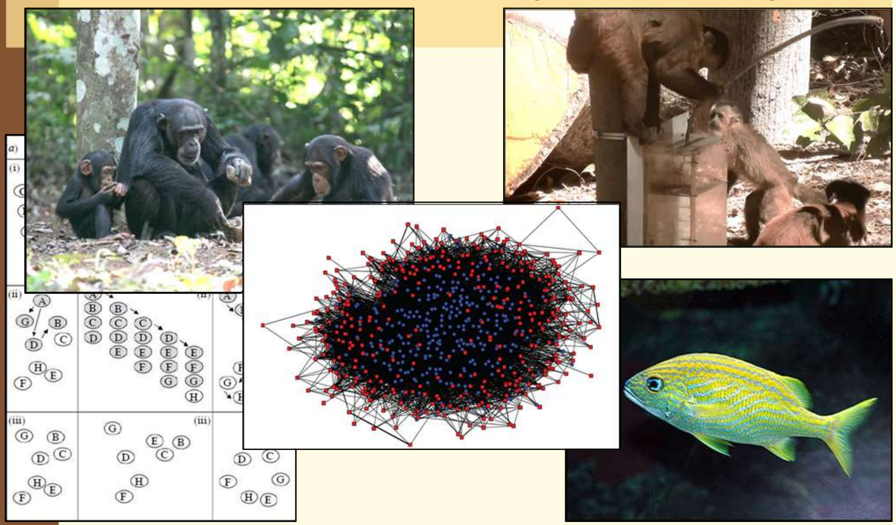
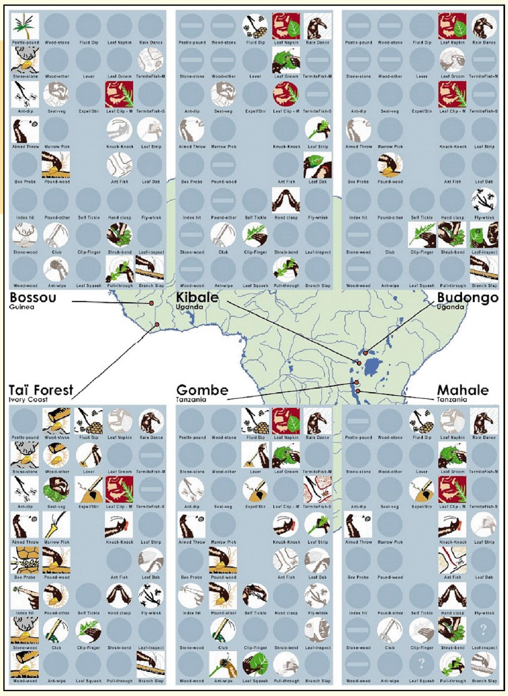
Animal social learning in the laboratory and in the wild: improving methodologies



Cultures in chimpanzees

39 distinct behavioral patterns, including the use of tools, foraging, grooming and courtship behaviors, are customary or habitual in some communities but absent in others, discounted the cases that allowed for ecological explanations.

Whiten, Goodall, McGrew, Nishida, Reynolds, Sugiyama, Tutin, Wrangham & Boesch 1999



A Guide to the Cultures of Chimpanzees

In an effort to catalogue variations among chimpanzees, we asked researchers working at six sites across central Africa to classify chimpanzee behaviors in terms of occurrence or absence in seven communities. (There are two communities at Mahale.) They key categories were customary behavior, which occurs in most or all members of one age or sex class; habitual, which is less common but which still occurs repeatedly; present; absent; and unknown. Certain behaviors are absent for ecological reasons (eco): for example, chimpanzees do not use hammers to open coula nuts at Budongo, because the nuts are not available. The survey turned up 39 chimpanzee rituals that are labeled as cultural variations; 18 are illustrated below. -A.W. and C.B.

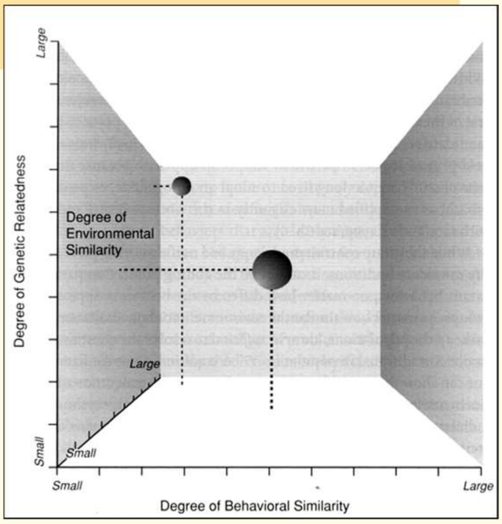
	BOSSOU	TAI FOREST	GOMBE	MAHALE M-GROUP	MAHALE K-GROUP	KIBALE	BUDONGO
Hammering nuts To crack open nutritious coula nuts, chimpanzees use stones as rudimentary hammers and anvils.	**customary**	**customary**	absent	absent	absent	absent (eco?)	absent (eco?)
Pounding with pestle With stalks of palm trees acting as makeshift pestles, chimpanzees can pound and deepen holes in trees.	**customary**	absent	absent	absent (eco?)	absent (eco?)	absent (eco?)	absent (eco?)
Fishing for termites Chimpanzees insert thin, flexible strips of bark into termite mounds to extract the in- sects, which they then eat.	absent	absent (eco?)	**customary**	absent	**customary**	absent (eco?)	absent (eco?)
Wiping ants off stick manually Once the ants have swarmed almost half- way up sticks dipped into the insects' nests, chimpanzees pull the sticks through their fists and sweep the ants into their mouths.	present	absent	**customary**	absent	absent	absent	absent
Eating ants directly off stick After a few ants climb onto sticks inserted into the nests, chimpanzees bring the sticks directly to their mouths and eat the ants.	**customary**	**customary**	**present**	absent	absent	absent	absent
Removing bone marrow With the help of small sticks, chimpanzees eat the marrow found inside the long bones of monkeys they have killed and eaten.	absent	**customary**	absent	absent	absent	absent	absent
Sitting on leaves A few large leaves apparently serve as protection when chimpanzees sit on wet ground.	present	**habitual**	absent	absent	absent	**present**	absent
Fanning Flies To keep flies away, chimpanzees utilize leafy twigs as a kind of fan.	absent	**habitual**	present	absent	absent	absent	**habitual**
Tickling self A large stone or stick can be used to probe especially ticklish areas on a chimpanzee's own body.	absent	absent	**habitual**	absent	absent	absent	absent

Customary, habitual, present or absent behaviours

Criticism of the "Group Comparison" method

Fragaszy & Perry 2003

Behavioral traditions **defined** by SBL; Intergroup variation is **not** required. (comparisons between populations DO NOT show mechanisms)



"False positives" and "false negatives"

Cultural differences in chimpanzees?

Stick tools in army ants dipping

Differences in sticks' length and capture techniques:
Gombe: "pull-through"
X Taï: "direct mouthing"
BUT: Humle & Matsuzawa 2002:

Bossou:
Both techniques:

Lenght varies as a function of ants' behavior (different species)

Cultural differences in chimpanzees?

BUT:
Möbius, Boesch, Koops, Matsuzawa & Humle (2008)

Chimpanzees at two long-term study sites in West Africa (Bossou/Taï) prey on the same five army ant species but adopt different strategies.

Controlled simulations of ant dipping and an ant survey at these two sites to evaluate alternative ecological explanations that could account for the observed differences in behaviour: **ant speed explained differences in tool length within Bossou but not between Bossou and Taï; results do not support an ecological basis underlying the lack of dipping at ant trails in Taï chimps; neither ant aggressiveness (…) nor yield when using tools could explain why, unlike Bossou chimpanzees, Taï chimpanzees do not use tools to harvest *Dorylus* epigaeic species**.

An interaction of cultural and ecological factors shapes the differences in army ant predation between Taï and Bossou chimpanzees.

A "Process" Model of Traditions
Fragaszy 2003

"A tradition is a behavioral practice that is shared among members of a group; is performed repeatedly over a period of time (…); and depends to a measurable degree on social contributions to individual learning for its appearance in new practitioners"

Distribution:
socialization ("species-typical") x
conventionalization (groups/individuals)

Duration: trans-generational x "fads"

Contribution of social context:
longitudinal studies, ontogeny etc

A "Process" Model of Traditions
Fragaszy 2003

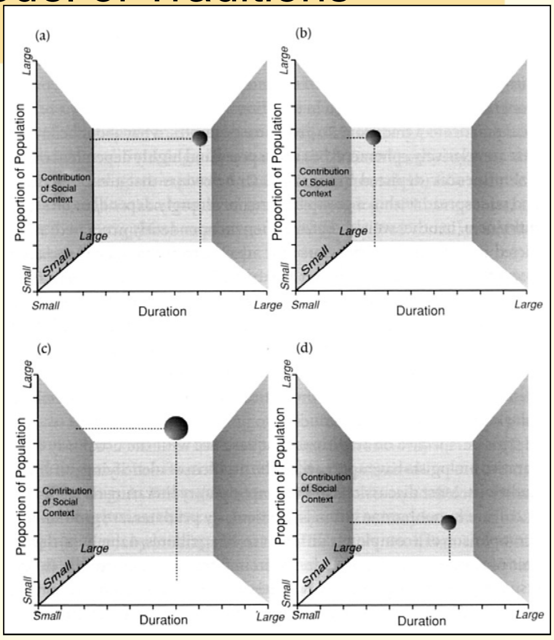
"Tradition space":

A. "Tradition"

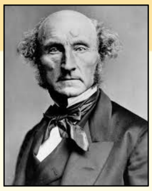
B . "Fad"

C. Durable & widespread behavior, not very dependent on SBL

D. SBL, but few individuals...



Fragaszy 2003



Methods to study traditions

(J. S. Mill:
four methods of inductive reasoning using comparative evidence:)

Causal Inference:

Joint Method of **Agreement** and **Difference**.

One variable held constant
X
One variable manipulated

This kind of experimental study is hardly feasible under natural conditions...

Fragaszy 2003

Correlation:

Method of **Residues**: one subtracts the magnitude of a phenomenon known to be associated with one set of conditions from its magnitude observed in a different, but closely related, set of conditions. We attribute the difference in the magnitude of the phenomenon to the differing conditions.
Ex: grooming rate x presence or absence of a particular parasite

Method of **Concomitant Variations**: comparison of the size of a phenomenon between two or more circumstances; concordance between behavioral similarity in pairs of animals within a group
Ex: Perry et al 2003: traditions in white-faced capuchins
Panger et al 2004. foraging technique x the proportion of time in proximity
van Schaik 2003: party size and presence of traditions in orangutans

None provides clear **causal** evidence

Fragaszy 2003

What evidence for social learning can we expect to collect from naturalistic observations?

"Field observers can document social contexts in which behaviors occur, changes over time in individual performance, and intragroup variation in behavior at a particular time; they also can seek comparable evidence about specific practices in other groups of the same species or related species. All of these kinds of evidence are useful to establish that social context aids a member of a group to acquire a behavior that others in the same group also perform".

Refining the comparative approach

Difficulty of studying the acquisition of behaviors in the field
Indirect evidence: spatial-temporal patterns
Complementarity of approaches

"The overall spatiotemporal patterns revealed by comparative studies, notwithstanding, can be useful in many ways; first, they show us which behaviors are species-typical, and which are rare or unique to particular populations, and this can guide investigative strategies; they can help to identify correlations between behavioral traits and prominent genetic or ecological factors (such as subspecies' distributions or very different environments), and, sometimes, to detect telltale clues of socially influenced behaviors, such as behavioral discontinuities associated with geographical barriers to intergroup diffusion"

van Schaik 2003

Refining the comparative approach

van Schaik 2003

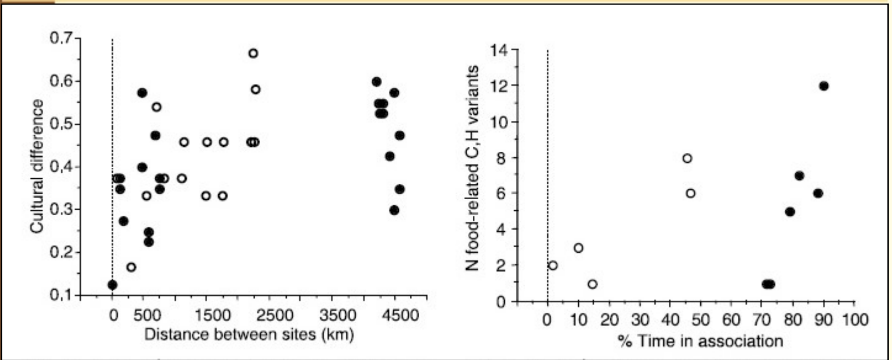
Hypothesis of the "Opportunities for Social Learning"

(van Schaik et al 1999:)
Social tolerance during gregarious foraging optimizes **invention** and **maintenance** of tool use techniques by social learning

Toolkit size should reflect an equilibrium between the **introduction rate** (innovation or diffusion) and the **rate of extinction** (by transmission failure)

Group/party sizes / interindividual distances / duration of association → toolkit sizes

Refining the "comparative" approach



van Schaik et al 2003

chimpanzees ● / orangutans○

The hypothesis of "innovation-and-diffusion"

Geographic distance and cultural differences
Association time and size of local repertoires

Fragaszy 2003

Longitudinal Methods:

How a characteristic comes about or changes through time in an individual and in groups.

Ontogeny and Socially-Biased Learning

- Birdsong
- Terkel's rats
- Stone-handling in Japanese macaques
- Nut-cracking in chimpanzees and capuchin monkeys
- …

Patterns of social diffusion of innovations

- Spontaneous (luck!)
- Experimentally-induced

Ontogenetic studies: development of lithic tools use

Development, social tolerance and opportunities for SBL

Resende & Ottoni 2002, Resende 2004, Ottoni, Resende & Izar 2005

Nut cracking observation
Exploration of nutcracking sites

Tool use in nut cracking by capuchin monkeys (Cebus apella): opportunities for social learning

Resende & Ottoni 2001

- Observation and scrounging
- Young observers seem to discriminate the proficiency of their potential "targets"

(Ottoni, Resende & Izar 2005)

Ontogenetic studies: development of lithic tools use

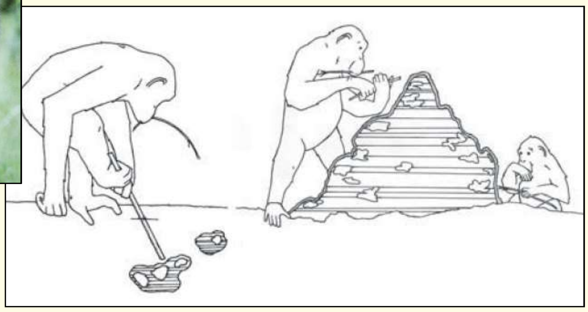
Observation & scrounging opportunities

X joined PET II group in 9/2003…

Z, in 2/2004

X and Z, introduced subadults:
X associated with peripheral proficient female and learned;
Z became a (delayed) scrounger...

Ontogenetic studies



Chimpanzees: acquisition of the use of probes to collect termites: faster in young females (who spend more time with mothers)

Lonsdorf et al 2004

Ontogeny of a Social Custom in Wild Chimpanzees: Age Changes in Grooming Hand-Clasp at Mahale
Nakamura & Nishida 2013

The ontogeny of GHC showed several dissimilarities with that of tool use and was more an extension of the development of typical grooming behavior. For example, infants did not try to perform GHC initially; instead, mothers were more active in the earliest stages.

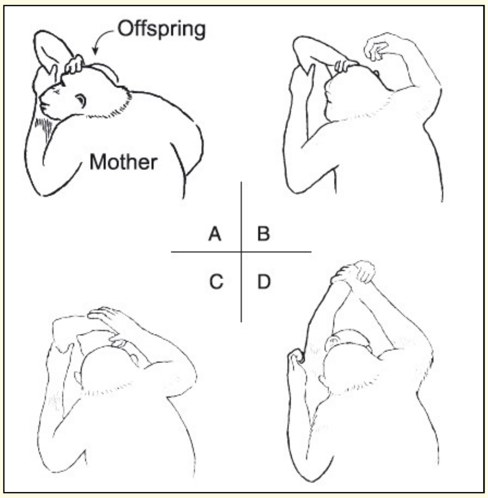
These results suggest that not all socially learned cultural behaviors are acquired in the way of learning tool use. There may be various ways of learning behavioral patterns that are performed continuously in a group and that consequently comprise culture in chimpanzees.

Ontogeny of a Social Custom in Wild Chimpanzees: Age Changes in Grooming Hand-Clasp at Mahale
Nakamura & Nishida 2013

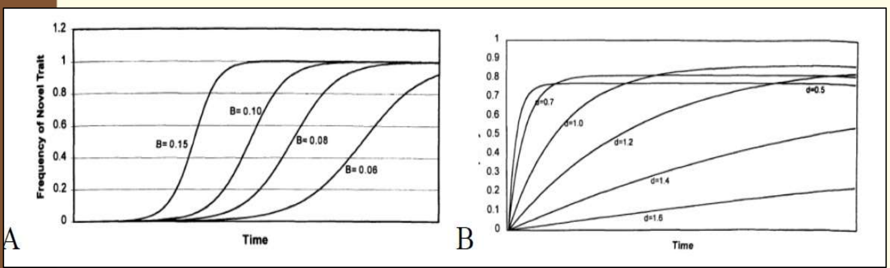
1st. HCH:
With mother: ~4-6yo
w. nonrelated females: ~ 9yo
w. adult males: ~11yo

A mother "molding" the offspring gesture

(Obs: remember Washoe and Loulis!)



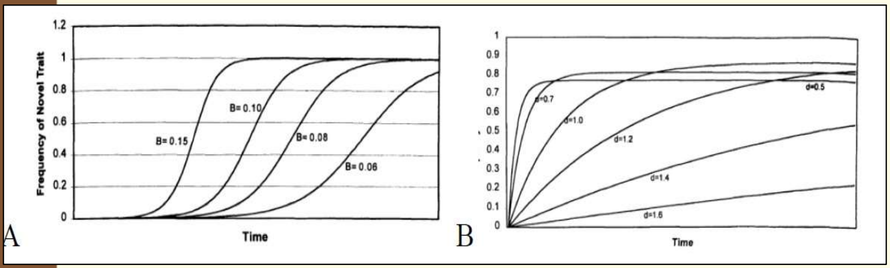
Evidence of SBL: "Diffusion Curves"?



(A) curves biased by cultural transmission ("S" Format)
(B) "individual" learning curves ("R" Format) [Henrich 2001]

Criticism:
Effects of social context and conditions of acquisition
Lefebvre (1995): scrounging may slow down the learning curve (false negative); if the latency of individual learning shows a normal distribution, the acquisition of a behavior by "trial-and-error" may, at the population level, describe a diffusion with an S-shaped curve (false positive).
Laland & Kendal (2003): it is rare to follow the innovation of a behavior: researchers might find curves that seem to be slowing down (R-shape) when they are in fact describe diffusion in its final stage (false negative of SBL).
Hoppitt et al (2010): Social structure and stage of diffusion: false positives or negatives. Neophobia and reinforcement for completed sub-stages might result in S-shaped diffusion curves (false positive).

Evidence of SBL: "Diffusion Curves"?

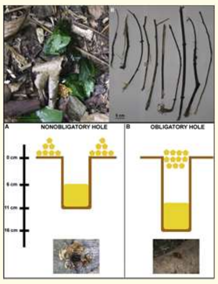


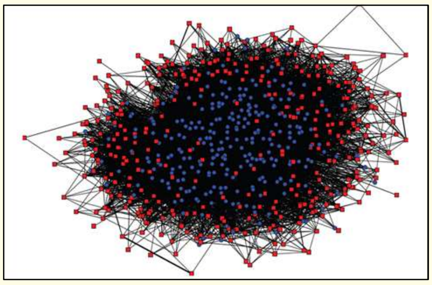
(A) curves biased by cultural transmission ("S" Format)
(B) "individual" learning curves ("R" Format) [Henrich 2001]

Laland & Kendal 2003:
"Reasoning as to the nature of the learning processes underlying the diffusion of an innovation on the basis of the shape of its diffusion curve is premature in the absence of a truly satisfactory body of theory that makes detailed predictions based on an extensive modeling of the relevant processes. The suggestion that asocial learning is likely to lead to linear increase over time and social learning to acceleratory or sigmoidal diffusion should now be regarded as discredited"

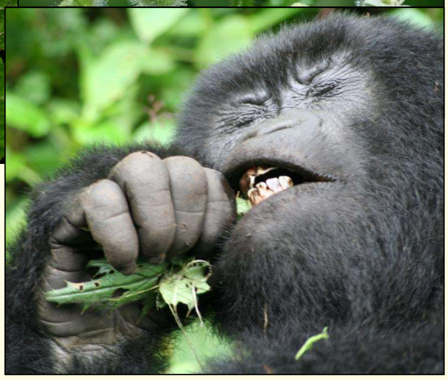
Comparative experimental studies: Laboratory & Nature

Comparative experimental studies:
Wild populations' studies





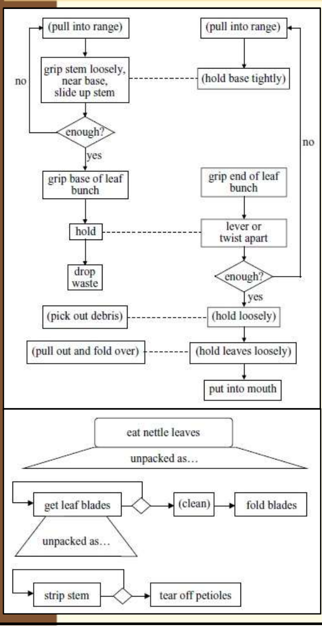
Byrne & Russon (1998): "action-level imitation"?



Irritating leaves' processing by one population of mountain gorillas (*Gorilla beringei beringei*) in subalpine moss forest and temperate meadows of volcanoes in Rwanda, Zaire, and Uganda (others eat "easier" items such as fruit)

Byrne (2003): Imitation as behaviour parsing

Nettle processing by mountain gorillas



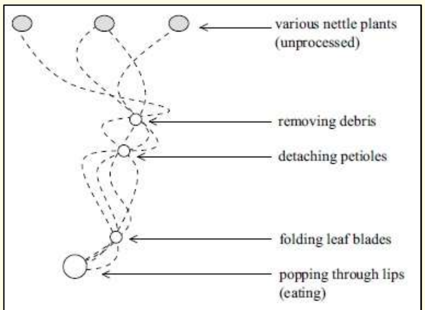


Figure 2. Nettle processing may be viewed as paths through a two-dimensional space of transformations, where each transformation is an action that may be applied. Because each plant is potentially unique in form, each is represented as a different starting point. The manual operations that are applied will vary on each occasion, so no paths overlap perfectly. However, certain operations are critical for success, and these are represented as points where all paths converge. These convergence points define the *essential* actions that must always be performed for eventual success, and may allow them to be recognized among the many inessential, idiosyncratic movements in a typical real sequence.

Byrne & Russon (1998): “action- level imitation”?

Table 1. *Levels of imitation*[a]

Impersonation	Pick out a strand of green galium from the mass with any precision grip of the left hand and transfer the hold to a power grip by the other fingers of this hand, then repeat this cycle while still holding the picked strands in a power grip of the other fingers of the left hand, until the bundle is sufficiently large. Then fold in any loose strands by using the right hand to bend in any loose strands while loosening and regrasping the mass of stems in the left hand, or, if this is easier at the time, by letting go with the finger and thumb of the left hand so that the bundle is held only by other fingers, then rocking the hand to allow grasping of both loose and gripped strands by finger and thumb again, then repeat this process so that the other fingers grasp the bundle firmly, and repeat the whole cycle until all strands are held. Then grip the bundle of galium loosely with the left hand half-open, pick out any debris with a pad-to-pad precision grip of the first finger and thumb of the right hand. Then grip the bundle tightly with the left hand and eat by feeding into the mouth until full, then shear off the rest by a molar bite, repeating when mouth empty again.
	Pick out a strand of green galium from the mass, then repeat this while still holding already picked strands until the bundle is sufficiently large. Then fold in any loose strands with the other hand (or with a rocking motion of the hand holding the bundle with repeated letting go and regrasping of strands if this is easier at the time). Then grip the bundle of galium loosely with the hand half open, pick out debris with the first finger and thumb of the other hand. Then grip tightly and eat with shearing bites.
Program level	Repeatedly pick green strands of galium with one hand, then use the other hand to fold in loose strands, then hold the bundle loosely with one hand and remove debris with the other hand, then eat.
	Pick a bundle of galium, tidy it up, remove debris from it, then eat.
Goal emulation	Eat galium.

Standardization of nettle processing technique (with differences in motor details) is an evidence of social learning? (BUT no other populations to be compared...)

Tennie, Hedwig, Call & Tomasello (2008)
An Experimental Study of Nettle Feeding in Captive Gorillas

Tennie et al (2008) presented western lowland gorillas (*Gorilla gorilla gorilla*) with highly similar nettles. Twelve gorillas in three different groups (including also one nettle-naïve gorilla) used the same program-level technique as wild mountain gorillas (with differences mainly on the action level).

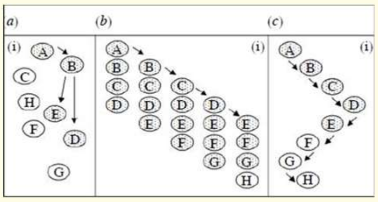
On the other hand, chimpanzees, orangutans, and bonobos did not show these program-level patterns, nor did the gorillas when presented with a plant similar in structural design but lacking stinging defenses.

Authors’ conclusion: although certain aspects (i.e. single actions) of this complex skill may be owing to social learning, **at the program level gorilla nettle feeding derives mostly from genetic predispositions and individual learning of plant affordances**.

Comparative experimental studies: Laboratory & Nature

Comparative experimental studies:
Wild populations' studies

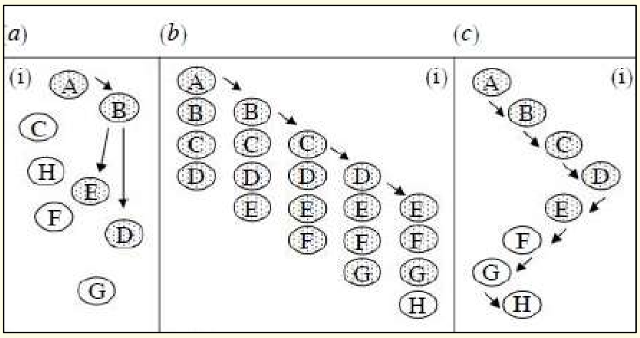
Cultural diffusion experiments with captives



The spread of traditions: experimental designs

Whiten & Mesoudi 2008

(a) open diffusion
(b) replacement method
(c) linear chain



+

- two groups/models, different techniques seeded
- control groups, no model, individual learning

Whiten, Horner & de Waal (2005)

Conformity to cultural norms of tool use in chimpanzees

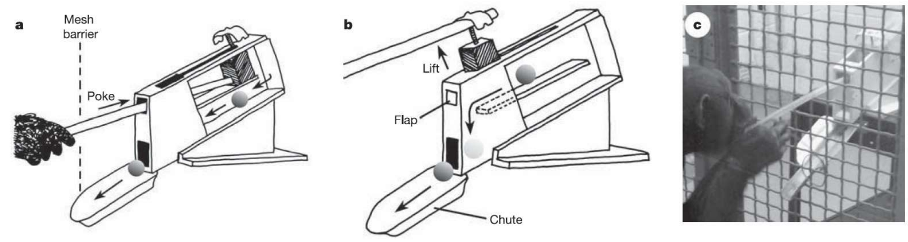


Figure 1 | Two techniques for gaining food from the 'Pan-pipes' apparatus. For each technique, the chimpanzee must insert a stick-tool through mesh caging to contact the apparatus and free a desirable food item that is trapped behind a blockage in the upper of two pipes. The food then rolls down a chute into the chimpanzees' enclosure. The Pan-pipes were 12 cm outside of the enclosure. **a**, In the Poke method, the stick-tool is inserted under the front flap, pushing the blockage back along the ramp so that the food is knocked off and rolls forward underneath. **b**, In the Lift method, the stick-tool is passed under hooks, allowing the blockage to be lifted and the food to roll forward. **c**, Chimpanzee GG performing the Poke method. A video of Pan-pipe operation can be found in the Supplementary Information.

A high-ranking female from each of two groups was trained to adopt one of two different tool use techniques ("two-action") for obtaining food from the same 'pan-pipe' apparatus, then re-introduced to her respective group.

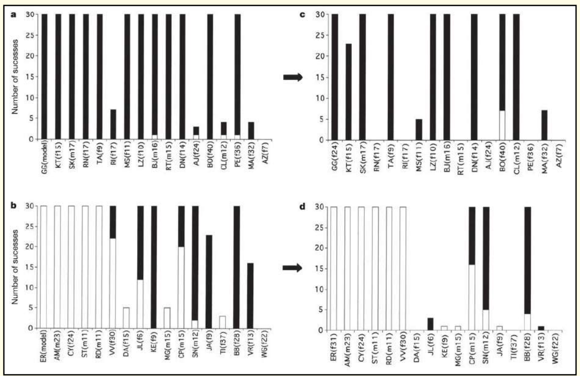
Whiten, Horner & de Waal (2005)

Conformity to cultural norms of tool use in chimpanzees

All but two of 32 chimpanzees mastered the new technique under the influence of their local expert, whereas none did so in a third population lacking an expert. Most chimpanzees adopted the method seeded in their group, and these traditions continued to diverge over time.

A: "Poke" seeded
B: "Lift" seeded
C/D: re-tests
(2 months later)

Black: "Poke"
White: "Lift"



A subset of chimps that discovered the alternative method went on to match the predominant approach of their group ("conformity bias"?)

Transmission of multiple traditions within and between chimpanzee groups

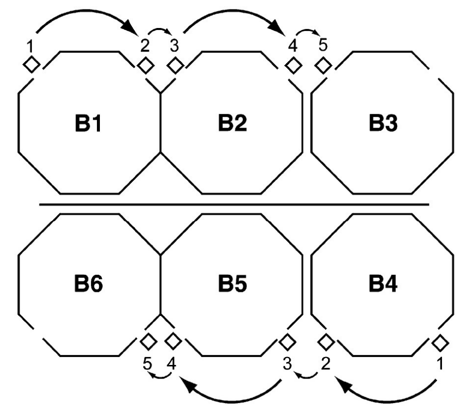
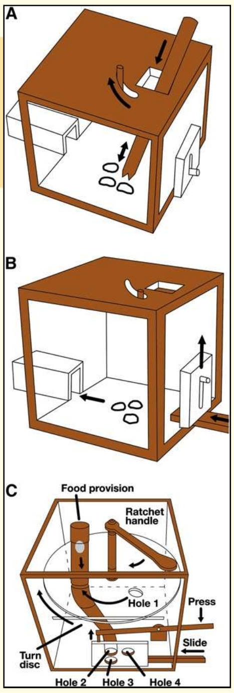


Figure 1. Compound Configuration

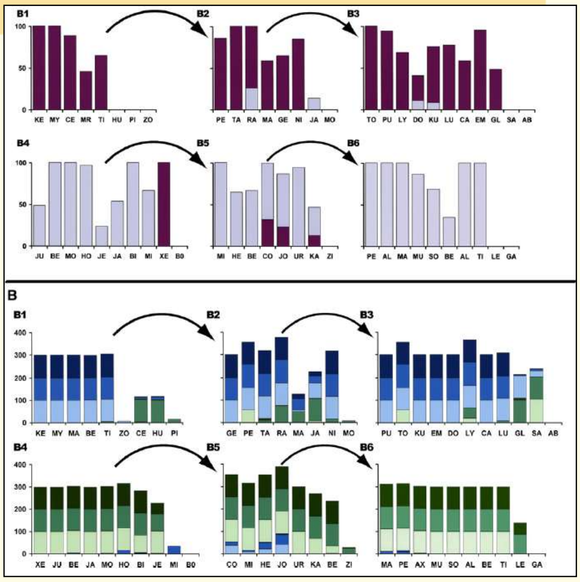


Whiten et al 2007

Transmission of multiple traditions within and between chimpanzee groups

A: Probing task, initiated by trained models KE in group B1 (stab method) and JU in group B4 (slide technique). Number of **stab** (dark) and **slide** (light) actions by each chimpanzee, capped at their first 100 successes.

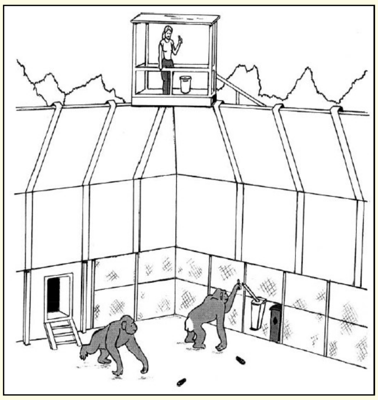
B: number of successful **ratchet** (light green), **slide** (midgreen), **ratchet-then-slide** (dark green), **turn** (light blue), **press** (midblue), and **turn-then-press** (dark blue) actions by each chimpanzee.

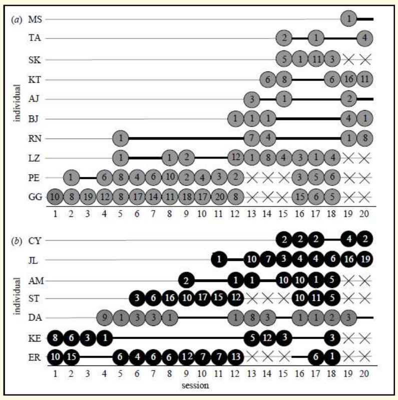


Whiten et al 2007

Spread of arbitrary conventions among chimpanzees: a controlled experiment

2 groups x 2 “traditions”: dropping a token in a bucket x dropping it in a pipe to get a reward (in other place)

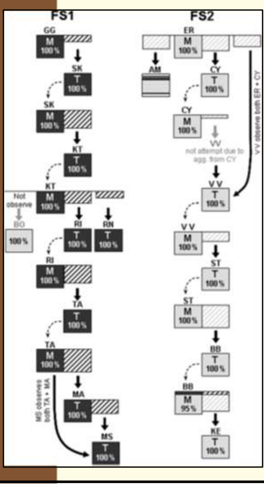


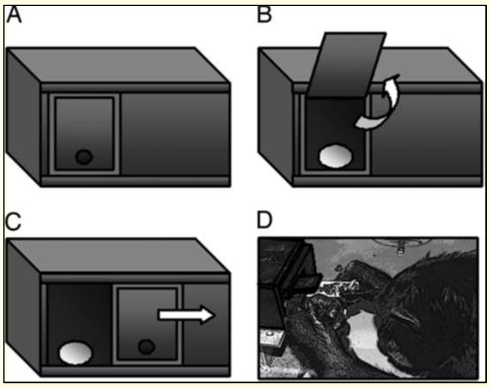


Bonnie, Horner, Whiten & de Waal 2007
~*Sapajus* sp: Lonsdorf et al. 2016

Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children

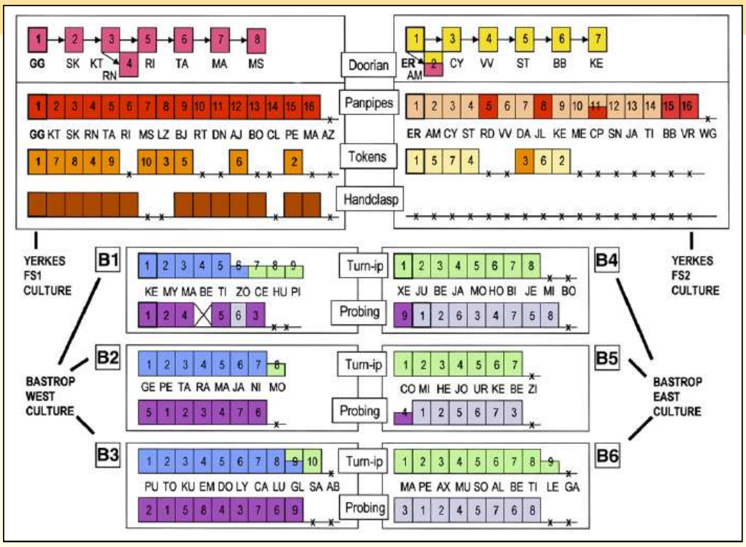
“Doorian fruit” apparatus: two-action





Horner, Whiten, Flynn & de Waal 2007

Transmission of multiple traditions within and between chimpanzee groups



Whiten et al 2007

Orangutan cultural diffusion chains

Dindo, Stoinski & Whiten 2010

Orangutans (zoo-living subjects):

Diffusion-chain paradigm

Observation of a conspecific performing a novel foraging method:

Foraging box with **two possible methods** for extracting food

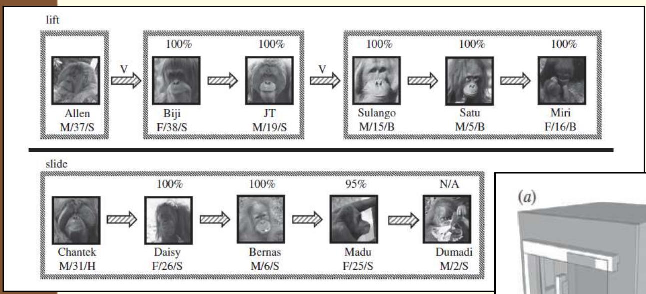
In a socially housed group of five orangutans, the dominant male was trained to use **one** technique to retrieve food. He then performed this technique in the presence of another group member, who was then allowed to forage. After several trials, the observer became the model for the next individual.

A second experimental group of six individuals was introduced to the alternative method.

The model-seeded technique was successfully transmitted along both experimental chains, with significant preferences for the model method. These results are consistent with claims for social transmission of foraging methods in wild orangutans.

Orangutan cultural diffusion chains
Dindo, Stoinski & Whiten 2010

Evidence of SBL in the wild restricted to mother-offspring interactions (X rehabilitation captives)



v = videotaped demonstration
"**Lift**" observers: all 20/20 lift
"**Slide**" observers:
2x20/20,1x19/20,1x0(inf.) slide

"Two-action" puzzlebox

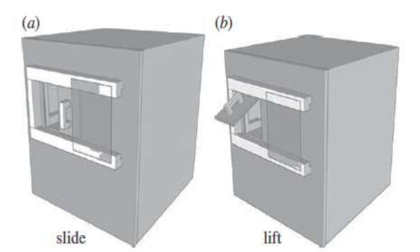


Figure 2. The box is shown (*a*) when the door is slid open and (*b*) when the door is lifted open.

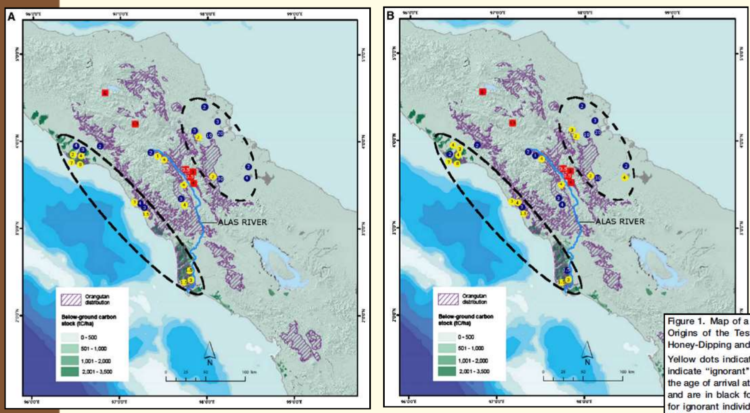
Sumatran orangutans differ in their cultural knowledge but not in their cognitive abilities
Gruber, Singleton & van Schaik 2012

Cultural, genetic and environmental influences analyzed in parallel in captivity to determine their influences on tool use: Sumatran orangutan *(Pongo abelii)* **orphans** from tool-using and non-tool-using regions that differed in both genetic and cultural backgrounds exposed to a **raking task** and a **honey-dipping task**.

Orangutans from both regions were equally successful in raking; however, swamp orangutans were more successful than Langkat orangutans in honey dipping, where previously acquired knowledge was required.

Mixed-model analysis: **performance in dipping task did not predict performance in raking (not genetic and no learning transfer).**

Sumatran orangutans differ in their cultural knowledge but not in their cognitive abilities
Gruber, Singleton & van Schaik 2012



A larger analysis suggested that the Alas River could constitute a geographical barrier to the spread of this cultural trait.

Figure 1. Map of a Northern Section of Sumatra Showing the Origins of the Tested Orangutans and Their Results in the Honey-Dipping and Raking Tasks

Yellow dots indicate "knowledgeable" individuals; blue dots indicate "ignorant" individuals. Numbers inside the dots are the age of arrival at the quarantine center of a given individual and are in black for knowledgeable individuals versus white for ignorant individuals. The blue line is the Alas River. The green gradient shows the below-ground carbon stock: darker regions correspond to the swamp areas. The elongated dashed circle indicates individuals belonging to the swamp population; the shorter dashed circle indicates individuals belonging to the Langkat population. Red squares indicate individuals that were excluded from the geographical analysis because they originated from a major city or could not be assigned to a population. Map adapted from [29] with permission of authors.
(A) Honey-dipping task.
(B) Raking task.

Sumatran orangutans differ in their cultural knowledge but not in their cognitive abilities
Gruber, Singleton & van Schaik 2012

"Honey-dipping individuals were on average less than 4 years old, but this behavior is not observed in the wild before 6 years of age. Our results suggest first that genetic differences between wild Sumatran populations cannot explain their differences in stick use; however, their performances in honey dipping support a **cultural differentiation in stick knowledge**. The results suggest that the honey-dippers were too young when arriving at the quarantine center to have possibly mastered the behavior in the wild individually, suggesting that they arrived with pre-established mental representations of stick use or, simply put, "**cultural ideas**.""

Comparative experimental studies: Laboratory & Nature

Comparative experimental studies: Wild populations' studies

Cultural diffusion experiments with captives

Comparative experimental studies in the wild

Reader & Biro 2010

Survey: field experiments
+ wild animals brought into captivity

Social learning in nonhuman animals, *excluding* examples of social information use where learning has not been definitively demonstrated (cases in which behavior has not been measured in the absence of either the producers of social information [*demonstrators*] or their artifacts)/ cases of social information use without learning.

23 studies (covering 20 species) that demonstrate social learning in the field and 3 studies that provide no evidence for social learning.

Reader & Biro 2010

Field experiments:

(1) manipulating physical aspects of the environment

(2) manipulating individual behavior
(including manipulation of individual presence)

(3) manipulating transmission routes, or

(4) some combination of these.

Reader & Biro 2010

Manipulating the environment or populations wholesale: Coral reef fish translocation studies.

1. if social learning is involved, the translocated population should, so far as possible, maintain its established traditions.

2. if the new location was previously home to another, now absent, population, the new arrivals will not necessarily adopt the traditions of the individuals that previously lived there.

3. if the new locale contains suitable demonstrators (e.g., members of the local population who exhibit a putative tradition), translocated individuals may acquire any putatively traditional behaviors that these local "demonstrators" exhibit.

All three of these predictions hold true in the case of spatial behavior in coral reef fish.

Migration routes, mating sites: experiments

Haemulon flavolineatum

Individuals moved to other populations **X** to locations where populations have been removed.
Helfman & Schultz (1984)

Thalassoma bifasciatum

Tanslocated individuals do not adopt mating sites used by removed population
Warner (1988)
Only removal of FEMALES resulted in mating site loss
Warner (1990)

Natural translocations: Interpopulation migrations.

[Methodological and ethic constraints to field experimentation...]

Grooming handclasp in chimpanzees of Mahale, Tanzania (etc) that differs in the details of its performance between different communities. At Mahale, a female (Gwakulo) changed somehow the way she performed the grooming handclasp after moving between two adjacent communities; in the other hand, individuals in her new group began to perform the style preferred by Gwakulo, but only in interactions with her (Nakamura & Uehara, 2004) [more complex than predicted by McGrew & Tutin 1978, McGrew et al 2001]

Reader & Biro 2010

Manipulating the environment: Novel resources or tasks.

Provision of various resources that are otherwise unavailable to discover whether a behavior is locale specific because of local knowledge or because of differences in local resources.

Bossou: *Panda* and *Coula* nuts, experimental nutcracking sites (Matsuzawa 1994, Matsuzawa & al 2001)

Natural translocations

"Natural experiment" Transmission of nut (*Coula*) cracking behavior to Bossou (Yo, migrant female from Mt. Nimba)
Yamakoshi & Matsuzawa 1993

"Although the presentation of novel resources or tasks can determine the readiness of a population to utilize them and potentially can exclude social learning as an explanation, **proof of social learning is not possible with such a manipulation**" (R&B 2010)

Social learning and conformity in vervet monkeys' foraging decisions

van de Waal, Borgeaud & Whiten 2013

Wild vervet monkeys will abandon personal foraging preferences in favor of group norms new to them.

Groups first learned to avoid the bitter-tasting alternative of two foods. Presentations of these options untreated months later: all new infants naïve to the foods adopted maternal preferences.
Males who migrated between groups where the alternative food was eaten switched to the new local norm.

Reader & Biro 2010

Manipulating the environment: Novel resources or tasks.

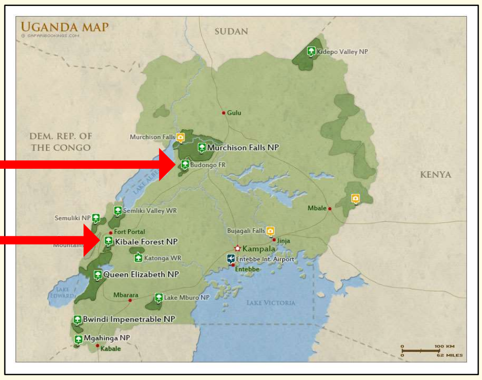
Gruber, Muller, Strimling, Wrangham, and Zuberbühler (2009):

Identical manipulations with two communities of chimpanzees living under highly similar ecological conditions but with considerably divergent tool use repertoires.

Uganda:

Sonso
(Budongo Forest)

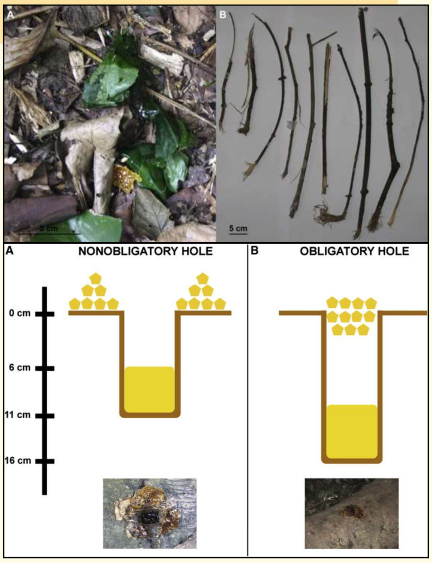
Kanyawara
(Kibale National Park)
[habitual probe users]



Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task

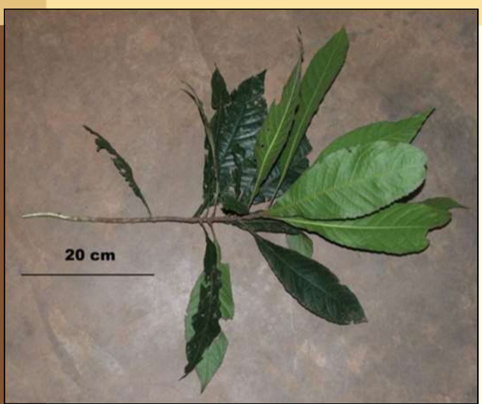
Chimp communities in similar environments with distinct "tool-kits" : Only habitual probe users (Kanyawara) produced them to solve the 2nd problem (20 out of 24), and only 2 out of 11 Sonso individuals produced leaf-sponges

Gruber et al 2009



Community-specific evaluation of tool affordances in wild chimpanzees

Gruber, Muller, Reynolds, Wrangham & Zuberbühler 2011

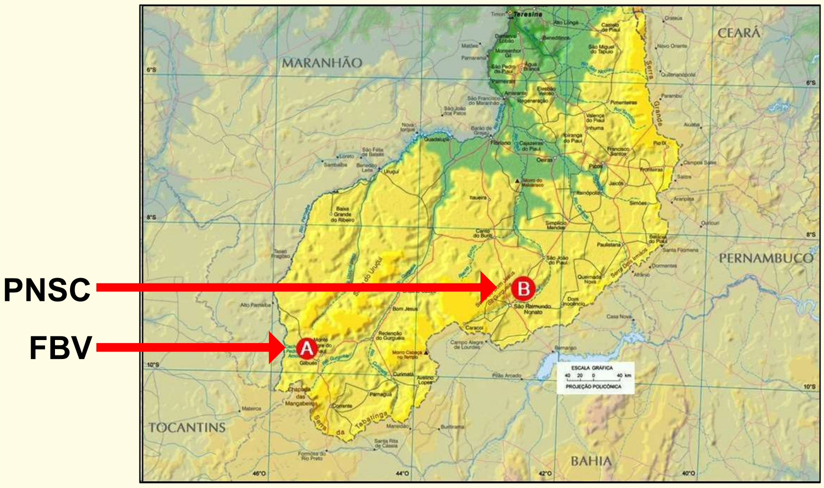


Exp.1:
Honey in a hole + branch of *Alstonia*
Sonso: discarded the stick, made sponges with leaves;
Kaniwara: discarded the leaves, made probe with stick

Exp.2 (Sonso): leafy stick already inserted in the hole. No one used it as a probe; 9 out of 20 tried with hands; only one chimpanzee manufactured a leaf sponge and succeeded.

Problem-solving with the use of probes:
Comparing bearded capuchin populations with distinct *tool-kits*
Ottoni & Cardoso (2014)

P. N. Serra da Capivara (probe users) x Faz. Boa Vista



Problem-solving with the use of probes:
Comparing capuchin populations with distinct *tool-kits*
Ottoni & Cardoso (2014)

Only PNSC monkeys (probe users) solved the task

Problem-solving with the use of probes:
Comparing capuchin populations with distinct *tool-kits*
Ottoni & Cardoso (2014)

FBV monkeys did not solve the task

Problem-solving with the use of probes:
Comparing capuchin populations with distinct *tool-kits*
Ottoni & Cardoso (2014)

Contrary to our expectations, FBV monkeys did not try to use stones (but SC monkeys did)

Problem-solving with the use of probes: Comparing capuchin populations with distinct *tool-kits* Ottoni & Cardoso (2014)

Transport and (attempted) use of **stone tools (PNSC):** Adult male transports stone and probe to the box in his first visit.

Reader & Biro 2010

Manipulating individual behavior:

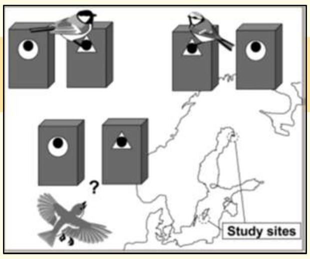
Altering the behavior of key individuals by explicit training or exposure to specific stimuli or through direct control by experimenters causing key individuals to provide pertinent information to other group members.

Foraging in fish and mammals

Reader et al. (2003): **foraging site choice** by guppies. One of the sites contained locally captured fish held within a transparent container ("demonstrators"). Fish preferentially entered the feeding site with the shoal; this preference was maintained in a subsequent test phase (demonstrator shoal no longer present)

van de Waal et al (2010) foraging in free-living vervet monkeys: **dominant individuals monopolized a feeding task** → a single demonstrator in each group.

Reader & Biro 2010



Manipulating individual behavior: Habitat selection and mobbing responses in birds.

Seppänen and Forsman (2007): manipulated apparent nest site choices of resident great and blue tits before the arrival of two species of migratory flycatchers by painting **circles on the front of tit nestboxes and triangles on nearby empty nestboxes (or vice versa)**. The late-arriving migrants copied the apparent nest site choices of the resident tits, demonstrating social learning from heterospecifics.

Davies & Welbergen (2009). Mobbing call playback caused reed warblers (*Acrocephalus scirpaceus*) to mob cuckoo or parrot models presented to them, while their nesting neighbors could observe. Subsequent tests of model presentations to the neighboring birds found that **mobbing responses to the cuckoo**, a harmful brood parasite at the study site, were acquired and maintained even 6 days later, whereas **mobbing of parrots, not a brood parasite, was not acquired by the neighbors** (~ Mineka & Cook 1988: macaques' social learning of avoidance of snakes x flowers)

Reader & Biro 2010

Closing the gap between the laboratory and the wild

Importance of field experiments: not only feasible, but a vital part of understanding social learning

Experiments with captives, on the other hand, have shown that behavior patterns originally ascribed to social learning may not require social information for their development – but that does not rule out a role for social learning of that behavior in natural circumstances.

Field experiments sometimes provide evidence for processes not yet demonstrated in the lab – or produce results contrary to those from the lab.

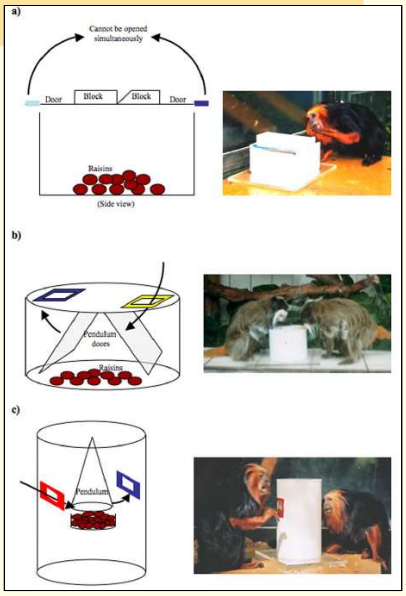
Field research also helps to create captive methodologies that better reflect conditions in the wild.

Refining the statistical tools for the analysis of social diffusion data

Option-bias analysis

Kendal, Kendal et al., 2009

If alternative forms of bias can be ruled out (e.g., genetic, ecological), the level of homogeneity of behavior within a population potentially provides a metric that can be used probabilistically to detect a social influence on learning. OBA compares the observed level of homogeneity to a sampling distribution generated utilizing randomization and other procedures.



Network-based diffusion analysis (NBDA)

(Franz & Nunn, 2009; Hoppitt, Boogert, & Laland, 2010; Hoppitt, Kandler, Kendal & Laland, 2010)

Use of the social network of a group to identify social learning:

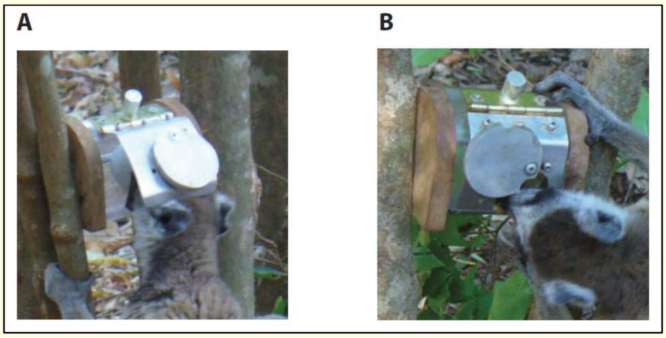
Theory of directed social learning: information is transmitted or directed through subsections of nonhuman primate populations at different rates, according to age, sex, status, or association patterns. In NBDA, social learning opportunities are assumed to be constrained by a social network: the probability of learning from skilled individuals is dictated by the strength of others' connections to them.

The approach requires the following as inputs:
(1) **a social network**, which may be asymmetrical (ex: grooming) or symmetrical (ex: social proximity, play);

(2) **diffusion data** represented as
(a) the order of acquisition (OADA; Hoppitt, Boogert, & Laland, 2010) or (b) the timing of acquisition (TADA; Franz & Nunn, 2010) of a novel behavior pattern

Evidence for social learning in wild lemurs (*Lemur catta*)
Kendal et al. (2010)

Option-Bias Analysis and Network-Based Diffusion Analysis applied for the first time to data from the wild. "Contrary to common thought regarding the cognitive abilities of prosimian primates, our evidence is consistent with social learning within subgroups in the ring-tailed lemur."



O-B: ...
NBDA: +++

Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales
Allen, Weinrich, Hoppitt & Rendell 2013

Lobtail feeding (innovation observed in 1980): striking the water's surface one to four times with the ventral side of the fluke, followed by a bubble-feeding sequence.

NBDA used to reveal the cultural spread of a naturally occurring foraging innovation, lobtail feeding, through a population of humpback whales (*Megaptera novaeangliae*) over a period of 27 years. Support for models with a social transmission component was 6 to 23 orders of magnitude greater than for models without. Coupled with existing knowledge about song traditions, these results show that this species can maintain multiple independently evolving traditions in its populations.

Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales

Allen, Weinrich, Hoppitt & Rendell 2013

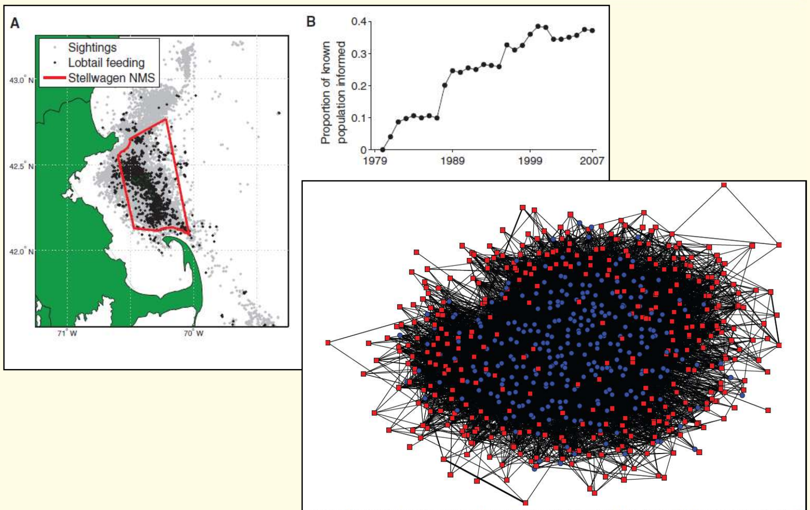
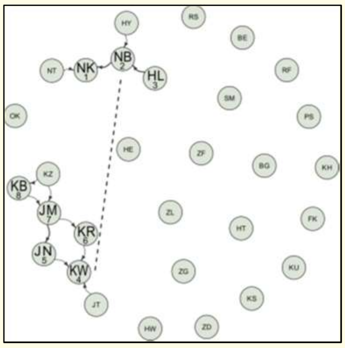


Fig. 2. Social network of whales sighted at least 20 times. Blue nodes are individuals observed lobtail feeding, red nodes are those never observed lobtail feeding. The network was laid out by spring-embedding using Netdraw (25) software.

Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees

Hobaiter *et al*. 2014

Spread of two novel tool-use variants, "**moss-sponging**" and "**leaf-sponge re-use**" (Sonso chimp community, Budongo Forest, Uganda)



"We (...) found strong evidence that diffusion patterns of moss-sponging, but **not** leaf-sponge re-use, were significantly better explained by social than individual learning. The most conservative estimate of social transmission accounted for 85% of observed events, with an estimated 15-fold increase in learning rate for each time a novice observed an informed individual moss-sponging.

Kin-based cultural transmission of tool use in wild chimpanzees

Lamon *et al* 2017

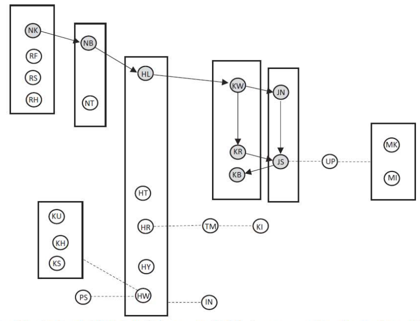


Fig. 3. Model of the two-dimensional transmission pattern. Circles represent all individuals seen moss-sponging at least once between 2011 and 2014. The eight original moss-spongers from Hobaiter *et al.*'s study (*2*) are represented in gray. The arrows represent the social transmission found by Hobaiter *et al.* (*2*). The rectangles represent matrilines in which vertical social learning took place, the main transmission mechanism involved in the spread. The dashed lines represent the possible learning path of the cases ($n = 7$) in which individuals acquired the behavior in the absence of vertical transmission because individuals did not have moss-sponging kin, suggesting learning from individuals that they were highly associated with (linked with the individual with the highest association index).

3 years later, moss-sponging was still present in the individuals that acquired the behavior shortly after its emergence and (...) it had spread further, to other community members. Our field experiment suggests that this secondary radiation and consolidation of moss-sponging is the result of transmission through matrilines, in contrast to the previously documented association-based spread among the initial cohort. We conclude that the spread of cultural behavior in wild chimpanzees follows a sequential structure of **initial proximity-based horizontal transmission followed by kin-based vertical transmission**.

Network-Based Diffusion Analysis

"Of course, **NBDA and other purely statistical approaches to analysing observational data are essentially correlational and thus do not necessarily imply cause**. To interpret such data, one has to try to rule out alternative potential explanations — in this case, for example, that the order of acquisition observed in the chimpanzees resulted not from social learning but from rank-based queuing to gain access to the waterhole, with each lower-ranked individual happening to watch the previous higher ranker before they got their turn".

(Whiten 2014)

Effects of social dynamics on the diffusion of novel behaviors in groups of wild capuchin monkeys in Serra da Capivara

Ottoni, Coelho & Kendal (2016), Coelho, Ottoni & Kendal (in prep.)

Lift X Pull

Ottoni, Kendal & Coelho (2016)

Experimental approaches to social diffusion

Experimentally induced innovation & diffusion

Serra da Capivara (SCNP)

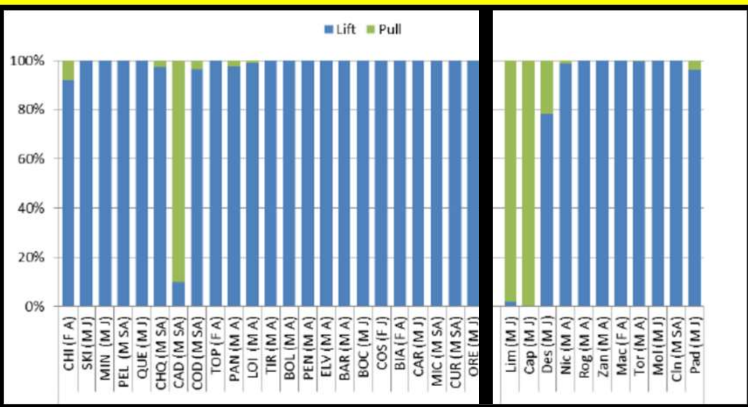
2 Groups:
Jurubeba (JB) &
Pedra Furada (PF)

Problem box


Two-action: lift (seeded in JB) x pull (seeded in PF)
Food reward (corn, peanuts and raisins)
Presence of observers: 5m / 10m

Problem box (two-action)

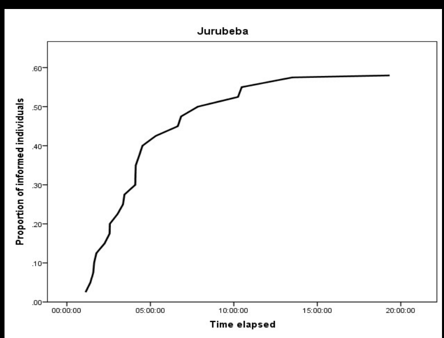
Two-action: Option Bias Analysis (Kendal 2009)

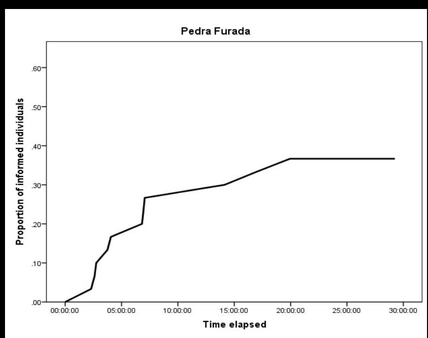


Jurubeba (*lift* seeded)

Pedra Furada (*pull* seeded)

Diffusion of novel trait - NBDA





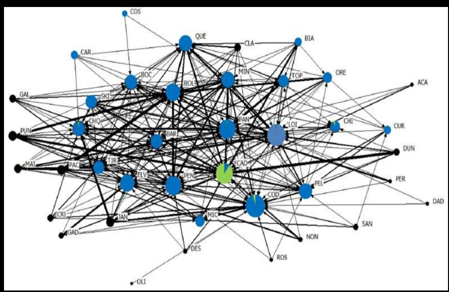
JURUBEBA: 57% group members

PEDRA FURADA: 37% group members

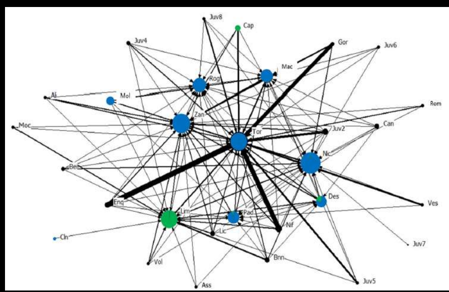
TADA: time each individual first solved the task

NBDA - Social model: informed by Observation networks

G1 – Jurubeba (JB)



G2 – Pedra Furada (PF)



NBDA – Asocial model: Individual parameters (1)

- *(AS1) Dominance hierarchy*. Monopolisation of the task by dominant individuals OR avoidance of knowledgeable subordinates of solving the task in the presence of dominants can slow down the rate of diffusion (and lead to erroneous identification of social learning)
- *(AS2) Neophobia*. Individual differences in neophobia can also alter the rate of diffusion of a novel trait (again leading to an erroneous identification of social learning). To control for this, two variables depicting neophobia were input in the analysis to inform the asocial model:
  - the level of avoidance of and interaction with novel objects (*nephobia1*) and
  - the latency to touch novel objects (*neophobia2*).



NBDA – Asocial model:
Individual parameters (2)

- *(AS3) Opportunity to approach the task*. The frequency with which individuals were registered approaching the task (coming within 5 meters of it) when it was not being manipulated by any conspecifics. This variable indicates variation in the likelihood with which individuals could approach the lift-pull task, be it due to monopolisation, neophobia or other unknown factors.

NBDA interpretation
AIC: Akaike Information Criterion

$\Delta AIC = AIC_{\text{social model}} - AIC_{\text{asocial model}}$

IF diffusion of the trait is best explained by the individual-level variables: ASOCIAL LEARNING factors may account for for the diffusion rate described.

$\Delta AIC \geq 2$

IF a model combining these asocial influences and the opportunities to observe conspecifics solving the task (observation networks) is a better fit to the diffusion data: SOCIAL LEARNING is likely occurring

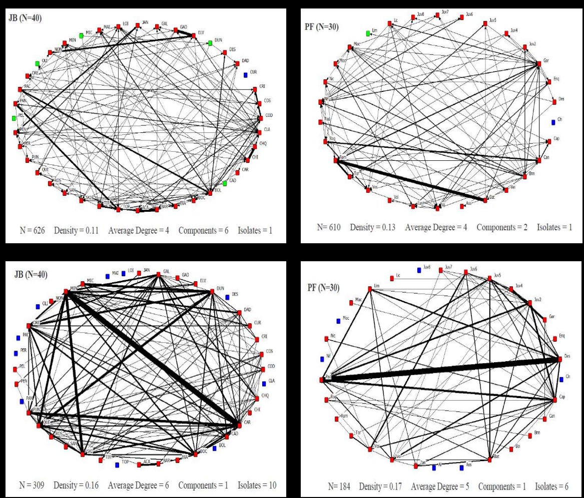
$\Delta AIC \leq -2$

NBDA: results

Network informing the social model	Jurubeba		Pedra Furada	
	ΔAIC	Akaike weights (ω)	ΔAIC	Akaike weights (ω)
Observation < 5 meters	-4.39*	0.90	-2.10*	0.74
Observation > 5 meters	-1.54		1.00	

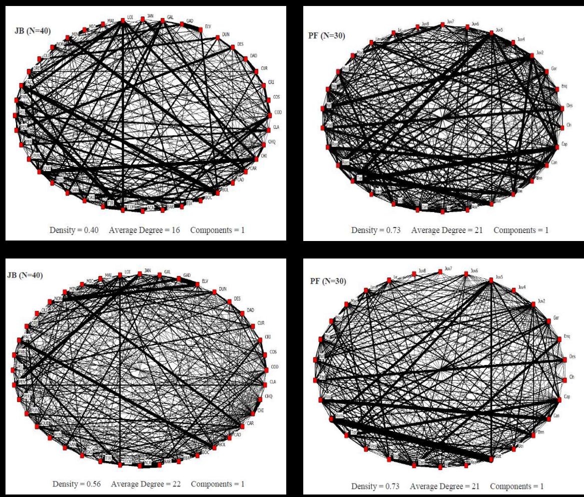
Opportunities for social learning outside the experimental set-up

- *Grooming networks:*
- *Play networks:*



Opportunities for social learning outside the experimental set-up

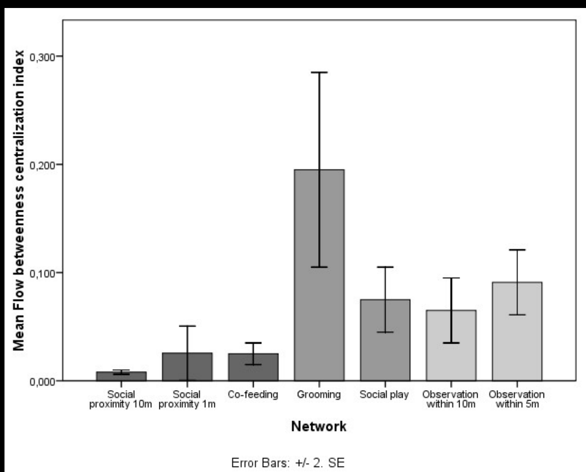
- *Co-feeding networks*
- *Social proximity networks (1m)*



Social Network Analysis:

How might the network structure influence the opportunities of social learning?

Flow betweenness centralization index: the degree to which the network flow was concentrated along paths including more central individuals.



NBDA – other social networks

Grooming → Social Model

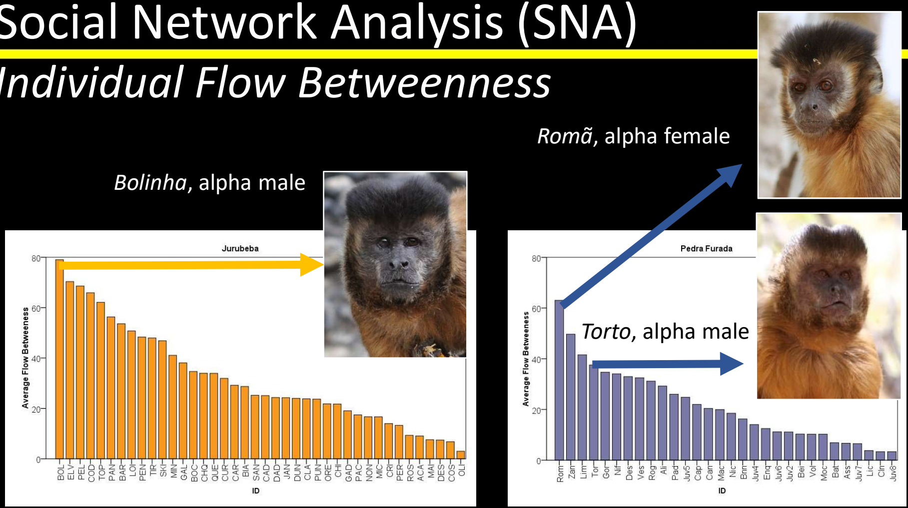
Play → Asocial Model

Network informing the social model	Jurubeba ΔAIC	Jurubeba Akaike weights (ω)	Pedra Furada ΔAIC	Pedra Furada Akaike weights (ω)
Grooming	-6.31*	0.96	-2.87*	0.81
Social proximity	-5.43*	0.94	0.77	
Co-feeding	-6.98*	0.97	0.51	
Play	2.00	0.73	2.00	0.73

$\Delta AIC = AIC_{social\ model} - AIC_{asocial\ model}$

Social Network Analysis (SNA)

Individual Flow Betweenness



Average *Flow Betweenness* from *Co-feeding*, *Grooming*, *Social play,* and *Observation* networks for each member of JU and PF groups.

Concluding remarks

These results provide direct evidence for social learning in wild bearded capuchin monkeys, supporting claims of culture in this clade.

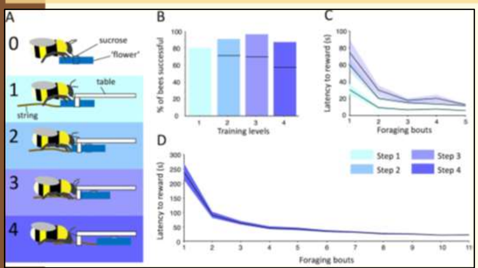
The NBDA finding that the social model informed by close-range observation predicted the diffusion pattern of the novel foraging behavior, points to the importance of social tolerance in the dissemination of knowledge through these groups.

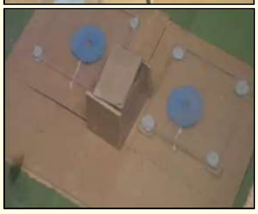
The densely connected social networks recorded for capuchin groups at SCNP imply that they form cohesive groups despite their unusually large size – and large social groups would be expected to generate a greater number of innovations.

The combination of large group sizes and tolerant and cohesive social networks may explain the uniquely large “tool-kit” found in SCNP bearded capuchin monkeys’ population.

Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect

Alem et al 2016





Bumblebees can be trained to pull a string to access a reward, but most could not learn on their own. Naïve bees learned how to pull strings by observing trained demonstrators from a distance. Once one bee knew how to string pull, over time, most of the foraging bees learned from the initially trained bee or from bees who had learned from the trained bee, even after the initial demonstrator was no longer available.

Stimulus/local enhancement + trial-and-error and perceptual feedback (but no means-end understanding (~ connected x disconnected strings)

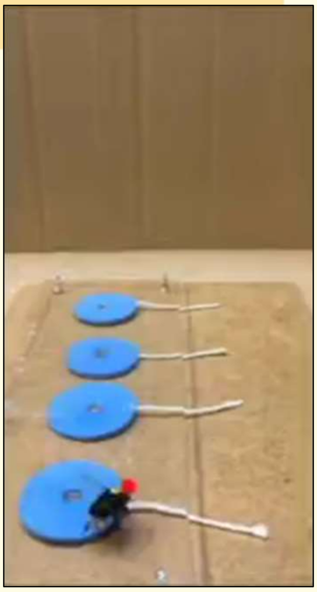
Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect
Alem et al 2016

Transmission Chain Experiment

(1) A single demonstrator per colony trained to pull the string; (2) pairs of bees allowed to engage with the string pulling task; (3) diffusion of the technique among the foraging population tracked; (4) NBDA analysis.

After 150 paired foraging bouts, a large proportion of each of the test colonies' forager population learnt to string pull, whereas none of the control colony foragers did. Additional foraging bouts (2 colonies): the technique continued to spread among the foragers. Learners progressively changed their foraging behaviors from scroungers to competent string pullers. The technique spread across sequential sets of learners, whereby some bees that learnt the technique never interacted with the seeded demonstrator.

[Obs: bees do not cooperate to pull the string but in fact hinder each other's efforts to some degree]



Next lecture:
Social Learning in Humans and Non-humans:
Continuity x Discontinuity
Cumulative Culture