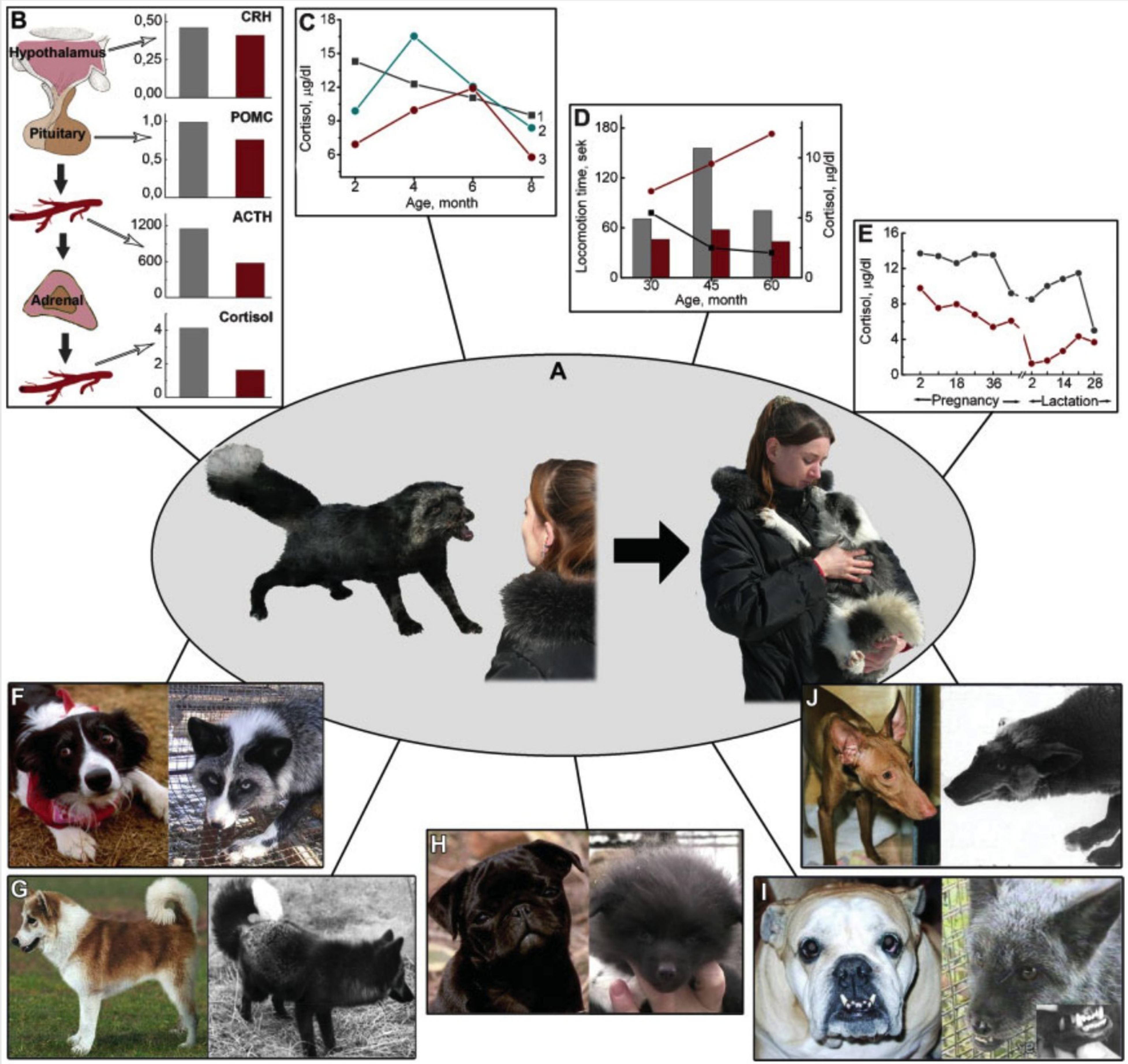
Domestication

Brian O'Meara
EEB464 Fall 2018

Learning objectives

- What has been the history of domestication?
- What traits change?
- Why do traits change?
- Can nonhuman organisms domesticate others?



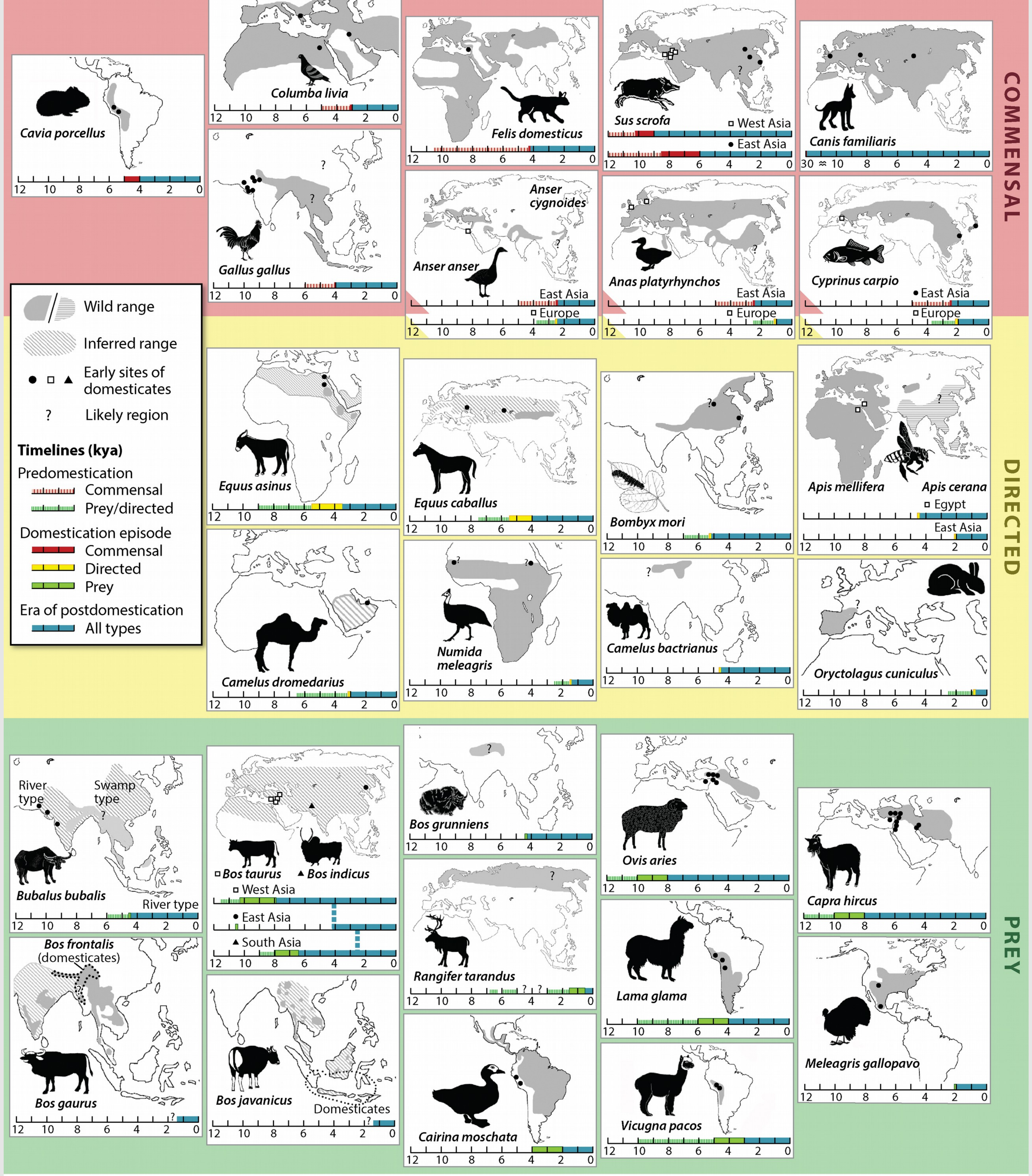
Trut et al. 2009

Does fast response to selection go against Darwin?

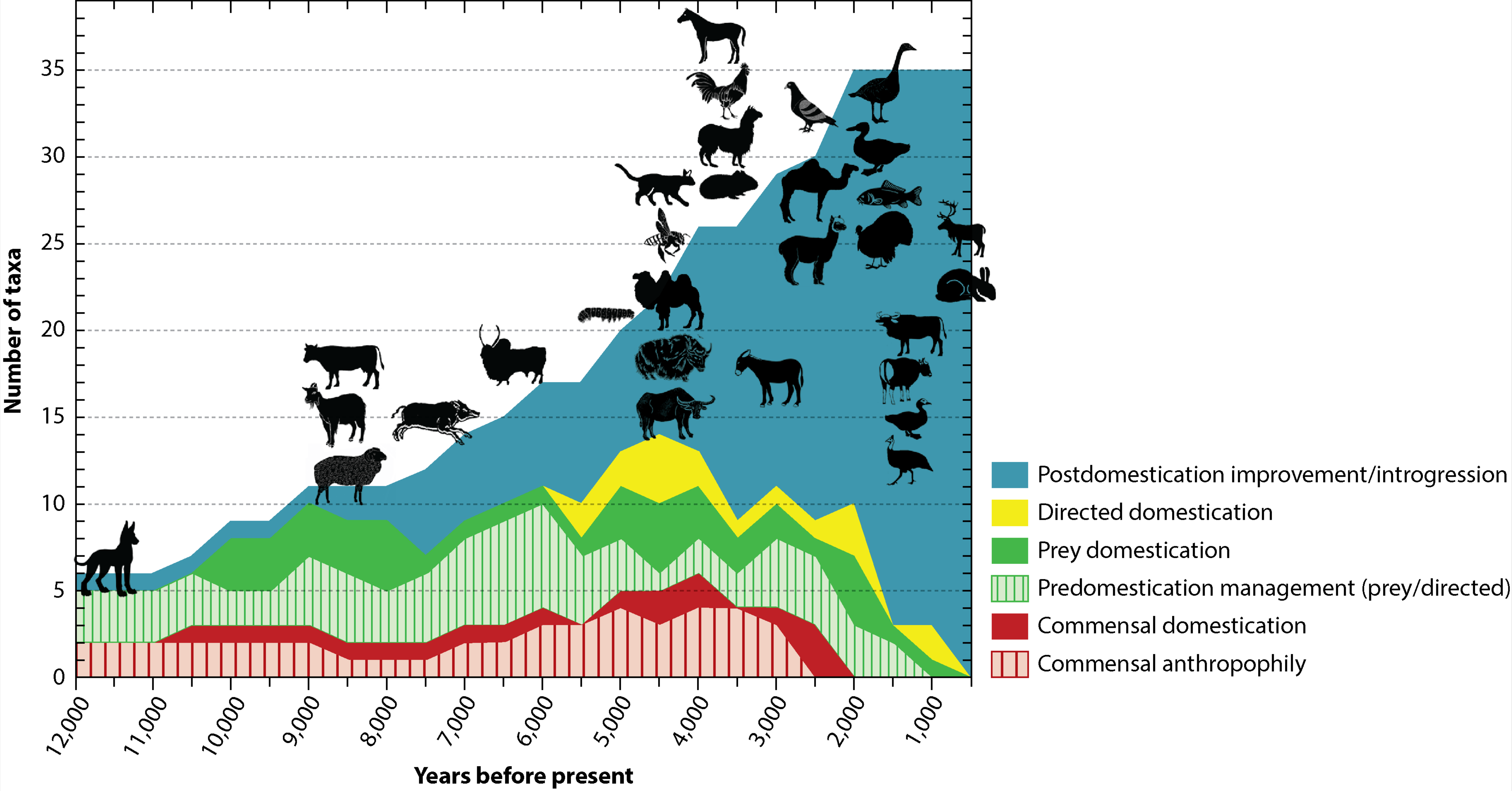
Why would traits besides the one being selected on change?

How would you test this?

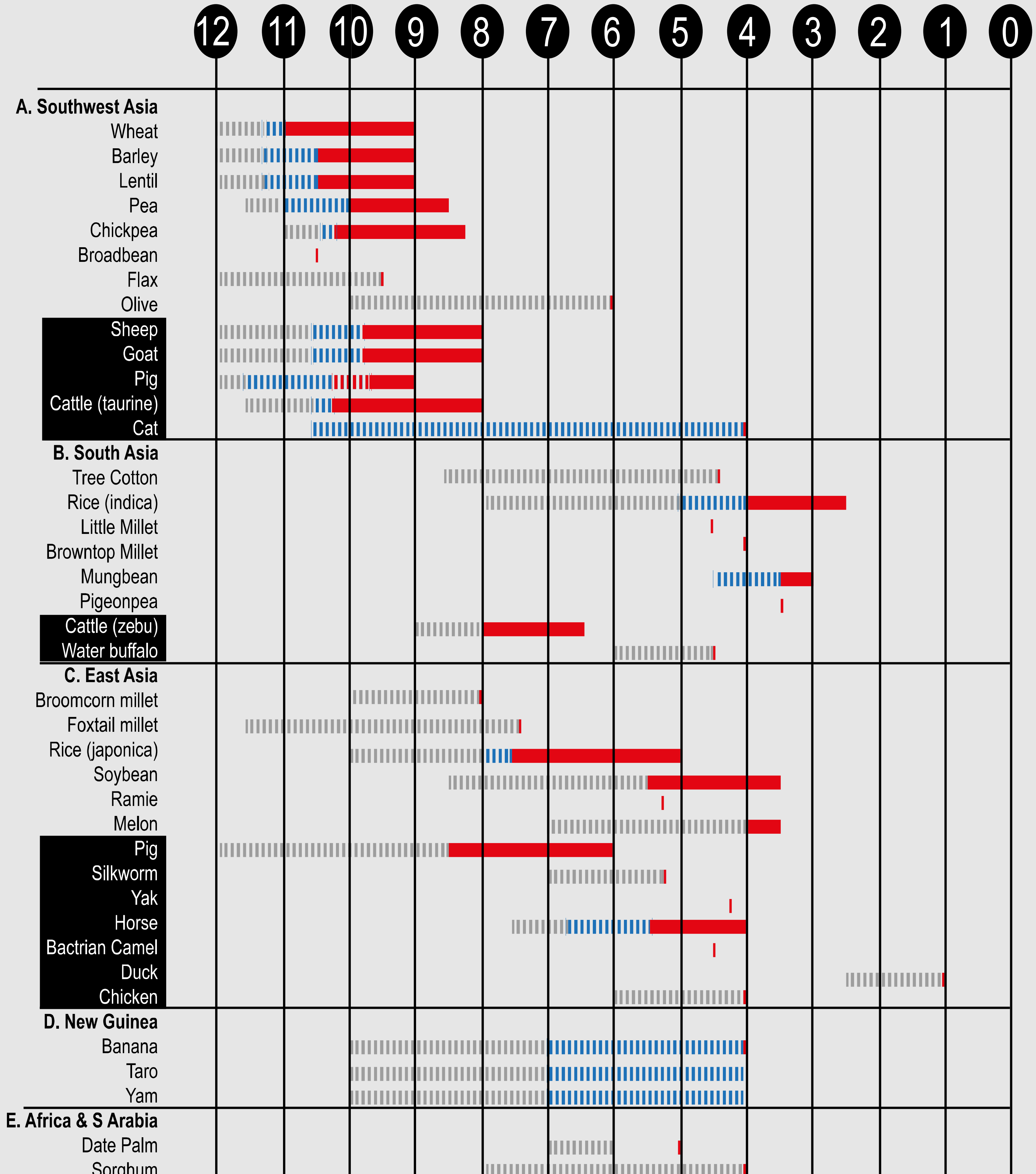
Vincent Musi for National Geographic.



Larson G, Fuller DQ. 2014.
Annu. Rev. Ecol. Evol. Syst. 45:115–36



Larson G, Fuller DQ. 2014.
Annu. Rev. Ecol. Evol. Syst. 45:115–36



explanations, however, have proved unsatisfying for a number of researchers, and significant tensions remain between camps advocating different explanatory blueprints. The issue poses an important remaining challenge in domestication research (25) (see below).

Early Domestication Stages

The initial stages of the multispecies networks involved in domestication were critical because humans acted as: (*i*) dispersal agents (managing the reproduction of cultivated plants and controlling the mobility, range and density of domestic livestock); (*ii*) agents of (conscious or unconscious) selection, favoring the reproductive success of particular behavioral and phenotypic variants); and (*iii*) ecosystem modifiers, who (along with natural environmental changes) alter the developmental conditions and hence the characteristics of associated organisms.

So what is a domesticated plant or animal and how does it differ from its wild ancestor? From a present-day perspective, it is possible to recognize suites of common traits that make up the so-called "domestication syndrome" (26–28), and presumably many of

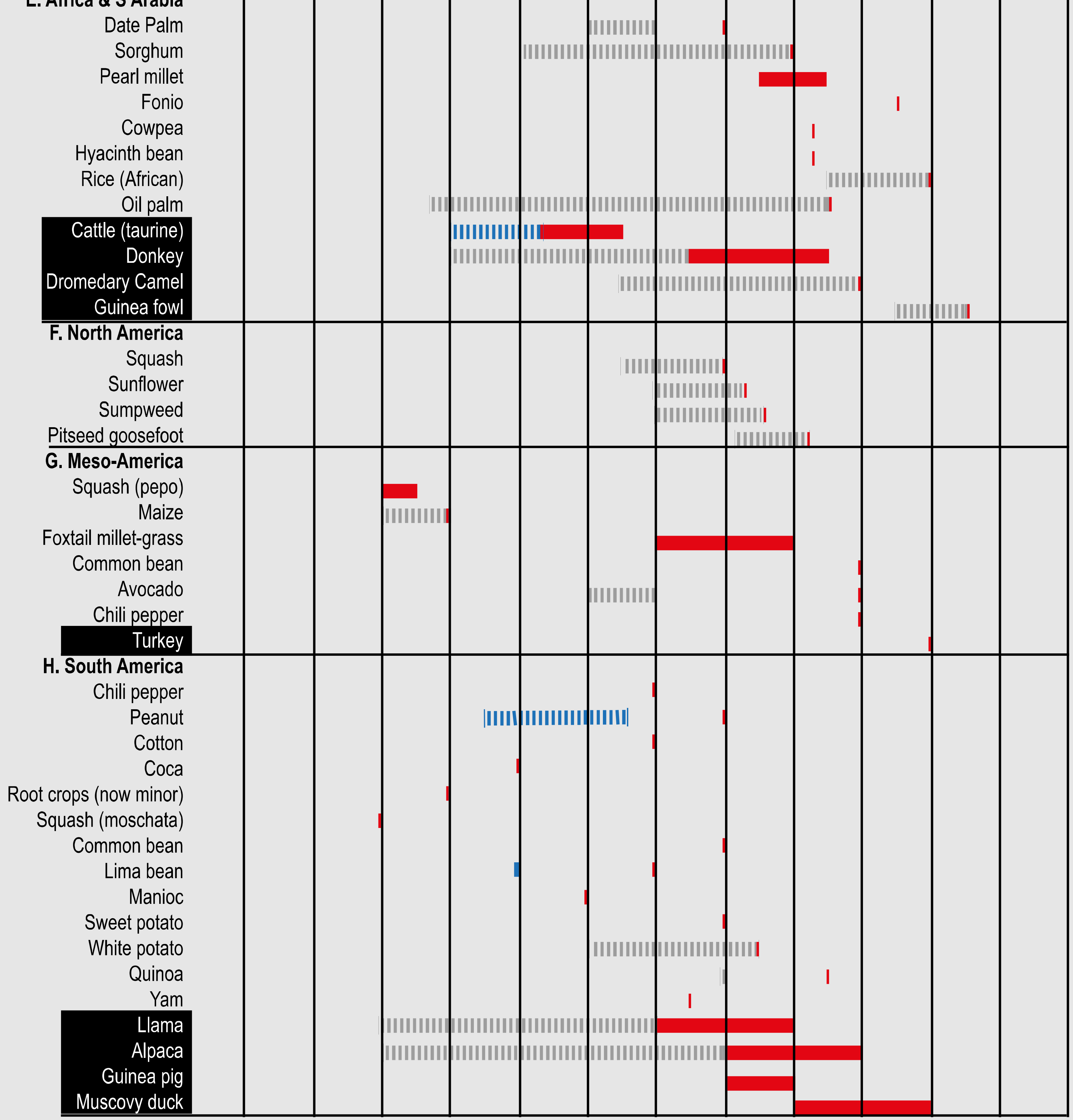


Fig. 2. A chronological chart listing the regions where, and the time frames over which, key plants and animals were domesticated. The numbers in the black circles represent thousands of years before present. Gray dashed lines represent documented exploitation before domestication or posited as necessary lead-time to domestication. Blue dashed lines represent either the management of plants or animals (including translocation) or predomestication cultivation of plants, neither of which were associated with morphological indications of domestication. Red bars frame the period over which morphological changes associated with domestication are first documented and a short, solid red bar represents the latest time by which domestication occurred. Although early Holocene plant domesti-

drome" (26–28), and presumably many of these were key to early selection along the wild-to-domesticated trajectory. In plants, the syndrome is defined by a wide variety of traits that, depending on the species, may include: a reduced ability to disperse seeds without human intervention, reduction in physical and chemical defenses, reduction in unproductive side-shoots, reduction in seed dormancy, bigger seeds, more predictable and synchronous germination, and in some seed-propagated species, bigger and more inflorescences. In animals, these traits include: endocrine changes, increased docility, altered reproduction pattern and output, altered coat color, floppy ears, facial neotony, usually a reduction in size, and other changes in body proportions (26). Recent genetic and archaeological research, however, has demonstrated that not all of these traits arose at the same time in either plants or animals. In addition, it has been helpful to separate genes that controlled the traits that were under early selection (domestication genes) from those that were selected later to produce diversified and improved crops and animals (improvement genes) (4).

The strength of selection for "domestication syndrome" gene variants and their speed of fixation remains controversial. Although strong selection with rapid evolution of domestication traits within as little as 100–

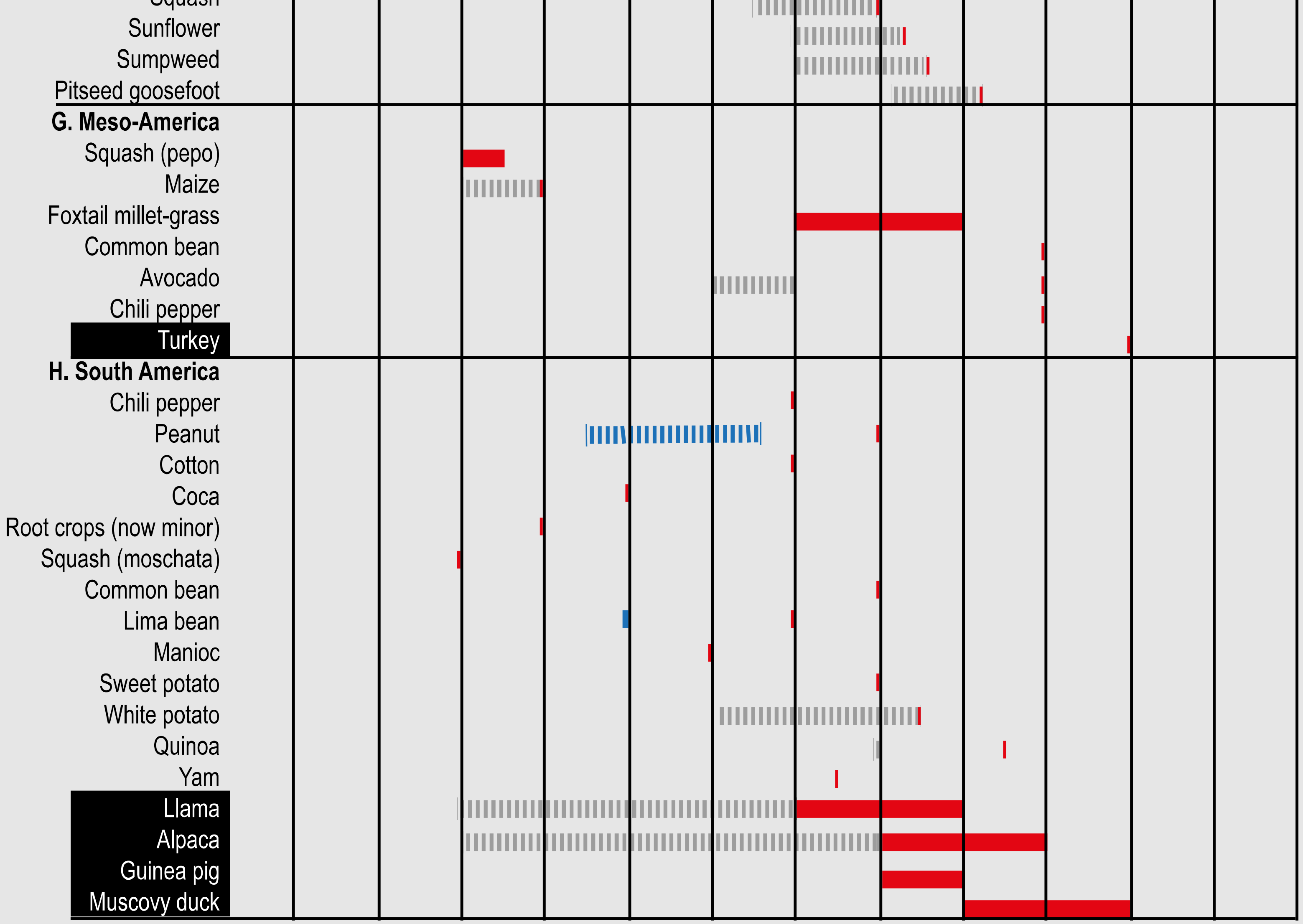


Fig. 2. A chronological chart listing the regions where, and the time frames over which, key plants and animals were domesticated. The numbers in the black circles represent thousands of years before present. Gray dashed lines represent documented exploitation before domestication or posited as necessary lead-time to domestication. Blue dashed lines represent either the management of plants or animals (including translocation) or predomestication cultivation of plants, neither of which were associated with morphological indications of domestication. Red bars frame the period over which morphological changes associated with domestication are first documented and a short, solid red bar represents the latest time by which domestication occurred. Although early Holocene plant domestication took place independently in both the Old and New Worlds, early Holocene animal domestication was restricted to the Near East. In addition, the majority of plants and animals on this list were domesticated in the middle Holocene. Additional details and references associated with each taxon are found in Table S1. Letters *A–H* correspond to those found in Fig. 1.

unproductive side-shoots, reduction in seed dormancy, bigger seeds, more predictable and synchronous germination, and in some seed-propagated species, bigger and more inflorescences. In animals, these traits include: endocrine changes, increased docility, altered reproduction pattern and output, altered coat color, floppy ears, facial neotony, usually a reduction in size, and other changes in body proportions (26). Recent genetic and archaeological research, however, has demonstrated that not all of these traits arose at the same time in either plants or animals. In addition, it has been helpful to separate genes that controlled the traits that were under early selection (domestication genes) from those that were selected later to produce diversified and improved crops and animals (improvement genes) (4).

The strength of selection for "domestication syndrome" gene variants and their speed of fixation remains controversial. Although strong selection with rapid evolution of domestication traits within as little as 100–200 y has been suggested (8, 9, 29), recent archaeological studies have questioned these conclusions, at least for cereal domestication.

How many plant species have been fully domesticated by humans?

1. 25
2. 100
3. 250
4. 500
5. 1000

- 250 plant species have been fully domesticated
- 2500 partially domesticated
- 160 plant families

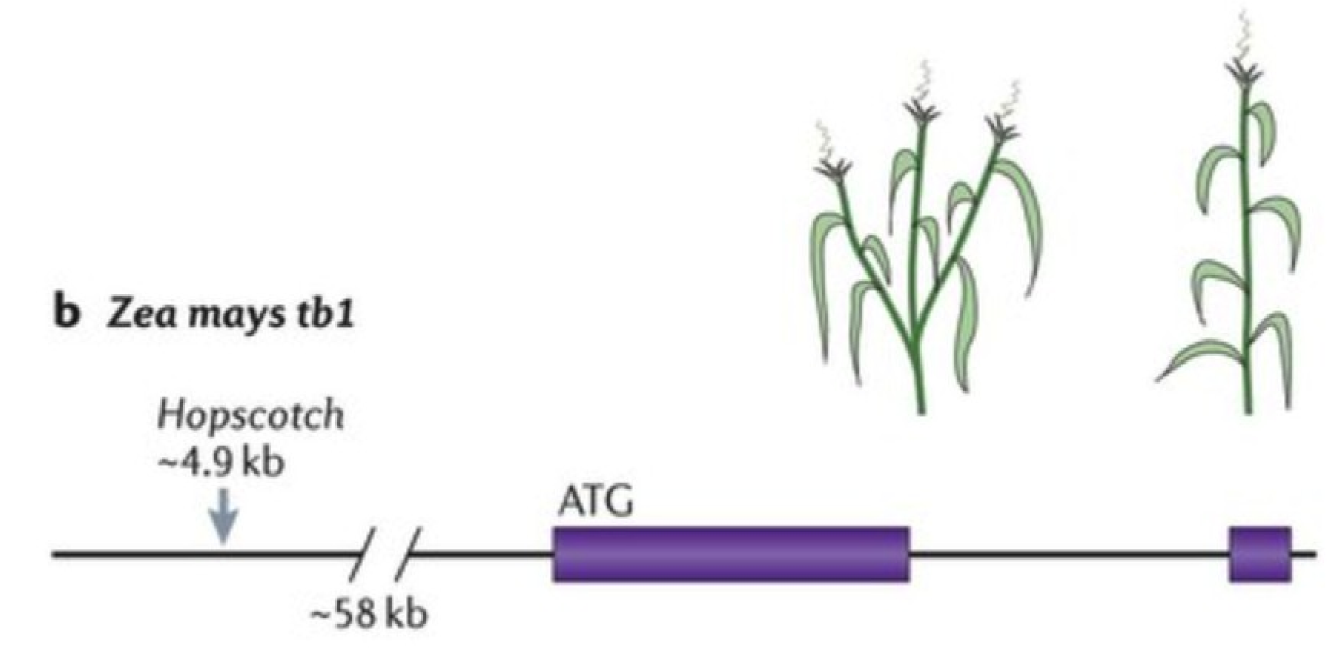
Meyer & Purugganan 2013

	Stage 1	Stage 2	Stage 3	Stage 4
Seed crop	• Larger seeds • Resource allocation • Thinner seed coat, and increased seed softening and ornamentation • Inflorescence architecture (including shape, number and determinacy) • Increased yield potential and productivity • Loss of dormancy • Determinate growth	• More seeds • Increased seed size variation • Pigment change • Flavour change • Change in starch content • Non-shattering seeds‡ • Reduced germination inhibition	• Reduced vernalization • Reduced photoperiod sensitivity • Modified hormone sensitivity • Synchronized flowering time • Shortened or extended life cycle • Dwarfism	• Increased yield • Increased abiotic stress toleranc • Increased biotic stress tolerance • Improved eating quality
Root and Tuber	• Flavour change • Resource allocation • Change in starch content • Ability to thrive in modified landscape • Reduced branching	• Reduced toxicity • Vegetative propagation and reduced sexual propagation • Abiotic stress tolerance • Biotic stress tolerance • Extended harvest season	• Hybridization using effect of heterosis • Promotion of allogamy • Increased yield	• Improved nutritional quality • Improve multiplication ability and rate
Fruit	• Flavour change • Resource allocation • Larger seed size • Larger fruit size • Shortened life cycle • Softer fruit	• Increased fruit size variation • Selfing breeding system	• Improved pollination success • Reduced fruit shedding • Continuous fruiting	• Delayed ripening • Increased post-harvest quality and delayed senescence • Increased yield • Increased abiotic stress toleranc • Increased resistance • Attractiveness and even ripening

*Examples in annual or short-lived perennial fruits, roots and seeds are shown. Fewer general traits could be identified for less well-characterized crops, such as leaf crops and long-lived perennial species, and these were therefore excluded. ‡A Stage 1 trait in some crop species.

Meyer & Purugganan 2013

Selection is a hallmark of domestication and should leave molecular footprints in the genomes of crop species. The first domestication gene that was isolated — the maize tb1 locus — has a 60–90-kb selective sweep that occurred upstream of the 5′ end of the protein-coding region. This sweep, which is defined as an extended region of low nucleotide diversity, spans the Hopscotch transposable element insertion in the cis-regulatory region that regulates tb1 expression. Early genome-scale surveys in maize suggested that as many as 2–4% of genes in this cereal crop species were under positive selection, but recent work indicates that a much larger percentage (~7.6%) of the maize genome has been affected by domestication and diversification. Recent studies also reveal that selective sweeps are prevalent in the genomes of other crops, such as mungbean, rice and tomato.



Meyer & Purugganan 2013

- Can nonhuman organisms domesticate other species?
- How?
- Do the species change in the same way species change with human domestication?