physiologically castrated,[1] and the effects were practically the same as would have occurred had she been castrated with a knife.

Incidents similar in principle sometimes occur among the mammals. A familiar example is the free-martin (see chapter 35), which is a heifer born twin with a bull. Such heifers are usually barren and often are quite masculine in appearance. Examination usually shows that the sex organs are in a rudimentary or abnormal condition. No doubt some other cases, besides free-martins, where females are quite masculine in appearance are really cases of poor functioning of the ovaries. Perhaps some males do not appear normally masculine because their testes are in some way functioning subnormally.

Thus, one of the reasons which the breeder has for seeking masculinity in his males and femininity in his females is that such evidence is some indication of the normal health and functioning of the primary sex glands. Certainly there are many exceptions to this rule, and probably it is not worth much attention if the seller will guarantee that the animal in question is a sure breeder. H. H. Wing tells of a bull which sired three very good daughters in the Cornell University herd but, on account of his feminine appearance, was sold before his daughters' merits became known. It should be added that the physiology of hormone action is not simple. There are many reactions and complicated interactions of the hormones from the sex glands with the hormones from other sources.

ABNORMAL DIVISION OF CHROMOSOMES

A second mechanism which may cause deviations from normal sex characteristics is abnormal behavior of the chromosomes. Definite evidence of this exists for Drosophila and some other laboratory organisms. It is reasonable to suppose that such behavior would occur occasionally among the mammals. Sex is not determined simply by whether the number of *X*-chromosomes present is one or two, but depends upon a balance between the effects of genes trending toward femaleness and genes trending toward maleness, most of the former being present on the *X*-chromosomes and most of the genes trending toward maleness being scattered on the autosomes. Normally, the presence of one or of two *X*-chromosomes throws the balance completely in one direction or completely in the other. If the chromosomes do not divide regularly, as happens in rare cases, an individual may have a few more or less than the normal number of chromosomes. This may keep the balance from turning definitely toward maleness or toward femaleness and may result

[1] "Spayed" is the word more commonly used in connection with females in animal breeding, but "castrated" may be used for either sex in scientific writings.

in intersexes of various kinds. Some of these intersexes are so extreme as to be sterile, but less extreme ones are sometimes fertile. In Drosophila this process is known to have produced occasional individuals which are more feminine than normal females or more male than normal males—the so-called "super females" and "super males." These are sterile. Winge has reported a case in which abnormal division of the chromosomes in a species of fish resulted in one race becoming homozygous for the *X*-chromosomes. Another pair of chromosomes, which evidently was not homozygous for all the genes affecting the expression of sex, took over the function of normally throwing the balance toward maleness or toward femaleness in each individual. In fishes, amphibians, and birds it appears that the balance normally thrown toward maleness or femaleness by the chromosome mechanism can more easily be reversed by genes on other chromosomes or by environmental conditions than is the case among the mammals.

Such chromosomal intersexes as were not sterile would transmit to some of their progeny the abnormal chromosome balance which caused them to deviate from the normal expression of sex characteristics. If a similar condition exists among mammals, some forms of intersexual conditions may be inherited. The use of breeding animals showing intersexuality might result in increasing the amount of intersexuality in the next generation. It seems improbable that this occurs often enough among the mammals to deserve much attention, but it is a possibility.

GENES AFFECTING SECONDARY SEXUAL CHARACTERISTICS

A third cause of variations in masculinity and femininity is the action of definite genes affecting the expression of the secondary sexual characteristics. Several of those are known in Drosophila and some, such as the genes for "hen feathering" in poultry, are known in other animals. No doubt some of these exist in all kinds of animals and also in such plants as exist in separate sexes (are "dioecious"). In fact, the results of abnormal chromosome behavior just discussed are difficult to explain on any other basis than that there are various genes affecting the expression of sex differences, a high proportion of the genes operating toward femaleness being located on the *X*-chromosome while most of those which operate toward maleness are located on the autosomes.

Further evidence about the existence of such genes comes from race crosses. These have been most extensively studied by Goldschmidt in the gypsy moth, Lymantria. Crosses between certain races of these produce intersexes of various degrees of intersexuality, while others produce normal individuals. A given cross always behaves in the same manner. That is, the results are orderly and definite. It seems likely that the normal balance between maleness and femaleness is caused by somewhat different combinations of genes in different races. In any comparatively pure race the balance falls definitely in one direction or the other. When two races which differ in the genes controlling this balance are crossed, the delicate balance required to throw the mechanism of sex determination in one direction or the other is likely to be upset. We do not know how general this is in the animal world, especially among the mammals. It may be so rare that it scarcely deserves mentioning. Perhaps the best general evidence on this subject is that from the sex-ratio in species crosses. Sometimes this is not disturbed at all, but often it is. Wherever there is a disturbance the heterogametic sex is usually the more violently affected. Among the common farm animals the mule is nearly always sterile, although a few cases of fertile mare mules have been reported. No cases are on record of a fertile male mule, but in fairness it should be added that the circumstances are such that fertility in the male mule would be more rarely detected than in the female. In the crosses between domestic cattle and the American bison, the few males produced have all been sterile, but most of the females have been fertile.

The nature and degree of secondary sexual differences vary from race to race within the same species. There is a somewhat greater difference in temperament between bulls and cows of the dairy breeds than in beef breeds, although a part of this may be a result of differences in the way they are managed. In some breeds of sheep, horns are a masculine trait; in others they appear in both sexes; in still others, neither sex has horns. No breed of sheep normally has horned ewes but hornless rams. In man, many racial differences occur in the expression of sex-differences. In the races from northwestern Europe and around the Mediterranean region, the men are generally rather heavily bearded. Some of the European peoples and most of the peoples of eastern Asia as well as the original natives of the two Americas are scantily bearded. The various negro races of Africa differ much among themselves in this respect. The beard is regarded as a secondary sexual characteristic in man, but its degree of expression varies from race to race, and that variation is not accompanied by corresponding variations in masculinity. In practically all races the height of the men is greater than that of the women, but the proportion of this difference varies from race to race.

Specific genes affect the expression of the secondary sexual characteristics, and many seem to have no direct bearing on reproduction itself. No doubt many of the differences in masculinity and femininity which we see or discuss in our breeding selections are the effects of such genes. While such genes may have no direct physiological importance, yet so long as the customers desire masculinity in the males and femininity in the females it will be to the breeder's interest to produce the kind of animals they want to buy. Probably users of dairy cattle would be better off if gentleness and meekness had always been sought by breeders of dairy bulls. Many of the dangers of handling aged bulls would have been diminished.

SUMMARY

Masculinity in males and femininity in females to some extent are expressions of the functioning of the testes or ovaries in secreting hormones. Absence of masculinity in males or of femininity in females may indicate lowered functioning of these glands, which might in some cases be extreme enough to cause these individuals to be irregular in breeding or even sterile. The importance of evidences of masculinity and femininity has often been exaggerated. The most valid reason for desiring manifestations of normal secondary sex differences is that those may be a partial guarantee that the animal will be a regular breeder.

Abnormal chromosome distribution may on rare occasions disturb the balance of gene action which normally determines complete maleness or complete femaleness. The resulting intersexes, if fertile, may transmit an abnormal number of chromosomes to some of their offspring, thereby leading to some inheritance of this intersexuality.

Some genes definitely affect the expression of sex differences without any detectable effect on the real efficiency of the animal in reproducing itself. These lead to inherited differences in the expression of secondary sexual characteristics. The breeder will need to pay some attention to these differences if his customers do.

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CHAPTER 35

Hermaphroditism and Other Abnormalities Pertaining to Sex

The simplest form of reproduction is that in which one organism merely divides into two and it is impossible to say which is mother and which is daughter. This is common among protozoa and bacteria. In the plant kingdom asexual reproduction has been maintained in various specialized forms (such as budding, sprouting from roots, etc.) even among the highest plants. None of the higher animals has maintained asexual reproduction except in the form of parthenogenesis, although truly remarkable regenerative powers are still possessed by animals as complicated as many of the worms. Many species of insects, such as the aphids and the bees, can reproduce parthenogenetically. Sex exists among them, and sexual reproduction occurs at times, but at other times the females lay unfertilized eggs which can develop without fertilization into mature individuals.

SEXUAL REPRODUCTION

The union of two individuals to form many others occurs occasionally among even the simplest protozoa and bacteria. In the simplest form it is impossible to distinguish which of the uniting individuals is male and which is female. In such cases the union is usually called by some such term as "conjugation." In some cases of conjugation it is possible by physiological means to show that the conjugants are different in kind and therefore might be said to belong to different sexes. In some of these cases there are more than two such forms. If they were called sexes, there would be more than two sexes. Other terms more precise but less common than male and female are used to describe such forms.

Sexual reproduction possesses a tremendous evolutionary advantage over asexual reproduction. In a species reproducing asexually, 100 new mutations would only mean the existence of 101 pure breeding genotypes from among which natural selection could choose. With sexual reproduction there is the opportunity for trying out each new mutation in combination with all the others. Therefore, 100 new mutations in a sexually reproducing species make possible 2^{100} new true-breeding genotypes. This is an enormously greater number. The possibility of finding some combination among that number which would be superior to the previous combinations is tremendously increased. This is the fundamental biological importance of sexual reproduction. It is such a big advantage that all but the very simplest plants and animals have evolved ways of reproducing sexually, at least occasionally. Many species, especially among the plants, have retained asexual reproduction for part of their life history but at intervals reproduce sexually. This combines certain advantages of both methods.

HERMAPHRODITISM

Sexual reproduction does not require that the sexes must be in separate individuals. In many of the simpler animals and in most plants the same individual has both male and female reproductive organs; that is, is truly hermaphroditic. Among the vertebrates, only a few fishes are functionally hermaphroditic, but many animals as highly organized as the mollusks and round worms are normally hermaphroditic. The date palm and several of the temperate zone trees, such as the mulberry, are typical examples of the few higher plants which have the sexes in separate individuals.[1] Many other plants—hemp for example—normally exist as separate male and female individuals; but it is easily possible to reverse the sex or to make them hermaphroditic by controlling environmental conditions, such as hours of illumination. Geneticists have even succeeded in producing races of corn which are dioecious, although corn is typically monoecious, the tassel bearing the male organs while the ear and its parts are the female organs.

That the animal kingdom has prevailingly adopted sexual reproduction in a form where the sexes are in separate individuals while the plant kingdom has prevailingly stayed with hermaphroditism naturally calls for an explanation. For many species, separate sexes make possible such a division of labor that a male and female individual together can leave more descendants than two hermaphroditic individuals could. Wherever the anatomy and habits of life of the species were such that division of labor between the sexes conferred this advantage, it was but natural that the species should ultimately give up hermaphroditism. Since plants do not move about, they have little to gain by a division of labor among the two parents. They had much to gain by securing cross-

[1] The botanists call such species "dioecious" and restrict the words "male" and "female" to the gametophyte generation. This usage does not correspond to the common and zoological usages of "male" and "female" but is customary in most botanical writings.

fertilization, at least occasionally, because permanent and complete self-fertilization would destroy the genetic advantage of sexual reproduction in making possible new combinations of genes. The plant world is full of remarkable mechanisms for promoting cross-fertilization. As long as plants have the advantage of occasional cross-fertilization, not much more is to be gained by being dioecious. With the higher animals the situation is quite different. Many of them take remarkable care of their young. In most cases much is gained by having one parent specialized to look after the young directly, the other specialized for obtaining food, for combat, for protection, and perhaps for other duties. The animals which have carried this specialization and division of labor farthest are the social insects, such as ants and bees, with their workers, soldiers, drones, queens, and other classes. The mode of reproduction among the mammals is especially extreme in involving considerable disability of the mother during the bearing and the early rearing of the young. In most mammals the male has become specialized for greater efficiency in combat, in the procuring of food, etc., which at least partly compensates for the fact that his direct contributions to the rearing of the young are less.

SO-CALLED HERMAPHRODITES AMONG MAMMALS

Cases of partial hermaphroditism[2] are reported frequently in medical literature. Mammalian embryos all go through early stages in which it is difficult to be sure of the sex of the individual. That is to say, the embryos seem to have the anatomical potentiality of developing into either sex. Which way the development turns is usually determined by the sex chromosome mechanism, which normally throws the balance definitely one way or the other. Then, as differentiation proceeds, many organs develop in a way which is irreversible. Occasionally this balance is not turned so definitely, and some of the organs develop in one direction and some in the other. Almost all combinations of this can exist, but the development of some of the organs precludes the development of the organs of the other sex so that functional hermaphroditism is impossible. A few cases of birds which were functional females at one time in their lives and later became functional males have been reported. The accessory sex organs in mammals are more specialized, and the development of those organs is less reversible; therefore, functional sex-reversal seems impossible among mammals. Even in birds it is impossible for one individual to be a functional male and a functional female at the same time.

Probably the things most likely to upset the normal balance of the

[2] Colloquially called "morphadites" by many stockmen.

sex-determining mechanism are abnormal chromosome divisions or the action of definite genes on the development of the sex organs. At other times the cause of the abnormal development is a hormonal disturbance, such as exists in the case of the free-martin.

Many of the more frequent cases of supposed hermaphroditism are only incomplete embryological development of some of the sex organs. Similar embryological accidents sometimes affect parts of the body not related to sex. Such may be illustrated by the case of hare-lip or cleft palate, which occurs frequently in man. The upper lip in man develops embryologically as a center piece and two pieces Irom the side. These normally grow together at an early stage. The lines of their union are still more or less visible in the adult and give the human upper lip its typical slight approach to a three-lobed condition. Sometimes one or both of these unions fail to be completed. The result is an individual with an upper lip divided into two or, in extreme cases, three parts. This is known as hare-lip. Often the defective union extends back through the palate and impairs speech. In a similar way, embryological accidents in the development of the sex organs often result in superficial appearance of hermaphroditism. The condition called hypospadias, which occasionally occurs in farm animals, is a case of this. In it the individual is truly a male but bears some superficial resemblance to a female and is incapable of reproduction because the urethral groove does not complete its development to form a closed tube. Most so-called hermaphrodites among mammals are really males whose development is imperfect. The extreme cases, of course, are sterile; but some of the milder cases may be capable of reproduction.

Hermaphroditism which has its origin in definite genes or in chromosomal disturbances may be inherited to some extent. The actual evidence of this comes from goats and pigs, where bermaphroditism occurs more frequently in certain families than in others. Where the hermaphroditism has its origin in an embryological accident of some kind, it will not have any hereditary tendency unless the original cause of the embryological peculiarity was partly hereditary.

THE FREE-MARTIN

In cattle the developing fetal membranes of twins usually grow together where they come in contact. If enough of the blood vessels on the two sets of membranes grow together, the blood of the two twins is mingled and some of that from each twin actually flows in the blood vessels of the other. This does no damage when both are males or both are females; but, when one is a male and the other is a female, the hormones secreted by the male develop first and exert enough influence on the female to prevent her normal sex development. The extent to which her development is altered varies greatly, presumably depending on how early the blood vessels fuse together and on how complete the fusion is. Occasionally the membranes do not fuse at all, or least the blood vessels on them do not grow together, and the male and female twins born are both quite normal. According to data from 283 such females tested, only about 1 in 12 among heifers born twins with bulls are fertile. The bull is not affected, presumably because his sex organs start to differentiate earlier and never permit those of the female to reach the stage where they can hamper the male's development. The free-martin condition is very rare in animals other than cattle. Why the membranes of twins should so frequently fuse in cattle and so rarely in other animals is not clear.

The proportion of twin births in cattle is generally low, being something like 1 twin birth among every 200 births in "beef cattle" and 1 twin birth among every 50 to 60 in "dairy breeds." The females of the unlike-sexed twins will rarely have any other value than that of veal or beef. The occurrence of a free-martin means practically no loss to the producer of commercial beef cattle. It means at least a small loss to the producers of dairy cattle, because normally it costs them more to raise a cow than the cow will be worth for beef. It is among breeders of purebred cattle that the free-martin causes the greatest loss. When a heifer is born twin with a bull the question immediately arises as to whether it will be profitable to keep her long enough to learn whether she will be a breeder. The answer will depend in part upon how valuable she would be if she did prove fertile. If she is of an ordinary family, neither of her parents nor many of her brothers and sisters being of outstanding merit, it will probably not be worth while to raise her if that is going to cost much more than her beef value at maturity. If her value as a breeding animal would be high, then it might be wise to keep her in the hope that she will be fertile. For example, suppose it will cost about $75 to raise this heifer until she is three years old, and that her probable beef value at that time will be only $50. The loss incurred in raising each heifer which proves to be barren would therefore be $25. If she is of such valuable breeding and individuality that if fertile she would be worth $350 at the age of three years, that would be $275 more than it cost to raise her. In the long run one such heifer which did prove fertile would pay for the loss on 11 which did not. If her breeding value were still higher, it would be wise to raise her. If her probable mature breeding value would be only $125, not enough profit could be made on the occasional successful case to make up for the many where the heifer was finally proved barren. That is a rough outline of what should be considered when one is deciding whether to keep such a twin heifer to maturity. The situation may be further modified by other evidence. Many of the free-martins show evidences of abnormality, especially a distinctly enlarged clitoris or a fold of skin containing a cord along the median plane of the body just above the rear attachment of the udder, even at birth. If the individual appears to be abnormal at birth, attempting to raise it for breeding purposes is almost useless. On the other hand, if the heifer appears absolutely normal at birth, the chances of her being fertile are higher than the general average of about 1 in 12.

SCIENTIFIC ASPECTS OF HERMAPHRODITISM

To the practical breeder all hermaphrodites or partial approaches to that condition are only annoying sources of loss and are evidence of nature's blunders. To the physiologist or embryologist they are full of interest because they may throw light on the interplay of hormones and organ development and give him new information about this subject. Nature has performed for him experiments which he could not perform for himself. For example the free-martin shows him the equivalent of castration of the female embryo and partial transplantation of the male gonads at an extraordinarily early stage which he could not achieve in his laboratory. For this reason the literature of physiology and embryology has far more cases of this kind reported than corresponds to the financial importance of the subject to the practical breeder.

SUMMARY

Sexual reproduction makes it possible for each new mutation to be tried in combination with all previously existing genes. This is such an important evolutionary advantage that nearly all species have developed ways of reproducing sexually, although many of the plants and some animals as specialized as insects, retain the ability to reproduce asexually at times. Even in many of the simplest organisms, an occasional generation of conjugation or sexual reproduction may occur.

The separation of the sexes into different individuals brings advantages from a division of labor. These are small or non-existent in the case of most plants but are considerable in nearly all higher animals.

The embryos of the higher animals usually have the anatomical potentiality of developing into either sex. Normally the sex-chromosomes throw the balance definitely in one direction or the other. Many of the changes in the developing sex organs are irreversible. Sometimes the normal sex-determining balance may be upset by chromosomal abnormalities or by the effect of definite genes in such a way that development does not proceed definitely toward the one sex or the other but toward one sex in some organs and toward the other sex in others. Various grades of hermaphroditism result. In dioecious plants and in some of the lower animals this normal balance can sometimes be upset by certain environmental conditions.

Tendencies to hermaphroditism seem sometimes to be inherited. The evidence of this among the mammals comes mostly from goats and pigs.

Many of the cases of supposed hermaphroditism are merely embryological accidents, usually occurring in an individual which was originally male but develops imperfectly during its embryology.

The free-martin is an especially interesting case, sometimes regarded as hermaphroditic but really the result of partial hormonal castration during embryonic development.

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CHAPTER 36

Gestation Periods

A certain length of gestation is characteristic of each species; but, like other characteristics, the lengths of individual gestation periods vary. The actual union of the ovum and spermatozoon may be several hours after the successful service. The gestation period is measured as the number of days between the day of service and the day of birth of the young, since the exact hour of fertilization will not be known.

In most of the animal kingdom except the mammals the fertilized eggs hatch outside the body of the mother. There are exceptions to this general rule. For example, there are some snakes and some fish in which hatching takes place inside the body of the mother and others in which it takes place outside, but in either case the young hatch in a similar stage of development. Their embryology is more like that of birds than like that of mammals. Even among the mammals a few of the most primitive—for example, the duck-bill of Australia—lay eggs which hatch outside their bodies in somewhat the same way as do those of birds. In many of the primitive mammals (the "marsupials"), the eggs hatch within the body of the mother, but development proceeds only a short way before the young are born at a very immature stage. After they leave the mother's body, they are nourished and carried by the mother in a pouch. The only North American representative of these mammals is the common opossum.

In the higher mammals ("Placentalia"), the ovum not only starts its development within the body of the mother but develops a special mechanism, the placenta, by which its blood vessels come into close contact but not actual union with those of the mother. Through the placenta food and oxygen from the mother diffuse to the embryo, and the carbon dioxide and other waste products from the embryo diffuse into the blood of the mother. The placenta enables the embryo to develop far before birth, while it is still sheltered against an environment hostile in many respects. Because of the better care the mother can provide, no such enormous number of fertilized eggs need be started on the road to development in order that a few shall reach maturity safely as is the case with most lower animals, e.g., the thousands or even millions of eggs spawned per female among fishes.

All the higher mammals share the evolutionary advantages of the placental mechanism, but they differ widely in the degree of maturity which their young attain before they are born. For example, the young of rabbits are born without their hair, with their eyes closed, and are fully dependent on their mother for many days. At the other extreme, although both are rodents, the young guinea pig is born fully equipped with hair, with its eyes open, is able to eat lettuce and cabbage before it is a day old and under favorable circumstances can even survive without a foster mother if its own mother dies at its birth. Most farm animals are intermediate in this respect.

CAUSES OF VARIATION IN GESTATION LENGTH

Within the species there are breed differences which are usually slight but can be detected when large numbers of each breed are compared (see *Jour. Ani. Sci.* 2:50–52 and 4:13–14 for examples). Within the breed there are no doubt individual differences, although it is rare that one female is so different from the average of the breed and has enough gestations that one could be certain that she really differs from the breed to which she belongs. A common cause of variation is disease, such as abortion. Environmental conditions not usually classified as disease may sometimes bring about a shortening or lengthening of the gestation period. The season of the year in which pregnancy begins has a slight effect on the length of the gestation period in some cases. There is some evidence to indicate that nutritional conditions, even when not severe enough to be actually pathological, may affect the length of gestation. Within a species large litters are usually carried for a shorter time than small litters. Various workers have at times detected an influence of the sex of the offspring upon the length of time it is carried, but the evidence is contradictory. This is probably never a major cause of variation. For example, Uppenborn reports from a study of 5,600 cases that stallion foals are carried an average of $1.6 \pm .2$ days longer than mare foals—a real difference, but not a practically important one. On the same subject Mauch reports an average of $1.7 \pm .5$. The size of the offspring may influence the length of time it is carried. First gestations are often a little shorter than later ones.

"NORMAL" AND "ABNORMAL" GESTATION PERIODS

There is no entirely satisfactory test to determine whether a particular gestation is normal in length or otherwise. This problem comes up in a practical way most frequently in connection with cattle when the question is raised as to whether a given gestation terminated normally or in an abortion. Abortion may occur at all stages from the time when the embryo is so small that it escapes detection, to the stage of a gestation period practically normal in length. The "average length of gestation" is a statistical composite picture of many individual cases, no one of which may perhaps have been of exactly the average length. Some variation is normal and is just as characteristic of the species as is variation in other traits or organs.

As a practical guide to normal and abnormal gestations, Table 21 shows the standard deviation of gestation lengths for the farm animals. Approximately two-thirds of all gestation periods may be expected to differ from the average by less than the standard deviation. A useful rule is to suspect of being abnormal any gestation differing from the species average by more than the standard deviation. Where the breed or herd average is known and is based on reliable numbers, deviations should be figured from it instead of the species average, of course. Any gestation differing from the average by more than twice the standard deviation is likely to be abnormal and calls for examination as to whether there may not be some diseased condition which needs attention, or whether perhaps there may not have been some mistake in the breeding date.

The standard deviations in Table 21 were calculated from actual data which may in some cases have included errors in breeding dates or may have included as normal some gestation periods which really were terminated by abortion at such an advanced stage that the offspring was able to live. So far as they could be detected, all such cases were excluded from these data, but it is unlikely that all were detected.

TABLE 21

GESTATION PERIODS IN COMMON MAMMALS

A. Summarized from published actual counts various breeds and places:

Kind of Animal	No. of Gestations Included in Average	Average Length of Gestation	Standard Deviation of Individual Gestation Lengths
Horses	28,456	335.9	About 10 or 11 days
Ass	14	366.9	12 days
Mares bred to jacks	2,338	350	About 19 days
Cattle	27,810	282.1	About 5 days
Swine	6,535	114.3	2.2 days
Sheep	4,417	149.1	2.4 days
Goats	6,761	150.8	3.3 days
Dog	147	61.3	3.1 days
Rabbit	1,540	31.4	1.1 days
Silver fox	797	52.2	0.9 days

B. Quoted from various books:

Kind of Animal	Average Length of Gestation Periods
Farm animals:	
Jennet	About 12 months. Quite variable
Mare	About 11 months. Quite variable
Cow	280 to 285 days. 283 is most frequently stated
Ewe	147 to 150 days
Doe (goat)	149 to 154 days
Sow	112 to 114 days
Bitch	58 to 67 days, usually about 63
Cat	60 to 64 days. Some state 50 days
Laboratory animals:	
Rabbit	31 days
Chinchilla	111 days
Hamster	15 days
Guinea pig	69 days
Mouse	21 days
Rat	21 days
Other animals, about which there is less certainty:*	
Bear	6 months. Recent evidence indicates that this is too short
Beaver	4 months. Another writer states 65 days
Buffalo	10–12 months. (315 days with $\sigma = 5.5$ days in the Asiatic buffalo)
Camel	13 months
Dromedary	12 months
Elephant	20–24 months
Ferret	42 days
Fisher	352 days
Fitch	43 days
Fox	52 days
Giraffe	14 months
Lion	3½ months
Marten	267 days
Mink	51 days
Monkey	7 months
Muskrat	21 days
Nutria	140 days
Opossum	12½ days
Otter	55 days
Prjewalsky's horse	356–359 days
Puma	79 days. One writer says 15 weeks
Raccoon	65 days
Reindeer	8 months
Seal	11–12 months
Skunk	40 days. Some state 63 days
Squirrel	28 days
Tiger	22 weeks
Walrus	One year
Wolf	60 days to 63 days
Zebra	Same as the horse

* For more details see: *Breeding Data on Fur Bearing Animals*, special circular dated June, 1933, from the Department of Veterinary Science, University of Wisconsin; or: Kenneth, J. H. 1943. Gestation; a table and bibliography. Edinburgh. Oliver and Boyd.

The practical effect of including a few errors of this kind is to make the standard deviations a little larger and the means a little smaller than they would otherwise be.

PRACTICAL USES FOR KNOWING THE LENGTHS OF GESTATION PERIODS

First of all the caretaker needs to know when to prepare for the young by isolating the prospective dam and fixing things so that she can take good care of her new-born. It is not safe to rely entirely upon the breeding calendar in doing this, both because individual animals may vary distinctly from the expected date and because, after all, that animal actually may have been bred at some other date than the one recorded for it.

Another practical use for the knowledge of gestation length is in settling cases of disputed parentage where a female may have been bred to two different males at different heat periods and the young is born at a time which does not correspond exactly to either service date. Often such cases cannot be satisfactorily settled, and the only honorable thing to do is to regard the offspring as a grade or at best as a purebred not eligible to registry.

Observing gestation lengths carefully may help some in disease control by enabling the breeder to quarantine each female several days before she is due to produce her young and by calling his attention immediately to any which deviate enough from expectation that they are likely to need veterinary attention.

CHAPTER 37

Sex Ratios

The proportions of the two sexes are approximately equal in all the vertebrates. There are other animals among which sex ratios are normally very far from equality. For example, in some of the gall flies the males may be as rare as 1 or 2 per cent of the population. There are slight but consistent deviations from equality in the sex ratio even among the higher animals. A summary of the usual percentage of males among the total births for several species is shown in Table 22.

These are the sex ratios among those actually born. Sometimes these are called secondary ratios to distinguish them from the primary ratios which exist at the time of conception. The secondary sex ratio can differ from the primary one if there are differences in the prenatal mortality of the two sexes. Such differences are known to exist in several species. Apparently it is the general rule among the mammals that the prenatal and also the immediate postnatal mortality is higher among males than among females. It is usually impossible to determine the primary sex ratio directly. In practically all writings on the subject the sex ratio stated is that at birth unless otherwise specified. Some writers even distinguish a tertiary sex ratio, which would be the ratio of the sexes existing at maturity or at some other age—perhaps at weaning time for the farm animals. The tertiary sex ratio is so influenced by postnatal conditions of management that it is rarely used.

Sex ratios are usually expressed as the number of males per hundred females or as the percentage of male births among all births studied. The first method has the disadvantage that anything producing a certain effect on one sex would magnify the proportion more than if it produced the same effect on the other sex. For example, if anything occurred to destroy one-fourth of the males and the sexes had really been present in exactly equal number at the start, the sex ratio would be stated as 75 males to 100 females. On the other hand, if something had destroyed one-fourth of the females, the sex ratio would be stated as 133 males to 100 females. In the latter case the deviation would at first glance appear larger, although the amount of change is really

TABLE 22

SEX RATIOS IN SEVERAL SPECIES OF ANIMALS

Animal	Percentage of Males Among All Births	Approximate Number of Births Studied	Author, Date, or Notes
Farm animals:			
Horse	49.7	1,111,908	Düsing
"	48.9	34,497	Richter
"	49.3	11,261	Uppenborn
"	49.7	62,002	Schlechter
"	49.1	4,109	Lauprecht, 1932
"	49.9	25,560	Darwin
Mule	44.3	1,416	Craft, 1933
Cattle	50.5	3,559	Gowen and Pearl
" (dairy)	49.4	13,000	Roberts, 1930, and Roberts and Yapp, 1928
"	51.5	124,000	Johansson, 1932
"	49.9	20,579	Engeler, 1933
"	52.2	11,450	Ward, 1941
Sheep	49.5	91,640	Chapman and Lush, 1932
"	49.0	127,587	Henning, 1939
Goat (Angoras)	50.1	3,000	Lush, *et al.*, 1930
Swine	52.3	23,000	McPhee, *et al.*, 1932
"	50.6	48,000	Krallinger, 1930
"	51.1	3,639	Hetzer, *et al.*, 1933
"	50.1	5,373	Kozelhua, 1940
Dog	51.5	50,000	Whitney, 1927
"	52.8	159,304	Winzenburger, 1936
"	52.4	324,323	Druckseis, 1935
Cat	55.0	653	Jones, 1922 (embryos only)
Chicken	49.4	102,143	Jull, 1940
"	50.8	23,273	At eight weeks. Hays, 1941
Other mammals:			
Man	50.7 to 51.7	....	Various authors
"	51.4	....	At birth. Crew, 1937
"	52.4	....	Stillbirths. Crew, 1937
Rat	51.2	....	Cuénot
Mouse	50.0 to 54.1		
Rabbit	51.1	....	....
Guinea pig	50.8	....	Ibsen
" "	49.4	2,014	Schott, 1930

the same. When expressed as percentages of the total births, such changes would appear of equal size, regardless of the sex in which they occurred.

CAUSES OF VARIATION IN SEX RATIOS

The deviations of sex ratios from exact equality are small, but some of them are based on too large numbers to be accidental. Hence they have aroused the interest of biologists, out of all proportion to the economic importance of such small deviations. There is an enormous literature on the subject of sex ratios and the causes of their deviations from exact equality. Crew's book[1] will serve as an introduction to that subject, but one has only to look under "sex ratios" in the indexes of *Biological Abstracts* or of the *Experiment Station Record* to note the large amount written on that subject.

The usual cause of deviations from equality where the numbers are small is chance. Among a group of 32 cows having 5 calves each, the most probable single result is that one cow will have only heifer calves and one only bull calves, five cows will each have one daughter and four sons and another five will each have four daughters and one son. The remaining 20 will each have two sons and three daughters or two daughters and three sons. It is to be expected that extreme deviations will occur just by chance. Those are sometimes impressive to persons who do not have firsthand familiarity with the wide variation which chance can produce in small samples.

The most probable causes for the slight but real differences found between sex ratios and exact equality are differential mortality of the embryos of the two sexes and differences in the motility or longevity of the two kinds of spermatozoa. The latter would lead to the initial production of more embryos of one sex, even though the two kinds of gametes were produced in equal numbers. Among the mammals mortality is a little higher among the males than among the females at all ages, but the reverse is true in birds. Sex-linked lethal genes are well known in Drosophila and lead to abnormal sex ratios. Dr. King's partial success[2] in selecting two strains of rats for a high and a low sex ratio may have been based on such lethals or on lethals which affected only one sex. In plants there is good evidence of differences in the rates at which various kinds of pollen tubes grow down through the maternal tissue to reach the ovules. It is doubtful that anything as extreme as this is important in the higher animals; yet there might be enough of it to explain the slight deviations from exact equality which actually exist.

[1] Crew, F. A. E., 1927, *The genetics of sexuality in animals*, Cambridge: The University Press.

[2] *Journal of Experimental Zoology*, 27:1–35.

Various investigators have found that differences in sex ratios were sometimes associated with such things as race, season of the year, year-to-year differences, excessive sexual activity, etc.; but none of these are large enough to be economically important, although they do challenge the investigator to explain them. Species crosses sometimes result in an unequal sex ratio, but such crosses are too rare to be important in practical animal breeding. The cause in these cases is the disturbed balance between two different sets of sex-determining genes. For example, Cole and Painter found 332 males but only 10 females among hybrids between the pigeon and the ring dove. Sex was not determined on 418 others which died in the first week of incubation or on 89 others which died later. Presumably high mortality among the females was the main cause of the extreme sex ratio. In pigeons the females are heterogametic.

THE POSSIBILITY OF SEX CONTROL

It seems unlikely at present that the breeder will ever be able to control the sex of the young produced. Apparently such control would require either some treatment which would destroy the fertilized eggs which are of one sex but leave unharmed those of the other sex, or it would require some sort of treatment before fertilization which would separate the two kinds of spermatozoa or would kill one kind and leave the other unharmed. The first method, even if such a highly selective treatment were discovered, would be impractical in the case of multiple births because it would merely reduce the fertility by eliminating those of the undesired sex without much if any compensating increase in those of the desired sex. The second method conceivably might be of some practical use but would require some chemical or some method of treatment so delicately balanced that it would destroy spermatozoa of one kind without harming those of the other kind or would separate one kind from the other without harming the fertilizing ability of the desired kind. The improbability of there being such a treatment, or of finding it even if it does exist, becomes evident when it is considered that in the farm animals the two kinds of spermatozoa would be exactly alike in well over 90 per cent of the material they contain.

There have been an enormous number of theories of sex control and sex determination. Drelincourt, writing in the seventeenth century, named 276 "false theories" of sex determination. It is only fair to add that his own theory was the two hundred seventy-seventh false one! Geddes and Thomson, writing in 1901, estimated that the number of published theories of this kind had doubled since Drelincourt's time. Many of these theories are so vague or mystical that it is not possible to test them experimentally. Such are the theories which invoke differences in "potency," "mental states," and the like. Many of those which have a physical basis are susceptible to experimental tests. All which have been tested so far can be explained on the chromosome theory of sex determination. Even the cases of sex reversal have only shown that certain environmental circumstances may at times be powerful enough to turn the balance in the other direction from that in which the chromosome mechanism would normally have thrown it. The same thing has been done in dioecious species of plants, such as hemp, where sex reversal can be accomplished by the proper combination of environmental circumstances.

Any theory of sex determination, no matter how absurd, will be right in about half of the cases, just as a matter of chance. The laws of chance permit small samples to deviate widely from the expected average.[3] Hence it is to be expected that even the most absurd theories will sometimes seem to fit rather well a sample consisting of a few cases. Not many years ago a man who thought he had discovered such a theory of sex determination advertised widely in livestock magazines that if breeders would pay him 50 cents per head he would tell them how to get calves of the desired sex. He guaranteed to refund the money whenever the results were not as he had predicted. Now he could be expected to be right half of the time, just as a matter of chance. If he had obtained enough business, this would have been a profitable undertaking for him, because at the most he would only have to return half the money he took in. Moreover, many probably would not ask for their money back or would lose their receipts, etc. In this particular case the man making these advertisements seemed to be sincere in his belief that he had discovered some natural law and was only trying to profit from his discovery as an inventor would from a patent. No doubt he would have been indignant if he had been accused of fraud. The critical test in such cases is to predict what the future sex will be in enough cases to give the laws of chance an opportunity to work out. If the predictions are not correct in significantly more than half the cases, there is no real evidence to support the supposed method of sex control. The subject has enough appeal to popular interest that any supposed new discovery bearing on it is almost sure to get headlines and wide publicity.[4]

[3] *Human Biology* 9:99–103.

[4] *Journal of Heredity,* 24:264–74.

CHAPTER 38

Fertility and Breeding Efficiency

The number of young produced per female per year or other unit of time is one of the most important factors in successful animal production. The cost of producing and maintaining the breeding females and breeding males must be met from the sale of their products and from the salvage value of those parents which are still alive when their breeding usefulness is ended. As long as they are kept for breeding, beef cattle and swine produce nothing for sale except their offspring. Dairy cattle, sheep, goats, horses, and poultry produce milk, wool, mohair, work, and eggs, respectively, in addition to producing their offspring. Even in these animals a considerable part of the income—in sheep, more than half of it—comes from the sale of young stock not needed for replacements. Also, the amount of milk a dairy cow produces in her lifetime depends much upon the frequency with which she freshens. Unless it has a high advertising value which the breeder is in a position to use, a phenomenally high record for one lactation may be unprofitable if that lactation is preceded by a long dry period and if the cow is not bred again until well along in her lactation. The production of wool by sheep, mohair by goats, and work by horses are almost the only returns in animal husbandry which do not depend closely upon reproductive activity.

The number of young produced could be counted at various ages for the purposes of measuring breeding efficiency. From the standpoint of profits and losses it might be most logical to count the number which reach marketing age. From the standpoint of finding the causes of high or low breeding efficiency, more information can be had by counting the number of young weaned or the number born alive among the mammals or the number of birds hatched or the number of eggs laid among poultry.

The subject of breeding efficiency receives attention in varying degrees in different branches of animal husbandry. Ranchers pay much attention to percentage calf crop, which is usually based on the number of calves branded, and to lamb crop, which is usually based on the number of lambs weaned or on the number which come back from the summer range wherever summer and winter ranges are separated. Poultrymen are much concerned with hatching percentages. Swine growers often refer to the number of pigs weaned per sow and also to the number farrowed per litter. Dairymen citing a cow's record often add that she calved again within a certain number of months or carried a calf a certain number of days during the lactation. Only a few dairymen keep definite count of their percentage calf crop, as beef raisers do, or keep track of the average length of time between calvings in their herds. Horsemen sometimes refer to their colt crop, but the number of mares on each farm is usually so small that each man thinks and speaks of his colts individually. Lambert, *et al.* report[1] 65 live colts per year per 100 mares bred. A similar figure for Austria is 52 colts.[2]

Variations in breeding efficiency are the net results of a complicated interplay of genetic and environmental circumstances. Genetic causes usually play a minor part in individual cases, being generally overshadowed in importance by circumstances of nutrition, temporary state of health of the dam, accident, and disease. Yet genetic causes often play a large part in differences between the averages of groups, such as breeds or herds.

FERTILITY

In popular usage fertility is the ability of an animal to produce large numbers of living young. The inability to produce any offspring at all is sterility. Either sex may be sterile, but stockmen usually speak of sterile females as "barren." Sterile is usually an absolute term meaning that the individual is incapable, for the time at least, of producing any young at all; but fertile is ordinarily a relative term, and high and low fertility are used to describe differences between the numbers of young per litter or differences in the frequencies of pregnancies.

In technical writings a distinction is sometimes made between fecundity, fertility, and prolificacy. In that case fecundity is the potential capacity of the female to produce functional ova, regardless of what happens to them after they are produced; fertility is the ability to produce living young or, in the case of poultry, to produce eggs which will start to develop; and prolificacy is a relative term used to express whether many or few offspring result from a given mating or from a certain individual during its lifetime. The distinction between fecundity and fertility is easily illustrated in poultry where a hen may have high fecundity but her eggs may be low in fertility or hatchability; that is, she may lay many eggs but only a few of those will start development

[1] *Proc. Amer. Soc. An. Prod.*, pp. 358–65, 1939.

[2] Züchtungskunde, 13:210.

if incubated or perhaps only a few of those which start to develop will go far enough to hatch into living chicks. Prolificacy is usually applied only to females or to groups, such as breeds, strains, or herds. These distinctions are sometimes necessary for precision in scientific writings but are unimportant in a practical way so far as concerns the mammals. Fertility is used here to mean in a comparative sense the ability of parents to produce large numbers of young.

The number of functional ova released is the first limitation on fertility, but the number actually fertilized may be much less. Failure to be fertilized may result from several circumstances. The spermatozoa may be few in numbers or low in vitality. Normally the male ejaculates millions of spermatozoa at each service; therefore, the number of these does not usually limit the number of young born. There is good evidence, however, that in occasional instances the male is so near the borderline of sterility that the number of normal spermatozoa is low enough to prevent the litter from being as large as it would otherwise be.

The spermatozoa retain their ability to fertilize the ova for only a few hours after they are released in the female genital tract. In some species the ova seem to be liberated at a certain stage in or just after the heat period. If service occurs too early, the spermatozoa are dead before the ova are liberated. If service occurs too late, the ova have passed the period when they could have been fertilized. In dairy cattle the probability of conception is highest when inseminations are made in the middle or later part of the heat period. There is some evidence[3] that the number of pigs per litter in swine may be increased by allowing two services, one early and one late in heat. Partially offsetting this is the danger of exhausting the male by so many services that the number or vitality of the spermatozoa in his future services to other sows would be diminished enough to lose more than was gained by the extra service. It is possible thus to exhaust the males, but the experimental evidence indicates that such exhaustion rarely becomes an actual fact.

Occasionally a given mating produces no results although both individuals later prove fertile in other matings. For example, a given mating is made two or three times without success; then the same female is mated to another male and conception occurs. Naturally such cases can be interpreted in several different ways. Possibly conception would have resulted if she had been mated at that time to the first male. The usual number of services per conception in herds of dairy cattle, not complicated by the presence of contagious abortion, is something like 1.8 to 2.5. With that high a percentage of unsuccessful services under what

[3] Missouri Agr. Exp. Sta., Bul. 310, p. 15.

may be regarded as average conditions, it is not surprising that there would be occasional cases where the same service is repeated three or more times without success and yet if repeated one more time would result in conception.

NUMBER OF YOUNG BORN

Many of the ova which are fertilized die before they reach the stage when they could be born normally. A few of these deaths may be the results of lethal genes for which the embryos are homozygous and which stop development at a certain stage. Others may be mere embryological accidents which prevent some vital organ in the embryo from developing as it should. A portion of those deaths may be the result of overcrowding in the uterus, or of insufficient nutrition, particularly with animals which have such large litters as swine and rabbits do. Part of the evidence for this is the fact that large litters have a higher proportion of embryos which do not complete development than small litters do. Some embryos die from the consequences of infections in the uterus.

Embryos which die before completing their normal development may gradually disintegrate and be resorbed. After they are completely resorbed, normal reproductive functioning of the female may be resumed. Sometimes, especially if bacteria are present, some putrefaction begins, and the embryo along with the residues of its membranes may be aborted. If the embryo which died is one of a large litter, many of which are still alive, as is usually the case with swine and rabbits, it will normally be expelled along with the others when they are born. If it died when it was extremely small, it may have had time to be resorbed before this takes place. Even if it is not resorbed, it is often so small that it is not noticed. If it did not die until shortly before the time of normal birth, the breeder will merely note that there is a stillborn individual in that litter. Many of the stillborn young in such animals as swine have no doubt been dead for several days before birth.

VITALITY AFTER BIRTH

The percentage of those which die between birth and marketable age varies greatly with different kinds of animals. Much of this can be controlled by sanitation and careful management. On farms where swine are fairly well managed, something like two-thirds to three-fourths of the pigs born are weaned. By far the larger proportion of those which are not weaned are dead at birth or die within the first 48 hours after birth. Reasonably exact and useful information about the average percentage of lambs, calves, and colts born which survive at least to weaning time is lacking. Ranchmen often speak of a 70 per cent calf crop, but in most regions that is more nearly a goal than an average of what is actually achieved. Western sheepmen speak of an 80 or 90 per cent lamb crop but do not so conventionally use any one figure as cattlemen do. The vitality of twin colts is especially low as compared with twins in other species. Uppenborn found that only 14 per cent of the colts born as twins lived beyond the age of one year.

As the young animal grows older its mother's influence on its fate becomes less and the effects of its own genes become relatively more important. It is common practice in some of the sow testing work in Sweden and Germany to use the weight of the litter at three or four weeks of age as a measure of the sow's productivity. By putting the weighing date as late as three or four weeks, they measure not only the sow's fertility but also her ability to care for her pigs and produce plenty of milk for them. Soon after three weeks of age the pigs begin to eat other feed, and then weights are affected more and more by their own individual abilities.

AGE AT FIRST BREEDING

Breeding efficiency can be lowered seriously by postponing the first breeding to a needlessly late age. Females bred at a very early age are apt to appear stunted, especially during the first lactation; but their size when mature is affected very little by their having been bred early. Extensive comparisons of early and delayed breeding with several classes of livestock were made at the Missouri Station many years ago and with beef cattle at the Oregon Station and with sheep at the North Dakota Station more recently. These comparisons have shown distinct advantages from breeding early with no disadvantages more serious than a more stunted appearance of the early-bred females during their first lactations. In dairy cattle, for instance, heifers bred to calve first at less than 24 months of age produce almost as much in their first five lactations as do heifers bred to calve first at more than 34 months. Moreover, the early-bred heifers finish their fifth lactations at an average age some 15 months less than that of the late-bred heifers. Thus, almost as much production is attained; and the feed and other maintenance costs for over a year are saved. Breeding could be at such an early age that difficulties at parturition would cause much trouble, but actually that rarely happens. Troubles at parturition seem about as frequent with older females as with younger ones.

INTERVALS BETWEEN PREGNANCIES

Breeding efficiency of a herd or flock as a whole may be seriously lowered by having long intervals between successive pregnancies. In some branches of animal husbandry the breeding policy in this respect is fixed primarily by the feed resources. An extreme example is the range cattleman or sheepman whose feed resources may be abundant from April to October but whose animals may have to get along on a submaintenance ration through the winter. If he cannot have his calves and lambs dropped before the middle of spring so that they can be grown largely on the abundant feed of the next few months, he may prefer to let the cows and ewes remain unbred until next year, rather than have out-of-season calves and lambs. Moreover, ewes will normally breed only at certain seasons of the year. For such men the problem of keeping breeding efficiency high is concentrated in a short season of the year and is mainly one of getting as nearly as possible 100 per cent of the cows or ewes to conceive during that time.

For dairymen and swine producers and for beef growers in the farming regions, there is also the possibility of increasing breeding efficiency by rebreeding reasonably soon after calving or farrowing. Theoretically it is possible to overdo this by breeding females so soon after the gestation period is ended that their strength and reserve vitality can be so exhausted that they will not produce strong offspring. Actually it is doubtful whether such damage is often done. Natural physiological checks and balances will guard against this danger to some extent as they do in a state of nature. The females may fail to come in heat if their reserves of health are low. Meanwhile each month that they are unnecessarily kept from reproducing adds to the overhead costs of their maintenance, which must be divided among the offspring they do produce. There is even some possibility that each additional ovulation adds to the scar tissue in the ovaries and thereby lowers fertility. Moreover, each additional month brings the animal nearer the end of its productive lifetime when one of its offspring, which might otherwise be available for sale, must be kept to replace it.

These considerations make it likely that the wisest general policy is to breed for the first time at an age early enough to favor the highest lifetime production and to rebreed at almost tbe earliest opportunity after each pregnancy. The data so far analyzed make it seem likely that lifetime production by dairy cows is higher with frequent breeding and many short lactations than it is with longer but fewer lactations. Even when a dairyman rebreeds promptly it is difficult to keep the average calving interval under 13 months. By raising two litters per year swine growers who are equipped to take care of fall-farrowed pigs can reduce very much the costs per pig of maintaining the breeding herd. In some of the dairy regions of northwestern Europe where there is a large surplus of skimmilk, as in Denmark, some swine producers wean their pigs at an early age and attempt to average two and one-half litters per year per sow, although few of them actually achieve that. The average number of litters produced per scored sow per year was 1.88 in the recognized swine centers of Denmark for the five years ending September 1, 1934.

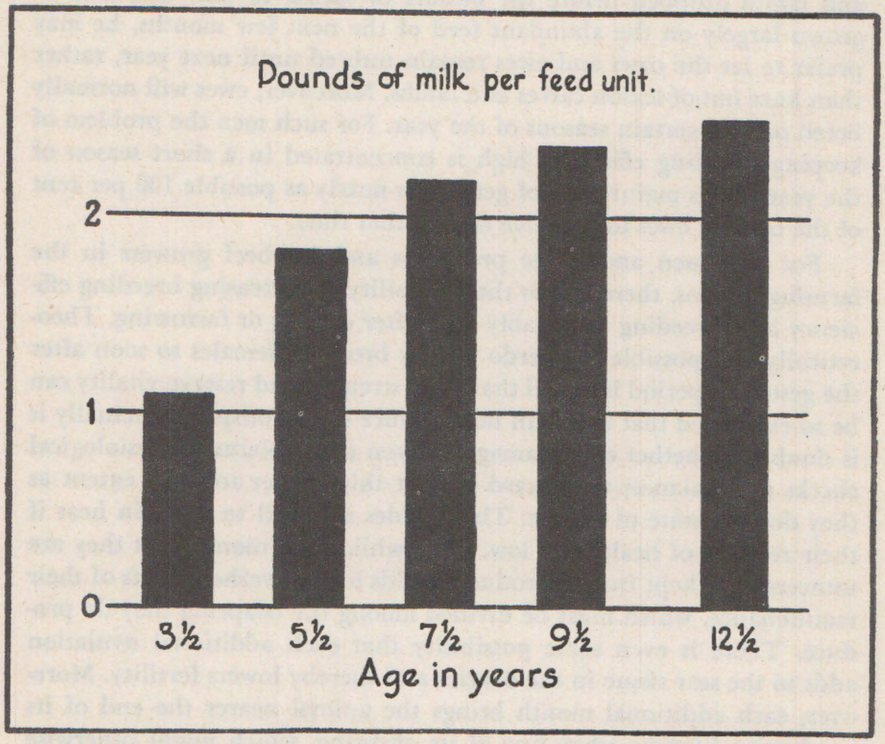

FIG. 49. "It pays to have cows which last a long time." Chart from cow-testing associations in Denmark showing how the returns in milk per unit of feed eaten by a cow during her whole lifetime increase rapidly with the increasing length of her productive life. (From *Kvaegavlen i Jylland,* 1933.)

LONGEVITY

The length of life of the parent is an important part of breeding efficiency, both from the economic standpoint and because it affects the possibilities of improving the breed. The expenses of rearing the parent until it is of breeding age are only partially met in most cases by the salvage value of the parents which are still alive to be sold when they are through producing young. Figure 49 shows a Danish analysis of cow-testing association data. The amount of milk produced per unit of feed eaten by the cow for her entire lifetime increases sharply as the cow's lifetime becomes longer. The longevity of the parents has an important effect on the possibilities of improving the breed by selection because it affects the percentage of young which must be saved merely for replacements. Several studies of dairy cattle indicate that under average conditions about 20 to 30 per cent of the cows are replaced each year. This means a productive life of four years or a little less and that something over 60 per cent of the heifer calves born must be saved for replacements. Seath reports an average of 3.78 calvings per cow's lifetime for Jerseys and Holsteins in Louisiana. Barker in Canada gives 6.1 years for the average life expectancy of dairy females and 6.0 years for registered beef cattle. The most favorable figure yet reported from studying any large body of data is that of Engeler, who found that the herdbook cows of the Brown Swiss breed averaged 4.56 calves during their entire lives, but that 69 per cent of the heifer calves born to herdbook cows were used for breeding. Range sheep in Nevada produced 57 lambs at market age per 100 ewes turned with the rams, but there was a complete turnover of the ewe flock in five years. About 53 per cent of the ewe lambs born would be needed for replacements.[4]

TWINS

Twins are a special case of fertility, particularly interesting in animals where births are normally single. In some breeds of sheep there are more twin births than single births.[5] In some other breeds less than one-fifth of the births are twins. Goats are rather similar to sheep in the frequency of twinning. Johansson summarized the records of nearly a million births in cattle and found that 1.88 per cent of all births in "dairy breeds" were twins. The corresponding figure for "beef breeds" was only 0.44 per cent. Engeler, studying 14,111 births in Brown Swiss cattle, found that 97.3 per cent were single births, 2.7 per cent were twins, .03 per cent were triplets, and there was one case of quadruplets. Sanders, studying more than a million and a quarter cattle records, found that 99.2 per cent were single births. Twins are about as rare in horses as they are in cattle. Uppenborn found that 1.5 per cent of all pregnancies among some 11,000 cases in horses were twins. Lauprecht, studying the records of about 1,500 mares, each of which had foaled several times, found that 1.5 per cent of all births were twin births. Except for the case of identical twins, which are common in man but rare in the farm animals, twins are not apt to be any more alike genetically than are full brothers and sisters born at different times. They are usually more like each other outwardly, however, because they have been subject to the same intrauterine environment before birth and often are reared under much the same environment afterward.

[4] Nevada Agr. Exp. Sta., Bul. 145.

[5] *Scientific Agriculture*, 22:11–17, 1941.

Variations in the tendency to produce twins are inherited to some extent. The result is that the general frequency of twinning is stronger in some individuals and races than in others, but things other than heredity play the major part in determining whether any particular birth shall be a twin birth.

IDENTICAL TWINS

About 50 per cent of the like-sexed twins in man are identical. These start as a single fertilized egg but very early in their embryology divide into two separate individuals. If this division occurs early enough, they may even have completely separate sets of fetal membranes. Usually they have a single chorion but separate amnions. There are cases where the division is not complete; then the result is some form of a double monster, ranging from almost complete separation (the so-called "Siamese twins") to just a faint beginning of the doubling. At large fairs there will often be some kind of a side-show exhibiting living or mounted freaks of this kind from various domestic animals.

Where the separation is complete the result is two separate individuals, of unusual genetic interest because they will be alike in all their genes. Their coefficient of relationship will be 100 per cent, although they may not be any more homozygous than the average of their breed or species. Comparisons of these twins with ordinary fraternal twins (for which the coefficient of relationship is usually 50 per cent) give us much of our information about the importance of heredity in human affairs. In most cases both kinds of twins are subjected to much the same environment, yet the resemblance between identical twins is so much greater than the resemblance between fraternal twins that there is rarely any doubt as to whether a given pair of twins is identical if more than three or four traits are considered. This remarkable similarity of identical twins has been observed from ancient times. Those rare cases where identical twins were reared apart under distinctly different environments provide interesting evidence on the importance of heredity and environment in man.

Identical twins are a subject of much popular interest but of little practical importance to the breeder. They are rare in the farm animals. Johansson estimates that 6.0 ± 1.2 per cent of all twin births in cattle are identical. Bonnier's estimate is 8.5 per cent. Although they are rare, enough have been assembled at different times and places by Kronacher in Germany, Bonnier in Sweden, and McMeekan in New Zealand to yield some interesting information on the interplay between heredity and environment. Kronacher has given detailed descriptions of many cases from cattle, including some which were double monsters, and has emphasized their usefulness as sources of information about the heritability of various characteristics. Identical twins seem to be much rarer in sheep and horses if, indeed, they occur at all. There are other animals in which they are not so rare. For instance, in the nine-banded armadillo the normal mode of reproduction is to produce four in a litter, the four litter mates being identical quadruplets.

TWINS WHICH ARE NOT FULL BROTHERS

Cases are frequently reported where two individuals are born in the same litter but are by different sires. Use is sometimes made of this in crossbreeding experiments to furnish a more adequate control for comparing the purebreds with the crossbreds. Boars of different breeds are mated to a sow which belongs to the same breed as one of the boars. Usually the resulting litter will contain some pigs by each boar. If the breeds are so chosen that the crossbreds can be distinguished from the purebreds by their color, this procedure provides nearly a perfect control of environmental conditions. Somewhat more spectacular cases are sometimes produced in animals which normally produce but one or two young at a time. Thus, Angora does have been known to produce twins, one of which was sired by an Angora buck while another was sired by a Toggenburg buck. A Guernsey nurse cow at the Iowa State College produced twins, one sired by a Hereford and the other by an Aberdeen-Angus bull.[6] Cases are on record where a mare has produced twins, one of which was sired by a horse while the other was sired by a jack. Such cases are conspicuous but illustrate no new principle. Such twins are genetically half brothers but, because of being exposed to so nearly identical environment, are apt to resemble each other more than ordinary half brothers do.

TWINS BORN AT DIFFERENT TIMES

Normally in farm animals when one pregnancy has begun, the female does not come in heat again until it is terminated. This is the general rule, but exceptions occur. When a second pregnancy begins before the preceding one is terminated, the usual consequence is that the second embryo and membranes are expelled also at the time the first pregnancy is terminated, no matter if the second embryo is still so immature that it has no chance of living outside the mother's body. Rarely it will happen that the second embryo is not expelled but continues its development normally and a second birth occurs several weeks or even months after the first one. Because such things as this are so rare and contrary to usual experience, they are apt to be reported when they do occur. Descriptions of such cases often appear in medical literature as well as in stock breeding writings.

[6] *Journal of Heredity*, 31:306.

MANAGEMENT WHICH PROMOTES BREEDING EFFICIENCY

Most individual variations in fertility within a breed are probably matters of management. The principal ways to get high fertility are the general ones of keeping the animals as free from disease as possible and in a reasonably good nutritive condition. The probability of conception and the number of young per conception can be noticeably increased in sheep and swine, and probably in cattle also, by having the females in fair condition and then distinctly improving or increasing their ration about two or three weeks before breeding begins. This is called "flushing" and is widely practiced by sheepmen and swine growers. Range cattlemen occasionally practice it where the price of a suitable concentrate, such as cottonseed meal, is not prohibitive. The percentage calf crop on the range is noticeably higher following a year when grazing was unusually good early in the breeding season. Other specific management to increase breeding efficiency includes breeding at a reasonably early age, fairly prompt rebreeding, having enough males (especially under range conditions) that they will find all females in heat and will not have their fertility impaired by overwork, giving the males extra feed during the breeding season, allowing only one or two services to each female (often practical under farm conditions but not under range conditions, of course), etc.

Artificial insemination is sometimes useful in overcoming sterility. It is sometimes used to breed a female at a distant place to some highly prized male without the expense of transporting one to the other. If artificial insemination is used extensively it permits the keeping of fewer sires and thereby effects a saving in maintenance costs. Against this must be charged the costs of the special apparatus or skilled labor required. By making it unnecessary to save so many sires, selection of the sires can be more intense. That should lead to somewhat more rapid progress although not in proportion to the number of sires which the artificial insemination permits discarding. For example, by reference to Table 12 it will be seen that if 100 per cent represents the progress resulting from selection among the males in one generation when 10 per cent of all males must be saved, then 117 per cent would represent the progress expected if only 5 per cent of the males needed to be saved, 139 per cent would represent the expected progress if only 2 per cent of the males need to be saved and 150 per cent would represent the progress to be expected if only 1 per cent needed to be saved. These figures concern only that part of the progress which is made by selecting the sires. The increasing intensity of selection among the sires would not increase the actual merit of the offspring so rapidly, however, because selection among the females contributes something to that, and this selection among females would not be altered by the use of artificial insemination. It appears, therefore, that the widespread use of artificial insemination would increase the rates of progress somewhat but not enough to change the prospects for breed improvement very radically.

GENETIC MEASURES TO PROMOTE BREEDING EFFICIENCY

So far as individual variations in fertility have a hereditary basis, they are subject to selection; and the average of the herd or flock in this respect can be changed by the same breeding methods used for changing other characteristics. That differences in fertility are often inherited is evident from a number of facts, such as the breed differences which exist in sheep and swine. Breeds of cattle also differ in the percentages of twins which they produce. Genetic literature contains many cases of inheritance of definite malformations which result in sterility. Superficially it seems a contradiction of terms to speak of the inheritance of sterility, since a sterile individual would not leave offspring. Nevertheless, sterility can be inherited just as lethal genes are; that is, carried along in heterozygous condition. Each different gene which definitely produces sterility must be of low frequency in the breed (just as lethal genes are) because of the intense natural selection against it. There might, however, be many such genes each in a different allelic series, each individually rare and yet enough of them that all together they would cause a noticeable amount of sterility in the whole breed. Data collected by Pearson on the number of children per family are interpreted by Fisher as showing that about 40 per cent of the observed variability in human family size is genetic in origin. There is conclusive evidence that part of the variation in longevity in Drosophila and in man is inherited,[7] but the direct evidence for farm animals is still fragmentary.

There is automatically some selection for high fertility, since those individuals with more offspring have more chances to get their sons or daughters saved for breeding purposes. This may be canceled by the breeder's selection for large size and excellent appearance. Individuals born in large litters may be initially handicapped by the greater competition and crowding. This is distinctly the case with twins in horses and, although less extreme, is noticeable with twins in cattle, sheep, and goats. Also, in swine the birth weights decrease and the mortality increases as litter size increases; although size of litter is by no means the major factor affecting birth weights and mortality, and its influence on weaning weight is comparatively unimportant. Moreover, the sow which has just nursed a large litter to weaning time is often thinner and

[7] Consult Pearl's *The Biology of Death*.

appears less attractive than one which has just weaned a few or none. Unless careful attention is paid to their records of production, the more productive sow is apt to be culled on account of her appearance whenever any culling is done. All this results in some tendency to select breeding animals which are below average in fertility themselves or come from parents of low fertility. In a similar way some selection for low fertility takes place in nature and may hold in equilibrium the selection which would otherwise favor the more fertile strains. Under many circumstances the most desirable condition with respect to fertility is neither the maximum nor the minimum. In the very largest litters all of the individuals are so handicapped that they cannot struggle through to maturity as successfully as those in smaller litters. On the other hand, those in the least fertile strains leave comparatively few offspring when they could have reared a larger number to maturity with almost equal success. This seems certain to cause some variation in litter size to be epistatic so far as profitability is concerned. Studies with swine have led to the general conclusion that a litter size of something like 9 to 12 pigs born alive leads to the largest net profit. If the litters are larger than this they contain too high a percentage of stillborns, and the survivors are too small at weaning time. If the litters are smaller than nine, incomplete nse is made of the sow's ability to nurse and rear pigs. None of the breeds of swine in the United States seem to be in danger of exceeding this optimum as a general average for the breed, although individual sows do exceed it frequently in single litters. Litter size in swine has a rather low repeatability; the intraherd correlation between the sizes of sncccessive litters from the same sow being of the order of one-sixth.[8] In selecting for litter size it would be unreasonable to expect actually to achieve each generation much more than about one-sixth of what is reached for in the selections, especially since the boars could express their inheritance only indirectly through the performance of their daughters.

The important practical step is to keep a reasonably complete and up-to-date record of each female's actual production and to lay heavy emphasis on that in all selections. By keeping the record in the form of lifetime production, some emphasis is automatically laid on longevity. The selection differential which can actually be made for productivity is usually small, even when the breeder thinks he is paying much attention to that. It is often an eye-opening experience to average the records on that point and see just what has been accomplished. For example, in the course of one breeding experiment at the Iowa Station (unpublished) in which much emphasis was laid on selecting for large litters, the data for 143 gilts farrowing in the first six years showed an average

[8] USDA Technical Bulletin. No. 836. 1942.

of 7.9 pigs per litter. The 92 gilts which were saved to produce at least one more litter averaged 8.4 pigs in their first litters. The selection differential actually achieved at this first culling was thus only one-half pig per litter. If the variance in litter size is about one-tenth hereditary in the simple additive manner—a reasonable assumption as far as the present evidence goes—and if selection of the boars out of prolific dams had an equal effect, this selection would increase the average litter size about one-twentieth of a pig per generation. With about 2½ years per generation, such selection would require 50 years to increase the size of the litter one pig! These computations are somewhat too pessimistic since they omit the selection which takes place after the second and later litters and the selection which takes place in saving gilts only from the larger litters in the first place. In these same data the additional selection differential achieved in culling sows after their second litters was .24 pig per litter. Selection for large litters continued all through the lives of the sows and in selecting gilts and young boars in the first place. It is within reason to expect that the improvement in litter size might be several times as rapid as indicated in the estimate above. The example illustrates two things: (1) that the selection differential actually achieved for fertility may be small even when much attention is paid to it; and (2) that such computations may be used in setting up standards of the average progress which may reasonably be expected.

SUMMARY

The number of young produced per female per year or other unit of time is important in determining profits in animal husbandry. It is also important in determining the percentage of young which must be saved to replace their parents and in thereby setting limits on the intensity of selection possible, especially among the females.

Fertility is limited in the first place by the number of ova produced. It is further limited by failure of some of the ova to become implanted or, if implanted, to develop normally enough to result in living young at birth.

Those which die between birth and weaning cause further loss in breeding efficiency. Much of this loss comes from faults of management, but some is from inherent weakness of the dam and the young. As the young grow older, their own inherent vitality and other characteristics play a larger part in their fate, and the characteristics of their dam play a correspondingly lesser part.

For mammals the first convenient stage for measuring differences in fertility is when the young are born. For economic reasons or for convenience, the number of young produced is often counted first at weaning time.

Fraternal twins or triplets are no more like each other genetically than ordinary full brothers and sisters. They are apt to be a little more like each other outwardly because of having been exposed to the same peculiarities of environment.

Identical twins, which are common in man but rare in the farm animals, are cases where a single fertilized ovum has later developed into two separate individuals. Such cases are unusually interesting to students of heredity because the two twins have identical inheritance. Their unusual likeness, as compared with that of ordinary fraternal twins, furnishes an opportunity to estimate the relative importance of heredity and environment.

Individuals born of the same mother at the same time may occasionally be half brothers, having been sired by different males.

In very rare cases a second pregnancy begins before the preceding pregnancy has terminated. Usually the younger embryo is expelled along with the older when the older one is born. In rare cases the younger embryo is retained and may be born several weeks or months later.

Longevity of the parents is important in breeding efficiency both because it spreads the cost of their rearing over a longer productive life and because it permits more intense selection of the smaller percentage of replacements needed.

Policies of management which promote breeding efficiency include such things as: keeping the animals reasonably free from disease and in good nutritive condition, flushing, breeding at a reasonably early age, fairly prompt rebreeding, not having too many females per male, giving the male extra feed during the breeding season, etc.

Genetic ways of promoting breeding efficiency consist of selecting the more fertile animals, with especial emphasis on their lifetime production of young. While it is probable that most of the ordinary individual variations in fertility are matters of management, yet some of these variations are hereditary, and some degree of success can be had by selecting for them, using the same methods as are used in breeding for other characteristics which can be manifested in one sex only. To do such selecting it is essential that up-to-date records of lifetime productivity be kept on each female.

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CHAPTER 39

General Considerations

In the preceding chapters each of the methods by which the breeder can change the genetic composition of a breed has been examined to see what it will and what it will not do and hence under what circumstances it would be useful. Before passing to the individual breeder's plans for his own procedure it is appropriate to review for a moment what each of the tools available to him will do best.

Selection—i.e., differences in the number of offspring which different kinds of individuals are permitted to have—is the most effective method for changing the frequency of genes and the genetic averages of the breed for various characteristics. It is naturally the method the breeder considers first because his profit or loss will depend mostly upon the average merit of the stock which he produces for sale. So far as genes produce effects which are consistently desirable in all combinations with other genes, the changes produced by selection are permanent (unless and until equally effective counter-selection has taken place); but insofar as the effects of the genes are desirable in some combinations and undesirable in others, many of the changes which selection produces when it is first practiced are lost within a generation or two if selection ceases. Selection produces only slight changes in the homozygosity or uniformity of a population unless it continues over many generations. If there is much epistasis, selection may increase uniformity rather sharply when first practiced; but continued selection is necessary to hold that increase in uniformity. Selection does not change the uniformity of the next generation nearly as much as it changes the average. The usefulness of selection can almost be summarized by saying that it usually carries the breeder toward his goal but is almost powerless to do much toward "fixing" characteristics. In cases where there is much epistasis, the rate of progress in changing the herd or breed average slackens considerably after the first few generations.

Inbreeding is in many respects a perfect complement to selection; it can do what selection cannot do, and can do feebly or not all that which selection can do well. Inbreeding is uniquely powerful as a means of