

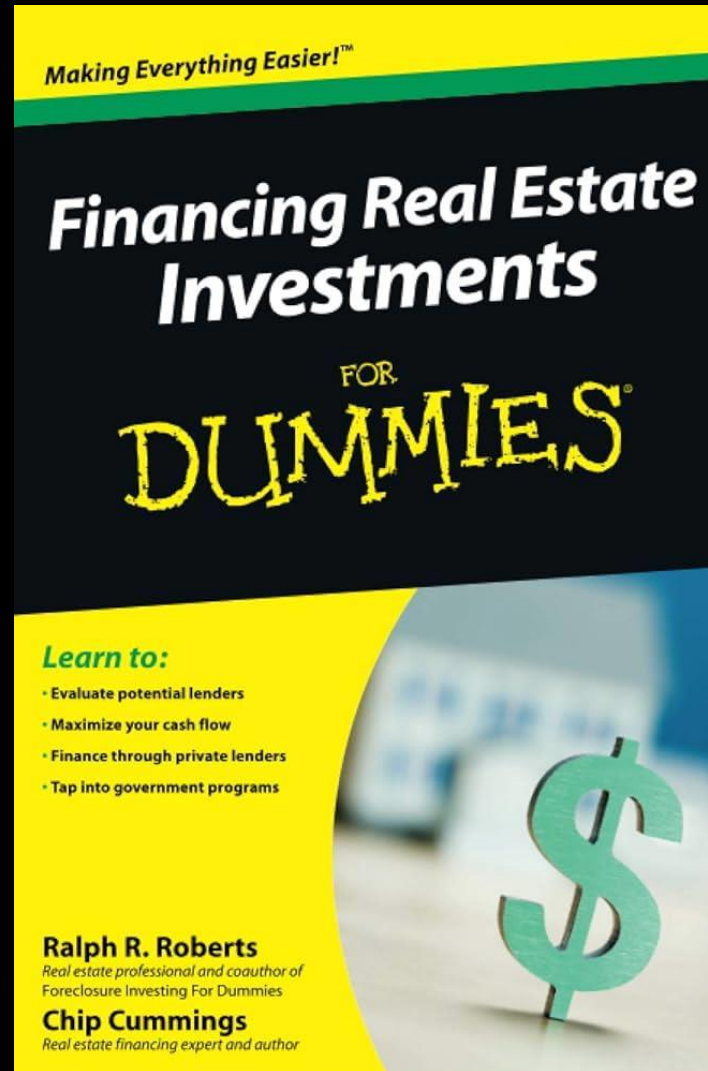
A black and white photograph showing a large colony of bats hanging upside down from the ceiling of a cave. The bats are densely packed in some areas, particularly on the left side of the frame, and more sparsely distributed on the right. The cave ceiling is rough and textured. The lighting is somewhat dim, highlighting the silhouettes and features of the bats.

“My Field for Dummies”: Exploring the social lives of bats

Gerry Carter
Ecology and Evolutionary Biology
Princeton University
Howard Hughes Medical Institute
socialbat.org

“My field for dummies”

“My field for dummies”



“My field for dummies”

Making Everything Easier!™

***Studying social
behavior (in bats)***

FOR
DUMMIES®



“My field for dummies”

“My field for dummies”

Scientific fields are defined, not by the facts,
but by the questions we ask.

“My field for dummies”

Scientific fields are defined, not by the facts,
but by the questions we ask.

The goal of research is not “facts”.
It is better questions.

“My field for dummies”

Do bats have social relationships?

Well, what is a social relationship?

And how do we measure that across species?

And do “social relationships” require special adaptive traits?

If so, how do these traits vary with ecology?

“My field for dummies”

“My field for dummies”

We are all dummies
when it comes to
the social lives of bats.



Social integration in humans



Social integration
is fundamental to
human wellbeing



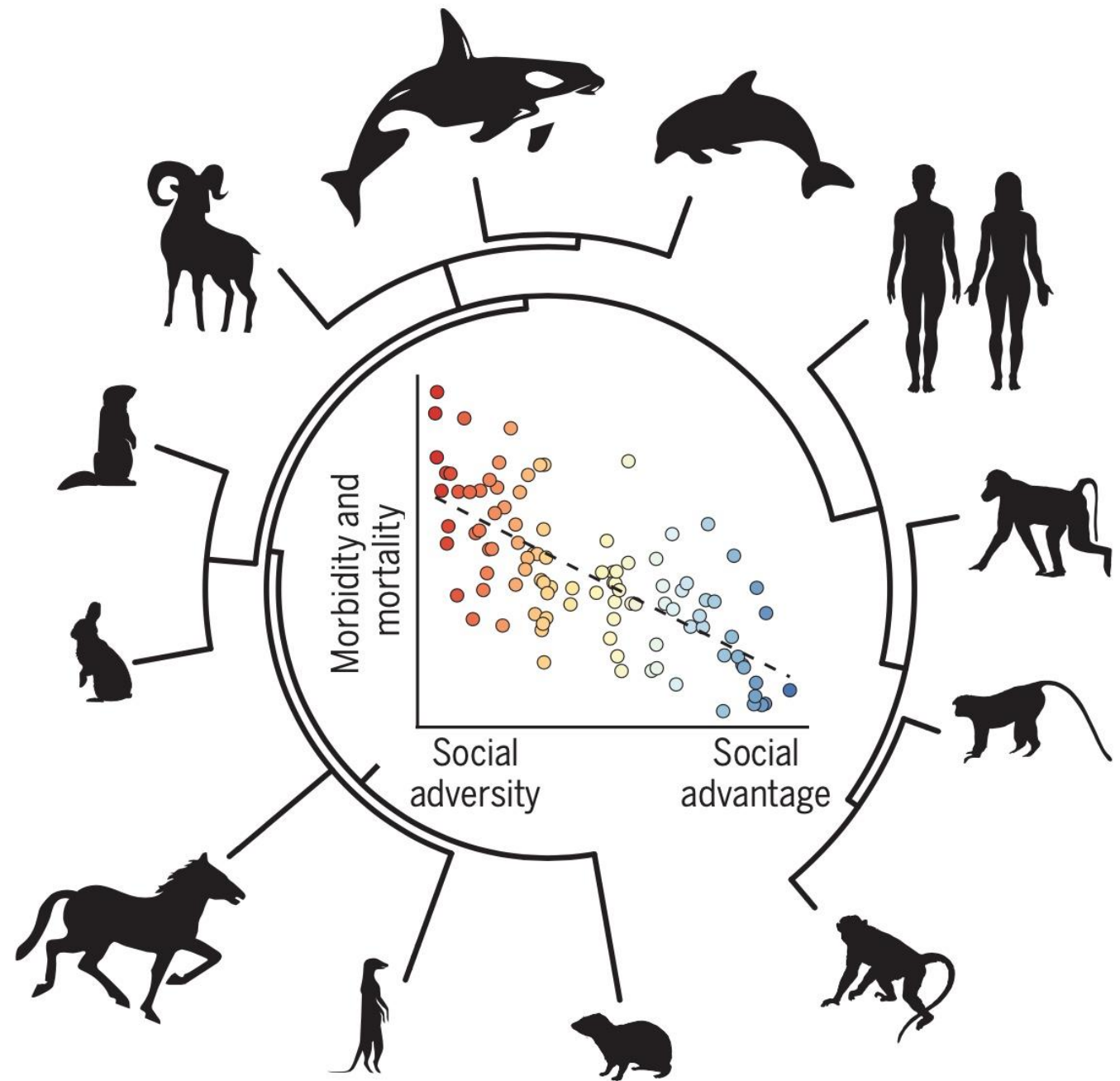
Poor social integration predicts reduced health and lifespan



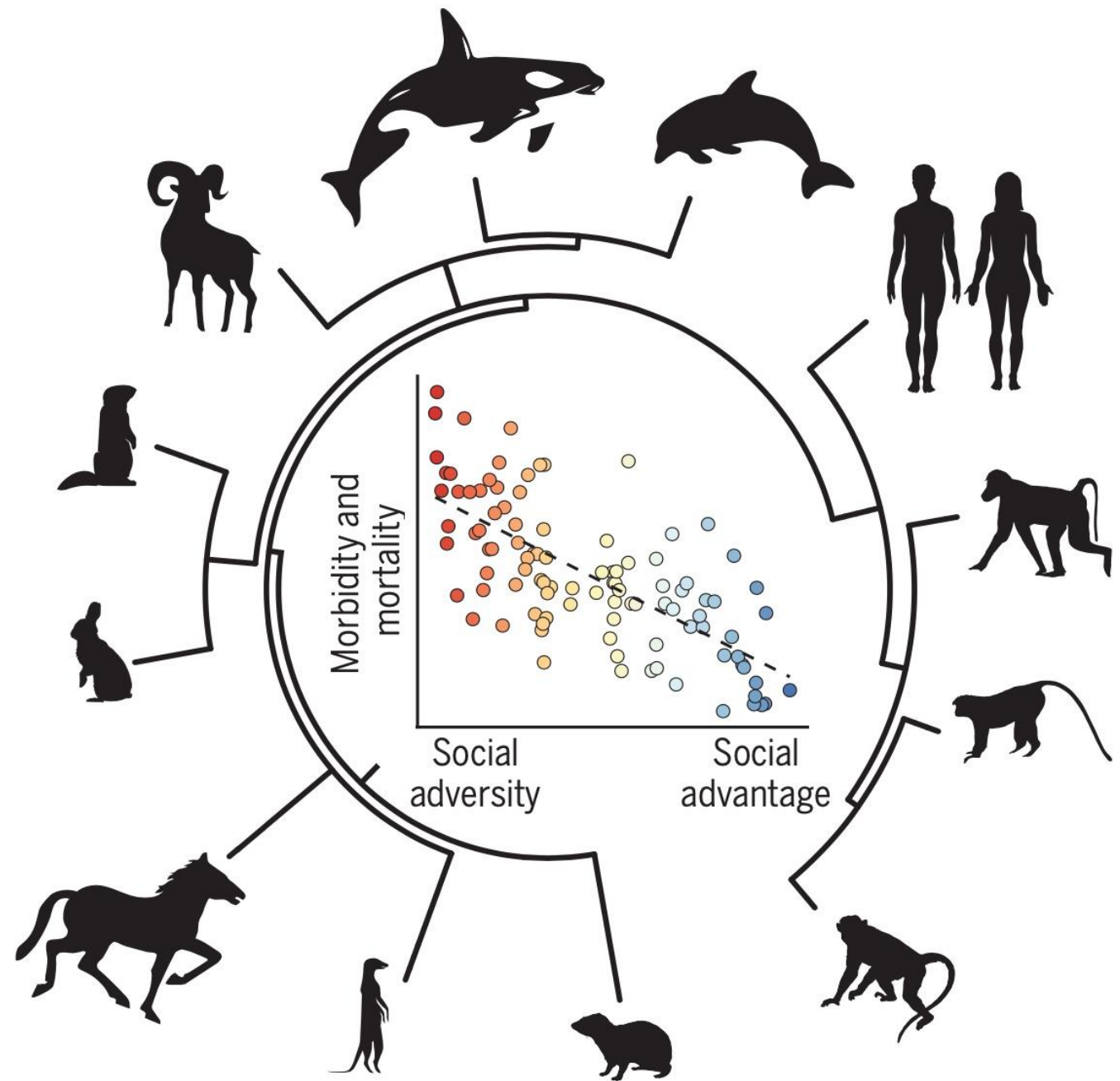
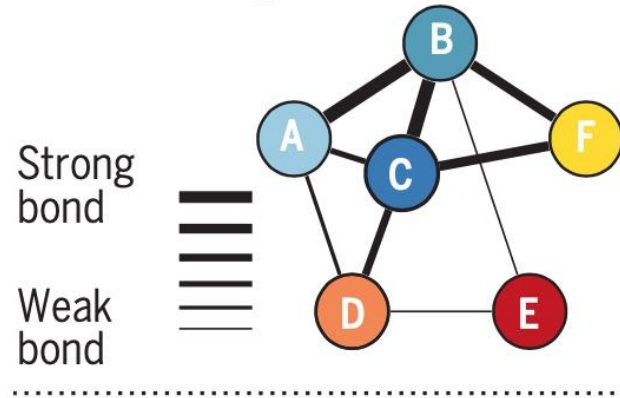
- depression and anxiety
- stress and inflammation
- increased infection
- cardiovascular disease
- cancer
- cognitive decline
- delayed recovery
- premature death

e.g. Holt-Lunstad et al. 2010; Leigh-Hunt et al. 2017

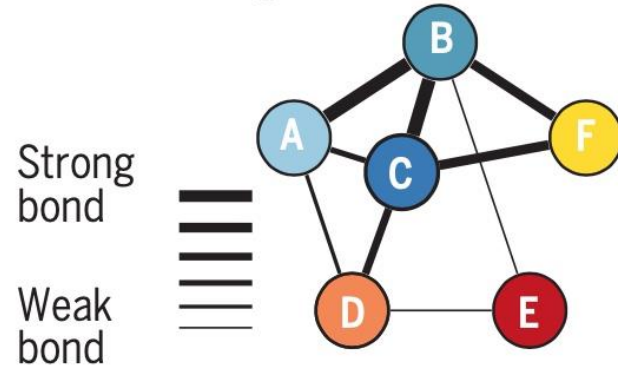
Other
social
mammals
also need
connection



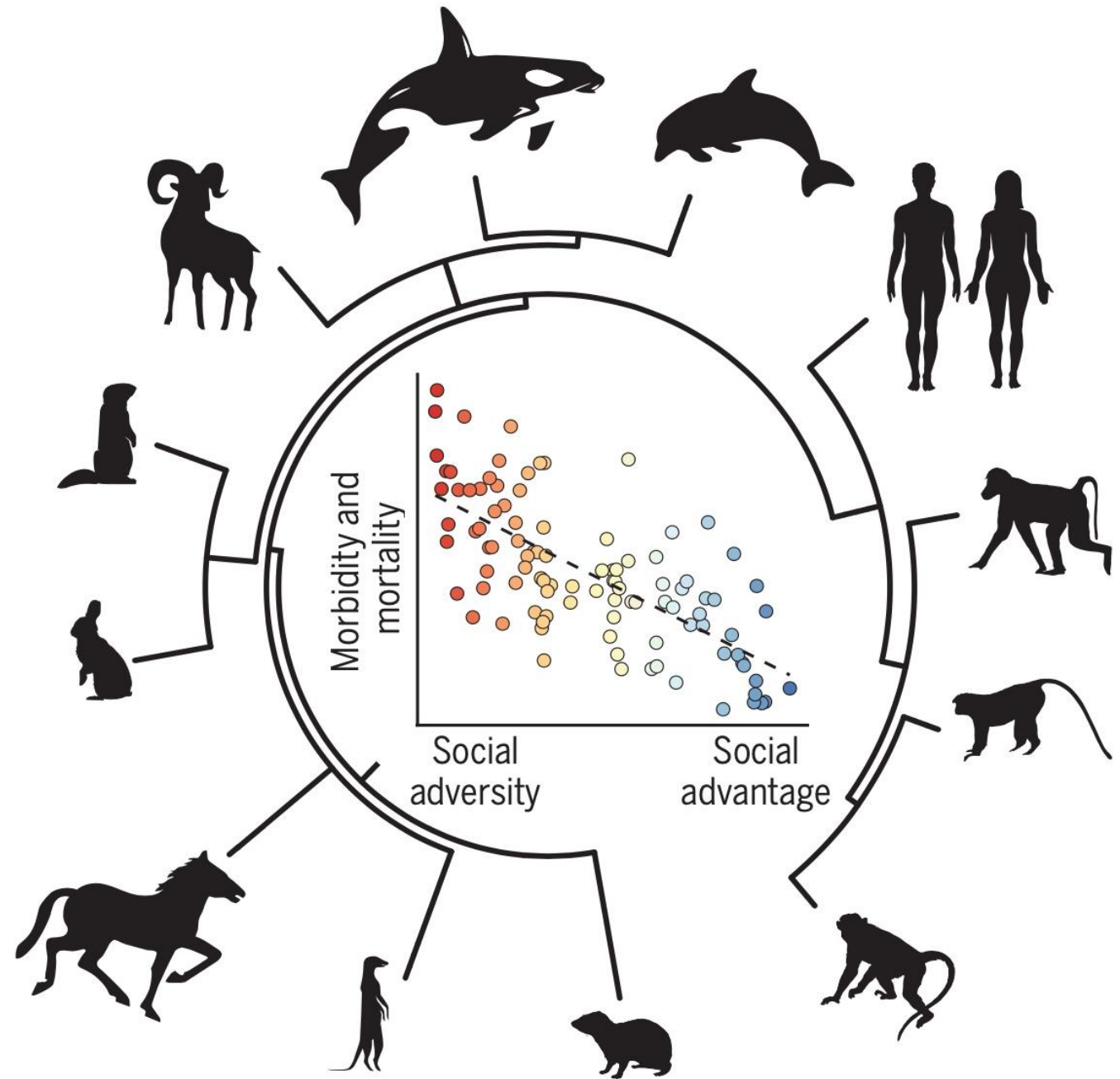
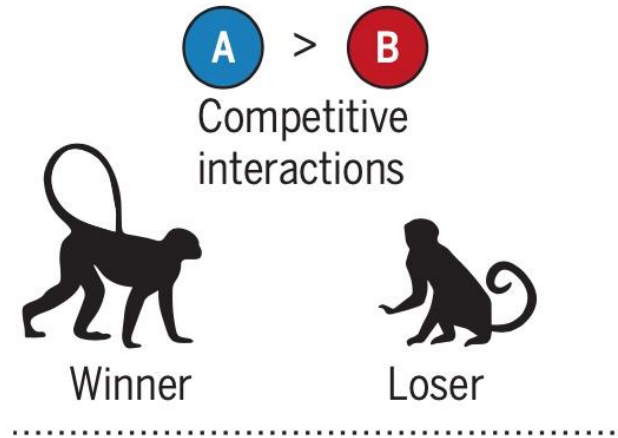
Social integration



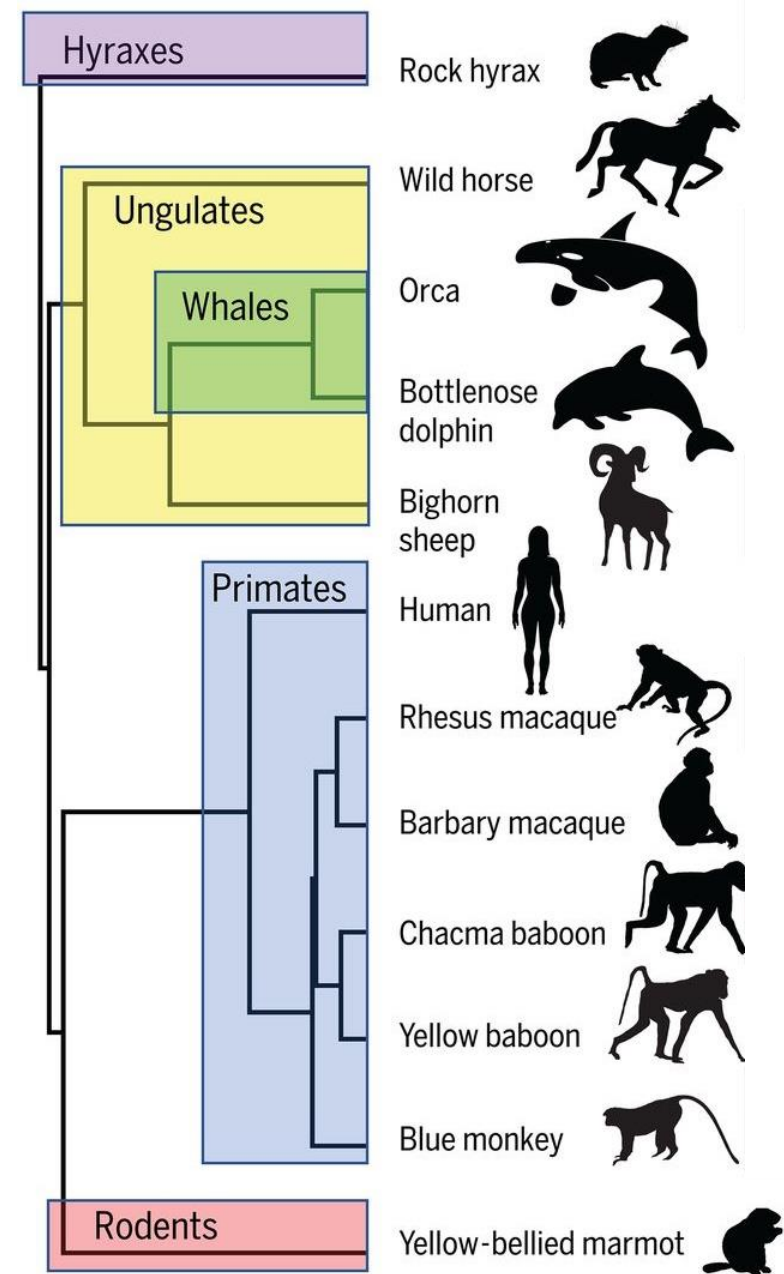
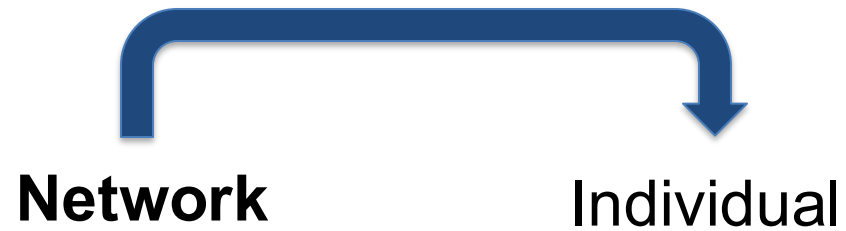
Social integration



Social status

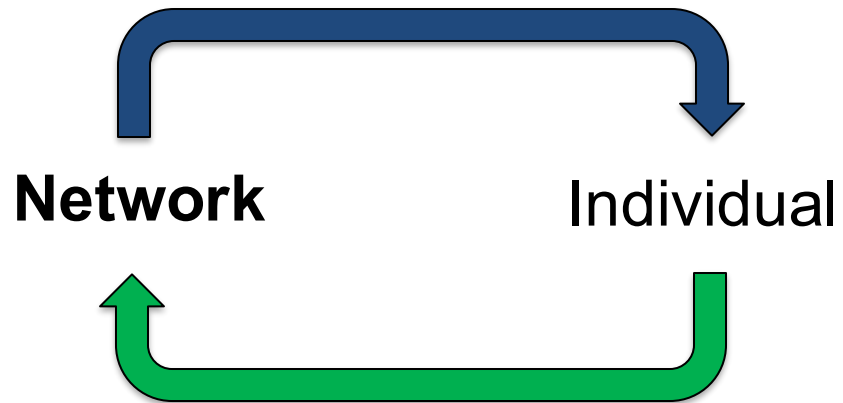


How do social relationships
influence individual success?

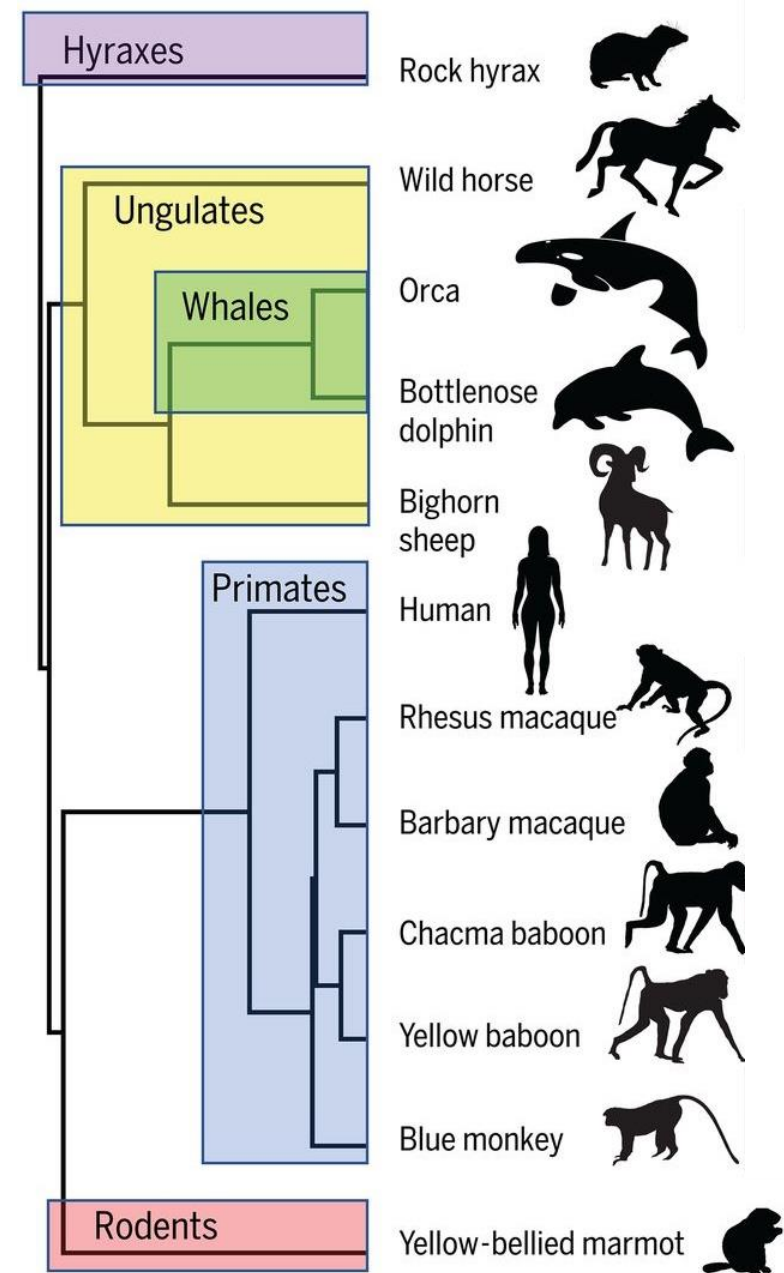




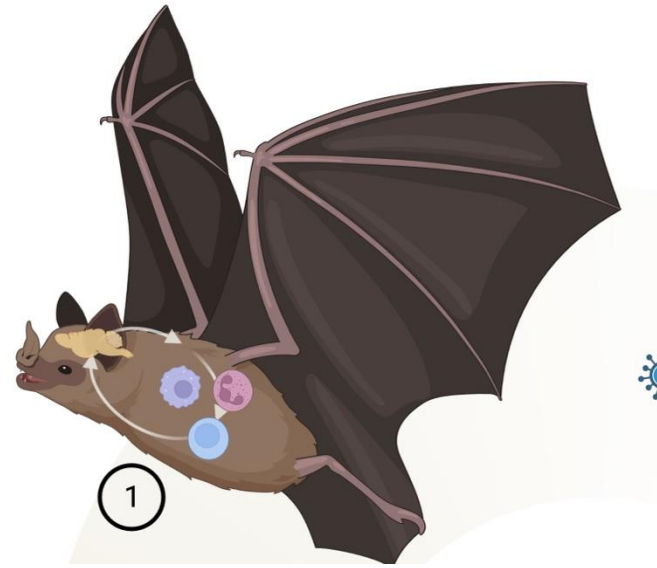
How do social relationships
influence individual success?



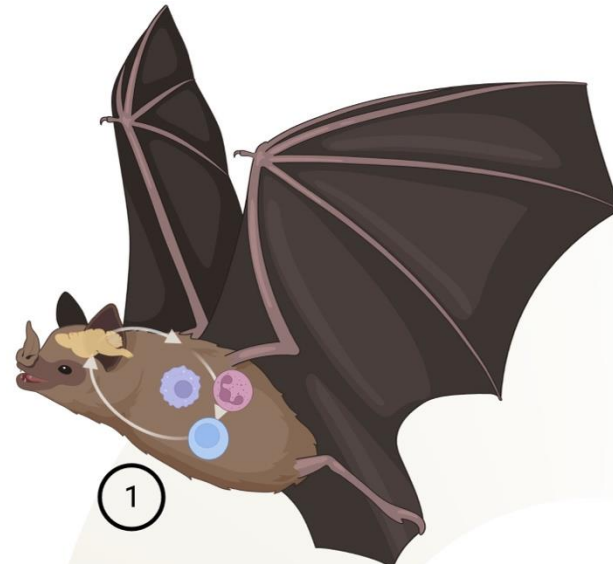
How do individuals build and
regulate their relationships?



What is a “social relationship”?



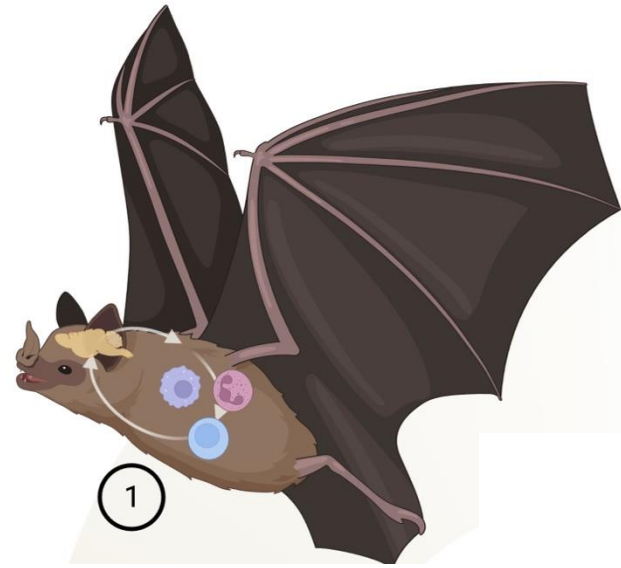
Individual bats can have
social traits.
How do these evolve?



Individual bats can have
social traits.
How do these evolve?

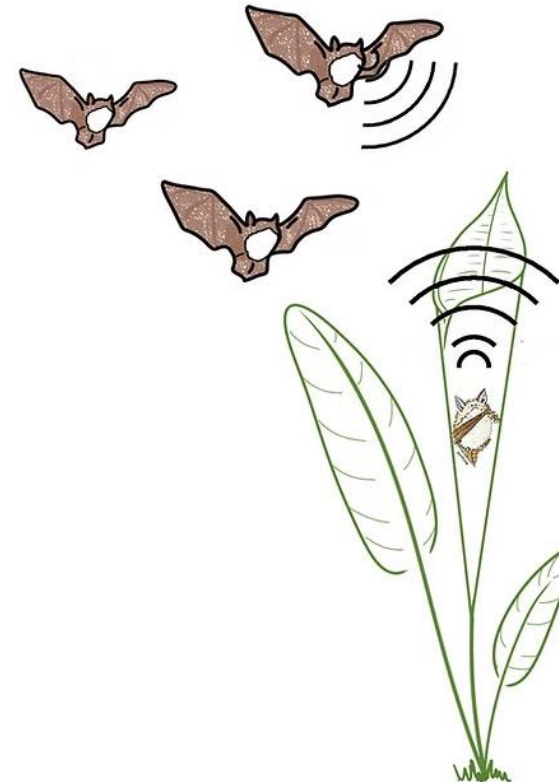
*Example: females vary in
maternal care*





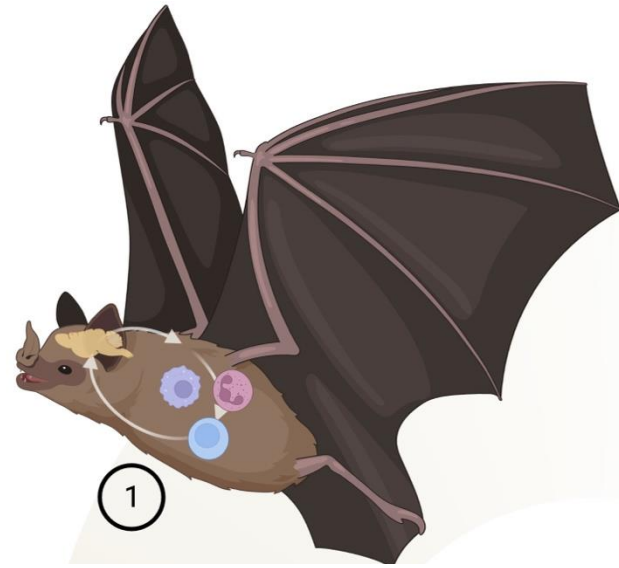
Individual bats can have
social traits.
How do these evolve?

*Example: bats vary in their
investment in contact calling*



Christian Ziegler
Minden Pictures

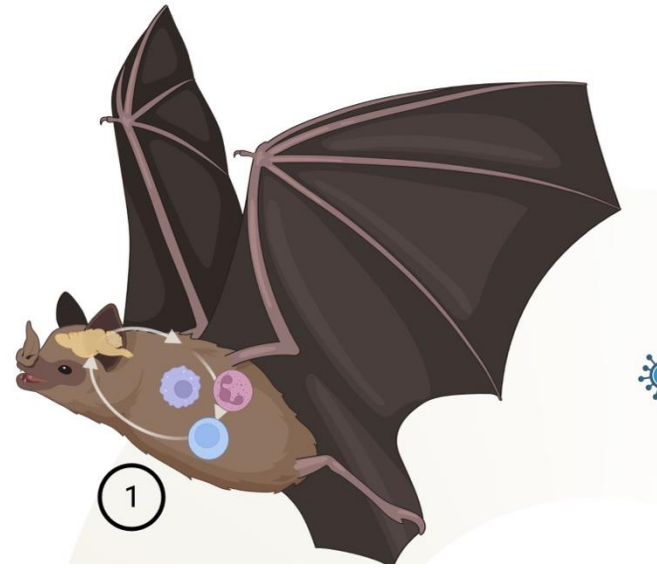
Chaverri et al. 2013 Behav Ecol
Chaverri & Gillam 2015 Roy Soc Open Science
Chaverri et al. 2020 Behav Ecol Sociobiol
Charrerri et al. 2024 Phil Trans B



Individual bats can have
social traits.
How do these evolve?

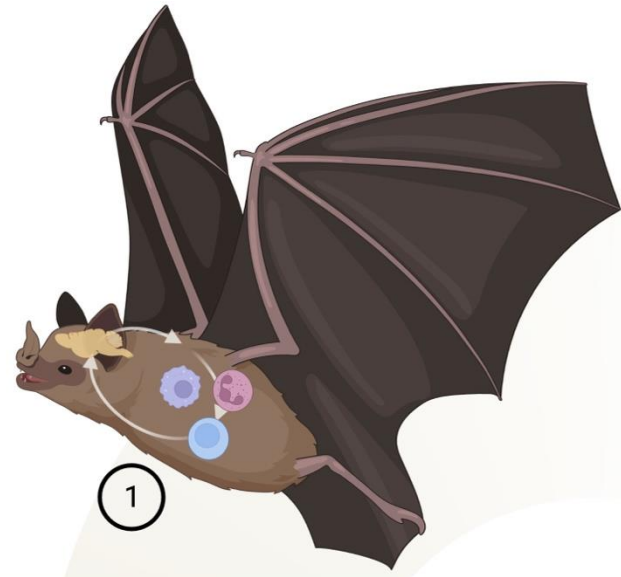
Individuals differ in rates of...

- *Calling*
- *Fighting*
- *Social clustering*
- *Social foraging*
- *Social learning*
- *Social grooming*
- *Food sharing*

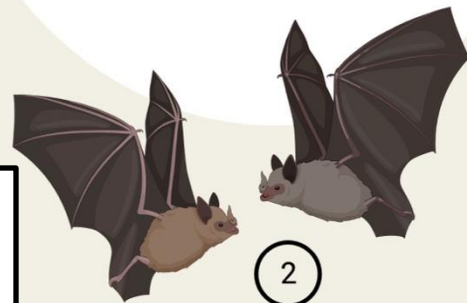


Individual bats can have
social traits.
How do these evolve?

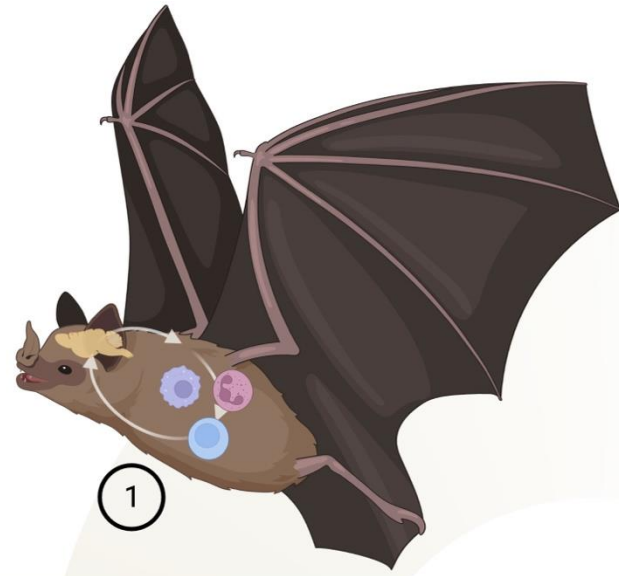
Natural selection favors social traits that **propagate one's genetic lineage.**
Therefore, social traits tend to have the appearance of being **strategic.**
So, we can ask: “**Why did this trait evolve? What is its function?**”



Individual bats can have
social traits.
How do these evolve?



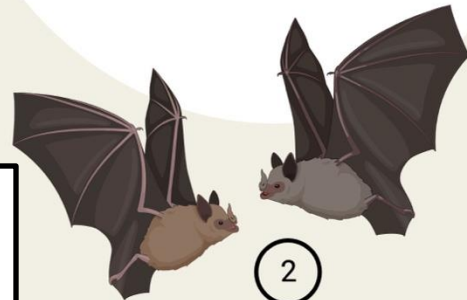
Pairs can have
social relationships.
How do these form?



Individual bats can have
social traits.
How do these evolve?

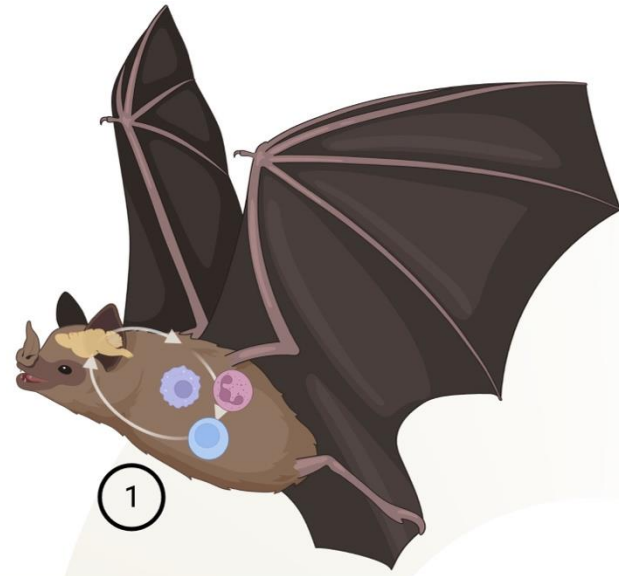


In *Pipistrellus kuhlii*,
juveniles experimentally
reared together formed
enduring relationships



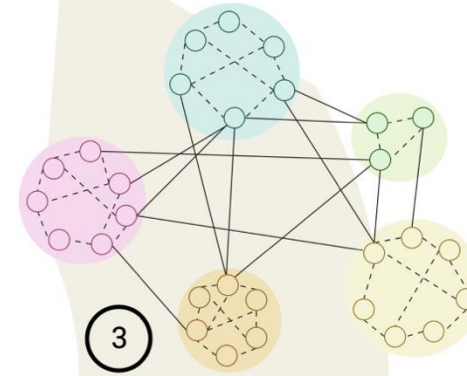
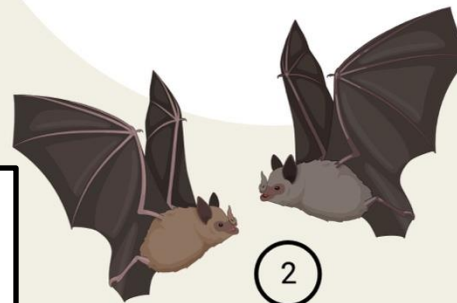
Pairs can have
social relationships.
How do these form?

Ancillotto et al. 2012 Ethology

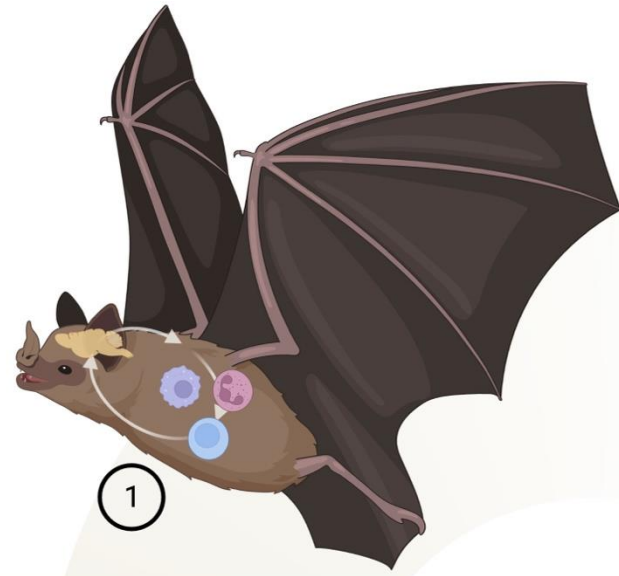


Individual bats can have
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How do these evolve?

Pairs can have
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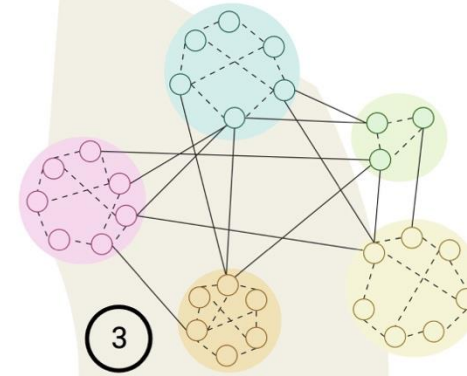
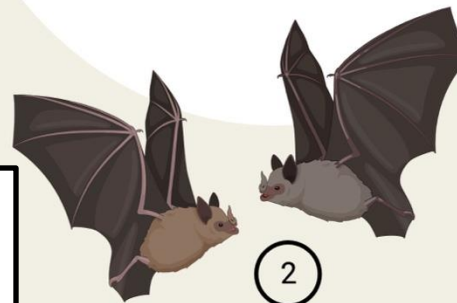


Groups form
social networks.
How are these structured?



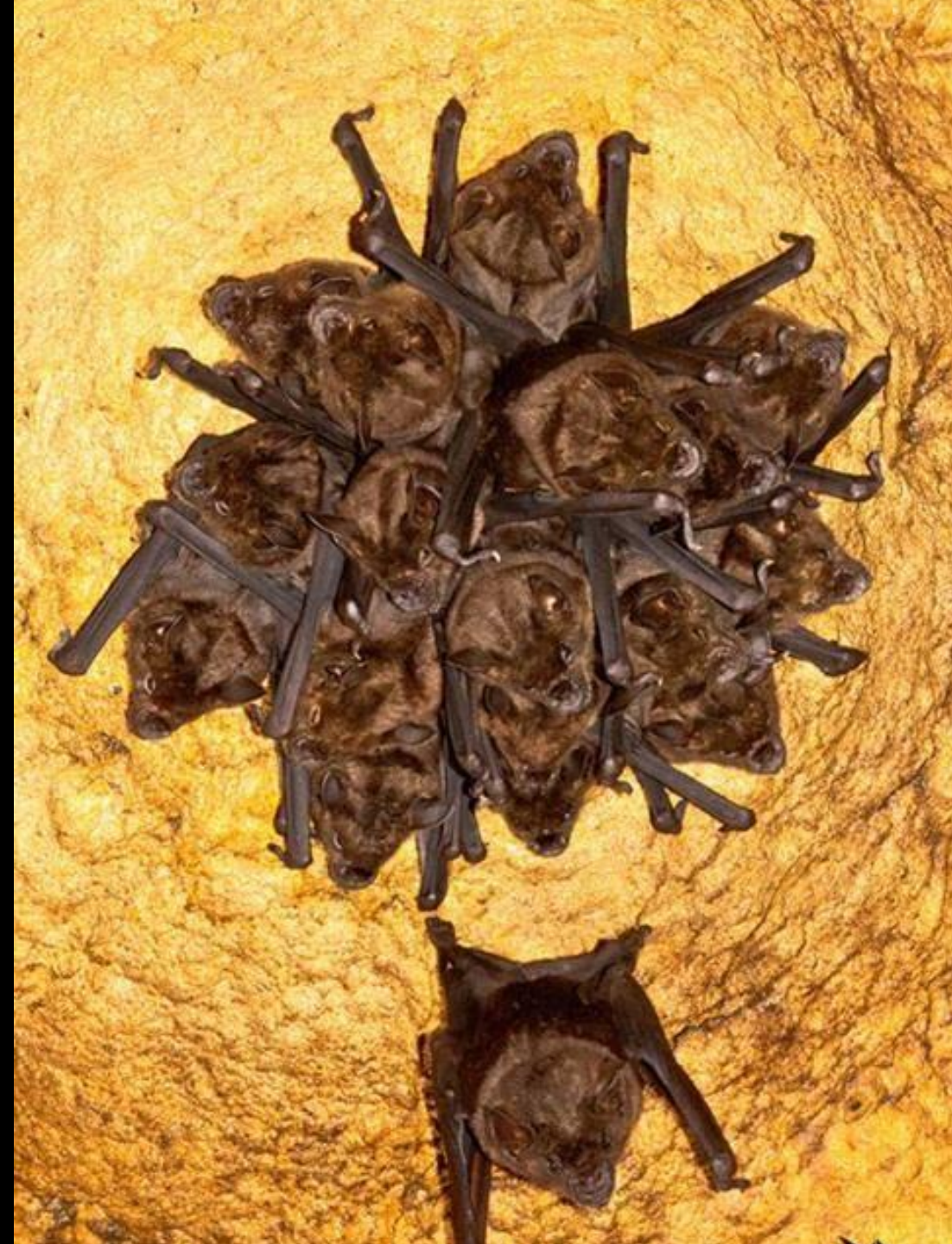
Individual bats can have
social traits.
How do these evolve?

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How do these form?



Groups form
social networks.
How are these structured?

An example of a bat society:
Greater spear-nosed bats (*Phyllostomus hastatus*)
live in stable groups of nonkin



McCracken & Bradbury 1977 Science
McCracken & Bradbury 1981 BES
Wilkinson & Boughman 1998 Anim Behav
Boughman & Wilkinson 1998 Anim Behav
Wilkinson et al. 2016 Phil Trans B

An example of a bat society:
Greater spear-nosed bats (*Phyllostomus hastatus*)
live in stable groups of nonkin



Boughman 2006 Behav Ecol Sociobiol
Bohn et al 2009 Behav Ecol Sociobiol
Wilkinson et al. 2016 Phil Trans B

An example of a bat society:
The carnivorous bat *Vampyrum spectrum* lives
in family groups with biparental care



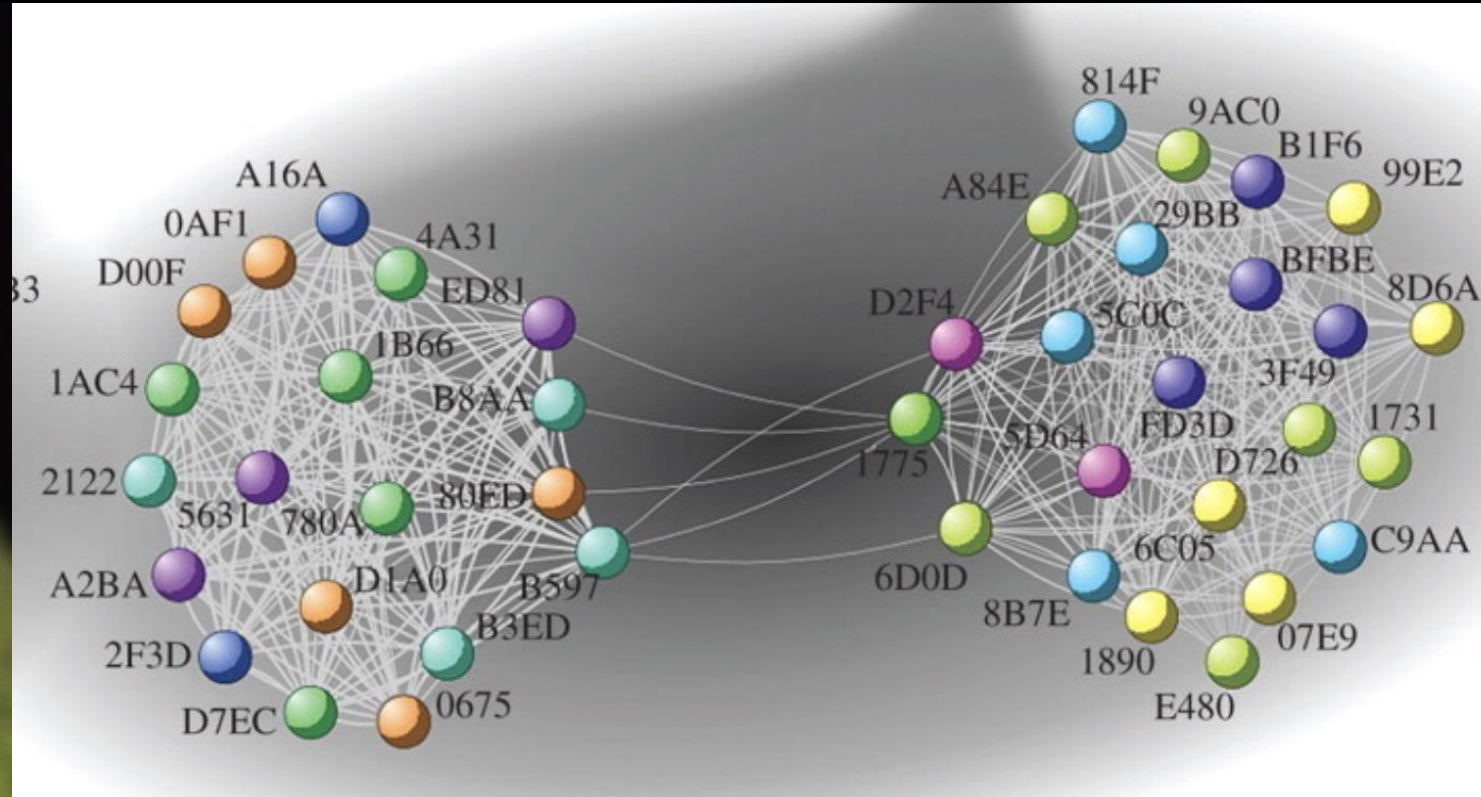
Vehrencamp et al. 1977 J Mamm
Martínez-Fonseca et al. 2022 PLOS One
Tietge et al. 2025 BioRxiv



José G. Martínez-Fonseca

Most bats have “fission-fusion” social dynamics

Bechstein's bat

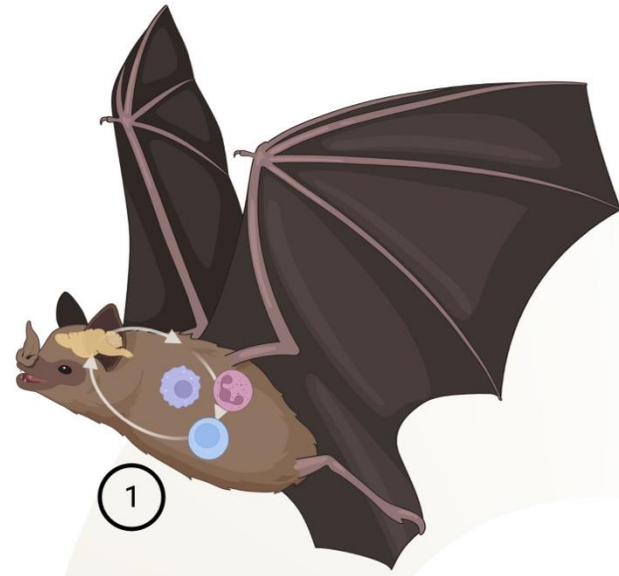


Kerth et al. 2011 Proceedings B

Wilkinson 1985 Behav Ecol Sociobiol
Willis & Brigham 2004 Proceedings B
Kerth et al. 2011 Proceedings B
Patriquin & Ratcliffe 2016 Sociality in Bats
Wilkinson et al. 2019 Behav Ecol Sociobiol

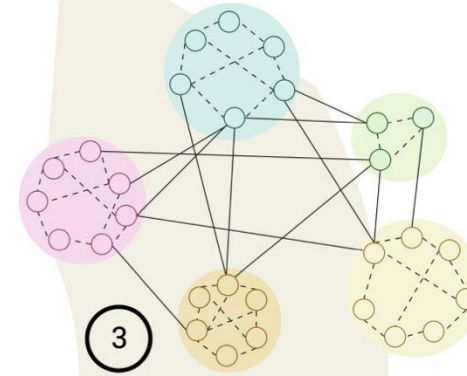
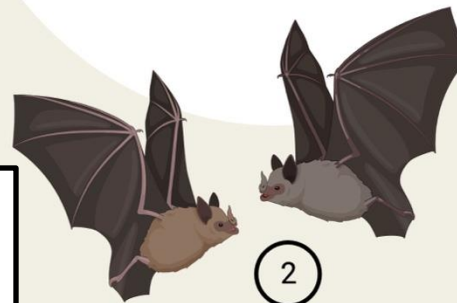
What's
going on
in here?



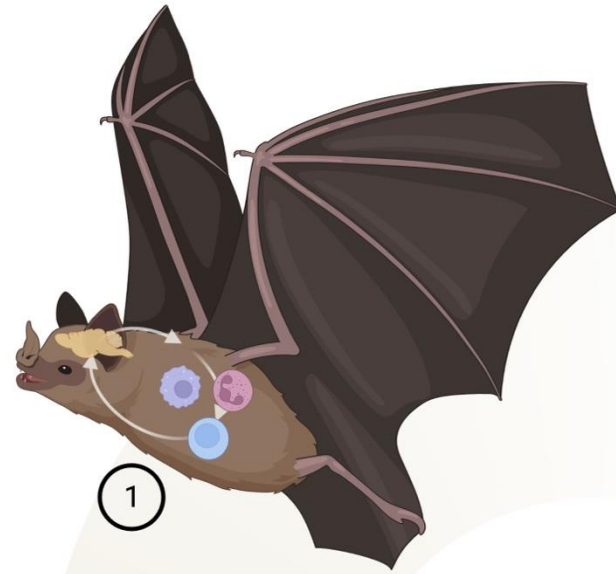


Individual bats can have
social traits.
How do these evolve?

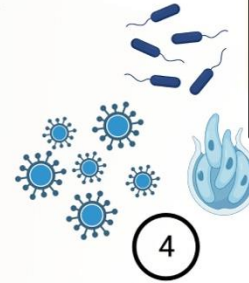
Pairs can have
social relationships.
How do these form?



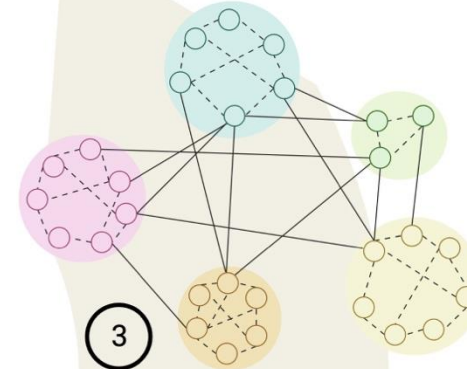
Groups form
social networks.
How are these structured?



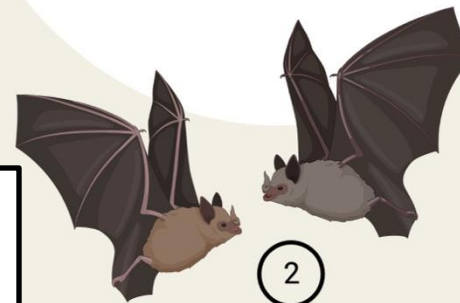
Individual bats can have
social traits.
How do these evolve?



**What are the
consequences?**
... for individuals, evolution,
conservation, disease, etc



Groups form
social networks.
How are these structured?



Pairs can have
social relationships.
How do these form?

Traits → Strategies → Relationships → Networks → Consequences

Traits → Strategies → Relationships → Networks → Consequences



A case study:
food sharing in common vampire bats

Vampire bats often fail on hunts.
They starve to death quickly.

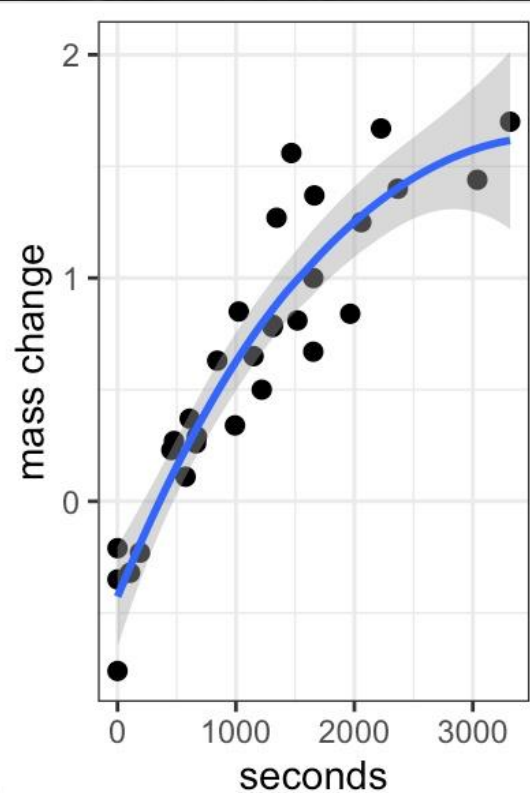


Vampire bats often fail on hunts.
They starve to death quickly.

They depend on food donations
from socially bonded partners

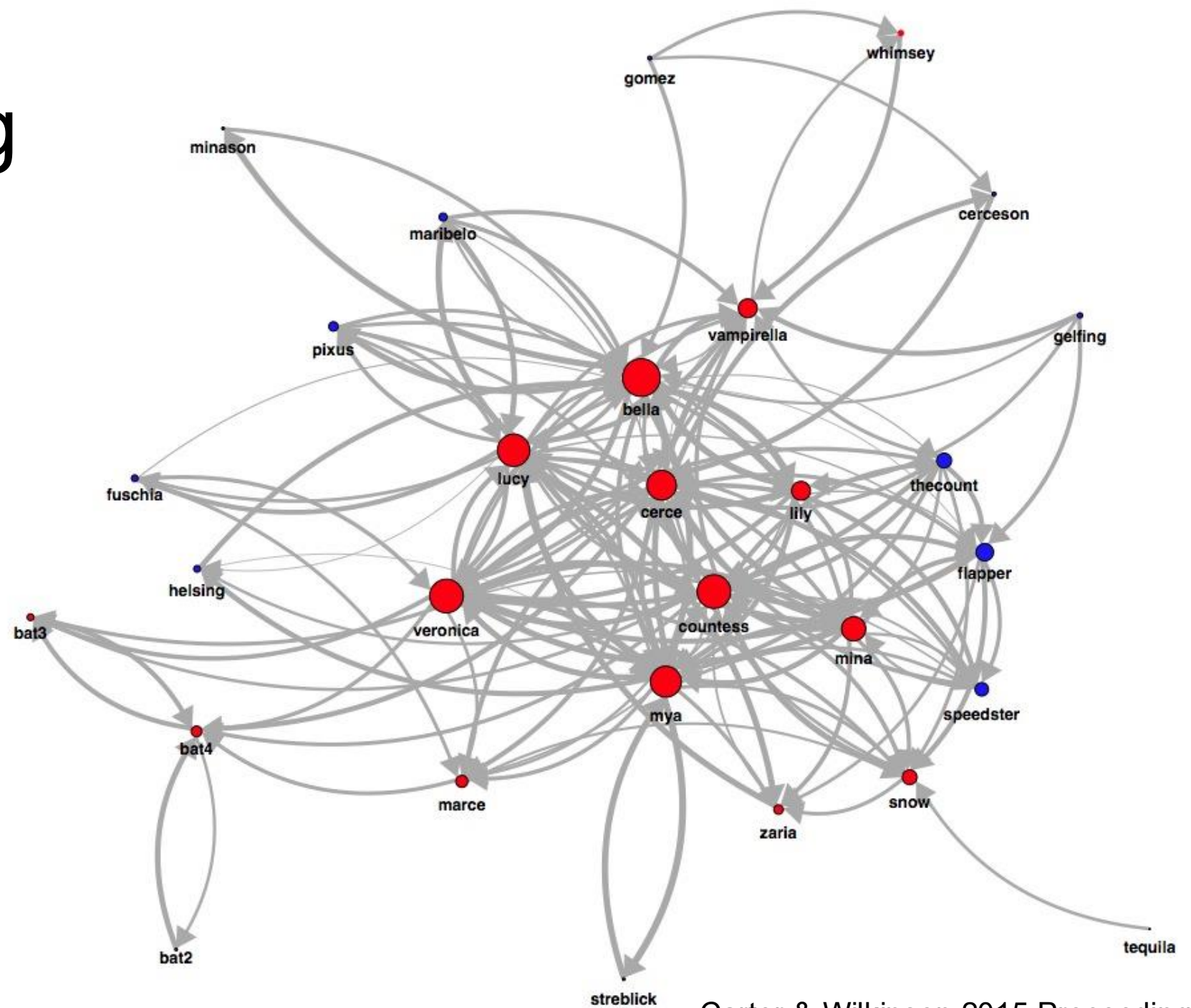


regurgitated
food donation



Food-sharing network

~1300 observations
over 4 years



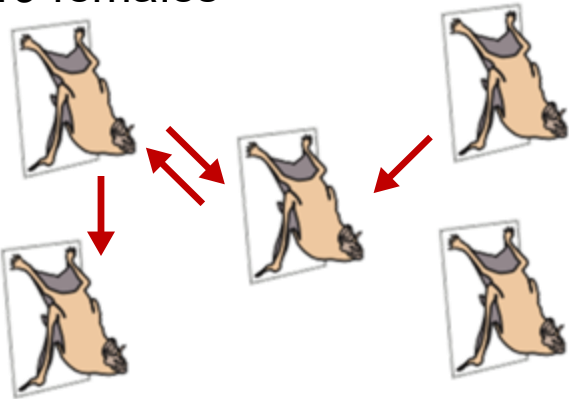


Studying relationship formation

Separate groups

57 fasting trials, 6 months

19 females



2 weeks

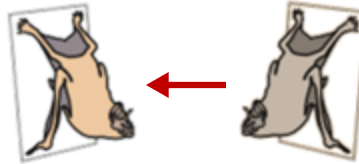
8 females



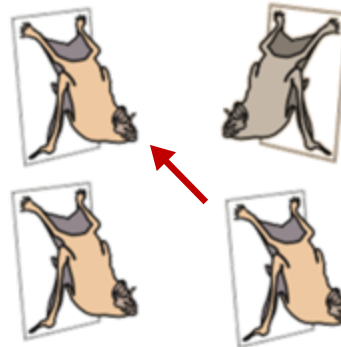
Controlled introductions

106 fasting trials, 93 days

10 pairs

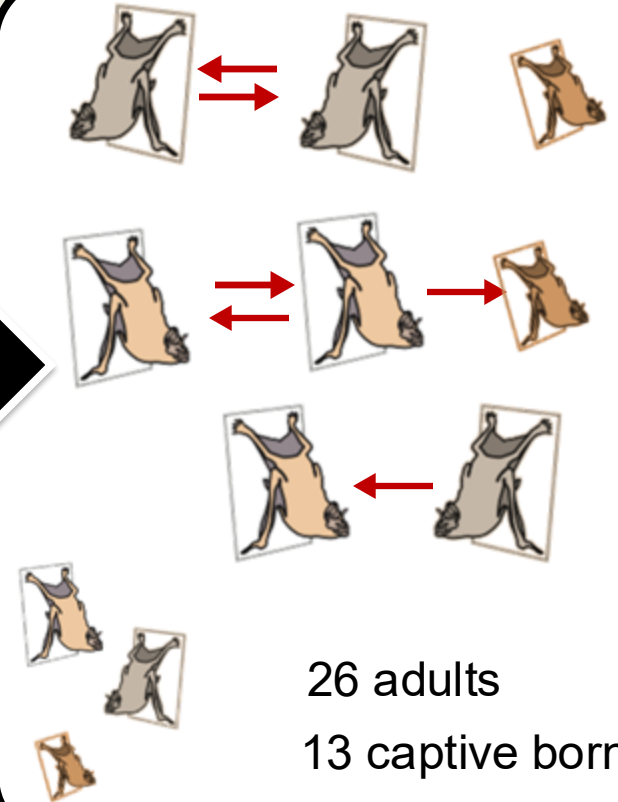


8 quartets



Mixed group

532 fasting trials, 303 days



26 adults
13 captive born

Traits → Strategies → Relationships → Networks → Consequences

Why do vampire bats feed non-kin?

Traits → Strategies → Relationships → Networks → Consequences



Traits → Strategies → Relationships → Networks → Consequences



Prolonged maternal care

7 months of gestation!

10 months of nursing!

29.5 year longevity!

social grooming



among bats, **vampire bats** are exceptional social groomers

Myotis bechsteinii

~0.1% from Kerth et al. 2003



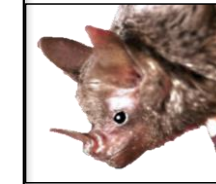
Artibeus

0.5%



Carollia

0.1%



Desmodus

3.7%



Eidolon

0.3%



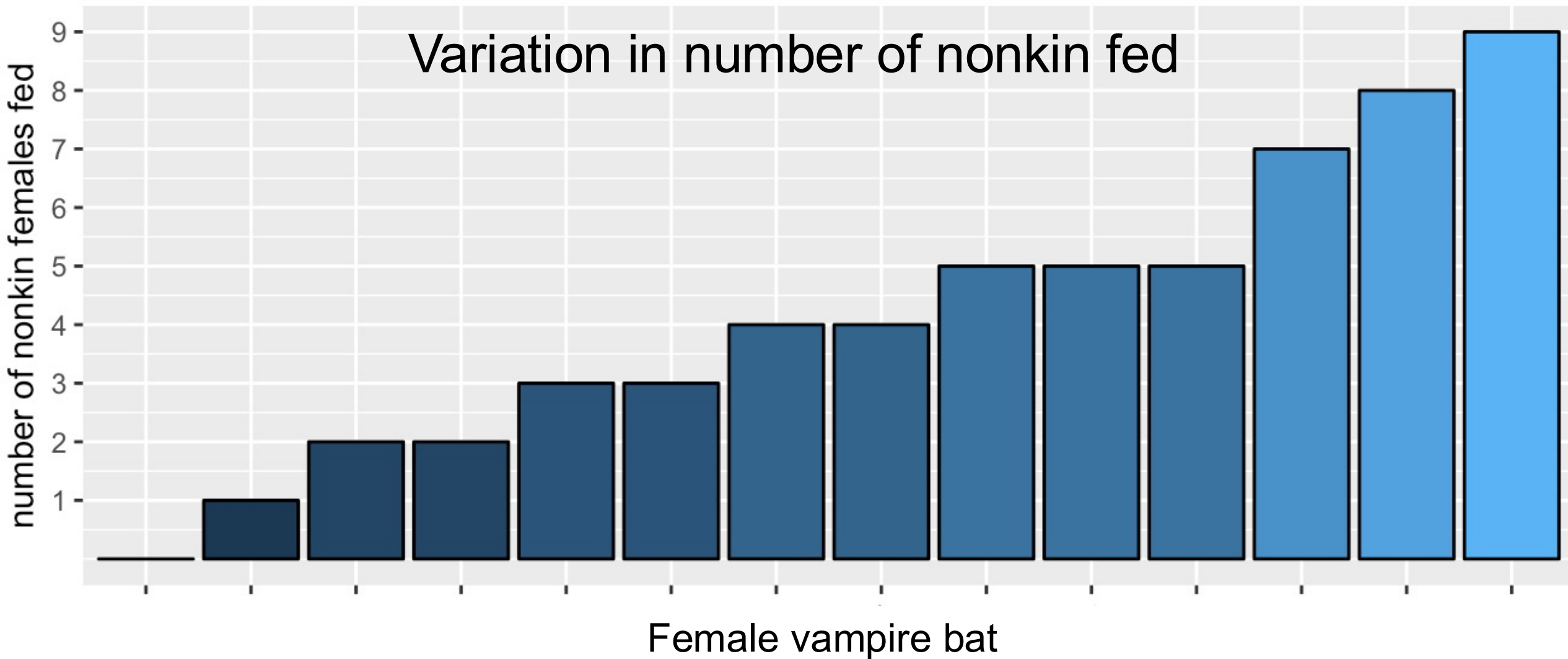
Rousettus

0.1%



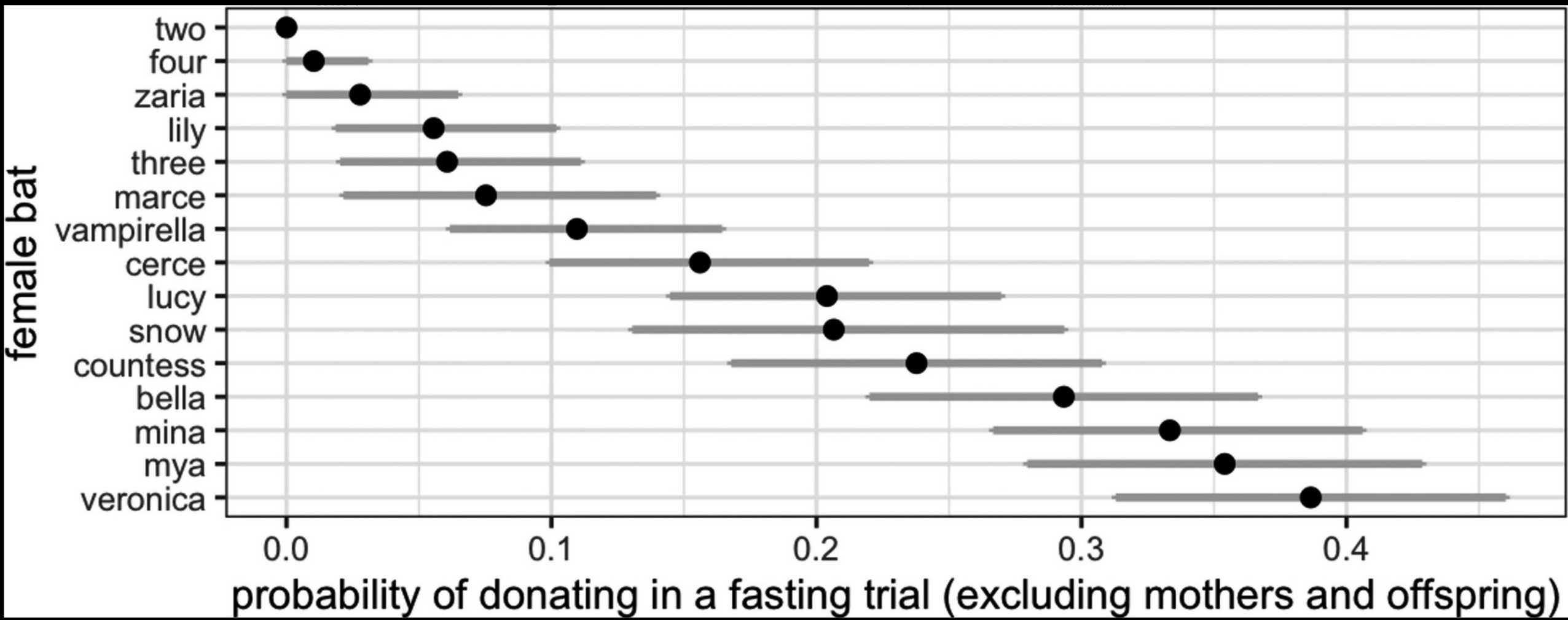
time spent allogrooming (%)

Traits → Strategies → Relationships → Networks → Consequences



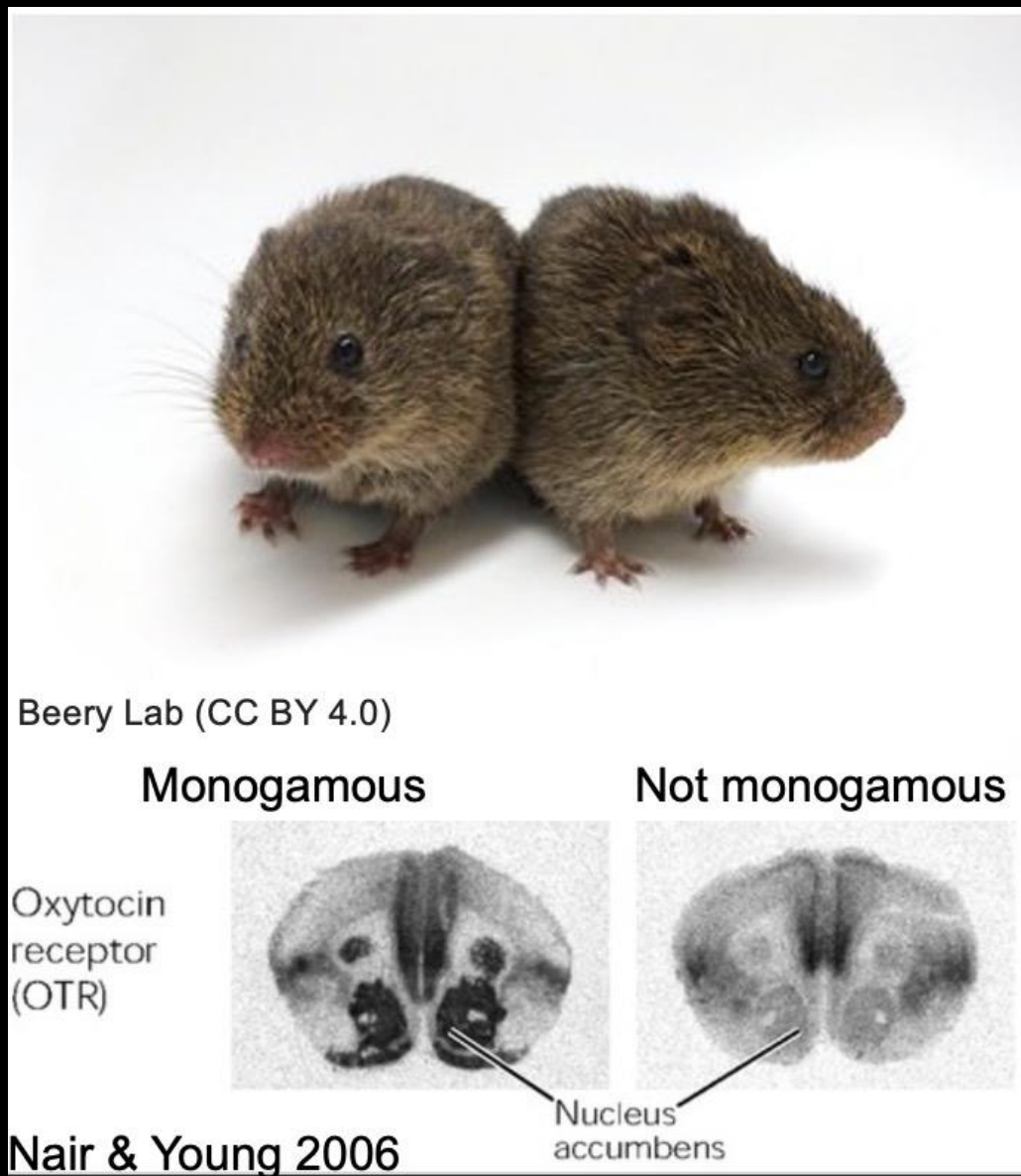
Traits → Strategies → Relationships → Networks → Consequences

Variation in “cooperativeness”



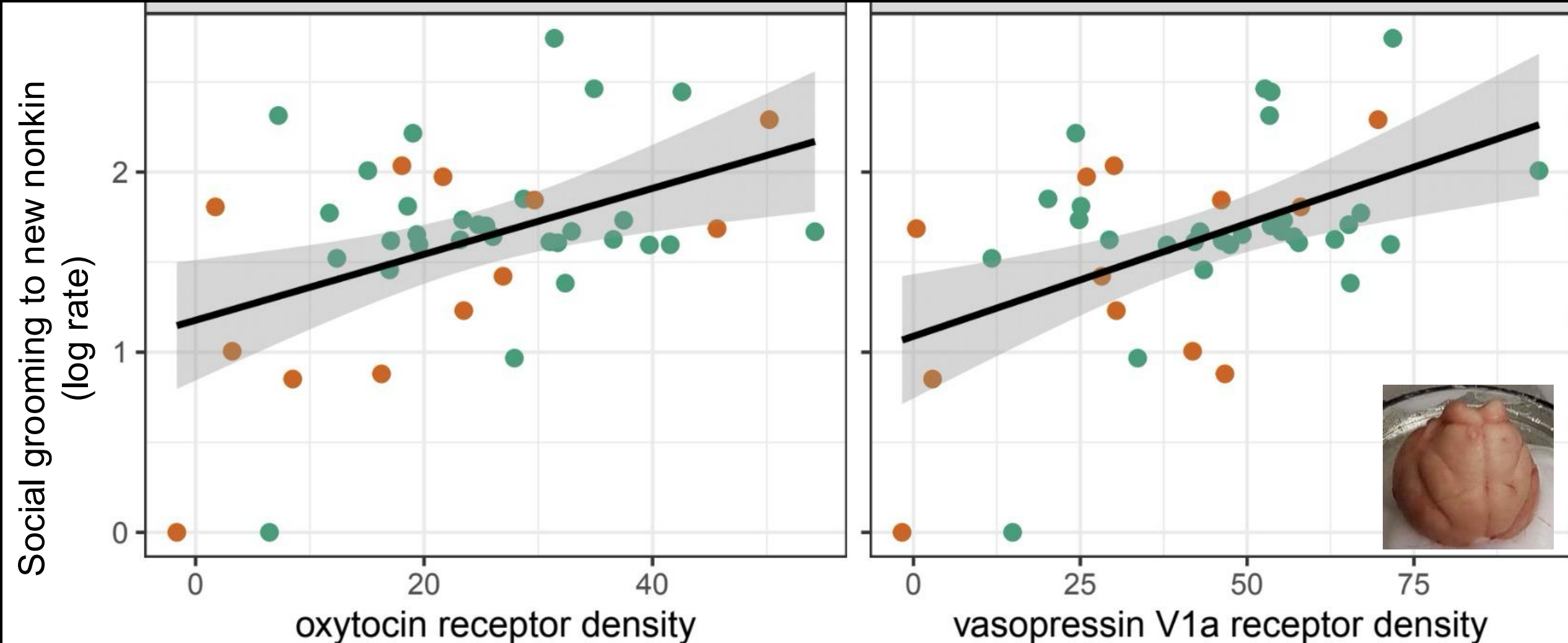
Traits → Strategies → Relationships → Networks → Consequences

Variation in the
“social brain”



Traits → Strategies → Relationships → Networks → Consequences

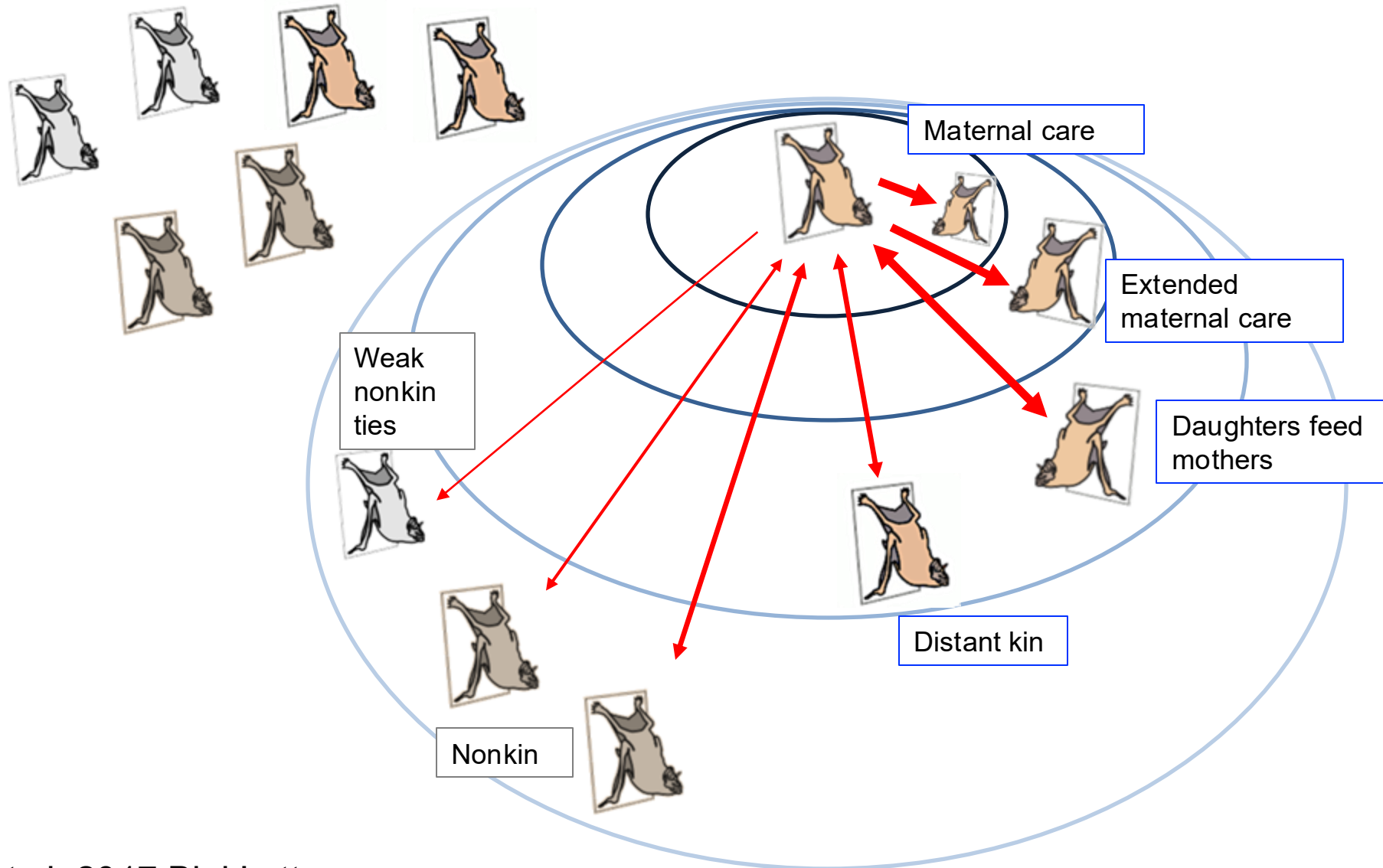
Oxytocin and vasopressin receptors in the vampire bat nucleus accumbens predict nonkin social bonding



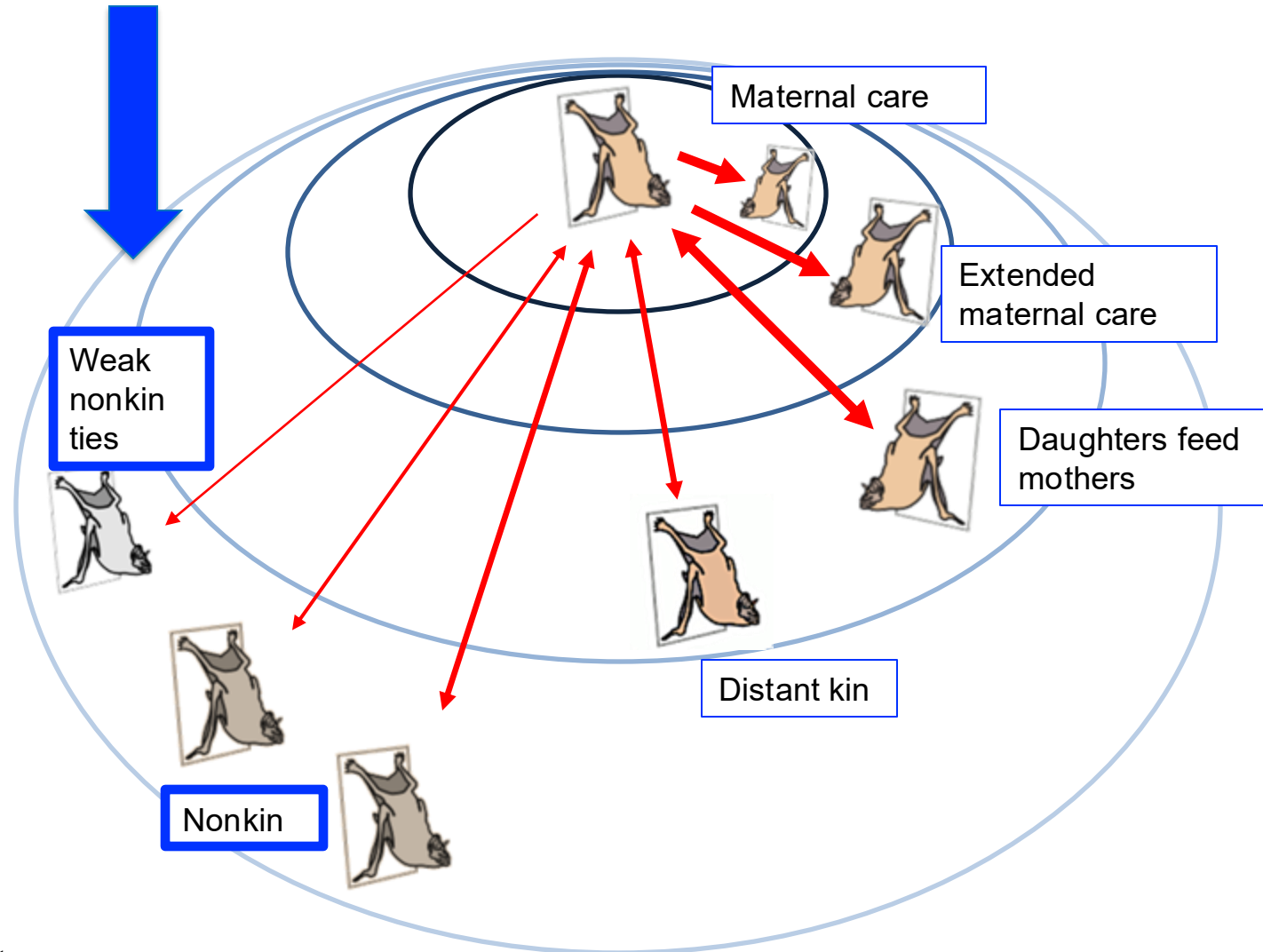
Traits → **Strategies** → Relationships → Networks → Consequences



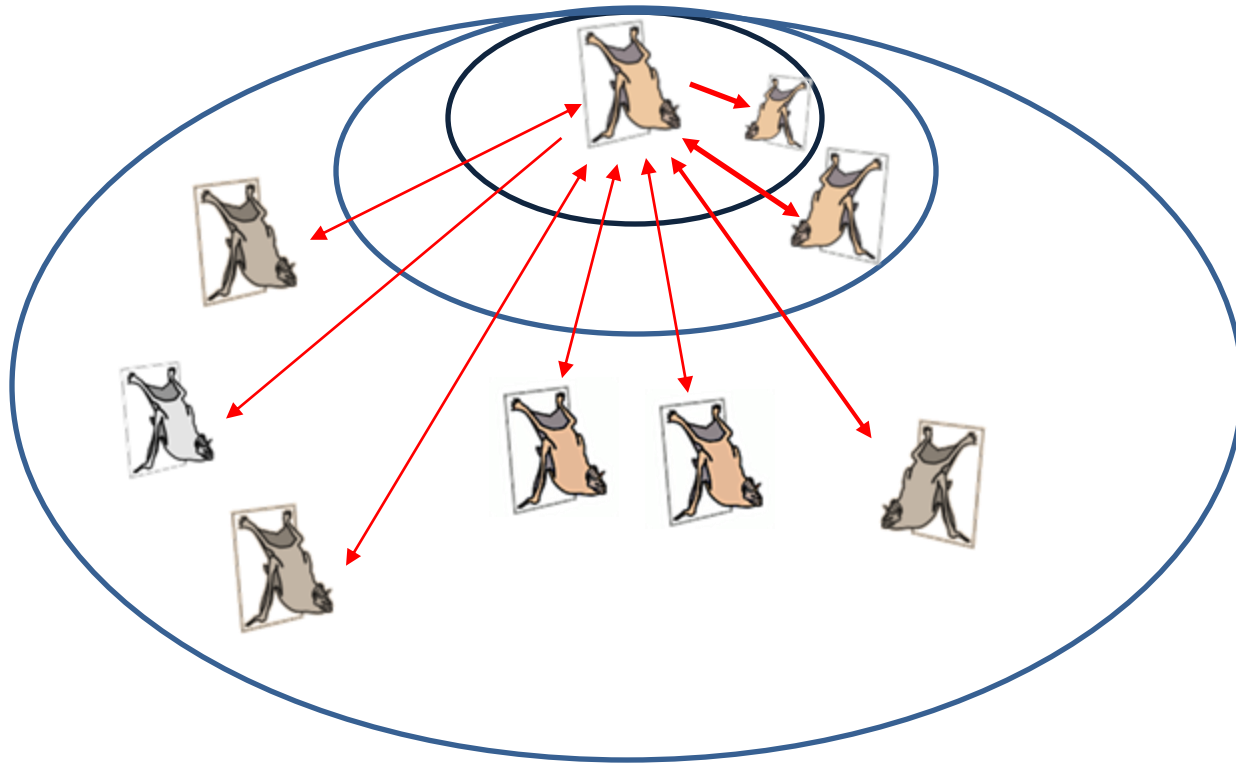
Helping is a *cooperative investment*.



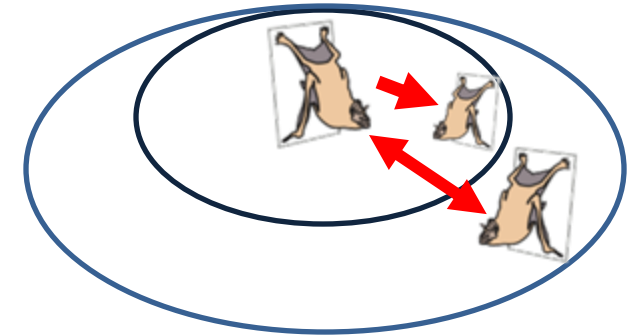
If you already have strong kin bonds, why form new weak nonkin bonds?



Which is better: quantity or quality?

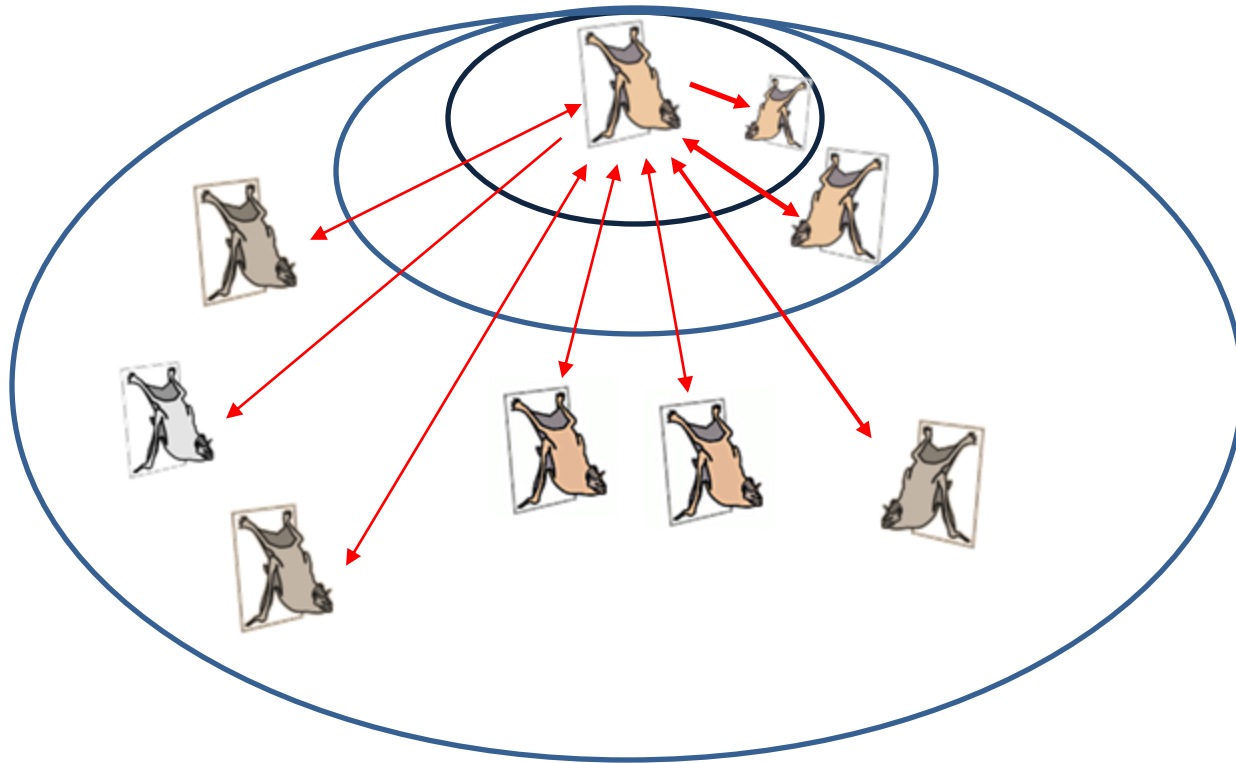


“Quantity”
More nonkin bonds

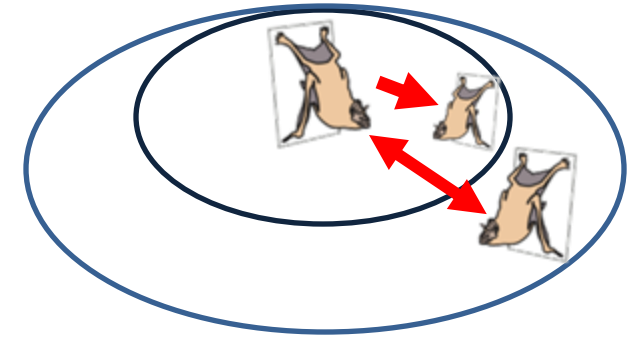


“Quality”
Fewer stronger bonds

“Social bet-hedging” = bats diversify cooperative investments across multiple partners because each partner’s availability is uncertain



“Quantity”
More nonkin bonds



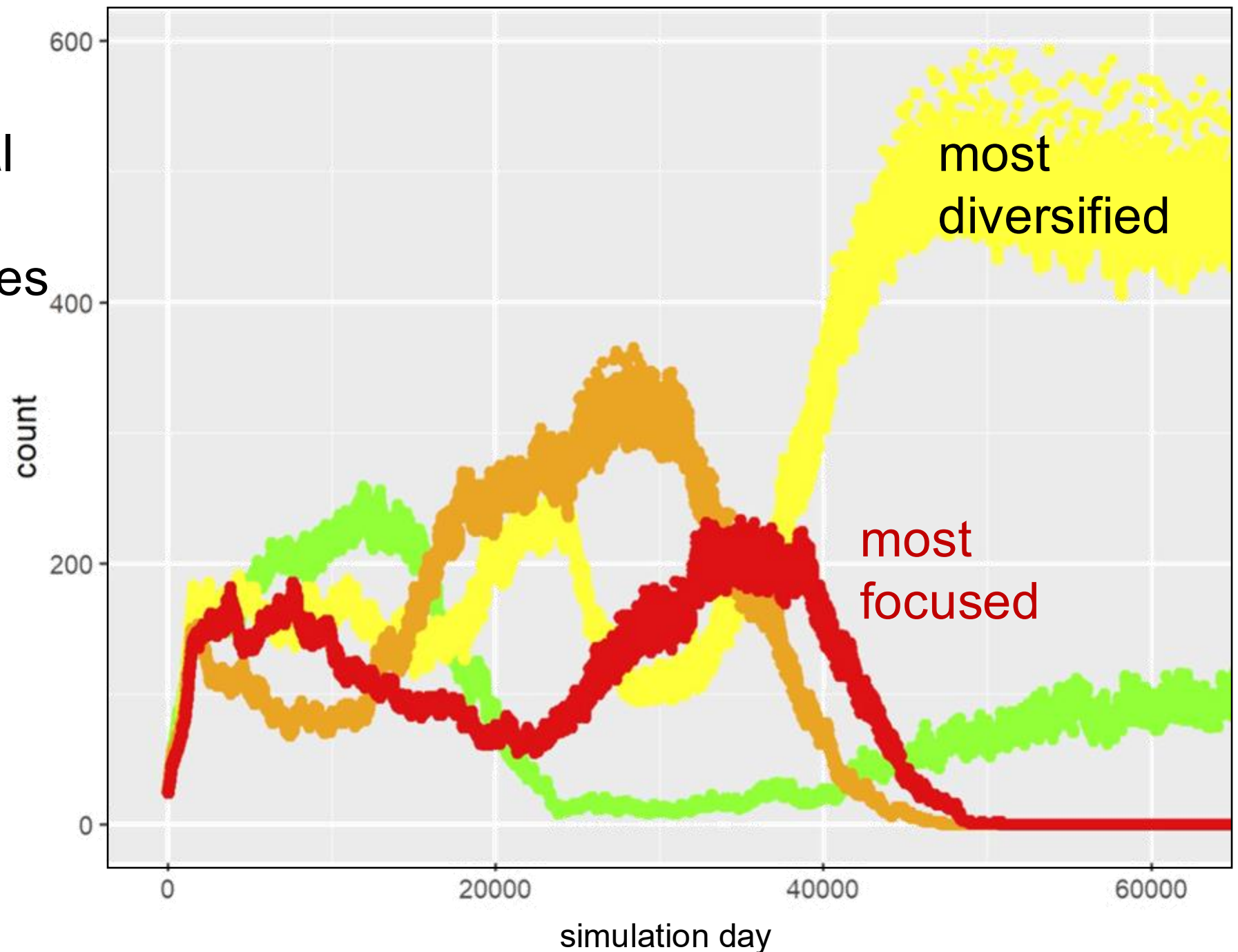
“Quality”
Fewer stronger bonds

Bats that help more nonkin cope
better with partner removal.

Carter et al. 2017 Biol Letters



Agent-based
simulations of social
evolution show that
diversifying strategies
are selected under
social uncertainty



Traits → Strategies → Relationships → Networks → Consequences



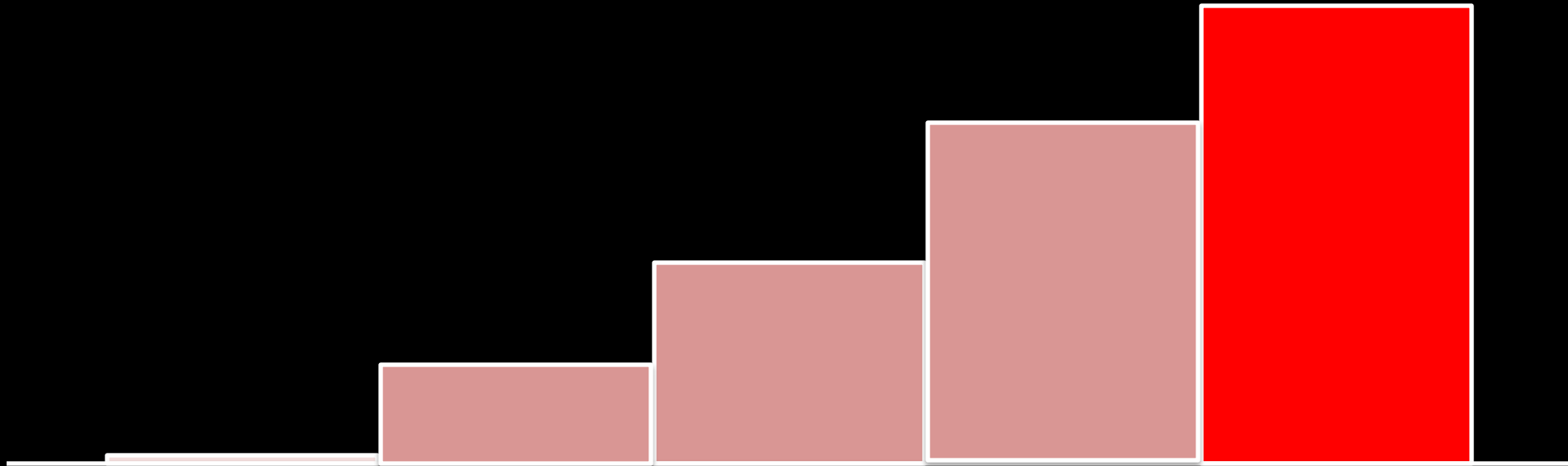
Bats form new relationships outside their matriline (family)
because matriline are too small to fully support them.

But how do bats form new relationships?

“Raising the stakes” or “Testing the waters”

a cooperative strategy for developing new cooperative relationships

Clustering (no cost) → Grooming (low cost) → Food sharing (high cost)



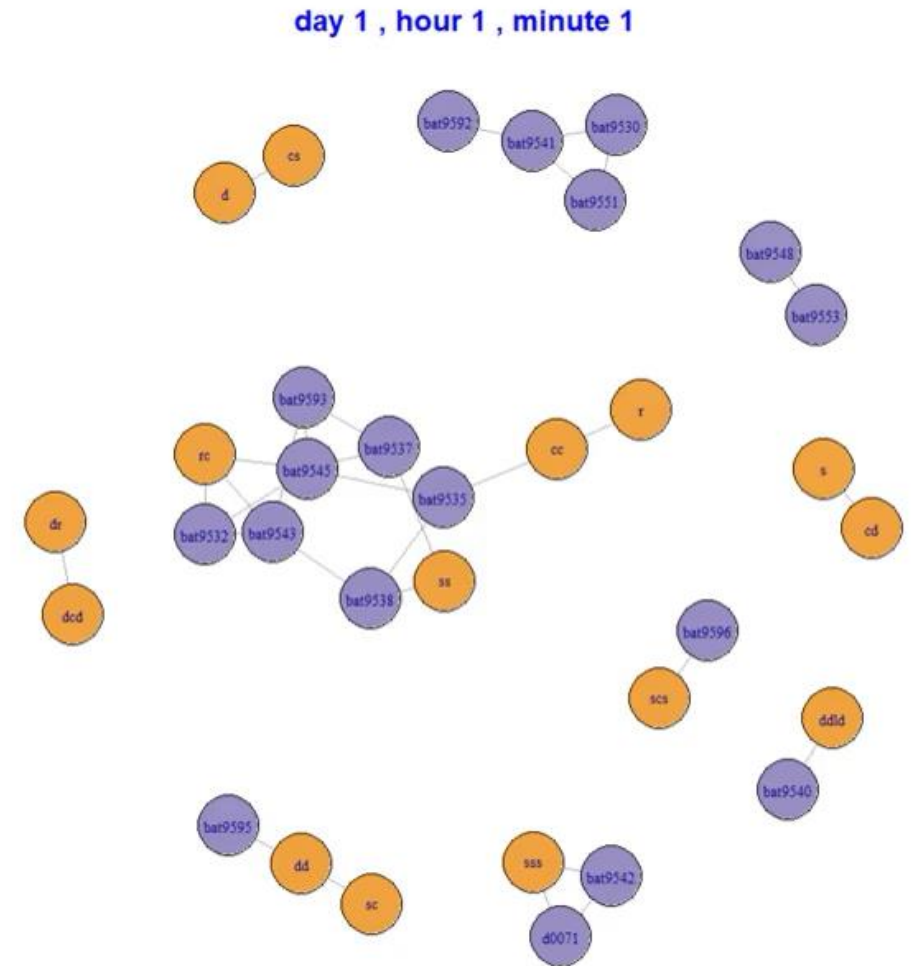
Traits → Strategies → Relationships → **Networks** → Consequences



Traits → Strategies → Relationships → **Networks** → Consequences



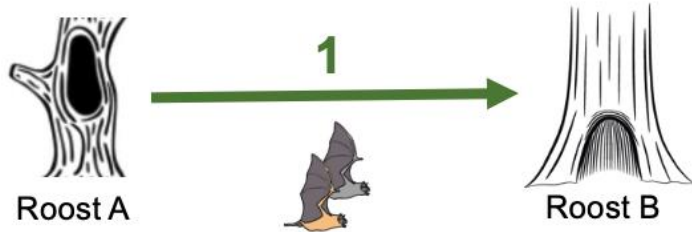
Ripperger*, Carter* et al. 2019 Current Biology
Ripperger et al. 2020 PLOS Biology
Ripperger & Carter 2021 PLOS Biology



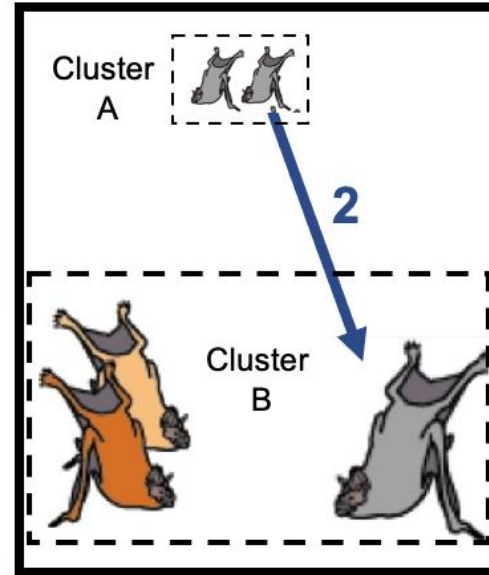
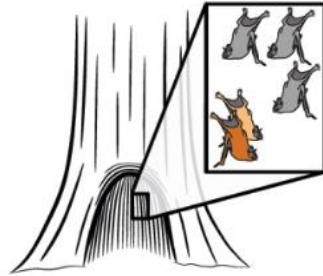
Test group
Control group

Social networks are shaped by nested scales of movement

Roost sharing
and switching

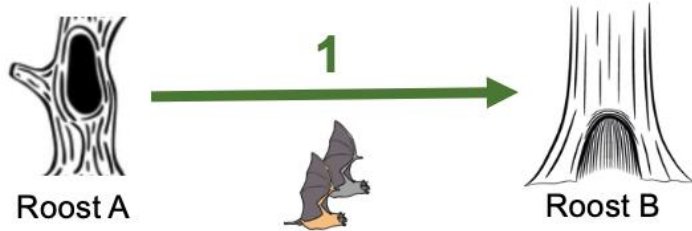


Clustering
and cluster
switching

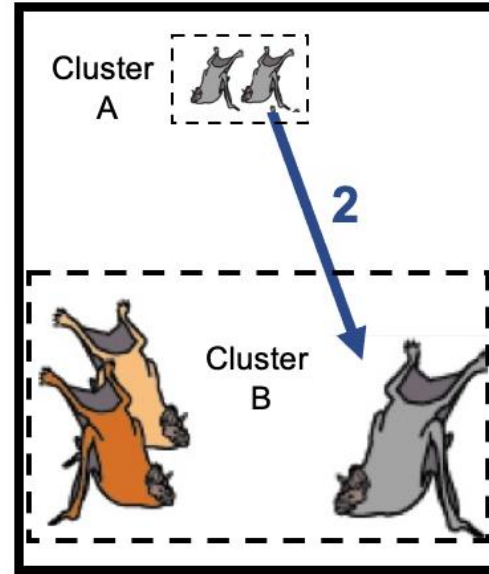
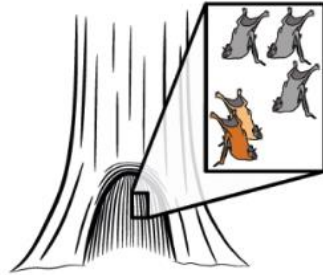


Social networks are shaped by nested scales of movement

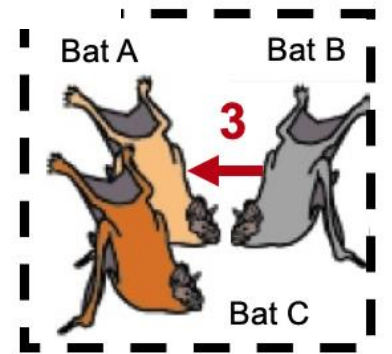
Roost sharing
and switching



Clustering
and cluster
switching

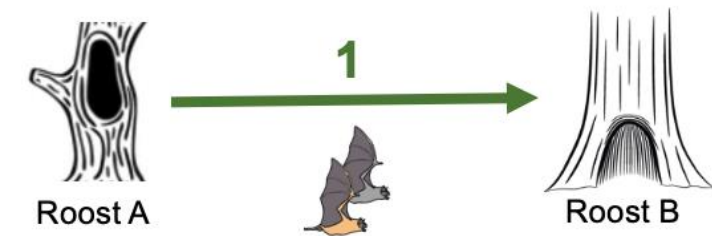


Choosing
interaction
partner

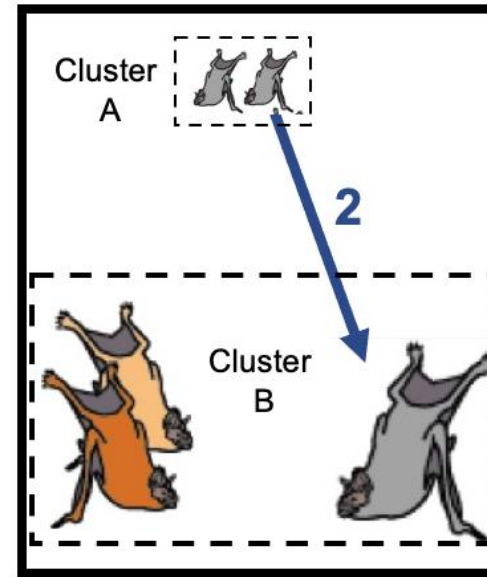
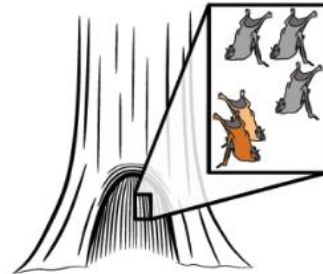


Social networks are shaped by nested scales of movement

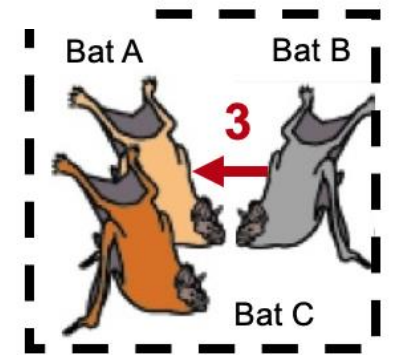
Roost sharing and switching



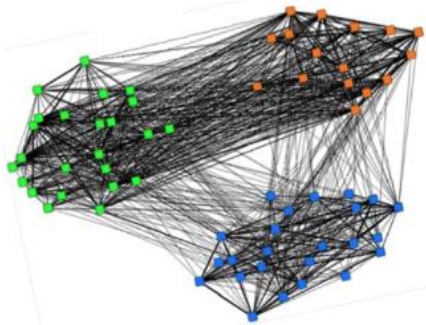
Clustering and cluster switching



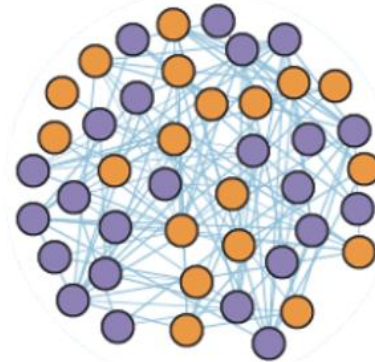
Choosing interaction partner



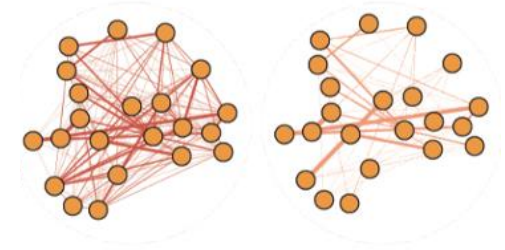
Co-roosting



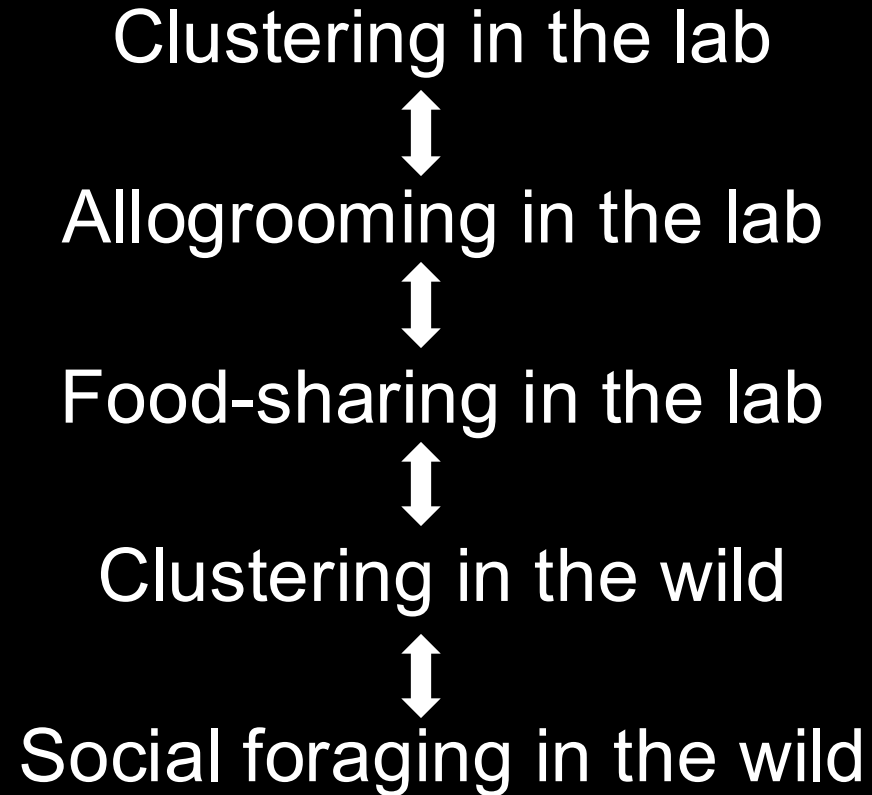
Close proximity



Cooperative behavior

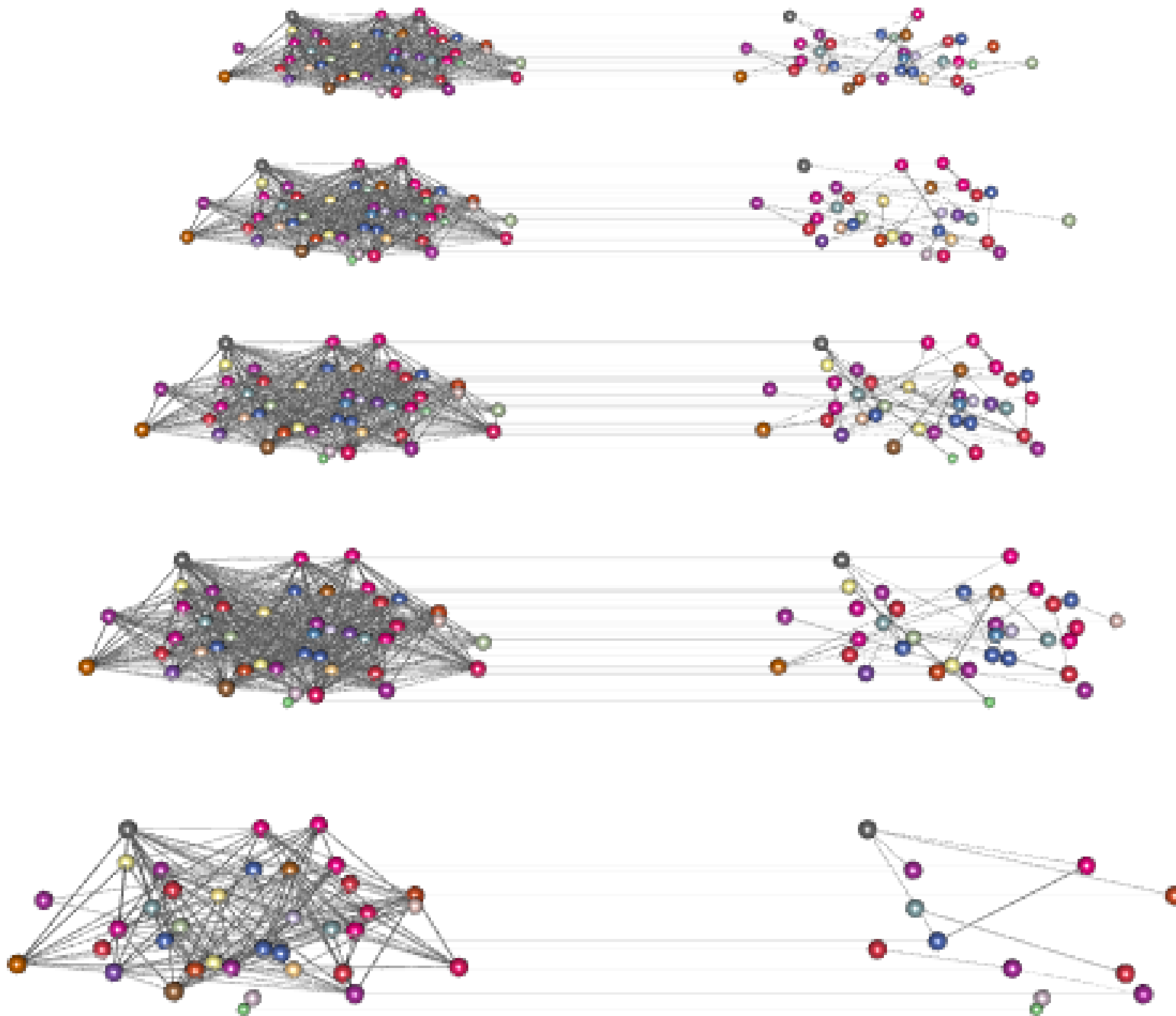


Relationships and networks persist across context



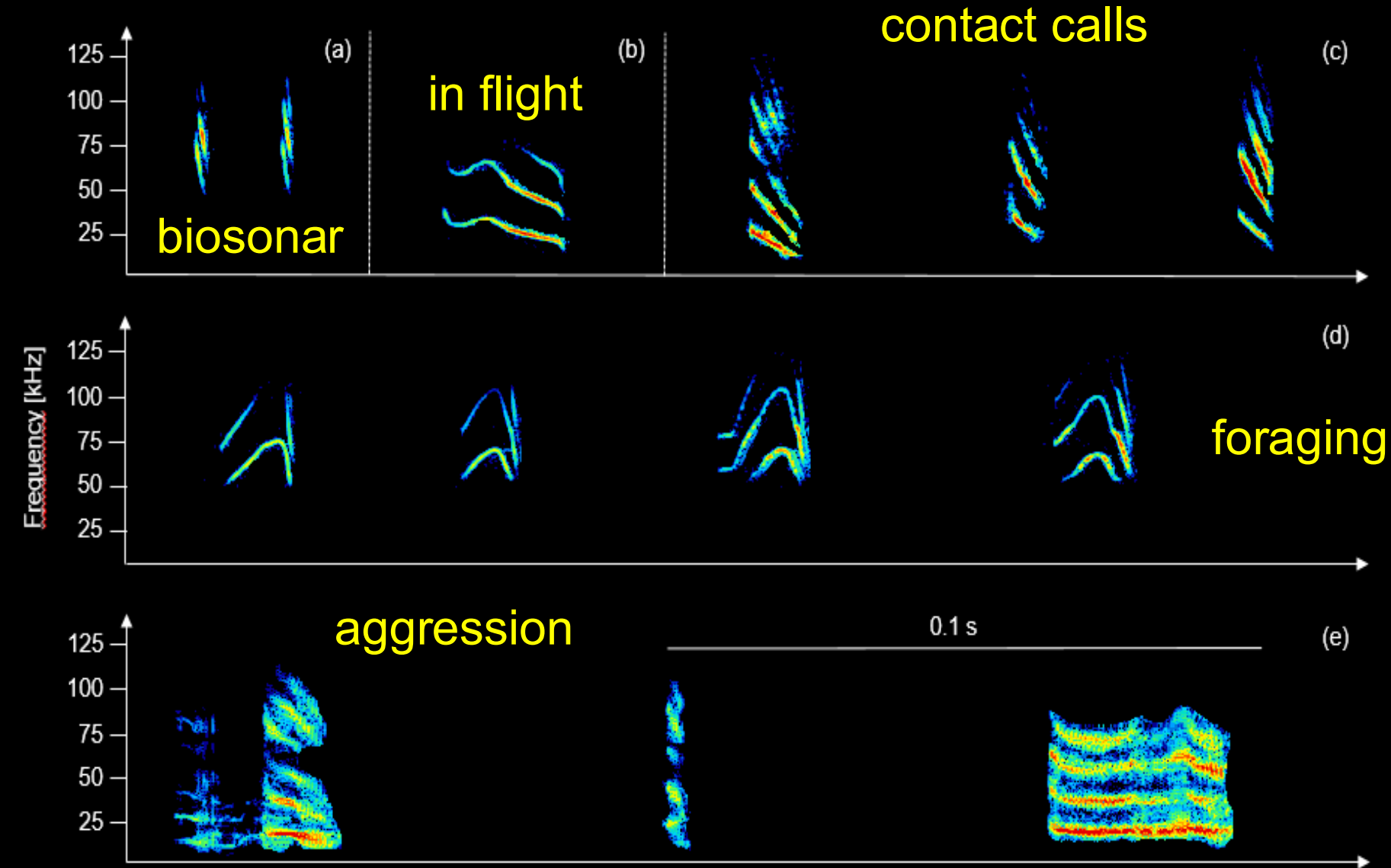
Inside
hollow
tree

Outside
roost on
cattle
pasture





Calls made during social foraging

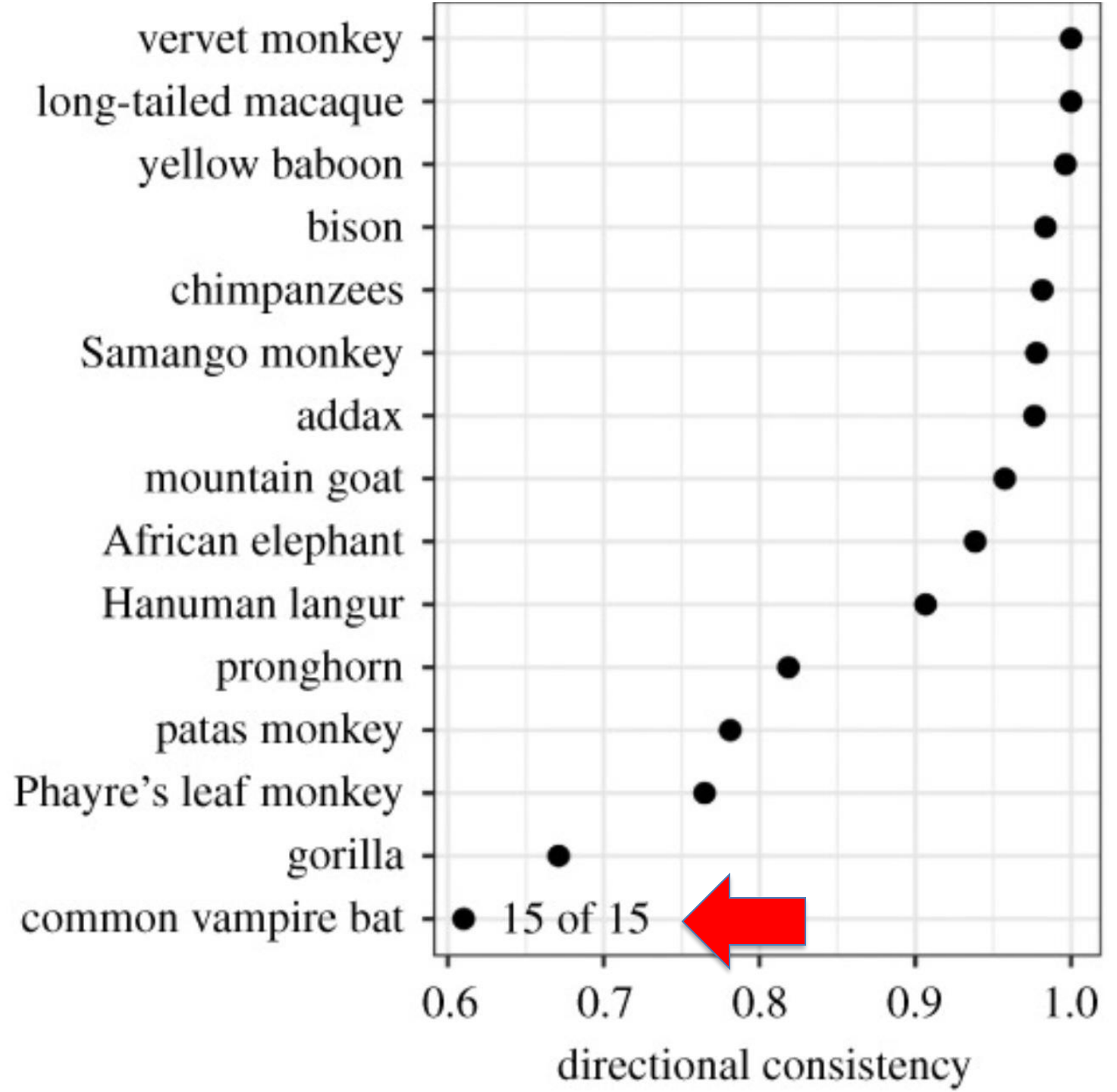


Traits → Strategies → Relationships → Networks → Consequences

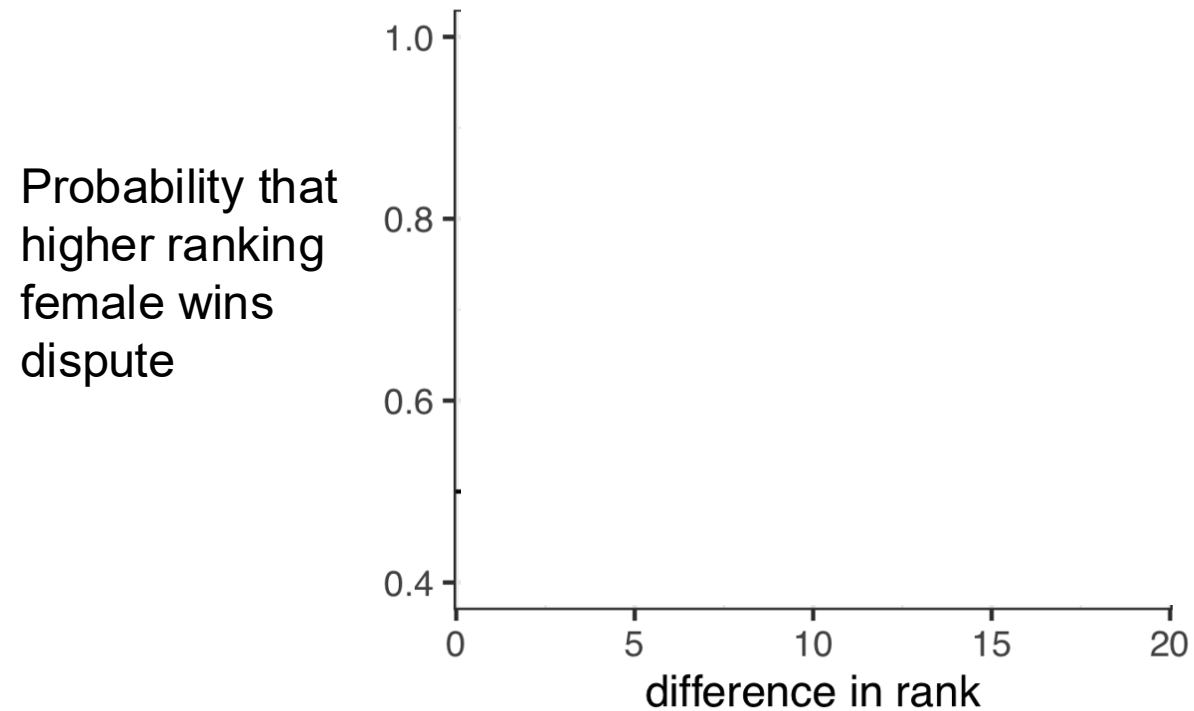


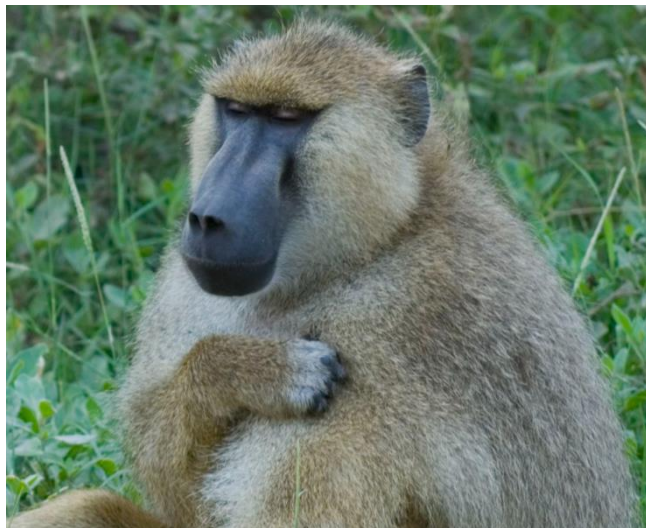
What about dominance hierarchies?

Female vampires
lack a strong
dominance
hierarchy relative
to other mammals



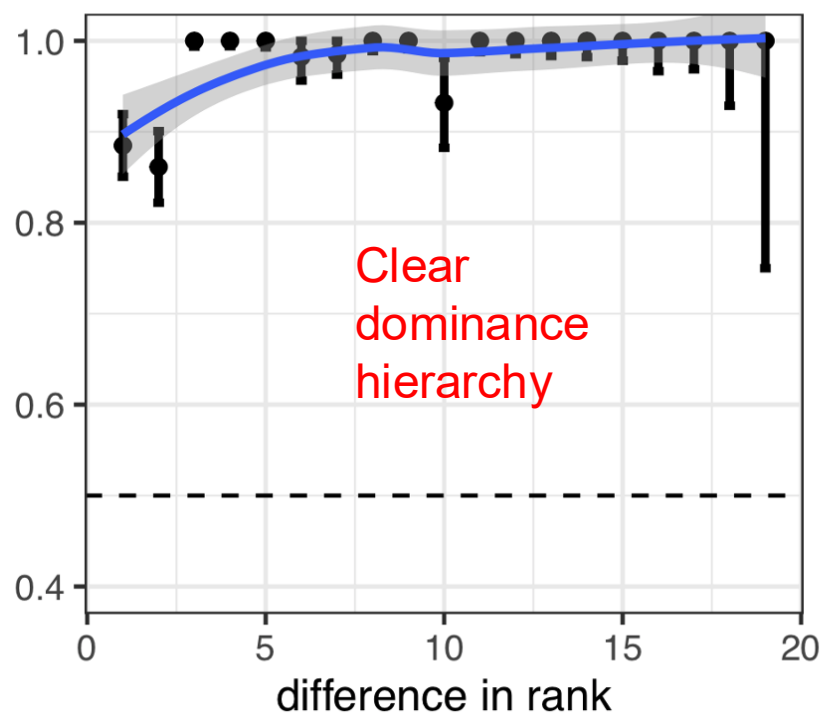
Visualizing a dominance hierarchy

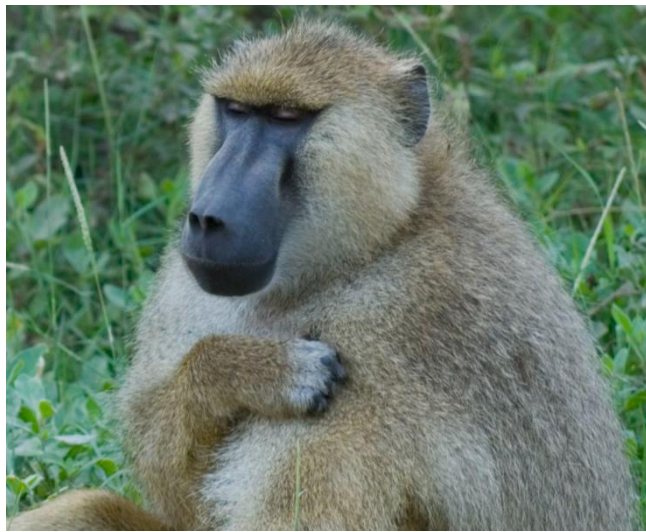




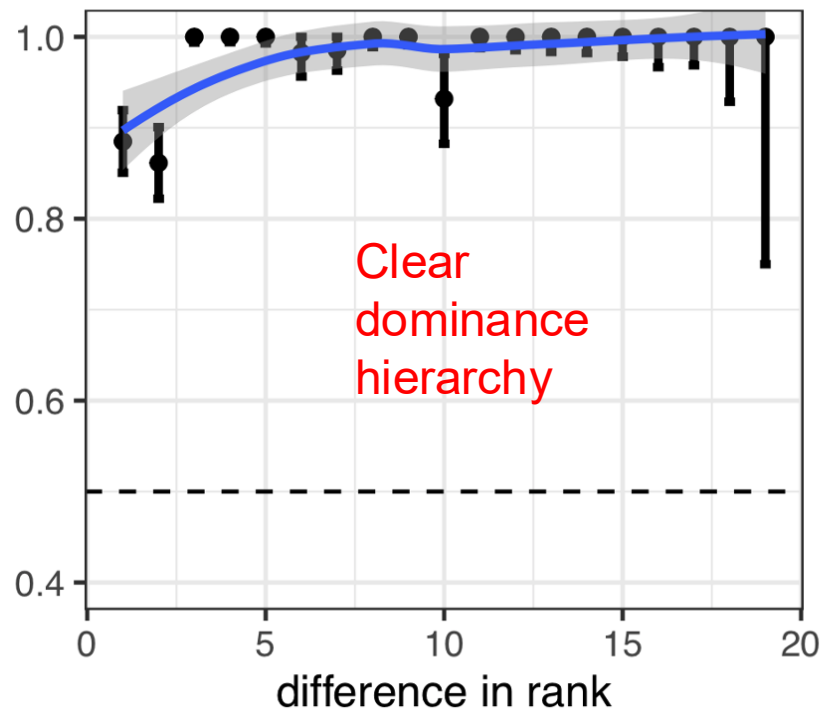
female yellow baboons

Probability that
higher ranking
female wins
dispute

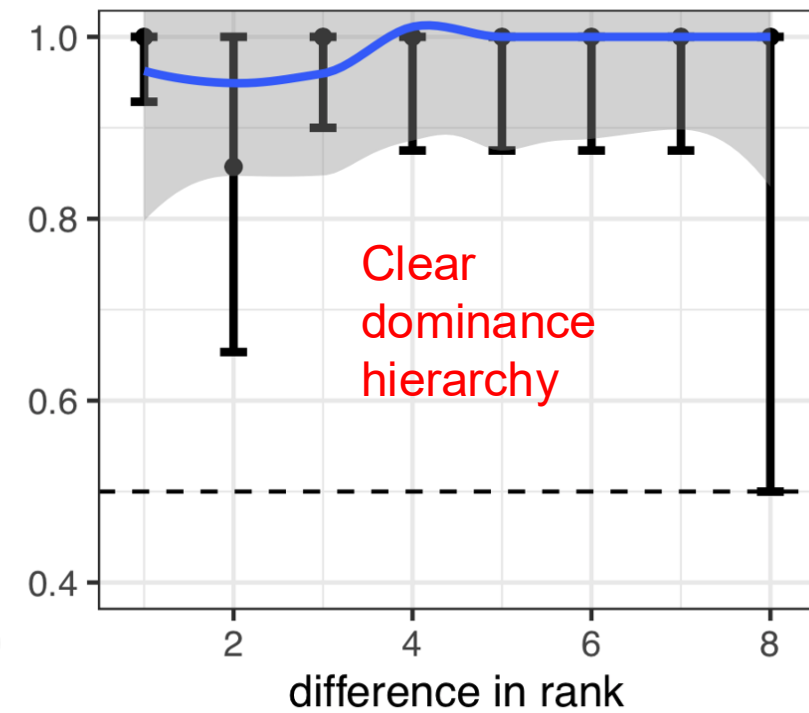




female yellow baboons

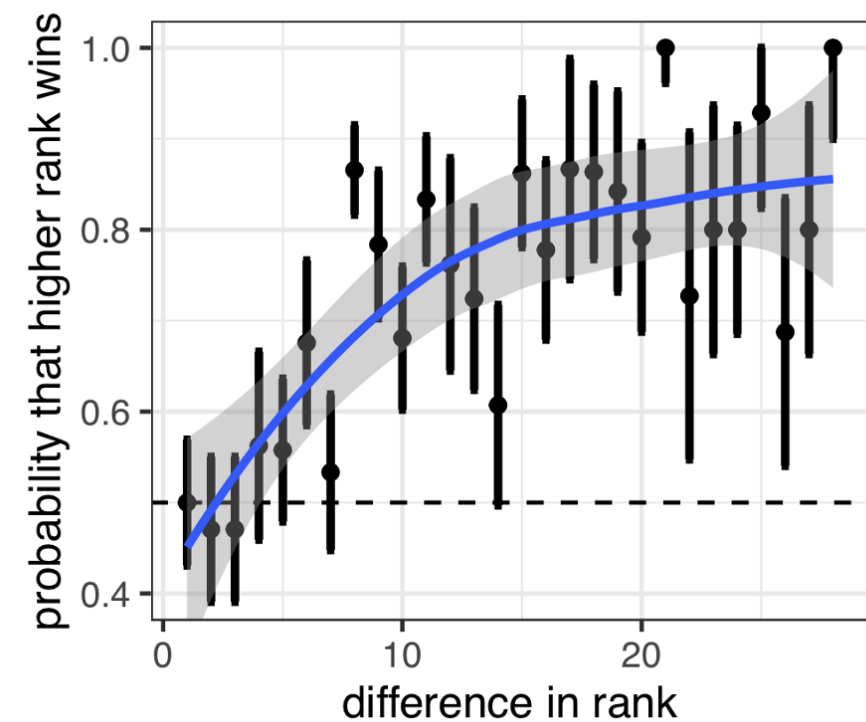


female long-tailed macaques

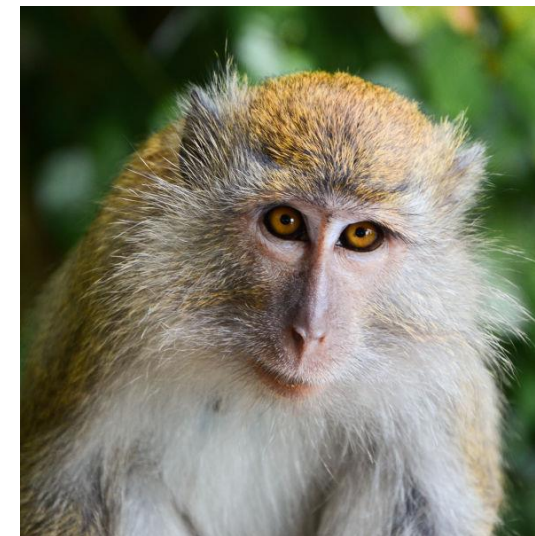
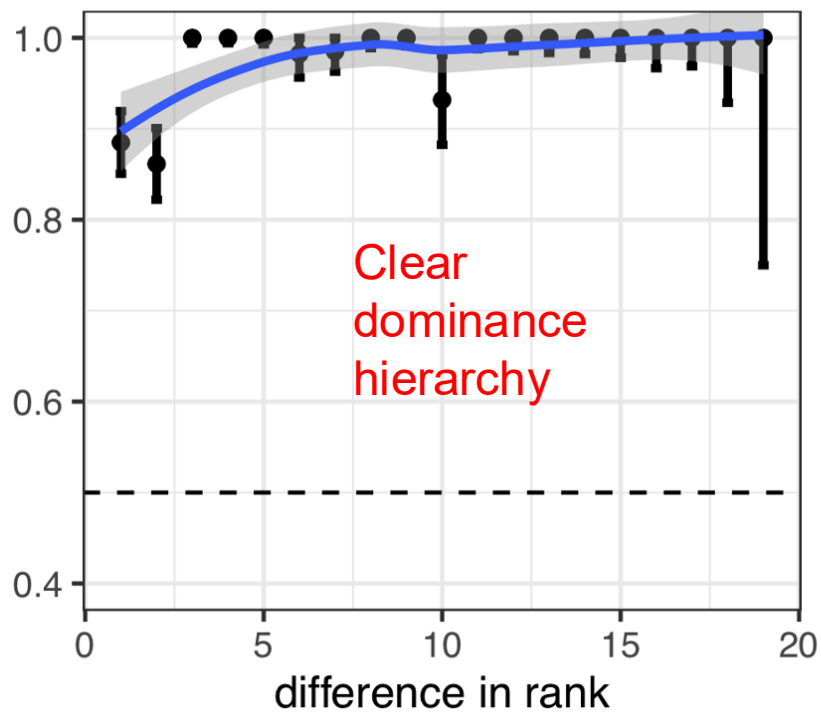




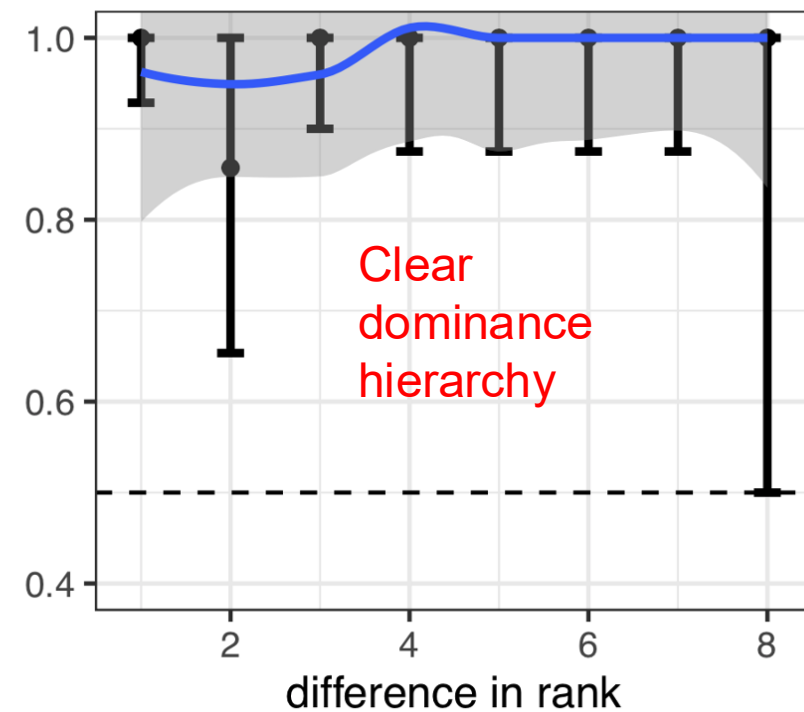
female vampire bats



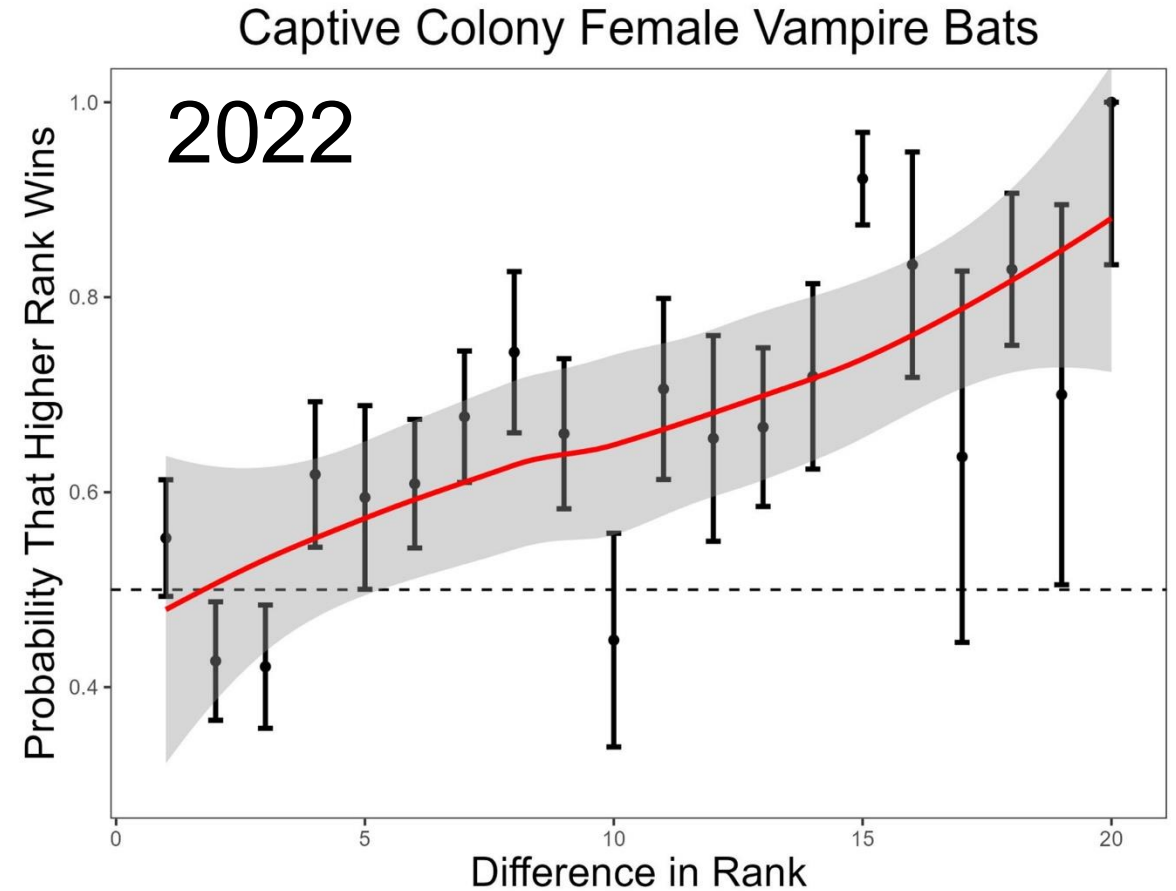
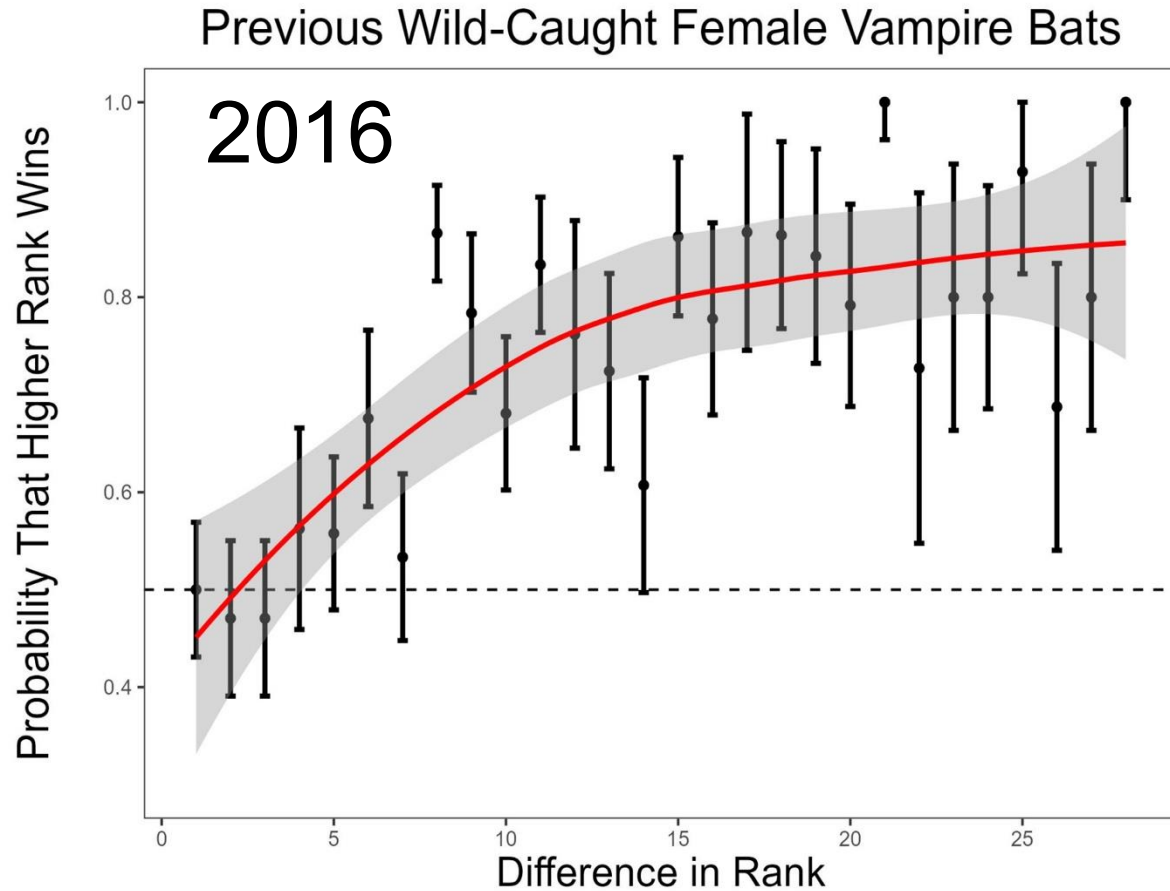
female yellow baboons



female long-tailed macaques



How well does social structure replicate across groups?



Traits → Strategies → Relationships → Networks → **Consequences**



Traits → Strategies → Relationships → Networks → Consequences

An example of social evolution feedbacks



Only some bats share food
and reciprocate.



Individual variation in helping
results from mutation, migration,
and behavioral flexibility.

Traits → Strategies → Relationships → Networks → Consequences

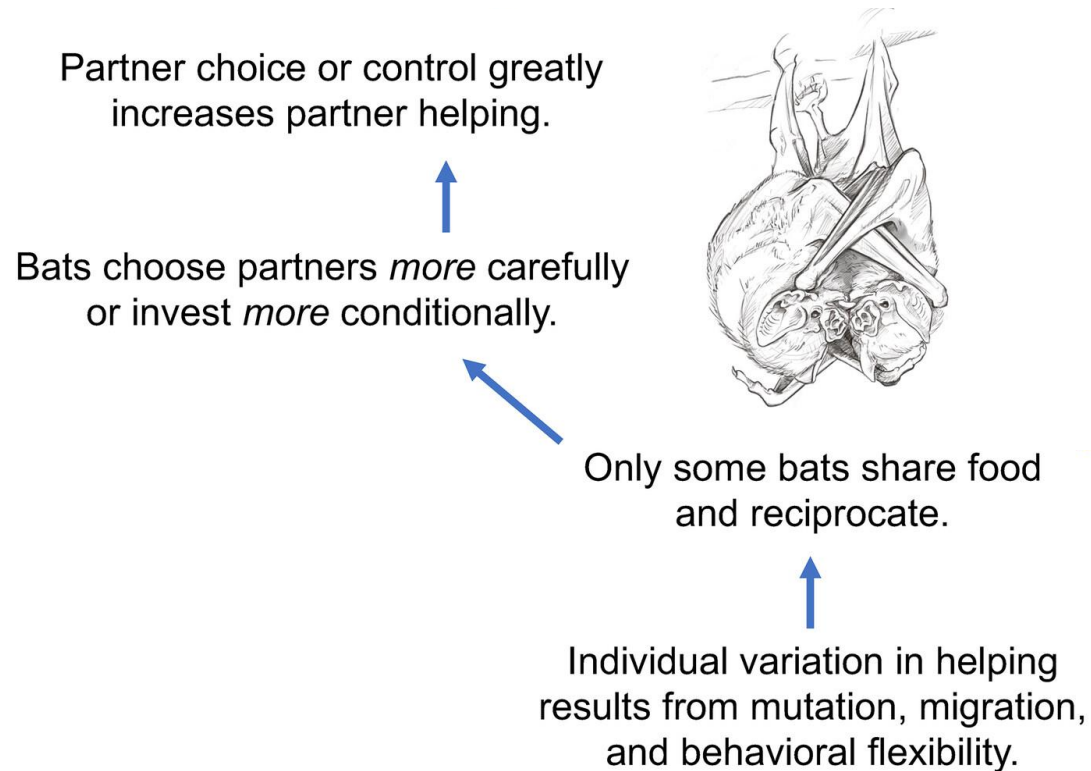
Bats choose partners *more* carefully
or invest *more* conditionally.



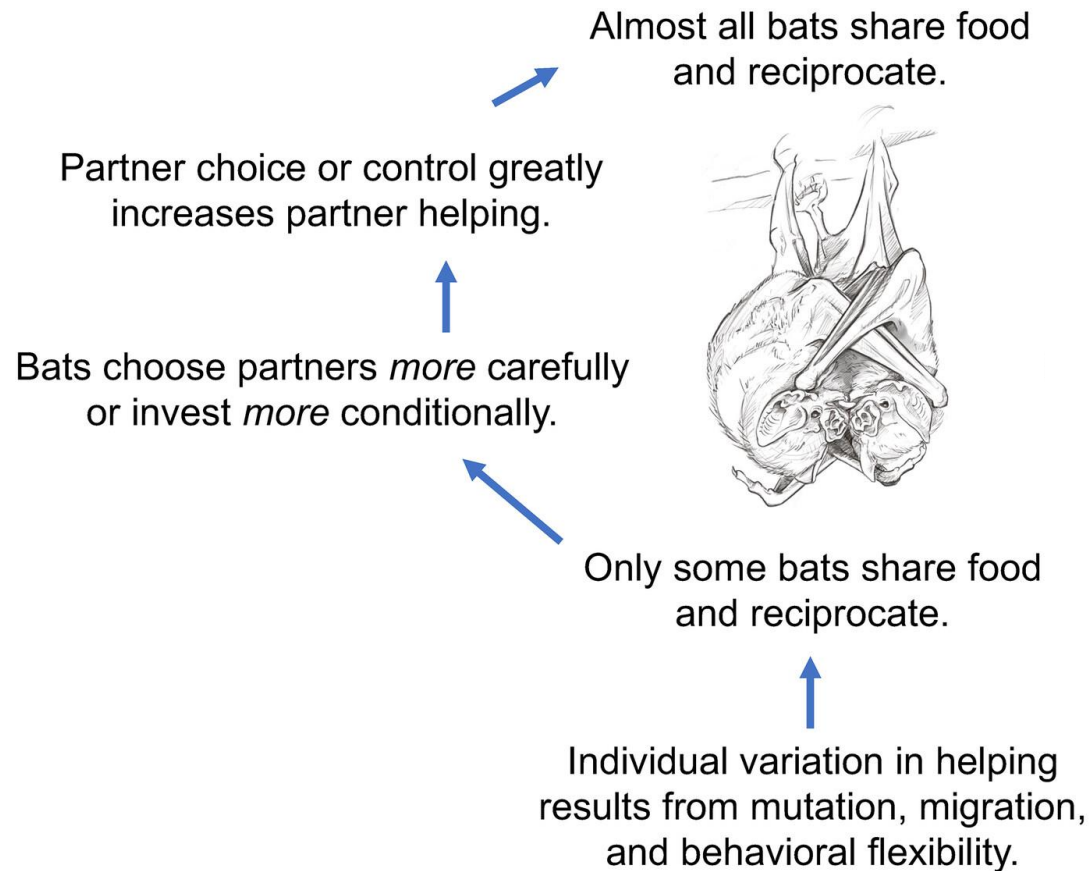
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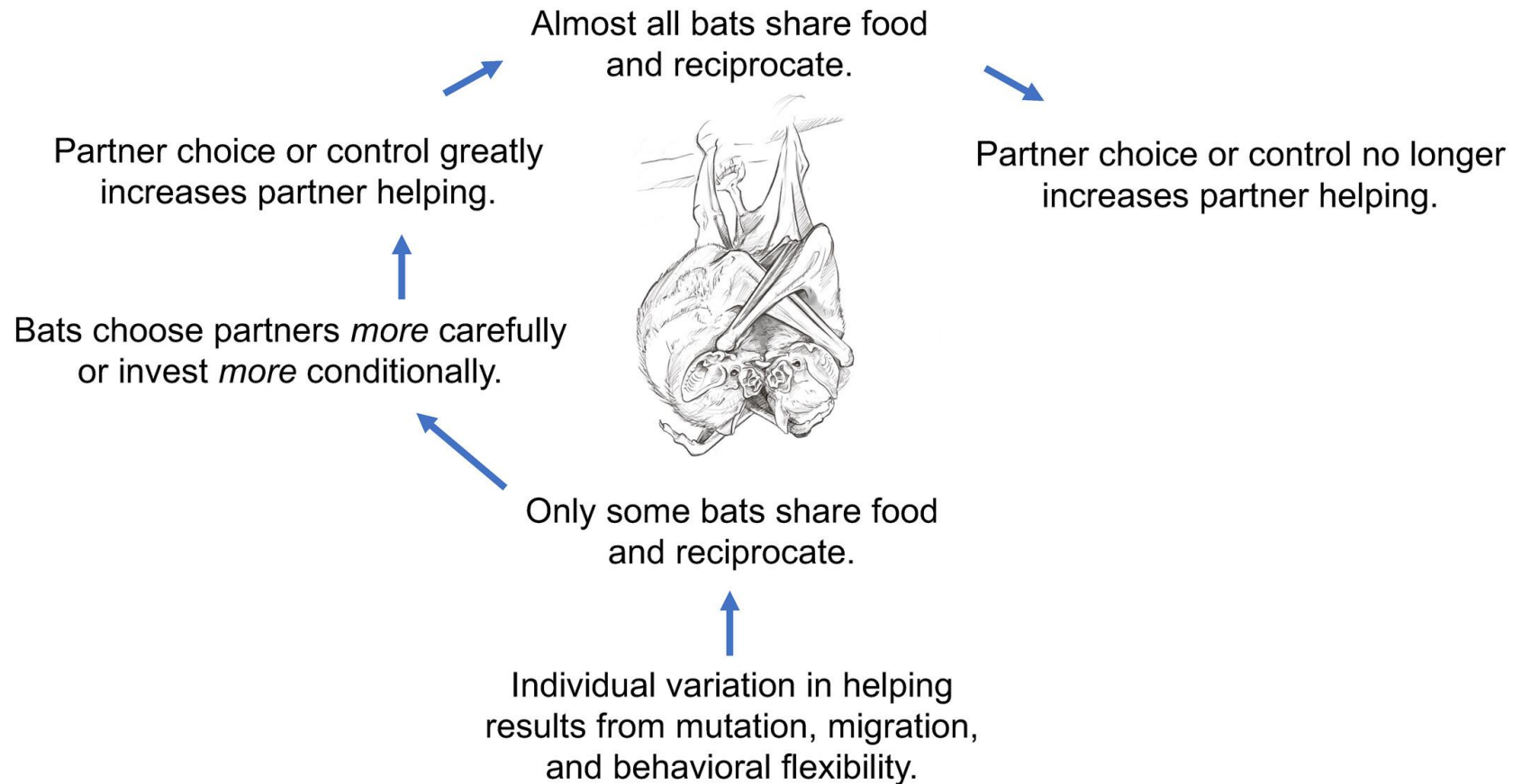
Traits → Strategies → Relationships → Networks → Consequences



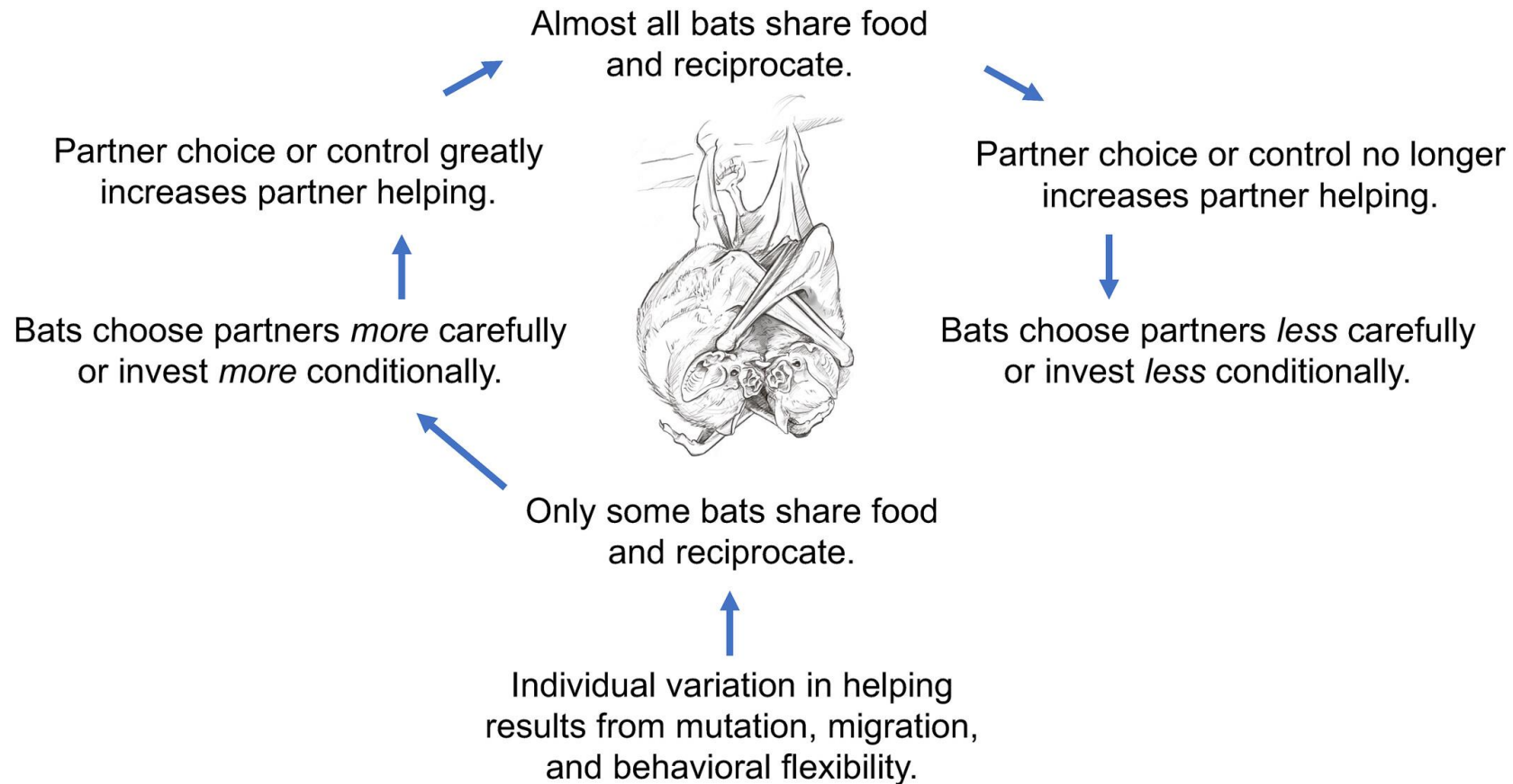
Traits → Strategies → Relationships → Networks → Consequences



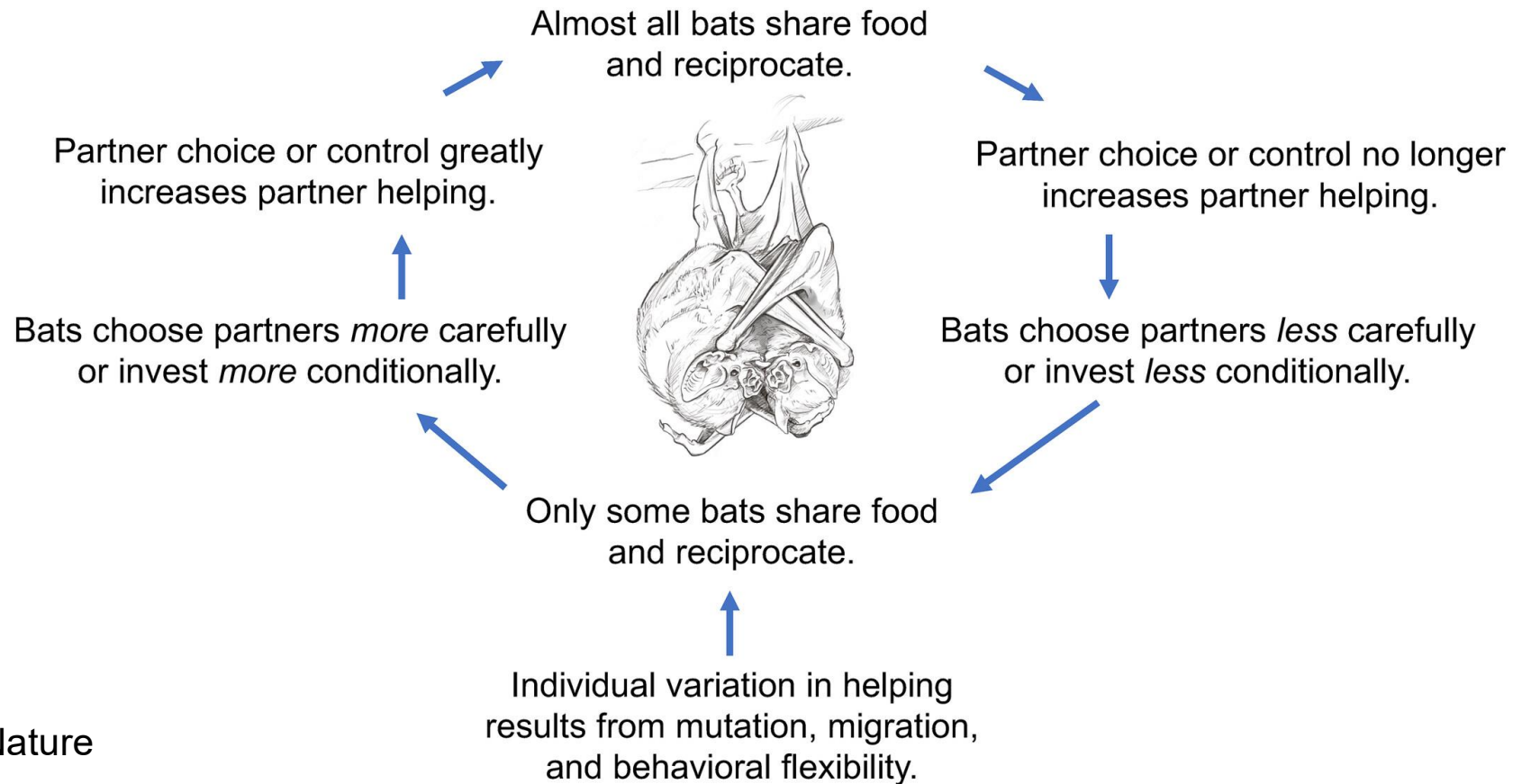
Traits → Strategies → Relationships → Networks → Consequences



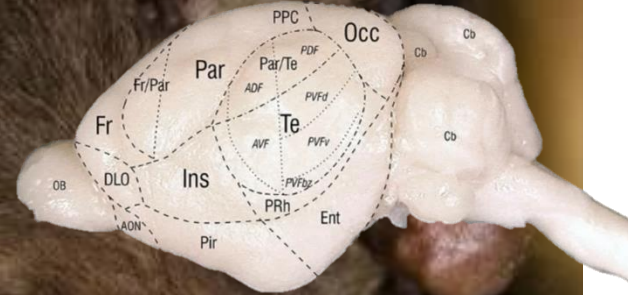
Traits → Strategies → Relationships → Networks → Consequences



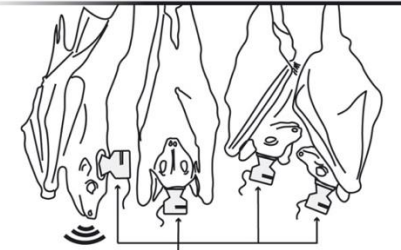
Traits → Strategies → Relationships → Networks → Consequences



Egyptian fruit bats as an emerging model system in social neuroscience



Multi-animal neural and audio recordings during freely occurring group vocal interactions



Wireless neural data loggers

NEUROSCIENCE

Social place-cells in the bat hippocampus

David B. Omer, Shir R. Maimon, Liora Las,^{*†} Nachum Ulanovsky^{*†}

Neuroscience

A unifying mechanism governing inter-brain neural relationship during social interactions

Wujie Zhang[✉], Maimon C Rose, Michael M Yartsev[✉]

SOCIAL NEUROBIOLOGY

Cortical representation of group social communication in bats

Maimon C. Rose[†], Boaz Styr[†], Tobias A. Schmid, Julie E. Elie, Michael M. Yartsev^{*}

Some final questions

To what extent does social integration impact individual health across different bat species?

How is bat social behavior and social structure shaped by ecology?

How does social structure shape social traits (including cognition)?

Questions



Southern Bent-winged bat
Steve Bourne



PRINCETON
UNIVERSITY

hhmi

Howard Hughes
Medical Institute



Alexander von Humboldt
Stiftung/Foundation



Sherri and Brock Fenton

