



### **Supporting Information for**

Evolving around humans: a universal definition for domestication

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#### **This PDF file includes:**

Supporting text

Figure S1

Table S1 and Table S2

SI References

## Supporting Information Text

### Lab model origins

The individuals used to establish nearly all major laboratory model organisms may have come from populations that were either human exploiters or domestic. Here, we describe several of the species from Table 2 in more detail.

**Dogs.** Purpose-bred beagles were established as the first standardized laboratory dog model in the 1940s using dogs sourced from hunting or show breeders(1). The choice of beagles was likely due to the breed's prevalence, although their health, small size, and ability to be group- or singly-housed have also been suggested as factors.

**Fruit Flies.** The fruit flies used to start the first experimental inbred lines were collected by leaving fruit on windowsills(2). The earliest use of fruit flies traces back to 1900 by C.W. Woodworth, a graduate student of W.E. Castle, who acquired his flies by leaving Concord grapes on a windowsill. W.E. Castle later collected more flies using the same technique, substituting bananas for grapes. Thomas Hunt Morgan, who popularized the use of *Drosophila* in genetics through a series of seminal experiments, sourced his flies either from Castle's inbred strain or by using the windowsill technique.

**Maize.** Laboratory strains of maize were developed from crop varieties, including unusual strains found at agricultural 'corn shows' (3). The use of maize as a model organism traces back to inheritance studies performed in 1869 by Gregor Mendel. Today, hundreds of maize inbred lines are described, and the most widely used were developed from crop varieties. For example, B73 was developed at Iowa State University from an Iowa Stiff Stalk Synthetic maize population (4), W22 was developed at the University of Wisconsin and is notable for its unusual purple pigmentation(5), and MO17 is an inbred representative of Lancaster, an heirloom field corn variety.

**Mice.** Many of the inbred strains of mice now used in laboratories were originally purchased from people breeding mice as pets(6, 7), and even the "wild" mice crossed into lab strains may have been commensal. The most prolific early provider of mice was Abbie Lathrop of Granby, Massachusetts(8, 9), who started as a mouse fancier who occasionally sold mice to local children. When her advertisements requesting mice for breeding were misunderstood as advertisements offering mice for sale, her business grew. Her customers included Clarence Cook Little, who created the first inbred strains (including the C57 and C58 strains) during his coat color experiments. Lathrop and others did use some "wild" (possibly commensal) mice in their breeding programs. For example, when L.C. Strong at Cold Spring Harbor Laboratory outcrossed laboratory mice with "wild" mice, the wild mice were in fact captured from a commensal population living in a pigeon coop(6).

**Rats.** Most laboratory rat strains were likely started using pet rats or rats caught in urban environments(10). The creation of laboratory rat strains was first undertaken by Dr. Helen Dean King at the Wistar Institute in Philadelphia, who bred and distributed rats through the 1940s, and many modern laboratory rat strains are descended from these strains(10–13). While the original four albino rats are known to have been provided by H.H. Donaldson, Donaldson's own papers give inconsistent information on their origins, mentioning European dealers and "wild" rats(14). More is known about other laboratory strains. For example, Dr. King established the rat strain now known as Brown Norway using rats captured in the city of Philadelphia(14). Similarly, the Long-Evans rat strain was created using two female Wistar rats and a male caught on the campus of the University of California, Berkeley, and the Sprague-Dawley rat strain was started using rats captured at the Oscar Mayer company dump(15, 16).

**Nematode.** The first nematodes (*Caenorhabditis elegans*) used in research, in 1676, were found in a bottle of wine and dubbed "vinegar eels" by Antonie van Leeuwenhoek, the inventor of the microscope(17). The founders of the Bergerac strain were collected from garden soil

(18) and the founders of the Bristol strain were collected from mushroom compost (19).

**Sand Fleas.** Populations of sand fleas (*Parhyale hawaiiensis*) are found in tropical waters worldwide. However, the lab cultures of *Parhyale* were developed by William Browne using animals that had opportunistically colonized the seawater filtration system of the Shedd Aquarium in Chicago, Illinois in 1997(20).

**Yeast (*Saccharomyces cerevisiae*).** Carl and Gertrude Lindegren, who started their work in yeast in the 1940s used commercial baking yeast from various locations to produce their laboratory strains. They also used strains previously isolated by Emil Mrak from rotting figs in Merced, California in the late 1930s. Another strain was isolated by C. Kurtzman from rotting bananas in Costa Rica (21).

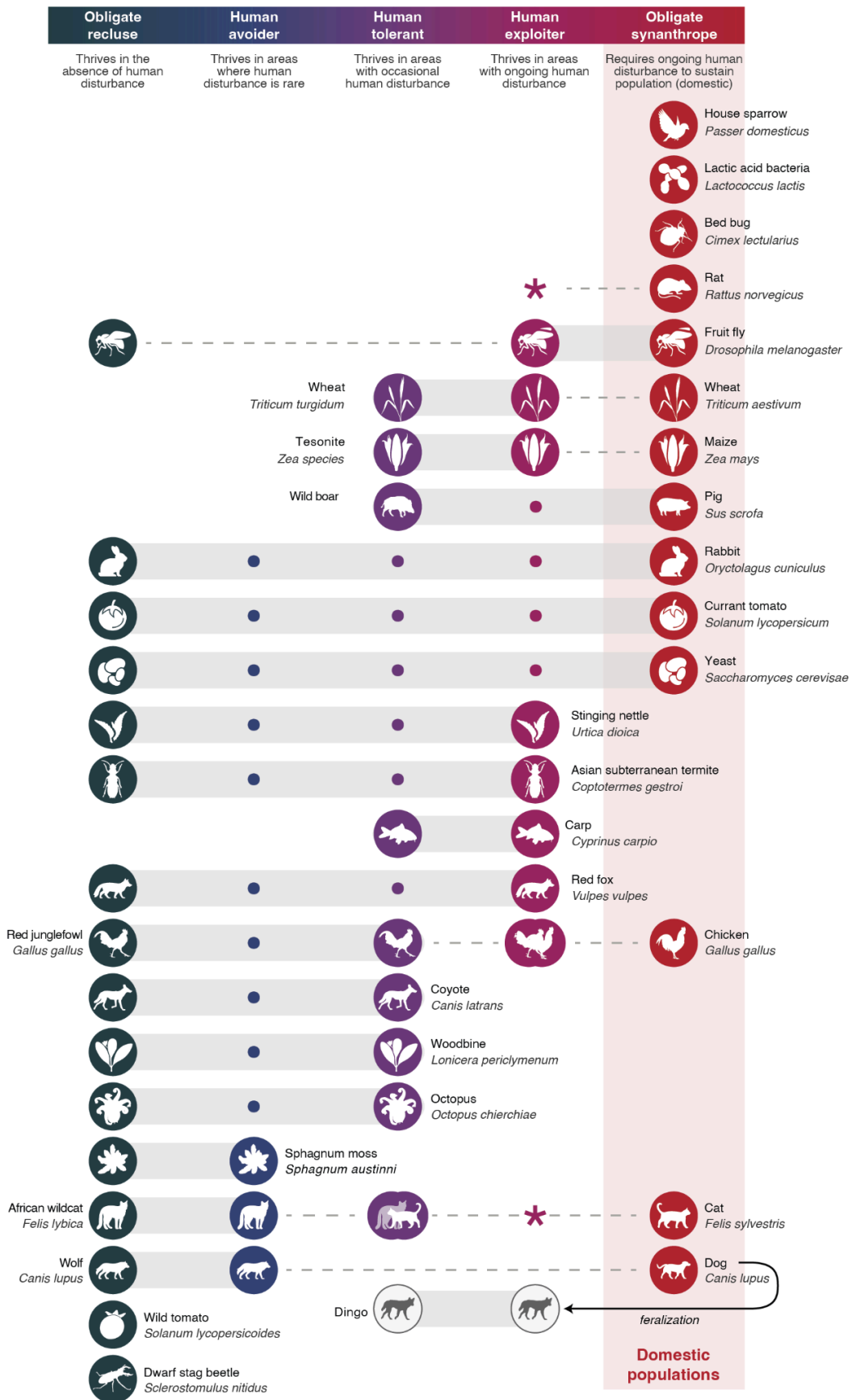
**South African clawed frog (*Xenopus laevis*).** Populations of *Xenopus* thrive in slow-moving, turbid water, including many human-created waterways that have allowed for their expansion outside of their native habitat (22). By the time *Xenopus* became a popular laboratory model for developmental biology in the 1940s and 1950s, they were easily acquired from commercial labs in Europe and the United States using *Xenopus* for pregnancy testing. These animals were originally acquired from commercial dealers in South Africa to meet the demand(23).

**Zebrafish (*Danio rerio*).** Populations of zebrafish thrive in slow-flowing waterways with sandy substrates, including many human-created environments such as canals created for irrigation, paddy fields, and ponds created for aquaculture of other species (24). The original lab strain was purchased from a pet store in Oregon selling ornamental fish (25). Mitochondrial evidence suggests the source population was from near the capital city Kolkata (26).

**Arabidopsis.** The earliest seed collections were established by Friedrich Laibach, a German botanist. Laibach sent four strains to the Hungarian botanist Barna Györfy in 1955. When Dr. Györfy's student, George Rédei, set up his own lab at the University of Missouri, Columbia, in 1956, he brought seeds from one of these four strains (labeled Landsberg) with him. Subsequent work revealed that the Landsberg seeds were not isogenic, and they are the source for several wild-type lines (including the Columbia wild type) as well as Rédei's early mutants (e.g. Landsberg *erecta*). Although little is known from historical records about where Friedrich Laibach collected his seeds, genetics is helping address this gap. Lines developed from Laibach's seeds (including Columbia and Landsberg *erecta*) were used to develop the earliest Arabidopsis genome data resources(27) and subsequent comparisons between plants from different parts of the world have confirmed that the Columbia strain shares significant ancestry with individuals from North Germany (28).

### **Classification of captive populations**

The definition can be used to assess the domestication status of any self-sustaining population. Captive populations are often sink populations that cannot sustain themselves without direct human intervention, and thus cannot be independently assessed for their position on the domestication spectrum. When individuals in captivity are a subpopulation of a self-sustaining population, their domestication status is that of the parent population. For example, a dog breed like poodles can be inferred to be domestic because the source population (dogs) is domestic, but poodles cannot be independently assessed for their domestication status.



**Figure S1. The domestication spectrum.** This is an expanded version of Figure 2, illustrating how the new definition can be operationalized. Populations are categorized along a spectrum of domestication types defined by their relationship with anthropogenic environments. Each row is a species (or broader clade for maize and wheat). Circles (both with silhouettes or without) indicate that populations are described in the corresponding category. Gray areas show the likely range of the domestication spectrum occupied by populations in that species or subspecies. Dashed lines demarcate categories in species with wild and domestic subspecies for which no populations are observed. Overlapping circles with silhouettes represent populations with admixture between wild and domestic subspecies. Asterisks indicate that populations are observed in that category only as a result of human translocations.

Term	Type	Relationship between human and non-human populations
Parasitic	Asymmetric (+/-)	One population benefits and the other is harmed
Mutualistic	Symmetric (+/+)	Both populations benefit
Interspecific competition	Symmetric (-/-)	Both populations are harmed
Commensal	Asymmetric (+/0)	One population benefits and the other neither benefits nor is harmed
Amensalism	Asymmetric (-/0)	One population is harmed and the other neither benefits nor is harmed

**Table S1. Mutualism is one of five types of symbiotic relationships that may exist between human and non-human populations.** Identifying the type of symbiosis that characterizes a given relationship requires measuring its effect on the evolutionary fitness of both populations.

Neologism	Definition	Ref.	Species & populations described
#1 Auto-domestication	#1 Sudden appearance of tameness in a population of wild animals primarily through habituation	(29)	Bighorn Sheep ( <i>Ovis canadensis canadensis</i> ); Cape buffalo ( <i>Syncerus caffer</i> )
	#2 When domestication occurs without human involvement	(30)	Cat
	#3 When members of a species manage the environment and reproductive opportunities of other members of the same species. Used to explain human morphological and behavioral phenotypes considered by author to be degenerate and maladaptive	(31)	Human
#2 De-domestication	#4 The establishment of a self-sustaining population of animals in the wild from a domestic source population, or the intentional creation of wild populations from a domestic source population (used interchangeably with re-wilding)	(32)	Heck cattle ( <i>Bos taurus</i> ); Konik horse ( <i>Equus ferus</i> )
		(33)	European rabbit ( <i>Oryctolagus cuniculus</i> ) bred to be wild-type from domestic populations
	#5 The evolution of wild-like traits and the ability to live outside of human management (equated with feralization)	(34)	Dingo ( <i>Canis lupus dingo</i> ); feral Kauai chicken ( <i>Gallus gallus</i> ); Tibetan sheep ( <i>Ovis aries</i> ); Weedy eggplant ( <i>Solanum melongena</i> ); Tibetan semi-wild wheat ( <i>Triticum aestivum</i> ); Weedy rice ( <i>Oryza sativa</i> )
	#6 The practice of releasing domestic populations into the wild or into a managed park to alter the ecosystem or for human sport or profit	(35)	Feral chickens in Hawaii; feral rabbits in Australia ( <i>Oryctolagus cuniculus</i> ); feral swine; Weedy rice ( <i>Oryza sativa</i> )
	#7 The process of a domestic species evolving to no longer require human control. Used to explain why some domestic species have pest populations.	(36)	Cat; Dog; Fruit tree (Apple tree); Fruit tree (Olive tree); Fruit tree (Orange tree); Horse; Pig
	#8 Undergoing the evolutionary process of domestication in reverse	(37)	
#3 Endosymbiotic domestication	#9 A mutualistic relationship leading to an endosymbiotic relationship	(38)	Organelle (e.g. mitochondria)
#4 Hyper-domestic	#10 An abnormally high expression of traits associated with domestication in species that have undergone self-domestication	(39)	Human
#5 Hypo-fomestic	#11 An abnormally low expression of traits associated with domestication in species that have undergone self-domestication (as a result of reduced neural crest activity)	(40)	Human
#6 Peri-domestic	#12 Domestic populations that have evolved to become "wild", which is defined as no longer being in a mutualistic relationship with humans or under human control	(36)	Cat; Dog; Fruit tree (Apple tree); Fruit tree (Olive tree); Fruit tree (Orange tree); Horse; Pig
	#13 Outdoor environments near houses	(41)	Mosquito ( <i>Anopheles</i> species)
	#14 Populations that are adapted to the human environment but are not under human control	(36)	Fruit fly ( <i>Drosophila melanogaster</i> ); House mouse ( <i>Mus musculus</i> )
	#15 Undefined, but used broadly to refer to uncontrolled domestic populations and urban wildlife	(42)	Feral cat; Black rat ( <i>Rattus rattus</i> ); Gull (no species name); Squirrel (no species name)
#7 Pre-	#16 Before domestication (as determined by lack of	(43)	Gazelle ( <i>Gazella gazella</i> ) hunting

Neologism	Definition	Ref.	Species & populations described
domestication	physiological changes or not specified)	(44)	Domestic cattle ( <i>Bos taurus</i> )
		(45)	Wild relative of domestic corn ( <i>Zea mays</i> spp. <i>parviglumis</i> )
	#17 Early harvesting/cultivation/breeding of a species Not yet physically distinguishable as domestic. Used to explain why some genetic changes predate domestication in the archeological record	(46)	Javan porcupine ( <i>Hystrix javanica</i> )
		(47)	Goat during the mid Pre-Pottery Neolithic B (no species name)
		(48)	Plants
		(49)	Wild plants
#8 Proto-domestication	#18 An evolutionary step that involves a non-human population living closer to humans without being controlled by humans	(50)	Dogs( <i>Canis lupus familiaris</i> )
		(51)	Fox ( <i>Vulpes vulpes</i> )
	#19 An evolutionary step that involves a nonhuman population undergoing unconscious selective pressure from humans prior to intentional human selection	(52)	Landrace fruit
	#20 Populations that due to hybridization have both behaviors and morphological traits that are midway between the wild and domestic populations	(53)	Pig
		(43)	Gazelle ( <i>Gazella gazella</i> )
	#21 Populations that undergo management and culling by humans, but do not experience any other human control	(47)	Gazelle (no species name); Goat ( <i>Capra aegagrus</i> ) in the Southern Levant; Nubian Ibex ( <i>Capra ibex nubiana</i> )
(54)		Truffle ( <i>Tuber melanosporum</i> )	
#9 Re-domestication	#22 Creating domestic populations with increased tameness by selectively breeding of the wild relatives of current domestic populations	(55)	Chicken ( <i>Gallus gallus</i> )
		(56)	Cereals; Ground cherry ( <i>Physalis pruinosa</i> ); Tomato (no species name)
#10 Self-domestication	#24 Domestication occurring without any human involvement	(57)	
		(35)	
		(58)	Dog
	#25 Domestication through selection for prosociality and against aggression.	(59)	Belyaev's fox ( <i>Vulpes vulpes</i> ); Bonobos ( <i>Pan paniscus</i> ); Dog; Human
	#26 Selection for reduced aggression in wild populations leading to the development of traits associated with domestication	(60)	Bonobo ( <i>Pan paniscus</i> )
	#27 Selection in human populations due to social pressure favoring less violence	(57)	Human
	#28 The production of domestication-associated traits in a population that is not captive nor under human control, but is experiencing selective pressures similar to those in populations that are captive or under human control	(61)	Human
	#29 When humans domesticate themselves	(35)	Human
#30 When selection for increased sociality in wild species leads to the development of traits associated with domestication	(62)	African elephant ( <i>Loxodonta africana</i> and <i>Loxodonta cyclotis</i> ); Asian elephant ( <i>Elephas maximus</i> )	

Neologism	Definition	Ref.	Species & populations described
	#31 When selection for reduced fear in a wild species leads to the development of traits associated with domestication	(63)	Ansell's mole rat ( <i>Fukomys anselii</i> )
	#32 When selection for tameness in a wild species results in the development of traits associated with domestication	(64)	Marmoset ( <i>Callithrix jacchus</i> )
#11 Semi-domestication	#33 Populations of a non-domestic species that are being bred or cultivated in captivity	(65)	White-lipped peccary ( <i>Tayassu pecari</i> )
		(66)	Fence post tree ( <i>Gliricidia sepium</i> )
			Mango ginger ( <i>Curcuma amada</i> )
	(67)	Deer mouse ( <i>Peromyscus maniculatus bairdii</i> )	
	#34 Populations that are no longer under human control, but that are still useful to humans	(68)	Passion fruit ( <i>Passiflora edulis</i> )
		(66)	Lima bean ( <i>Phaseolus lunatus</i> )
	#35 Populations that are under partial or indirect human control	(69)	Asian elephant ( <i>Elephas maximus L.</i> ); Camel ( <i>Camelus spp. L.</i> ); Hunted ungulate
		(70)	Mongoose ( <i>Herpestes ichneumon</i> ).
(71)		Reindeer ( <i>Rangifer tarandus</i> )	
#36 Populations that spend part of their life cycle indoors and part of it outdoors	(72)	Muga silk worm ( <i>Antheraea assamensis</i> )	
#12 Super-domestication	#37 Selection for increased usefulness using genetic editing technology	(73)	Canola ( <i>Brassica napus L.</i> )
#13 Trans-domestication	#38 When a wild species is moved by humans out of its native range and is then undergoes domestication	(74)	Cluster or Guar bean ( <i>Cyamopsis tetragonoloba</i> )

**Table S2.** Neologisms that modify the word domestication are common. We documented 13 of these terms with at least 38 distinct definitions. Many attempt to address the ambiguity inherent in earlier attempts to define domestication.

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