CHAPTER IX.

THE EVIDENCE FROM SECONDARY SEXUAL CHARACTERS CONTINUED. — THE CAUSE OF THE EXCESSIVE MODIFICATION OF MALE CHARACTERS.

The Explanation of Daines Barrington and Wallace—Reasons for considering it inadequate—Darwin's explanation—History of domesticated races shows that this does not go to the root of the matter—The view that the male is more exposed than the female to the action of selection—A more fundamental explanation is needed—This is furnished by our theory of heredity—Special difficulties—Summary.

THE sexual characteristics of animals have been made the subject of considerable discussion by various naturalists, and among birds especially there have been many attempts to explain why the female has not acquired the same ornaments as the male.

The Explanations of Daines Barrington and Wallace.

Wallace points out that conspicuous ornaments and brilliant plumage would render the female bird prominent while incubating, and would thus enable enemies to detect the presence of the nest. He believes that since incubating females are exposed to this danger, natural selection has acted, by the destruction of the most conspicuous females, to gradually produce races in which the females have nothing to render them conspicuous.

In 1773 the Hon. Daines Barrington called attention (*Phil. Trans.* 1773, p. 164) to the fact that singing birds are all small, and he believes that this arises from

the difficulty larger birds would have in concealing themselves if they called the attention of their enemies by loud notes. He also says that he conceives it is for the same reason that no hen bird sings, because this talent would be still more dangerous during incubation, and he suggests that the inferiority of the female bird in point of plumage may be due to the same cause.

This argument, that the dull color and lack of ornament in female birds is a direct adaptation to their peculiar life, has been elaborated by Wallace. (*On Natural Selection*, p. 231.) He says that in the struggle for existence incessantly going on, protection or concealment is one of the most general and most effectual means of maintaining life, and it is by modifications of color that this protection can be most readily obtained, since no other character is subject to such numerous and rapid variations. He says that, as a general rule, the female butterfly is of dull and inconspicuous colors, even when the male is most gorgeously arrayed, and that in all these cases the difference can be traced to the greater need of protection for the female, on whose continued existence, while depositing her eggs, the safety of the race depends.

Since a male insect is, by its structure and habits, less exposed to danger, it does not need any special means of protection, as the female does, to balance the greater danger to which she is exposed, and Wallace believes that on account of this danger, and because of her greater importance to the existence of the species, the female insect always acquires this protection in one way or another through the action of natural selection.

He also says that "the female bird, while sitting on her eggs in an uncovered nest, is much exposed to the attacks of enemies, and any modification of color which

rendered her more conspicuous would often lead to her destruction, and that of her offspring. All variations in this direction in the female would therefore, sooner or later, be eliminated, while such modifications as rendered her inconspicuous by assimilating her to surrounding objects, as the earth or the foliage, would, on the whole, survive the longest, and thus lead to the attainment of those brown or green and inconspicuous tints which form the coloring (of the upper surface at least) of the vast majority of female birds which sit upon open nests." As a proof that this is the true explanation of the dull plumage and lack of ornaments in so many female birds, he states that wherever the nest is domed or covered, or so placed as to conceal the sitting bird, the plumage is strikingly gay and conspicuously colored in both sexes; but that in those species where there is a strong contrast in colors, and the male is gay and conspicuous, while the female is dull and obscure, the nest is open, and the sitting bird is exposed to view.

Reasons for Holding that this Explanation is Inadequate.

The argument of Wallace, which is fully stated in the essay above quoted, is briefly, that the dull plumage of so many female birds, as contrasted with the gay colors of the males, has been directly acquired in the females by the destruction of the most conspicuous ones, and the natural selection of the inconspicuous varieties.

Darwin has discussed it at length in his essay on sexual selection, and has given many reasons for refusing to give it unqualified acceptance, but I will give here a few additional reasons for believing that the phenomena in question depend upon some more fundamental law. In the first place, we must bear in mind that,

even among birds, the male differs from the female by the possession of numerous secondary sexual characters besides brilliant plumage, and that many of these, like the spurs of male Gallinaceæ, are not at all conspicuous. Bechstein (*Naturgesch Deutschland*) says that a breed of fowls formerly existed in Germany in which the hens were furnished with spurs, but that they could not be allowed to sit on their own eggs, as, although they were good layers, the spurs disturbed the nest and broke the eggs; and it might perhaps be urged that the absence of spurs in the females of wild species of Gallus may be due to the selection, for this reason, of females without spurs; but we must recollect that natural selection acts upon every part of the organism, and would, if the female were as liable as the male to give rise to hereditary variations, have acted, during the evolution of spurs, to bring the structure and habits of the female into harmony with these new weapons, so that she could enjoy their protection without injury to her eggs.

Darwin says that when we think of the multitude of birds which with impunity gladden the country with their songs during the spring, it does not seem probable that the females have been saved from acquiring this power on account of the danger to which they would have been exposed by attracting the attention of birds and beasts of prey.

If female birds have had the power of song, it would certainly seem simpler for them to have acquired the habit of restraining their voices in dangerous places than to suppose that the power has been removed by natural selection.

Wallace's view fails to account for the fact that the plumage of allied species of females is, as a rule, much more alike than that of the males; and this fact is quite

inexplicable if the dull colors of the females are due to direct modification by natural selection.

Again, we must recollect that among the lizards, where the females do not incubate, the males are often much more conspicuously colored than the females, and the females of allied species are more alike than the males. Here the dull colors of the females as compared with those of the males cannot be accounted for by the natural selection of those females which are least exposed to danger during incubation.

Among fishes the same rule is adhered to, and the males are usually more conspicuous than the females, and here the female is certainly no more exposed to danger than the male. "As far as there is any difference, the males, from being generally of smaller size, and from wandering about more, are exposed to greater danger than the females; and yet when the sexes differ, the males are almost always the most conspicuously colored. The ova are fertilized immediately after being deposited, and when this process lasts for several days, as in the case of the salmon, the female during the whole time is attended by the male. After the ova are fertilized they are, in most cases, left unprotected by both parents, so that the males and females, as far as oviposition is concerned, are equally exposed to danger, and both are equally important for the production of fertile ova; consequently the more or less brightly colored individuals of either sex would be equally liable to be destroyed or preserved, and both would have an equal influence on the colors of their offspring or the race." (Darwin, *Sexual Selection*, Vol. II, p. 19.)

The male stickleback does all the work of building the nest, and after the eggs are laid and fertilized he drives the females away, and performs for a long time

the duties of a nurse with exemplary care and vigilance, gently leading back the young to the nest when they stray too far. Yet the male is more brilliantly colored than the female, and his colors are especially brilliant and conspicuous during the breeding season.

I shall show farther on that the males of domesticated breeds of fowls and pigeons are more conspicuous and diversified than the females, but as fancy pigeons are reared in confinement, and are protected from every danger, this cannot be due to the natural selection of *the best-protected females.*

We must conclude, then, that the brilliant plumage of male birds is due to some more general and fundamental cause than the one proposed by Wallace, since female reptiles which do not incubate, and female fishes which are even less exposed to danger than the males, and female domesticated birds which are thoroughly protected from enemies, all follow the same law.

The fact that many structures which are not at all conspicuous are confined, like gay plumage, to male birds, also indicates the existence of an explanation more fundamental than the one proposed by Wallace, and this latter explanation gives no reason why the females of allied species should so often be almost exactly alike when the males are very different.

Darwin's Explanation.

Darwin has given a different explanation, and he believes that the greater modification of males throughout the animal kingdom is chiefly due to sexual selection. He has devoted more than five hundred pages to the development of this idea in his essay on sexual selection (*Descent of Man*, Part II.), and he has marshalled an overwhelming array of facts with mas-

terly skill. The attempt to point out within the limits of a single chapter the errors of his conclusion is beset with many difficulties, and I shall be compelled to treat the subject with brevity, and to leave unsaid much which might be urged did space permit.

As an introduction to the discussion of the subject, I shall quote Darwin's statement of the meaning of the term "sexual selection." He says: "This depends on the advantage which certain individuals have over other individuals of the same sex and species in exclusive relation to reproduction. When the two sexes differ in structure in relation to different habits of life, they have, no doubt, been modified through natural selection, accompanied by inheritance limited to one and the same sex. So, again, the primary sexual organs, and those for nourishing and protecting the young, come under the same head; for those individuals which generated or nourished their offspring best, would leave, *cæteris paribus*, the greatest number to inherit their superiority; while those which generated or nourished their offspring badly, would leave but few to inherit their weaker powers. As the male has to search for the female, he requires for this purpose 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. . . . When the two sexes follow exactly the same habits of life, and the male has more highly developed sense organs or locomotive organs than the female, it may be that these in their perfect state are indispen-

sable 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 the less well-endowed males, if time were allowed them, would succeed in pairing with the females; and they would in all other respects, judging from the structure of the female, be equally well adapted for their ordinary habits of life. In such cases sexual selection must have come into action, for 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. 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 fortified through sexual selection, that is, by the advantage acquired by certain males over their rivals. But in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection. . . . There are many structures and instincts which must have been developed through sexual selection, such as the weapons of offence and the means of defence possessed by the males for fighting with and driving away their rivals—their courage and pugnacity—their ornaments of many kinds—their organs for producing vocal or instrumental music, and their glands for emitting odors; most of these latter structures serving only to allure or excite the females. That these characters are the result of sexual and not of ordinary selection is clear, as unarmed, unornamented, or unattractive males would succeed equally well in the battle for life, and in leav-

ing a numerous progeny, if better endowed males were not present. We may infer that this would be the case, for 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 they are, in many respects, interesting, but more especially as they depend 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 the strangest 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. In the same manner as man can improve the breed 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. Through repeated deadly contests, a slight degree of variability, if it led to some advantage, however slight, would suffice for the work of sexual selection; and it is certain that secondary sexual characters are eminently variable.

"In the same manner as man can give beauty, according to his standard of taste, to his male poultry—can give to the Sebright bantam a new and elegant plumage, an erect and peculiar carriage—so it appears that in a state of nature female birds, by having long selected the more attractive males, have added to their beauty. . . . It is certain that with almost all animals there is a struggle between the males for the possession of the fe-

males. . . . Of the males the strongest, and, with some species, the best armed, drive away the weaker males; and the former would then unite with the more vigorous and best nourished females, as these are the first to breed. 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; 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. But in a multitude of cases the males which conquer other males do not obtain possession of the females independently of choice on the part 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, as has been actually observed in some cases, that they would at the same time prefer the most vigorous and lively males. . . . And this apparently has sufficed during a long course of generations to add not only to the strength and fighting power of the males, but likewise to their various ornaments or other attractions. . . . To sum up on the means through which, so far as we can judge, sexual selection has led to the development of secondary sexual characters: It has been shown that the largest number of vigorous offspring will be reared from the pairing of the strongest and best armed males, which have conquered other males, with the most vigorous and best-nourished females, which are the first to breed in the spring. Such females, if they select the most attractive and, at the same time, vigorous males, 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."

The Study of Domesticated Races shows that this Explanation does not go to the Root of the Matter.

This long extract will, I hope, fully explain to those readers who are not familiar with Darwin's essay, the nature of sexual selection. It will be seen that he attributes the greater modification of the males as compared with the females, in most of the groups of animals where the sexes differ, to the fact that the males have struggled with each other for the possession of the females, or have been chosen by the females. This process, long continued, is believed to have resulted in the perpetuation of the strongest, best armed, or most attractive males.

I fully acknowledge the great potency of sexual selection, and believe with Darwin that it must act in essentially the manner described by him, but I do not believe that it goes to the root of the matter.

Fortunately there is a simple experimental test which is easily tried and gives a satisfactory solution of the question whether the phenomena do or do not depend upon something more fundamental than the exposure of the male to the action of selection.

If we take animals in which the sexes differ but little, and prevent them from following their own inclinations,

and pair them without any reference to their own preferences, and continue this for a number of generations, until we have produced a number of divergent races or breeds; if we then find that the males of these breeds differ more from each other than the females, we must conclude that there is, behind the action of selection, some more deep-seated law, which determines that males shall, as a rule, be more modified than females.

Domesticated Pigeons.

The study of domesticated pigeons is extremely interesting in this connection, for it shows conclusively that the tendency which we have shown to exist in nearly all groups of bisexual animals, the tendency of the male to deviate more than the female from the typical structure of allied forms, cannot be attributed exclusively to the fact that the male is more exposed than the female to the action of either sexual or ordinary selection.

There are more than two hundred wild species of the pigeon family, and throughout the whole group there is an almost total absence of external difference between the sexes. In a few species the plumage is somewhat more brilliantly colored in the male than it is in the female, and it is stated that in one species, *Carpophaga oceanica*, the excrescence at the base of the beak is a sexual character, but these differences between the sexes are slight and exceptional.

In domesticated pigeons, on the contrary, the sexes often differ considerably, and it is a remarkable fact that here, as in so many other groups of the animal kingdom, "the characteristics of the different breeds are often most strongly displayed in the male bird." (Darwin, *Variation*, Vol. I. p. 199.) In many cases the sexes are

alike; thus the female trumpeter has a tuft like that of the male, and the hood of the Jacobin and the frill of the turbit are alike in both sexes; but wherever the sexes do differ the males are, as a rule, more modified than the females.

In all ordinary domesticated breeds as well as in most wild species, the number of tail-feathers is twelve, but in the fan-tail breed there are from thirty to forty, and they are permanently expanded like a fan. We must believe that this deviation from the typical number of tail-feathers in the pigeon family is due to recent modification, and we find that the number is often much greater in the male fan-tail than it is in the female.

The pouter pigeon is a very remarkable domestic breed. All domestic pigeons have some slight power of inflating the crop, but this power is so greatly developed in the pouter breed that the bird is able to blow himself up like a balloon, and Darwin says that after one of his pouters had swallowed a good meal of peas, he could hear the peas rattle as if in a bladder as the bird flew through the air with its crop inflated. Darwin says that the males pout more than the females, and glory in this power, and strut about puffed up with wind and pride. He also says that it is a very unusual thing for the female to excel in pouting. We must therefore believe that the male pouter has departed further than the female from ordinary pigeons.

The tumbling habit of tumbler pigeons is perhaps the most remarkable of all the hereditary modifications of domestic animals which man has produced. The following account of the English tumbler is quoted by Darwin from Brent: "Every few seconds over they go, one, two, or three somersaults at a time. Here and there a bird gives a very quick and rapid spin, re-

volving like a wheel, though they sometimes lose their balance and make a rather ungraceful fall, in which they occasionally hurt themselves by striking some object. They begin to tumble almost as soon as they can fly; at three months old they tumble well but still fly *strong; at five or six months they tumble excessively,* and in the second year they mostly give up flying on account of their tumbling so much and so close to the ground. Some fly round with the flock, throwing a clean somersault every few yards, till they are obliged to settle from giddiness and exhaustion. These are called air-tumblers, and they commonly throw from twenty to thirty somersaults in a minute, each clear and clean. I have one red cock that I have on two or three occasions timed by my watch, and counted forty somersaults in the minute. Others tumble differently. At first they throw a single somersault, then it is doubled till it becomes a continuous roll, which puts an end to flying, for if they fly a few yards, over they go, and roll till they reach the ground. Thus I had one kill herself, and another broke his leg. Many of them turn over only a few inches from the ground, and will tumble two or three times in flying across their loft. These are called house-tumblers, from tumbling in the house."

The tumbling habit is shared by both sexes, but as in the case of the *pouter, it is the male which excels.*

The carrier and barb races of domestic pigeons are characterized by the presence of naked carunculated skin over the beak and around the eyes, and in both of these races this feature is most pronounced in the males. These illustrations are sufficient to show that the distinctive characteristics of each breed of domesticated pigeons are either alike in both sexes, or else most de-

veloped in the males, and that the males of allied breeds differ from each other more than the females.

The individuals of choice breeds of domestic pigeons are not allowed to follow their own inclinations and to pair at will, but they are very carefully watched by the breeder, for reasons which have no reference to the inclinations of the birds, so that there is no chance for sexual selection, nor does the breeder confine his attention to the male sex especially, but seeks to improve the female as well as the male; and Mr. Eaton asserts in his "Treatise on the Almond Tumbler" that a hen tumbler would be worth twice as much money as a cock if she had the characteristics of the breed equally well developed.

We find, then, that among the two hundred or more wild species of the pigeon family, where sexual selection has every chance to act, there is no great difference between the sexes; but that in the more valuable domesticated breeds, where all choice is precluded, and sexual selection out of the question, the males are, as a rule, more modified than the females whenever the sexes differ. We must therefore conclude that the greater modification of the males, in pigeons at least, is not due to the fact that the male is more exposed than the female to the action of selection, but that the male has more tendency than the female to depart from the ancestral type. In pigeons, at least, we must believe that something within the animal determines that the male should lead and the female follow, in the evolution of new breeds.

Domesticated Animals in General.

When we study other domesticated animals in the same way, we find that in some cases, as in horses, there is little difference between the sexes, and in other cases

the efforts of the breeder are directed towards a peculiarity of one or the other sex, as when cattle are reared for the sake of their milk, or when fowls are kept for fighting, or for their eggs; but whenever the sexes do differ we find that the same law exists, and that the males of allied races differ from each other more than the females. Regarding sheep, Darwin says that there is a strong tendency for characters which have been acquired under domestication to become attached exclusively to the male sex, or to be much more highly developed in the male than in the female. As illustrative of this law he refers, among other instances, to the fact that the accumulation of fat in the fat-tailed sheep of the plains of India is greater in the male than in the female, and the mane of the African maned race is far more developed in the ram than in the ewe.

Among fowls, every one is familiar with the fact that the males of different breeds are, as a rule, much more different than the females, and that most of the breeds are distinguished from each other by peculiarities in organs which, like the comb, spurs, and long tail-feathers, are confined to the male. As a rule there is considerable difference between the sexes of fowls, but exceptions are not at all unusual, and in many breeds the sexes can hardly be distinguished. The males and females of the gold and silver laced Sebright bantam can be barely distinguished from each other, except by the comb, wattles, and spurs, for they are colored alike, and the males have not hackles, nor the flowing, sickle-like tail feathers. In one breed of game fowls the males and females are said to resemble each other so closely that the cocks have often mistaken their hen-feathered opponents in the cock-pit for real hens, and have lost their lives by the mistake, for although the cock is dressed in

the feathers of the hen, he retains all his courage and high spirit.

In a few cases the females of allied breeds differ more than the males, and Darwin refers to two strains of black-breasted red games, in which the cocks were so much alike that they could not be distinguished, while the hens were partridge-brown in the one case and fawn-brown in the other. The pencilling which is characteristic of the Hamburg hen is almost absent in the male, but as a rule the various breeds of fowls are distinguished by peculiarities of organs which are almost or entirely confined to the males.

Of the comb Darwin says that it differs much in the various breeds, and its form is eminently characteristic of each kind with the exception of the Dorkings. A single deeply serrated comb is the typical and most common form. It differs much in size, being immensely developed in Spanish fowls; and in a local breed called Redcaps, it is sometimes upwards of three inches in breadth at the front, and more than four inches in length, measured to the end of the peak behind. In some breeds the comb is double, and when the two ends are cemented together it forms a "cap comb;" in the "rose comb" it is depressed, covered with small projections, and produced backwards; in the horned and Créve-Cœur fowl it is produced into two horns; it is triple in the pea-combed Brahmas, short and truncated in the Malays, and absent in the Guelderlands. In the tasselled game a few long feathers arise from the back of the comb, and in many breeds a crest of feathers replaces the comb. The crest, when little developed, arises from a fleshy mass, but when much developed, form a hemispherical protuberance of the skull. In the best Polish fowls it is so largely developed that the birds can hardly pick up their

food, and they are said to be particularly liable to be struck by hawks.

With reference to variation in the plumage of the male fowl Darwin says (*Variation*, p. 307): "As in some orders of birds the males display extraordinarily shaped feathers, such as naked shafts with disks at the end, etc., the following case may be worth giving. In the wild *Gallus bankiva*, and in our domestic fowls, the barbs which arise from each side of the extremities of the hackels are naked or not clothed with barbules, so that they resemble bristles; but Mr. Brent sent me some scapular hackels from a young Birchen Duckwing game-cock, in which the naked barbs became densely reclothed with barbules towards their tips, so that these tips, which were dark colored with a metallic lustre, were separated from the lower parts by a symmetrically-shaped transparent zone formed of the naked portions of the barbs. Hence the colored tips appeared like little separate metallic disks. The sickle feathers in the tail, of which there are three pair, and which are eminently characteristic of the male sex, differ much in the various breeds. They are scymater-shaped in some Hamburgs, instead of being long and flowing as in the typical breeds. They are extremely short in the Cochins, and are not at all developed in Hennies. They are carried, together with the whole tail, erect in Dorkings and games, but droop much in Malays and some Cochins. Sultans are characterized by an additional number of lateral sickle feathers. The spurs vary much, being placed higher or lower on the shank; being extremely long and sharp in games, and blunt and short in Cochins."

The number of the spurs varies, some fowls having as many as five on each leg; their position on the leg also varies in different breeds.

These extracts are sufficient to show that organs which are confined to the cock are especially variable, and that the characteristics of each breed are chiefly modifications of their male parts.

It is therefore evident that the males of the various breeds are as a rule much more different from each other than the females, in fowls, as well as in sheep, pigeons and other domestic animals. The rule is by no means universal, however, and there are a few remarkable exceptions. I have already mentioned two cases of black-breasted red game fowls, in which the females were quite distinct, while the males of the two forms could not be distinguished. The breed of domestic ducks known as the Call Duck is remarkable for its small size and from the extraordinary loquacity of the female, while the drake only hisses like ordinary drakes.

Darwin gives (*Variation*, Vol. I. p. 309) an interesting account of the origin of the crest in Polish fowls. He says that in most fowls head ornaments of all kinds are more fully developed in the male than in the female; but in Polish fowls the crest or top-knot, which in the male replaces the comb, is equally developed in both sexes. "In certain sub-breeds, which from the hen having a small crest are called lark-crested, a single upright comb sometimes almost entirely takes the place of the crest in the male. From this latter case, and from some facts presently to be given with respect to the protuberance of the skull in Polish fowls, the crest in this breed ought perhaps to be viewed as a feminine character which has been transferred to the male. . . . At the present day all the breeds of Polish fowls have the great bony protuberance on their skulls, which includes part of the brain and supports the crest, equally developed in both sexes. But formerly in Germany the skull of

the hen alone was protuberant. Blumenbach, who particularly attended to abnormal peculiarities in domestic animals, states, in 1813, that this was the case; and Bechstein had previously, in 1793, observed the same fact. This latter author . . . . expressly states that he never observed this protuberance in male fowls. Hence there can be no doubt that this remarkable character in the skulls of Polish fowls was formerly in Germany confined to the female sex, but has now been transferred to the males, and has thus become common to both sexes."

These few cases are clearly exceptional, and the study of domesticated animals shows us that, as a rule, the males of allied breeds, like the males of wild species, are more different from each other than the females. We cannot attribute this difference to sexual selection, for most of our domesticated animals, especially those of pure blood, are prevented by man from following their own inclination in the selection of mates. Neither can we assert that man has devoted especial attention to the selection and modification of males, and has aimed at changes in those organs which are most developed in males, for, among pigeons at least, the opposite of this is the case, and a female bird of equal excellence is more valued than a male. We are thus forced to conclude not only that "among domesticated animals the male is more variable than the female" (Darwin, *Sexual Selection*, Vol. I. p. 266), but also that organs which are confined to males, or unusually developed in them, are more apt than organs which are confined to females, to transmit their variations, and thus to give rise to hereditary race modifications. As our domesticated races show, by their close similarity to natural species, that the causes which have produced them are very similar to those which have acted upon wild organisms, we are justified

in doubting, from the analogy of domesticated animals, whether the excessive modification of the males of wild animals is due entirely to the fact that males are more exposed than females to the action of selection. As the study of domesticated races leads us to the conclusion that something within the animal compels the male to lead and the female to follow in the evolution of new breeds, we must believe that a similar law regulates in the same way the evolution of wild organisms. The study of domesticated races, like the study of wild species, also compels us to believe that this law is not immutable, but that variations which originate in a female may become hereditary, although this is somewhat rare, as compared with the hereditary establishment of male modifications.

The View that the Male is more Exposed than the Female to the Action of Selection.

According to Darwin the excessive exposure of the male to the action of selection, natural and sexual, is the cause of his great modification. He points out that the distinctive characters of the male are, in many cases at least, of especial use to him, as a male, and he shows that the individuals which possess these peculiarities are benefited by them, and have therefore been preserved, while the females, deriving no advantage from them, have not been thus selected.

No one can doubt the truth of this statement, but it does not go to the root of the matter. The question is not how peculiarities useful to the male alone have been restricted to that sex, but why the female has not acquired another set of characteristics to fit her for her peculiar needs. No one can doubt that a hen might have special organs, as useful to her for the care and pro-

tection of her brood, and for her own defence while incubating, as the cock's spurs and ornaments are in another way to him: nor can we doubt that such organs would be preserved and perfected by natural selection if proper variations should appear and should become hereditary.

Among the mammalia the peculiar organs of the male, his so-called secondary sexual characters, are often of great use to him in ways which are not connected with reproduction. This is especially true of his weapons of offence, for the bull not only uses his horns in fighting with other males for the females, but also in protecting himself and the rest of the herd from enemies. The elephant uses his tusks in many ways. He tears down trees with them for the sake of the foliage, and he rips open palm trees in order to obtain the nutritious farinaceous core. He uses them to prod the ground to discover whether it is firm enough to bear his weight, and with them he attacks and kills his enemies. Many mountain goats, when they accidentally fall from great heights, strike upon their strong and elastic horns, and thus break the force of the blow. In fact, most of the weapons which occur in male animals are used for defence or protection, as well as in their conflicts with other males. The presence of these organs often saves the life of their possessor, and it would therefore seem as if they would be more modified by natural selection than by sexual selection, for natural selection usually means death to the unarmed male, while the result of sexual selection is simply a decreased number of descendants. But natural selection acts upon the female as well as the male, and as the care and protection of the young usually falls to the female mammal, it would seem as if she as well as the male ought to have special weapons of de-

fence. The welfare of the race does not depend upon the number of young which are born, but upon the number which grow up; and if we take two cases, one variety in which the male has special weapons which enable him to drive away his rivals and thus to produce a great number of children, and another variety in which the female has special weapons which enable her to protect her young from enemies, and thus rear them all in safety, it certainly seems as if the modification would be most sure of perpetuation in the second case, and that the second variety should, in time, exterminate the first.

As a matter of fact we do find that the weapons of mammals exist in many cases in the female, but they are most developed and most modified in the male, and it is hard to understand why variations of this kind should not more frequently arise and become hereditary in the female, unless something besides sexual selection determines that males should be more plastic than females.

The modification of the female is certainly quite possible, for there are numbers of cases in all groups of the animal kingdom where the females alone have some peculiar characteristic which is not directly concerned in reproduction.

Thus Darwin says (*Variation*, Vol. I. p. 333): "The tarsi of the front legs are dilated in many male beetles or are furnished with broad cushions of hairs; and in many genera of water-beetles they are armed with a round flat anchor, so that the male may adhere to the slippery body of the female. It is *a much more unusual circumstance* that the females of some water beetles (Dytiscus) have their elytra deeply grooved, and in *Acilius sulcatus* thickly set with hairs, as an aid to the male."

We have seen that the males of many species of crustacea have various parts of their bodies especially modi-

fied for clinging to the female, and we can understand that natural selection will perpetuate modifications of this kind, for the males which adhere most firmly to the females will leave the greatest number of descendants, who will inherit their peculiarity; but the same rule would hold good if certain females were so modified as to afford a good surface for the male to cling to, as we may see from the fact that in a few forms the females are thus modified.

Fritz Müller has described certain species of amphipod crustacea, of the genus Melita, in which the female does have special hook-like processes for the male to cling to, and cases of this kind are sufficiently numerous to show that when a useful female modification does appear it becomes hereditary. In all cases where the sexes are separated and different from each other, the female undoubtedly might be benefited by peculiar organs as frequently as the male. How then are we to account for the remarkable fact that the cases of male modification of this kind are so very much more numerous than the instances of female modification?

Darwin concludes that we must believe that the male is more variable than the female, and we shall subsequently see that this is so, and the reason for it. Still the female does vary, and vary greatly, and unless there is some reason why female variations should be less apt than male variations to become hereditary, the great preponderance of special male modifications is incomprehensible.

The Male more Eager than the Female.

Darwin attributes this to the greater eagerness of the male. He says (*Sexual Selection*, Vol. I. p. 263): "Throughout the animal kingdom, when the sexes

differ from each other in external appearance, it is the male which, with rare exceptions, has been chiefly modified: for the female still remains more like the young of her own species, and more like the other 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."

He points out that it is the males that fight together and display their charms before the females; that among mammals, birds, fishes, reptiles, and batrachians, the male is known to be much more eager than the female; that among insects it is a law that the male seeks the female; that among spiders and crustacea the males are more active and erotic than the females, and that in these latter groups the organs of sense and of locomotion are often more highly developed in the male than in the female. The female, on the other hand, is, with the rarest exceptions, less eager than the male: she is coy, requires to be courted, and may often be seen for a long time endeavoring to escape from the male.

He gives the following explanation of the manner in which the male has been rendered more eager than the female, so that he searches for her and plays the more active part in courtship in so many widely distinct classes of animals:

"It would be no advantage and some loss of power if both sexes were mutually to search for each other; but why should the male almost always be the seeker? With plants, the ovules after fertilization have to be nourished for a time; hence the pollen is necessarily brought to the female organs—being placed on the stigma, through the agency of insects or of the wind, or by the spontaneous movements of the stamens, and with the algæ, etc., by the locomotive power of the antherozooids. With lowly

organized animals permanently affixed to the same spot, and having their sexes separated, the male element is invariably brought to the female; and we can see the reason, for the ova, even if detached before being fertilized and not requiring subsequent nourishment and protection, would be, from their larger relative size, less easily transported than the male element. Hence, plants and many of the lower animals are in this respect analogous. In the case of animals not affixed to the same spot, but enclosed within a shell, with no power of protruding any part of their bodies, and in the case of animals having little power of locomotion, the males must trust the fertilizing element to the risk of at least a short transit through the waters of the sea. It would, therefore, be a great advantage to such animals, as their organization became perfected, if the males, when ready to emit the fertilizing element, were to acquire the habit of approaching the female as closely as possible. The males of various lowly organized animals have thus aboriginally acquired the same habit which would naturally be transmitted to their more highly developed male descendants; and in order that they should become efficient seekers, they would have to be endowed with strong passions. The acquirement of such passions would naturally follow from the more eager males leaving a larger number of offspring than the less eager."

Need for a more Fundamental Explanation.

This is all undoubtedly true, as far as it goes, but it does not cover the whole ground. The sexual passion of the male is undoubtedly stronger, as a rule, than that of the female, and as the existence of the species depends upon the strength of this passion, there will undoubtedly be a selection of the most eager males.

We must recollect, however, that the sexual passion is not the only one upon which the perpetuation of the species depends. The parental feeling or passion is fully as important, and as a rule this is most developed in the female. In the same way that the males which are best fitted for pleasing and commanding the females are naturally selected, those females which are best adapted for protecting, feeding, and educating the young would be picked out from generation to generation. If any hereditary variation should appear which contributed in any way to this end, it would be at least as valuable to the species as an extra ornament or a new color in the male; and there are certainly as many possible ways to improve a female animal as there are to improve a male. If these variations of parts which are confined to the female, or which are of use only or chiefly in this sex, are as apt as the similar parts of a male to give rise to hereditary modifications, we should expect the evolution of new improvements in the female body to keep pace with the improvement of the male body.

We should expect, when allied species are compared, to find that the females differ from each other as much as the males; and that while the males are gradually becoming more and more specialized for conflict and rivalry with other males, and for winning the favor of the females, the females are becoming specialized along another path, for the better care and protection of their young. The fact that we find nothing of the kind; that evolution shows itself especially in the males, while the females remain comparatively stationary, shows that we must search for some other explanation than the one given by Darwin. We are, therefore, compelled to recognize, in the general rule that the male is more modified than the female, the evidence of some cause

more fundamental and general than the great exposure of the male, through the intensity of the sexual passion, to the influence of selection; for the parental instinct is fully as important for the welfare of the race as the sexual instinct, and the former is, as a rule, most developed in the female, just as the latter is greatest in the male, and it might be expected to lead to the selection and modification of females, as the latter passion does to the modification of males.

The Theory of Heredity Furnishes the Only Adequate Explanation.

We must acknowledge that the great body of facts detailed in the beginning of this chapter have no adequate explanation, except on the hypothesis that a part which is present, or functional, or most important in the male alone, is very much more likely than a part which is limited to females in the same way, to give rise to hereditary variations. The facts receive a ready explanation on the hypothesis that there is an especial adaptation for the transmission to the egg of gemmules thrown off by the cells of the male body, while their transmission in the female is not thus provided for, but is due to accident. According to this view we must, in animals where the sexes have long been separated, look to the cells of the male body for the origin of a large proportion of the variations which have gradually been accumulated in the past to give species their present character; and we must regard secondary sexual characters as differing from ordinary specific characteristics, simply in being especially useful to one sex, usually the male, or in being disadvantageous to the other sex, so that natural selection has developed them to a greater degree in one sex than in the other.

It will be seen that the evidence from this source is, as far as it goes, very similar to the evidence from hybrids. A reciprocal cross between two species furnishes a means of analyzing the influence of the two sexes, and of distinguishing, to some slight degree, the effect of each sexual element in heredity. The study of sexual character gives us another means of doing the same thing on a more limited scale.

As each cell of the body may throw off gemmules, there is no way of showing that a variation in a part which is alike in both sexes, is due to the transmission of gemmules from the cells of one parent rather than from those of the other, but the case is different with a part which is more developed in one sex than it is in the other. In this case we should, according to our theory of heredity, expect it to throw off gemmules most frequently in the sex in which it is of most functional importance, and as we suppose that there is an especial arrangement for the transmission to the egg of those gemmules which originate in the male body, we can see that an organ which is most important in the body of the male is much more likely to give rise to hereditary modification than one which is most important, and therefore most prolific of gemmules, in the female body.

The *history of secondary sexual characters is*, therefore, what our theory of heredity would lead us to expect, and no other explanation which has ever been proposed fully accounts for all the phenomena.

Instances of Female Modification.

We should not expect, however, to find secondary sexual characters exclusively confined to males, but simply more general than they are in females, and as a matter of fact we do meet with many cases where the female has been more modified than the male.

I will now give a few of those which seem to me to be most opposed to my general conclusion.

Female Modification.

In certain species of the amphipod crustacean genus Melita, the females differ from all other amphipods by having the sexual lamellæ of the penultimate pair of feet produced into hook-like processes, of which the males lay hold with the hands of the first pair. In another amphipod, *Brachyscelus,* the male possesses, like all other amphipods, a pair of posterior antennæ, but they are absent in the female, so that the latter differs more than the male from allied forms. Darwin states that the females of certain water-beetles, as *Dytiscus Acilius* and *Hydroporus,* have their wing-covers grooved or thickly set with hairs or punctured, in order to enable the male to cling to the slippery surface of their hard and polished bodies.

The call duck is a domesticated breed which receives its name from its extraordinary and exceptional loquacity, and as this loquacity is confined to the female, while the male hisses like other ducks, we must regard this as a case of female modification. We know from the statements of Blumenbach and Bechstein that, previously to the year 1813, the great bony protuberances on the skull which characterize the Polish breed of fowls, were confined to the females, although they are now equally developed in both sexes. There can be no doubt that this peculiarity originated in the females, and was subsequently inherited by the males.

Among the Phasmidæ or spectre insects the females alone, in some species, show a most striking resemblance to leaves, while the males show only a rude approximation, and Darwin has pointed out that, as we can

hardly believe that such a resemblance is disadvantageous to the males, we must conclude that the females alone have varied, and that these variations have been preserved and augmented by natural selection for the sake of protection, and have been transmitted to the female offspring alone.

In two species of Birds of Paradise, *Paradisia apoda* and *Paradisia Papuana*, the females differ from each other more than do their respective males; the female of the latter species having the under surface pure white, while the female of *P. apoda* is deep brown beneath.

The males of two species of shrikes (*Oxynotus*) in the islands of Mauritius and Bourbon, differ but little in color, while the females differ much, so that the female of the Bourbon species might at first sight be mistaken for the young of the Mauritius species. In this case there seems to be every reason for believing that the female of the Mauritius species has varied, while the male has remained unmodified.

Semper states (*Animal Life*) on the authority of Dr. Hagen that the females of many species of cave-beetles are blind, while the males have perfect eyes. As we may feel confident that these beetles are descended from ordinary forms, we must regard this as an instance of female modification.

The remarkable shell which is secreted by the large fan-like arms of the paper nautilus (Argonauta) occurs in the females alone, and it probably owes its origin to female modification, although it it not impossible that our recent species may be descended from a form in which the male had a shell.

The most remarkable cases of female modification are those which are presented by polymorphic insects.

Papilio turnus is one of our common yellow butter-

flies, and it is found over almost the whole of temperate North America. In New England and New York the sexes are alike, but south of lat. 42° some of the females are black, and they are so different from the yellow male and the northern yellow female, that they were for a long time regarded as a distinct species, and have received a specific name, *Papilio glaucus.* Between lat. 42° and lat. 37° both forms are found, and Prof. Uhler of Baltimore, has reared the yellow female *Papilio turnus*, and the black one, *P. glaucus*, from the same lot of eggs, but further south only the black female is found, although the male is exactly like that which in New England is associated with the yellow female alone.

Wallace has recorded a number of similar cases among the Malayan *Papilionidæ*, of which *Papilio Memnon* is one of the most striking. In this species there are two kinds of females, one closely resembling the male, and the other differently colored, and furnished with long spatulate tail-like elongations of the hinder wings. These tails are not present on the wings of the male nor on those of the second female, although they are found in both sexes of other species of Papilio, and in some other less specialized genera of the Papilio family. The males, the tailed and the tailless females have all been reared from a single group of eggs, so there is no doubt that they all belong to the same species.

Wallace has given other cases in which the same male form is found associated, in different countries, with their three different female forms.

It is possible, and indeed probable, that in some of these cases certain females have resembled the male, while others have either remained unmodified or else have reverted back to an ancestral form.

Darwin refers to a case of sexual dimorphism which

occurs in several species of the dragon flies of the genus Agrion, in which a certain number of females are of an orange color, and thus differ from the males and ordinary females.

He suggests that this is probably a case of reversion, for in the true Libellulæ, whenever the sexes differ in color, the females are always orange or yellow, so that, supposing Agrion to be descended from some primordial form having the characteristic sexual colors of the typical Libellulæ, it would not be surprising that a tendency to vary in this manner should occur in the females alone.

This explanation seems to apply to several of the recorded cases of female polymorphism, but not to all, and we must acknowledge that in these cases the female shows, in a far greater degree than the male, a tendency to deviate from the primitive form of the species, and to give rise to new race modifications.

We have already called attention to the fact that among the Crustacea there are many cases of male polymorphism, and many cases of the same kind are known among male insects; as well as many cases, besides those I have mentioned, of female polymorphism.

In many of the social insects we have most profound structural modifications, and most complex instincts, which can only have arisen in females; and as allied species of social insects differ from each other in characters which are confined to the females, we must acknowledge that in these forms there is no lack on the part of this sex of a power to give rise to hereditary race modifications.

That facts of this kind present a serious difficulty I cannot deny, but we must recollect that our hypothesis does not demand that the power to transmit variations should be confined exclusively to males, but simply that

it should be much more active in them than it is in the females, and we certainly find that this is the case. I believe that we may, in justice, conclude that, with greater knowledge of the few cases where females give evidence that they have this power to an exceptional degree, the difficulty will disappear, for they are certainly deviations from a general rule, and they must therefore be regarded as special cases, to be studied by themselves. It is interesting to notice that both parthenogenesis and female race-modification are more frequent among the Anthropods than in most other groups of animals, and that parthenogenesis is known to occur in the Lepidoptera and in the social insects, two of the groups where great modifications can be most clearly traced to a female origin. It is not improbable that the power of the egg to develop without fertilization, and its power to store up and transmit gemmules, may be related in some way, so that when the one power is acquired the other is also.

Every one is aware that we meet, in the most diverse groups of animals, with structures and instincts which are confined to the females; such as the brood-chambers of Daphnia, the ovipositor of the ichneumon fly, the sting of the honey bee, the marsupial pouch of the opossum, the nest-building and incubating instincts of birds, or the nursing habit of female mammals. We must bear in mind, however, that in many of these cases a male origin for the successive variations is not out of the question. The fact that the male Hippocampus and not the female has an incubatory pouch, and that mammæ are present in most male mammals, certainly shows the possibility of a male origin for these structures, and as many male birds either share in the work of nest-building and incubating or aid the female in this duty, there

is certainly no difficulty in believing that these instincts have had a male origin.

The remarkable instinct which leads some species of cuckoo and crow blackbirds to lay their eggs in the nests of other species, must have originated in females, and a collection of all the cases which must be explained in the same way would make a formidable list, but the fact would still remain true, that among animals with separate sexes, male modifications are very much more frequent than female modifications, and this is all that our theory requires.