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# Using animal history to inform current debates in gene editing farm animals: A systematic review

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There is growing interest in gene editing farm animals. Some alterations could benefit animal welfare (e.g., improved heat tolerance in cattle with the "slick" gene), the environment (e.g., reducing methane emissions from cattle with induced pluripotent stem cells), and productivity (e.g., higher weight gains in cattle with the "double muscling" gene). Existing scholarship on the acceptability of such modifications has used myriad approaches to identify societal factors that shape the ethics and governance of this technology. We argue that integrating historical approaches—particularly from the relatively new and burgeoning field of animal history—offers a form of "anticipatory knowledge" that can help guide discussions on this topic. We conducted a systematic review of the animal history literature in English, German, and Spanish to identify the influence of political, scientific, economic, social, and cultural factors on the development and acceptance of such technologies. We identified analogous structures and fault lines in past debates about farm animals that provide insights for contemporary discussions about gene editing. Those analogous structures include the market power of meatpackers or the racialized precepts in livestock breeding, and fault lines, like the disconnect between states and citizens over the direction of food systems. Highlighting these similarities demonstrates how external forces have shaped—and will continue to shape—the acceptance or rejection of emerging biotechnologies as applied to farm animals.

KEYWORDS
**animal history, gene editing (CRISPR/Cas9), biotechnology, animal welfare, sustainability, agriculture, anticipatory knowledge**

## Introduction

Gene editing is a controversial technology whose proponents claim it can address current challenges in animal agriculture. As temperatures rise due to climate change, periods of warm weather can negatively impact the welfare of dairy cows (Polsky and von Keyserlingk, 2017) and milk production (Osei-Amponsah et al., 2020). One approach to mitigate heat stress is to incorporate gene editing techniques (e.g., TALENS and CRISPR-Cas9) to improve the animal's ability to regulate its body temperature (Dang et al., 2019). The prolactin receptor "slick" gene derives its nickname from the fact that cattle inheriting it have a short and sleek hair coat, an observation first described as a random genetic mutation in the Senepol breed of the Caribbean. Using gene editing tools, scientists have incorporated the slick gene into Holsteins and other cattle breeds—thereby improving heat tolerance with shorter hair coats (see Figure 1) (Dikmen et al., 2014; Hansen, 2020). This and other applications of gene editing have been criticized as upholding intensive agricultural practices (Devolder, 2021; Hock, 2021), potentially undermining public trust in an ever-evolving food system.

While gene editing for bovine thermoregulation might seem new, there is a history of acclimatizing cattle to cope with warmer places. In 1911, for instance, a British- and French-owned beef syndicate hired Murdo Mackenzie, a Scotsman and the esteemed manager of the Matador Ranch in Texas, to set up new operations in South America (Wilcox, 2008). Mackenzie and the Brazil Land, Cattle, amd Packing Company imported 900 Hereford and Shorthorn bulls from the United States to cross with "creole" herds in Brazil. However, the reception of "foreign stock" was not positive: many Brazilian farmers viewed these cattle as too frail to withstand the intense sun of the tropical grasslands and rejected the notion of "upgrading" their herds with these purebreds. This reaction was underpinned by local breeders who placed greater value on the heat- and disease-resistance traits of the Zebu cattle from India. Murdo's son John Mackenzie echoed this sentiment in the 1920s, stating: "With few exceptions the native Brazilian prefers cattle of the Brahma [Zebu] type" (Wilcox, 2008, p. 378). As corporations in the global North attempted to replicate a model of cattle production across the world, North American and European expertise about temperate-adapted breeds did not translate well when implemented under tropical ranching conditions. Brazilians chose Zebus over Herefords because the former's traits were deemed as more suitable to local environmental conditions (Wilcox, 2017).

This historical example of cultural preferences for Zebu cattle suggests that gene editing for improved heat tolerance will confront past legacies that influence its adoption. A recent survey in Brazil suggests that citizens objected less to gene editing technology itself than potential intended uses and beneficiaries (Yunes et al., 2021). Some participants argued that genomic alteration was "unnatural" because human intervention violated the animal's integrity, while some questioned the profit motives behind genetic traits based on their perceived value to the farmer. Still others preferred alternatives such as providing cattle with shade or crossing them with heat-tolerant Zebu breeds (Yunes et al., 2021). Public attitudes appear most accepting toward gene editing when the introduced traits are perceived to provide a social good, for example, to animal welfare or the environment (Ritter et al., 2019; Kramer and Meijboom, 2020). While crossbreeding with Zebu for heat tolerance traits might compromise other animal characteristics, public affinities toward the breed as an alternative to gene editing come from a deeper context.

We argue that incorporating an historical dimension can inform current debates about gene editing farm animals by offering "anticipatory knowledge", extracting lessons from the past that turn hindsight into foresight (Simon et al., 2021). Animal history is anticipatory because past experiences help to shape present and future expectations (Neustadt and May, 1986; Oreskes and Conway, 2014). Examining why past technologies were adopted (or not) can prepare stakeholders to identify and anticipate similar factors in the present. As a precedent for showing why historical approaches can provide insights, we turn to the example provided by Holloway and Bear (2017) who investigated the adoption of milking technologies. They found that UK farmers held comparable anxieties in the transition from hand- to machine-milking (1930s—1960s) as farmers did in the shift almost half a century later from machine- to automated-milking (1990s—2010s). They identified a concern about the technology weakening "stockmanship" as farmers went from milking cows by hand (intimate human-animal relationships) to milking by machine (humans and animals co-present but distanced). Given this historical context, the arrival of automated-milking systems could be seen as both a barrier (neglecting the herd) or an opportunity (freeing of time to allow for more individualized care) (Holloway, 2007). In a systematic review of scholarly literature for and against using gene editing on animals, De Graeff et al. (2019) commented that "arguments raised previously, in different contexts or in older but related debates, may be relevant for the current discussion of genome editing." Synthesizing recent works in animal history is about revisiting these older but related debates to uncover historical lessons from precursors such as selective breeding or artificial insemination (Kramer and Meijboom, 2020). It also enables scholars to discern which historical cases are likely analogous to gene editing. Our central research question was thus: how and why can animal history contribute to contemporary discussions of, and developments in, gene editing farm animals?

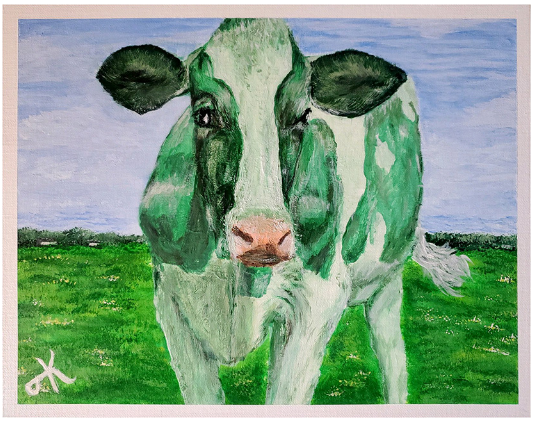

FIGURE 1
An artistic rendition of "greening Holsteins" to represent enhancing climate adaptation in cattle with gene editing tools. *Eco-stein*, original artwork by Patricia Knoblauch, 2021. Used with permission.

# Methods

## Approach

Historians have traditionally dismissed animals within their scholarship, arguably conveying that they were unimportant. This exclusion likely occurred because the history profession took shape during the latter half of the nineteenth century, a time when farm animals were largely driven out of cities (McNeur, 2014; Atkins, 2016; Robichaud, 2019). Instead of treating animals as legitimate actors in shaping the past, historians of science viewed them as passive objects of study (Haraway, 1989) or, for agricultural historians, as mere economic inputs (Randhawa, 1986). The more recent shift to accepting that animals do matter can be attributed to the rise of animal rights activism of the 1970s (Singer, 1975) and scientific concern about the biodiversity crisis of the 1980s (Wilson, 1988). In response, historians have begun to examine the roles of animals in history, concluding that the past looks quite different when centering animals as subjects with needs, desires, and abilities (Ritvo, 1987; Krüger et al., 2014). This new emphasis on non-human animals as co-creating the past has made "animal history" a distinct sub-field. Animal historians argue that we better understand continuity and change over time by investigating human-animal interactions, rather than analyzing people and power alone (Fitzgerald et al., 2018; Way et al., 2020).

The approaches of animal history are interdisciplinary because animals held myriad roles within society. Animal-focused scientists—such as veterinarians, ethologists, ecologists, and animal welfare researchers—have developed methods to better comprehend non-human sentience and sociability. Historians apply these insights to analyze how animals themselves experienced the past; for example, when interpreting the urban presence of street dogs before twentieth-century leash laws were enforced (Wang, 2019). Animal historians also rely on the work of philosophers and theorists to point out moments of "non-human agency" when animals helped or hindered human actions. For instance, the antislavery and animal protection movements during the nineteenth century based their moral outrage about plantation agriculture on the shared bodily suffering of enslaved Africans and draft animals (Boisseron, 2018). The discipline can provide additional insights by employing anthropocentric archives from non-traditional perspectives, such as reading government reports about war or journal entries about frontier life "against the grain" to obtain textual traces about the lives of horses or oxen (Tucker and Russell, 2004; Ahmad, 2016). The cumulative effect has been to reconstruct multispecies stories that question human exceptionalism, as well as highlight the interdependency between animals and people (Walker, 2013; Nance, 2015).

## Review

Our review of the animal history literature involved a three-phase process [see diagram in Figure 2; Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) model; Page et al., 2021]. We began the identification phase in July–August 2021 using search engines, databases, and targeted journals to gather sources. One researcher (Wright) conducted English- and Spanish-language searches on Google Scholar and WorldCat based on a combination of key words: animal history, cattle, pigs, sheep, horses, livestock breeding, historia de animales, historia de vacas, historia de ovejas, historia de cerdos, historia de caballos, and historia de ganaderia. Wright reviewed the first 50 results among thousands listed (Godin et al., 2015). Wright also completed English-language searches in the journals of *Agricultural History*, *Agricultural History Review*, *Environment and History*, *Environmental History*, *ISIS*, *Journal of the History of Biology*, and *Technology and Culture* due to the prevalence of animal history scholarship within those publications. Another researcher (Tworek) conducted German-language searches in H-Soz-Kult with the key words: Tiergeschichte, Kuh, Kühe, Pferd, Pferde, Schwein, Schweine, Schäfe, Stier, Stiere, and Zucht. The searches resulted in 5,362 records total.

During the screening phase (September–October 2021), we read each synopsis and table of contents in books, as well as abstracts in articles, based on the eligibility criteria as noted in Table 1. After removing duplicates ($n$ = 2,538), we excluded records for non-scholarly publications ($n$ = 159), being unavailable in English, Spanish, or German ($n$ = 8), not employing animal history methodologies ($n$ = 2,455) and centering non-farm animals ($n$ = 105). We then read the full text and excluded records that did not relate to gene editing or

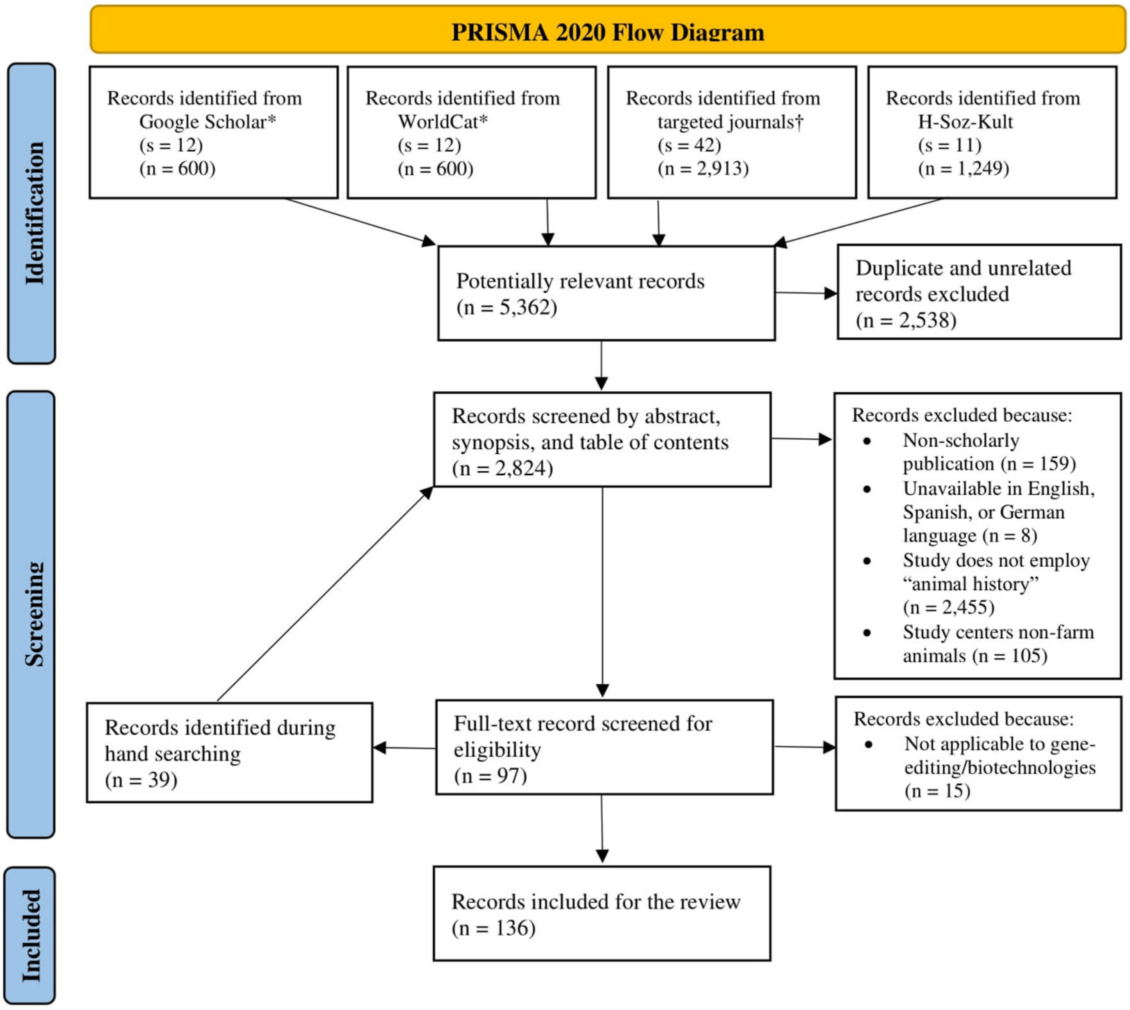


FIGURE 2
Three-phase systematic review process depicting number of searches (s), number of records screened (*n*), and included in the final synthesis. *It was unmanageable to review entire Google Scholar and WorldCat searches (Godin et al., 2015) so the first 50 hits were screened for potential records in the search results. †Targeted journals included: *Agricultural History, Agricultural History Review, Environment and History, Environmental History, ISIS, Journal of the History of Biology, Studies in History and Philosophy of Science, and Technology and Culture*. Diagram from: Page et al. (2021).

biotechnology ($n = 15$). We used hand searching, or adding citations from other sources in which they were cited, which resulted in 39 additional records. Collectively, 136 total sources met our inclusion criteria.

## Results

Before turning to a qualitative synthesis of these sources, a brief quantitative analysis demonstrates the tremendous intellectual energy in, and diversity of, animal history. Of those studies included in the review, 52% ($n = 71$) were published within the last 10 years, offering the ability to answer research questions that were not possible a decade ago during public debates about using transgenic techniques to produce genetically modified organisms. In descending order by region for those studies bounded in a single country, Europe made up the largest share at 25% ($n = 34$), North America was 17% ($n = 23$), Latin America and the Caribbean were 13% ($n = 18$), Asia and Australasia were 11% ($n = 15$), and Africa was 7% ($n = 10$). Moreover, 27% ($n = 36$) of the studies were transnational or comparative. We periodized studies based on their temporal coverage (see Table 2) into three distinct eras: Agro-Pastoral (Earliest Times-1700 CE) ($n = 25$), Imperial State (1700–1945) ($n = 82$), and Welfare State (1945-Present) ($n = 29$). Taken together, the studies we reviewed demonstrate how larger structural forces in agriculture shaped animal bodies (conformation) over time and across space,

TABLE 1 Eligibility criteria for review.

| Inclusion criteria | Exclusion criteria |
|---|---|
| • Scholarly book, article, dissertation, or thesis | • Non-scholarly publication |
| • Available in English, Spanish, or German language | • Unavailable in English, Spanish, or German language |
| • Study employs "animal history" methodologies (i.e., treats non-human animals as historical agents) | • Study does not employ "animal history" methodologies |
| • Study centers farm animals (i.e., cows, sheep, pigs, water buffaloes, and horses) | • Study centers non-farm animals |
| • Applicable lessons for gene editing or other biotechnologies | • Not applicable to gene editing or other biotechnologies |

despite farm animals sometimes resisting or confounding these changes (Greene, 2009). We now turn to a narrative to explore our findings.

## Agro-pastoral period (earliest times-1700 CE)

Because livestock performed myriad functions within human societies, selection pressures on animals were broad. For instance, Bray (2018) has argued that medieval Chinese officials placed more value on cattle, sheep, and pigs for their workforce or ceremonial needs than as sources of nutrition. Agricultural treatises (*nongshu* 農書) written during the Song dynasty (960–1279 CE) considered livestock as inferior to crops. Unlike European mixed farming systems in which livestock manure connected animal husbandry to crop growing, Chinese farming was cereal-intensive with legumes used to enrich fields (Sterckx et al., 2018). As Mikhail (2014) has detailed, the most valuable animal in Ottoman Egypt was the *jāmusa*, or water buffalo, as this multi-purpose creature provided labor, transportation, and sustenance. Egyptian peasants in the 1500s relied on buffalo cows to dig and dredge irrigation canals, carry grain to sovereigns, turn waterwheels, plow soil, and provide milk—resulting in unconscious selecting for a broad suite of traits. The adoption of steam engines with coal power in the nineteenth century finally lessened the longstanding need for bulkier livestock with traits for muscle power (Hribal, 2003; Greene, 2009).

Animal bodies and behaviors were as diverse as the polities they encountered (Kreiner, 2017). The flexibility of domesticated pigs allowed them to fit into many places and political structures (Albarella et al., 2007). Take, for example, porcine typologies in the Pacific World. Voyagers from New Guinea and Southeast Asia traveling in outrigger canoes brought their pigs when populating remote Oceania circa 3,000 years ago (Sand, 2021). Across the Polynesian islands, commoners kept the "village pig"—a pig with a small, slim, and hairy conformation—to scavenge until the rare occasion when the king or chief rounded up all the pigs for a festival. In contrast, starting in the sixteenth century on the Kyukyu islands, Okinawan families kept the "house pig"—a pig that was somewhat larger, rounder, and pot-bellied—to preserve diplomatic ties with Chinese officials, who had ancient proscriptions against eating draft animals like oxen (Sand, 2021). This example provides evidence that pig "types" varied depending on the political arrangements in which an animal population was embedded (Osypińska and Zurawski, 2020).

Aside from the body politic, biological changes to farm animals like dairy cattle resulted in reciprocal changes in humans. Kumar et al. (2015) has noted that multiple ancient texts of India offered practical advice on cattle breeding, including the Hindu treatise *Vishnu Purana* (circa 200 CE) that stated a valuable bull was the offspring of a heavy milker, had sturdy limbs, and proved capable of protecting the entire herd—revealing the value systems of South Asian dairying culture. McInerney (2010) has shown that ancient Greek pastoralists valued the coloration of cattle and tried to influence hide heredity through a system of castration and culling. For example, the third century BCE mathematician Archimedes used those breeding principles to calculate the herd size of four types—milk white, dark, tawny, and dapple—found in Homer's epic *The Odyssey* (McInerney, 2010). By developing dairying culture, those human populations in sub-Saharan Africa, Europe, Middle East, and South Asia have high frequencies of gene mutations that allow for continued production into adulthood of the enzyme lactase, specialized for the digestion of the milk sugar lactose (Wiley, 2014). Thus, the coevolutionary relationship between people and animals involved genetic changes in both directions.

Before a system of breed improvement began in the eighteenth century, human control over livestock was often tenuous; feral cattle and pigs often interbred with wild relatives such as aurochs or boars (Ajmone-Marsan et al., 2010; Kreiner, 2017). The Spanish term *cimarrones*, or literally the "wild ones", was originally applied to stray livestock (Del Río Moreno, 1996; Hribal, 2003). Because pigs were known for their delinquency—eating crops, raiding food stores, defiling gravesites, injuring people—medieval communities in Europe adopted rules that the animal's proprietor was responsible for damages, with fines applied for wandering animals (Jørgensen, 2013). For instance, a 1649 Code of Laws in Russia penalized livestock owners for animal-related losses (Glagoleva, 2010). Structural changes between 1550 and 1700 enabled English farmers to have tighter command over livestock breeding. Enclosing the "commons" with fences gave breeders control over which individual farm animal could mate in a flock or herd (Netz, 2004). The importation

TABLE 2 Characteristics (y-axis) of human-animal relationships in agriculture across three eras (x-axis).

| | Agro-pastoral (earliest times-1700 CE) | Imperial state (1700–1945) | Welfare state (1945-Present) |
|---|---|---|---|
| **Livestock breeding** | Unconscious selection of traits (selective hunting, altering environments, labor demands, husbandry practices, etc.) | Methodical selection for production traits | Selection increasingly mediated by biotechnologies (AI, IVF, cloning, etc.) |
| **Animal bodies** | Multi-purpose generalists: food, labor, transportation, ceremony | Specialized toward one purpose; greater consistency of type | Acceleration of biological changes across generations due to scientific understanding of genotypes (quantitative genetics, molecular genetics, etc.) |
| **Key ideologies** | Diverse depending on place and political structure | For colonial elites, social hierarchies imposed on breeds and reinforced by animal improvement | Regardless of ideological commitments, agricultural intensification sought for food security—and thus political legitimacy |
| **Key spaces** | Local environments shaped animal traits and constitution (i.e., "every soil has its stock") | Empires sent "improved" animal breeds to different environments to upgrade "native" stock | Laboratories become breeding sites for genetic engineering of desired traits |
| **Key practices** | Culling and castration shaped characteristics of herds, flocks, etc.; feeding and grazing on the commons created more intermixing among animals | With global movement of animals, state veterinarian services established to help control livestock epizootics (rinderpest, hog cholera, sheep pox, etc.) with quarantines, slaughtering, and inoculations. | Regulatory agencies grow in size and strength to ensure food safety based on technical concerns |
| **Public involvement** | Concern about livelihoods since most people practiced forms of animal husbandry | Concern about animal cruelty (e.g., live animal transport) and animal diseases (e.g., cull-and-slaughter measures) | Concern about animal welfare, sustainability, food justice even though fewer people in agriculture |
| **Case study** | Sty feeding in medieval China vs. pannage in medieval Europe influenced porcine constitution | Mutton and wool trade in Australasia and Greater Pacific for improved sheep | Artificial insemination and frozen bull semen led to Holsteinization of global dairy industry |
| **Included sources** | Russell, 1987; Del Río Moreno, 1996; Malcolmson and Mastoris, 1998; Hribal, 2003; Netz, 2004; Terrisse, 2004; Wood and Orel, 2005; Albarella et al., 2007; Wood, 2007; Ajmone-Marsan et al., 2010; Costlow and Nelson, 2010; Glagoleva, 2010; McInerney, 2010; White, 2011; Jørgensen, 2013; Mikhail, 2014; Poczai et al., 2014; Wiley, 2014; Kumar et al., 2015; Kreiner, 2017, 2020; Bray, 2018; Schwartz, 2018; Sterckx et al., 2018; Osypińska and Zurawski, 2020; Sand, 2021 | Ritvo, 1987, 2010; Wilcox, 1992, 1999, 2008, 2017; Melville, 1997; Amaral, 1998; Li, 2000; Hernández, 2001; Zarrilli, 2001; Grundy, 2002; Thurtle, 2002; Derry, 2003, 2015, 2020; Anderson, 2004; Crosby, 2004; Elofson, 2004; Orland, 2004; Schrepfer and Scranton, 2004; Bankoff et al., 2007; Kevles, 2007; Fitzgerald, 2008; Flórez-Malagón et al., 2008; Gaudilliere et al., 2009; Greene, 2009; Van Ausdal, 2009, 2012; Appuhn, 2010; Brown and Gilfoyle, 2010; Milne, 2010; Nelson, 2010; Swart, 2010a,b; Knab, 2011; Matz, 2011a,b; Russell, 2011; Weisiger, 2011; Lopes and Riguzzi, 2012; Mishra, 2012; Woods R. J. H., 2012; Breen, 2013; García Garagarza, 2013; Peden, 2013; Skabelund, 2013; Fischer, 2015; Mwatwara and Swart, 2015; Tyrrell, 2015, 2018, 2019; Uribe Mendoza, 2015; Woods, 2015, 2017a,b; Brown, 2016; Hove and Swart, 2016; Pawley, 2016, 2018, 2020; Pelozatto Reilly, 2016; Rosenberg, 2016, 2017, 2020; Saha, 2016; Saraiva, 2016; Specht, 2016, 2020; Del Rosario García Huerta and Ruiz Gómez, 2017; LeCain, 2017; Cushing, 2018; Ford, 2018; Mendoza, 2018; Zelinger, 2018, 2019; Donald, 2019; Conz, 2020; Kirchberger, 2020; Sunseri, 2021; Wedekind, 2021 | Howkins and Merricks, 2000; Bieleman, 2005; Brassley, 2007; Franklin, 2007; Wilmot, 2007; Theunissen, 2008, 2012, 2020; Langston, 2010; Smith-Howard, 2010, 2017a,b; Woods A., 2012; Sayer, 2013; Saucier and Parsons, 2014; Smith, 2014; García-Sancho, 2015; Funes-Monzote, 2016; Schmalzer, 2016; Villanueva, 2017; Derry, 2018; Schneider, 2018; Anderson, 2019; Fleischman, 2020; Funes-Monzote and Palmer, 2020; Kassen, 2020; Settele, 2020; Woods, 2022 |

of new fodder crops—clovers, ryegrass, turnips—and the drainage of "water meadows" for more arable land facilitated improved animal diets (Russell, 1987). Better animal nutrition, in turn, meant livestock reached sexual maturity faster—thereby shorting generation intervals. These external shifts allowed European breeders to reproduce phenotypes more consistently in farm animals (Wood and Orel, 2005; Poczai et al., 2014).

Crossbreeding to create another typology, the "capitalist pig," provides a clear example of the shift from unconscious to methodical selection (White, 2011). Feeding practices unintentionally shaped porcine bodies over millennia; in medieval Europe, hogs were let loose in forests to scavenge for acorns and beechnuts, known as pannage, resulting in a lean and hardy physique (Malcolmson and Mastoris, 1998; Kreiner, 2020). In contrast, Chinese hogs were fed human food scraps and housed in pens that restricted their movements, leading to a rounder body type and fattier meat. Around 1700, British breeders began importing pigs from China for crossing with their own stock. The resulting breeds, including Yorkshire, Berkshire, and Suffolk hogs, combined the characteristics of the two types: better able to withstand living in crowded pens and reach slaughter weight quickly (see Figure 3). As White (2011) has noted, these same physical qualities later allowed pork production to flourish under industrial capitalism. Biological innovation often preceded mechanical innovation as animals were often seen as technologies of industrialization (Russell, 2011). This more mechanistic view toward animals and the rise of breed improvement set the stage for imperial states to globalize their approaches over the next few centuries.

## Imperial state period (1700-1945)

During this period, imperialism and capitalist industrialization combined to create more standardized approaches to genetic modification that sought to maximize economic productivity from animal bodies (Anderson, 2019; Kassen, 2020). Livestock breeders facilitated industrializing farms by seeking ways to alter farm animals to become more useful for intensive production (Fitzgerald, 2008). Just as factories resulted in product standardization, animal bodies became more specialized and uniform, often to better serve a single purpose (e.g., for meat, milk, hide, or fleece; Schrepfer and Scranton, 2004; Pawley, 2016). Breeders focused on selecting for production traits, such as maximizing weight gain which reduced time to slaughter, thus serving economic goals. English tenant farmer Robert Bakewell (1725-1795) is often credited with developing the methods for breed improvement (Woods, 2017b). Bakewell used in-breeding, or mating closely related animals, for greater consistency of type in his pursuit of "improved" breeds. By the nineteenth century, intellectual property in living things—namely stud animals—was protected through breeding associations and registered pedigrees (Kevles, 2007). The ability to protect and promote these breeds was facilitated by growth in urban centers connected by railroad networks, enabling the formation of national markets (Matz, 2011a). A clear example of this occurred in 1806 in Switzerland where the Council of Bern created local stud books and organized cattle exhibitions. At national shows, breeders developed shared definitions for what made one group of animals distinct from another. These ideals could then become further standardized by codifying them in pedigrees; in 1874, Swiss breeders created the first herd book *Schweizer Braunvieh Rasse* (Swiss Brown Race) to lay out criteria for the pursuit of an archetype (Orland, 2004).

Imperial states reinforced the market expansion of improved livestock (Mishra, 2012; Fischer, 2015; Kirchberger, 2020). For beef cattle in the Americas, an oligopoly of US-based meatpackers drove breed selection from the Spanish-introduced Longhorns that were prevalent in the 1600s toward British-bred Herefords by the 1870s (Del Rosario García Huerta and Ruiz Gómez, 2017). Longhorn cattle, first joining conquistadors on expeditions from the Iberian Peninsula, underwent a process of feralization over the following 80–200 generations as Spanish imperial administrators left these animals to fend for themselves on the open range from Mexico to the Río de la Plata until they were rounded back up for slaughter (Zarrilli, 2001; García Garagarza, 2013; Specht, 2016; LeCain, 2017). Both the gauchos of the Argentine pampas and cowboys of the Canadian prairies came to rely on the Spanish Longhorn, a hardy and independent breed that could defend itself with its sharp, scimitar-like horns from predators like jaguars or wolves and withstand being driven long distances on horseback to market (Elofson, 2004; Hernández, 2001; Pelozatto Reilly, 2016). But as Specht (2020) has revealed, Chicago's Beef Trust—dominated by a small group of firms like Armor, Swift, and Morris—wanted animals that gained weight quickly and held fatty flesh; in contrast, Longhorns, when butchered, were known for lean and stringy meat. Chicago's Beef Trust decided to preferentially choose Hereford cattle. The resulting market force led to near universal adoption of the Hereford breed, achieved by exporting bulls from Britain to the North American West and the South American countries of Argentina and Uruguay, where Chicago's Beef Trust owned subsidiaries (Grundy, 2002). This example illustrates how larger structural forces, like economic centralization under capitalism, influenced breeding decisions.

This period also saw the rise of public institutions and campaigns against animal cruelty that laid the groundwork for resistance to certain agricultural interventions. Brutality toward animals going to market was one such example that spurred public concern for more humane treatment. In 1824, the Royal Society for the Prevention of Cruelty to Animals (RSPCA) formed to enforce a new law in Britain that fined drovers and butchers for flagrant abuses to livestock (Li, 2000). As Donald (2019) has reported, over 70% of RSPCA membership by the late nineteenth century was women—reflecting an empathy developed for sentient creatures who also suffered under male domination. For instance, RSPCA member Frances Maria Thompson was distraught after seeing cattle and sheep driven to the London's Smithfield market in a "pitiable state" (Donald, 2019, p. 77). Gendered forms of animal protection also sprung up elsewhere in the British Empire, including in New South Wales which served as a major source of live animal exports to South Africa and India. Critics spoke about the harsh conditions for livestock—overcrowding below the ship's deck and a lack of water—on long oceanic voyages (Cushing, 2018). Some commercial freighters responded by developing better-equipped vessels; the *Mary Mildred* featured two hemp ropes on the top deck so cattle could walk around and have fresh air, plus moveable troughs for drinking. New technologies helped to assuage instead of abolish unsettling practices (for anticruelty legislation in the Russian Empire, see Nelson, 2010).

With live animal trade, the increased risk of epizootics crossing borders encouraged state veterinary services to control diseases through quarantines, compulsory slaughters, and inoculations (Appuhn, 2010; Brown and Gilfoyle, 2010; Knab, 2011; Uribe Mendoza, 2015; Ford, 2018). In 1914, when 20,000 cattle died from a rinderpest outbreak in Manchuria, Japanese veterinarians blamed the "callousness of the Chinese" for infections (Perrins, 2010, p. 158). In response, the Japanese-owned South Manchuria Railway established the Cattle Disease Research Institute, which implemented a mandatory immunization program of Chinese herds through mobile veterinary corps. Like Japanese veterinarians in East Asia, US veterinarians denigrated Mexicans through the animals they handled. In 1911, the Bureau of Animal Industry (BIA) constructed the first federally funded fence along the US-Mexico divide to limit the spread of the tick-borne cattle illness called Texas fever (Mendoza, 2018). Restricting the ability of "diseased Mexican cattle" to freely cross the border allowed BIA officials to inspect herds at ports-of-entry and, if needed, direct them to dipping stations (Lopes and Riguzzi, 2012). To avoid the challenges associated with live animal quarantine, Leibig's Extract of Meat Company in German South West Africa (modern-day Namibia) began exporting beef extract and cubes in 1906 made from "scrub" Zebu cattle (Sunseri, 2021). Veterinary knowledge about animals served to ameliorate perceived and real challenges that came with the imperial expansion of animals (Krätli, 2010; Skabelund, 2013; Brown, 2016; Ford, 2018; Conz, 2020; Wedekind, 2021).

Social hierarchies created to justify empires profoundly influenced animal husbandry (Thurtle, 2002; Tyrrell, 2015; Zelinger, 2019). The importation of foreign beef cattle to Brazil provides an example of how race and xenophobia affected breeding practices. After slavery was abolished in Brazil in 1888, the national government—controlled by descendants of Portuguese settlers—initiated a policy of *branqueamento*, or "whitening", among the majority African and Amerindian population (Agier, 1995). Just as state officials encouraged human immigration from Europe to "improve the race", cattle breeders imported Herefords, Shorthorns, and other purebred European stock to cross with their native "creole" herds. However, as Wilcox (2017) has noted, cattle improvement schemes were limited by the realities of tropical ranching in Latin America. Instead of choosing temperate breeds, ranchers in the Brazilian state of Mato Grosso brought in humped Zebu bulls from India. Ranchers in tropical Brazil and Colombia observed advantages with Zebus given the hotter climates; their lighter and short haired hides were better adapted to warm temperatures (Flórez-Malagón et al., 2008; Van Ausdal, 2012). Racialized thinking impeded acceptance, as exemplified by nationalist scientists like Assis Brasil and Eduardo Cotrim who disparaged the Indian breed as an "Asiatic plague" and "Hindu idol." Nevertheless, Zebu crosses prevailed, becoming the standard for Brazilian stock by the mid-twentieth century. In this case, racial categories and nationalist pride initially hindered the adoption of better-adapted cattle breeds (for a related discussion on the whitening campaign in southern Rhodesia, see Hove and Swart, 2016).

Class tensions and gender norms also shaped livestock breeding. If inbreeding methods meant "like begets like," then nobility in Britain insisted that they should only marry within the landowning class to preserve social purity (Milne, 2010). Because animal breeding involved controlling sexual reproduction to create offspring that served human ends, gendered ideas about what animal intercourse should, or should not, look like became part of the practice. Rosenberg (2016) has asserted that US agricultural experts used animal breeding to promote heteronormative sexuality in the rural countryside. In 1911 a pair of Colorado breeders wrote to *Berkshire World and Corn Belt Stockman's* columnist, A. J. Lovejoy, about a young boar that was more interested in mounting old boars than young sows. In response to the query, Lovejoy recommended the animal be castrated since he did not meet the cultural expectations of heterosexual reproduction. Similarly, Pawley (2018) has argued that livestock breeders in eighteenth-century Britain used extraordinary measures to overcome the seasonality of sheep intercourse based on popular understandings of women's sexuality. Commercial breeders made use of aphrodisiac herbs (i.e., turnips and saltwater grass) to prompt ewes' sexual desires outside of the "blossoming" period between July and September when they normally went into estrus. Again, livestock breeding intersected with preexisting categories of race, class, and gender (Terrisse, 2004; Ritvo, 2010; Swart, 2010b; Rosenberg, 2017, 2020).

Animals also subverted the hierarchies of empire. Saha (2016) has contended that cattle informed Burma's separation from British India. Burmese oxen had evolved to be a stockier build, given their use as draft animals, while Indian cows were a leaner, dairy type. Although British colonial officials sought to "improve" Burmese stock during the 1850s, they reversed course in the 1900s as rice hauling came to dominate commerce. When Burma split from British India in 1937, Burmese nationalists justified separation by pointing to different regional breeds. Like Burmese cattle, horses in southern Africa supported political autonomy. Swart (2010a) has argued that "Basotho ponies" became a distinctive type through the independence struggle of Basutoland (now Lesotho). Dutch Boers developed the utilitarian Cape horse, or "Caper", in southern Africa with stock imported from across the world (Bankoff et al., 2007). In 1806, when British imperial administrators had replaced the Dutch East Indies Company in managing the Cape Colony, English Thoroughbreds were the preferred breed for horse racing and status boasting. Indigenous peoples eventually described as "Sotho" had formed small chiefdoms to the north. King Moshoeshoe adopted horses of the colonists, using newfound equine mobility to consolidate black African groups under a centralized mountain stronghold, Thaba Bosiu, by the early nineteenth century (Swart, 2010a). The characteristics of the Basotho horse were the result of both natural and artificial section; the former led to compact animals with strong hooves (shaped by the steep, rugged terrain) and the latter led to animals suitable for agricultural labor and long endurance rides (shaped by selectively mating ponies with these traits). Horses and other domesticated animals could assist empires, but they also created political power for resisting colonialism (Melville, 1997; Crosby, 2004; Weisiger, 2011; Wiley, 2014).

Under imperial expansion, a tension emerged among breeders between either favoring a "universal" type that could thrive anywhere or adapting "native" stock to specific regions. For instance, breeders within the British Empire were concerned about whether the stock of their home islands would "acclimatize" when introduced to colonies and quasi-colonies in the Americas, Australia, New Zealand, and South Africa (Woods, 2017b). This concern, rooted in the seventeenth century dictum "every soil has its stock", was based on the notion that the character of place shaped the character of type, leading to the rise of a wide variety of local breeds. For example, imported Spanish Merinos to Australia and New Zealand—known for fleece—thrived in the colder high country while British Longwools—known for flesh—did better in warmer coastal areas (Peden, 2013). The introduction of refrigerated steamships enabled a transoceanic mutton trade in the late nineteenth century (Woods R. J. H., 2012; Woods, 2015). In response, New Zealand farmers crossed Merinos and Longwools to create an all-purpose breed, the Corriedale, that was better able to cope with a range of island conditions. Woods (2017b) has argued the creation of this "native" sheep distanced breeders from their colonial past; breeding sought to resolve contradictions that came with animals of empire (Anderson, 2004; Saraiva, 2016). The 250 years of imperial expansion created institutions, hierarchies, attitudes, and tensions that affect people, animals, and their interactions up to today.

## Welfare state period (1945-present)

After World War II, empires and nation-states pursued agricultural intensification for food security—and thus political legitimacy (Schneider, 2018). While 1945–1989 is often seen through the lens of Cold War competition between two superpowers with opposing ideologies, animal history tells a story of surprising global convergence. The recent book titles of *Communist Pigs* (2020), *Capitalist Pigs* (2019), and *Fascist Pigs* (2016) are telling for their ideological breadth. As Fleischman (2020) has contended, pigs reared on opposite sides of the world, in East Germany and Iowa, were nearly identical during the 1970s given the global consensus around the importance of producing cheap meat. Although different mechanisms were used to achieve this goal, the German Democratic Republic (GDR) used Stasi agents to promote land collectivization while the US Department of Agriculture relied on debt to force the agribusiness mantra of "get big or get out," both governments pushed farm consolidation. After the 1948 fallout between Josef Stalin and Yugoslav leader Josip Broz Tito, the Socialist Federation of Yugoslavia became a key player in linking communist and capitalist blocs. In 1970, Yugoslavia delivered hundreds of breeding boars to East Germany, which enabled pig breeders to preferentially use hybrids as they delivered improved weight gain and had a high tolerance for disease resistance when reared in confined spaces. The GDR was not alone in this breeding approach: by 1978, more than 80% of pigs in East Germany and 90% in the United States were hybrids. Despite the Berlin Wall marking a divide between market capitalism and state communism, Settele (2020) observed that agricultural production in the "two Germanys" was more similar than different. Feeding citizens through the mass production of animals worked to sway or solidify public attitudes about the different political regimes (Cullather, 2010; Smith, 2014; Schmalzer, 2016).

A useful illustration about how agricultural intensification transcended political ideologies is the collaboration between Canada and Cuba. Funes-Monzote and Palmer (2020) have argued that Cold War geopolitics forced Cuba to become more self-sufficient in food production. After the 1959 Revolution, Fidel Castro sought to reduce Cuban reliance on US imports, setting the goal that each Cuban child should have access to a liter of nationally-produced milk per day. When the US government authorized an economic embargo on the country in 1961, Cuba turned to Canada for help with breeding stock. French agronomist and adviser Julien Coléou recommended crossing Cuban cows with Holsteins for improved milk production, opening the door for exporting 20,000 Canadian Holsteins to Cuba and hence transforming the predominantly

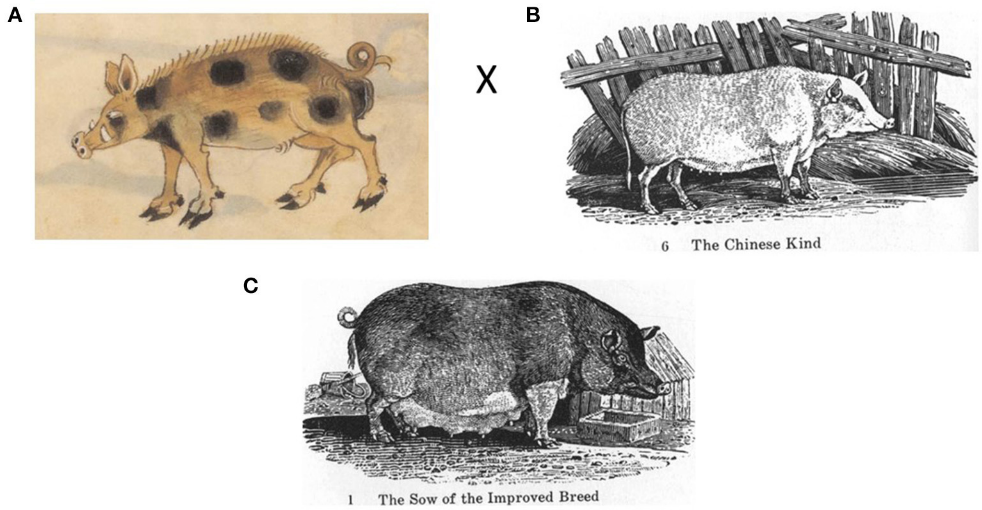


FIGURE 3
Porcine typologies—**(A)** the "pannage pig" of medieval Europe; **(B)** the "sty pig" of medieval China, and **(C)** the "capitalist pig" of improved breeds—illustrated the shift from unconscious selection to methodical selection in animal breeding. Image Credits: The British Library Board: Shelfmark/Page: Add. 42130, f.19v, used with permission. The Memorial Edition of Thomas Bewick's Works, vol III: A General History of Quadrupeds (Newcastle-upon-Tyne: Bernard Quatich, 1885). Courtesy of Oberlin College Library.

Zebu herds to hybrid stock. Cuban veterinarians, some of whom trained in Canada, opened artificial insemination (AI) centers to support this transition (Funes-Monzote, 2016). Cuba's dairy production reached 1.1 billion liters of fluid milk annually between 1981 and 1989, making the island nation the sixth largest producer in Latin America. Castro even claimed a Canadian Holstein stud bull, Rosafe Signet, as a revolutionary hero after his offspring, Ubre Blanca (White Udder), broke the world record for total milk yield, previously held by an American cow (see Figure 4). On a 1976 visit to Cuba, Prime Minister Pierre Trudeau remarked that "creating new breeds of cattle" was a mutual interest "despite the differences between a Latin American tropical country and a northern continental nation of harsh climate" (Funes-Monzote and Palmer, 2020, p. 147). This example illustrates how nation-states can converge in their desire to shape animal bodies for food security.

During this period, governments increasingly turned to biotechnologies for mediating livestock selection (Wilmot, 2007). AI, a reproductive technology that circumvented sexual intercourse by introducing sperm to a cervix manually, was implemented as a "public service" in the dairy industry to ease breeders' pushback for disrupting their occupational identity (Derry, 2015). The UK government alleviated domestic concerns by instituting national AI centers that would combat wartime food rationing by rationalizing milk production. In 1951, 20% of cows in England and Wales were impregnated by AI; by 1958, that figure rose to 58% (Wilmot, 2007). In the Netherlands, breeders vowed not to use Holstein semen for nationalistic and cultural reasons: they wanted to protect their renowned

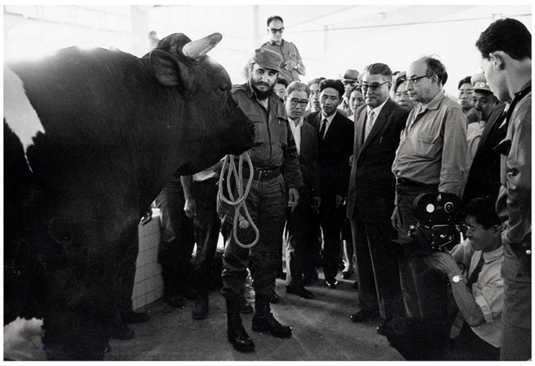

FIGURE 4
Fidel Castro with imported Holstein bull, Rosafe Signet, 1967. The Cuban-Canadian connection in dairy production exemplified how nation-states across the ideological spectrum converged on shaping animal bodies for food security. Photograph from Keystone Press/Alamy Stock Photo. Used with permission.

Friesian breed from North American bulls (Theunissen, 2008). At mid-century, Dutch farmers favored selecting animals on physical appearance too, while the North American industry had shifted to a more quantitative approach. The Dutch perspective is summarized in the words of one breeder who stated: "That's all very well, but a computer can't look at my cows" (Theunissen, 2012, p. 295). Opinion began to shift after the U.N.'s Food and Agriculture Organization sponsored experiments during the mid-1970s, conducted by Maria Stolzman in Poland, using Holstein bulls from Canada, United States, New Zealand, and Israel, and proving that the daughters of these sires had milk yields higher than those of their Friesian counterparts. The "Holsteinization" of Dutch herds eventually won out and frozen sperm insemination rates in the Netherlands rose from 3.5% in 1968 to 72.2% by 1975 (Theunissen, 2020). As the UK and Dutch examples demonstrate, how governments subsidized the implementation of biotechnologies like AI mattered in their adoption.

Scientific authority over livestock practices expanded as laboratories became key players in the breeding technology domain. Pig farmers in the United Kingdom did not use AI until the 1970s due to fears of disease risk from technicians being the vehicle for introducing new bacteria to pigs in indoor facilities (Brassley, 2007). However, Dr. Christopher Polge of Cambridge's Animal Research Station, in collaboration with the Milk and Livestock Commission (MLC), developed "semen extenders" increasing the longevity of fresh sperm. This new preservation method, when combined with mail service and the MLC agents teaching farmers how to inseminate pigs as part of their extension activities, resulted in the rapid adoption of AI (Brassley, 2007). New technologies still could unsettle traditional boundaries; Franklin (2007) conveyed that Dolly the Sheep, the first mammal to be cloned from adult genetic material, caused public stir because scientists redefined how sexual reproduction was conventionally understood. As Margaret Thatcher's neoliberal government sought to replace public expenditures with private contracts at universities, Scotland's Roslin Institute received sponsorship by PPL Therapeutics for the technique's potential to extract valuable human enzymes (García-Sancho, 2015). This industry partnership enabled Roslin's researchers to demonstrate that viable livestock could be developed from cells in a petri dish (Franklin, 2007).

Critiques of agricultural intensification emerged inside and outside of food systems. Just as the aftermath of World War II was a turning point for expanded welfare states to meet the basic needs of people (e.g., policies for universal healthcare, social housing, etc.; Castles et al., 2010), the period was also transformative for thinking more expansively about the care of animals (Woods A., 2012). In dairy production, wartime labor shortages in Europe and North America led to the adoption of milking machines (Bieleman, 2005), and although milk output increased, so did udder infections. To help control this increased risk of disease, antibiotic drugs were increasingly used to keep dairy yields high and mastitis rates low (Woods, 2007; Smith-Howard, 2017a). Some US dairy farmers, as early as the 1960s, rejected the use of antibiotics and adopted organic methods despite the lack of financial premiums for doing so (Saucier and Parsons, 2014). For example, one farmer (Kevin Engelbert) explained that even though his father had been using antibiotic treatments weekly to keep mastitis at bay on his upstate New York herd, he decided to stop "pushing the cows", arguing that his approach improved animal health (Saucier and Parsons, 2014). Increased acceptance of organic milk as healthier than conventional milk took place in the 1990s, driven in part by concerns associated with the use of recombinant bovine somatotropin (rBST) (Smith-Howard, 2017b).

As an outsider, Ruth Harrison's 1964 book *Animal Machines*, which criticized the adoption of battery cages in poultry egg production among other farm practices, stirred competing definitions of what constituted animal welfare (Sayer, 2013). After a Harrison-inspired petition asking for "the end of factory farms" was sent to the UK's Ministry of Agriculture, Fisheries, and Food with 250,000 signatures, Parliament established a special committee, chaired by MP Francis Brambell, charged with investigating the treatment of farm animals. In 1965, the Brambell Report recommended that livestock be provided basic rights, coined the "Five Freedoms", including freedom from hunger and thirst, freedom from injury and disease, and freedom to express normal behaviors. Important though it was, the report left room for different stakeholders to emphasize different elements of what they considered vital to the animal. For instance, large egg producers defended battery cages, stating the technology improved animal welfare by limiting the spread of disease (freedom of disease), while animal activists declared they did not, and raised concerns related to the bird's restriction of movement (freedom to express natural behaviors) (Sayer, 2013). Animal activists from the 1960s onwards have increasingly voiced concerns on how livestock are raised, processed, and marketed (Howkins and Merricks, 2000; Villanueva, 2017).

Regulatory agencies, which grew in size and capacity, tried to balance the conflicting values between states and citizens concerning animal agriculture. In the 1950s, US pharmaceutical companies marketed the synthetic hormone diethylstilboestrol (DES), which was first approved for prenatal care in pregnant women, as a feed additive for beef cattle to gain weight more quickly (Langston, 2010). Despite growing evidence that DES exposure led to cancer, the Food and Drug Administration (FDA) allowed the chemical to remain in livestock production so long as no detectable residues were found in the meat itself. The US Department of Agriculture increased its testing population from 192 to 6,000 head of cattle in 1971, reporting no residues but withholding 10 cases of extremely high levels (Langston, 2010). After congressional hearings, the FDA was forced in 1972 to phase out DES as a feed additive based on the risks to human health. Like growth hormones, Woods (2022) has argued that vaccine development for bovine viral diarrhea (BVD) was motivated by state interests pivoting around World War II: national security, agricultural policies, and technological fixes. Under a joint US-Canada program initially charged with defending North America against the potential use of rinderpest as a biological weapon, New York State veterinarians first identified BVD in 1946 as a transmissible disease in cattle herds. This need for vaccines gained traction when agricultural policies encouraged intensification, increasing herd sizes and stock densities, and farmers began speaking of "shipping fever" and "feedlot disease" in their herds (Woods, 2022). Despite growing public concerns around animal welfare, regulatory states funded and promoted technological fixes to sustain agricultural intensification rather than more extensive approaches.

## Discussion

This historical synthesis has found three pertinent historical lessons to inform contemporary debates about gene editing farm animals.

### Selection pressures vary with time

Our review has shown how selection pressures on farm animals were quite broad during the Agro-Pastoral Period (reflecting the range of uses from ceremonial purposes to labor, transportation to food), narrowed during the Imperial State Period (with breeds more specialized around a single function like maximizing meat, milk, or fleece), and broadened again during the Welfare State Period (based on a range of values around animal welfare and sustainability). Our review has also identified a growing disconnect during the most recent period between states that greatly valued agricultural intensification for food security (Saraiva, 2016; Schmalzer, 2016; Anderson, 2019; Fleischman, 2020) and their citizenry who valued a range of other concerns such as animal welfare and environmental impact (Saucier and Parsons, 2014; Villanueva, 2017). These findings suggest that gene editing farm animals will more likely be accepted if the emerging biotechnology aligns with societal concerns over state desires, as well as a broad over narrow set of values. This finding may partly explain why contemporary surveys in Brazil (Yunes et al., 2021), Norway (Bratlie et al., 2020), and the United Kingdom (Nuffield Council on Bioethics, 2021) have all demonstrated that ordinary people are most open to gene editing when they believe its applications will benefit some form of social good, such as animal welfare, sustainability, or food justice.

The strong link to enhanced production traits in the Imperial State Period reveals another historical precedent likely to influence gene editing use. Our review provides evidence that uneven power relations between those who controlled "improved" breeds and those who did not, generated resistance to these animals of empire (e.g., Swart, 2010b; Saha, 2016; Woods, 2017b). It will likely continue to be a source of conflict as most patents for gene-edited animals are held by private companies in the global North (Then, 2016). Profit motives have influenced the selection of production traits since the Imperial State Period, and people have disputed this emphasis since the Welfare State Period (Saucier and Parsons, 2014; Sayer, 2013; Smith-Howard, 2017b). Given those contentions, we should anticipate that biotechnologies seen to primarily provide production benefits to private actors, such as gene editing for the double muscle trait (more meat on the animal) or docility trait (less stress hormones during slaughtering), will generally have the lowest public approval (Bratlie et al., 2020; Ankeny et al., 2021; Naab et al., 2021; Busch et al., 2022). Animal history matters in these debates because historical approaches can help identify power structures in the past for understanding current (and future) selection pressures.

### What was old is new again

Purveyors of past biotechnologies have routinely stressed their newness to attract investment capital (Franklin, 2007; Pawley, 2020) while at the same time emphasizing their oldness to assuage public concerns (Center for Food Integrity, 2021). Historical knowledge can establish what represents a rupture from the past and what does not. Consider the practice of dehorning cattle. Prior to this practice, overcrowding at slaughterhouses during the late nineteenth century led to cattle goring each other; to remediate these injuries beef processors started removing the horns—first in Ireland (1870), then in the United States (1883) and Canada (1888) (Derry, 2015). After the RSPCA successfully lobbied British Parliament that dehorning inflicted unnecessary pain on animals, a new law in 1889 banned this practice. Concurrently, breeders suggested cattle could be "dehorned naturally" by crossing with polled Angus or Galloway breeds (Derry, 2015). In 1890, Canadian authorities arrested Ontario farmer Chauncy Smith for the then illegal act of dehorning. When this legal challenge went to the courts, a resulting commission—made up of veterinarians and farmers—recommended that the horns simply be removed during calfhood (disbudding) and using painkillers for more humane treatment. The contemporary proposal of introducing the polled trait to horned cattle breeds through gene editing can be seen as a new method to address an old issue which has been contested over time (Hennig, 2018).

The coevolutionary history of cattle and people, however, suggests there might come a time when horns are a useful or desirable trait again. Under open-range conditions of the Americas between the sixteenth and nineteenth centuries, Longhorns were valuable as they could defend themselves from wolves and jaguars when their human handlers were absent (Pelozatto Reilly, 2016; Specht, 2016). The introduction of barbed wire fences and predator eradication campaigns finally made these horns less important (Elofson, 2004; Netz, 2004). But if consumer demand for "grass-finished beef" leads to animals reared more extensively (Rowntree et al., 2016), and if "rewilding" efforts restore native carnivores to rural landscapes (Wolf and Ripple, 2018), horned cattle varieties could have utility once more. This thought-experiment highlights the reciprocal relationship between biology and culture that influence livestock traits (Derry, 2018). Historical approaches show that the future is open to many possibilities, countering the narrative frame of technological determinism that portrays the adoption of gene editing techniques or other biotechnologies as inevitable (Devolder, 2021).

## Biology, culture, and equity

Our review has also demonstrated that the eugenics movement, conventionally restricted to the early twentieth century, was not an anomaly in time as racialized thinking developed through animal breeding over the Imperial State Period (Milne, 2010; Wilcox, 2017; Pawley, 2018; Zelinger, 2019). Examining past injustices in animal agriculture, and the colonial systems that underpinned it, can offer a knowledge base for informing culturally responsive approaches to gene editing tools (Feliú-Mójer, 2020). For example, Hudson et al. (2019) found that the Māori people of New Zealand were not opposed to gene editing outright but did express strong views about the biotechnology if *taonga* (precious) species, or plants and animals protected by the 1840 Treaty of Waitangi, were involved.

Inserting the slick gene into cattle could be viewed as an important climate adaptation tool, helping livestock to adjust to warming temperatures. However, given that approaches to acclimatizing breeds in the past were bound up in empire (Peden, 2013; Wilcox, 2017; Woods, 2017b), gene editing for bovine thermoregulation might be seen in another cultural context as further expanding the hoofprint of where cattle can be raised, including farther into the Indigenous-held territories of the Amazon (Skidmore et al., 2021). Tanner and Walch-Solimena (2019) observed that "there are considerable cultural differences, rooted in historical experience, in the approach to the risks and opportunities associated with new biotechnologies" (p. 25). Animal history helps researchers and policymakers to better understand and respect the cultural differences, rooted in historical experience, in which they research and govern.

One current debate about gene editing farm animals is whether the process or its products should fall under pre-existing regulations (Charpentier et al., 2019; Cotter et al., 2020). For example, the US Food and Drug Administration very recently made a "low-risk determination" on introducing the slick trait in cattle through CRISPR-Cas9, based on its natural appearance as a genetic mutation in some breeds (Food Drug Administration, 2022). However, regulatory processes tend to focus discussions to technical concerns about food safety (Langston, 2010; Woods, 2022) and the "safe enough" narrative allows science and technology to dictate governance and ethics, rather than the other way around (Woopen et al., 2021). Who gets to define value in gene editing depends on which actors have power. In animal agriculture, power has historically been held by corporate meatpackers (Amaral, 1998; Specht, 2020; Sunseri, 2021), state veterinary services (Krätli, 2010; Brown, 2016; Ford, 2018; Conz, 2020; Wedekind, 2021), and large breeding associations (Orland, 2004; Kevles, 2007; Matz, 2011b). Given that technical authority in breeding has shifted to smaller numbers of actors over the last 300 years (Brassley, 2007; García-Sancho, 2015; Theunissen, 2020), public trust in gene editing could be built through more equitable practices that incorporate concerns of historically marginalized communities, such as women (Donald, 2019), and those who have experienced colonization (Weisiger, 2011; Breen, 2013).

## Limitations

Our review was limited in its geographic asymmetry and the livestock species considered. Studies about animals in the global North, particularly the United States ($n = 18$) and Great Britain ($n = 13$), were overrepresented in this review, indicating a need for more animal histories based in the global South. Moreover, studies about domesticated farm animals that originated on the Eurasian continent were disproportionate. The historical examination of other animals, such as the llama, turkey, Muscovy duck, and reindeer, could yield valuable insights about human-animal relationships in agriculture (Wakild, 2021), particularly of Indigenous practices.

# Conclusion

Animal history is a new and burgeoning field of historical inquiry that can help to answer questions relevant to contemporary issues such as gene editing farm animals. Unlike statistical modelers who attempt to offer predictions about the future (Aykut et al., 2019), historians deliver lessons by way of parables (Glassberg, 2014). Historical approaches offer a form of "anticipatory knowledge" because the past creates legacies that influence the present and reveal multiple scenarios for the future (Simon et al., 2021). By recounting past breeding practices, history prepares stakeholders for how new biotechnologies like gene editing might disrupt or adjust to older patterns in animal husbandry. For instance, AI in cows unsettled the Dutch dairy culture by selecting animals with formulas over features, and AI in pigs adapted to the preference among British farmers to breed their own animals. In bioethical decision-making, the quandary of "what should we do?" has a wider perspective for answers if preceded by reflecting on the historical question of "how did we get here?" (Neustadt and May, 1986; Oreskes and Conway, 2014). Historical approaches can be anticipatory because varied experiences in the past help to shape our collective expectations for the present and future. Animal history acts to temper both unbridled faith in human control over animals and the resolute belief that animal bodies are unchanged or natural. Because history captures longer time trends instead of brief snapshots, the discipline counteracts short-sighted, present-oriented thinking that often guides policy debates (Guldi and Armitage, 2014). Historical methods are about identifying patterns and processes in the past so that stakeholders can learn which guiding logics to keep and which to discard. Like collaborations between historians and ecologists (Higgs et al., 2014), animal historians and animal-focused scientists have much to gain from increased dialogue.

## Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

## Author contributions

WW identified English- and Spanish-language sources for the review. HT identified those in German. WW and HT independently read all included records, responsible for the synthesis found in the Section Results, and as well as the interpretation in the Section Discussion. MvK, KK, and DW provided input on the research question and study design, as well as provided comments, and suggestions on earlier drafts of the paper. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Publisher's note



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