Processing of novel food reveal payoff and rank-biased social learning in a wild primate

C. Canteloup[1,2*], M.B. Cera[1], B.J. Barrett[3,4,5]† & E. van de Waal[1,2]†

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

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

[3] Max Planck Institute for Animal Behavior, Department for the Ecology of Animal Societies, Konstanz, Germany

[4] University of Konstanz, Department of Biology, Konstanz, Germany

[5] Max Planck Institute of Evolutionary Anthropology, Department of Human Behavior, Ecology, and Culture, Leipzig, Germany

† These authors contributed equally to this work

[*]corresponding author: Charlotte Canteloup (charlotte.canteloup@gmail.com)

Abstract

Cultural complexity is strongly shaped by the efficiency by which new knowledge is propagated. Different social learning strategies (SLS), where individuals biasedly learn particular behaviors or from specific demonstrators, can contribute to an individual's success. While SLS have been mostly studied in isolation, their interaction and the interplay between individual and social learning is less understood. We performed a field-based open diffusion experiment in a wild primate. We provided two groups of vervet monkeys with a novel food, unshelled peanuts, and documented how three different peanut opening techniques spread within the groups. We analyzed data using hierarchical Bayesian dynamic learning models that explore the integration of multiple SLS with individual learning. We show that vervets

preferentially use the technique yielding the highest observed payoff, and also bias attention toward individuals of higher rank. This shows that traditions may arise when individuals integrate information about the efficiency of a behavior alongside cues related to the rank of a demonstrator.

Introduction

Organisms may learn about their environment and acquire new skills individually, by trial and error, or socially, by directly observing and copying others' behavior (1). Social learning has been considered adaptive since organisms may gain fitness benefits when learning from others, especially in a changing environment (2). Socially transmitted behaviors resulting in animal cultural traditions have been described in diverse taxa and domains such as songbird vocal dialects (3), tool use in crows (4), hunting techniques in whales (5), social conventions, extractive foraging techniques and manipulation behaviors in numerous primates (6-8).

Social learning biases direct an individual's attention towards a behavior based on its content, relative frequency in a population, or its association with a particular type of demonstrator. These biases are typically, but not always, assumed to be shortcuts to acquiring adaptive behavior and are theoretically well explored (10-12). Content-biases focus on characteristics of the observed behavior such as a bias towards better payoff. Much theoretical work has explored the evolution of payoff-biased learning (13, 14), which is useful when payoffs are stochastic or adaptive behavior is rare. Empirical work in humans show payoff-bias for its concurrent use with other social learning strategies (15). In some cases, payoff-biased learning might be under-utilized by humans (16). Researchers have recently expanded their investigation of payoff-biased learning to wild animals. Wild capuchins adopted the most

51 successful and efficient technique when processing novel fruits (17). Great tits do not use
52 payoff-biased learning but acquire a high payoff foraging technique through a combination of
53 positive frequency-dependent learning and individual learning that is highly sensitive to
54 personal experiences in payoffs (18). Male vervet monkeys, but not females, used the technique
55 displayed by male demonstrators more when a difference in payoff was introduced with males
56 receiving more food than females (19). The prevalence of payoff-biased learning is likely
57 underestimated in wild populations particularly if adaptive behavior is common, easy to
58 innovate, or if there is a single optimal solution (17).

59 Context biases focus on other cues, such as their frequency in a population (e.g.
60 preferentially use the most common behavior or the one exhibited by the majority of
61 individuals: conformity bias) or particular traits of models (e.g. preferentially use the behavior
62 displayed by familiar, prestigious, related, or similarly aged individuals: (20)). Such biases have
63 been reported in various animal species. "Moss sponging" by chimpanzees (21) and "sponging"
64 by dolphins (22) were both transmitted within matrilines; "Shelling", another foraging
65 technique, spread non-vertically among associated dolphins (23). Younger female guppies
66 chose the mate choice of older females (24). Capuchins and chimpanzees used the foraging
67 method displayed by older individuals (17, 25). In female-philopatric vervet monkeys, females
68 were preferentially chosen over males as demonstrators (26), but demonstrators were all of
69 high-rank. The techniques used by higher-ranked individuals were preferentially chosen by
70 chimpanzees (27) and vervet monkeys (28) when researchers simultaneously tested for several
71 biases. Animals also conform to the most frequently observed behavior: in vervet monkeys,
72 dispersing males conformed to the local foraging norm, abandoning their native preference
73 (29); great tits and chimpanzees disproportionately adopted the most frequent local foraging
74 technique (30, 31 but see 32); nine-spined sticklebacks preferentially chose the feeder favored
75 by the majority of individuals, even when this feeder was less rewarding than an alternative

(33). Fruit flies chose their mating partner according to the preference of the majority of copulating conspecifics (34). All these findings suggest that different contextual characteristics strongly influence social learning patterns. However, relatively little research has investigated how organisms jointly integrate multiple social learning strategies with individual experience.

Open diffusion experiments with experimentally trained demonstrators in the wild have been well utilized (18, 29, 30), and show what types of social learning animals are capable of in a well-defined experimental context. However, open diffusion experiments without experimentally trained demonstrators may better show how traditions endogenously arise in the wild in more realistic social settings; yet, they are rare (17, 28).

Recently developed dynamic statistical models including Network Based Diffusion Analysis (hereafter NBDA: (35, 36) and Experience-Weighted Attraction models (hereafter EWA: (15, 17, 37)) are powerful statistical modeling approaches to identify evidence for social learning and the pathways of social transmission. NBDA is useful to identify an evidence for social learning and the typical pathways of social transmission but it only analyzes the initial spread of a new behavior, i.e. the origin of a cultural tradition. It cannot thus evaluate what social learning strategies individuals use to inform behavioral choice once they have learned multiple options (36). Nor can NBDA examine how individuals uniquely combine individual and social information – the combination of which makes social learning adaptive. EWA models analyze the entire unique behavioral sequence chosen by each individual and investigate how this is influenced over time by both personal experience and observation of others, i.e. the origin and maintenance of a cultural tradition (15, 17). EWA models permit extant theoretical models of social learning strategies to be turned into statistical models to examine which strategy, or combination of strategies, best predict the behavior of individuals. These predictions are conditional upon an individual's unique personal experiences and opportunities

for observing social information, thus linking individual variation in behavior to population-level cultural dynamics.

This study aims to determine which social learning strategies – content-biased: frequency-dependent; payoff-biased and/or context biased: based on demonstrator specificities (sex, kin and rank) - are responsible for the transmission of novel food processing techniques - peanut shelling - in wild vervet monkeys (*Chlorocebus pygerythrus*). Here, we offered a novel food – unshelled peanuts – to two groups of wild vervet monkeys: Noha (hereafter 'NH') and Kubu (hereafter 'KB') during four months of field experiments. We recorded the exact time of each peanut consumption event and the identity of observers at each time to construct a dynamic observation network. We described the three different peanut extraction techniques used by monkeys: crack with the hand (hereafter 'CH'; Movie S1: https://youtu.be/BkiTJyxp3gQ); crack with the mouth from the side of the peanut (hereafter 'CMS'; Movie S2: https://youtu.be/3JOAH4khnjk) and crack with the mouth from the top of the peanut (hereafter 'CMT'; Movie S3: : https://youtu.be/ikcFeAjVZqI). We then analyzed data from this experiment with EWA models. We predict, in accordance with another study focusing on context biases (28), that higher-ranked vervet monkeys are more influential demonstrators than others. We hypothesize that other content biases, such as frequency or payoff based (i.e. the most successful technique), would also be possible. The major interest of this study remains in assessing the weight of each social learning strategy in a single analysis combining individual and social information through the use of a field open diffusion experiment with no trained model.

Results

Effects of group, rank, sex and age on success, manipulation and observation

In NH, 25 individuals (9 adults; 12 juveniles; 4 infants) succeeded in opening 2104 peanuts and attempted to open a further 1401 peanuts. In KB, 9 individuals (5 juveniles; 4 infants) succeeded in opening 45 peanuts and 10 individuals (6 juveniles; 4 infants) attempted to open 102 peanuts (Table S1). We found an effect on rank and sex both on the rate of peanut opening successes and on the rate of manipulation. Higher rankers succeeded significantly more to extract peanuts (GLMs: estimate=-2.67; standard error=0.67; t value=-4.00; P=0.0004) and manipulated more peanuts than lower rankers (estimate=-2.22; standard error=0.65; t value=-3.56; P=0.002). Males succeeded significantly more to extract peanuts (18/24 males; 16/29 females; estimate=1.12; standard error=0.32; t value=3.56; P=0.001) and manipulated significantly more peanuts than females (19/24 males; 16/29 females; estimate=0.93; standard error=0.32; t value=2.95; P=0.007).

The latency of first success ranged from 2.03 minutes (122s) to 448.1 minutes (26,886s) in NH (mean=218.35 min (13,101.52s); standard error of the mean=25.29 min (1517.54s)) and from 78.95 min (4737s) to 393.6 min (23,616s) in KB (mean=223.33 min (13,400.89s); standard error of the mean=38.85 min (2330.88s); Table S1). The innovator in NH was a low-ranked, newly immigrated adult male at the first exposure to peanuts (Avo) while, in KB, it was an infant male (Aar) at the third exposure. We found a significant effect of age on latency of first peanut opening success. Juveniles had a lower latency compared to infants (GLMs: estimate=-0.57; standard error=0.25; t value=-2.34; P=0.05), but we found no significant difference between infants and adults (estimate=0.13; standard error=0.31; t value=0.41; P=0.91) nor between juveniles and adults (estimate=-0.45; standard error=0.25; t value=-1.82; P=0.16). We found no significant difference between groups (estimate=-0.16; standard error=0.24; t value=-0.67; P=0.51), between males and females (estimate=0.12; standard

error=0.21; t value=0.57; P=0.58) and no significant effect of rank (estimate=-0.11; standard error=0.42; t value=-0.26; P=0.80) on latency of first success.

We found no clear difference in the rate of observation of successes between groups (GLMs: estimate=2.79; standard error=1.66; t value=1.68; P=0.10), between high rankers and low rankers (estimate=-1.64; standard error=0.86; t value=-1.91; P=0.07), between adults and infants (estimate=0.64; standard error=0.59; t value=1.08; P=0.29), between adults and juveniles (estimate=-0.007; standard error=0.42; t value=-0.017; P=0.99) nor between males and females (estimate=0.81; standard error=0.44; t value=1.85; P=0.08) . We found no evidence for any difference on the rate of observation of manipulations between groups (estimate=2.42; standard error=1.36; t value=1.78; P=0.09), between high and low rankers (estimate=-1.56; standard error=0.83; t value=-1.89; P=0.07), between adults and infants (estimate=0.57; standard error=0.58; t value=0.98; P=0.33), between adults and juveniles (estimate=-0.01; standard error=0.41; t value=-0.03; P=0.98) and between males and females (estimate=0.79; standard error=0.42; t value=1.88; P=0.07).

We found effects of rank, age and sex on the rate of being observed when manipulating and successfully opening peanuts. High-rankers were observed significantly more than low-rankers when succeeding (GLMs: estimate=-3.61; standard error=0.65; t value=-5.57; P<0.001) and manipulating (estimate=-3.31; standard error=0.65; t value=-5.08; P<0.001). Adults were observed significantly more than juveniles when succeeding (estimate=-0.91; standard error=0.29; t value=-3.12; P=0.004) and manipulating (estimate=-0.73; standard error=0.29; t value=-2.56; P=0.02). Males were observed significantly more than females when successfully opening (estimate=1.15; standard error=0.27; t value=4.20; P<0.001) and manipulating peanuts (estimate=1.02; standard error=0.28; t value=3.63; P=0.001).

EWA model interpretations

For most individuals, and at the population level, we found that CMS was the most successful, and became the most common technique in the population. CMS was successful on 46.8% occasions in NH and 24.8% in KB over all manipulations. This was followed by CMT (8.1% in NH, 5.4% success in KB) and CH (5.1% in NH, 0.7% in KB). Overall, we found the best support for the global model which receives the most weight and has the lowest WAIC value (Support 100%; Table 1) and predicts well at the population-level (Fig. 1) and across all individuals (Fig. 2; Fig. S1). Model predictions from the global model show that the highest-payoff behavior became the most common for nearly all individuals in the population (Fig. 2; Fig. 3 and Fig. S1). The parameters' magnitudes and certainties in the global model, as well as WAIC score and parameter estimates in individual models, suggest that payoff-bias, followed by rank-bias, were the two singular most important learning strategies (Table 1; Table 2). Figure 3 shows predictions for five evaluated models for a single individual ('Gran' in NH). In this case, all models allow the highest payoff behavior (CMS; displayed in purple) to become the most common in the population. The global model tends to show more uncertainty around any particular prediction, whereas models evaluating pure individual learning strategies tend to be overconfident in their estimates, less accurate, or do not perform well for all individuals in the population. Payoff-biased and rank-biased learning models perform well, but do not adequately predict the frequency of all three behaviors across the entire time series, whereas frequency-dependent learning over-predicts the frequency of the most common, high-payoff behavior. The individual learning model's predictions are overconfident, tend to drift around, and underestimate the frequency of CMS, particularly at the beginning of the time series. We found little support that individuals preferentially used the technique displayed by females or individuals of the same sex (Table 1). Kin-biased learning might be important for a few, but not most individuals. We encourage readers to examine Figure S1, as we believe it is the most informative about model fit compared to real data and is informative about individual variation.

Variation between individuals and groups in parameters

We see considerable variation between the two groups and among individuals for many varying effects parameters in these models, this occurred for several reasons. In KB, fewer individuals participated in the experiment and they had fewer foraging bouts generating more uncertain estimates as reflected by the population posterior mean estimates in Table 2. They were also less likely to observe social information, based on the 20-minute time windows we selected in this analysis. For these reasons, many of the individual-level parameter estimates of varying effects have tighter 89% High Posterior Density Intervals than the population mean estimates. Posterior estimates of group-level varying effects also differ greatly for some parameters. These estimates are more precise and parameter values related to social learning are higher for NH due to the greater number of individuals who participated to the experiment. This can be visualized when looking at the shaded HPDIs around model predictions in Figure S1 for individuals in both groups of different sample sizes. It is also visualized in Figures S2-S4. Estimates of σ extracted from the variance-covariance matrix of the global model are in Figure S5.

Sensitivity to attraction scores (λ)

Females (Posterior Mean (λ_f=8.38; [89% HPDI: 4.01-14.86]) are more sensitive than males (λ_m=6.27 [3.35-10.35]) to differences in attraction scores while juveniles are more sensitive than adults (λ_j=10.04 [5.45-17.07]; λ_a=5.22 [2.64-9.03]). A higher attraction score typically means that individuals are more sensitive to personally-experienced differences of behavioral payoffs. The direction of these effects is consistent across nearly all evaluated models (Table 2). We see considerable variation in varying effects of λ at the group and individual level (Fig. S2A), but much of this is due to sampling differences.

Weight given to recent experiences (ϕ)

Overall, we see small values for ϕ, suggesting that individuals tend to weight past experience more heavily than recent experience; memory strongly influences behavior. Adults tend to weight new experiences more heavily than juveniles (ϕ_a=0.08 [0.02-0.17]; ϕ_j=0.04 [0.01-0.08]). We see little support for sex differences (ϕ_f =0.06 [0.02-0.12]; ϕ_m=0.05 [0.01-0.11]). The direction and magnitude of these effects are consistent across all evaluated models (Table 2). Groups and individuals (particularly in KB) tend to have larger and more uncertain estimates of ϕ as a wider range of parameter values can predict the observed data (Fig. S2B).

Weight given to social information (γ)

In the global model, social information influences behavior slightly more heavily for adults than juveniles (γ_a=0.23 [0.05-0.48]; γ_j=0.20 [0.05-0.38]), and for females than males (γ_f =0.23 [0.05-0.43]; γ_m=0.20 [0.04-0.43]). However, these patterns are not consistent across all models. This is because for each individual model, one learning bias might be particularly salient for a particular age or sex class. We can gain insight into this from comparing predictions from the global model to models representing individual learning strategies (Fig. S2C). For example, the payoff-bias learning model has higher values of γ for juveniles and females (γ_j=0.31 [0.13-0.50] ; γ_a=0.28 [0.11-0.49]; γ_f =0.30 [0.13-0.51]; γ_m=0.28 [0.11-0.49]), while the rank-bias learning model has higher values for of γ for adults and males (γ_a=0.29 [0.12-0.50]; γ_j=0.18 [0.07-0.33]; γ_m=0.27 [0.11-0.47]; γ_f =0.20 [0.08-0.37]).

Payoff-bias

We find reliable support for payoff-biased learning, for nearly all individuals in the population (Fig. S3A). Of the social learning biases, we also see the most salient differences

between age and sex classes. Juveniles rely more on payoff-biased social learning than adults ($\beta pay_{j=}$1.24 [-0.36-2.76]; βpay_j=0.45 [-1.06-1.97]), while females rely more heavily on it than males (βpay_f=1.07 [-0.49-2.63]; βpay_m=0.62 [-0.88-2.08]). Of the EWA models representing individual learning strategies, payoff-biased learning had the lowest WAIC value (Table 1) and its predictions were most similar to the global model for most individuals in the population. Similar differences and stronger effect sizes were estimated in the payoff-biased learning model when compared to the global model (Table 2).

Rank-bias

We also see good support for rank-biased social learning for most individuals in the population, although there is more uncertainty around these predictions (Fig. S3B). The global model suggests that adults are more likely to learn from high ranking individuals than juveniles ($\beta rank_a$=1.26 [-0.25,2.72] ; $\beta rank_j$=0.80 [-0.85,2.53]), and females are more likely to learn from high-ranking individuals than males ($\beta rank_f$=1.18 [-0.40,2.75]; $\beta rank_m$=0.89 [-0.60,2.48]). These differences between age and sex parameters are much smaller in the rank-biased learning model (Table 2). This is likely because higher ranking individuals are more successful than low ranking individuals. When including both rank and payoff in the global models, differences in reliance on rank cues, instead of payoff cues, emerge.

Frequency-dependence

On average, the population tends to be somewhere between linear and slightly positive-frequency-dependent. We see posterior means slightly larger than 1 for most individuals (Fig. S4). However, boundary conditions (f^c>0) often make posterior point estimates misleading; nearly half of the posterior mass for many individuals and all age and sex classes lies in a parameter space consistent with anti-conformity. The frequency-dependent learning model

estimated a stronger degree of conformist transmission, but it often under-predicts the probability of an individual choosing a less common behavior.

Matrilineal kin-, Female- and Same-sex biased learning

We see some evidence for matrilineal kin-biased learning (Table 2), but this might only be for some individuals in the population (Fig. S3C). We see little evidence for sex-biased and female-biased transmission (Table 2; Fig. S3D; Fig. S3E).

Discussion

In the present study we used a time-series model predicting each technique's probability of being chosen in order to infer which social learning strategies were utilized in two groups of wild vervet monkeys when learning to process unshelled peanuts, a novel food. The best supported statistical model, and evidence from a suite of models, suggests that vervet monkeys used the most successful, highest payoff technique, and displayed by the higher ranked demonstrators. We found weak support for a positive frequency-dependent conformity bias defined as 'use the most observed technique'. We also found no evidence that they show a bias toward the technique displayed by females, individuals of the same sex, or related individuals. They do not ignore social information and also use individual learning. We reported high variation between groups and among individuals for many parameters in the models. This is due to the difference in data sample size between the two groups; one group (NH) with many more participants eating peanuts than the other (KB). Finally, we reported effects of age, sex and rank on individual and social learning which are discussed in the remainder of the discussion.

Note that we avoided using the term "copying" across the manuscript which is strongly associated to "imitation" by some scholars (38, 39), although not by all (9, 40). Here, we do not make any assumption and conclusion regarding the social learning mechanisms (action form copying versus non-form copying/socially mediated individual learning: 39) implied in the acquisition of the peanuts processing techniques. We acknowledge that the three peanuts processing techniques we describe are within the Zone of Latent Solution of vervet monkeys (39) and we do not claim for form copying, i.e. that vervet monkeys faithfully copied the exact movements – the form of the behavior - displayed by their conspecifics.

Wild vervet monkeys acquire novel food processing technique via payoff-biased learning

We found the strongest support for the global model suggesting that vervet monkeys use multiple social learning strategies simultaneously. Here, payoff- and rank-biased learning guided diffusion of peanut processing techniques in both groups of wild vervet monkeys. These results do not fully align with those of a previous study on vervet monkeys at our field site (19). In Bono and colleagues' study, payoff consisted of a different quantity of food provided by a two-action design – one item versus five. In our study, socially observed payoffs were an individual's mean observed probability of a technique being successful in the previous 20 minutes. Bono et al. found that only males chose the technique used by the male model more when it received five food items compared to a female model receiving only one item (19). We find that females and juveniles relied more on payoff-biased social learning than males and adults conversely. We believe this discrepancy in results can be explained by methodological differences between both studies. First, in Bono and colleagues' study (19), only two models, a male and a female, that were both adults and of high rank, were available in each group, while in our study, numerous individuals of both sexes and various ages and ranks could opportunistically serve as demonstrators. Second, we tested here behavioral responses of

individuals towards a novel and unknown food while Bono and colleagues (19) tested monkeys in a two-action box experiment filled with known food. It is possible that monkeys got accustomed to boxes' affordance across the numerous experiments of this kind they had experienced in previous years at the Inkawu Vervet Project. Different strategies could be at play in different environmental contexts, i.e. in a usual foraging situation *versus* an unprecedented one. Our results suggest thus that females - the philopatric sex – are maybe less conservative in their social learning than previously thought and that their conservatism decreases in a novel context after an environmental change. When it has been suggested that females would stick to their habits compared to males who are expected to show more behavioral flexibility (19), our findings challenge this hypothesis and filled a gap. Females possibly possess more detailed knowledge than males about the distribution of existing food resources or objects such as boxes they encounter in their territory, which could make them a valuable source of directed social learning in these common situations. However, we suggest that when facing an unknown foraging situation, females can show flexibility, decrease their conservatism and rely more than males on the social information available.

Other recent studies used a similar multilevel dynamic learning model in great tits (18) and in capuchins (17). Great tits have been found to switch to an alternative higher payoff variant when given a choice between a low and a high payoff option (18). As we found in vervet monkeys, young birds were more likely to use social information than older birds (18). Barrett and colleagues (17) offered *Sterculia apetala* fruits to a naïve group of wild capuchins and followed the spread of the processing techniques. They found that, of multiple biases, payoff-biased social learning was the one responsible for the spread of the most successful techniques (17), and that age was a strong predictor in the heterogeneity of learning among individuals. We can hypothesize that this maintained preference for CMS technique could be at the origin

348 of cultural transmission of peanut processing techniques if this food was made available on the
349 long term in vervet monkeys' environment.
350
351 Rank also matters: vervet monkeys preferentially used the technique displayed by higher
352 rankers
353 Here, we also report a rank bias in agreement with the 'use preferentially the behavior
354 displayed by higher-ranked individuals' strategy found in chimpanzees (27) and vervet
355 monkeys (28). In this latter study, we used another modeling approach – NBDA - to identify
356 the typical pathways of transmission of boxes opening techniques in an open diffusion
357 experiment. We tested whether the diffusion followed specific social networks representing
358 different pathways of learning such as learning from females, older individuals, related
359 individuals or higher rankers. We discovered evidence of a transmission bias favoring learning
360 from higher-ranked individuals, with no evidence for age, sex or kin bias (28). Present results
361 are thus in accordance with these previous findings. We could not in this previous study test for
362 frequency-dependent learning and payoff-biased learning nor for the interplay between the use
363 of social and individual information, but this is precisely what we assessed here. This means
364 that higher rankers are not only considered as models for the first learning event but that this
365 bias is maintained across time.
366 While higher rankers were manipulating more boxes and were more successful, they
367 were not observed more than low rankers in our previous study (28). Instead, observations of
368 higher-ranked individuals had a greater effect on observers' behavior than observations of
369 lower-ranked individuals. Here, we found that higher rankers manipulated and successfully
370 processed more peanuts, probably because they can monopolize access to food. We did not find
371 any difference in observation rate between individuals but, we reported that higher rankers,
372 adults and males were observed more than lower rankers, juveniles and females. This difference

373 might be due to experimental novelty arousing a different attentional pattern. Indeed, in a box
374 experiment, vervet monkeys showed a selective attention to female models (26) when all
375 models were of high rank. This is in accordance with literature on chimpanzees and capuchins
376 in which older and more proficient nut crackers are more observed than others (41, 42).
377
378 No clear evidence of conformity, kin or sex biased learning
379 We tested for frequency-dependent learning with a model estimating whether
380 individuals used i) positively frequency dependence as conformity bias; ii) unbiased
381 transmission/copy proportional to frequency and iii) negative frequency dependence/anti-
382 conformity- bias toward copying rarer traits. We found little evidence for any frequency-
383 dependent learning, our population being slightly positive frequency-dependent. A previous
384 study on vervet monkeys reported that migrant males conformed to their new group norm by
385 abandoning their natal feeding preference, thus following a functional definition of conformity
386 (29). The authors' claim of conformity (29) has been considered a premature conclusion
387 regarding the mechanism of conformity, as the authors did not have the observational data of
388 who the males attended to before switching and could not prove that the males observed the
389 foraging choice of a majority before switching (43). Here, we did not test for such a conformity
390 bias based on the number of individuals using the same processing technique, but we rather
391 tested for a conformity bias based on the frequency of technique used. We thus tested whether
392 individuals were i) more likely to use a technique frequently observed; ii) as likely to use a
393 technique as it is observed or iii) less likely to use it. Such biases have been tested in great tits
394 where the establishment of a foraging tradition has been found to rely on positive frequency-
395 dependence; individuals adopting the most frequent local variant (30). Barrett and colleagues
396 (18) found no evidence for a conformity bias but they found evidence of weak anti-conformity
397 meaning that rare techniques attracted more attention in capuchins.

We found no evidence for kin- or sex-biased social learning. Previous studies reported that infant vervet monkeys ate the same food as their mother (29) and that females were preferred as models over males (26). However, these studies tested for a single bias at a time while we tested here for several biases simultaneously, weighting each strategy against the other which makes the analysis more powerful. Our results are furthermore consistent with a previous study testing for several model biases in a single analysis that did not identify neither any such biases (28). We believe that testing for several biases in a single analysis allow to disentangle between potential confounding factors such as age, sex and rank and can highlight instances of equifinality where multiple social learning strategies produce the same signature in a population (44).

Sociodemographic effects on individual variation in social and individual learning

In the present study, the two innovators were an infant and a low-ranking adult male. In another open diffusion experiment (28), the alpha male and female were the two innovators in the same two groups when tested one year before. We believe that this difference can be linked to the aforementioned experiments' methodological considerations. In Canteloup and colleagues' study (28), groups were tested in a two-action box experiment for which individuals may get accustomed to boxes' affordances despite the use of new design. Some studies suggested that juveniles and low rankers are often innovators (45, 46) although this depends on the type of behavior (47), while other studies suggest neophilia and boldness have been found to better predict innovation (48). We hypothesize that innovators' identity also depends on task novelty. Monkeys being neophobic, an unknown food can be considered as a source of stress, which suggests that low rankers were the initiators and that juveniles were quicker to first succeed to extract peanuts because of their usual limited access to resources. When the task is not completely new, dominants are more expected to be the innovators.

We reported that, in the global model, social information influenced behavior more heavily in adults than juveniles and in females than males, but these patterns were not consistent across all models. In the payoff model, social information influenced behavior more heavily for juveniles and females whereas in the rank model, adults and males relied more on social information. Despite being in disagreement with what has been previously found in vervet monkeys (19), this suggests that juveniles and females would be more sensitive to behaviors' payoffs while adults and males would be more sensitive to rank cues associated with a demonstrator. Overall, we found that adults weighed past experience more heavily than recent experience compared to juveniles, suggesting that memory strongly influences their behavior as previously found in birds and capuchins (17, 18).

Conclusions

We show that payoff bias could be at the origin of the spread of novel food processing techniques in vervet monkeys, and that this content bias likely acts concurrently with rank-biased learning. EWA models consider exactly what and whom individuals had uniquely observed both prior to their observing a successful solution and after they learn how to solve the task. This detailed time-varying modeling approach makes the analysis particularly powerful in uncovering the interplay between personal and social information use, which makes social learning adaptive and efficient. Because it is very rare that first innovation event and its spread are recorded through observational studies, we believe that controlled experiments coupled with dynamic, theory-informed modeling are a good approach to track the diffusion of new behaviors and to disentangle between different social learning strategies.

Materials and Methods

448

449 Experimental model and subject details

450 We studied two groups of wild vervet monkeys (*Chlorocebus pygerythrus*): 'Noha'
451 (NH) and 'Kubu' (KB). NH was composed of 34 individuals (5 adult males; 9 adult females;
452 11 juveniles males; 9 juveniles females) and KB was composed of 19 individuals (1 adult male;
453 6 adult females; 6 juveniles males; 6 juveniles females; Table S1). Males were considered as
454 adults once they dispersed, and females were considered as adults after they gave their first
455 birth. Individuals that did not fulfill these criteria were considered as juveniles (28). Each group
456 had been habituated to the presence of human observers: since 2010 for NH and since 2013 for
457 KB. All individuals were identifiable thanks to portrait photographs and specific individual
458 body and face features (scars, colors, shape etc.).

459 Ethics guidelines: Our study adhered to the "Guidelines for the use of animals in
460 research" of Association for Study of Animal Behavior and was approved by the relevant local
461 authority, Ezemvelo KZN Wildlife, South Africa.

462

463 Study site

464 The study was conducted at the Inkawu Vervet Project (IVP) in a 12,000-hectare private
465 game reserve: Mawana (28°00.327S, 031°12.348E) in KwaZulu Natal province, South Africa.
466 The vegetation of the study site consisted in a savannah characterized by a mosaic of grasslands
467 and clusters of trees of the typical savannah thornveld, bushveld and thicket patches. Mawana
468 houses various species of animals including elephants, hippopotamus, giraffes, zebras and
469 numerous species of antelopes. The common predators of vervet monkeys consist of leopards,
470 hyenas, jackals, caracals, servals and several species of snakes and raptors.

471

472 Hierarchy establishment

473 Agonistic interactions (aggressor behavior: stare, chase, attack, hit, bite, take place;
474 victim behavior: retreat, flee, leave, avoid, jump aside) were collected from May 2018 to
475 October 2018, aside from experiment days, on all the adults and juveniles of both groups via
476 *ad libitum* sampling (49) and food competition tests (i.e. corn provided to the whole group from
477 a plastic box). Data were collected by CC, MBC and different observers from the IVP team.
478 Before beginning data collection, observers had to pass an inter-observer reliability test with
479 80% reliability for each data category between two observers. Data were collected on tablets
480 (Vodacom Smart Tab 2) equipped with the Pendragon version 8.

481 Individual hierarchical ranks were determined by the outcome of dyadic agonistic
482 interactions recorded *ad libitum* and through food competition tests using Socprog software
483 version 2.7 (50). Hierarchies in both groups were significantly linear (NH: h' = 0.27; $P <$
484 0.0001; KB: h' = 0.42; $P < 0.0001$) and ranks were assessed by I&SI method (51).

485

486 Open diffusion experiment

487 The experimental apparatus consisted of provisioning the group with two transparent
488 rectangular plastic boxes (dimensions: 34x14x12 cm) containing unshelled peanuts in
489 quantities (about 2 kg) to avoid a single individual monopolizing the boxes. The monkeys had
490 never been provided with peanuts before the experiment and peanuts were not available in their
491 environment. Thus, unshelled peanuts were a novel, nutritious food that required processing to
492 be extracted from their shells before consumption.

493 Experiments took place at sunrise at monkeys' sleeping sites during the dry, food-scarce
494 winter to maximize their motivation for novel food. The two boxes of peanuts were offered to
495 the monkeys, spaced by about 1 to 10 meters from each other. CC led the experiment with the
496 help of two to four field assistants. All monkeys were free to come to the boxes within the
497 constraints of the social group dynamics. Experiments were video recorded using JVC cameras

498 (EverioR Quad Proof GZ-R430BE) to which the experimenter said aloud the identities of the
499 actor and of the attending neighbors for each manipulation event. A manipulation event was
500 defined either as an attempt to extract a peanut from its shell (i.e. the individual acted on the
501 peanut failing to fully open it and to get access to the food) or as a success (i.e. the individual
502 succeeded to fully open a shell and to extract the peanut from the shell). A conspecific was
503 considered as attending when it had its head or body oriented in an unobstructed line towards
504 the subject manipulating the peanut and was located within 0-30m from the actor. Several
505 individuals could thus be registered as attending to one or several actors simultaneously.

506 The open diffusion experiments ran from May 2018 to August 2018 to have a maximum
507 of individuals participating in the experiment. A total of 11 sessions of open diffusion
508 experiment were run in NH and 10 in KB. The average duration of an experimental session was
509 46:46 minutes for NH and 42:47 minutes for KB.

510

511 Video analysis

512 All video recordings were later analyzed by MBC with Media Player Classic Home
513 Cinema software version 1.7.11. Twenty percent of the video were analyzed by CC and inter-
514 observer reliability was substantial ($\kappa = 0.78$). During video analysis in slow motion or frame
515 by frame, the following variables were encoded: date, exact time of each manipulative event,
516 actor identity, the technique used (crack with hand: 'CH'; crack with mouth from the top of the
517 peanut: 'CMT'; crack with mouth from the side of the peanut: 'CMS'; see Movies S1-S3) and
518 the identity of attending individuals.

519

520 Quantification and statistical analysis

521 Following Barrett and colleagues (17), we used a suite of hierarchical experience-
522 weighted attraction (EWA) models to analyze data collected in the open-diffusion experiment.

523 EWA models are time-series models that evaluate the joint influence of personal experience
524 and social information on the probability of individual displaying a behavior (37). While
525 originally a tool in behavioral economics, they are being further developed and utilized in cross-
526 taxa studies of cultural transmission (16-18, 27, 52).

527 This analytical approach has several strengths: It permits evaluation of multiple
528 hypothesized learning strategies, utilizes a dynamic social learning network unique to each
529 individual, and links individual variation in behavior and cognition to population level-cultural
530 dynamics. Working with time-series of behavior unique to each individual is important as
531 population-level signatures can often be misleading (53) or exhibit equifinality, particularly if
532 individuals vary in experience, observation opportunities or the social learning strategies they
533 employ (44). The mathematical specification of our analytical approach also minimizes
534 ambiguity of what types of social learning we are evaluating. This is important as verbal
535 definitions are imprecise, and terminologies are differently interpreted in studies of social
536 learning. Most importantly, this approach links theory to data. Instead of using a theoretically
537 uninformed analytical approach to find results consistent with theory, we bypass quantitative
538 proxies and translate theoretical models to statistical models. We discuss the models in
539 mathematical detail in the supplemental material.

540 We fit a series of EWA models evaluating the following learning strategies:

541 1. Individual learning

542 2. Frequency-dependent learning (using preferentially behavior using information about
543 its frequency in population)

544 3. Female-biased learning (bias toward using preferentially the technique displayed by
545 females in group i.e. matrilineal sex in vervets)

546 4. Matrilineal kin-biased learning (bias towards using preferentially the technique
547 displayed by closely related individuals)

5. Compare means payoff-biased learning (using preferentially most successful or efficient behavior)

6. Rank-biased learning (using preferentially the technique displayed by high-ranking individual)

7. Sex-biased learning (using preferentially behaviors of individuals that are the same sex as you)

8. Global model that includes 1-7.

For each behavioral choice, social information used by an actor was the average value of each cue observed in a time window of 20 minutes prior to the observation (Table 3). As individuals access social information at different timescales, and this window choice was somewhat arbitrary, we also evaluated social info at 30, 10, and 5-minute timescales. These analyses yielded similar results and were robust to time windows.

We ran the models using regularizing priors and a Cholesky decomposition for estimating varying effects. They were fit using RStan version 2.19.3 (54). Models were compared using widely applicable information criteria (WAIC). Reproducible model code and data can he found here: https://github.com/bjbarrett/vervet_peanut_EWA

EWA Model Specification

EWA models have two parts: a set of expressions that specify how individuals accumulate experience and a second set of expressions that specify the probability of each option being chosen. Accumulated experience is represented by *attraction scores*, $A_{ij,t}$, unique to each behavior i, individual j, and time t. We update $A_{ij,t}$ with an observed payoff $\pi_{ij,t}$:

$$A_{ij,t+1} \quad (1-\phi_j)A_{ij,t} + \phi_j \pi_{ij,t}$$

The parameter ϕ_j controls the importance of recent payoffs in influencing attraction scores. When ϕ_j is high, more weight is given to recent experience over past experiences – memory has less of an influence on behavioral choice. This parameter is unique to an individual j, and we also estimate how it varies by age-class and sex.

Attraction scores are converted into probabilities of behavioral choice with a standard multinomial logistic choice rule:

$$Pr\left(i \vee A_{ijt}, \lambda_j\right) \quad \frac{exp\left(\lambda_j A_{ij,t}\right)}{\sum_k exp\left(\lambda_j A_{kj,t}\right)} = I_{ij}$$

λ_j controls sensitivity to differences in attraction scores on behavioral choice and is unique to an individual j. A very large λ_j ,means the option with the largest attraction score is nearly always selected. Choice is random with respect to attraction score when $\lambda_j = 0$. Individuals were assigned a payoff of zero, $\pi_{ij,t} = 0$, if they failed to open a peanut. If they were successful $\pi_{ij,t} = 1$.

Social learning may directly influence choice distinctly from individual learning. $S_{ij} = S\left(i \vee \Theta_j\right)$ is the probability an individual j chooses behaviour i on the basis of a set of social cues and parameters Θ_j. Behavioral choice is a convex combination specified by:

$$Pr\left(i \vee A_{ij,t}, \Theta_j\right) = \left(1 - \gamma_j\right) I_{ij,t} + \gamma_j S_{ij,t}$$

where γ_j is the weight assigned to social cues bounded by 0 and 1.

Social cues are incorporated into $S_{ij,t}$ by use of a multinomial probability expression with a log-linear component $B_{ij,t}$ that is an additive combination of cue frequencies. The probability of displaying each behavior i, solely as a function of social cues, is:

$$S_{ij,t} \quad \frac{N_{ij,t}^{f_c} expB_{ij,t}}{\sum_m N_{mj,t}^{f_c} expB_{mj,t}}$$

$N_{ij,t}$ are the observed frequencies of each technique i at time t by individual j. The exponentiated parameter f_c controls the amount and type of frequency dependence. When $f_c = 1$, social learning is unbiased by frequency and techniques influence choice in proportion to their occurrence (sometimes referred to as unbiased transmission). When $f > 1$, social learning is positive frequency-dependent or conformist. When $f < 1$, social learning is negative frequency-dependent, and a bias is shown towards rare behaviors.

Other social cues associate with individuals (i.e. rank, age, or relatedness) or behaviors (i.e payoffs), are incorporated via:

$$B_{ijt} \quad \sum_k \beta_k$$

B_{ijt} is the sum of the products of the influence parameters β_k and the cue values $\kappa_{k,ijt}$. Cues evaluated in these models are explained in detail in Table 3.

Other statistics

We used generalized linear models (GLMs) with quasi-Poisson error and log link function to test for the effect of group, normalized rank, sex and age on i) the latency of first success of shelling a peanut; ii) the number of peanut shelling successes; iii) the number of peanuts manipulation (attempts + successes); iv) the number of successes observed; v) the number of manipulations observed; vi) the number of times being observed when succeeding and vii) the number of times being observed when manipulating. We added the log of the time each individual had to process peanuts once they first succeeded as an offset (a standard

statistical technique for converting a Poisson GLM for analysis of counts into a model for analyzing counts per unit of time). All tests were performed with package lme4.

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Figures and Tables

Figure 1

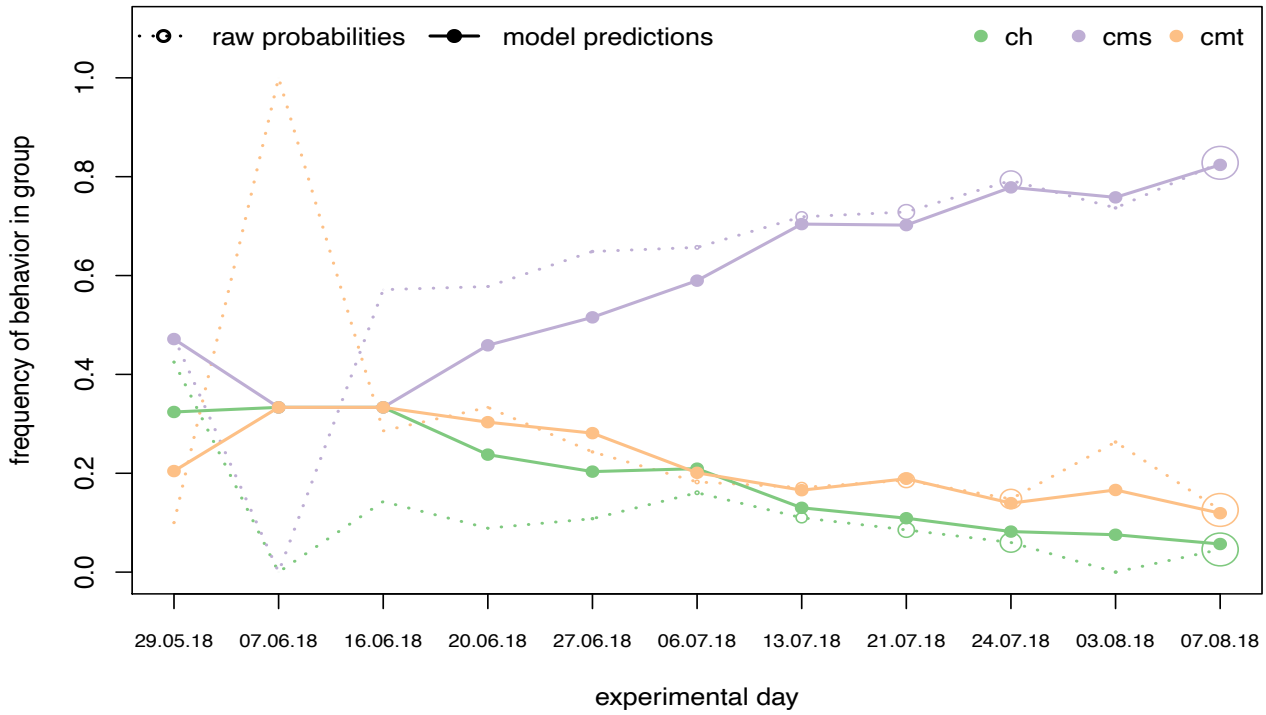

Figure 1. Daily mean group probability of processing techniques over experimental days for NH. Filled lines and points are global model predictions. Dashed lines and circles are probabilities of raw data. Diameter of points of raw data scales with daily sample size.

Figure 2

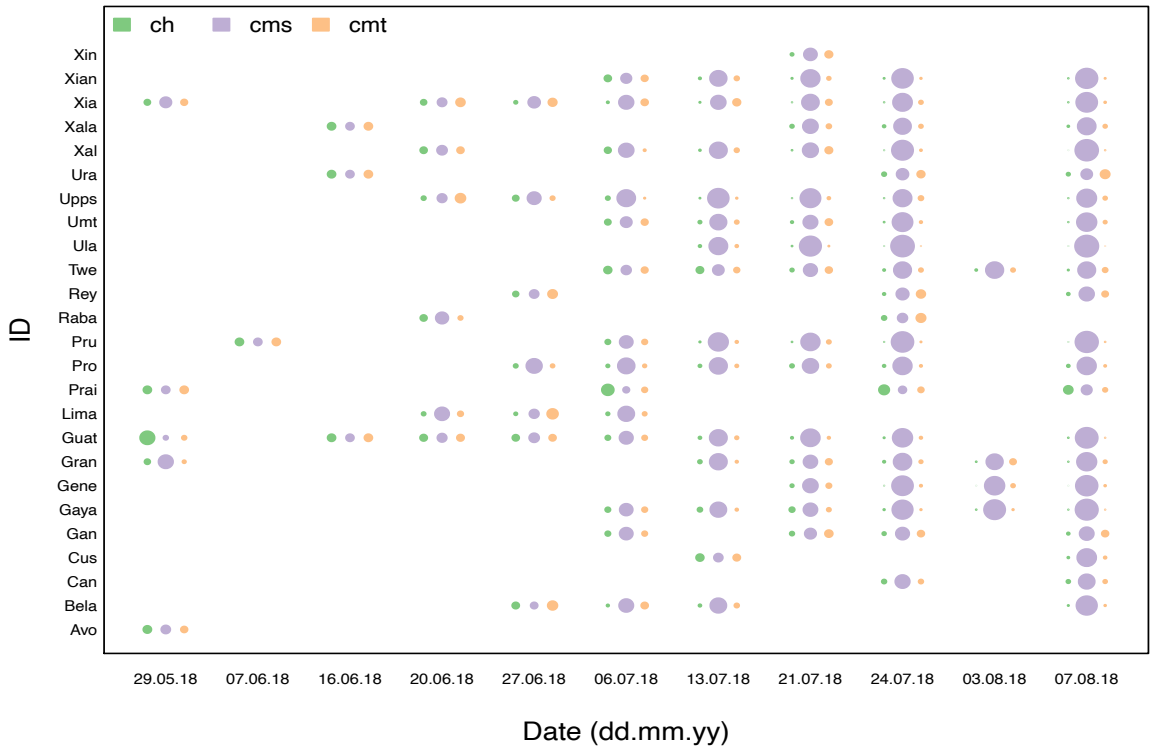

Figure 2. Visualization of posterior estimates from the global model of daily mean probability of processing techniques across all foraging individuals in NH. Point diameter scales with probability, with many individuals approaching fixity of CMS on the final day.

Figure 3

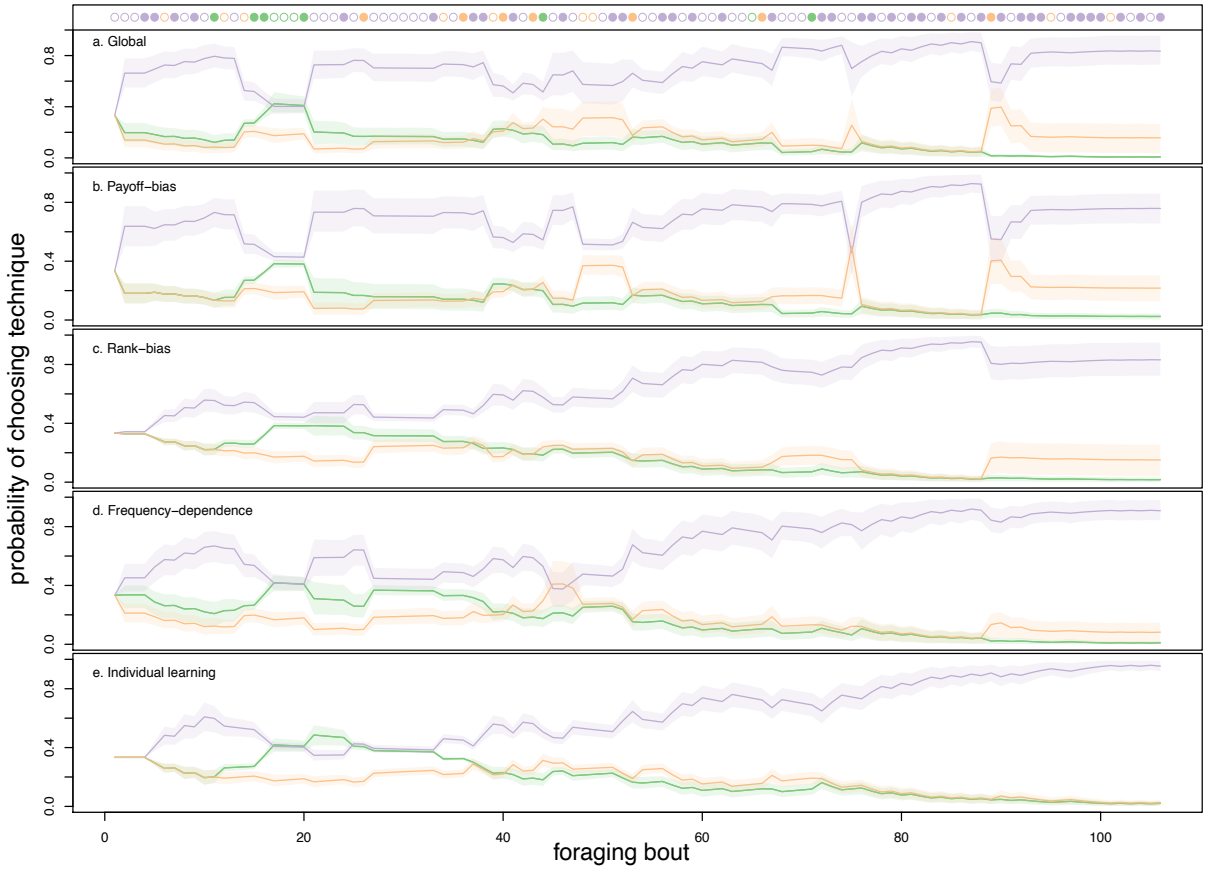

Figure 3. Model predictions of the probability of using a technique across foraging bout from five models for the behavioral time series of individual 'Gran' in NH group. Colors correspond to the three processing techniques (purple: 'CMS'; orange: 'CMT'; green: 'CH'). Line shows posterior mean at each timestep, shaded interval is a 89% High Posterior Density Intervals (HPDI). Points along top row are raw data showing observed behavioral choice at each foraging bout. Filled circles are successes, empty circles are failures.

Table 1

Model	WAIC	SE	dWAIC	weight
Global Model	4707.71	91.09	0.00	1.00
Payoff-bias	4756.90	91.12	49.18	0.00
Rank-bias	4780.21	90.55	72.50	0.00
Frequency-dependence	4796.59	90.92	88.88	0.00
Matrilineal Kin Bias	4856.82	92.46	149.11	0.00
Same-sex-bias	4874.49	92.68	166.78	0.00
Female-bias	4875.25	92.73	167.54	0.00
Individual learning	4920.83	92.00	213.12	0.00

Table 1. Widely applicable information criteria estimates for all evaluated models with a 20 minute window of social information. Standard errors, difference in WAIC and model weight are included.

Table 2

Parameter	Global	Payoff-bias	Rank-bias	Freq-dep.	Kin-bias	Female-bias	Sex-bias	Ind. learn.
λ_f	8.38	20.89	19.17	8.79	15.76	13.73	13.55	7.31
λ_m	6.27	16.93	14.86	6.24	14.69	13.66	13.41	6.36
λ_j	10.04	20.37	19.94	10.73	16.72	15.42	15.13	9.31
λ_a	5.22	17.22	14.22	5.09	13.81	12.14	12.02	4.99
ϕ_f	0.06	0.04	0.04	0.06	0.04	0.05	0.05	0.06
ϕ_m	0.05	0.04	0.04	0.05	0.04	0.04	0.04	0.05
ϕ_j	0.04	0.03	0.03	0.04	0.03	0.03	0.03	0.05
ϕ_a	0.08	0.05	0.05	0.07	0.05	0.06	0.06	0.07
γ_f	0.23	0.30	0.20	0.21	0.14	0.13	0.13	
γ_m	0.20	0.28	0.26	0.21	0.16	0.13	0.13	
γ_j	0.20	0.31	0.18	0.16	0.12	0.09	0.09	
γ_a	0.23	0.28	0.28	0.26	0.19	0.18	0.18	
f_f^c	1.26			1.66				
f_m^c	1.04			1.29				
f_j^c	1.08			1.60				
f_a^c	1.20			1.33				
$\beta_f em_f$	-0.03					-0.01		
$\beta_f em_m$	0.09					-0.16		
$\beta_f em_j$	-0.05					-0.20		
$\beta_f em_a$	0.11					0.03		
$\beta_k in_f$	0.53				1.07			
$\beta_k in_m$	0.75				1.00			
$\beta_k in_j$	0.63				0.98			

$\beta_k in_a$	0.65			1.09	
$\beta_p ay_f$	1.07	1.46			
$\beta_p ay_m$	0.62	0.87			
$\beta_p ay_j$	1.24	1.46			
$\beta_p ay_a$	0.45	0.87			
$\beta_r ank_f$	1.18		2.37		
$\beta_r ank_m$	0.89		2.25		
$\beta_r ank_j$	0.80		2.22		
$\beta_r ank_a$	1.26		2.40		
$\beta_s ex_f$	-0.40				0.17
$\beta_s ex_m$	-0.80				0.00
$\beta_s ex_j$	-0.86				-0.07
$\beta_s ex_a$	-0.34				0.24

Table 2. Posterior mean estimates of learning parameters for all evaluated EWA models. Subscripts correspond to male (m), female (f), adult (a), and juvenile (j).

Table 3

Model	**Social and Individual Cues**
1) Individual learning	$\pi_{ij,t} = 1$ if successful, 0 if not
2) Frequency-dependence	$N_{ij,t}$= count of times j observed demonstrators perform behavior i
3) Female-bias	$\kappa_{k,ijt}$= 1 if adult female, 0 otherwise
4) Matrilineal kin-bias	$\kappa_{k,ijt}$= coefficient of relatedness, r, between observer j and demonstrator
5) Payoff-biased learning	$\kappa_{k,ijt}$= mean observed payoff, $\overline{\pi_{ij,t}}$, of behavior i observed by j
6) Rank-bias	$\kappa_{k,ijt}$= rank of demonstrator determined by I&SI method
7) Sex-bias	$\kappa_{k,ijt}$= 1 if same sex as observe, 0 if different
8) Global model	all cues in 1-7

Table 3. Individual information and social cues used in the EWA models. Models 2-8 also incorporate individual experience from model 1. Information observed at timestep t for models 2-8 was the mean of each cue, κ evaluated in the 20 minutes prior to timestep t.