

Diffusion Dynamics of Socially Learned Foraging Techniques in Squirrel Monkeys

Nicolas Claidière,¹ Emily J.E. Messer,¹ William Hoppitt,² and Andrew Whiten^{1,*}

¹Centre for Social Learning and Cognitive Evolution, School of Psychology and Neuroscience, University of St Andrews, St Andrews KY16 9JP, Scotland, UK

²Department of Life Sciences, Anglia Ruskin University, Cambridge CB1 1PT, UK

Summary

Social network analyses [1–5] and experimental studies of social learning [6–10] have each become important domains of animal behavior research in recent years yet have remained largely separate. Here we bring them together, providing the first demonstration of how social networks may shape the diffusion of socially learned foraging techniques [11]. One technique for opening an artificial fruit was seeded in the dominant male of a group of squirrel monkeys and an alternative technique in the dominant male of a second group. We show that the two techniques spread preferentially in the groups in which they were initially seeded and that this process was influenced by monkeys' association patterns. Eigenvector centrality predicted both the speed with which an individual would first succeed in opening the artificial fruit and the probability that they would acquire the cultural variant seeded in their group. These findings demonstrate a positive role of social networks in determining how a new foraging technique diffuses through a population.

Results

Social network analysis (SNA) should prove to be useful and powerful in the study of social learning. Social learning, and in particular observational learning, relies on close proximity between individuals. In turn, proximity patterns often reflect particular social relationships, hence predicting that social learning will depend on the pattern of relationships between individuals [11]. Accordingly, it has recently been proposed that the study of social learning should make use of SNA to quantify patterns of social interactions and/or proximity that are likely to lead to the transmission of newly learned behaviors [12–20].

Just three published studies so far have explored the expected utility of SNA to test the hypothesis that social learning of foraging techniques occurs according to patterns of association. To date, these studies failed to find evidence that association coefficients predict the spread of behavior [12, 21, 22]. However, as pointed out by Kendal et al. [21], it is important to identify a social network appropriate to the task being studied. Here, for the first time, we monitored the copresence (the time dyads of monkeys spent together) near the foraging site to identify relevant social networks during a social learning experiment. We followed a standard “open group diffusion” procedure [23], in which one individual of each of two groups,

the model, was trained to open a “pivotage” artificial fruit using one of the two alternative techniques (see [Figure 1](#) and [Movie S1](#) available online). Once each model was trained, other individuals were given the opportunity to watch the model manipulating the pivotage and were then given access to it (see [Supplemental Experimental Procedures](#) for experimental details). We chose to train the alpha male of each group because alpha male squirrel monkeys typically monopolize feeding resources in the wild [25], making them a focus of attention and therefore likely models for social learning of foraging behavior.

Among the various measures that can be used to quantify the position of an individual in a network, Eigenvector centrality (hereafter, EV-centrality) is of particular interest for social learning studies. The EV-centrality of an individual increases with the strength of its social connections and more so when these connections are established with central individuals (individuals who themselves have numerous and strong connections [26]). EV-centrality therefore reflects the connections of the individual with the entire network, whereas other measures typically consider only local connections. Since a foraging innovation cannot arise in every individual's local network, it is individuals that are well connected to the whole network that are likely to learn the innovation earlier, if it diffuses through the group by observational learning. We therefore hypothesized that if the monkeys rely on observational learning, those with a high EV-centrality should tend to solve the task earlier and use the same technique as the model (see [Supplemental Information](#) for a discussion of the effect of different network measures). By contrast, if individuals do not rely on observational learning, their performance will more likely be linked to individual factors such as attention, motor control, or strength. Importantly, EV-centrality is independent of the total time spent in the experimental zone and does not simply reflect the total time spent observing the model (see [Supplemental Experimental Procedures](#) for full explanation of this consideration). Accordingly, we compared the effect of EV-centrality with that of age on the probability of monkeys being successful early in the experiment and of using a technique which matched that used by the original model. We used age as an indirect measure of nonsocial factors since age is linked to both cognitive and physical development and was not correlated with EV-centrality in our data ($r_s = -0.30$, $n = 15$, $p = 0.28$, 95% CI = $[-0.76, 0.20]$).

Attention and Motivation Increases after Observation of a Model

We found that individuals tended not to pay attention to a potential source of food for long if they did not find a solution to access the food quickly. Four control individuals out of five, without the benefit of watching a model, never managed to open the pivotage despite spending on average 20 min in the experimental zone (min = 16 min; max = 29 min) but soon losing interest (the rate at which the experimental apparatus was touched quickly decreased with the number of sessions; $r_s = -0.48$, $n = 4$, $p = 0.014$, 95% CI = $[-0.73, -0.13]$).

By contrast, during the open diffusion experiment, we found that a total of 15 individuals out of 22 (excluding models) were

*Correspondence: aw2@st-andrews.ac.uk





Figure 1. The Pivotage Being Opened

The artificial fruit could be opened in two ways, using either “lift” (top) or “pivot” (bottom). The door was held shut by a small magnet that prevented it from accidentally opening. Once the door was opened, monkeys could reach in and retrieve a reward from a small platform. To mimic natural conditions in which the food could be hidden from view (insects consumed by squirrel monkeys are often cryptic, for instance, see [24]), the door and the food container were opaque, so the food was not visible unless the door was opened.

successful at opening the pivotage and 21 individuals managed to move the door at least once during the test sessions (see Table S1). When compared to the one individual out of five who was successful in the control condition, these results confirm that a basic effect of the model is to maintain the attention and motivation necessary to learn a technique to gain food (individuals in the test condition were more likely to move the door than individuals in the control condition; Fisher’s Exact test, $p = 0.0014$).

Effect of Social Networks on the Spread of the Newly Introduced Technique

To analyze the factors influencing the potential spread of the alternative techniques in the two groups, we used a

generalized estimating equation (GEE). Two different actions that lead to the same result are unlikely to be of precisely the same difficulty; there is nearly always one that is easier to learn or to perform than the other. As a result, the diffusion and stability of the newly introduced techniques may be different in the two groups. We therefore included the effect of a group identity variable (effectively indicating which technique was demonstrated) and its interaction with other variables (age and EV-centrality). Furthermore, because the influence of observation on learning should manifest early on, we used the first 30 successes of each individual (excluding models) in our analysis of technique choice. The number of successes matching the technique of the model compared to the total number of successes (up to a total of 30) was used as the dependent variable. The GEE included EV-centrality, age, and group identity as main factors and interactions between group identity and age, and group identity and EV-centrality. We also controlled for the possibility that the time spent in the experimental foraging zone and the time spent observing the model might influence the technique used by including these two variables successively in the model. We found no significant effect of the time spent in the experimental zone (Wald chi-square = 1.70, degrees of freedom [df] = 1, $p = 0.19$) or the time spent observing the model (Wald chi-square = 0.13, df = 1, $p = 0.72$), and inclusion of these variables had little impact on the estimated effect of EV-centrality. This shows that EV-centrality is directly responsible for the technique learned and both variables were accordingly removed from the final model.

Despite the fact that models performed both techniques in the first test sessions, and a majority of individuals discovered and used both techniques at some stage (Figure 2 and Movie S1), we found strong evidence of a difference in the technique that the two groups used (Wald chi-square = 8.23, df = 1, $p = 0.004$; Figure 3). This shows that squirrel monkeys were more likely to learn the technique that was first introduced and performed by the model and therefore that they learned the techniques of their successful group mates.

We also found a group by EV-centrality interaction (Wald chi-square = 5.27, df = 1, $p = 0.022$). In the West group, more central individuals were more likely to be successful using the action used by the model, an effect we did not find in the East group (West group: Wald chi-square = 4.97, df = 1, $p = 0.026$; East group: Wald chi-square = 0.72, df = 1, $p = 0.40$). In the West group, by back-transforming the log odds ratio, we found that there was a 14.1% increase in the odds of using the model’s technique for every 1% increase in EV-centrality (EV-centrality varied between 2% and 43% in the West group). By contrast, the effects of age (Wald chi-square = 0.002, df = 1, $p = 0.96$) and of the interaction between group identity and age (Wald chi-square = 0.085, df = 1, $p = 0.77$) were small and nonsignificant, so these were removed from the final model. Furthermore, we found that across both groups, EV-centrality was strongly negatively correlated with the session in which individuals first solved the task ($r_s = -0.79$, $n = 15$, $p = 0.001$, 95% CI = [−0.96, −0.30]) but age was not ($r_s = 0.03$, $n = 15$, $p = 0.92$, 95% CI = [−0.51, 0.57]). Confirming this result, we found a positive correlation between the total number of successes and EV-centrality ($r_s = 0.62$, $n = 15$, $p = 0.013$, 95% CI = [0.14, 0.95]) but not age ($r_s = 0.15$, $n = 15$, $p = 0.60$, 95% CI = [−0.44, 0.65]). Therefore, as predicted, individuals with high EV-centrality tended to solve the task earlier than individuals with low EV-centrality and individuals who solved the task earlier had more time to be successful and to become efficient at the task.

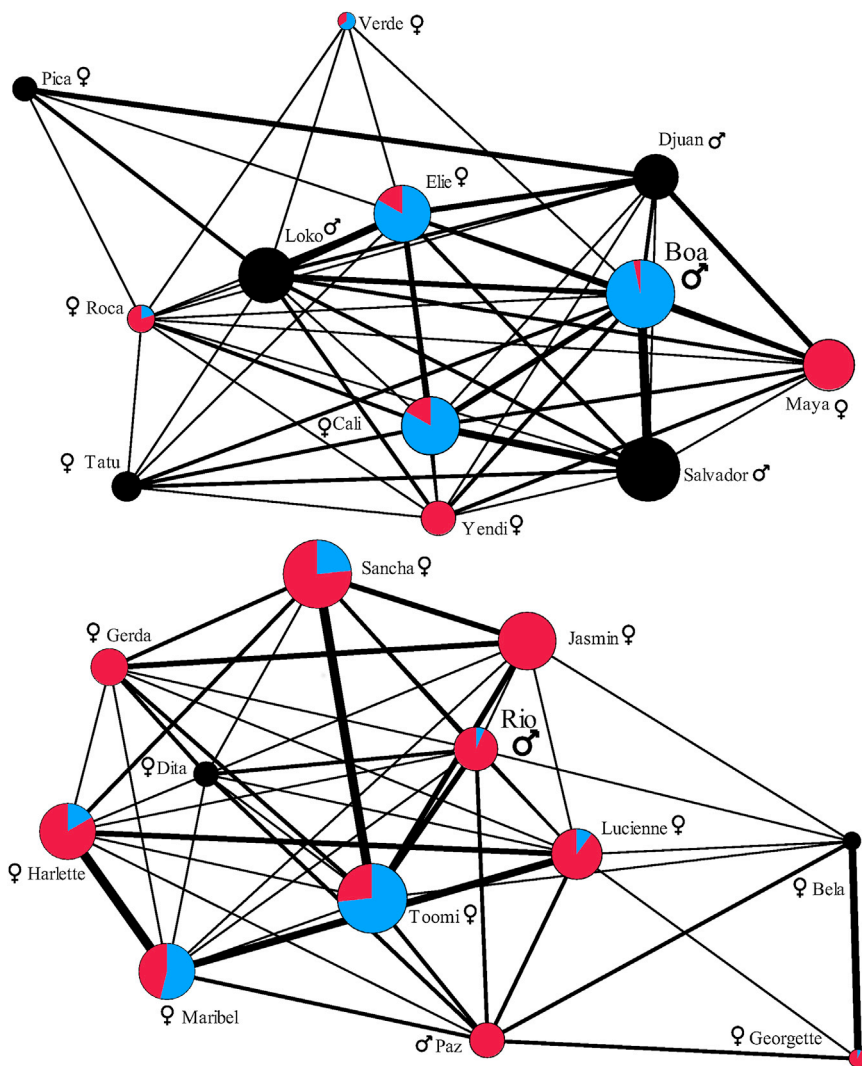


Figure 2. Experimental Sociograms for the Two Groups

Sociograms of East group (top) and West group (bottom). Link size is proportional to bond strength. Node size is proportional to the Eigenvector centrality. Node color indicates the actions performed by each monkey: the pie chart represents the proportion of successful lifts (blue) and pivots (red) for a maximum of 30 successes; a black circle represents individuals who never opened the pivotage successfully.

Discussion

Our results provide evidence of social learning in common squirrel monkeys [see also 29]. Naive, control individuals showed initial interest in the novel pivotage, but this interest soon eroded when they failed to open it. In contrast, once they watched a proficient model retrieve reward(s), the majority of individuals learned to solve the task. The actions of a single successful individual are thus sufficient to maintain interest from most naive individuals and facilitate their learning. It is unclear if the status of the initial model within the social network is important because this was not a variable we could manipulate: indeed this question is challenging to study experimentally because it requires multiple tests with different models [see 30 for a study with multiple models].

Individuals in each group were more likely to use the technique used by their model than individuals in the other group, confirming that techniques diffused through social learning. This finding adds to a recently growing

Progressive Erosion of the Difference between Groups

As in many previous studies [e.g., 10, 27, 28], the preference for the model's technique did not prevent a progressive erosion of the difference in the techniques exhibited in the two groups (Figure 4). To analyze the change in behavior across time, we used a GEE in which, as previously, the dependent variable was the number of successes matching the modeled technique compared to the total number of successes (up to 30). The subject variable was the individual monkey (excluding models), and a session by group (East or West) interaction defined the within subject variable.

For the West group, there was strong evidence that the preference for the model's option decreased over time (Wald test: $\chi^2 = 10.1$, $df = 1$, $p = 0.001$), with the fidelity to the model (odds of copying the model) decreasing by an estimated 22.5% per session (95% CI = 9.3%–33.8%). There was little evidence of such a decrease in the East group (Wald test: $\chi^2 = 0.34$, $df = 1$, $p = 0.56$; 95% CI = 11.9% decrease to 7.1% increase). Correspondingly, there was evidence of a greater decrease over time in the West group than the East group (Wald test: $\chi^2 = 5.69$, $df = 1$, $p = 0.017$), with the ratio of effects (East/West) estimated at 0.80 (95% CI = 0.66–0.96).

literature that has provided evidence for the spread through social learning of foraging techniques [6, 8, 9, 23, 29, 31–36]. Social learning may be of particular significance to squirrel monkeys in the wild because their diet includes prey such as Lepidopterans and Orthopterans, which are typically cryptic and sometimes toxic [24, 25], so that social learning about foraging is likely to be highly adaptive.

The group differences in the technique preferred imply a social learning process that goes beyond the local enhancement effect that may account for the difference between baseline control monkeys and those who observed a model, since the alternative techniques were both performed at the same location. Candidate processes would include imitation (copying monkeys' lifting versus pivoting actions) or emulation (reproducing lifting versus pivoting movements of the door) but our experiment was not designed to discriminate between these (see [29] for a recent experiment designed to make such a distinction in Bolivian squirrel monkeys).

Of more general significance in our study is the demonstration that social factors, captured here by the EV-centrality of individuals in their social network, mattered more than nonsocial factors, represented by age, in determining how quickly

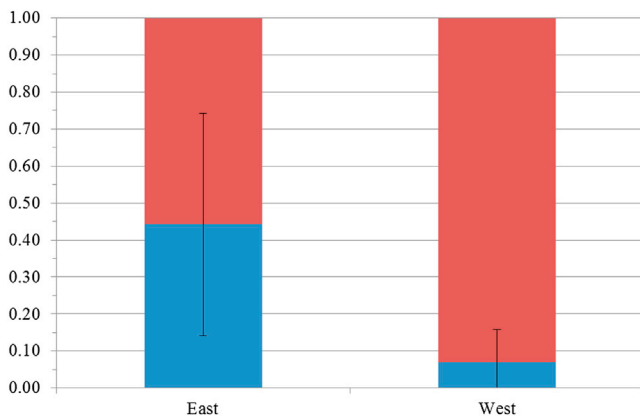


Figure 3. Between-Groups Social Learning Effect

The probability of performing lift was higher in the East group (with a lift model) than in the West group (with a pivot model), as predicted by the social learning hypothesis. On the y axis is the probability of performing lift (blue) over the alternative pivot (red) technique. The values reported are the estimated means and 95% confidence intervals (CIs) of the mean from the GEE model described in the text.

individuals solved the task and whether they used the same technique as the model. It is important to distinguish between two different goals that one might have when identifying social networks to understand social learning. The first, our primary objective here, involves testing whether close proximity has an effect on learning, and thus whether there is evidence for social transmission in a group context. The fact that we found an effect of EV-centrality on technique acquisition shows that close proximity can predict learning. A second objective would be to identify which relationships can predict the observation of other individuals. We did not directly address this question, but we note that individuals from the same matriline had higher association coefficients than nonmatriline members in our networks (matriline pairs, $n = 16$, median = 0.16, SE = 0.04; nonmatriline pairs, $n = 79$, median = 0.03, SE = 0.01; Mann-Whitney $U = 1,078.5$, $n = 95$, $p = 7.008 \times 10^{-6}$; unknown pairs, $n = 15$). This shows that maternal relatedness between individuals affected their participation in the task and their EV-centrality. Furthermore, although EV-centrality is a summary measure that is based on association coefficients between pairs of individuals, we find that it accurately predicts social learning. In less controlled environments, such as an open diffusion context or in the wild, SNA and its associated network statistics thus represent useful alternatives to the detailed modeling of each individual's behavior.

More central individuals could access the pivotage in the presence of various others, independently from the total time spent in the experiment. They thus had more opportunities to witness already successful individuals and to learn from them, indirectly acting as models to others as a result. To the best of our knowledge, this is the first experiment showing that the social network can predict both the speed of acquisition of an action and the probability of using the technique witnessed the most. This is important because despite the fact that the strength of association between two individuals could be expected to influence their probability of learning from each other, previous studies have not confirmed this relationship [12, 21, 22]. A possible explanation for the difference between the findings of this study and previous ones is the origin of the association matrices. Here, we used the copresence of

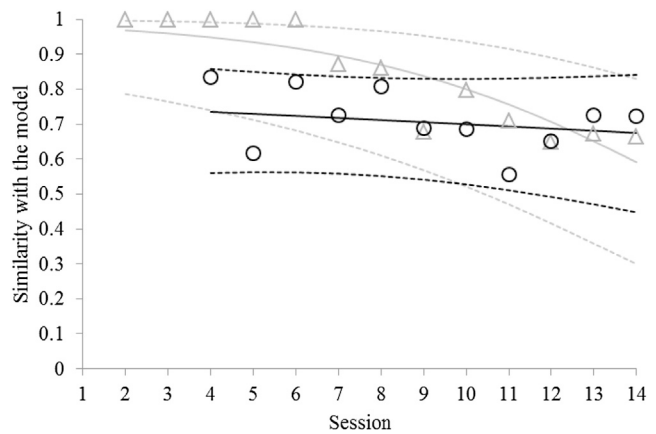


Figure 4. Erosion of Group Differences over Time

Similarity with the model-trained technique (number of actions matching that of the model divided by the total number of actions) for the East (black circles) and West (gray triangles) groups across the 14 test sessions. The solid lines represent the mean and the dotted lines the 95% CI results from the GEE model described in the main text. Individuals started to be successful in the West group earlier than in the East group (second and fourth sessions, respectively).

individuals in proximity to the artificial fruit as the source of our association coefficients, rather than a measure independent of the foraging context (such as grooming or other affiliative behaviors as are typically measured in nonforaging contexts; with the exception of [18]).

The group differences our experiment created progressively disappeared through time. This erosion of differences might be due to limited fidelity of social transmission and/or individuals being progressively more likely to change their technique as they become more expert at the task and explore it further. Indeed, even the trained models discovered and began to evidence both techniques during the early test trials. Both factors are likely to be important but other analyses, perhaps fitting models representing different individual and social learning effects, will be required to disentangle such potential effects.

The progressive erosion of group difference also speaks to the more general issue of the role of social learning in explaining cultural stability. Social learning is widespread among animals [37, 38] but there are important differences in the extent to which different species develop stable group-specific behaviors [6, 7]. This suggests that although social learning is necessary for culture, it will not in itself necessarily sustain stable, between-group diversity in behavior. In the present experiment, for instance, the squirrel monkeys relied on social learning to solve the task and acquire a particular technique but this did not lead to stable group differences in behavior. To achieve a better understanding of the origin of culture, we therefore need a deeper analysis of the factors responsible not only for the spread but also for the stability of behaviors among groups of individuals over time [27, 39].

Conclusion

Our results indicate that EV-centrality, but not age, plays an essential role in the spread of new foraging techniques by affecting both the speed of learning and the technique learned. The study of social learning should therefore make use of SNA to quantify patterns of social interactions and/or proximity that are likely to lead to the transmission of newly learned

behaviors. However, our results also highlight the importance of choosing a measure of association linked to the task being studied rather than obtained in a different context when studying social learning.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two tables, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.05.036>.

Acknowledgments

We are very grateful to Mark Bowler, Cédric Sueur, and Erica van de Waal for comments on an earlier version of the manuscript. We are also thankful to Andy Burnley for constructing the apparatus and to Charlotte MacDonald and the Living Links Animal Keeping Care Staff for their assistance with the monkeys. E.M. gratefully acknowledges funding from the Cross Trust and W.H. was supported by a BBSRC grant (BB/I007997/1).

Received: March 26, 2013

Revised: May 17, 2013

Accepted: May 22, 2013

Published: June 27, 2013

References

- Croft, D.P., James, R., and Krause, J. (2008). *Exploring Animal Social Networks* (Princeton: Princeton University Press).
- Whitehead, H. (2008). *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis* (Chicago: University of Chicago Press).
- Krause, J., Lusseau, D., and James, R. (2009). Animal social networks: an introduction. *Behav. Ecol. Sociobiol.* 63, 967–973.
- Sueur, C., Jacobs, A., Amblard, F., Petit, O., and King, A.J. (2011). How can social network analysis improve the study of primate behavior? *Am. J. Primatol.* 73, 703–719.
- Sueur, C., Deneubourg, J.-L., Petit, O., and Couzin, I.D. (2011). Group size, grooming and fission in primates: a modeling approach based on group structure. *J. Theor. Biol.* 273, 156–166.
- Laland, K.N., and Galef, B.G., eds. (2009). *The Question of Animal Culture* (Cambridge: Harvard University Press).
- Whiten, A., Hinde, R.A., Laland, K.N., and Stringer, C.B. (2011). Culture evolves. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366, 938–948.
- Gruber, T., Müller, M.N., Strimling, P., Wrangham, R., and Zuberbühler, K. (2009). Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Curr. Biol.* 19, 1806–1810.
- Müller, C.A., and Cant, M.A. (2010). Imitation and traditions in wild banded mongooses. *Curr. Biol.* 20, 1171–1175.
- van de Waal, E., Borgeaud, C., and Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science* 340, 483–485.
- Coussi-Korbel, S., and Frigaszy, D.M. (1995). On the relation between social dynamics and social learning. *Anim. Behav.* 50, 1441–1453.
- Boogert, N.J., Reader, S.M., Hoppitt, W., and Laland, K.N. (2008). The origin and spread of innovations in starlings. *Anim. Behav.* 75, 1509–1518.
- Franz, M., and Nunn, C.L. (2010). Investigating the impact of observation errors on the statistical performance of network-based diffusion analysis. *Learn. Behav.* 38, 235–242.
- Franz, M., and Nunn, C.L. (2009). Network-based diffusion analysis: a new method for detecting social learning. *Proc. Biol. Sci.* 276, 1829–1836.
- Hoppitt, W., Boogert, N.J., and Laland, K.N. (2010). Detecting social transmission in networks. *J. Theor. Biol.* 263, 544–555.
- Voelkl, B., and Noë, R. (2010). Simulation of information propagation in real-life primate networks: longevity, fecundity, fidelity. *Behav. Ecol. Sociobiol.* 64, 1449–1459.
- Hoppitt, W., and Laland, K.N. (2011). Detecting social learning using networks: a users guide. *Am. J. Primatol.* 73, 834–844.
- Aplin, L.M., Farine, D.R., Morand-Ferron, J., and Sheldon, B.C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proc. Biol. Sci.* 279, 4199–4205.
- Mann, J., Stanton, M.A., Patterson, E.M., Bienenstock, E.J., and Singh, L.O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. *Nat Commun* 3, 980.
- Rutz, C., Burns, Z.T., James, R., Ismar, S.M.H., Burt, J., Otis, B., Bowen, J., and St Clair, J.J.H. (2012). Automated mapping of social networks in wild birds. *Curr. Biol.* 22, R669–R671.
- Kendal, R.L., Custance, D.M., Kendal, J.R., Vale, G., Stoinski, T.S., Rakotomalala, N.L., and Rasamimanana, H. (2010). Evidence for social learning in wild lemurs (*Lemur catta*). *Learn. Behav.* 38, 220–234.
- Schnoell, A.V., and Fichtel, C. (2012). Wild redfronted lemurs (*Eulemur ruffifrons*) use social information to learn new foraging techniques. *Anim. Cogn.* 15, 505–516.
- Whiten, A., and Mesoudi, A. (2008). Establishing an experimental science of culture: animal social diffusion experiments. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 363, 3477–3488.
- Sussman, R.W. (2000). *Primate Ecology and Social Structure, Volume 2: New World Monkeys* (Upper Saddle River: Pearson Custom Publishing).
- Boinski, S. (1999). The social organizations of squirrel monkeys: Implications for ecological models of social evolution. *Evol. Anthropol.* 8, 101–112.
- Newman, M.E.J. (2004). Analysis of weighted networks. *Phys. Rev. E Stat. Nonlin. Soft Matter Phys.* 70, 056131.
- Claidière, N., and Sperber, D. (2010). Imitation explains the propagation, not the stability of animal culture. *Proc. Biol. Sci.* 277, 651–659.
- Thornton, A., and Malapert, A. (2009). The rise and fall of an arbitrary tradition: an experiment with wild meerkats. *Proc. Biol. Sci.* 276, 1269–1276.
- Hopper, L.M., Holmes, A.N., Williams, L.E., and Brosnan, S.F. (2013). Dissecting the mechanisms of squirrel monkey (*Saimiri boliviensis*) social learning. *PeerJ* 1, e13.
- Horner, V., Proctor, D., Bonnie, K.E., Whiten, A., and de Waal, F.B.M. (2010). Prestige affects cultural learning in chimpanzees. *PLoS ONE* 5, e10625.
- Whiten, A., Horner, V., and de Waal, F.B. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature* 437, 737–740.
- Dindo, M., Thierry, B., and Whiten, A. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proc. Biol. Sci.* 275, 187–193.
- Sherry, D.F. (2008). Social learning: nectar robbing spreads socially in bumble bees. *Curr. Biol.* 18, R608–R610.
- Wilkinson, A., Kuenstner, K., Mueller, J., and Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biol. Lett.* 6, 614–616.
- Hopper, L.M., Schapiro, S.J., Lambeth, S.P., and Brosnan, S.F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Anim. Behav.* 81, 1195–1202.
- van de Waal, E., Claidière, N., and Whiten, A. (2013). Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. *Anim. Behav.* 85, 71–76.
- Heyes, C., and Galef, B.G., eds. (1996). *Social Learning in Animals: The Roots of Culture* (San Diego: Academic Press).
- Hoppitt, W., and Laland, K. (2008). Social processes influencing learning in animals: a review of the evidence. *Adv. Stud. Behav.* 38, 105–165.
- Claidière, N., and Sperber, D. (2010). The natural selection of fidelity in social learning. *Commun. Integr. Biol.* 3, 350–351.