

PART TWO

SEXUAL SELECTION

CHAPTER VIII.

PRINCIPLES OF SEXUAL SELECTION.

WITH animals which have their sexes separated, the males necessarily differ from the females in their organs of reproduction; and these are the primary sexual characters. But the sexes often differ in what Hunter has called secondary sexual characters, which are not directly connected with the act of reproduction; for instance, the male possesses certain organs of sense or locomotion, of which the female is quite destitute, or has them more highly-developed, in order that he may readily find or reach her; or again the male has special organs of prehension for holding her securely. These latter organs, of infinitely diversified kinds, graduate into those which are commonly ranked as primary, and in some cases can hardly be distinguished from them; we see instances of this in the complex appendages at the apex of the abdomen in male insects. Unless indeed we confine the term "primary" to the reproductive glands, it is scarcely possible to decide which ought to be called primary and which secondary.

The female often differs from the male in having organs for the nourishment or protection of her young, such as the mammary glands of mammals, and the abdominal sacks of the marsupials. In some few cases also the male possesses similar organs, which are wanting in the female, such as the receptacles for the ova in certain male fishes, and those temporarily developed in certain male frogs. The females of most bees are provided with a special apparatus for collecting and carrying pollen, and their ovipositor is modified into a sting for the defense of the larvae and the community. Many similar cases could be given, but they do not here concern us. There are, however, other sexual differences quite unconnected with the primary reproductive organs, and it is with these that we are more especially concerned such as the greater size, strength, and pugnacity of the male, his weapons of offence or means of defence against rivals, his gaudy colouring and various ornaments, his power of song, and other such characters.

Besides the primary and secondary sexual differences, such as the foregoing, the males and females of some animals differ in structures related to different habits of life, and not at all, or only indirectly, to the reproductive functions. Thus the females of certain flies (Culicidae and Tabanidae) are blood-suckers, whilst the males, living on flowers, have mouths destitute of mandibles.* The males of certain moths and of some crustaceans (e. g. *Tanais*) have imperfect, closed mouths, and cannot feed. The complementary males of certain cirripedes live like epiphytic plants either on the female or the hermaphrodite form, and are destitute of a mouth and of prehensile limbs. In these cases it is the male which has been modified, and has lost certain important organs, which the females possess. In other cases it is the female which has lost such parts; for instance, the female glow-worm is destitute of wings, as also are many female moths, some of which never leave their cocoons. Many female parasitic crustaceans have lost their natatory legs. In some weevil-beetles (Curculionidae) there is a great difference between the male and female in the length of the rostrum or snout;*(2) but the meaning of this and of many analogous differences, is not at all understood. Differences of structure between the two sexes in relation to different habits of life are generally confined to the lower animals; but with some few birds the beak of the male differs from that of the female. In the *Huia* of New Zealand the difference is wonderfully great, and we hear from Dr. Buller*(3) that the male uses his strong beak in chiselling the larvae of insects out of

decayed wood, whilst the female probes the softer parts with her far longer, much curved and pliant beak: and thus they mutually aid each other. In most cases, differences of structure between the sexes are more or less directly connected with the propagation of the species: thus a female, which has to nourish a multitude of ova, requires more food than the male, and consequently requires special means for procuring it. A male animal, which lives for a very short time, might lose its organs for procuring food through disuse, without detriment; but he would retain his locomotive organs in a perfect state, so that he might reach the female. The female, on the other hand, might safely lose her organs for flying, swimming, or walking, if she gradually acquired habits which rendered such powers useless.

* Westwood, *Modern Classification of Insects*, vol. ii., 1840, p. 541. For the statement about *Tanais*, mentioned below, I am indebted to Fritz Muller.

*(2) Kirby and Spence, *Introduction to Entomology*, vol. iii., 1826, p. 309.

*(3) *Birds of New Zealand*, 1872, p. 66.

We are, however, here concerned only with sexual selection. This depends on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction. When, as in the cases above mentioned, the two sexes differ in structure in relation to different habits of life, they have no doubt been modified through natural selection, and by inheritance, limited to one and the same sex. So again the primary sexual organs, and those for nourishing or protecting the young, come under the same influence; for those individuals which generated or nourished their offspring best, would leave, *ceteris paribus*, the greatest number to inherit their superiority; whilst those which generated or nourished their offspring badly, would leave but few to inherit their weaker powers. As the male has to find the female, he requires organs of sense and locomotion, but if these organs are necessary for the other purposes of life, as is generally the case, they will have been developed through natural selection. When the male has found the female, he sometimes absolutely requires prehensile organs to hold her; thus Dr. Wallace informs me that the males of certain moths cannot unite with the females if their tarsi or feet are broken. The males of many oceanic crustaceans, when adult, have their legs and antennae modified in an extraordinary manner for the prehension of the female; hence we may suspect that it is because these animals are washed about by the waves of the open sea, that they require these organs in order to propagate their kind, and if so, their development has been the result of ordinary or natural selection. Some animals extremely low in the scale have been modified for this same purpose; thus the males of certain parasitic worms, when fully grown, have the lower surface of the terminal part of their bodies roughened like a rasp, and with this they coil round and permanently hold the females.*

* M. Perrier advances this case (*Revue Scientifique*, Feb. 1, 1873, p. 865) as one fatal to the belief in sexual election, inasmuch as he supposes that I attribute all the differences between the sexes to sexual selection. This distinguished naturalist, therefore, like so many other Frenchmen, has not taken the trouble to understand even the first principles of sexual selection. An English naturalist insists that the claspers of certain male animals could not have been developed through the choice of the female! Had I not met with this remark, I should not have thought it possible for any one to have read this chapter and to have imagined that I maintain that the choice of the female had anything to do with the development of the prehensile organs in the male.

When the two sexes follow exactly the same habits of life, and the male has the sensory or locomotive organs more highly developed than

those of the female, it may be that the perfection of these is indispensable to the male for finding the female; but in the vast majority of cases, they serve only to give one male an advantage over another, for with sufficient time, the less well-endowed males would succeed in pairing with the females; and judging from the structure of the female, they would be in all other respects equally well adapted for their ordinary habits of life. Since in such cases the males have acquired their present structure, not from being better fitted to survive in the struggle for existence, but from having gained an advantage over other males, and from having transmitted this advantage to their male offspring alone, sexual selection must here have come into action. It was the importance of this distinction which led me to designate this form of selection as Sexual Selection. So again, if the chief service rendered to the male by his prehensile organs is to prevent the escape of the female before the arrival of other males, or when assaulted by them, these organs will have been perfected through sexual selection, that is by the advantage acquired by certain individuals over their rivals. But in most cases of this kind it is impossible to distinguish between the effects of natural and sexual selection. Whole chapters could be filled with details on the differences between the sexes in their sensory, locomotive, and prehensile organs. As, however, these structures are not more interesting than others adapted for the ordinary purposes of life, I shall pass them over almost entirely, giving only a few instances under each class.

There are many other structures and instincts which must have been developed through sexual selection- such as the weapons of offence and the means of defence- of the males for fighting with and driving away their rivals- their courage and pugnacity- their various ornaments- their contrivances for producing vocal or instrumental music- and their glands for emitting odours, most of these latter structures serving only to allure or excite the female. It is clear that these characters are the result of sexual and not of ordinary selection, since unarmed, unornamented, or unattractive males would succeed equally well in the battle for life and in leaving a numerous progeny, but for the presence of better endowed males. We may infer that this would be the case, because the females, which are unarmed and unornamented, are able to survive and procreate their kind. Secondary sexual characters of the kind just referred to, will be fully discussed in the following chapters, as being in many respects interesting, but especially as depending on the will, choice, and rivalry of the individuals of either sex. When we behold two males fighting for the possession of the female, or several male birds displaying their gorgeous plumage, and performing strange antics before an assembled body of females, we cannot doubt that, though led by instinct, they know what they are about, and consciously exert their mental and bodily powers.

Just as man can improve the breeds of his game-cocks by the selection of those birds which are victorious in the cock-pit, so it appears that the strongest and most vigorous males, or those provided with the best weapons, have prevailed under nature, and have led to the improvement of the natural breed or species. A slight degree of variability leading to some advantage, however slight, in reiterated deadly contests would suffice for the work of sexual selection; and it is certain that secondary sexual characters are eminently variable. Just as man can give beauty, according to his standard of taste, to his male poultry, or more strictly can modify the beauty originally acquired by the parent species, can give to the Sebright bantam a new and elegant plumage, an erect and peculiar carriage- so it appears that female birds in a state of nature, have by a long selection of the more attractive males, added to their beauty or other attractive qualities. No doubt this implies powers of discrimination and taste on the part of the female which will at first appear extremely improbable; but by the facts to be adduced hereafter, I hope to be able to shew that the females actually

have these powers. When, however, it is said that the lower animals have a sense of beauty, it must not be supposed that such sense is comparable with that of a cultivated man, with his multiform and complex associated ideas. A more just comparison would be between the taste for the beautiful in animals, and that in the lowest savages, who admire and deck themselves with any brilliant, glittering, or curious object.

From our ignorance on several points, the precise manner in which sexual selections acts is somewhat uncertain. Nevertheless if those naturalists who already believe in the mutability of species, will read the following chapters, they will, I think, agree with me, that sexual selection has played an important part in the history of the organic world. It is certain that amongst almost all animals there is a struggle between the males for the possession of the female. This fact is so notorious that it would be superfluous to give instances. Hence the females have the opportunity of selecting one out of several males, on the supposition that their mental capacity suffices for the exertion of a choice. In many cases special circumstances tend to make the struggle between the males particularly severe. Thus the males of our migratory birds generally arrive at their places of breeding before the females, so that many males are ready to contend for each female. I am informed by Mr. Jenner Weir, that the bird-catchers assert that this is invariably the case with the nightingale and blackcap, and with respect to the latter he can himself confirm the statement.

Mr. Swaysland of Brighton has been in the habit, during the last forty years, of catching our migratory birds on their first arrival, and he has never known the females of any species to arrive before their males. During one spring he shot thirty-nine males of Ray's wagtail (*Budytes raii*) before he saw a single female. Mr. Gould has ascertained by the dissection of those snipes which arrive the first in this country, that the males come before the females. And the like holds good with most of the migratory birds of the United States.* The majority of the male salmon in our rivers, on coming up from the sea, are ready to breed before the females. So it appears to be with frogs and toads. Throughout the great class of insects the males almost always are the first to emerge from the pupal state, so that they generally abound for a time before any females can be seen.*(2) The cause of this difference between the males and females in their periods of arrival and maturity is sufficiently obvious. Those males which annually first migrated into any country, or which in the spring were first ready to breed, or were the most eager, would leave the largest number of offspring; and these would tend to inherit similar instincts and constitutions. It must be borne in mind that it would have been impossible to change very materially the time of sexual maturity in the females, without at the same time interfering with the period of the production of the young- a period which must be determined by the seasons of the year. On the whole there can be no doubt that with almost all animals, in which the sexes are separate, there is a constantly recurrent struggle between the males for the possession of the females.

* J. A. Allen, on the "Mammals and Winter Birds of Florida," Bulletin of Comparative Zoology, Harvard College, p. 268.

*(2) Even with those plants in which the sexes are separate, the male flowers are generally mature before the female. As first shewn by C. K. Sprengel, many hermaphrodite plants are dichogamous; that is, their male and female organs are not ready at the same time, so that they cannot be self-fertilised. Now in such flowers, the pollen is in general matured before the stigma, though there are exceptional cases in which the female organs are before-hand.

Our difficulty in regard to sexual selection lies in understanding how it is that the males which conquer other males, or those which prove the most attractive to the females, leave a greater number of

offspring to inherit their superiority than their beaten and less attractive rivals. Unless this result does follow, the characters which give to certain males an advantage over others, could not be perfected and augmented through sexual selection. When the sexes exist in exactly equal numbers, the worst-endowed males will (except where polygamy prevails), ultimately find females, and leave as many offspring, as well fitted for their general habits of life, as the best-endowed males. From various facts and considerations, I formerly inferred that with most animals, in which secondary sexual characters are well developed, the males considerably exceeded the females in number; but this is not by any means always true. If the males were to the females as two to one, or as three to two, or even in a somewhat lower ratio, the whole affair would be simple; for the better-armed or more attractive males would leave the largest number of offspring. But after investigating, as far as possible, the numerical proportion of the sexes, I do not believe that any great inequality in number commonly exists. In most cases sexual selection appears to have been effective in the following manner.

Let us take any species, a bird for instance, and divide the females inhabiting a district into two equal bodies, the one consisting of the more vigorous and better-nourished individuals, and the other of the less vigorous and healthy. The former, there can be little doubt, would be ready to breed in the spring before the others; and this is the opinion of Mr. Jenner Weir, who has carefully attended to the habits of birds during many years. There can also be no doubt that the most vigorous, best-nourished and earliest breeders would on an average succeed in rearing the largest number of fine offspring.* The males, as we have seen, are generally ready to breed before the females; the strongest, and with some species the best armed of the males, drive away the weaker; and the former would then unite with the more vigorous and better-nourished females, because they are the first to breed.*(2) Such vigorous pairs would surely rear a larger number of offspring than the retarded females, which would be compelled to unite with the conquered and less powerful males, supposing the sexes to be numerically equal; and this is all that is wanted to add, in the course of successive generations, to the size, strength and courage of the males, or to improve their weapons.

* Here is excellent evidence on the character of the offspring from an experienced ornithologist. Mr. J. A. Allen, in speaking (Mammals and Winter Birds of E. Florida, p. 229) of the later broods, after the accidental destruction of the first, says, that these "are found to be smaller and paler-coloured than those hatched earlier in the season. In cases where several broods are reared each year, as a general rule the birds of the earlier broods seem in all respects the most perfect and vigorous."

*(2) Hermann Muller has come to this same conclusion with respect to those female bees which are the first to emerge from the pupa each year. See his remarkable essay, "Anwendung der Darwin'schen Lehre auf Bienen," Verh. d. V. Jahrg., xxix., p. 45

But in very many cases the males which conquer their rivals, do not obtain possession of the females, independently of the choice of the latter. The courtship of animals is by no means so simple and short an affair as might be thought. The females are most excited by, or prefer pairing with, the more ornamented males, or those which are the best songsters, or play the best antics; but it is obviously probable that they would at the same time prefer the more vigorous and lively males, and this has in some cases been confirmed by actual observation.* Thus the more vigorous females, which are the first to breed, will have the choice of many males; and though they may not always select the strongest or best armed, they will select those which are vigorous and well armed, and in other respects the most attractive. Both sexes, therefore, of such early pairs would as above explained, have an advantage over others in

rearing offspring; and this apparently has sufficed during a long course of generations to add not only to the strength and fighting powers of the males, but likewise to their various ornaments or other attractions.

* With respect to poultry, I have received information, hereafter to be given, to this effect. Even birds, such as pigeons, which pair for life, the female, as I hear from Mr. Jenner Weir, will desert her mate if he is injured or grows weak.

In the converse and much rarer case of the males selecting particular females, it is plain that those which were the most vigorous and had conquered others, would have the freest choice; and it is almost certain that they would select vigorous as well as attractive females. Such pairs would have an advantage in rearing offspring, more especially if the male had the power to defend the female during the pairing-season as occurs with some of the higher animals, or aided her in providing for the young. The same principles would apply if each sex preferred and selected certain individuals of the opposite sex; supposing that they selected not only the more attractive, but likewise the more vigorous individuals.

Numerical Proportion of the Two Sexes. - I have remarked that sexual selection would be a simple affair if the males were considerably more numerous than the females. Hence I was led to investigate, as far as I could, the proportions between the two sexes of as many animals as possible; but the materials are scanty. I will here give only a brief abstract of the results, retaining the details for a supplementary discussion, so as not to interfere with the course of my argument. Domesticated animals alone afford the means of ascertaining the proportional numbers at birth; but no records have been specially kept for this purpose. By indirect means, however, I have collected a considerable body of statistics, from which it appears that with most of our domestic animals the sexes are nearly equal at birth. Thus 25,560 births of race-horses have been recorded during twenty-one years, and the male births were to the female births as 99.7 to 100. In greyhounds the inequality is greater than with any other animal, for out of 6878 births during twelve years, the male births were to the female as 110.1 to 100. It is, however, in some degree doubtful whether it is safe to infer that the proportion would be the same under natural conditions as under domestication; for slight and unknown differences in the conditions affect the proportion of the sexes. Thus with mankind, the male births in England are as 104.5, in Russia as 108.9, and with the Jews of Livonia as 120, to 100 female births. But I shall recur to this curious point of the excess of male births in the supplement to this chapter. At the Cape of Good Hope, however, male children of European extraction have been born during several years in the proportion of between 90 and 99 to 100 female children.

For our present purpose we are concerned with the proportions of the sexes, not only at birth, but also at maturity, and this adds another element of doubt; for it is a well-ascertained fact that with man the number of males dying before or during birth, and during the first two years of infancy, is considerably larger than that of females. So it almost certainly is with male lambs, and probably with some other animals. The males of some species kill one another by fighting; or they drive one another about until they become greatly emaciated. They must also be often exposed to various dangers, whilst wandering about in eager search for the females. In many kinds of fish the males are much smaller than the females, and they are believed often to be devoured by the latter, or by other fishes. The females of some birds appear to die earlier than the males; they are also liable to be destroyed on their nests, or whilst in charge of their young. With insects the female larvae are often larger than those of the males, and would consequently be more likely to be

devoured. In some cases the mature females are less active and less rapid in their movements than the males, and could not escape so well from danger. Hence, with animals in a state of nature, we must rely on mere estimation, in order to judge of the proportions of the sexes at maturity; and this is but little trustworthy, except when the inequality is strongly marked. Nevertheless, as far as a judgment can be formed, we may conclude from the facts given in the supplement, that the males of some few mammals, of many birds, of some fish and insects, are considerably more numerous than the females.

The proportion between the sexes fluctuates slightly during successive years: thus with race-horses, for every 100 mares born the stallions varied from 107.1 in one year to 92.6 in another year, and with greyhounds from 116.3 to 95.3. But had larger numbers been tabulated throughout an area more extensive than England, these fluctuations would probably have disappeared; and such as they are, would hardly suffice to lead to effective sexual selection in a state of nature. Nevertheless, in the cases of some few wild animals, as shewn in the supplement, the proportions seem to fluctuate either during different seasons or in different localities in a sufficient degree to lead to such selection. For it should be observed that any advantage, gained during certain years or in certain localities by those males which were able to conquer their rivals, or were the most attractive to the females, would probably be transmitted to the offspring, and would not subsequently be eliminated. During the succeeding seasons, when, from the equality of the sexes, every male was able to procure a female, the stronger or more attractive males previously produced would still have at least as good a chance of leaving offspring as the weaker or less attractive.

Polygamy. - The practice of polygamy leads to the same results as would follow from an actual inequality in the number of the sexes; for if each male secures two or more females, many males cannot pair; and the latter assuredly will be the weaker or less attractive individuals. Many mammals and some few birds are polygamous, but with animals belonging to the lower classes I have found no evidence of this habit. The intellectual powers of such animals are, perhaps, not sufficient to lead them to collect and guard a harem of females. That some relation exists between polygamy and the development of secondary sexual characters, appears nearly certain; and this supports the view that a numerical preponderance of males would be eminently favourable to the action of sexual selection. Nevertheless many animals, which are strictly monogamous, especially birds, display strongly-marked secondary sexual characters; whilst some few animals, which are polygamous, do not have such characters.

We will first briefly run through the mammals, and then turn to birds. The gorilla seems to be polygamous, and the male differs considerably from the female; so it is with some baboons, which live in herds containing twice as many adult females as males. In South America the *Mycetes caraya* present well-marked sexual differences, in colour, beard, and vocal organs; and the male generally lives with two or three wives: the male of the *Cebus capucinus* differs somewhat from the female, and appears to be polygamous.* Little is known on this head with respect to most other monkeys, but some species are strictly monogamous. The ruminants are eminently polygamous, and they present sexual differences more frequently than almost any other group of mammals; this holds good, especially in their weapons, but also in other characters. Most deer, cattle, and sheep are polygamous; as are most antelopes, though some are monogamous. Sir Andrew Smith, in speaking of the antelopes of South Africa, says that in herds of about a dozen there was rarely more than one mature male. The Asiatic Antelope saiga appears to be the most inordinate polygamist in the world; for Pallas*(2) states that the male drives away all rivals, and collects a herd of about a hundred females and kids together; the female is hornless and has softer hair, but does not otherwise differ much from the male. The wild horse of

the Falkland Islands and of the western states of N. America is polygamous, but, except in his greater size and in the proportions of his body, differs but little from the mare. The wild boar presents well-marked sexual characters, in his great tusks and some other points. In Europe and in India he leads a solitary life, except during the breeding-season; but as is believed by Sir W. Elliot, who has had many opportunities in India of observing this animal, he consorts at this season with several females. Whether this holds good in Europe is doubtful, but it is supported by some evidence. The adult male Indian elephant, like the boar, passes much of his time in solitude; but as Dr. Campbell states, when with others, "It is rare to find more than one male with a whole herd of females"; the larger males expelling or killing the smaller and weaker ones. The male differs from the female in his immense tusks, greater size, strength, and endurance; so great is the difference in these respects that the males when caught are valued at one-fifth more than the females.*⁽³⁾ The sexes of other pachydermatous animals differ very little or not at all, and, as far as known, they are not polygamists. Nor have I heard of any species in the Orders of Cheiroptera, Edentata, Insectivora and rodents being polygamous, excepting that amongst the rodents, the common rat, according to some rat-catchers, lives with several females. Nevertheless the two sexes of some sloths (Edentata) differ in the character and colour of certain patches of hair on their shoulders.*⁽⁴⁾ And many kinds of bats (Cheiroptera) present well-marked sexual differences, chiefly in the males possessing odoriferous glands and pouches, and by their being of a lighter colour.*⁽⁵⁾ In the great order of rodents, as far as I can learn, the sexes rarely differ, and when they do so, it is but slightly in the tint of the fur.

* On the Gorilla, Savage and Wyman, Boston Journal of Natural History, vol. v., 1845-47, p. 423. On Cynocephalus, Brehm, Illustriertes Thierleben, B. i., 1864, s. 77. On Mycetes, Rengger, Naturgeschichte der Säugethiere von Paraguay, 1830, ss. 14, 20. On Cebus, Brehm, *ibid.*, s. 108.

*⁽²⁾ Pallas, Spicilegia Zoolog., fasc. xii., 1777, p. 29. Sir Andrew Smith, Illustrations of the Zoology of S. Africa, 1849, pl. 29, on the Kobus. Owen, in his Anatomy of Vertebrates (vol. iii., 1868, p. 633) gives a table shewing incidentally which species of antelopes are gregarious.

*⁽³⁾ Dr. Campbell, in Proc., Zoolog. Soc., 1869, p. 138. See also an interesting paper by Lieut. Johnstone, in Proceedings, Asiatic Society of Bengal, May, 1868.

*⁽⁴⁾ Dr. Gray, in Annals and Magazine of Natural History, 1871, p. 302.

*⁽⁵⁾ See Dr. Dobson's excellent paper in Proceedings of the Zoological Society, 1873, p. 241.

As I hear from Sir Andrew Smith, the lion in South Africa sometimes lives with a single female, but generally with more, and, in one case, was found with as many as five females; so that he is polygamous. As far as I can discover, he is the only polygamist amongst all the terrestrial Carnivora, and he alone presents well-marked sexual characters. If, however, we turn to the marine Carnivora, as we shall hereafter see, the case is widely different; for many species of seals offer extraordinary sexual differences, and they are eminently polygamous. Thus, according to Peron, the male sea-elephant of the southern ocean always possesses several females, and the sea-lion of Forster is said to be surrounded by from twenty to thirty females. In the North, the male sea-bear of Steller is accompanied by even a greater number of females. It is an interesting fact, as Dr. Gill remarks,* that in the monogamous species, "or those living in small communities, there is little difference in size between the males and females; in the social species, or rather those of which the males have harems, the males are

vastly larger than the females."

* "The Eared Seals," *American Naturalist*, vol. iv., Jan. 1871.

Amongst birds, many species, the sexes of which differ greatly from each other, are certainly monogamous. In Great Britain we see well-marked sexual differences, for instance, in the wild-duck which pairs with a single female, the common blackbird, and the bullfinch which is said to pair for life. I am informed by Mr. Wallace that the like is true of chatterers or Cotingidae of South America, and of many other birds. In several groups I have not been able to discover whether the species are polygamous or monogamous. Lesson says that birds of paradise, so remarkable for their sexual differences, are polygamous, but Mr. Wallace doubts whether he had sufficient evidence. Mr. Salvin tells me he has been led to believe that humming-birds are polygamous. The male widow-bird, remarkable for his caudal plumes, certainly seems to be a polygamist.* I have been assured by Mr. Jenner Weir and by others, that it is somewhat common for three starlings to frequent the same nest; but whether this is a case of polygamy or polyandry has not been ascertained.

* The Ibis, vol. iii., 1861, p. 133, on the Progne widow-bird. See also on the *Vidua axillaris*, *ibid.*, vol. ii., 1860, p. 211. On the polygamy of the capercaillie and great bustard, see L. Lloyd, *Game Birds of Sweden*, 1867, pp. 19, and 182. Montagu and Selby speak of the black grouse as polygamous and of the red grouse as monogamous.

The Gallinaceae exhibit almost as strongly marked sexual differences as birds of paradise or humming-birds, and many of the species are, as is well known, polygamous; others being strictly monogamous. What a contrast is presented between the sexes of the polygamous peacock or pheasant, and the monogamous guinea-fowl or partridge! Many similar cases could be given, as in the grouse tribe, in which the males of the polygamous capercaillie and black-cock differ greatly from the females; whilst the sexes of the monogamous red grouse and ptarmigan differ very little. In the Cursores, except amongst the bustards, few species offer strongly-marked sexual differences, and the great bustard (*Otis tarda*) is said to be polygamous. With the Grallatores, extremely few species differ sexually, but the ruff (*Machetes pugnax*) affords a marked exception, and this species is believed by Montagu to be a polygamist. Hence it appears that amongst birds there often exists a close relation between polygamy and the development of strongly-marked sexual differences. I asked Mr. Bartlett, of the Zoological Gardens, who has had very large experience with birds, whether the male tragopan (one of the Gallinaceae) was polygamous, and I was struck by his answering, "I do not know, but should think so from his splendid colours."

It deserves notice that the instinct of pairing with a single female is easily lost under domestication. The wild-duck is strictly monogamous, the domestic-duck highly polygamous. The Rev. W. D. Fox informs me that out of some half-tamed wild-ducks, on a large pond in his neighborhood, so many mallards were shot by the game-keeper that only one was left for every seven or eight females; yet unusually large broods were reared. The guinea-fowl is strictly monogamous; but Mr. Fox finds that his birds succeed best when he keeps one cock to two or three hens. Canary-birds pair in a state of nature, but the breeders in England successfully put one male to four or five females. I have noticed these cases, as rendering it probable that wild monogamous species might readily become either temporarily or permanently polygamous.

Too little is known of the habits of reptiles and fishes to enable us to speak of their marriage arrangements. The stickle-back (*Gasterosteus*), however, is said to be a polygamist;* and the male during the breeding-season differs conspicuously from the female.

To sum up on the means through which, as far as we can judge, sexual selection has led to the development of secondary sexual characters. It has been shewn that the largest number of vigorous offspring will be reared from the pairing of the strongest and best-armed males, victorious in contests over other males, with the most vigorous and best-nourished females, which are the first to breed in the spring. If such females select the more attractive, and at the same time vigorous males, they will rear a larger number of offspring than the retarded females, which must pair with the less vigorous and less attractive males. So it will be if the more vigorous males select the more attractive and at the same time healthy and vigorous females; and this will especially hold good if the male defends the female, and aids in providing food for the young. The advantage thus gained by the more vigorous pairs in rearing a larger number of offspring has apparently sufficed to render sexual selection efficient. But a large numerical preponderance of males over females will be still more efficient; whether the preponderance is only occasional and local, or permanent; whether it occurs at birth, or afterwards from the greater destruction of the females; or whether it indirectly follows from the practice of polygamy.

The Male generally more modified than the Female.- Throughout the animal kingdom, when the sexes differ in external appearance, it is, with rare exceptions, the male which has been the more modified; for, generally, the female retains a closer resemblance to the young of her own species, and to other adult members of the same group. The cause of this seems to lie in the males of almost all animals having stronger passions than the females. Hence it is the males that fight together and sedulously display their charms before the females; and the victors transmit their superiority to their male offspring. Why both sexes do not thus acquire the characters of their fathers, will be considered hereafter. That the males of all mammals eagerly pursue the females is notorious to every one. So it is with birds; but many cock birds do not so much pursue the hen, as display their plumage, perform strange antics, and pour forth their song in her presence. The male in the few fish observed seems much more eager than the female; and the same is true of alligators, and apparently of batrachians. Throughout the enormous class of insects, as Kirby remarks, "the law is that the male shall seek the female."* Two good authorities, Mr. Blackwell and Mr. C. Spence Bate, tell me that the males of spiders and crustaceans are more active and more erratic in their habits than the females. When the organs of sense or locomotion are present in the one sex of insects and crustaceans and absent in the other, or when, as is frequently the case, they are more highly developed in the one than in the other, it is, as far as I can discover, almost invariably the male which retains such organs, or has them most developed; and this shews that the male is the more active member in the courtship of the sexes.*(2)

* Kirby and Spence, Introduction to Entomology, vol. iii., 1826, p. 342.

*(2) One parasitic hymenopterous insect (Westwood, Modern Class. of Insects, vol. ii., p. 160) forms an exception to the rule, as the male has rudimentary wings, and never quits the cell in which it is born, whilst the female has well-developed wings. Audouin believes that the females of this species are impregnated by the males which are born in the same cells with them; but it is much more probable that the females visit other cells, so that close inter-breeding is thus avoided. We shall hereafter meet in various classes, with a few exceptional cases, in which the female, instead of the male, is the seeker and wooer.

The female, on the other hand, with the rarest exceptions, is less

eager than the male. As the illustrious Hunter* long ago observed, she generally "requires to be courted"; she is coy, and may often be seen endeavouring for a long time to escape from the male. Every observer of the habits of animals will be able to call to mind instances of this kind. It is shown by various facts, given hereafter, and by the results fairly attributable to sexual selection, that the female, though comparatively passive, generally exerts some choice and accepts one male in preference to others. Or she may accept, as appearances would sometimes lead us to believe, not the male which is the most attractive to her, but the one which is the least distasteful. The exertion of some choice on the part of the female seems a law almost as general as the eagerness of the male.

* Essays and Observations, edited by Owen, vol. i., 1861, p. 194.

We are naturally led to enquire why the male, in so many and such distinct classes, has become more eager than the female, so that he searches for her, and plays the more active part in courtship. It would be no advantage and some loss of power if each sex searched for the other; but why should the male almost always be the seeker? The ovules of plants after fertilisation have to be nourished for a time; hence the pollen is necessarily brought to the female organs-being placed on the stigma, by means of insects or the wind, or by the spontaneous movements of the stamens; and in the Algae, &c., by the locomotive power of the antherozoids. With lowly-organised aquatic animals, permanently affixed to the same spot and having their sexes separate, the male element is invariably brought to the female; and of this we can see the reason, for even if the ova were detached before fertilisation, and did not require subsequent nourishment or protection, there would yet be greater difficulty in transporting them than the male element, because, being larger than the latter, they are produced in far smaller numbers. So that many of the lower animals are, in this respect, analogous with plants.* The males of affixed and aquatic animals having been led to emit their fertilising element in this way, it is natural that any of their descendants, which rose in the scale and became locomotive, should retain the same habit; and they would approach the female as closely as possible, in order not to risk the loss of the fertilising element in a long passage of it through the water. With some few of the lower animals, the females alone are fixed, and the males of these must be the seekers. But it is difficult to understand why the males of species, of which the progenitors were primordially free, should invariably have acquired the habit of approaching the females, instead of being approached by them. But in all cases, in order that the males should seek efficiently, it would be necessary that they should be endowed with strong passions; and the acquirement of such passions would naturally follow from the more eager leaving a larger number of offspring than the less eager.

* Prof. Sachs (Lehrbuch der Botanik, 1870, S. 633) in speaking of the male and female reproductive cells, remarks, "verhalt sich die eine bei der Vereinigung activ, ... die andere erscheint bei der Vereinigung passiv."

The great eagerness of the males has thus indirectly led to their much more frequently developing secondary sexual characters than the females. But the development of such characters would be much aided, if the males were more liable to vary than the females- as I concluded they were- after a long study of domesticated animals. Von Nathusius, who has had very wide experience, is strongly of the same opinion.* Good evidence also in favour of this conclusion can be produced by a comparison of the two sexes in mankind. During the Novara expedition*(2) a vast number of measurements was made of various parts of the body in different races, and the men were found in almost every case to present a greater range of variation than

the women; but I shall have to recur to this subject in a future chapter. Mr. J. Wood,*⁽³⁾ who has carefully attended to the variation of the muscles in man, puts in italics the conclusion that "the greatest number of abnormalities in each subject is found in the males." He had previously remarked that "altogether in 102 subjects, the varieties of redundancy were found to be half as many again as in females, contrasting widely with the greater frequency of deficiency in females before described." Professor Macalister likewise remarks*⁽⁴⁾ that variations in the muscles "are probably more common in males than females." Certain muscles which are not normally present in mankind are also more frequently developed in the male than in the female sex, although exceptions to this rule are said to occur. Dr. Burt Wilder*⁽⁵⁾ has tabulated the cases of 152 individuals with supernumerary digits, of which 86 were males, and 39, or less than half, females, the remaining 27 being of unknown sex. It should not, however, be overlooked that women would more frequently endeavour to conceal a deformity of this kind than men. Again, Dr. L. Meyer asserts that the ears of man are more variable in form than those of a woman.*⁽⁶⁾ Lastly the temperature is more variable in man than in woman.*⁽⁷⁾

* Vortrage uber Viehzucht, 1872, p. 63.

*⁽²⁾ Reise der Novara: Anthropolog. Theil, 1867, ss. 216-269. The results were calculated by Dr. Weisbach from measurements made by Drs. K. Scherzer and Schwarz. On the greater variability of the males of domesticated animals, see my Variation of Animals and Plants under Domestication, vol. ii., 1868, p. 75.

*⁽³⁾ Proceedings of the Royal Society, vol. xvi., July, 1868, pp. 519 and 524.

*⁽⁴⁾ Proc. Royal Irish Academy, vol. x., 1868, p. 123.

*⁽⁵⁾ Mass. Medical Society, ii., No. 3, 1868, p. 9.

*⁽⁶⁾ Archiv fur Path. Anat. und Phys., 1871, p. 488.

*⁽⁷⁾ The conclusions recently arrived at by Dr. J. Stockton Hough, on the temperature of man, are given in the Pop. Sci. Review, Jan. 1, 1874, p. 97.

The cause of the greater general variability in the male sex, than in the female is unknown, except in so far as secondary sexual characters are extraordinarily variable, and are usually confined to the males; and, as we shall presently see, this fact is, to a certain extent, intelligible. Through the action of sexual and natural selection male animals have been rendered in very many instances widely different from their females; but independently of selection the two sexes, from differing constitutionally, tend to vary in a somewhat different manner. The female has to expend much organic matter in the formation of her ova, whereas the male expends much force in fierce contests with his rivals, in wandering about in search of the female, in exerting his voice, pouring out odoriferous secretions, &c.: and this expenditure is generally concentrated within a short period. The great vigour of the male during the season of love seems often to intensify his colours, independently of any marked difference from the female.* In mankind, and even as low down in the organic scale as in the Lepidoptera, the temperature of the body is higher in the male than in the female, accompanied in the case of man by a slower pulse.*⁽²⁾ On the whole the expenditure of matter and force by the two sexes is probably nearly equal, though effected in very different ways and at different rates.

* Prof. Mantegazza is inclined to believe ("Lettera a Carlo Darwin," Archivio per l'Anthropologia, 1871, p. 306) that the bright colours, common in so many male animals, are due to the presence and retention by them of the spermatic fluid; but this can hardly be the case; for many male birds, for instance young pheasants, become brightly coloured in the autumn of their first year.

*⁽²⁾ For mankind, see Dr. J. Stockton Hough, whose conclusions are

given in the Popular Science Review, 1874, p. 97. See Girard's observations on the Lepidoptera, as given in the Zoological Record, 1869, p. 347.

From the causes just specified the two sexes can hardly fail to differ somewhat in constitution, at least during the breeding-season; and, although they may be subjected to exactly the same conditions, they will tend to vary in a different manner. If such variations are of no service to either sex, they will not be accumulated and increased by sexual or natural selection. Nevertheless, they may become permanent if the exciting cause acts permanently; and in accordance with a frequent form of inheritance they may be transmitted to that sex alone in which they first appeared. In this case the two sexes will come to present permanent, yet unimportant, differences of character. For instance, Mr. Allen shews that with a large number of birds inhabiting the northern and southern United States, the specimens from the south are darker-coloured than those from the north; and this seems to be the direct result of the difference in temperature, light, &c., between the two regions. Now, in some few cases, the two sexes of the same species appear to have been differently affected; in the *Agelaius phoeniceus* the males have had their colours greatly intensified in the south; whereas with *Cardinalis virginianus* it is the females which have been thus affected; with *Quiscalus major* the females have been rendered extremely variable in tint, whilst the males remain nearly uniform.*

* Mammals and Birds of E. Florida, pp. 234, 280, 295.

A few exceptional cases occur in various classes of animals, in which the females instead of the males have acquired well pronounced secondary sexual characters, such as brighter colours, greater size, strength, or pugnacity. With birds there has sometimes been a complete transposition of the ordinary characters proper to each sex; the females having become the more eager in courtship, the males remaining comparatively passive, but apparently selecting the more attractive females, as we may infer from the results. Certain hen birds have thus been rendered more brightly coloured or otherwise ornamented, as well as more powerful and pugnacious than the cocks; these characters being transmitted to the female offspring alone.

It may be suggested that in some cases a double process of selection has been carried on; that the males have selected the more attractive females, and the latter the more attractive males. This process, however, though it might lead to the modification of both sexes, would not make the one sex different from the other, unless indeed their tastes for the beautiful differed; but this is a supposition too improbable to be worth considering in the case of any animal, excepting man. There are, however, many animals in which the sexes resemble each other, both being furnished with the same ornaments, which analogy would lead us to attribute to the agency of sexual selection. In such cases it may be suggested with more plausibility, that there has been a double or mutual process of sexual selection; the more vigorous and precocious females selecting the more attractive and vigorous males, the latter rejecting all except the more attractive females. But from what we know of the habits of animals, this view is hardly probable, for the male is generally eager to pair with any female. It is more probable that the ornaments common to both sexes were acquired by one sex, generally the male, and then transmitted to the offspring of both sexes. If, indeed, during a lengthened period the males of any species were greatly to exceed the females in number, and then during another lengthened period, but under different conditions, the reverse were to occur, a double, but not simultaneous, process of sexual selection might easily be carried on, by which the two sexes might be rendered widely different. We shall hereafter see that many animals exist, of which neither sex

is brilliantly coloured or provided with special ornaments, and yet the members of both sexes or of one alone have probably acquired simple colours, such as white or black, through sexual selection. The absence of bright tints or other ornaments may be the result of variations of the right kind never having occurred, or of the animals themselves having preferred plain black or white. Obscure tints have often been developed through natural selection for the sake of protection, and the acquirement through sexual selection of conspicuous colours, appears to have been sometimes checked from the danger thus incurred. But in other cases the males during long ages may have struggled together for the possession of the females, and yet no effect will have been produced, unless a larger number of offspring were left by the more successful males to inherit their superiority, than by the less successful: and this, as previously shewn, depends on many complex contingencies.

Sexual selection acts in a less rigorous manner than natural selection. The latter produces its effects by the life or death at all ages of the more or less successful individuals. Death, indeed, not rarely ensues from the conflicts of rival males. But generally the less successful male merely fails to obtain a female, or obtains a retarded and less vigorous female later in the season, or, if polygamous, obtains fewer females; so that they leave fewer, less vigorous, or no offspring. In regard to structures acquired through ordinary or natural selection, there is in most cases, as long as the conditions of life remain the same, a limit to the amount of advantageous modification in relation to certain special purposes; but in regard to structures adapted to make one male victorious over another, either in fighting or in charming the female, there is no definite limit to the amount of advantageous modification; so that as long as the proper variations arise the work of sexual selection will go on. This circumstance may partly account for the frequent and extraordinary amount of variability presented by secondary sexual characters. Nevertheless, natural selection will determine that such characters shall not be acquired by the victorious males, if they would be highly injurious, either by expending too much of their vital powers, or by exposing them to any great danger. The development, however, of certain structures- of the horns, for instance, in certain stags- has been carried to a wonderful extreme; and in some cases to an extreme which, as far as the general conditions of life are concerned, must be slightly injurious to the male. From this fact we learn that the advantages which favoured males derive from conquering other males in battle or courtship, and thus leaving a numerous progeny, are in the long run greater than those derived from rather more perfect adaptation to their conditions of life. We shall further see, and it could never have been anticipated, that the power to charm the female has sometimes been more important than the power to conquer other males in battle.

LAWS OF INHERITANCE.

In order to understand how sexual selection has acted on many animals of many classes, and in the course of ages has produced a conspicuous result, it is necessary to bear in mind the laws of inheritance, as far as they are known. Two distinct elements are included under the term "inheritance"- the transmission, and the development of characters; but as these generally go together, the distinction is often overlooked. We see this distinction in those characters which are transmitted through the early years of life, but are developed only at maturity or during old age. We see the same distinction more clearly with secondary sexual characters, for these are transmitted through both sexes, though developed in one alone. That they are present in both sexes, is manifest when two species, having strongly-marked sexual characters, are crossed, for each transmits the characters proper to its own male and female sex to the hybrid offspring of either sex. The same fact is likewise

manifest, when characters proper to the male are occasionally developed in the female when she grows old or becomes diseased, as, for instance, when the common hen assumes the flowing tail-feathers, hackles, comb, spurs, voice, and even pugnacity of the cock. Conversely, the same thing is evident, more or less plainly, with castrated males. Again, independently of old age or disease, characters are occasionally transferred from the male to the female, as when, in certain breeds of the fowl, spurs regularly appear in the young and healthy females. But in truth they are simply developed in the female; for in every breed each detail in the structure of the spur is transmitted through the female to her male offspring. Many cases will hereafter be given, where the female exhibits, more or less perfectly, characters proper to the male, in whom they must have been first developed, and then transferred to the female. The converse case of the first development of characters in the female and of transference to the male, is less frequent; it will therefore be well to give one striking instance. With bees the pollen-collecting apparatus is used by the female alone for gathering pollen for the larvae, yet in most of the species it is partially developed in the males to whom it is quite useless, and it is perfectly developed in the males of *Bombus* or the humble-bee.* As not a single other hymenopterous insect, not even the wasp, which is closely allied to the bee, is provided with a pollen-collecting apparatus, we have no grounds for supposing that male bees primordially collected pollen as well as the females; although we have some reason to suspect that male mammals primordially suckled their young as well as the females. Lastly, in all cases of reversion, characters are transmitted through two, three, or many more generations, and are then developed under certain unknown favourable conditions. This important distinction between transmission and development will be best kept in mind by the aid of the hypothesis of pangenesis. According to this hypothesis, every unit or cell of the body throws off gemmules or undeveloped atoms, which are transmitted to the offspring of both sexes, and are multiplied by self-division. They may remain undeveloped during the early years of life or during successive generations; and their development into units or cells, like those from which they were derived, depends on their affinity for, and union with other units or cells previously developed in the due order of growth.

* H. Muller, "Anwendung der Darwin'schen Lehre, &c.," Verh. d. n. V. Jahrg., xxix. p. 42.

Inheritance at corresponding Periods of Life. - This tendency is well established. A new character, appearing in a young animal, whether it lasts throughout life or is only transient, will, in general, reappear in the offspring at the same age and last for the same time. If, on the other hand, a new character appears at maturity, or even during old age, it tends to reappear in the offspring at the same advanced age. When deviations from this rule occur, the transmitted characters much oftener appear before, than after the corresponding age. As I have dwelt on this subject sufficiently in another work,* I will here merely give two or three instances, for the sake of recalling the subject to the reader's mind. In several breeds of the fowl, the down-covered chickens, the young birds in their first true plumage, and the adults differ greatly from one another, as well as from their common parent-form, the *Gallus bankiva*; and these characters are faithfully transmitted by each breed to their offspring at the corresponding periods of life. For instance, the chickens of spangled Hamburgs, whilst covered with down have a few dark spots on the head and rump, but are not striped longitudinally, as in many other breeds; in their first true plumage, "they are beautifully pencilled," that is each feather is transversely marked by numerous dark bars; but in their second plumage the feathers all become spangled or tipped with a dark round spot.*(2) Hence in this breed

variations transmitted at, and been transmitted to, three distinct periods of life. The pigeon offers a more remarkable case, because the aboriginal parent species does not undergo any change of plumage with advancing age, excepting that at maturity the breast becomes more iridescent; yet there are breeds which do not acquire their characteristic colours until they have moulted two, three, or four times; and these modifications of plumage are regularly transmitted.

* The Variation of Animals and Plants under Domestication, vol. ii., 1868, p. 75. In the last chapter but one, the provisional hypothesis of pangenesis, above alluded to, is fully explained.

*(2) These facts are given on the high authority of a great breeder, Mr. Teebay; see Tegetmeier's Poultry Book, 1868, p. 158. On the characters of chickens of different breeds, and on the breeds of the pigeon, alluded to in the following paragraph, see Variation of Animals, &c., vol. i., pp. 160, 249; vol. ii., p. 77.

Inheritance at corresponding Seasons of the Year. - With animals in a state of nature, innumerable instances occur of characters appearing periodically at different seasons. We see this in the horns of the stag, and in the fur of arctic animals which becomes thick and white during the winter. Many birds acquire bright colours and other decorations during the breeding-season alone. Pallas states,* that in Siberia domestic cattle and horses become lighter-coloured during the winter; and I have myself observed, and heard of similar strongly marked changes of colour, that is, from brownish cream-colour or reddish-brown to a perfect white, in several ponies in England. Although I do not know that this tendency to change the colour of the coat during different seasons is transmitted, yet it probably is so, as all shades of colour are strongly inherited by the horse. Nor is this form of inheritance, as limited by the seasons, more remarkable than its limitation by age or sex.

* *Novae species Quadrupedum e Glirium ordine*, 1778, p. 7. On the transmission of colour by the horse, see Variation of Animals and Plants under Domestication, vol. i., p. 51. Also vol. ii., p. 71, for a general discussion on "Inheritance as limited by Sex."

Inheritance as Limited by Sex. - The equal transmission of characters to both sexes is the commonest form of inheritance, at least with those animals which do not present strongly-marked sexual differences, and indeed with many of these. But characters are somewhat commonly transferred exclusively to that sex, in which they first appear. Ample evidence on this head has been advanced in my work on Variation under Domestication, but a few instances may here be given. There are breeds of the sheep and goat, in which the horns of the male differ greatly in shape from those of the female; and these differences, acquired under domestication, are regularly transmitted to the same sex. As a rule, it is the females alone in cats which are tortoise-shell, the corresponding colour in the males being rusty-red. With most breeds of the fowl, the characters proper to each sex are transmitted to the same sex alone. So general is this form of transmission that it is an anomaly when variations in certain breeds are transmitted equally to both sexes. There are also certain sub-breeds of the fowl in which the males can hardly be distinguished from one another, whilst the females differ considerably in colour. The sexes of the pigeon in the parent-species do not differ in any external character; nevertheless, in certain domesticated breeds the male is coloured differently from the female.* The wattle in the English carrier pigeon, and the crop in the pouter, are more highly developed in the male than in the female; and although these characters have been gained through long-continued selection by man, the slight differences between the sexes are wholly due to the form of inheritance which has prevailed; for they have arisen, not from, but

rather in opposition to, the wish of the breeder.

* Dr. Chapuis, *Le Pigeon Voyageur Belge*, 1865, p. 87. Boitard et Corbie, *Les Pigeons de Voliere, &c.*, 1824, p. 173. See, also, on similar differences in certain breeds at Modena, *Le variazioni dei Colombi domestici*, del Paolo Bonizzi, 1873.

Most of our domestic races have been formed by the accumulation of many slight variations; and as some of the successive steps have been transmitted to one sex alone, and some to both sexes, we find in the different breeds of the same species all gradations between great sexual dissimilarity and complete similarity. Instances have already been given with the breeds of the fowl and pigeon, and under nature analogous cases are common. With animals under domestication, but whether in nature I will not venture to say, one sex may lose characters proper to it, and may thus come somewhat to resemble the opposite sex; for instance, the males of some breeds of the fowl have lost their masculine tail-plumes and hackles. On the other hand, the differences between the sexes may be increased under domestication, as with merino sheep, in which the ewes have lost their horns. Again, characters proper to one sex may suddenly appear in the other sex; as in those sub-breeds of the fowl in which the hens acquire spurs whilst young; or, as in certain Polish sub-breeds, in which the females, as there is reason to believe, originally acquired a crest, and subsequently transferred it to the males. All these cases are intelligible on the hypothesis of pangenesis; for they depend on the gemmules of certain parts, although present in both sexes, becoming, through the influence of domestication, either dormant or developed in either sex.

There is one difficult question which it will be convenient to defer to a future chapter; namely, whether a character at first developed in both sexes, could through selection be limited in its development to one sex alone. If, for instance, a breeder observed that some of his pigeons (of which the characters are usually transferred in an equal degree to both sexes) varied into pale blue, could he by long-continued selection make a breed, in which the males alone should be of this tint, whilst the females remained unchanged? I will here only say, that this, though perhaps not impossible, would be extremely difficult; for the natural result of breeding from the pale-blue males would be to change the whole stock of both sexes to this tint. If, however, variations of the desired tint appeared, which were from the first limited in their development to the male sex, there would not be the least difficulty in making a breed with the two sexes of a different colour, as indeed has been effected with a Belgian breed, in which the males alone are streaked with black. In a similar manner, if any variation appeared in a female pigeon, which was from the first sexually limited in its development to the females, it would be easy to make a breed with the females alone thus characterised; but if the variation was not thus originally limited, the process would be extremely difficult, perhaps impossible.*

* Since the publication of the first edition of this work, it has been highly satisfactory to me to find the following remarks (the *Field*, Sept., 1872) from so experienced a breeder as Mr. Tegetmeier. After describing some curious cases in pigeons, of the transmission of colour by one sex alone, and the formation of a sub-breed with this character, he says: "It is a singular circumstance that Mr. Darwin should have suggested the possibility of modifying the sexual colours of birds by a course of artificial selection. When he did so, he was in ignorance of these facts that I have related; but it is remarkable how very closely he suggested the right method of procedure."

On the Relation between the Period of Development of a Character and its Transmission to one Sex or to both Sexes. - Why certain

characters, and other characters by one sex alone, namely by that sex in which the character first appeared, is in most cases quite unknown. We cannot even conjecture why with certain sub-breeds of the pigeon, black striae, though transmitted through the female, should be developed in the male alone, whilst every other character is equally transferred to both sexes. Why, again, with cats, the tortoise-shell colour should, with rare exceptions, be developed in the female alone. The very same character, such as deficient or super-numerary digits, colour-blindness, &c., may with mankind be inherited by the males alone of one family, and in another family by the females alone, though in both cases transmitted through the opposite as well as through the same sex.* Although we are thus ignorant, the two following rules seem often to hold good- that variations which first appear in either sex at a late period of life tend to be developed in the same sex alone; whilst variations which first appear early in life in either sex tend to be developed in both sexes. I am, however, far from supposing that this is the sole determining cause. As I have not elsewhere discussed this subject, and it has an important bearing on sexual selection, I must here enter into lengthy and somewhat intricate details.

* References are given in my *Variation of Animals and Plants under Domestication*, vol. ii., p. 72.

It is in itself probable that any character appearing at an early age would tend to be inherited equally by both sexes, for the sexes do not differ much in constitution before the power of reproduction is gained. On the other hand, after this power has been gained and the sexes have come to differ in constitution, the gemmules (if I may again use the language of pangenesis) which are cast off from each varying part in the one sex would be much more likely to possess the proper affinities for uniting with the tissues of the same sex, and thus becoming developed, than with those of the opposite sex.

I was first led to infer that a relation of this kind exists, from the fact that whenever and in whatever manner the adult male differs from the adult female, he differs in the same manner from the young of both sexes. The generality of this fact is quite remarkable: it holds good with almost all mammals, birds, amphibians, and fishes; also with many crustaceans, spiders, and some few insects, such as certain Orthoptera and Libellulæ. In all these cases the variations, through the accumulation of which the male acquired his proper masculine characters, must have occurred at a somewhat late period of life; otherwise the young males would have been similarly characterised; and conformably with our rule, the variations are transmitted to and developed in the adult males alone. When, on the other hand, the adult male closely resembles the young of both sexes (these, with rare exceptions, being alike), he generally resembles the adult female; and in most of these cases the variations through which the young and old acquired their present characters, probably occurred, according to our rule, during youth. But there is here room for doubt, for characters are sometimes transferred to the offspring at an earlier age than that at which they first appeared in the parents, so that the parents may have varied when adult, and have transferred their characters to their offspring whilst young. There are, moreover, many animals, in which the two sexes closely resemble each other, and yet both differ from their young: and here the characters of the adults must have been acquired late in life; nevertheless, these characters, in apparent contradiction to our rule, are transferred to both sexes. We must not however, overlook the possibility or even probability of successive variations of the same nature occurring, under exposure to similar conditions, simultaneously in both sexes at a rather late period of life; and in this case the variations would be transferred to the offspring of both sexes at a corresponding late age; and there would then be no real contradiction to the rule that variations occurring late in life are

transferred exclusively to the sex in which they first appeared. This latter rule seems to hold true more generally than the second one, namely, that variations which occur in either sex early in life tend to be transferred to both sexes. As it was obviously impossible even to estimate in how large a number of cases throughout the animal kingdom these two propositions held good, it occurred to me to investigate some striking or crucial instances, and to rely on the result.

An excellent case for investigation is afforded by the deer family. In all the species, but one, the horns are developed only in the males, though certainly transmitted through the females, and capable of abnormal development in them. In the reindeer, on the other hand, the female is provided with horns; so that in this species, the horns ought, according to our rule, to appear early in life, long before the two sexes are mature and have come to differ much in constitution. In all the other species the horns ought to appear later in life, which would lead to their development in that sex alone, in which they first appeared in the progenitor of the whole family. Now in seven species, belonging to distinct sections of the family and inhabiting different regions, in which the stags alone bear horns, I find that the horns first appear at periods, varying from nine months after birth in the roebuck to ten, twelve or even more months in the stags of the six other and larger species.* But with the reindeer the case is widely different; for, as I hear from Prof. Nilsson, who kindly made enquiries for me in Lapland, the horns appear in the young animals within four or five weeks after birth, and at the same time in both sexes. So that here we have a structure, developed at a most unusually early age in one species of the family, and likewise common to both sexes in this one species alone.

* I am much obliged to Mr. Cupples for having made enquiries for me in regard to the roebuck and red deer of Scotland from Mr. Robertson, the experienced head-forester to the Marquis of Breadalbane. In regard to fallow-deer, I have to thank Mr. Eyton and others for information. For the *Cervus alces* of N. America, see Land and Water, 1868, pp. 221 and 254; and for the *C. Virginianus* and *C. stronglyloceros* of the same continent, see J. D. Caton, in Ottawa Acad. of Nat. Sc., 1868, p. 13. For *Cervus eldi* of Pegu, see Lieut. Beaven, Proceedings of the Zoological Society, 1867, p. 762.

In several kinds of antelopes, only the males are provided with horns, whilst in the greater number both sexes bear horns. With respect to the period of development, Mr. Blyth informs me that there was at one time in the Zoological Gardens a young koodoo (*A. strepsiceros*), of which the males alone are horned, and also the young of a closely-allied species, the eland (*A. oreas*), in which both sexes are horned. Now it is in strict conformity with our rule, that in the young male koodoo, although ten months old, the horns were remarkably small, considering the size ultimately attained by them; whilst in the young male eland, although only three months old, the horns were already very much larger than in the koodoo. It is also a noticeable fact that in the prong-horned antelope,* only a few of the females, about one in five, have horns, and these are in a rudimentary state, though sometimes above four inches long: so that as far as concerns the possession of horns by the males alone, this species is in an intermediate condition, and the horns do not appear until about five or six months after birth. Therefore in comparison with what little we know of the development of the horns in other antelopes, and from what we do know with respect to the horns of deer, cattle, &c., those of the prong-horned antelope appear at an intermediate period of life, - that is, not very early, as in cattle and sheep, nor very late, as in the larger deer and antelopes. The horns of sheep, goats, and cattle, which are well developed in both sexes, though not quite equal in size, can be felt, or even seen, at birth or soon afterwards.*(2) Our rule, however, seems to fail in some

breeds of sheep, for instance merinos, in which the rams alone are horned; for I cannot find on enquiry,*⁽³⁾ that the horns are developed later in life in this breed than in ordinary sheep in which both sexes are horned. But with domesticated sheep the presence or absence of horns is not a firmly fixed character; for a certain proportion of the merino ewes bear small horns, and some of the rams are hornless; and in most breeds hornless ewes are occasionally produced.

* *Antilocapra Americana*. I have to thank Dr. Canfield for information with respect to the horns of the female: see also his paper in Proceedings of the Zoological Society, 1866, p. 109. Also Owen, *Anatomy of Vertebrates*, vol. iii., p. 627.

*⁽²⁾ I have been assured that the horns of the sheep in north Wales can always be felt, and are sometimes even an inch in length, at birth. Youatt says (*Cattle*, 1834, p. 277), that the prominence of the frontal bone in cattle penetrates the cutis at birth, and that the horny matter is soon formed over it.

*⁽³⁾ I am greatly indebted to Prof. Victor Carus for having made enquiries for me, from the highest authorities, with respect to the merino sheep of Saxony. On the Guinea coast of Africa there is, however, a breed of sheep in which, as with merinos, the rams alone bear horns; and Mr. Winwood Reade informs me that in one case observed by him, a young ram, born on Feb. 10th, first shewed horns on March 6th, so that in this instance, in conformity with rule, the development of the horns occurred at a later period of life than in Welsh sheep, in which both sexes are horned.

Dr. W. Marshall has lately made a special study of the protuberances so common on the heads of birds,* and he comes to the following conclusion: - that with those species in which they are confined to the males, they are developed late in life; whereas with those species in which they are common to the two sexes, they are developed at a very early period. This is certainly a striking confirmation of my two laws of inheritance.

* "Über die knöchernen Schadelhöcker der Vogel", in the *Niederland. Archiv für Zoologie*, B. i., Heft 2, 1872.

In most of the species of the splendid family of the pheasants, the males differ conspicuously from the females, and they acquire their ornaments at a rather late period of life. The eared pheasant (*Crossoptilon auritum*), however, offers a remarkable exception, for both sexes possess the fine caudal plumes, the large ear-tufts and the crimson velvet about the head; I find that all these characters appear very early in life in accordance with rule. The adult male can, however, be distinguished from the adult female by the presence of spurs; and conformably with our rule, these do not begin to be developed before the age of six months, as I am assured by Mr. Bartlett, and even at this age, the two sexes can hardly be distinguished.* The male and female peacock differ conspicuously from each other in almost every part of their plumage, except in the elegant head-crest, which is common to both sexes; and this is developed very early in life, long before the other ornaments, which are confined to the male. The wild-duck offers an analogous case, for the beautiful green speculum on the wings is common to both sexes, though duller and somewhat smaller in the female, and it is developed early in life, whilst the curled tail-feathers and other ornaments of the male are developed later.*⁽²⁾ Between such extreme cases of close sexual resemblance and wide dissimilarity, as those of the *Crossoptilon* and peacock, many intermediate ones could be given, in which the characters follow our two rules in their order of development.

* In the common peacock (*Pavo cristatus*) the male alone possesses spurs, whilst both sexes of the Java peacock (*P. muticus*) offer the

unusual case of being furnished with spurs. Hence I fully expected that in the latter species they would have been developed earlier in life than in the common peacock; but M. Hegt of Amsterdam informs me, that with young birds of the previous year, of both species, compared on April 23rd, 1869, there was no difference in the development of the spurs. The spurs, however, were as yet represented merely by slight knobs or elevations. I presume that I should have been informed if any difference in the rate of development had been observed subsequently.

* (2) In some other species of the duck family the speculum differs in a greater degree in the two sexes; but I have not been able to discover whether its full development occurs later in life in the males of such species, than in the male of the common duck, as ought to be the case according to our rule. With the allied *Mergus cucullatus* we have, however, a case of this kind: the two sexes differ conspicuously in general plumage, and to a considerable degree in the speculum, which is pure white in the male and greyish-white in the female. Now the young males at first entirely resemble the females, and have a greyish-white speculum, which becomes pure white at an earlier age than that at which the adult male acquires his other and more strongly-marked sexual differences: see Audubon, *Ornithological Biography*, vol. iii., 1835, pp. 249-250.

As most insects emerge from the pupal state in a mature condition, it is doubtful whether the period of development can determine the transference of their characters to one or to both sexes. But we do not know that the coloured scales, for instance, in two species of butterflies, in one of which the sexes differ in colour, whilst in the other they are alike, are developed at the same relative age in the cocoon. Nor do we know whether all the scales are simultaneously developed on the wings of the same species of butterfly, in which certain coloured marks are confined to one sex, whilst others are common to both sexes. A difference of this kind in the period of development is not so improbable as it may at first appear; for with the Orthoptera, which assume their adult state, not by a single metamorphosis, but by a succession of moults, the young males of some species at first resemble the females, and acquire their distinctive masculine characters only at a later moult. Strictly analogous cases occur at the successive moults of certain male crustaceans.

We have as yet considered the transference of characters, relatively to their period of development, only in species in a natural state; we will now turn to domesticated animals, and first touch on monstrosities and diseases. The presence of supernumerary digits, and the absence of certain phalanges, must be determined at an early embryonic period- the tendency to profuse bleeding is at least congenital, as is probably colour-blindness- yet these peculiarities, and other similar ones, are often limited in their transmission to one sex; so that the rule that characters, developed at an early period, tend to be transmitted to both sexes, here wholly fails. But this rule, as before remarked, does not appear to be nearly so general as the converse one, namely, that characters which appear late in life in one sex are transmitted exclusively to the same sex. From the fact of the above abnormal peculiarities becoming attached to one sex, long before the sexual functions are active, we may infer that there must be some difference between the sexes at an extremely early age. With respect to sexually-limited diseases, we know too little of the period at which they originate, to draw any safe conclusion. Gout, however, seems to fall under our rule, for it is generally caused by intemperance during manhood, and is transmitted from the father to his sons in a much more marked manner than to his daughters.

In the various domestic breeds of sheep, goats, and cattle, the males differ from their respective females in the shape or development of their horns, forehead, mane, dewlap, tail, and hump on the

shoulders; and these peculiarities, in accordance with our rule, are not fully developed until a rather late period of life. The sexes of dogs do not differ, except that in certain breeds, especially in the Scotch deerhound, the male is much larger and heavier than the female; and, as we shall see in a future chapter, the male goes on increasing in size to an unusually late period of life, which, according to rule, will account for his increased size being transmitted to his male offspring alone. On the other hand, the tortoise-shell colour, which is confined to female cats, is quite distinct at birth, and this case violates the rule. There is a breed of pigeons in which the males alone are streaked with black, and the streaks can be detected even in the nestlings; but they become more conspicuous at each successive moult, so that this case partly opposes and partly supports the rule. With the English carrier and pouter pigeons, the full development of the wattle and the crop occurs rather late in life, and conformably with the rule, these characters are transmitted in full perfection to the males alone. The following cases perhaps come within the class previously alluded to, in which both sexes have varied in the same manner at a rather late period of life, and have consequently transferred their new characters to both sexes at a corresponding late period; and if so, these cases are not opposed to our rule: - there exist sub-breeds of the pigeon, described by Neumeister,* in which both sexes change their colour during two or three moults (as is likewise the case with the almond tumbler); nevertheless, these changes, though occurring rather late in life, are common to both sexes. One variety of the canary-bird, namely the London Prize, offers a nearly analogous case.

* Das Ganze der Taubenzucht, 1837, ss. 21, 24. For the case of the streaked pigeons, see Dr. Chapuis, *Le Pigeon Voyageur Belge*, 1855, p. 87.

With the breeds of the fowl the inheritance of various characters by one or both sexes, seems generally determined by the period at which such characters are developed. Thus in all the many breeds in which the adult male differs greatly in colour from the female, as well as from the wild parent-species, he differs also from the young male, so that the newly-acquired characters must have appeared at a rather late period of life. On the other hand, in most of the breeds in which the two sexes resemble each other, the young are coloured in nearly the same manner as their parents, and this renders it probable that their colours first appeared early in life. We have instances of this fact in all black and white breeds, in which the young and old of both sexes are alike; nor can it be maintained that there is something peculiar in a black or white plumage, which leads to its transference to both sexes; for the males alone of many natural species are either black or white, the females being differently coloured. With the so-called cuckoo sub-breeds of the fowl, in which the feathers are transversely pencilled with dark stripes, both sexes and the chickens are coloured in nearly the same manner. The laced plumage of the Sebright bantam is the same in both sexes, and in the young chickens the wing-feathers are distinctly, though imperfectly laced. Spangled Hamburgs, however, offer a partial exception; for the two sexes, though not quite alike, resemble each other more closely than do the sexes of the aboriginal parent-species; yet they acquire their characteristic plumage late in life, for the chickens are distinctly pencilled. With respect to other characters beside colour, in the wild-parent species and in most of the domestic breeds, the males alone possess a well-developed comb; but in the young of the Spanish fowl it is largely developed at a very early age, and, in accordance with this early development in the male, it is of unusual size in the adult female. In the game breeds pugnacity is developed at a wonderfully early age, of which curious proofs could be given; and this character is transmitted to both sexes, so that the hens, from their extreme pugnacity, are now

generally exhibited in separate pens. With the Polish breeds the bony protuberance of the skull which supports the crest is partially developed even before the chickens are hatched, and the crest itself soon begins to grow, though at first feebly;* and in this breed the adults of both sexes are characterised by a great bony protuberance and an immense crest.

* For full particulars and references on all these points respecting the several breeds of the fowl, see *Variation of Animals and Plants under Domestication*, vol. i., pp. 250, 256. In regard to the higher animals, the sexual differences which have arisen under domestication are described in the same work under the head of each species.

Finally, from what we have now seen of the relation which exists in many natural species and domesticated races, between the period of the development of their characters and the manner of their transmission- for example, the striking fact of the early growth of the horns in the reindeer, in which both sexes bear horns, in comparison with their much later growth in the other species in which the male alone bears horns- we may conclude that one, though not the sole cause of characters being exclusively inherited by one sex, is their development at a late age. And secondly, that one, though apparently a less efficient cause of characters being inherited by both sexes, is their development at an early age, whilst the sexes differ but little in constitution. It appears, however, that some difference must exist between the sexes even during a very early embryonic period, for characters developed at this age not rarely become attached to one sex.

Summary and concluding remarks.- From the foregoing discussion on the various laws of inheritance, we learn that the characters of the parents often, or even generally, tend to become developed in the offspring of the same sex, at the same age, and periodically at the same season of the year, in which they first appeared in the parents. But these rules, owing to unknown causes, are far from being fixed. Hence during the modification of a species, the successive changes may readily be transmitted in different ways; some to one sex, and some to both; some to the offspring at one age, and some to the offspring at all ages. Not only are the laws of inheritance extremely complex, but so are the causes which induce and govern variability. The variations thus induced are preserved and accumulated by sexual selection, which is in itself an extremely complex affair, depending, as it does, on the ardour in love, the courage, and the rivalry of the males, as well as on the powers of perception, the taste, and will of the female. Sexual selection will also be largely dominated by natural selection tending towards the general welfare of the species. Hence the manner in which the individuals of either or both sexes have been affected through sexual selection cannot fail to be complex in the highest degree.

When variations occur late in life in one sex, and are transmitted to the same sex at the same age, the other sex and the young are left unmodified. When they occur late in life, but are transmitted to both sexes at the same age, the young alone are left unmodified. Variations, however, may occur at any period of life in one sex or in both, and be transmitted to both sexes at all ages, and then all the individuals of the species are similarly modified. In the following chapters it will be seen that all these cases frequently occur in nature.

Sexual selection can never act on any animal before the age for reproduction arrives. From the great eagerness of the male it has generally acted on this sex and not on the females. The males have thus become provided with weapons for fighting with their rivals, with organs for discovering and securely holding the female, and for exciting or charming her. When the sexes differ in these respects,

It is also, as we have seen, an extremely general law that the adult male differs more or less from the young male; and we may conclude from this fact that the successive variations, by which the adult male became modified, did not generally occur much before the age for reproduction. Whenever some or many of the variations occurred early in life, the young males would partake more or less of the characters of the adult males; and differences of this kind between the old and young males may be observed in many species of animals.

It is probable that young male animals have often tended to vary in a manner which would not only have been of no use to them at an early age, but would have been actually injurious- as by acquiring bright colours, which would render them conspicuous to their enemies, or by acquiring structures, such as great horns, which would expend much vital force in their development. Variations of this kind occurring in the young males would almost certainly be eliminated through natural selection. With the adult and experienced males, on the other hand, the advantages derived from the acquisition of such characters, would more than counterbalance some exposure to danger, and some loss of vital force.

As variations which give to the male a better chance of conquering other males, or of finding, securing, or charming the opposite sex, would, if they happened to arise in the female, be of no service to her, they would not be preserved in her through sexual selection. We have also good evidence with domesticated animals, that variations of all kinds are, if not carefully selected, soon lost through inter-crossing and accidental deaths. Consequently in a state of nature, if variations of the above kind chanced to arise in the female line, and be transmitted exclusively in this line, they would be extremely liable to be lost. If, however, the females varied and transmitted their newly acquired characters to their offspring of both sexes, the characters which were advantageous to the males would be preserved by them through sexual selection, and the two sexes would in consequence be modified in the same manner, although such characters were of no use to the females: but I shall hereafter have to recur to these more intricate contingencies. Lastly, the females may acquire, and apparently have often acquired by transference, characters from the male sex.

As variations occurring later in life, and transmitted to one sex alone, have incessantly been taken advantage of and accumulated through sexual selection in relation to the reproduction of the species; therefore it appears, at first sight, an unaccountable fact that similar variations have not frequently been accumulated through natural selection, in relation to the ordinary habits of life. If this had occurred, the two sexes would often have been differently modified, for the sake, for instance, of capturing prey or of escaping from danger. Differences of this kind between the two sexes do occasionally occur, especially in the lower classes. But this implies that the two sexes follow different habits in their struggles for existence, which is a rare circumstance with the higher animals. The case, however, is widely different with the reproductive functions, in which respect the sexes necessarily differ. For variations in structure which are related to these functions, have often proved of value to one sex, and from having arisen at a late period of life, have been transmitted to one sex alone; and such variations, thus preserved and transmitted, have given rise to secondary sexual characters.

In the following chapters, I shall treat of the secondary sexual characters in animals of all classes, and shall endeavour in each case to apply the principles explained in the present chapter. The lowest classes will detain us for a very short time, but the higher animals, especially birds, must be treated at considerable length. It should be borne in mind that for reasons already assigned, I intend to give only a few illustrative instances of the innumerable structures by the aid of which the male finds the female, or, when found, holds her. On the other hand, all structures and instincts by

the aid of which the male conquers other males, and by which he allures or excites the female, will be fully discussed, as these are in many ways the most interesting.

Supplement on the proportional numbers of the two sexes in animals belonging to various classes.

As no one, as far as I can discover, has paid attention to the relative numbers of the two sexes throughout the animal kingdom, I will here give such materials as I have been able to collect, although they are extremely imperfect. They consist in only a few instances of actual enumeration, and the numbers are not very large. As the proportions are known with certainty only in mankind, I will first give them as a standard of comparison.

Man. - In England during ten years (from 1857 to 1866) the average number of children born alive yearly was 707,120, in the proportion of 104.5 males to 100 females. But in 1857 the male births throughout England were as 105.2, and in 1865 as 104.0 to 100. Looking to separate districts, in Buckinghamshire (where about 5000 children are annually born) the mean proportion of male to female births, during the whole period of the above ten years, was as 102.8 to 100; whilst in N. Wales (where the average annual births are 12,873) it was as high as 106.2 to 100. Taking a still smaller district, viz., Rutlandshire (where the annual births average only 739), in 1864 the male births were as 114.6, and in 1862 as only 97.0 to 100; but even in this small district the average of the 7385 births during the whole ten years, was as 104.5 to 100: that is in the same ratio as throughout England.* The proportions are sometimes slightly disturbed by unknown causes; thus Prof. Faye states "that in some districts of Norway there has been during a decennial period a steady deficiency of boys, whilst in others the opposite condition has existed." In France during forty-four years the male to the female births have been as 106.2 to 100; but during this period it has occurred five times in one department, and six times in another, that the female births have exceeded the males. In Russia the average proportion is as high as 108.9, and in Philadelphia in the United States as 110.5 to 100.*(2) The average for Europe, deduced by Bickes from about seventy million births, is 106 males to 100 females. On the other hand, with white children born at the Cape of Good Hope, the proportion of males is so low as to fluctuate during successive years between 90 and 99 males for every 100 females. It is a singular fact that with Jews the proportion of male births is decidedly larger than with Christians: thus in Prussia the proportion is as 113, in Breslau as 114, and in Livonia as 120 to 100; the Christian births in these countries being the same as usual, for instance, in Livonia as 104 to 100.*(3)

* Twenty-ninth Annual Report of the Registrar-General for 1866. In this report (p. xii.) a special decennial table is given.

*(2) For Norway and Russia, see abstract of Prof. Faye's researches, in *British and Foreign Medico-Chirurg. Review*, April, 1867, pp. 343, 345. For France, the *Annuaire pour l'An 1867*, p. 213. For Philadelphia, Dr. Stockton-Hough, *Social Science Assoc.*, 1874. For the Cape of Good Hope, Quetelet as quoted by Dr. H. H. Zouteveen, in the Dutch translation of this work (vol. i., p. 417), where much information is given on the proportion of the sexes.

*(3) In regard to the Jews, see M. Thury, *La Loi de Production des Sexes*, 1863, p. 25.

Prof. Faye remarks that "a still greater preponderance of males would be met with, if death struck both sexes in equal proportion in the womb and during birth. But the fact is, that for every 100 still-born females, we have in several countries from 134.6 to 144.9 stillborn males. During the first four or five years of life, also,

more male children die than females, for example in England, during the first year, 126 boys die for every 100 girls- a proportion which in France is still more unfavourable."* Dr. Stockton-Hough accounts for these facts in part by the more frequent defective development of males than of females. We have before seen that the male sex is more variable in structure than the female; and variations in important organs would generally be injurious. But the size of the body, and especially of the head, being greater in male than female infants is another cause: for the males are thus more liable to be injured during parturition. Consequently the still-born males are more numerous; and, as a highly competent judge, Dr. Crichton Browne,*⁽²⁾ believes, male infants often suffer in health for some years after birth. Owing to this excess in the death-rate of male children, both at birth and for some time subsequently, and owing to the exposure of grown men to various dangers, and to their tendency to emigrate, the females in all old-settled countries, where statistical records have been kept,*⁽³⁾ are found to preponderate considerably over the males.

* British and Foreign Medico-Chirurg. Review, April, 1867, p. 343. Dr. Stark also remarks (Tenth Annual Reports of Births, Deaths, &c., in Scotland, 1867, p. xxviii.) that "These examples may suffice to show that, at almost every stage of life, the males in Scotland have a greater liability to death and a higher death-rate than the females. The fact, however, of this peculiarity being most strongly developed at that infantile period of life when the dress, food, and general treatment of both sexes are alike, seems to prove that the higher male death-rate is an impressed, natural, and constitutional peculiarity due to sex alone."

*⁽²⁾ West Riding Lunatic Asylum Reports, vol. i., 1871, p. 8. Sir J. Simpson has proved that the head of the male infant exceeds that of the female by $\frac{3}{8}$ ths of an inch in circumference, and by $\frac{1}{8}$ th in transverse diameter. Quetelet has shown that woman is born smaller than man; see Dr. Duncan, Fecundity, Fertility, and Sterility, 1871, p. 382.

*⁽³⁾ With the savage Guarany of Paraguay, according to the accurate Azara (Voyages dans l'Amérique merid., tom. ii., 1809, pp. 60, 179), the women are to the men in the proportion of 14 to 13.

It seems at first sight a mysterious fact that in different nations, under different conditions and climates, in Naples, Prussia, Westphalia, Holland, France, England and the United States, the excess of male over female births is less when they are illegitimate than when legitimate.* This has been explained by different writers in many different ways, as from the mothers being generally young, from the large proportion of first pregnancies, &c. But we have seen that male infants, from the large size of their heads, suffer more than female infants during parturition; and as the mothers of illegitimate children must be more liable than other women to undergo bad labours, from various causes, such as attempts at concealment by tight lacing, hard work, distress of mind, &c., their male infants would proportionably suffer. And this probably is the most efficient of all the causes of the proportion of males to females born alive being less amongst illegitimate children than amongst the legitimate. With most animals the greater size of the adult male than of the female, is due to the stronger males having conquered the weaker in their struggles for the possession of the females, and no doubt it is owing to this fact that the two sexes of at least some animals differ in size at birth. Thus we have the curious fact that we may attribute the more frequent deaths of male than female infants, especially amongst the illegitimate, at least in part to sexual selection.

* Babbage, Edinburgh Journal of Science, 1829, vol. i., p. 88; also p. 90, on still-born children. On illegitimate children in

It has often been supposed that the relative age of the two parents determine the sex of the offspring; and Prof. Leuckart* has advanced what he considers sufficient evidence, with respect to man and certain domesticated animals, that this is one important though not the sole factor in the result. So again the period of impregnation relatively to the state of the female has been thought by some to be the efficient cause; but recent observations discountenance this belief. According to Dr. Stockton-Hough,*⁽²⁾ the season of the year, the poverty or wealth of the parents, residence in the country or in cities, the crossing of foreign immigrants, &c., all influence the proportion of the sexes. With mankind, polygamy has also been supposed to lead to the birth of a greater proportion of female infants; but Dr. J. Campbell*⁽³⁾ carefully attended to this subject in the harems of Siam, and concludes that the proportion of male to female births is the same as from monogamous unions. Hardly any animal has been rendered so highly polygamous as the English race-horse, and we shall immediately see that his male and female offspring are almost exactly equal in number. I will now give the facts which I have collected with respect to the proportional numbers of the sexes of various animals; and will then briefly discuss how far selection has come into play in determining the result.

* Leuckart, in Wagner's Handwörterbuch der Phys., B. iv., 1853, s. 774.

*⁽²⁾ Social Science Association of Philadelphia, 1874.

*⁽³⁾ Anthropological Review, April, 1870, p. cviii.

Horses.- Mr. Tegetmeier has been so kind as to tabulate for me from the Racing Calendar the births of race-horses during a period of twenty-one years, viz., from 1846 to 1867; 1849 being omitted, as no returns were that year published. The total births were 25,560,* consisting of 12,763 males and 12,797 females, or in the proportion of 99.7 males to 100 females. As these numbers are tolerably large, and as they are drawn from all parts of England, during several years, we may with much confidence conclude that with the domestic horse, or at least with the race-horse, the two sexes are produced in almost equal numbers. The fluctuations in the proportions during successive years are closely like those which occur with mankind, when a small and thinly-populated area is considered; thus in 1856 the male horses were as 107.1, and in 1867 as only 92.6 to 100 females. In the tabulated returns the proportions vary in cycles, for the males exceeded the females during six successive years; and the females exceeded the males during two periods each of four years; this, however, may be accidental; at least I can detect nothing of the kind with man in the decennial table in the Registrar's Report for 1866.

* During eleven years a record was kept of the number of mares which proved barren or prematurely slipped their foals; and it deserves notice, as shewing how infertile these highly-nurtured and rather closely-interbred animals have become, that not far from one-third of the mares failed to produce living foals. Thus during 1866, 809 male colts and 816 female colts were born, and 743 mares failed to produce offspring. During 1867, 836 males and 902 females were born, and 794 mares failed.

Dogs.- During a period of twelve years, from 1857 to 1868, the births of a large number of greyhounds, throughout England, were sent to the Field newspaper; and I am again indebted to Mr. Tegetmeier for carefully tabulating the results. The recorded births were 6878, consisting of 3605 males and 3273 females, that is, in the proportion of 110.1 males to 100 females. The greatest fluctuations occurred in 1864, when the proportion was as 95.3 males, and in

1867, as 116.3 males to 100 females. The above average proportion of 110.1 to 100 is probably nearly correct in the case of the greyhound, but whether it would hold with other domesticated breeds is in some degree doubtful. Mr. Cupples has enquired from several great breeders of dogs, and finds that all without exception believe that females are produced in excess; but he suggests that this belief may have arisen from females being less valued, and from the consequent disappointment producing a stronger impression on the mind.

Sheep. - The sexes of sheep are not ascertained by agriculturists until several months after birth, at the period when the males are castrated; so that the following returns do not give the proportions at birth. Moreover, I find that several great breeders in Scotland, who annually raise some thousand sheep, are firmly convinced that a larger proportion of males than of females die during the first year or two. Therefore the proportion of males would be somewhat larger at birth than at the age of castration. This is a remarkable coincidence with what, as we have seen, occurs with mankind, and both cases probably depend on the same cause. I have received returns from four gentlemen in England who have bred lowland sheep, chiefly Leicesters, during the last ten to sixteen years; they amount altogether to 8965 births, consisting of 4407 males and 4558 females; that is in the proportion of 96.7 males to 100 females. With respect to Cheviot and black-faced sheep bred in Scotland, I have received returns from six breeders, two of them on a large scale, chiefly for the years 1867-1869, but some of the returns extend back to 1862. The total number recorded amounts to 50,685, consisting of 25,071 males and 25,614 females or in the proportion of 97.9 males to 100 females. If we take the English and Scotch returns together, the total number amounts to 59,650, consisting of 29,478 males and 30,172 females, or as 97.7 to 100. So that with sheep at the age of castration the females are certainly in excess of the males, but probably this would not hold good at birth.*

*I am much indebted to Mr. Cupples for having procured for me the above returns from Scotland, as well as some of the following returns on cattle. Mr. R. Elliot, of Laighwood, first called my attention to the premature deaths of the males, - a statement subsequently confirmed by Mr. Aitchison and others. To this latter gentleman, and to Mr. Payan, I owe my thanks for large returns as to sheep.

Of Cattle I have received returns from nine gentlemen of 982 births, too few to be trusted; these consisted of 477 bull-calves and 505 cow-calves; i. e., in the proportion of 94.4 males to 100 females. The Rev. W. D. Fox informs me that in 1867 out of 34 calves born on a farm in Derbyshire only one was a bull. Mr. Harrison Weir has enquired from several breeders of Pigs, and most of them estimate the male to the female births as about 7 to 6. This same gentleman has bred rabbits for many years, and has noticed that a far greater number of bucks are produced than does. But estimations are of little value.

Of Mammalia in a state of nature I have been able to learn very little. In regard to the common rat, I have received conflicting statements. Mr. R. Elliot, of Laighwood, informs me that a rat-catcher assured him that he had always found the males in great excess, even with the young in the nest. In consequence of this, Mr. Elliot himself subsequently examined some hundred old ones, and found the statement true. Mr. F. Buckland has bred a large number of white rats, and he also believes that the males greatly exceed the females. In regard to moles, it is said that "the males are much more numerous than the females":* and as the catching of these animals is a special occupation, the statement may perhaps be trusted. Sir A. Smith, in describing an antelope of S. Africa*(2) (*Kobus ellipsiprymnus*), remarks, that in the herds of this and other species, the males are few in number compared with the females: the natives believe that they are born in this proportion; others believe that the younger males are

expelled from the herds, and Sir A. Smith says, that though he has himself never seen herds consisting of young males alone, others affirm that this does occur. It appears probable that the young when expelled from the herd, would often fall a prey to the many beasts of prey of the country.

* Bell, History of British Quadrupeds, p. 100.

*(2) Illustrations of the Zoology of S. Africa, 1849, pl. 29.

BIRDS.

With respect to the Fowl, I have received only one account, namely, that out of 1001 chickens of a highly-bred stock of Cochins, reared during eight years by Mr. Stretch, 487 proved males and 514 females; i. e., as 94.7 to 100. In regard to domestic pigeons there is good evidence either that the males are produced in excess, or that they live longer; for these birds invariably pair, and single males, as Mr. Tegetmeier informs me, can always be purchased cheaper than females. Usually the two birds reared from the two eggs laid in the same nest are a male and a female; but Mr. Harrison Weir, who has been so large a breeder, says that he has often bred two cocks from the same nest, and seldom two hens; moreover, the hen is generally the weaker of the two, and more liable to perish.

With respect to birds in a state of nature, Mr. Gould and others* are convinced that the males are generally the more numerous; and as the young males of many species resemble the females, the latter would naturally appear to be the more numerous. Large numbers of pheasants are reared by Mr. Baker of Leadenhall from eggs laid by wild birds, and he informs Mr. Jenner Weir that four or five males to one female are generally produced. An experienced observer remarks,*(2) that in Scandinavia the broods of the capercaillie and black-cock contain more males than females; and that with the Dal-ripa (a kind of ptarmigan) more males than females attend the leks or places of courtship; but this latter circumstance is accounted for by some observers by a greater number of hen birds being killed by vermin. From various facts given by White of Selborne,*(3) it seems clear that the males of the partridge must be in considerable excess in the south of England; and I have been assured that this is the case in Scotland. Mr. Weir on enquiring from the dealers, who receive at certain seasons large numbers of ruffs (*Machetes pugnax*), was told that the males are much the more numerous. This same naturalist has also enquired for me from the birdcatchers, who annually catch an astonishing number of various small species alive for the London market, and he was unhesitatingly answered by an old and trustworthy man, that with the chaffinch the males are in large excess: he thought as high as 2 males to 1 female, or at least as high as 5 to 3.*(4) The males of the blackbird, he likewise maintained, were by far the more numerous, whether caught by traps or by netting at night. These statements may apparently be trusted, because this same man said that the sexes are about equal with the lark, the twite (*Linaria montana*), and goldfinch. On the other hand, he is certain that with the common linnet, the females preponderate greatly, but unequally during different years; during some years he has found the females to the males as four to one. It should, however, be borne in mind, that the chief season for catching birds does not begin till September, so that with some species partial migrations may have begun, and the flocks at this period often consist of hens alone. Mr. Salvin paid particular attention to the sexes of the humming-birds in Central America, and is convinced that with most of the species the males are in excess; thus one year he procured 204 specimens belonging to ten species, and these consisted of 166 males and of only 38 females. With two other species the females were in excess: but the proportions apparently vary either during different seasons or in different localities; for on one occasion the males of *Campylopterus hemileucurus* were to the females as 5 to 2, and on another

occasion*(5) in exactly the reversed ratio. As bearing on this latter point, I may add, that Mr. Powys found in Corfu and Epirus the sexes of the chaffinch keeping apart, and "the females by far the most numerous"; whilst in Palestine Mr. Tristram found "the male flocks appearing greatly to exceed the female in number."*(6) So again with the *Quiscalus major*, Mr. G. Taylor says, that in Florida there were "very few females in proportion to the males,"*(7) whilst in Honduras the proportion was the other way, the species there having the character of a polygamist.

* Brehm (*Illustriertes Thierleben*, B. iv., s. 990) comes to the same conclusion.

*(2) On the authority of L. Lloyd, *Game Birds of Sweden*, 1867, pp. 12, 132.

*(3) *Nat. Hist. of Selborne*, letter xxix., ed. of 1825, vol. i., p. 139.

*(4) Mr. Jenner Weir received similar information, on making enquiries during the following year. To shew the number of living chaffinches caught, I may mention that in 1869 there was a match between two experts, and one man caught in a day 62, and another 40, male chaffinches. The greatest number ever caught by one man in a single day was 70.

*(5) *Ibis*, vol. ii. p. 260, as quoted in Gould's *Trochilidae*, 1861, p. 52. For the foregoing proportions, I am indebted to Mr. Salvin for a table of his results.

*(6) *Ibis*, 1860, p. 137; and 1867, p. 369.

*(7) *Ibis*, 1862, p. 187.

FISH.

With fish the proportional numbers of the sexes can be ascertained only by catching them in the adult or nearly adult state; and there are many difficulties in arriving at any just conclusion.* Infertile females might readily be mistaken for males, as Dr. Gunther has remarked to me in regard to trout. With some species the males are believed to die soon after fertilising the ova. With many species the males are of much smaller size than the females, so that a large number of males would escape from the same net by which the females were caught. M. Carbonnier,*(2) who has especially attended to the natural history of the pike (*Esox lucius*), states that many males, owing to their small size, are devoured by the larger females; and he believes that the males of almost all fish are exposed from this same cause to greater danger than the females. Nevertheless, in the few cases in which the proportional numbers have been actually observed, the males appear to be largely in excess. Thus Mr. R. Buist, the superintendent of the Stormontfield experiments, says that in 1865, out of 70 salmon first landed for the purpose of obtaining the ova, upwards of 60 were males. In 1867 he again "calls attention to the vast disproportion of the males to the females. We had at the outset at least ten males to one female." Afterwards females sufficient for obtaining ova were procured. He adds, "from the great proportion of the males, they are constantly fighting and tearing each other on the spawning-beds."*(3) This disproportion, no doubt, can be accounted for in part, but whether wholly is doubtful, by the males ascending the rivers before the females. Mr. F. Buckland remarks in regard to trout, that "it is a curious fact that the males preponderate very largely in number over the females. It invariably happens that when the first rush of fish is made to the net, there will be at least seven or eight males to one female found captive. I cannot quite account for this; either the males are more numerous than the females, or the latter seek safety by concealment rather than flight." He then adds, that by carefully searching the banks sufficient females for obtaining ova can be found.*(4) Mr. H. Lee informs me that out of 212 trout taken for this purpose in Lord Portsmouth's park, 150 were males and 62 females.

* Leuckart quotes Bloch (Wagner, Handwörterbuch der Phys., B. iv., 1853, s. 775), that with fish there are twice as many males as females.

*(2) Quoted in the Farmer, March 18, 1869, p. 369.

*(3) The Stormontfield Piscicultural Experiments, 1866, p. 23. The Field newspaper, June 29, 1867.

*(4) Land and Water, 1868, p. 41.

The males of the Cyprinidae likewise seem to be in excess; but several members of this family, viz., the carp, tench, bream and minnow, appear regularly to follow the practice, rare in the animal kingdom, of polyandry; for the female whilst spawning is always attended by two males, one on each side, and in the case of the bream by three or four males. This fact is so well known, that it is always recommended to stock a pond with two male tenches to one female, or at least with three males to two females. With the minnow, an excellent observer states, that on the spawning-beds the males are ten times as numerous as the females; when a female comes amongst the males, "she is immediately pressed closely by a male on each side; and when they have been in that situation for a time, are superseded by other two males."*

* Yarrell, Hist. British Fishes, vol. i., 1826, p. 307; on the *Cyprinus carpio*, p. 331; on the *Tinca vulgaris*, p. 331; on the *Abramis brama*, p. 336. See, for the minnow (*Leuciscus phoxinus*), Loudon's Magazine of Natural History, vol. v., 1832, p. 682.

INSECTS.

In this great class, the Lepidoptera almost alone affords means for judging of the proportional numbers of the sexes; for they have been collected with special care by many good observers, and have been largely bred from the egg or caterpillar state. I had hoped that some breeders of silk-moths might have kept an exact record, but after writing to France and Italy, and consulting various treatises, I cannot find that this has ever been done. The general opinion appears to be that the sexes are nearly equal, but in Italy, as I hear from Professor Canestrini, many breeders are convinced that the females are produced in excess. This same naturalist, however, informs me, that in the two yearly broods of the ailanthus silk-moth (*Bombyx cynthia*), the males greatly preponderate in the first, whilst in the second the two sexes are nearly equal, or the females rather in excess.

In regard to butterflies in a state of nature, several observers have been much struck by the apparently enormous preponderance of the males.* Thus Mr. Bates,*(2) in speaking of several species, about a hundred in number, which inhabit the upper Amazons, says that the males are much more numerous than the females, even in the proportion of a hundred to one. In North America, Edwards, who had great experience, estimates in the genus *Papilio* the males to the females as four to one; and Mr. Walsh, who informs me of this statement, says that with *P. turnus* this is certainly the case. In South Africa, Mr. R. Trimen found the males in excess in 19 species;*(3) and in one of these, which swarms in open places, he estimated the number of males as fifty to one female. With another species, in which the males are numerous in certain localities, he collected only five females during seven years. In the island of Bourbon, M. Maillard states that the males of one species of *Papilio* are twenty times as numerous as the females.*(4) Mr. Trimen informs me that as far as he has himself seen, or heard from others, it is rare for the females of any butterfly to exceed the males in number; but three South African species perhaps offer an exception. Mr. Wallace*(5) states that the females of *Ornithoptera croesus*, in the Malay Archipelago, are more common and more easily caught than the males; but this is a rare butterfly. I may here add, that in

Hyperythra, a genus of moths, Guenee says, that from four to five females are sent in collections from India for one male.

* Leuckart quotes Meinecke (Wagner, Handwörterbuch der Phys., B. iv., 1853, s. 775) that the males of butterflies are three or four times as numerous as the females.

* (2) The Naturalist on the Amazons, vol. ii., 1863, pp. 228, 347.

* (3) Four of these cases are given by Mr. Trimen in his *Rhopalocera Africae Australis*.

* (4) Quoted by Trimen, Transactions of the Ent. Society, vol. v., part iv., 1866, p. 330.

* (5) Transactions, Linnean Society, vol. xxv., p. 37.

When this subject of the proportional numbers of the sexes of insects was brought before the Entomological Society,* it was generally admitted that the males of most Lepidoptera, in the adult or imago state, are caught in greater numbers than the females: but this fact was attributed by various observers to the more retiring habits of the females, and to the males emerging earlier from the cocoon. This latter circumstance is well known to occur with most Lepidoptera, as well as with other insects. So that, as M. Personnat remarks, the males of the domesticated *Bombyx yamamai*, are useless at the beginning of the season, and the females at the end, from the want of mates.* (2) I cannot, however, persuade myself that these causes suffice to explain the great excess of males, in the above cases of certain butterflies which are extremely common in their native countries. Mr. Stainton, who has paid very close attention during many years to the smaller moths, informs me that when he collected them in the imago state, he thought that the males were ten times as numerous as the females, but that since he has reared them on a large scale from the caterpillar state, he is convinced that the females are the more numerous. Several entomologists concur in this view. Mr. Doubleday, however, and some others, take an opposite view, and are convinced that they have reared from the eggs and caterpillars a larger proportion of males than of females.

* Proceedings, Entomological Society, Feb. 17, 1868.

* (2) Quoted by Dr. Wallace in Proceedings, Entomological Society, 3rd series, vol. v., 1867, p. 487.

Besides the more active habits of the males, their earlier emergence from the cocoon, and in some cases their frequenting more open stations, other causes may be assigned for an apparent or real difference in the proportional numbers of the sexes of Lepidoptera, when captured in the imago state, and when reared from the egg or caterpillar state. I hear from Professor Canestrini, that it is believed by many breeders in Italy, that the female caterpillar of the silk-moth suffers more from the recent disease than the male; and Dr. Staudinger informs me that in rearing Lepidoptera more females die in the cocoon than males. With many species the female caterpillar is larger than the male, and a collector would naturally choose the finest specimens, and thus unintentionally collect a larger number of females. Three collectors have told me that this was their practice; but Dr. Wallace is sure that most collectors take all the specimens which they can find of the rarer kinds, which alone are worth the trouble of rearing. Birds when surrounded by caterpillars would probably devour the largest; and Professor Canestrini informs me that in Italy some breeders believe, though on insufficient evidence, that in the first broods of the ailanthus silkmoth, the wasps destroy a larger number of the female than of the male caterpillars. Dr. Wallace further remarks that female caterpillars, from being larger than the males, require more time for their development, and consume more food and moisture: and thus they would be exposed during a longer time to danger from ichneumons, birds, &c., and in times of scarcity would perish in greater numbers. Hence it

appears quite possible that in a state of nature, fewer female Lepidoptera may reach maturity than males; and for our special object we are concerned with their relative numbers at maturity, when the sexes are ready to propagate their kind.

The manner in which the males of certain moths congregate in extraordinary numbers round a single female, apparently indicates a great excess of males, though this fact may perhaps be accounted for by the earlier emergence of the males from their cocoons. Mr. Stainton informs me that from twelve to twenty males, may often be seen congregated round a female *Elachista rufocinerea*. It is well known that if a virgin *Lasiocampa quercus* or *Saturnia carpini* be exposed in a cage, vast numbers of males collect round her, and if confined in a room will even come down the chimney to her. Mr. Doubleday believes that he has seen from fifty to a hundred males of both these species attracted in the course of a single day by a female in confinement. In the Isle of Wight Mr. Trimen exposed a box in which a female of the *Lasiocampa* had been confined on the previous day, and five males soon endeavored to gain admittance. In Australia, Mr. Verreaux, having placed the female of a small *Bombyx* in a box in his pocket, was followed by a crowd of males, so that about 200 entered the house with him.*

* Blanchard, *Metamorphoses, Moeurs des Insectes*, 1868, pp. 225-226.

Mr. Doubleday has called my attention to M. Staudinger's* list of Lepidoptera, which gives the prices of the males and females of 300 species or well-marked varieties of butterflies (*Rhopalocera*). The prices for both sexes of the very common species are of course the same; but in 114 of the rarer species they differ; the males being in all cases, excepting one, the cheaper. On an average of the prices of the 113 species, the price of the male to that of the female is as 100 to 149; and this apparently indicates that inversely the males exceed the females in the same proportion. About 2000 species or varieties of moths (*Heterocera*) are catalogued, those with wingless females being here excluded on account of the difference in habits between the two sexes: of these 2000 species, 141 differ in price according to sex, the males of 130 being cheaper, and those of only 11 being dearer than the females. The average price of the males of the 130 species, to that of the females, is as 100 to 143. With respect to the butterflies in this priced list, Mr. Doubleday thinks (and no man in England has had more experience), that there is nothing in the habits of the species which can account for the difference in the prices of the two sexes, and that it can be accounted for only by an excess in the number of the males. But I am bound to add that Dr. Staudinger informs me, that he is himself of a different opinion. He thinks that the less active habits of the females and the earlier emergence of the males will account for his collectors securing a larger number of males than of females, and consequently for the lower prices of the former. With respect to specimens reared from the caterpillar-state, Dr. Staudinger believes, as previously stated, that a greater number of females than of males die whilst confined to the cocoons. He adds that with certain species one sex seems to preponderate over the other during certain years.

* *Lepidopteren-Doubletten Liste*, Berlin, No. x., 1866.

Of direct observations on the sexes of Lepidoptera, reared either from eggs or caterpillars, I have received only the few following cases:*

* See following table.

So that in these eight lots of cocoons and eggs, males were produced in excess. Taken together the proportion of males is as 122.7 to 100 females. But the numbers are hardly large enough to be trustworthy.

On the whole, from these various sources of evidence, all pointing in the same direction, I infer that with most species of Lepidoptera, the mature males generally exceed the females in number, whatever the proportions may be at their first emergence from the egg.

	Males	Females
The Rev. J. Hellins* of Exeter reared, during 1868, imagos of 73 species, which consisted of	153	137
Mr. Albert Jones of Eltham reared, during 1868, imagos of 9 species, which consisted of	159	126
During 1869 he reared imagoes from 4 species consisting of	114	112
Mr. Buckler of Emsworth, Hants, during 1869, reared imagos from 74 species, consisting of	180	169
Dr. Wallace of Colchester reared from one brood of <i>Bombyx cynthia</i>	52	48
Dr. Wallace raised, from cocoons of <i>Bombyx pernyi</i> sent from China, during 1869	224	123
Dr. Wallace raised, during 1868 and 1869, from two lots of cocoons of <i>Bombyx yamamai</i>	52	46
Total	934	761

* This naturalist has been so kind as to send me some results from former years, in which the females seemed to preponderate; but so many of the figures were estimates, that I found it impossible to tabulate them

With reference to the other orders of insects, I have been able to collect very little reliable information. With the stag-beetle (*Lucanus cervus*) "the males appear to be much more numerous than the females"; but when, as Cornelius remarked during 1867, an unusual number of these beetles appeared in one part of Germany, the females appeared to exceed the males as six to one. With one of the Elateridae, the males are said to be much more numerous than the females, and "two or three are often found united with one female; * so that here polyandry seems to prevail." With *Siagonium* (Staphylinidae), in which the males are furnished with horns, "the females are far more numerous than the opposite sex." Mr. Janson stated at the Entomological Society that the females of the bark feeding *Tomicus villosus* are so common as to be a plague, whilst the males are so rare as to be hardly known.

* Gunther's Record of Zoological Literature, 1867, p. 260. On the excess of female *Lucanus*, *ibid*, p. 250. On the males of *Lucanus* in England, Westwood, Modern Classification of Insects, vol. i., p. 187. On the *Siagonium*, *ibid.*, p. 172.

It is hardly worthwhile saying anything about the proportion of the sexes in certain species and even groups of insects, for the males are unknown or very rare, and the females are parthenogenetic, that is, fertile without sexual union; examples of this are afforded by several of the Cynipidae.* In all the gall-making Cynipidae known to Mr. Walsh, the females are four or five times as numerous as the males; and so it is, as he informs me, with the gall-making Cecidomyiidae (Diptera). With some common species of saw-flies

(Tenthredinae) Mr. F. Smith has reared hundreds of specimens from larvae of all sizes, but has never reared a single male; on the other hand, Curtis says,*(2) that with certain species (*Athalia*), bred by him, the males were to the females as six to one; whilst exactly the reverse occurred with the mature insects of the same species caught in the fields. In the family of bees, Hermann Muller,*(3) collected a large number of specimens of many species, and reared others from the cocoons, and counted the sexes. He found that the males of some species greatly exceeded the females in number; in others the reverse occurred; and in others the two sexes were nearly equal. But as in most cases the males emerge from the cocoons before the females, they are at the commencement of the breeding-season practically in excess. Muller also observed that the relative number of the two sexes in some species differed much in different localities. But as H. Muller has himself remarked to me, these remarks must be received with some caution, as one sex might more easily escape observation than the other. Thus his brother Fritz Muller has noticed in Brazil that the two sexes of the same species of bee sometimes frequent different kinds of flowers. With respect to the Orthoptera, I know hardly anything about the relative number of the sexes: Korte,*(4) however, says that out of 500 locusts which he examined, the males were to the females as five to six. With the Neuroptera, Mr. Walsh states that in many, but by no means in all the species of the odonatous group, there is a great overplus of males: in the genus *Hetaerina*, also, the males are generally at least four times as numerous as the females. In certain species in the genus *Gomphus* the males are equally in excess, whilst in two other species, the females are twice or thrice as numerous as the males. In some European species of *Psocus* thousands of females may be collected without a single male, whilst with other species of the same genus both sexes are common.*(5) In England, Mr. MacLachlan has captured hundreds of the female *Apatania muliebris*, but has never seen the male; and of *Boreus hyemalis* only four or five males have been seen here.*(6) With most of these species (excepting the Tenthredinae) there is at present no evidence that the females are subject to parthenogenesis; and thus we see how ignorant we are of the causes of the apparent discrepancy in the proportion of the two sexes.

* Walsh in the American Entomologist, vol. i., 1869, p. 103. F. Smith, Record of Zoological Lit, 1867, p. 328.

*(2) Farm Insects, pp. 45-46.

*(3) "Anwendung der Darwin'schen Lehre," Verh. d. n. Jahrg., xxiv.

*(4) Die Strich. Zug oder Wanderheuschrecke, 1828, p. 20.

*(5) "Observations on N. American Neuroptera," by H. Hagen and B. D. Walsh, Proceedings, Ent. Soc. Philadelphia, Oct., 1863, pp. 168, 223, 239.

*(6) Proceedings, Ent. Soc. London, Feb. 17, 1868.

In the other classes of the Articulata I have been able to collect still less information. With spiders, Mr. Blackwall, who has carefully attended to this class during many years, writes to me that the males from their more erratic habits are more commonly seen, and therefore appear more numerous. This is actually the case with a few species; but he mentions several species in six genera, in which the females appear to be much more numerous than the males.* The small size of the males in comparison with the females (a peculiarity which is sometimes carried to an extreme degree), and their widely different appearance, may account in some instances for their rarity in collections.*(2)

8888

* Another great authority with respect to this class, Prof. Thorell of Upsala (On European Spiders, 1869-70, part i., p. 205), speaks as if female spiders were generally commoner than the males.

*(2) See, on this subject, Mr. O. P. Cambridge, as quoted in Quarterly Journal of Science, 1868, page 429.

Some of the lower crustaceans are able to propagate their kind sexually, and this will account for the extreme rarity of the males; thus von Siebold* carefully examined no less than 13,000 specimens of *Apus* from twenty-one localities, and amongst these he found only 319 males. With some other forms (as *Tanais* and *Cypris*), as Fritz Muller informs me, there is reason to believe that the males are much shorter-lived than the females; and this would explain their scarcity, supposing the two sexes to be at first equal in number. On the other hand, Muller has invariably taken far more males than females of the *Diastylidae* and of *Cypridina* on the shores of Brazil: thus with a species in the latter genus, 63 specimens caught the same day included 57 males; but he suggests that this preponderance may be due to some unknown difference in the habits of the two sexes. With one of the higher Brazilian crabs, namely a *Gelasimus*, Fritz Muller found the males to be more numerous than the females. According to the large experience of Mr. C. Spence Bate, the reverse seems to be the case with six common British crabs, the names of which he has given me.

* *Beitrage zur Parthenogenesis*, p. 174.

The proportion of the sexes in relation to natural selection.

There is reason to suspect that in some cases man has by selection indirectly influenced his own sex-producing powers. Certain women tend to produce during their whole lives more children of one sex than of the other: and the same holds good of many animals, for instance, cows and horses; thus Mr. Wright of Yeldersley House informs me that one of his Arab mares, though put seven times to different horses, produced seven fillies. Though I have very little evidence on this head, analogy would lead to the belief, that the tendency to produce either sex would be inherited like almost every other peculiarity, for instance, that of producing twins; and concerning the above tendency a good authority, Mr. J. Downing, has communicated to me facts which seem to prove that this does occur in certain families of short-horn cattle. Col. Marshall* has recently found on careful examination that the *Todas*, a hill-tribe of India, consist of 112 males and 84 females of all ages- that is in a ratio of 133.3 males to 100 females. The *Todas*, who are polyandrous in their marriages, during former times invariably practised female infanticide; but this practice has now been discontinued for a considerable period. Of the children born within late years, the males are more numerous than the females, in the proportion of 124 to 100. Colonel Marshall accounts for this fact in the following ingenious manner. "Let us for the purpose of illustration take three families as representing an average of the entire tribe; say that one mother gives birth to six daughters and no sons; a second mother has six sons only, whilst the third mother has three sons and three daughters. The first mother, following the tribal custom, destroys four daughters and preserves two. The second retains her six sons. The third kills two daughters and keeps one, as also her three sons. We have then from the three families, nine sons and three daughters, with which to continue the breed. But whilst the males belong to families in which the tendency to produce sons is great, the females are of those of a converse inclination. Thus the bias strengthens with each generation, until, as we find, families grow to have habitually more sons than daughters."

* *The Todas*, 1873, pp. 100, 111, 194, 196.

That this result would follow from the above form of infanticide seems almost certain; that is if we assume that a sex-producing tendency is inherited. But as the above numbers are so extremely scanty, I have searched for additional evidence, but cannot decide whether what I have found is trustworthy; nevertheless the facts

are, perhaps, worth giving. The Maories of New Zealand have long practised infanticide; and Mr. Fenton* states that he "has met with instances of women who have destroyed four, six, and even seven children, mostly females. However, the universal testimony of those best qualified to judge, is conclusive that this custom has for many years been almost extinct. Probably the year 1835 may be named as the period of its ceasing to exist." Now amongst the New Zealanders, as with the Todas, male births are considerably in excess. Mr. Fenton remarks (p. 30), "One fact is certain, although the exact period of the commencement of this singular condition of the disproportion of the sexes cannot be demonstratively fixed, it is quite clear that this course of decrease was in full operation during the years 1830 to 1844, when the non-adult population of 1844 was being produced, and has continued with great energy up to the present time." The following statements are taken from Mr. Fenton (p. 26), but as the numbers are not large, and as the census was not accurate, uniform results cannot be expected. It should be borne in mind in this and the following cases, that the normal state of every population is an excess of women, at least in all civilised countries, chiefly owing to the greater mortality of the male sex during youth, and partly to accidents of all kinds later in life. In 1858, the native population of New Zealand was estimated as consisting of 31,667 males and 24,303 females of all ages, that is in the ratio of 130.3 males to 100 females. But during this same year, and in certain limited districts, the numbers were ascertained with much care, and the males of all ages were here 753 and the females 616; that is in the ratio of 122.2 males to 100 females. It is more important for us that during this same year of 1858, the non-adult males within the same district were found to be 178, and the non-adult females 142, that is in the ratio of 125.3 to 100. It may be added that in 1844, at which period female infanticide had only lately ceased, the non-adult males in one district were 281, and the non-adult females only 194, that is in the ratio of 144.8 males to 100 females.

* Aboriginal Inhabitants of New Zealand (Government Report), 1859, p. 36.

In the Sandwich Islands, the males exceed the females in number. Infanticide was formerly practised there to a frightful extent, but was by no means confined to female infants, as is shown by Mr. Ellis,* and as I have been informed by Bishop Staley and the Rev. Mr. Coan. Nevertheless, another apparently trustworthy writer, Mr. Jarves,*⁽²⁾ whose observations apply to the whole archipelago, remarks:- "Numbers of women are to be found, who confess to the murder of from three to six or eight children," and he adds, "females from being considered less useful than males were more often destroyed." From what is known to occur in other parts of the world, this statement is probable; but must be received with much caution. The practice of infanticide ceased about the year 1819, when idolatry was abolished and missionaries settled in the islands. A careful census in 1839 of the adult and taxable men and women in the island of Kauai and in one district of Oahu (Jarves, p. 404), gives 4723 males and 3776 females; that is in the ratio of 125.08 to 100. At the same time the number of males under fourteen years in Kauai and under eighteen in Oahu was 1797, and of females of the same ages 1429; and here we have the ratio of 125.75 males to 100 females.

* Narrative of a Tour through Hawaii, 1826, p. 298.

*⁽²⁾ History of the Sandwich Islands, 1843, p. 93.

In a census of all the islands in 1850,* the males of all ages amount to 36,272, and the females to 33,128, or as 109.49 to 100. The males under seventeen years amounted to 10,773, and the females under the same age to 9593, or as 112.3 to 100. From the census of 1872, the proportion of males of all ages (including half-castes) to

females, is as 125.36 to 100. It must be borne in mind that all these returns for the Sandwich Islands give the proportion of living males to living females, and not of the births; and judging from all civilised countries the proportion of males would have been considerably higher if the numbers had referred to births.*(2)

* This is given in the Rev. H. T. Cheever's *Life in the Sandwich Islands*, 1851, p. 277.

*(2) Dr. Coulter, in describing (*Journal R. Geograph. Soc.*, vol. v., 1835, p. 67) the state of California about the year 1830, says that the natives reclaimed by the Spanish missionaries, have nearly all perished, or are perishing, although well treated, not driven from their native land, and kept from the use of spirits. He attributes this, in great part, to the undoubted fact that the men greatly exceed the women in number; but he does not know whether this is due to a failure of female offspring, or to more females dying during early youth. The latter alternative, according to all analogy, is very improbable. He adds that "infanticide, properly so called, is not common, though very frequent recourse is had to abortion." If Dr. Coulter is correct about infanticide, this case cannot be advanced in support of Colonel Marshall's view. From the rapid decrease of the reclaimed natives, we may suspect that, as in the cases lately given, their fertility has been diminished from changed habits of life.

I had hoped to gain some light on this subject from the breeding of dogs; inasmuch as most breeds, with the exception, perhaps, of greyhounds, many more female puppies are destroyed than males, just as with the Toda infants. Mr. Cupples assures me that this is usual with Scotch deerhounds. Unfortunately, I know nothing of the proportion of the sexes in any breed, excepting greyhounds, and there the male births are to the females as 110.1 to 100. Now from enquiries made from many breeders, it seems that the females are in some respects more esteemed, though otherwise troublesome; and it does not appear that the female puppies of the best-bred dogs are systematically destroyed more than the males, though this does sometimes take place to a limited extent. Therefore I am unable to decide whether we can, on the above principles, account for the preponderance of male births in greyhounds. On the other hand, we have seen that with horses, cattle, and sheep, which are too valuable for the young of either sex to be destroyed, if there is any difference, the females are slightly in excess.

From the several foregoing cases we have some reason to believe that infanticide practised in the manner above explained, tends to make a male-producing race; but I am far from supposing that this practice in the case of man, or some analogous process with other species, has been the sole determining cause of an excess of males. There may be some unknown law leading to this result in decreasing races, which have already become somewhat infertile. Besides the several causes previously alluded to, the greater facility of parturition amongst savages, and the less consequent injury to their male infants, would tend to increase the proportion of live-born males to females. There does not, however, seem to be any necessary connection between savage life and a marked excess of males; that is if we may judge by the character of the scanty offspring of the lately existing Tasmanians and of the crossed offspring of the Tahitians now inhabiting Norfolk Island.

As the males and females of many animals differ somewhat in habits and are exposed in different degrees to danger, it is probable that in many cases, more of one sex than of the other are habitually destroyed. But as far as I can trace out the complication of causes, an indiscriminate though large destruction of either sex would not tend to modify the sex-producing power of the species. With strictly social animals, such as bees or ants, which produce a vast number of

sterile and fertile females in comparison with the males, and to whom this preponderance is of paramount importance, we can see that those communities would flourish best which contained females having a strong inherited tendency to produce more and more females; and in such cases an unequal sex-producing tendency would be ultimately gained through natural selection. With animals living in herds or troops, in which the males come to the front and defend the herd, as with the bisons of North America and certain baboons, it is conceivable that a male-producing tendency might be gained by natural selection; for the individuals of the better defended herds would leave more numerous descendants. In the case of mankind the advantage arising from having a preponderance of men in the tribe is supposed to be one chief cause of the practice of female infanticide.

In no case, as far as we can see, would an inherited tendency to produce both sexes in equal numbers or to produce one sex in excess, be a direct advantage or disadvantage to certain individuals more than to others; for instance, an individual with a tendency to produce more males than females would not succeed better in the battle for life than an individual with an opposite tendency; and therefore a tendency of this kind could not be gained through natural selection.

Nevertheless, there are certain animals (for instance, fishes and cirripedes) in which two or more males appear to be necessary for the fertilisation of the female; and the males accordingly largely preponderate, but it is by no means obvious how this male-producing tendency could have been acquired. I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future.