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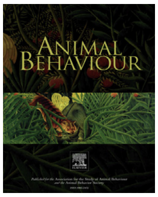

Lack of conformity to new local dietary preferences in migrating captive chimpanzees

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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.

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

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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).