Genetic adaptation to starch in dogs

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The following is an excerpt from *Feeding Miss Lilly: on feeding dogs a great, nature-inspired diet; revised edition* (Dr Christine King; Anima Books, 2022).

… there were no grains or grain-based foods in Miss Lilly's daily diet. Some dogs do OK with a little grain in their diets, but many do not, mine included. Miss Lilly came to tolerate the occasional dog cookie (thank you, Uncle Walter!) or discarded hamburger bun by the side of the road (dog manna!), but she did best when I excluded grains and other starchy foods (potatoes, sweet potatoes, most legumes) from her daily diet. That, too, is species-appropriate.

What’s the problem with grain?

Few foods are inherently and universally “bad,” and the cereal grains are no exception.[1] Grains are not bad; they’re just misused. Mostly they’re overused. A lot. Even in human diets. And they just don’t belong in any great amount in a carnivore’s diet, not even that of a facultative carnivore.

The modern cereal grains (wheat, corn, oats, barley, rice, *etc.*) aren’t even that great a food for herbivores and omnivores — at least, not in the large quantities we’re typically feeding or eating. A lot of attention has been paid to gluten and other proteins in certain grains (*e.g.,* wheat) as a cause of disease, and rightly so. But in my experience, not enough concern has been applied to the *starch* content of cereal grains.

the up-side

Cereal grains have been deliberately selected over the centuries to be very high in starch. Compare, for example, the size of an oat or rice kernel with those of wild oats or wild rice, or with any other grass seed for that matter. The domestic kernel is much larger than its wild counterpart because its central portion is bloated with the starchy material that is turned into flour during milling.

The high starch content of cereal grains — 45% to 75% starch[2], depending on the crop — makes them quite calorie-dense (*i.e.,* concentrated calories), which is the whole point: grains are a compact form of energy that is easy to grow, harvest, store, transport, trade, and make into high-calorie food.

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[1] By “grain,” I mean the *cereal grains* (wheat, corn, oats, barley, rice, sorghum, millet, spelt, kamut, rye, triticale, *etc.*). Most grain-producing plants are members of the Grass family, and they are best called *cereal* grains, as grain simply means “small particle” (*e.g.,* grain of sand). Not all small seeds are cereal grains; for example, sesame, chia, buckwheat, quinoa, and amaranth seeds are not cereals.

[2] Source: equi-analytical.com/common-feed-profiles/

In addition, foods made with cereal grains are considerably less expensive to produce than foods made with high-quality animal products. There's value in that. However, there's also a down-side.

the down-side

Even though grains have been a significant component of human diets for thousands of years, genetically we still haven't fully adapted to using grains as a primary food source. The changes in diet which followed the domestication of grasses for the mass production of grain have not been accompanied by sufficient changes in the human genome to prevent the diseases commonly caused by high-grain diets — and we're omnivores!

Dogs and cats, being *carnivores,* are even less well adapted to using cereal grains as a major food source. Compared with wolves, dogs have made some genetic adaptations in this regard (especially in the gene that codes for pancreatic amylase),[3] but clearly not enough. [More on this later.]

Gluten, lectins, phytates, and other plant molecules are implicated in the grain-related health problems, but *starch* may be every bit as problematic.

Starch is a carbohydrate-storage molecule that is made by plants. It is stored, among other places, in the seeds, where it serves as a little energy "backpack" once the seed has fallen to the ground. Sprouting, or germination, activates the enzymes in the seed that transform the starch into readily usable energy for initial root, stem, and leaf growth.

As an energy source for animals (and humans), starch must first be broken down into smaller sugar molecules before it can be absorbed by the intestine and used for energy production in the body. There are several different digestive enzymes involved in this process, and any one of them can limit the complete digestion, absorption, and utilization of starch.

Starch is also readily broken down ('fermented') and used for energy by the bacteria and other microbes in the gut.[4] Carbohydrate-fermenting ('saccharolytic') microbes are found throughout the digestive tract, including in the mouth, so to some extent there is always a race between enzymatic digestion and microbial fermentation of any starchy food.

The more starch there is in a meal, the more microbial fermentation will feature in its breakdown, because enzymatic digestion of starch is rate-limited: there's only so much starch a body can break down with its digestive enzymes in a given amount of time.

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[3] For example, 'Diet adaptation in dog reflects spread of prehistoric agriculture' [doi: 10.1038/hdy.2016.48] and 'Dietary variation and evolution of gene copy number among dog breeds' [doi:10.1371/journal.pone.0148899].

[4] The 'gut' is generally considered to comprise the parts of the digestive tract that are located within the abdomen (belly): the stomach, small intestine, and large intestine (cecum and colon). That's what I mean when I refer to the gut. The 'digestive tract' as a whole includes every part from mouth to anus. The 'digestive system' may also include the liver and pancreas, depending on the context.

For example, in horses 2 grams of starch per kilogram of body weight is enough to cause spillover of starch into the large intestine.[5] There, it is rapidly fermented by the gut microbes. And that's in a *herbivore,* whose digestive system is *designed* to make use of plant material *exclusively.*

The trouble with the microbial fermentation of starch is that it yields lactic acid and carbon dioxide, both of which alter the environment within the gut, and not for the better. In sufficient amounts, the gas produced can cause bloating, cramping, or simply flatulence (excessive 'farting'). But a more insidious problem is that many of the other gut microbes are inhibited or killed off by the increase in acidity of the gut contents.

The large swings in acidity and microbial stress/distress with each high-starch meal can cause persistent, low-grade inflammation and compromise of the intestinal barrier, a situation commonly referred to as 'leaky gut'.

Leaky gut is well named, because microbes and microbial products that are normally confined to the gut are absorbed into the bloodstream when the intestinal barrier is compromised,[6] taxing the liver, activating the immune system, altering brain chemistry (via the gut–brain axis) — in fact, affecting every organ and tissue in the body to some extent.

Cooking makes most forms of starch more digestible and thus more available to the body, although there are still some enzymatic steps required in order for cooked starches to be digested and absorbed. However, cooking still leaves some *resistant* starch that cannot be enzymatically digested; it can only be broken down by the gut microbes, with the aforementioned consequences when consumed in large amounts.

So, cereal grains — and in fact *any* starchy food — for all their legitimate calorie-dense advantage, are not all they're cracked up to be. Or perhaps it would be better to say that eating them is not without problems. What constitutes "too much" starch depends somewhat on the individual (as some adaptation does occur), but mostly it depends on the species.

dogs and starch

Being carnivores, dogs are not well equipped to make good use of dietary starch in anything more than small amounts. Dogs do produce some carbohydrate-specific digestive enzymes, but all-in-all

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[5] 'Diet-dependent modular dynamic interactions of the equine cecal microbiota.' [doi: 10.1264/jsme2.ME16061]

[6] A recent study in horses measured the numbers of intestinal bacteria found in the lymph nodes that drain the intestine (the mesenteric lymph nodes) and in the liver.

Horses on a *high-grain* diet (49% starch) had 2–17 times as many bacteria in their mesenteric lymph nodes, and 10–35 times as many bacteria in their liver, compared with horses on a *high-fiber* diet (19% starch). These differences were statistically significant and they show that, even in a species adapted for an exclusively plant-based diet, a high-starch diet results in a leaky gut. [doi: 10.1111/jpn.13643] their digestive secretions are geared toward getting most of their energy needs met from animal fats, proteins, glucose (found in blood and tissues), and glycogen (a glucose-storage molecule found mostly in liver and muscle — *i.e.,* an *animal source* carbohydrate-storage molecule).

The dog's digestive system is simply not well adapted to making use of large amounts of starch, even after all this time living alongside humans. Sprouted or fermented grains may be better digested by dogs, as they are by humans. Even so, grass seeds don't form a significant part of the diet in wild canids, other than in the gut contents of their prey (where they have already been digested by enzymes and fermented by microbes), so we would be wise to follow suit when feeding our domestic dogs.

Most commercial dog- and cat-foods rely heavily on cereal grains or other starchy plants (for example potato, sweet potato, tapioca, peas). That's mostly because starchy foods are relatively cheap and animal products relatively expensive to grow and process, and pet-food manufacturing is a business.

As for the "grain-free" label on some dry and canned foods, that's typically a crafty marketing ploy, because grain-free generally doesn't mean *starch*-free. While these foods are indeed grain-free, *most are not starch-free;* other starchy foods are used in place of the cereal grains.

Think of it this way: just as you can't make a cookie without using some sort of flour, you can't make a kibble without some sort of starch.[7] If the starch doesn't come from grain, it has to come from some other starchy food. But either way, it's not a species-appropriate food source for a carnivore.

We can blame the pet-food manufacturers only so far, though. After all, they're simply making a profit by providing us with what we say we want: a cheap and easy way to feed our pets. On the one hand, they've trained us to think that dogs are supposed to eat dog-food and cats to eat cat-food. But on the other hand, *we've* trained *them* to meet our demand for quick, simple, and inexpensive pet-foods.

One of the penalties we're paying for our over-reliance on cereal grains and other starchy foods is the epidemic of obesity and related metabolic and endocrine (hormonal) disorders, such as type II diabetes and probably thyroid and adrenal gland disorders as well, in humans *and* animals.

In addition to their effects on the gut, high-starch meals cause a rapid increase in blood glucose, which triggers the release of insulin into the bloodstream from the pancreas. In small amounts, insulin is not only beneficial, it's essential. However, repeatedly or persistently high levels of insulin are problematic. This dynamic — the need for moderation or balance, the Goldilocks effect — is a critical one, wherever we look in the body.

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[7] Cookies *can* be made with nut flour (*e.g.,* almond meal), but they need a binder such as egg white if they are to be starch-free and not crumble in your hand.

Another consequence of high-starch diets is the prevalence of chronic digestive disorders often grouped under the umbrella term 'inflammatory bowel disease' (IBD). Anal sac problems[8] could go here, too, although they more rightly belong with the chronic skin conditions, including persistent itchiness (atopic dermatitis) and ear infections (otitis externa), that we commonly see with a leaky gut.

In fact, I think we can lay many chronic inflammatory and degenerative disorders at the door of this ill-conceived dietary strategy. They include periodontal disease, osteoarthritis, heart disease, kidney disease, cataracts, senility, cancer — *i.e.,* the customarily age-related diseases.

In recent years, there's been an avalanche of research published on how our gut microbes influence not just digestion but our entire health and well-being. In short, what we eat can either make us well or make us ill — and make us "glad, sad, or mad" — because the makeup and activity of our gut microbes depend in large part on what we eat. (The gut microbes are discussed in more depth in Chapter 4 of *Feeding Miss Lilly*.) It would be a gross oversimplification to blame every disease on a high-starch diet, but the evidence against high-starch diets is compelling.

In my clinical experience and my adventures with Miss Lilly, these disorders can be improved, sometimes dramatically, simply by cutting out grains and other starchy foods. While age-related disorders may still develop over time, it is possible to delay their appearance and slow their advancement with a species-appropriate diet which, for dogs, includes little or no starch.

...same goes for legumes

By the way, similar arguments can be made about the overuse of beans, peas, lentils, and other pulses (the generic term for legume seeds) in the diets of dogs and cats (and humans).[9] Tofu and other soy products fit here, as they are made from soybeans.

Legumes are primarily used as an alternate source of protein in vegetarian and vegan meals. However, legumes may also contain quite a bit of starch (30% to 50% starch for many varieties of beans and lentils[10]) and other rapidly-fermentable carbohydrates (hence the gas!). Not as much as grains, but enough to cause problems when overeaten. It's interesting that pea starch is commonly used in grain-free pet-foods...

Legumes are gluten-free; but in addition to starch, they contain several potentially troublesome molecules, including lectins and phytates, whose negative effects have earned them the label 'anti-nutrients.' *Anti-nutrients!* Harmful rather than helpful.

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[8] Just for fun: anal sac disease was probably the underlying cause of Tricki Woo's baneful condition which Mrs Pumphrey referred to as "flop-bot" in James Herriot's book *All Creatures Great and Small.* Tricki Woo was overweight, being fed all manner of high-calorie human foods by the overly indulgent Mrs Pumphrey.

[9] Green beans and pea pods (*e.g.,* snow peas, sugar snap peas) are exceptions because their seeds are immature, so they are high in fiber and low in starch.

[10] USDA FoodData Central: fdc.nal.usda.gov/index.html

A disturbing link has recently been found between a particular form of degenerative heart disease (dilated cardiomyopathy, or DCM) and the predominance of plant proteins (especially legumes) in the dog's diet.[11] There are numerous factors involved in DCM, but legumes rate a mention.

Reliance on plant proteins is most common in vegetarian and vegan dog-foods, but legumes also show up in grain-free and novel-protein dog-foods, and "boutique" brands (small companies that strive to distinguish themselves in the crowded pet-food marketplace).

I did include some cooked legumes in Miss Lilly's diet, but never very much, not very often, and only for extra variety (a concept I discuss in Chapter 3).

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On the next two pages are illustrations which show that one genetic adaptation to a high-starch diet in dogs — expression of the gene which codes for pancreatic amylase[*] — varies by breed, particularly by where the breed *originated* and its historical relationship with human agricultural activity.

[*] Pancreatic amylase is a starch-digesting enzyme produced by the pancreas and secreted into the small intestine after a meal. Its activity is the first step in breaking down dietary starch into small sugar molecules that can then be absorbed by the intestine. (In many species, including dogs, amylase is also secreted in the saliva. Pancreatic amylase deals with the starch that escaped digestion by salivary amylase.)

The gene coding for the production of pancreatic amylase is called AMY2B (amylase type 2-B), to distinguish it from *salivary* amylase (AMY1, amylase type 1). In general, the more copies of an amylase gene a species expresses, the better adapted the species is to a high-starch diet.

However, it's not quite as simple as that. There is *enormous* variation in AMY2B expression among individuals within the same species, and even within the same race or breed. In addition, ***being able to digest more starch does not diminish the adverse health effects of a high-starch diet;*** it simply shifts the harmful effects from the *gut* (disordered gut microbes, leaky gut) to the *circulation* (metabolic and endocrine diseases such as obesity, type II diabetes, and thyroid and adrenal gland disorders).

The last two pages show how much variation there is in *salivary* amylase (AMY1) expression between and within species, and how gene copy number is only *somewhat* related to salivary amylase *activity.*

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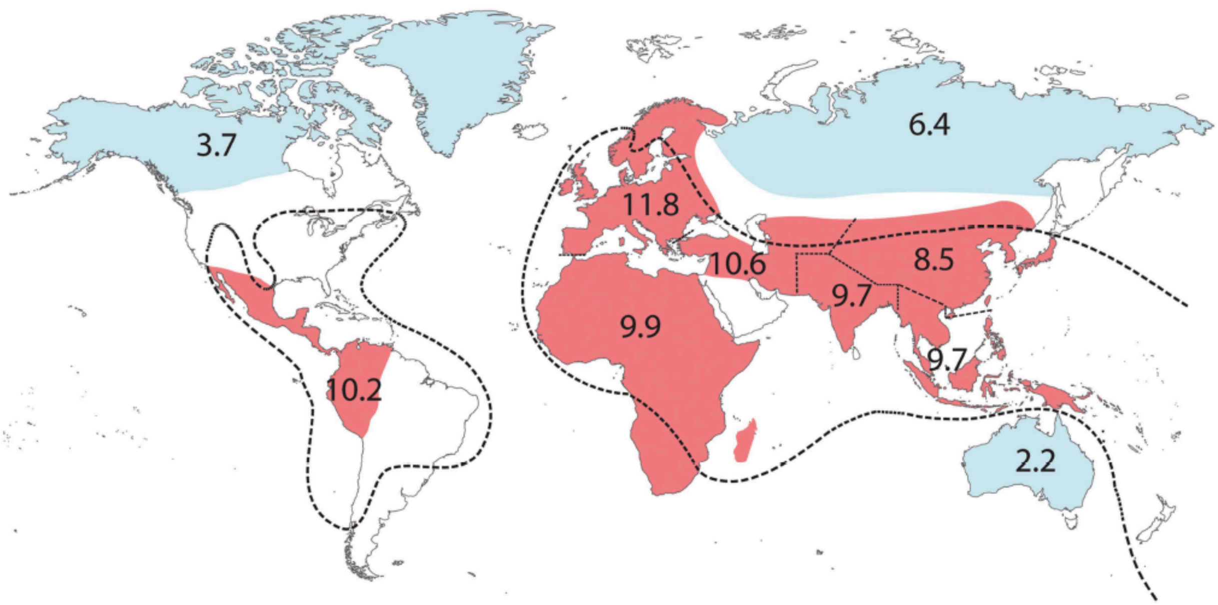
[11] 'Review of canine dilated cardiomyopathy in the wake of diet-associated concerns.' [doi: 10.1093/jas/skaa155]



Average AMY2B (pancreatic amylase) gene copy number in various dog breeds, grouped by origin into 10 global regions: Europe (11.8), Africa (9.9), Southwest Asia (10.6), South Asia (9.7), East Asia (8.5), Southeast Asia (9.7), Australia (2.2), Central America (10.2), Arctic America (3.7), and Arctic Asia (6.4).

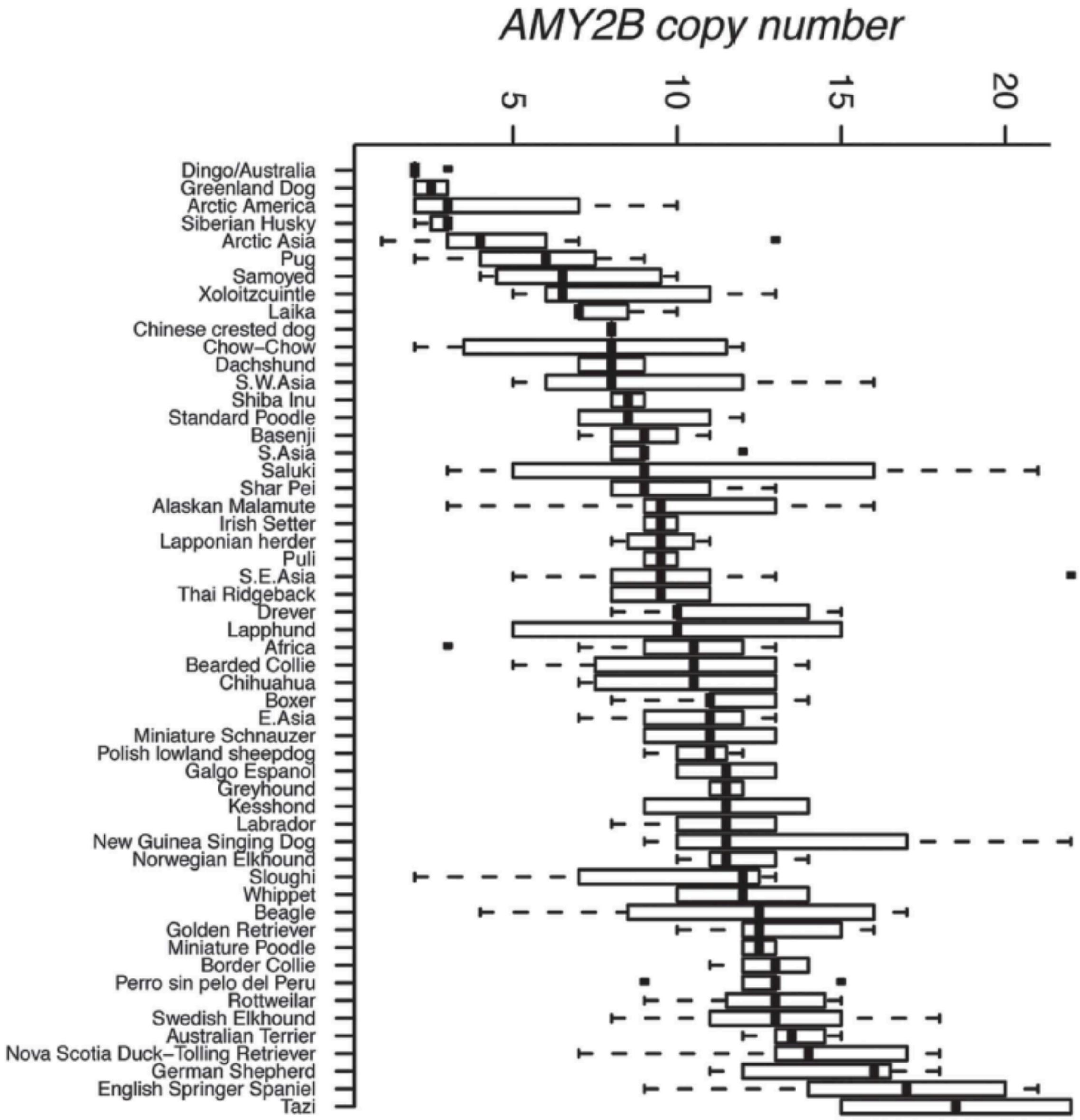
Dashed lines: approximate extent of prehistoric agriculture.

Colours: regions sampled, red for agrarian (agricultural) and blue for nonagrarian societies.

Gene copy numbers for specific dog breeds are detailed on the next page.

From Arendt M, Cairns KM, Ballard JWO, *et al.* Diet adaptation in dog reflects spread of prehistoric agriculture. *Heredity* 2016, 117: 301–306. doi: 10.1038/hdy.2016.48.

Number of copies of the gene that codes for pancreatic amylase (AMY2B)
in various dog breeds, representing 46 breeds and 8 global regions.



Vertical black bars: median copy number. (The **median** splits the group into two equal halves, with 50% of tested dogs at or above that number and the other 50% at or below it. *It may not be the same as the average*.)

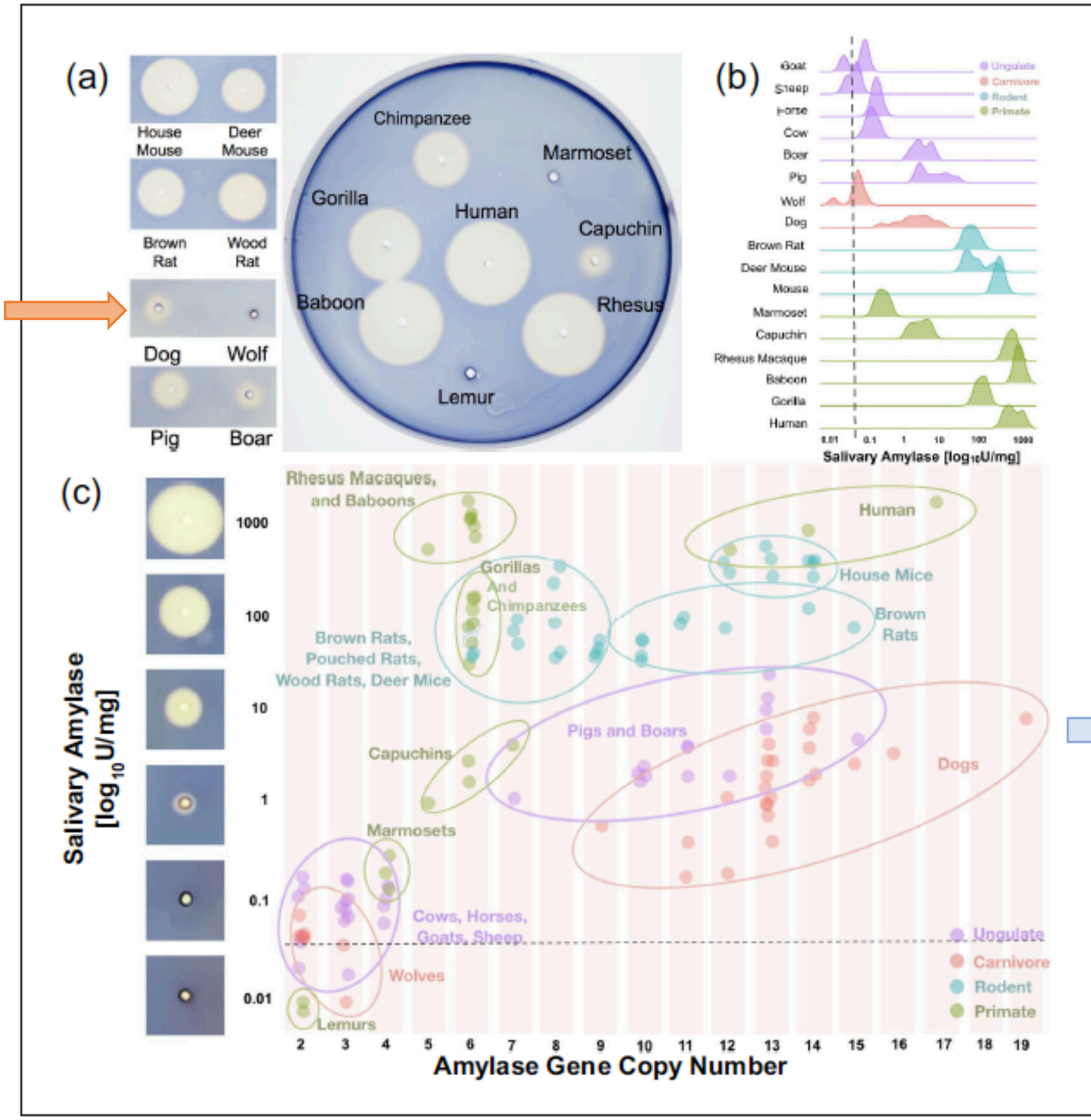
Horizontal boxes: interquartile range (IQR). (The IQR represents the middle 50% of dogs tested. *It may not be symmetrical above and below the median.*)

Whiskers: minimum to maximum values for the tested dogs.

Black squares: outliers (individual dogs with abnormally high or low copy numbers).

From Arendt M, Cairns KM, Ballard JWO, *et al.* Diet adaptation in dog reflects spread of prehistoric agriculture. *Heredity* 2016, 117: 301–306. doi: 10.1038/hdy.2016.48.

Salivary amylase activity and its relationship to AMY1 (salivary amylase) gene copy number in various species.



next page

(a) 'Petrie dishes' showing the zone of starch lysis (enzymatic digestion) caused by salivary amylase in various species. Note the difference between dogs and wolves (orange arrow). Also note how much smaller the zone is in dogs than in humans. This difference is also illustrated in panel **(c)**. Panel **(b)** shows that, while dogs may have as many copies of AMY1 as humans, salivary amylase *activity* is much lower in dogs.

From Pajic P, Pavlidis P, Dean K, *et al.* Independent amylase gene copy number bursts correlate with dietary preferences in mammals. *eLife* 2019, 8: e44628. doi: 10.7554/eLife.44628.

Here are the specific dog breeds and data from the AMY1 study summarised on the previous page, along with the data for the wolves and wolf x dog crosses sampled in that study.

Dog breed	**Number of dogs**	**AMY1 gene copies per dog**	**Salivary amylase activity (units/mg)***
Australian Cattle Dog (Blue Heeler)	2	13–14	2.24–2.34
Beagle	1	13	1.35
Boxer	1	14	4.43
French Bulldog	1	11	0.46
German Sheperd x Beagle	1	13	0.87
Golden Retriever	3	13–19	3.88–8.87
Hound (unspecified)	2	13–14	0.05–1.69
Labrador Retriever	6	9–14	0.68–3.27
Labrador x Pitbull	1	12	0.22
Labrador mix (Tucker)	1	13	0.47
Newfoundland	1	12	1.34
Pitbull	2	13–14	3.24–9.09
Pitbull x Bulldog	1	14	6.96
Sheepdog mix (unspecified)	1	15	3.00
Siberian Husky	1	11	0.20
Total/Average	**25**	**13**	**2.62**
Range		**9–19**	**0.05–9.09**
Wolf	11	average: 2 range: 2–3	average: 0.046 range: 0.010–0.080
Wolf x dog	2	8–9	n/a

* units per milligram of total salivary protein

The log_{10} scale used in panel **(b)** on the previous page is a bit misleading, as it visually diminishes the magnitude of the difference in salivary amylase activity between dogs and humans. Compared with the range of values in the five humans tested (508–1,590 units/mg), the range of **salivary amylase activity in dogs was at least 56 times *lower* than in humans**, and at the extreme ends of the range it was 31,800 times lower in dogs!

Circled: breeds with highest values for salivary amylase activity. Although there were only 1–3 dogs in each group, might these dogs represent those at heightened risk for obesity and other metabolic or endocrine disorders associated with high serum insulin concentrations? This possibility is worth further study.

From Pajic P, Pavlidis P, Dean K, *et al.* Independent amylase gene copy number bursts correlate with dietary preferences in mammals. *eLife* 2019, 8: e44628. doi: 10.7554/eLife.44628.

