

THEORIES OF HUMAN UNIQUENESS (PART 2)



HEB 1330: Primate Social Behavior
24 November 2020

TODAY

- Self-domestication hypothesis
- Cooperative breeding hypothesis

NATURE OF HUMAN-PRIMATE DIFFERENCES

- Sociality: social vs ultra-social
- Communication: imperative vs informative
- Cognition: empirical vs hypothetical
- Social learning: traditions vs. cumulative culture

What were the selection pressures underlying human-unique traits?

3 THEORIES OF HUMAN UNIQUENESS

- Cultural niche hypothesis
- Cooperative breeding hypothesis
- Self-domestication hypothesis

SELF-DOMESTICATION HYPOTHESIS

- Selection against aggression during the course of human evolution has facilitated the high levels of prosociality, tolerance, and cooperation that characterize human society

SELF-DOMESTICATION HYPOTHESIS

- Fox domestication experiment
- Domestication syndrome
- Self-domestication in humans?
- Self-domestication in primates?

DOMESTICATION

- Artificial selection for tameness/selection against (reactive) aggression

DOMESTICATION

- Artificial selection for tameness/selection against (reactive) aggression
- *Self-domestication*: natural selection favoring tameness/reduction in aggression

FOX DOMESTICATION

Belyaev's fox-breeding experiments:
selection for “low reactivity to humans”

- Given food while stroked / handled monthly, 1-6 months old
- Scored at 7-8 months.



Strong reaction
Excluded



Low fear
Chosen for breeding

Low inbreeding coefficient (.02-.07)

Trut L (1999) Early canid domestication: the farm-fox experiment. *Am Sci* 3-4, 160-169

FOX DOMESTICATION

Many unselected consequences



Floppy ears



Short legs, short tail



Curly tail

FOX DOMESTICATION

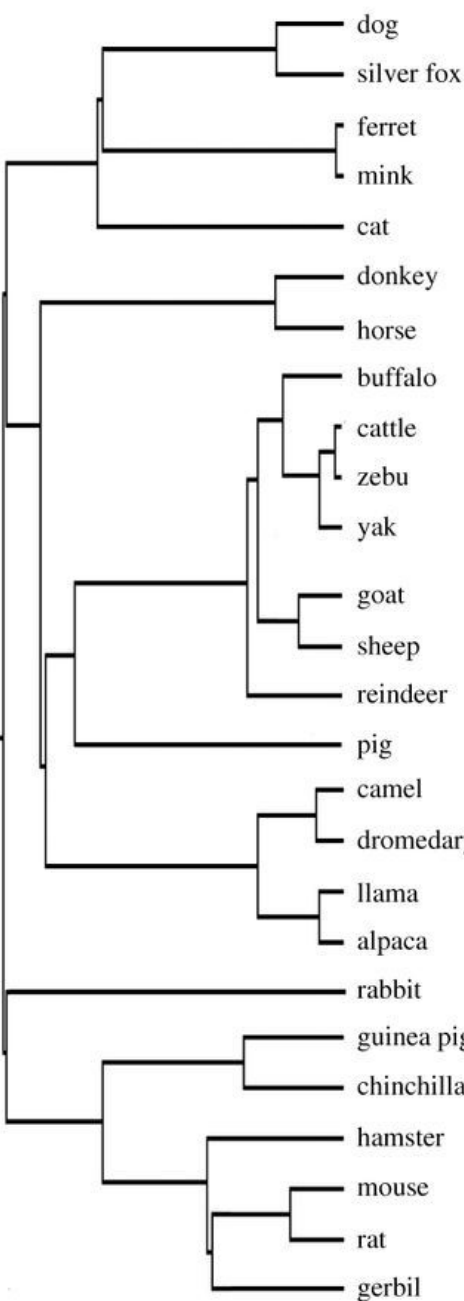


Alisa, one of two Novosibirsk foxes living as pets in a wealthy home outside St. Petersburg, is friendly with her human companions and with the family's yellow Labrador too.

DOMESTICATION SYNDROME

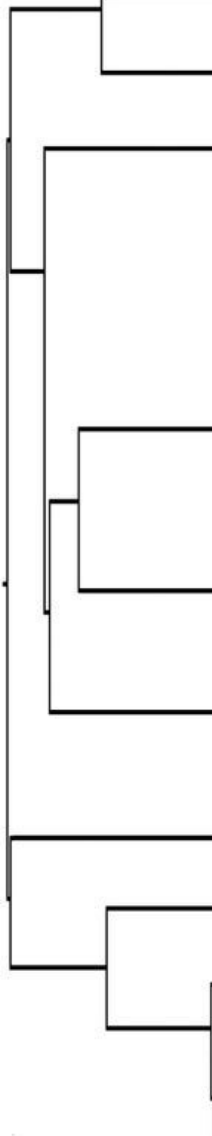


























- Domestication syndrome: suite of traits not selected for, but somehow linked to reduction in aggression

DOMESTICATION SYNDROME

		occur in all individuals/have occurred in early domesticated forms of a species							occur in some varieties/breeds of a species									pathway of domestication	
		increased tameness	decreased brain size	decreased heart weight	shorter muzzle	reduced tooth size	increased variability of vertebrae count*	change in caudal vertebrae count**	more frequent oestrus cycles	floppy ears	curly tail	supernumerary toes	disproportionate dwarfism***	depigmentation	increased skin area; skin folds	hairlessness	wool		curly hair
	dog	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	C
	silver fox	X	x (?)		X				X	X	X			X					D
	ferret	X	X	X										X					D
	mink	X	X											X					D
	cat	X	X		X			X		X	X		X	X		X	X		C
	donkey	X	X							X				x (?)					D
	horse	X	X				X			X		X	X	X		X			D
	buffalo	X												X					P
	cattle	X	X		X					X			X	X	X	X	X		P
	zebu	X								X				x (?)	X				P
	yak	X	X											X					P
	goat	X	X		X					X	X			X	X		X		P
	sheep	X	X		X				X		X			X	X	X	X	X	P
	reindeer	X													X				P
	pig	X	X	X	X	X	X				X	X	X	X	X	X	X	X	C
	camel	X	X												X				D
	dromedary	X	X												X				D
	llama	X	X	X									X		x (?)			X	P
	alpaca	X	X	X										X	X	X		X	P
	rabbit	X	X	X							X				X	X	X	X	D
guinea pig	X	X	X							x (?)				X				C	
chinchilla	X													x (?)				D	
hamster	X													X				C/D	
mouse	X		X	X	X				X					X		X	X	C	
rat	X	X	X						X					X				C	
gerbil	X	X							X					x (?)				D	

DOMESTICATION SYNDROME

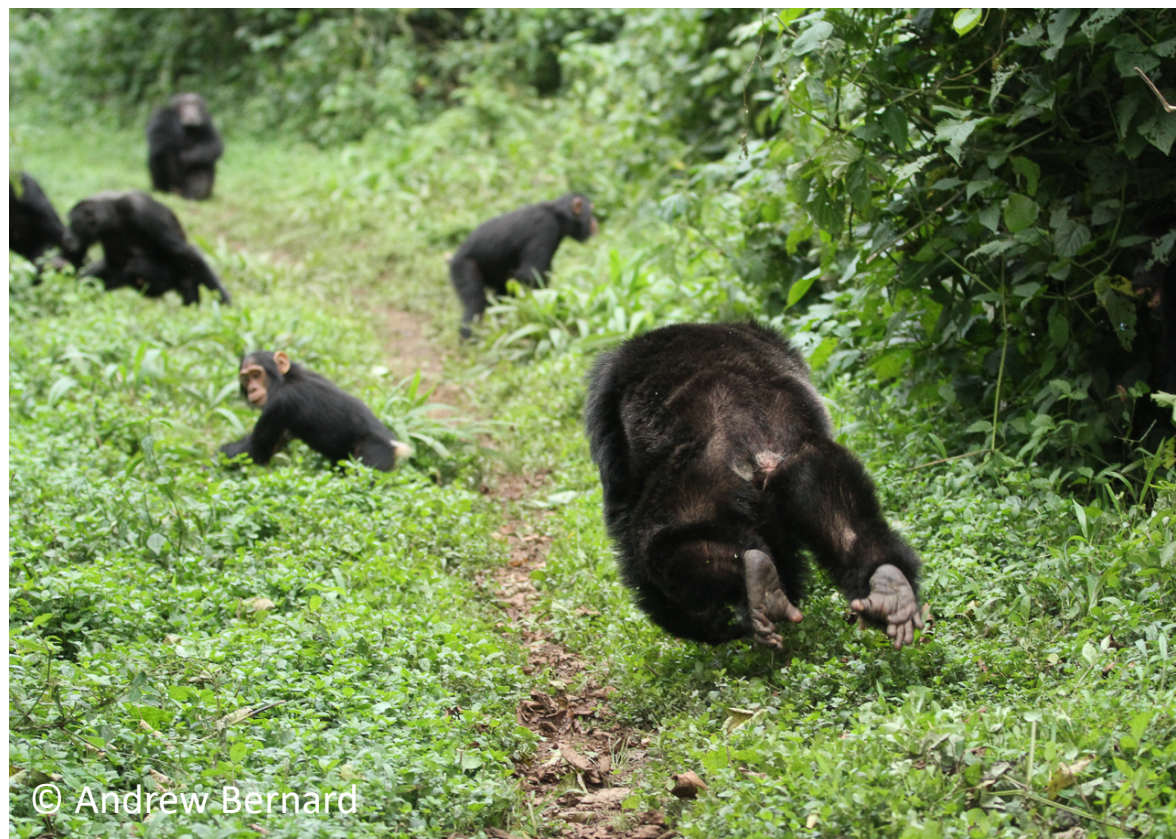
- Do humans exhibit traits of the domestication syndrome?

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	ferret		X	X	X									X					D
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	cat		X	X		X			X		X	X		X	X		X	X	C
	donkey		X	X							X				X (?)				D
	horse		X	X				X			X		X	X	X		X		D
	buffalo		X												X				P
	cattle		X	X		X					X		X	X	X	X	X		P
	zebu		X								X				X (?)	X			P
	yak		X	X											X				P
	goat		X	X		X				X	X			X	X		X		P
	sheep		X	X		X			X		X			X	X	X	X	X	P
	reindeer		X												X				P
	pig		X	X	X	X	X	X			X	X	X	X	X	X	X	X	C
	camel		X	X											X				D
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chinchilla		X												X (?)					D
hamster		X												X					C/D
mouse		X		X	X	X			X					X		X		X	C
rat		X	X	X					X					X					C
gerbil		X	X						X					X (?)					D

DOMESTICATION SYNDROME

- Do humans exhibit traits of the domestication syndrome?

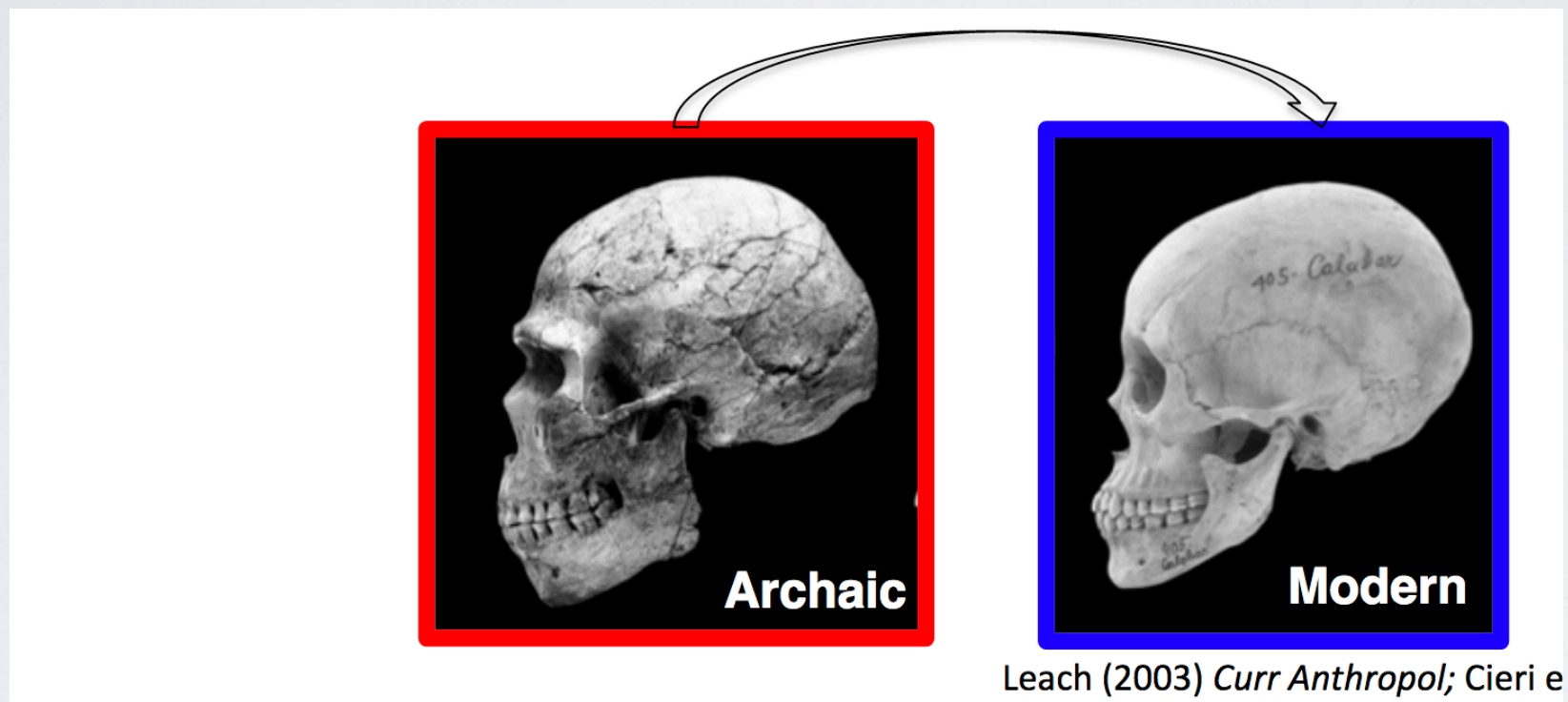
Human males 'scuffle' at $\sim 1/1000^{\text{th}}$ chimpanzee rate
Reactive aggression very reduced in humans



© Andrew Bernard

DOMESTICATION SYNDROME

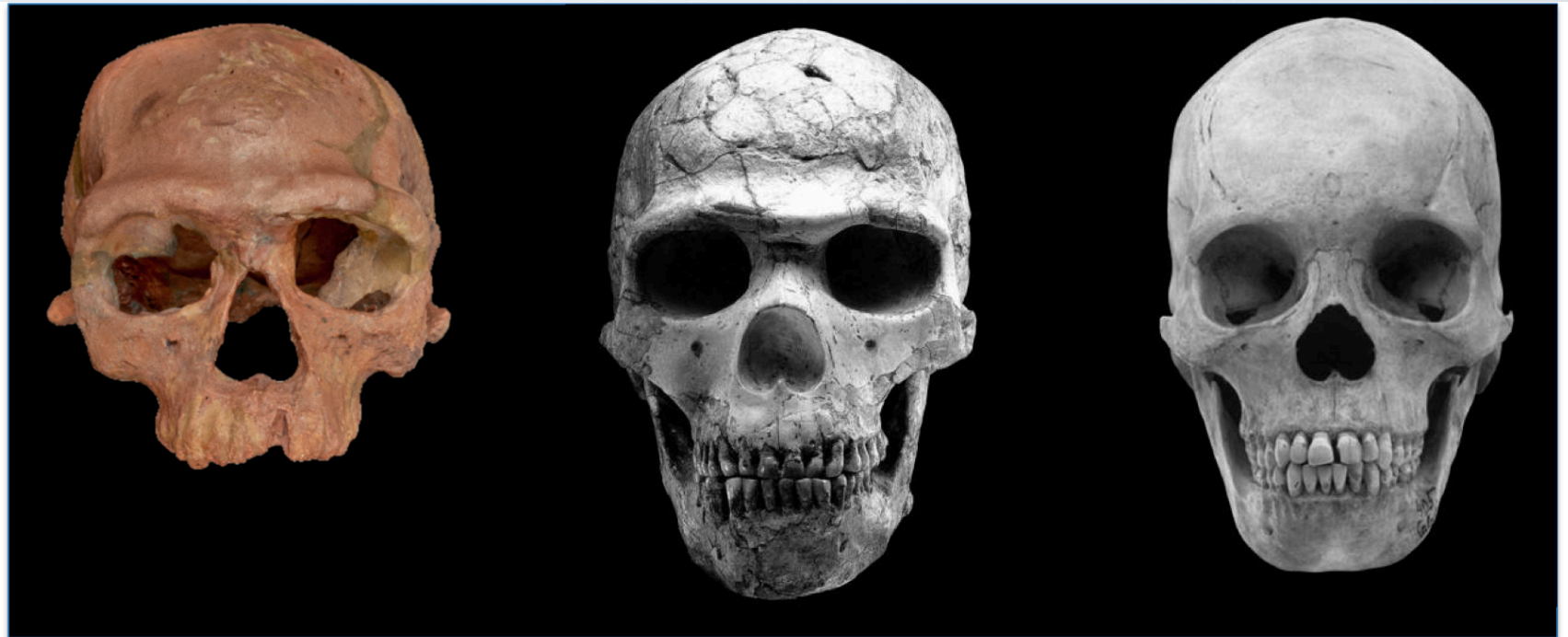
- Do humans exhibit traits of the domestication syndrome?



- Lighter body
- Shorter face, smaller teeth
- Juvenilization of skull and skeleton
- 10-15% brain reduction in las 30,000 years

DOMESTICATION SYNDROME

- Do humans exhibit traits of the domestication syndrome?



Jebel Irhoud
H. sapiens (?)
350-280 ka
Stringer & Galway-
Witham 2017

Skhul 5
H. sapiens
110 ka
© D. Brill
Cieri et al 2014

African
H. sapiens
Recent
© D. Brill
Cieri et al 2014⁵²

- Lighter body
- Shorter face, smaller teeth
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DOMESTICATION SYNDROME

- **Do humans exhibit traits of the domestication syndrome?**



- Increased vocal flexibility due to effects of domestication?

DOMESTICATION SYNDROME

- **Do humans exhibit traits of the domestication syndrome?**



- Homosexual preference (to the exclusion of heterosexual preference) a result of domestication?

DOMESTICATION SYNDROME

- Do humans exhibit traits of the domestication syndrome?



Vitiligo=depigmentation from domestication?

2 ROUTES TO HUMAN SELF-DOMESTICATION

- Cultural niche: social institutions and norms favor less aggressive individuals, who follow rules, etc (Prof. Henrich)
- Selective coalitionary proactive aggression, aka capital punishment (Prof. Wrangham)

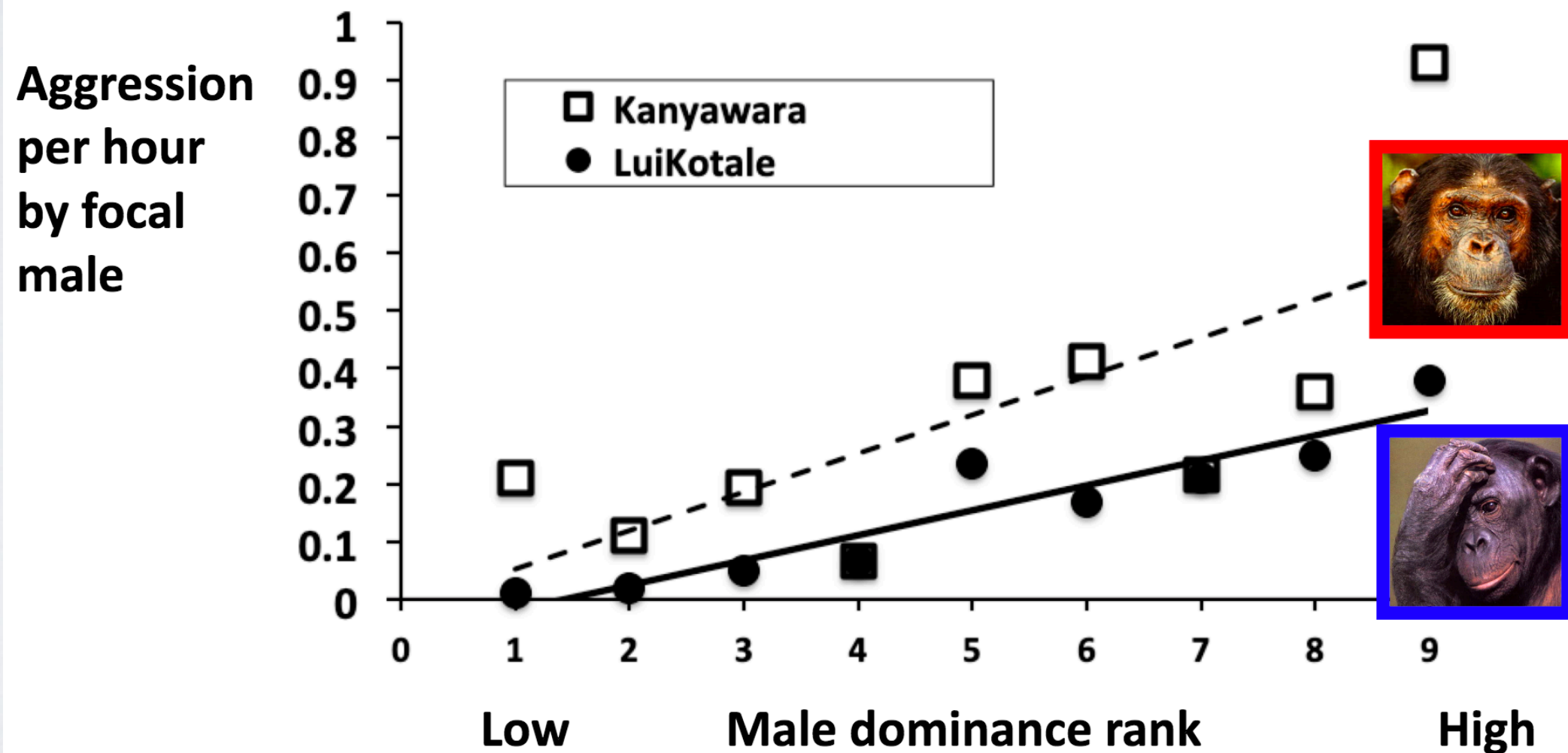
SELF-DOMESTICATION IN PRIMATES?

- Bonobos
- Marmosets

BONOBOS

Bonobos & chimpanzees: contact + non-contact aggression

- (1) higher-ranking males more aggressive
- (2) chimpanzees ca. 2x more aggressive than bonobos



Data: Muller & Wrangham (2004) *Anim Behav* 67, 113-123; Surbeck et al (2012) *Anim Behav* 83, 659-669

BONOBOS



©FRANS LANTING

BONOBOS



BONOBOS

- Plausible domesticated traits in bonobos

Morphology

- reduced cranial capacity and telencephalon
- juvenilized cranium
- smaller canine teeth
- reduction of pigment in lips and tail

Behaviour & Psychology

- delays in psychological development
- increased tolerance & decreased xenophobia resulting in less aggression
- increased adult play & sexual behaviour
- decrease in predatory motivation
- altered levels of emotional reactivity

Neurobiology & Psychology

- altered HPA axis
- altered serotonergic system
- altered size, organization or connectivity of occipital frontal cortex and amygdala
- altered levels or reactivity of androgens

Figure 1. A model of bonobo evolution due to selection for tolerance and against aggression.

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Figure 1. A model of bonobo evolution due to selection for tolerance and against aggression.

Features in bonobo society that led to non-aggression being favored?

MARMOSETS

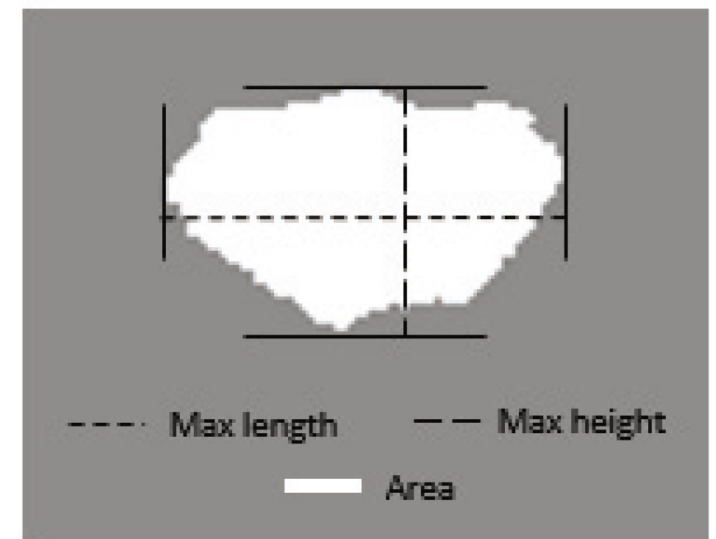
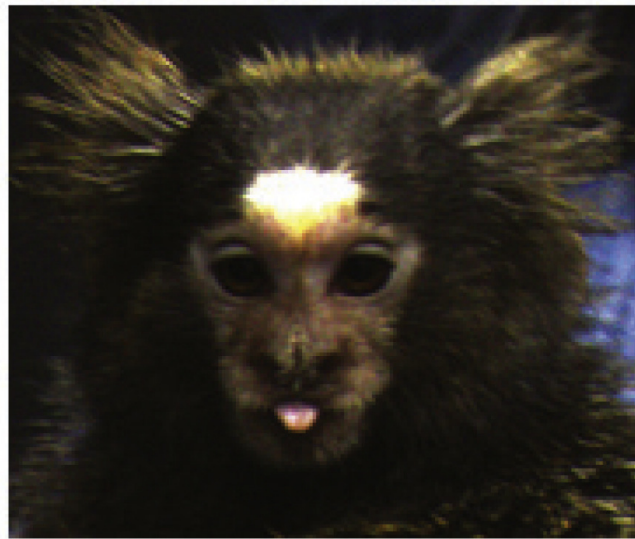
- White patch on forehead is thought to be part of domestication syndrome
- Size and rate of growth of white patch varies between individuals
- Are size and growth rate linked to degree of domestication?

A

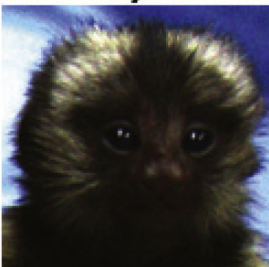


MARMOSETS

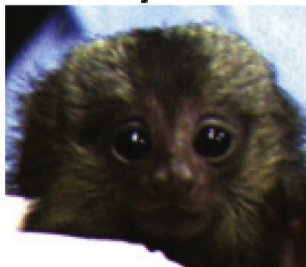
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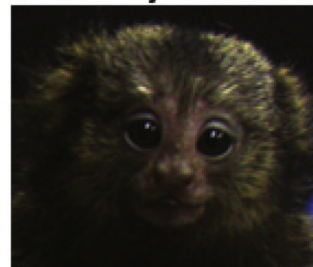
Day 4



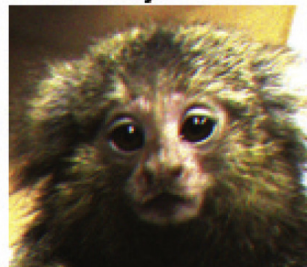
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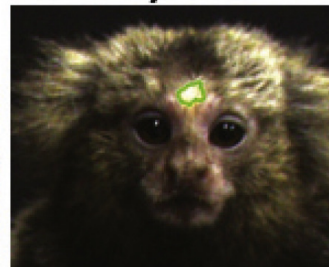
Day 49



Day 74



Day 103



Day 124



Day 152

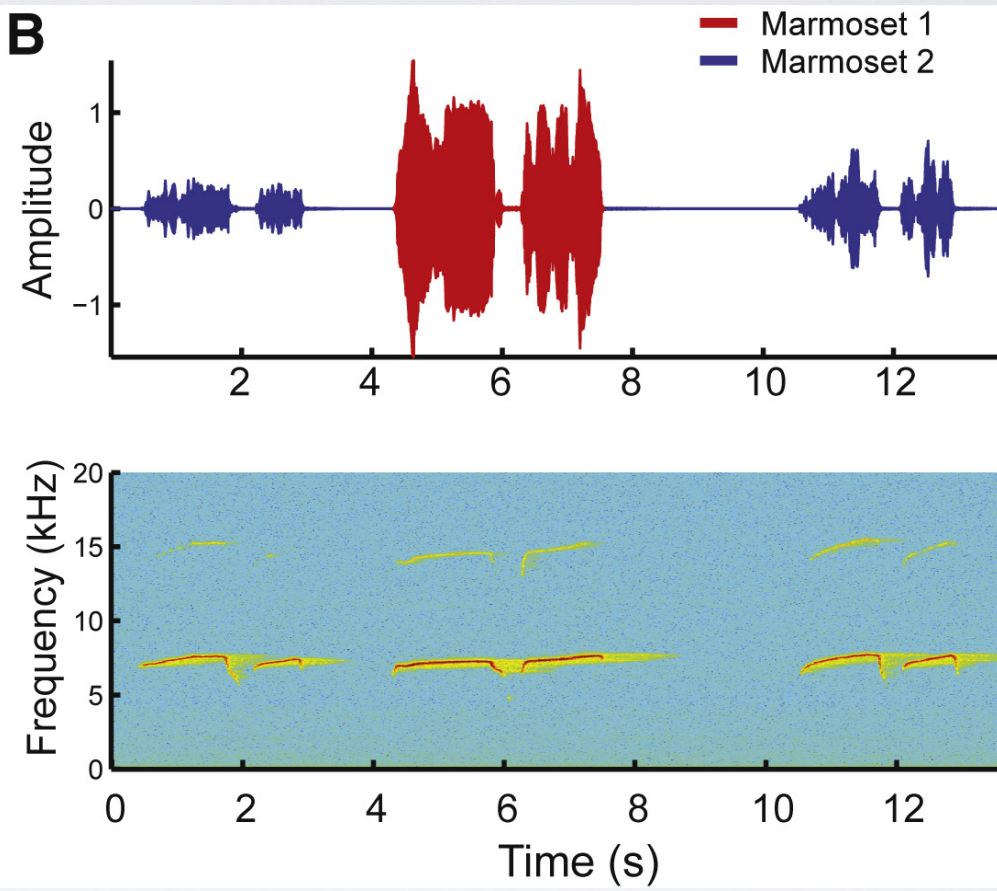


MARMOSETS

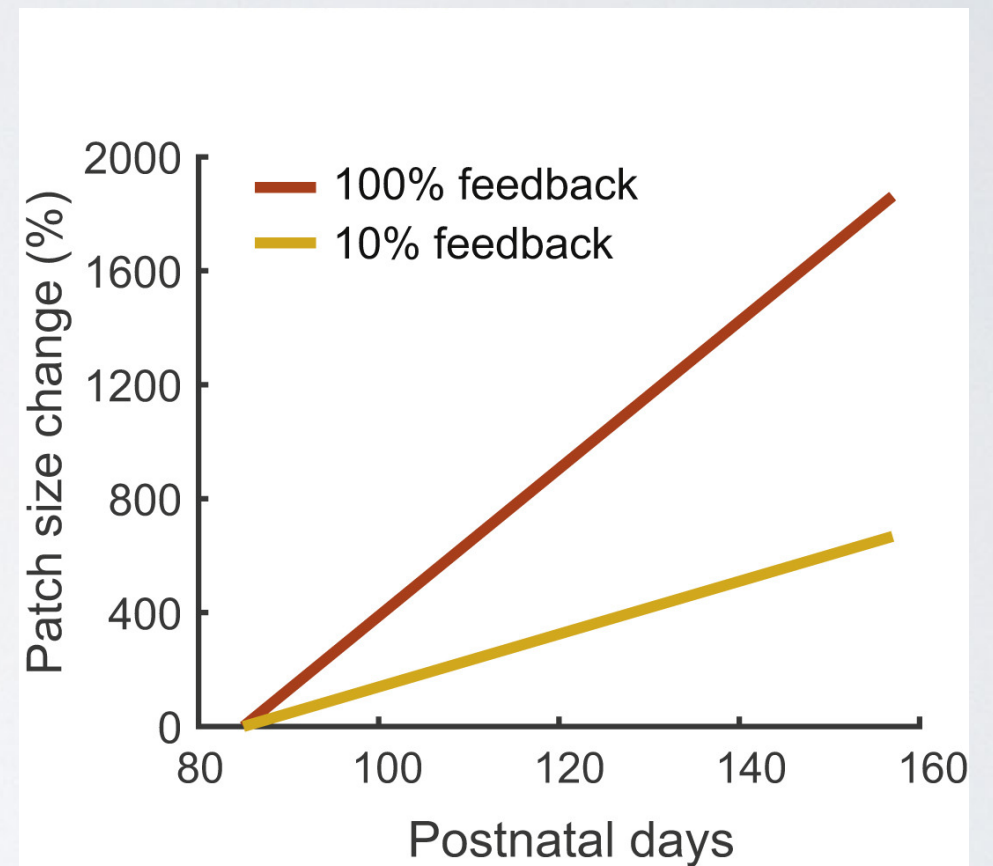
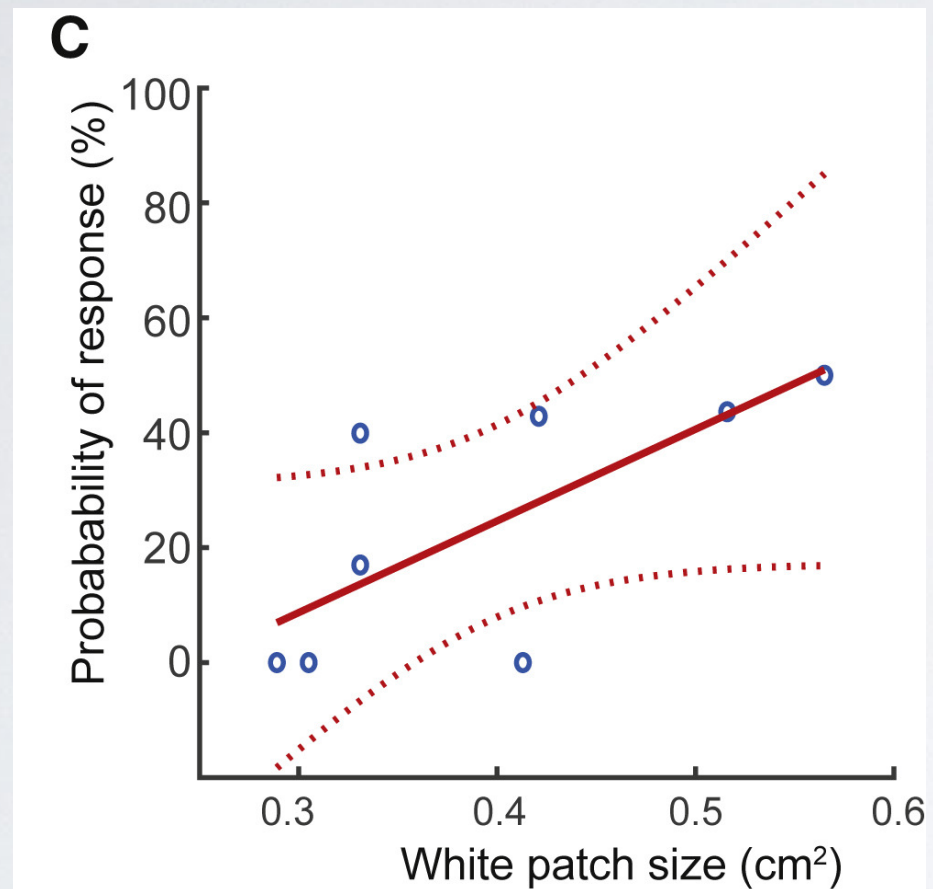
A



B



MARMOSETS



SELF-DOMESTICATION HYPOTHESIS

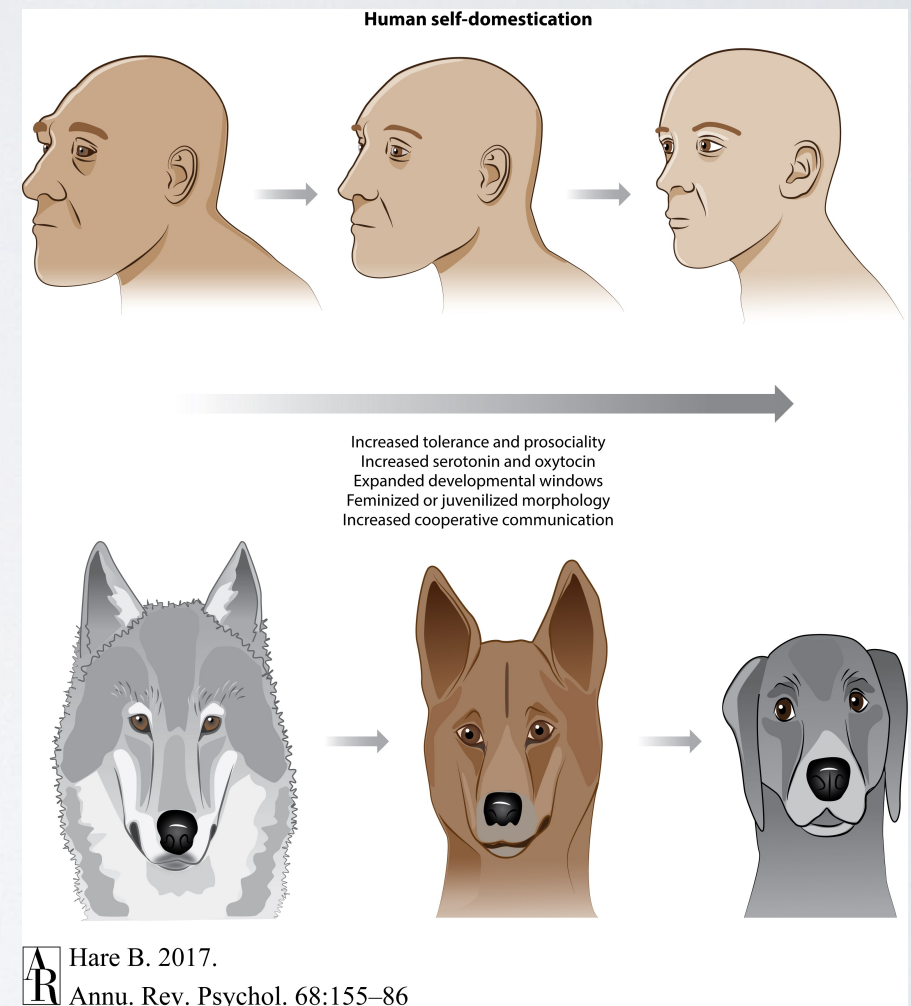
Table 1 Evidence for domestication syndrome in modern humans

	Dog versus wolf ^a	Experimental fox versus control fox ^a	Bonobo versus chimpanzee ^a	Holocene humans versus Lower Paleolithic humans
Aggression	Lower-intensity inter- and intragroup aggression in feral dogs	Experimental but not control foxes are nonaggressive toward humans	Lower intensity inter- and intragroup aggression in bonobos	Intragroup tolerance allows and is favored due to demographic pressure in Holocene humans (Cieri et al. 2014, Henrich 2015)
Physiology	Dogs show a muted stress response when interacting with humans	Higher basal serotonin and lower corticosteroids in experimental foxes	Bonobos have more a passive coping response to social stress	Holocene humans exhibit morphologically inferred reductions in neonatal androgens and pubertal testosterone levels and increased brain serotonin and oxytocin availability (Cieri et al. 2014, Nelson et al. 2011)
Morphology	Dogs show reduced cranial capacity and depigmentation of the coat	Experimental foxes show a feminized skull and depigmentation of the coat	Bonobos show reduced cranial capacity, feminized faces, and depigmentation of lips and tail tufts	Holocene humans exhibit a modest reduction in cranial capacity, feminized faces, globular cranial development, and depigmentation of the sclera (Cieri et al. 2014, Hublin et al. 2015, Tomasello et al. 2007)
Prosocial behavior	Dogs are more attracted to humans than to conspecifics	Experimental foxes are more attracted to and interested in playing and interacting with humans as adults	Bonobos exhibit more play and sociosexual behavior as adults, voluntarily share food, and are more food tolerant	Holocene humans exhibit extreme levels of intragroup food sharing, helping, and social bonding (Kramer 2014, Warneken 2015)
Expanded developmental window	Period of socialization with humans begins earlier and lasts longer in dogs; dogs retain the juvenile vocal repertoire into adulthood	Period of socialization with humans begins earlier and lasts longer in experimental foxes; experimental foxes retain the juvenile vocal repertoire into adulthood	Nonreproductive sociosexual behaviors that create tolerance emerge early and last throughout adulthood in bonobos; cognitive skills related to spatial memory and social inhibition exhibit delayed development in bonobos	Holocene humans exhibit early-emerging social cognition and graded brain development with extreme delays in synaptic pruning of cortical regions (Casey & Caudle 2013, Somel et al. 2009, Wobber et al. 2014)
Social cognition	Dogs are more sensitive to human social cues	Experimental foxes are more sensitive to human social cues	Bonobos attend to eyes and exploit a human's gaze more and show increased cooperative flexibility	Holocene humans exhibit increases in cooperative communication, cultural ratcheting, and coordinated defense against out-groups, as well as expanded social networks (Cieri et al. 2014, Hare 2011)

^aNonhuman comparisons are based on Hare et al. (2012)

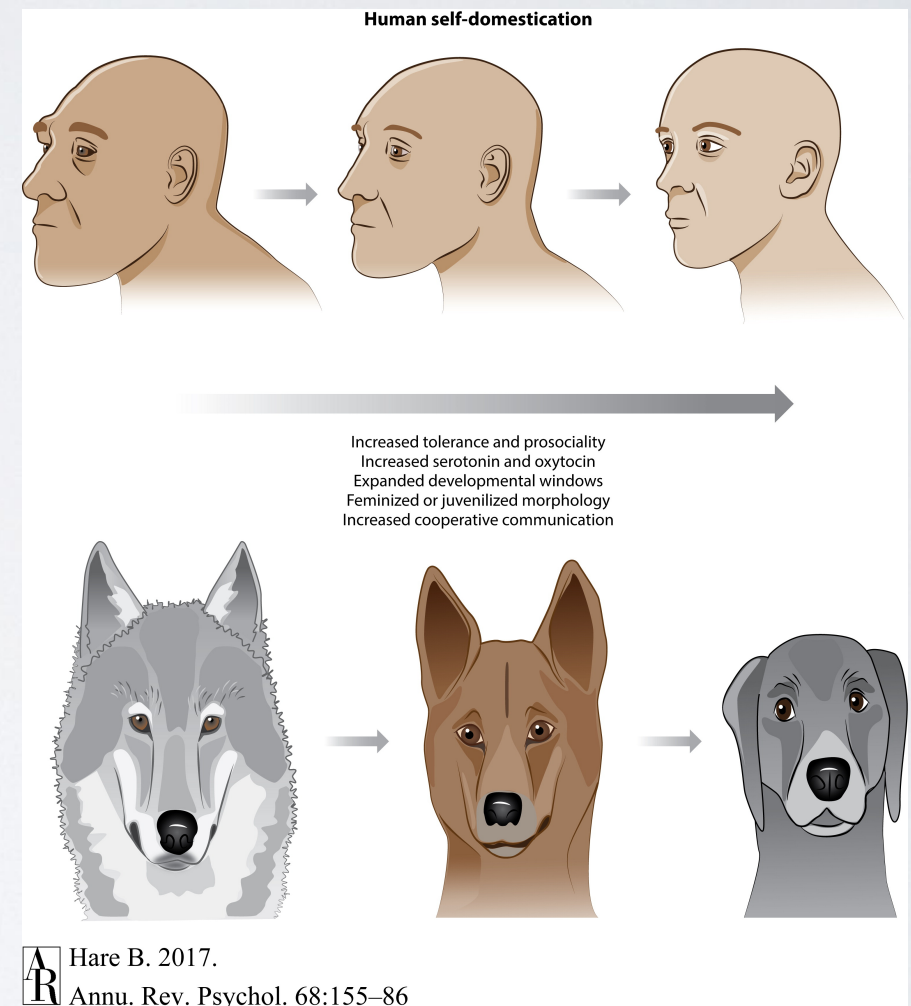
SELF-DOMESTICATION HYPOTHESIS

- Prosociality and cooperation
- Language
- Brain size
- High-fidelity social learning
- Theory of mind
- Life history



SELF-DOMESTICATION HYPOTHESIS

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COOPERATIVE BREEDING HYPOTHESIS

COOPERATIVE BREEDING

- Social system in which non-parents (alloparents) provide care for infants
- Often involves reproductive suppression (i.e., the alloparents or 'helpers' do not have their own offspring)
- Examples: meerkats, red wolves, naked mole rats, callitrichids



CALLITRICHIDAE

- Offspring often stay as adults (delayed dispersal)
- Twins (80% pregnancies):
 - total 20% mother's weight
 - need carriage, food, protection
- Non-breeders help with:
 - vigilance against predators
 - territorial defense
 - allo-parenting
- Alloparenting performed by:
 - juveniles
 - non-breeding adults
 - polyandrous males



Lottker et al. (2004, 2007) *Am J Primatol*

ARE HUMANS COOPERATIVE BREEDERS?

<div> <div>Alloparents = Helpers</div> <div> <div>Allomothers</div> <div>Care-givers</div> </div> </div>				
Mother	(likely) Sire	Weaned offspring	Others	
++	+++	++	++	Callitrichids ¹
++	(+)	++	++	Capuchin monkeys ^{2,3,4,9}
+++	0	0	(+)	Squirrel monkeys ^{2,3,10}
++	+++	(+)	0	Owl & Titi monkeys ^{2,3}
+++	0	0	(+)	OWMs & Great apes ^{2,3}
+++	+(+)	+(+)	+(+)	Humans ^{11,12}

ARE HUMANS COOPERATIVE BREEDERS?

- In cooperative breeding species, an infant's provisioning needs surpass that of a single mother
- If alloparental support likely to be insufficient, mothers will abandon newborn
- Cotton-top tamarins: 12% of infants abandoned when older offspring present; 57% of infants abandoned when other offspring were too young to help
- Compared to most primates, humans are very sensitive to levels of allomaternal support and infant defects; occasionally abandon/kill own infants
- Humans, Tamarins, Marmosets are only primates that regularly (though rarely) abandon infants



ARE HUMANS COOPERATIVE BREEDERS?

- Non-breeding group of alloparents?
- Grandmothers!
- Living beyond ability to reproduce is uncommon
- Post-menopausal longevity may be an adaptation supporting the unusual combination of short-interbirth intervals and long juvenile period



Grandma Schamberg with 2 grandkids

COOPERATIVE BREEDING HYPOTHESIS

- Why would cooperative breeding lead to the evolution of humans' unique traits?



COOPERATIVE BREEDING HYPOTHESIS

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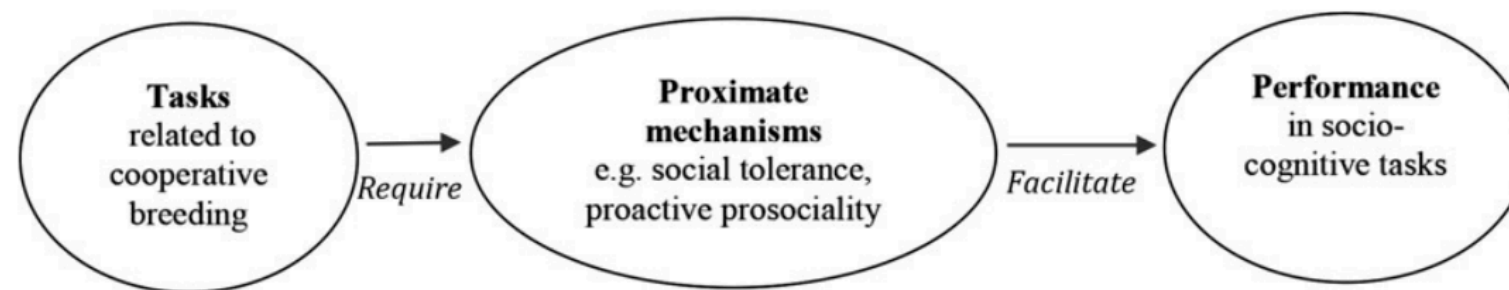


Figure 1 The hypothesized pathway for a link between cooperative breeding and socio-cognitive performance. The cooperative breeding hypothesis predicts that cooperative breeding – or extensive allomaternal care – is associated with a set of proximate mechanisms necessary to support and enable allomaternal behaviours. At the same time, these proximate mechanisms facilitate performance (but not necessarily ability) in a variety of socio-cognitive tasks. For instance cooperatively breeding primates show increased levels of social tolerance, which is necessary to ensure smooth infant transfers in the canopy. At the same time, however, social tolerance also facilitates performance in social learning tasks (see text).

COOPERATIVE BREEDING AND THEORY OF MIND

- Evidence that parental care is linked to ToM abilities?
 - Across taxa, females more socially responsive than males
 - Boys and girls readily console, but boys require stronger signal of distress
 - Mothers respond to weaker signals of infant stress than fathers
 - Women outperform men in mentalizing tasks (may reflect ability or motivation)

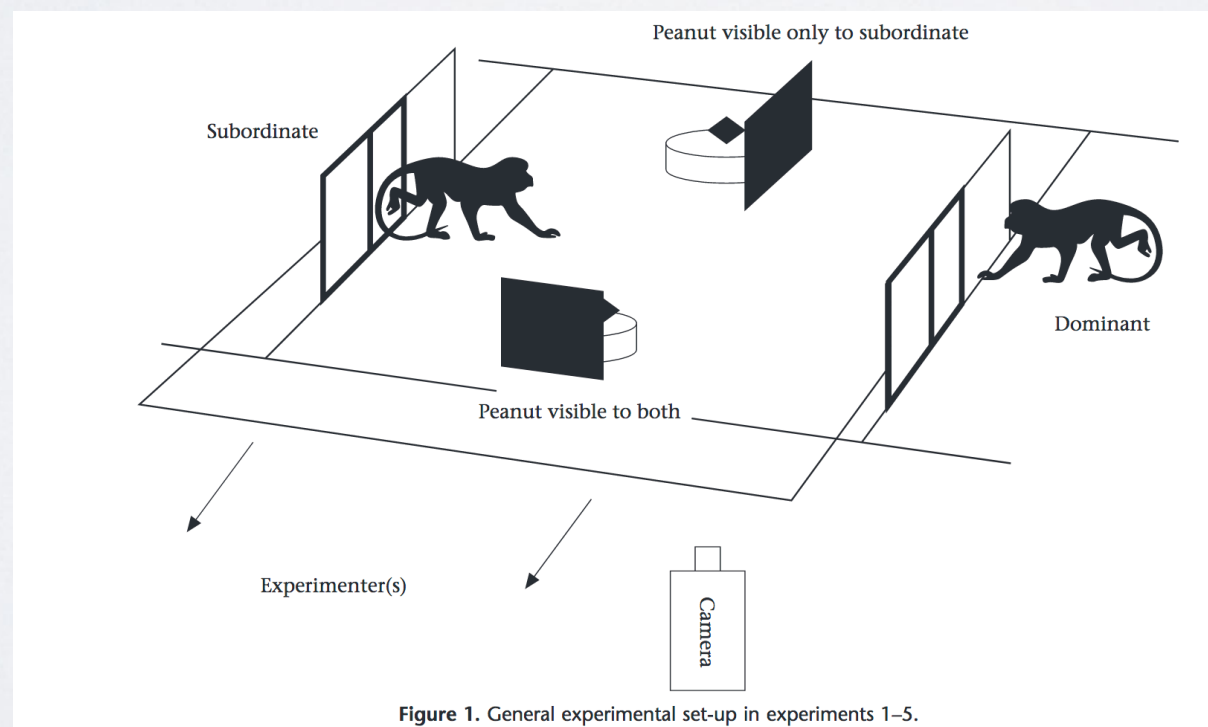


COOPERATIVE BREEDING AND THEORY OF MIND

- **Prediction:** Widespread alloparental care should favor increased social sensitivity, mindreading in alloparents. Cooperative breeding species should outperform independently breeding species on ToM tasks

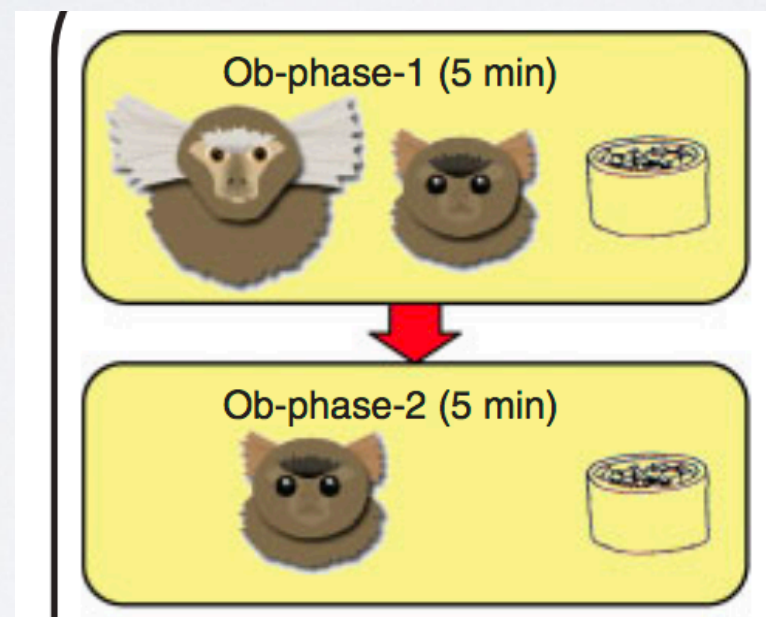
COOPERATIVE BREEDING AND THEORY OF MIND

- **Prediction:** Widespread alloparental care should favor increased social sensitivity, mindreading in alloparents. Cooperative breeding species should outperform independently breeding species on ToM tasks
- **Result:** Marmosets demonstrated theory of mind-like ability in task that Hare et al. (2000) developed for chimpanzees. Big-brained capuchins failed the test.



COOPERATIVE BREEDING AND THEORY OF MIND

- **Prediction:** Widespread alloparental care should favor increased social sensitivity, mindreading in **alloparents**. Cooperative breeding species should outperform independently breeding species on ToM tasks
- **Result:** Mothers modify vocal behavior based on attentional state and age of infant



- Mothers vocalized when 11-15 week old infants were not paying attention to foraging task, but did not vocalize when they were paying attention.
- Mothers did not vocalize in presence of 19-23 week-old infants (nor when alone).

COOPERATIVE BREEDING AND THEORY OF MIND

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COOPERATIVE BREEDING AND THEORY OF MIND

- **Prediction:** Widespread alloparental care should favor increased social sensitivity, mind reading in **care recipients**. Cooperative breeding species should outperform independently breeding species on ToM tasks
- **Result:** In humans, performance on false belief test associated with number of older siblings

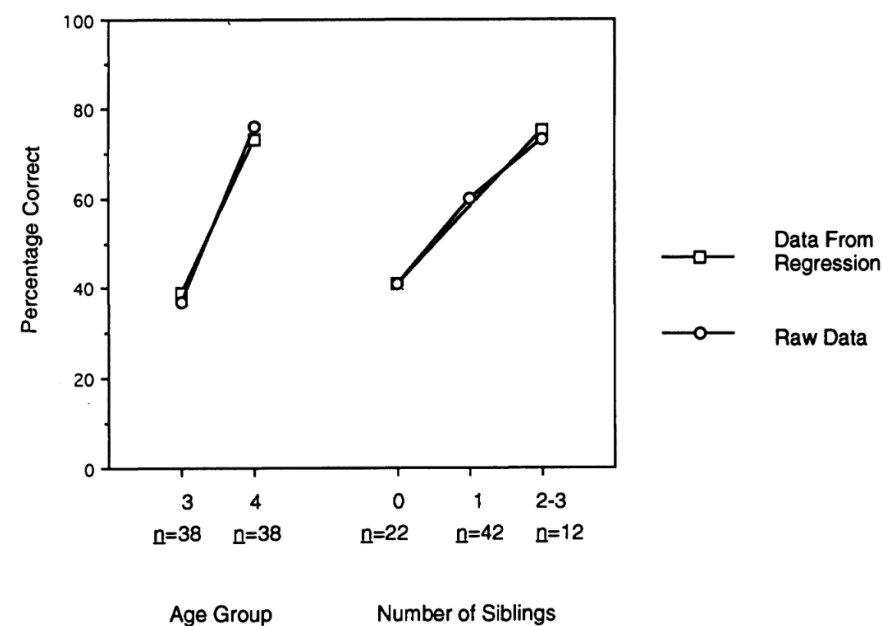


FIG. 1.—Percent children giving correct answer to the belief question in Experiment 1, according to age and family size. Three-year-olds: mean = 3-6; 4-year-olds: mean = 4-4; regression equation for age: $Y = 1.78x - 6.66$; regression equation for size: $Y = .74x - 1.11$.

COOPERATIVE BREEDING AND COMMUNICATION

- Vocal communication more common when individuals spatially/visually separated
- Great apes mother-infant pairs rarely need to vocalize with one another because offspring is usually on mother
- In cooperative breeders, infant often held by alloparents; often cannot see mother.
- Infants may benefit from signals to alloparents to elicit care/provisioning
- Infants often different color from adults in species with alloparental care (e.g., most colobines)



Javan Langurs

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Dusky leaf monkey

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Black and white colobus

COOPERATIVE BREEDING AND VOCAL COMMUNICATION

- **Prediction:** Cooperative breeding species should exhibit more complex mother-infant vocal communication than independently breeding species

COOPERATIVE BREEDING AND VOCAL COMMUNICATION

- **Prediction:** Cooperative breeding species should exhibit more complex mother-infant vocal communication than independently breeding species
- **Result:** Among all primate infants, only humans and marmosets babble. Marmoset babbling may be seems to be associated with caregiving.

Table 1. Within subject differences in behavioral contexts during bouts of pigmy marmoset babbling (PMB) and periods of not babbling

	Mean number of observations per min		
	PMB	No PMB	Significance
Social behavior relating to infant-caregiver			
Infant being carried by caregiver	0.49	0.38	N.S.
Infant climbed on or was picked up by caregiver	0.33	0.02	*
Infant approached a caregiver	0.18	0.06	*
Caregiver approached infant	0.27	0.07	*
Infant being groomed by caregiver	0.11	0.03	*
Infant huddling with family members	0.29	0.14	*
Infant behavior unrelated to caregivers			
Infant drinking water or eating	0.07	0.11	N.S.
Infants' other behavior	0.56	0.31	*
Infant moving independently	0.85	0.43	*
Infant playing	0.13	0.08	N.S.

*Results are based on the mean number of observations per min, pooled over 754 observed PMB bouts for all eight subjects, aged 1–20 weeks (Wilcoxon matched pairs signed-rank test, two-tailed). *, significant; N.S., not significant.*

COOPERATIVE BREEDING AND TEACHING

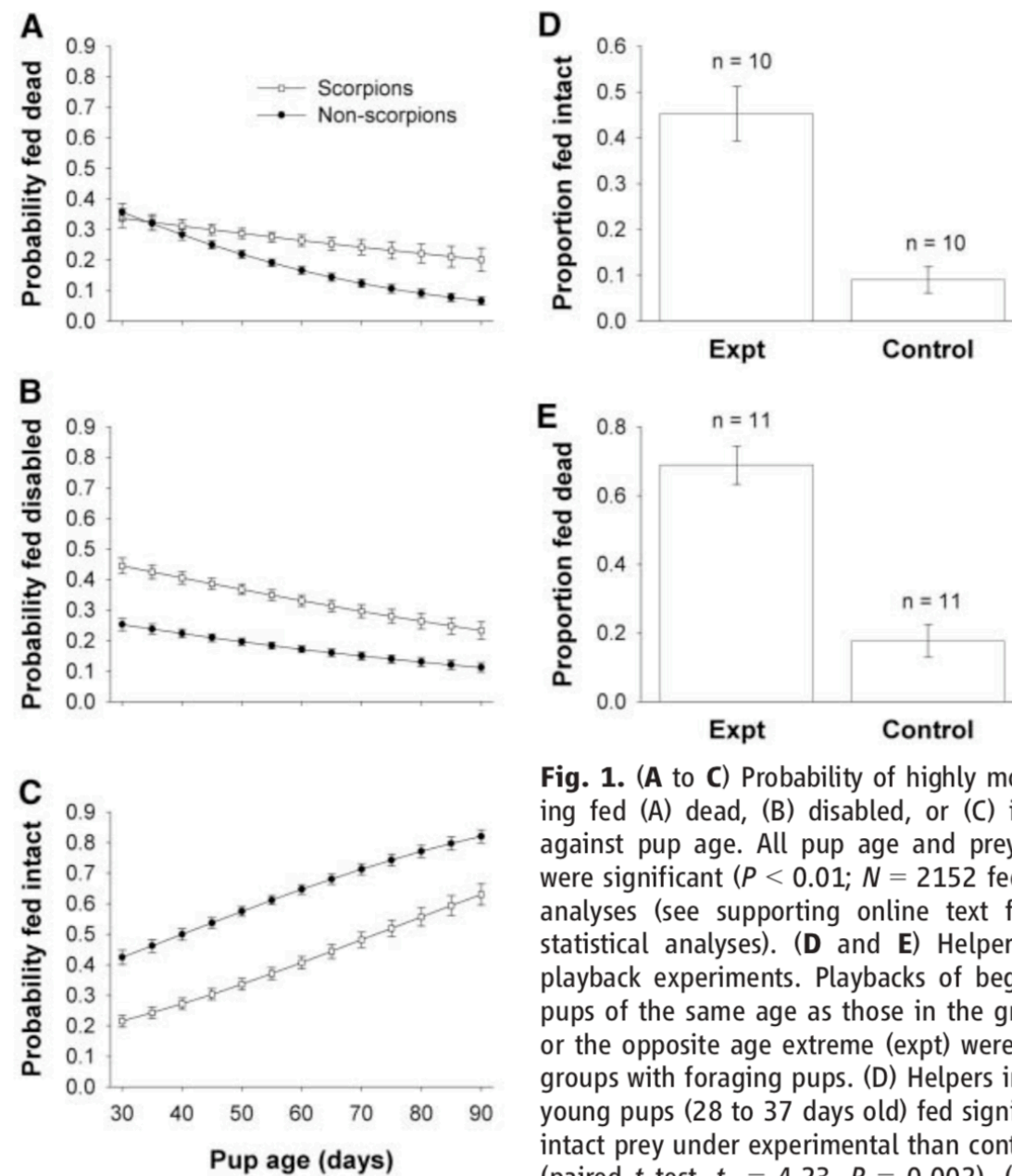


Fig. 1. (A to C) Probability of highly mobile prey being fed (A) dead, (B) disabled, or (C) intact plotted against pup age. All pup age and prey type effects were significant ($P < 0.01$; $N = 2152$ feeds) in GLMM analyses (see supporting online text for details of statistical analyses). (D and E) Helper response to playback experiments. Playbacks of begging calls of pups of the same age as those in the group (control) or the opposite age extreme (expt) were broadcast to groups with foraging pups. (D) Helpers in groups with young pups (28 to 37 days old) fed significantly more intact prey under experimental than control playbacks (paired t test, $t_9 = 4.23$, $P = 0.002$). (E) Helpers in groups with old pups (71 to 86 days old) fed

significantly more dead prey under experimental than control playbacks (paired t test, $t_{10} = 4.81$, $P = 0.001$).

<https://science.sciencemag.org/> on November 24, 2020



COOPERATIVE BREEDING HYPOTHESIS IN HUMANS

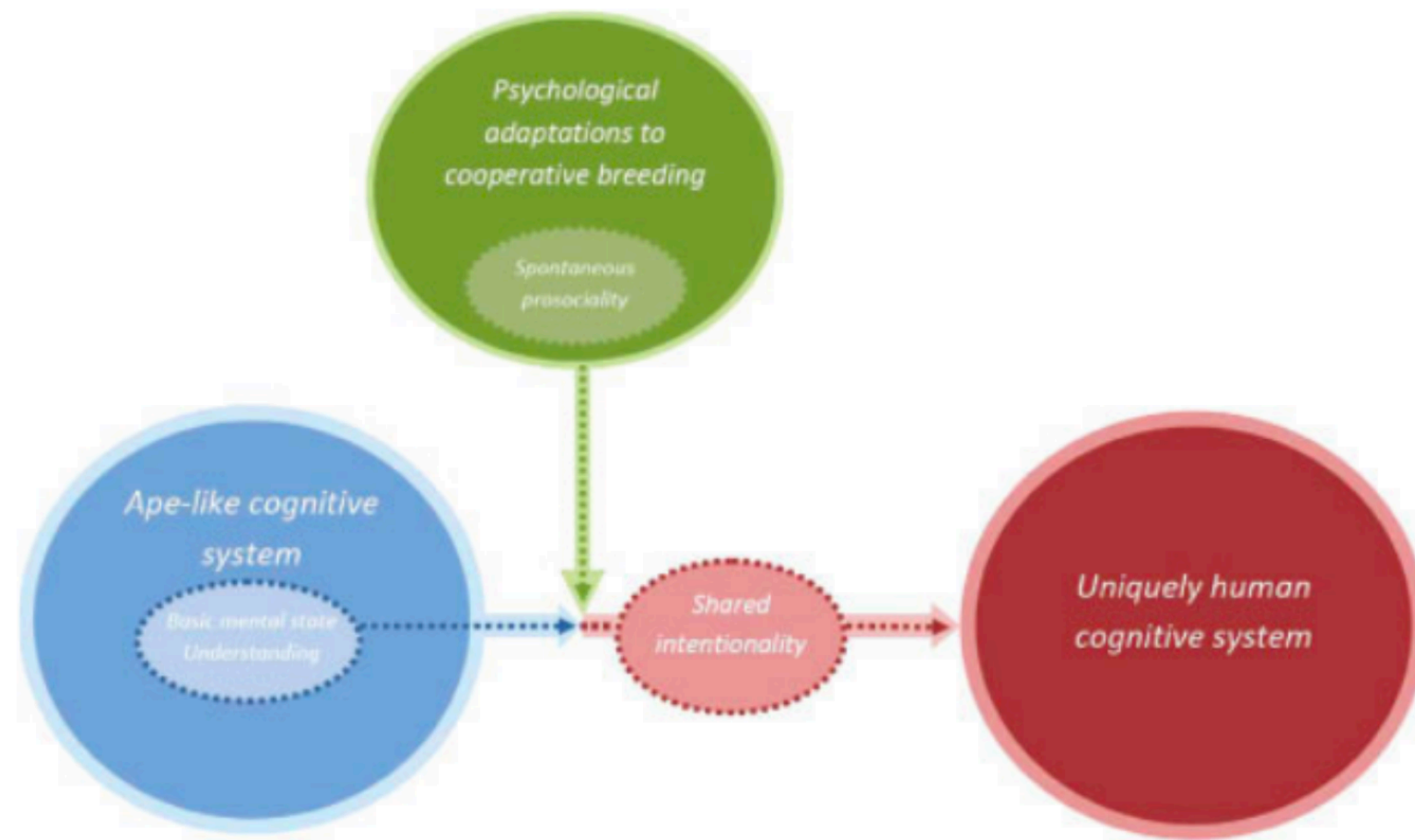
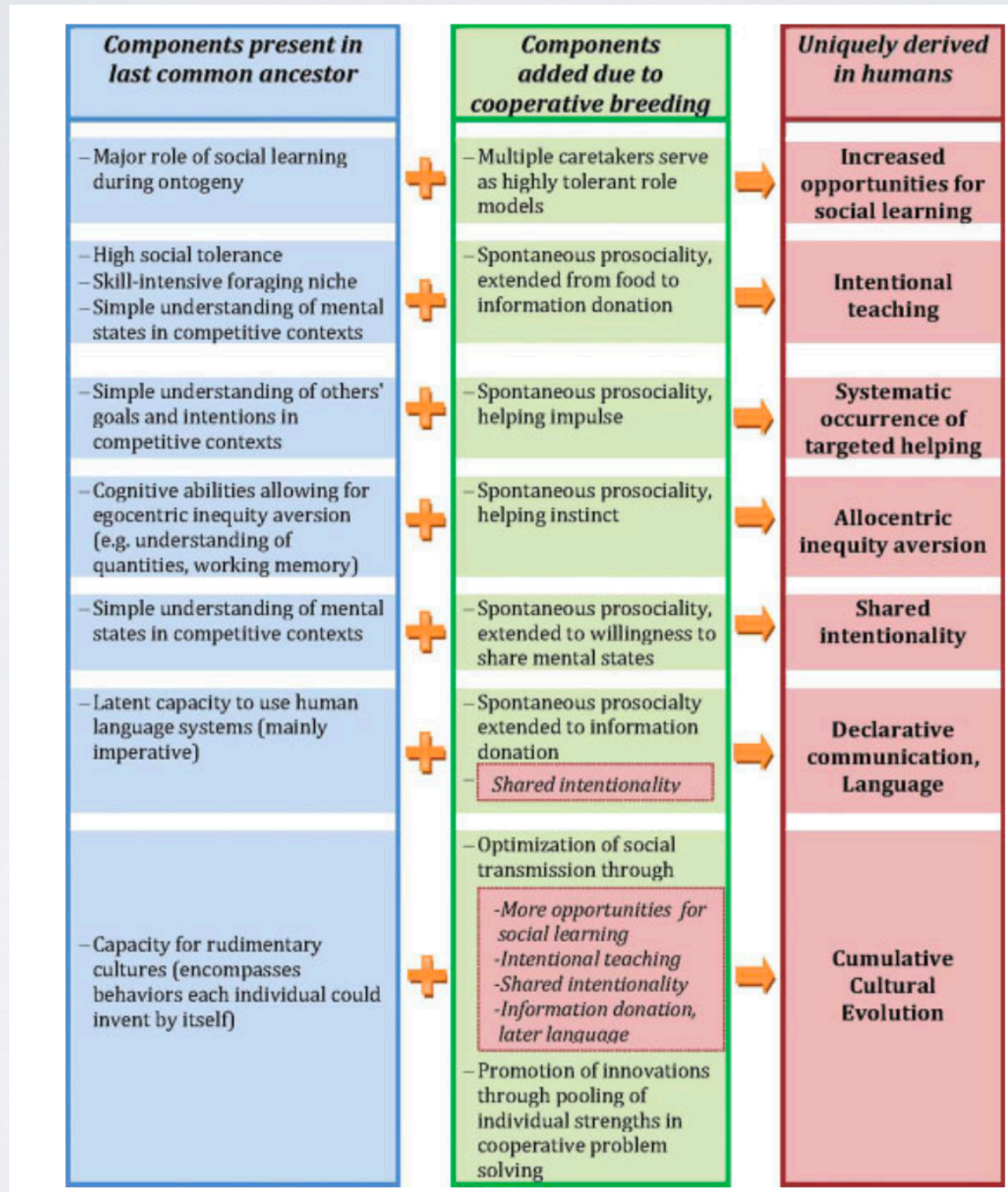


Figure 1. The role of cooperative breeding in the transition from ape-like to uniquely human cognition. In many species, engaging in shared care plus provisioning is likely to be accompanied by psychological adaptations such as increased social tolerance and spontaneous prosociality. These can increase cognitive performance in the social domain, as seen in callitrichids. In humans, however, spontaneous prosociality was added to an already ape-like cognitive system, among others capable of basic mental state understanding. In addition to the cognitive consequences observed in other cooperatively breeding species, this enabled the emergence of shared intentionality. Shared intentionality (see glossary) has been identified as a key difference between humans and other great apes; it is responsible for the emergence of uniquely human cognitive systems both phylogenetically and ontogenetically.²² (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

COOPERATIVE BREEDING HYPOTHESIS AND EVOLUTION OF HUMAN-UNIQUE TRAITS



CONVERGENT EVOLUTION IN HUMANS AND CALLITRICHIDS

- High levels of prosociality
- Above average ToM?
- Infant babbling
- Infant abandonment
- Short inter-birth interval

Ingredients in humans' special sauce?

- Prosociality and cooperation
- Language
- Brain size
- Social learning (over-imitation and high-fidelity copying)
- Theory of mind
- Long lifespan (esp. post-reproductive lifespan)

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QUESTIONS...ABOUT ANYTHING?