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Practical animal breeding as the key to an integrated view of genetics, eugenics and evolutionary theory: Arend L. Hagedoorn (1885–1953)

Bert Theunissen

Descartes Centre for the History and Philosophy of the Sciences and the Humanities, Utrecht University, Netherlands

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ABSTRACT

In the history of genetics Arend Hagedoorn (1885–1953) is mainly known for the 'Hagedoorn effect', which states that part of the changes in variability that populations undergo over time are due to chance effects. Leaving this contribution aside, Hagedoorn's work has received scarcely any attention from historians. This is mainly due to the fact that Hagedoorn was an expert in animal breeding, a field that historians have only recently begun to explore. His work provides an example of how a prominent geneticist envisaged animal breeding to be reformed by the new science of heredity. Hagedoorn, a pupil of Hugo de Vries, tried to integrate his insights as a Mendelian geneticist and an animal breeding expert in a unified view of heredity, eugenics and evolution. In this paper I aim to elucidate how these fields were connected in Hagedoorn's work.

1. Arend Hagedoorn

The Hagedoorn effect, named after the Dutch geneticists Arend Lourens Hagedoorn and his wife Anna Cornelia, states that a substantial part of the changes in variability that populations undergo over time are due, not to natural selection, but to chance effects. It was Ronald E. Fisher, the statistician and population geneticist, who published the first mathematical treatment of the effect and gave it its name in 1922, in a paper he was prompted to write by the Hagedoorns' exposition of the phenomenon in their 1921 book *The Relative Value of the Processes Causing Evolution*.[1]

Historians of population genetics are familiar with the Hagedoorns' book as an early contribution to the debate on what would later come to be called random genetic drift, yet for the rest, Arend Hagedoorn's work has received scarcely any attention from historians.[2] This is mainly due, it seems, to the fact that, for most of his career, Hagedoorn's focus was on practical animal breeding, a field that historians of science have only recently begun

E-mail address: l.t.g.theunissen@uu.nl

[1] A. L. Hagedoorn and A. C. Hagedoorn-Vorstheuvel La Brand, *The Relative Value of the Processes Causing Evolution* (The Hague: Martinus Nijhoff 1921); the book was co-authored by Hagedoorn's wife and lifelong collaborator. R. A. Fisher, 'On the Dominance Ratio,' *Proceedings of the Royal Society of Edinburgh 42* (1921–1922) 321–341, on p. 328. Fisher also wrote a very critical review of the Hagedoorn's book in *Eugenics Review 13* (1922) 467–470.

[2] Basic information on Hagedoorn's life and work (in Dutch) can be found in a commemorative issue, published after his death, of the journal of the Dutch Genetics Society, titled 'Het leven en werken van dr A. L. Hagedoorn,' *Erfelijkheid in Praktijk 15* (November 1954), nr 4/5. For a short obituary in English see Michael Pease, 'Dr. A. L. Hagedoorn,' *Nature 173*, no. 4393 (1954) 60–61.

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to explore in depth. It is becoming increasingly clear now what a rich field the history of animal breeding offers for studying science and technology relations.[3] Hagedoorn was an internationally well-known figure in this field in the first half of the twentieth century, when geneticists began to think about how the 'art of breeding' might be turned into a science on the basis of the new insights provided by Mendelian genetics.

An early adopter of Mendelism, Hagedoorn lived and worked as a geneticist in the USA, France, Germany and the Netherlands. He spent a substantial part of his time and energy trying to convince livestock farmers to reform their breeding practices, and he was invited by animal breeders and farmers in, among other countries, Great Britain, Rhodesia, South Africa and Australia to explain the principles of scientific breeding to them. His book *Animal Breeding*, first published in London in 1939, went through five editions and was reprinted ten times. He also published books on plant breeding and poultry breeding.[4]

Hagedoorn's work and career illustrate how a prominent Mendelian geneticist envisaged animal breeding to be informed by the new science of heredity. Furthermore Hagedoorn, having studied biology in Amsterdam with the originator of the mutation theory, Hugo de Vries, was interested in evolutionary questions. Especially in the early decades of his career he tried to integrate his insights as a Mendelian geneticist and animal breeding expert in a unified view of heredity and evolution. Finally Hagedoorn and his wife and lifelong co-worker, Anna Cornelia Vorstheuvel La Brand, a medical doctor, brought their expertise in the fields of genetics and animal breeding to bear on questions relating to the nature and future of humankind. It has often been noted that the views and methods of animal breeders were a source of inspiration for eugenicists, yet the connection deserves to be investigated in more detail. The views expressed by the Hagedoorns, even though they were highly critical of the Dutch eugenics movement, vividly illustrate how closely the fields might indeed be intertwined for scientists who were active in both.

My first aim in this paper is to elucidate how Arend Hagedoorn's views in the fields of genetics, evolutionary theory and animal breeding were connected. As Jon Harwood has recently underlined, the relation between biology and agriculture should not be seen as a unidirectional one in which new biological knowledge provided a driving force of agricultural innovation. Agriculture generated problems and provided generalisations, models and metaphors that stimulated basic scientific research and theorizing.[5] Hagedoorn's work presents a clear example of this two-way relationship. His ideas on genetics, evolution and practical breeding are in fact inseparable. I shall argue, for instance, that the 'Hagedoorn effect' was as much a product of his experiences in the field of practical breeding as of his purely scientific work.

Secondly, I shall discuss a concrete example of how Hagedoorn's views on breeding were received by those who were supposed to be the beneficiaries of his work, the practical breeders. The interest in animal and plant breeding that historians of science have recently taken up is partly inspired by the opportunities it provides to study the interactions between scientific and practical workers, and the encounter of their different kinds of expertise. Hagedoorn's case illustrates some of the complexities involved in the interaction, testifying to the fact that what is customarily seen as the twentieth century transformation of animal breeding 'from art to science', did not simply boil down to the application of scientific knowledge to practical problems.

2. Mendelian genetics and animal breeding

After having studied biology with Hugo de Vries in Amsterdam and having received his doctorate from Jacques Loeb in Berkeley in 1909, Arend Hagedoorn became involved in solving the many hereditary puzzles that challenged the early Mendelians.[6] In his high school and student years he had been an avid breeder of pigeons, mice and bantam chicken, and in the 1910s, like geneticists such as Lucien Cuénot, R. C. Punnett and Florence M. Durham, he studied hereditary phenomena that proved amenable to a Mendelian approach, such as the inheritance of coat colour in small rodents and poultry.[7] An adherent of Johannsen's pure line theory, he sided with the opponents of William Castle's view that the genes themselves might be changed by selection. For instance in the early 1910s, when he was working as a genetics adviser at the Vilmorin seed company in France, Hagedoorn showed that the pure lines of wheat varieties that had been cultivated by the company for more than fifty years had not changed at all, despite sustained selection for the best phenotypes. Castle's finding that variations might go beyond the normal range of variability of a character, could be explained by assuming that the character in question was influenced by multiple Mendelian factors, Hagedoorn and others argued.[8]

As to the nature of the genes, he followed investigators such as his mentor Loeb and Richard Goldschmidt in adhering to a quantitative, physico-chemical view of gene action. In 1911 Hagedoorn suggested that genes were autocatalytical enzymes. His paper attracted quite some attention at the time, yet the more elaborate

[3] To give a few recent examples: R. J. Wood and V. Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel* (Oxford: Oxford University Press 2001); Margaret E. Derry, *Bred for Perfection. Shorthorn Cattle, Collies, and Arabian Horses since 1800* (Baltimore & London: Johns Hopkins University Press 2003); J. Harwood (ed.), 'Special Issue on Biology and Agriculture', *Journal of the History of Biology 39* (2006) 237–406; S. Wilmot (ed.), 'Between the Farm and the Clinic: Agriculture and Reproductive Technology in the Twentieth Century. Special issue,' *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences 38* (2007) 303-530; Bert Theunissen, 'Darwin and His Pigeons. The Analogy Between Artificial and Natural Selection Revisited,' *Journal of the History of Biology 45* (2012) 179–212; Bert Theunissen, 'Breeding for Nobility or for Production? Cultures of Dairy Cattle Breeding in The Netherlands 1945–1995', *Isis 103* (2012) 278–309; Abigail Woods, 'Rethinking the History of Modern Agriculture: British Pig Production, c.1910–65,' *Twentieth Century British History 23* (2012) 165–191; Margaret E. Derry, *Art and Science in Breeding: Creating Better Chickens* (Toronto: University of Toronto Press 2012).

[4] A. L. Hagedoorn, *Animal Breeding* (London: Lockwood 1939). The book also appeared in a Spanish translation: *Cría de animales* (Madrid: Tecnos 1966); A. L. Hagedoorn, *Plant Breeding* (London: Lockwood 1950); A. L. Hagedoorn and Geoffrey Sykes, *Poultry Breeding: Theory and Practice* (London: Lockwood 1953).

[5] Harwood, 'Special Issue on Biology and Agriculture,' Introduction, 239.

[6] Under Loeb's supervision, Hagedoorn had conducted experiments on hybridization and artificial parthenogenesis. His doctoral research was published as 'On the Purely Maternal Characters of the Hybrids Produced from Eggs of Strongylocentrotus', *Archiv für Entwicklungsmechanik der Organismen 27* (1909) 1–20.

[7] See for instance A. L. Hagedoorn, 'The Genetic Factors in the Development of the Housemouse, which Influence the Coat Colour', *Zeitschrift für inductive Abstammungs- und Vererbungslehre 6* (1911) 97–136; 'On Tricolor Coat in Dogs and Guinea-pigs', *The American Naturalist 46* (1912) 682–683.

[8] See for instance A. L. Hagedoorn, 'Selection in Pure Lines. Fifty Years' Work in Wheat by Vilmorin Shows Not One of the Varieties Changed in Any Way by these Generations of Selection', *The American Breeders' Magazine 4* (1913) 165–168; 'Studies on Variation and Selection', *Zeitschrift für inductive Abstammungs- und Vererbungslehre 11* (1914) 145–183. For Hagedoorn's role at the Vilmorin Company, see Jean Gayon and Doris T. Zallen, 'The Role of the Vilmorin Company in the Promotion and Diffusion of the Experimental Science of Heredity in France, 1840–1920,' *Journal of the History of Biology 31* (1998) 241–262. For the debate between Hagedoorn (and others) and Castle, see W.B. Provine, *Sewall Wright and Evolutionary Biology* (Chicago & London: University of Chicago Press 1986) 69–70. For Johannsen and Castle see W. B. Provine, *The Origins of Theoretical Population Genetics* (Chicago & London: The University of Chicago Press 1971) 90–129.