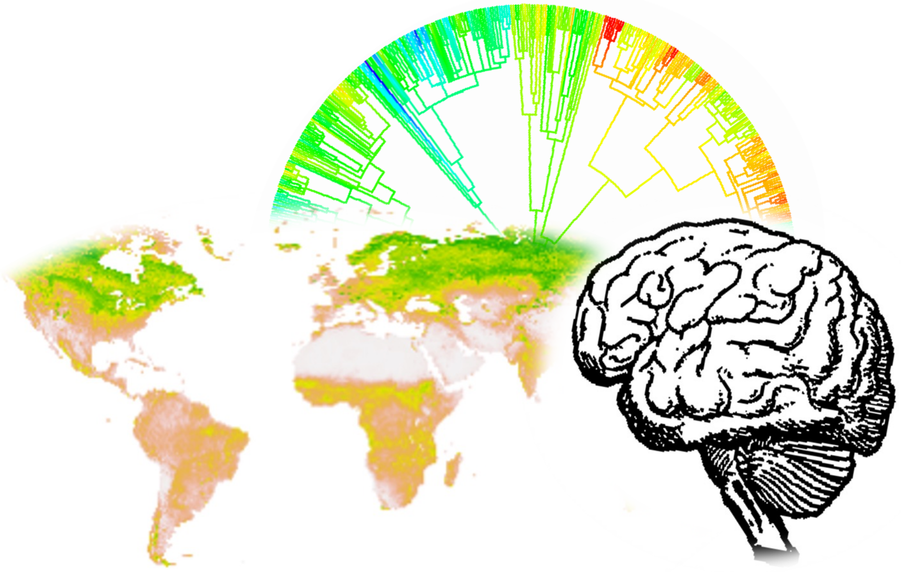
Social and Ecological Aspects of Brain Size Evolution

A Comparative Approach



PhD Thesis Defence

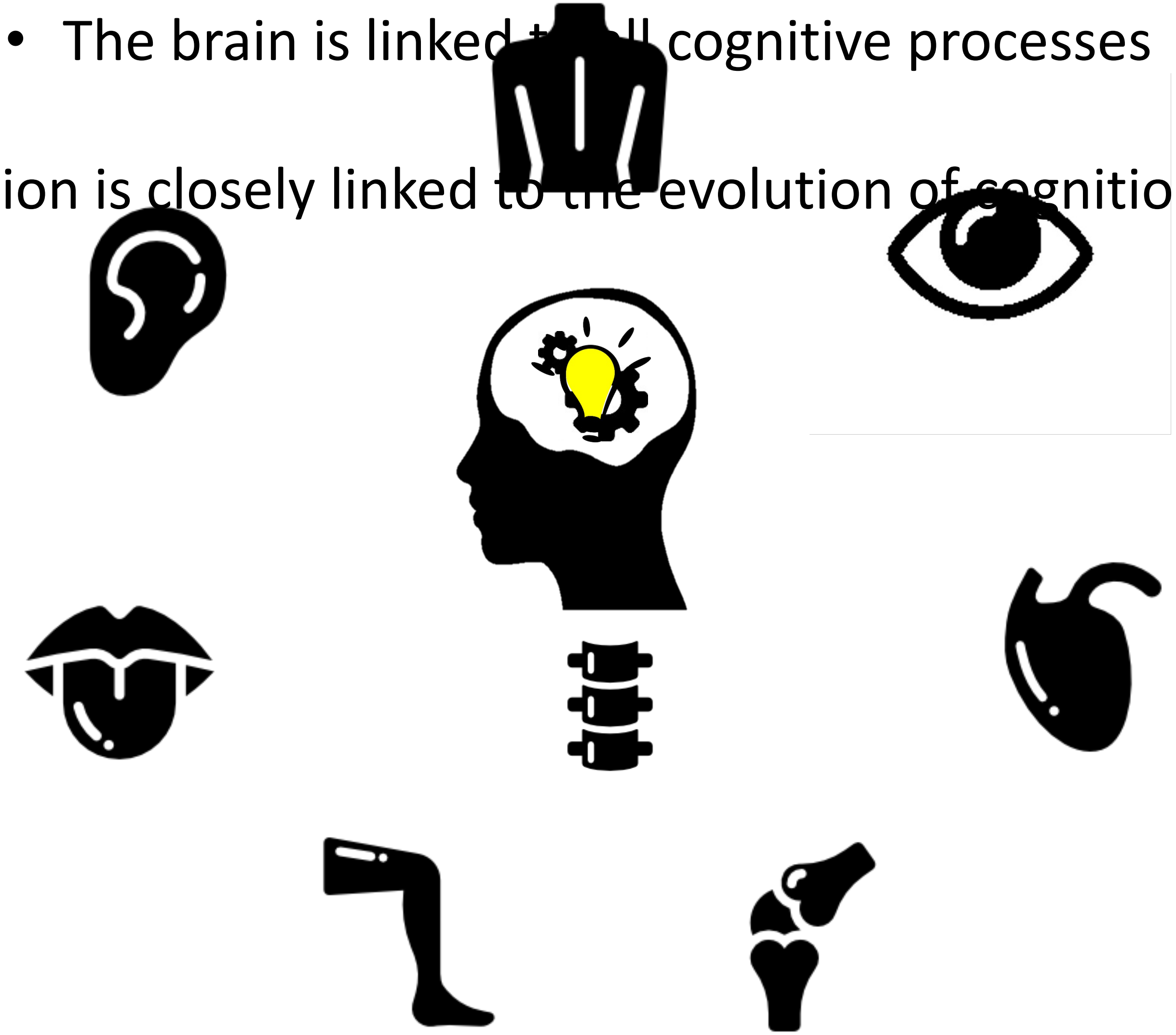
Sereina M. Graber

1st of September 2017

Supervised by Dr. Karin Isler and Prof. Dr. Carel van Schaik

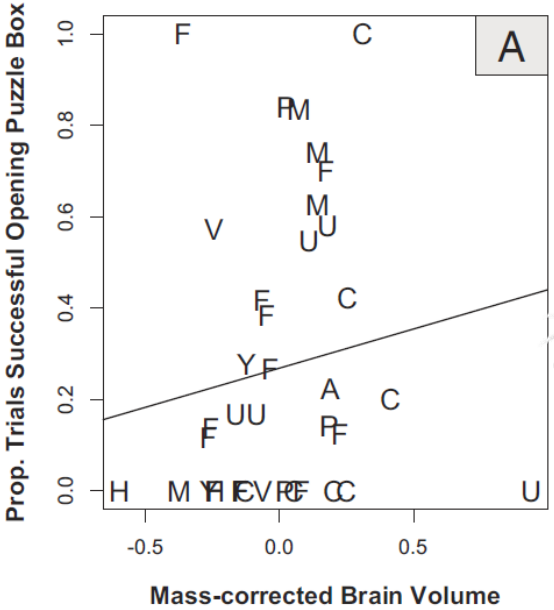
Why Study Brain Size Evolution?

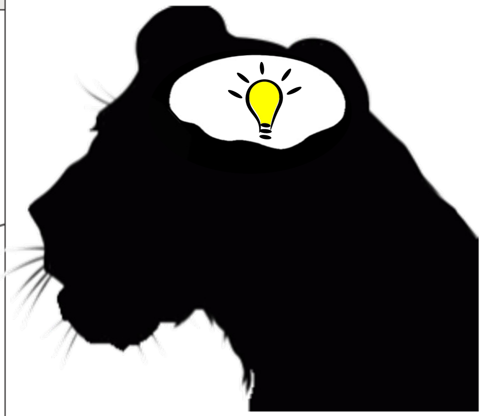
- The brain is linked to all cognitive processes
- Brain size evolution is closely linked to the evolution of cognition and intelligence



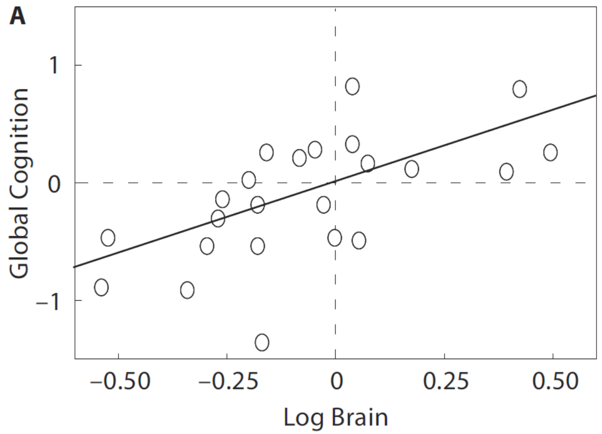
Larger Brained Species Are More Intelligent

Benson-Amram et al. 2016

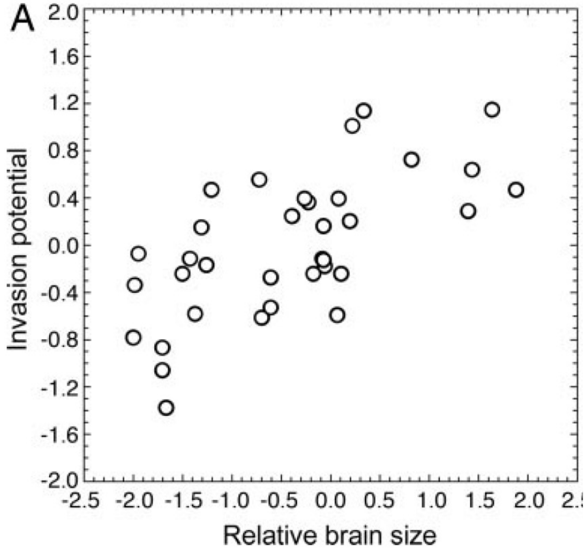




Deaner et al. 2007

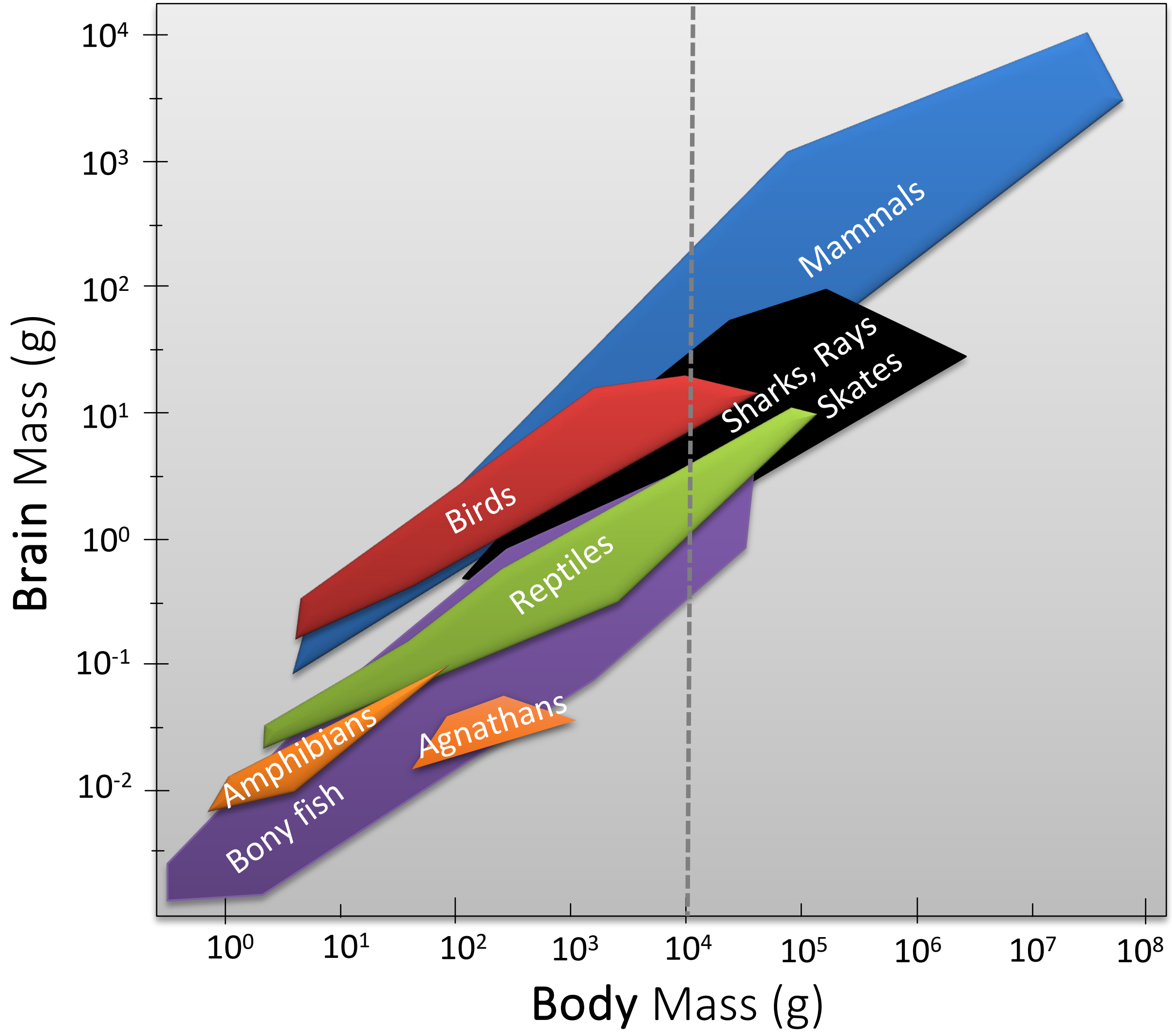


Sol et al. 2005



Byrne & Whiten 1988, Harvey & Krebs 1990, Dunbar 1995, Byrne 1997, Reader & Laland 2002, Lefebvre et al. 2004, Deaner et al. 2007, Burkart et al. 2017

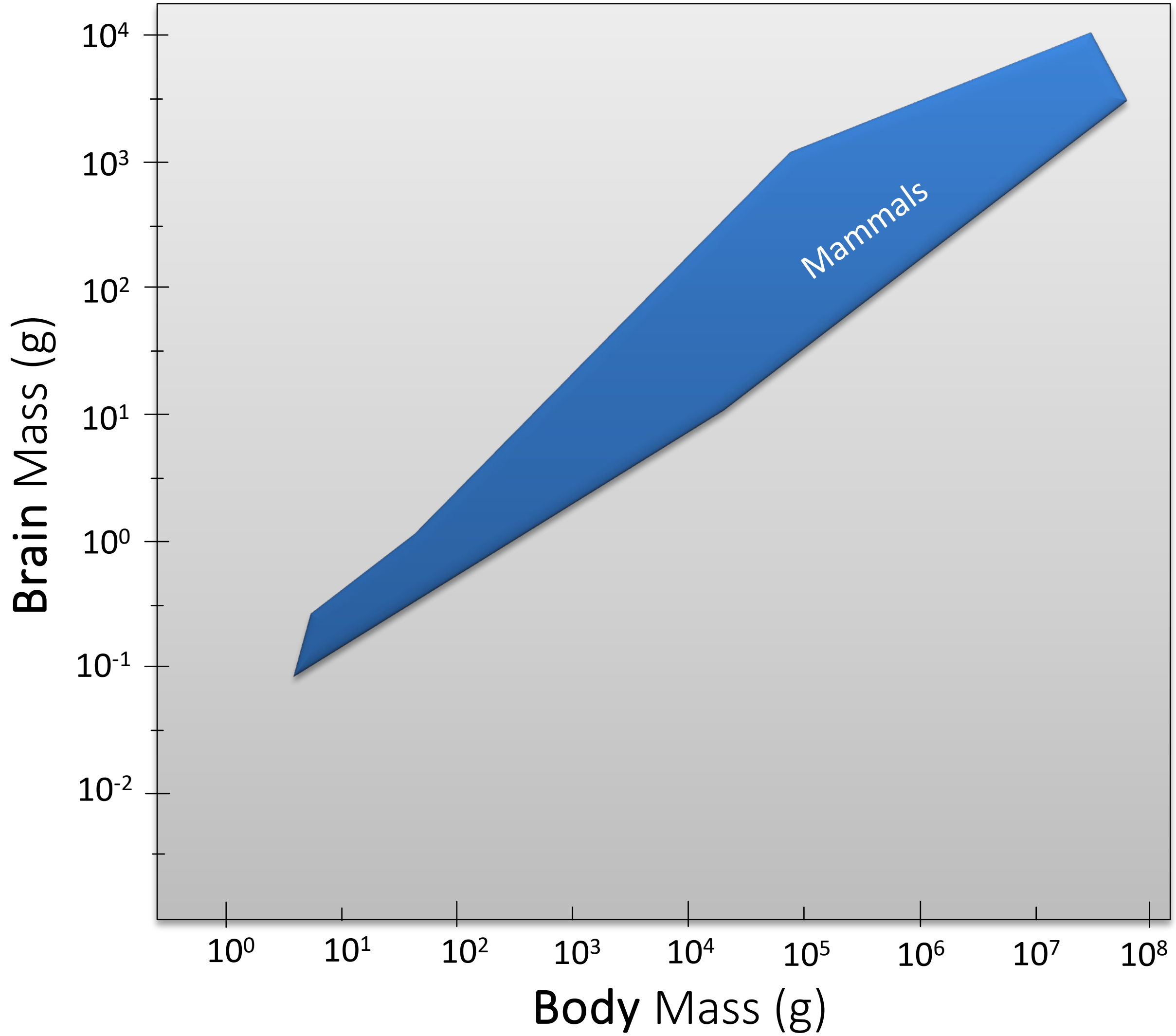
Relevant Phenomenons in Brain Size Evolution



- **Much variation in relative brain size**
  - between lineages
  - within lineages

J. van Woerden 2011, modified from Jerison 1973

Relevant Phenomenons in Brain Size Evolution



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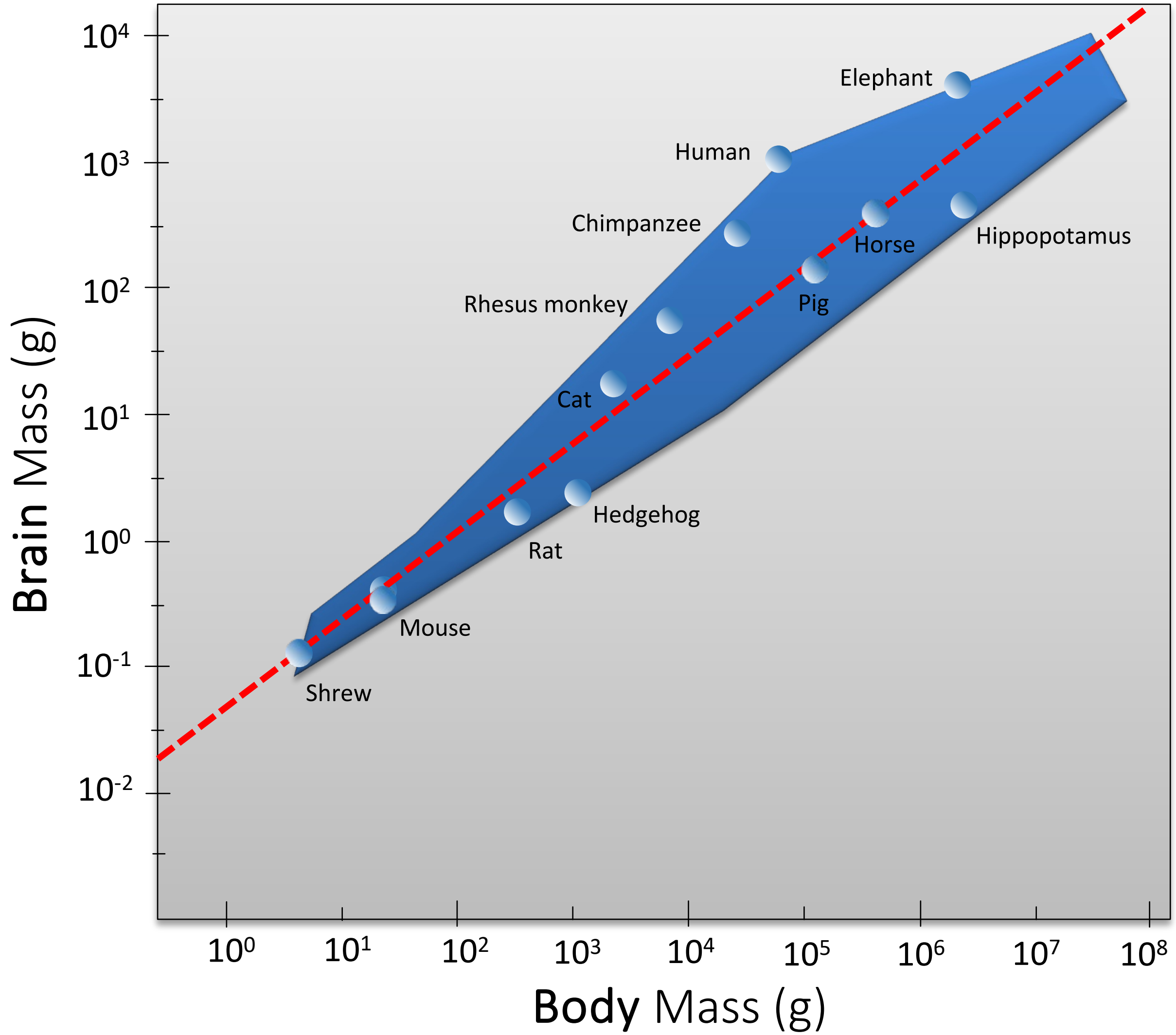

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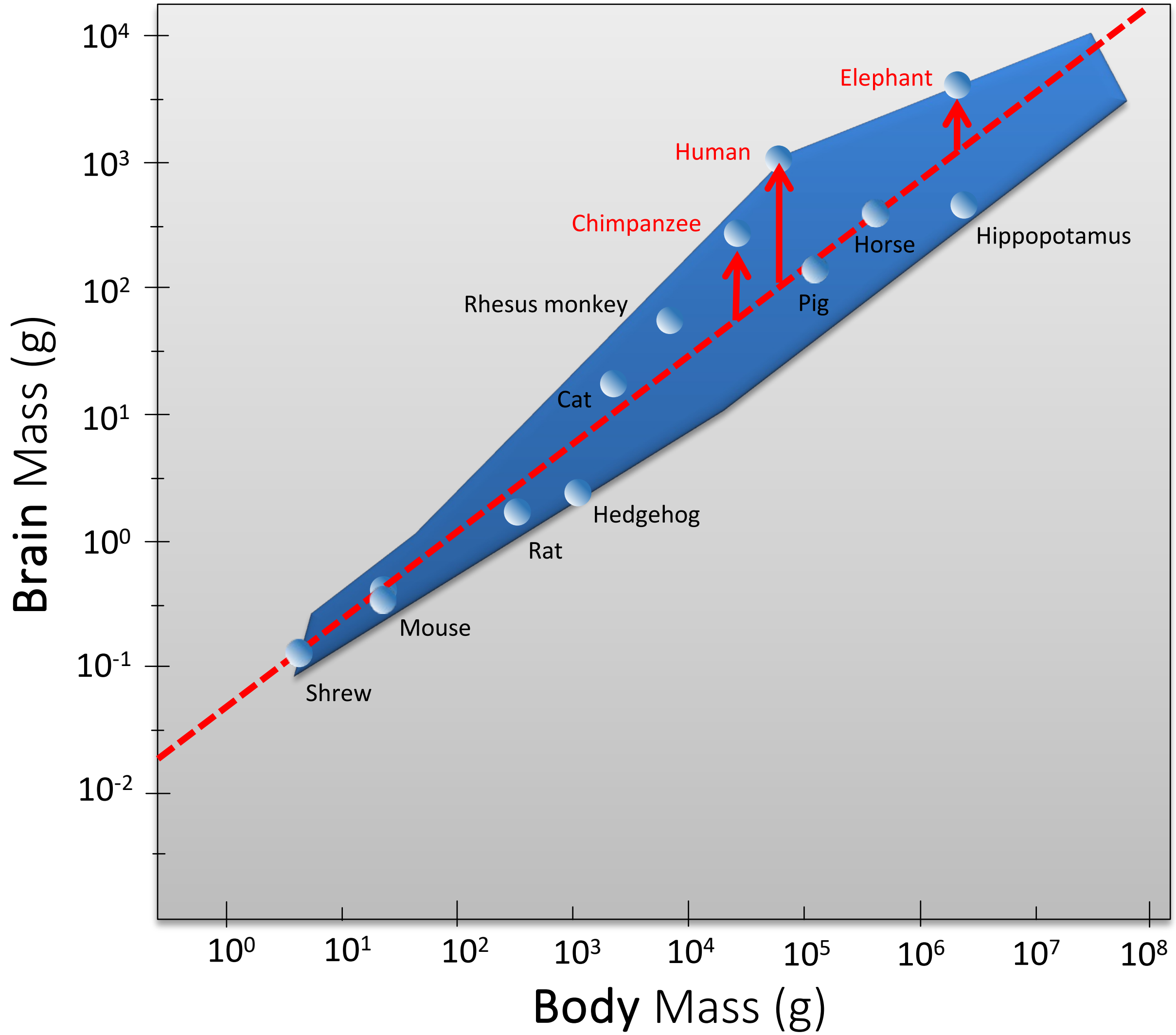

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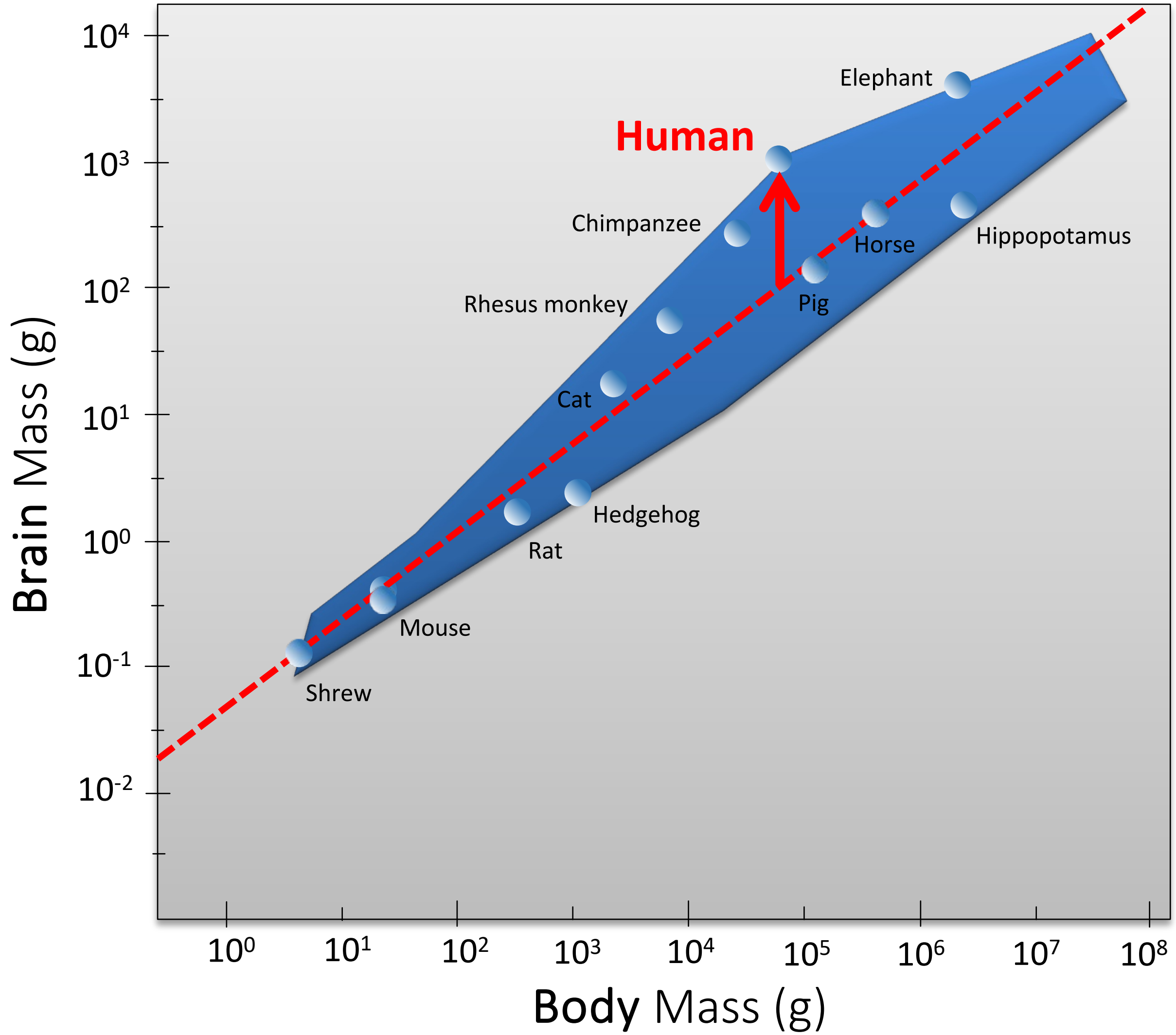

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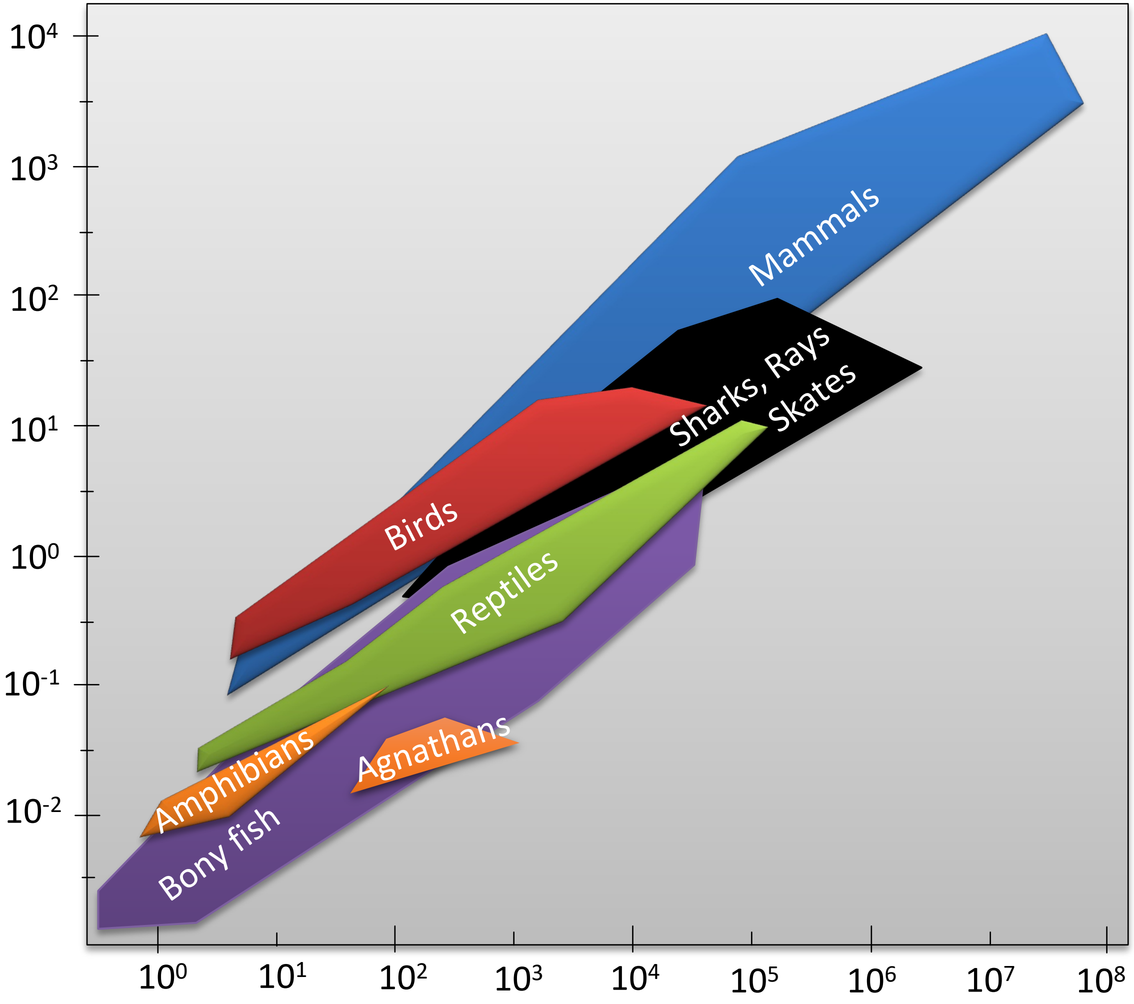


- Much variation in relative brain size
  - between lineages
  - within lineages

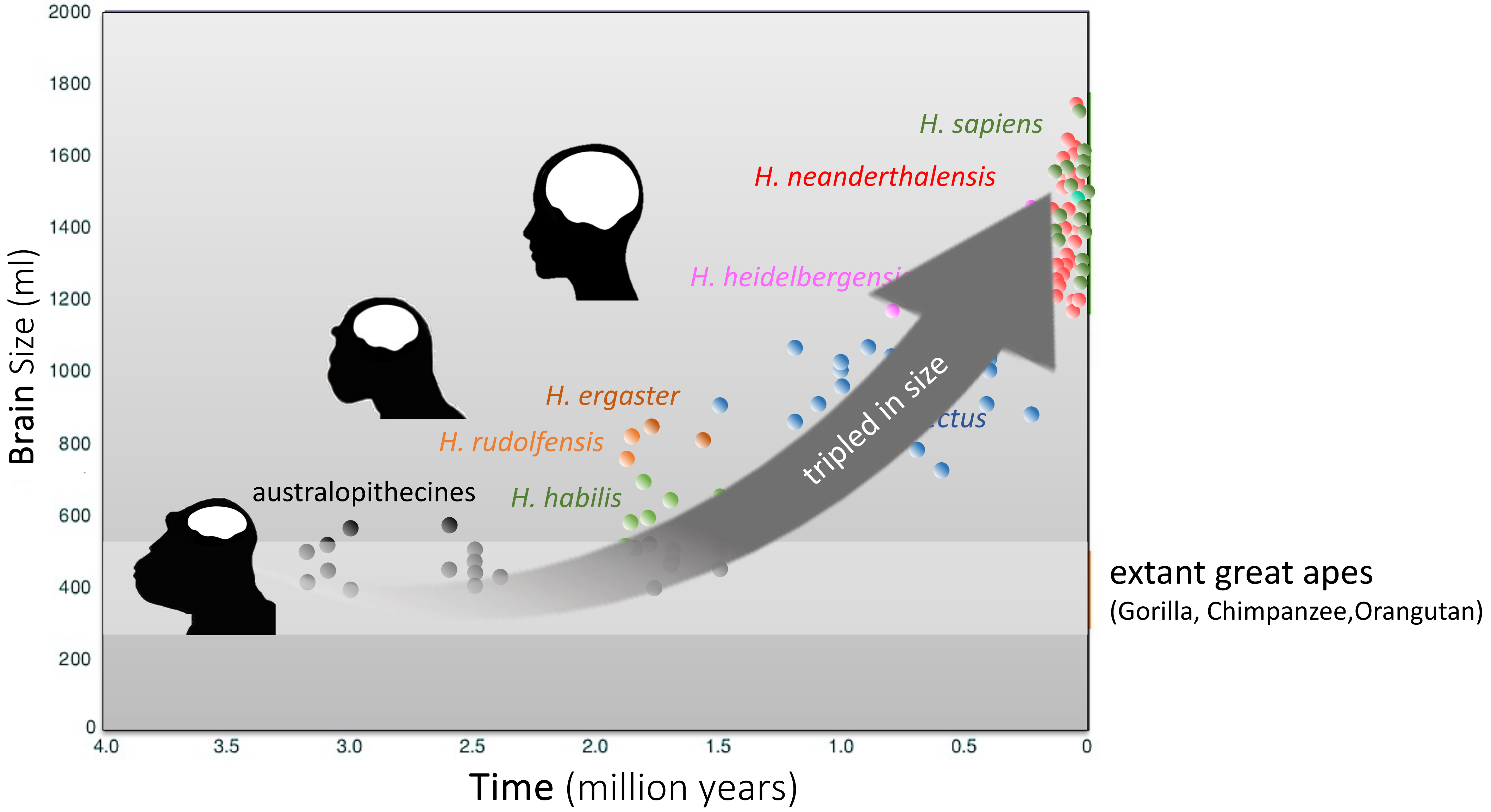
- **Evolutionary trend to encephalization**

  (Marsh's rule: Jerison 1973)

  Brains get relatively larger over evolutionary time

J. van Woerden 2011, modified from Jerison 1973

Brain Size Increased Over Time in Human Lineage



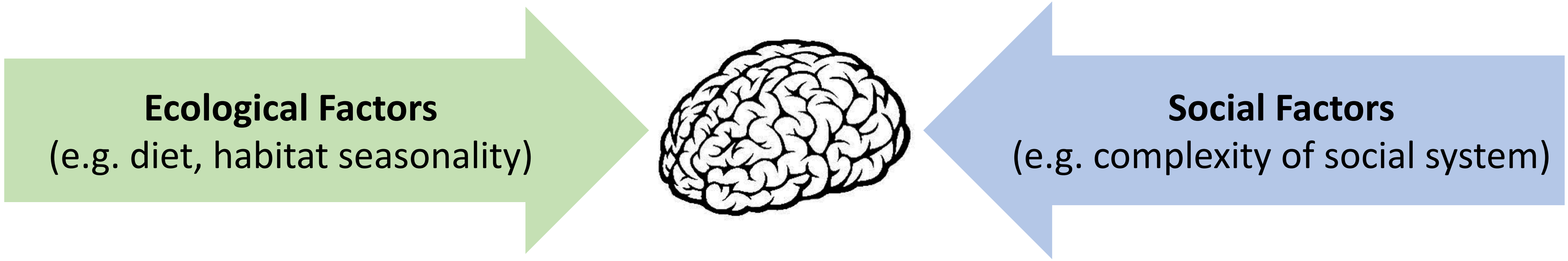
modified from Holloway 2004

Questions

Why did some species/taxa grow larger brains than others?

What led to our unmatched relative brain size?

Hypotheses Explaining Brain Size Evolution



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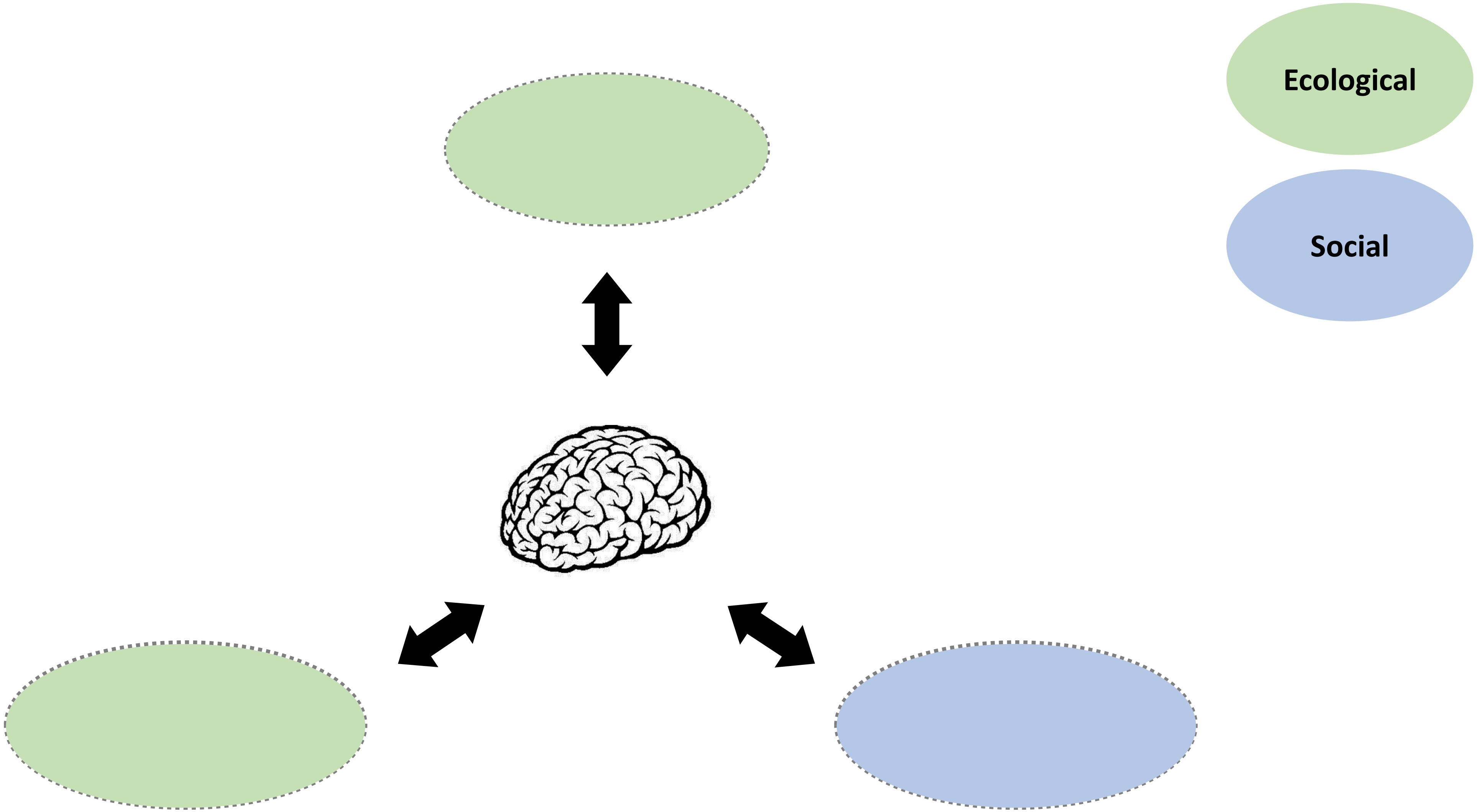

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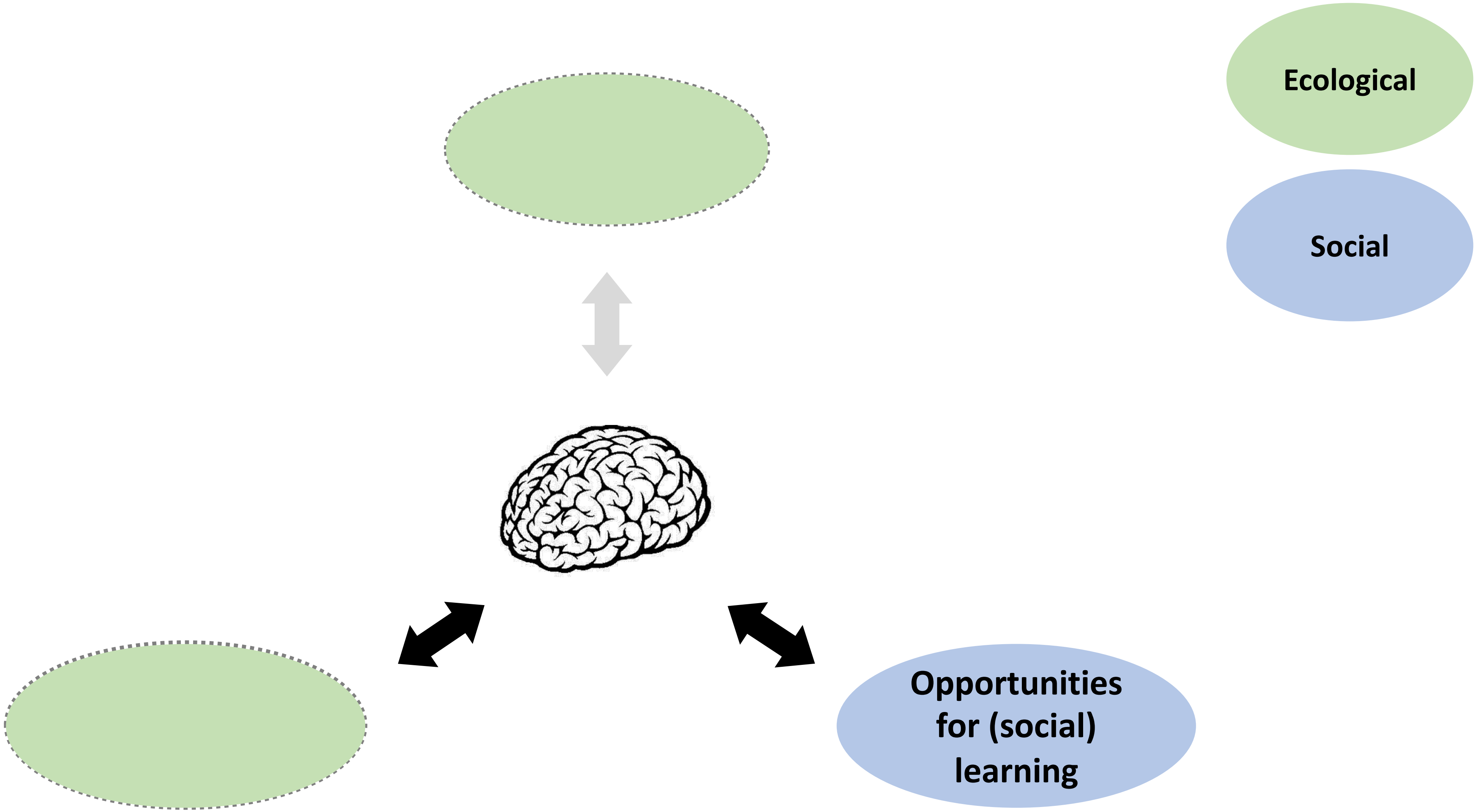

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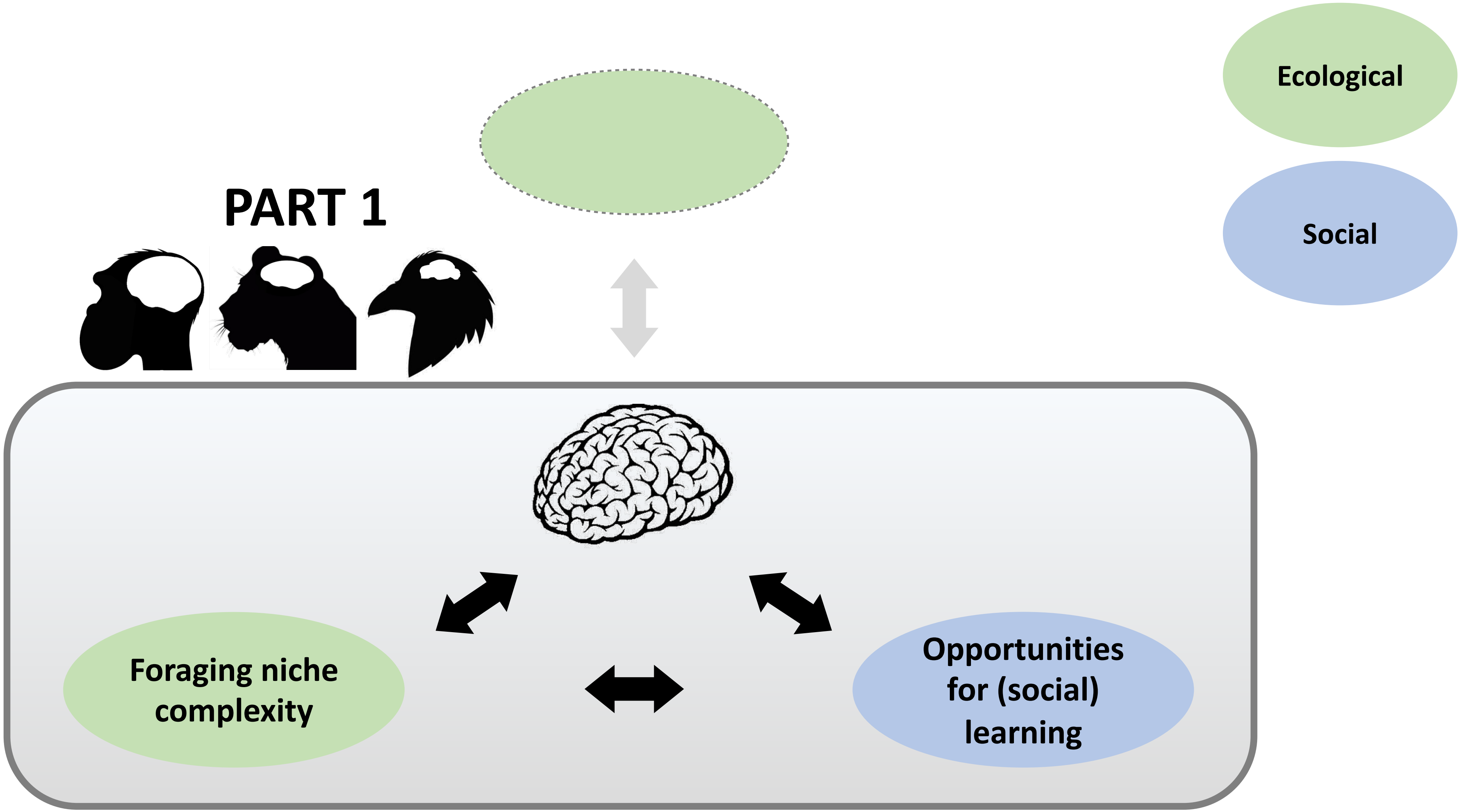
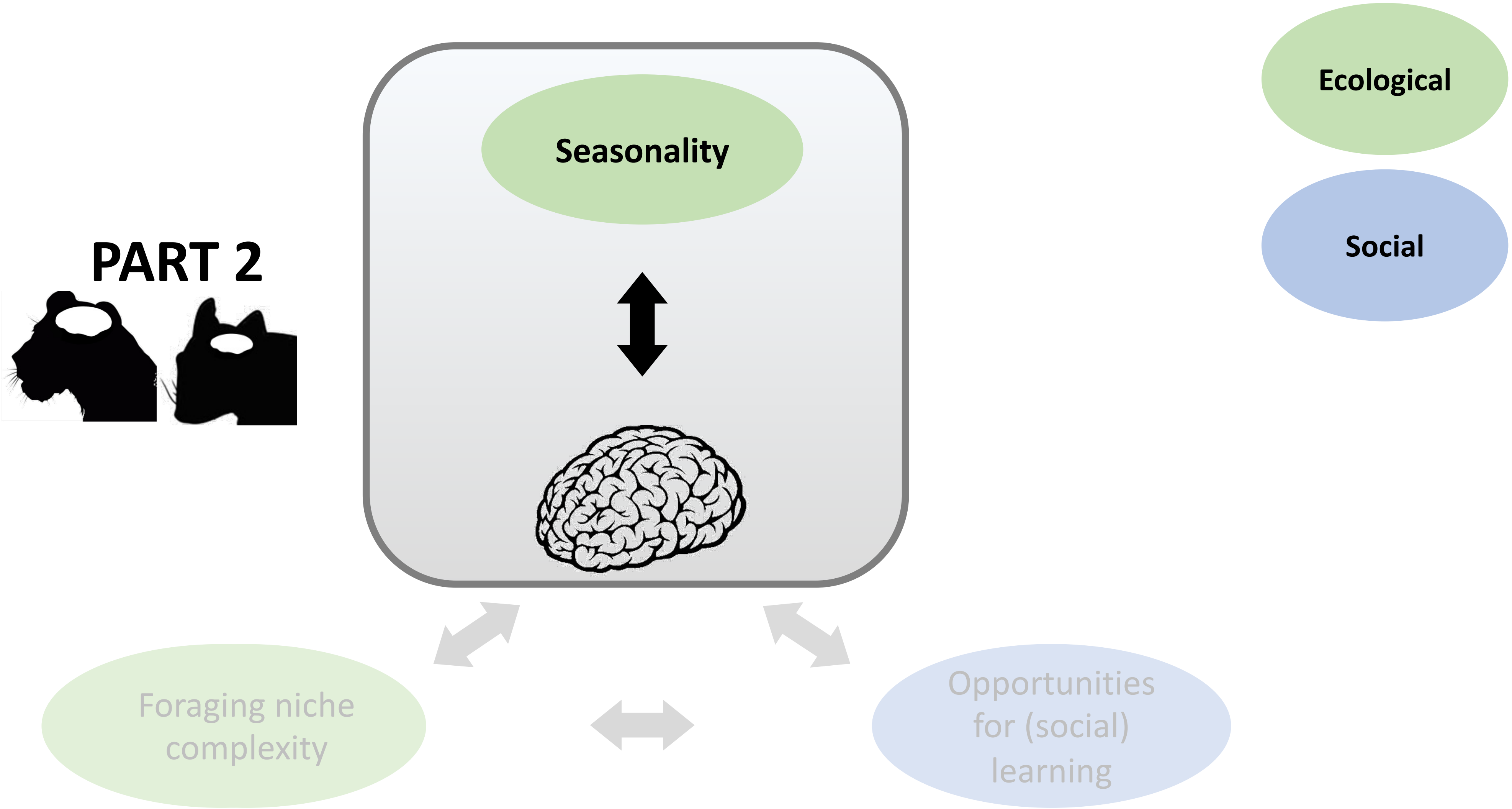
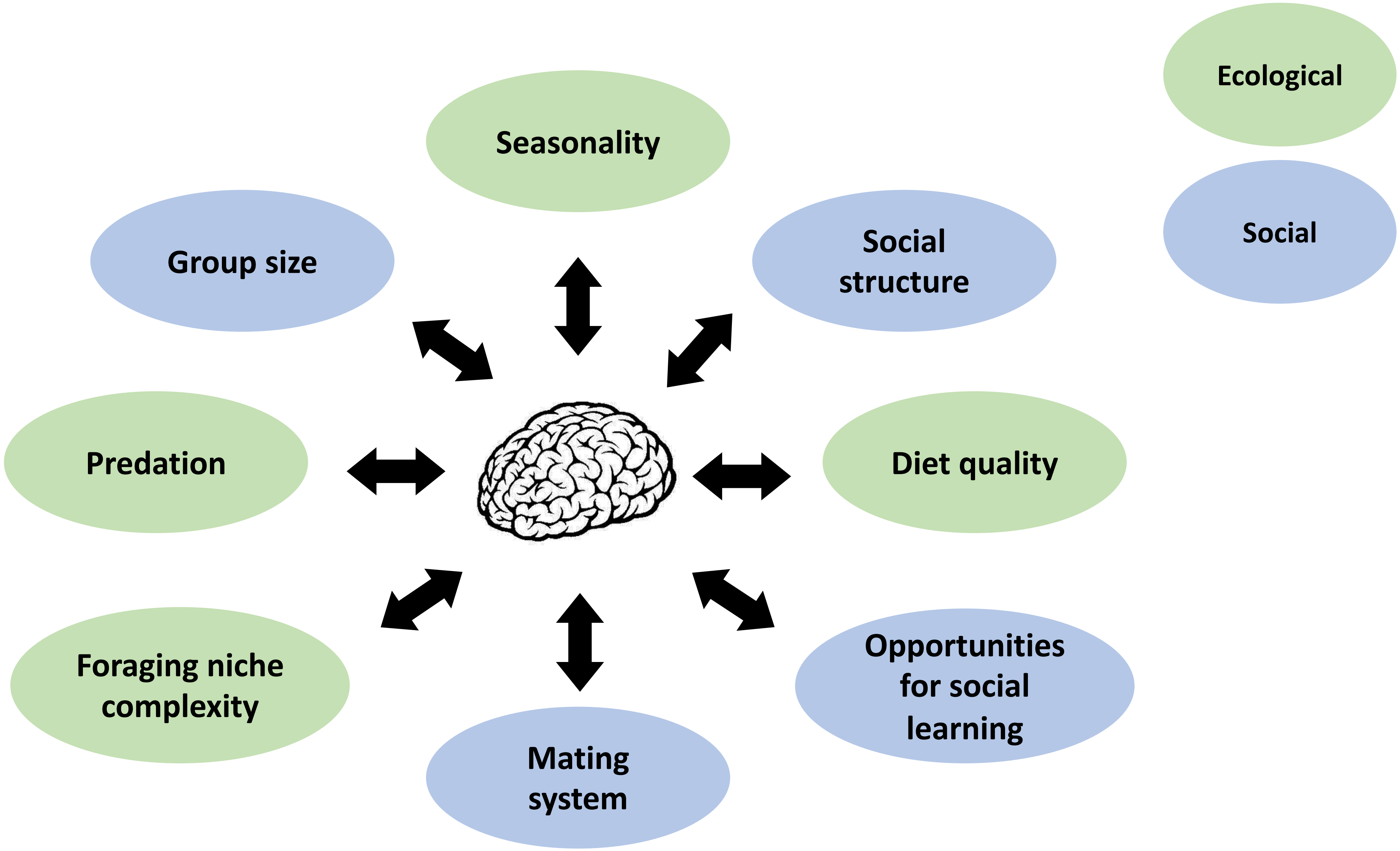


Ecological
Social
PART 1
Foraging niche complexity
Opportunities for (social) learning

Overview


Ecological
Social
Seasonality
PART 2
Foraging niche complexity
Opportunities for (social) learning

Overview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Group size
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Predation
Diet quality
Foraging niche complexity
Mating system
Opportunities for social learning

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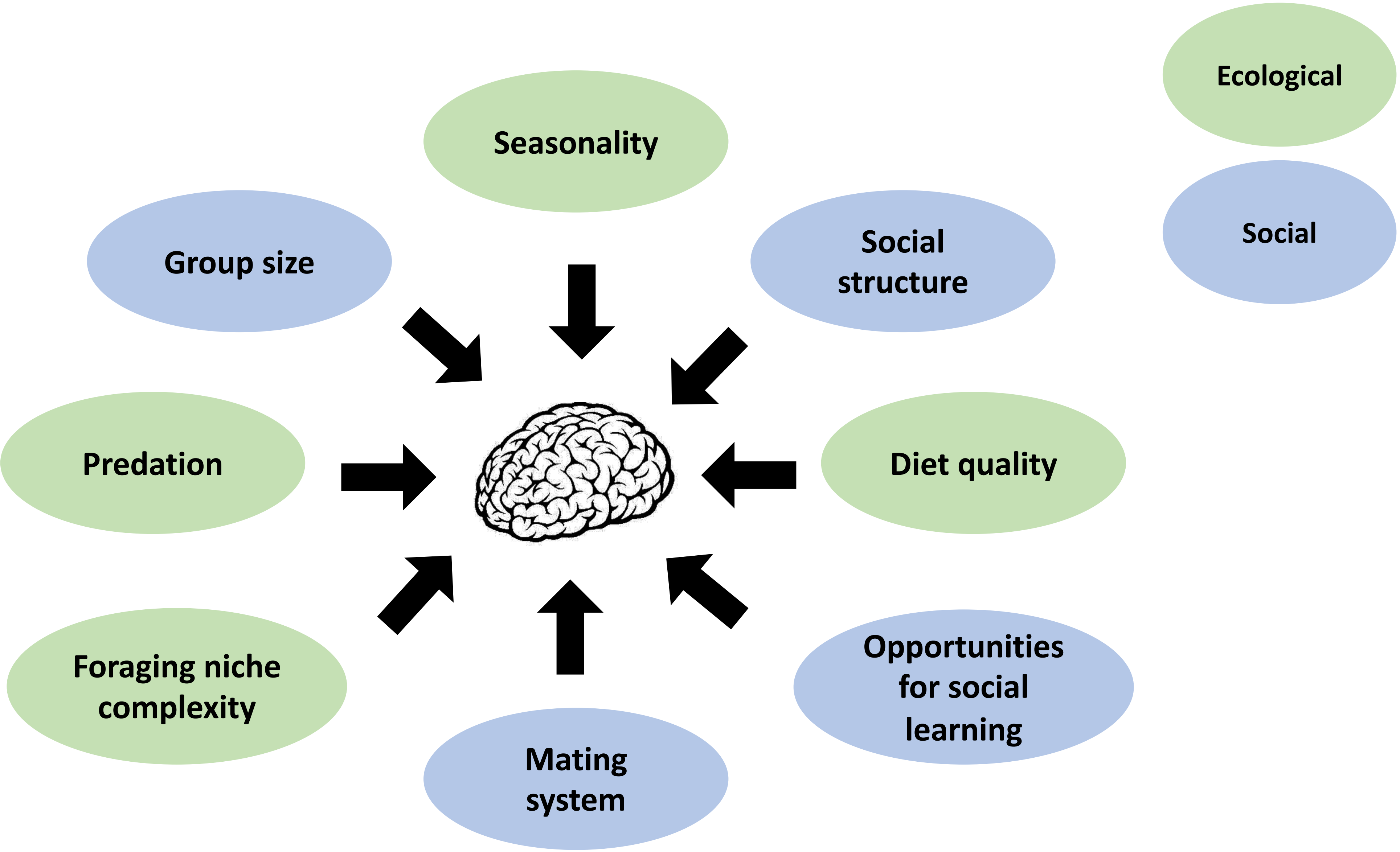
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Ecological
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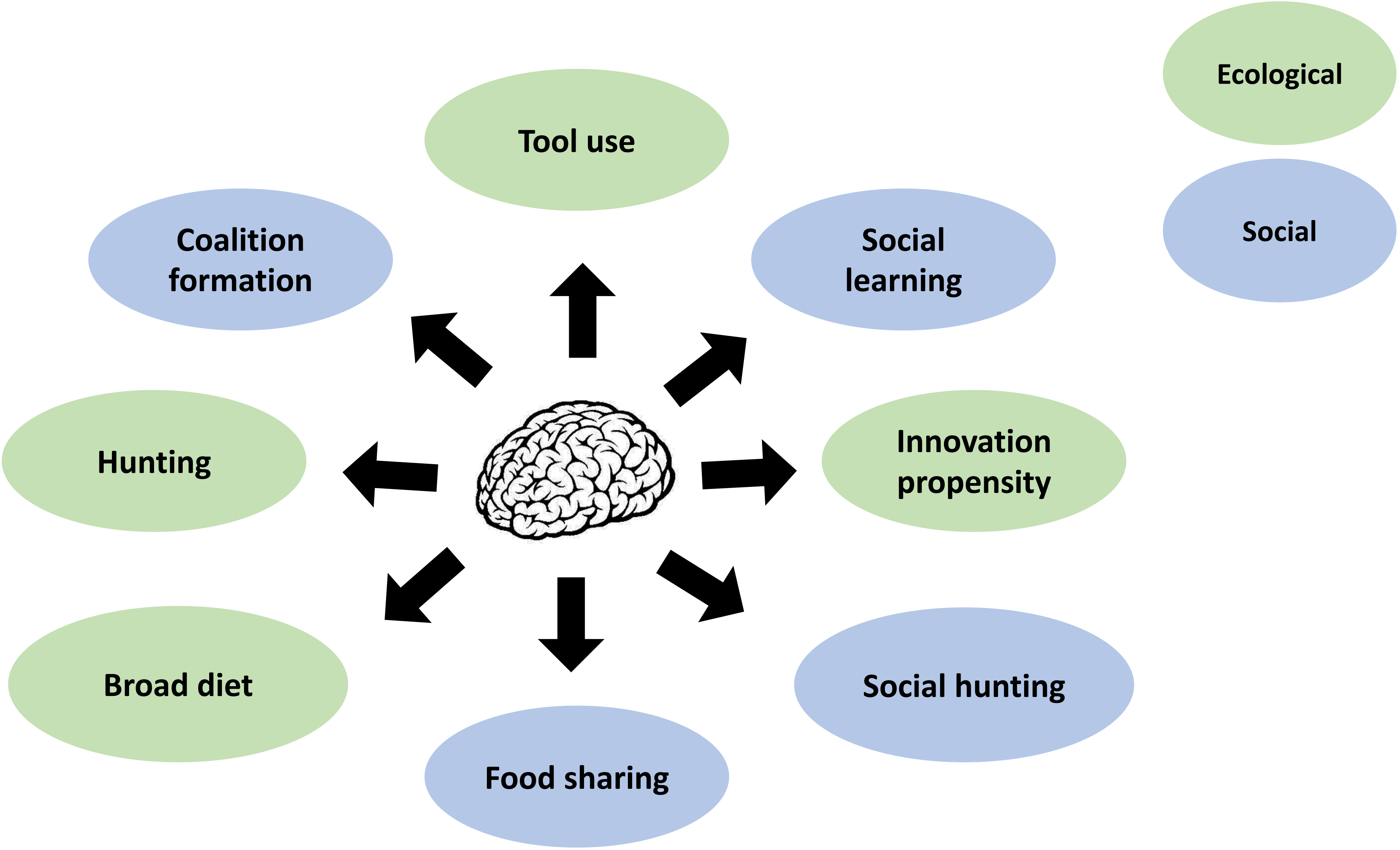
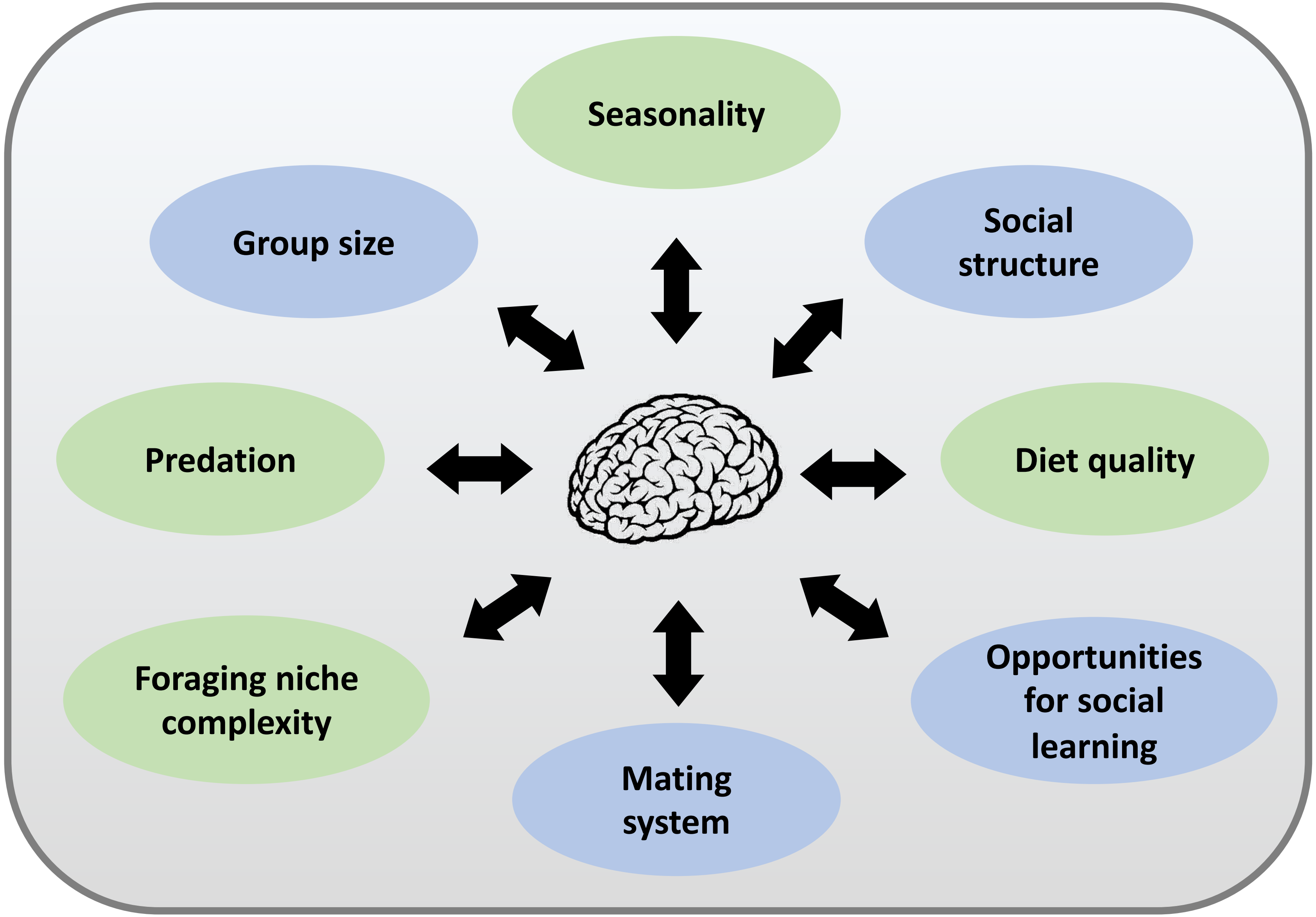


Ecological
Social
Tool use
Coalition formation
Social learning
Hunting
Innovation propensity
Broad diet
Social hunting
Food sharing

Overview

PART 3



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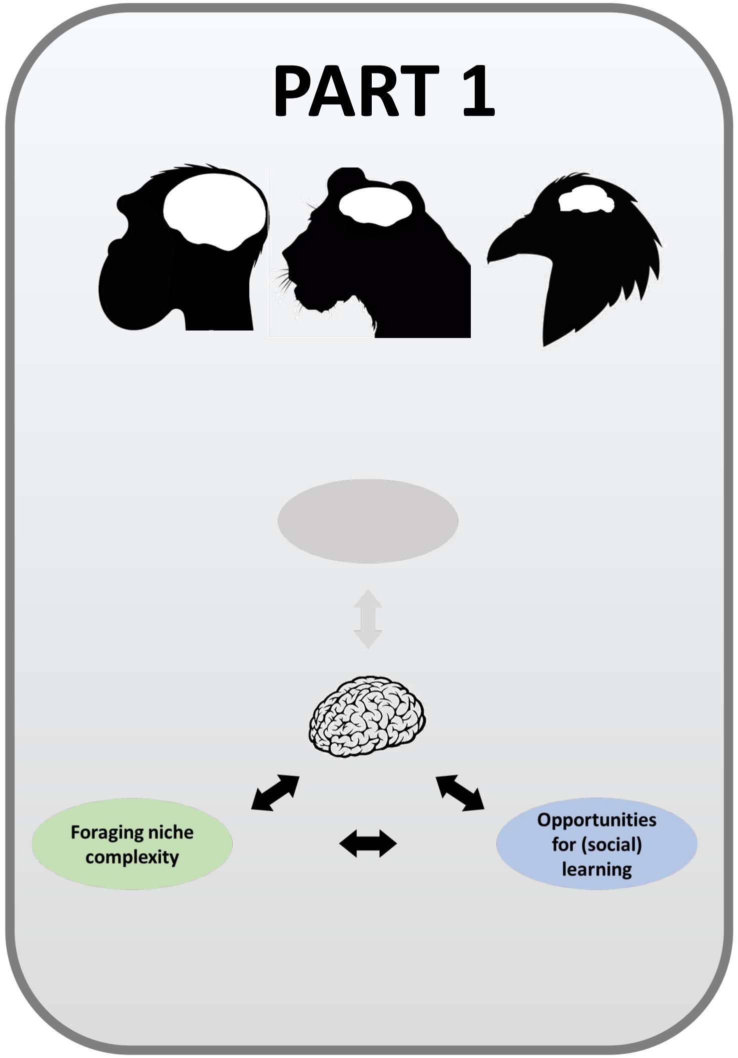

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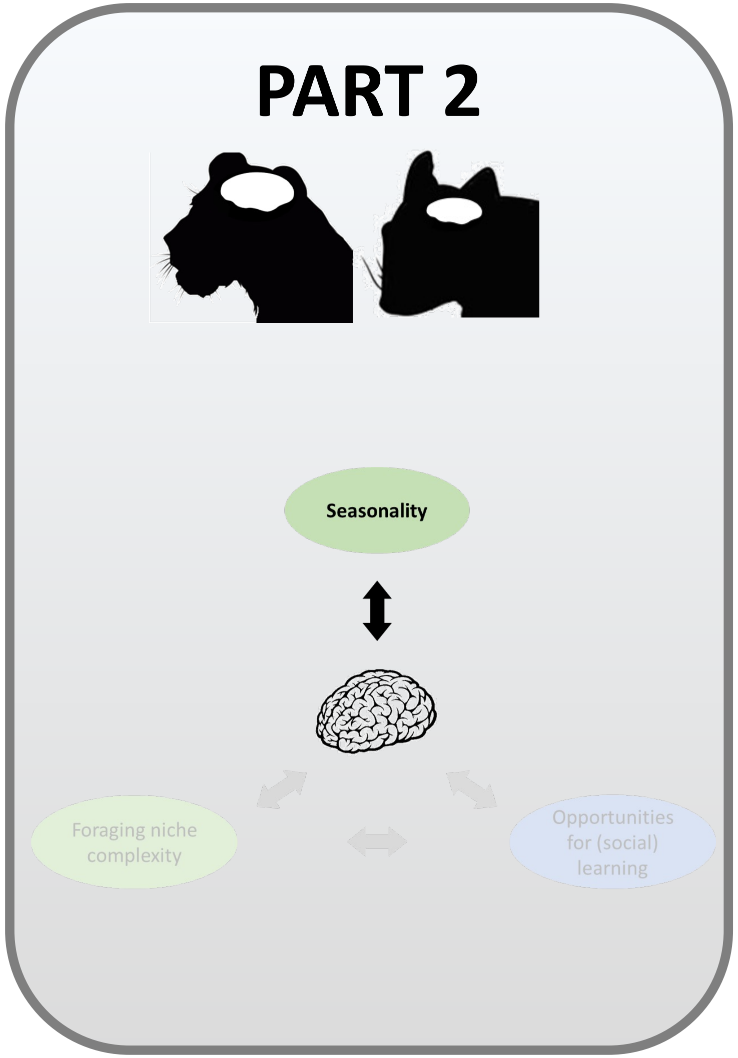

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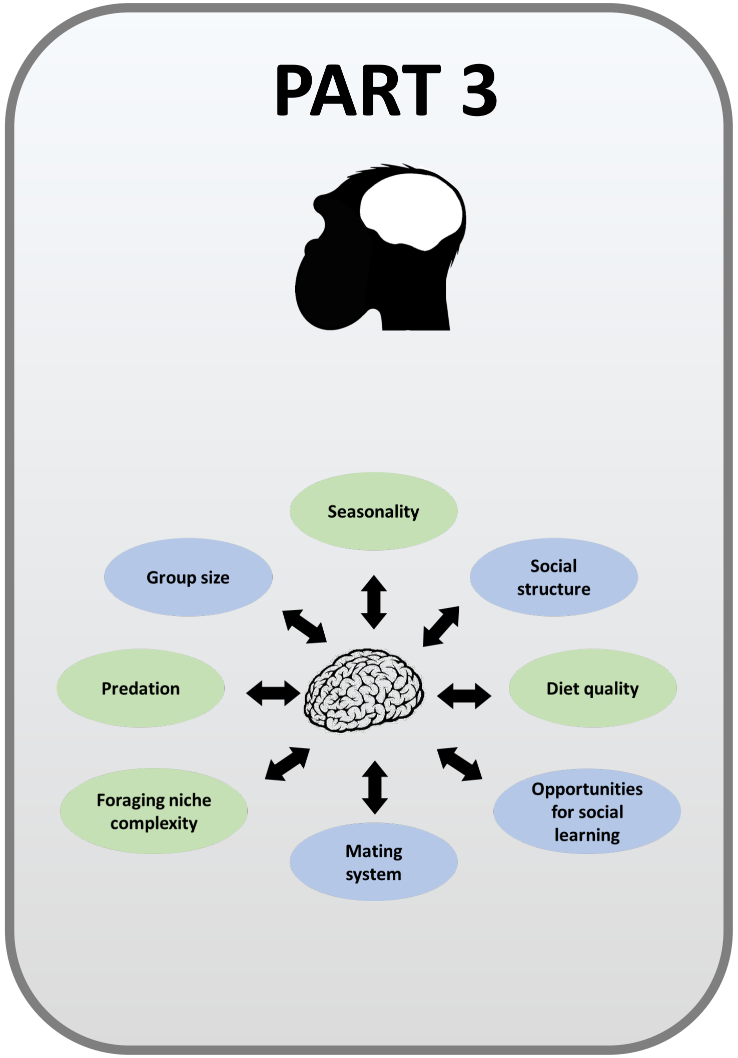
Seasonality
Foraging niche complexity
Opportunities for (social) learning



PART 3
Seasonality
Group size
Social structure
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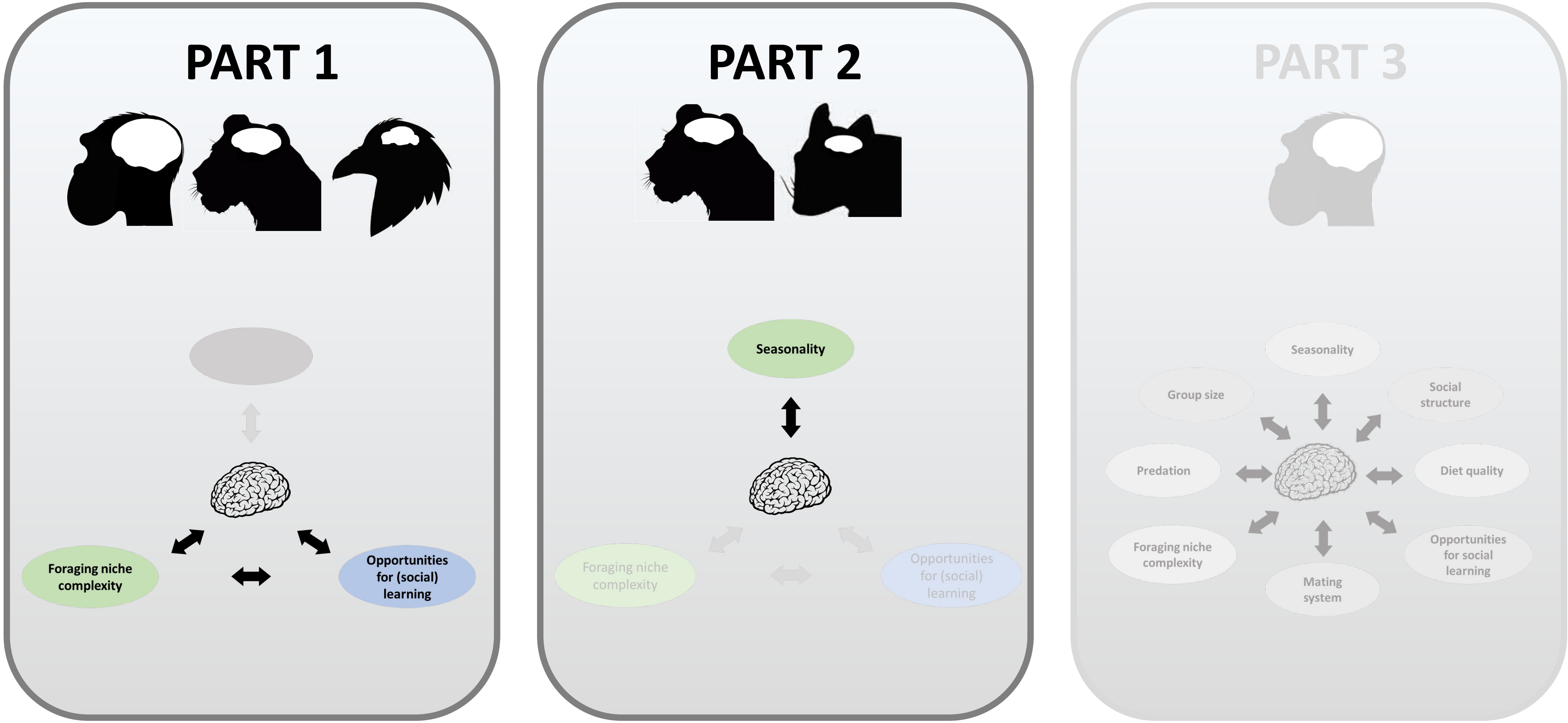
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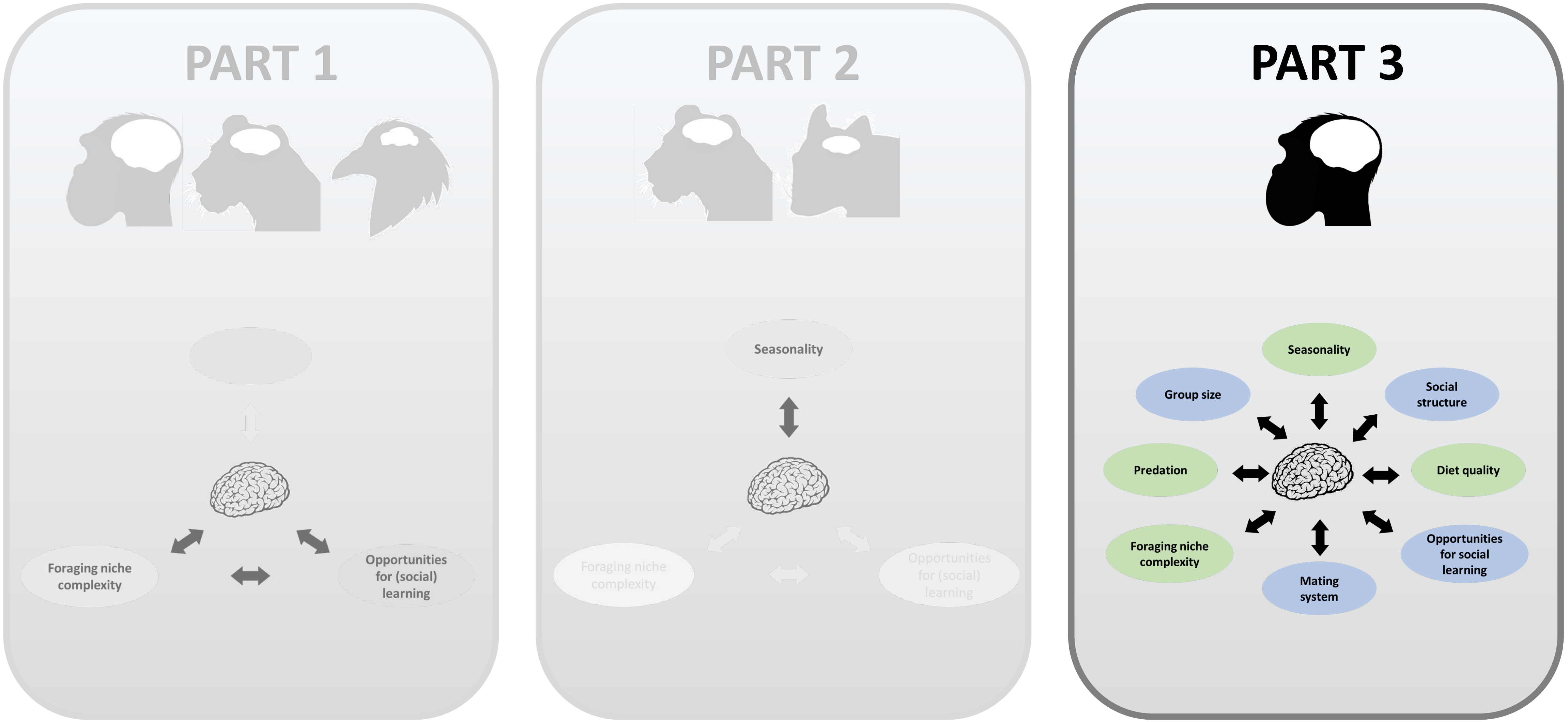
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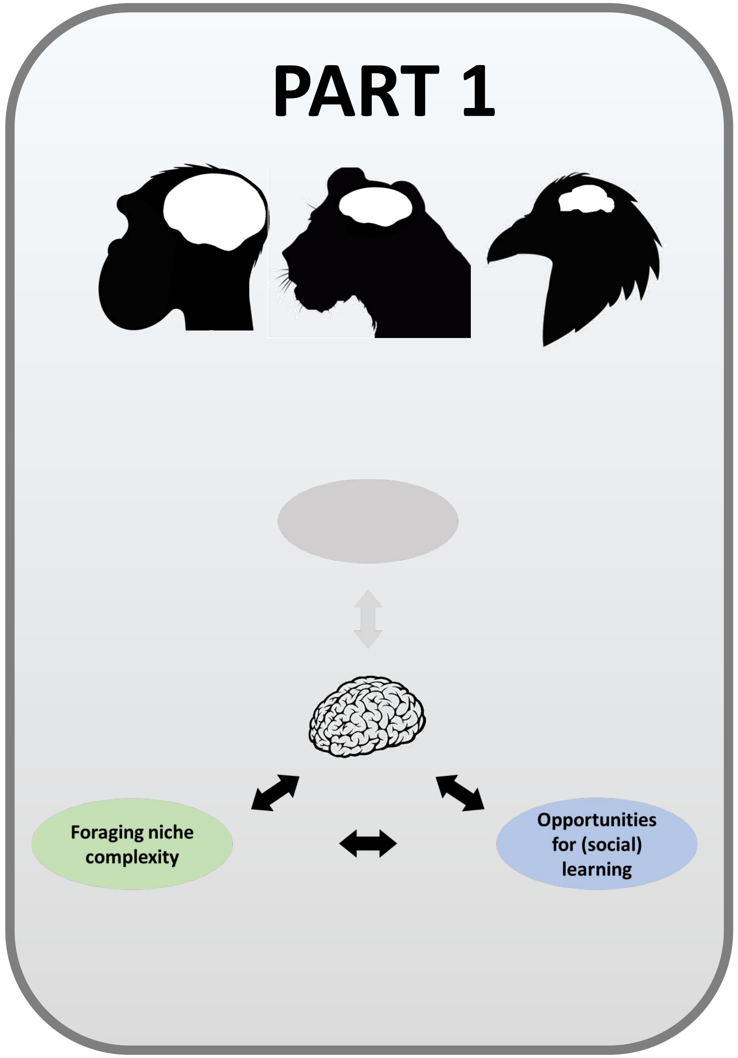
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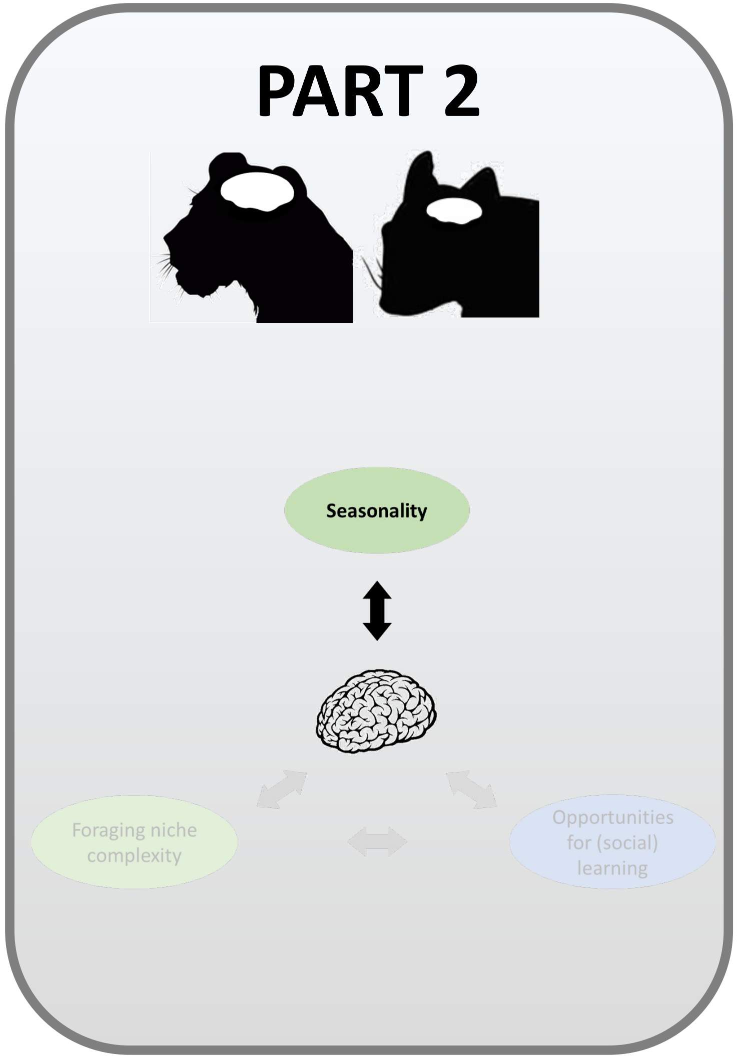
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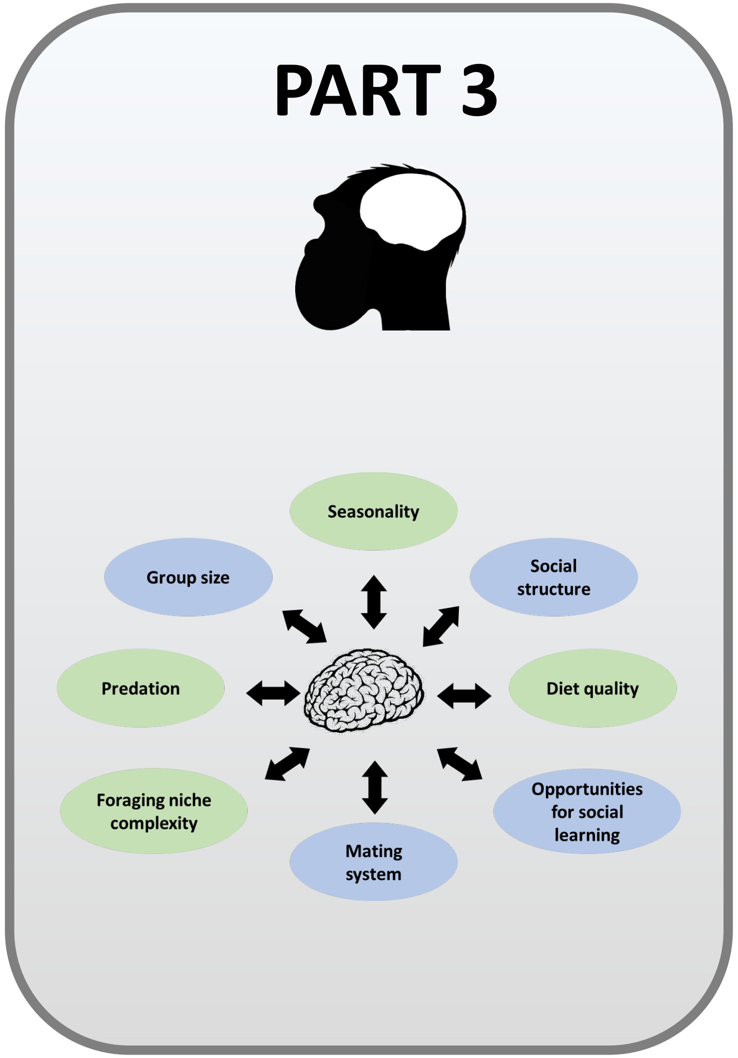
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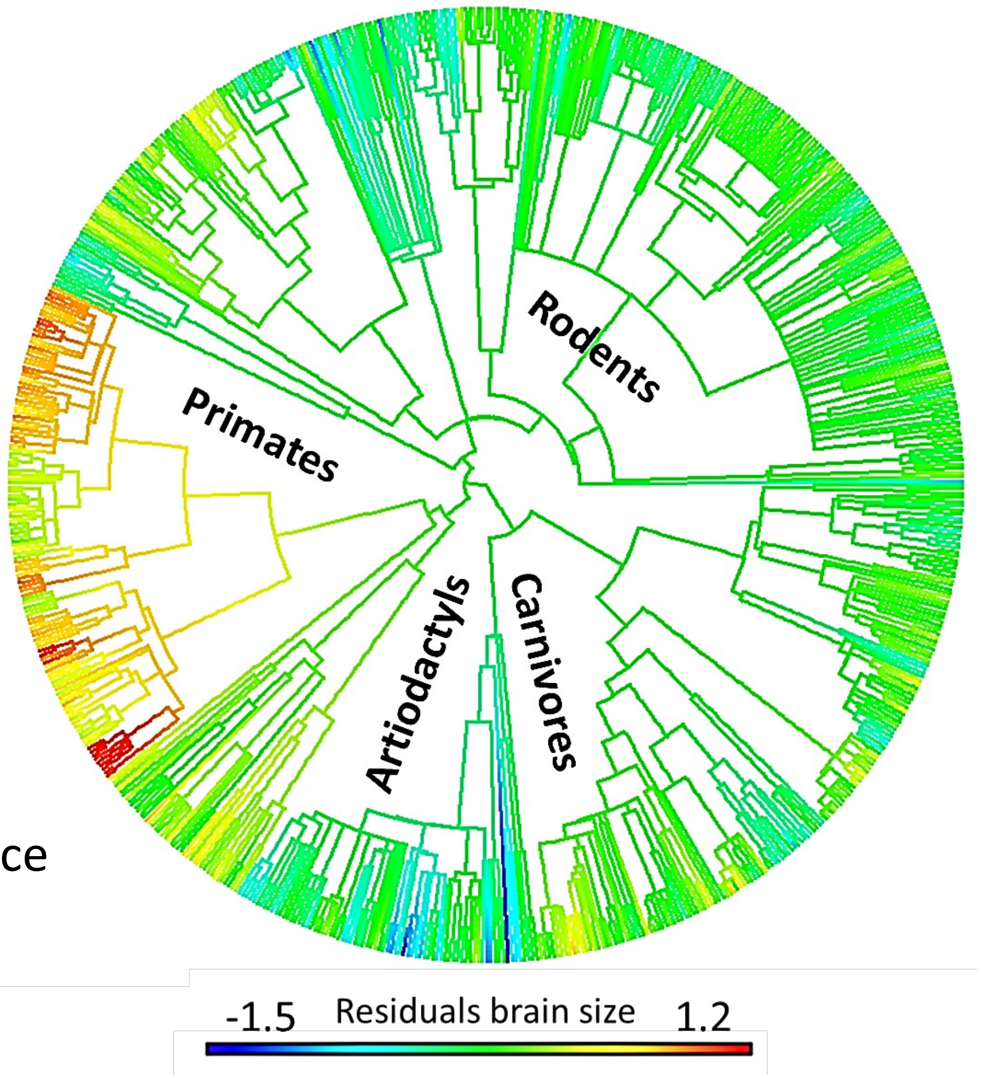
Phylogenetic Comparative Approach

- **General patterns across species on a large evolutionary scale**
- **Selection experiments are difficult**
  → patterns of correlated evolution!
- **Phylogenetic dependence**
  Variation clusters along more closely related species
- **Phylogenetic comparative methods**
  Statistical models need to control for phylog. dependence



Felstenstein 1985, Nunn 2011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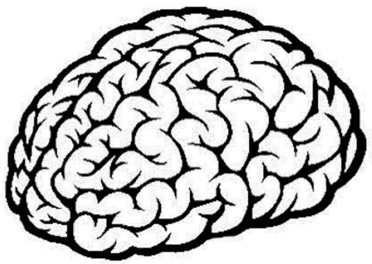
Opportunities for learning and foraging niche complexity

PART 1

skills are not innate, but need to be learned

complex skills require enhanced cognition...

...and deliver energy to maintain a large brain

more opportunities to learn → **Complex foraging niche** ↔ 

Schuppli and Graber et al. 2016, Schuppli et al. 2012

Opportunities for learning and foraging niche complexity

AFR is positively correlated with foraging niche complexity

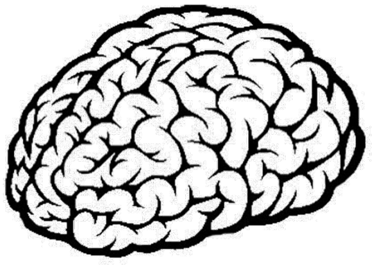
Foraging niche complexity is positively correlated with brain size

Slow development

+

Complex foraging niche

+

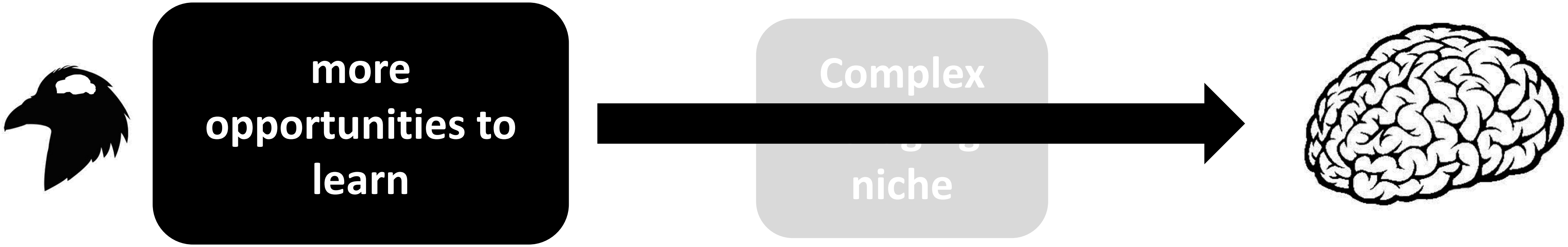


- Slow development provide species with more time to learn (energetic buffer)
- Increased behavioral flexibility linked to the evolution of cognition

Schuppli and Graber et al. 2016, Schuppli et al. 2012

Opportunities for social learning and brain size

PART 1



Graber et al. in prep.

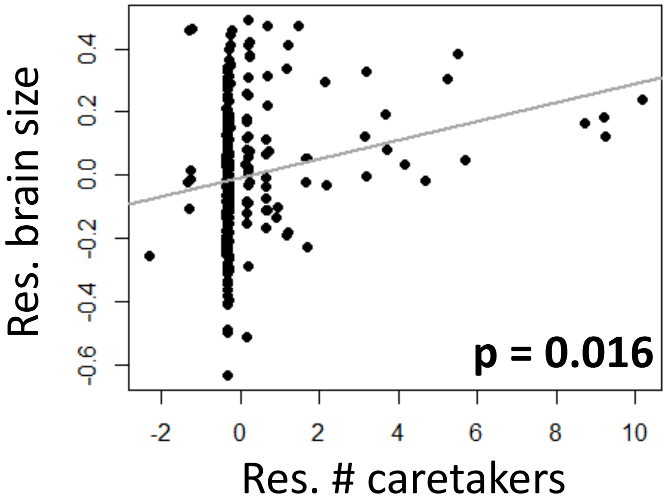
Opportunities for social learning and brain size

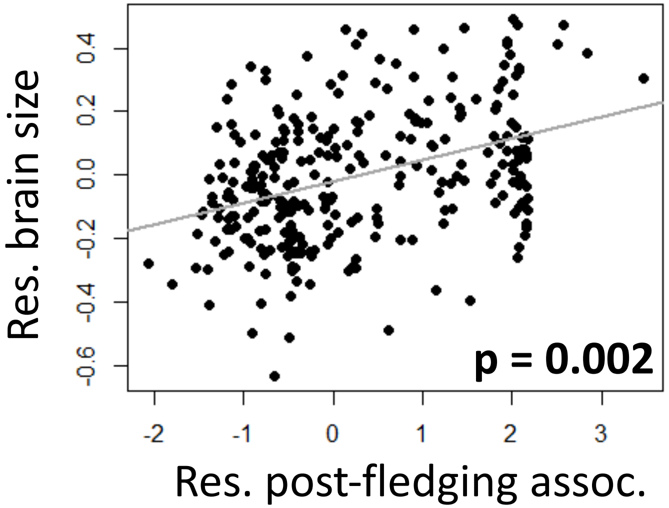
PART 1

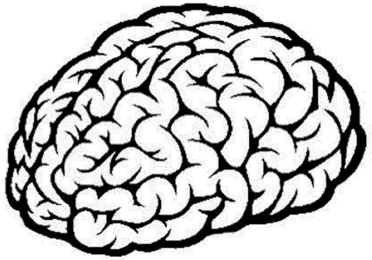
more opportunities for social learning

↑ number of caretakers

↑ duration post-fledging association







Graber et al. in prep.
data by M. Griesser, K. Isler and S. Graber

Opportunities for social learning and brain size

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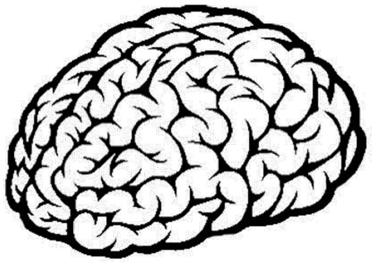
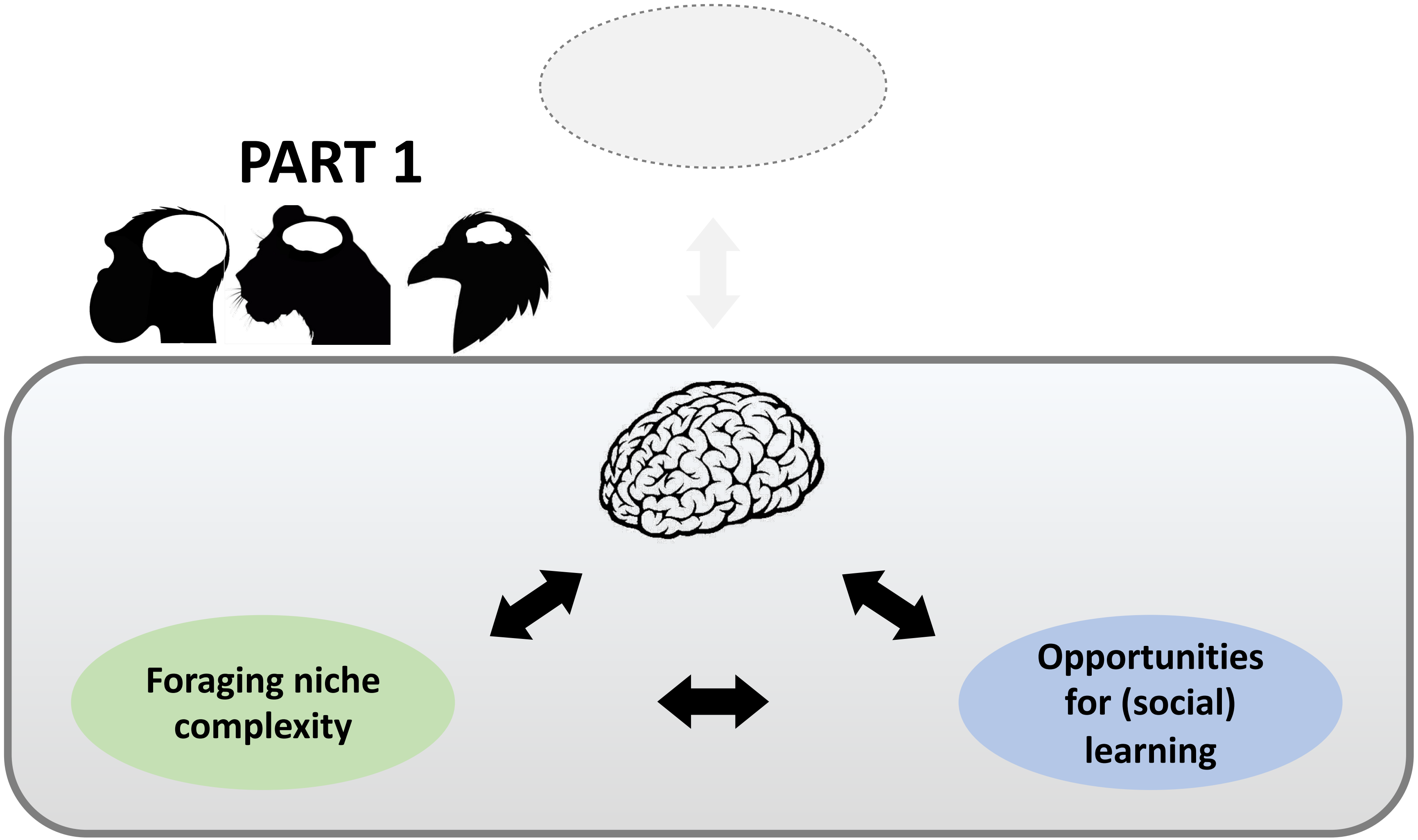
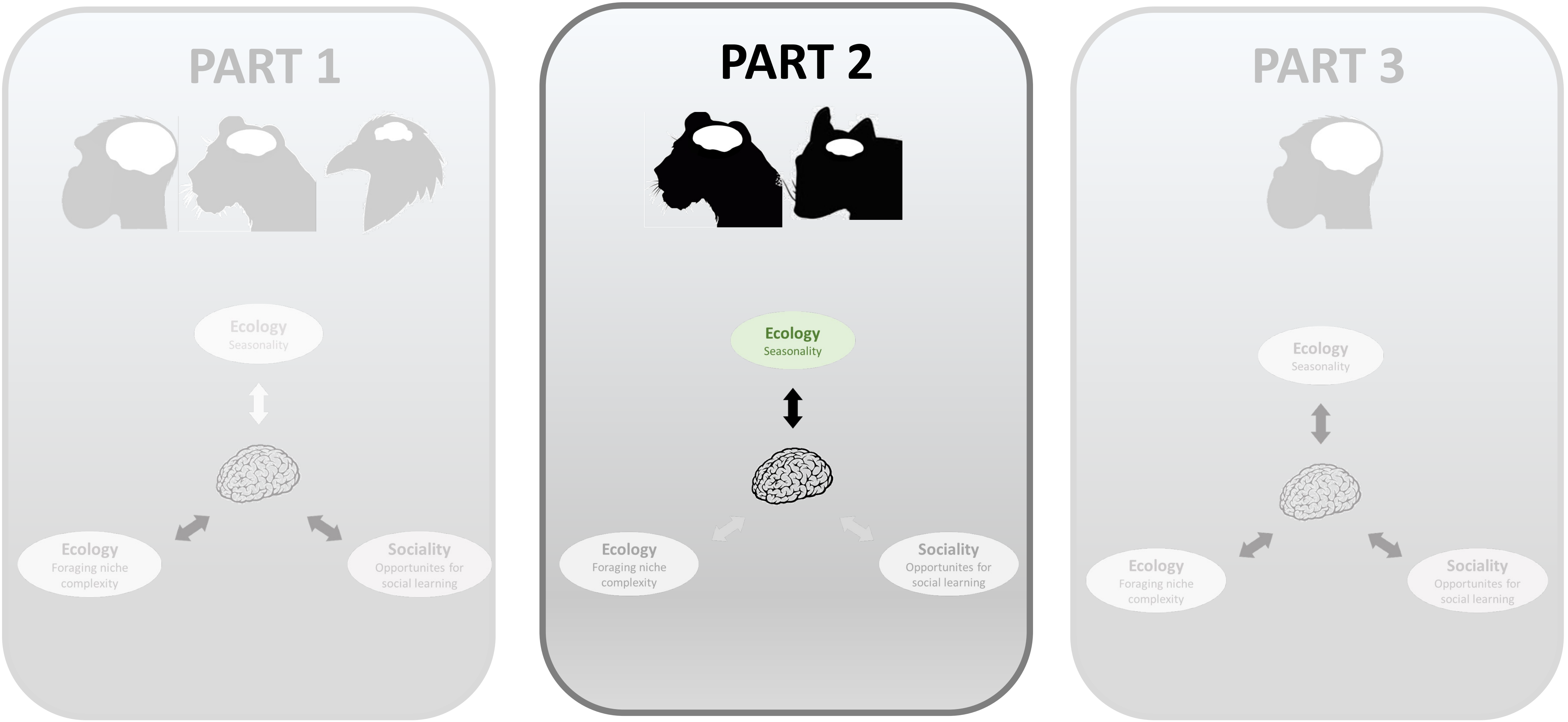


Opportunities for socially mediated learning of complex skills drive the evolution of brain size

Conclusions

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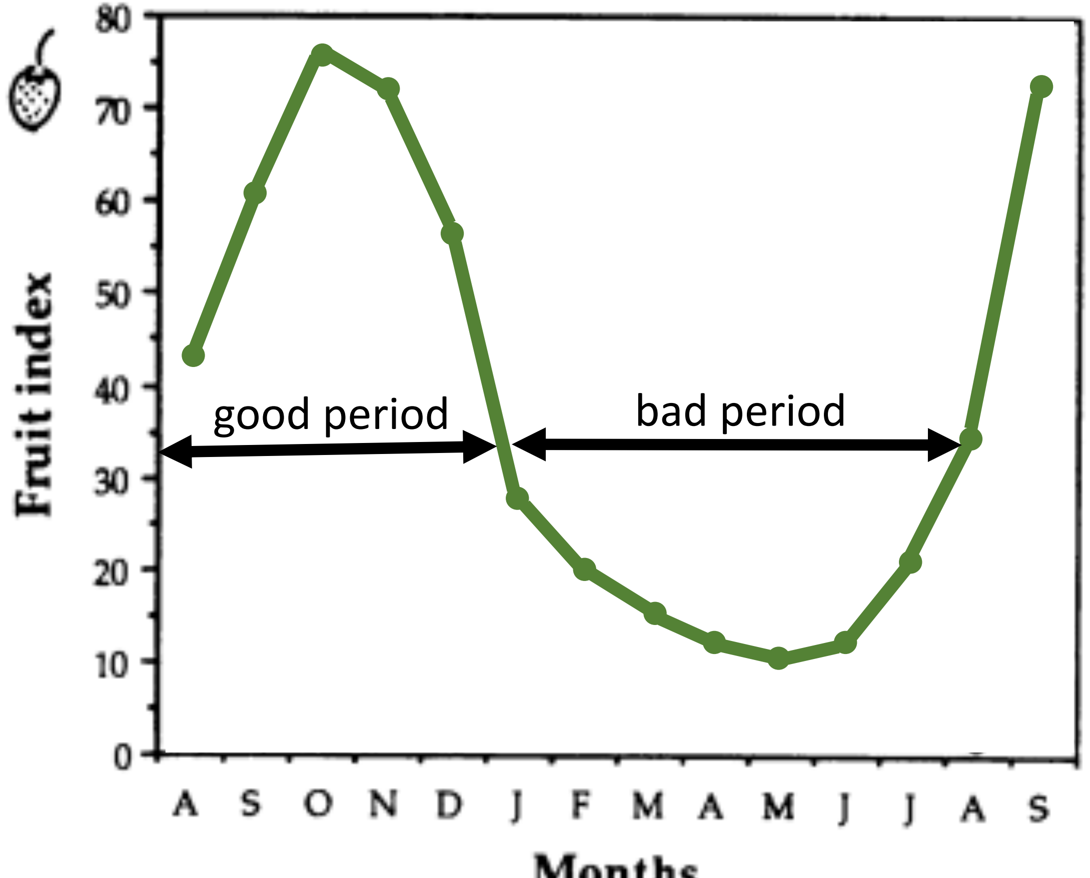
Seasonality and its Effects on Brain Size Evolution

PART 2

What is seasonality?

Seasonality = recurrent fluctuations in climatic conditions and environmental productivity over the year

Seasonal habitats → periods with less food available



J. van Woerden modified from Peres 1994, van Woerden 2011

Explaining brain size evolution from cost and benefit perspective

PART 2

Cost perspective
Expensive brain framework

Larger brain → increase energy turnover → stabilized energy intake (avoid starvation)

Larger brain → change in energy allocation

Benefit perspective
Cognitive buffer hypothesis

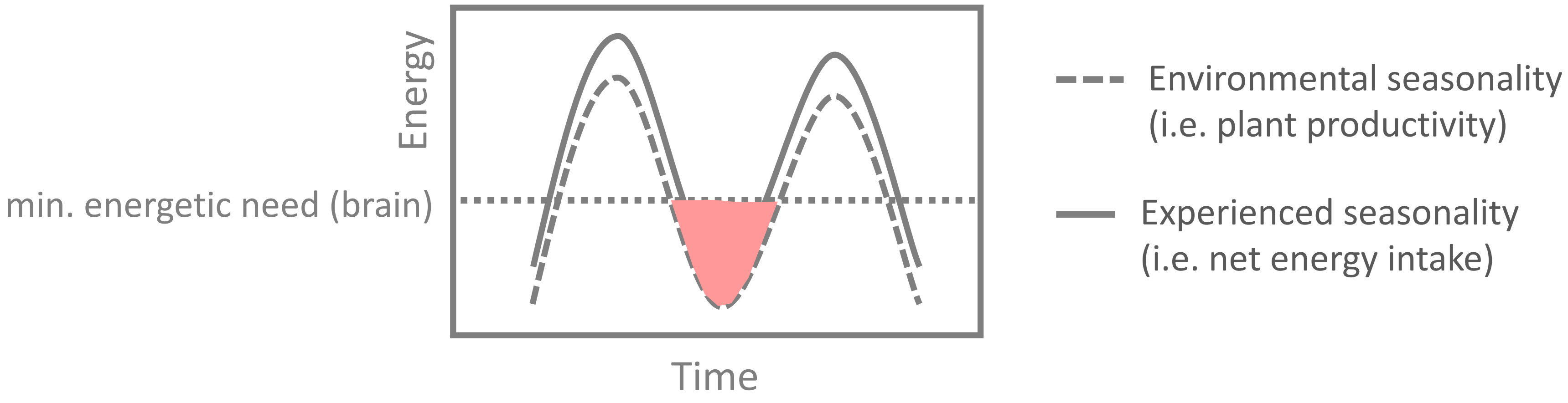
Enhanced cognition of enlarged brains allows for

- enhanced spatial memory
- enhanced food acquisition skills
- general enhanced behavioral flexibility

→ larger-brained species are better at responding to seasonal fluctuations and unpredictable changes in the environment

Isler and van Schaik 2009, Navarrete et al. 2011, Allman et al. 1993, Sol et al. 2009

Costs vs. Benefits



Expensive Brain Hypothesis

Cognitive Buffer Hypothesis

van Woerden et al. 2010, 2012, 2014

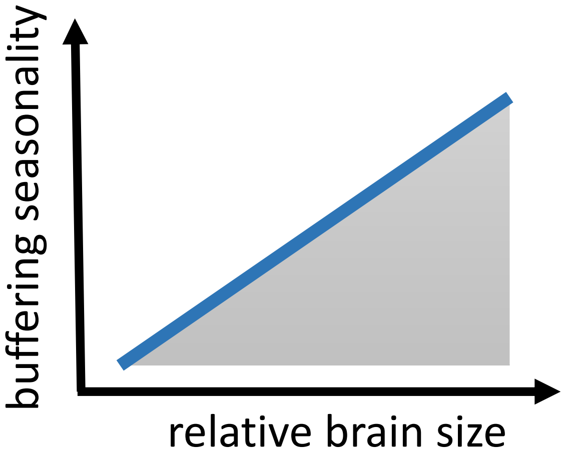
Expensive Brain vs. Cognitive Buffer Hypothesis

Expensive Brain Hypothesis

The more **experienced** seasonality, the **smaller** the relative brain size

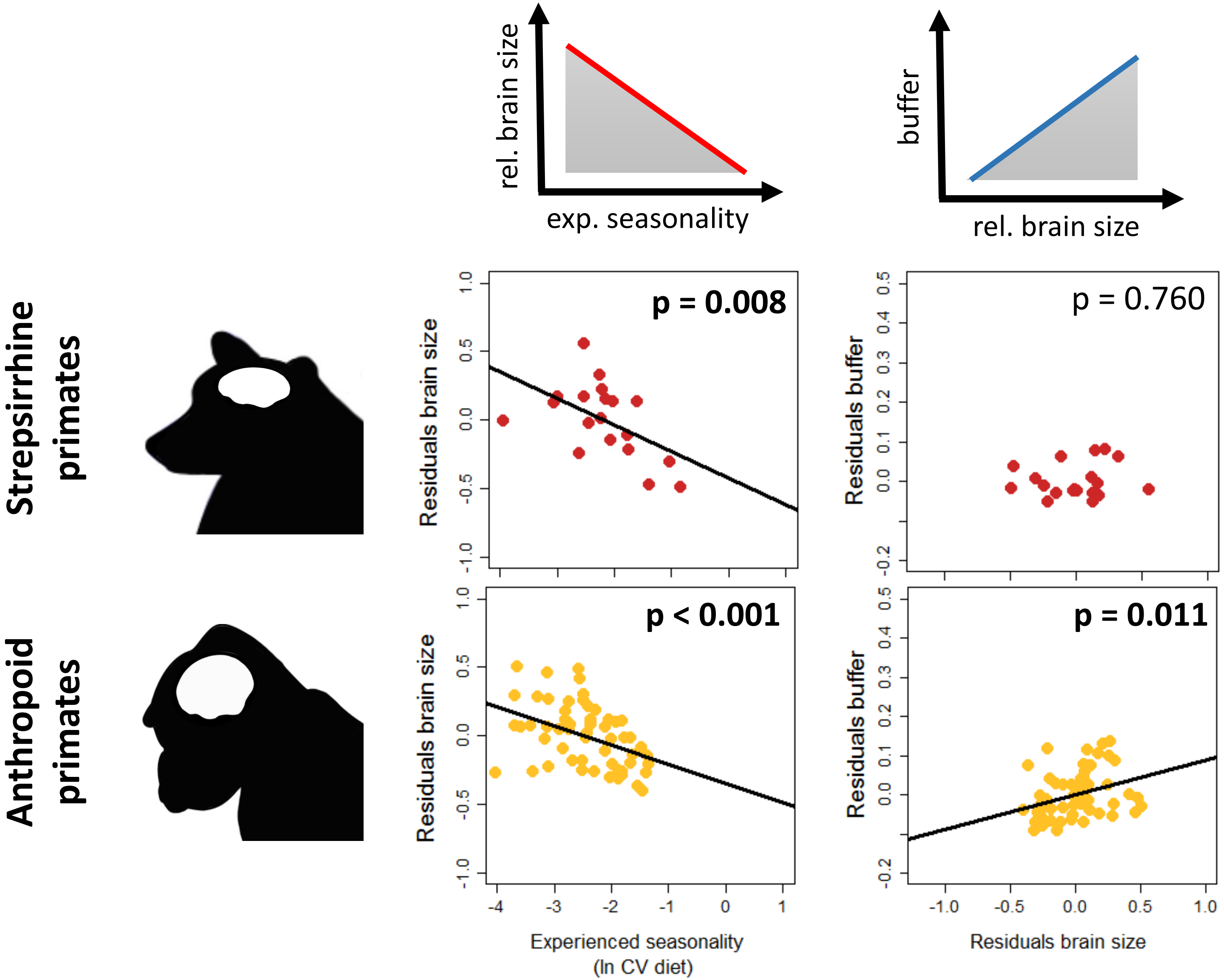
Cognitive Buffer Hypothesis

The more **cognitive buffering** – the larger the **difference** between the experienced and environmental seasonality – the **larger** the relative brain size



Expensive brain vs. cognitive buffer hypothesis in primates

PART 2



PhD thesis
Janneke van Woerden

data from van Woerden et al. 2014

PART 2

Brain Size and Body Mass Data

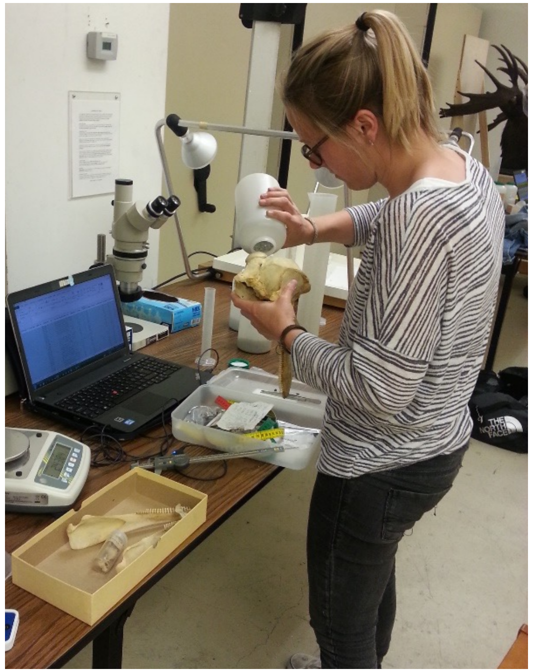
1 Brain size

- endocranial volume measurements based on glass beads
- total of **1974** specimens at 3 museums (USA)

The Field Museum

American Museum of Natural History

Smithsonian



2 Body mass

from established database by K. Isler
(literature research, based on wild study populations)

Seasonality Data

PART 2

1 **Environmental seasonality**

coefficient of variation (CV) over the year in **N**ormalized **D**ifference **V**egetation **I**ndex (NDVI)

GIMMS database 1981-2004, Tucker et al. 2005

2 **Experienced seasonality**

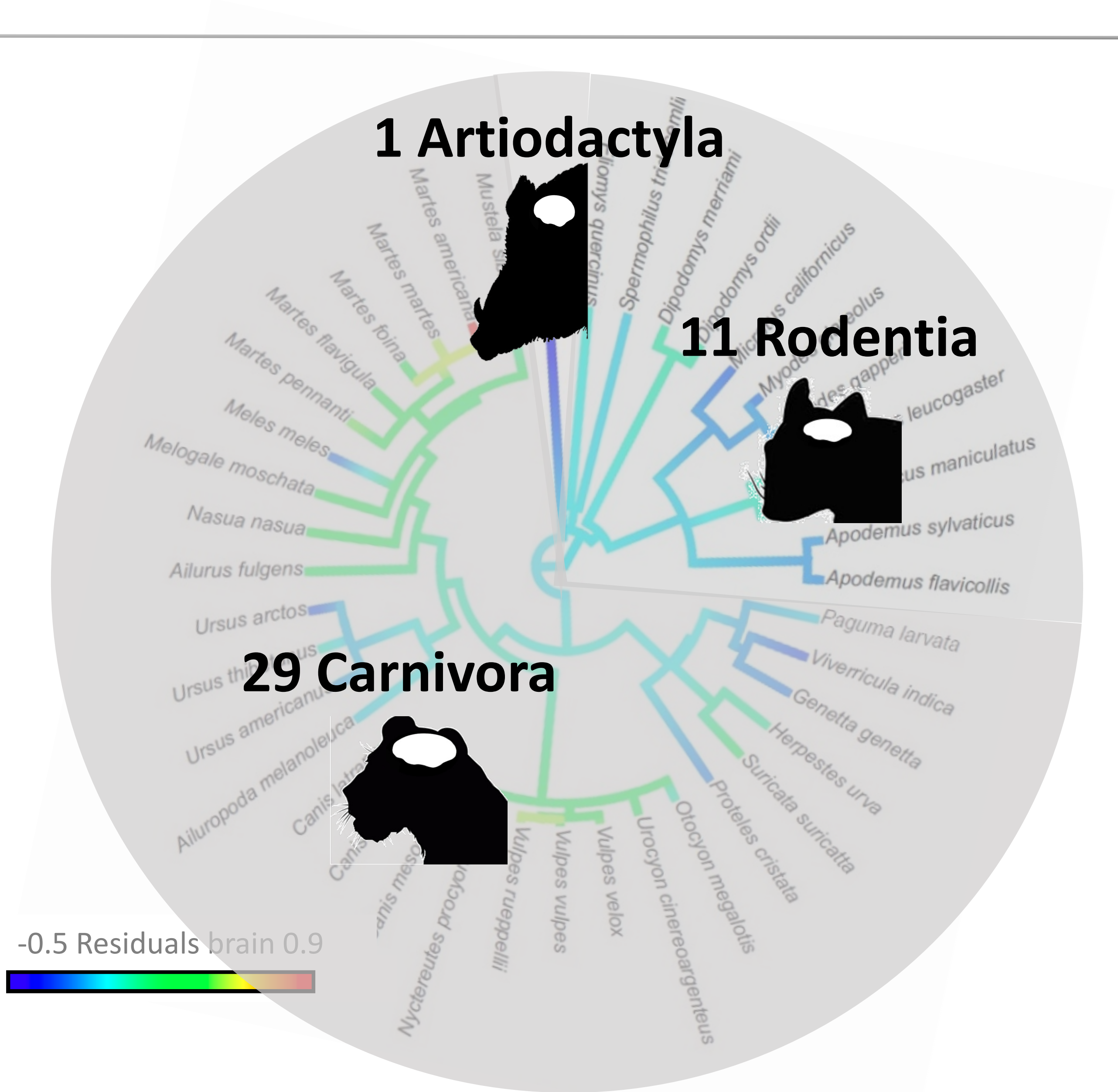
- seasonal diet composition: monthly frequency of occurence in scats/stomach contents
- CV in food category with highest nutritional value

3 **Buffer = environmental – experienced seasonality**

CV NDVI – CV diet

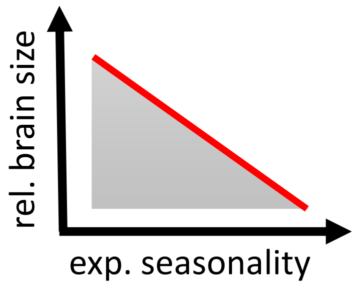
Data: Carnivora & Rodentia

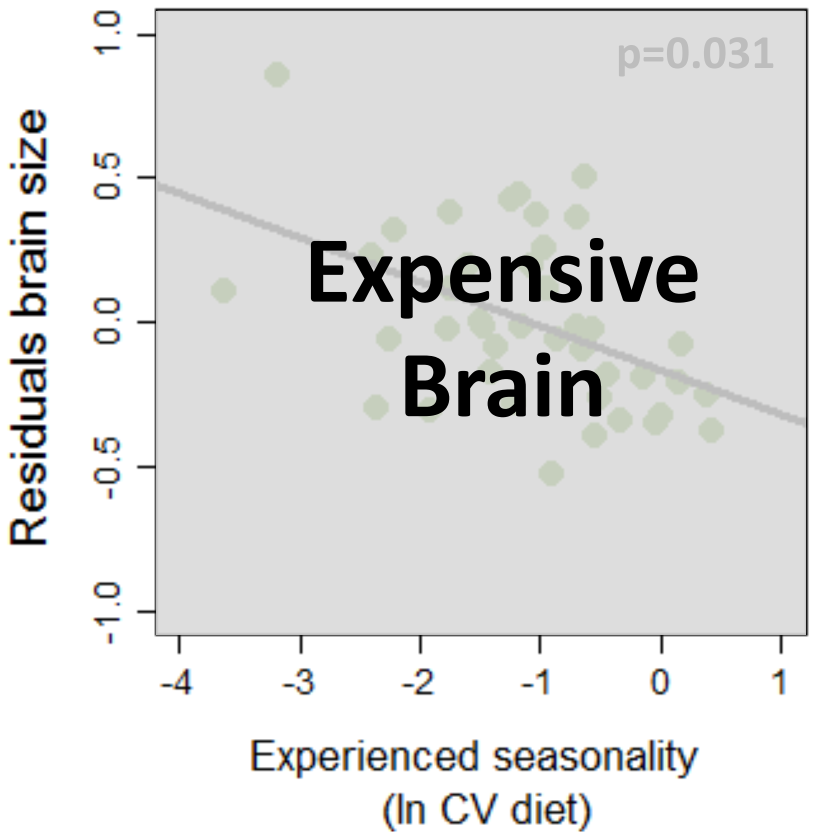
PART 2



Graber et al. submitted in Brain, Behavior and Evolution

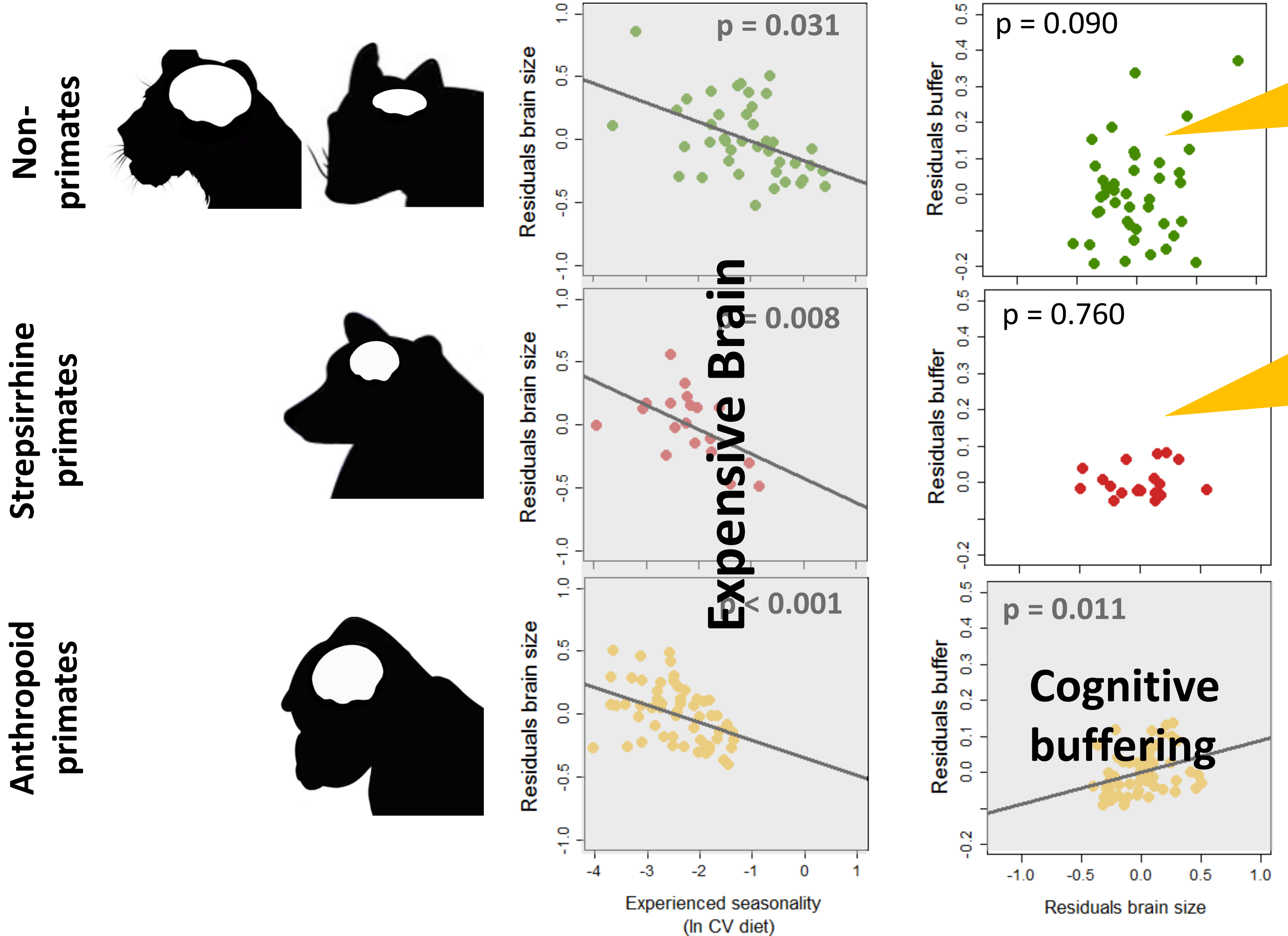
Expensive brain but no cognitive buffer effect!





Graber et al. submitted in Brain, Behavior and Evolution

Energy Always Matters!

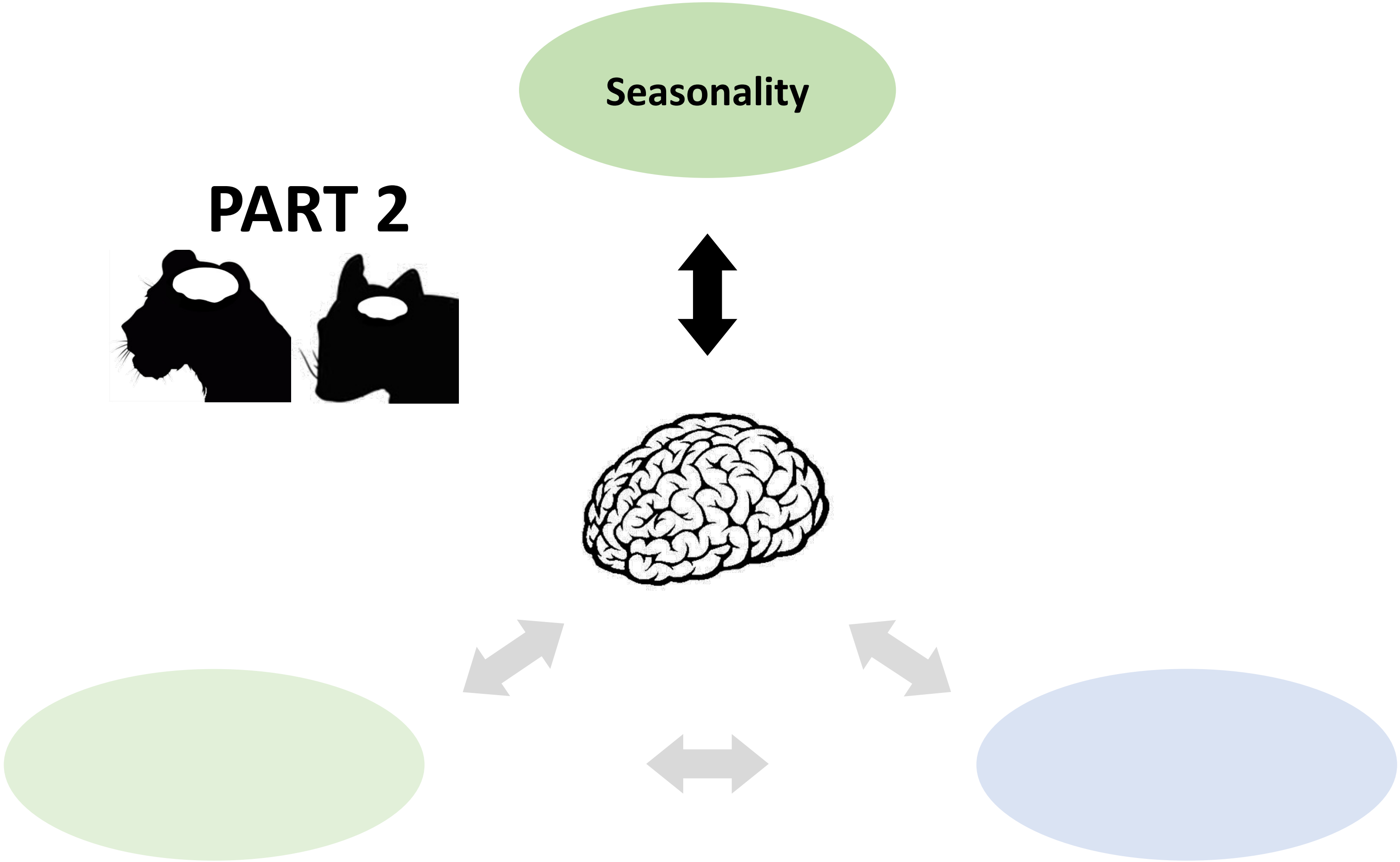


Alternative strategies
- Shift in diet
  -> energy-rich food[1]
- Hibernation, fat storage[1,2]

Alternative strategies
- High birth seasonality[3]
- Reduced BMR[4]
- Torpor/Hibernation[5]
- Fat storage

[1]Graber et al. submitted, [2]Heldstab et al. 2017 , [3]Janson and Verdolin 2005, [4]Genoud 2002, [5]Dausmann et al. 2004, Schülke and Ostner 2007

Conclusions



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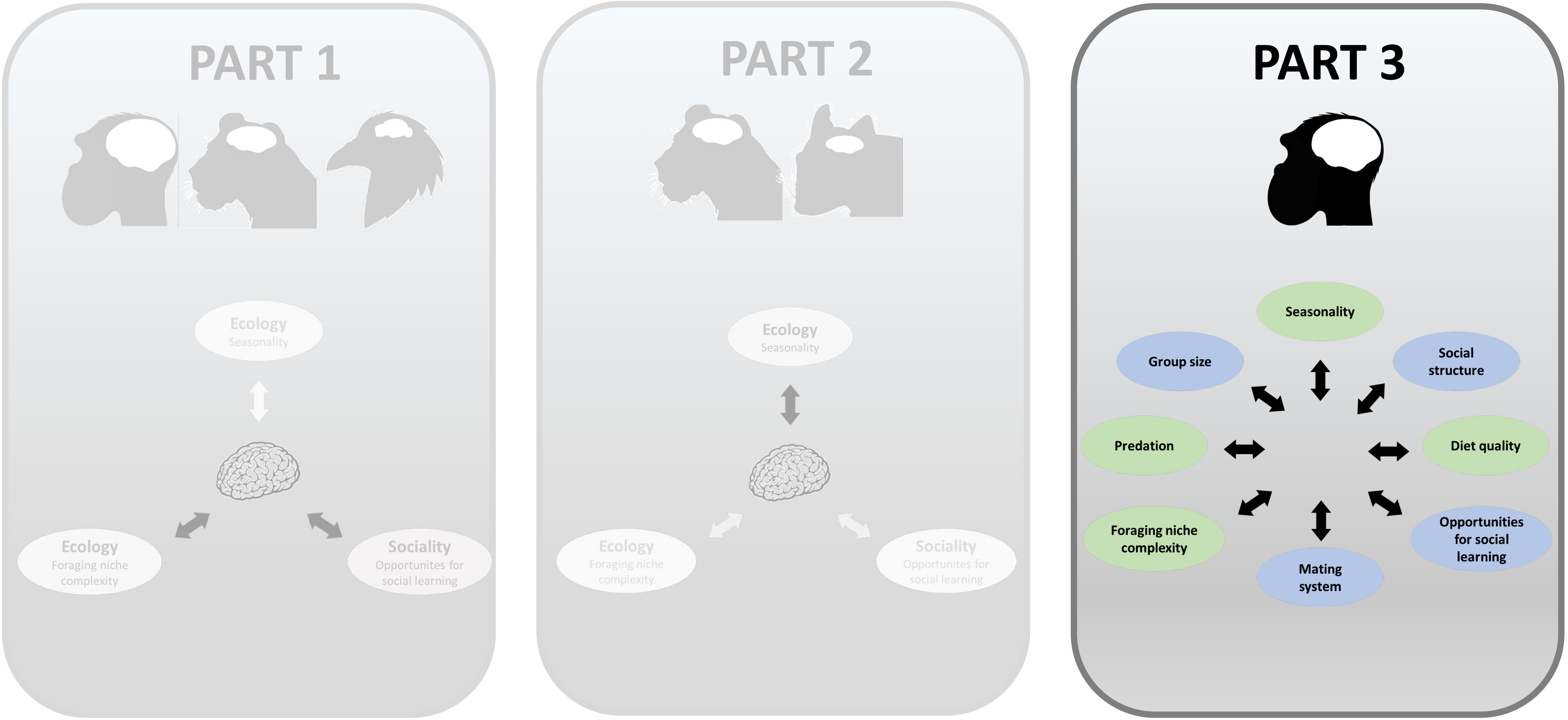

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Diet quality
Foraging niche complexity
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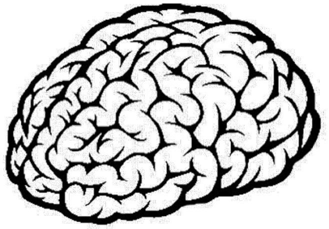
Mating system

Shortcomings of previous studies

Ecological Factors
(e.g. diet, habitat seasonality)



Social Factors
(e.g. group size)

Social Brain Hypothesis

Species living in larger and more complex groups need larger brains

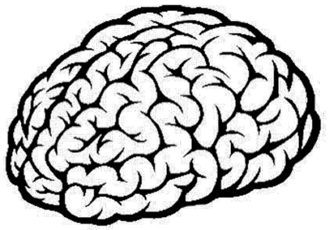
...but

vs.

Dunbar 1998, van Schaik et al. 2012, Holekamp 2007, Holekamp et al. 2015

Shortcomings of previous studies

Ecological Factors
(e.g. diet, habitat seasonality)

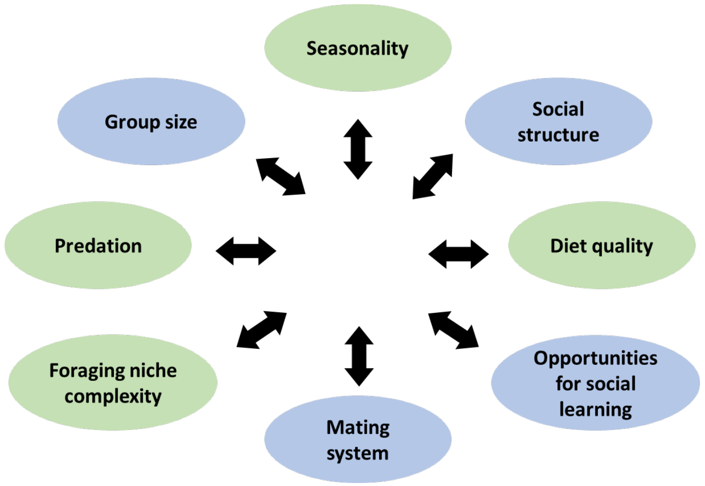


Social Factors
(e.g. group size)

- Tested only one or the other domain
- Simple ad-hoc measurements
- Evidence for general behavioral flexibility
  Selective benefits vs. cognitive consequences!

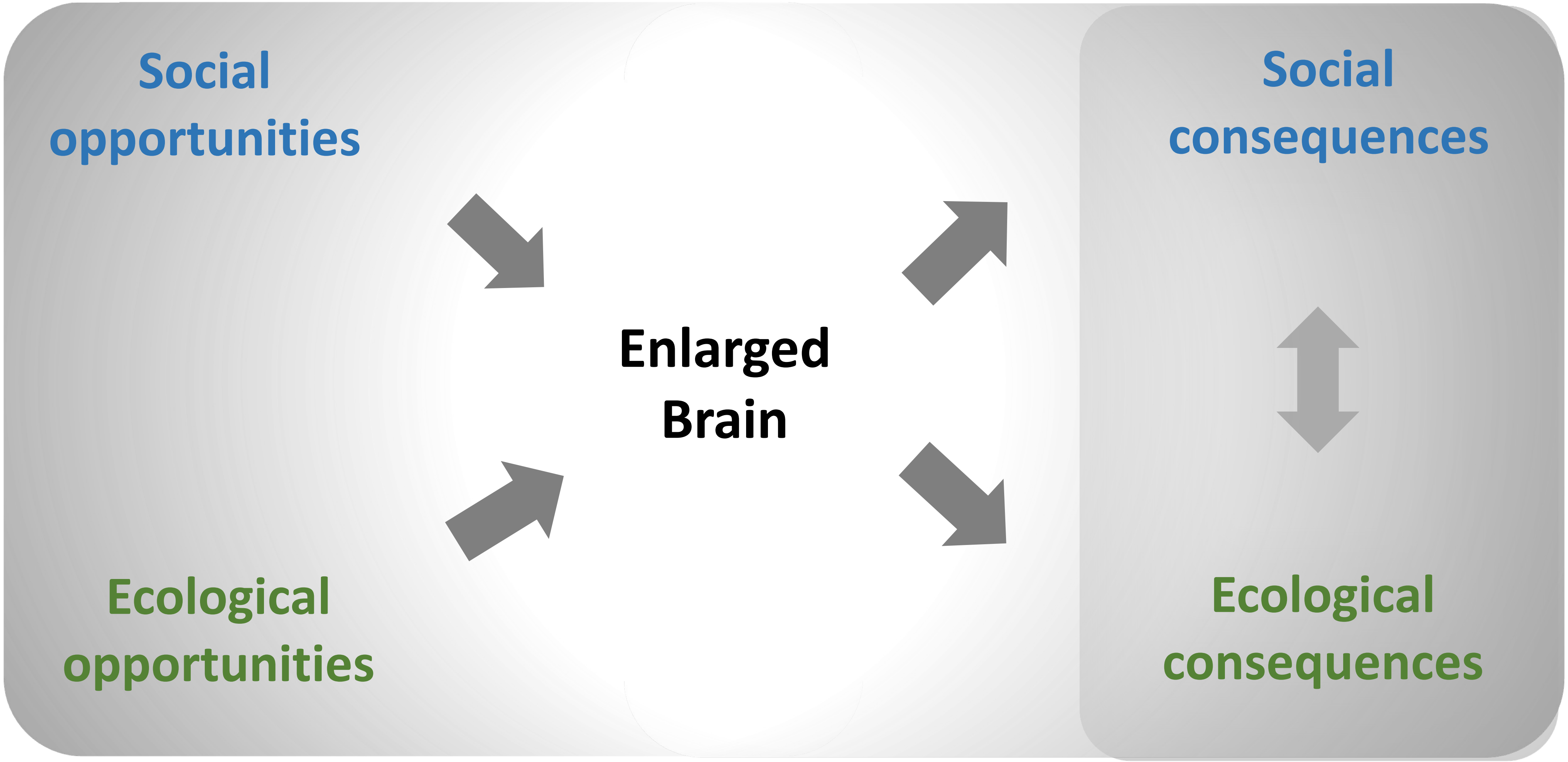
New approach needed!

☺ Include a broad range of social and ecological variables



☺ Systematic distinction between possible **selective pressures** and **cognitive consequences** of enlarged brains

Concept of Opportunities and Consequences



Facilitation of enlarged brains

Direct effects of enlarged brains

General behavioral flexibility

Graber et al. in review

Opportunity and Consequence Variables

Social opportunities

social system
group size
gregariousness
fission-fusion
home range overlap
vocal terr. advertisement
dispersal
mating system
body size dimorphism
visual trait dimorphism
cooperative breeding

$N_{spp.}$=67

Ecological opportunities

activity
habitat
substrate
predation risk
mobility in ranging area
environmental seasonality
% insects and meat in diet
% fruits and seeds in diet
% leaves in diet
extractive foraging
diet quality

$N_{spp.}$=50

Enlarged Brain

Opportunity and Consequence Variables

Social opportunities $N_{spp.}=67$

social system
group size
gregariousness
fission-fusion
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Ecological opportunities $N_{spp.}=50$

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extractive foraging
diet quality

Enlarged Brain

Social consequences $N_{spp.}=60$

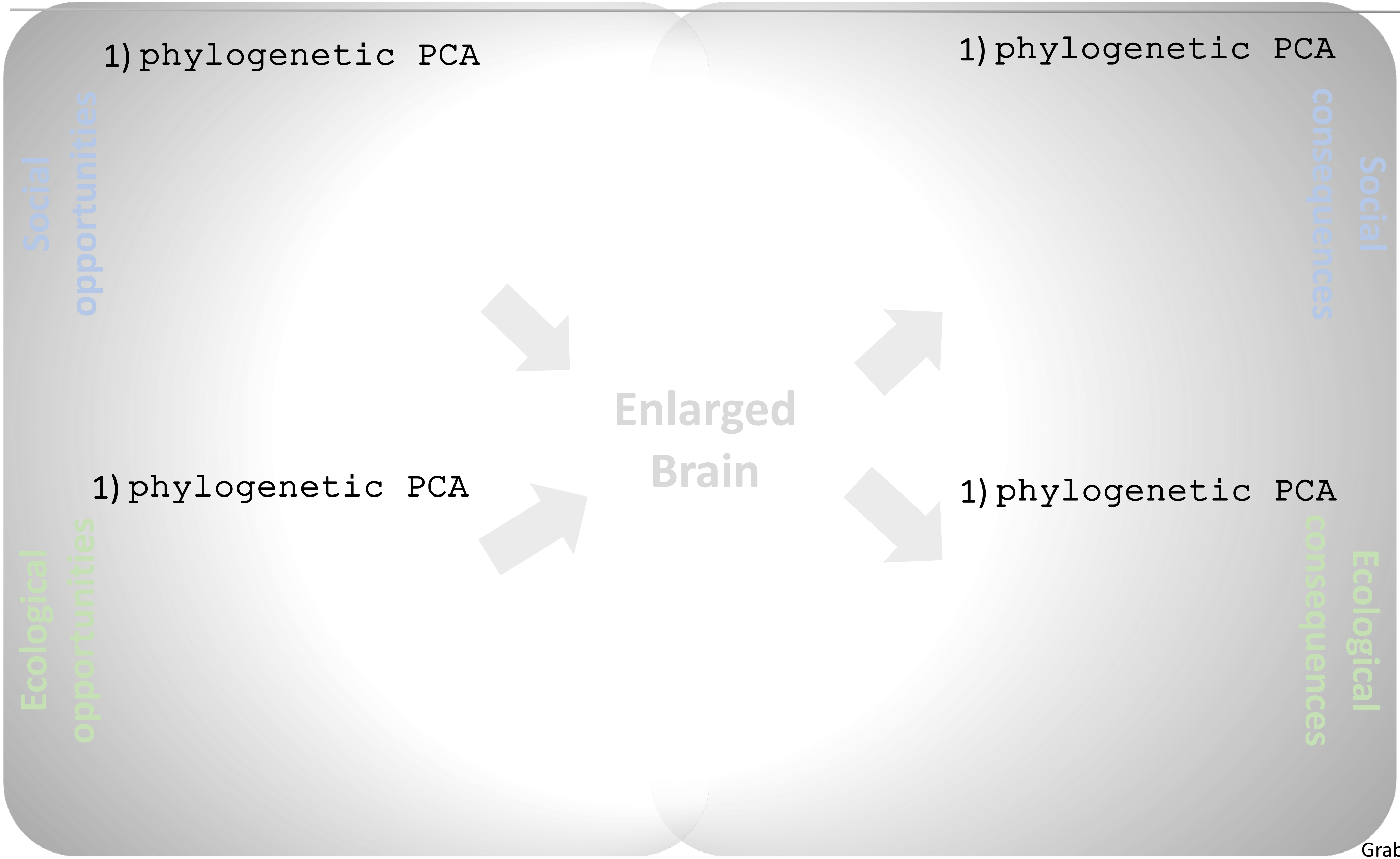
social learning frequency
coalition formation
social hunting
food sharing among adults

Ecological consequences $N_{spp.}=53$

buffering env. Seasonality
innovation frequency
diet breadth
hunting
tool use

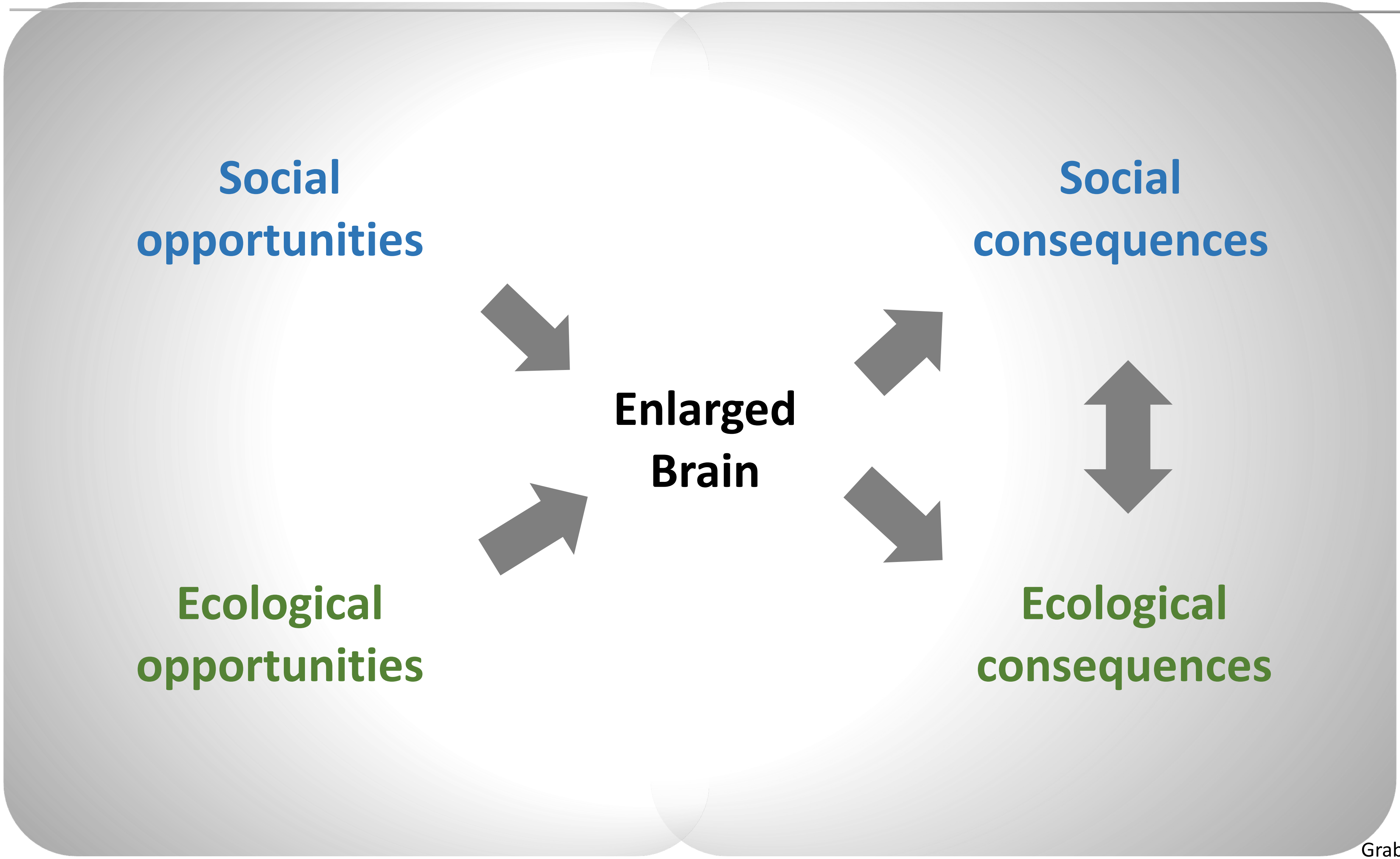
Graber et al. in review

1. Phylogenetic Principal Component Analysis (PCA)



Graber et al. in review

2. Phylogenetic Path Analysis



Graber et al. in review

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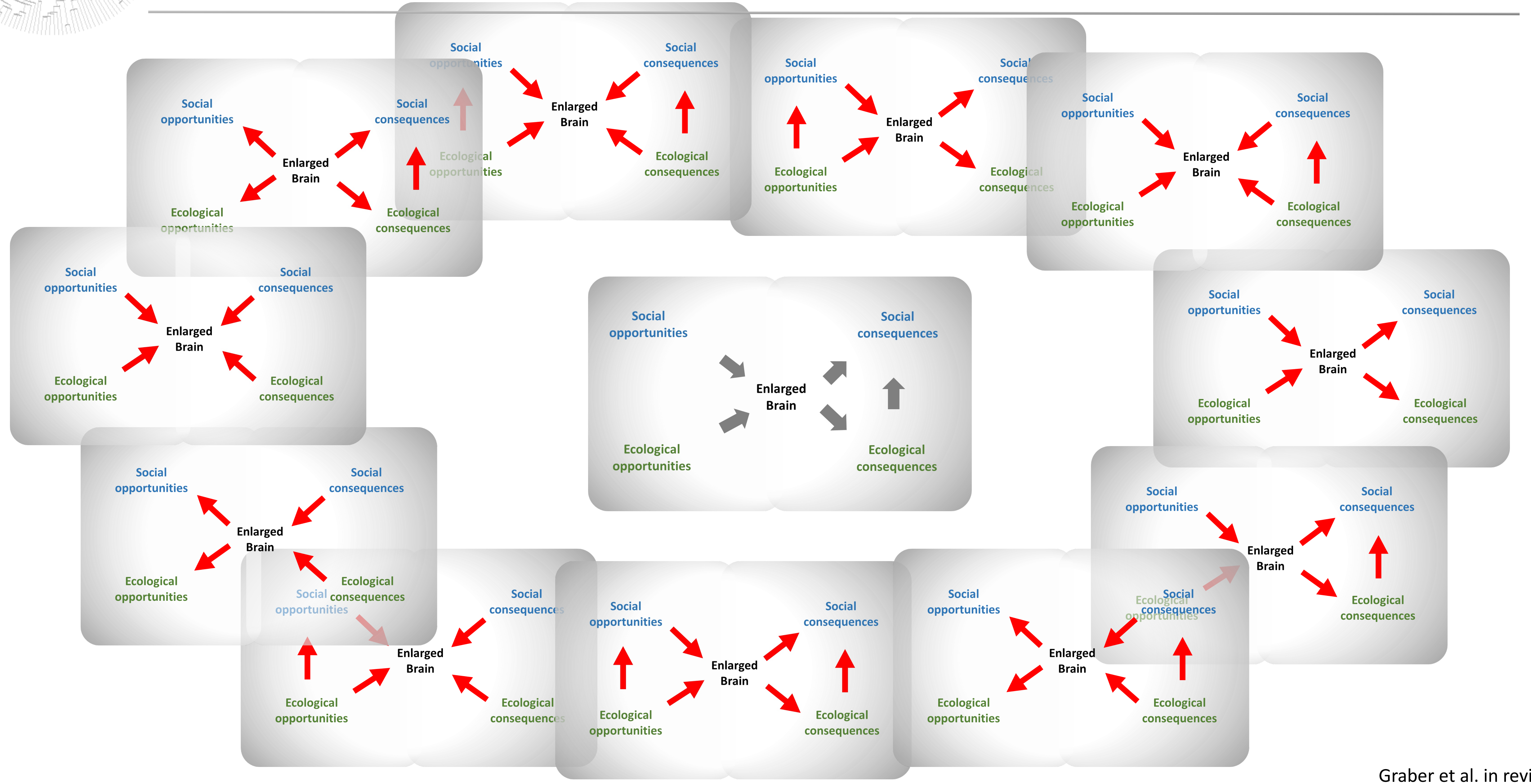

Graber et al. in review

Phylogenetic PCA

Social opportunities	PC1	PC2
multi-male-female group	0.05	**0.66**
home range overlap	0.31	0.09
vocal terr. advertisement	**-0.60**	-0.46
group size	**0.51**	0.42
gregariousness	-0.26	**0.65**
fission-fusion	**0.57**	-0.12
dispersal	-0.08	-0.42
polygynandry	0.25	**0.60**
body size dimorphism	**0.77**	-0.25
visual trait dimorphism	**0.66**	**-0.59**
cooperative breeding	-0.41	-0.17
Proportion explained	0.22	0.20

group size
cohesion
sex. dimorph.

social system
mating system

Enlarged
Brain

Graber et al. in review

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Ecological opportunities	PC1	PC2
diurnality	-0.38	-0.34
wooded habitat	0.02	**-0.65**
arboreality	0.03	**-0.50**
Predation risk	0.39	0.30
mobility in raning area	0.33	0.46
environmental seasonality	0.25	**0.50**
% insects and meat in diet	**0.52**	-0.47
% fruits and seeds in diet	**0.70**	0.05
% leaves in diet	**-0.92**	0.06
extractive foraging	0.15	0.47
diet quality	**0.90**	-0.33
Proportion explained	0.26	0.18

diet quality

habitat complexity

Enlarged Brain

Graber et al. in review

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Proportion explained	0.26	0.18

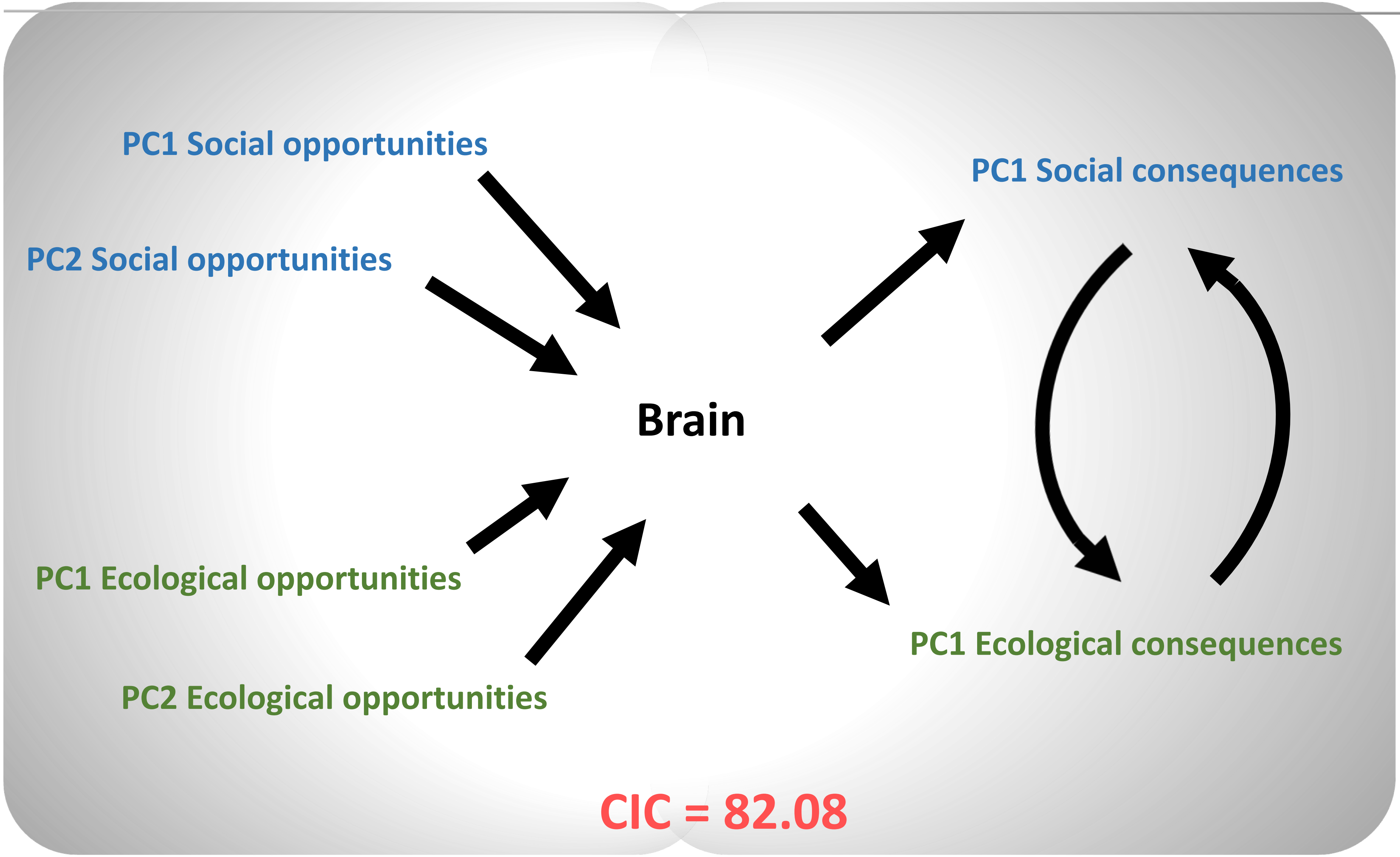
Enlarged Brain

Social consequences	PC1
Social learning frequency	**0.78**
Coalition formation	**0.73**
Social hunting	**0.86**
Food sharing among adults	**0.63**
Proportion explained	0.57

Ecological consequences	PC1
Buffering env. seasonality	0.11
Diet breadth	0.47
Hunting	**0.77**
Tool use	**0.82**
Innovation frequency	**0.79**
Proportion explained	0.42

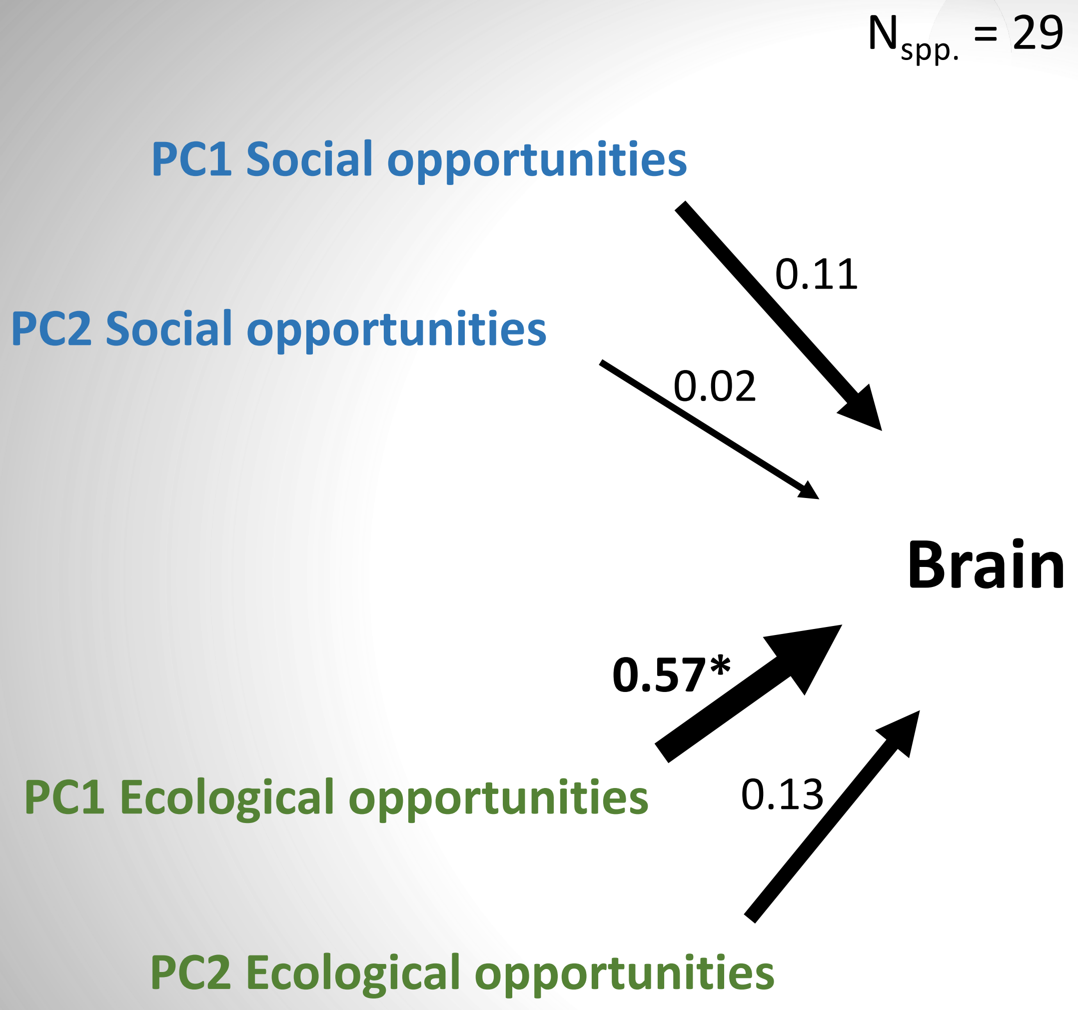
Graber et al. in review

Path Analysis: confirmation of concept of opportunities and consequences



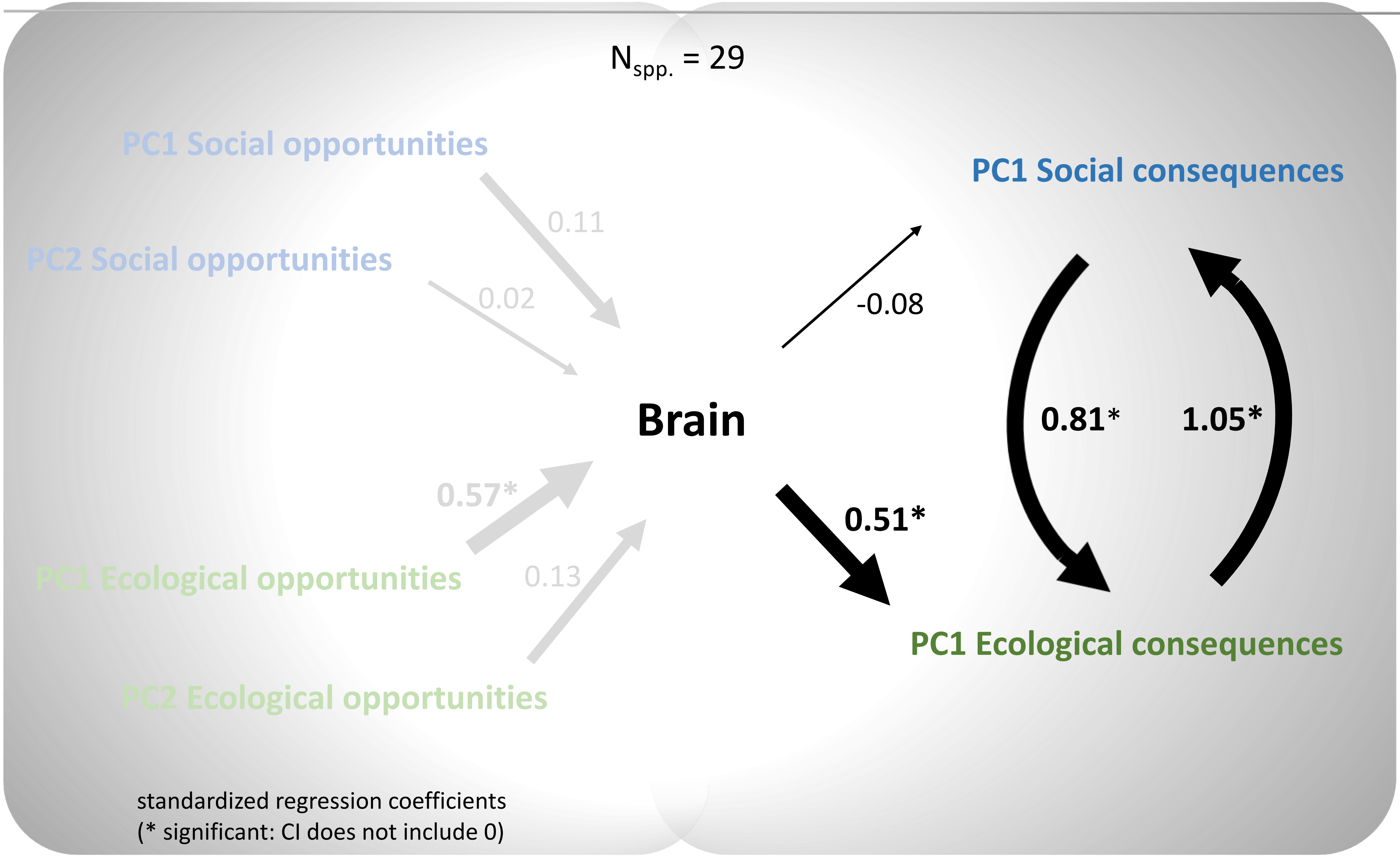
Path Analysis: confirmation of concept of opportunities and consequences

Ecological rather than social opportunities lead to enlarged brains



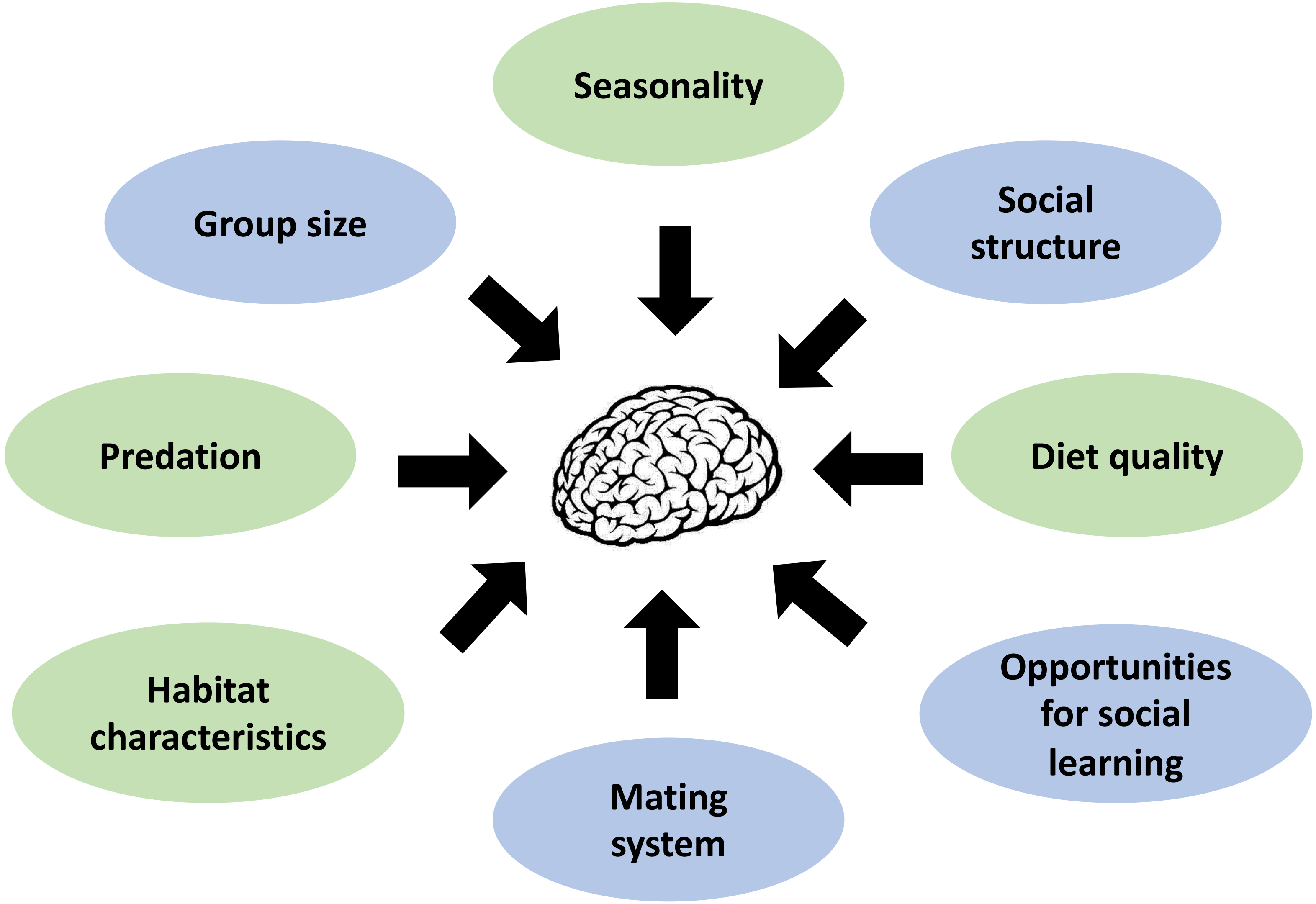
standardized regression coefficients
(* significant: CI does not include 0)

Enlarged brain allows for complex social and ecological cognitive abilities



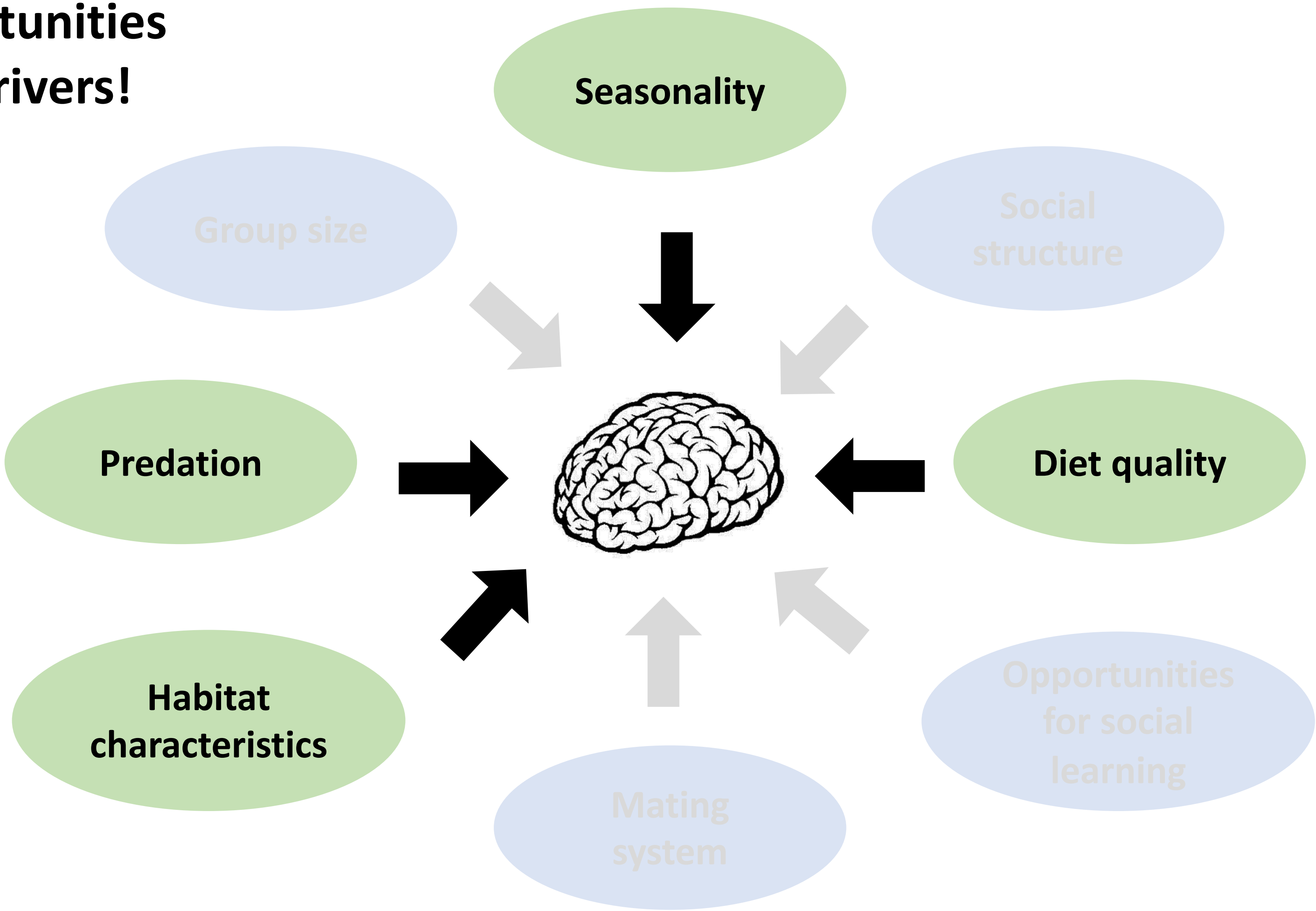
PART 3

Conclusions



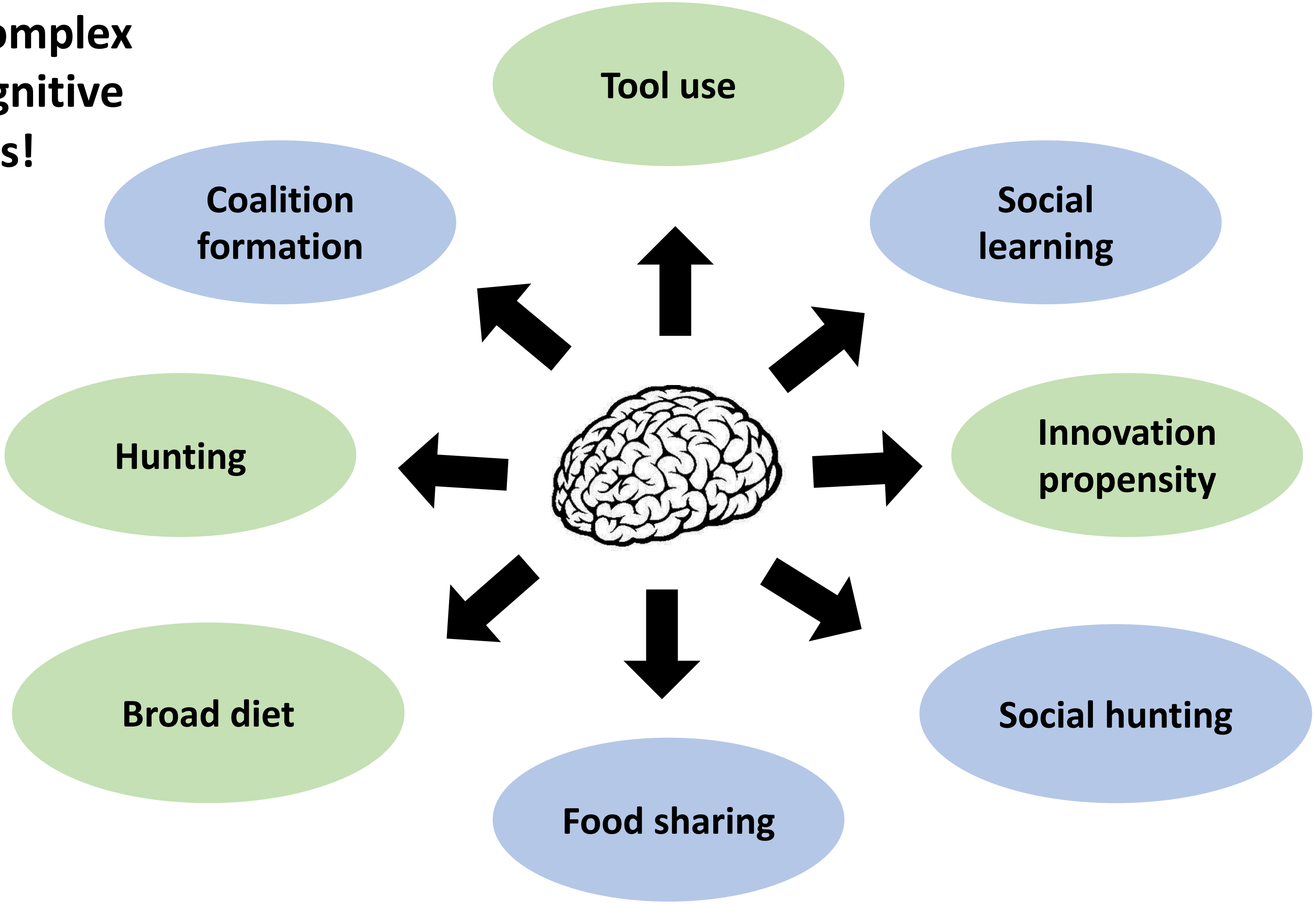
Conclusions

Ecological opportunities are the main drivers!



Conclusions

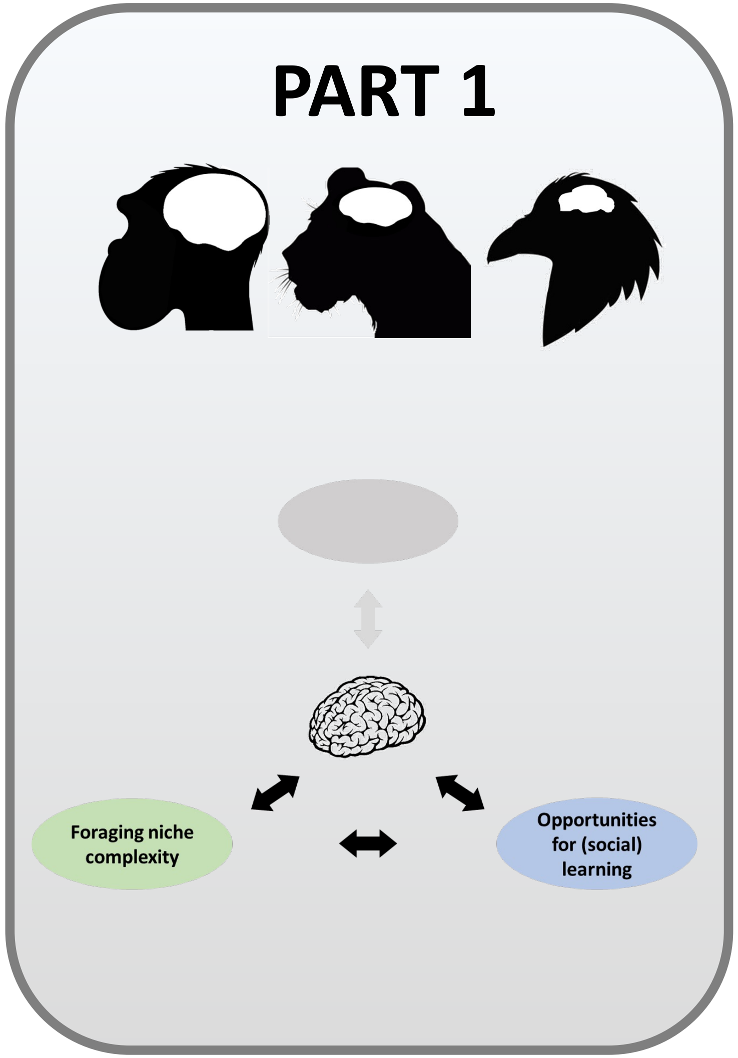
Large brains allow for a variety of more complex socio-and eco-cognitive consequences!

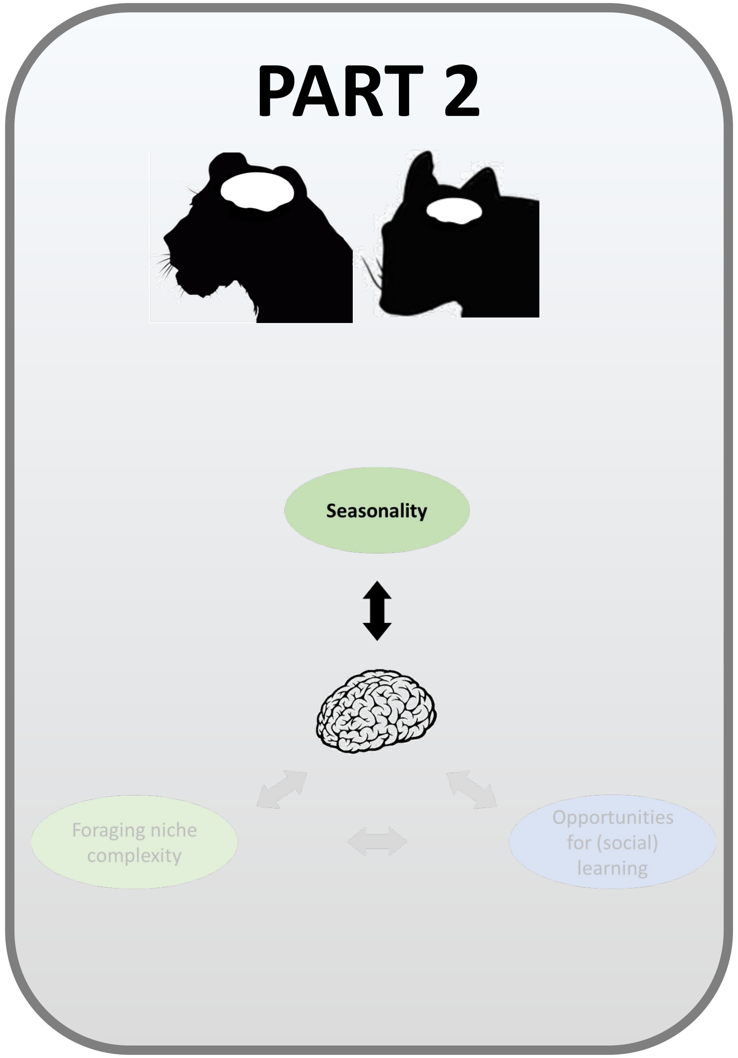


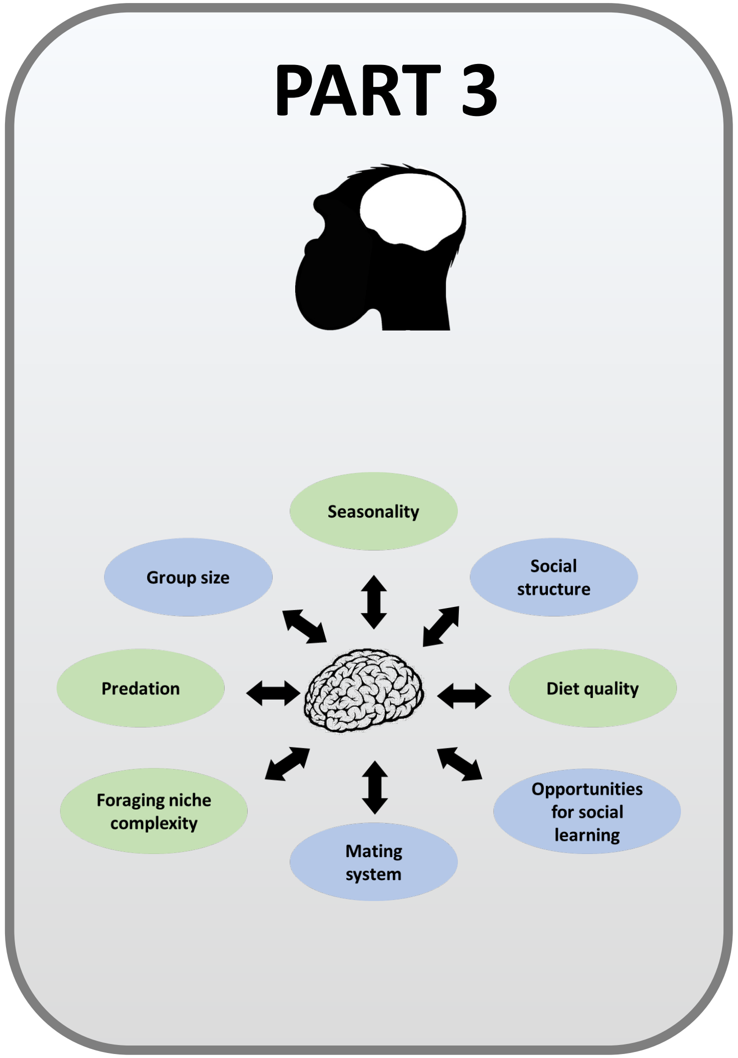
Conclusions

Social complexity could only become prominent in lineages **where ecological preconditions** had already allowed for the evolution of larger brains**.**

Summary


PART 1
Foraging niche complexity
Opportunities for (social) learning


PART 2
Seasonality
Foraging niche complexity
Opportunities for (social) learning


PART 3
Seasonality
Group size
Social structure
Predation
Diet quality
Foraging niche complexity
Opportunities for social learning
Mating system

Summary

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Opportunities for (social) learning
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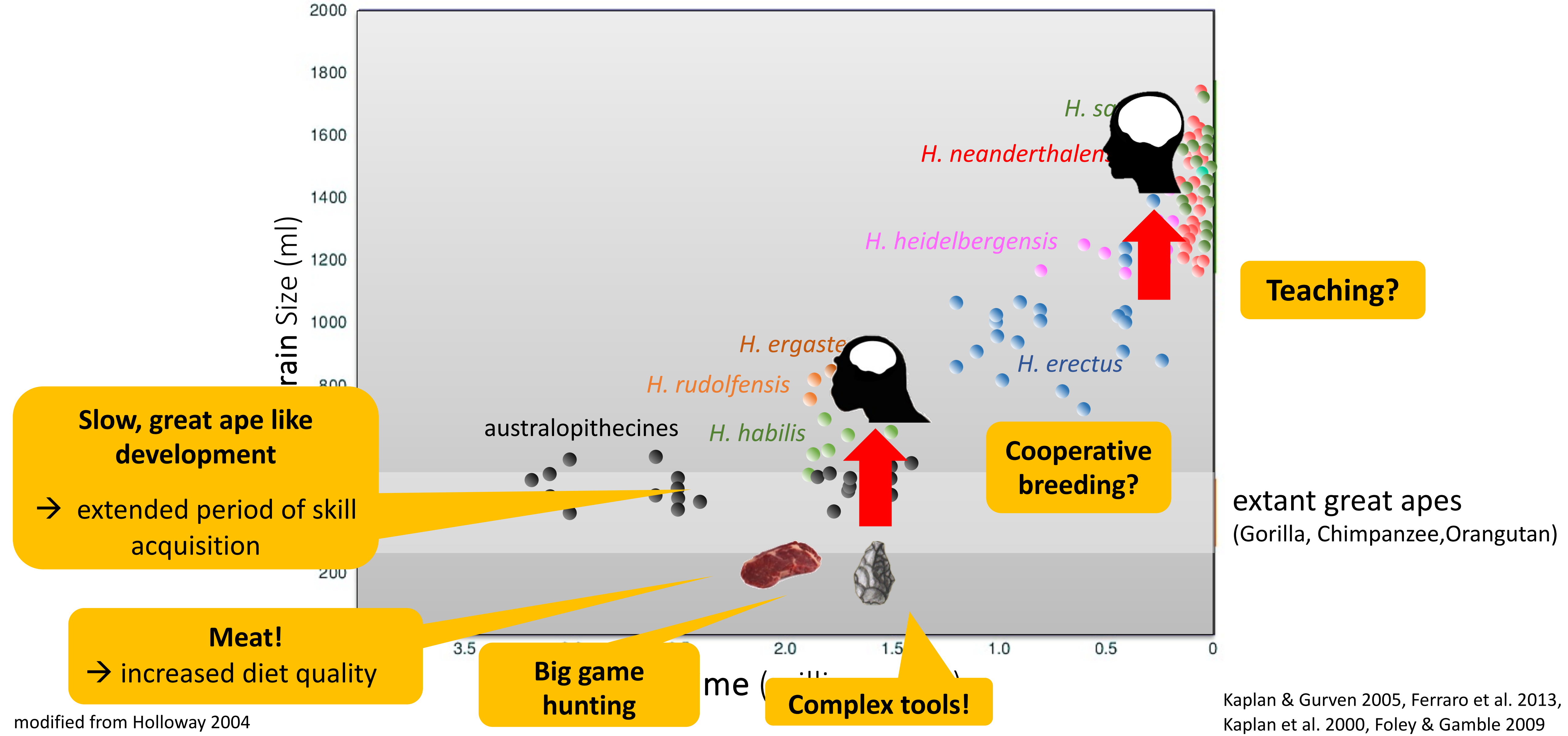
What about human brain size evolution?

How did our ancestors do it?



modified from Holloway 2004

Kaplan & Gurven 2005, Ferraro et al. 2013, Kaplan et al. 2000, Foley & Gamble 2009

Thank you!

Karin Isler
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Sandra Heldstab

Laura Damerius

Erik Willems
Szymon Drobniak
Michael Griesser
Reinhard Furrer

Coop-Peer-Action

Werner, Christine und Adriel Graber

Kern, Vogel, Kümin, sDenze, Fäb

Steff

Schmöpelinios

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FNSNF
SWISS NATIONAL SCIENCE FOUNDATION

Universität Zürich UZH

Thank you!

How did our ancestors do it?