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The introduction of Mendelism in Iceland

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SUMMARY
This paper analyzes the development of the theoretical rules at the basis of the breeding programs in Iceland from 1900 until the 1930s. This development was closely tied to the establishment of breeding societies in Iceland, and the introduction of a breeding method based on best yield calculations which was imported to Iceland from Denmark and England (optimization calculation in modern parlance). In the first decades of the 20th-century breeding was pre-Mendelian; the practitioners did not understand the heredity of characters as was made possible with Mendel's laws. In 1905 the first attempt was made at introducing Mendelism to Iceland with the publication of the book called *Heritability and Breeding* (*Ættgengi og Kynbætur*). It completely failed. A decade later a somewhat more successful attempt was made by the agronomist Páll Zóphóníasson. He tried to introduce the practical aspect of Mendelism to Icelandic farmers/breeders. He persisted in his efforts, but it was difficult to persuade them of the virtues of the Mendelian methodology. Zóphóníasson published the results of his own research based on Mendelian genetics in 1930 and 1934 which were noticed abroad, e.g., by the geneticists William E. Castle and Otto Lous Mohr. What characterizes this story is that Iceland neither had University based training or research in genetics, nor were there any institutions in that field. The history of animal genetics in Iceland in this period is the story of individuals trying to introduce novel ideas into a society where little had been thought about these matters.

Key words: animal breeding, history of genetics, Mendel, Mendelism, Páll Zóphóníasson, pure lines, Wilhelm Johannsen.

YFIRLIT
Páll Zóphóníasson og mendelsk erfðafræði í búfjárkynbótum á Íslandi

Í greininni er fjallað um fræðilegar reglur sem lagðar voru til grundvallar í kynbótaumræðunni á Íslandi á fyrstu áratugum 20. aldar, en sú umræða var nátengd stofnun fyrstu kynbótafélaganna. Tilkoma þeirra um síðustu aldamót markaði tímamót í íslenskum landbúnaði. Með þeim var í fyrsta sinn reynt að byggja upp almennan grundvöll fyrir skipulegar kynbætur á Íslandi. Notkun bestunaraðferða, og síðar mendelskrar erfðafræði, opnaði fyrir möguleika á mun markvissari kynbótum en áður höfðu þekkst hér á landi. Umbótasinnarnir lögðu áherslu á að kynbætur hefðu lítt verið stundaðar meðal íslenskra bænda og brýnna úrbóta væri því þörf, en þeir voru ekki samstiga í ráðleggingum sínum til bænda. Boðberar bestunaraðferðarinnar, búfræðingarnir Guðjón Guðmundsson og Hallgrímur Þorbergsson, vöruðu t.d. við of mikilli notkun skyldleikaræktar, aðhylltust erfðir áunninna eiginleika og töldu ekki mögulegt að sameina tvö eða fleiri góð einkenni í sama stofninum. Árið 1905 kom út bók danska plöntusjúkdómafræðingsins F. Kölpin Ravn *Ættgengi og kynbætur*, í íslenskri þýðingu Helga Jónssonar grasafræðings, þar sem margt af því sem Guðjón og Hallgrímur héldu fram var dregið í efa. Í þessari bók var erfðafræði Mendels, og notagildi hennar í kynbótum, í fyrsta sinn kynnt Íslendingum. Bókin vakti nánast enga athygli. Tíu árum seinna var gerð önnur tilraun til þess að vekja athygli á mendelskri erfðafræði meðal íslenskra bænda. Þar var að verki Páll Zóphóníasson, búfræðikandídat. Á árunum 1914–1934 fjallaði hann ítarlega um notagildi mendelskrar erfðafræði í kynbótum á búfénaði þar sem hann, í krafti erfðafræði Mendels, hafnaði erfðum áunninna eiginleika, lagði áherslu á notagildi skyldleikaræktar og að bændur gætu sameinað tvo eða fleiri eiginleika

í búfjárstofnum sínum. Páll byggði umfjöllun sína mest á erlendum ritum, en árið 1930 og 1934 birti hann niðurstöður eigin rannsókna í *Búnaðarritinu* og *Nordisk Jordbrugsforskning*. Vöktu niðurstöður rannsókna hans á gulri fitu í sauðfé, sem orsakast af víkjandi erfðavísi, athygli erlendra vísindamanna. Þar á meðal var bandaríski erfðafræðingurinn William E. Castle, einn frægasti erfðafræðingur 20. aldar, sem birti stutta grein um rannsóknir Páls í *Journal of Heredity* árið 1934. Íslenskir bændur virðast ekki hafa verið mjög móttækilegir fyrir boðskap Páls og er í greininni reynt að varpa ljósi á ástæður þess.

ESTABLISHMENT OF BREEDING SOCIETIES IN ICELAND

Systematic large-scale animal breeding in Iceland is a recent development. It dates back to the beginning of the 20th-century when farmers in certain rural districts joined forces and established breeding societies. The objective was to raise more productive livestock, e.g. cows with higher milk yield, which could also be used for breeding purposes. In the 18th and primarily the 19th-century isolated attempts had been made in this direction by importing sheep and even bulls.[1] These breeding efforts had a limited effect on the Icelandic livestock populations, especially sheep. Moreover the imported sheep sometimes brought diseases with them which had serious and lasting effects on sheep farming in Iceland.[2]

Farmers in Europe and America started establishing breeding societies and groups to register pedigrees in the 19th-century. In Denmark the first cattle breeding societies were established around 1850, but Icelandic farmers had to wait until 1900 for a written account of the Danish breeding effort.[3] The following year the Icelandic Agricultural Society (Búnaðarfélag Íslands, established 1837) supported a young consultant, Guðjón Guðmundsson (1872–1908), to travel to England and study cattle breeding practices and to investigate the market prospects for Icelandic agricultural products in England. In 1897 the import of living Icelandic sheep to England had been seriously restricted and the price for salted lamb plummeted causing a crisis in Icelandic agriculture. This fact together with growing urbanization in Iceland spurred interest in cattle breeding resulting in Guðmundsson's journey.[4] Upon his return he began laying the ground for establishing the first cattle breeding societies in Iceland, by setting down rules of operation for them.[5] The Icelandic Agricultural Society started for the first time to work systematically on livestock breeding when Guðmundsson was hired, in 1902, as its first breeding consultant. Prior to his arrival Icelandic farmers had limited knowledge of systematic breeding practices and "record keeping barely existed".[6]

The purpose of the cattle breeding societies was to increase the productivity of dairy cows in each district, by raising stock, which yielded most milk, at least cost. The fat content of the milk was also supposed to be raised. Their aim was to implement a breeding program on farms directed at increasing milk productivity by using a breeding method based on best yield calculation. By keeping records of both the amounts of fodder each cow ingested and the milk it produced, cows giving most milk for

1 Stefánsson 1910 and Þorbergsson 1929. For an account of animal and plant breeding practices in Europe in the 18th-century and the former part of the 19th see Orel 1996, 10–35.

2 *Alþingi* 1931. Enclosure with parliamentary bill 21 which authorized importation of sheep.

3 Cooke 1997, 64; Sigurðsson 1900. Iceland was a Danish dependency at that time.

4 Jóhannesson 1937, 277–278; Bjarnason 1905, 181–185; Erlingsson 1998b, 68–73.

5 Guðmundsson 1902.

6 Þórarinsson *et al.* 1988, 602.

least cost and possessing the required fat content could be chosen for further breeding. Individual farmers were encouraged to keep such records and an inspector was supposed to be hired by each society to supervise the record keeping.[7] Genealogical tables were also supposed to be kept whereby, it was hoped, the efficiency of this breeding method could be considerably increased. With the aid of these tables the breeder should be able to determine the offspring of each cow, and choose calves for further breeding. Guðmundsson emphasized this with an example of two cows, one yielded 3548 liters of milk in one year, the other 1680. The first one ate 3150 kilograms of fodder that year, the other 2478. Other expenses being equal and considering calves and cow manure he concluded that "according to these calculations the first cow gave 169.40 krónur in pure profit over that year, the other only 19.32 krónur."[8] Furthermore it was important to know the fat content of the milk because:

> *yielding a lot of fat milk from a relatively small amount of fodder is based*, like most other advantages or disadvantages in animals, on heredity. The easiest way to produce a good cow variety is *to use only those animals for breeding which possess the above mentioned qualities*... [It] is vital that the animals are sturdy and flawless, but this demands that the selection of the breeding animals, their upbringing, feeding, caring and shelter is in order.[9]

Like Guðmundsson pointed out, keeping records and breeding selectively was not enough! The living conditions of the animals also had to be improved. For many centuries livestock in Iceland had been kept outside most of the winter and those kept inside had not been fed much.[10] In the case of milk production a real increase first occurred in the 17th and 18th-century (see Figure 1). It is likely that by then the cows were being treated better, i.e. in food and shelter, for serious breeding effort were still in the distant future. The early 20th-century breeding consultants knew that a successful breeding program had to be accompanied with improved feeding and housing of the animals.[11]

The first cattle breeding societies were founded 1902–1903, but started serious work only in 1904–1905, in 1904 seven societies had been established.[12] In 1914 there were 24 societies operative and their breeding farms harbored 14% of the cattle population in Iceland.[13] Sheep farmers had also established similar societies, the first in 1898. But they were less successful than the cattle breeding societies. In 1919 only 7 breeding societies were opera-

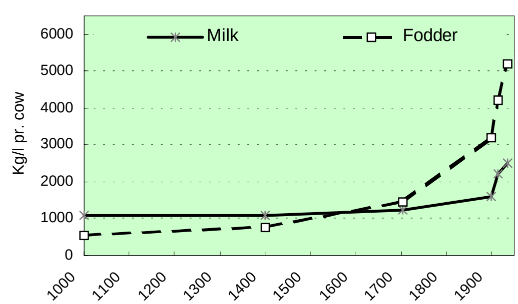

Figure 1. Development of milk production in Iceland from 1000–1934 in relation to fodder ingestion per individual.[14]

1. mynd. Samband mjólkurframleiðslu og fóðurnotkunar á hverja kú á Íslandi á tímabilinu 1000–1934.

7 Guðmundsson 1903, 135–139.

8 Guðmundsson 1903, 134.

9 *Ibid.*, 134. Emphasis in original.

10 Zóphóníasson 1914, 52–61. It contains an account of cattle farming from the 9th-century land was first settled to the first years of this century.

11 Þorbergsson 1906, 191–194; 1907, 95–100 & 1908, 315–319.

12 Guðmundsson 1904, 39.

13 Jóhannesson 1937, 308–309. Similar numbers from Denmark were 17% and from Norway 5%.

14 Sigðurðsson 1937, 315–316.

tive, but their number increased steadily the following years.[15] A striking measure of the success of the cattle breeding societies is that the average milk productivity per cow increased from 1600 liters to 2500 in the years 1900–1934 (see Figure 1). How much the best yield breeding method contributed to this dramatic increase is uncertain, since it coincided with a dramatic increase in the amount of fodder provided for each cow, from 3200 to 5200 kg in the years 1900–1934. It seems likely that this increase in fodder consumption, along with better shelters being provided for the cows,[16] explains a major portion of the increased milk production. This seeming fact does not, however, affect my overall aim, which is to analyze the theoretical rules Icelandic consultants emphasized in their writings about breeding. No matter how effective the breeding efforts were in the first decades of the 20th-century, this discussion has a value of its own. It gives an opportunity to monitor how a new idea was brought to Iceland and to analyze the rhetoric used to promote this idea, i.e. Mendelism. It should be noted that the rhetoric used in the promotion and demarcation of new knowledge often leads to an underestimation of the old practices, when the actors "consciously or otherwise, discursively construct working definitions of science that function, for example, to exclude various non- or pseudo-sciences so as to sustain their (perhaps well earned) position of epistemic authority …".[17] This should be kept in mind as this story progresses.

THE THEORETICAL BASIS OF ANIMAL BREEDING IN ICELAND

The pre-Mendelian tradition

1903–1913. The establishment of the breeding societies meant that farmers had to be instructed how to carry out their breeding efforts. In their writings, during the first decade of the 20th-century Guðmundsson and Hallgrímur Þorbergsson (1880–1961), another breeding consultant for the Icelandic Agricultural Society, emphasized the "scientific" fact that it was impossible to combine in a single animal (one variety) different qualities like good meat and wool production. The farmers were advised by Guðmundsson that: "While breeding sheep, for example, we may not try to produce a variety that is good for both milk, meat and wool production, for these qualities are more or less exclusive. The science and experience of the educated nations has a long time ago shown this to be true."[18] Based on this fact Guðmundsson and Þorbergsson discussed general breeding rules.

When farmers in Iceland chose breeding animals, they normally based their choice on the external appearances of the animals.[19] The efficiency of the breeding could be improved considerably by using simple best yield calculations, but even more by combining them with rules based on genealogy. Guðmundsson stated two rules based on this principle, which he called the two main breeding rules:

> (1) The breeding animals have to possess those qualities which the farmer wants their descendants to have.... (2) The breeding animal should be vigorously built and be descended from a vigorous stock, which is free of any hereditary flaws... These two main rules show us that a knowledge of the kinship of breeding animals is essential for all those who want to improve their stock, since genealogical records are all over considered instrumental in the improvement of livestock breeding.[20]

For these simple rules to be effective the farmer had to control the mating of the animals

15 Jónsson 1901; Guðmundsson 1903, 139–146; Jóhannesson 1937, 296–301.
16 Sigðurðsson 1937, 313–314.
17 Taylor 1996, 5.
18 Guðmundsson 1903, 127. See also Þorbergsson 1906, 184–185.
19 Þorbergsson 1906, 191.
20 Guðmundsson 1903, 127.

and keep pedigree records, which Icelandic farmers did not usually do.[21] These rules can be put into practice by using one of the three following breeding methods: "to choose the best individuals of the locally adapted stock, to blend unbred [animals] with bred ones, and to buy bred [animals] from abroad or from other regions and keep them unblended."[22] Þorbergsson admitted it was problematic to determine which of these methods was best. The first minimized the risk of infectious diseases, but as it was very time consuming it was only a realistic option for "calm" farmers who were conscious of what they wanted to accomplish with their breeding efforts. The second and the third methods, though useful per se, were barely applicable in Iceland in this period.

Regarding sheep Þorbergsson claimed there were no distinct sheep varieties in Iceland and that it had no breeding characteristics.[23] Hence it would be difficult to blend unbred sheep with bred ones in Iceland unless foreign varieties were imported.[24] Yet previous disasters that had resulted from the importation of sheep made Icelandic farmers reluctant to try this method.[25] The number of breeders who wanted to import sheep for breeding purposes as well as availing themselves of rules two and three increased in this period, until limited import was authorized in 1931 by a parliamentary act.[26] The 1933 importation of Karakul-sheep resulted in yet another disaster for Icelandic sheep farmers, the imported sheep brought with it the slow viral disease meadi-visna.[27]

A central issue in breeding was the acceptable level of inbreeding in the population. It was well known that inbreeding could have deleterious consequences, so the only reliable "rule" was not to mate closely related animals. This was the message Icelandic farmers got early in the 20th-century from the consultants Guðmundsson and Þorbergsson. The farmers were admonished that available evidence demonstrated that if this rule of thumb was violated "the descendants would often become infertile, weak, suffer from nervous diseases, become disfigured, the bones would soften and the yield of wool would deteriorate."[28] Still Guðmundsson and others knew that inbreeding could be used effectively if certain rules were followed.[29] Moreover, they knew that breeders in Europe and the United States, by relying on these rules, had applied inbreeding successfully to create new varieties, and that this was based on the fact that inbreeding not only yields bad or unwanted features but also may bring forth desirable qualities. Yet they discouraged the use of inbreeding in Iceland because they were still locked up in the old tradition.

21 Þorbergsson 1907, 100; Zóphóníasson 1930a, 62–63; Þórarinsson *et al*. 1988, 602. Fitzgerald (1990, 10–22) and Cooke (1997, 70–71) give analogous examples form corn breeding practices in Illinois and from poultry breeding at the Maine Agricultural Experiment Station, respectively, at the turn of the century.

22 Þorbergsson 1906, 186.

23 *Ibid.*, 196. "no breeding characteristics" meaning that the Icelandic sheep population was too variable to speak of any distinctive characters.

24 Nevertheless attempts were made at improving the sheep population in certain districts by breeding them with "varieties" from other districts. See Guðmundsson 1911.

25 Einarsson & Einarsson 1916; Þorbergsson 1929, 30–31. In 1762 and 1856 the parasitic ant *Psoroptes ovis*, which causes dermatological disease in sheep, was brought to Iceland with imported sheep.

26 Þorbergsson 1909; Þorbergsson 1917; Lotz 1932; Zóphóníasson 1932ab; Alþingi 1931, parliamentary bill nr 21.

27 Þórarinsson *et al.* 1988, 596–601.

28 Þorbergsson 1906, 187–188. The editors added in a footnote that these conditions were not caused by the fact that the individuals were related but because they possessed some weaknesses.

29 Guðmundsson 1903, 131; Stefánsson 1905, 136.

The Mendelian tradition

1905–1914. Mendelism was introduced to Iceland in 1905, in a book called *Heritability and Breeding* (*Ættgengi og kynbætur*) published by the Icelandic Literary Society. It was a translation of *Forplantning og Arvelighed* written by the Danish plant pathologist Frederik Kölpin Ravn (1875–1920) in 1904. Ravn summed up for the general public, "those issues, which concern the heritability of the characters from parent to offspring….".[30] He discussed the difference between sexual and asexual reproduction; quantitative characters and their distribution referring to the British naturalist Francis Galton (1822–1911) and his law of regression; the inheritance of acquired characters; origin of new species; and Mendel's law of heredity; Johannsen's pure-line theory and how inbreeding could be used positively in animal and plant breeding.

Ravn emphasized that inbreeding was not necessarily harmful. Research had shown that certain diseases could express themselves in the offsprings of closely related parents and stay in the family for generations, but the reverse was also known. To illustrate this Ravn mentioned a region in France where marriages between closely related individuals was customary. Nevertheless "these rural people are handsome and vigorously built and the above mentioned illnesses [e.g. deafness and nervous diseases] have never appeared in this region."[31] The breeding of domestic animals demonstrated this even better; special varieties had been produced based on inbreeding and experiment with rats had shown that intensive inbreeding for 18–20 generations had no visible effects on the animals.

Discussing Mendel's laws, discovered by the Czech monk Gregor Mendel (1822–1884) in the 1860's, Ravn described his experiment with the varieties of *Pisum sativum*, which had either green or yellow seeds.[32] Ravn demonstrated that yellow is dominant versus green in the F_1 generation. In the F_2 generation the ratio between the yellow and green seeds is 3:1 and those individuals in F_2 or later generations, that do not breed true for either color will always have offsprings with the 3:1 ratio. Ravn did not explain how these ratios could be explained by the behavior of certain factors in the reproductive cells during their production, as Mendel and his successors had done.[33]

At the turn of the 20th-century Carl Correns (1864–1933) and William Bateson[34] (1861–1926) had demonstrated that not all traits are inherited in a dominant/recessive fashion. Some traits like the red and white flower varieties in the common bean plant (*Mirabilis jalapa*) are semi-dominant, i.e. the F_1 offsprings exhibit a mixture of the parental traits.[35] Ravn noted that black and white people had brown offsprings and that the offsprings of the red and white varieties of the common bean plant were pink. Mendel's law could explain the inheritance of some of these intermediate hybrids. Yet he did not distinguish between the simple Mendelian inheritance of the flower color and the much more complex inheritance of color in humans.

Finally, Ravn discussed the inheritance of two independent parental traits in their offsprings.[36] Yet he did not discuss how the 9:3:3:1 ratio resulted from combining two 3:1 ratios. Although Ravn's discussion of Mendelism left much to be desired, his conclusions concern-

30 Ravn 1905, 4.
31 *Ibid.*, 28.
32 Mendel [1865] 1958. In this English translation of Mendel's original paper this and his other hybridization experiments are described.
33 Ravn 1905, 58–61.
34 1900 and 1902, respectively. It was William Bateson who, in 1905, coined the term "genetics" (Darden 1977, 87).
35 Mayr 1982, 735.
36 Ravn 1905, 71–74.

ing the possible value of Mendelism for animal breeding were important. Ravn stated that if the character one wants to "fix" follows "Mendel's rule" it was conceivable that a variety could be produced, which had this character fixed, even when different varieties were crossed. The optimal results were to be expected if the character was recessive.

Previously Icelandic farmers had been told to avoid producing a variety with two desirable traits and inbreeding due to its deleterious side effects. But Mendelian genetics demonstrated the effectiveness of inbreeding and that different individual characters were sometimes inherited independently (independent assortment), hence it should be possible to produce varieties which had more than one desirable quality if each of them obeyed "Mendel's rule". Therefore Ravn's message could have undermined the writings of Icelandic breeding consultants, yet it fell on deaf ears. Ravn's book was rarely mentioned in the period 1905–1919 nor was the real thrust of the book understood. In 1907 Eggert Briem (1879–1939), an educated Icelandic farmer, claimed that "this field of study [Mendelian genetics] is of great interest to natural scientists and farmers."[37] Yet either he did not fully understand "this field of study" or he skipped the chapter on Mendelian genetics for he referred only to the section where Ravn discussed the difficulties 19th-century hybrid experimenters faced when trying to explain the heredity of parental character in the F_2 generation. He used this outdated information to advise farmers how to proceed with their breeding efforts. In retrospect, this is not surprising for Briem had very limited means to understand these novel ideas, coming from a country where systematic animal breeding had barely started. It is, though, interesting to compare Briem's remarks with what the British zoologist Walter E. Collinge had to say in 1907 about the application of Mendel's laws in animal breeding. Collinge, coming from a country where systematic breeding had a long history, observed that

> the application of Mendel's Law [] bids fair to revolutionize [animal breeding]. Hitherto the dominant factors in any particular animal or breed have, to a very large extent, been lost sight of. We have muddled horribly in the past. We have been looking after the "general purpose cow" instead of the production of first-rate dairy cattle and high grade grazing cattle. The horse-breeder and flock-master have trodden in the same path, forgetting that it is not sufficient that the latter should produce only a big sheep, with meat or high quality, and lose sight of the wool and the production of twins.[38]

Mendelism surfaced again when Páll Zóphóníasson (1886–1964), a leading Icelandic agronomist, wrote his first article in 1914 concerning Mendel's laws of inheritance and Johannsen's pure-line theory. He began working in agriculture in 1909 having finished his studies in agronomy in Denmark. He taught at the agricultural school at Hvanneyri in Borgarfjörður in the west of Iceland from 1909 to 1920 when he became headmaster of the agricultural school at Hólar in Hjaltadalur in the north of Iceland. He resigned this position in 1928 to become a breeding consultant for the Icelandic Agricultural Society. Furthermore, from 1934–1959 he was a Member of Parliament (Alþingi) for the Rural Alliance Party (Framsóknarflokkur), and from 1951–1958 he was the director of the Icelandic Agricultural Society (búnaðarmálastjóri).[39] In a series of additional articles he filled in the missing details in Ravn's discussion about Mendelism and cast it in a practical form. In 1919 Zóphóníasson noted that Ravn's book

> is the first, and until now nearly the only text, which has been written in Icelandic about the new heritability research. I find it appropriate

37 Briem 1907, 31.

38 Collinge 1907, 100.

39 See more detailed biographical notes in Steinþórsson 1965, 4–25.

to make some additions, mainly with livestock breeding in mind.[40]

1914–1934. In his 1914 article in *Búnaðarritið* Páll Zóphóníasson outlined the three stages of proper breeding programs. In the first stage the breeding animals were chosen with the aid of best yield calculations based on productivity reports; animals which had productivity well above the average were chosen. Nevertheless, if one looked closely at each animal thus selected the variability in the offspring became apparent. Some had above average productivity others below, but all would eventually revert back to the average (according to Galton's law of regression). He argued as follows:

> The direct descending lines are different, and the second stage of all breeding programs is to identify the best direct descending lines and breed them pure. The breeding societies are unable to achieve this goal unless pedigrree records are kept along with the productivity records... as a consequence of the difference between the direct descending lines it is possible to make all the [animals] as good as the average [animal] in the best descending line.[41]

In the second stage the breeder identifies "the best direct descending lines" and breeds "them pure". The third stage was based on exploiting the rare appearance of individuals, which excelled; so-called mutants. The new characters they possessed were usually "fixed in the animal in which it first appeared, so it can be used to produce a new variety."[42] The power of this breeding method had been illustrated in 1701 when a male lamb was born on a farm in North America with much shorter legs than other members of this variety. Subsequently this ram was used to produce Ancon, a short-legged sheep variety.[43] Zóphóníasson's scheme for breeding resembles Wilhelm Johannsen's (1857–1927) general views on selection and evolution.[44] Zóphóníasson's notion of "direct descending lines" is obviously derived from Johannsen's pure-line theory, which he developed after a series of selection experiments on self pollinating beans in 1900–1902.[45] But since animals do not self-reproduce it was far from obvious that the principles of Johannsen's pure-line theory could be applied to animal breeding, but as Ravn pointed out it was of vital importance to see if that was possible.[46] Ravn thought, "it was very likely that [the pure-line theory] could be applied to animals".[47] Zóphóníasson, being educated at the Agricultural College in Copenhagen where Ravn taught until 1905 and Johannsen from 1905, most likely brought the pure-line theory and Ravn's optimism home with him from Denmark.

Zóphóníasson claimed that cattle breeding in Iceland although in its initial stage was ready to enter the second stage. Breeding programs in the second stage aimed, as we have seen, at producing direct descending lines (Johannsen's pure-lines) and varieties which did better than the average individual. This could be accomplished by "getting populations with the character fixed, or populations, which either have the desired characters *as recessive*, or have them *as a pure break-up from those who are*

40 Zóphóníasson 1919, 59.
41 Zóphóníasson 1914, 84–85.
42 *Ibid.*, 85.
43 Þorbergsson 1915, 75–76.
44 Johannsen claimed that natural selection alone was ineffective in the creation of new species because of the tendency of the selected characters to revert to the ancestral state (Galton's law of regression). The only way new species could be created was through mutations. But natural selection still had a place in Johannsen's evolutionary theory, by acting as a sieve it would eliminate the unfit but not create anything new. In *Elemente der exakten Erblichkeitslehre* (1909) Johannsen defined the basic concepts of genetics: "gene", "genotype" and "phenotype". See Roll-Hansen 1978 & 1989.
45 Ravn 1905, 45–53; Erlingsson 1998b, 80–82; Roll-Hansen 1978.
46 Ravn 1905, 52.
47 *Ibid.*, 100.

dominant."[48] He explained what he meant by dominant and recessive by referring to farmers who could breed a cattle population where all the individuals had horns (recessive character).[49]

Zóphóníasson shared his interest in Johannsen's pure-line theory with the American geneticist Raymond Pearl (1879–1940). Pearl started in 1908 to apply Johannsen's theory in his work on the breeding of poultry. He knew that the theory had never been applied to vertebrates but was aware, as Ravn had been, that it was of great scientific interest to see if it could be applied to them. But after four years of experimental work Pearl realized that Johannsen's pure-line theory was of limited practical use, even though he believed that it was of scientific value, i.e. regarding the genotype/phenotype distinction. "Thus Pearl stopped short of advocating the pure-line theory for practical breeders, concluding that the 'fact simply is that a pure line in the strict sense of Johannsen can not by definition exist in an organism reproducing as the domestic fowl does'". Hence Pearl abandoned Johannsen's theory and turned his attention exclusively to Mendelism and its application in animal breeding,[50] something Zóphóníasson also appears to have done for he does not mention the pure-line theory in any of his later publications.

In a number of articles, published during the period 1916–1934, Zóphóníasson extended Ravn's discussion of Mendelism and made it easier to use, as his American counterpart had done, by explaining "how genetics made breeding results understandable and [describing] the ways in which genetics could help breeders improve their practical results". But unlike Pearl, who felt that his application of genetics had only helped breeders "to understand the techniques they had already mastered",[51] Zóphóníasson was addressing Icelandic farmers, who had only recently been introduced to systematic breeding practices. In his 1916–1917 articles Zóphóníasson explained the inheritance of a single character,[52] which differed in the parents and showed how the inheritance of this character could follow two routes, i.e. the previously mentioned 3:1 ratio and 1:2:1 ratio in the F_2 generation.[53] Explanation of how these ratios could arise by referring to factors in the germ cells, which segregated during meiosis, was also included.[54] Zóphóníasson mentioned briefly the inheritance of two characters, which differed in the parents by tabulating the 9:3:3:1 ratio.[55] Two years later he published an article on Mendelian genetics deepening his earlier exposition. Moreover, he mentioned sex-linked inheritance of characters and that acquired characters where not inherited.[56]

What characterized Zóphóníasson's writings in this period was his firm belief that different characters in the same individuals were inherited independently. He asserted that "from this it also follows that the old theory, which states that it is impossible to unite in the same

48 Zóphóníasson 1914, 86. By pure break he meant those individuals that bred true (were homozygous) for the dominant character. Emphasis in original.

49 *Ibid.*, 86–90.

50 Cooke 1997, 75–83. Quote is on pp. 78–79.

51 *Ibid.*, 82.

52 Zóphóníasson 1916–1917.

53 If the F_1 offsprings exhibit a blending of the parental characters, both the two parental characters and the blended one will appear in F_2. The ratio is 1:2:1, i.e. offsprings with the blended character appear twice as frequently as those with each of the parental characters. The offsprings with the parental characters will breed true but those with the blended character will have offspring in the 1:2:1 ratio.

54 Zóphóníasson 1916–1917, 50–51 (I).

55 *Ibid.*, 59 (II).

56 Zóphóníasson 1919.

individual certain qualities like high body weight and high milk yield in sheep... is totally wrong."[57] He correctly demonstrated the falsity of the old theory, which I discussed above, but the early Mendelian belief in the absolute independence of the inheritance of separate characters turned out to be wrong. In 1911 the American geneticist Thomas H. Morgan (1866–1945) noted that "instead of random segregation in Mendel's sense we find 'associations of factors' that are located near together in the chromosomes."[58] Zóphóníasson did not know this when he wrote his articles, but in a footnote in his 1919 article he stated that "Now 1919 – two years after this article was written – it has been confirmed, that certain characters constitute exceptions from this [absolute independence]. They seem to be tight together, and have to be inherited inseparably together."[59] He was referring to he fact that some genes, which are on the same chromosome, are invariably inherited together, what is termed linkage. Only in 1930 did Zóphóníasson explain linkage in writing. He did this in a long article, published in *Búnaðarritið*, where he discussed many aspects of modern genetics with numerous examples (some from his own research).[60] This was the first time results of animal research based on Mendelian genetics were published by an Icelander.

Zóphóníasson's research

In 1930 and 1934 two articles by Zóphóníasson were published in the Danish agricultural journal *Nordisk Jordbrugsforskning* where he described the results of his genetical research on Icelandic sheep. His findings concerning yellow fat in sheep were also made public in a letter by the American geneticist William E. Castle (1867–1962), "one of the most ingenious experimenters in early genetics",[61] to *The Journal of Heredity* in 1934.[62] Castle got a word of Zóphóníasson's research when the Norwegian geneticist Otto Lous Mohr (1886–1967) informed Castle about them on his visited to Harvard University.[63] Castle was interested in Zóphóníasson's research on yellow fat in sheep because he had earlier done research on a similar condition in rabbits, caused by a recessive gene.[64]

Zóphóníasson noted that sheep breeding in Iceland had not followed a definite plan and that improvements were necessary. Farmers had, though, tried to improve their sheep stocks by choosing for further breeding, lambs that seemed to fulfil their expectations.[65] He also noted that until quite recently Icelandic sheep farmers had almost exclusively employed breeding rams which were unrelated to their own stock. This fear of inbreeding was in Zóphóníasson's opinion strange, as he knew of some cattle farmers that had relied on inbreeding. He supported this claim with a pedigree from a farm in Dalasýsla in the west of Iceland; similar pedigrees were available from other farms. It

> is very strange to know how afraid farmers in general are of inbreeding. This is especially common in sheep breeding, where farmers buy rams from other farms, often without knowing what they are getting, because as the farmers

57 Zóphóníasson 1919, 70. In his article on plant breeding in Britain from 1900 until 1920 Paolo Palladino quotes V.E. Vilkins' 1926 report on the status of agricultural research in Britain where he emphasized, as Zóphóníasson did, that "by scientific methods of breeding it may be possible to combine in one variety several desirable qualities..." (Palladino 1993, 304).

58 Morgan 1911, 384. See also Kimmelman 1983, 175–178.

59 Zóphóníasson 1919, 68.

60 Zóphóníasson 1930a.

61 Mayr 1982, 785. On Castle's live see Provine 1986, 34–63.

62 Castle 1934, 223.

63 Mohr 1934, 223.

64 Castle 1933.

65 Zóphóníasson 1934, 217.

> say 'the sheep are getting too related and need to get new blood'.[66]

Nevertheless, few farmers had started using breeding (sperm) rams from their own stock. The prerequisite for this breeding method was to keep detailed records of the offsprings of each ewe. The farmers needed to keep pedigree records.[67] Based on these records the farmers could select breeding lambs on the basis of their relations to individuals, which had the desired characteristics. This made the selection more purposeful "and one goes from mass selection to selection based on genealogy and the individuals themselves".[68] The ineffectiveness on mass selection had been clearly demonstrated in the early 20th-century; Raymond Pearl had for example clearly demonstrated this in 1908 in terms of poultry breeding.[69]

The Icelandic sheep population was at that time very variable (color, with or without horns, body shape and many hereditary diseases). Zóphóníasson noted that therefore it was not surprising that farmers who were trying to improve their stock with inbreeding stumbled unexpectedly onto one thing or another which they had not expected,[70] referring to recessive genes which hitherto had been rarely expressed in homozygous condition because of the lack of inbreeding. Zóphóníasson added that

> inbreeding is the best possible way to "fix" certain characters in any variety. It has been used, more or less, in the production of most varieties which are approximately fixed... But inbreeding is a very expensive breeding alternative if the variety, which the farmer wants to improve, has any serious flaws [meaning recessive genes]... But inbreeding is the only possible way to rid the population of them. Only with it can the flawed individuals be found, and only then can one get rid of them... if sublethal or other serious flaws are not in the population, then inbreeding should, without a doubt, be used as a way of improving it.[71]

Inbreeding could reduce the time it took to "fix" certain characters in the population, but it could cause the expression of lethal or sublethal syndromes caused by recessive genes. Here we have a much subtler understanding of the effects of inbreeding than in the case of Zóphóníasson's predecessors. In northern Europe diseases caused by recessive genes had usually vanished before research based on Mendelian genetics gained momentum. The fact that inbreeding was uncommon in Iceland meant that these genes were relatively common which provided very good material for genetical studies of the effects of these recessive genes in the sheep population. As an example of this, Zóphóníasson demonstrated that a lethal syndrome affecting lambs, characterized by a short and bulky body, weakened legs, unusually large skull, etc., so called bulldog lambs, was caused by a recessive gene.[72] Zóphóníasson also figured out the inheritance of color in Icelandic sheep. His results indicated that the brown color in Icelandic sheep is recessive relative to the black and white colors, and that there were two kinds of the black color, one recessive and one dominant relative to the white color.[73] Zóphóníasson's results coincide with results published by two British geneticists in 1930 on color inheritance in British sheep.[74] It should

66 Zóphóníasson 1930a, 62.
67 Hólmjárn 1916.
68 Zóphóníasson 1934, 217.
69 Cooke 1997, 70–75.
70 *Ibid.*, 62–63.
71 Zóphóníasson 1930a, 63–64.
72 Zóphóníasson 1930b, 327–329 & 1930a, 46–47; Erlingsson 1998b, 96–97. Similar syndrome was known to affect calves, so called *bulldog* calves (Mohr 1930, 15), which is where Zóphóníasson got the name for the lamb syndrome.
73 Zóphóníasson 1934, 221–222; Erlingsson 1998b, 99–100.
74 Roberts and White 1930, 187.

be noted that Zóphóníasson conducted his research independent of the British one. Finally I will describe Zóphóníasson's conclusions concerning yellow fat in sheep in some detail, since it got so much publicity.

Yellow fat was occasionally observed in sheep in Iceland.[75] It was a serious drawback, for meat with yellow fat could not be exported. Farmers thought the yellow fat was caused by something the sheep ingested during the summer grazing in the mountains, but Zóphóníasson thought it was quite obvious that this condition was caused by a recessive gene which in a homozygous condition caused the yellow fat.[76] He knew of yellow fat from 17 farms. As a rule 3–4 years after a new ram was bought to the farm yellow fat appeared in the lambs.

What made it difficult for Zóphóníasson to reach a firm conclusion about the causes of yellow fat was the fact that the matings on these farms were uncontrolled, so genealogical records were unavailable. Yet the farmers could still link the lambs born with yellow fat to the daughters of the purchased rams or their sons. Zóphóníasson's inquiry revealed that the purchased rams on all the 17 farms stemmed from farms where yellow fat had previously occurred. When the farmers replaced these rams with new rams from farms where yellow fat had not occurred, no more lambs with yellow fat emerged. One of Zóphóníasson's examples was as follows:

> In 1928 Mr. Z- visited a farm, Esphof, where a number of "yellow" individuals had occurred. It turned out that seven years ago a ram had been bought from a distant farm, and yellow individuals did not appear unless both their mother and father might descend from the ram mentioned. At the advice of Mr. Z- the farmer bought a new unrelated ram, and then no more yellow individuals appeared until last year, when he got three yellows. But in this case he had used rams that were bred on his own farm. Later Mr. Z- has visited the farm from which the first ram had been bought. At this farm yellow lambs had appeared occasionally for many years.[77]

These data were not beyond a doubt, yet Zóphóníasson thought it very likely that a recessive gene caused yellow fat, which in homozygous condition caused the yellow fat. Castle agreed with this conclusion:

> ...the communication which follows... indicates clearly that the yellow fat mutation which occurs among sheep in Iceland – but, so far as my information goes, is unknown elsewhere – is a simple recessive character in inheritance.[78]

Zóphóníasson's research was a considerable feat considering that he was working alone without any formal institutional or financial support; he was totally dependent on the good will of Icelandic farmers in his data collection. All of Zóphóníasson's published research, were conducted before 1928, while he was a teacher and later schoolmaster at the agricultural schools at Hólar and Hvanneyri, respectively. In 1929, when he had become a breeding consultant for the Icelandic Agricultural Society (IAS), he asked the IAS Assembly for financial assistance to enable him to continue his work, but his request was declined.[79] This fact and his increased involvement in Icelandic politics led his research efforts to a halt.

In spite of his university degree Zóphóníasson was, by modern standards, an amateur re-

75 Zóphóníasson 1934, 218; Castle 1934, 246–247; Zóphóníasson 1930a, 43.

76 They were both right. In the grass the sheep ingests there are carotene pigments, which are broken down to a colorless substance in the liver. "This reducing mechanism is lacking in yellow-fat rabbits [and sheep], and so the carotene passes unreduced and yellow into the fat storage tissue." Castle 1933, 947.

77 Castle 1934, 246–247. Castle's letter to *The Journal of Heredity* includes his letter from O.L. Mohr, where this and there other examples of yellow fat are given.

78 Castle 1934, 246.

79 Zóphóníasson 1930a, 45.

searcher, akin to his hero Gregor Mendel,[80] since our current understanding of the sciences and scientists is centered on a salaried researcher working within a university or institute. Science became

> 'professional' in the sense that the... amateur was beginning to be replaced by professional (salaried) man as the model type of person who pursued the knowledge of nature. In producing this new professional of science, a great part was played by the universities and other institutions of higher learning".[81]

Professionalization, or disciplinary building,[82] in the biological sciences started in the early 19th-century and has been an ongoing process ever since.[83] The professionalization of genetics started in the early 20th-century and revolved around establishing genetics as an independent discipline, in an already firmly established institutional setting. Experimental biology was, for a variety of reasons,[84] first to gain footing in the United States, with the geneticist T.H. Morgan as the leading figure,[85] while countries like Germany, France and Britain lagged behind.[86] The rise of genetics in the agricultural sciences followed a similar path, i.e. with the United States leading the way:

> The independence of American agricultural research centers from the farming community was obtained, and maintained, at least in part, by the development of the Mendelian theory of heredity as an essential pre-requisite for the development of breeding practices. Not surprisingly, the growth of genetics was particularly vigorous in the United States. This hard-won independence was never in question in the Great Britain, and thus the need to foster work on the genetic foundations of breeding was less urgent.[87]

In this respect it is interesting to note that the director of the Scottish Plant Breeding Station (est. in the 1910's) and Britain's leading commercial breeder Edwin Sloper Beaven (1857–1941) were skeptical about the practical utility of Mendelian genetics in breeding. Zóphóníasson noted a similar example from Denmark where breeding consultants did not apply, or were skeptical about the application of, Mendelian genetics in their work, but according to Zóphóníasson things were moving on. Thus in 1930 two of Denmark's state consultants in cattle breeding had recently died, yet their positions could not be immediately filled because the Danish breeding societies insisted that the new consultants be educated in Mendelian genetics, so they could pass this new way of thinking to other consultants. In light of this development in Denmark Zóphóníasson noted that "here at home there is still no understanding concerning these matters, but hopefully it will gradually change here as elsewhere."[88] But Zóphóníasson's vision was still far off. State supported, professional, agricultural research started on a small scale in Iceland in 1935, with the establishment of the Industry Section of the University of Iceland (Atvinnudeild Háskólans), while systematic research in genetics and breeding was still looming behind the horizon.

CONCLUSION

The introduction of breeding societies, with their emphasis on improved husbandary prac-

80 Olby 1985, 89–108.
81 Cunningham & Williams 1993, 423. For a critical survey of the role the sciences play in modern society see Fuller 2000.
82 Golinski 1998, 66–98.
83 Bowler 1996, 25–39; Kohler 1990.
84 Harwood 1987.
85 Sapp 1983, 334–341; Falk 1995, 241–246; Harwood 1993, 33–45.
86 Harwood 1993; Burian *et al*. 1988; Palladino 1994.
87 Palladino 1994, 432.
88 Zóphóníasson 1930c, 46.

tices and the best yield breeding method, marked a clear break with the past in Icelandic agriculture. For the first time farmers were presented with systematic ways to improve their livestock, where increased fodder consumption and better shelters played a key role. The best yield method was also of value, for now farmers had an alternative to choosing breeding animals merely based on external appearances. In the rapidly expanding sector of dairy production these new methods were quickly adopted, but in sheep breeding changes came more slowly.[89]

In his pioneering work Páll Zóphóníasson tried to introduce a new breeding method based on Mendelian genetics,[90] thus undermining the theoretical rules his predecessors had relied on. He tried to persuade farmers that with this novel technique they could improve their breeding efforts more than had already been accomplished with the recently acquired best yield breeding method. The latter method being relatively well established in cow breeding, Zóphóníasson commented wryly on the strategy of sheep farmers who avoided the best yield method and chose breeding animal only on the basis of external appearances:

> But even though something can be accomplished with this method [that is basing choice of breeding animal on external appearances only], it has to be likened to blind man's buff. You never know what you will catch, and it is very sad to have now, in 1930, to use it at all agricultural exhibitions around the country as the main way to select breeding animals.[91]

Zóphóníasson's belief in Mendelism resembles that of Rowland Biffen (1874–1949), a British botanist and breeder, and Fritz von Wettstein (1895–1945), a German geneticist. Biffen argued that the only possible way to improve breeding would be through further elaboration of the newly rediscovered Mendelian theory and the subsequent reorganization of breeding practices in light of the results of the genetic research.[92] Wettstein's comment on the status of German agriculture in 1930 was analogous to Zóphóníasson's:

> It is depressing to note that agriculture is so reluctant to learn [how to apply genetics to breeding] and to apply what we know... It is not right, nor is it comprehensible, that German agriculture has not followed the example of Sweden, America and other countries where the practical application of experimental genetics long ago became common sense.[93]

According to Jonathan Harwood rhetorical statements like these, made by the early "Mendelian enthusiast", were often exaggerated and unwarranted, since the "old" breeding methods were not as obsolete as the enthusiasts indicated. Harwood has divided the early Mendelian enthusiasts into roughly two groups. Some of them were agricultural scientists and geneticists that appealed to the scientific legitimacy they thought Mendelism conferred on them, or they "had [an] obvious axe to grind". Others were agronomists, who wrote papers on Mendelism "aimed at a general agricultural audience and often concluding with an appeal for increased support" of genetic research. Harwood claims that the Mendelian enthusiasts in Germany had a limited success in promoting their new ideas among general breeders. One of the reasons was that many of them "assumed that variation arose, not just by mutation and recombination, but via broadly neo-Lamarckian [e.g. inheritance of acquired characteristics] mechanisms".[94] Another rea-

89 Zóphóníasson 1916–1917, 137 (I); Þórarinsson *et al.* 1988, 602–612; Bjarnason 1905, 181.
90 Vilhjálmsson & Erlingsson 1998.
91 Zóphóníasson 1930a, 50.
92 Palladino 1993, 302.
93 Harwood, unpublished manuscript A. Did theory transform practice? Mendelism and plant-breeding in Gemany, 1880–1920.
94 Jonathan Harwood, unpublished manuscript B. The reception of genetic theory among academic plant-breeders in Germany, 1900–1930. See Bowler 1983, 58–140 for a discussion on neo-Lamarckism.

son focuses on the role economical and applicational factors played in the reluctance of general breeders to adopt the new "Mendelian" breeding methods; these methods were costly and often did not result in anything better than the old methods.[95] Kathy J. Cooke has argued similarly. She claims that the rediscovery of Mendel's laws in 1900 led to an unwarranted "'marketing' of Mendelism over the next few years… [S]cientists [] prophesied 'glittering possibilities'… [that] remained largely unfulfilled."[96]

Zóphóníasson was definitely a Mendelian enthusiast of the latter kind, i.e. an agronomist writing for the general audience and appealing for research funding. The German model does, though, only partially explain Zóphóníasson's lack of success of implementing Mendelism in Iceland. Neo-Lamarckism was something Zóphóníasson had to face and he confronted it head on.[97] The application argument is, on the other hand, hardly relevant to the situation in Icelandic agriculture. As we have seen systematic animal breeding had only recently been introduced to Iceland so instead of having to confront well established and widespread breeding practices with new ideas, i.e. Mendelism, Zóphóníasson was filling a vacuum, being forced to implement basic breeding methods, i.e. the best yield method and pedigree records, parallel to his Mendelian methodology.[98] It is important to recall that Iceland was, at that time, a poor and isolated country, with many small and ineffective farms. This might have caused some of the farmers to realize that their farming was too small in scale to make the application of Mendelian or older systematic breeding methods practical. Poverty may have been crucial; it is costly in the short term to keep some of the "best" animals for breeding.

Finally it is worth noting that Zóphóníasson's amateurish status might have played a role in his lack of success in implementing Mendelism. Recent research has shown that members of the public (or the Icelandic farmers community) do not react simply to technical content [e.g. papers on Mendelism], but to a complex of contextual, institutional, and personal representations of science and scientific knowledge. "The public uptake (or not) of science is not based upon intellectual capability as much as social-institutional factors having to do with social access, trust, and negotiation as opposed to imposed authority."[99] If this is the case Zóphóníasson had several things working against him. As was noted above he was working without any formal institutional support and as science had not been introduced in Iceland as a practice, in the period this study covers, we

95 Jonathan Harwood, unpublished manuscripts A and B. Zóphóníasson was well aware of the cost that could follow breeding based on Mendelian principles. In his discussion of yellow fat he observed that this research was beyond the means of individual farmers so state support was necessary (Zóphóníasson 1934, 119). Earlier he also stated that "inbreeding is a very expensive breeding alternative if the variety, which the farmer wants to improve, has any serious flaws" (Zóphóníasson 1930a, 63–64).

96 Cooke 1997, 63.

97 We have already seen Guðmundsson and Þorbergsson expound neo-Lamarckian ideas, e.g. their emphasis on breeding only one character in each individual (on other neo-Lamarckian elements in their writings, see e.g. Guðmundsson 1903, 129; Þorbergsson 1906, 185. See also Þorbergsson 1915, 73). This is related to the idea that each individual has a finite amount of energy at its disposal and "if more is spent on one quality, then less is available for other qualities. This is what everyday experience teaches us" (Finnbogason 1903, 9). See Erlingsson 1998a, 73–86 for a discussion of neo-Lamarckian ideas in the Icelandic literature on evolution 1900–1940. On Zóphóníasson's rebuttal of neo-Lamarckism, see e.g. Zóphóníasson 1930a, 46–48.

98 Whether the economic argument bears on this case cannot be answered currently since the data used in this research does not allow me to give any conclusive answers.

99 Wynne 1991, 116.

can hardly talk about any "personal representations of science" among Icelandic farmers. Taking this into account the picture that emerges of Zóphóníasson is of an individual, who used the technical content of his knowledge to introduce new knowledge in Iceland, which he often did by talking down to Icelandic farmers and his predecessors and thus even slightly alienating them. With this in mind it seems obvious that Zóphóníasson had few social/institutional factors working in his favor, which might partially explain why Icelandic farmers ignored the message delivered by this Mendelian enthusiast.[100]

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100 Despite Zóphóníasson's lack of success in implementing the modern breeding method in Iceland he was a successful consultant. In his years as a consultant the number of cattle breeding societies increased steadily, from 23 in 1927 to over 100 in the early 1940s.

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