

ON THE INTERFACE OF GENETICS, CULTURAL AND ECOLOGICAL DYNAMICS:

SOCIAL LEARNING AND THE EMERGENCE OF FORAGING CULTURES.

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General questions

Q: how do social influences on learning affect behavioural inheritance?

Q: how does behavioural inheritance affect evolution?

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Q: how does behavioural inheritance affect evolution?

Context:

Foraging: *Learning what to eat*

Primates: *are kept in mind*

Baseline: *trial-and-error*

Opportunity-based Modelling

ToDo Principle (Hogeweg & Hesper 1981):

- Behavioural structured by opportunities
- Simple behaviour → behavioural complexity

Opportunity-based approach

a given behaviour is dependent on the opportunities for that behaviour.

➔ implement simple behaviour and see what happens

Opportunity-based model

Individual-based behaviour

- individuals live in groups and learn while foraging
- **non-identical individuals:** learning makes a difference and can be observed
- **time-dependence:** learning history

Opportunity-based model

Individual-based behaviour

- individuals live in groups and learn while foraging
- **non-identical individuals:** learning makes a difference and can be observed
- **time-dependence:** learning history

Diverse spatial environment

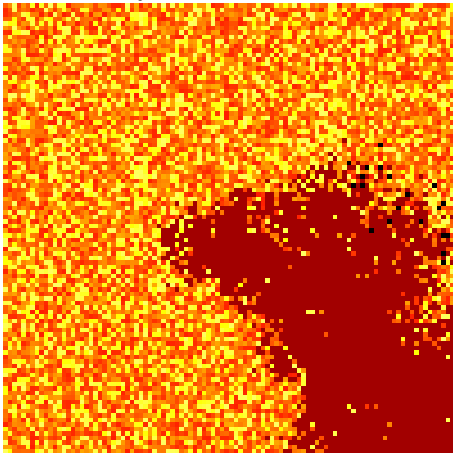
- **there is something to learn!**
- **spatial variation:** affects what food is where

↳ **affects what you learn where → opportunities for learning**

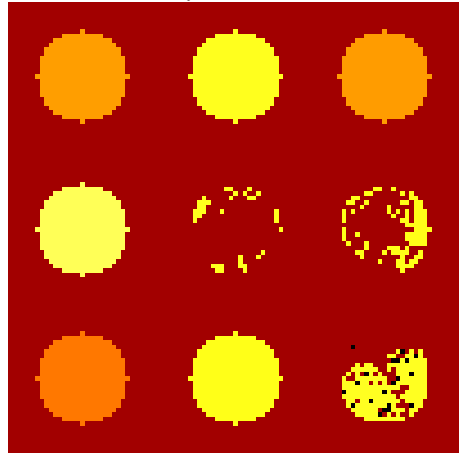
Model: Environment

- Many resources with different qualities
- Resources placed on 2D grid: resource distribution
- Resources replenished at beginning of each year

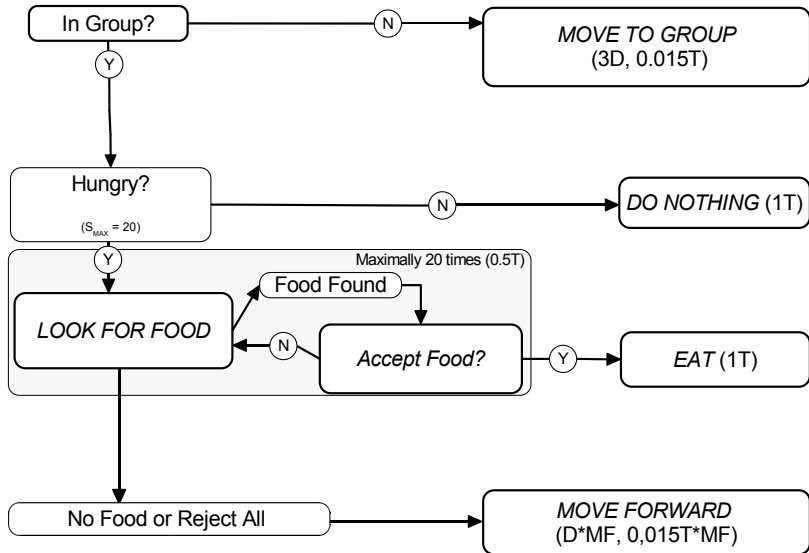
Uniform distribution



Patchy Distribution



Model: Individual behaviour rules



Model: Trial-and-Error Learning

1) Discovering new resources (TRIALS)

↳ fixed probability to try unknown resources: TRIAL RATE

Model: Trial-and-Error Learning

1) Discovering new resources (TRIALS)

➔ fixed probability to try unknown resources: TRIAL RATE

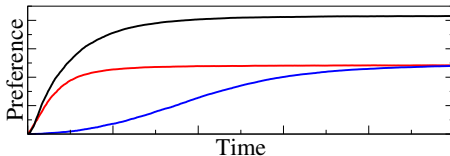
2) Developing resource preferences (RE-INFORCEMENT LEARNING)

$pref_r$ = individual's energy estimate for resource r

E_{avg} = average energy (quality) per item digested

$pref_{avg}$ = average preference / item digested

$$pref_r := pref_r + (PU \cdot \frac{S_r}{S_T} \cdot (E_{avg} - pref_{avg})) \quad (1)$$



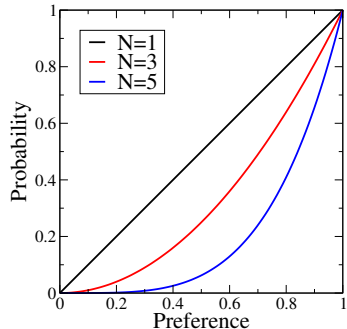
Food choice and model feedbacks

$$prob = \left(\frac{pref_r}{pref_{exp}} \right)^N \quad (2)$$

Pre_{exp}: expectation of quality of food in the environment

if *pref_r* > *pref_{exp}* **then** *pref_{exp}* = *pref_r*

else *pref_{exp}* := *pref_{exp}* * 0.999



Food choice and model feedbacks

$$prob = \left(\frac{pref_r}{pref_{exp}} \right)^N \quad (3)$$

Pre_{exp}: expectation of quality of food in the environment

if *pref_r* > *pref_{exp}* **then** *pref_{exp}* = *pref_r*

else *pref_{exp}* := *pref_{exp}* * 0.999

Feedback:

$$pref_r := pref_r + \left(PU \cdot \frac{S_r}{S_T} \cdot (E_{avg} - pref_{avg}) \right) \quad (4)$$

↓

↑

$(pref_r / pref_{exp})^N \rightarrow$ FORAGING AND EATING

Part 1: Trial-and-Error Baseline experiments

- **Effect environment on learning opportunities?**

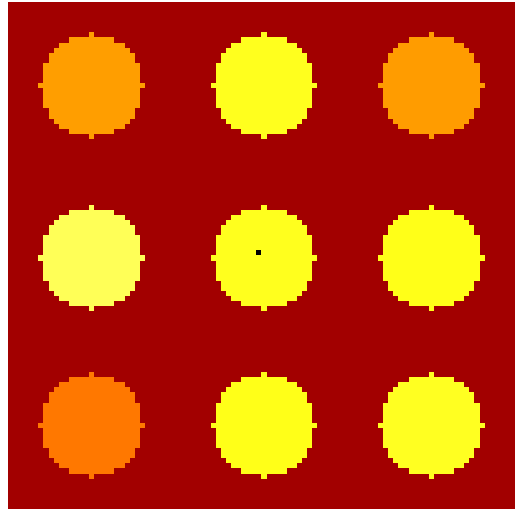
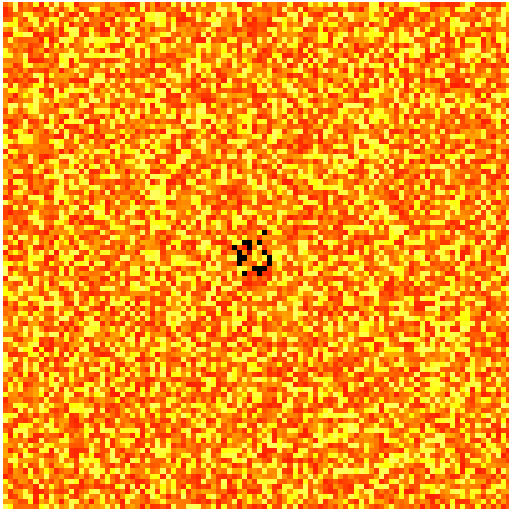
Uniform vs Patchy

- **Effect grouping on learning opportunities?**

Gregarious vs Solitary

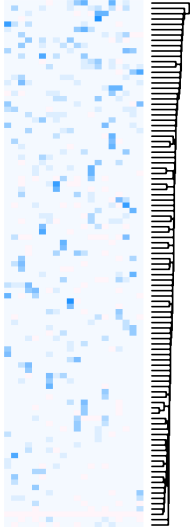
Baseline experiments: study diet development in 20 naïve individuals for 50 years.

Uniform and Patchy

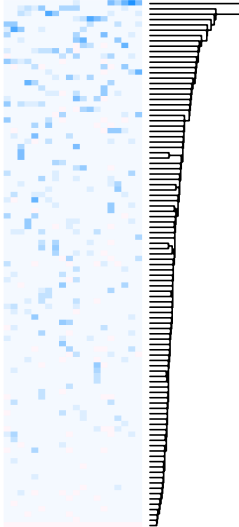


Results: Uniform Distribution

Grouping
INDIVIDUALS



Solitary
INDIVIDUALS

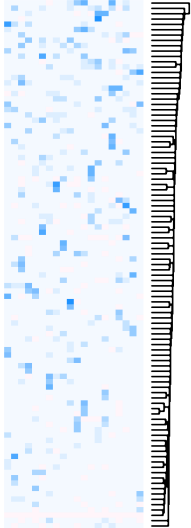


Resources

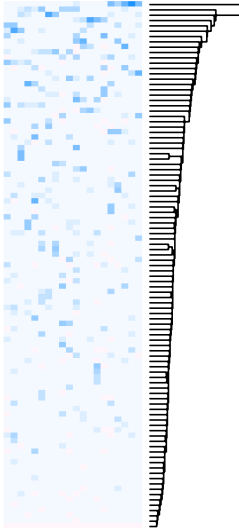
Clustering: Manhattan distances and single linkage

Uniform compared to Patchy

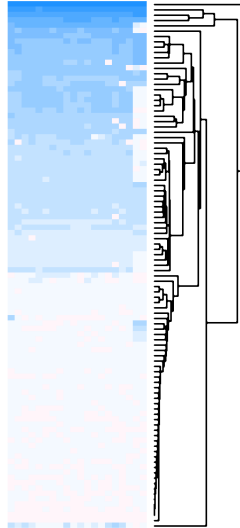
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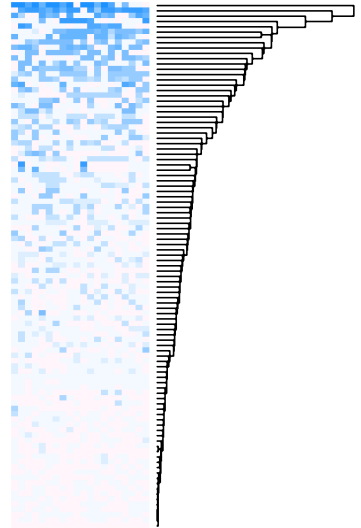
Solitary
INDIVIDUALS



Grouping
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Resources

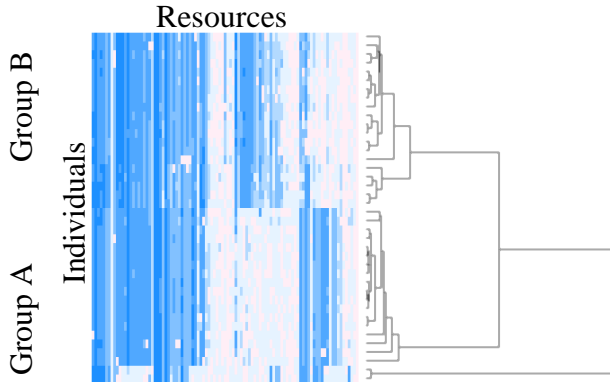
Clustering: Manhattan distances and single linkage

UNIFORM

PATCHY

Results: Patchy

Different groups in the exact same environment after 10 years



Clustering: correlation distances and average linkage

So far

- Resource distributions have profound impact
(not type of learning)
 - ↳ **Uniform**: local depletion of opportunities by groups
 - ↳ *divergence in diet*
 - ↳ **Patchy**: local sharing of opportunities in groups
 - ↳ *convergence in diet*
 - ↳ *group-level diets*

Part 2: Diet inheritance by trial-and-error?

Does convergence in learning in patches lead to diet traditions?

↳ **are group-level diets inherited?**

Part 2: Diet inheritance

Does convergence in learning in patches lead to diet traditions?

↳ **are group-level diets inherited?**

Transmission Chain Experiments (cf Curio 1978)

- Each year oldest individual is replaced by naïve individual (group replaced every 20 years)
- 20 year initialization period: to establish stable age distribution
- Compare 2 groups in the exact same environment *over 90 years*

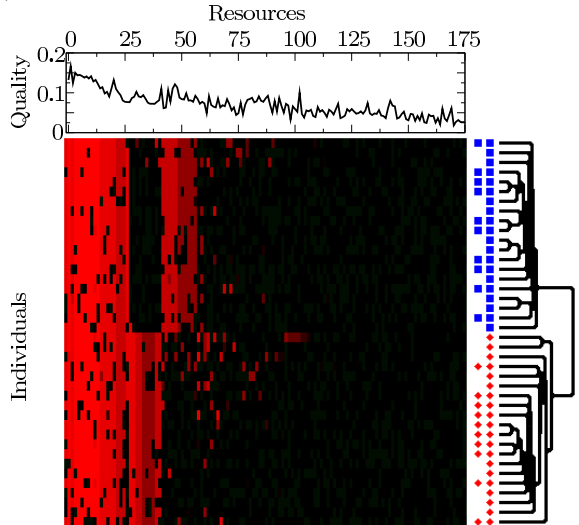
Important parameters:

- **MF** = distance moved forward after not finding food
- **Foraging selectivity (N)** $\rightarrow (pref_r/pref_{exp})^N$

Results: Transmission of group-specific diets

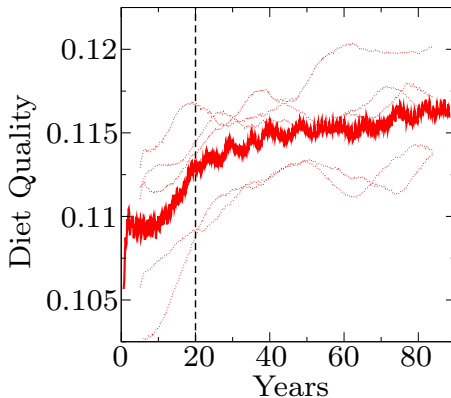
*Comparing 2 groups over 2 generations (at year 40 and year 80)
($N=3$, $MF=10$, 250 resources):*

- Diet traditions even with $TR=1.0$
- Convergence on high quality resources
- Divergence on lower quality resources



Clustering: correlation distances and average linkage

Results: Cumulative increase in diet quality



- Diet quality **increases over generations**
- Cumulative group-level process **beyond single individuals**

Contrasting cultural phenomena

TRADITIONS



CONSERVATIVE

CUMULATIVE CHANGE

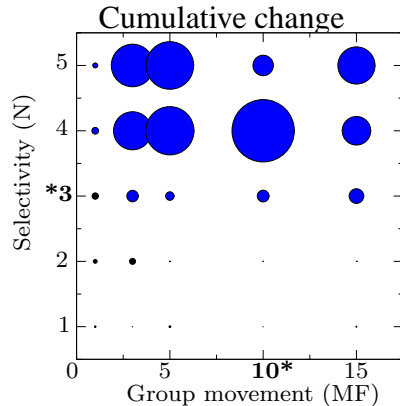
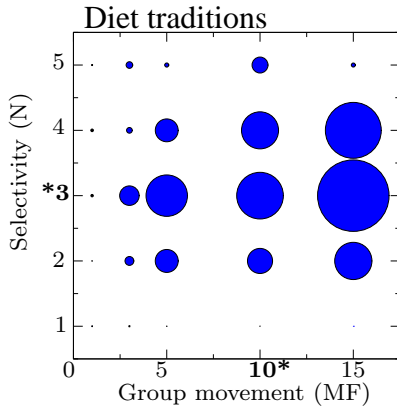


“PROGRESSIVE”

MUTUALLY EXCLUSIVE?

WHEN DO THEY OCCUR?

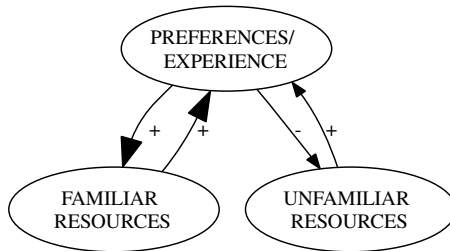
When traditions and cumulative change?



- **Move Forward:** ratio time $\frac{PREFEREDPATCH}{NON-PREFEREDPATCH}$

- **Selectivity:** TRANSITION TRADITIONS TO CUMULATIVE PROCESS

Role selectivity



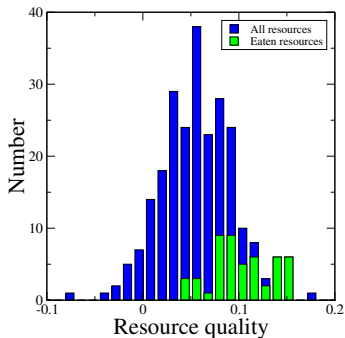
- *Positive feedback foraging* and preferences → **familiarity bias**
- *Selectivity*: **discrimination** between preferences
- *Selectivity*: **enhanced bias to high quality**
- *Selectivity*: **enhanced familiarity biases (variation)**

When traditions?

Convergence due to grouping > divergence due to selectivity

Traditions: shared familiarity biases

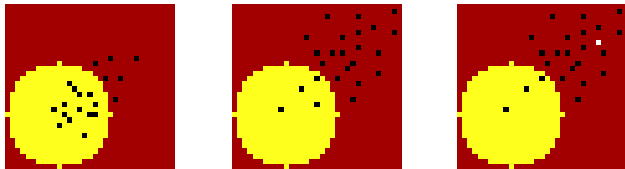
Resource distribution: familiarity biases on low quality resources



When accumulation?

Convergence due to grouping < divergence due to selectivity

Variation in group → selection of shared preferences
(high quality)



Naïves → learn from “selected” resources

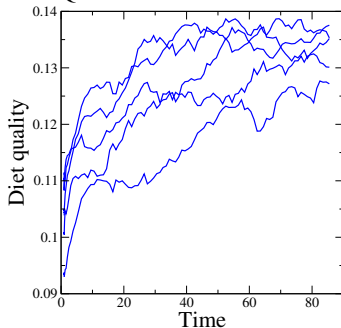
Naïves → add to variation in group → add to selection process

Positive feedback:

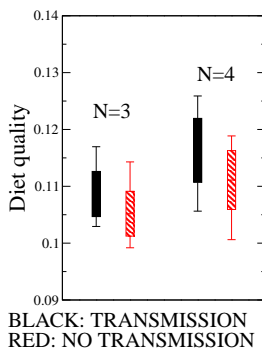
naïves inheriting selectivity *and* contributing to it

Accumulation through positive feedback

DIET QUALITY OF 1 YEAR OLDS



EFFECT NAÏVES ON DIET QUALITY



Groups → *context for selecting diet*

Naïves → *add to variation and group's selectivity*

As selectivity increases

Low selectivity

“open-minded individuals”

- grouping > selectivity
- low intra-group variation
- high inter-group variation
- naïves inherit *group diet*

“traditional groups”

As selectivity increases

Low selectivity

“open-minded individuals”

- grouping > selectivity
- low intra-group variation
- high inter-group variation
- naïves inherit *group diet*

“traditional groups”

High selectivity

“stubborn individuals”

- selectivity > grouping
- high intra-group variation
- low inter-group variation
- naïves inherit *selectivity*

“progressive groups”

Discussion: What do we get with Trial-and-Error?

Depends on resource distributions (opportunities):

- *Divergent learning:*

 - ↳ grouping and locally depletable opportunities

- *Convergent learning and group-level diets:*

 - ↳ grouping and shared opportunities

Discussion: What do we get with Trial-and-Error?

Depends on resource distributions (opportunities):

- *Divergent learning:*

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 - ↳ grouping and shared opportunities

Constrasting cultural phenomena:

- *Traditions:*

 - ↳ population dynamics and group-level diets

- *Cumulative change:*

 - ↳ population dynamics and group-level selectivity

We get a lot!

Conclusions

Social influences on learning as *side-effects* of grouping

- ↳ arise independent of adaptive consequences, i.e. “for free”
- ↳ obligatory: individuals do not have a choice (opportunity)

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Diet culture follows **from convergent trial-and-error learning**

- ↳ does not require sophisticated cognition
- ↳ also side-effect of grouping (“for free”)
- ↳ “obligatory”: choice between traditions (selective) and/or cumulative change (strongly selective)

Future work

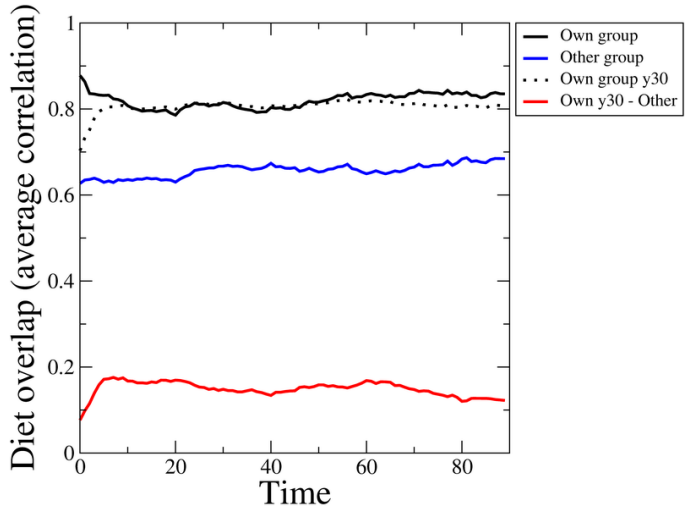
What about observational learning?

↳ Q: what are its additional effects on diet culture?

How does diet culture feedback on evolution?

↳ evolution of the digestive system

Diet traditions



Accumulation

Linear regressions on diet quality

