to interact and explore novelty differs between captive and wild individuals.

In the broadest sense, curiosity is described as "*the motivation to seek information about something unfamiliar*" (Berlyne 1950; Loewenstein 1994; Byrne 2013; Kidd and Hayden 2015; Gross et al. 2020). This 'novelty-seeking' is notably in the absence of any immediate external reward (Wang and Hayden 2019). In humans, psychologists commonly address curiosity through questionnaires and self-reports (see overview in Gross et al. 2020). In non-human animals, however, identifying curiosity requires measures of more specific behavioural components describing readiness and motivation to gather information about something unfamiliar, outside the context of general survival activities (Mettke-Hofmann et al. 2002; Byrne 2013; Hall et al. 2018). Moreover, given the high risks present in most natural environments, many animals have intrinsically strong neophobia, potentially preventing them from engaging in novelty exploration (Barnett

1958; Greenberg 1990a; Mettke-Hofmann et al. 2002). Therefore, it is likely that overcoming neophobia is foundational for when and how wild animals can pursue curiosity driven exploration. Generally, the term neophobia is used to describe "*fear*" of novelty (Greenberg 1990a, 1990b, 2003; Fox and Millam 2007; Greggor et al. 2016a, 2016b), but since we cannot always infer fearful emotions of animals from novel object test paradigms, the more commonly used definition is "*novelty avoidance*" (Misslin and Cigrang 1986; Benson-Amram et al. 2013; Forss et al. 2015; Greggor et al. 2015; Rasolofoniaina et al. 2020). The contrasting response of closely approaching novel stimuli, or preferring novelty over familiarity is termed neophilia (Day et al. 2003; Greenberg 2003; Kaulfuß and Mills 2008). Crucially, one needs to keep in mind that being explorative is *not* the opposite of being neophobic. Instead, explorative behaviours encompass multiple motivational actions relevant to gain information about something unfamiliar (Greenberg 2003; Biondi et al. 2010; Carter et al. 2012; Forss et al. 2017). Therefore, an animal can be both neophobic and simultaneously have a strong exploration tendency (Moretti et al. 2015; Forss et al. 2017). Here we refer to curiosity as a positive response to novel stimuli expressed through the *combination* of low neophobia (measured as readiness to approach something new) and subsequent explorative behaviours used by an individual to gather knowledge of new encountered stimuli (measured as exploration events, e.g., handling, sniffing etc.) (Damerius et al. 2017a).

One extreme case leading to reduced neophobia is the risk-free existence of captive animals (Barnett 1958; Brown et al. 2013). The "*captivity effect*" or "*captivity bias*" refers to measurable intra-species cognitive differences between individuals from natural- and captive environments (Haslam 2013; Forss et al. 2015; van Schaik et al. 2016; Rössler et al. 2020). Beyond neophobia, a captivity effect has also been described for other behaviours like innovation (Benson-Amram et al. 2013; Rössler et al. 2020) and tool use (Kummer and Goodall 1985; Gruber et al. 2010; Shumaker et al. 2011; Haslam 2013). Variation in activity budgets between wild and captive animals (Veasey et al. 1996; Yamanashi and Hayashi 2011) forms the foundation of the argument that the captivity effect results from wild animals being more occupied with foraging and predator vigilance than captive conspecifics (Kummer and Goodall 1985; Brown et al. 2013; Amici et al. 2020). Accordingly, "*the free time hypothesis"* and "*the excess energy hypothesis"* propose that captive animals have a surplus of energy and a lower cognitive load allowing for higher levels of exploration and innovativeness than wild conspecifics, who are occupied searching for food, mating partners or shelter (Kummer and Goodall 1985; Laidre 2008a; McCune et al. 2019; Amici et al. 2020). For example, captive hyenas (*Crocuta crocuta*) are less neophobic and more explorative than wild conspecifics, thereby outperforming them in certain problem-solving tasks (Benson-Amram et al. 2013). On the other hand, wild Mexican jays (*Aphelocoma wollweberi*) were faster problem-solvers than captive conspecifics (McCune et al. 2019) and wild-caught and laboratory raised Goffins cockatoos (*Cacatua goffiniana*) differed mainly in their motivation to *participate* in an experimental task, but not in their innovation rates (Rössler et al. 2020). Yet, if and what elements of captive life increase exploration tendencies is less clear. Findings from both primates and birds suggest that frequent exposure to human-made artefacts increases task performance as a result of habituation to artificial materials (Gajdon et al. 2004; Laidre 2008b; van de Waal and Bshary 2011; Damerius et al. 2017a; 2017b). In some primate species, like the great apes, neophobia towards novelty is so high that it can be challenging to perform cognitive tasks through presentation of anthropogenic materials in their natural habitats (Forss et al. 2015; Kalan et al. 2019). Despite being exposed to novel objects for multiple months, wild orangutans (*Pongo abelii* & *Pongo pygmaeus*) only explored them on the rare occasions when they first observed a familiar human interact with the objects (i.e., human presence induced a curious response) (Forss et al. 2015). In captive orangutans, researchers found that individuals' degree of human orientation was positively correlated with exploration tendency, which in turn enhance their problem-solving skills (Damerius et al. 2017b). Thus, it is likely that, in some species, the captivity effect results from human habituation; captive animals show lower neophobia due to reduced risk perception regarding humans, and they develop stronger interest in novelty following increased experience with anthropogenic artefacts (van de Waal and Bshary 2011; Damerius et al. 2017a, 2017b).

In the present study, we examined the foundations of curiosity by investigating neophobia and exploration tendencies in wild and captive vervet monkeys (*Chlorocebus pygerythrus*), using both novel-food and novel-object paradigms. Vervet monkeys are a particularly interesting species to address curiosity as they are opportunistic foragers and successfully inhabit anthropogenic environments like agricultural and urban areas, where they frequently exploit human food sources (Wimberger and Downs 2010; Thatcher et al. 2019). As a highly generalist and “nuisance” species, we expect them to show low levels of neophobia and high exploratory tendencies towards novel stimuli (Greenberg 2003; Sol et al. 2011; Tryjanowski et al. 2016; Griffin et al. 2017; Barrett et al 2019; Jarjour et al. 2020).

Specifically, we aimed to investigate whether curiosity in vervet monkeys is related to habituation to humans or due to low environmental risk and increased free time per se. In the first case, we compared the responses to novel stimuli of captive monkeys to those of wild habituated and wild unhabituated individuals. We predicted that if there existed a captivity effect, wild monkeys (habituated and unhabituated) would show less interest in unfamiliar objects and foods than captive conspecifics. To address the influence of human habituation on curiosity, we performed a separate test to compute the habituation index of each habituated vervet group. We predicted that groups with higher habituation indices would show more curious responses towards the battery of novel stimuli. In addition, for the wild habituated monkeys, we evaluated whether the habitat structure of the location where the experiments were conducted had any influence on the monkeys' responses. Here our prediction was that certain habitat structures, like high grass or open savannah, possibly impose higher predation risk and that monkeys would therefore be less motivated to explore in these habitat structures, compared to when the experiments were performed underneath a tree, providing a more protected location. Because sociality is expected to reduce risk perception and presence of group members has been shown to increase approaches to novel objects in other species (Stöwe et al. 2006; Moretti et al. 2015; Forss et al. 2017), we predicted that in riskier habitat structures monkeys would approach more in a social context, accompanied by one or more group members. Lastly, given that captive and wild monkeys vary in their experiences with human-made artefacts, we used foods and objects of natural and artificial characteristics to evaluate any potential effect of stimuli features.

Methods

Subjects and study sites

We collected data on wild vervet monkeys (*Chlorocebus pygerythrus*) during February and March 2020 at the Inkawu Vervet Project (IVP) field site, located in Mawana game reserve (28°00.327S, 031°12.348E) in KwaZulu-Natal, South Africa. The study site is home to multiple wild groups of vervet monkeys, six of which are habituated to humans, regularly observed by researchers, and partake in experimental studies. Our data set comprised four of these groups, three of which are habituated since 2010 (Baie Dankie: N=57, Noha: N=39, Lemon Tree: N=24) and the fourth since 2013 (Kubu: N=19). In addition, the study area sustains at least three unhabituated groups, with many more living throughout the rest of the reserve. To enable data collection on unhabituated monkeys and to record any potential interactions with the novel stimuli, we placed motion triggered video camera traps below two known sleeping trees of an unhabituated group (Congo: N=11).

We collected data on the captive population in March 2020 at the Wild Animal Trauma Centre & Haven (WATCH) vervet sanctuary, in Vryheid, KwaZulu Natal, South Africa. At the time of data collection, the WATCH sanctuary housed three groups of vervet monkeys. For logistical reasons we only included two groups in our study (Poena: N=17 and Boeta: N=3). Most of the monkeys arrived at the sanctuary and were cared for by humans since they were a few weeks old, and only a few individuals arrived at a later life stage. At first, infant monkeys arriving at a very young age are housed indoors and bottle nursed by human caretakers. Once they reach three months of age, they are slowly integrated into a group of conspecifics of mixed ages. Since the goal is to release these individuals back into their natural habitat (if circumstances allow), caretakers, and occasionally researchers, limit their contact with the monkey groups as much as possible.

Experimental set up

Habituated groups

We presented all four habituated groups with eight novel stimuli representing distinct materials, structures and odours. We categorized four of these items as human-made or processed: boiled pasta (green, red, natural coloured), popcorn, toy mice (with Baldrian herb scent) and plastic toy cars (yellow, blue, green, red). One item, white seashells, represented a completely natural occurring object. We chose the remaining three items to have “naturalistic features”: fish (dead organic material in form of canned sardines), beef meatballs (raw organic material), rubber butterflies of different colours (man-made material which mimics naturally occurring organisms) (Supplementary information (SI) Fig.S1). We randomized the order of presentation of the novel stimuli across groups to avoid order effects and presented one type of novel stimulus at a time, on the ground, always with several items of each type to avoid potential monopolization by higher-ranking group members. To attract the wild monkeys' attention to the experimental area, prior to the start of the experiment we placed a handful of familiar food (corn) in the middle of the area where the novel items were spaced out. The habituated monkeys are used to eating corn as this food item has been introduced during both the habituation process as well as during previous experimental studies (van de Waal et al. 2013; van de Waal et al. 2017). Our main goal was to record any potential behavioural reactions towards the novel stimuli *after* the monkeys had been attracted to the area (within 20 meters) and thus seen the novel stimuli. We did all experiments during the early mornings one to two hours after dawn and we presented only one category of novel stimuli per group per day. We video recorded all experiments with Sony handycams HDR-CX200, two mounted on tripods from different angles, and a third that was handheld by an observer zooming in on any observed explorative behaviours. We presented all novel stimuli to the monkeys for 20 minutes, to allow enough time for lower-ranking individuals to also approach in case the most dominant individuals were present at the start of the experiment preventing the lower rankers from approaching. Because the microhabitats vary slightly across groups as well as within each groups' home range, depending on their location on the day of our experiments, we categorized each experimental set up into three distinct habitat structures: open savannah (no canopy protection and no high grass), high grass (high grass but no canopy protection) and below tree (the experimental area was protected by canopy). In the open savannah, vervet monkeys are exposed to aerial predators like eagles and monkeys are observed to restrict their movement in high grass as the study area is home to a high abundance of pythons, capable of capturing vervet monkeys. Consequently, below trees represents the safest habitat structure for the monkeys as the tree canopy serves as protection from aerial predators and these areas do not have high grass.

Unhabituated group

The unhabituated group would not tolerate any human presence, as individuals from this group run away when human observers approach. They were however already habituated to eat corn when placed out in their habitat. We used an identical set up as with the habituated group, where we placed a small amount of corn in the middle of the area with the novel items. To record data from the unhabituated group we placed the video camera traps in a way that they captured two different angles of the novel items, which we presented to the monkeys below two of their known sleeping trees. We used all the same novel stimuli as those used for the habituated groups. Because of the uncertainty regarding when the group would pass by the experimental location or when the monkeys would exactly use those sleeping trees, we presented the novel stimuli for two days in a row (unless a recording of any approaches by the group took place before the end of two consecutive days). Recordings from the camera traps thus allowed us to distinguish whether the group approached the novel stimuli on a single or multiple visits. For comparisons with the other group types, we only used the responses observed during the first visit.

Captive groups

At the WATCH sanctuary, we placed the novel stimuli in the main enclosure of the monkeys, who we moved into a side enclosure during the preparation of the experiment, and then let back into their normal enclosure. We used the same experimental protocol as for the habituated groups, including categories and numbers of novel stimuli, experimental duration, video camera placements and recordings. As the captive monkeys were not used to corn, we used a few peanuts instead as the familiar food that would attract their attention to the experimental area.

Video coding and measurements

We coded all behavioural responses from video recordings. We recorded the number of close proximity approaches – those made to within 1 meter of any of the multiple novel stimuli (food or item) – by any monkey that was present within a 20-meter radius of the experimental location. As we defined a close proximity approach as each time a monkey approached within 1 meter the novel stimuli, in any case where a monkey left the experimental area and then approached within 1 meter again, this represented two approaches. For each approach that was made to the experimental area, we also distinguished whether or not the approach was made alone (when no other monkey was present within 1 meter of the novel stimuli) or socially (when there was at least one other monkey present within 1 meter of the novel stimuli). Once a monkey made physical contact with a novel item (0 meters), we coded following exploration events: the number of smelling and tasting events, the number of times a monkey touched the novel item by hand, the number of times when a monkey chewed/ bit the novel stimuli and the number of times a monkey lifted and moved an item. We then summed these behaviours into one exploration score labelled *number of exploration events* for each group and item. For each novel food item, we additionally scored whether or not a monkey tasted it, defined as an event where a monkey licked a novel food item, or every time a monkey put its lips onto a food item without ingesting it. All definitions of the coded behaviours as well as the frequencies of approaches and exploration events per group can be found in the ethogram in Table S1 and Fig. 4S in the Supplementary material.

Habituation test

To estimate the variation in human habituation among groups, we additionally performed a habituation test with the wild-habituated and captive groups. During this test, we exposed the monkeys to a human male that they had never seen before. The wild habituated groups are familiar with researchers and project volunteers who attempt to distinguish themselves from other humans such as poachers by always wearing a turquoise blue cap while in the presence of the monkeys. In the habituation test, the man was dressed all in black clothes and wore a black cap. The man walked calmly towards the group of the monkeys shaking a Tupperware with corn as this is a familiar signal to the monkeys when they participate in research experiments. In the wild setting the man then placed the closed box with corn at his feet and as a group level habituation index, we measured the proportion of monkeys that approached the man to a distance of one meter out of all the monkeys present within 20 meters. In the captive setting the man placed himself right at the enclosure mesh and placed peanuts right at his feet, which were in touchable distance to the monkeys. This test lasted 20 minutes in total.

Statistical analyses

We conducted the statistical analyses in R (version 3.6.1; R Core Team, 2019) and RStudio (version 1.2.5031; RStudio Team, 2020). We z-transformed covariates (habituation index and group size) to have a mean of zero and standard deviation of one before including them in the models to facilitate the interpretation of the coefficient estimates (Schielzeth 2010).

We first conducted a series of Spearman correlations to investigate whether any of the response measures (number of close proximity approaches, number of exploration events and number of individuals within each group that tasted the food items) were correlated (Table 2). Since the number of individuals that tasted the different stimuli strongly correlated with the other response measures and this variable contained multiple missing values (N=24) we excluded this variable from further analysis.

To address the study aims we fitted four different Generalized Linear Mixed Models (glmm) to the data (Table 1). We checked all models (Model 1a ,1b, 2, 3) for overdispersion and overall stability (see Supplementary material) and z-transformed continuous variables (Habituation index and group size) before including them as fixed effects (Table 1). We draw inference by comparing the full model with a reduced (null) model lacking the predictors of interest but containing all other model elements (Forstmeier and Schielzeth 2011) using a likelihood ratio test (test "Chisq'' in the R function anova, (Dobson 2002). We implemented this approach in order to avoid "cryptic multiple testing" and to maintain type 1 error rates at the desired nominal level of 0.05 (Forstmeier and Schielzeth 2011). We calculated individual p values for each predictor using the function drop1 and R squared using the function r.squaredGLMM.

In the first model (Model 1a), we investigated the effects of group type (3 levels: wild habituated, wild unhabituated and captive) and stimuli type (8 levels, see above) on the number of approaches (response variable, count data) observed in a given group. For Model 1a, which had a poisson error structure and log link function, we fitted the function glmer from the package lme4 (Bates et al. 2014). To account for group identity, we included the random intercept of group ID (7 levels, see above) into the model. We also included the logarithm of group size as an offset term to account for the different number of individuals in each of the groups.

In order to evaluate variation in close proximity approaches in relation to habituation level, we fitted a second model (Model 1b) using the same response variable, random structure and the same offset as in Model 1a, but we changed the fixed effect structure. In addition to group type (2 levels: wild habituated and captive) and object type, we included the habituation index into Model 1b. As unhabituated groups did not have a habituation index, we excluded this group from those models where this variable was included (Model 1b and Model 2, see below).

In Model 2, we evaluated potential differences in explorative behaviour among the different group types (2 levels: wild habituated and captive), habituation level and stimuli type (8 levels). Similar to Models 1a and 1b, in Model 2 we included the random intercept of group ID as well as group size as an offset. To avoid overdispersion problems, we fitted this model using a quasipoisson model with a negative binomial distribution and the optimizer "bobyqa".

In Model 3, we evaluated whether the proportion of social approaches varied according to habitat structure, habituation level and stimuli type. In Model 3 we only included data from wild habituated groups as these groups were the only ones that had been tested at locations with different habitat structures (below tree; N = 14, high grass; N = 10, open savannah; N = 13). Model 3 was a binomial model with a response variable in the form of a matrix containing two columns corresponding to the number of social approaches and the number of individual approaches per trial (Baayen et al. 2008). By using such response variable, we account for the different number of approaches observed in different trials. Given that binomial models do not allow including offsets, we included group size as a control predictor. As before, we also included the random intercept of group ID was included in the model (although note that in this case group ID only had 4 levels, which is the threshold generally used to substitute a fixed by a random effect, meaning that it could have also been included as a control predictor).

Table 1: Descriptions of the different model structures. Variables preceded by a "z" indicate that this variables were z-transformed before being introduced in the models. Group size was log transformed before being introduced as an offset.

Model	Response variable	Fixed effects	Random effect	Offset
1a	Number of approaches	Stimuli type (8 levels); Group type (3 levels)	Group ID (7 levels)	log Group size
1b	Number of approaches	Stimuli type (8 levels); Group type (2 levels)[1]; z-Habituation index	Group ID (6 levels)	log Group size

2	Number of exploratory events	Stimuli type (8 levels); Group type (2 levels)[1]; z-Habituation index	Group ID (6 levels)	log Group size
3	Two-column matrix including number of social approaches and number of individual approaches per trial	Stimuli type (8 levels); Habitat structure (3 levels); z-Habituation index; z-Group size[3]	Group ID (4 levels)[2]	-

1. Wild habituated groups were excluded from the model as they did not poses a habituation index.
2. Only wild habituated groups
3. Included as control predictor

Results

Relationship between response measurements

We found that all three response measures were significantly correlated among one another. The strongest correlation was found between the number of individuals tasting the novel stimuli and the number of exploratory events observed in a group. Correlation coefficients and p values of the correlations can be found in Table 2.

Table 2: Coefficients and p values in parenthesis resulting from the correlation analyses performed among curiosity measures.

	N approaches	N exploratory events	N tasting individuals
N approaches	1	0.47 (<0.001)	0.45 (0.01)
N exploratory events	-	1	0.61 (<0.001)
N tasting individuals	-	-	1

Factors influencing approaches to novel stimuli

Model 1a was overall significantly different from its corresponding null model (likelihood ratio test: $X^2=70.94$, df=9, p<0.001; R^2 full model=0.5; SI: Table 3S). Group type and stimuli type both had significant effects on monkeys' approaches to the novel stimuli (group type: df=2, p<0.001; stimuli type: df=7, p<0.001). More specifically, we found that the three group types significantly differed among them (Fig. 1), with captive groups presenting the highest average number of close approaches to the novel objects and foods (captive-wild habituated: $p<0.001$, Hedge's g=0.89; captive-wild unhabituated: $p<0.001$, Hedge's g= 1.16; wild habituated-wild unhabituated: p=0.048, Hedge's g=2.23).

The visualization of the effects of stimuli type on the number of approaches by group (SI: Fig. 2S) suggested that the differences among stimuli indicated by the model were driven by the high number of approaches in the largest captive group (Poena). To determine if this was the case, we fitted Model 1a again, but removed the data from the Poena group. In this case, we found that although the full-null model comparison was significant (likelihood ratio test: X^2=20.92, df=9, p=0.013; R^2 full model=0.41) and the significant effect of group type remained (p=0.002), stimuli type did not have a significant effect on the number of approaches (p=0.34).

Model 1b (SI: Table 3S) was overall significant both when the Poena group was included and excluded (with Poena: likelihood ratio test: X^2=66.83, df=9, $p<0.001$; R^2 full model=0.5; without Poena: likelihood ratio test: X^2=18.18, df=9, p=0.03; R^2 full model=0.41). In neither case did the habituation index (with Poena: p=0.84, without Poena: p=0.19) nor the group type (with Poena: p=0.08, without Poena: p=0.09) have significant effects on the number of close approaches observed in the different groups.

Factors influencing exploration tendency

Model 2 was overall significant according to the full-null model comparison (likelihood ratio test: X^2=67.28, df=9, $p<0.001$; R^2 full model=0.68, SI: Table 5S). All test predictors had a significant effect on the response (habituation index: $p<0.001$, Figure 2; stimuli type: p=0.001) although the significance of group type (i.e., difference in exploration events between captive and wild habituated groups) was marginal (p=0.047, Hedge's g= 0.58). Visual assessment of the data suggested that the statistical differences in exploration tendency based on stimuli type were not driven by a particular group (SI: Fig. 3S). Differences in exploratory events based on stimuli type were investigated by changing the predictor's reference category (SI: Fig. 3S, Table 6S).

Habitat structure and novelty approaches

Model 3 was overall significant according to the full-null model comparison (likelihood ratio test: X^2=30.29, df=10, p<0.001; R^2 full model=0.68, SI: Table 7S). We found that the proportion of social approaches varied significantly across stimuli types (p<0.001). However, the proportion of social approaches did not significantly differ based on habitat structure (p=0.47, Fig. 3) or habituation index (p=0.99).

Discussion

The effect of human habituation on curiosity

As opportunistic foragers, we would expect vervet monkeys to show relatively low neophobia in order to optimize their foraging niche (Greenberg and Mettke-Hofmann 2001; Greenberg 2003; Mettke-Hofmann 2014; Barrett et al. 2019). Our results, however, showed that within this species, neophobia levels were conditional on environment (captive and wild) and habituation level (Fig. 1). Wild individuals approached novel stimuli significantly less than captive conspecifics and, as predicted, within the wild sample, unhabituated monkeys approached novel items less than habituated individuals (Fig. 1). This contrasts with both the *"free time"* and *"excess energy"* hypotheses (Kummer and Goodall 1985; Laland and Reader 1999; Reader and Laland 2001; Amici et al. 2020), which would predict that both types of wild vervet groups (habituated and unhabituated) have similar approach frequencies, since they live in the same environment and therefore experience similar predation pressure, food abundance and presumably are in need for similar amount of foraging and vigilance activities. Moreover, we exposed the wild unhabituated group to the novel stimuli longer than the habituated monkeys, due to the set up by the video camera traps. Thus, the need for wild individuals to attend to other activities during the experiments cannot account for the observed differences in the number of approaches between these group types. As such, our data does not support the "*free time*" or "*excess energy hypotheses*". Rather, we propose *the habituation hypothesis* as a possible explanation of our findings, and discuss this more below.

Besides differences in the number of close approaches between monkeys from captive and wild habitats, the wild habituated monkeys made an intermediate number of approaches, in-between their captive and wild unhabituated conspecifics (Fig. 1). The captive monkeys in our sample had never (or only at very early age) experienced any negative reinforcement when approaching anything unfamiliar as they spent all their life within a risk-free, food provisioned habitat and thereby probably have a positive perception of humans. This experience was reflected in the results of the habituation test, as almost all captive monkeys approached the man to the closest possible distance. Of course, we cannot account for the fact that the captive monkeys experienced a barrier between them and the unknown human as he was standing outside the enclosure mesh, however given that the more habituated wild monkeys also approached to same distance suggest that habituation to humans and/or human artefacts reduces approach neophobia. In contrast to the captive monkeys, the wild monkeys at IVP are exposed to both negative and positive human interactions. Besides researchers (which are distinguished by their blue caps) who sporadically provide food through field experiments, they occasionally encounter poachers, hunters and people living in villages just outside the reserve fence. Accordingly, the wild habituated monkeys in our sample have become accustomed to humans and human artefacts but also experience the hazards of natural environments. It is possible that during the experiments, the wild habituated monkeys perceived researcher presence as a safety indicator, or associated us with occasional feeding opportunities, which possibly raised their motivation to approach the novel stimuli compared to the unhabituated group. Yet, within the sample of habituated wild monkeys, habituation index did not predict the number of approaches (SI: Table 4S and Fig. 2S), but groups with higher habituation indices had stronger exploration tendencies (Fig. 2). It is also worth emphasising that the majority of the habituated IVP monkeys avoid very close proximity even to familiar humans (Erica van de Waal, personal observation). These findings imply that a significant effect of habituation is the increased motivation to interact and manipulate novel stimuli, rather than just daring to come closer to humans or their artefacts, or expecting to obtain food from them. All together, these findings support our hypothesis that habituation to humans and/or their artefacts facilitates curiosity towards novelty in vervet monkeys.

Going beyond this, within the wild habituated groups, we found lower explorative tendencies in Lemon Tree and Kubu compared to Baie Dankie and Noha. Indeed, the human-related experiences vary between the habituated groups. The home range of Lemon Tree is located furthest away from the IVP station; and in previous years, both Lemon Tree and Kubu have encountered hunters/villagers more frequently than other groups. During the habituation process of the monkeys at IVP, Lemon Tree showed a delay in their habituation compared to the other habituated groups (Erica van de Waal, personal communication). Thus, it is plausible that the effect of human habituation on novelty responses is relative to the ratio of neutral-positive (researcher) encounters to neutral-negative (non-researchers, poachers and hunters) encounters experienced by a group. Furthermore, both Lemon Tree and Kubu have participated in fewer field experiments, and thereby experienced less exposure to manufactured materials and food rewards. Moreover, we found that the groups with the higher habituation indices (Poena, Boata, Noha and Baie Dankie) explored the plastic cars and rubber butterflies more than the two groups with lower habituation index (Kubu, Lemon Tree) (SI: Fig. 3S). Although these groups have more experiences with colourful items and anthropogenic materials, they also explored seashells more than the other groups, an item that was novel but represents a completely natural material (SI: Fig. 3S). These observations suggest that it was not the material per se that captured their interest but rather that habituation brings about a general change in their curiosity towards unfamiliar items, showing strong support for our habituation hypothesis.

Stimuli type and curiosity

The different stimuli types that we presented to the monkeys, did not influence the number of close approaches observed across groups, implying that since all items were new to the monkeys of all groups, each individual needed to approach first in order to judge whether or not to engage in further exploration. The categorization of man-made/ processed versus more naturalistic stimuli did not have any general effect on responses (SI: Fig. 3S and Fig. 2S). Instead, the data suggest that items that emit a characteristic odour (fish, meatballs, cat toy mice, boiled pasta) might be less explored on average than non-smelly items. Furthermore, both captive and wild vervet monkeys seemed reluctant to taste the strong-smelling food items fish and meatballs. Former experiments introducing novel foods have demonstrated that it indeed takes vervet monkeys multiple exposures to novel food before they accept it as a food source (Canteloup et al. 2020; Canteloup et al. 2021) and sociality plays a role in that monkeys are more likely to eat novel food after first observing a conspecific do so (Pooja et al. in prep). Thus, it is likely that monkeys perceive an unknown smell as repulsive and therefore explored such items less. One could argue that popcorn emits similar levels of odour as boiled pasta, yet popcorn was explored much more by the monkeys, especially by the two groups Baie Dankie and Noha (SI: Fig. 3S). These groups regularly participate in field experiments rewarded with soaked corn, and thus it is possible that the monkeys of Baie Dankie and Noha associated the smell of popcorn with soaked corn, and thereby had a more positive association with the smell of popcorn compared to the other odours. Future experiments should investigate further the effect that odour cues have on novelty responses and exploration tendencies.

Habitat structure and novelty responses

Compared to the wild habituated groups, it is worth noting that the experiments with the unhabituated wild group always took place underneath a familiar, frequently used sleeping tree, where the monkeys are presumably relatively safe from aerial predators, and with no high grass to obscure potentially hidden snakes, yet this did not seem to increase their motivation to approach (Fif.1). Furthermore, even though open savannah exposes vervet monkeys to large birds and areas of tall grass can hide predatory snakes (Seyfarth et al. 1980), habitat structure had no influence on the motivation to approach novelty during our experiments (Fig. 3a). Previous findings suggest that vervet monkeys at IVP vocalize to recruit social partners, especially close to the river (Mercier et al. 2017), proposing that monkeys experience the river bank as a high-risk area. Thus, distance to the river could potentially be a more relevant variable to assess the influence of habitat on novelty responses. In our sample, habitat structure had no effect on whether or not a monkey approached alone or in a social context (Fig. 3b). This finding was somewhat unexpected, given that sociality has been reported to reduce the risk involved in approaching something new (Stöwe et al. 2006; Moretti et al. 2015), and watching a conspecific interact with novelty also increases exploration tendencies (Forss et al. 2017). Of course, social influences may also constrain an animal’s motivation to interact with novel stimuli due to monopolization or potential fear of aggression from conspecifics.

Study limitations

Our study was limited by the inclusion of a single unhabituated group (Congo). Clearly, multiple groups of this category would be needed to verify the effect of habituation across wild monkeys. Moreover, the fact that the Lemon Tree group showed as equally low habituation index as the Kubu group despite the fact that monkeys in Lemon Tree have been regularly exposed to researchers for three years more than Kubu raises the question of to what extent within group dynamics potentially influence the monkey's response to novelty. Kubu is a small group with a large proportion of juveniles and in many species, vervet monkeys included, juveniles seem to be more explorative than adults (Fairbanks and McGuire 1993; Bergman and Kitchen 2009; Thornton and Samson 2012; Debeffe et al. 2013). Considering within group dynamics, will also help to evaluate what effects life-history and sociality have on curiosity. Thus, in the future we intend to investigate these data at the individual level to clarify how potential within group variation may also contribute to the observed pattern between groups.

Conclusion

One way to detect curiosity in animals is to introduce something novel into their familiar environment and measure their motivation to overcome potential neophobia and explore it. In doing so, we found evidence that curiosity in vervet monkeys is expressed through a combination of reduced neophobia (willingness to approach into close proximity) together with a variety of explorative behaviours like smelling, touching and tasting something previously unknown (Table 2). Our findings, that captive and wild habituated vervet monkeys responded more positively towards unfamiliar items than unhabituated conspecifics, despite the fact that all wild monkeys are exposed to similar risks in their natural habitat, support our conclusion that the main driver of curiosity in our sample was habituation level to humans and human-made artefacts, rather than risk constraints or time constraints of life in the wild. Consequently, our findings highlight the importance to account for the captivity effect and habituation levels when conducting cognitive research across settings.

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Figures

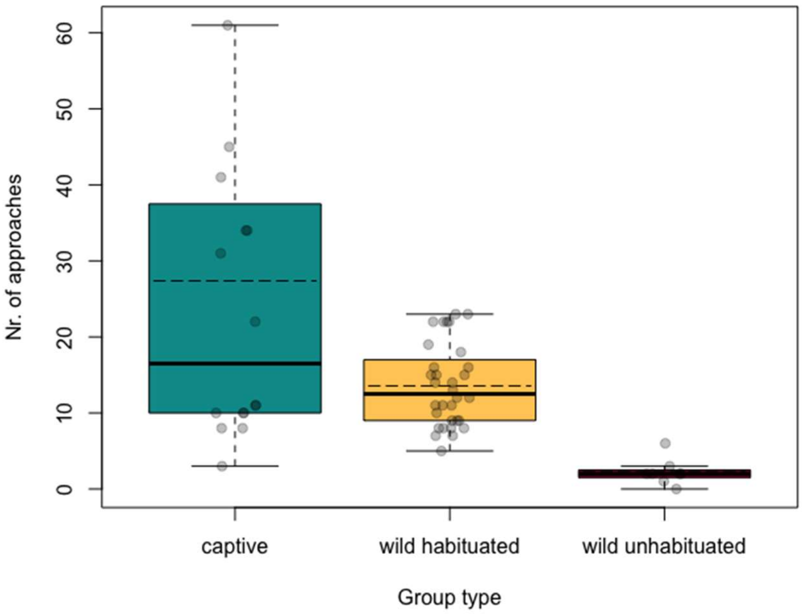

Fig. 1: Boxplots of the number of approaches performed by each group type. Each point corresponds to a trial ($N_{captive}$=16, $N_{wild\ habituated}$=32, $N_{wild\ unhabituated}$=8). Dashed lines correspond to the group means and solid lines correspond to the group medians.

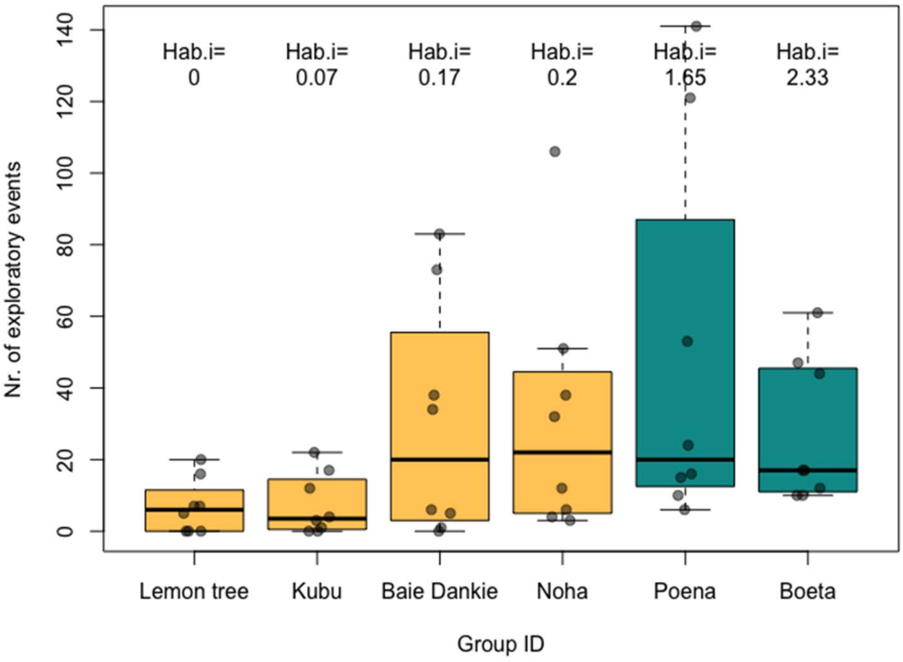

Fig. 2: Boxplots of the number of exploratory events observed in each of the groups. Hab.i represents the habituation index calculated for each group. Green boxes correspond to the captive groups and yellow boxes correspond to wild habituated groups

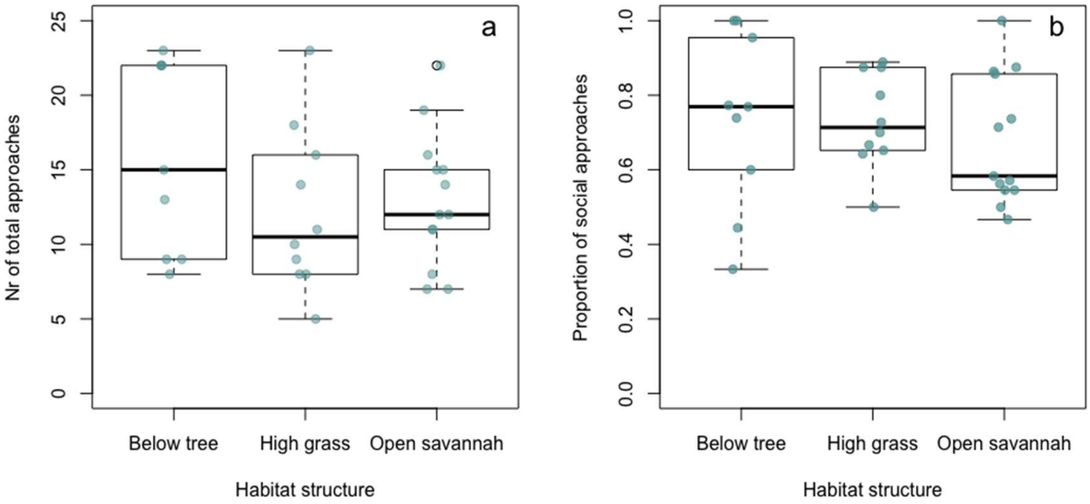

Fig. 3: a) Boxplots of the number of total close approaches observed in the different habitat structures and **b)** the proportion of social approaches out of the total number of approaches (individual and social) observed in each of the experimental locations featuring different habitat structures. Each dot corresponds to a trial.