Role of immigrants and muzzle contacts in the uptake of a novel food by wild vervet monkeys

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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 observed whether dispersing males could introduce this innovation into groups and compare uptake between groups. 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 another group. Uptake of the novel food was fastest in groups where immigrant males ate first and younger individuals were most likely to 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, were targeted towards knowledgeable adults the most, and juveniles and naïve individuals initiated the most. Knowledgeable adult males were targeted but rarely initiated muzzle contacts, whereas knowledgeable adult females were targeted and initiated them, emphasising an adult sex difference in seeking social information. We highlight the potential of immigrants as vectors of information, enabling rapid behavioural adaptation and population level culture.

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 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, behavioural responses are crucial to adapt fast enough when circumstances change rapidly and genetic adaption would not 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. Exploration, on the other hand, involves behaviours that seek information about novel stimuli. Whilst seeming to be opposites of one spectrum, neophobia and exploration are likely motivated by different needs and served by different mechanisms, and it is possible to express high or low levels of both, simultaneously [6]. 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 [8] 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 long-lived species to adapt their behaviour quickly to changing circumstances, for example to exploit a novel resource introduced into the current habitat (e.g. [9]). Nonetheless, if explorative conspecifics or individuals that uniquely possess particular knowledge are present, one might rather learn from them via social learning. Indeed, many studies of diverse species in captivity have found that observing a conspecific eat a novel food reduces neophobic responses (reviewed in [6]: e.g. marmosets [10], rooks [11], aye-ayes [12], as well as humans [13]). In the wild, a study on jackdaws found the same [14], and similarly, wild baboons handled a novel food for longer after seeing a demonstrator do so, though this was dependent on their personality [15]. 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. Moreover, the individual differences of the observed conspecifics may be important. In addition, in wild groups, dispersing individuals can import information or behavioural innovations, upon immigration, into new groups [16–19], thus facilitating the spread of information at the population level, but experimental evidence focused on multiple groups is lacking.

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. [15,18,20–23], and see review in [24]). However, for Old World monkeys, detailed olfactory information, in a foraging context, may be acquired through muzzle contact behaviour – the act of one individual bringing their muzzle into very close proximity with another’s [25–28]. Indeed, previous studies found that, whilst foraging, muzzle contacts were most commonly initiated by infants and juveniles towards adults [28,29], which supports the 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. [28] also suggest that muzzle contacts are constrained by social tolerance, due to the necessary close proximity, which may constrain information transmission. 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 [30]. 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 in their lives, producing considerable adult individual heterogeneity in groups. Furthermore, frequently dispersing males could serve as vectors of information between groups, potentially facilitating behavioural adaptation to their large geographical range [30]. In a previous study by our team [20], two groups (NH, KB) of wild vervet monkeys were provided with a novel food that required extraction (peanuts in shells) before consumption. The results supported social transmission of the opening techniques used to extract peanuts, based on visual attention to demonstrators [20]. In the present study, we presented this novel food to three more groups (AK, BD, LT) of the same study population, to study five groups in total. Our first line of investigation here concerned 1) innovation of extracting and eating the novel food. Second, utilizing natural dispersals of males between our study groups, we investigated 2a) variation between groups in their uptake of the novel food according to who innovated, or initiated eating, and 2b) demographic (age, sex, rank) variation in in uptake of the novel food. Third, we analysed 3a) the rate of muzzle contacts as groups' had more exposure and therefore increased familiarity with the food; and 3b) whether knowledge of the food, age, sex and / or rank influenced muzzle contact behaviour.

As questions 1) and 2a) were largely exploratory, we did not make specific predictions. Regarding question 2b) we expected uptake to be more likely in younger monkeys, 2b) during the first exposure, and over four exposures, due to previous work suggesting that juveniles take more risks [31] and are less neophobic [32–35] than adults. Regarding question 3a) we expected muzzle frequency to decrease as groups had more exposures to the novel food due to its likely function in obtaining information acquisition. In 3b) we expected an effect of knowledge, specifically for naïve monkeys to initiate more, and knowledgeable monkeys to be targeted more. Similarly, we expected an effect of age, with juveniles more likely initiators and adults more likely targets.

These combined approaches broaden our understanding of routes to behavioural adaptation to exploit a novel resource in the wild, and the potential contribution to this of dispersal.

RESULTS

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 Table S1 and detailed description in Materials and Methods).

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

1) Innovation

When presented with a novel food, in groups that had new immigrant males (AK_{20}, BD, LT, NH), new immigrants were the first to extract and eat peanuts: at the first exposure in BD, LT and NH, and at the second exposure in AK_{20}. Two of these males were previously

naïve to peanuts and individually innovated the solution (*Avo* in NH, *Bab* in LT); and two imported the innovation from NH into their new groups (*Pro* in BD and *Yan* in AK_{20}; see Fig. 1). In all four cases, the males had been present in the group for less than three months prior. In KB an infant (*Aar*) innovated at the third exposure (see Table S1), and in AK_{19} no one innovated during their single exposure. There were no new immigrant males within the last three months in AK_{19} at the time of their exposure to peanuts, nor in KB at any of their exposures.

2a) Variation in the uptake of novel food according to who ate first

During the first exposure to peanuts in BD, LT and NH, when new immigrant males initiated eating peanuts, we observed that the following percentages of these groups learned to extract and eat peanuts during that exposure: BD: 31%; LT: 20%; NH: 9% (Fig. 2a). In the first exposures in AK_{19} and KB, no monkeys learned to extract and eat peanuts. After an immigrant male ate in AK_{20}, at the second exposure in that group (but the first exposure with a new immigrant male, who was knowledgeable about peanuts) 30% 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). 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).

2b) Demographic variation in the uptake of the novel food

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 more likely to extract and eat peanuts than both adults (GLMM, Tukey HSD: Estimate = 1.38, Standard error = 0.51, z = 2.70, p = 0.012) and infants (Est. = 2.12, SE = 0.74, z = 2.85, p = 0.011), but no difference between infants and adults (Est. = -0.74, SE = 0.70, z = -1.05, p = 0.538). Rank showed a non-significant trend (Est. = -1.48, SE = 0.81, z = -1.83, p = 0.067) with high rankers more

likely than low rankers to extract and eat peanuts. There was no main effect of sex (Est. = 0.63, SE = 0.42, z = 1.50, p = 0.134). Over four exposures, we found a significant main effect of age, with juveniles more likely to extract and eat peanuts than adults (Est. = 1.62, SE = 0.54, z = 3.00, p = 0.008) and infants (Est. = 1.92, SE = 0.64, z = 3.02, p = 0.007), but no difference between infants and adults (Est. = -0.30, SE = 0.54, z = -0.55, p = 0.845). We also found a significant main effect of rank, with high rank individuals more likely than low rank individuals to eat (GLMM: Est. = -2.66, SE = 0.80, z = -3.70, p < 0.001). We found no main effect of sex (Est. = 0.27, SE = 0.41, z = 0.66, p = 0.510).

3a) Muzzle contact frequency in groups

Here, in the groups where large proportions of monkeys had started to eat peanuts over four exposures (AK_{20}, BD and LT), we recorded 569 muzzle contacts in total. We found that exposure number (1-4) had a significant effect on the rate of muzzle contact, with the rate decreasing as groups had more exposures to peanuts (LME: Est. = -0.71, SE = 0.27, t = -2.63, p = 0.030).

3b) Individual variation in muzzle contact behaviour

In the final analysis, with the simple model (see Materials and Methods) we found significant main effects of both knowledge (Est. = 1.63, SE = 0.24, z = 6.67, p < 0.001) and age (Est. -3.51, SE = 0.68, z = -5.18, p < 0.001) on individuals' status as initiators or targets of muzzle contacts. Knowledgeable individuals and adults were more likely to be targets rather than initiators of muzzle contact, compared to naïve individuals and juveniles/infants respectively. We did not find significant main effects of sex or rank (sex: Est = 0.72, SE = 0.65, z = 1.12, p = 0.26; rank: Est. = 0.025, SE = 0.021, z = 1.19, p = 0.236).

When removing rank but adding interactions between knowledge and age and knowledge and sex to the model, we found significant interactions between both, knowledge and age (Est. = -1.79, SE = 0.52, z = -3.48, p < 0.001; Fig. 3A, left), and knowledge and sex (Est. = 1.60, SE = 0.54, z = 2.93, p = 0.003; Fig. 3A, right). In Figure 3A (left) we can see

clearly the effect of knowledge on adults, but not on juveniles. In Figure 3A (right) we see that the effect of knowledge on males and females is generally similar, but slightly stronger in males.

In the three-way interaction model, the interaction between knowledge, age and sex was not significant (Est. = -2.11, SE = 1.31, z = -1.62, p = 0.106; Fig. 3B).

DISCUSSION

By looking at the uptake of a novel food by members of five groups of wild vervet monkeys, we found evidence for new immigrant males as fast innovators, and as vectors of information between groups. We saw faster uptake of the novel food by groups when new immigrant males, rather than infants or juveniles, ate first. We also found effects of age and rank on uptake of the food. In addition, as groups had more exposures to the food, muzzle contact behaviour decreased. Between dyads involved in muzzle contacts, both knowledge and age, and interactions between knowledge and age, and knowledge and sex influenced whether individuals were initiators or targets. Below we discuss the contributions of these results to our perspectives on the potential value of dispersing individuals in transmission of behavioural adaptations to novel circumstances around populations.

1) Innovation

Fast innovation to exploit a novel resource by new immigrants, in this case at the first exposure to a novel food, could be linked to a dispersal state by physiological conditions related to dispersal. Whilst the sample size of our study is low, the fact that no monkeys innovated during the first exposures to peanuts in groups with no new immigrants supports this too. Dispersal has indeed previously been associated with exploration and boldness (i.e. low neophobia) in several taxa, with associated neurochemical variation, both within (ontogenetically) and between individuals [36]. Moreover, evidence links lower serotonergic activity with: earlier dispersal in rhesus macaques [37], greater social impulsivity in vervet

monkeys [38], and reduced harm avoidance in humans [39]; 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 [40], 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 [41]. We suggest rather that the unique individual, social and environmental factors that prompt a male to disperse [42] may trigger a transitory exploratory behavioural syndrome [43] 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 [40] also supports this. Future work focused 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.

2a) Individual variation in uptake of a novel food according to who ate first

When immigrant males extracted and ate a food that was novel to their new groups, i.e. during the first exposure to it (in BD, LT and NH), 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 the other (BD), the male had learned to extract and eat the food in his previous group. Similarly, in AK, uptake of the novel food began precisely when a new immigrant imported the innovation during the group's second exposure. In contrast, following innovation by an infant in KB at their third exposure, no other individuals followed in extracting and eating peanuts during this 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 learned 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. One 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 [18,20]. 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 [20]). 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 all 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 [20,44]. It is nonetheless likely that various interactions of socioecological factors affect the influence of juveniles in overcoming food neophobia in the wild.

Moreover, whilst previous experiments suggested that high-ranked adult philopatric females are preferred over high-ranked adult males as models to learn from [22], 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 while being 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, or more exploratory juveniles of high rank, may play important roles in generating and facilitating the spread of behavioural adaptations to exploit novel resources and face rapid environmental changes.

2b) Demographic variation in the uptake of the novel food

In the first exposure juveniles were most likely to eat, and over four exposures, both infants and juveniles were more likely to eat than adults were. These results suggest that younger animals overcome neophobia faster than adults, corresponding closely with results regarding risk-taking in another population of vervet monkeys [31], and work in other species suggesting that juveniles are overall more exploratory and less neophobic [32–35].

High rank individuals were more likely to eat over the whole experiment, probably due to preferential access to the resource as it became more familiar.

3a) Muzzle contact frequency in groups

At the group level, frequency of muzzle contact decreased as groups had more exposures to the novel food. This demonstrates the relevance of the behaviour in the context of unknown or rarely encountered foraging items, because as the food became more familiar to the monkeys, they sought olfactory information from their conspecifics less frequently. This result concurs with findings from a similar study in wild olive baboons [25].

3b) Individual variation in muzzle contact behaviour

In individual monkeys, knowledge of the novel food predicted whether they were more likely to be initiators or targets of muzzle contacts. Knowledgeable individuals were more likely to be targets and naïve individuals were more likely to be initiators. This shows strong support that, in the presence of a novel resource, individuals use this behaviour to seek specific information from others who demonstrate having that information. We do not make claims related to knowing what others know, but rather assume that seeing a group member

eating an unknown resource prompts the initiation of muzzle contact towards that individual. This result further corroborates the finding in 3a) of decreasing muzzle contact frequency with increased exposure to the resource, and the overall function of muzzle contact in soliciting foraging information.

Age was also a significant predictor, with adults more likely to be targets, and juveniles more likely to be initiators. This concurs with previous findings of younger vervet monkeys targeting adults with muzzle contacts during natural foraging [28,29], as well as our team's previous study where adults were preferentially observed eating this novel food [20]. This suggests adults are generally preferred sources of information and juveniles are not. Moreover, age also interacted with knowledge, whereby becoming knowledgeable increased adults' likelihood of becoming targets rather than initiators much more than it did for juveniles, and naïve adults were still more likely to be targets than knowledgeable juveniles (Fig. 3A, left). This suggests that juveniles are *not* preferred sources of information, even when knowledgeable regarding a new resource, which may impede information flow. Nonetheless, as discussed in section 2b), this impediment may be overcome by older or higher-ranked juveniles. Indeed, we can expect high-ranked juveniles to gain access to preferred resources over lower-ranked adults as well as lower-ranked juveniles. Nevertheless, any age-related impediment to information flow is likely an adaptive mechanism as juveniles' greater curiosity combined with lack of experience is risky; but their reliance on adults to gain information presents as an adaptive mitigation to this risk.

Intriguingly, whilst we found no significant main effect of sex, sex did interact with knowledge. Inspection of the plot in Fig. 3A (right) shows that whilst gaining knowledge affected both males and females similarly, this effect appears to be slightly stronger in males. Bearing in mind that juveniles (both males and females) are very unlikely to be targets, as shown by both, the main effect of age, and the interaction of knowledge and age (Fig. 3A, left), we can assume that this stronger effect in males is driven by adult males. Indeed, by plotting the three-way interaction between knowledge, age and sex (Fig. 3B),

whilst non-significant, we can see the effect of knowledge is strongest for adult males, but it is slightly stronger for juvenile males than females too. This likely drives the interaction between knowledge and sex in the two-way interaction model (Fig. 3B) too. Nonetheless, the biggest difference remains between adults and juveniles, and is similar for both sexes.

What remains, however, is that knowledge made adult males almost exclusively targets and not initiators (Fig. 3B). Adult females, on the other hand, did still initiate muzzle contacts, as seen by their more intermediate probability of being targets or initiators. Given that our results show strong support for the function of muzzle contact in acquiring information about novel resources, this adult sex difference is particularly interesting. That adult females still initiate muzzle contacts, even when knowledgeable, suggests that they still seek social information even when they have first-hand experience. This is in line with the assertion that they 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. This implies that they very quickly rely on their own information, which arguably reflects boldness or low neophobia. This may be related to their status as dispersers, given that during dispersal they must fend for themselves and have no group-mates to rely on. Alongside results from our previous study [20], where males were more likely to be observed extracting and eating peanuts, this shows support for the potential role of dispersing male vervet monkeys in generating and transmitting novel information within groups, and transferring it between groups.

Ideas and Speculation

Taking all of the evidence together, from this and other studies, we propose a prominent role of dispersing male vervet monkeys in generating and transmitting novel behavioural adaptations between groups. Dispersing adult males are more likely to generate novel information than adult females, given the associated risks of doing so, and they are more likely to be learned from quickly than explorative juveniles. Moreover, they are the only ones that can transmit information between groups, which can allow population level adaptation. This could help facilitate the species' widespread distribution and fast adaptation to human-modified environments, similar to the breadth of that of many macaque and baboon species (e.g. [45,46]), also living in multi-male multi-female groups. Spotted hyenas (*Crocuta crocuta*) also live in large multi-male multi-female groups, unique among large carnivores to maintain a similarly large distribution, further motivating greater attention to this proposed hypothesis of the impact of regular immigration to fast adaptation for socially learning species in a changing world.

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 [47]. We urge future research to investigate whether physiological mechanisms exist that might underpin a transitory dispersal syndrome characterised by heightened exploration and reduced neophobia that is triggered during, or triggers, dispersal. Moreover, we suggest further research, in diverse species, into whether dispersers transmit valuable information between groups, as this can have major implications for population fitness, especially in the context of the rapid anthropogenic change that most animal populations now face. This can have further implications for short- and long-term conservation efforts, informing wildlife management tasked with, for example,

the maintenance of wildlife corridors beyond the borders of groups to allow intergroup transfer, or establishing most appropriate group composition for long term adaptation and survival of groups to be reintroduced to the wild.

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 [21].

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 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 Table S1).

Ethics guidelines: Our study 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.

Hierarchy establishment

Agonistic interactions (aggressor behaviour: stare, chase, attack, hit, bite, take place; victim behaviour: retreat, flee, leave, avoid, jump aside) were collected *ad libitum* [48] on all adults and juveniles of each group. These data were collected throughout one year

preceding the experiment 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 [43] 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 hierarchical ranks were determined by the outcome of dyadic agonistic interactions using Socprog software version 2.7 [44]. Linearity of hierarchies are reported in supplementary material (SM2). Ranks were assessed by I&SI method [45].

Peanut exposures

We provided each group with a highly nutritious novel food that required extraction before consumption – unshelled peanuts – 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 motivation to engage in food-rewarded experiments.

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}; Table S1). Figure 1 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 for another study [19], and *Yan* had observed many others eating peanuts. *Yan* was the first to eat in AK in 2020 (Fig. 1).

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. One box of peanuts was offered per exposure in AK_{20}, BD and LT, which lasted up to one hour, after which the monkeys usually left the vicinity. In AK_{19}, the exposure of one box of peanuts lasted approximately five minutes, after which the monkeys left the vicinity. 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 (Table S1). Here we present results for each group from the first four exposures *from the first eating event* in each 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 $AK_{19\text{-}20}$, 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.

To analyse muzzle contacts in groups where many individuals started eating the novel food quickly, GL counted frequencies of muzzle contacts in videos of AK_{20}, BD and LT. PD and MC identified individuals involved in all muzzle contacts in AK_{20}, BD and LT.

Data analysis

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 who extracted and ate peanuts (question 2b) i) at the first exposure (AK_{19}, BD, KB, LT & NH) and ii) over the four exposures ($AK_{19\text{-}20}$, BD, KB, LT & NH). In each model, we considered age, sex and rank (normalised rank) as fixed effects and group was included as random effect.

Muzzle contact frequency over repeated exposure to novel food

We investigated muzzle contact behaviour in groups where large proportions of the groups started to extract and eat peanuts over the first four exposures (AK_{20}, BD, LT). We ran a linear regression model to investigate the effect of exposure to the novel food on muzzle contact rate (question 3a). The normality of the residuals was verified on the basis of the QQ plot shape to use a linear model. Muzzle contact rate was calculated as the total number of muzzle contacts observed within 2 m of the food, during each exposure, divided by the total duration (in minutes) of each exposure. Muzzle contact rate was the outcome variable, with exposure number (1-4) as the predictor. For BD and LT we excluded exposures 4 and 3, respectively, due to circumstances resulting in very small proportions of these groups present at these exposures. We ran the same model including these outlier exposures and present these results in the supplementary material (SM3).

Factors influencing whether individuals are initiators and targets of muzzle contact

Finally, we ran three binomial GLMMs to investigate question 3b) factors affecting whether individuals involved in muzzle contacts were initiators or targets. Due to very low

numbers of infants ever being targets of muzzle contacts, we merged the infant and juvenile age categories for this analysis. Our first simple model included individuals' knowledge of the novel food at the time of each muzzle contact (knowledgeable = previously succeeded to extract and eat peanuts; naïve = never previously succeeded to extract and eat peanuts) and age, sex and rank as fixed effects. Individual was included as a random effect. The second model was the same, but we removed rank and added interactions between: knowledge and age; and knowledge and sex. The third model was the same as the second, but we also added a three-way interaction between knowledge, age and sex. We interpreted interactions by visual inspection of plots made using R package 'interactions' [49].

Statistics were computed in R Studio (R version 4.0.3), and linear regression was done with the base R stats package [50]. GLMMs were done using the 'lme4' package [51].

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

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Tables and figures

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.

Group	Group size	Exposure number						**Total**
		1	2	3	4	5	6	
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

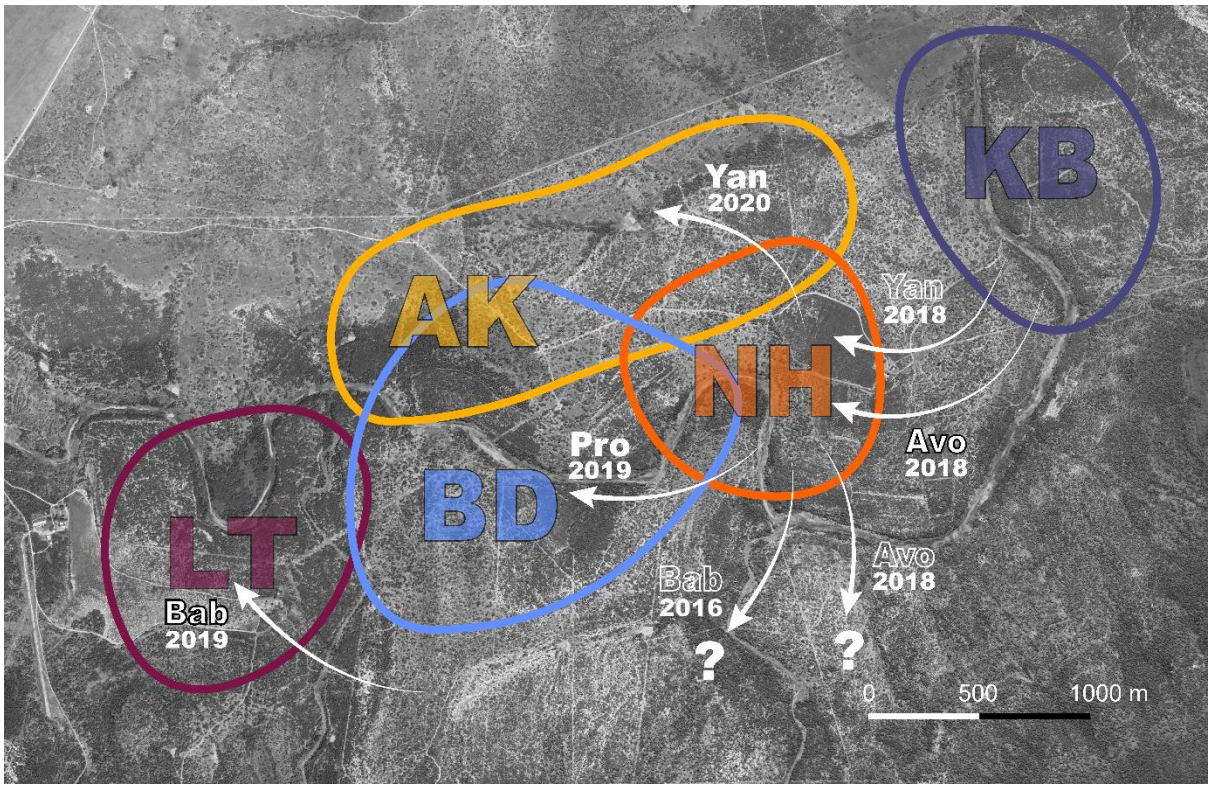

Figure 1. Aerial view of study area with coloured shapes showing a rough estimate of group home-ranges for study groups AK, BD, KB, LT and NH. White arrows with annotations represent relevant dispersals. Names of males and year of dispersal are shown. Black outlined text indicates the immigrant innovators 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.

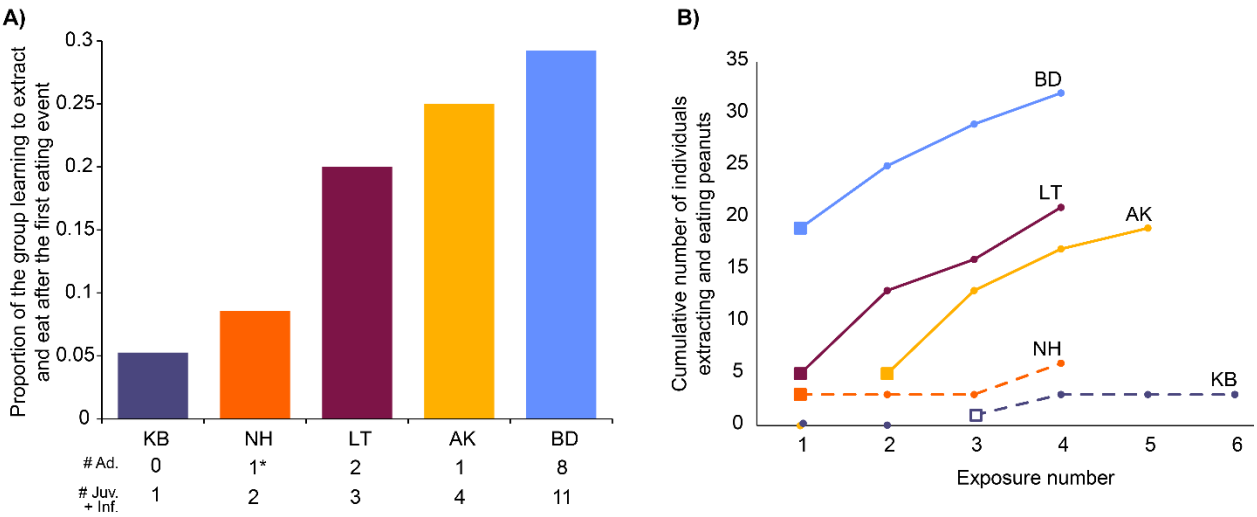

Figure 2. Uptake of extracting and eating peanuts in each group. A) Shows the proportion of each group that started eating when the first eating event took place. Total numbers of individuals, split by age, are shown below the x-axis. In NH the asterisk highlights the one adult which was the innovator 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).

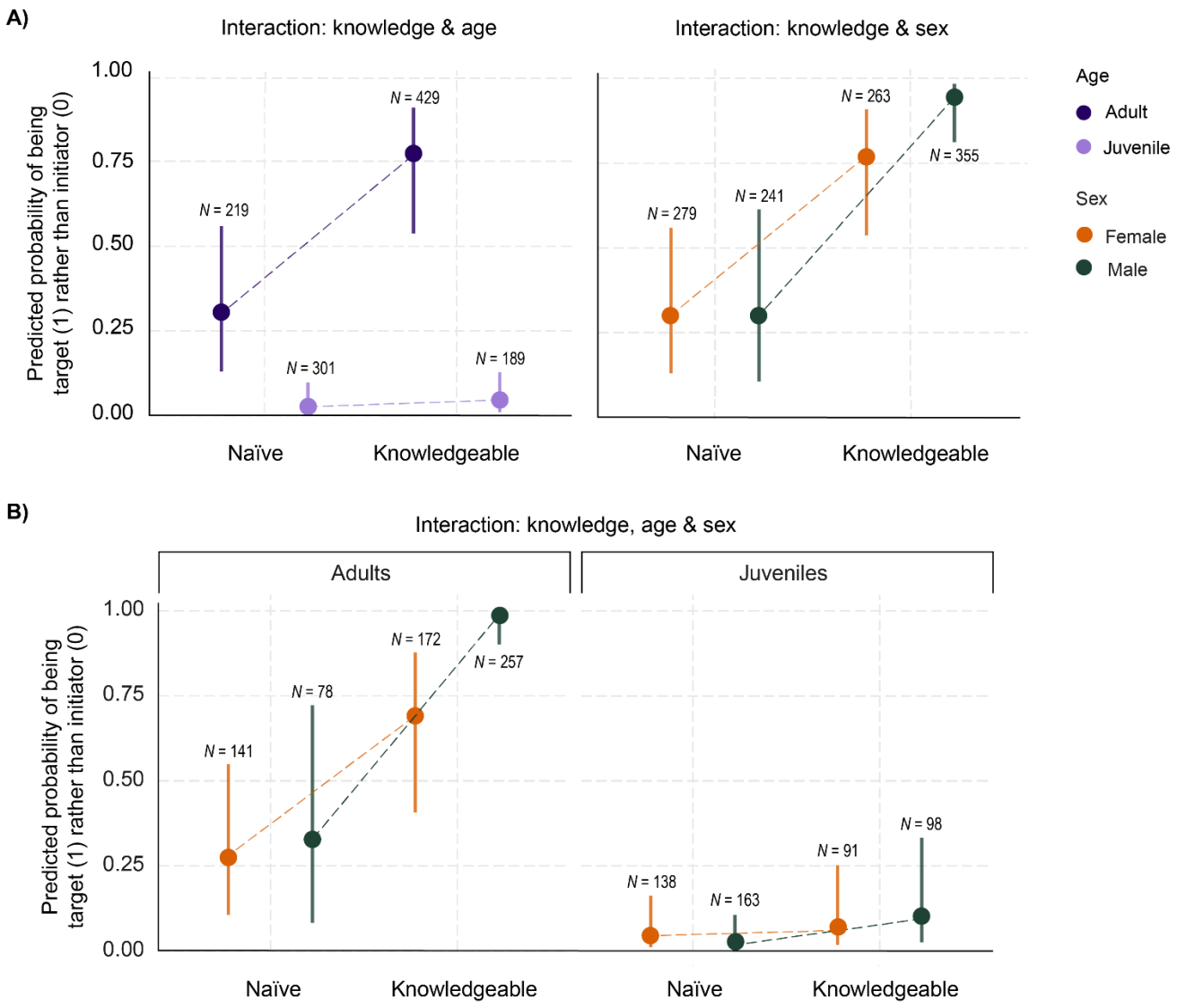

Figure 3. Plots illustrating significant interactions between the effects of A) left: knowledge and age, and right: knowledge and sex on the likelihood of individuals being initiators rather than targets of muzzle contact; and B) shows the (non-significant) three-way interaction between knowledge, age and sex. Solid circles show predicted probabilities, and extending bars show 95% confidence intervals (visualised using ‘cat_plot’ function from R package

‘interactions’ [49]). *N* is the number of muzzle contact interactions engaged in by each age/sex category).