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Shifts in Circulating Concentrations of Glucose in Domesticated Mammals: Is There a Consistent Adaptation to Domestication?

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Abstract

There have been marked changes in amylase gene number during human evolution resulting in shifts in carbohydrate metabolism. This has been related to utilization of starch. Similarly, there are changes in enzymes related to carbohydrate metabolism in dogs. Again, this has been linked to improving starch utilization following domestication. It was questioned as circulating concentrations of glucose is a good indicator of putative differences in carbohydrate metabolism across domesticated animals. Domesticated bovids had lower ($p < 0.001$) circulating concentrations of glucose than wild species in their respective sub-families. Circulating concentrations of glucose were consistently lower ($p < 0.001$) in domesticated animals compared to either closely related wild species or the mean for wild species in their sub-families (or families where there is insufficient data available). It is suggested that shift to lower circulating concentrations of glucose in domesticated animals is related to greater starch intake following domestication in a manner akin to the shifts in carbohydrate metabolism and amylase gene number in human evolution.

Keywords

Circulating Glucose, Livestock, Domestication

1. Introduction

The ability both to digest dietary poly/disaccharides and to absorb monosaccharides is critically important. Moreover, it is crucial to control carbohydrate metabolism and maintain circulating concentrations of glucose in animals as much as in people. During human evolution, there has been the acquisition of multiple copies of amylase gene (*AMY*1). This presumably allows greater utilization of starch (earlier work reviewed [1] [2]).

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Concentrations of amylase in the saliva are related to amylase gene copy number; there being markedly higher amylase concentrations with increasing numbers of amylase 1 genes [2] [3]. Elevated amylase is associated with improvements in both the digestion of starchy foods [3] [4] and in glucose tolerance [5]. Following consumption of starch, there were smaller increases in circulating concentrations of glucose in subjects with high compared to those with low salivary amylase concentrations [5]. Moreover, plasma concentrations of insulin rose earlier [5]. In contrast, *AMY*1 gene number does not show the increases in frugivorous chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) [2]. The present communication examines whether analogous shifts in carbohydrate metabolism occurred during domestication of mammals with the increases in consumption of starch in the diet.

It has recently been suggested that the ability to thrive on a diet rich in starch was a key feature in the early domestication of dogs. There are signals of selection being reported in ten genes related to starch digestion and fat metabolism in dogs [6]. The impact of these genomic shifts on glucose metabolism in dogs has not been reported. It is questioned whether there may be marked differences in circulating concentrations of glucose in dogs compared to the ancestral grey wolf. Moreover, there is a single report that circulating concentrations of glucose are lower in domesticated pigs than in wild pigs [7]. The aim of the present study was to determine whether there is a systematic shift in the basal circulating concentrations of glucose in domesticated species.

2. Materials and Methods

2.1. Database

There is a large but diffuse literature containing data on serum biochemistry and hematological parameters of wild animals, most commonly determined on blood samples obtained at capture. A database of basal plasma/serum glucose concentrations in vertebrate species was assembled based on the literature to allow analysis of putative physiological shifts with evolutionary/taxonomic status, ecological parameters and other environmental factors. Circulating concentrations of glucose would be expected to exhibit marked differences e.g. between fed and fasted in mono-gastric omnivorous animals. However, domestic animals and the descendants of their ancestral wild species are predominantly either ancestrally carnivores or either rumen or hind gut fermenters relying on gluconeogenesis. Circulating concentrations of glucose is widely reported as a serum/plasma biochemical parameter in wild mammals following capture.

On causal inspection of the database, there appeared to be a relationship between domestication and serum/plasma concentration of glucose with lower levels in domesticated species. The data base was then queried systematically to determine whether circulating concentrations of glucose are different in domesticated species compared to either descendant of the ancestral species or to the taxonomic sub-family or family which the domesticated species belongs.

2.2. Statistical Analysis

Comparisons between circulating concentrations of glucose in domesticated species and descendants of the same (or very closely related) species or the mean for the sub-family [and where there is available data on insufficient numbers of species ($n < 3$)—the family] were analyzed by both Student's paired t test and by split plot analysis of variance (ANOVA) followed by Tukey's range test.

3. Results

Table 1 and **Table 2** summarize circulating concentrations of glucose in domesticated animals and, respectively, either animals of closely related wild species or the means for wild animals in the sub-families (or where there are insufficient data points in families). The circulating concentrations of glucose were uniformly lower in domesticated animals than descendant animals of the ancestral species of the domestic animals or those in closely related wild species (**Table 1**). Moreover, within the exception of the cat, circulating concentrations of glucose were lower in domesticated animals than in wild species of their respective sub-families/families (**Table 2**).

Table 3 compares the circulating concentrations of glucose in domesticated and the respective wild species (**Table 1** and **Table 2**). Circulating concentrations of glucose are 33.7% lower ($p < 0.001$) in domesticated animals compared to matched ancestral or closely related wild mammalian species and 40.1% lower ($p < 0.001$) in domesticated animals and wild species than in their respective sub-families/families (**Table 3**).

There was a marked difference ($p < 0.001$) in the circulating concentrations of glucose between domesticated

Table 1. Comparison of circulating concentrations of glucose in domestic and closely related/ancestral wild species.

Domesticated species	Wild ancestral or closely related species	Serum/plasma glucose (m·Moles·L^{-1})	Reference
Alpaca (*Vicugna pacos*)		6.4	[7] [8]
	Vicuñas (*Vicugna vicugna*)	9.1	[9] [10]
Cat (*Felis silvestris*)		8.1	[11]
	European Wildcat (*Felis silvestris*)	9.3	[12]
Dog (*Canis lupo familiaris*)*		3.4	[13] [14]
	Grey wolf (*Canis lupo*)	6.6	[15]-[18]
Ferret (*Mustela putorius furo*)		5.8	[19]
	European Polecat (*Mustela putorius*)	9.3	[20]
Horse (*Equus ferus*)		5.6	[21]-[23]
	Przewalski horse (*Equus przewalskiprzewalski*)‡	7.2	[25]
Llama (*Lama glama*)		5.5	[7] [26]
	Guanaco (*Lama guanicoe*)	7.6	[27]
Pig (*Sus scrofa domestica*)†		5.3	[28] [30]
	European Wild Boar (*Sus scrofa*)	9.3	[28] [31] [33]
Reindeer (*Rangifer tarandus*)		4.0	[33]
	Caribou (*Rangifer tarandus caribou*)	8.3	[34]

*Compared to 3.1 m·Moles·L^{-1} in stray dogs [35]; ‡The only surviving true wild horse species [24]; †Compared to 7.8 m·Moles·L^{-1} in Texas feral pigs [36].

animals and wild species in the taxonomic sub-families *Bovinae* and *Caprinae* in the Family *Bovidae* (**Table 3**). Circulating concentrations of glucose were 57.1% lower in domesticated bovids (**Table 3**).

4. Discussion

Circulating concentrations of glucose were consistently lower in domesticated animals than in either matched ancestral species/closely related wild mammalian species (**Table 1** and **Table 3**) or other members of the same taxonomic sub-family/family (**Table 2** and **Table 3**). The difference in circulating concentrations of glucose in domesticated animals is a general phenomenon. These were observed irrespective of the following:

- Nutrition—*i.e.* whether the domesticated species was a ruminant, hind gut fermenter (horse, ass and rabbit) or predominantly carnivore (dog, ferret).
- Classification/evolutionary relationships—being observed in species from the Orders—*Actiodactyla* (bovids, camelids, deer and pigs), *Carnivora* (dogs, ferrets), *Lagomorpha* (rabbits) and *Perissodactyla* (horses and donkeys).

Genomic studies in dogs and horses support a shift in carbohydrate metabolism in domesticated species with increasing consumption of starch. The ability to thrive on a diet rich in starch was a key feature in the early domestication of dogs. Signals of selection have been reported in ten genes related to starch digestion and metabolism in dogs [6]. Moreover in horses, there is evidence again for selection for genes related to carbohydrate metabolism [50].

The present communication would support it being the selection associated with domestication itself rather than subsequently being response for the difference in circulating concentrations of glucose. There was not a relationship ($r^2 < 0.2$; $p > 0.45$) between the duration of time since domestication and the differences in circulating concentrations of glucose between domesticated animals and either closely related wild species or the mean for the sub-family/family (data not shown).

While the domestic cat is considered within the domestic animals, it can be argued that cats should be consi-

Table 2. Comparison of circulating concentrations of glucose with wild members of the same sub-family or family.

Domesticated Species	Wild Species in Same Taxonomic Group	Serum/Plasma Glucose ($m \cdot Moles \cdot L^{-1}$)	Reference
Cattle (*Bos primigenius formerly Bos taurus*)[a]		5.2	[37] [38]
Gayal-Domesticated Gaur (*Bos gaurus*)		2.7	[39]
Water Buffalo (*Bubalus bubalis*)		3.2	[40]
	Non-Domesticated-Subfamily *Bovinae*[‡]	8.0 ± (8) 0.6	
Sheep (*Ovis aries*)		4.1	[41] [42]
Goat (*Capra aegagrus hircus*)		4.2	[43] [44]
	Non-Domesticated-Subfamily *Caprinae*[‡]	9.4 ± (6) 0.7	
Alpaca (*Vicugna pacos*)		6.4	[7] [8]
Camel (*Camelus dromedaries*)		4.1	[26] [45]
Llama (*Lama glama*)		5.5	[7] [26]
	Non-Domesticated-Family *Camelidae*[‡]	8.3 ± (2) 0.8	
Pig (*Sus scrofa domestica*)		5.3	[28]-[30]
	Non-Domesticated-Family *Suidae*[‡]	6.1 ± (4) 1.14	
Reindeer (*Rangifer tarandus*)		4.0	[33]
	Non-Domesticated-Family *Cervidae*[‡]	7.9 ± (14) 0.5	
Dog (*Canis lupo familiaris*)		3.4	[13] [14]
	Non-Domesticated-Subfamily Caninae[‡]	7.1 ± (11) 0.8	
Cat (*Felis silvestris*)		8.1	[11]
	Non-Domesticated Subfamily *Felinae*[‡]	7.6 ± (11) 0.8	
Ferret (*Mustela putorius furo*)		5.8	[19]
	Non-Domesticated Subfamily *Mustelinae*[‡]	9.5	
Donkey or Ass (*Equus africanus asinus*)		4.1	[23] [46] [48]
Horse (*Equus ferus*)		5.6	[21] [23]
	Non-Domesticated-Family *Equidae*[‡]	7.6 ± (5) 0.6	
Rabbit (*Oryctolagus cuniculus*)		6.8	[13] [49]
	Non-Domesticated-Family *Leporidae*[‡]	10.2 ± (4) 1.6	

[‡]Data on wild animal in the same taxa on the domesticated animals is shown as mean ± (n = number of species) S.E.M.

dered as commensal rather than domesticated [51]. Cats are obligate carnivores that were "domesticated" about 5300 BP [51] [52]. Selection is thought to have been focused traits related to hunting ability [51] [52]. It is not surprising that cats are on outlier with little, if any, difference in circulating concentrations of glucose with either a closely related species (**Table 1**) or wild species within the (**Table 2**).

It might be argued that the greater circulating concentration of glucose in wild species is an artifact of their capture, environment or nutritional state. This does not appear to be the case. Similar concentrations of glucose are reported in captive wolves and those in the wild [53]. Moreover, there was no difference in circulating concentrations of glucose between fed and fasted states in wolves [15].

It might be questioned as to whether the lower concentration of glucose in domestic animals reflects an effect of human activity. One way to address this is comparison of glucose in domesticated animals that have reverted

Table 3. Comparison of circulating concentrations of glucose mean + (n =) S.E.M. in domesticated and wild species.

	Serum/Plasma Glucose (m·Moles·L^{-1})	
I. Comparison between domesticated animals and wild species in the *Bovidae* subfamilies *Bovinae* and *Caprinae*		
Domesticated species$^{\Delta}$	3.9 ± (5) 0.53^{a}	
Wild species		8.6 ± (14) 0.50^{b}
II. Comparison between domesticated animals and matched ancestral or closely related wild mammalian species$^{\Delta}$		
Domesticated species	5.5 ± (8) 0.51^{a}	
Ancestral or closely related wild species		8.3 ± (8) 0.38^{b}
III. Comparison between domesticated animals and mean for wild species within same family or subfamily†		
Domesticated species$^{\Delta}$	4.9 ± (16) 0.36^{a}	
Matched family or sub-family wild species		8.2 ± (16) 0.25^{b}

$^{\Delta}$Data shown in **Table 1**; †Where information is available on sufficient species (>3); data shown in **Table 2**; ^{a,b}Different superscript letters indicate difference $p < 0.001$.

to the wild. Circulating concentrations of glucose in feral adult horses, stray dogs and feral goats are the same as in domesticated animals [35] [54] [56] but higher in young burros [57] and wild horses samples at some locations [54]. It is unclear the extent to which feral pigs in the USA represent the descendants of introduced Eurasian wild pigs/wild boar (*Sus scrofa*) [58] and/or escaped domesticated pigs. The assumption is that feral pigs are predominantly Eurasian wild pigs. The range where feral pigs are found is increasing in part by further introductions. Circulating concentrations of glucose in feral pigs in the Texas, USA (7.8 mM) [36] are between those of wild pigs (9.3 mM) and domestic pigs (3.7 mM) (**Table 1**). This supports feral pigs, at least in Texas, being the result of hybridization between wild pigs and escaped domestic pigs. Based on circulating concentrations of glucose, it is estimated that about three quarters of the background of feral pigs is from wild pigs.

The present study provides evidence that domesticated animals have reduced circulating concentrations of glucose. What is not known include the following: Do the differences in circulating concentrations of glucose reflect amylase gene number as in humans [1]-[5] and dogs [6]? Is there are systematic shifts in the "set point" of the homeostatic mechanism in domestic animals including insulin secretion? Are there assumptions about ideal diets that do not adequately address differences in domestication?

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