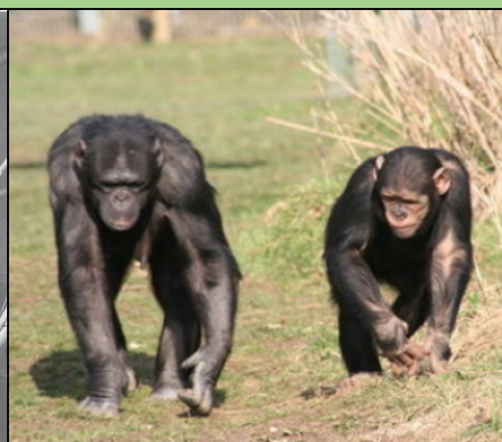
Cultural Ecology

Implications of animal culture for ecology and evolution

Max-Planck-Institut
für Verhaltensbiologie

Lucy Aplin

This Lecture

1. **Is culture adaptive?**
   - Social learning - contexts, trade-offs & social learning strategies
   - Culture as local adaptation

2. **How does the environment affect selection for culture?**
   - Necessity drives innovation vs the opportunity hypothesis

3. **Culture in changing environments**
   - Diffusion of innovations
   - Behavioural flexibility: cultural buffers, cultural traps

4. **Co-evolutionary dynamics**
   - Gene culture co-evolution
   - Speciation
   - Cultural intelligence hypothesis

This Lecture

1. **Is culture adaptive?**
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   - Culture as local adaptation

Core Principles of Behavioural Ecology

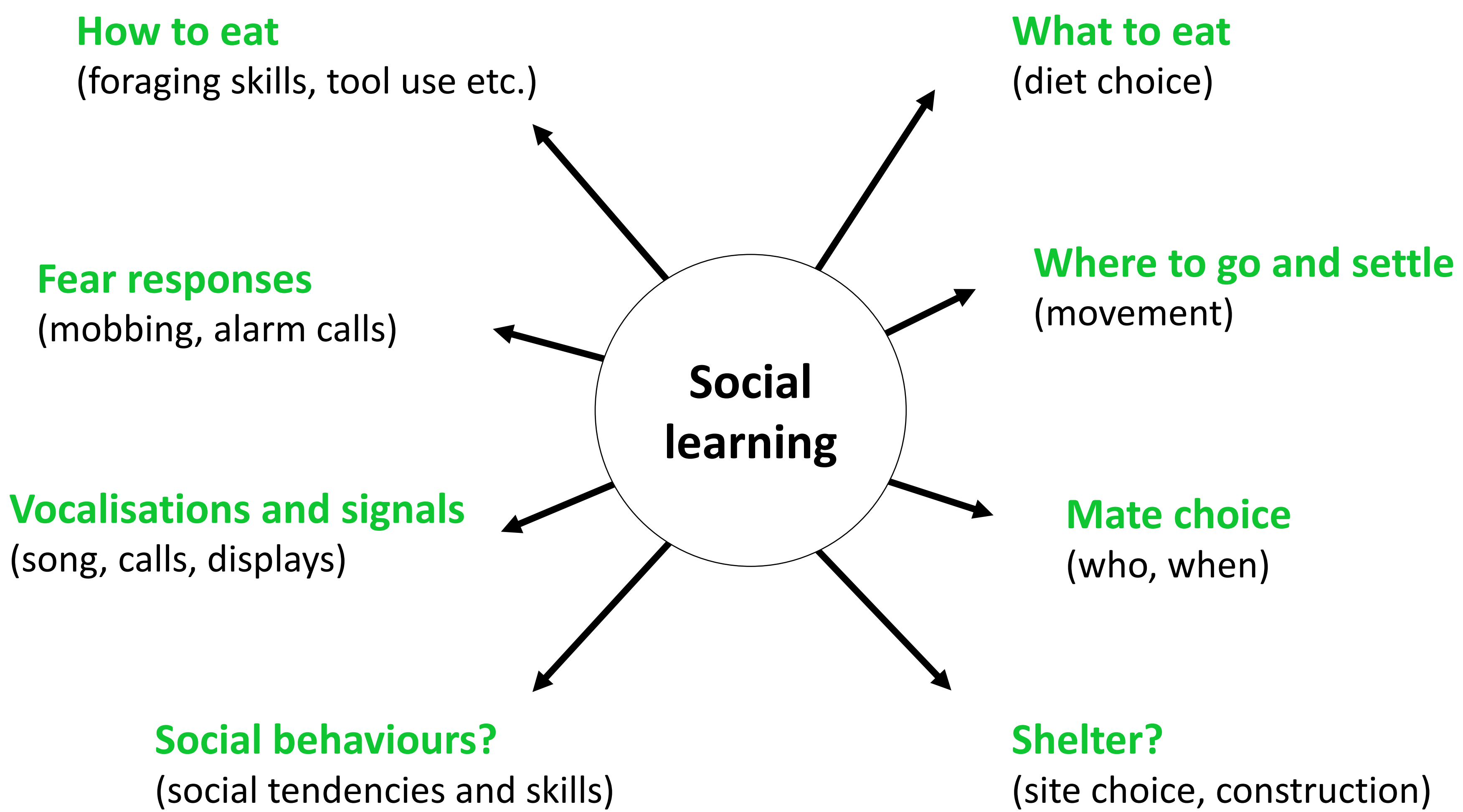
Variation, Selection and Inheritance**:** key components of Darwinian (and cultural) evolution.

Fitness: An individual‘s (or phenotype‘s) contribution to the gene pool of the next generation (survival + reproduction).

Adaptations**:** Evolved solutions to recurrent environmental problems of survival and reproduction.

Adaptive Behaviour**:** Any behaviour that contributes directly or indirectly to an individuals fitness, and is thus subject to the forces of natural selection.

1a. Is culture adaptive: contexts, trade-offs & SLSs



1a. Is culture adaptive: contexts, trade-offs & SLSs

- Social learning is not always adaptive; the information could be wrong, inappropriate or out of date.

- The best quality information is most likely obtained through trial and error learning. The most “reliable” results will come from genetically fixed behaviour.

So when should you use social learning?

When Learning > Fixed Behaviour
and
When Social Information > Asocial Information

1a. Is culture adaptive: contexts, trade-offs & SLSs

When Learning > Fixed Behaviour
and
When Social Information > Asocial Information

1. When environments vary too fast for fixed behaviour, but slow enough that learned information is still relevant.

2. In social species (when there is opportunity), and when juveniles are social with experienced adults.

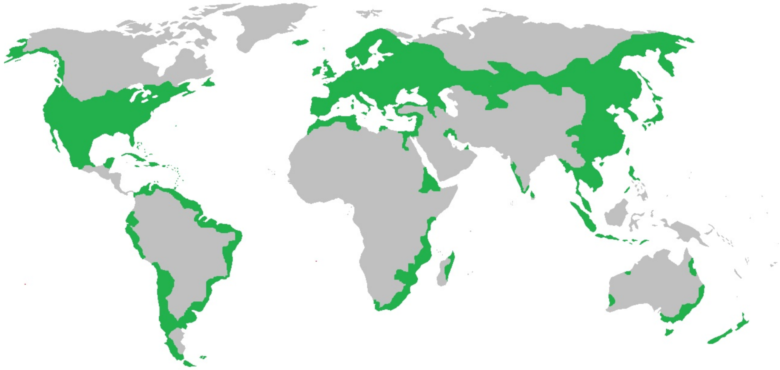
3. When asocial learning is risky, costly or hard to undertake.

4. Or when social information (and the collective pooling of information) outperforms personal information.

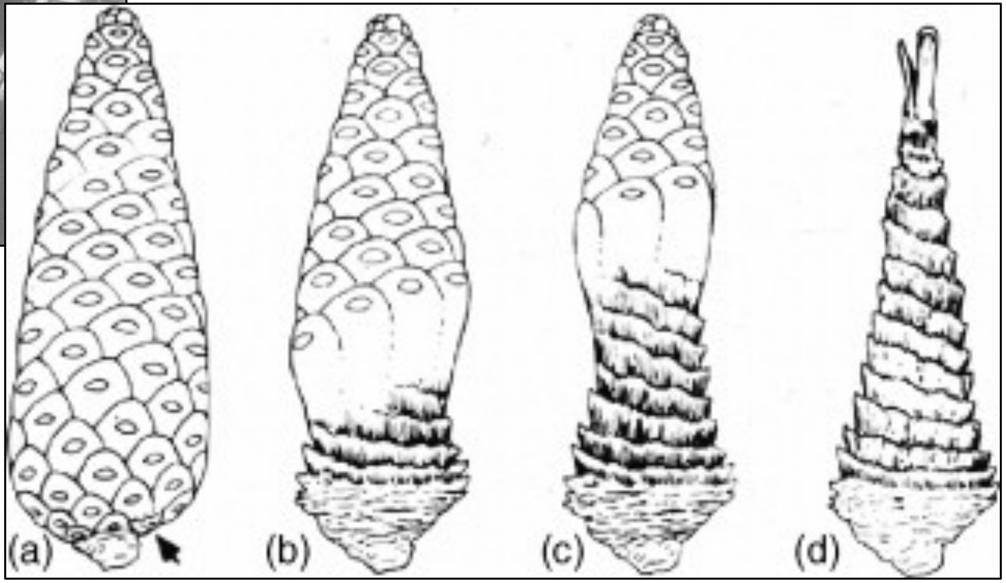
5. When being the same as others in your group matters (mate choice, ‘symbolic markers’).

1b. Is culture adaptive: invasive population

Aisner & Terkel (1992)

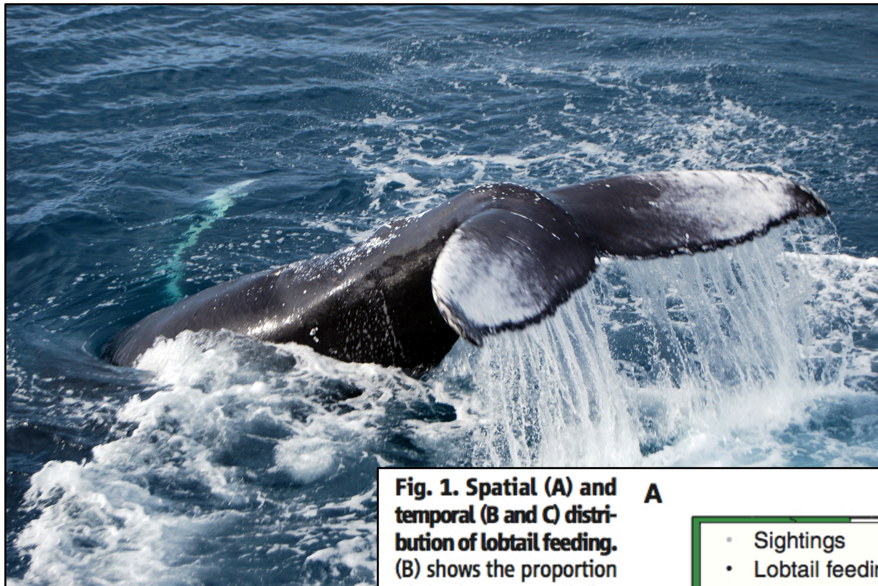


Pine-cone stripping behaviour in invasive black rats (*Rattus rattus*) living in forests of Jerusalem pine in Israel



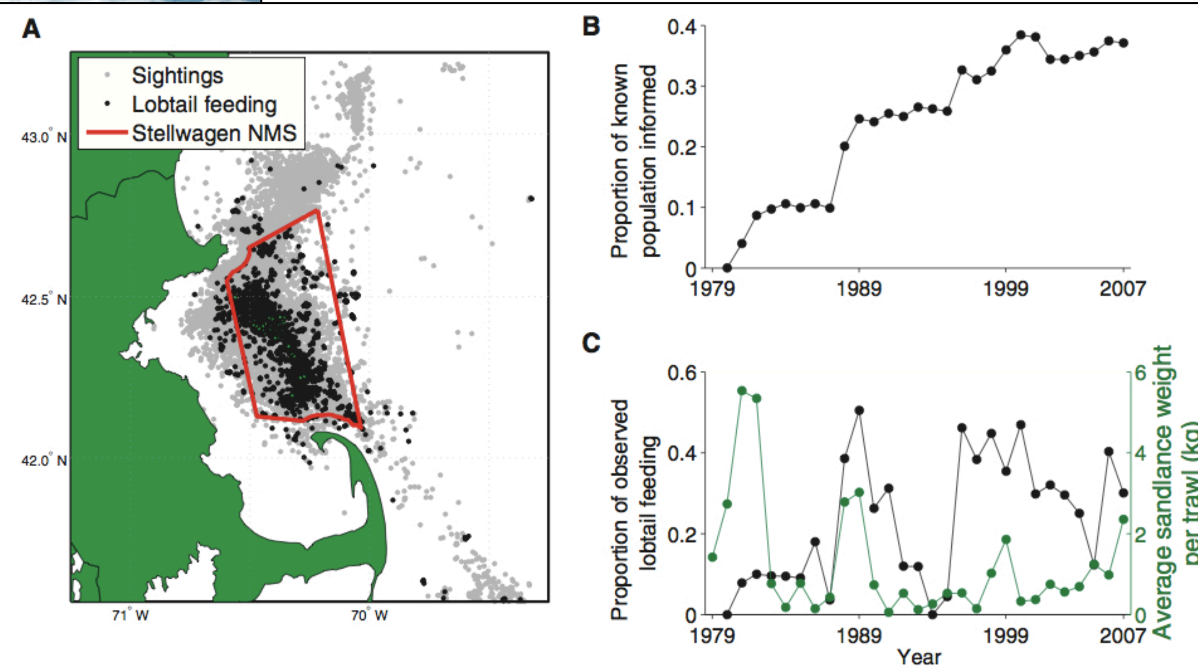
Schematic diagram of pinecones being efficiently stripped of their scales in the efficient manner taking advantage of the architecture of the pinecone. In: CM Heyes & BG Galef, Jr. Eds. Social Learning in Animals the Roots of Culture. San Diego: Academic Press (Figure 5).

1b. Is culture adaptive: innovation and uptake



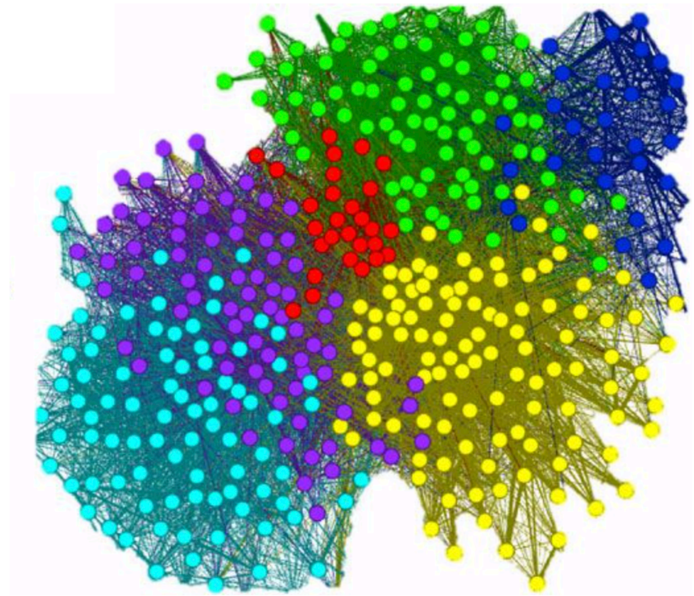
Lob-tail feeding innovation in humpback whales (*Megaptera novaeangliae*) feeding on sand lance in the gulf of Maine.

Fig. 1. Spatial (A) and temporal (B and C) distribution of lobtail feeding. (B) shows the proportion of the known population each year that were also known to be informed, and (C) shows the proportion of observed feeding events each year that were lobtail feeding, along with sand lance abundance in research trawls (27).



Allen et al. (2013) *Science*

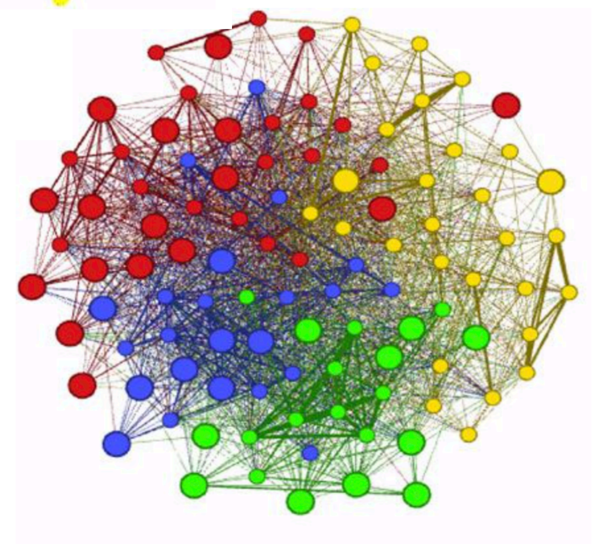
1b. Is culture adaptive: a fitness advantage



<- Shows six clusters for the entire network (439 dolphins). Spongers are in the purple and light blue clusters.

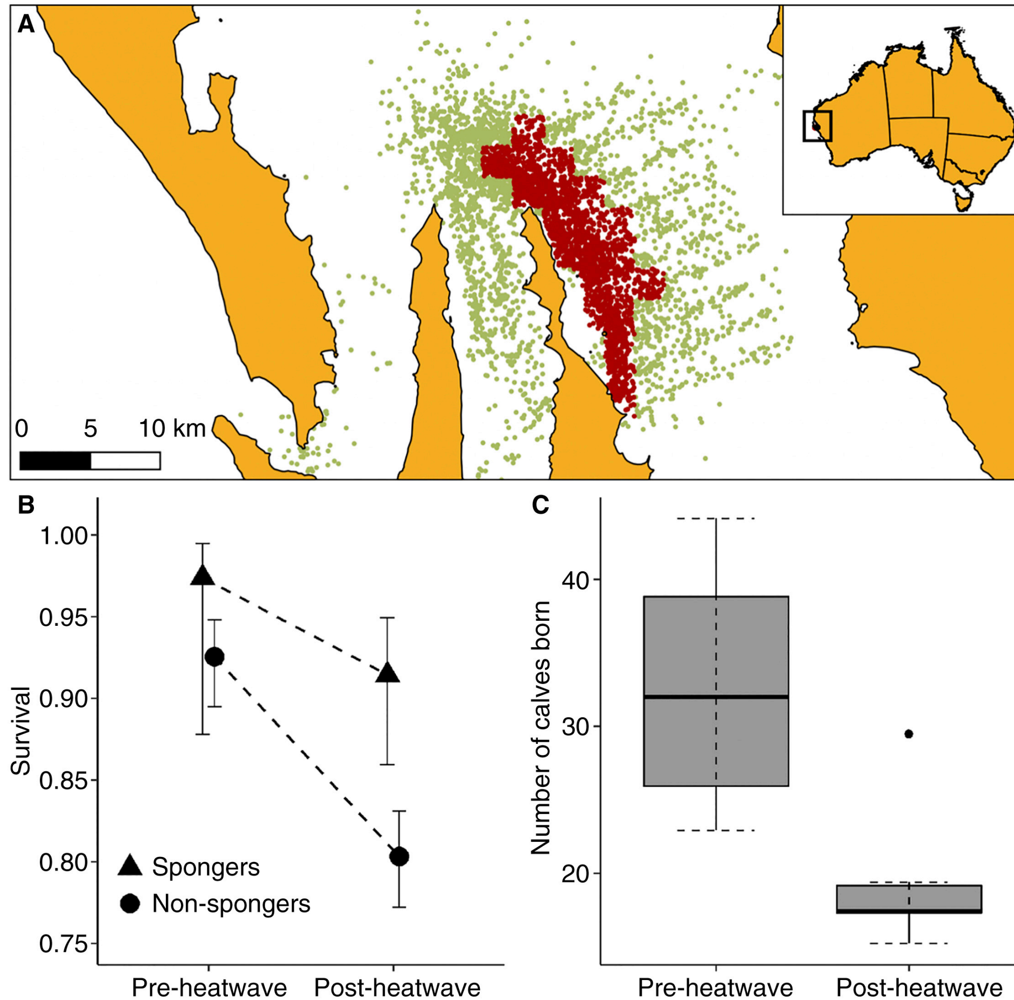
Sponge tool use in bottlenose dolphins (*Tursiops aduncus),* and it's affect on survival and reproduction after a marine heatwave

-> Shows four clusters for the 105 dolphins in the core sponger area. Larger nodes are spongers. Ties are weighted by the affinity index and represent clear cliques of spongers and non-spongers with a few interesting exceptions.



Wild et al. (2019) *Biology Letters;* Mann et al. (2012) *Nature Communications;* Tyne et al (2012) *Marine Ecology;* Krutzen et al. (2014) *PRSB*

1b. Is culture adaptive: a fitness advantage



Sponge tool use in bottlenose dolphins (*Tursiops aduncus),* and it's affect on survival and reproduction after a marine heatwave

Wild et al. (2019) *Current Biology*

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2. **How does the environment affect selection for culture?**
    - Necessity drives innovation vs the opportunity hypothesis

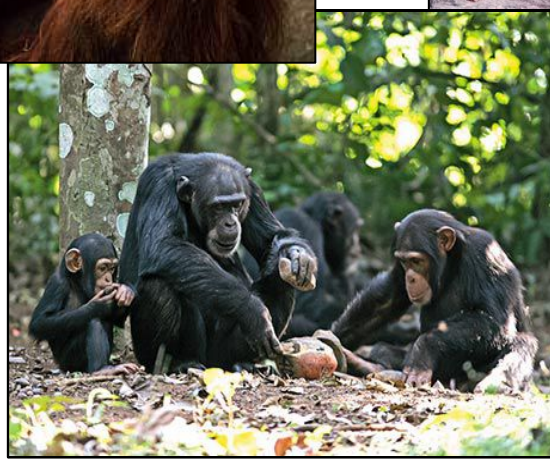
2a. Environmental drivers for culture

NECESSITY

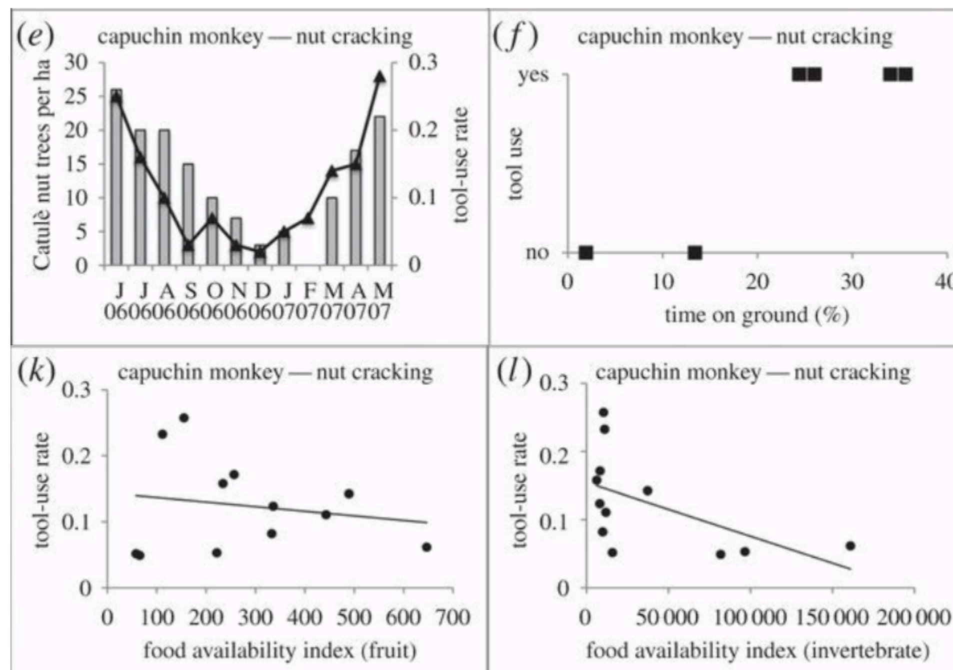
vs

OPPORTUNITY & FREE TIME

2a. Necessity vs Opportunity: Material culture in primates



(*e*) tool-use rate to crack nuts by capuchin monkeys and catulè nut availability. (*f*) tool use in nut cracking and % time on ground across capuchin monkey sites.



(*k*) tool-use rate to crack nuts in relation to food availability index of fruit; (*l*) tool-use rate to crack nuts in relation to food availability index of invertebrates

Koops et al. (2014) Biology Letters

2a. Necessity vs Opportunity: Material culture in primates

Review of evidence for Opportunity and Necessity:

"The conclusion from these studies regarding the ecological influences on feeding tool use … is that opportunity, not necessity, is the main driver… (ecological) opportunities influence occurrence of tool use, and likely the species' cultural repertoires. The resources extracted using tools (nuts, honey, insects) are among the nutritionally richest in primate habitats. Hence, extraction pays off, and not just during times of food scarcity. "

Koops et al. (2014) *Biology Letters*

2a. Material culture in primates

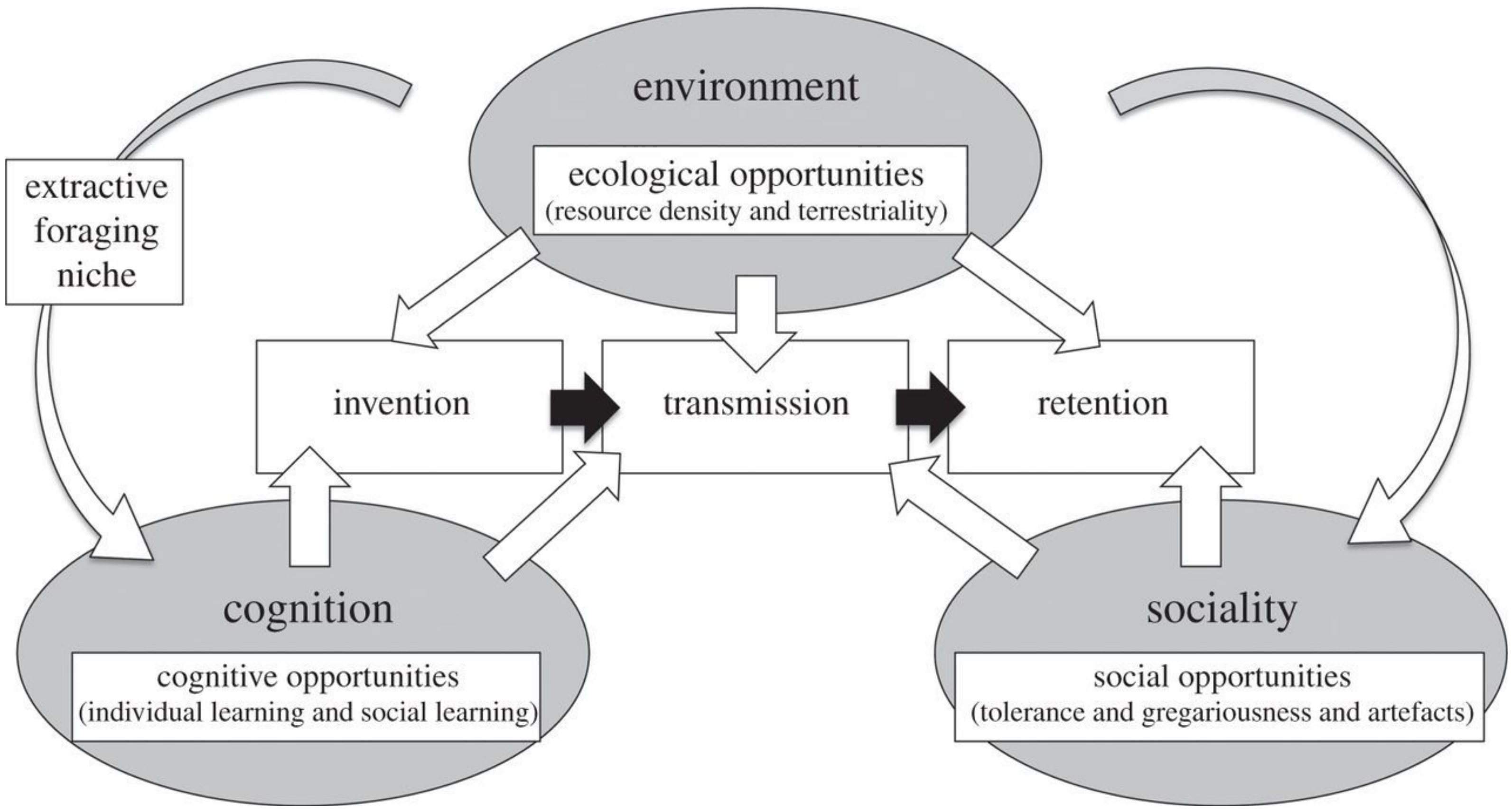


Figure 2. The three-factor model of primate material culture (modified from reference [10] by adding 'environment' and 'retention'). White arrows, direct influence; black arrows, causal sequence.

Koops et al. (2014) Biology Letters

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3. **Culture in changing environments**
    - New cultures: diffusion of innovations
    - Existing cultures: cultural buffers, cultural traps

3a. Changing environments: diffusion of innovations

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Innovation rates, brain size and behavioural flexibility are associated with invasion success & urbanisation

e.g. Sol et al. PNAS 2005, Sol et al. An Beh 2013

3a. Changing environments: diffusion of innovations

3a. Changing environments: diffusion of innovations

New or changed environment

↓

Novel challenge or opportunity

↓

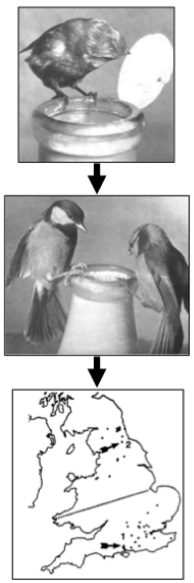
An innovation in behaviour

↓

Social learning & transmission → **Adaptive Cultural Trait**

Fisher & Hinde (1949) *British Birds*; Aplin et al. (2016) *Current Opinions*

3a. Changing environments: diffusion of innovations



Novel challenge or opportunity

↓

Behavioural Innovation

↓

Social learning and transmission

↓

Population-level change in behaviour

↓

Ecological or Evolutionary Consequences

Transmission modes

-Horizontal transmission facilitates the rapid within-generation spread of information [78]. Overlapping generation times will allow for longer term persistence.

Developmental constraints

-Innovations should spread more extensively in species with open-ended learning [54,78], and may diffuse slowly in species where learning is restricted to developmentally sensitive periods [19].

Social learning biases

-Individuals can have learning rules determining when, what and whom they copy [35]. These will interact with innovator identity and environmental conditions to alter diffusion rates; e.g. if individuals preferentially copy dominant individuals and innovators tend to be subdominants, this mismatch may prevent innovations from spreading [87].

Social foraging strategies

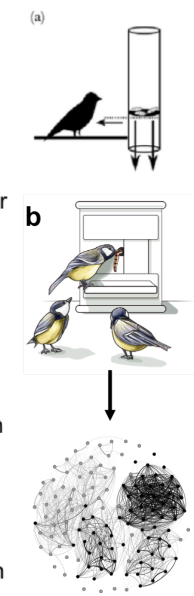
-Scrounging may either prevent or promote social learning, depending on the species and behaviour transmitted (e.g. scrounging prevented the learning of foraging behaviour in pigeons [38]). Information will also likely be acquired faster in more egalitarian societies where individuals can't monopolise resources [88].

Social networks

-Information spreads faster on well-connected networks and in fission-fusion societies [54]. Relatively well-connected individuals spread and receive information faster [44,46]. Novel behaviours may feedback to network structure [66].

Population demographics

-The spread and persistence of new behaviours will be ultimately constrained by population dynamics, including population sizes, dispersal rates, mortality rates and longevity [37].



Aplin et al. (2016) *Current Opinions*

3a. Changing environments: diffusion of innovations

Aplin et al. (2015) Nature

3a. Changing environments: diffusion of innovations

New or changed environment

↓

Novel challenge or opportunity

↓

Innovation

↓

Social learning and transmission

↓

Cultural behaviour

↓

Ecological consequences?

3a. Changing environments: diffusion of innovations

New or changed environment

↓

Novel challenge or opportunity

↓

Innovation

↓

Social learning and transmission

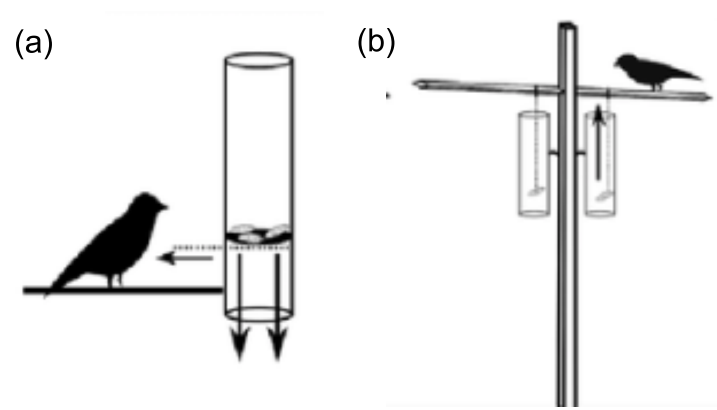
↓

Cultural behaviour

↓

Ecological consequences?

- High number of foraging innovations in Lefebvre's database
- "Lifestyle" associated with innovativeness: broad diet, winter resident, non-hoarder, social foraging and learning…
- 44% of birds solved (moderately repeatable)



Cole et al. 2011 *Anim Behav*; Morand-Ferron et al. 2011 *Behav Ecol;* Cole et al. 2012 *Curr Biol*

3a. Changing environments: diffusion of innovations

New or changed environment

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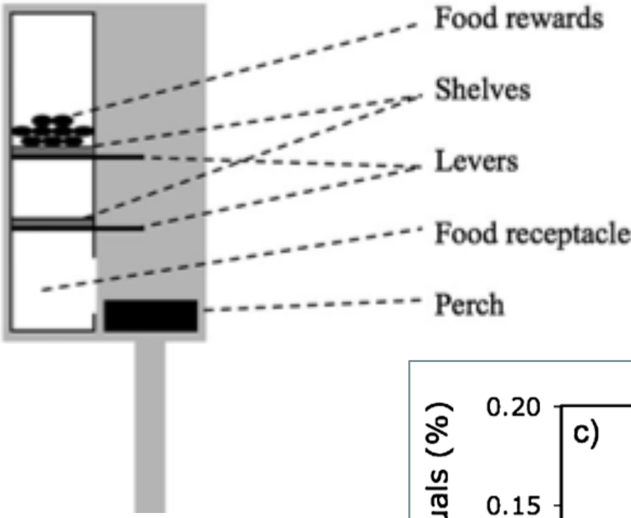


Necessity drives innovation?

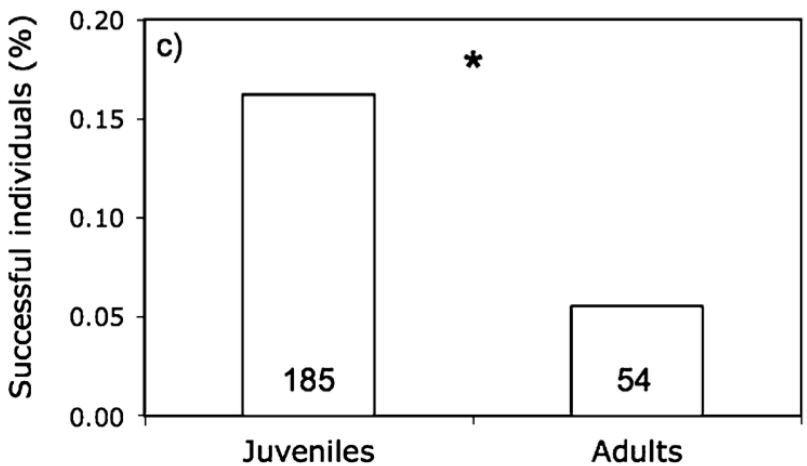
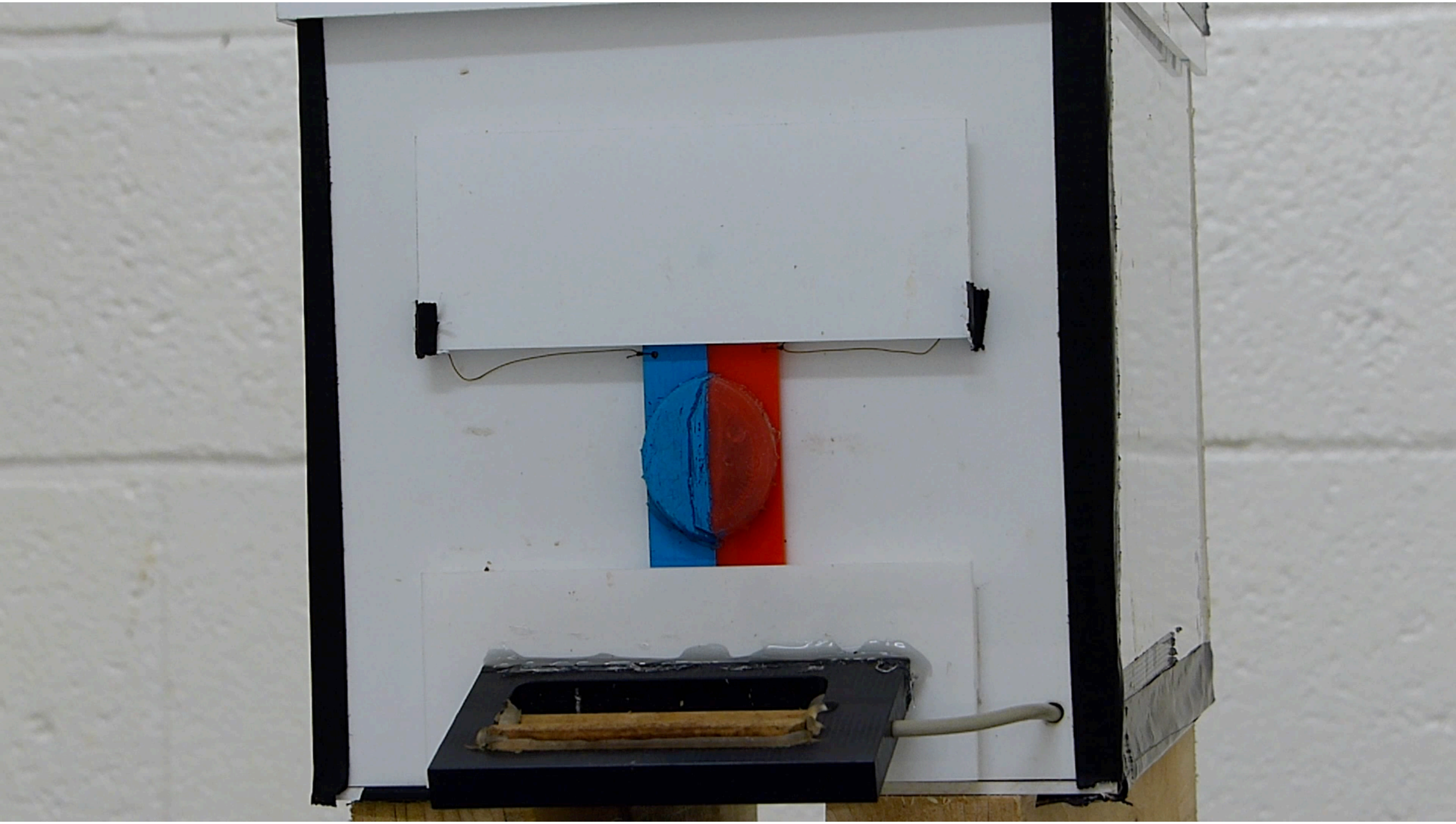


Figure 3
Percentage of individuals that solved the problem at least once in the field according to (a) species, (b) sex, and (c) age class. Numbers in bars indicate sample size for each category. "n.s." indicates no significant difference in a GLMM on problem-solving success, whereas the "*" indicates $P < 0.05$.

Cole et al. 2011 *Anim Behav*; Morand-Ferron et al. 2011 *Behav Ecol;* Cole et al. 2012 *Curr Biol*

3a. Changing environments: diffusion of innovations



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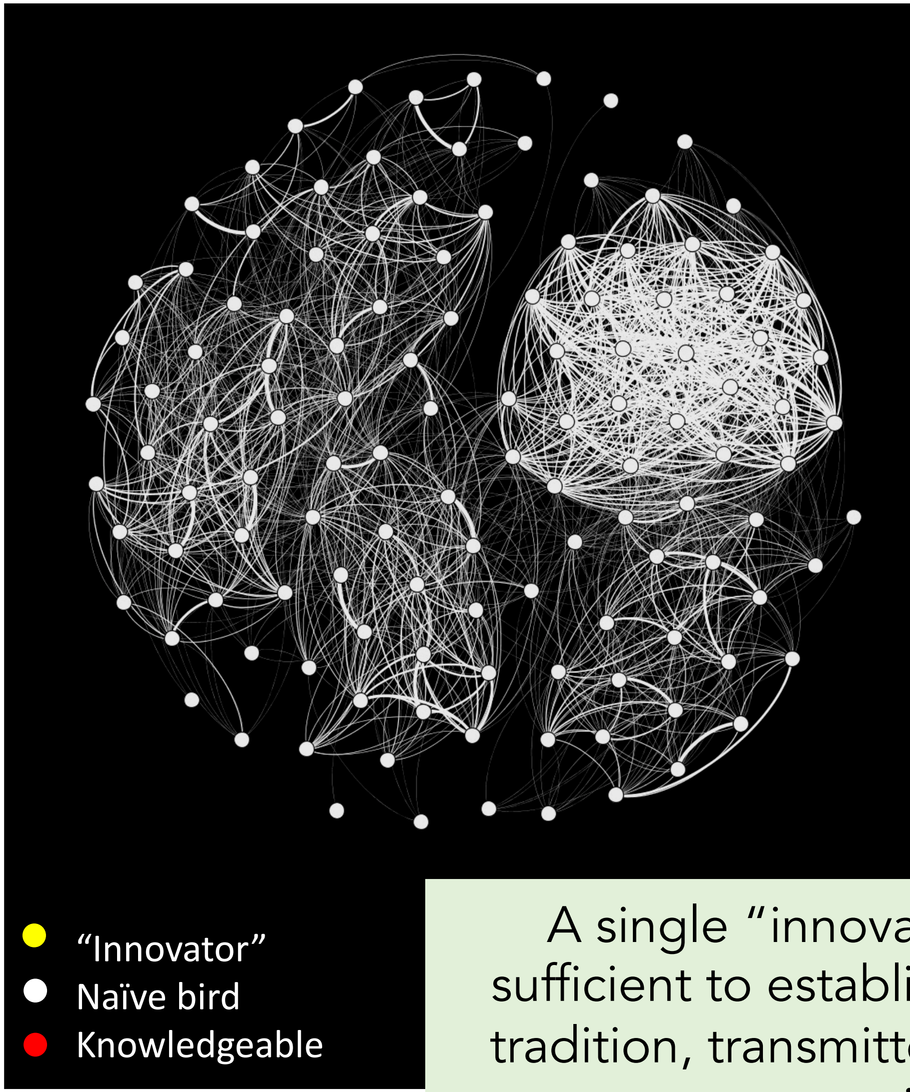
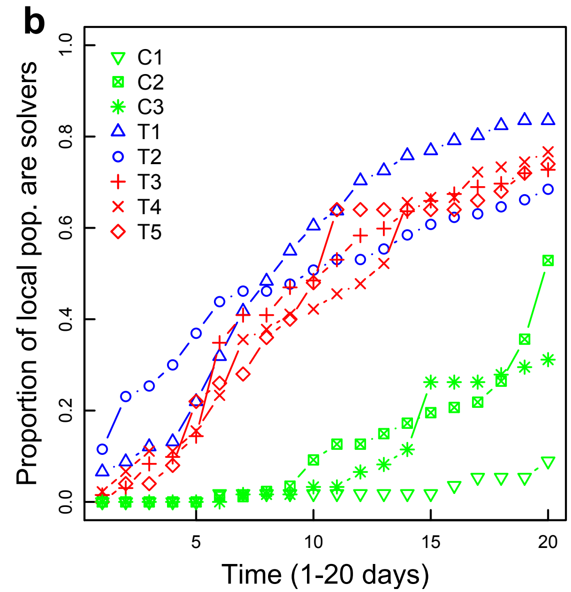
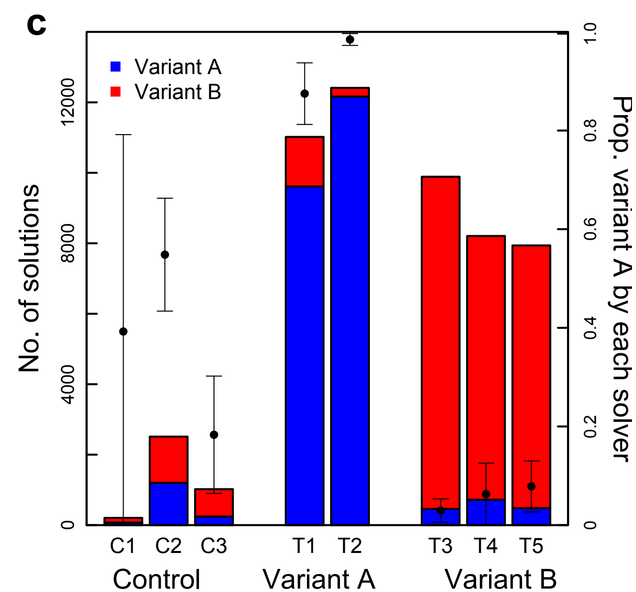




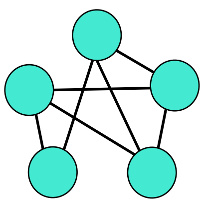


A single “innovator” is sufficient to establish a new tradition, transmitted to the next **generation**.

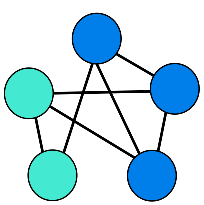
Aplin et al. (2015) Nature

3a. Changing environments: diffusion of innovations

Social Foraging Strategies



Social Networks



Population Demographics

Novel challenge or opportunity

↓

Behavioural Innovation

↓

Social learning and transmission

↓

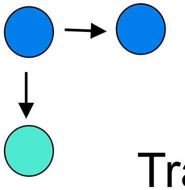
Group-level change in behaviour

↓

Culture! Ecological/Evolutionary implications?

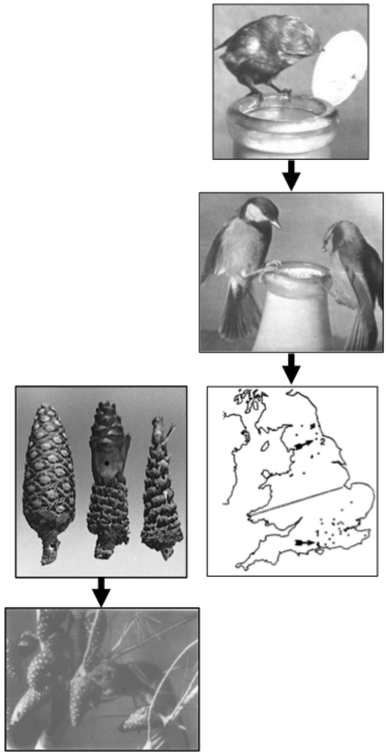
Cognition, Individual Variation, Development

Learning Biases & Mechanisms



Modes of Transmission

3a. Changing environments: diffusion of innovations



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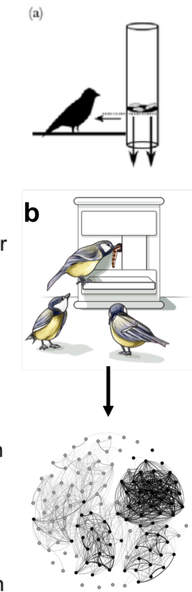


Aplin et al. (2016) *Current Opinions*

3a. Changing environments: diffusion of innovations

Video source: earthOCEANtv on Youtube

3a. Changing environments: diffusion of innovations

Behavioural interaction between southern right whales (*Eubalaena australis*) and kelp gulls (*Larus dominicanus*)

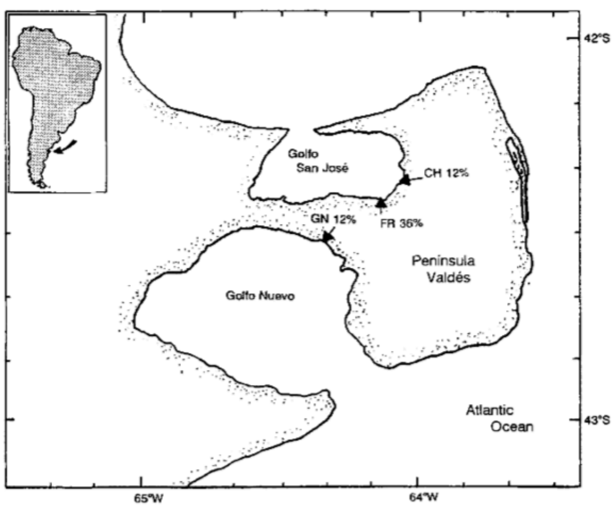


Figure 1. Map of Península Valdés, Argentina, showing the observation sites and the proportion of 5-min intervals with gull attacks at each site. CH: Cliff Hut; FR: Fracaso; GN: Golfo Nuevo.

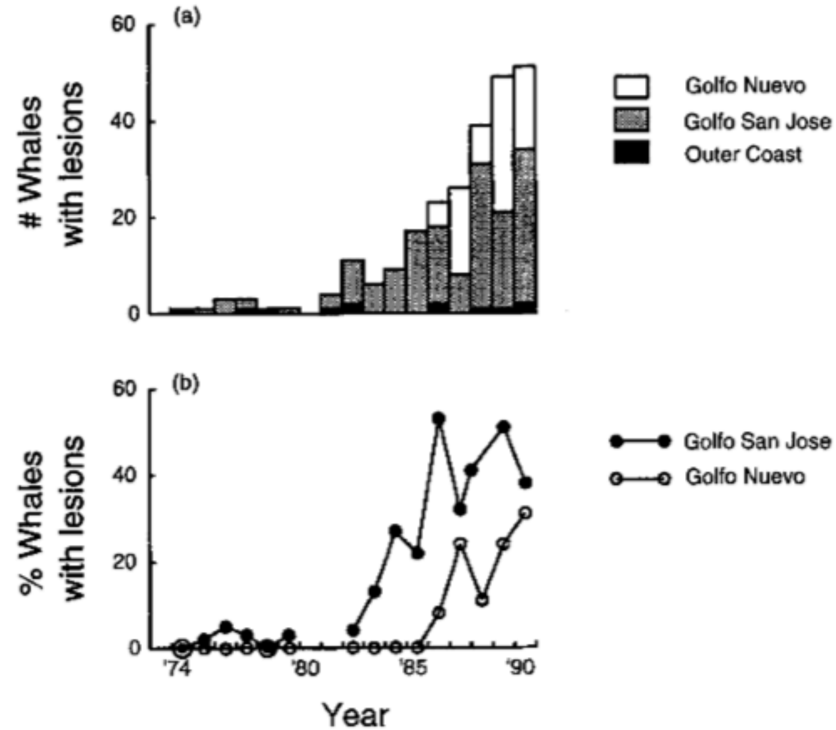


Figure 6. Temporal increase in (a) number and (b) proportion of right whales at Península Valdés with lesions on their backs. Whales with lesions did not appear in Golfo Nuevo until 1986 (1980 and 1981 excluded because of poor survey coverage).

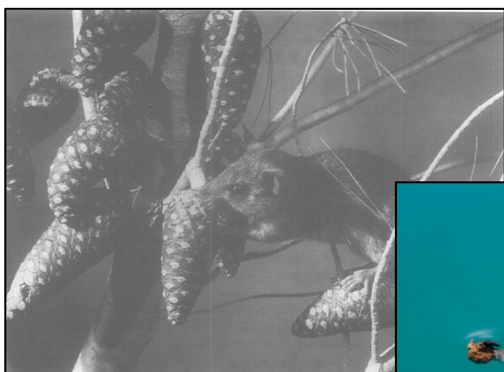
Rowntree et al. (2006) *Marine Mammal Science*; Sironi et al. (2009) I *Whaling Commission;* Fazio et al. (2015) *Marine Biology*

3b. Culture in changing environments: buffers and traps

CULTURAL BUFFERS

vs

CULTURAL INERTIA & TRAPS



Zohar & Terkel (1994) Animal Behaviour; Wild et al. (2019) Current Biology; Whitehead ??

3b. Culture in changing environments: buffers and traps

Cultural inertia**:** a reliance on cultural transmission may introduce a time-lag to cultural change in response to changing environments, particularly in the case of frequency-dependent behaviour. Cultural traps: maladaptive traditions caused by changing environments and out-of-date or locally inappropriate information.

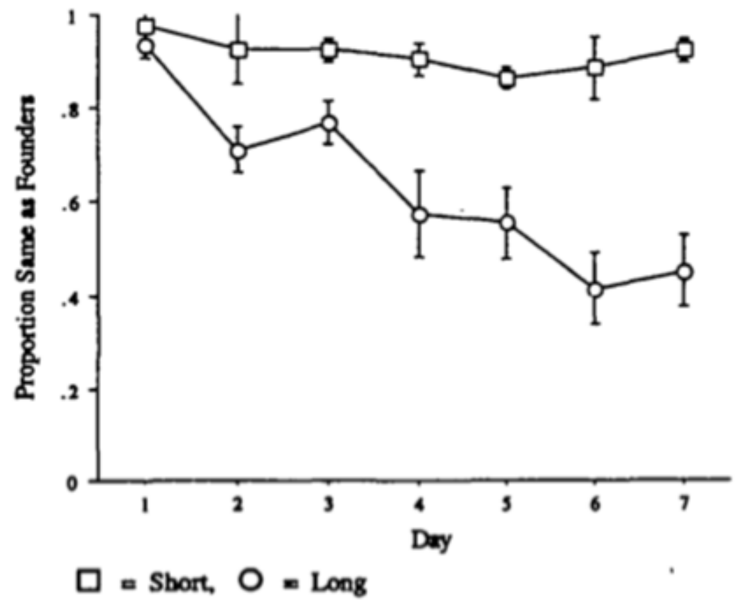


Figure 3
Proportion (mean ± SE) of times that experimental subjects took the same hole as their founders over 7 days. The route preference traditions are much more stable for populations with founders trained to take the short route ($n = 4$) than for populations with founders trained to take the long route ($n = 8$).

Guppies (*Poecilia reticulata*) trained on a long route to food (suboptimal behaviour) influenced their shoal for several days before the group switched to the shorter route.

Galef (1995) Animal Behaviour; Whitehead & Richer (2009) Evolution & Human Behaviour; Laland & Williams (1998) *Behavioral Ecology*

3b. Culture in changing environments: buffers and traps

<u>Translocation experiments in fish</u>: populations of blue headed wrasse (SPSP) share mating sites, that are socially learned. After initial translocation, new sites are selected, but after a second translocation, sites are re-used.

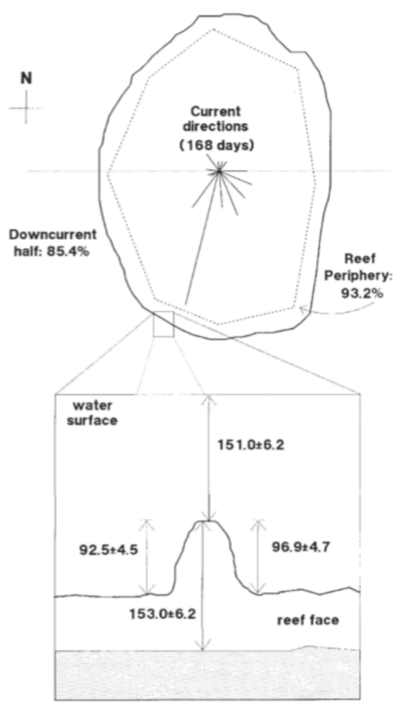


Fig. 1 Depiction of the physical characteristics of spawning sites used by the bluehead wrasse, compiled from measurements of 103 sites on 25 reefs. Top, site distribution on a composite reef as a percentage of the total sites sampled. Daily current direction data for 168 days are superimposed on the reef outline; mean (± one angular deviation) current direction was 172.8°±49.5°. Reef periphery was designated as all areas <2 m from the reef edge. Measurements (cm) of mean (± one standard error) site depth and vertical projection from the reef edge are shown in the lower part of the figure.

Table 1 Influence of pre-manipulation site usage on the location of mating sites

	Total sites available	Sites used before	Sites used after	Sites used before and after	Contingency table analysis
Experimental reefs					
PV20 (1983)	24	6	6	2	$P = 0.48$
PT32 (1984)	35	10	10	5	$P = 0.09$
WI26 (1983)	29	7	8	4	$P = 0.07$
PT31 (1984)	43	6	7	2	$P = 0.25$
PV8 (1984)	34	7	13	5	$P = 0.06$
PV21 (1986)	40	7	6	1	$P = 0.71$
Control reefs					
PV19 (1983)	43	8	8	8	$P < 0.001$
PV21 (1984)	40	7	7	7	$P < 0.001$
PV9 (1984)	45	12	12	12	$P < 0.001$

Warner (1988) Nature; Warner (1992) American Naturalist

3b. Culture in changing environments: buffers and traps

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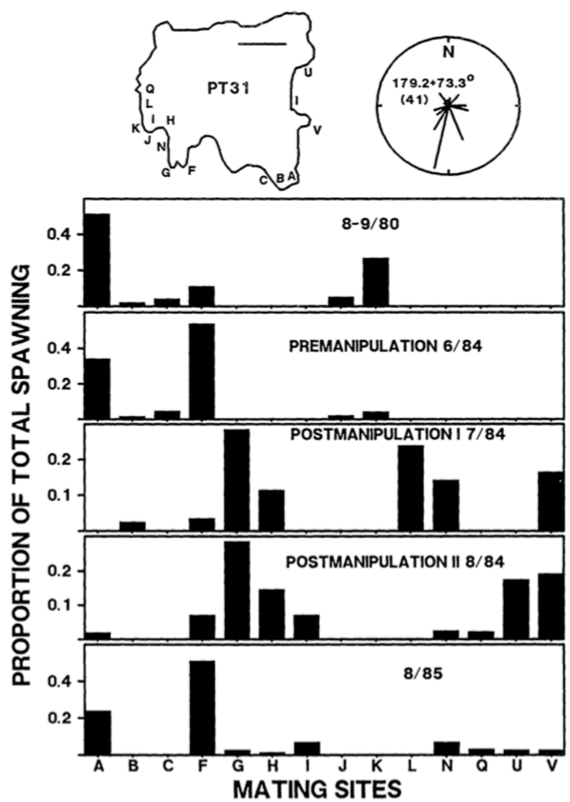


Influence of Pre-Manipulation Mating-Site Use on the Location of Mating Sites after Replacement of Residents with Naive Populations

Site and Dates	Total Sites Available	No. of Sites Used before	No. of Sites Used after	No. of Sites Used before and after	*P**
Experimental Reefs					
Reef PT31					
Manipulation I (6/23–7/26/84)	43	6	7	2	0.25
Manipulation II (8/11–8/28/84)	43	7	9	5	0.002
Reef PV8					
Manipulation I (6/6–7/31/84)	34	7	13	5	0.06
Manipulation II (8/14–8/30/84)	34	13	13	9	0.005
Reef PV21					
Manipulation I (6/30–7/17/86)	40	7	6	1	0.71
Manipulation II (7/31–8/10/86)	40	6	6	5	<0.001
Control Reefs					
Reef PV19 (6/13–6/30/83)	43	8	8	8	<0.001
Reef PV21 (7/23–8/10/84)	40	7	7	7	<0.001
Reef PV9 (6/15–7/3/84)	45	12	12	12	<0.001

* Probabilities are given for a contingency-table analysis using a one-tailed Fisher's exact test. The null hypothesis is that the sites used after the manipulation represent a random draw from the available pool, with no influence of past use.

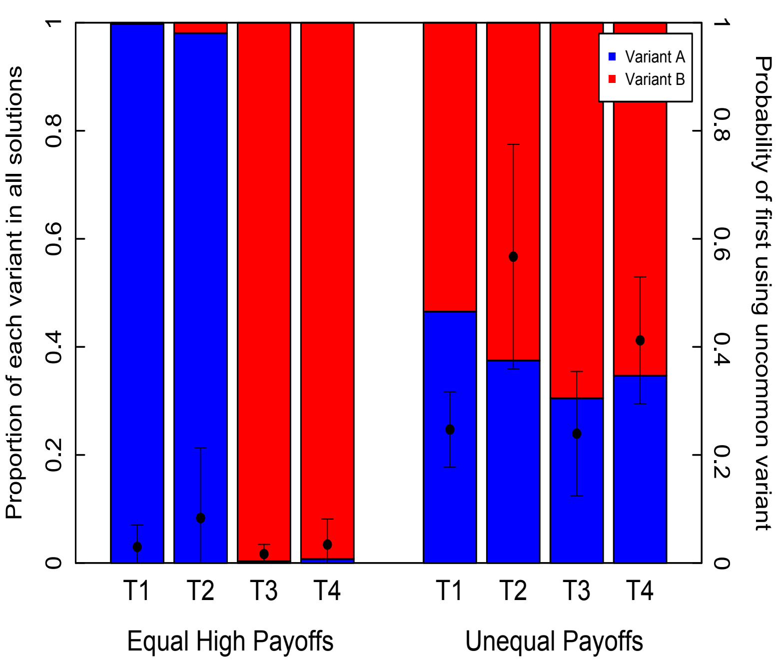
Warner (1988) Nature; Warner (1992) American Naturalist

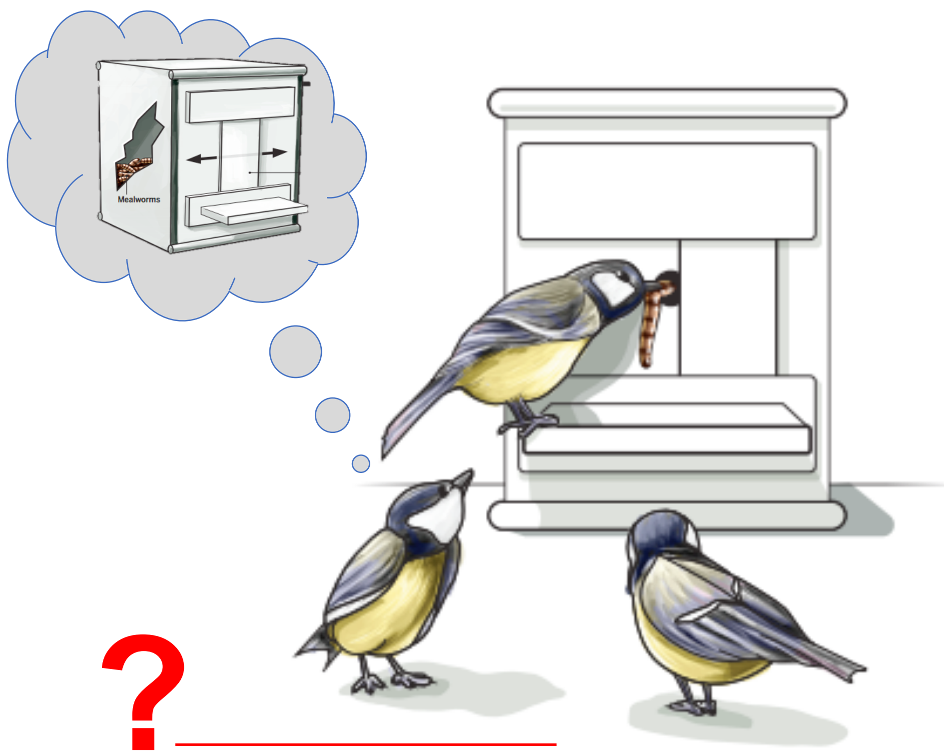
3b. Culture in changing environments: buffers and traps

Suboptimal traditions in conformist birds: Experiments in great tits (*parus major*) show that populations can switch to a more optimal tradition rapidly after conditions change. This switch is not prevented by conformity, however individual and social variation is important.

3b. Culture in changing environments: buffers and traps

<u>Suboptimal traditions in conformist birds:</u> Experiments in great tits (*parus major*) show that populations can switch to a more optimal tradition rapidly after conditions change. This switch is not prevented by conformity, however individual and social variation is important.

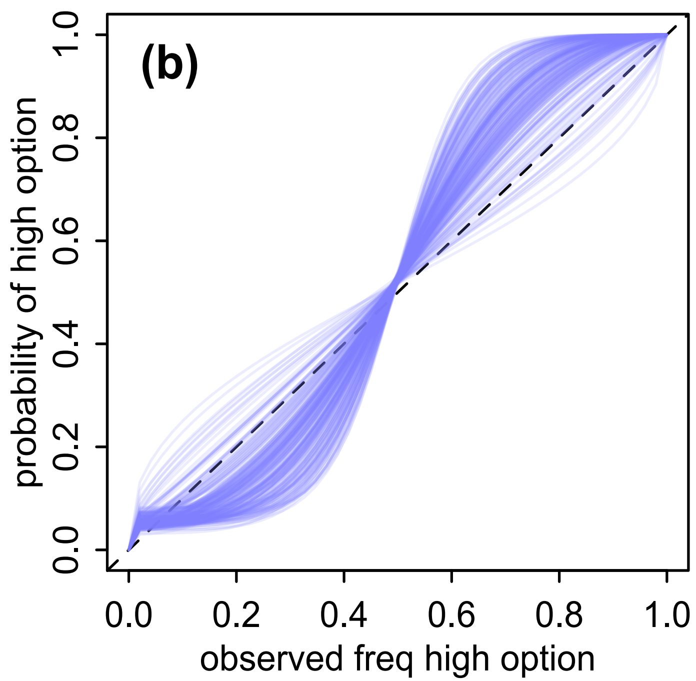


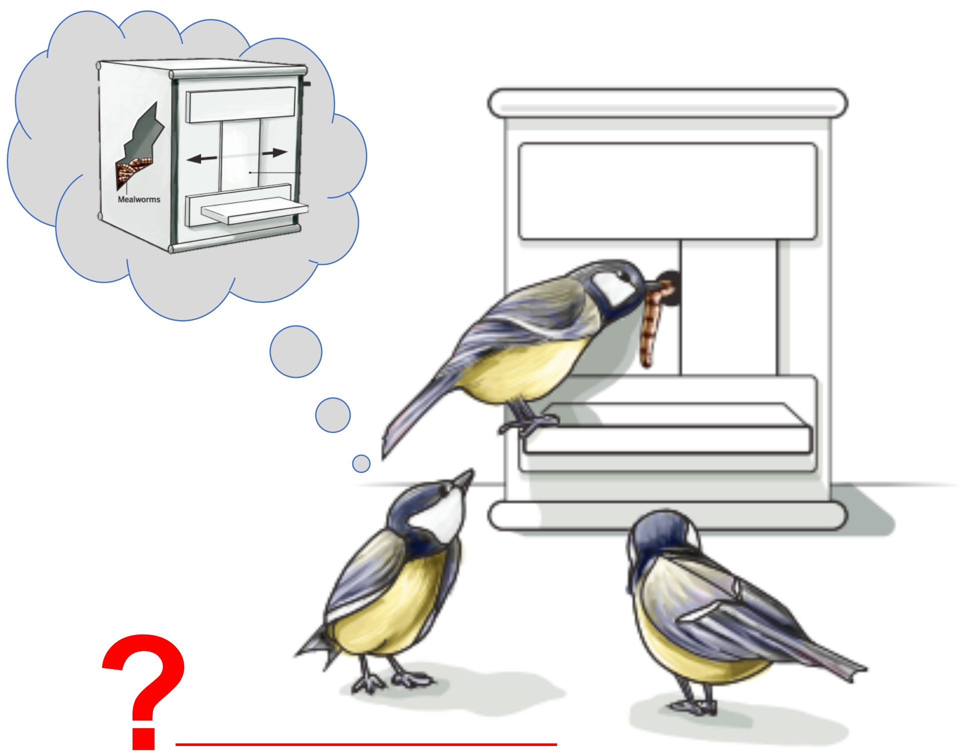


Aplin *et al.* (2017) PNAS

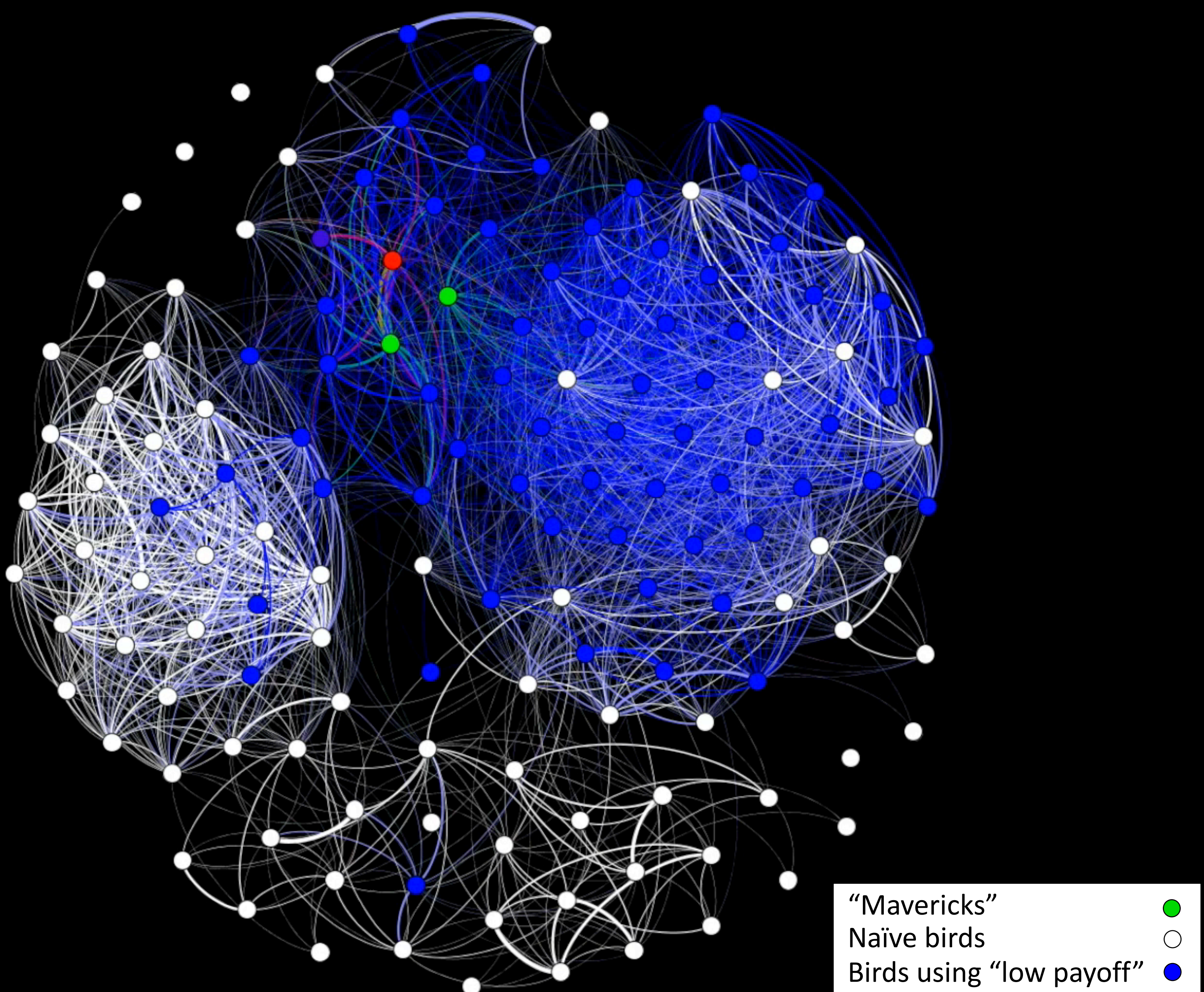
3b. Culture in changing environments: buffers and traps

<u>Suboptimal traditions in conformist birds:</u> Experiments in great tits (*parus major*) show that populations can switch to a more optimal tradition rapidly after conditions change. This switch is not prevented by conformity, however individual and social variation is important.





Aplin *et al.* (2017) PNAS



Aplin *et al*. (2017) *PNAS*

This Lecture

1. **Is culture adaptive?**
   - Social learning - contexts, trade-offs & social learning strategies
   - Culture as local adaptation (pine cone stripping)

2. **How does the environment affect selection for culture?**
   - Necessity drives innovation vs the opportunity hypothesis

3. **Culture in changing environments**
   - New cultures: diffusion of innovations
   - Existing cultures: cultural buffers, cultural traps

4. **Co-evolutionary dynamics**
   - Gene culture co-evolution
   - Speciation
   - Cultural intelligence hypothesis

4a. Gene-culture co-evolution

"Cultural adaptations affect population structures as well as the physical and social environment that elicits genetic evolution. Thus, **cultural behaviour may select for particular functional genes, influence patterns of genetic diversity, and spark speciation.** When cultural activity is an important determinant of fitness**, it can generate selection for traits that further enhance cultural competencies**, allowing genes and culture to coevolve reciprocally"

Whitehead et al. (2019)

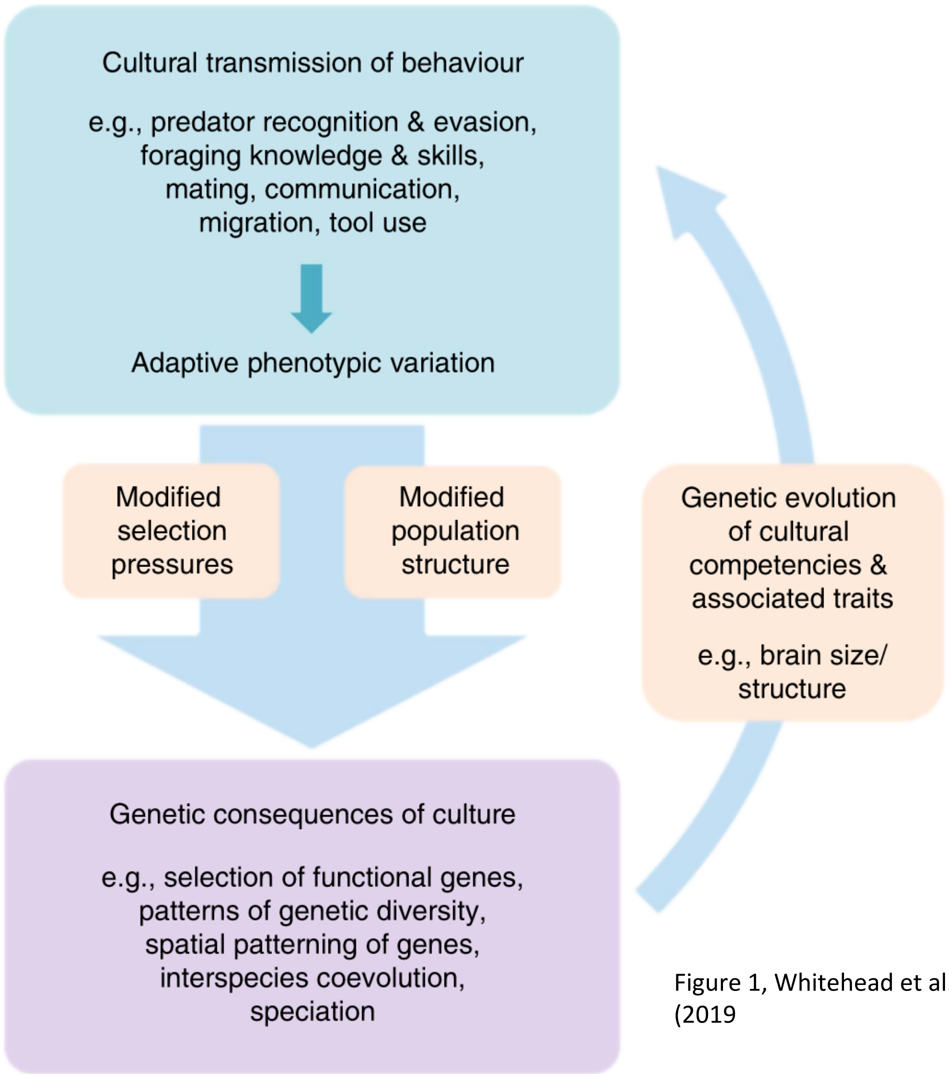
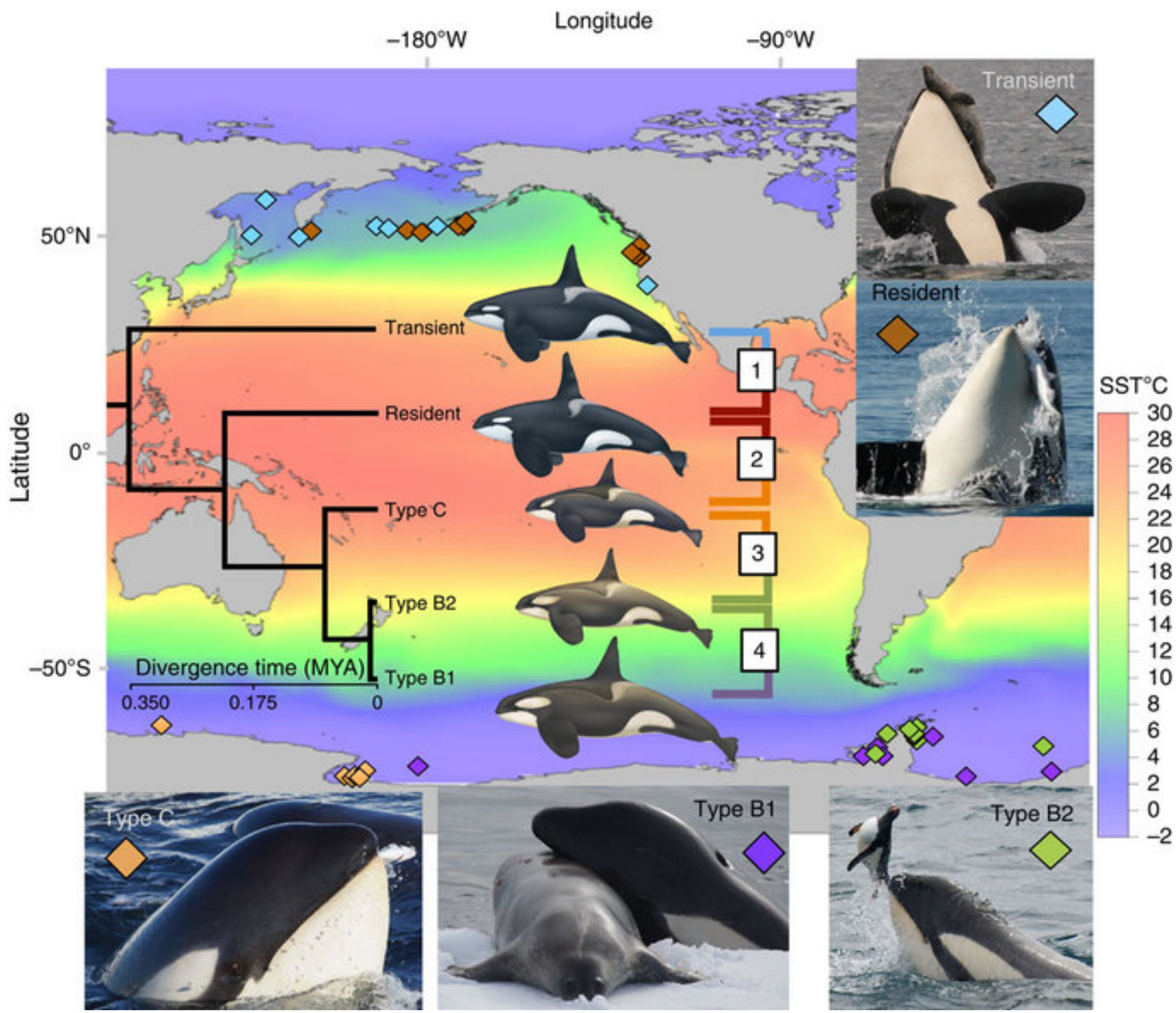


Figure 1, Whitehead et al. (2019

Whitehead et al. (2019) *Nature Communications*

4a. Gene-culture co-evolution: evidence from killer whales



Foote et al. (2016) *Nature Communications;* Whitehead (2017) *PNAS*

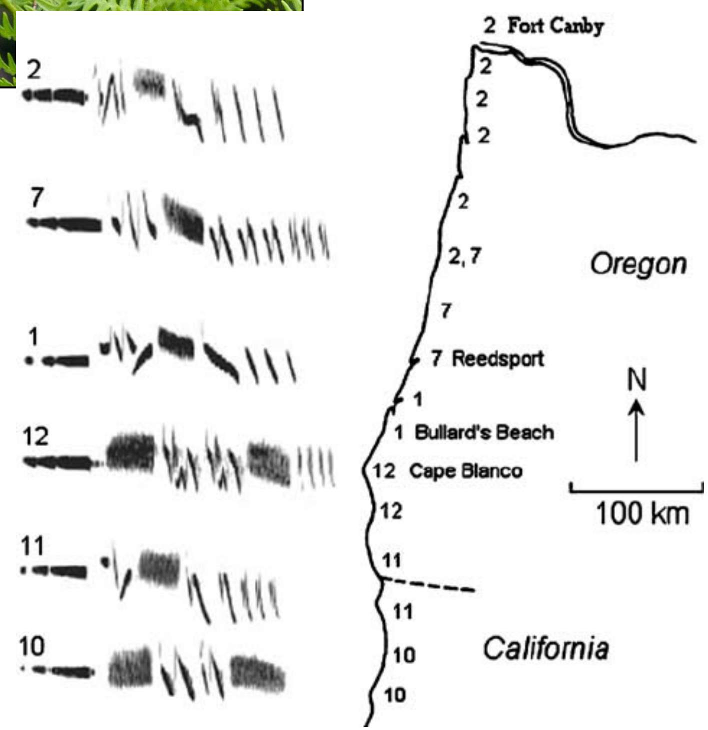
4b. Speciation through reproductive isolation in birds

White-rumped Shama, Hawaii, © Benjamin Clock and Macaulay Library

4b. Speciation through reproductive isolation in birds

Family Thraupidae (Tanagers)

Family Furnariidae (ovenbirds and woodcreepers)



Mason et al. (2016) *Evolution;* Nelson (2000) *Animal Behav;* Lipshutz et al. (2017) Molecular Ecology

4c. Cultural intelligence hypothesis

<u>Cultural intelligence hypothesis</u> argues that social learning and culture will affect evolution for intelligence, and feedback to an increasing reliance on cultural knowledge.

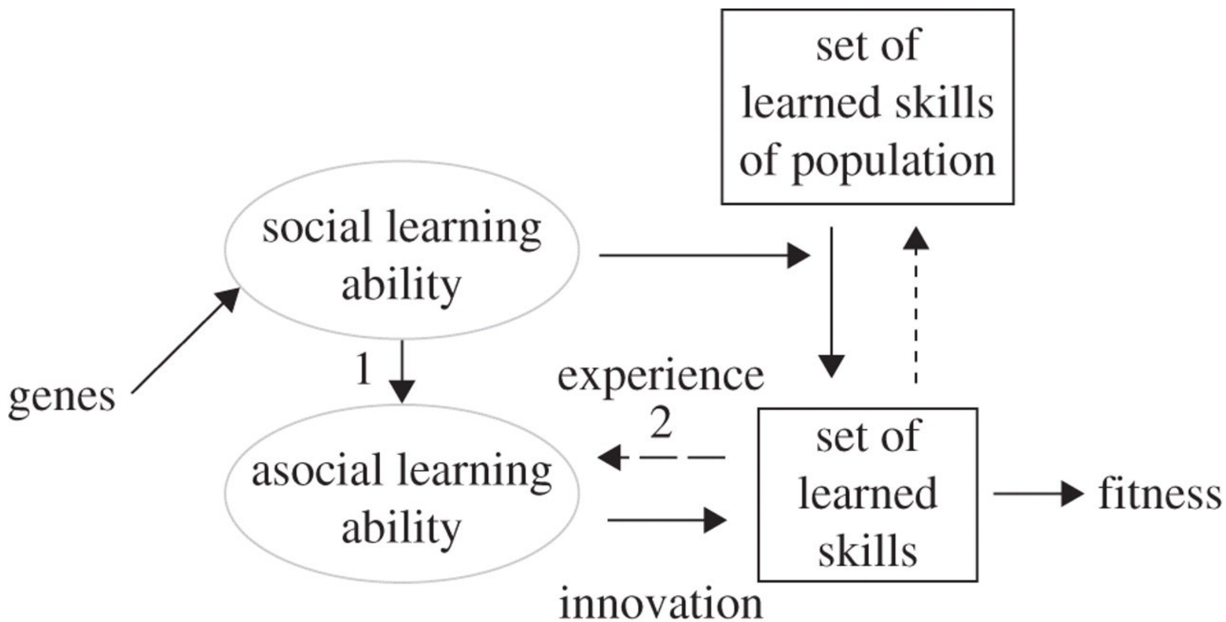


Figure 2. The evolution of intelligence through cultural feedback. Selection on an increased set of learned skills is achieved by improved social learning. Owing to the high cognitive overlap, social learning improves the asocial (individual)-learning ability (i.e. intelligence; shown by arrow 1). More learned skills also improve the latter through stronger experience effects (arrow 2).

Van Schaik & Bukart (2011) Phil Trans; Street et al. (2017) PNAS

4c. Cultural intelligence hypothesis

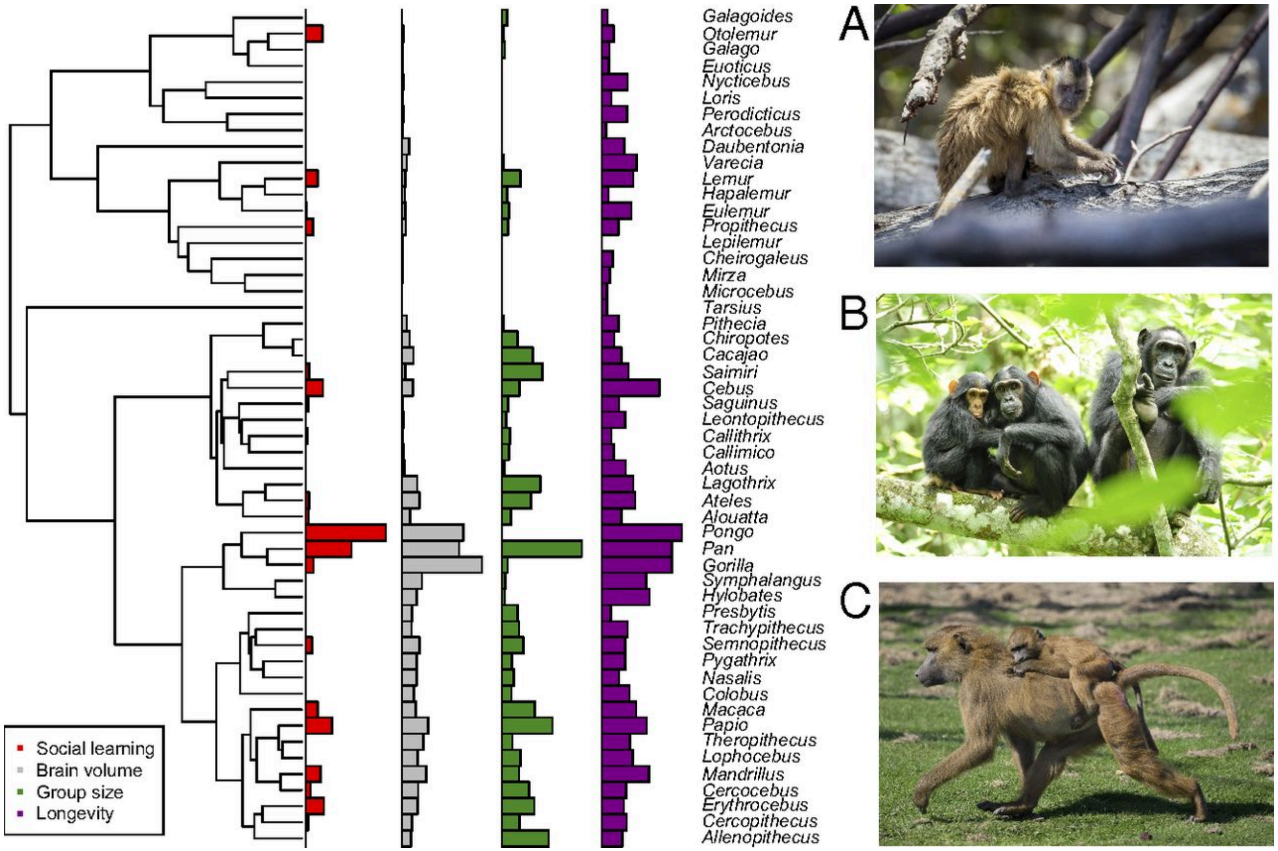


Figure 2: Summary of raw data on social learning, absolute brain volume, group size, and longevity for 52 primate gener. Images show (*A*) bearded capuchin (*Cebus libidinosus*), (*B*) chimpanzees (*Pan troglodytes*), and (*C*) guinea baboons (*Papio papio*), illustrating lineages that represent convergent coevolution of high social learning abilities, large brain volumes, complex social relationships, and long lifespans.

Van Schaik & Bukart (2011) Phil Trans; Street et al. (2017) PNAS

Ecology & Evolution

Suggested Reading

1. Whiten, A. (2017). " Culture extends the scope of evolutionary biology in the great apes." Proceedings of the National Academy of Sciences 114: 7790-7797.

2. Aplin, L. M. (2016). "Understanding the multiple factors governing social learning and the diffusion of innovations." Current Opinion in Behavioral Sciences 12: 59-65.

3. Galef, B. G. (1994) "Why behaviour patterns that animals learn socially are locally adaptive." Animal Behaviour 49: 1325-1334.

4. Koops, K., Visalberghi, E., & van Schaik, C. P. (2014). " The ecology of primate material culture ". Biology Letters. 10: 20140508.

5. Whitehead, H., Laland, K. N., Rendell, L., Thorogood, R., & Whiten, A. (2019). "The reach of gene-culture coevolution in animals." Nature Communications 10: 2405

6. Slabbekoorn, H., & Smith, T. B. (2002). "Bird song, ecology and speciation. " Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 357: 493-503.

7. Street, S. E., Navarrete, A. F., Reader, S. M., & Laland, K. N. (2017). " Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates." Proceedings of the National Academy of Sciences. 114: 7908-7914.