SECOND EDITION

ANIMAL GENETICS

Frederick B. Hutt

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1807 1982

John Wiley & Sons
New York • Chichester • Brisbane • Toronto • Singapore

Library of Congress Cataloging in Publication Data:

Hutt, Frederick Bruce, 1897–
Animal genetics.

Includes bibliographical references and indexes.
1. Animal genetics. I. Rasmusen, Benjamin. II. Title.

QH432.H87 1982 591.15 81-19671
ISBN 0-471-08497-2

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

To Randall Knight Cole,
geneticist, skilled poultry breeder,
and, since 1935,
esteemed colleague of the senior author

PREFACE

This edition, like the first one, is written primarily for students in agricultural and veterinary colleges. During the 17 years that have elapsed since the first edition, there have been many advances in our knowledge of heredity in domestic animals. It is not surprising that changes have been necessary in every chapter.

These advances have resulted less from the discovery of new principles of genetics than from the application of the old ones, with new techniques, to the diligent investigation of genetic variation in domestic animals.

Much of this newer research has dealt with variations in physiology. Accordingly, this edition devotes a whole new chapter to blood groups and protein polymorphisms. It was written by Dr. Rasmusen, who has also contributed revisions and additions throughout the book. The former chapter on biochemical genetics has been rewritten and enlarged to cover various kinds of genetically aberrant physiology.

Advances in cytological techniques have extended our knowledge of the chromosomes, which can now be individually identified (Chapter 6). When they go astray, it is possible to identify the ones that have done so and the effects of the mishap (Chapters 18 and 19).

As in the first edition, a special effort has been made to illustrate principles with examples drawn from domestic animals. These are not all cows and horses. Let us not forget that the mouse is a semi-domestic animal, albeit one not usually welcome. That "wee, sleekit, cowerin', timorous beastie" (as Burns called it) is famous for having the most extensive chromosome map of any mammal, including man (Chapter 10). No horse is likely ever to attain similar distinction.

Illustrative examples from plants or from man have been mostly replaced by suitable material from domestic animals. As in the first edition, a special effort has been made to dip only lightly into statistics, and to administer the irreducible minimum of them in small doses. These are scattered through several chapters wherever they best fit in.

We should like to thank collectively the people who have generously provided photographs for the 30 new illustrations or permission to use material published elsewhere. For these last, an effort has been made in the legends to give credit not only to the original author but also to the original publication. When that credit reads *from*, the original illustration is unaltered; when it reads *after*, slight alterations were made (at our request) by the publishers' artists. We are especially indebted to Prof. Ingemar Gustavsson of the Royal Veterinary College, Uppsala, Sweden, who provided several photographs, and to the *Journal of Heredity*, which did likewise. For other acknowledgments, see those for the first edition.

We have not strained any friendships by asking colleagues to read special chapters, but we are greatly indebted to one anonymous reviewer, who, taking his task more conscientiously than do most reviewers, submitted no fewer than 67 suggestions. We accepted 70 percent of them!

Frederick B. Hutt
Benjamin A. Rasmusen

ACKNOWLEDGMENTS
IN THE FIRST EDITION

I must thank, first of all, Professor F. A. E. Crew, for his book, *Animal Genetics*, published in 1925. As it was one of the magnets which drew me to his laboratory in Edinburgh, it played no small role in the chain of events which led eventually to the writing of this second book bearing that same title. Since the two are separated by 39 years, it is inevitable that my *Animal Genetics* should differ greatly from its predecessor, but I hope, nevertheless, that my professor will approve his pupil's handiwork.

I am particularly grateful to my colleagues, Professors C. H. Uhl, A. M. Srb, and R. K. Cole, who read individual chapters of the manuscript, and made many helpful suggestions; and to Professor Clyde Stormont, who read the whole manuscript, suggested several improvements which have been made, and undoubtedly saved me from more than one *lapsus calami* (which, translated freely, means: glaring error), some of which would have sent the reviewers into transports of unrestrained delight.

My thanks also go to all those who aided the cause either by providing photographs or by giving permission to use illustrations already published elsewhere. Rather than list their names here, I have made acknowledgments in each case in the legend of the illustration concerned. With respect to illustrations that have appeared elsewhere, an effort has been made to give credit both to the original author and to the original publication. Thirty-two of them appeared originally in the *Journal of Heredity*, and for many of these which were no longer available from the authors, the editor, Barbara Kuhn, kindly provided the original prints.

Special thanks are due to Miss Donna Hower who drew all the diagrams in Chapters 2, 4, 5, and 7 which show segregation in F_2 generations, and also redrew Figures 5 and 6 in Chapter 12.

Dr. H. P. A. de Boom of the Veterinary Laboratory at Ondestepoort, in South Africa, not only contributed the three pictures of his remarkable "baboon dogs," but also generously allowed me to cite his unpublished findings about them. Dr. H. C. Rowsell of the Ontario Veterinary College kindly contributed the latest extensions in his pedigree of hemophilia B in Cairn Terriers.

I am indebted also to the late Sir Ronald Fisher, and to Messrs. Oliver and Boyd, Ltd., of Edinburgh, for permission to reprint Table 4-4 from their book, *Statistical Methods for Research Workers*.

Finally, I must thank my secretary, Mrs. James L. Morrison, not only for her remarkable ability to turn none-too-legible manuscript into beautiful typescript, but also for keeping in good order the almost endless details about illustrations, tables, references, proofs, indices, and correspondence that lie behind every book. Only other authors and secretaries who have fought with them the battle of a book can fully appreciate how much such help can contribute to the ultimate victory in that battle.

F. B. H.

CONTENTS

CHAPTER 1

Genetics

"Genetics," said Bateson, when he proposed that name in 1906 for the youngest child in the family of biological sciences, "is the science dealing with heredity and variation, seeking to discover laws governing similarities and differences in individuals related by descent."

These terms, *heredity* and *variation*, should be defined according to genetic usage before we go any further. The geneticist's concept of inheritance is a bit more specialized than those of some others who use the term. There is no quarrel with the man who says that he "inherited" his father's farm. That usage, long familiar not only to happy legatees, but also to disappointed ones, and to lawyers who thrive on disputes between the two kinds, has nothing to do with biological inheritance

A dictionary tells us that heredity in the biological sense is the "hereditary transmission of the physical and psychical characters of parents to their offspring." That is a fairly good definition, but hardly a perfect one, for it does not rule out the transmission from parent to offspring of something *not* hereditary in the geneticist's special concept of heredity. In the *genes*, or units of inheritance that a chick receives through the nucleus of its mother's ovum and from the nucleus of its father's spermatozoön that fertilized the egg, are contained all the chick's hereditary potentialities. Some of these, like the color of its downy feathers and the shape of its comb, are evident at hatching. Others, like the color of its adult plumage, its ultimate size, or its capacity to lay eggs, become evident at maturity.

The hen sometimes *transmits* something to the chick that is not inherited through the genes. The egg can carry a bacterium which (in some cases) multiplies and gives the chick pullorum disease during the first week after hatching. Similarly, a mouse can receive in its mother's milk a carcinogenic agent that later causes the mouse to develop mammary cancer. These diseases are thus transmitted from parent to offspring, but are not truly inherited as are traits caused by the genes. Of course, as we shall see later, among those genes are some that determine whether or not the young animal can withstand the transmitted infection or will succumb to it. Conditions passed in a germ cell from parent to offspring, but outside the nucleus and not through genes, are sometimes said to be transmitted by *cytoplasmic inheritance* to distinguish them from heredity through the genes.

Let us not overlook the word *variation* in Bateson's definition. Some of that variation is caused by heredity, but much of it is caused by the environment. The innumerable debates of yesteryear on the relative importance of heredity and environment are less common nowadays, but as geneticists we can be sympathetic to both sides. Most of us have devoted considerable effort to determining how much of the variation in some plant or animal is caused by genes and how much by environment. Sometimes we try to exclude all environmental variation from experiments in order to show up differences that are caused by heredity. At other times, various environments, and even conditions of stress, are deliberately imposed to reveal genetic differences in ability to tolerate them.

The familiar saying, "Like begets like," has long been the guiding principle for animal breeders who select their ideal animals and reproduce them in the hope of getting further generations of similarly ideal descendants. Unfortunately, as those who have tried it know, like does not always beget like. It is true that cows beget calves and sows beget piglets. Similarly, Holstein-Friesians usually beget black and white Holstein-Friesians, but occasionally their calf is red and white. It is even more discouraging when the breeder finds that 300-egg hens do not regularly have 300-egg daughters, and, similarly, that the calf from the cow yielding 30,000 pounds of milk cannot do the same. The geneticist's business is to find out why such variations occur, to determine in what proportions the variant types are to be expected, and to learn how to make more likely the probability that ideal animals will beget ideal offspring.

Scope of Genetics

Genetics is not just a matter of 3:1 ratios. Some of the most important traits with which we are concerned in agriculture do not segregate in any recognizable ratios whatever. Differences in ability to produce eggs, milk, wool, meat, and other characteristics are certainly inherited, but, as we shall see later, the genetic bases for such variations are much more complicated than the basis for the difference between black calves and red ones. Sometimes the environmental influences far outweigh the genetic ones. Part of the geneticist's task is to discover the optimum environment for the maximum expression of the inherited potentialities.

Geneticists are concerned with genes, with the chromosomes that carry them, and with the cells in which those chromosomes are found. Animal geneticists have not yet delved as deeply into cytology as have plant geneticists, but we are equally concerned about the normal behavior of chromosomes and the mechanisms by which chromosomes are transmitted from one generation to the next. We would like to know much more about the extent to which they may interfere with fertility and viability when chromosome behavior is aberrant.

Developmental genetics deals with the question: How does the invisible gene produce the visible character? For example: How do genes for albinism cause some animals to lack melanic pigment? How do genes for inherited dwarfism in various species cause the retardation of growth that the breeder of bantam fowls likes and the breeder of Hereford cattle does not? How do genes for determination of sex make some animals males and others females? These are all good genetical problems, even though none deals with simple 3 : 1 ratios.

Another important field of genetics is concerned with the study of mutations, or changes in the germ plasm. There is ample evidence that these occur in nature. Many of them have been preserved by breeders to differentiate breeds of domesticated animals and horticultural varieties of plants. Most seem to be undesirable, but others have proven useful in agriculture, and some geneticists have studied the feasibility of inducing further mutations that might raise productivity beyond the current high levels to which it has been brought by selection.

Finally, genetics is inseparably bound to the big question of how evolution of species and subspecies has been brought about. This entails a study of the frequencies of various genes in wild animals and the relation of those genes to the "fitness" of different individual animals to survive. Statistical geneticists study the frequency of genes of various kinds in breeds, flocks, and herds of domestic animals, and devise elaborate schemes to show how those frequencies might (theoretically) be altered by different methods of selection.

Importance of Genetics in Agriculture

There are a number of good reasons why people who breed domestic animals, or keep them for profit, or minister to their afflictions, should know something about genetics. Since we are concerned primarily with increasing the yields of milk, fat, eggs, wool, meat, or some other desirable product, we should know how to manipulate to best advantage the genetic variations affecting these characteristics. The risks and results of inbreeding are better understood with some basic knowledge of how the genes behave. Conversely, high levels of productivity in improved breeds and strains can often be raised still higher by the mysterious power of the hybrid vigor that results when suitable strains are crossed. Geneticists would like to know how to make that hybrid vigor more amenable to their control.

Breeders of domestic animals are concerned about inherited defects. These range all the way from inconsequential downy feathers between a chick's toes, through assorted congenital weaknesses, to lethal abnormalities of form or function. Not all such defects are inherited. A little knowledge of genetics helps to distinguish the ones that are from those that are not and facilitates the elimination of undesirable genes. Differences among animals in ability to tolerate disease are clearly inherited, and a start has been made on producing disease-resistant strains of fowls, heat-resistant breeds of cattle, and other animals particularly adapted to environments where some similar stress is inevitable. Genetic ability to withstand stress can also cause problems in agriculture, as is shown by the houseflies and other insects which, by natural selection and without any help from geneticists, have bred their strains so highly resistant to DDT. The codling moths and mites that have become resistant to various toxins illustrate nicely the fact that animals differ in genetic ability to withstand stress of one kind or another, and that such differences can be accumulated by selection.

It is to be hoped that the animal geneticist will also develop a point of view conducive to the genetical improvement of the species with which he works. The veterinarians who guard the health of our domestic animals and the doctors who do the same for man have much in common. Both try to heal the sick. The doctors ministering to man, however, try to keep all of their parents alive to the last possible gasp. This humanitarian practice is usually appreciated by the patient, but it is not always the best thing for the human race. Some of those patients have genetic defects that should not be inflicted on later generations. In such cases it would be ideal if the patient could be kept alive, and in the best health possible, but with some assurance that his bad genes would go no further. However, most twentieth-century doctors seem no more concerned about later generations than was their revered Hippocrates, who lived in an age that antedated the Roman chariot. Their duty, as they see it, is to the individual in this generation, not to those in later ones.

The veterinarian can do somewhat better with his patients. Many of them also have genetic weaknesses and defects that should never be passed on to later generations. Here the veterinarian with a knowledge of genetics can be of great help, not only to his own clients but also to those of his successors, if he will advise against the reproduction of defective animals and do whatever he can to prevent it. There is no reason why genetic defects should not be repaired, or otherwise overcome, provided that this is done to permit raising the animal to a marketable age; but it is to be hoped that such repairs will not be knowingly made by veterinarians in animals that might be used for reproduction. At least one veterinarian has repeatedly refused requests to sew up umbilical hernia in bull calves. That is sound eugenics. On the other hand, a specific form of impotency in bulls was frequently repaired by veterinarians in a European country until they learned that the defect was caused entirely by heredity. Thereafter the curative operations ceased. In short, the veterinarian can think of the individual, but also of the race.

Finally, even a little knowledge of genetics is helpful to those who might otherwise be overawed by some of the sensational tales in the daily press. Newspapers delight in providing the public with heart-rending and hair-raising reports of the routine operations of heredity in the human species. These range from the now-familiar plight of the erythroblastotic baby, through the victims of hemophilia, of muscle dystrophy, or of other inherited disasters, to the perennial enthusiasm over the possibility of controlling sex, and the titillating speculation about the probable sex of children not yet born. On top of all this, there has been added in recent years many a controversial column about the risks of future generations that might be induced in the present one by environmental agents of various kinds. The frustrating sense of fatalism often engendered by some of these harrowing tales is less likely to bother the reader whose leavening knowledge of genetics permits him to read between the lines.

These few applications of genetics just considered do not exhaust the list, and current studies of genetic variations in the biochemical and physiological processes of domestic animals suggest that important new applications recently found are only forerunners of others to follow in the future. Advances in knowledge of the blood antigens of domestic animals have made immunogenetics a useful tool for identifying paternity and verifying pedigrees.

Beginnings

Genetics has flourished as a science only since the turn of the century. Progress in that time has been so rapid that it is difficult to believe how slow was the advancement in knowledge of reproduction and heredity up to 1900. Not till 1672, when de Graaf discovered that mammalian ovaries produce eggs equivalent to the eggs of birds, was it recognized that the female's contribution to the next generation comes from such eggs. Five years later Leeuwenhoek and his student, Hamm, discovered in mammalian semen the innumerable "animalcula" which we now know as spermatozoa.

For about a century thereafter a great controversy raged between Ovists, who held that the new life developed entirely from the ovum (with the seminal fluid acting merely as a stimulant), and the Animalculists, who believed that the individual developed entirely from the spermatozoön. One of the Animalculists, Hartsoeker, looking down his microscope at human sperm, believed that he saw in the head thereof a tiny "homunculus" shaped like a man (Fig. 1-1) and all ready to develop when planted in the proper environment! We must remember that in those early days the microscopes were not as good as they are now. In any case, Hartsoeker should be enshrined in the annals of

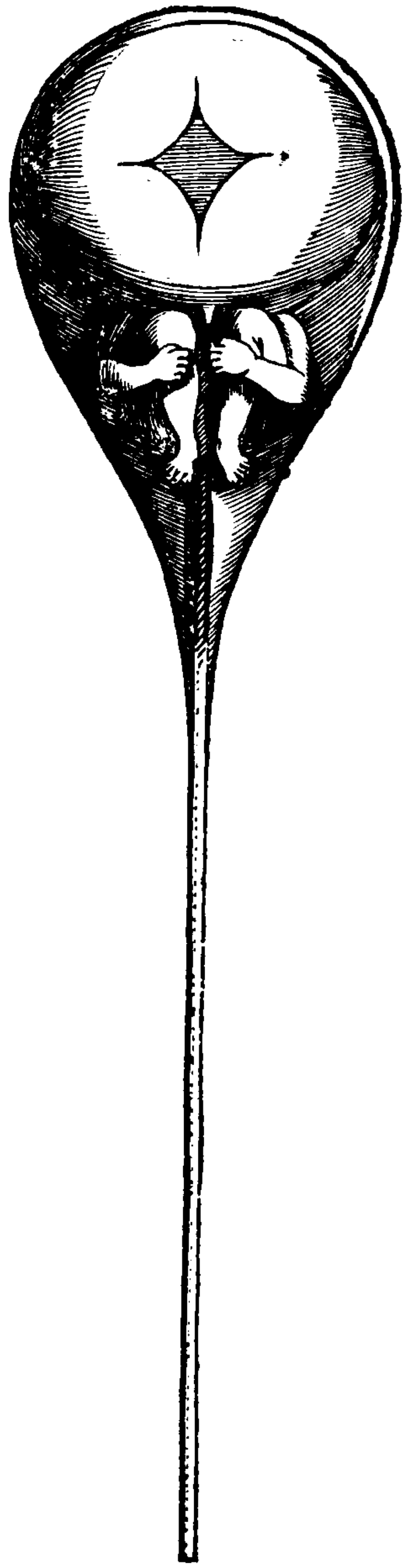

FIG. 1-1 The "homunculus," as Hartsoeker pictured it in his *Essai de Dioptrique*, Paris, 1694.