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Lack of conformity to new local dietary preferences in migrating captive chimpanzees

Gillian L. Vale^{a,b}, Sarah J. Davis^{a,b}, Erica van de Waal^c, Steven J. Schapiro^b, Susan P. Lambeth^b, and Andrew Whiten^{a,*}

^aCentre for Social Learning and Cognitive Evolution, and Scottish Primate Research Group, School of Psychology & Neuroscience, University of St Andrews, St Andrews, U.K ^bNational Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, The University of Texas MD Anderson Cancer Center, Bastrop, TX, U.S.A ^cAnthropological Institute and Museum, University of Zurich, Zurich, Switzerland

Abstract

Conformity to the behavioural preferences of others can have powerful effects on intragroup behavioural homogeneity in humans, but evidence in animals remains minimal. In this study, we took advantage of circumstances in which individuals or pairs of captive chimpanzees, *Pan troglodytes*, were ‘migrated’ between groups, to investigate whether immigrants would conform to a new dietary population preference experienced in the group they entered, an effect suggested by recent fieldwork. Such ‘migratory-minority’ chimpanzees were trained to avoid one of two differently coloured foods made unpalatable, before ‘migrating’ to, and then observing, a ‘local-majority’ group consume a different food colour. Both migratory-minority and local-majority chimpanzees displayed social learning, spending significantly more time consuming the previously unpalatable, but instead now edible, food, than did control chimpanzees who did not see immigrants eat this food, nor emigrate themselves. However, following the migration of migratory-minority chimpanzees, these control individuals and the local-majority chimpanzees tended to rely primarily upon personal information, consuming first the food they had earlier learned was palatable before sampling the alternative. Thus, chimpanzees did not engage in conformity in the context we tested; instead seeing others eat a previously unpalatable food led to socially learned and adaptive re-exploration of this now-safe option in both minority and majority participants.

*Correspondence: A. Whiten, School of Psychology & Neuroscience, University of St Andrews, St Andrews KY16 9JP, U.K. aw2@st-andrews.ac.uk (A. Whiten).

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.12.007>.

Author Contributions

G.L.V. collected the data and carried out the statistical analyses; G.L.V. and A.W. drafted the manuscript with all authors contributing to the final manuscript; the original conception of the methodology was the work of A.W. and E.W.; the original methodology was adapted for captive chimpanzees by G.L.V. and A.W.; S.D. conducted inter-rater reliability, S.P.L. conducted and monitored all chimpanzee ‘migrations’ and provided on-site logistical support along with S.J.S.

Keywords

conformity; cultural transmission biases; culture; social learning; social-learning strategies

Many of the daily choices faced by animals require decisions about whether to engage in personal exploration of the environment (asocial learning) or instead to exploit the existing knowledge of others by learning socially (Kendal, Coolen, van Bergen, & Laland, 2005; Kendal, Coolen, & Laland, 2009; Laland, 2004). Evolutionary theory predicts that if appropriate decision-making rules can be economically employed, social learning will itself be selective. Such selectivity may be pursued through heuristics termed social learning strategies (Laland, 2004), or transmission biases (Boyd & Richerson, 1985; Henrich, 2001), which dictate who, what, when or even how to copy. The identification of such heuristics has proved instructive in understanding how cultures evolve in humans and other species (Kendal et al., 2015; Rendell et al., 2011). A variety of social learning strategies have recently been identified in diverse animal taxa (Kendal et al., 2009; Laland, 2004; Rendell et al., 2011), such as preferentially copying ‘dominant’ or ‘knowledgeable’ individuals (Kendal et al., 2015). One particularly powerful social learning strategy is conformist copying of majority behaviour, shown by mathematical modelling to facilitate intergroup cultural diversity and intragroup homogeneity (Boyd & Richerson, 1985), especially in spatially variable environments (Nakahashi, Wakano, & Henrich, 2012). Conformist copying is predicted to be adaptive, insofar as it can support the rapid uptake and maintenance of local information, by the copying of traits that are common among individuals already familiar with their environment. Social psychologists often refer to such effects in terms of two kinds of ‘social norms’. In the words of one such authority, ‘In addition to perceptions of what most others approve (the injunctive social norm), there is a second social normative type (the descriptive social norm) that also directs behaviour forcefully. Descriptive social norms refer to one’s perception of what most <http://dx.doi.org/10.1016/j.anbehav.2016.12.007> others actually do’ (Cialdini, 2007, p. 264). It is the latter phenomenon we focus on here.

Authors have defined the concept of conformity in various other ways over the years (Claidiere & Whiten, 2012; van Leeuwen & Haun, 2014). Originally, social psychologists emphasized conformity as the subjugation of personal knowledge or behaviour in favour of an alternative displayed by a majority of others. The classic work of Asch (1956), in which participants were prepared to express agreement with the clearly incorrect perceptual judgements of a group of experimental confederates, is an example of this form of conformity. Human deference to such group responses has since been replicated many times and has been shown to be sensitive to a number of factors, such as cultural context, audience presence and group size (Bond & Smith, 1996; see Bond, 2005; Morgan & Laland, 2012).

It is this sense of conformity we address in the present paper concerning our closest primate relative, the chimpanzee, *Pan troglodytes*. However, to avoid confusion, we first note that some students of cultural evolution have defined conformity in the more specific sense of a disproportionate tendency for individuals to copy a majority, even without subjugation of known behaviours (Boyd & Richerson, 1985; Whalen & Laland, 2015), a phenomenon that has been labelled ‘conformist transmission’ (van Leeuwen & Haun, 2014; Whalen &

Laland, 2015). Theoretical simulation studies have suggested that such conformist transmission may readily evolve in populations of social learners, although strong conformist tendencies can also be maladaptive in preventing the spread of potentially beneficial innovations (Henrich & Boyd, 1998; Kandler & Laland, 2013; Wakano & Aoki, 2007). Recent studies in fish and birds, respectively, have suggested that such disproportionate copying of majorities may occur in nonhuman animals (e.g. great tit, *Parus major*: Aplin et al., 2015a; nine-spined stickleback, *Pungitius pungitius*: Pike & Laland, 2010) although this conclusion has proved controversial (Aplin et al., 2015b; van Leeuwen, Kendal, Tennie, & Haun, 2015; Whiten & van de Waal, in press).

In intermediate levels of environmental change and patterns of spatial heterogeneity, social learning becomes an adaptive strategy (reviewed in Vale, Carr, Dean, & Kendal, 2017). Conformity may be an important social learning strategy when migrating to a new area and entering a new group (Boyd & Richerson, 1985), where there is scope for uncertainty about the optimal ways to behave. ‘Copy when uncertain’ is one of the other principal social learning strategies highlighted in studies of both humans and nonhuman species (Kendal et al., 2009, 2015; Laland, 2004). Recent evidence consistent with ‘copy when uncertain’ and/or ‘conformity’ comes from a small but growing set of field experiments. In one, after four groups of wild vervet monkeys, *Chlorocebus aethiops*, were trained to prefer just one of two differently coloured corn provisions by making one severely distasteful, nine of 10 males migrating between groups after the distasteful additive was removed were found to quickly abandon their earlier learned preference in favour of the other colour if they entered a group where a majority was eating this (van de Waal, Borgeaud, & Whiten, 2013). More recently, a similar effect was documented in wild great tits that abandoned an earlier learned preference to peck one side of an artificial foraging device in favour of the opposite method, if this was shown by a majority of the new community they entered (Aplin et al., 2015a,b). There is thus a growing, if still small and controversial, literature consistent with the existence of this form of conformity to new community behaviours in the particular circumstance of migrating to a new and unfamiliar social and physical context (van Leeuwen et al., 2015; Whiten & van de Waal, in press).

In the present study of chimpanzees, we focused on conformity as originally defined in the social psychology literature: adherence to group preferences at the expense of discarding known or existing personal preferences or behaviours. Specifically, we investigated whether individuals become flexible in their behavioural options due to the social influences of a group of conspecifics. Evidence of such a disposition has recently been presented for wild chimpanzees living in neighbouring communities that are each characterized by differing preferences for nut-cracking hammer materials in different seasons (Luncz & Boesch, 2014; Luncz, Mundry, & Boesch, 2012). This cannot be easily explained by genetics, given intergroup transfer and breeding, nor by local environments, since the habitat is similar across the relevant ranges. However, we note a caveat regarding the role that environment could play in social transmission via niche construction, if communities’ preferred tools accumulate near nut-bearing trees, thus encouraging their subsequent use. The authors of these studies have concluded that the differences represent different cultural traditions. Females display the behavioural profiles that are characteristic of their community, despite having transferred from other communities, an effect accordingly interpreted as conformity

to local traditions, involving the abandonment of earlier tool preferences (Luncz & Boesch, 2014). This interpretation is supported by tracking of a female migrant that initially displayed the behavioural profile of her natal community, but over time adopted that of her new adopted community, and by follow-up studies of changes in tool preferences of a larger sample of females (Luncz, Wittig, & Boesch, 2015). A possible parallel to this effect in the vocal domain is the recent tracing of progressive adoption of a local vocalization dialect at the expense of their original one by chimpanzees introduced into a new group in a zoo (Watson et al., 2015a; but see Fisher, Wheeler, & Higham, 2015; Watson et al., 2015b for further debate). Such results are consistent with an earlier experimental study of the diffusion of experimentally seeded alternative tool use patterns in different groups of captive chimpanzees, some of whom discovered the alternative technique, yet reconverged on the profile of the majority of their group (Whiten, Horner, & de Waal, 2005). However, it is unclear whether other social learning strategies, such as a tendency to copy certain individuals or recently observed behaviours, as well as individual learning tendencies, such as reverting back to a behaviour due to habit formation, may explain such occurrences of behavioural reconvergence (van Leeuwen & Haun, 2013; van Leeuwen & Haun, 2014; van Leeuwen et al., 2015).

Given these emerging findings, in the present study, we experimentally tested for conformity by exploiting an unusual (perhaps unique) opportunity, in which a statistically viable sample of individuals or pairs of chimpanzees were moved to new groups in a large US primate facility, as part of efforts to enhance welfare and social enrichment during the transfer of a number of chimpanzees to a new facility. Echoing the field experiment of van de Waal et al. (2013) with wild vervet monkeys, we first exposed chimpanzee subjects to two differently coloured foods, one of which was made unpalatable, so participants would learn to avoid it. The group receiving the migrants was taught to prefer the other colour of food. After allowing time for immigrant chimpanzees to then observe the new, reversed group preference, we tested whether, like the immigrant males in the vervet study, the immigrants would conform by changing the food option they chose to ingest.

METHODS

Animals

A total of 60 chimpanzees, housed at the National Center for Chimpanzee Care (NCCC) Michale E. Keeling Center for Comparative Medicine and Research of the University of Texas MD Anderson Cancer Center, were included in this study (mean age = 30.7 years, range 13–53 years; 32 female).

Migratory-minority Subjects

Eleven chimpanzees (five female, termed migratory-minority individuals) provided the migratory subjects for the study. These chimpanzees were migrated into nine new groups all housed at the same facility. Migration refers to the physical movement of these chimpanzees to new groups that were housed in a different enclosure to the former housing of the migratory-minority individuals. Migratory-minority individuals moved to their new enclosures/groups either individually or in pairs (see Table 1). In the wild, females leave

their natal groups to migrate to other groups (Nishida et al., 2003; Pusey, Williams, & Goodall, 1997), but to provide a reasonable sample size, this study recorded the behaviour of both migratory males and females. Following these migrations, the average group size was five (range 3–10, Table 1).

Local-majority Subjects

Migratory-minority chimpanzees were relocated into nine groups of chimpanzees ($N = 37$ chimpanzees, 19 female). These groups were termed local-majority individuals to indicate that they received the migrating chimpanzees, remaining in their enclosure rather than themselves relocating, and to denote that their group sizes were always greater than the number of migrating chimpanzees they received (Table 1 outlines the variation in local-majority group sizes and the number of migrating chimpanzees they received). One local-majority subject failed to participate in this study.

Control Groups

Twelve chimpanzees (eight female) formed our control groups (two groups consisting of seven and five chimpanzees). Control groups received no migrating individuals. These controls allowed the assessment of whether chimpanzees, with an induced food preference, may change their food preferences despite not receiving migrating chimpanzees trained on a different dietary preference. One control individual failed to participate in the study.

Ethical Note

Chimpanzees were not moved specifically for this study. Instead, we exploited the fact that in a colony reorganization, these chimpanzees were to be moved to new groups to promote enhanced welfare and to sustain large group sizes or to restructure existing groups. Some chimpanzee movements were designed to also make smaller groups for these chimpanzees' movement to a new facility. All chimpanzees chose whether to participate in the study. Chimpanzees were not deprived of food or water. Ethical approval was granted for this study by the Institutional Animal Care and Use Committee (IACUC approval number 0894-RN01) and the University of St Andrews' Animal Welfare and Ethics Committee.

Materials

Two sources of food (toasted oats) were provisioned in two differently coloured (green and orange) feeders (36×4 inches and 2 inches high, see Supplementary video) located on the outside of the chimpanzee enclosures. The feeders were positioned flush against the enclosure mesh so that chimpanzees could reach through the mesh to gain access to the provisioned food. To distinguish between the two food sources, food was also coloured either green or orange (using food dye) and placed in the corresponding colour feeder. Chimpanzees have been shown to perceive colours like humans do (Matsuzawa, 1985), so the present study used colour to distinguish between the two food sources. To induce food preferences, one food source (green or orange, counterbalanced) was made unpalatable by treating it with Fooley Ultra-Bitter Training Aid (see Table 1), to which food dye was added before spraying the mixture into the food until it was coated. Fooley Ultra-Bitter Training Aid is a bitter liquid used to deter pets from chewing household items.

Procedure

We followed the general procedure of van de Waal et al. (2013), previously applied to wild vervet monkeys.

Training phase

To establish food colour preferences, we ran an initial training phase in which all chimpanzees (migratory-minority, local-majority, control individuals) were provisioned with orange and green food in two adjacent, differently coloured feeders, one of which (orange or green) was made unpalatable by spraying it with Fooey Ultra-Bitter Training Aid (Table 1 and Supplementary video). To ascertain whether migratory-minority subjects adopt the food choice of their new group, different food colour preferences were always induced in resident local-majorities and the individuals who would be migrating into them (migratory-minorities). We followed this procedure until both coloured foods were sampled by at least 80% of subjects and until a maximum of one animal per session sampled the unpalatable food across three consecutive sessions. Each session lasted for 20 min, during which the food sources were refilled when nearly depleted. To rebait, both food sources were simultaneously removed from, refilled and then repositioned within reach of the subjects. Both food sources were refilled using this procedure when one or both were nearly depleted. This ensured there was always access to both food sources. This method was employed to prevent biasing chimpanzees' food selections should only one source remain within their reach. In situations where two chimpanzees, housed together, were moving to new groups, they were trained as a pair (see also Appendix Table A1). For local-majorities, all training was conducted in a group setting.

Group stabilization and observation phase

Following the migratory-minorities' movements into new groups, and a habituation period that allowed the newly formed groups time to stabilize, migrants were given the opportunity to observe the local-majority consume the food colour that these migrants had learned was unpalatable (observation phase). Habituation periods were determined by the chimpanzee colony manager and based on behavioural monitoring of the newly formed groups' interactions. As groups stabilized at different rates and, in some cases, chimpanzee movements were delayed, the interval between the training and observation phase varied across groups (mean = 33, range 7–68 days). During the observation phase, the food that local-majority chimpanzees were trained to discriminate as unpalatable was again treated with Fooey Ultra-Bitter Training Aid. To allow only observation of the local-majority food preference, migratory-minority individuals voluntarily separated from the local-majority, while remaining in visual contact through areas of wire mesh of the enclosures. Voluntary separation was achieved by calling the subject's name and waiting for the chimpanzee to separate from the group. Upon separation, the individual received a food reward. A minimum of two, 30 min observation sessions were conducted, during which the attendance levels of migratory-minority individuals were recorded in situ at 1 min intervals. Additional observation sessions were run following subjects' failure to attend to the local-majority consuming food on more than 15 intervals of 1 min until this criterion was met. An individual was recorded as attending to the local-majority if its head was oriented towards

the local-majority while they were consuming food. In practice, only a single individual required an additional observation session. Control groups, which did not receive migrating chimpanzees, did not participate in an observation phase.

Test phase

In the test phase, conducted the day after the observation phase, chimpanzees, now as a group, were provisioned with untreated orange and green food for three 30 min sessions. This phase allowed an assessment of whether chimpanzees switched their food preferences to match those of their new companions (previously unpalatable, 'unPal', food) and for controls, whether they stuck with their induced food preference (previously palatable, 'Pal', food), when both foods were palatable. Again, participation was voluntary. All food sampling was continuously coded, noting the start and end time of the feeding bout and the type of food that was consumed. This allowed the calculation of the overall consumption times of each food type. Chimpanzee food selections during three 30 min test sessions were also coded by a second researcher and inter-rater reliability was 100%. Owing to a limited sample size, data were analysed using nonparametric, two-tailed, statistical tests. The dependent variable was the proportion of time chimpanzees spent consuming previously unPal food (time spent consuming previously unPal food (s)/total time spent consuming previously unPal and Pal food).

Following Kendal et al. (2015) dominance rank was assessed by using three chimpanzee experts' ratings using a three-point categorical dominance scale ranking each chimpanzee of each group as either 'high', 'medium' or 'low' dominance. Ratings were given for the newly formed chimpanzee groups once they had stabilized; for the controls, ratings were given for their already stable groups. Inter-rater reliability was high (intraclass correlation, $ICC_{2,1} = 0.831$, $P < 0.001$; see section Group stabilization and observation phase above, for details of how group stabilization was determined). As in Kendal et al. (2015), the modal rank was selected for the few cases of rank disagreements.

RESULTS

The proportion of time spent consuming previously unPal food differed between groups (migratory-minority/local-majority/controls: Kruskal–Wallis test: $H_2 = 11.10$, $N = 58$, $P = 0.004$). Both migratory-minority chimpanzees (median = 0.107) and local-majority chimpanzees (median = 0.285) spent proportionately more time consuming their previously unPal food than did controls (median = 0.00; Mann–Whitney U test: $U = 21.00$, $N_{\text{controls}} = N_{\text{migratory-minority}} = 11$, $P = 0.008$; $U = 74.00$, $N_{\text{controls}} = 11$, $N_{\text{local-majority}} = 36$, $P = 0.002$, respectively; Fig. 1; see Appendix Tables A2–A5 for individual and group food preferences), suggesting that chimpanzees in both categories were affected by witnessing others eating the alternative food. There was no difference in the proportion of time migratory-minority chimpanzees and local-majority chimpanzees spent consuming their previously unPal foods (Mann–Whitney U test: $U = 166.00$, $N_{\text{local-majority}} = 36$, $N_{\text{migratory-minority}} = 11$, $P = 0.420$; Bonferroni adjustment applied with alphas set at 0.017). Latencies to first sample the previously unPal food also did not differ between local-majority (median = 1800 s) and

migratory-minority (median = 630 s) chimpanzees (Mann–Whitney U test: $U = 105.00$, $N_{\text{local-majority}} = 29$, $N_{\text{migratory-minority}} = 9$, $P = 0.39$; see Appendix for additional results).

There was no difference in the proportion of time local-majority individuals spent consuming the previously unPal food, or in their latency to first sample this food, according to dominance rank (high/medium/low proportion of time spent consuming unPal food, Kruskal–Wallis test: $H_2 = 1.135$, $N = 36$, $P = 0.564$; high/medium/low latency, Kruskal–Wallis test: $H_2 = 2.063$, $N = 29$, $P = 0.356$). This suggests that food switching was not due to competition from more dominant individuals. Moreover, three of the migratory-minority, ranked ‘high’, ‘medium’ and ‘low’, displayed overall preferences for the previously unPal food (see Appendix). This suggests that competition did not deter some chimpanzees (of any rank) from consuming the food preferred by the local-majority.

All local-majority individuals, except one female, that sampled the previously unPal food during the test phase did so only after a migrant had already sampled it. Local-majority individuals sampled the unPal food after observing, on average, just 2 (median) unPal food sampling events (range 0–8 events, $N = 29$; ‘events’ account for observing the same individual sample the food multiple times), or watching, on average, 1 (median) individual sample unPal food (range 0–4). As migratory-minorities were exposed to an observation phase in which they observed the local-majority consume the food they knew to be unPal, all migratory-minority subjects, during the test phase, that sampled the unPal food did so only after observing the local-majority consume it.

Although social learning influenced the food sampled by local-majority and migratory-minority chimpanzees, chimpanzees overall relied preferentially upon personal information, tending to first consume the known Pal food before sampling the previously unPal food (49 of 58 chimpanzees, chi-square goodness-of-fit test: $\chi^2_1 = 27.59$, $P < 0.001$). The food that was consumed first (Pal/unPal) did not differ between groups (migratory-minority/local-majority/controls: Fisher’s exact test = 3.00, $P = 0.262$). The high prevalence in first consuming known Pal food suggests that the variation in the time it took groups to stabilize (mean = 33, range 7–68 days) did not influence chimpanzees’ first food selections. Only one of the 11 migratory-minority individuals first sampled the previously unPal food they had witnessed the residents eat. This female chimpanzee took longer to sample any of the food (321 s) than other migratory-minority individuals (mean = 18 s, range 0–109 s), and, in this sense, appeared more uncertain than the others, before making her novel choice. There appeared to be no sex differences in the food first sampled by migratory-minority individuals given that all, except this one female, selected the known Pal food first. Overall, the median proportion of time migratory-minority males spent consuming unPal food was 0.093 (inter-quartile range, IQR = 0.34) and for migratory-minority females was 0.147 (IQR = 0.79). Migratory-minority females, on average (median), sampled the previously unPal food after 894 s (IQR = 2689.50) and migratory-minority males did so after 276 s (median, IQR = 2798.50). The average time taken to first sample the known Pal was equivalent across sexes (female migratory-minority: median = 5.00 s, IQR = 1854; male migratory-minority: median = 4.50 s, IQR = 27.25; note that there are too few participants to perform inferential statistics to determine possible sex differences).

DISCUSSION

We assessed whether migrating chimpanzees would opt to switch to a conflicting dietary preference displayed by the resident group they moved to. Both migratory-minority and local-majority chimpanzees spent proportionately more time consuming their previously unPal food than control groups that received no migrating chimpanzees. This suggests that exposure to other animals consuming the alternative food encouraged food exploration through social learning, despite participants' prior experience of marked unpalatability in this option. However, we found that instead of conforming, migratory-minority chimpanzees initially, and overall, relied upon personal information, preferring to sample the food they knew to be palatable.

Adaptive behaviour requires individuals to be informed by acquiring relevant information from their surroundings, either by personal exploration (asocial learning), observing others (social learning) or both (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Simultaneous employment of personal and social learning could lead to better informed individuals than when concentrating on one information source alone. While our chimpanzees appeared not to engage in conformity, we did observe bidirectional information exchange between migratory-minority and local-majority individuals. Indeed, only nine of the 47 local-majority and migratory-minority chimpanzees failed to sample the food that they had learned was very unpalatable. This switching between information sources encouraged food exploration and maximized the amount of food available to subjects. This capacity to nimbly switch behavioural responses (socially and asocially learned) has implications for cultural evolution in changing environments, wherein established behaviours can periodically become redundant (Boyd & Richerson, 1985).

Other studies have also recently reported a lack of conformity in captive chimpanzees (Haun, Rekers, & Tomasello, 2014; van Leeuwen, Cronin, Schütte, Call, & Haun, 2013), a result with which the current study is consistent. This is despite chimpanzees being shown to have a disposition to copy a majority over a minority behaviour when they are task naïve (Haun, Rekers, & Tomasello, 2012) and wild migratory female chimpanzees apparently transitioning to the behaviour of their new group (Luncz & Boesch, 2014; although see van Leeuwen & Haun, 2013; van Leeuwen & Haun, 2014; van Leeuwen et al., 2015).

Several different factors might account for the lack of a disposition to conform reported in this study. First, there is a countervailing tendency in chimpanzees for conservative behaviour, that is, to persevere with a known behaviour despite the availability of a behavioural alternative that is within participants' capacity to learn, noted in several recent studies (Haun et al., 2014; Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008; although see Manrique, Volter, & Call, 2013 and Davis et al. 2016, for cases of flexible behaviour in chimpanzees when past solutions become unavailable or very costly). However, as local-majority and migratory-minority chimpanzees proceeded to sample both previously Pal and unPal foods, social information was sufficient to overcome the conservative Pal food preference documented in control chimpanzees. Given evidence in the literature for the opposite tendencies of both conservatism and conformity/social

learning in chimpanzees, a key question for future research is identification of the factors that throw the switch between these opposing dispositions.

A further question is whether the conformity documented in wild chimpanzees may arise from alternative copying strategies such as copying dominant individuals (Kendal et al., 2015; see van Leeuwen & Haun, 2013; van Leeuwen & Haun, 2014; van Leeuwen et al., 2015). That local-majority chimpanzees sampled the previously unPal food following the observation of, on average, only one individual sampling this food indicates that conformity was not required for flexible behaviour. This is reminiscent of Norway rats, *Rattus norvegicus*, which switched from food known to be palatable to foods thought to be toxic or less palatable after interacting with a conspecific that ate the undesirable food (Galef & Whiskin, 2008). Such findings highlight the need for future migration studies to include single demonstrator–observer pairs to assess whether behavioural switching requires social information from one or many individuals.

A second possible explanation for our results concerns the costs of alternative options. Theoretical analyses indicate that reliance upon social information should increase as the costs associated with acquiring or using personal information increase (Boyd & Richerson, 1985; Feldman, Aoki, & Kumm, 1996). This has been termed the ‘costly information hypothesis’, which depicts an evolutionary trade-off between acquiring (or using) accurate, but costly (personal) information versus less accurate, but cheap (social) information (Boyd & Richerson, 1985). It is noteworthy that the chimpanzees in the present study acquired accurate personal information of the Pal food coupled with little cost in its subsequent use. Conversely, conformity to social information incurred the potential costs of consuming a food personally known to be distasteful, coupled with competition from the new group if opting to sample it; the strong conformity effect reported by van de Waal et al. (2013) for migrating male vervet monkeys occurred most prominently when males could approach the locally preferred food without a higher-ranked resident present. Such circumstances could plausibly reduce the incentive for chimpanzees in the present study to conform to the new dietary preference of resident chimpanzees. However, dominance rank did not appear to predict how much time chimpanzees spent consuming the previously unPal food or when they first sampled it. Rather, a bias towards personal information may have been reinforced by a lack of prior exposure in these chimpanzees to potentially noxious foods and general risk when engaging in individual exploration: the collection and use of personal information may have very little cost in captive populations. A lack of risk experienced by captive animals, when presented with novel objects and foods, has been suggested to explain the neophilic responses of captive animals compared to the neo-phobic responses of their wild counterparts (Forss, Schuppli, Haiden, Zweifel, & van Schaik, 2015). Thus, it may be more costly for wild populations, which are likely to have experienced costs for ignoring social information, to ignore the dietary choices of local individuals.

A third possible explanation for the lack of conformity observed relates to informational uncertainty. Theoretical analyses also suggest that individuals should use social information when they are uncertain, whether induced by prior information being unreliable, a lack of prior personal information (Boyd & Richerson, 1988), personal information becoming outdated (Boyd & Richerson, 1985, 1988), the accumulated knowledge of conspecifics

being more reliable (Giraldeau, Valone, & Templeton, 2002), or through environmental variability (Boyd & Richerson, 1985). Environmental heterogeneity in the present study, introducing uncertainty, may not have been within the right parameters for chimpanzees to adopt the dietary preference of their group. Modelling studies and theoretical considerations suggest that social learning pays under intermediate levels of environmental change, or with moderate levels of spatial heterogeneity, where change is not so rapid as to require asocial learning, or so slow that adaptive behaviour can evolve through natural selection (reviewed in Vale et al., 2017). In the present study, environmental variability was introduced by chimpanzees' migrations to a new enclosure with new residents. However, all enclosures at the research site provide rather similar ecological conditions, and migratory-minority and local-majority chimpanzees were not necessarily unfamiliar to one another in all cases. Accordingly, environmental variability may not have been sufficient to elicit any conformist dispositions, compared to that experienced by wild animals migrating to distant locations and groups.

Nevertheless, we did observe social information use in chimpanzees exposed to conspecifics consuming previously unPal food. Here, personal knowledge of the unPal food was conflicted by new information, which could explain the chimpanzees' sampling of this previously distasteful food. This may suggest social learning occurred as uncertainty about the palatability of the two food options increased. Accordingly, it is plausible that the forgoing of old solutions in favour of group preferred solutions, documented in wild populations, could occur because of environmental and social uncertainty, as much as from the number of demonstrators modelling the new behaviour (see van Leeuwen et al., 2015; Whiten & van de Waal, in press, for discussion).

In conclusion, conspecifics foraging on one of two available food sources provided migratory-minority and local-majority individuals with social information regarding the quality of resources (Dall et al., 2005). Chimpanzees' resource site selections have been shown to be influenced by the selections of others when they lack prior personal experience (Haun et al., 2012; Vale, Flynn, Lambeth, Schapiro, & Kendal, 2014). In contrast to this, our findings suggest that even persuasive social information (multiple individuals to learn from) was mostly disregarded by chimpanzees when they possessed conflicting prior personal information. This reliance on personal information, coupled with the local-majority chimpanzees' deviation from an established group preference, suggests that chimpanzees did not engage in conformity in the present context and raises the possibility that matching majority preferences in other contexts may be driven by alternative nonconformist biases. Nevertheless, our results suggest flexible learning in chimpanzees. Specifically, exposure to other animals consuming alternative food encouraged food exploration through social learning. Such flexible use of learning strategies has important implications for chimpanzees' ability to track potential shifts in circumstances by updating their prior knowledge.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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APPENDIX. ADDITIONAL RESULTS

Local-majority groups spent proportionally more time consuming Pal food in test 1 (median = 1.00) than in test 3 (median = 0.61; $W = -2.07$, $P = 0.038$). There were no significant differences in the proportion of time local-majority groups spent consuming Pal food between test 1 and test 2 (median = 0.58; $W = -1.82$, $P = 0.069$) or between test 2 and test 3 ($W = -0.889$, $P = 0.374$). Comparable analyses were not conducted for migratory-minority chimpanzees due to a small sample size.

Immigrant chimpanzees moved to new groups as a pair or individually (see Appendix Table A1, Fig. A1 for the proportion of time migratory-minority chimpanzees spent consuming food according to local-majority group sizes). The average proportion of time spent consuming the previously unPal food, during the test phase, by chimpanzees that moved as a

pair was 0.459 ([median], IQR = 0.78, $N= 4$ chimpanzees) compared to 0.078 ([median], IQR = 0.15, $N= 7$) by chimpanzees that migrated alone. Immigrant chimpanzees that moved as a pair sampled the previously unPal food, on average, earlier (median = 475.50 s, IQR = 2668.50, $N= 4$) than individually moved chimpanzees (median = 1158.00 s; IQR = 2798.50, $N= 5$).

Table A1

Majority size and proportion of unpalatable (unPal) and palatable (Pal) foods consumed by migratory-minority subjects

Group	Migratory-minority subject	Majority size	unPal	Pal
PH	EY	4	0.65	0.35
PH	DE	4	0.29	0.71
GP	GI	2	0	1
AX	JE	2	0.11	0.89
NK	MC	4	0.08	0.92
SA	JSE	7	0.06	0.94
SA	GE	7	0.98	0.02
HA	ME	2	0.72	0.28
JY	PR	2	0.15	0.85
MO	RR	5	0	1
ALX	SM	9*	0.08	0.92

* One local-majority did not participate, failing to sample any food.

Figure A1. Proportion of time spent consuming previously unPal food by migratory-minority individuals according to their local-majority group size.

Food preferences during the test phase varied between individuals, as assessed by comparing food consumption times to what would be expected by chance alone (binomial tests, see Appendix Tables 2–4). Three migratory-minority individuals preferred the previously unPal food (of ‘low’, ‘medium’ and ‘high’ dominance rank, one male) and eight the previously Pal

food (one chimpanzee of ‘low’, five chimpanzees of ‘medium’ and two chimpanzees of ‘high’ dominance rank, five male); 12 local-majority individuals preferred the previously unPal food, 23 the previously Pal food and one displayed no preference; all 11 control individuals displayed a preference for the previously Pal food.

Table A2

Time spent consuming unpalatable (unPal) and palatable (Pal) food during the test phase and migratory-minority individual food preferences

Group	Individual	Sex	Previously Pal	Previously unPal	Binomial <i>P</i>	Food preference
PH	EY	F	1444	2667	<0.001	Previously unpalatable
PH	DE	M	1443	589	<0.001	Previously palatable
GP	GI	F	4149	0	<0.001	Previously palatable
AX	JE	M	2106	252	<0.001	Previously palatable
NK	MC	M	1724	146	<0.001	Previously palatable
SA	JSE	F	1703	106	<0.001	Previously palatable
SA	GE	F	9	504	<0.001	Previously unpalatable
HA	ME	M	1257	3211	<0.001	Previously unpalatable
JY	PR	F	2511	434	<0.001	Previously palatable
MO	RR	M	2570	0	<0.001	Previously palatable
ALX	SN	M	2116	178	<0.001	Previously palatable

Food preferences were determined using the binomial test (probability set at 0.5).

Table A3

Time spent consuming unpalatable (unPal) and palatable (Pal) food during the test phase and local-majority individual food preferences

Group	Individual	Sex	Previously Pal	Previously unPal	Binomial <i>P</i>	Food preference
PH	CE	F	21	3288	<0.001	Previously unpalatable
PH	PH	M	4916	0	<0.001	Previously palatable
PH	SY	F	1135	17	<0.001	Previously palatable
PH	LE	M	688	2014	<0.001	Previously unpalatable
GP	PY	F	3040	802	<0.001	Previously palatable
GP	GP	M	3355	0	<0.001	Previously palatable
AX	TU	M	529	81	<0.001	Previously palatable
AX	AX	M	2705	56	<0.001	Previously palatable
NK	BA	F	191	322	<0.001	Previously unpalatable
NK	MY	F	257	101	<0.001	Previously palatable
NK	NK	M	291	881	<0.001	Previously unpalatable
NK	CK	M	170	8	<0.001	Previously palatable
SA	MI	F	4244	0	<0.001	Previously palatable
SA	PH	M	8	0	0.008	Previously palatable
SA	SA	F	1237	3385	<0.001	Previously unpalatable
SA	PN	M	24	80	<0.001	Previously unpalatable
SA	TI	M	136	336	<0.001	Previously unpalatable

Group	Individual	Sex	Previously Pal	Previously unPal	Binomial <i>P</i>	Food preference
SA	TO	M	0	162	<0.001	Previously unpalatable
SA	SE	M	1078	151	<0.001	Previously palatable
HA	UA	F	2441	1097	<0.001	Previously palatable
HA	HA	F	0	3247	<0.001	Previously unpalatable
JY	JY	M	2482	1537	<0.001	Previously palatable
JY	CY	M	1384	53	<0.001	Previously palatable
MO	KT	F	0	2266	<0.001	Previously unpalatable
MO	NA	F	2880	1424	<0.001	Previously palatable
MO	AE	F	1639	297	<0.001	Previously palatable
MO	MO	M	1336	1319	0.756	No preference
MO	CI	F	1957	0	<0.001	Previously palatable
ALX	MN	M	1930	0	<0.001	Previously palatable
ALX	AA	F	1838	0	<0.001	Previously palatable
ALX	BTA	F	417	857	<0.001	Previously palatable
ALX	SPE	F	925	131	<0.001	Previously palatable
ALX	GE	M	300	591	<0.001	Previously unpalatable
ALX	AX	M	1243	352	<0.001	Previously palatable
ALX	TA	F	107	142	0.031	Previously unpalatable
ALX	MN	F	13	99	<0.001	Previously palatable

Food preferences were determined using the binomial test (probability set at 0.5).

Table A4

Time spent consuming unpalatable (unPal) and palatable (Pal) food during the test phase and controls' individual food preferences

Group	Individual	Sex	Previously Pal	Previously unPal	Binomial <i>P</i>	Food preference
AK	ZE	F	1277	25	<0.001	Previously palatable
AK	HD	M	2914	0	<0.001	Previously palatable
AK	CA	F	499	12	<0.001	Previously palatable
AK	AL	M	3310	0	<0.001	Previously palatable
AK	MY	F	1637	15	<0.001	Previously palatable
AK	MA	F	2542	999	<0.001	Previously palatable
AK	TA	F	2638	154	<0.001	Previously palatable
JI	JA	M	964	0	<0.001	Previously palatable
JI	BE	F	767	0	<0.001	Previously palatable
JI	TK	F	2623	0	<0.001	Previously palatable
JI	QY	F	3520	0	<0.001	Previously palatable

Food preferences were determined using the binomial test (probability set at 0.5).

There was slight variation in group food preferences, as assessed by comparing food consumption times to what would be expected by chance alone (binomial tests, see Appendix Table A5). Data were collated from all participants (including migratory-minority individuals) to assess whether there was convergence on either Pal or unPal food. Pal food represents the food that was previously Pal to the local-majority and controls (thus being

previously unPal to the minority). Seven of the experimental groups displayed a preference for the food that was known to be Pal to the local-majority, one group displayed no preference and one preferred the food known to be unPal to the local-majority. Both our controls displayed a preference for their known Pal food during the test phase (see Appendix Table A5).

Table A5

Overall group preferences for feeding on unpalatable (unPal) and palatable (Pal) food observed during the test phase

Group Pal	Group unPal	Binomial <i>P</i>	Food preference
7337	5826	<0.001	Previously palatable
3486	2243	<0.001	Previously palatable
5652	5601	0.637	No preference
1085	3036	<0.001	Previously unpalatable
7812	7876	0.615	Previously palatable
10016	8206	<0.001	Previously palatable
4300	4101	0.031	Previously palatable
6395	4951	<0.001	Previously palatable
6950	4288	<0.001	Previously palatable
14817	1433	<0.001	Previously palatable
7874	0	<0.001	Previously palatable

Food preferences were determined using the binomial test (probability set at 0.5). Control groups are indicated in bold.

Figure 1.

Median proportion of time spent consuming previously unPal food (black horizontal line) according to subject group. Boxes represent the interquartile ranges. Whiskers represent the minimum and maximum proportion of time spent consuming previously unPal food that are not outliers (unclassified outliers represented by circles or extreme cases by asterisks).

Number, sex and induced food preference of migrating chimpanzees and the local-majority to which they migrated

Table 1

Group	Migratory-minority			Local-majority		
	N	Number of females	Induced food preference	N	Number of females	Induced food preference
PH	2	1	Orange	4	2	Green
GP	1	1	Green	2	1	Orange
AX	1	0	Orange	2	0	Green
NK	1	0	Green	4	2	Orange
JY	1	1	Orange	2	0	Green
SA	2	2	Green	7	2	Orange
HA	1	0	Orange	2	2	Green
NK	1	0	Green	9	6	Orange
MO	1	0	Green	5	4	Orange