

The mammalian brain under domestication: Discovering patterns after a century of old and new analyses

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Abstract

Comparisons of wild and domestic populations have established brain reduction as one of the most consistent patterns correlated with domestication. Over a century of scholarly work has been devoted to this subject, and yet, new data continue to foster its debate. Current arguments, both for and against the validity of brain reduction occurring in domestic taxa, have repeatedly cited a small set of reviews on this subject. The original works, their sampling, methodological details, and nuances of results that would be key to establishing validity, particularly in light of new data, have not been investigated. To facilitate and encourage a more informed discussion, we present a comprehensive review of original brain reduction literature for four mammalian clades: Artiodactyla, Perissodactyla, Carnivora, and Glires. Among these are studies that generated the most cited brain reduction values in modern domestication literature. In doing so, we provide a fairer stage for the critique of traits associated with domestication. We conclude that while brain reduction magnitudes may contain error, empirical data collectively support the reduction in brain size and cranial capacity for domestic forms.

KEYWORDS

allometry, Artiodactyla, encephalization, skull

1 | INTRODUCTION

Differences in brain form between wild and domestic populations have been documented since at least the early 1900s (Herre, 1952; Klatt, 1912a, 1921). Mammals have been studied most, with reports of brain size reduction in domesticated Artiodactyla, Perissodactyla, Carnivora, Glires (Kruska, 1988), but the phenomenon has also been described in birds (Cnotka, 2006; Rehkamper et al., 2008; Sánchez-Villagra, 2022). Collectively, mammalian studies on this subject constitute over a century of research. However, reviews of domestication processes have repeatedly cited only a subset of these works, in support of brain reduction as a principal feature of the 'domestication syndrome' (Clutton-Brock, 1999; Herre &

Röhrs, 1990; Kruska, 1988; Price, 2002; Rehkamper et al., 2008; Wilkins et al., 2014; Wright et al., 2020; Zeder, 2012). Recently, the validity of this brain reduction pattern has been put into question (K. A. Lord, Larson, Coppinger, et al., 2020; K. A. Lord, Larson, Karlsson, et al., 2020; Wright et al., 2020), mainly as a consequence of genetic work highlighting the complexities of identifying truly wild ancestors of domesticated species (MacHugh et al., 2017; Orlando et al., 2013; Owen et al., 2014). It appears unlikely that any living wild population is directly ancestral to extant domesticated, due to introgression or admixture (gene flow between wild and domestic forms or between different wild populations), or extinction (Larson & Fuller, 2014; MacHugh et al., 2017). Consequently, there are legitimate concerns that proxies commonly used to characterize

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wild populations are not appropriate (K. A. Lord, Larson, Coppinger, et al., 2020; K. A. Lord, Larson, Karlsson, et al., 2020). Groups traditionally sampled as wild counterparts of domestics are, rather, closely related species or subspecies (Girdland Flink et al., 2014; Larson & Fuller, 2014; K. A. Lord, Larson, Coppinger, et al., 2020; MacHugh et al., 2017).

Another concern over brain reduction studies has been the use of body mass to correct for overall size differences (Clutton-Brock, 1999; Healy, 2021; Hemmer, 1990; Mason, 1984). Husbandry practices or breeding protocols, especially of livestock, often select for larger body mass, resulting in higher percentages of muscle or subcutaneous/intramuscular fat for domestics compared to wild populations (Hemmer, 1990; Kruska, 1988, 2011). The critique is that this may “inflate” or overestimate body size and bias brain reduction values in domestics (Clutton-Brock, 1999; Hemmer, 1990). However, all studies are not performed equally. Methods for measuring brain and body size vary across studies, and most make an effort to correct for differences in body mass composition. Thus, any argument for or against the validity of brain reduction in domestics should evaluate not only taxonomy, but also the methodological details of any cited work.

Our response to these concerns is that studies of brain change related to domestication will likely always be approximations, with different methodologies achieving different degrees of reliability and accuracy. Despite this, the collective of studies overwhelmingly supports a pattern of brain reduction correlated with a range of domestication “types.” Domestication is a process involving different degrees of animal-human interaction. In investigating brain size changes associated with it, it is fundamental to specify if the matter at hand is the initial domestication, associated with selection for tameness, or the intense selection associated with the creation of breeds. In reporting brain reduction values, summaries and overviews of this subject most often cite the work of Kruska (1988) (Clutton-Brock, 1999; Price, 2002; Rehkamper et al., 2008; Sánchez-Villagra, 2022; Wright et al., 2020; Zeder, 2012). The important work of Kruska (1988), however, mainly summarized the results of other studies. Then and now, original studies that generated those results, mostly published between 1920 and 1980, are rarely cited or scrutinized in terms of methods or taxonomy. Their reliability is variable given modern genetics, taxonomy, and methodologies. Hence, the purpose of this study is to provide a critical review of this fundamental primary literature, to facilitate a more informed discussion of this subject.

For each work evaluated, we report all relevant methodological details, including the metric compared (brain mass or endocranial volume [EV]), methods for measuring brain and body size, sample composition, and an evaluation of wild/domestic status in light of current genomics. The review is organized by clades, in the following order: Artiodactyla, Perissodactyla, Carnivora, and Glires, then by publication date within each group. Where possible a “most reliable” study is identified for each taxon, and discussed in the text.

We also report our own calculations of brain size change, based on newly gathered data for four artiodactyls: domestic pigs (*Sus domesticus*), llamas (*Lama glama*), alpacas (*Vicugna pacos*), and goats (*Capra hircus*). We use foramen magnum breadth (FM) to adjust for

body size differences. FM is a less well-known but established body size proxy proposed by Radinsky (1967), and was an available metric across our datasets. The use of different body size proxies not only illustrates the variation in brain reduction magnitudes resulting from different methods, but also the persistence of the reduction signal despite those varying methods. For goats, this is the first allometric test of brain size change under domestication.

2 | METHODOLOGY

2.1 | Literature search

Our literature search began with the references cited in recent (c. 1990 onwards) overviews of mammalian brain size change under domestication. These overviews (Clutton-Brock, 1999; Hemmer, 1990; Price, 2002; Rehkamper et al., 2008; Sánchez-Villagra, 2022; Wright et al., 2020; Zeder, 2012) mostly cite various works by D. Kruska, and predominantly Kruska (1988). Kruska (1988) cites the original brain reduction studies which are mostly based on dissection work and mass comparisons. These original works often do not appear in internet searches, are often in German, and are printed only in archaic journals. Except for works inaccessible through our combined library resources, we obtained the majority of these publications. The original works were critiqued, as well as studies referenced therein, and those referenced within the latter. Thus, we reviewed publications dating back to 1912–1920. Additionally, we performed a Google Scholar search for each taxon using these keywords: brain + size + change + domestication + [taxon] or [common name]. The combined efforts yielded 62 works for evaluation (Table 1). From these, we discuss in the text-only studies testing for *total brain size* change ($n = 34$). Anatomical or cytoarchitectural descriptions, studies specific to one brain region (olfactory, visual, etc.), ontogenetic works, and overviews were reviewed very simply (Table 1).

2.2 | Evaluation of studies

Older studies tended to provide sparser methodological details (i.e., use of common names only, no measurement details, and no sample sizes), and their data sources were at times unclear. Such appears to be the reporting style of the time, particularly before 1950. For as many groups as possible, we deemed as “more reliable” those studies which reported most of the following: (1) taxonomic identifications, (2) sample sizes, (3) methods for measuring brain and body size, (4) definitions of proxies, and (5) calculations. Their results are depicted in cladogram form in Figure 1 and should be interpreted with the caveats discussed for each, in the main text below.

Most studies calculating *relative* brain size differences between wild and domestic forms used what we refer to as the “allometric mass method.” This involves linear regressions of log-transformed brain and body mass proxies for wild and domestic samples. The use of body mass on the x-axis is a way of “correcting” for overall size

TABLE 1 Brain change studies reviewed in current work

Artiodactyla				% Total mean brain size change				Method for measuring brain size		Method used for size correction		Units	
Author(s)	Year	Title	Group	% Total mean brain size change	Domestic sample	Wild sample	Metric measured	Fresh mass	Brain mass	Fresh mass	Basilar length	log(g)	vs. mm
Herre and Thieme	1965	Studien an Gehirnen südamerikanischer Tylopoden	Llama, guanaco, alpaca	Serial reduction: guanaco to llama to alpaca. average: 19% ^a	15 <i>Llama glama</i> and <i>Vicugna pacos</i> ; mixed ages	17 <i>L. guanicoe</i> ; mixed ages	Brain mass	Fresh mass	Brain mass	Fresh mass	Basilar length	log(g)	vs. mm
Gorgas	1966	Betrachtung zur Hirnschädelkapazität zentralasiatischer Wildsäugtiere und ihrer Hausformen	Camels	~20%–30%	10 <i>Camelus bactrianus</i> (Trampeltier); 8 <i>C. dromedarius</i>	13 <i>C. ferus</i>	EV ^b	No details	No details	No details	Basilar length	mm	vs. mm
Röhrs and Kruska	1969	Der Einfluss der Domestikation auf das Zentralnervensystem und Verhalten von Schweinen	Pigs	na	na	na	na	na	na	na	na	na	na
Kruska	1970a	Über die Evolution des Gehirns in der Ordnung Artiodactyla Owen, 1848, insbesondere der Teilordnung Suina Gray, 1868	Multiple	na	na	na	na	na	na	na	na	na	na
Kruska	1970b	Vergleichend cytoarchitektonische Untersuchungen an Gehirnen von Wild und Hausschweinen	Pigs	33.6%	116 <i>Sus domesticus</i> (various sources; 8 breeds)	18 <i>S. scrofa</i> (published sources)	Brain mass	Fresh mass	Brain mass	Fresh mass	Basilar length	log(g) vs. log (kg)	Wild: net body mass = gross minus intestines; Domestic: net body mass = gross minus 45%
Kruska	1972	Volumenvergleich optischer Hirnzentren bei Wild und Hausschweinen	Pigs	na	na	na	na	na	na	na	na	na	na
Kruska	1973	Domestikationsbedingte Größenänderungen verschiedener Hirnstrukturen bei Schweinen	Pigs	na	na	na	na	na	na	na	na	na	na
Kruska and Stephan	1973	Volumenvergleich allokortikaler Hirnzentren bei Wild- und Hausschweinen	Pigs	na	na	na	na	na	na	na	na	na	na
Kruska and Röhrs	1974	Comparative quantitative investigations on brains of feral pigs from the Galapagos Islands and of European domestic pigs	Pigs	0.0%	Regression from Kruska 1970b	8 feral European domestic pigs from Galapagos	Brain mass	Fresh mass	Brain mass	Fresh mass	Basilar length	log(g)	Wild: net body mass = gross minus viscera; Domestic: net

TABLE 1 (Continued)

Artiodactyla		Group	% Total mean brain size change	Domestic sample	Wild sample	Metric measured	Method for measuring brain size		Units
Author(s)	Year						Title	Method used for size correction	
Ebinger	1974	Sheep	23.9%	78 <i>Ovis aries</i> (44 North German Moorland, 34 Blackhead)	6 <i>O. musimon</i> Islands; mixed ages, males only	Brain mass	Fresh mass	Gross mass	g vs. g body mass: gross minus 45% (Kruska 1970b)
Röhrs and Ebinger	1978	Pigs	18.5%	49 <i>Sus domesticus</i> (published sources)	58 <i>S. scrofa</i> (published sources)	EV	EV: pellets (1.5 and 4 mm)	Basilar length	log(cm) vs. log (cm)
Röhrs and Ebinger	1978	Sheep	22.8%	68 <i>Ovis aries</i>	42 <i>O. ammon</i> (ten subspecies)	EV	EV: pellets (1.5 and 4 mm)	Basilar length	log(cm) vs. log (cm)
Kruska	1980	Llama, guanaco, and alpaca	17.6%	17 <i>Llama glama</i> and <i>Vicugna pacos</i> (various sources)	24 <i>L. guanicoe</i>	Brain mass	Fresh mass	Net body mass = gross minus viscera and fur	log(g)
Kruska	1982	Tylopods	na	na	na	na	na	na	na
Plogmann and Kruska	1990	Pigs	na	na	na	na	na	na	na
Kruska	2009	Pigmy hog	na	na	na	na	na	na	na

(Continues)

TABLE 1 (Continued)

Artiodactyla										
Author(s)	Year	Title	Group	% Total mean brain size change	Domestic sample	Wild sample	Metric measured	Method for measuring brain size	Method used for size correction	Units
Bondel	2017	Vergleichende Morphometrische Untersuchungen am Gehirn von <i>Sus scrofa</i> f. domestica.	Pigs	41.4%	117 <i>Sus domesticus</i> (various German landraces); ages/sex estimated	93 <i>Sus scrofa</i> (from Ebersberg forest)	Brain mass	Formulin-fixed mass	Gross mass	g vs. kg
Balcarcel, Sánchez-Villagra et al.	2021	Singular patterns of skull shape and brain size change in the domestication of South American camelids	Guanaco, llama, vicuña, alpaca	llamas: 15.4% alpacas: 6.8%	9 <i>Llama glama</i> ; 8 <i>Vicugna pacos</i> ; adults only (Herre & Thiede, 1965; Kruska, 1980)	24 <i>L. guanicoe</i> ; 8 <i>V. vicugna</i> ; adults only (Herre & Thiede, 1965; Kruska, 1980)	Brain mass	Fresh mass	Net body mass = gross minus viscera and fur	log(g)
Balcarcel et al.	2021	Intensive human contact correlates with smaller brains: differential brain size reduction in cattle types	Cattle	25.6% mean reduction in domestics. Variable reduction by breed type	317 <i>Bos taurus</i> (71 breeds)	13 <i>B. primigenius</i>	EV	Predictive model based on external cranial dimensions	Muzzle width	log(mm ²) vs log (mm)
Perissodactyla										
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Method for measuring brain size	Method used for size correction	Units
Herre	1958	Einflüsse der Umwelt auf das Säugetiergehirn	Donkeys	~15% larger brains in feral donkeys	<i>Equus asinus</i> ; sample size not provided	"Feral donkeys" (feral for 50 years); sample size not provided	Brain mass	No details	No details	No details
Gorgas	1966	Betrachtung zur Hirnschädelkapazität zentralasiatischer Wildsäugtiere und ihrer Hausformen	Horses	~20%–30%	13 "primitive household" horses from Mongolia and Kazakhstan	10 <i>E. przewalskii</i>	EV	No details	Basilar length	mm vs. mm
Kruska	1973	Cerebralisation, Hirnevolution und domestikationsbedingte Hirngrößenänderungen innerhalb der Ordnung Perissodactyla Owen, 1848 und ein Vergleich mit der Ordnung Artiodactyla Owen, 1848	Equidae: horses, zebras, and donkeys	16%	36 <i>Equus caballus</i> ; 11 <i>E. asinus</i>	2 <i>E. zebra</i> ; 7 <i>E. quagga</i>	Brain mass	Brain mass (mostly from Crile and Quiring 1940)	Body mass (mostly from Crile and Quiring 1940)	log(g) vs. log(kg)

TABLE 1 (Continued)

Perissodactyla										
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Method for measuring brain size	Method used for size correction	Units
Röhrs and Ebing-er	1998	Sind Zooprzewalskipferde Hauspferde?	Horses	1. Mass: 16.0% 2. EV: 14.0%	13 "domestic horses" (various sources)	10 E. przewalskii (various sources)	Brain mass and EV	1. Mass: fresh mass 2. EV: no details	1. Mass: gross body mass 2. EV: basilar length	1. Mass: g 2. EV: mm vs. mm
Carnivora										
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Method for measuring brain size	Method used for size correction	Units
Klatt	1912b	Über die Veränderung der Schädelkapazität in der Domestikation	Cats	"5 ccm less" EV in domestics vs. "wild cats"	7 "house cats"	7 <i>Felis maniculata</i>	EV	No details	Basilar length	ccm vs. cm
Klatt	1912b	Über die Veränderung der Schädelkapazität in der Domestikation	Dogs	"30ccm less" EV in dogs vs. wolves and jackals	54 <i>Canis familiaris</i> ; mixed ages and breeds	88, of various wolf and jackal species	EV	No details	Basilar length	ccm vs. cm
Röhrs	1955	Vergleichende Untersuchungen an Wild- und Hauskatzen	Cats	~26% "rough estimate"	17 "domestic cats" (no pedigrees; 5 from Schleswig-Holstein, 12 from published sources)	4 "wild cats" (1 feral <i>Felis silvestris caucasica</i> , 2 from Harz Mountains and Hungary, 1 from Weber 1896, 1 feral from Schleswig-Holstein)	Brain mass	Brain mass/gross body mass (published data)	Gross body mass (published data)	g vs. g
Schumacher	1963	Quantitative Untersuchungen an Gehirnen mitteleuropäischer Musteliden	Martens, other mustelids	inconclusive	<i>Mustela furo</i> ; sample size not provided	Martens, polecats, ermines, mouse weasels	Brain mass	Fresh mass	1. Mass: no details 2. EV: full skull length	1. Mass: g 2. EV: cm ³ vs. mm
Kruska	1975	Über die postnatale Hirnentwicklung bei <i>Procyon cancrivorus cancrivorus</i>	Raccoon	na	na	na	na	na	na	na
Kruska	1977	On the postnatal development of the brain of the farm mink <i>Mustela vison</i> f. dom. (Mustelidae; Mammalia)	American mink	na	na	na	na	na	na	na

(Continues)

TABLE 1 (Continued)

Carnivora										
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Method for measuring brain size	Method used for size correction	Units
Kruska	1996	The effect of domestication on brain size and composition in the mink (<i>Mustela vison</i>)	American mink	19.6%	80 domestic <i>Mustela vison</i> , ranch mink; adults only	62 <i>M. vison energumenos</i> (captive/wild); adults only	Brain mass	Fresh mass	Net mass: gross minus viscera, fur and fat	log(g) vs. log(g)
Kruska and Schreiber	1999	Comparative morphometrical and biochemical-genetic investigations in wild and ranch mink (<i>Mustela vison</i> : Carnivora: Mammalia)	American mink	na	na	na	na	na	na	na
Steffen et al.	2001	Postnatal brain size decrease, visual performance, learning, and discrimination ability of juvenile and adult American mink (<i>Mustela vison</i> : Carnivora: Mammalia)	American mink	na	na	na	na	na	na	na
Kruska and Sidorovich	2003	Comparative allometric skull morphometrics in mink (<i>Mustela vison</i> Schreber, 1777) of Canadian and Belarus origin; taxonomic status	American mink	14.2%	103 <i>Mustela vison energumenos</i> (feral); adults only	90 <i>M. vison energumenos</i> and <i>M. vison lacustris</i> (wild and captive/wild); adults only	EV	EV	Basilar length	log(mm) vs. log (mm)
Tamlin et al.	2009	Separating wild from domestic American mink <i>Neovison vison</i> based on skull morphometrics	American mink	0.0%	131 domestic <i>Neovison vison</i> , ranch mink; adults, mixed sexes	248 wild mink, <i>N. vison</i> ; adults, mixed sexes	EV	EV (lead pellets, type #6)	Condylobasal length	log(cm) vs. log (mm)
Hecht et al.	2019	Significant neuroanatomical variation among domestic dog breeds	Dogs	na	na	na	na	na	na	na
Glires										
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Method for measuring brain size	Method used for size correction	Units
Frick and Nord	1963	Domestikation und Hingewicht	Mice	0.0%	laboratory albino mice (bred in lab for 100 yrs); no sample size; mixed ages; data	298 <i>M. musculus domesticus</i> (commensal); caught at	Brain mass	Fresh mass	Net mass = gross minus stomach and intestines	g, mg

(Continues)

TABLE 1 (Continued)

Glires						Method for measuring brain size			
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Method used for size correction	Units
Ebinger	1972	Vergleichend-quantitative Untersuchungen an Wild- und Laborratten	Rats	8.7%	from Seeliger 1961	Frankfurt zoo; mixed ages	Brain mass	Gross weight	g
					50 domestic <i>Rattus norvegicus</i> (Wistar and Sprague-Dawley strains); both sexes; adults only	73 wild <i>R. norvegicus</i> (brown rats)			
Fischer	1973	Vergleichende quantitative Untersuchungen an Wildkaninchen und Hauskaninchen	Rabbits	13.1%	33 domestic <i>O. cuniculus</i> ; various breeds	30 wild <i>O. cuniculus</i>	Brain mass	Gross mass	g
Sorbe and Kruska	1975	Vergleichende allometrische Untersuchungen an den Schädeln von Wander- und Laborratten	Rats	1. Mixed-variable method: 16.6% 2. EV: 5.9%	68 laboratory rats, <i>Rattus Norvegicus</i> (Sprague-Dawley strain)	50 <i>R. norvegicus</i> (single population)	EV	1. Mixed-variable: gross mass 2. EV: basilar length	1. Mixed-variable: gross mass 2. EV: cm ³ vs. gross mass 2. EV: cm ³ vs. mm
					na	na	EV: bead (1.5 mm)	na	na
Kruska	1975a	Vergleichend-quantitative Untersuchungen an den Gehirnen von Wander- und Laborratten. I. Volumenvergleich des Gesamthirns und der klassischen Hirnteile	Rats	na	na	na	na	na	na
Kruska	1975b	Comparative-quantitative investigations on brains of Norway and laboratory rats. II. Volumetric comparison of allocortical centers in the brain	Rats	na	na	na	na	na	na
Kruska and Schott	1977	Vergleichend-quantitative Untersuchungen an den Gehirnen von Wander- und Laborratten. III.	Rats	na	na	na	na	na	na

TABLE 1 (Continued)

Glires							Method for measuring brain size		Method used for size correction		Units	
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Brain mass	Fresh mass	Gross mass	log(g) vs. log(kg)	
		Volumenvergleich optischer Hirnzentren										
Ebinger et al.	1984	Hirngrößenänderung vom Wild zum Hausmeerschweinchen	Guinea pigs	13.4%	37 <i>Cavia aperea porcellus</i>	25 <i>C. aperea</i> (caught in Peru)	Brain mass	Brain mass	Fresh mass	Gross mass	log(g) vs. log(kg)	
Stuermer et al.	2003	Intraspecific allometric comparison of laboratory gerbils with Mongolian gerbils trapped in the wild indicates domestication in <i>Meriones unguiculatus</i> (Milne-Edwards, 1867) (Rodentia: Gerbillinae)	Mongolian gerbil	17.6%	50 domestic <i>Meriones unguiculatus</i> ; different breeding colonies; males only	19 wild <i>M. unguiculatus</i> caught in Mongolia; males only	Brain mass	Brain mass	Fresh mass	Net mass = gross minus intestines, skin, and subcutaneous fat	log(g)	
Kruska and Steffen	2013	Comparative allometric investigations on the skulls of wild cavies (<i>Cavia aperea</i>) versus domesticated guinea pigs (<i>Cavia porcellus</i>) with comments on the domestication of this species	Guinea pigs	1. Mixed-variable method: 16.2% 2. EV: 12.1%	76 <i>Cavia porcellus</i> ; adults, both sexes	93 <i>C. aperea</i> (single breeding colony); adults, both sexes	EV	EV: pellets (1.4 mm) and calibration cylinder.		1. Mixed-variable: gross mass 2. EV: full skull length	log(mg) vs. log (mg) 2. EV: log (mg) vs. log(mm)	
Kruska	2014	Comparative quantitative investigations on brains of wild cavies (<i>Cavia aperea</i>) and Guinea pigs (<i>Cavia porcellus</i>). A contribution to size changes of CNS structures due to domestication	Guinea pigs	14.2%	82 <i>Cavia porcellus</i> (indications of multiple breeds)	127 <i>C. aperea pamparum</i> (bred in captivity for 15+ years from Argentinian population)	Brain mass	Brain mass	Fresh mass	Net mass = gross minus viscera and body fat	log(g)	
Brusini et al.	2018	Changes in brain architecture are consistent with altered fear processing in domestic rabbits	Rabbits	Smaller brain in domestics, as measured by EQ: wild: 0.46, domestic: 0.22	8 domestic <i>Oryctolagus cuniculus</i> , from breeding center	8 wild <i>O. cuniculus</i> , from breeding center	EQ ^c	EQ ^c	Brain volume: MRI ^d and digital segmentation	na	1. ml vs. kg 2. ml vs. foot length in mm	
Multi-taxa and reviews												
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	Brain mass	Method for measuring brain size	Method used for size correction	Units	

(Continues)

TABLE 1 (Continued)

Multi-taxa and reviews						Method for measuring brain size			Method used for size correction		Units
Author(s)	Year	Title	Group	% Total brain size change	Domestic sample	Wild sample	Metric measured	measuring brain size	size correction	Units	
Klatt	1912	Über den Einfluß der Gesamtgröße auf das Schädelbild nebst Bemerkungen über die Vorgeschichte der Haustiere	Multiple	na	na	na	na	na	na	na	
Klatt	1921	Studien zum Domestikationsproblem Untersuchungen am Hirn	Multiple	na	na	na	na	na	na	na	
Herre	1956	Fragen und Ergebnisse des Domestikationsforschung nach Studien am Hirn	Multiple	na	na	na	na	na	na	na	
Herre and Rohrs	1973	Haustiere- zoologisch gesehen	Multiple	na	na	na	na	na	na	na	
Kruska	1987	How fast can total brain size change in mammals?	Multiple	na	na	na	na	na	na	na	
Kruska	1988	Effects of domestication on brain structure and behavior in mammals	Multiple	na	na	na	na	na	na	na	
Kruska	2005	On the evolutionary significance of encephalization in some eutherian mammals: effects of adaptive radiation, domestication, and feralization	Multiple	na	na	na	na	na	na	na	
Kruska	2007	The effects of domestication on brain size	Multiple	na	na	na	na	na	na	na	
Kruska	2011	Evolution, Domestikation und Feralisation. Auswirkungen auf das Gehirn bei placentalen Säugetieren	Multiple	na	na	na	na	na	na	na	

Note: Studies on total mean brain size change are in bold, listed chronologically within each clade. Taxonomy per Gentry et al. (2004), where possible. Basilar/condylobasal length = distance between prosthion and basion. Mixed-variable method = mass and volume units mixed.

^aCited in Herre and Rohrs (1973).

^bEV = endocranial volume.

^cEQ = encephalization quotient.

^dMRI = magnetic resonance imaging.

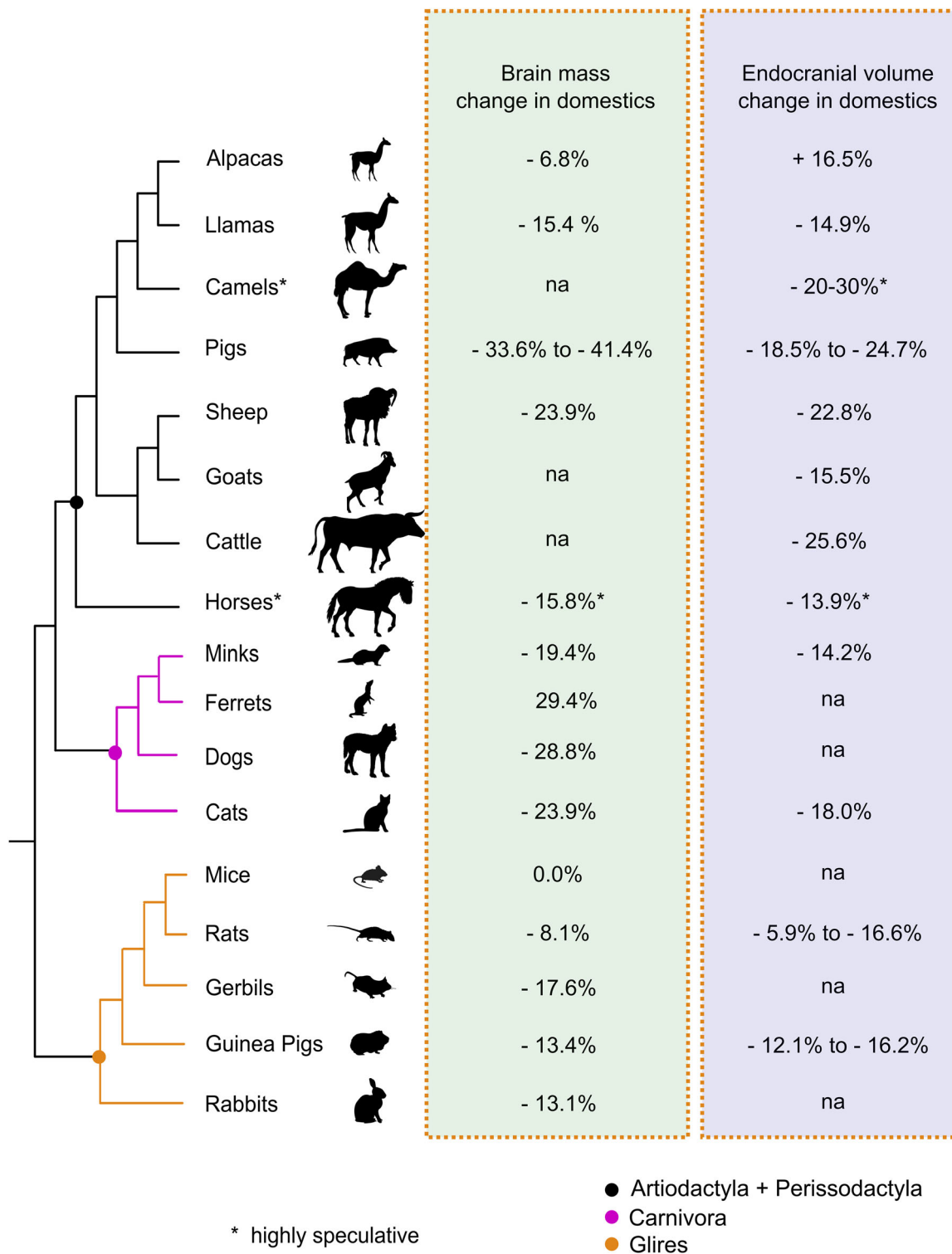


FIGURE 1 Graphical summary of brain size change between wild and domestic taxa here reviewed, and results of and newly analyzed data. For details and references see text and Table 1. Values should be interpreted while considering all caveats discussed in the main text for that group. Results of new analyses are in *bold*. Tree topology is based on Flynn et al. (2005) and Hassanin et al. (2012). Silhouettes credited to: phylopic.org; (aurochs) DFoidl (modified by T. Michael Keesey), (horse) Mercedes Yrayzoz (vectorized by T. Michael Keesey), (rat) Maija Karala, (gerbil) Flappiefh, and (rabbit) Anthony Caravaggi, <https://creativecommons.org/licenses/by-sa/3.0/>, <https://creativecommons.org/licenses/by-nc-sa/3.0/>, <https://creativecommons.org/licenses/by/3.0/deed.de>

differences, allowing the interpretation of relative, rather than absolute, mean brain size differences. The allometric scaling (i.e., the slopes in log-log space) of both regressions are then statistically tested for similarity. If this scaling does not differ between the wild and the domestic populations, the y -intercept difference is interpreted as the relative mean brain size difference between both samples, expressed as a percentage of wild brain mass (Kruska, 1988; Röhrs & Ebinger, 1978). Other studies tested for EV change, and generally used a skeletal proxy to “correct” for overall size differences (Kruska & Sidorovich, 2003; Radinsky, 1967; Röhrs & Ebinger, 1978). The most frequently-used proxy was basilar length, measured as the distance between the basion and prosthion (Röhrs & Ebinger, 1978). We refer to both of these body size correction methods as “allometric” corrections. Both the metric tested (brain mass or volume) and allometric “corrector” (body mass or some skeletal dimension) are relevant for the precision of results and for comparisons between studies. We note these variables for each work.

The way in which body mass is measured is also relevant to study comparability and reliability. Most studies allometrically corrected with “net” body mass, that is, gross mass minus viscera (most common) or minus some combination of intestines, stomach, fur, or subcutaneous fat. This was done to minimize error due to differences in body composition, that is, higher fat percentages or greater muscle mass, higher visceral weight, or heavier fur in domestic versus wild animals (Hemmer, 1990; Röhrs, 1955). We note these variables, and sampling age (adults or mixed ages), where available.

2.3 | New analyses

To test EV change in domestic versus wild pigs ($n = 29$ wild, $n = 22$ domestic) and goats ($n = 22$ wild, $n = 41$ domestic), llamas ($n = 18$ domestic) versus guanacos ($n = 83$ wild), and alpacas ($n = 14$ domestic) versus vicuñas ($n = 21$ wild), we took homologous skull measurements for all four groups (SD1). Specimens measured are housed at the Zoological Museums of the University of Zurich, Switzerland (ZMUZH); Nehring-Collection of Zoologische Sammlung der Königlichen

Landwirtschaftlichen Hochschule zu Berlin, Museum für Naturkunde Berlin, Germany (ZMB_Mamm.); Museum für Haustierkunde “Julius Kühn,” Martin-Luther-Universität Halle-Wittenberg, Germany (HTK); Museum National d'Histoire Naturelle, Paris, France (MNHN); Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN); Centro Nacional Patagónico, Puerto Madryn, Argentina (CENPAT); Museo de La Plata, Argentina (MLP); Zoologisches Institut/Populationsgenetik (former Institut für Haustierkunde), Christian-Albrechts-Universität zu Kiel, Germany (I.f.H); American Museum of Natural History, New York, USA (AMNH); Naturhistorisches Museum, Vienna, Austria (NMW); and the Zoological Museum of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg (ZIN RAS). All measurements except for those of *Sus domesticus* and some *Capra aegagrus* (taken by MG) were taken by the first author (AB). EV was estimated using the “all-Artiodactyla” predictive model from Finarelli (2011), based on braincase length, braincase width, and braincase height as in SD2 (Figure S1; Balcarcel, Sánchez-Villagra, et al., 2021).

Foramen magnum breadth (FM) was used as a proxy for body size for allometric correction. Radinsky (1967) found a correlation coefficient (r) between FM breadth and EV of 0.94–0.98 across three of the four mammalian clades reviewed here, and suggested it as a reliable body weight proxy (Radinsky, 1967). The actual relationship between FM breadth and body mass is not known for these groups, so we present our results with requisite caution. An ANCOVA model was applied to our data, with EV and FM as covariates. Regressions are in log-log space, and significance was established at $p < 0.05$. To test if FM breadth is influenced by domestication, we performed a preliminary ANCOVA on all four wild/domestic pairings using FM and total skull length as covariates, with wild/domestic status as cofactor (SD2). No slope or intercept differences were found between wild and domestic populations in any group.

Analyses were conducted in an R statistical environment (v. 1.2.5019) using the packages “dplyr” (Wickham et al., 2020), “MASS” (Venables & Ripley, 2002), and ‘ggplot2’ (Wickham, 2016). All data and calculations are in Supporting Information files SD1–SD3. Model statistics are in Table 2, and plots are in Figure 2. Results are discussed in the corresponding text below.

TABLE 2 ANCOVA statistics for regressions in Figure 2

Comparison	Intercept difference (encephalization difference)	p -value: intercept difference	p -value: slope difference
Guanaco (wild, $n = 83$) vs. llama (domestic, $n = 18$)	14.9% reduction in llamas (domestic)	<0.001	0.094 ^a
Vicuña (wild, $n = 21$) vs. alpaca (domestic, $n = 13$)	16.5% increase in alpacas (domestic)	0.001	0.523
Boar (wild, $n = 29$) vs. pig (domestic, $n = 22$)	24.7% reduction in pigs (domestic)	<0.001	0.221
Bezoar (wild, $n = 23$) vs. goat (domestic, $n = 41$)	15.5% reduction in goats (domestic)	0.012	0.729

Note: endocranial volume (EV) versus foramen magnum breadth (FM, as a proxy for body size) for the newly gathered data of wild and domestic South American camelids, pigs and goats. EV estimated with “All-Artiodactyla” formula from Finarelli (2011). Logged data. Intercept differences are interpreted as relative brain size differences. Significant values ($p < 0.05$) are in bold. Full model statistics in Supporting Information file SD3.

^aNearly significant slope differences, see text for discussion.

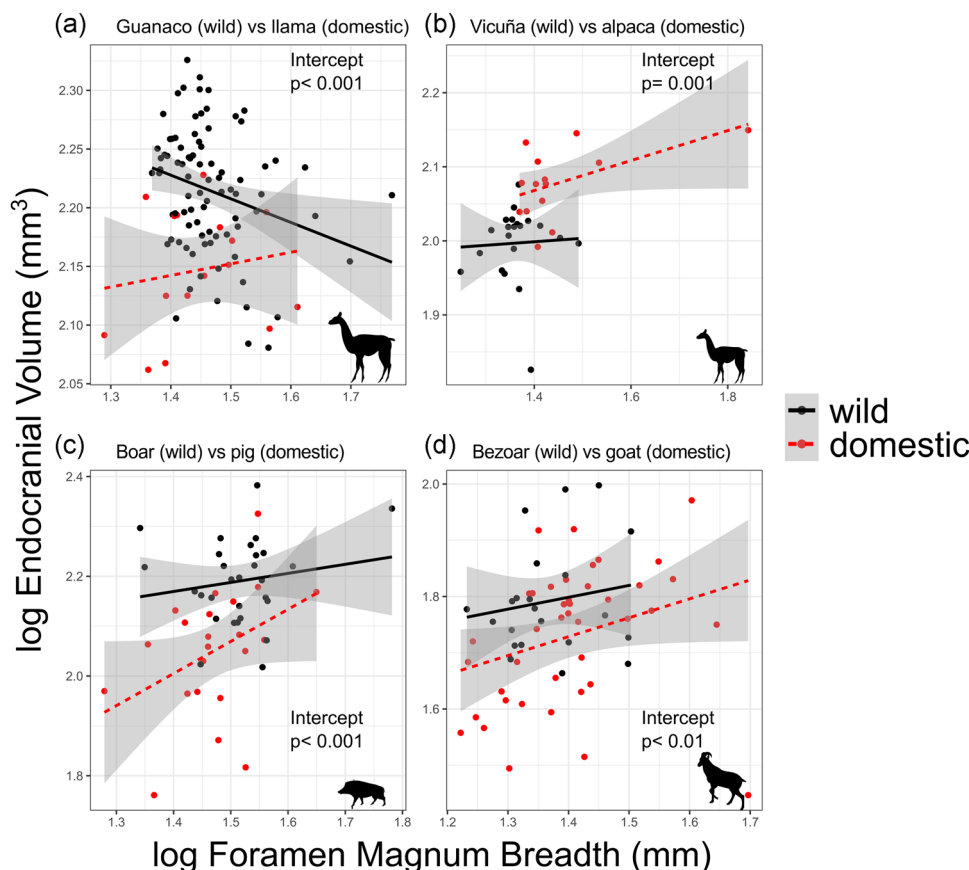


FIGURE 2 Regressions of endocranial volume (EV) versus foramen magnum breadth (FM, as a proxy for body size) for the newly gathered data of wild and domestic (a, b) South American camelids, (c) pigs, and (d) goats. EV estimated with “All-Artiodactyla” formula from Finarelli (2011) based on cranial height, width, and length. Full analyses in Supporting Information file SD3. p -values are for γ -intercept differences between wild and domestic regressions

3 | REVIEW

3.1 | Artiodactyla

3.1.1 | South American camelids

Until recently, studies on this group misclassified wild/domestic relationships among the four members, reflecting an earlier taxonomic understanding. Herre and Thiede (1965) compared three of the four camelids: guanaco (*L. guanicoe*, wild), llama (*Lama glama*, domestic), and alpaca (*V. pacos*, domestic) using the allometric mass method with brain mass versus net body mass (gross body mass minus viscera and fur). Samples were of mixed ages. Brain reduction was reported for both domestics (llamas and alpacas), but without a specific magnitude, and only in relation to the guanaco (wild). The current wild/domestic hypothesis for this group is as follows: *L. guanicoe* (wild)—*L. glama* (domestic), and *V. vicugna* (wild)—*V. pacos* (domestic; Kadwell et al., 2001). Based simply on a figure in this publication (Herre & Thiede, 1965, p. 158, fig. 6), a later work retrospectively reported 19% brain reduction for domestic llamas and alpacas compared to the guanaco (wild; Herre & Röhrs, 1973).

Kruska (1980) applied the same allometric method to a larger data set, using the same now-erroneous taxonomy, to calculate 17.6% brain reduction for llamas and alpacas, in comparison to the guanaco. A study in 2020 compiled the original data from these publications plus vicuña data, pruned it to include adults only, and applied the same allometric mass method. Brain reduction of 15.4% was calculated for llamas (domestic) and 6.8% for alpacas (domestic), compared to the guanaco (wild) and vicuña (wild), respectively (Balcarcel, Sánchez-Villagra, et al., 2021).

Based on newly acquired data, our analyses estimate EV reduction of 14.9% for llamas (domestic) compared to the guanaco (wild), when using foramen magnum breadth for allometric correction (Figure 2a, Table 2, Supporting Information file SD3), a result close to that based on brain mass calculations (15.4%; Balcarcel, Sánchez-Villagra, et al., 2021). This is in line with the pattern of lower-magnitude reductions for EV comparisons versus brain mass analyses (Röhrs & Ebinger, 1978). However, the slope difference between wild and domestic regressions is nearly significant ($p = 0.094$; Table 2), making our results somewhat tentative. In contrast, we find a 16.5% increase in EV for the alpaca (domestic) compared to the vicuña (wild; Figure 2B, Table 2, Supporting Information file SD3). Seemingly contradicting the general pattern,

this result is not entirely surprising, given the degree of hybridization between the alpaca (domestic form of vicuña) and the larger-bodied guanaco (wild) and llama (domestic), which confounds any potential signal of domestication (Balcarcel, Sánchez-Villagra, et al., 2021; Kadwell et al., 2001). Much less admixture has been detected in the llama (domestic form of guanaco; Kadwell et al., 2001), which makes the llama/guanaco comparison a more reliable model of domestication change.

3.1.2 | Camels

Brain size change in camels has only been addressed in one primary study, Gorgas (1966), wherein EV reduction in the range of 20%–30% was reported for a combined sample of domestic camels and horses. Small samples of Bactrian (*Camelus bactrianus*, domestic) and dromedary camels (*C. dromedarius*, domestic) were compared to wild *C. ferus*, using basilar length for allometric correction. Specific values have not been reported for any camel.

It is currently hypothesized that lineages of *C. ferus* (wild) and *C. bactrianus* (domestic) split long before the onset of “Old world” camel domestication, and that direct wild progenitors of Bactrian camels are extinct (Larson & Fuller, 2014; Mohandesan et al., 2017). For dromedaries, ancient DNA work has only constrained a hypothetical wild ancestral population (Almathen et al., 2016; Mohandesan et al., 2017), which renders further wild/domestic comparisons problematic for this group.

3.1.3 | Pigs

Brain reduction in domestic pigs is rather well-established by multiple methods and studies. Kruska (1970) compared 18 wild boar (*Sus scrofa*) to 81 domestic pigs (*S. domesticus*, from eight breeds) using the allometric mass method, and calculated 33.6% brain size reduction in domestics (Kruska, 1970). However, net body mass was measured differently for wild and domestic samples: wild net body mass = gross mass minus intestines; domestic net body mass = gross mass reduced by 45%. The rationale was that in domestics, viscera and body fat account for 10% and 35% of gross body mass, respectively (Kruska, 1970). An analysis based on consistent body mass measurements may provide different results. The most recent mass-based pig study is Bondel (2017), which used much larger samples (wild = 93, domestic = 117) to calculate brain size reduction of 41.4% in domestics. Here, it is unclear whether gross or adjusted mass was used for allometric correction.

EV reduction of 18.5% in domestic pigs was reported by Röhrs and Ebinger (1978), using larger samples than Kruska (1970) and basilar length for allometric correction. This study tested several taxa. For each one, calculations of EV change were consistently lower than those of brain mass—a potential indication that body mass and basilar length do not scale isometrically in these groups (Röhrs & Ebinger, 1978).

Our analysis of *Sus domesticus* (domestic) and *S. scrofa* (wild) yields EV reduction of 24.7% for domestics (Figure 2C, Table 2, Supporting Information file SD3)—a higher value than that calculated by Röhrs and Ebinger (1978) with basilar length (18.5%)—exemplary of the variation in results achieved by different methods (Figure 1), as well as the persistence of a reduction signal.

The wild/domestic status of *S. scrofa* (wild) and *S. domesticus* (domestic) is well supported, although it has been suggested that European domestic pigs (sampled in all studies here) have a mixed ancestry of local European and Middle Eastern wild progenitors (Larson & Fuller, 2014). A comparison using both wild populations would be relevant. For pig studies in general, another potential source of bias is that the two main pig “types” (lard or bacon) are bred for different body shapes—bacon pigs having longer frames than lard pigs (Ekarius, 2008), presumably for greater meat yields.

3.1.4 | Goats

Until now there have been no allometric tests of brain size change in domestic goats, only some empirical observations (Klatt, 1912b). We calculate a 15.5% reduction in EV for domestic goats (*Capra hircus*) compared to the wild Bezoar (*Capra aegagrus*; Figure 2D, Table 2, Supporting Information file SD3). The ancestry of domestic goats by *C. aegagrus* so far remains uncontested (Hemmer, 1990; Naderi et al., 2008; Zeder, 2001).

3.1.5 | Sheep

Brain size change in sheep has also been studied by multiple methods in various studies. Ebinger (1974) tested for both mass and EV change, sampling 78 domestic sheep (*Ovis aries*) of various German breeds and six European mouflons (*O. musimon*, wild). Brain mass reduction was calculated at 23.9% using the allometric mass method, but with gross body mass. EV reduction was calculated at 22.8% in domestics, using basilar length for allometric correction. Röhrs and Ebinger (1978) tested the same taxa but with more balanced samples than Ebinger (1974), 42 wild and 68 domestic sheep, but with very similar results: 22.1% EV reduction in domestics. In contrast to most other taxa, mass and volume methods generated similar reduction values in sheep. A possible explanation may be that body mass and basilar length scale somewhat isometrically in sheep.

It is hypothesized that European domestic sheep stem from Turkish and Iranian *O. orientalis anatolica* (wild; Hiendleder et al., 2002), and not from the European *O. musimon* (wild). Whole-genome sequencing suggests that *O. musimon* belongs to a separate clade, and is described by some as a “feral domesticate” (Hiendleder et al., 2002; Vigne et al., 2005). Nonetheless, *O. musimon* is considered a close relative that physically resembles the progenitor of *O. aries* (domestic; Hiendleder et al., 2002). A comparison of domestic sheep with *O. orientalis* (wild) would be informative, particularly since introgression between domestic sheep and local

wild populations is less of an issue in this group (Alberto et al., 2018) compared to others, that is, pigs (Larson & Fuller, 2014; Ottoni et al., 2013).

3.1.6 | Cattle

“Unpublished observations” of brain reduction in taurine cattle (*Bos taurus*, domestic) compared to aurochs (*B. primigenius*, wild) have been reported, but without supporting evidence (Kruska, 2011, 2014). An allometric mass method is not possible for this group due to the extinction of the aurochs in the 17th century (Mason, 1984). Hemmer (1990) reported EV reduction of 10%–20% for “feral” Chillingham cattle ($n = 10$) compared to aurochs ($n = 5$), but without providing data or a description of methods. A recent study did present an analysis of EV change between a sample of 13 aurochs and 317 domestic taurine cattle (*B. taurus*, domestic, multiple breeds), calculating 25.6% EV reduction in domestics when using muzzle width as allometric corrector (Balcarcel, Veitschegger, et al., 2021). This result was statistically tested and found to be independent of any muzzle size changes related to domestication.

Current genomic work confirms *Bos primigenius* as the wild progenitor of taurine cattle (Park et al., 2015). Given the extinction of aurochs nearly 400 years ago (Mason, 1984), and subsequent lack of admixture between them and domestic cattle, we would expect a clearer distinction between wild and domestic populations, potentially giving the cattle model of domestication greater explanatory power.

3.1.7 | Yak

Brain change in the domestic yak has been poorly studied. Gorgas (1966) collected wild (wildyak) and domestic (hausyak) yak data (taxonomy not specified), but for a very small sample (wild, $n = 5$; domestic, $n = 9$). A published plot of these data (Gorgas, 1966, p. 232) suggested reduced EV for domestics and sexual dimorphism in this variable. Notably, Gorgas (1966) did not observe sexual dimorphism in the horses and camels that were also sampled in this study.

3.2 | Perissodactyla

3.2.1 | Donkeys

Brain size change in domestic donkeys (*Equus asinus*) has only been studied in comparison to a feral population (Herre, 1958). Both populations were South American, and the feral population had been so for approximately 50 years. Sample sizes were not reported. Based on the allometric mass analysis, the non-feral domestic donkeys were found to have 15% smaller brains than the feral population. Feral animals are, by definition, domestics reintroduced into the wild,

so this study is more informative of feralization than domestication. Thus, we do not include this group in Figure 1.

The likeliest ancestor of the domestic donkey is *Equus africanus* (North African wild ass; Clutton-Brock, 1999; Gentry et al., 2004; Zeder et al., 2006), although some suggest it is a now-extinct wild subspecies (Wilson & Reeder, 2005). Morphological differences between wild and domestic donkeys are unclear (Zeder, 2012), mainly due to a lack of archaeological and osteological collections (Zeder et al., 2006), making this group a most intriguing model for further domestication studies.

3.2.2 | Horses

Brain reduction values reported for domestic horses are, at best, approximations. Gorgas (1966) calculated EV reduction of 20%–30%, but for a combined sample of domestic horses and camels. The wild/domestic sampling is also problematic in this study: domestics consisted of 13 “primitive household horses” from Mongolia and Kazakhstan, and the wild sample of 10 *E. przewalski* horses. The domestic taxon is undefined, and Przewalski's horses are no longer considered the true wild ancestors of domestic horses (Orlando et al., 2013). Lineages of *E. przewalski* and modern horses reportedly split approximately 38–72 Kya, before horse domestication began. Furthermore, most Przewalski's horses stem from captive populations (Orlando et al., 2013), which further reduces their representation of a true “wild” population due to the potential effects of captivity on skull morphology (O'Regan & Kitchener, 2005). However, as the only remaining nondomestic horse lineage, Przewalski's horses were used as the wild proxy in all but one of the studies reviewed here.

Kruska (1973) also examined the horse brain but in comparison to other equids, essentially stating little about domestication and more about phylogenetic brain size variation. *E. zebra* and *E. quagga*—two zebra species—together comprised the wild proxy, which was compared to a combined sample of domestic horses and donkeys. Using the allometric mass method, the study reported a 16% brain size reduction in domestic compared to wild equids, a result which the author admitted would be questioned due to its lack of specificity (Kruska, 1973). The study also appears to have used gross mass for allometric correction, potentially overestimating its results. Kruska (1973) cites Gorgas (1966) as also having calculated 16% brain reduction in horses—a point we contest, since Gorgas (1966) did not report specific values for either camels or horses.

The most rigorous horse study to date is Röhrs and Ebinger (1998), which tested brain mass and EV differences between 10 domestic horses and 13 *E. przewalski* specimens (Röhrs & Ebinger, 1978). Brain mass reduction of 15.84% was reported for domestics, using gross mass for allometric correction. EV reduced by 13.94%, using basilar length as a size corrector. It is noteworthy that for both domestic horses and sheep, mass and EV methods yield similar reduction values, suggesting similar scaling of body mass and basilar length in both groups.

3.3 | Carnivora

3.3.1 | Dogs

Klatt (1912) was one of the first to report brain size differences between wild and domestic dogs. However, his wild sample was a mix of wolves and jackals, some of the uncertain age, and analyses were not statistically tested. A more authoritative study is Röhrs and Ebinger (1978) which reported 28.8% brain mass reduction in domestic dogs (*Canis familiaris*, $n = 448$, multiple breeds) compared to wolves (*Canis lupus*, $n = 78$), using gross body mass for allometric correction. Data in this study were compiled from previous publications, but sources are not identified nor raw data provided. Röhrs and Ebinger (1978) also concluded that the allometry of EV and basilar length differs significantly between wolves and dogs, suggesting that basilar length is an inappropriate size proxy for the group (Röhrs & Ebinger, 1978). This allometric difference was not encountered in any other taxon here reviewed. We consider Röhrs and Ebinger (1978) as the most reliable brain size study for domestic dogs, given its methodology and sampling. Breed composition of the domestic sample is, unfortunately, not reported. Differences in breeding goals and protocols can have a significant effect on brain reduction, as has been shown in domestic cattle (Balcarcel, Veitschegger, et al., 2021).

Current genetic work points to an extinct Pleistocene wolf population as the wild ancestors of domestic dogs (Bergstrom et al., 2020). While contemporary wolf populations may not precisely reflect the wild ancestral state, they do represent the closest proxy.

3.3.2 | Cats

The majority of brain size studies on domestic cats are plagued with taxonomic and sampling issues, in light of current genomic hypotheses of species affiliation. At present, the consensus is that domestic cats stem mostly from *Felis lybica lybica* (Driscoll et al., 2009; Kitchener et al., 2017).

Klatt (1912) was also one of the earliest to test EV differences between wild and domestic cats. "Domestic cats" ($n = 7$) were compared to *Felis maniculata* (wild, $n = 7$), a close relative of, but not actually, the wild progenitor. Domestic cats reportedly had smaller EVs by 5 cm. No plots or methodological details were provided, which makes these data problematic.

Another problematic study is Röhrs (1955) which compared 17 "domestic cats" to a mixed sample ($n = 4$) of feral and "wild cats." Only one of the feral cats was identified as *Felis silvestris caucasica*, a closely related species of the domestic cat progenitor. Using a different method than other studies: proportional brain mass versus gross body mass, the study reported a "rough estimate" of 26% brain mass reduction for domestics (Röhrs, 1955).

With the largest data set and dual approaches, Röhrs and Ebinger (1978) provided the most thorough investigation of brain size change in this group. Brain masses of 90 domestic cats (*Felis catus*) were compared to a mix of regionally-diverse wild cats (*Felis silvestris*,

$n = 6$), referred to as "forest wild cats" from Europe/Asia and "feral cats" from North Africa/Asia. Using gross body mass for allometric correction, domestics were found to have 23.9% smaller brains than the wild sample. EV was reduced by 18% when using basilar length for size correction. An earlier study with even smaller samples had reported similar brain mass reduction (23.4%) between the same taxa (Herre & Röhrs, 1973).

3.3.3 | Ferrets

There are currently two candidates for the wild progenitor of the domestic ferret, *Mustela furo* (domestic): *M. putorius* (wild) or *M. eversmannii* (wild), with the latter having a strong case based on phylogenetic work (Kurose et al., 2008). It is relevant that all three taxa can successfully interbreed, but *M. putorius* and *M. furo* have the same chromosome number, and reportedly have more similar developmental biology compared to *M. eversmannii* (Kurose et al., 2008).

Schumacher's (1963) study was informative of relative brain size variation (both mass and volume metrics) across Mustelidae, by comparing several taxa: 32 ferrets, 15 polecats, 3 martens, 3 stoats, and 2 weasels. While not relevant to domestication, this study provided raw data that could be useful in future works.

We consider Espenkotter (1982) as the most comprehensive study on ferret brain size change, since it compared European polecats (*M. putorius*, wild) to domestic ferrets (*M. furo*), using the allometric mass method. Net and gross body masses were both reported, but it is unclear which was used for the analysis. However, sampling was not restricted to adults, so the report of 29.4% brain reduction in domestic ferrets is the average reduction across different growth stages (Espenkotter, 1982).

3.3.4 | Mink

Kruska (1996) studied the domestic American mink, or "ranch mink," known then as *Mustela vison*, and today as *Neovison vison* (Harding & Smith, 2009; IUCN, 2020; Wilson & Reeder, 2005). Using the allometric mass method, and *M. vison energumenos* as the wild form, Kruska (1996) calculated brain size reduction of 19.4% for ranch mink.

Kruska and Sidorovich (2003) added to the understanding of feralization rather than domestication by testing for EV change between a subspecies of wild *Mustela vison* (bred in captivity) and feral mink populations. The latter were found to have 14.2% reduced EV compared to captive-bred wild mink.

We consider Tamlin et al. (2009) as the most recent and comprehensive study on mink. It compared wild and domestic *M. vison*, as well as free-ranging, likely feral, and hybridized mink, to evaluate differences in EV. The study used much larger samples than Kruska (1996), including several populations of domestic farmed mink that were bred for different coat colors. All populations were from the same geographic origin, and basilar length was used for allometric

correction (Tamlin et al., 2009). No EV differences were found between the three samples. An additional morphometric analysis found no muzzle shortening in domestics, counter to the pattern in other domestic taxa (Owen et al., 2014; Sánchez-Villagra et al., 2016), as well as to findings in Kruska and Sidorovich (2003) for feral mink. The results of all three mink studies are incongruous, making this group worthy of further investigation. In particular, the lack of brain reduction in mink which are farmed for coat color, rather than for specific behaviors or musculoskeletal features, supports a correlation between brain size change (or lack of it) and breeding goals (Balcarcel, Veitschegger, et al., 2021).

3.4 | Glires

3.4.1 | Rabbits

Fischer (1973) calculated 13.1% brain size reduction in domestic rabbits (*Oryctolagus cuniculus domesticus*) using the allometric mass method, with gross mass as allometric corrector. A potential source of bias here is that domestic rabbits were four times heavier than wild rabbits. Another is that the author cautions the wild sample may have included feral individuals, given the prevalence of these in the sampling area (Fischer, 1973). Genetic studies generally support the domestication of rabbits from the European rabbit (*O. cuniculus cuniculus*) around 1400 years ago in Southern France (Carneiro et al., 2014), where Fischer (1973) collected his sample and where the wild population still exists.

The most recent rabbit study is Brusini et al. (2018), which used magnetic resonance imaging and reported brain reduction in domestic rabbits compared to wild ones (*Oryctolagus cuniculus*; I. Brusini, pers. comm.). Brain volumes were measured from digital renderings of the brain, and results were reported as differences in encephalization quotient (EQ): the ratio of observed brain volume to expected brain volume, after correcting for body weight (Brusini et al., 2018). Methods for measuring body weight were not reported and would be highly relevant, given the extreme body mass differences between wild and domestic samples (nearly fourfold). Wild rabbits reportedly had an EQ of 0.46, while domestic rabbits had an EQ of 0.22. A secondary analysis using foot length (mm) for allometric correction also found domestic rabbits to have smaller brains. However, the authors report absolute foot length differences between domestic and wild rabbits (Brusini et al., 2018) but nothing regarding relative foot size, which would be more relevant and informative.

3.4.2 | Mice

Mice are the only mammalian group whose brain size appears not to change under domestication. Frick and Nord (1963) found no differences in relative brain size between wild mice (*Mus musculus domesticus*) and domestic albino laboratory mice, using the allometric

mass method. Their wild sample size was not reported and the large domestic sample ($n = 298$) was bred in a laboratory setting for more than 100 years. Frick and Nord (1963) sampled various growth stages and whether this affects results could be further investigated. Despite competing hypotheses on the systematics of the genus *Mus* and the synonymy of subspecies within *Mus musculus*, there is consensus on the descent of domestic mice from *Mus m. domesticus* (Cucchi et al., 2012; Wilson & Reeder, 2005).

3.4.3 | Rats

The brain of the domestic laboratory rat (*Rattus norvegicus*, domestic) reportedly reduces by approximately 6%–17% compared to wild “brown” rats (*Rattus norvegicus*, wild), according to various studies using different methods. Ebinger (1972) calculated brain mass reduction of 8.7% in laboratory albino rats using gross body mass for allometric correction. Sorbe and Kruska (1975) found a 5.9% EV reduction in the same taxa, when using basilar length for allometric correction. When combining volume and mass methods (regressing EV vs. body mass), a 16.6% reduction in EV was detected (Sorbe & Kruska, 1975). We thus infer that basilar length and body mass do not scale isometrically in rats. At present, the status of *Rattus norvegicus* as the wild form of laboratory albino rats (Castle, 1947) appears uncontested.

3.4.4 | Gerbils

Stuermer et al. (2003) compared brain size in wild and “domestic” Mongolian gerbils, *Meriones unguiculatus*. The domestic sample was a “mixed reference” group from different “western” laboratory colonies (Stuermer et al., 2003). Using net body mass for allometric correction, they calculated 17.6% brain mass reduction in domestics compared to the wild sample. Body fat corrections for calculating net body mass were well documented, but only males were sampled. The authors also noted that mean body mass for the wild population was 11%–22% lower than in other studies, positing their sample may have been malnourished (Stuermer et al., 2003).

From our investigations, it is unclear if “domestic” populations of *Meriones unguiculatus* officially qualify as a domesticated form. Multiple studies refer to domestic *Meriones unguiculatus* (Clark & Galef, 1980; Eckrich et al., 2008; Stuermer & Wetzel, 2006; Stuermer et al., 2003), but some standard sources do not recognize a domestic variety (Wilson & Reeder, 2005).

3.4.5 | Guinea pigs

Ebinger et al., (1984) compared domestic guinea pigs (*Cavia porcellus*) with wild cavies (*Cavia aperea*), calculating a 13.4% reduction in brain mass in domestics when using gross body mass for allometric correction. Kruska and Steffen (2013) tested for EV change with a

much larger sample and reported a 12.1% EV reduction in domestics. However, their allometric corrector, basilar length, was found to be ~5% shorter in domestic guinea pigs compared to wild cavies (when corrected for size differences; Kruska & Steffen, 2013), likely overestimating their results. When combining metrics (regressing EV vs. body mass), the EV reduction was 16.2%, indicating that basilar length and body mass may not scale isometrically in this group.

The most rigorous brain size study on guinea pigs appears to be Kruska (2014), where brain mass reduction was found to be 14.2% in *Cavia porcellus* (domestic) compared to *Cavia aperea* (wild). The large sample (wild = 127, domestic = 82) included a variety of breeds, net body mass was used for allometric correction, and results were similar to those in Ebinger et al., (1984). Results of all guinea pig studies reviewed here are constrained to a range of 12.1%–16.2% brain size reduction in domestics.

Debates continue over which ancestral subspecies gave rise to domestic guinea pigs. *Cavia aperea tshudii* is reportedly a strong candidate (Spotorno et al., 2006), but recent mitogenomic work describes more complicated natural and genetic histories for guinea pigs around the globe (E. Lord et al., 2020).

4 | DISCUSSION AND SUMMARY

Among the studies reviewed here, some are more robust than others in regard to methodological or sampling critique, and thus remain as the best approximations of brain size change correlated with domestication. These include, for example, a ~34% brain mass reduction in domestic pigs (Kruska, 1970), ~24% brain mass reduction in domestic sheep (Ebinger, 1974), ~29% brain mass reduction in dogs compared to wolves (Röhrs & Ebinger, 1978), and ~15% brain mass reduction in llamas versus guanacos (Balcarcel, Sánchez-Villagra, et al., 2021).

4.1 | Artiodactyla

Among South American camelids, the guanaco-llama comparison appears to be the better domestication model compared to vicuña-alpaca, due to significant hybridization between the latter (Balcarcel, Sánchez-Villagra, et al., 2021; Kadwell et al., 2001). Both mass and volume analyses suggest brain reduction of approximately 15% in the llama compared to the guanaco. The alpaca is more a model of hybridization, indicated by brain and skull form features it shares with the three other members of the group (Balcarcel, Sánchez-Villagra, et al., 2021; Herre & Thiede, 1965). Breeding pressure is seemingly weaker in domestic camelids compared to other groups, and domestics remain in wild-like environments today (Wheeler, 1995, 2012). It is possible that South American camelids reflect an earlier state of domestication compared to other domestics (Balcarcel, Sánchez-Villagra, et al., 2021).

For camels, brain reduction of 20%–30% (Gorgas, 1966) is highly speculative, due to low sampling and bulk comparison with horses. However, this is the only report of its kind for this group. True wild

ancestors for both Bactrian and Dromedary camels are extinct (Mohandesan et al., 2017), so future work on this taxon will likely rely on *Camelus ferus* as the closest wild proxy.

For pigs, multiple studies concur on high magnitudes of brain reduction in the range of 25%–40%. The results may be skewed by their mixed ancestry by two wild populations, but most researchers agree that pigs display perhaps the highest percentages of brain reduction of all domestics (Kruska & Stephan, 1973; MacHugh et al., 2017; Zeder, 2012). A possible explanation is the intensity of breeding selection whereby diet, reproduction, mating, and longevity are manipulated by humans (Ekarius, 2008), likely resulting in high selection for tameness as well (Balcarcel, Veitschegger, et al., 2021).

For goats, our result of ~15% brain reduction in domestics is tentative due to small and unbalanced samples. Comparative results are lacking since this is the first goat analysis of its kind. However, wild ancestry by the Bezoar, *C. aegagrus*, is well supported (Naderi et al., 2008). Most sheep studies have used *O. musimon* as a wild form, which is a close relative (with a similar phenotype) of the true wild ancestor, *O. orientalis anatolica*, according to current genomics (Hiendleder et al., 2002). Future studies could sample *O. orientalis anatolica* for greater accuracy. However, sheep studies reviewed here consistently find brain reduction in the range of 23%–24% for domestics, regardless of method (Ebinger, 1974; Röhrs & Ebinger, 1978).

A single cattle study relying on a well-constrained wild ancestor, *B. primigenius*, and a large domestic sample reported ~26% brain reduction in domestics (Balcarcel, Veitschegger, et al., 2021). It used muzzle width as a body size proxy, so using a more conventional (perhaps postcranial) allometric corrector and a larger wild sample would be relevant. However, the study also detected differential brain reduction among different cattle breed types, suggesting that the brain responds variably to different types of domestication. Such analyses represent an opportunity to further test the plasticity of the mammalian brain.

The single yak study we reviewed is unreliable for multiple reasons (Gorgas, 1966). Yaks remain an unexplored group in this area of study.

4.2 | Perissodactyla

Horse brain studies remain speculative, based on the extinction of the wild ancestral population and much admixture in the closest available wild proxy. Numbers are similarly speculative for the donkey although they may have a reasonably constrained living wild population (Clutton-Brock, 1999; Zeder et al., 2006).

4.3 | Carnivora

For dogs, the calculation of ~29% brain reduction based on mass appears most reliable based on sample sizes and methodology (Röhrs

& Ebinger, 1978). A more accurate wild sample is currently not possible due to extinction (Bergstrom et al., 2020), so *Canis lupus* remains the best possible proxy. A prior analysis of EV change in dogs failed due to allometric differences between the wolf and dog skull (Röhrs & Ebinger, 1978). Comparative results are lacking. For cats, ~24% brain reduction based on mass also appears most reliable based on sample sizes and methodology (Röhrs & Ebinger, 1978), particularly since the wild sample included several different populations. However, cats and dogs are highly bred animals, which could confound a variety of selection pressures and phenotypes, more so than in other domestic groups. A parsing of breeds and/or landraces in these groups would provide further insights into the relationship between brain size and artificial selection.

Studies of brain reduction in domestic ferrets have some taxonomic issues, and the most thorough study is ontogenetic. Results of several mink studies are contradictory, ranging from 0% to 19% brain size reduction in domestics. These taxa require further study.

4.4 | Glires

Several studies concur that brain reduction is occurring in domestic rabbits. However, the value of ~13% reduction may be somewhat biased, since studies have not adjusted for higher fat deposits in the domestic populations.

For their mouse study, Frick and Nord (1963) appear to have used robust methods to find zero change in brain size in domestic compared to wild mice. However, the size of the wild sample is unclear. In rats, based on a reliable taxonomic framework, the brain of domestics appears to reduce between 6% and 17%. In both taxa, domestication is generally not for purposes of intense human relationships or docility, which makes the absence of, or low-magnitude, reduction intriguing (Balcarcel, Veitschegger, et al., 2021). Guinea pig brain reduction appears well constrained around 12%–16% based on multiple methods, with a wild proxy of sub-specific proximity. For gerbils, taxonomy and methods seem robust, and concur on brain reduction of ~17% for domestics.

4.5 | Persistent issues

Most studies testing for EV change have used basilar length as an allometric corrector. Given the numerous reports of snout shortening in some domestics compared to wild forms (Geiger et al., 2018; Heck et al., 2018; Owen et al., 2014), this proxy has a high likelihood of error. However, since the degree of rostral change is variable across domestic taxa (K. A. Lord, Larson, Coppinger, et al., 2020), any error is likely variable by species, and may be adjustable. In contrast, multivariate models for estimating EV have achieved accuracies of ~97%–98% (Finarelli, 2006, 2011). Concerns still remain in the variability of the relationship between EV and brain size. These issues also appear to be specific to species (Röhrs & Ebinger, 1978).

4.6 | Future steps

Future domestication studies can build on prior brain size studies by incorporating new genetic information, as was done for South American camelids (Balcarcel, Sánchez-Villagra, et al., 2021). Moreover, the phylogenetic resolution provided by genetics (MacHugh et al., 2017) broadens the spectrum of evolutionary models that can test for correlations between specific selection pressures and phenotypes. For example, examinations of well-defined breeds can be an important avenue of research as they allow clearer testing of the relationship between breeding goals and phenotypic effect (Balcarcel, Veitschegger, et al., 2021; Eusebi et al., 2021). In cattle, the magnitude of brain reduction appears correlated with the intensity of human contact and the degree of selection for or against docility. More aggressive, “wilder” cattle breeds appear to have larger relative brain sizes (Balcarcel, Veitschegger, et al., 2021). Subparts of the brain reportedly also display variable size changes under domestication. Most taxa experience the greatest reduction in the amygdala—a region that controls and processes fear (Kruska, 1988). In domestic rabbits, for example, reduction in amygdala size and changes in brain architecture are consistent with a reduction in emotional processing (Brusini et al., 2018).

In summary, evolutionary models associated with domestication including feralization, breeding, hybridization, or other distinction based on enhanced genetic resolution, may limit some insights but can be opportunities for others.

5 | CONCLUSIONS

Most domestication studies present a degree of methodological concern that should be made explicit when citing the results, as with most scientific work. Awareness of such concerns may encourage future studies. Brain reduction values certainly contain error, but as a collective, results firmly support a pattern of brain size reduction under domestication (Figure 1). The onus is on those claiming the lack of brain change following domestication, to provide robust tests against these observations. There is currently no clear pattern to the variation in brain reduction seen across or within clades (Finarelli, 2011; Kruska, 2011, 2014).

Studies in this area will remain as approximations with different degrees of probability due to extinction, hybridization, and the impossibility of precise ancestral reconstruction (Larson & Fuller, 2014), as with most reconstructions of a historical process, including ancient DNA studies which unavoidably also rely on proxies (Frantz et al., 2020). This does not preclude the significance of comparisons but it is fundamental to domestication work that the type of domestication investigated be defined, whether it be early phase, intensive breeding, or other (Sánchez-Villagra et al., 2017; Sánchez-Villagra, 2022; Zeder, 2012).

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

AUTHOR CONTRIBUTIONS

A. M. Balcarcel collected the majority of data, performed the literature review, translation, and writing of this manuscript. M. Geiger collected a portion of pig and goat data. M. Geiger and M. R. Sánchez-Villagra reviewed and translated literature, and critically revised the manuscript. M. Clauss advised on statistical tests and critically revised the manuscript. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Supplementary data file [SD1-SD3](#) provides all data and analyses in this study.

PEER REVIEW

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