Role of immigrant males 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 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 Table S1 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).

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 (Table S1).

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% (n = 65); LT: 20% (n = 25); NH: 9% (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% (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).

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 3.98 times (398%) more likely to extract and eat peanuts than adults, and 8.35 times (835%) more likely than infants, but there was no significant difference between infants and adults (Model 1, Table 3). Rank showed a non-significant trend, with lower ranked individuals 77% less likely, per unit of standardised rank, as higher ranked individuals to extract and eat peanuts. There was no significant effect of sex (Model 1, Table 3).

Over four exposures, we found a significant main effect of age, with juveniles 5.03 times (503%) more likely to extract and eat peanuts than adults, and 6.80 times (680%) 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, as high 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 611 muzzle contact interactions between 87 different individuals in all five 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: Est. = -0.05, df = 0.02, standard error (SE) = 15.91, t = -2.72, $p = 0.015$) and a significant main effect of the number of monkeys eating peanuts on the rate of muzzle contacts per minute (Est. = 0.19, df = 0.05, SE = 14.96, t = 3.78, $p = 0.002$), but no significant effect of exposure

number (Est. = -0.12, df = 0.19, SE = 14.73, t = -0.62, *p = 0.543*). The significant interaction shows that effect of exposure number depends on the number of monkeys eating (Figure 3). In Fig. 3A we can see that, for all the groups, when very few monkeys ate peanuts during that exposure, muzzle contact rate was very low, unless it was the first exposure. Contrastingly, when many monkeys ate peanuts, particularly in groups AK, BD and LT, there is a clear decrease in muzzle contact rate as the monkeys had more exposures to the peanuts. The interaction is also demonstrated in Fig. 3B, which shows predictions from the model of a strong decrease in muzzle contact rate across subsequent exposures when many monkeys are eating, but this is much weaker when few monkeys eat.

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 in the final model because the model was too complex to converge properly (SM3: Table S2). 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.

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), we observed that immigrant males 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* (Table S1), 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 and we believe these specific characteristics would counteract any effects of recent dispersal on innovation tendencies. Moreover, 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 take risks around novelty. 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, high rank individuals were significantly more likely to eat than lower rank individuals (with a non-significant trend in the same direction in the first exposure), probably due to preferential access to the resource as it became more familiar.

2a) Muzzle contact frequency in groups

When many monkeys were eating, the rate of muzzle contacts decreased over repeated exposure to the novel food. This 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).

There was also a significant main effect of the number of monkeys eating on the rate of muzzle contact. This is likely due to there being more opportunity to interact when more individuals are present. An alternative hypothesis could simply be that muzzle contacts are provoked by seeing conspecifics consume any provisioned food. 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 interaction with 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.

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 Table S1).

Ethical statement: 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.

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 supplementary material (SM2). 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}; Table S1). 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 (Table S1). 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.

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. 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) i) at the first exposure (AK_{19}, BD, KB, LT & NH; Model 1) and ii) over the four exposures ($AK_{19\text{-}20}$, 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 the group where they first ate, so all individuals were only considered once in those models.

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

We calculated muzzle contact rate as the no. of muzzle contact interactions occurring within 2 m of the food during each exposure, divided by the duration (in minutes) of that exposure. As we were interested in the effect of exposure to the novel food on muzzle contact rate, we used four exposures from the first eating event for each group, as this event marks when the novel food has been recognised as a viable food by at least one member of the group. 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 linear mixed effects model with muzzle contact rate (per minute) as the outcome variable, exposure number and number of monkeys eating as fixed effects, with an interaction between the two, and group as a random effect (Model 3). As this is a linear model with Gaussian distribution, effect sizes are reported as the regression coefficients.

Visual inspection of a Q-Q plot was used to verify the normality of residuals, and no over- or under-dispersion was detected.

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 here for two reasons. First, we did not have any theoretical basis to expect residing in different groups to have an effect here, since we were concerned with the effects of life history strategies of individuals on their information acquisition behaviour, which should not differ for individuals from different groups. Second, we had problems with model convergence when including it,

so given the reason above and following advice of statisticians, we did not include it in the final model. In the final model (Model 6) we removed the three-way interaction, as it was not significant (Supplementary material 3, Table S2), 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.

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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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.

		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

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

Model no.	Outcome	Predictors [1]	Effect size [2]	SE	z- value	*p*-value [3]
1	Eat in first exposure: yes/ no (binomial)	Age: Infant – Adult*	0.48	0.70	-1.05	0.538
		Juvenile – Adult*	3.98	0.51	2.70	***0.018***
		Juvenile – Infant*	8.35	0.74	2.90	***0.011***
		Sex (M)	1.89	0.42	1.50	0.134
		Standardised rank	0.23	0.81	-1.83	***0.067***
2	Eat in four exposures: yes / no (binomial)	Age: Infant – Adult*	0.74	0.54	-0.55	0.845
		Juvenile – Adult*	5.03	0.54	3.00	***0.008***
		Juvenile – Infant*	6.80	0.66	3.02	***0.008***
		Sex (M)	1.31	0.41	0.66	0.510
		Standardised rank	0.07	0.80	-3.31	***<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] Effect size is calculated as the odds ratio. [3] Bold italics show significant and marginally significant p-values at 0.05 level. *Indicates post-hoc multiple comparisons (with Tukey correction).

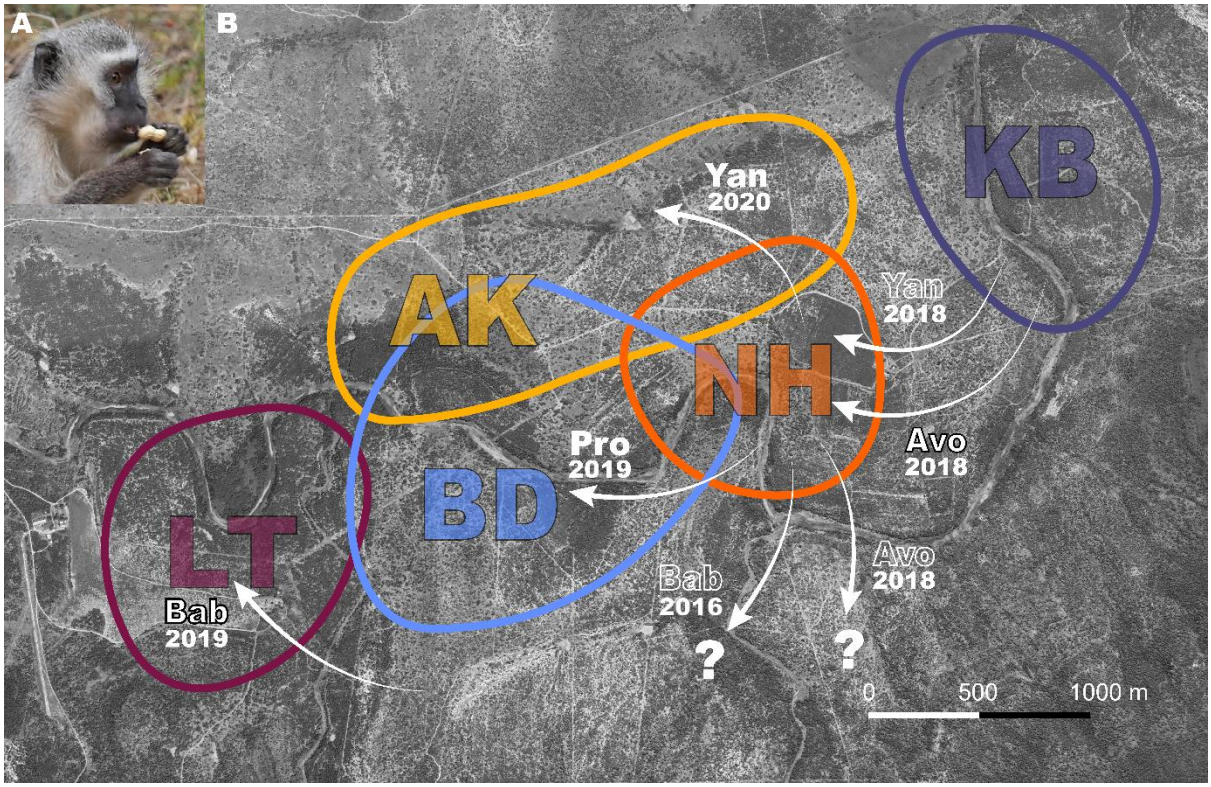

Figure 1. A) A vervet monkey holding unshelled peanut, about to open it. B) Aerial view of study area with coloured shapes showing a rough estimate of group home-ranges for study groups AK, BD, KB, LT and NH. White arrows with annotations represent relevant dispersals. Names of males and year of dispersal 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.

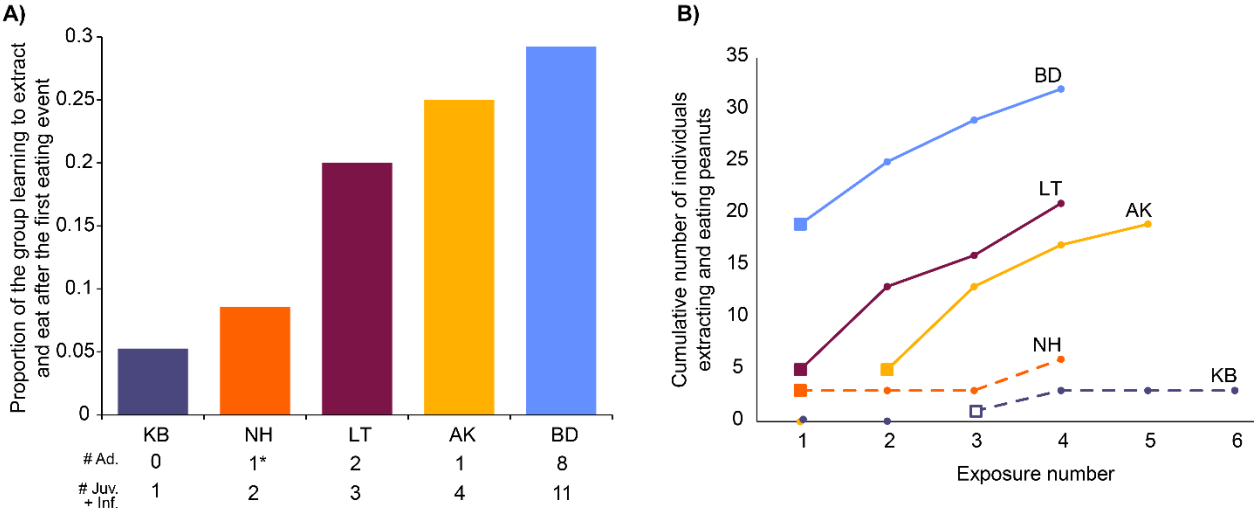

Figure 2. Uptake of extracting and eating peanuts in each group. A) Shows the proportion of each group that started eating when the first eating event took place. Total numbers of individuals, split by age, are shown below the x-axis. In NH the asterisk highlights the one adult which was the innovator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

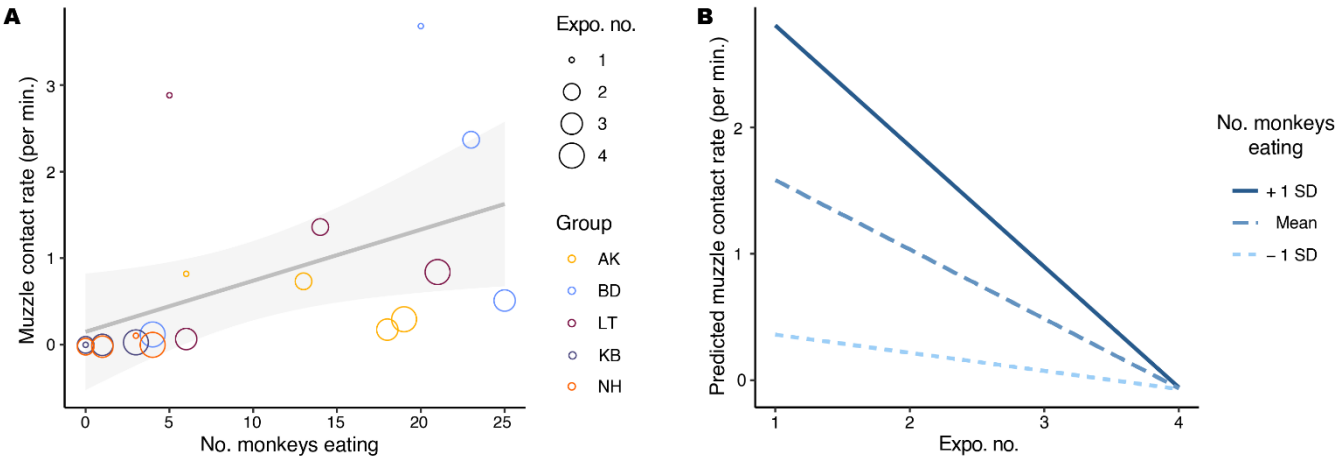

Figure 3. A. Variation in muzzle contact rate according to the number of monkeys eating and exposure number. The influence of exposure number is particularly clear in the points for AK, BD and LT where many monkeys started eating. Shading shows 95% CI. B. Model predictions based on the significant interaction between exposure number and number of monkeys eating. The effect of exposure number is large when many monkeys are eating, and this effect diminishes when fewer monkeys are eating.

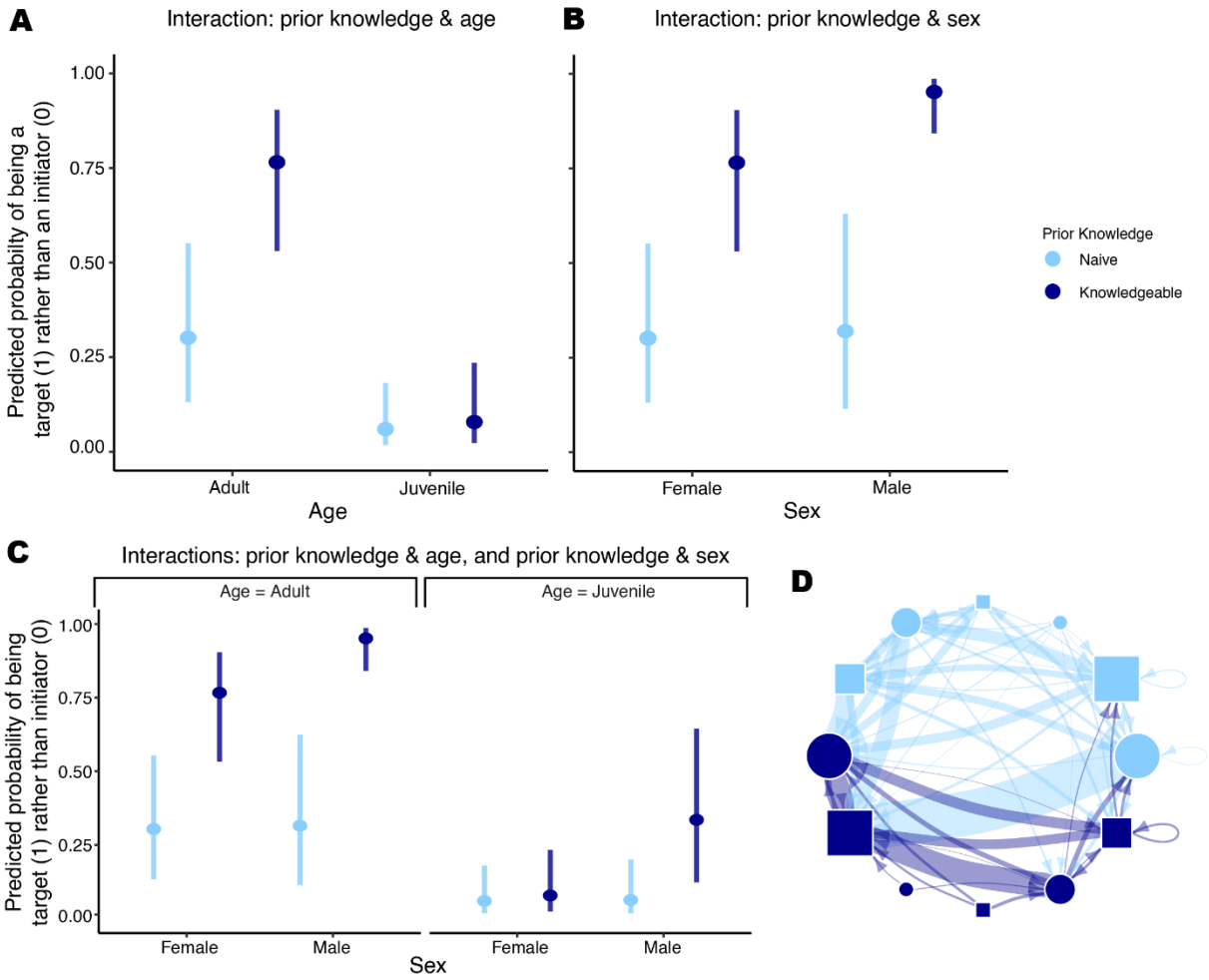

Figure 4. Plots illustrating significant interactions between the effects of A) knowledge and age, and B) knowledge and sex on the likelihood of individuals being initiators rather than targets of muzzle contact; and C) illustrates both interactions from the same model, but separated by age and sex. 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).