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Field experiments with wild primates reveal no consistent dominance-based bias in social learning

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Directed social learning suggests that information flows through social groups in a nonrandom way, with individuals biased to obtain information from certain conspecifics. A bias to copy the behaviour of more dominant individuals has been demonstrated in captive chimpanzees, *Pan troglodytes*, but has yet to be studied in any wild animal population. To test for this bias using a field experiment, one dominant and one low-ranking female in each of three groups of wild vervet monkeys, *Chlorocebus aethiops pygerythrus*, was trained on alternative methods of opening an 'artificial fruit'. Following 100 demonstrations from each model, fruits that could be opened either way were presented to each group and all openings were recorded. Overall, the dominant females were not attended to more than low-ranking females during the demonstrations, nor were their methods preferentially used in the test phase. We conclude that these monkeys show no overall bias to copy high-ranking models that would lead to a high-ranking model's behaviour becoming more prevalent in the group than a behaviour demonstrated by a low-ranking model. However, by contrast, there were significant effects of observer monkeys' rank and sex upon the likelihood they would match the dominant model. Additionally we found that the dominant models were more likely to stick to their initially learned method than were low-ranking models.

Research has increasingly revealed evidence for social learning abilities in a variety of animal taxa. Social learning can be highly beneficial, allowing an animal to avoid the costs associated with asocial learning (Laland, 2004). However, maladaptive information may also be transmitted (Laland & Williams, 1998) and therefore animals could benefit from copying only the most useful information. One way to obtain the best information may be to selectively copy certain individuals based upon individual characteristics, such as age, sex or past successes. It is also likely that animals may exhibit biased social learning based upon the social organization of a group (directed social learning, Coussi-Korbel & Fragaszy, 1995); greater time spent in proximity to certain individuals may increase the likelihood that they will become models for social learning. Research with a variety of nonhuman animals has yielded evidence for a range of biases based upon the identity of the model in social learning, including age (Choleris, Guo, Liu, Mainardi, & Valsecchi, 1997; Duffy, Pike, & Laland, 2009), sex (Katz & Lachlan, 2003; van de Waal, Renevey, Favre, & Bshary, 2010), position in the social network (Allen, Weinrich, Hoppitt, & Rendell, 2013; Claidière, Messer, Hoppitt, & Whiten, 2013) and kinship (van de Waal, Bshary, & Whiten, 2014). Findings of multiple social learning biases in the same species (Kendal et al., 2015) also suggest that biases may work in concert.

In addition to the aforementioned biases, it has been proposed that copying successful individuals may be an adaptive strategy (Boyd & Richerson, 1985; Henrich & Gil-White, 2001) and that social rank may be used as a proxy for this in nonhuman animals (Laland, 2004, although see Henrich & Gil-White, 2001). However few empirical studies have examined this issue. Dindo, Leimgruber, Ahmed, Whiten, and de Waal (2011) found no evidence of dominance-based biases in social learning or social attention in captive tufted capuchin monkeys, *Sapajus apella*, during an extractive foraging task. By contrast, two studies with captive chimpanzees, *Pan troglodytes*, found that chimpanzees preferred to copy a higher rather than lower ranked individual using tasks requiring both object manipulation (Kendal et al., 2015; although

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see ; Watson et al., 2017) and token exchange (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010), although dominance in the latter was confounded with age and past success on tasks. Based on these findings with chimpanzees, it has been suggested that such a bias towards copying dominant individuals could, in a similar way to conformist transmission (Boyd & Richerson, 1985), constrain intragroup variation and increase the between-group variation found in wild chimpanzees (Kendal et al., 2015). However, such a bias has not yet been assessed in wild populations.

The aim of the current study was, accordingly, to examine whether a dominance-based bias exists in a wild population of primates. Vervet monkeys, *Chlorocebus aethiops pygerythrus*, provide an ideal species to examine this issue as they have linear hierarchies (Cheney & Seyfarth, 1990) and have previously been shown to learn socially in experimental contexts (van de Waal, Claidière, & Whiten, 2015; van de Waal et al., 2010; van de Waal, Borgeaud & Whiten, 2013). While a previous study revealed a bias for individuals to preferentially attend to and copy female, rather than male, conspecifics (van de Waal et al., 2010), both sexes of models used in that study were dominant and so the effect of demonstrator rank upon social learning remains to be tested in this species.

To provide an experimental test for a bias to copy high-ranking, over low-ranking, models in a wild primate, we trained two models of differing rank within each of three groups to use alternative methods to open an 'artificial fruit' to gain a reward inside and gave both models the opportunity to demonstrate their method to their groupmates. We investigated whether a certain rank of model was attended to more in an experimental setting and whether the method they displayed was preferred over the other in an extractive foraging task.

METHODS

Study Site and Participants

The research was conducted at the Inkawu Vervet Project (IVP), located in the Mawana Game Reserve in KwaZulu-Natal, South Africa (28°00S, 031°12E). Experiments were conducted between May and December 2015 with five groups of vervet monkeys at the field site. Four were assigned to experimental conditions: Ankhase (AK), Baie Dankie (BD), Noha (NH) and Kubu (KB) and one acted as a control group (Lemon Tree (LT)). A total of 100 monkeys were exposed to the demonstration phase in the three two-model groups, while 42 monkeys participated in the test phase of the experiment from all five groups.

Ethical note

Ethical permission for this study was obtained from the University of St Andrews Ethics Committee and from the Ezemvelo Wildlife Board in South Africa. The study conforms to the ASAB/ABS guidelines for the Treatment of Animals in Behavioural Research and Teaching. All individuals were habituated to human presence and steps were taken to minimize any potential effects of the study, such as a limit on provisioning for experimental purposes.

General Protocol

Two models of differing rank were selected for each of the three 'two-model' groups (AK, NH and BD, see Table 1) and trained to demonstrate alternative methods for opening a baited artificial fruit. Model rank was determined by the outcome of dyadic conflicts recorded ad libitum and through regular observations of the order of access to food provided to the group by researchers since the habituation of the groups (between 2 and 5 years for each group). During this time the female hierarchies have remained highly stable, as is usual for vervet monkeys (Cheney & Seyfarth, 1990). Models defined as 'dominant' were the highest ranked females in their group, while 'low-rank' models were taken from the bottom half of the female hierarchy (positions six of 10 (AK), 11 of 12 (BD) and seven of 11 (NH)). All researchers collecting data at IVP were tested on monkey identification and interobserver reliability prior to data collection. Individual rank for all group members was calculated using the EloRating package in R (Neumann et al., 2011). In the control group (LT), no models were trained. In the fourth experimental group, KB, only a low-ranking model (a subadult female model who had her first offspring early in the test and was then ranked five of eight females) was trained to test the effects of a single model. Demonstrations and test sessions were conducted by J.B. and M.G., with the assistance of one or more trained field assistants, comprising volunteers and students at IVP.

Apparatus

To create two alternative behaviours in the two models, we used an 'artificial fruit', a polycarbonate box designed to mimic the characteristics of natural items that need to be opened to gain the edible fraction inside (hereafter simply 'box'). Access to the food reward inside required the opening of a small door on one side. The sides and top were painted black with only the door left transparent, to funnel the monkeys' attention to this part of the box. The base of the box tilted it back at a roughly 30 degree angle and two metal hooks allowed the box to be secured by hammering pegs into the ground.

One of two methods could open the door. First, the door was attached via a bolt in its top centre, allowing it to be pivoted around this bolt ('Pivot'). Second, the door contained a smaller section which was attached with hinges at the top, so this could be pushed inwards and upwards as an alternative means of opening ('Push'; see Fig. A1). Magnets held both door elements in place, so they could not be accidentally opened. A manual lock prevented one method of opening during training. Only one nonmodel attempted and failed to open the box during the demonstration phase and this individual later successfully opened the box in the test phase. All training, demonstration and tests were recorded using handheld Panasonic HD (HC-X920M) video cameras.

Training

The dominant female and a mid- to low-ranking female (hereafter low-ranking) from each of groups AK, NH and BD, and one low-ranking female from KB, were trained as demonstrators. Some females had been trained to approach boxes with patterned covers for a food reward during a previous study at the site (Borgeaud & Bshary, 2015). In the present study these covers were placed on top of the boxes during the training and demonstration phase to encourage the target females to approach the boxes; however, not all models had been trained on a cover, so covers were not used with Riss (low-ranking model, BD) and Ness (low-ranking model, KB).

Training was conducted over a period of 7–9 days on an opportunistic basis. Both models were usually trained on each day of training, in no particular order. The food reward used for each opening was a small piece of apple. The criterion for demonstration, which all models reached, was the successful opening of the box 10 times during two consecutive sessions, totalling 20 successful openings. The training was opportunistically conducted when there were few other monkeys in the area to minimize observation of the models being trained.