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Are cows pickier than goats? Linnaeus's innovative large-scale feeding experiment

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ABSTRACT

In 1749, Linnaeus published *Pan Svecicus*, a thesis that was defended by his student Nils Hesselgren. The thesis describes food preference trials in cows, goats, sheep, horses, and pigs, and includes 2325 tests with 643 plant species. The data had surprisingly little bearing on the text in the thesis, and even though the experiments quickly became internationally known, the data were merely repeated, rather than discussed. We have digitized the data and linked the species names to modern nomenclature and present the first analysis and discussion of the results. Pigs were most selective (eating 32% of the 204 plant species that were tested on all animals), followed by horses (59%), cows (66%), sheep (82%), and goats (85%). The ruminants (especially goats and sheep) had high overlap in food choice, and the pigs deviated most (despite the fact that pigs are more closely related to the ruminants than are horses). Among plant orders, Fabales and Poales were generally preferred, while Lamiales and Ranunculales were avoided, especially by cows and horses. Cows and horses were also more keen to avoid toxic plant species. All animals showed a preference for species that are today considered nutritious. We now make the data available, for further analyses in ecology, history of science, and other disciplines.

Keywords: Enlightenment period; food preferences; history of ecology; livestock; *Pan Svecicus*; toxic plants

INTRODUCTION

On 9 December 1749, the 20-year-old medical student Nils Hesselgren defended a *pro exercitio* thesis with the cryptic title *Pan Svecicus* at Uppsala University, Sweden. As was the normal practice at that time, the thesis was written or dictated by his supervisor, Carl Linnaeus (Linnaeus 1749), and Hesselgren's task was merely to publicly defend it (Lindberg 2016). The thesis describes food preferences in domestic animals—more than 2300 tests were made in which 643 plant species were presented to cows, goats, sheep, horses, and pigs, and it was recorded whether the animal ate the plant or not. This may well have been the first ecological experiment in the world (Egerton 2007), but more important is the stunning scale of the operation.

Linnaeus was driven by curiosity, but he also had strong ambitions (and even official assignments) to lead studies that should reveal plants, animals, minerals, farming practices, etc., that could be used to improve the Swedish household and national economy (Broberg 2023). This was most obvious in the accounts from his travels through Sweden, financed by scientific academies or initiated directly from the parliament for this very purpose. In *Flora Lapponica* (Linnaeus 1737) Linnaeus describes how he, during his journey to the Dalarna province in 1734, observed that horses indiscriminately ate most herbs, but avoided several species. This led him to initiate the feeding experiment, and he states that there are no previous scientific accounts dealing with choices of plants among livestock animals, and that this is therefore totally new science.

In the introduction to the thesis Linnaeus explains its title: *The ancients attributed the pastoral life to Pan, the care of flowers to Flora, hunting to Diana, and the cultivation of grain to Ceres* [the thesis was written in Latin, and we give quotes in italics from the English translation by Stillingfleet (1759), retaining his spelling]. In analogy with the Swedish Flora (encompassing the Swedish plants), Linnaeus introduces the Swedish Pan, *intending thereby to denote the five domestic quadrupeds, which live upon plants growing in Sweden; or the devouring army of Pan, which lays waste the provinces of the Swedish Flora*.

Despite thousands of observations, the thesis largely reiterates what Linnaeus and contemporaries already knew about animal feeding and plants that were selected, avoided, or presumed toxic

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to livestock. The collected data are hardly referred to, and the consequences of the findings are not discussed. *Pan Svecicus* nevertheless quickly became well known among European scholars. In England, the botanist Richard Pulteney, who was also Linnaeus's biographer, published 'Tables from Pan Suecus, accommodated to the English Plants' (Pulteney 1758, 1781). In his publication, Pulteney reproduced the data table from the second edition of *Pan Svecicus* (Linnaeus 1751). However, he left out a substantial number of species (around 190) that were rare or do not grow in England but, on the other hand, included about 20 English species that were not found in *Pan Svecicus* for which he provided his own data. For many species, he also added notes specifying what different authors had said on their usefulness in animal husbandry. Complete translations of *Pan Svecicus* were published in English [Stillingfleet 1759 (thesis text only)] and German (Höpfner 1778, Lippert 1785). Lippert, as Pulteney before him, supplemented information for all species on habitat, distribution, longevity, and flowering times to the data table.

As we were working on a Swedish translation of the Latin text (Feltenius *et al.* 2024), we were intrigued by the fact that no one seemed to have been particularly interested in the actual data for 275 years. Our aim here is to find out what the results in *Pan Svecicus* show. To what extent did the five animal species differ in specialization, and how much did their food choices overlap? Do similarities in food selection mirror how phylogenetically related the animals are, or how similar they are in their nutritional physiology (e.g. ruminants vs nonruminants)? Did the animals avoid species that Linnaeus considered toxic, or species that today are listed as toxic?

We are of course aware that the 18th century research methodology will not stand up to today's standards. Yet, we feel

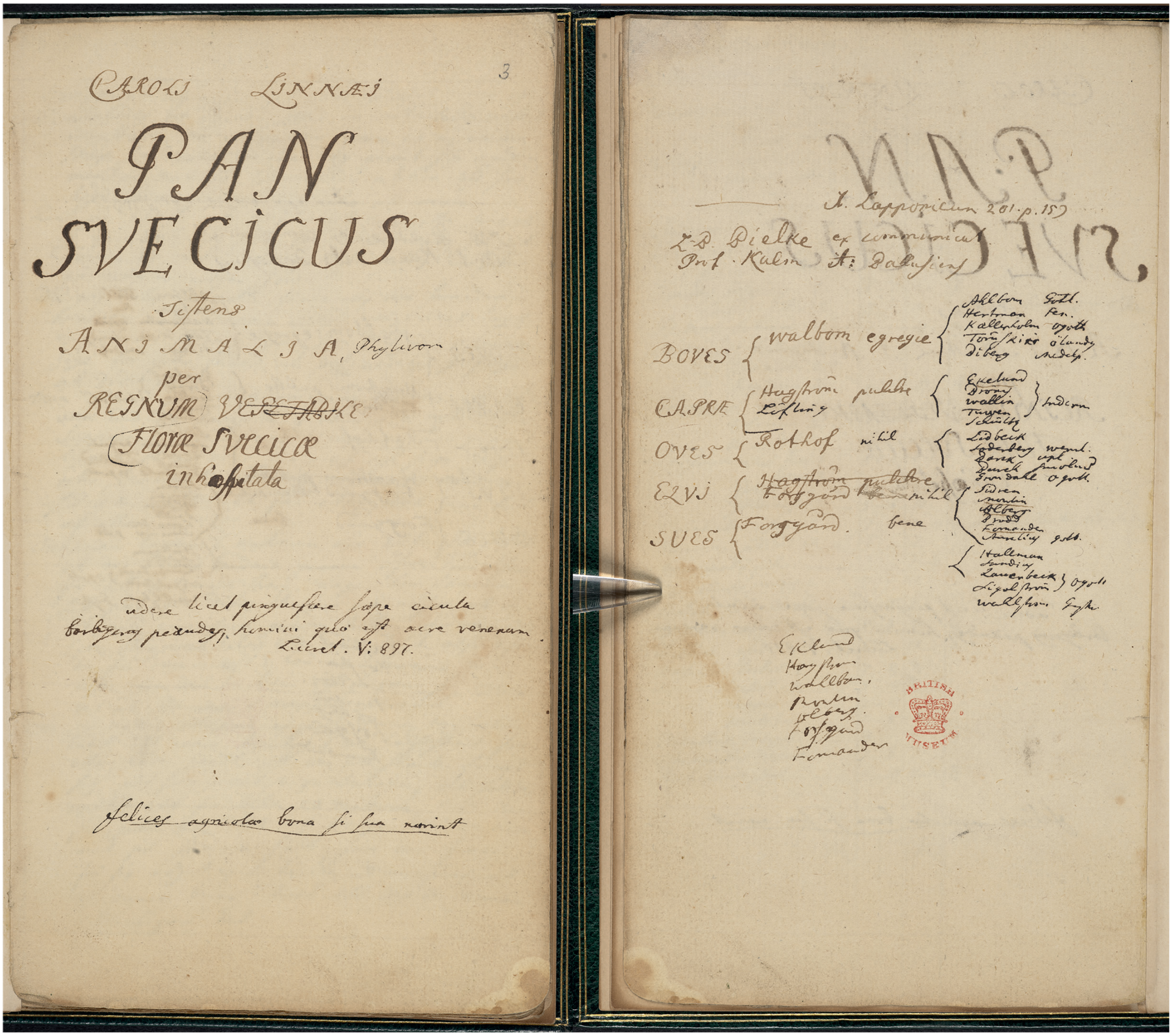

Figure 1. The first pages of Linnaeus's *Pan Svecicus* manuscript from the late 1740s in mixed Swedish and Latin, indicating how he had handed out responsibilities in the project (to the right). Five disciples had the main responsibility for each of the livestock species, and these had under them five or six people, from different parts of the country, who would carry out the feeding trials. The main contributors' efforts have been graded in the manuscript as *bene*, *egregie*, *pulchre*, *nihil* (well, excellently, beautifully, nothing) by Linnaeus. © British Library Board (Egerton MS 2039, pages f3r and f3v).

that the effort is worthwhile, and there are several aspects that make *Pan Svecicus* conspicuously modern. (i) The topic is still well worth studying; there are still gaps in our knowledge on the value of different wild plants for grazing domestic animals (Villalba *et al.* 2010). (ii) The number of observations is impressive, even with modern standards. (iii) In contrast to the 18th century solitary scientist, *Pan Svecicus* was built very much like a modern research programme, with Linnaeus as the Principal investigator, and with postdocs and advanced pupils given leading roles for each of the animal species, and each in charge of a group of students (Fig. 1). (iv) The species lists are linked to *Flora Svecica* (Linnaeus 1745) and thereby traceable to modern nomenclature. (v) The methods are well described. (vi) Raw data are available, a practice that has been the rule in scientific publications only in the last decade. We now make the data available with modern nomenclature.

MATERIALS AND METHODS

Editions and amendments to *Pan Svecicus*

In addition to the 1749 thesis, we extracted data from three later editions published in *Amoenitates academicae* in 1751, 1762, and (after Linnaeus's death) 1787. Quite a few entries from 1749 were changed, and the number of observations increased from 2325 to 2452 in 1751 and to 2492 in 1762. The 1787 edition had 2489 observations with very few changes, and we did not include it in our analysis.

In 1779, the Swedish physician and naturalist Pehr Gustaf Tengmalm published 'Attempts at an improved *Pan Svecicus*' (Tengmalm 1779–1780 in Swedish; Tengmalm 1790 in Latin) with 3083 observations. Tengmalm writes in the introduction that after *Pan Svecicus* was published, land management has 'gained considerable increase and improvement'. He particularly mentions the contributions of Pehr Kalm, Pehr Adrian Gadd, Peter Jonas Bergius, and Johan Låstbom, whose observations, together with those of some 'well-deserved foreigners' and a few of his own, form the basis of his attempt. The data in Tengmalm's tables are considerably extended, but strangely, some observations are deleted and some scores are changed compared with *Pan Svecicus*. However, no specific details on how the new data have been obtained—whether exactly the same methods have been used, or to what extent literature data have been included—are presented. In this paper we refer to the investigations as 'Pan 1749', 'Pan 1751', 'Pan 1762', 'Pan 1787', and 'Tengmalm'.

In 1774, another student of Linnaeus, Per Holmberger, defended the thesis *Esca avium domesticarum*, presenting results of feeding experiments in which geese, ducks, hens, and turkeys had been similarly tested (Linnaeus 1774).

Feeding procedure

The work began in 1747–48 when Linnaeus commissioned a large number of his students across the country to conduct feeding trials with the five most common domestic animals: cattle, goats, sheep, horses, and pigs. In the thesis he acknowledges the many difficulties with this kind of experiment, for example that some plants may be palatable in the spring but not later, just like *many people eat the nettle in the spring; but who could bear it afterwards?* Animals eat different parts of the plants, but in the experiment, a plant is considered as eaten if the animal eats the leaves. The procedure is described in some detail: *Next, the animals ought not to be over hungry, when we make our experiments, if we intend to make them properly. For they will greedily devour most kinds of plants at such a time, which they will absolutely refuse at another. Thus when they come immediately out of the house, they are not fit to make experiments upon; for then they are ravenous after every green thing that comes in their way. The best method is to make the experiments when their bellies are almost full, for they are hardly ever so intirely. Moreover the plants ought not to be handled by sweaty hands, some animals will refuse the most pleasing, and tasteful in that case. We ought to throw them on the ground, and if we find the animal refuses to eat them, we must mix them with others that we know they like; and if they still refuse them, we have a sure proof, especially if the fame be tryed with many individuals* (for direct quotes in italics we use the translation by Stillingfleet 1759). In addition, it is stated that some experiments were often repeated 10 times, often even 20 times. Hence, the experiments were replicated, and combined into one data point for each plant–animal combination.

In Linnaeus's data (Fig. 2) 1 indicates eaten and 0 not eaten; 11 clearly means that the plant is eagerly eaten. Entries 01 and 10 are also used but their meaning is unclear: both numbers indicate that *they sometimes eat the plants, sometimes despise them, or eat them when they are more familiar with them and more hungry*, but in his manuscript (Br Mus Egerton MS2039), Linnaeus gives a different view: '01 means that the species is not eaten fresh, but eaten if dried. 10 means that the species is eaten fresh, but not if dried.' Pulteney (1758) gives a translation that is hardly compatible with the original text: 'When both are found together in a column thus (10) or (01) they denote that the plant is sometimes eaten, and sometimes refused by the animal. The former of these is supposed to signify that it is generally eaten, but sometimes refused; the latter that it is generally refused, but sometimes eaten.' Because of these uncertainties we lump categories 01, 10, 1, and 11 in most analyses.

Nomenclature

In the data tables in *Pan Svecicus* (Fig. 2) the species were listed according to their number in the first edition of *Flora Svecica* (Linnaeus 1745) and we have suggested modern interpretations of the different species (Supporting Information Appendix S1). In cases where there are today more than one species for a particular Linnaean taxon, we have chosen the most likely species, based on its believed commonness in Linnaeus's time. Nomenclature follows the Swedish taxonomic database *Dyntaxa* (artfakta.se).

Toxic plant species and other plant traits

A list of species considered toxic or highly toxic to livestock was retrieved from the Swedish Veterinary Agency (SVA 2024). A few additional toxic species were added from Cooper and Johnson (1998), Frohne and Pfänder (2005), and Constable *et al.* (2016), and here we also included a species if the source listed a congeneric and ecologically similar species. From Constable *et al.* (2016) we also collected information on toxins found in the listed plant species, with additions from Cooper and Johnson

FLORA SVECICA

	Boves	*Capræ*	*Oves*	*Equi*	*Sues*
I. MONANDRIA					
1 Salicornia maritima	0	-	0	0	1
2 Hippuris aquatica	0	1	0	0	0
3 Callitriche paluſtris	-	-	-	-	-
II. DIANDRIA					
4 Liguſtrum vulgare	1	1	1	0	-
5 Circæa utraque	-	-	1	-	-
6 Veronica ternifolia	1	1	1	0	0
7 - - ſpicata	1	0	1	0	-
8 - - mas	-	1	1	1	-
9 - - ſcutellata	1	1	1	1	-
10 - - Beccab. oblong.	1	1	-	1	0
11 - - - - rotund.	1	1	0	0	0
12 - - Pſeudo Chamædrys	1	1	1	-	0
13 - - alpina	-	-	-	-	-
14 - - femina	-	1	-	-	-
15 - - clinopodifolia	-	-	-	-	-
16 - - caulic. adhærent.	1	1	1	-	-
17 - - oblongis caulic.	1	1	1	-	-
18 - - cymbalarifolia	1	1	1	-	-
19 - - rutæfolia	-	-	-	-	-
20 - - minima	-	-	-	-	-
21 Pinguicula vulgaris	-	0	0	-	-
22 - - alba	-	0	0	-	-
23 - - minima	-	0	0	-	-
24 Utricularia major	-	-	-	-	-
25 - minor	-	-	-	-	-
26 Verbena vulgaris	0/	0	1	0	-
27 Lycopus paluſtris	0	1	1	0	-
28 Salvia Hominum	0	1	1	0	-
29 Anthoxanthum vulgare	1	1	1	1	-

Sic Experimenta dedimus 2314. Ex hiſce conſtat

	edere	negligere	
Boves	276;	218	plantas.
Capras - -	449	- - - 126	
Oves - -	387	- - - 141	
Equos - -	262	- - - 212	
Sues - -	72	- - - 171	

Figure 2. Left: first page of the data table in *Pan Svecicus* (Linnaeus 1749) with species numbered according to the first edition of *Flora Svecica* (Linnaeus 1745). The columns are for cows (*Boves*), goats (*Caprae*), sheep (*Oves*), horses (*Equi*), and pigs (*Sues*). Right: list of total number of tests (2314) and number of plant species that were eaten or ignored by each animal.

(1998), Frohne and Pfänder (2005), and SVA (2024). We did not include species as toxic if the toxin was confined to seeds or fruits.

We retrieved information on the quality of certain plant species as fodder. We used data on the nutritional value of plants extracted from modern agricultural textbooks by Kotowski *et al.* (2023). From East-Central European historical sources (ca. 1775–1850) the same authors extracted local knowledge about livestock preferences. We coded these variables as −1 (negative nutritional value and not preferred by livestock in Kotowski's data) or 1 (positive nutritional value; preferred).

Statistical analysis

Analyses were made with the R software (R Core Team 2022). We used the packages *U.PhyloMaker* (Jin and Qian 2023) to visualize plant phylogeny based on megatree GBOTB.extended. WP.tre (Jin and Qian 2022), and *VennDiagram* (Chen 2022) and *nVennR* (Pérez-Silva *et al.* 2018) to construct Venn diagrams.

In Pan 1749, 643 plant species were tested, but each animal species was tested with a slightly different set of plants. To avoid bias, we performed analyses on the 204 species that were tested on all five animal species. To test the robustness of the results we then made analyses based on all observations. This procedure was followed also for later editions of *Pan Svecicus*.

RESULTS

Number of plant species eaten

A final table in *Pan Svecicus* summarizes the number of plant species that were eaten or ignored by the five tested animal species (Fig. 2). However, the numbers are incorrect, and, furthermore, the tables in the three later editions have the exact same numbers, despite the fact that more observations were included. The correct numbers (based on the raw data tables) for the five different editions of *Pan Svecicus* (incl. Tengmalm) are given in Table 1.

Table 1. The number of plant species tested, eaten, and percentage eaten for each animal species in the four editions of *Pan Svecicus* and in Tengmalm's investigation.

	Tested	Eaten	Eaten (%)
Pan 1749, 2325 tests			
Cow	502	331	65.9
Goat	565	482	85.3
Sheep	518	422	81.5
Horse	473	280	59.2
Pig	267	86	32.2
Pan 1751, 2452 tests			
Cow	525	339	64.6
Goat	568	484	85.2
Sheep	543	435	80.1
Horse	507	293	57.8
Pig	309	118	38.2
Pan 1762, 2492 tests			
Cow	538	339	63.0
Goat	566	483	85.3
Sheep	555	434	78.2
Horse	516	297	57.6
Pig	317	125	39.4
Pan 1787, 2489 tests			
Cow	537	340	63.3
Goat	566	484	85.5
Sheep	555	435	78.4
Horse	515	297	57.7
Pig	316	123	38.9
Tengmalm 1779, 3083 tests			
Cow	685	471	68.8
Goat	655	558	85.2
Sheep	661	507	76.7
Horse	665	412	62.0
Pig	417	239	57.3

In Pan 1749, there were 204 plant species tested on all five animal species, and in this set the percentages eaten were ranked as: pig, 32.4%; horse, 47.5%; cow, 62.3%; sheep, 80.4%; goat, 84.4%. Tengmalm's investigation was more balanced, with 400 plant species tested on all animals. The rank order remained, but with less difference between animals: pig, 57.5%; horse, 60.8%; cow, 67.0%; sheep, 74.2%; goat, 84.5%.

When all observations were included (Table 1) the percentage eaten plant species had nonoverlapping ranges for the five animals across the investigations: pig, 32.2–57.3%; horse, 57.6–62.0%; cow, 63.0–68.8%; sheep, 76.7–81.5%; goat, 85.2–85.5%.

Overlaps and differences in plant selection

Of the 204 species tested on all animals in Pan 1749, 35 species were eaten by all animals, and another 35 were eaten by all but pigs (Fig. 3). The ruminants—cows, goats, and sheep—shared another 29 species, and 23 species were eaten by goats and sheep only. Goat was the only animal with a substantial number of uniquely chosen species (12).

Based on the plants tested on all animals in Pan 1749, goat and sheep were most similar in their selection of plants. Pig deviated the most, but was more similar to horse than to the ruminants (Fig. 4). In Tengmalm's data (1779–1780) goat and sheep are still the most similar, but we see an increased similarity in other comparisons, especially between pig and horse.

The dendrogram depicting food selection almost mirrors the animal's phylogenetic tree (Fig. 4) with the ruminants in the Bovidae being most similar in food selection. There is one mismatch between the two trees: the even-toed pig (Suidae) was less similar to the other even-toad species (Bovidae in Artiodactyla) than was the odd-toed horse (Equidae in Perissodactyla).

Among the plant orders, Fabales and Poales were generally chosen by all animals, while Lamiales and Ranunculales were avoided (Fig. 5), and this was most clearly seen in cows and horses (the latter also preferring Asterales). These tendencies were present also when the calculations included all species in Pan 1749 and in Tengmalm (Supporting Information Table S1). The links between food preferences and plant phylogeny are illustrated in Figure 6.

Which kind of plants do the animals select?

Figure 7 shows the number of plant species avoided or eaten dependent on plant quality variables from Kotowski *et al.* (2023). There was a tendency for the animals to select plants with high nutritional value (upper graph in Fig. 7). More clearly, they (at least cows, sheep and horses) selected plants that in the East–Central European historical sources used by Kotowski *et al.* (2023) were considered as being preferred fodder (lower graph).

Do the animals avoid toxic species?

To avoid bias, we first analysed food preferences based on the restricted set of 204 species tested on all animals in Pan 1749. Based on toxicity in SVA (2024), only cows and horses tended to avoid toxic plants (Fig. 8). This effect was stronger when tested on the full data in Pan 1749, and the data added in the 1751 and 1762 editions gave the same results (Supporting Information Table S2). In Tengmalm's data, pig also selected against toxic plants, whereas the results for goat and sheep differed between the restricted and full data (Table S2).

Analyses of the species tested on all animals in Pan 1749 with toxicity instead based on Constable *et al.* (2016) yielded qualitatively the same results as in Figure 8 (Supporting Information Table S2).

Table 2 shows that quite a number of toxic, and even highly toxic species were consumed. Goats were the least discriminating (accepted 71 and 89% of the high- and low-toxicity species, respectively) followed by sheep. All animals accepted fewer of the offered high-toxicity than of low-toxicity species, but the avoidance of high-toxicity species was particularly obvious in cows. In Pan 1749, three highly toxic species were uniquely eaten by goats: *Cynoglossum officinale* L., *Hyoscyamus niger* L., and *Pteridium aquilinum* (L.) Kuhn. *Conium maculatum* L. was uniquely eaten by sheep, and another six highly toxic species were eaten only by goat and sheep (*Aconitum lycoctonum* L., *Convallaria majalis* L., *Daphne mezereum* L., *Frangula alnus* Mill., *Solanum dulcamara* L., and *Taxus baccata* L.). In Tengmalm's data there were considerably more cases with animals eagerly eating toxic plants, but the ranking of the animals was the same as in Pan 1749.

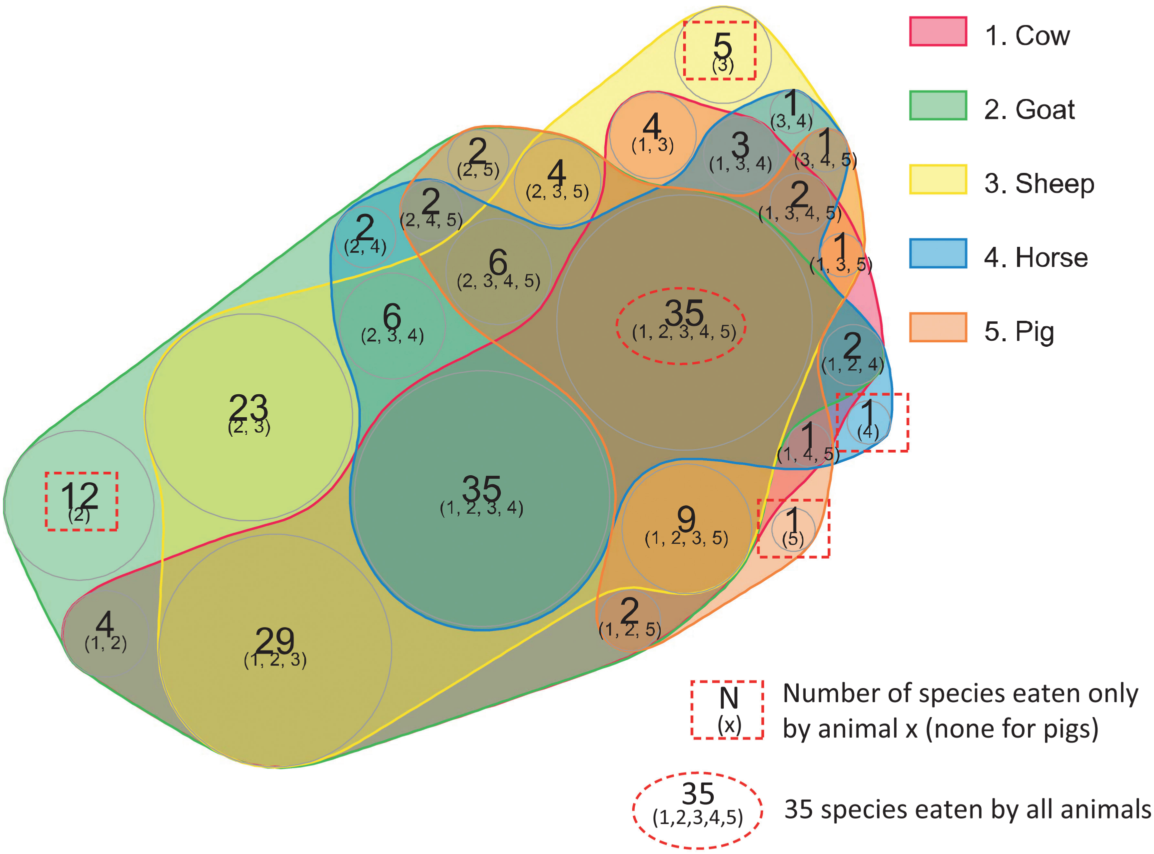

Figure 3. Venn diagram showing the number of plant species (n = 204) eaten by different combinations of animals in Pan 1749.

Confronting the text with the results

In the thesis, Linnaeus makes a number of additional statements, and it is of interest to check how well the text matches the results. In Table 3 we provide some examples, which, on balance, suggest that the text seems to be largely based on conventional wisdom at the time, not on the collected data.

DISCUSSION

Why the results from the impressive *Pan Svecicus* experiments have had so little scientific impact is a mystery. The publication was internationally well known, but the scholars who republished or translated *Pan Svecicus* at the time (Pulteney 1758, 1781, Stillingfleet 1759, Höpfner 1778, Lippert 1785) did not attempt to interpret or discuss the results.

Thereafter, the thesis has been largely neglected, apart from short summaries (e.g. Svanberg 1957, Ramsbottom 1959), while Linnaean biographers only mention *Pan Svecicus* briefly (Blunt 1984, Broberg 2023). However, Egerton (2007) stated that 'This was one of the earliest, if not the earliest, series of experiments on an ecological question, and surely the earliest such large-scale quantitative experiments.' It is also of historical importance, being one of the first publications in which Linnaeus used an attempt at a binomial nomenclature (Stearn 1959).

Our interest here is not primarily in science history, but in ecology: What do the data tell us, and what would the data have told Linnaeus? As an 18th century scientist he lacked the tools to numerically analyse the > 2300 observations, but given his analytical mind it is surprising that the text in *Pan Svecicus* largely reiterates what was known beforehand about animal feeding, making almost no use of the findings, and even ignoring observations that contradicted the conventional wisdom of the time (see above: *Confronting the text with the results*). It is possible that the thesis had been written first and that the experimental data were added very late in the publication process and defence. Perhaps stranger is that although data were successively added and revised in later editions (Linnaeus 1751, 1762, 1787) the text was not amended. After 275 years, it is time to let the data speak for themselves.

Bearing in mind that we are dealing with an 18th century experiment, the experimental procedure is surprisingly well described and reproducible. The results are also quite robust, as indicated by the fact that analyses with different data sets (complete data vs restricted to plants tested on all animals; different editions of *Pan Svecicus*; different indicators of plant toxicity) yield similar results.

Specialization and overlap in food choice

Modern studies on food preferences in livestock are usually set up as 'choice experiments' (also known as 'preference tests' or 'cafeteria experiments') in which the animal can choose between plants that are offered simultaneously (Meier *et al.* 2012). The approach in *Pan Svecicus*—offering one species at a time—is the only reasonable way in which such a large number of food plants can be tested. Rather than asking which of a few offered species the animal prefers, Linnaeus's experiment tells us which

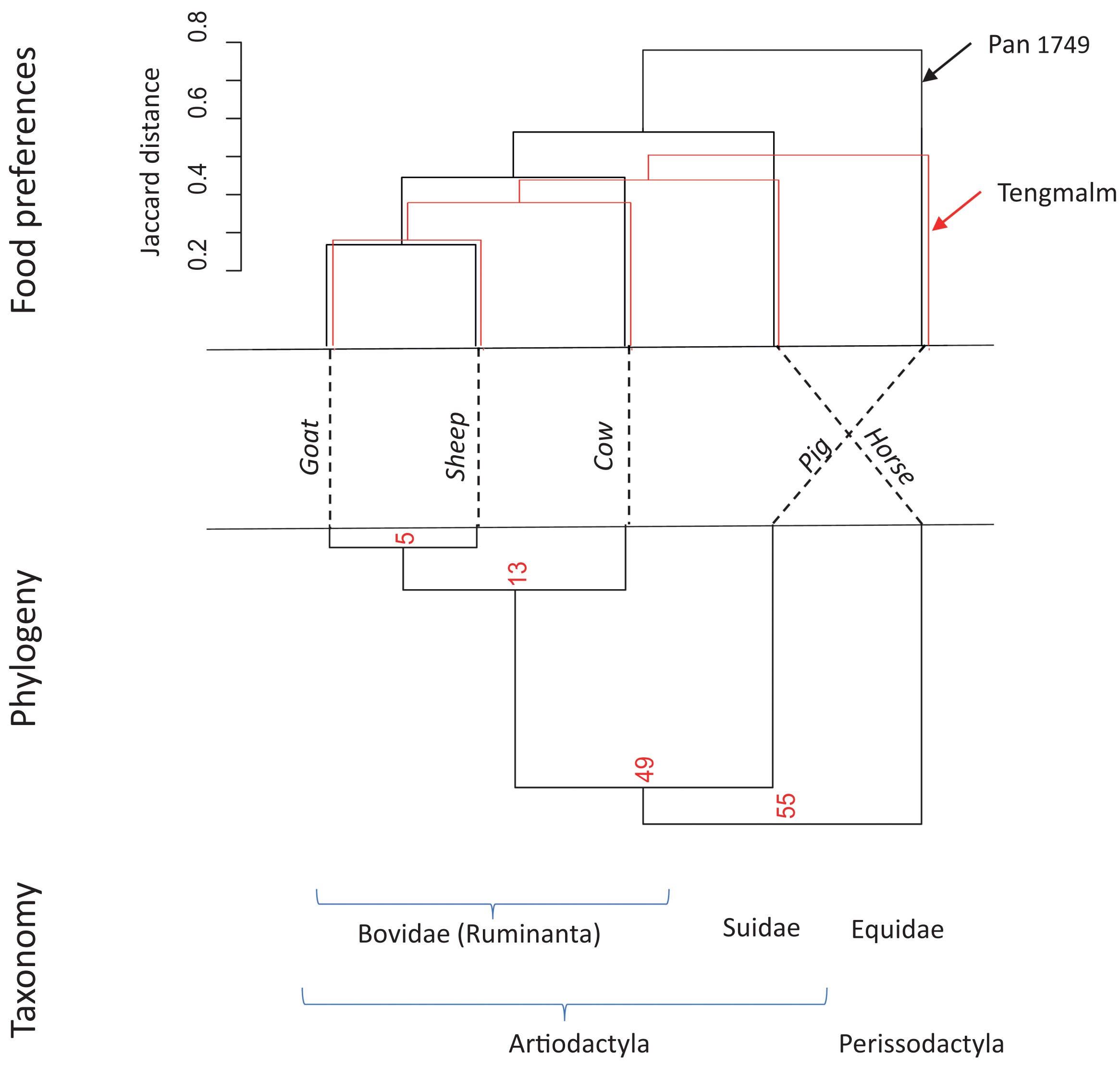

Figure 4. Upper tree: dissimilarity (Jaccard distance) in plant selection between the animal species in Pan 1749 (based on the 204 plant species tested on all animals) and Tengmalm (400 plant species). Lower tree: phylogenetic tree with branching events in million years.

of several hundred species were not accepted at all. This is no less interesting, but comparisons with modern literature must be made with this in mind.

To answer the question in our title, yes, cows were pickier than goats. In terms of number of species eaten there was a clear order of pickiness: pigs > horses > cows > sheep > goats, regardless of which subset of data that was tested, and for all editions of *Pan Svecicus* as well as for Tengmalm's data. But what if they are allowed to select in a mixed field? The animals differ in feeding behaviour. Cattle wrap the tongue around plants and tear, which makes them relatively nonselective. In contrast, sheep tend to nibble, which makes it possible to select species in a mixed sward. Goats are browsers and are used to sample a wide variety of foods including bark, as opposed to grazing a pasture. Pigs naturally root and can dig up roots and tubers that are inaccessible to other grazing stock. Payne and Murphy (2014) state that sheep and pigs are more discriminatory than cattle and more likely to reject feeds by taste and smell, which is the contrary to what is reported for sheep in *Pan*.

For the true herbivores (horse, cow, sheep, goat) it is striking how well the similarity in food preferences matches their relatedness (Fig. 4). The phylogeny also reflects their nutritional physiology, with the horse deviating from the ruminants. The pig deviated even more, despite being phylogenetically closer to the ruminants. One could have expected that the pig, being an omnivore, should be less choosy, but the opposite was observed.

We compared the preferences in Pan 1749 with independent sources from the Enlightenment period (Kotowski *et al.* 2023). For the ruminants, the preferred plant species in Pan 1749 were to a great extent species that Kotowski *et al.* (2023) classified as 'preferred by livestock' based on sources from ca 1775–1850. Goats, however, consumed quite a few species that were considered less preferred in Kotowski's classification (Fig. 7), which is in line with the observation that it was the least picky animal in Pan 1749. Pigs to a high degree declined plants that were considered positive for livestock, but pigs were probably not included as 'livestock' in the preference scoring in the historical data.

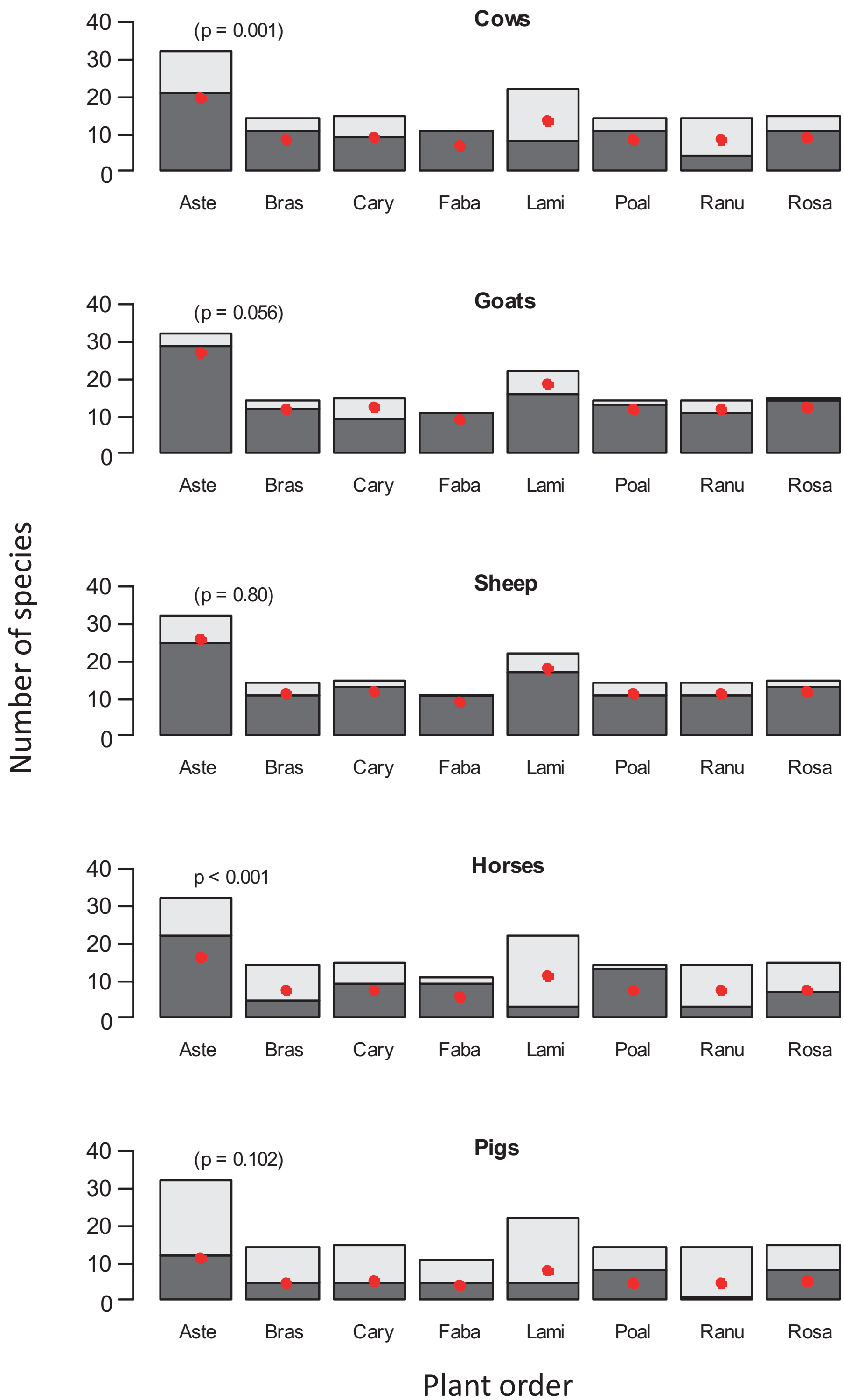

Figure 5. Number of species eaten (dark) and avoided (light) for the plant orders that included > 10 species (see Fig. 6 for full names of the plant orders). Data include 137 species in these orders tested on all animals in Pan 1749. The red dot shows the expected number of eaten plant species under the assumption that the animal selects the same proportion of all plant orders. *P*-values are for χ^2-tests for each animal (given in parentheses for tests that include some cells with low expected numbers).

Do animals have different preferences across the plant phylogeny?

Lamiales, the mint order, includes species that are often fragrant or odorous with medicinal uses and herbal spices (Frohne and Pfänder 2005), and Ranunculales, including the buttercups, generally contain toxic substances and are considered obnoxious (Frohne and Pfänder 2005). In the Pan 1749 data it is quite clear that cows and horses avoided plants from these orders (Fig. 6). With the extended data of Tengmalm this also holds for pigs, whereas goats and sheep remained quite neutral to these orders.

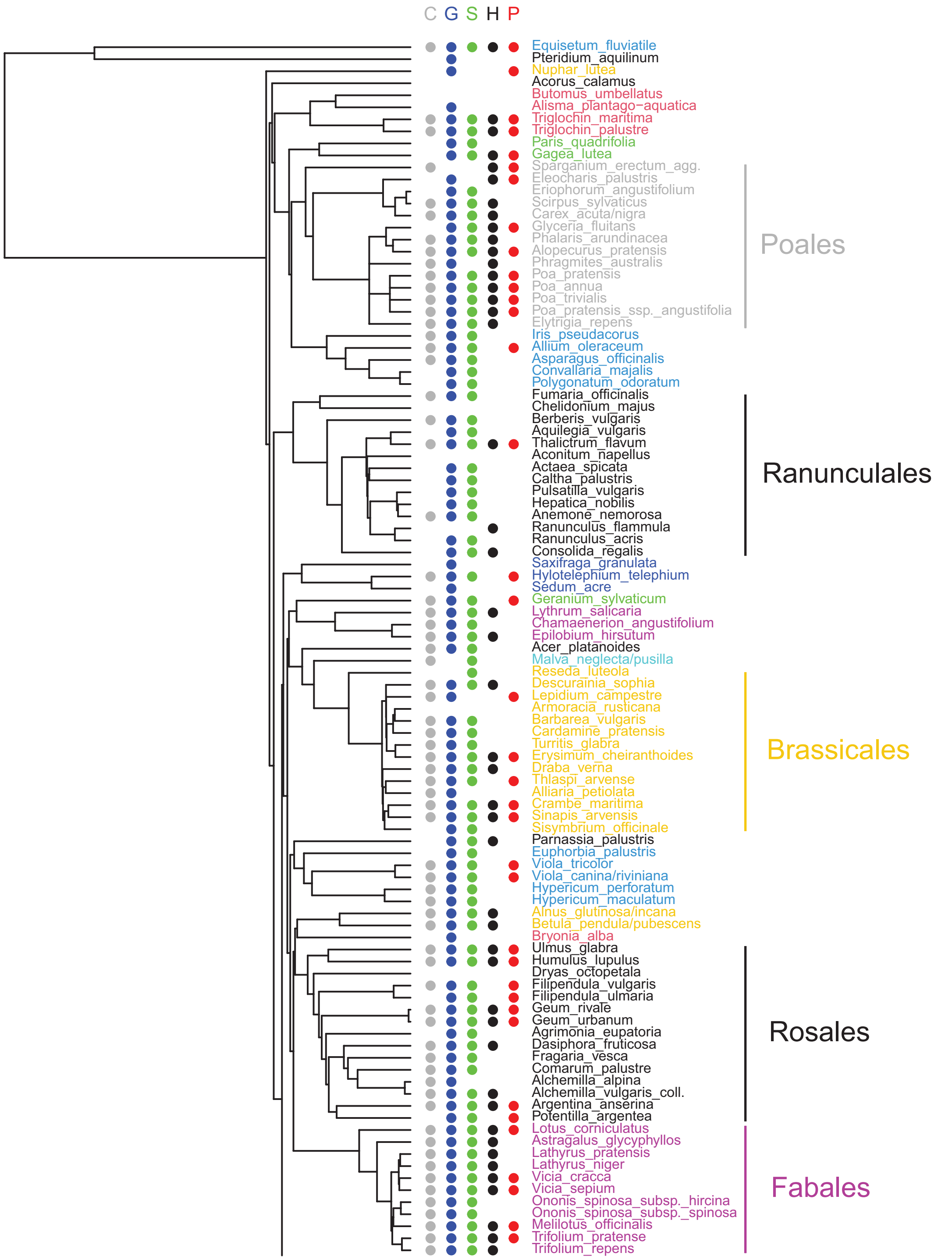

Figure 6. Phylogenetic tree with the 204 plant species tested on all animals in Pan 1749, with plant orders indicated by differently coloured species names. The orders with > 10 species (tested in Fig. 5) are named to the right. The two deviating species at the top are the pteridophytes *Equisetum fluviatile* and *Pteridium aquilinum*. The symbols show which plant species the animals accepted: C, cow, grey symbols; G, goat, blue; S, sheep, green; H, horse, black; P, pig, red.

In the early 18th century the practice of growing hay on fields in addition to using seminatural meadows started to develop across Europe (Kåhre 1996). A highly topical issue was the selection of species for hay, especially among legumes and grasses. There was an overall preference for the Fabales and Poales, but pigs were, perhaps unsurprisingly as they were not fed with hay, indifferent to them. Linnaeus (1742) had previously proposed *Medicago falcata* L. as a splendid candidate, being well adapted to Swedish conditions and suggested to be superior to imported species. In *Pan* all grazers accepted *M. falcata* (not tested on pigs), but Linnaeus made no reference to his earlier publication.

Do animals recognize nutritious or toxic plants?

How do the animals decide to eat or avoid a certain plant? Grazing animals are exposed to a variety of plants, and diet selection is complex and not fully understood. It has been suggested

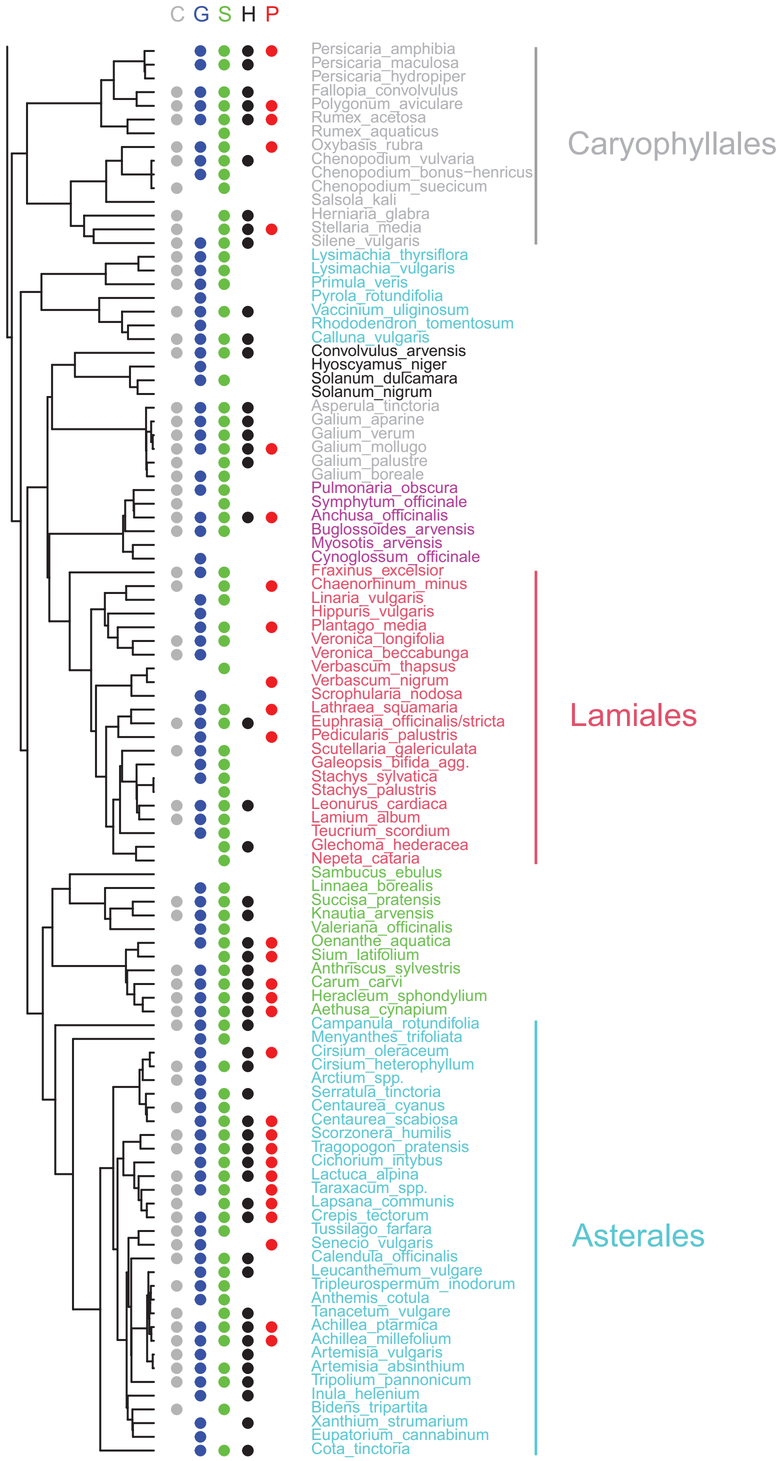

Figure 6. Continued

that animals learn which plants to eat and to avoid through interactions between the plant's flavour and the postingestive consequences of nutrients and toxins (Villalba *et al.* 2010). Further, social interaction with the mother or other members of the herd may influence feeding behaviour (Ralphs and Provenza 1999). We could not find data on relevant plant traits for all species but the results show that both positive and negative choices were made. All animals preferentially ate plants with positive nutritional value (Fig. 7), but only cows and horses clearly avoided toxic plants (Fig. 8). However, it is difficult to separate positive and negative signals since there may be trait correlations that differ among plant groups: leguminous plants could be both toxic and nutritious with nitrogen-based herbivore defence substances such as cyanogenic glycoside in *Trifolium* (Table 2) whereas less nutritious plants could also be toxic but with a non-nitrogen-based defence (Mattson 1980).

Regardless of data, cows and horses were best in avoiding toxic species. This result is surprising, considering the report that

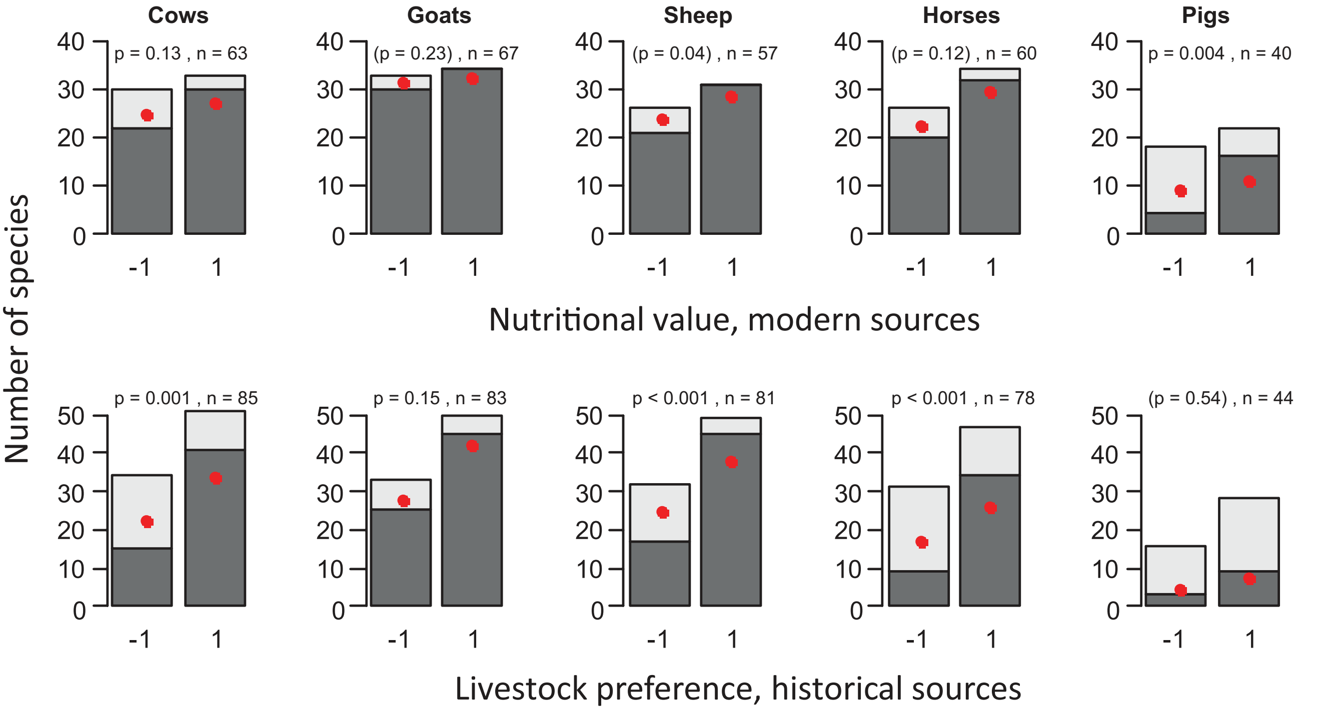

Figure 7. Number of plant species of different quality eaten (dark bars) or avoided (light bars) in Pan 1749. The species were classified according to nutritional value (upper graph) and historical sources on livestock preference (lower graph) by Kotowski *et al.* (2023). Plant traits are coded as negative (−1) or positive (1). The red dot shows the expected number of eaten plant species under the assumption that the animal selects the same proportion of the high- and low-quality group. *P*-values are for χ^2-tests for each animal (given in parentheses for tests that include some cells with low expected numbers); *n*, number of plant species tested.

Figure 8. Number of toxic and nontoxic plant species eaten (dark bars) and avoided (light bars) based on the 204 species tested on all animals in Pan 1749, and toxicity according to SVA (2024). The red dot shows the expected number of eaten plant species under the assumption that the animal selects the same proportion of toxic and nontoxic species. *P*-values are for χ^2-tests with Yates' correction for each animal.

sheep and pigs are more likely to reject feeds by taste and smell (Payne and Murphy 2014). Sheep and, particularly, goats consumed a surprisingly high percentage of the toxic plants. Among the 204 plant species tested on all animals in Pan 1749, 12 species were uniquely eaten by goats, including the highly poisonous species *Cynoglossum officinale*, *Hyoscyamus niger*, and *Pteridium*

Table 2. List of toxic species with observations on animal choices in the original *Pan Svecicus* (Linnaeus 1749) and in Tengmalm's data (Tengmalm 1779–1780).

		Pan 1749					Tengmalm				
Species	**Toxin**	**Cow**	**Goat**	**Sheep**	**Horse**	**Pig**	**Cow**	**Goat**	**Sheep**	**Horse**	**Pig**
Highly toxic species											
Aconitum lycoctonum	Aconitine[a]	0	1	10	0	–	0	1	0	1	0
Aconitum napellus	Aconitine[a]	0	0	0	0	0	0	0	0	10	0
Aethusa cynapium	Piperidine alkaloid	1	1	1	1	1	1	1	1	1	1
Agrostemma githago	Steroidal saponin	–	1	1	1	–	1	1	1	1	–
Chelidonium majus	Isoquinoline alkaloid	0	0	0	0	0	0	0	0	0	0
Cicuta virosa	Cicutoxin	0	1	1	1	–	0	0	0	0	0
Conium maculatum	Piperidine alkaloid	0	0	1	0	–	0	1	1	0	–
Convallaria majalis	Cardiac glycoside	0	1	1	0	0	0	1	1	11	0
Cynoglossum officinale	Pyrrol	0	1	0	0	0	0	0	0	0	0
Daphne mezereum	Daphnetoxin[a]	0	1	1	0	–	0	1	1	0	1
Datura stramonium	Tropane alkaloid	0	0	0	0	–	0	0	0	0	0
Euphorbia helioscopia	Cyanogenic glycoside	0	01	01	1	–	0	10	10	11	0
Euphorbia palustris	Cyanogenic glycoside	0	1	10	0	0	0	1	10	0	0
Euphorbia peplus	Cyanogenic glycoside	0	–	–	10	–	0	10	10	11	0
Frangula alnus	Anthraquinone	0	1	1	–	–	0	11	1	1	–
Glechoma hederacea		0	0	1	10	0	0	0	1	1	0
Hyoscyamus niger	Tropane alkaloid	0	01	0	0	0	0	0	0	0	0
Jacobaea vulgaris	Pyrrol	1	–	–	–	–	1	1	–	–	–
Oenanthe aquatica	Oenantotoxin	0	1	1	1	01	1	1	1	1	1
Pteridium aquilinum	Thiaminase	0	01	0	0	0	0	1	0	0	0
Senecio viscosus	Pyrrolizidine alkaloid	–	–	–	–	–	0	0	0	0	–
Senecio vulgaris	Pyrrolizidine alkaloid	1	1	0	0	1	1	1	0	0	1
Solanum dulcamara	Calcinogenic glycoside, steroidal alkaloid	0	1	1	0	0	0	1	1	0	0
Solanum nigrum	Calcinogenic glycoside, steroidal alkaloid	0	0	0	0	0	0	0	0	0	0
Taxus baccata	Taxine alkaloids	0	1	1	0	–	0	1	1	0	–
Eaten (% of offered high-toxicity)		**13**	**73**	**64**	**32**	**23**	**20**	**64**	**54**	**42**	**21**
Low-toxicity species											
Actaea spicata	Irritant oils	0	1	1	0	0	0	1	1	0	0
Alliaria petiolata	Glucosinolate[c]	1	1	0	0	0	1	1	0	0	0
Anemone nemorosa	Protoanemonine	10	1	1	0	0	10	1	1	0	0
Anemone ranunculoides	Protoanemonine	–	–	–	–	–	0	10	0	0	–
Armoracia rusticana	Glucosinolate	0	0	0	0	0	0	0	1	0	10
Artemisia absinthium	Thujone[a], tannins[c]	1	10	1	1	0	1	10	1	1	0

Table 2. Continued

Species	Toxin	Pan 1749					Tengmalm				
		Cow	Goat	Sheep	Horse	Pig	Cow	Goat	Sheep	Horse	Pig
Barbarea vulgaris	Irritant oils	1	10	10	0	0	1	10	1	0	0
Brassica campestris	Nitrate, disulphide, glucosinolate	1	1	–	–	–	1	1	1	0	11
Brassica napus	Nitrate, disulphide, glucosinolate	1	1	–	–	–	11	1	1	0	11
Brassica nigra	Nitrate, disulphide, glucosinolate	–	–	–	–	–	1	1	1	0	–
Caltha palustris	Protoanemonine	0	1	1	0	0	0	1	1	0	1
Cardamine pratensis		10	1	1	0	0	10	1	1	0	0
Carex vulpina	Cyanogenic glycoside	–	1	–	1	0	1	1	–	1	0
Chenopodium album	Cyanogenic glycoside, nitrate	1	1	1	–	11	1	1	1	1	11
Consolida regalis	Diterpene alkaloid[a], nor-diterpene alkaloid[a]	0	1	1	10	0	0	1	1	11	0
Convolvulus arvensis	Several alkaloids[b]	1	1	1	1	0	11	1	1	11	0
Cuscuta europaea		1	01	1	0	–	1	10	1	1	–
Cytisus scoparius	Neurogenic quinolizidine alkaloid	–	–	–	–	–	1	1	1	1	–
Dryopteris filix-mas	Thiaminase	0	1	0	–	–	0	1	0	0	0
Equisetum arvense	Thiaminase	0	1	0	0	–	0	1	0	0	0
Equisetum palustre	Thiaminase	–	1	–	–	–	0	1	0	0	0
Equisetum sylvaticum	Thiaminase	–	1	–	11	–	0	1	–	11	–
Euonymus europaeus	Cardiac glycoside	1	1	1	0	–	1	11	1	1	–
Fagopyrum esculentum	Fagopyrin	–	1	1	0	0	11	1	1	11	0
Ficaria verna	Protoanemonine	0	1	1	0	–	0	1	1	0	–
Fraxinus excelsior	Glycoside[b]	1	1	1	0	0	11	1	1	0	0
Hedera helix	Triterpene saponin	0	0	1	1	–	0	0	1	1	–
Hepatica nobilis	Protoanemonine	0	10	1	0	0	0	10	1	0	0
Heracleum sphondylium	Furocoumarin	1	1	1	1	1	1	1	1	1	1
Hypericum hirsutum	Dianthrone derivative, hypericin	–	–	–	–	–	1	0	1	–	–
Hypericum hirsutum/montanum	Dianthrone derivative, hypericin	–	–	1	0	–	–	–	–	–	–
Hypericum maculatum	Dianthrone derivative, hypericin	1	1	1	0	0	11	1	1	0	0
Hypericum montanum	Dianthrone derivative, hypericin	–	–	–	–	–	11	0	–	0	–
Hypericum perforatum	Dianthrone derivative, hypericin	1	1	1	0	0	11	1	1	0	0
Iris pseudacorus	Cardiac glycoside	1	1	01	0	0	10	1	10	0	0
Juncus articulatus	Cyanogenic glycoside	–	–	–	–	–	1	1	1	1	–
Juncus bufonius	Cyanogenic glycoside	–	–	–	1	–	1	1	1	1	–
Juncus bulbosus	Cyanogenic glycoside	1	1	1	1	–	1	1	1	1	–
Juncus conglomeratus	Cyanogenic glycoside	–	1	–	–	–	10	1	0	10	–
Juncus effusus	Cyanogenic glycoside	–	1	–	1	–	10	1	0	1	–
Juncus filiformis	Cyanogenic glycoside	–	–	–	–	–	–	1	1	–	–

Table 2. Continued

Species	Toxin	Pan 1749					Tengmalm				
		Cow	Goat	Sheep	Horse	Pig	Cow	Goat	Sheep	Horse	Pig
Juncus squarrosus	Cyanogenic glycoside	–	–	–	1	–	1	–	0	1	–
Ligustrum vulgare		1	1	1	0	–	11	1	11	0	0
Lolium temulentum	Nitrate	–	–	0	–	–	10	0	0	0	1
Lotus corniculatus	Cyanogenic glycoside	1	1	1	1	10	1	1	1	11	10
Lysimachia arvensis		1	1	0	–	–	1	1	0	–	–
Maianthemum bifolium	Glycoside[c], saponin[c]	–	1	–	–	1	0	1	0	11	–
Mercurialis annua	Mercurialin[b], trimethylamine[b], saponin[b]	–	–	–	–	–	0	1	0	0	–
Mercurialis perennis	Mercurialin[b], trimethylamine[b], saponin[b]	0	–	1	–	–	–	–	–	–	–
Narthecium ossifragum	Steroidal saponin	1	–	0	1	0	1	1	0	0	–
Oenanthe crocata	Oenantotoxin	1	–	1	1	–	1	–	0	1	–
Oenanthe fistulosa	Oenantotoxin	1	–	–	1	–	1	–	0	0	–
Oxalis acetosella	Oxalate[b]	01	1	1	–	1	10	1	1	1	1
Papaver rhoeas	Rhoeadine	1	1	1	0	–	1	1	10	0	–
Paris quadrifolia	Saponin[a]	0	1	1	0	0	0	1	1	0	0
Pedicularis lapponica	Glycoside[b]	–	1	1	–	–	–	1	1	–	–
Pedicularis palustris	Glycoside[b]	0	1	0	0	01	0	1	0	0	10
Pedicularis sceptrum-carolinum	Glycoside[b]	1	1	–	0	–	1	1	0	0	–
Pedicularis sylvatica	Glycoside[b]	0	–	–	–	0	0	1	0	0	0
Pulsatilla pratensis	Protoanemonine	–	–	–	–	–	0	1	0	0	0
Pulsatilla sylvestris	Protoanemonine	–	–	–	–	–	0	1	0	0	0
Pulsatilla vernalis	Protoanemonine	–	–	–	–	–	0	1	0	0	0
Pulsatilla vulgaris	Protoanemonine	0	1	1	0	0	0	1	1	0	0
Quercus robur	Tannins	1	1	1	1	–	1	1	1	1	1
Ranunculus acris	Protoanemonine	0	1	1	0	0	0	1	1	0	0
Ranunculus bulbosus	Protoanemonine	0	–	–	–	–	0	1	0	0	0
Ranunculus flammula	Protoanemonine	0	0	0	1	0	0	0	0	11	0
Ranunculus lingua	Protoanemonine	–	–	–	–	–	0	0	0	0	0
Ranunculus repens	Protoanemonine	–	1	–	1	–	0	1	10	1	–
Ranunculus sceleratus	Protoanemonine	0	1	0	–	–	0	1	0	0	–
Rhamnus cathartica	Anthraquinone	0	1	1	1	–	0	1	1	11	–
Rhinanthus angustifolius/minor	Glycoside[c]	10	1	1	10	–	11	1	1	10	–
Rhododendron tomentosum	Andromedotoxin, cardiac glycoside, grayanotoxin	0	1	0	0	0	0	1	1	1	1
Rumex acetosa	Oxalate[b]	1	1	1	1	1	11	1	11	1	1
Rumex acetosella	Oxalate[b]	–	1	1	1	1	0	1	11	1	1
Rumex aquaticus	Oxalate[b]	0	0	1	0	0	0	0	1	11	0

Table 2. Continued

Species	Toxin	Pan 1749					Tengmalm				
		Cow	Goat	Sheep	Horse	Pig	Cow	Goat	Sheep	Horse	Pig
Rumex crispus	Oxalate[b]	0	0	–	–	–	1	0	1	1	1
Rumex-hybrid	Oxalate[b]	–	–	–	–	0	1	–	–	1	0
Sinapis arvensis	Nitrate, disulphide, glucosinolate	1	1	1	10	1	1	1	1	10	1
Sium latifolium		0	0	01	1	1	0	0	1	11	1
Symphytum officinale	Pyrrolizidine alkaloid	1	0	1	0	0	1	0	10	1	0
Tanacetum vulgare	Sesquiterpene lactone	1	0	1	10	0	11	0	11	11	0
Thalictrum aquilegifolium	Protoanemonine	1	1	1	1	–	1	1	1	1	–
Thalictrum flavum	Protoanemonine	1	1	1	1	10	1	1	1	1	10
Thalictrum minus	Protoanemonine	–	–	–	–	10	1	1	1	1	1
Thlaspi arvense	Glucosinolate	1	1	10	0	1	1	1	0	0	1
Trifolium hybridum	Phyto-oestrogen	–	–	–	–	–	11	1	1	11	–
Trifolium repens	Cyanogenic glycoside, phyto-oestrogen	1	1	1	1	0	11	1	1	11	1
Trollius europaeus	Protoanemonine	0	1	1	0	–	0	1	1	0	–
Tussilago farfara	Pyrrolizidine alkaloid[a]	10	1	1	0	0	10	1	1	0	0
Vicia sativa	Cyanogenic glycoside	1	1	1	1	–	11	1	1	11	1
Vincetoxicum hirundinaria	Cynanchoside	0	1	0	0	–	0	11	0	10	0
Viola tricolor	Glycoside[c], methylsalicylat[c]	1	1	1	0	10	1	1	0	0	10
Eaten (% of offered low-toxicity)		**61**	**88**	**81**	**47**	**32**	**62**	**86**	**68**	**51**	**40**

Animal choices are given with the original code: –, not tested; Grey—0, not eaten; Yellow—10 or 01, sometimes eaten; Orange—1, eaten; Red—11, eagerly eaten. Presence of toxins is according to Constable *et al.* (2016) with additions: [a]Frohne and Pfänder (2005); [b]Cooper and Johnson (1998); [c]SVA (2024).

Table 3. List of statements on livestock preferences made in *Pan Svecicus*, some of which are consistent with the experimental results and some that are contradictory.

Statement in text	Experimental result
Linnaeus describes that farmers are surprised to see calves languish in fields covered by *Filipendula ulmaria* (L.) Maxim., not knowing that this plant is useless fodder for them, but highly nourishing for goats	Yes, *F. ulmaria* was rejected by cows but greedily eaten by goats
Linnaeus refers to his own previous observations (Linnaeus 1737) that horses discarded species that were considered harmful at the time: *Filipendula ulmaria*, *Valeriana officinalis* L., *Convallaria majalis*, *Angelica archangelica* L., *Chamaenerion angustifolium* (L.) Scop., *Comarum palustre* L., *Geranium sylvaticum* L., *Trollius europaeus* L., and *Aconitum lycoctonum*	Yes, the observations are supported by the data in the thesis, but this could also mean that Linnaeus used his previous observations without testing them again
On *Cicuta virosa* (water hemlock) Linnaeus writes: *In the spring, when the water hemlock is under water, so that the cows cannot smell it, they dye in heaps. But when the summer comes on and has dryed the ground, they are very carefull not to touch it*	Yes, in the experiments *C. virosa* was indeed refused by cows, but eaten by goats, sheep and horses. However, the toxin is most concentrated in the tuberous roots, rather than in the leaves that were used in the experiment (Schep *et al.* 2009)
Linnaeus states that it is well known that sheep eat poisonous plants in wetlands, and lists species that he suspects to be toxic	Some of the listed species are indeed considered as toxic today, and of these sheep accepted *Juncus* L. but avoided *Narthecium ossifragum* (L.) Huds. and *Ranunculus flammula* L
Horses are more selective than other creatures	Yes, they were indeed much more selective than the ruminants (Table 1).
Horses dislike Tetradynamia	Yes, there is a tendency that horses selected more against Brassicales than the ruminants (Fig. 5)
Goats seek more variation, and do not thrive well on a single plant species	Yes, they accepted more plant species than the other animals (Table 1)
Sheep choose *Festuca ovina* L. before anything else, as this plant makes them fatter than any other plant	Yes, sheep ate it eagerly
Euphorbia helioscopia L. has a *milky juice, which causes blotches in our skin and hurts our fibres, and therefore it is said to be poisonous*	*Euphorbia helioscopia* was eaten by horses, and sometimes by goats and sheep
Linnaeus writes that *Aconitum* (probably referring to the wild *A. lycoctonum*) kills the goat but not the horse	The contradictory result was that *A. lycoctonum* was eaten by goats and sometimes by sheep, but not by horses
Aconitum napellus L. (monkshood) is a nonnative species that Linnaeus had observed near Falun, and he states it is *generally left untouched by all the animals, that are accustomed to these places; but if forreign cattle are brought thither and meet with this vegetable, they venture to take too large a quantity of it, and are killed*	*Aconitum napellus* was tested on all animals, and eaten by none—a surprising result since it is unlikely that all animals would have been grazing around the restricted occurrences of *A. napellus*

aquilinum, and another six were eaten only by goats and sheep. However, our list of poisonous plants does not account for the fact that species and individuals vary in their susceptibility to different plants. For example, the microbes in the reticulorumen and hindgut in ruminants and horses, respectively, may differ in their ability to degrade individual toxins (Loh *et al.* 2020, Wunderlich *et al.* 2023). Additionally, there is a variety of detoxification enzymes in the liver and other organs which differ between species (Cheeke 1994).

When interpreting the animals' response to toxic plants there is a caveat: Linnaeus clearly states that only leaves were tested (as only these were relevant as fodder). A striking example is *Cicuta virosa* L. which was 'sometimes eaten' by goats, sheep, and horses (Table 2). This is a highly toxic plant, but the toxin is most concentrated in the tuberous roots, rather than in the leaves (Schep *et al.* 2009). However, in Tengmalm's data none of the animals accepted to eat *Cicuta*, and we wonder if Tengmalm may have modified the data because he knew that *Cicuta* is toxic. Our scepticism is based on the observation that Tengmalm's procedures are less well documented than in Pan 1749 and it is rather unclear how Tengmalm 'improved' *Pan Svecicus*.

The text cites American observations that *Kalmia angustifolia* L. immediately killed sheep in Virginia, and *K. latifolia* L. was very harmful to sheep in New York. At that time *Kalmia* was within the genus *Andromeda*, and as a scientist may do today, Linnaeus hypothesized that by analogy also the Swedish *Andromeda* species should be harmful to sheep. In the experiments sheep accepted *Andromeda vulgaris* (today *A. polifolia* L.), but not *A. caerulea* [*Phyllodoce caerulea* (L.) Bab.], *A. hypnoides* [*Harrimanella hypnoides* (L.) Coville], or the related *Ledum* (*Rhododendron tomentosum* Harmaja). From this Linnaeus could have drawn the conclusion that the European species are less harmful than their American congeners (in our modern sources only *Rhododendron tomentosum* is listed as toxic), but the comparative approach feels strikingly modern: *It is particularly to be noted upon this occasion, that the botany of America, a countrey so far disjoyned from us, gives a hint for considering things of the greatest use, of which the antients did not so much as dream.*

CONCLUSION

One of our aims with this publication is to make Linnaeus's data available in modern form to encourage scholars of botany and history of science to further explore them.

The motivation behind *Pan Svecicus* was practical. For example, how could agricultural practices be improved by selection of seeds for hay and how could the quality of grazing pastures be evaluated? But the applied aspects were overshadowed by a magnificent curiosity-driven approach, testing a huge range of plants beyond any practical interest.

Naturalists of the 18th century had limited means to evaluate quantitative data. The experimental procedure is reproducible, and with the huge number of trials, we are convinced that the results are solid: goats accepted the largest number of species followed by sheep, cows, horses, and pigs. The ruminants were similar in their plant preferences, and the omnivorous pig deviated from the grazers. The animals tended to select nutritious plant species, and (particularly cows and horses) to avoid toxic species.

The text in the thesis has virtually no basis in the tabulated data, and our conclusion is that Linnaeus prepared the text beforehand, and did not revise it when data came in from his students. A reason may be lack of time before printing of the thesis, but stranger is that later editions had updated tables with new data, but the text was identical (as was the table summarizing the observations). A striking observation, emphasizing that Linnaeus himself did not scrutinize or make much use of the data, is that the thesis ends with a famous quotation from Lucretius: 'For you may observe that bearded goats often grow fat on hemlock, which to men is rank poison' (Watson 1851), but the contradictory result in *Pan Svecicus* that poison hemlock (*Conium maculatum* L.) was uniquely eaten by sheep rather than goats is left without comment!

Science proceeds one step at a time. We must acknowledge the heroic efforts by Linnaeus and his team to collect valuable and accurate data, allowing conclusions to be drawn long after their time.

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

The data underlying this article are available in Supporting Information Appendix S1.

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