The evolution of intelligence in mammalian carnivores

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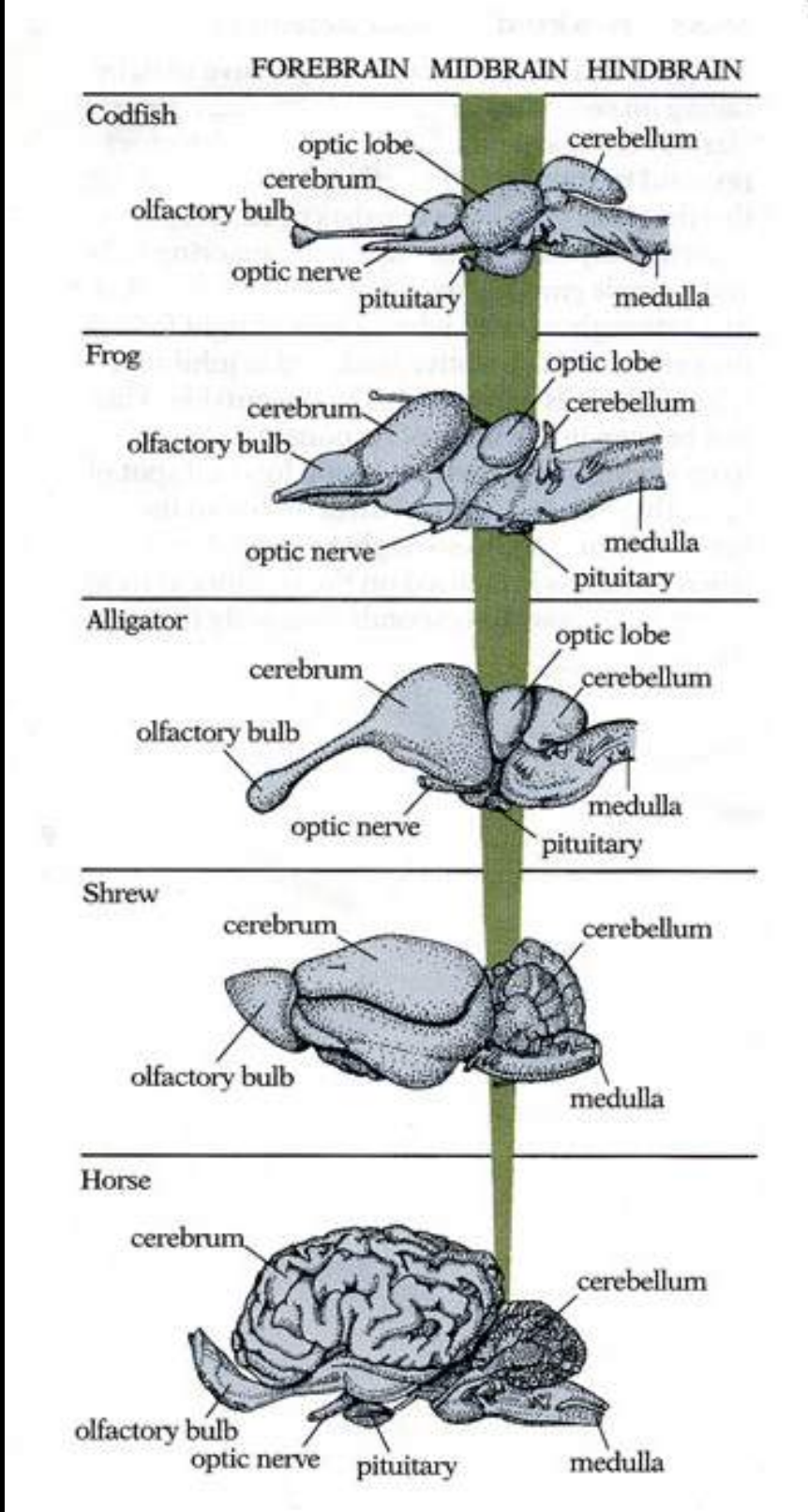
“Intelligence” broadly defined:

“Those processes by which organisms obtain & retain information about their environments, & use that information to make behavioral decisions” (Kamil 1987)

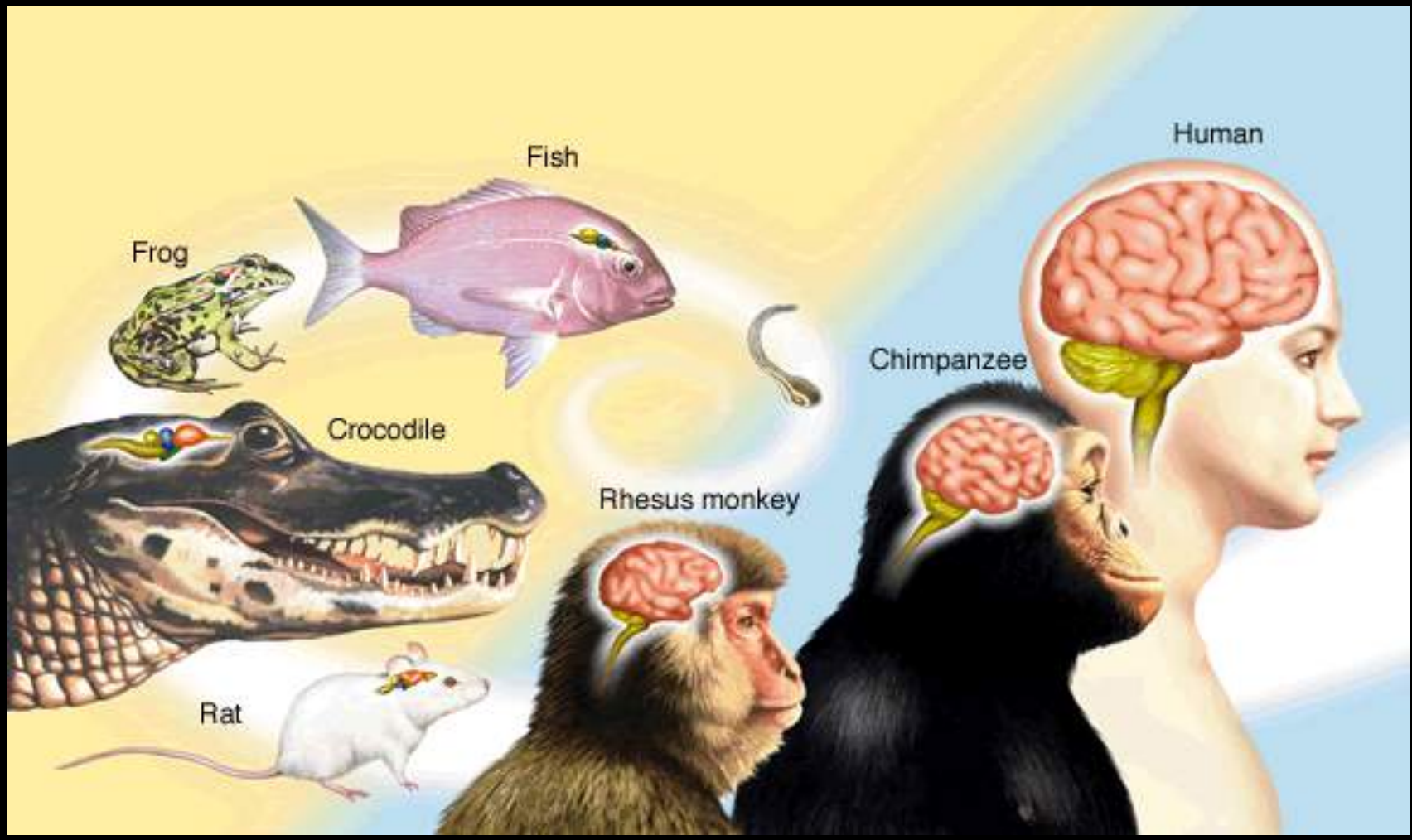
These processes are mediated by nervous systems that vary greatly in size & complexity

Despite the huge metabolic costs of neural tissue, mammals have relatively large brain:body ratios



Relative to other animals, including most other mammals, primates have relatively large brains, enlarged cortex, & sophisticated cognition.

Why?



H1: Big brains & great intelligence evolved to cope with complexity in the physical environment

H2: The ‘social complexity’ hypothesis: large brains evolved to cope with complexity in the social environment

H3: The ‘cognitive buffer’ hypothesis: large brains evolved to allow animals to cope with novel socio-ecological challenges & thus reduce mortality in changing environments

Where we began:
Testing the social complexity hypothesis

If the big brains found in primates were favored by social complexity,…

…then non-primates living in primate-like societies should exhibit cognitive abilities & brain features convergent with those in primates.

Eg: spotted hyenas

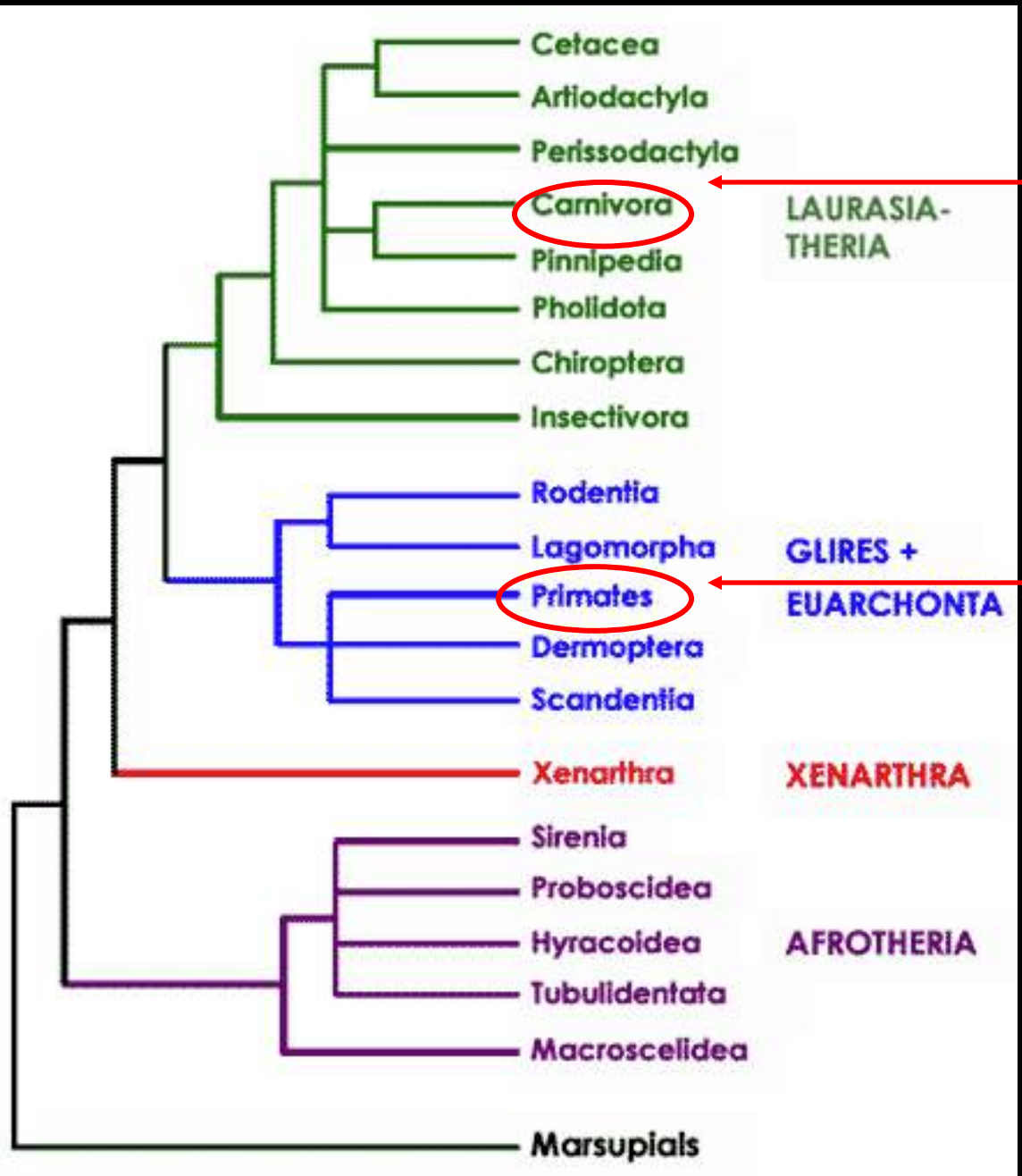
Spotted hyenas live in large, stable social groups called ‘clans,’ containing ≤ 130 individuals

Striking convergence: hyena clans & baboon troops are large, complex groups containing both kin & non-kin

- Mean within-group relatedness is low
- Multiple overlapping generations
- Multiple adults of both sexes
- Male dispersal & female philopatry
- Matrilineal kin sub-groups
- Hierarchical rank relationships

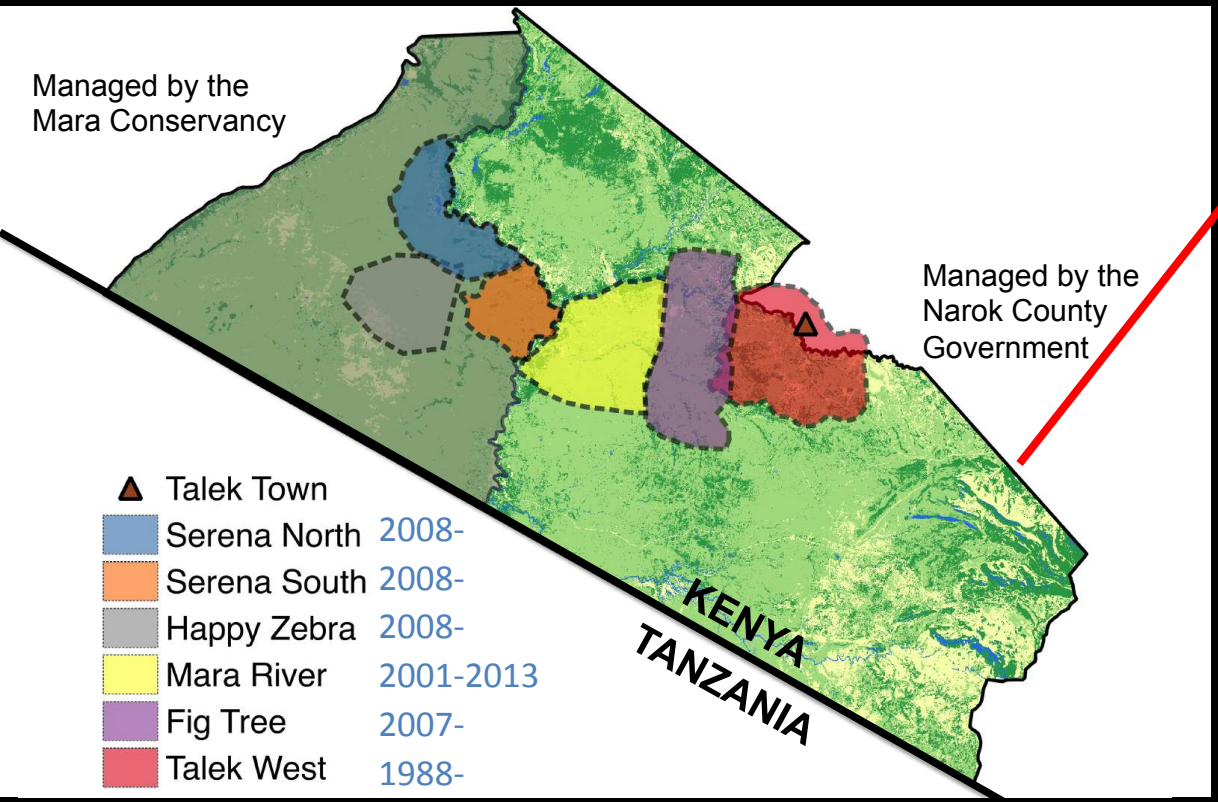
Group size, composition & structure have evolved convergently

Primates & carnivores last shared a common ancestor 90-100 MYA



Study of multiple clans in Kenya since 1988: clans contain 40 -130 hyenas

Masai Mara National Reserve



Individual recognition of hyenas

Daily observation from vehicles

A typical (low intensity) fight

Clans are structured by linear dominance hierarchies

Loser

Winner	MRPH	SEIN	WHO	MP	NAV	BAIL	MIG	BP	BOS
MRPH	--	24	14	13	28	11	14	21	4
SEIN		--	24	13	17	15	18	11	9
WHO			--	20	31	10	15	17	11
MP	1			--	36	27	12	15	14
NAV			2		--	19	29	13	17
BAIL						--	17	21	12
MIG							--	9	5
BP								--	3
BOS									--

Breeding females

Immigrant males

Both individuals and matrilines have ranks

Hyena Life history

Natal den → Communal den → Weaning → Puberty → Reproduction (females)

Puberty → Dispersal (males) → Immigration & reproduction (males)

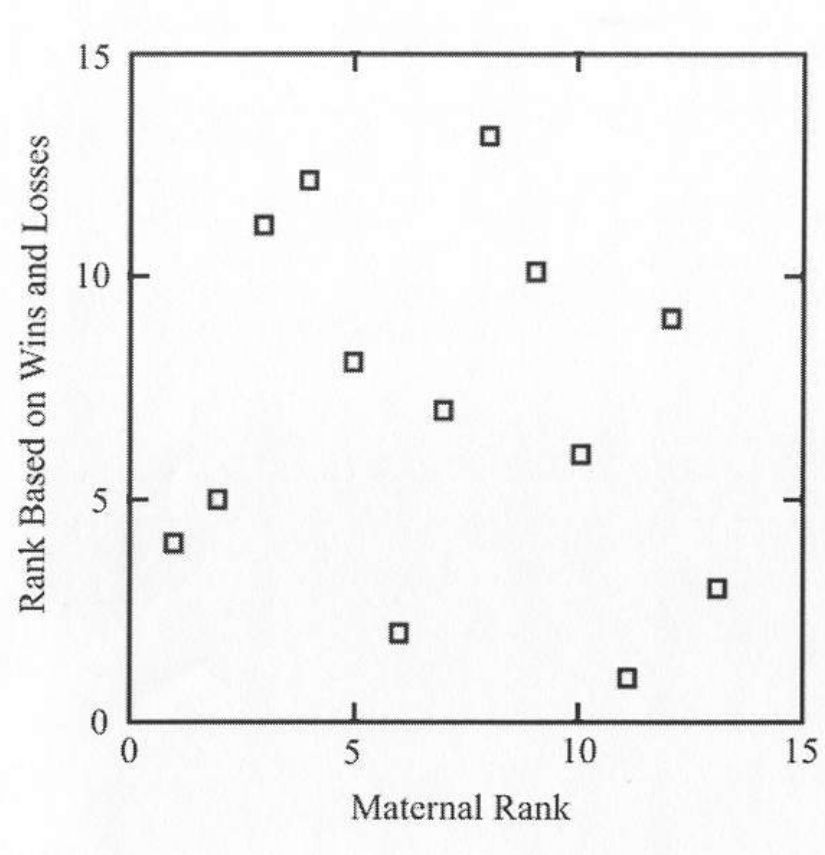
Max lifespan in nature is ~ 26 yrs

As in primates, hyena social rank is learned early in life

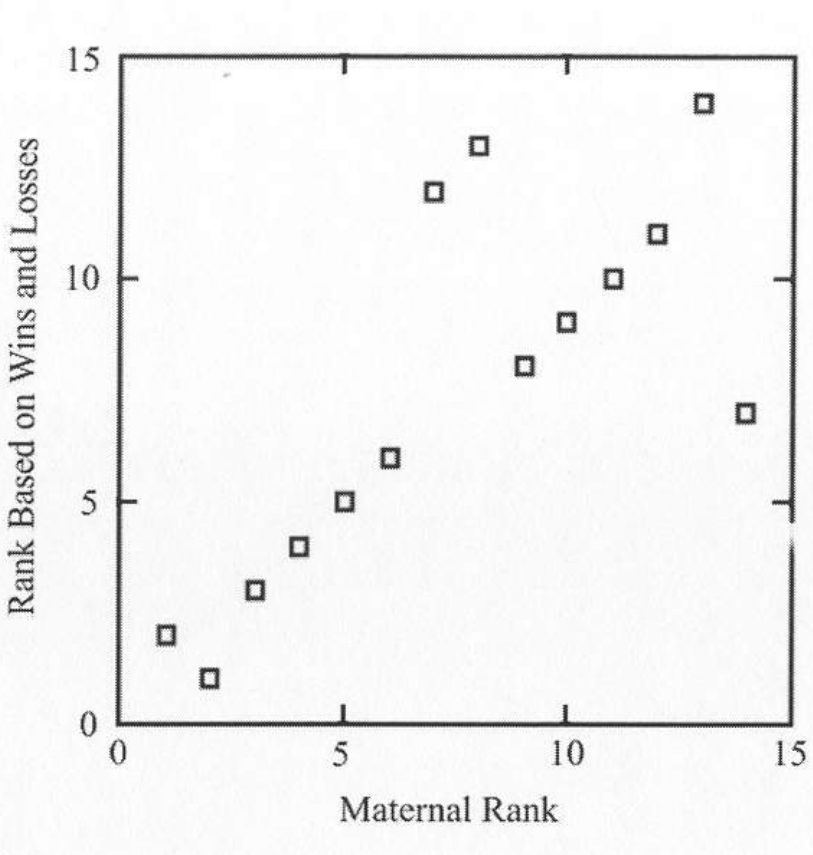
(Holekamp & Smale 1993)

Conducted repeated "bone" tests. Monitored fights among cubs when no adults present.

Test results for a cohort containing 13 cubs



4 Month Lapse



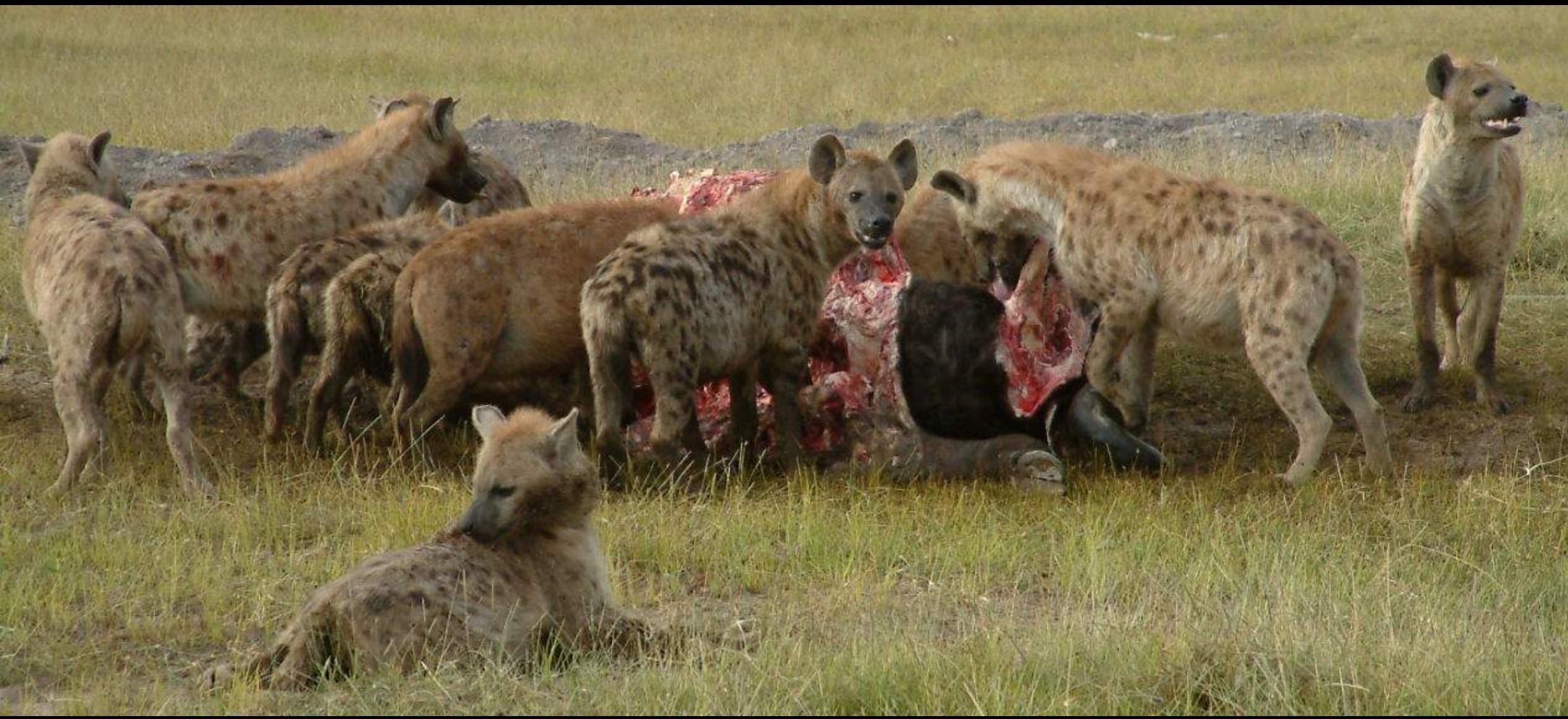
After 1-2 month
at the communal den

After 5-6 months
at the communal den

Rank acquisition complete by ~18 mo of age

(Holekamp & Smale 1993)

Patterns of resource competition: as in primates, outcomes are determined by social rank

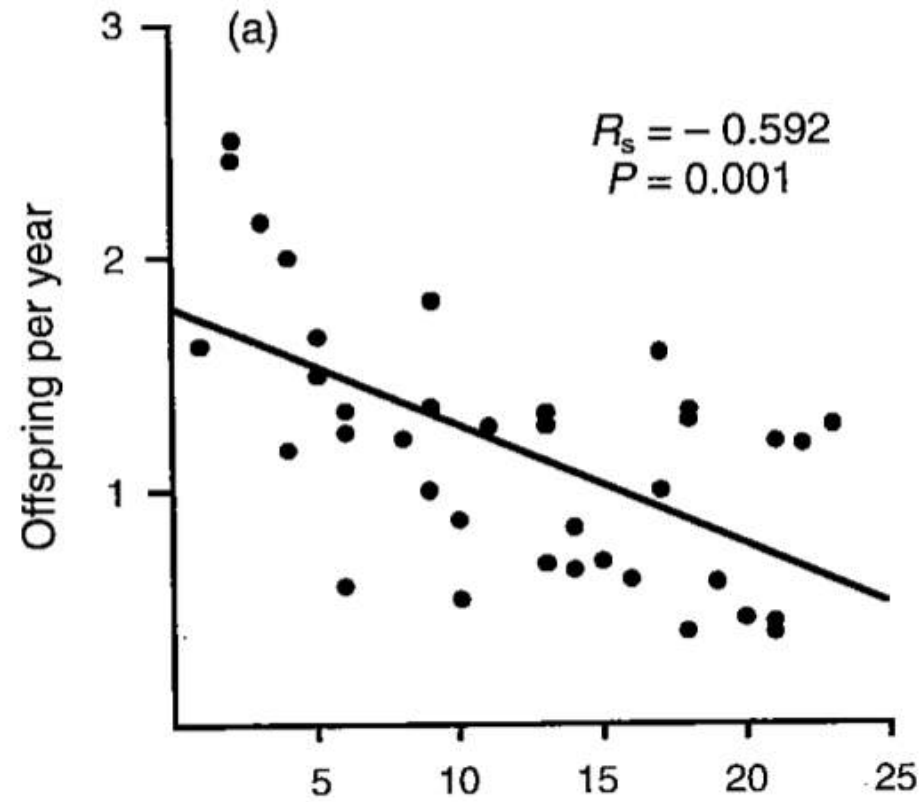


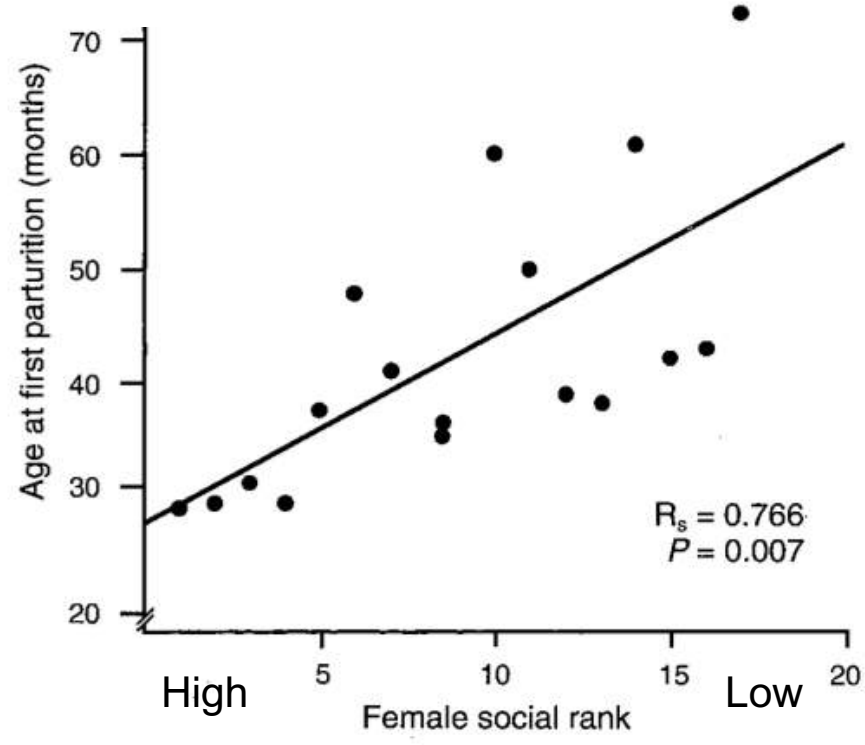
As in many primates, all adult female hyenas breed, but their reproductive success varies with social rank….

….and this has profound long-term fitness consequences.

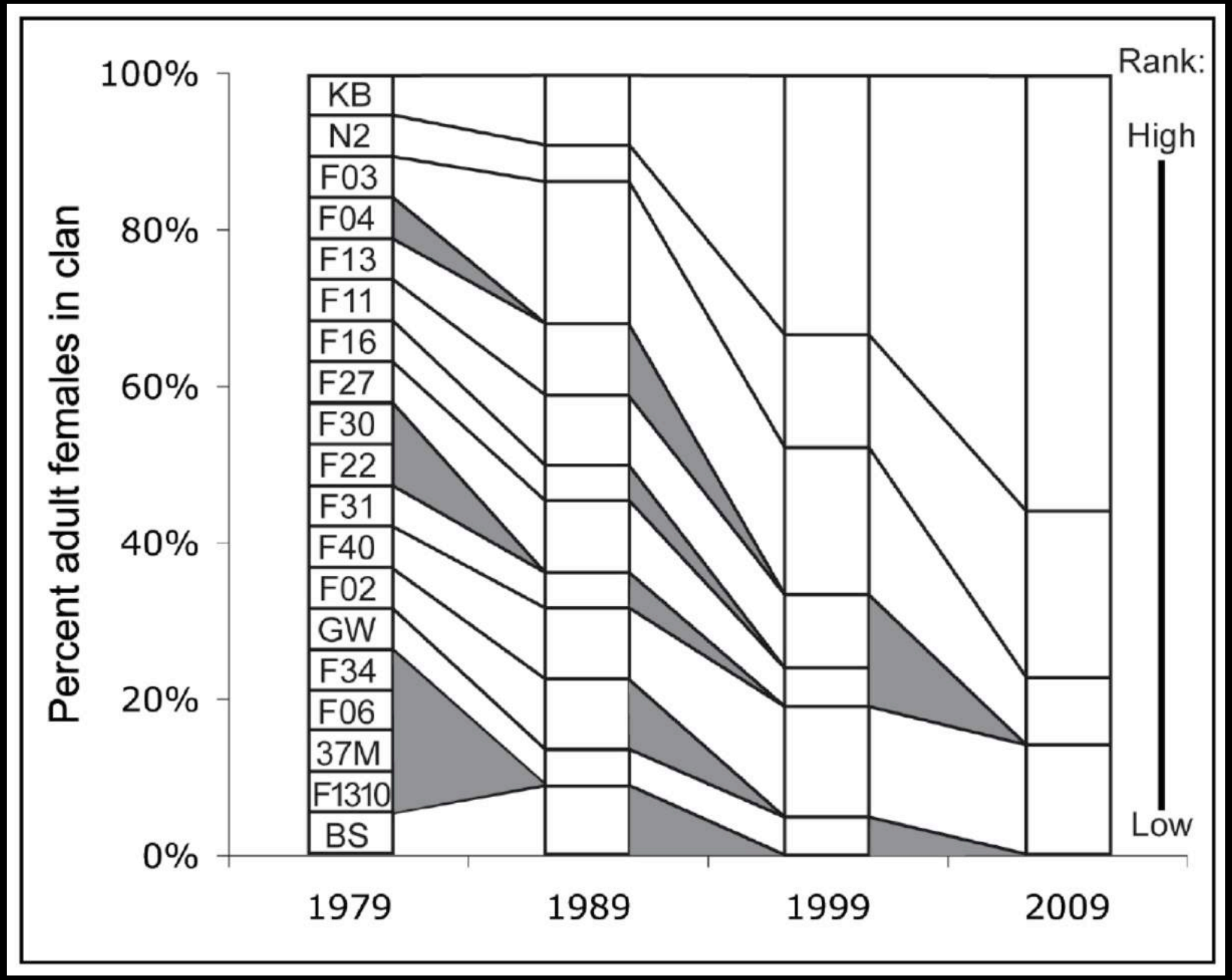
(Holekamp et al. 1996, *J. Reprod. Fert.*)

(Holekamp et al. 2012, *Molec. Ecol.*)



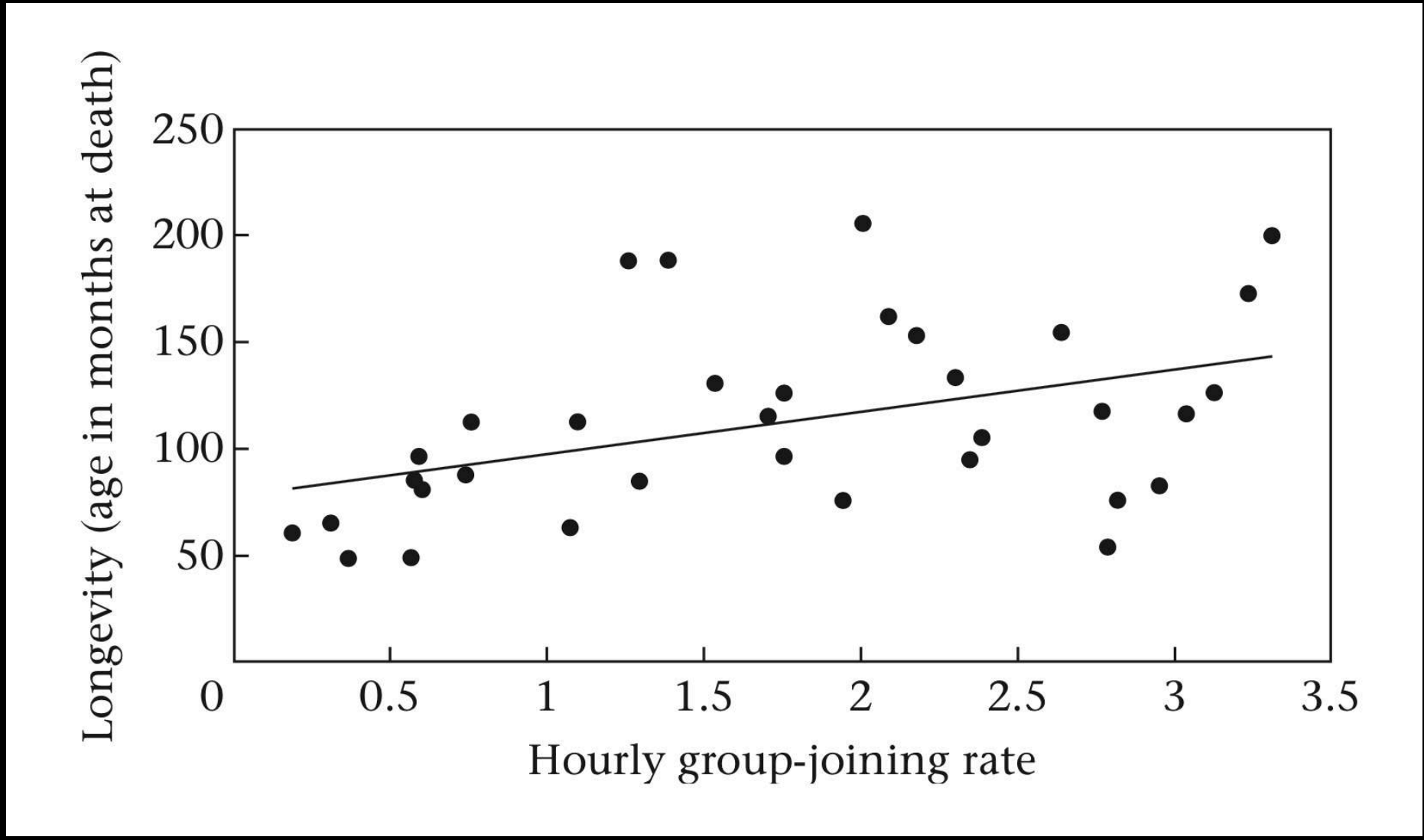


As in despotic primate societies, females' fitness varies with social rank



(Holekamp et al. 2012)

After controlling for rank, gregariousness affects fitness in hyenas, as it does in baboons



Generalized linear model: $t_{31} = 2.695$, $P = 0.011$

(Holekamp et al. 2015)

Spotted hyenas & cercopithecine primates have much in common

- Group size, composition & structure
- Life history patterns & social development
- Rank determines priority of resource access
- Fitness consequences of social rank & gregariousness

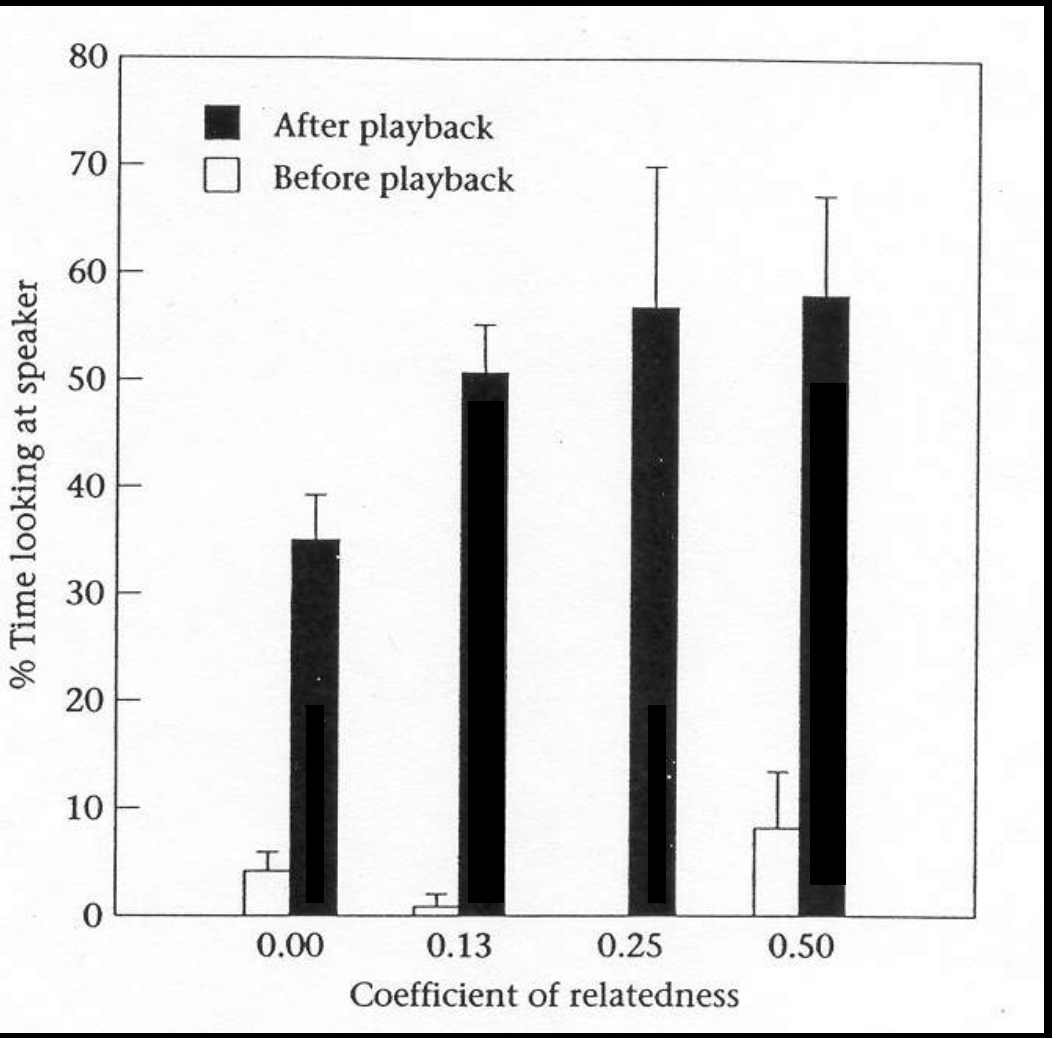
Are there <u>also</u> similarities in social cognition between these taxa?

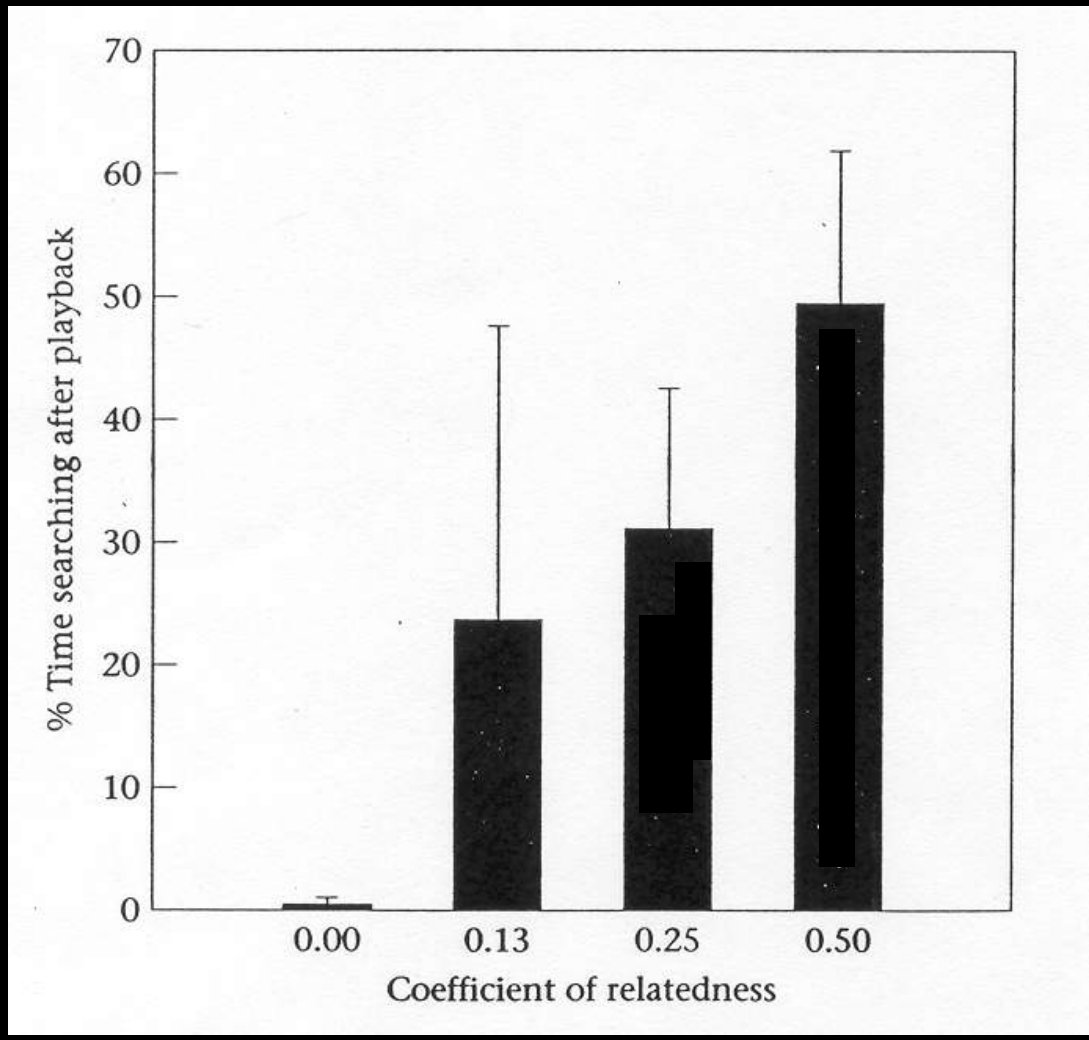
Hyenas & cercopithecine primates: social cognitive abilities & adaptive decision-making

- Individual recognition using multiple sensory modalities (Kruuk 1972; Holekamp et al. 1999; Benson-Amram et al. 2011)
- Reconcile after fights to repair social bonds (Wahaj et al. 2001)
- Kin-biased associations & nepotistic behavior (Holekamp et al. 1997; Smith et al. 2007)
- Recognize paternal as well as maternal kin (Van Horn et al. 2004; Wahaj et al. 2004)

Playback experiments with hyenas

Eg., Responses to cub distress calls vary with relatedness



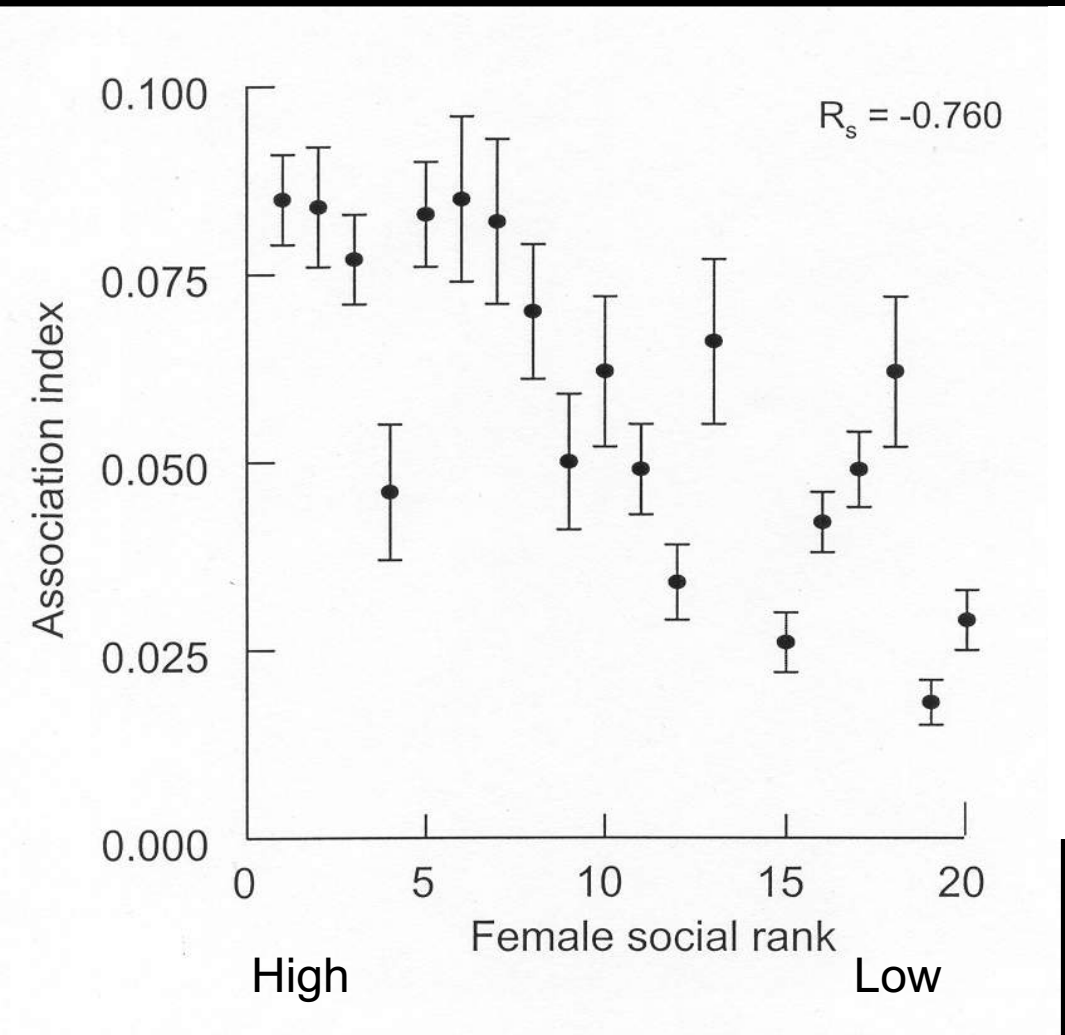


(Holekamp et al. 1999, *Anim. Behav.*)

Hyenas & cercopithecine primates: social cognitive abilities & adaptive decision-making

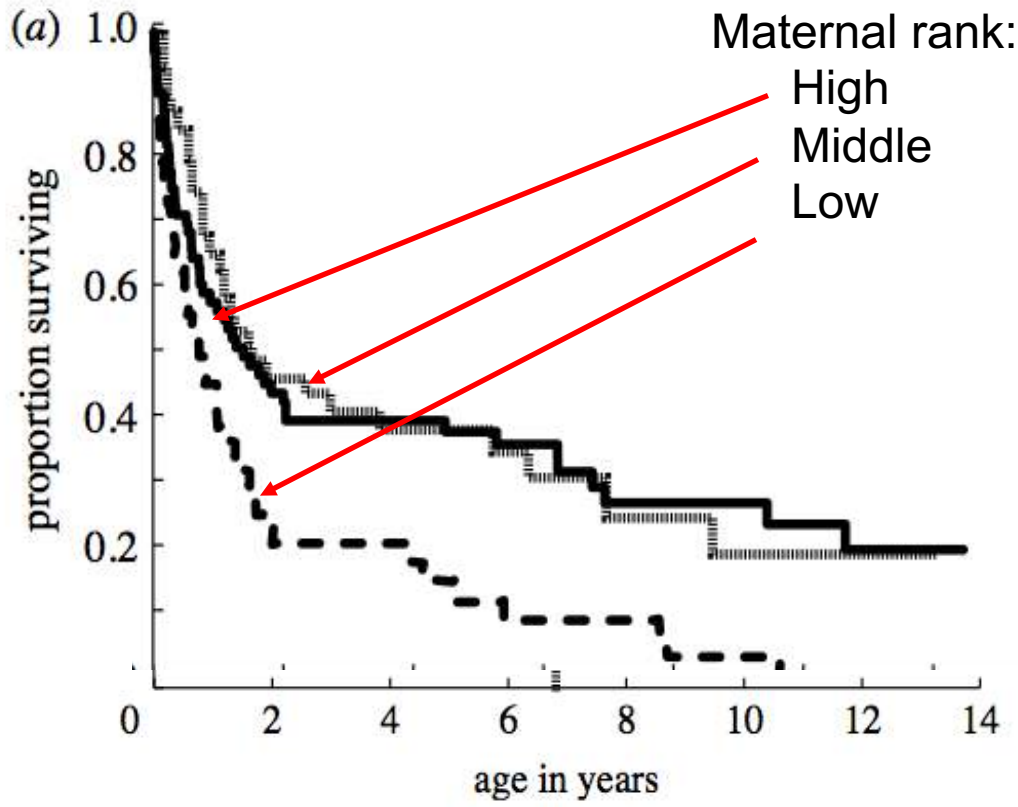
- Join forces to accomplish social goals (Engh et al. 2000, 2005; Smith et al. 2010)
- Recognize third-party relationships based on both rank & kinship (Engh et al. 2005)
- Track a great deal of information about their environments & use it to make adaptive social decisions (Smith et al. 2010)
- Recognize that social partners vary in their relative value, & choose accordingly (Szykman et al. 2001; Smith et al. 2007; Smith et al. 2011)

Eg., Adaptive use by males of knowledge about female social rank



Males initiate M-F associations & prefer higher-ranking females

(Szykman et al. 2001, *Behav. Ecol. Sociobiol.*)



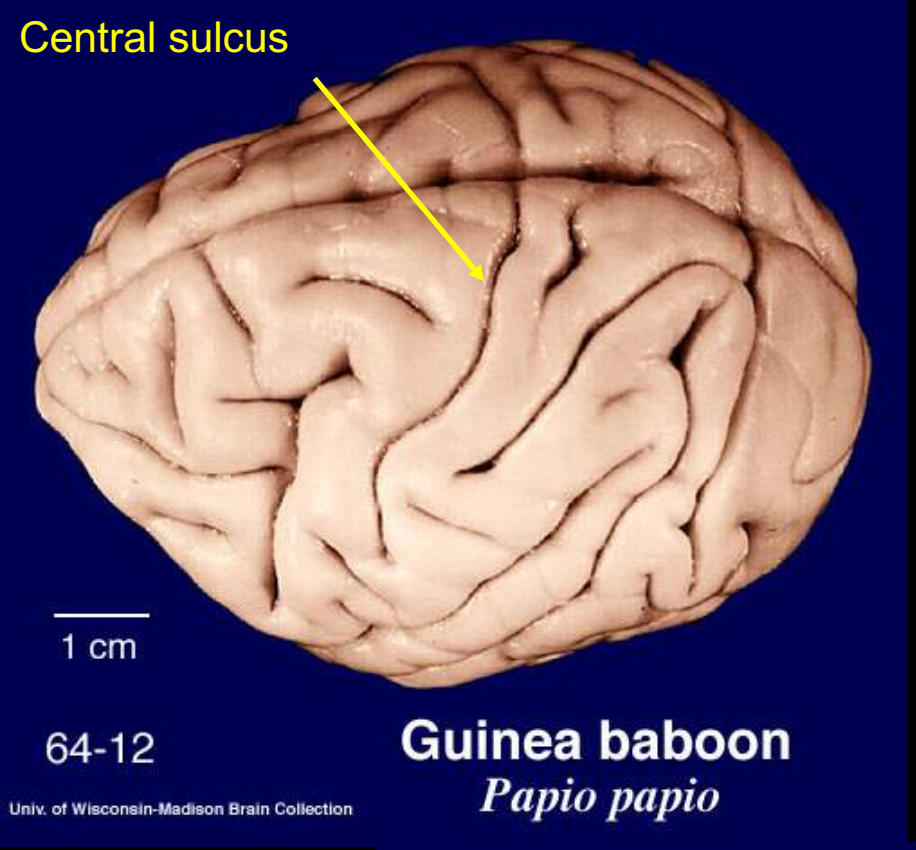
Cubs of higher-ranking females survive better

(Watts et al. 2009, *Proc. Roy. Soc. B*)

Summary: We find striking similarities in social cognition between
spotted hyenas &
cercopithecine primates

Behavioral data support the social complexity hypothesis

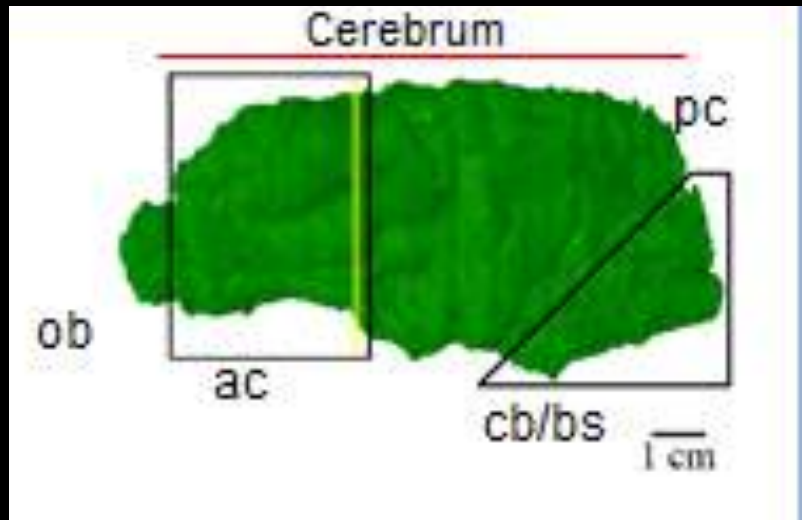
But what about the brain?



The ‘social brain’ hypothesis predicts convergent evolution between hyenas & primates regarding expansion of neural tissues mediating social behavior

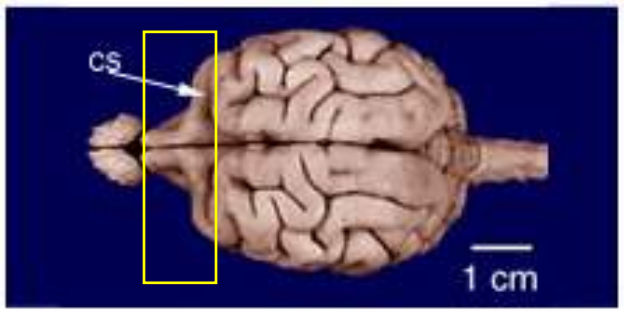
Comparative analysis of gross brain morphology based on “virtual brain” endocasts from CT scans

- Compare brains & brain regions
  among Hyaenid species (Sakai et al. 2011)

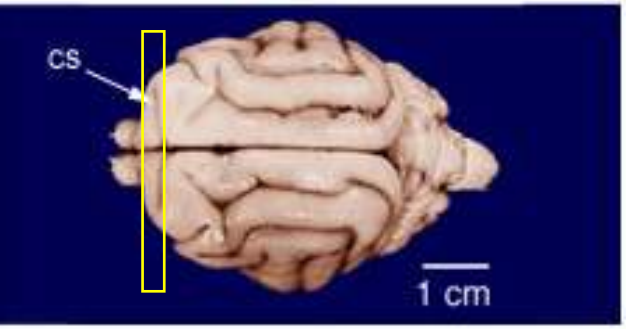


Comparison of spotted hyenas with less gregarious Hyaenid species

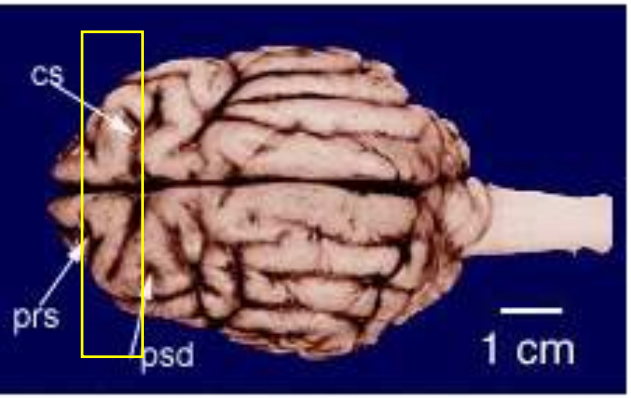
Cerebral hemispheres of 4 carnivores



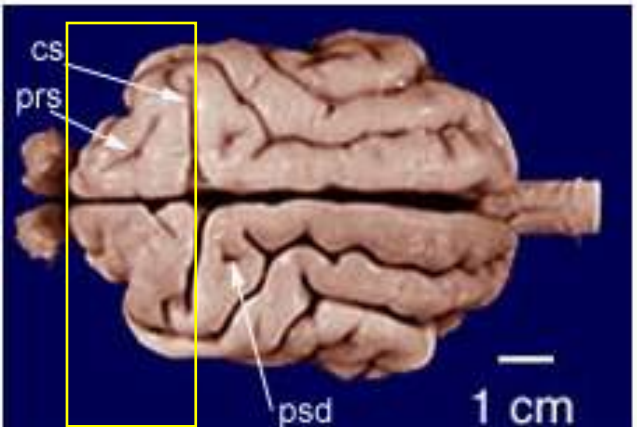
Raccoon



Cat



Dog

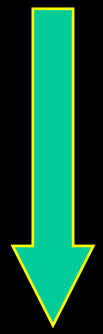


Spotted hyena

Yellow box indicates approximate area of frontal cortex (cortex rostral to the cruciate sulcus)

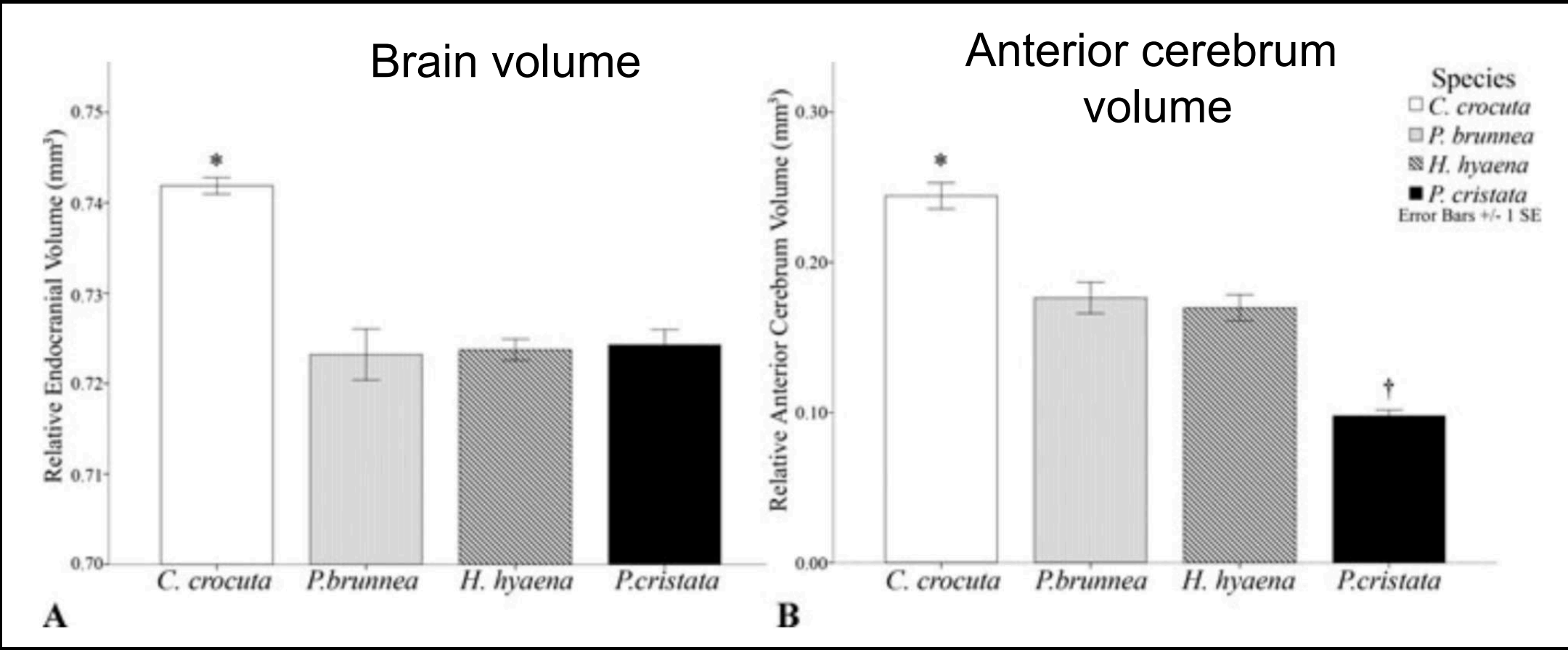
If social brain hypothesis is correct, then frontal cortex volume in Hyaenids should decrease as:

spotted hyena
brown hyena
striped hyena
aardwolf



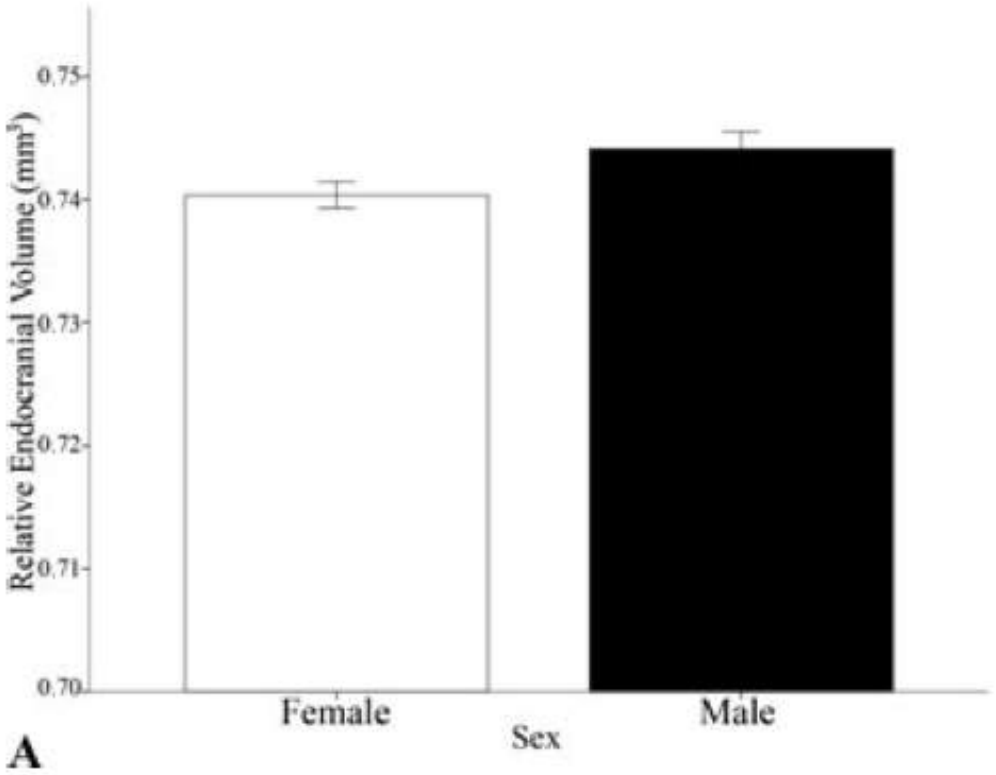
(Sakai et al. 2011 *Brain, Behav, Evol*)

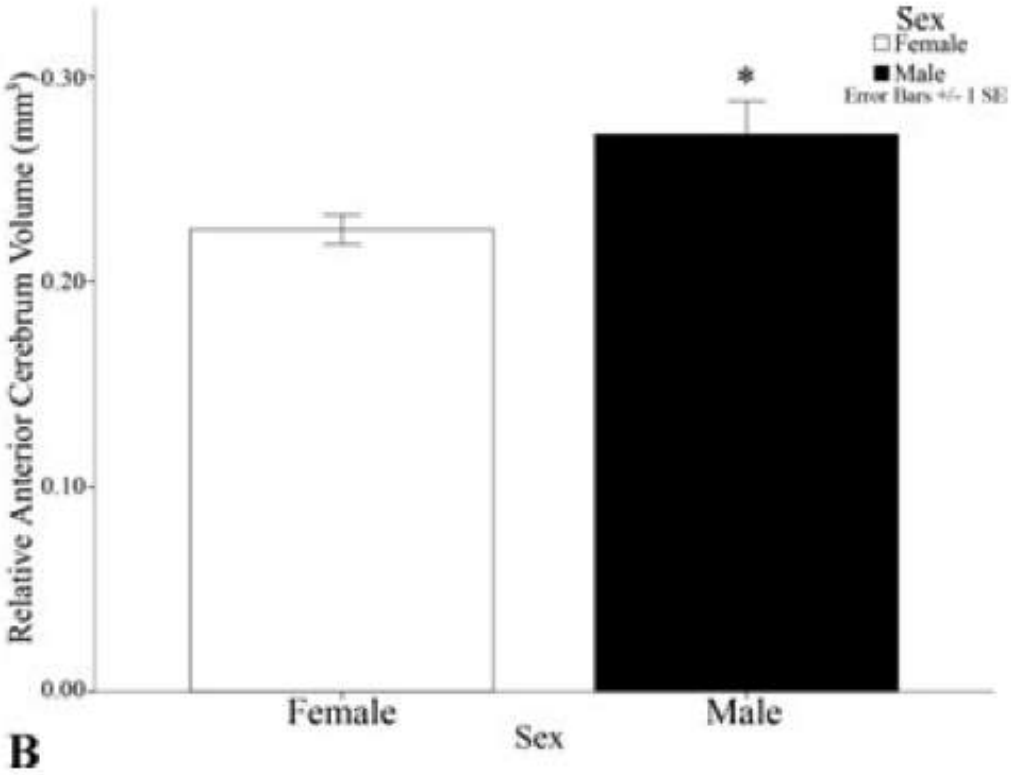
Spotted hyenas have the largest relative brain and frontal cortex volumes



(Sakai et al. 2011, *Brain, Behav Evol*)

Anterior cerebrum is proportionately larger in adult male (N=12) than female (N=18) spotted hyenas



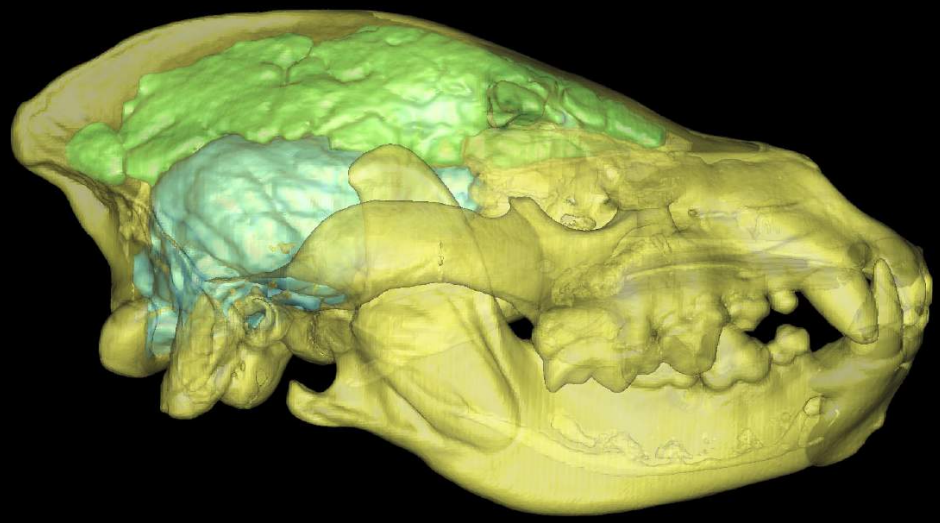


(Arsznov et al. 2010 *Brain, Behav. Evol.*)

Comparative brain analysis

- Whole brain and frontal cortex both larger in spotted hyenas than less gregarious Hyaenids
- Frontal cortex larger in male than female spotted hyenas

Behavioral and morphological data support the social complexity hypothesis

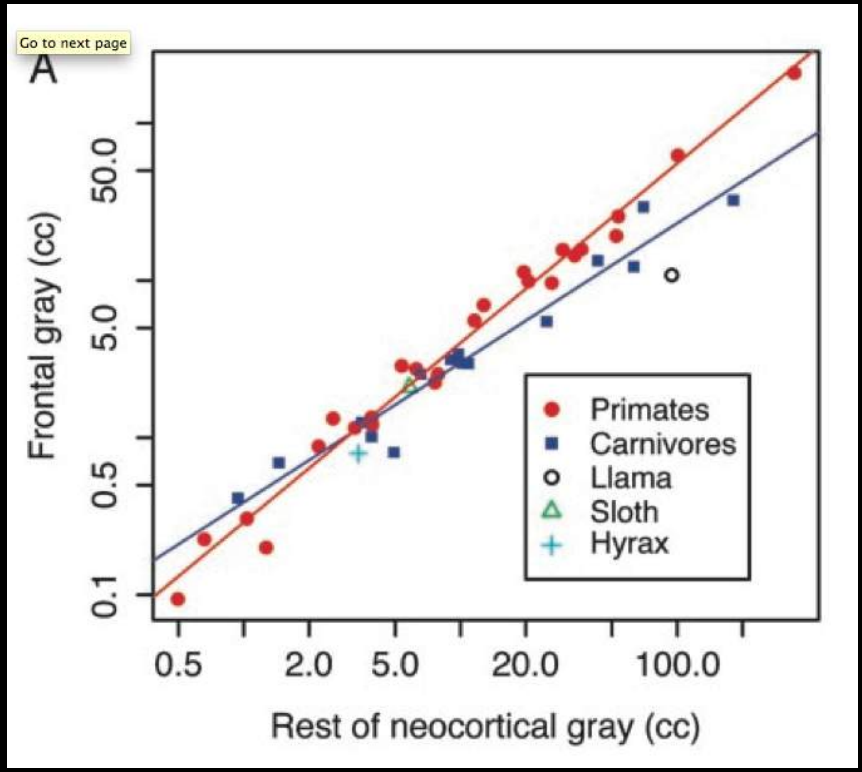


Caveats: The social complexity hypothesis can't explain:

1. Grade shifts in relative brain size & relative cortex size

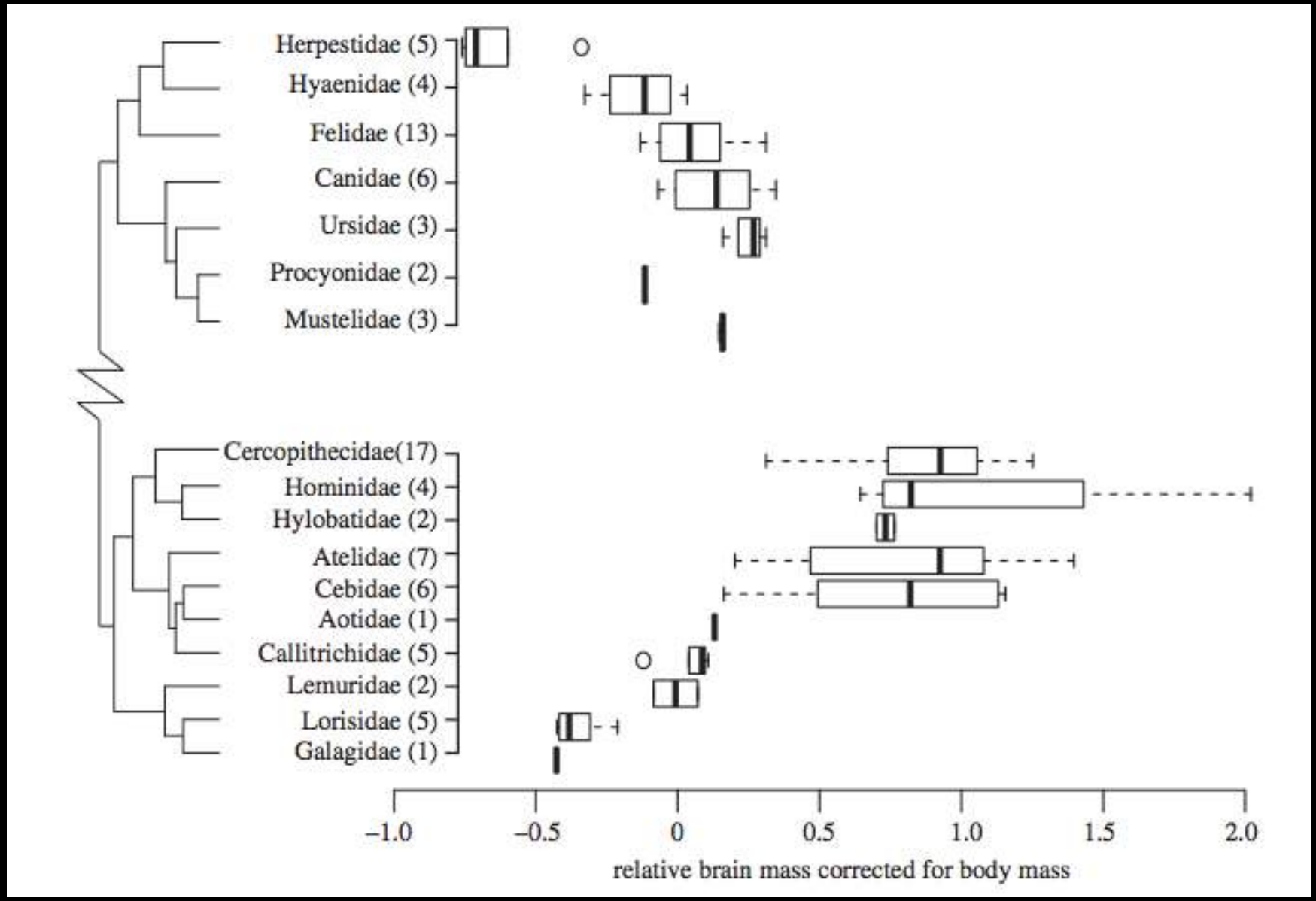
Primates vs. carnivores

(Bush & Allman 2004)



2. Species with high socio-cognitive abilities also excel in general intelligence

Brain size varies more within & among primate than carnivore families; variability affects evolvability. This may contribute to grade shifts.



(Holekamp et al. 2013)

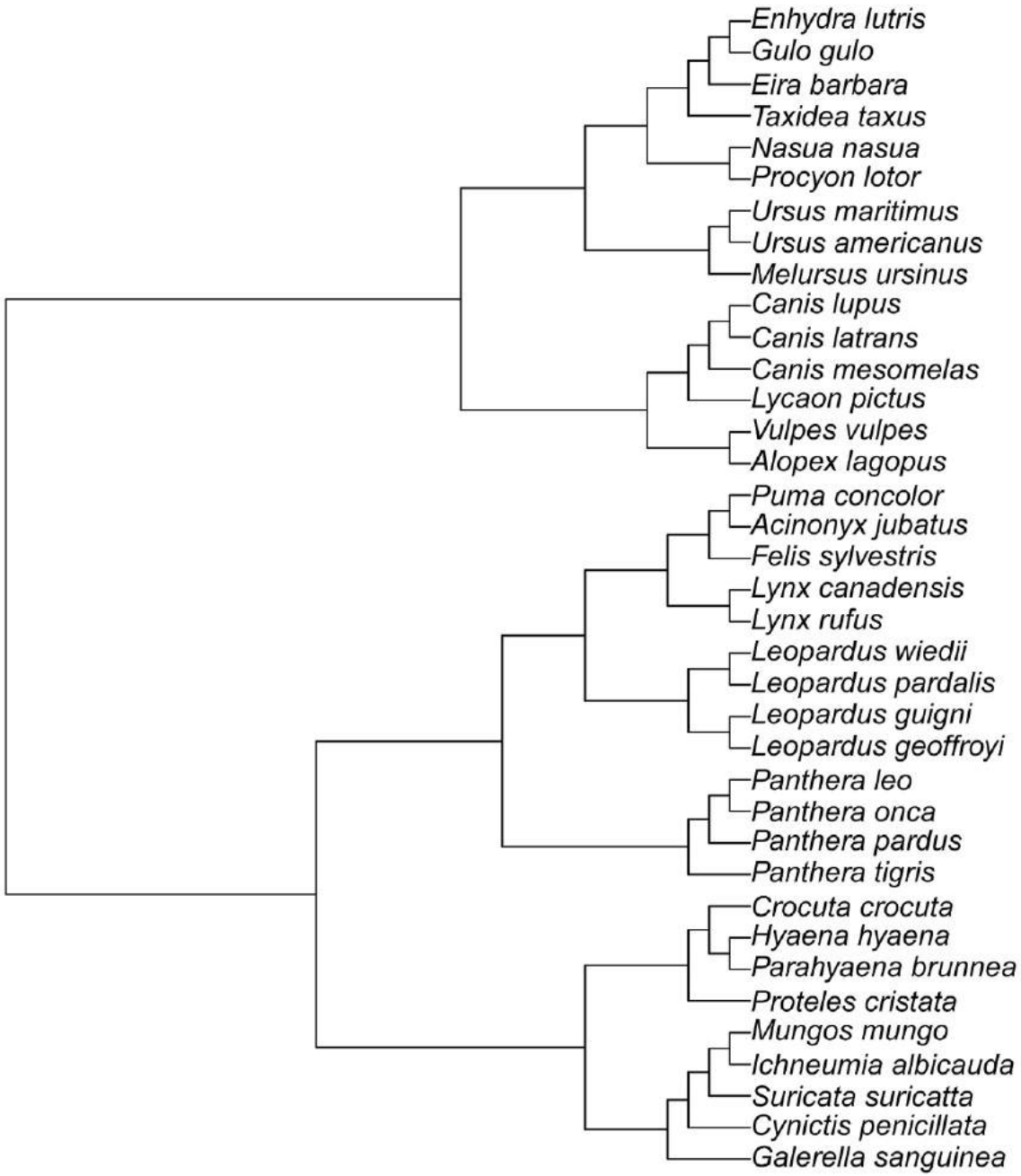
The problem of general intelligence

Phylogenetic analysis of brain & brain region volumes in carnivores

Used brain size as a proxy for general intelligence

(Swanson et al. 2012, *PLoS1*)

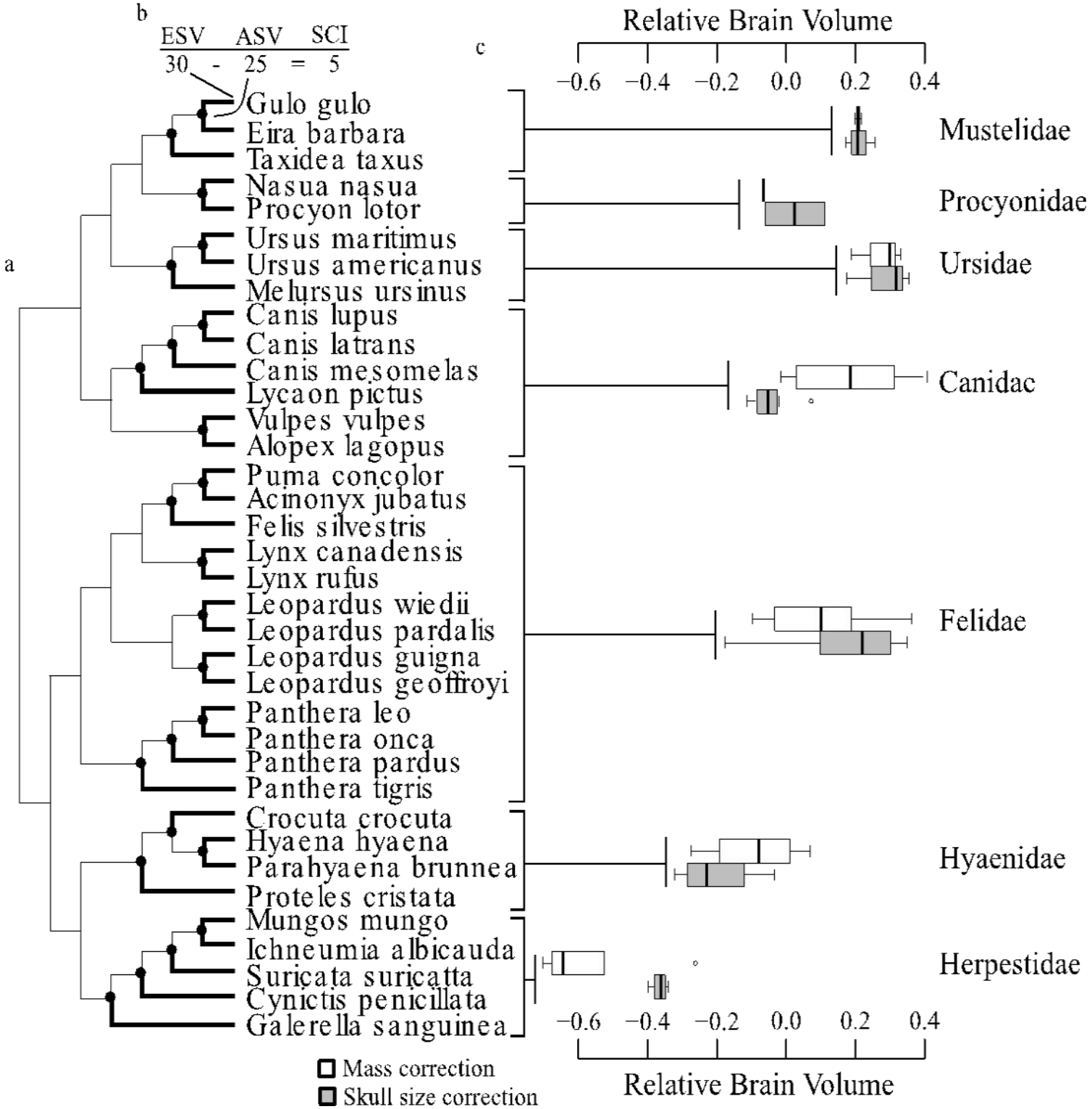
Multivariate phylogenetic analysis of mammalian carnivores



36 species
Multiple specimens per species
Measures of endocranial volume plus:

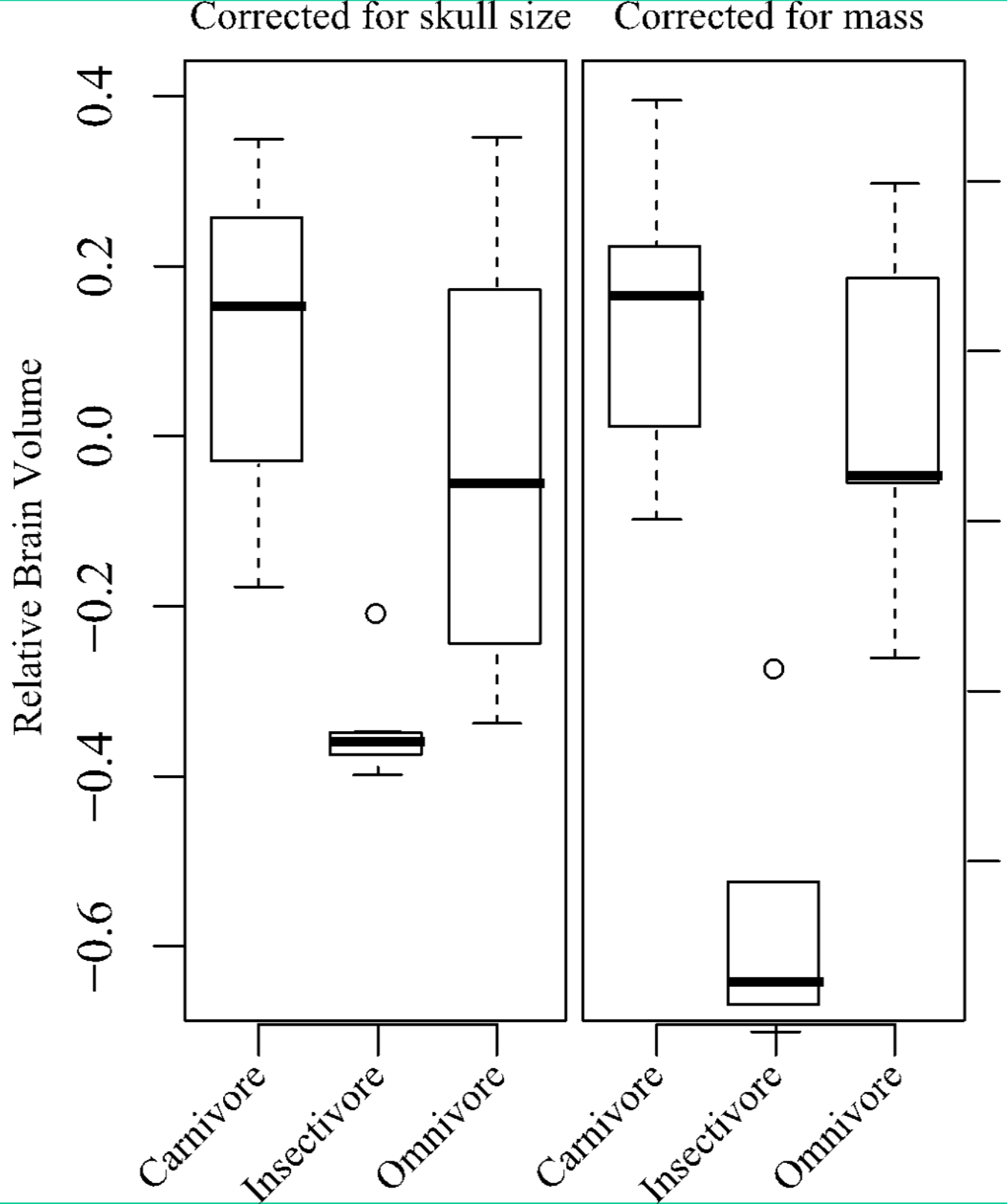
- Volume of each of multiple brain areas from CT scans
- Social complexity
- Diet
- Life history data
- Specimen sex

(Swanson et al. 2012, *PLoS1*)



Phylogeny Matters

(Swanson et al. 2012, *PLoS1*)



Diet matters

But sociality doesn't predict brain size

(Swanson et al. 2012, *PLoS1*)

Social problem-solving is remarkably similar in hyenas & baboons, yet general behavioral plasticity appears much greater in baboons

Plasticity is a hallmark of intelligence….
..but social complexity can't account for this difference

How does general intelligence evolve?

Can social selection pressures shape the evolution of general intelligence as well as social cognition?

How well do hyenas solve non-social problems?

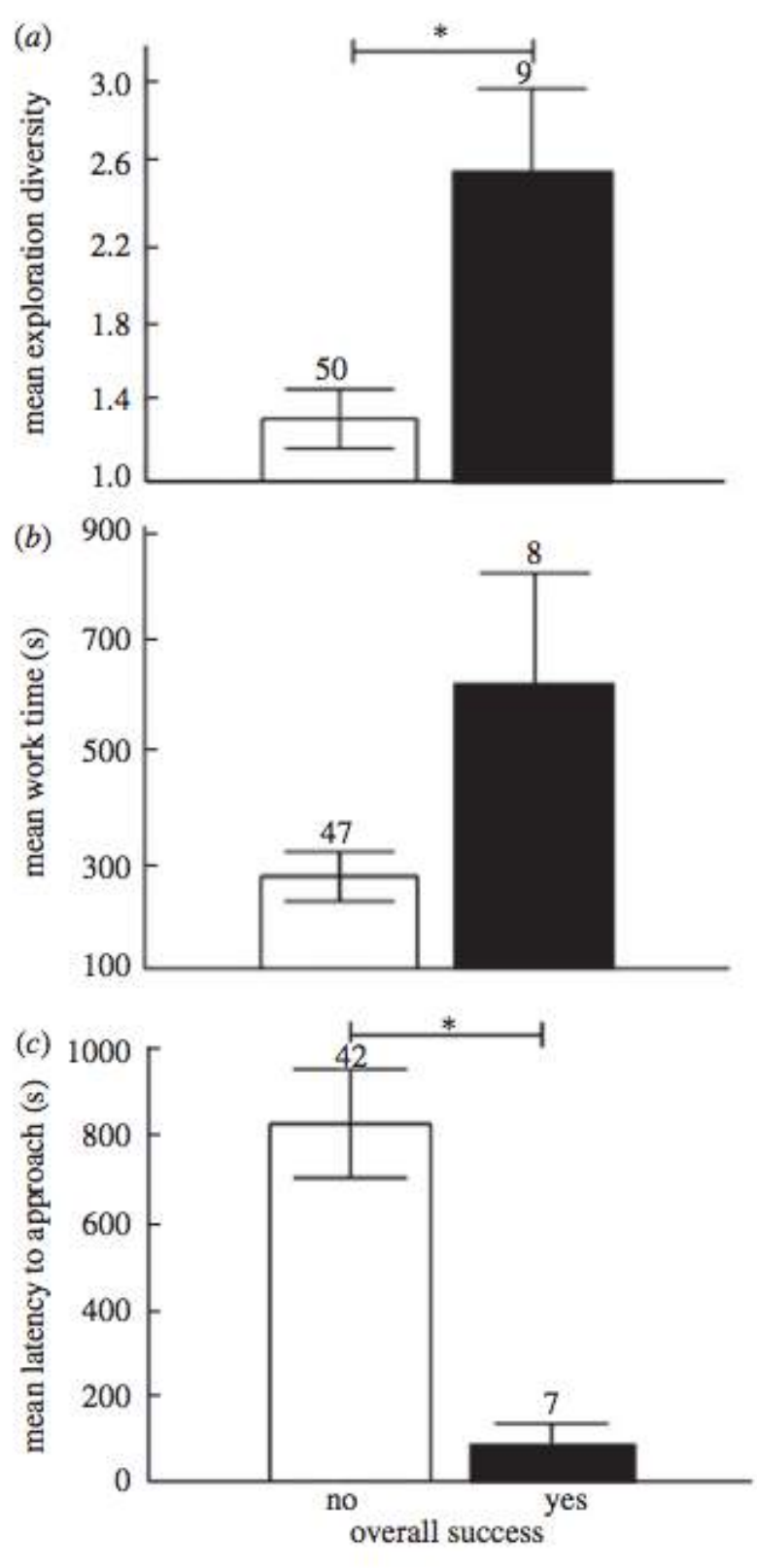
"Puzzle box" tests with wild hyenas

354 trials on 59 individuals from 3 study clans

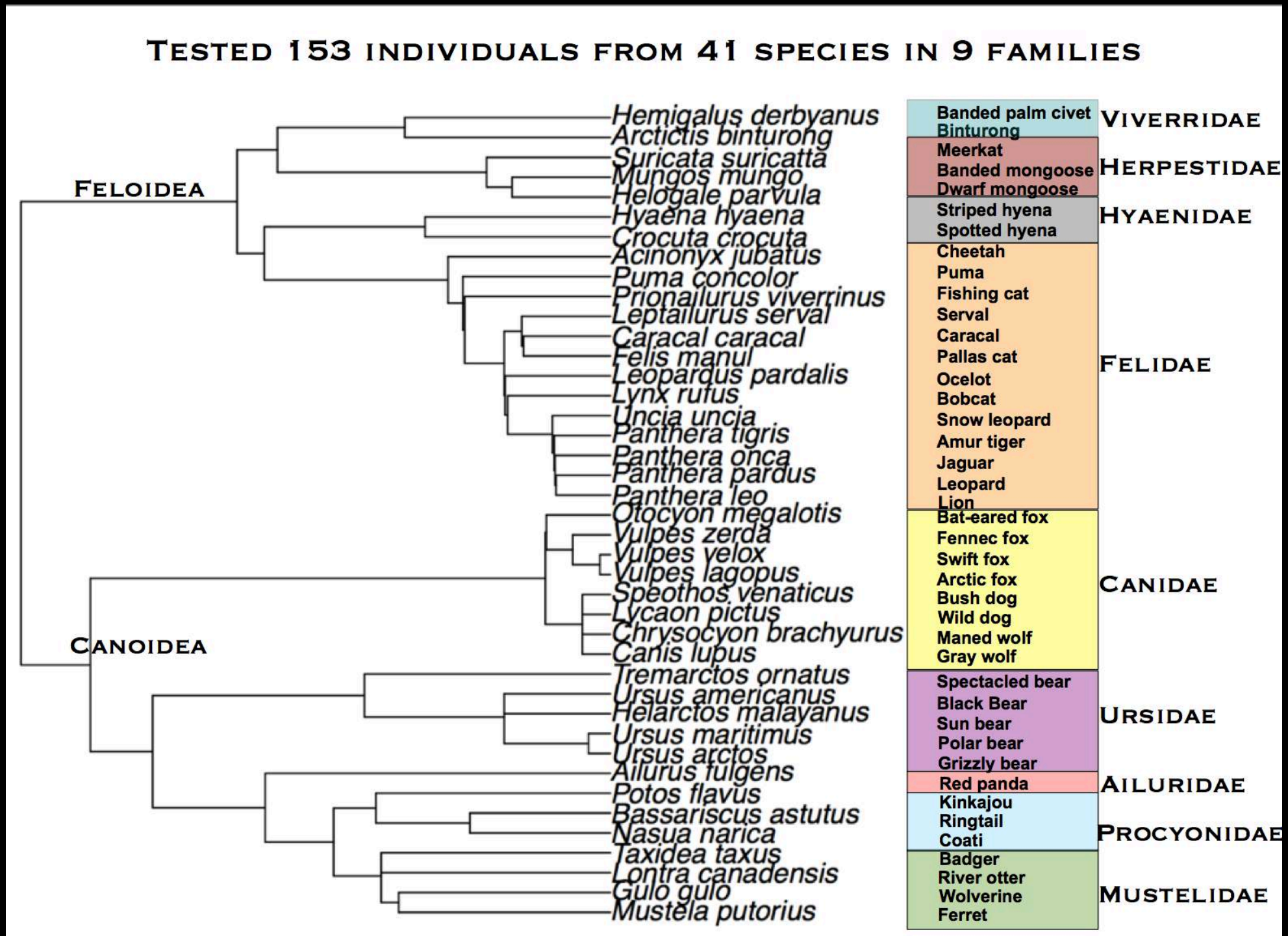
Innovation, persistence, & neophilia predict success in field puzzle box experiments

But only 9 of 59 wild subjects opened the box!

(Benson-Amram & Holekamp 2012, *Proc. Roy. Soc. B*)



Zoo study of problem-solving in carnivores: 9 zoos



Experimental set-up

Box size: scaled to body size
Bait: favorite food
Test location: home enclosure

Experimental set-up

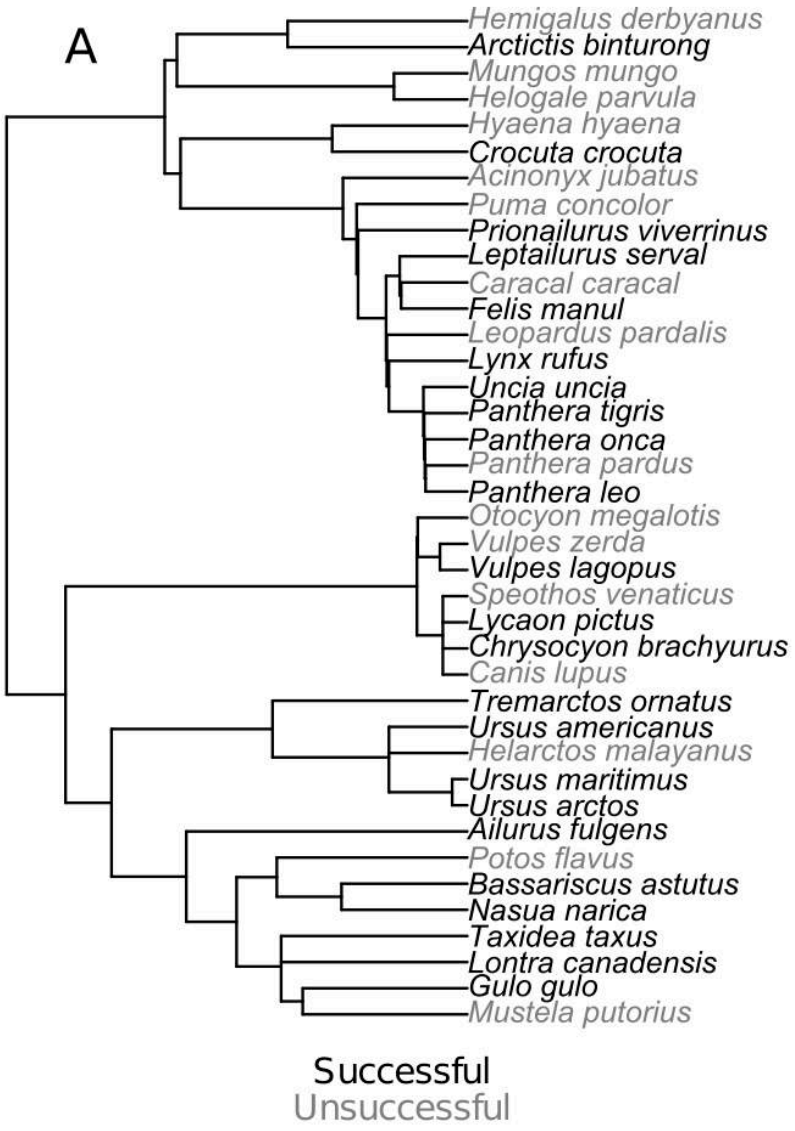
Video analysis & modeling

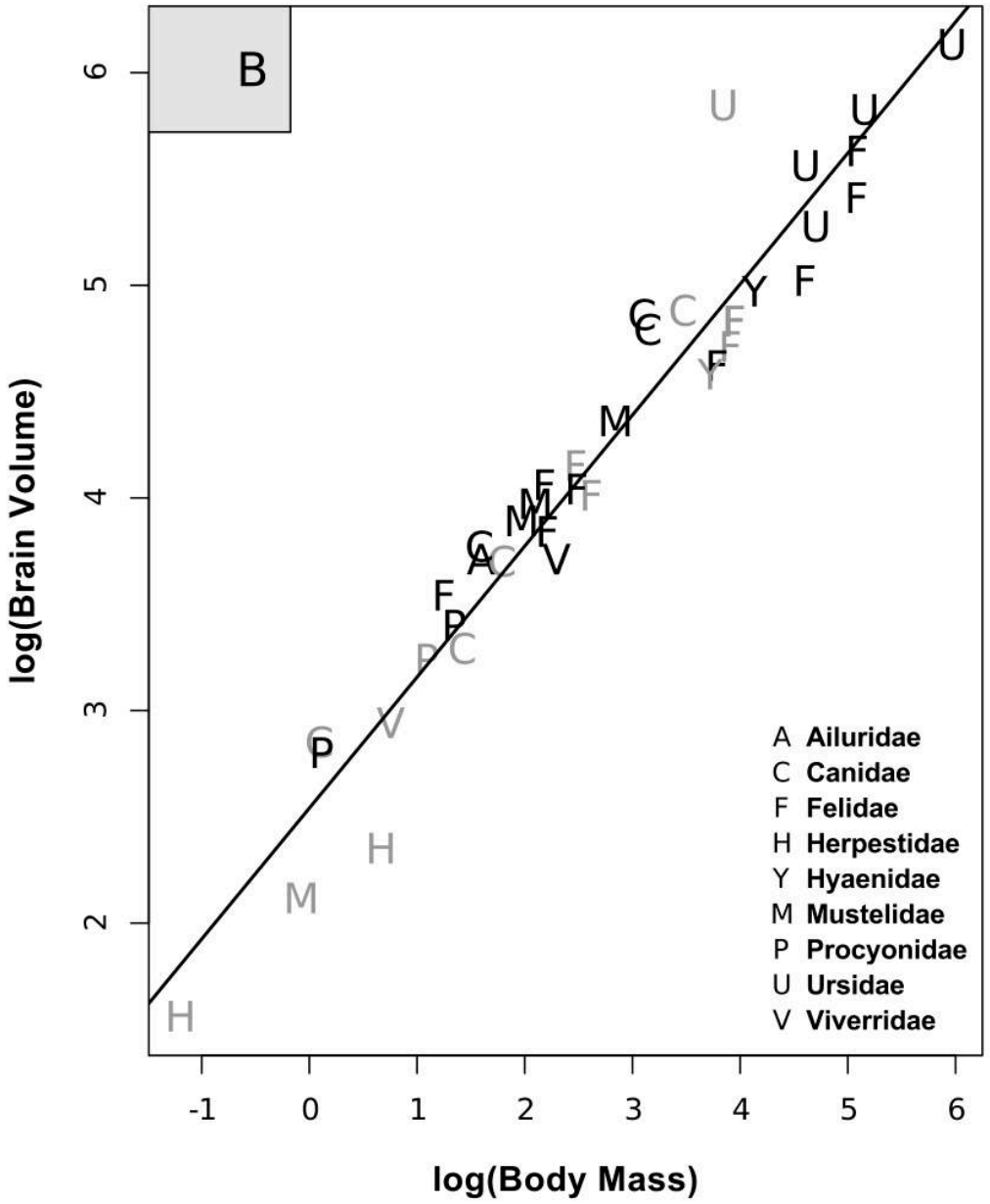
- Success opening box assessed in relation to
  - Performance measures
    - Work time
    - Number of different behaviors used
    - Neophobia
  - Sociality
  - Body size
  - Manual dexterity
  - Neuroanatomy

Problem-solving in captive carnivores

Bayesian phylogenetic generalized linear mixed-effects models
used to investigate predictors of success in opening the puzzle box

Carnivore brain volume varies with body mass

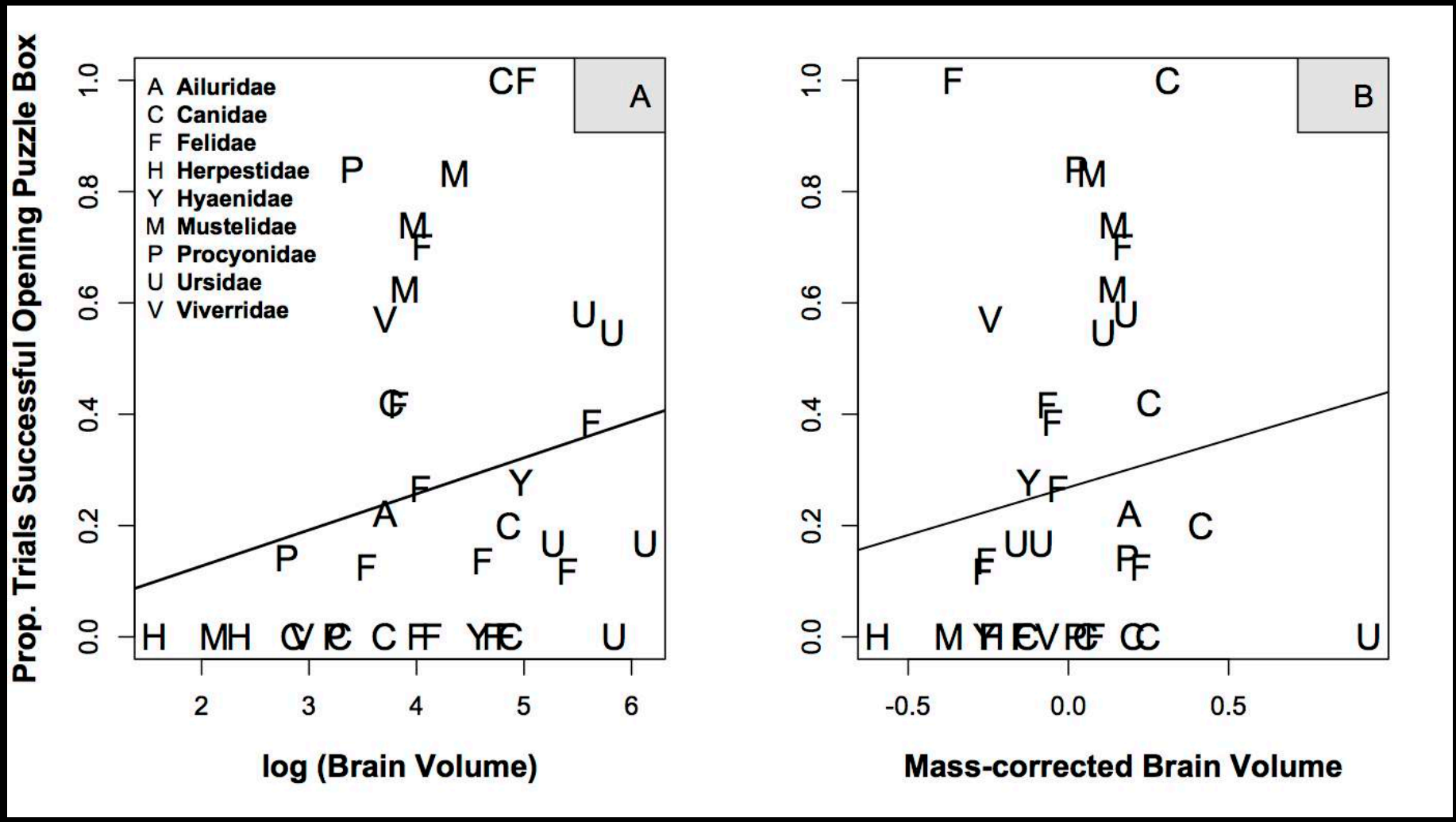




(Benson-Amram et al. 2016, *PNAS*)

Carnivores with larger brains were better at solving the problem.

But social species performed no better than solitary ones.



(Benson-Amram et al. 2016, *PNAS*)

Social complexity appears to promote convergent evolution in carnivores of

- social problem-solving
- size of specific brain regions (?)

But social complexity does not predict either brain size or ability to solve non-social problems

The evolution of general intelligence remains unexplained

What shapes the evolution of general intelligence?

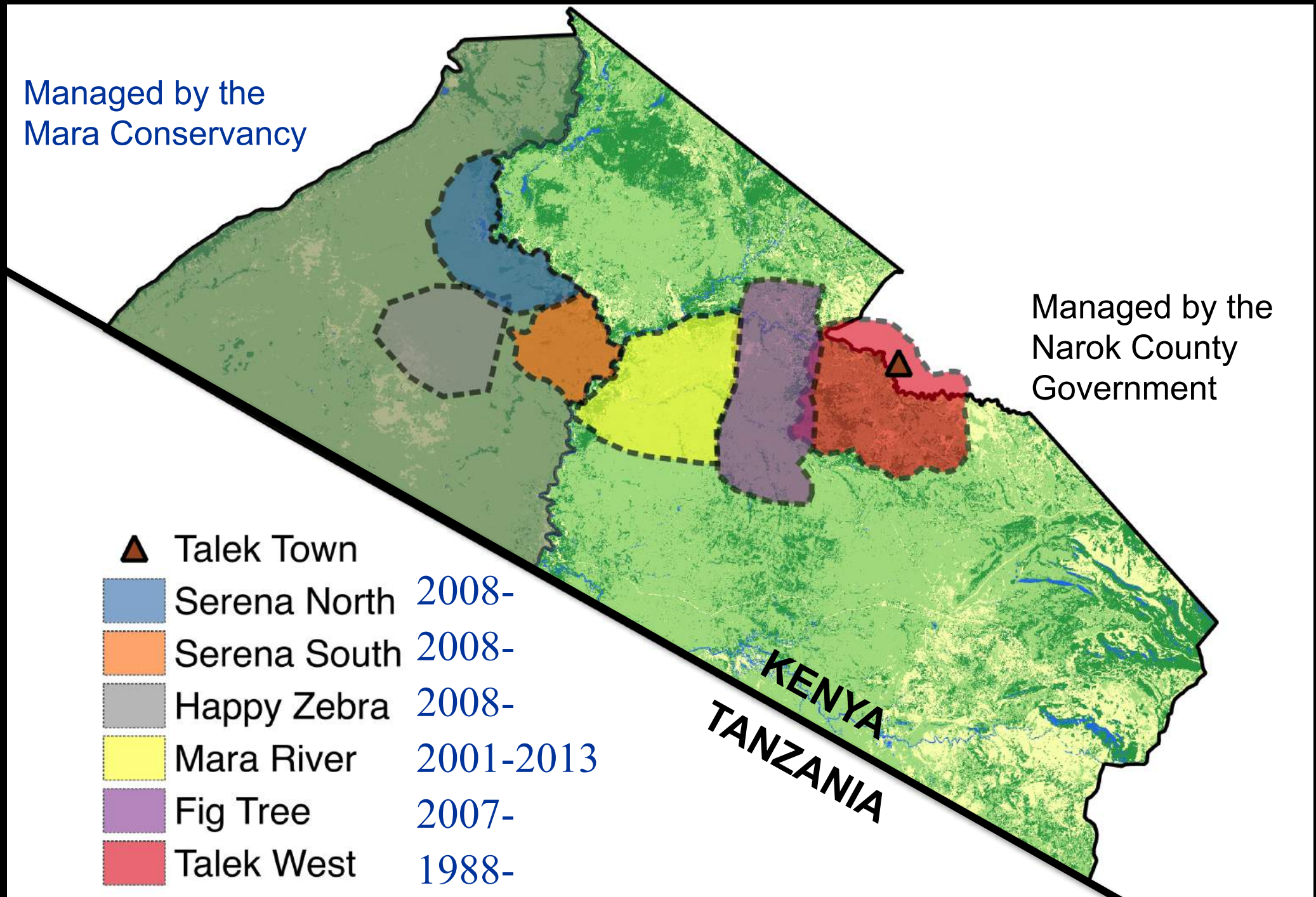
The cognitive buffer hypothesis (Allman, Sol, Reader & colleagues): large brains evolved to allow animals to cope with novel socio-ecological challenges & thus reduce mortality in changing environments

Where we're headed:

Testing predictions of the Cognitive Buffer hypothesis in the context of urbanization

- -Cities are evolutionarily novel environments
- -Cognitive testing across an urbanization gradient

Masai Mara National Reserve



Talek town 2009
Rapid urbanization in progress

Talek town 2013
Rapid urbanization in progress

Urban hyenas in Mekelle, Ethiopia: city-dwelling for ≥ 500 years

Compare performance among ancestral, rapidly urbanizing & fully urbanized populations

Serena: Stable ancestral environment

Talek: Rapidly urbanizing environment

Mekelle: Stable urban environment

Administer battery of 7 tasks:

Learning, memory behavioral flexibility & executive function

Calculate ‘g’ using a psychometric factor-analytical approach, & calculate selection gradient on ‘g’ in each habitat

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The Mara hyenas