CHAPTER VIII.

INSTINCT.

Instincts comparable with habits, but different in their origin --Instincts graduated -- Aphides and ants -- Instincts variable -- Domestic instincts, their origin -- Natural instincts of the cuckoo, molothrus, ostrich, and parasitic bees -- Slave-making ants -- Hive-bee, its cell-making instinct -- Changes of instinct and structure not necessarily simultaneous -- Difficulties of the theory of the Natural Selection of instincts -- Neuter or sterile insects -- Summary.

Many instincts are so wonderful that their development will probably appear to the reader a difficulty sufficient to overthrow my whole theory. I may here premise, that I have nothing to do with the origin of the mental powers, any more than I have with that of life itself. We are concerned only with the diversities of instinct and of the other mental faculties in animals of the same class.

I will not attempt any definition of instinct. It would be easy to show that several distinct mental actions are commonly embraced by this term; but every one understands what is meant, when it is said that instinct impels the cuckoo to migrate and to lay her eggs in other birds' nests. An action, which we ourselves require experience to enable us to perform, when performed by an animal, more especially by a very young one, without experience, and when performed by many individuals in the same way, without their knowing for what purpose it is performed, is usually said to be instinctive. But I could show that none of these characters are universal. A little dose of judgment or reason, as Pierre Huber expresses it, often comes into play, even with animals low in the scale of nature.

Frederick Cuvier and several of the older metaphysicians have compared instinct with habit. This comparison gives, I think, an accurate notion of the frame of mind under which an instinctive action is performed, but not necessarily of its origin. How unconsciously many habitual actions are performed, indeed not rarely in direct opposition to our conscious will! yet they may be modified by the will or reason. Habits easily become associated with other habits, with certain periods of time and states of the body. When once acquired, they often remain constant throughout life. Several other points of resemblance between instincts and habits could be pointed out. As in repeating a well-known song, so in instincts, one action follows another by a sort of rhythm; if a person be interrupted in a song, or in repeating anything by rote, he is generally forced to go back to recover the habitual train of thought: so P. Huber found it was with a

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

caterpillar, which makes a very complicated hammock; for if he took a caterpillar which had completed its hammock up to, say, the sixth stage of construction, and put it into a hammock completed up only to the third stage, the caterpillar simply re-performed the fourth, fifth, and sixth stages of construction. If, however, a caterpillar were taken out of a hammock made up, for instance, to the third stage, and were put into one finished up to the sixth stage, so that much of its work was already done for it, far from deriving any benefit from this, it was much embarrased, and, in order to complete its hammock, seemed forced to start from the third stage, where it had left off, and thus tried to complete the already finished work.

If we suppose any habitual action to become inherited--and it can be shown that this does sometimes happen--then the resemblance between what originally was a habit and an instinct becomes so close as not to be distinguished. If Mozart, instead of playing the pianoforte at three years old with wonderfully little practice, had played a tune with no practice at all, be might truly be said to have done so instinctively. But it would be a serious error to suppose that the greater number of instincts have been acquired by habit in one generation, and then transmitted by inheritance to succeeding generations. It can be clearly shown that the most wonderful instincts with which we are acquainted, namely, those of the hive-bee and of many ants, could not possibly have been acquired by habit.

It will be universally admitted that instincts are as important as corporeal structures for the welfare of each species, under its present conditions of life. Under changed conditions of life, it is at least possible that slight modifications of instinct might be profitable to a species; and if it can be shown that instincts do vary ever so little, then I can see no difficulty in natural selection preserving and continually accumulating variations of instinct to any extent that was profitable. It is thus, as I believe, that all the most complex and wonderful instincts have originated. As modifications of corporeal structure arise from, and are increased by, use or habit, and are diminished or lost by disuse, so I do not doubt it has been with instincts. But I believe that the effects of habit are in many cases of subordinate importance to the effects of instincts;--that is of variations produced by the same unknown causes which produce slight deviations of bodily structure.

No complex instinct can possibly be produced through natural selection, except by the slow and gradual accumulation of numerous, slight, yet profitable, variations. Hence, as in the case of corporeal structures, we ought to find in nature, not the actual transitional gradations by which each complex instinct has been acquired--for these could be found only in the lineal ancestors of each species--but we ought to find in the collateral lines of descent some evidence of such gradations; or we ought at least to be able to show that gradations of some kind are possible; and this we certainly can do. I have been surprised to find, making allowance for the instincts of animals having been but little observed, except in Europe and North America, and for no instinct being known among extinct species, how very generally gradations, leading to the most complex instincts, can be discovered. Changes of instinct may sometimes be facilitated by the same species having different instincts at different periods of life, or at different seasons of the year, or when placed under different circumstances, etc.; in which case either the one or the other instinct might be preserved by natural selection. And such instances of diversity of instinct in the same species can be shown to occur in nature.

Again, as in the case of corporeal structure, and conformably to my theory, the instinct of each species is good for itself, but has never, as far as we can judge, been produced for the exclusive good of others. One of the strongest instances of an animal apparently performing an action for the sole good of another, with which I am acquainted, is that of aphides voluntarily yielding, as was first observed by Huber, their sweet excretion to ants: that they do so voluntarily, the following facts show. I removed all the ants from a group of about a dozen aphides on a dock-plant, and prevented their attendance during several hours. After this interval, I felt sure that the aphides would want to excrete. I watched them for some time through a lens, but not one excreted; I then tickled and stroked them with a hair in the same manner, as well as I could, as the ants do with their antennae; but not one excreted. Afterwards, I allowed an ant to visit them, and it immediately seemed, by its eager way of running about to be well aware what a rich flock it had discovered: it then began to play with its antennae on the abdomen first of one aphis and then of another: and each, as soon as it felt the antennae, immediately lifted up its abdomen and excreted a limpid drop of sweet juice, which was eagerly devoured by the ant. Even the guite young aphides behaved in this manner, showing that the action was instinctive, and not the result of experience. It is certain, from the observations of Huber, that the aphides show no dislike to the ants: if the latter be not present they are at last compelled to elect their excretion. But as the excretion is extremely viscid, it is no doubt a convenience to the aphides to have it removed; therefore probably they do not excrete solely for the good of the ants. Although there is no evidence that any animal performs an action for the exclusive good of another species, yet each tries to take advantage of the instincts of others, as each takes advantage of the weaker bodily structure of other species. So again certain instincts cannot be considered as

absolutely perfect; but as details on this and other such points are not indispensable, they may be here passed over.

As some degree of variation in instincts under a state of nature, and the inheritance of such variations, are indispensable for the action of natural selection, as many instances as possible ought to be given; but want of space prevents me. I can only assert that instincts certainly do vary--for instance, the migratory instinct, both in extent and direction, and in its total loss. So it is with the nests of birds, which vary partly in dependence on the situations chosen, and on the nature and temperature of the country inhabited, but often from causes wholly unknown to us. Audubon has given several remarkable cases of differences in the nests of the same species in the northern and southern United States. Why, it has been asked, if instinct be variable, has it not granted to the bee "the ability to use some other material when wax was deficient?" But what other natural material could bees use? They will work, as I have seen, with wax hardened with vermilion or softened with lard. Andrew Knight observed that his bees, instead of laboriously collecting propolis, used a cement of wax and turpentine, with which he had covered decorticated trees. It has lately been shown that bees, instead of searching for pollen, will gladly use a very different substance, namely, oatmeal. Fear of any particular enemy is certainly an instinctive guality, as may be seen in nestling birds, though it is strengthened by experience, and by the sight of fear of the same enemy in other animals. The fear of man is slowly acquired, as I have elsewhere shown, by the various animals which inhabit desert islands; and we see an instance of this, even in England, in the greater wildness of all our large birds in comparison with our small birds; for the large birds have been most persecuted by man. We may safely attribute the greater wildness of our large birds to this cause; for in uninhabited islands large birds are not more fearful than small; and the magpie, so wary in England, is tame in Norway, as is the hooded crow in Egypt.

That the mental qualities of animals of the same kind, born in a state of nature, vary much, could be shown by many facts. Several cases could also be adduced of occasional and strange habits in wild animals, which, if advantageous to the species, might have given rise, through natural selection, to new instincts. But I am well aware that these general statements, without the facts in detail, can produce but a feeble effect on the reader's mind. I can only repeat my assurance, that I do not speak without good evidence.

INHERITED CHANGES OF HABIT OR INSTINCT IN DOMESTICATED ANIMALS.

The possibility, or even probability, of inherited variations of instinct in a state of nature will be strengthened by briefly considering a few cases under domestication. We shall thus be enabled to see the part which habit and the selection of so-called spontaneous variations have played in modifying the mental gualities of our domestic animals. It is notorious how much domestic animals vary in their mental qualities. With cats, for instance, one naturally takes to catching rats, and another mice, and these tendencies are known to be inherited. One cat, according to Mr. St. John, always brought home game birds, another hares or rabbits, and another hunted on marshy ground and almost nightly caught woodcocks or snipes. A number of curious and authentic instances could be given of various shades of disposition and taste, and likewise of the oddest tricks, associated with certain frames of mind or periods of time. But let us look to the familiar case of the breeds of dogs: it cannot be doubted that young pointers (I have myself seen striking instances) will sometimes point and even back other dogs the very first time that they are taken out; retrieving is certainly in some degree inherited by retrievers; and a tendency to run round, instead of at, a flock of sheep, by shepherd-dogs, I cannot see that these actions, performed without experience by the young. and in nearly the same manner by each individual, performed with eager delight by each breed, and without the end being known--for the young pointer can no more know that he points to aid his master, than the white butterfly knows why she lays her eggs on the leaf of the cabbage--I cannot see that these actions differ essentially from true instincts. If we were to behold one kind of wolf, when young and without any training, as soon as it scented its prey, stand motionless like a statue, and then slowly crawl forward with a peculiar gait; and another kind of wolf rushing round. instead of at, a herd of deer, and driving them to a distant point, we should assuredly call these actions instinctive. Domestic instincts, as they may be called, are certainly far less fixed than natural instincts: but they have been acted on by far less rigorous selection, and have been transmitted for an incomparably shorter period, under less fixed conditions of life.

How strongly these domestic instincts, habits, and dispositions are inherited, and how curiously they become mingled, is well shown when different breeds of dogs are crossed. Thus it is known that a cross with a bull-dog has affected for many generations the courage and obstinacy of greyhounds; and a cross with a greyhound has given to a whole family of shepherd-dogs a tendency to hunt hares. These domestic instincts, when thus tested by crossing, resemble natural instincts, which in a like manner become curiously blended together, and for a long period exhibit traces of the instincts of either parent: for example, Le Roy describes a dog, whose great-grandfather was a wolf, and this dog showed a trace of its wild parentage only in one way, by not coming in a straight line to his master, when called.

Domestic instincts are sometimes spoken of as actions which have become inherited solely from long-continued and compulsory habit, but this is not true. No one would ever have thought of teaching, or probably could have taught, the tumbler-pigeon to tumble--an action which, as I have witnessed, is performed by young birds, that have never seen a pigeon tumble. We may believe that some one pigeon showed a slight tendency to this strange habit, and that the long-continued selection of the best individuals in successive generations made tumblers what they now are; and near Glasgow there are house-tumblers, as I hear from Mr. Brent, which cannot fly eighteen inches high without going head over heels. It may be doubted whether any one would have thought of training a dog to point, had not some one dog naturally shown a tendency in this line; and this is known occasionally to happen, as I once saw, in a pure terrier: the act of pointing is probably, as many have thought, only the exaggerated pause of an animal preparing to spring on its prev. When the first tendency to point was once displayed, methodical selection and the inherited effects of compulsory training in each successive generation would soon complete the work; and unconscious selection is still in progress, as each man tries to procure, without intending to improve the breed, dogs which stand and hunt best. On the other hand, habit alone in some cases has sufficed; hardly any animal is more difficult to tame than the young of the wild rabbit; scarcely any animal is tamer than the young of the tame rabbit; but I can hardly suppose that domestic rabbits have often been selected for tameness alone; so that we must attribute at least the greater part of the inherited change from extreme wildness to extreme tameness, to habit and long-continued close confinement.

Natural instincts are lost under domestication: a remarkable instance of this is seen in those breeds of fowls which very rarely or never become "broody," that is, never wish to sit on their eggs. Familiarity alone prevents our seeing how largely and how permanently the minds of our domestic animals have been modified. It is scarcely possible to doubt that the love of man has become instinctive in the dog. All wolves, foxes, jackals and species of the cat genus, when kept tame, are most eager to attack poultry, sheep and pigs; and this tendency has been found incurable in dogs which have been brought home as puppies from countries such as Tierra del Fuego and Australia, where the savages do not keep these domestic animals. How rarely, on the other hand, do our civilised dogs, even when quite young, require to be taught not to attack poultry, sheep, and pigs! No doubt they occasionally do make an attack, and are then beaten; and if not cured, they are destroyed; so that habit and some degree

of selection have probably concurred in civilising by inheritance our dogs. On the other hand, young chickens have lost wholly by habit, that fear of the dog and cat which no doubt was originally instinctive in them, for I am informed by Captain Hutton that the young chickens of the parent stock, the Gallus bankiva, when reared in India under a hen, are at first excessively wild. So it is with young pheasants reared in England under a hen. It is not that chickens have lost all fear, but fear only of dogs and cats, for if the hen gives the danger chuckle they will run (more especially young turkeys) from under her and conceal themselves in the surrounding grass or thickets; and this is evidently done for the instinctive purpose of allowing, as we see in wild ground-birds, their mother to fly away. But this instinct retained by our chickens has become useless under domestication, for the mother-hen has almost lost by disuse the power of flight.

Hence, we may conclude that under domestication instincts have been acquired and natural instincts have been lost, partly by habit and partly by man selecting and accumulating, during successive generations, peculiar mental habits and actions, which at first appeared from what we must in our ignorance call an accident. In some cases compulsory habit alone has sufficed to produce inherited mental changes; in other cases compulsory habit has done nothing, and all has been the result of selection, pursued both methodically and unconsciously; but in most cases habit and selection have probably concurred.

SPECIAL INSTINCTS.

We shall, perhaps, best understand how instincts in a state of nature have become modified by selection by considering a few cases. I will select only three, namely, the instinct which leads the cuckoo to lay her eggs in other birds' nests; the slave-making instinct of certain ants; and the cell-making power of the hive-bee: these two latter instincts have generally and justly been ranked by naturalists as the most wonderful of all known instincts.

INSTINCTS OF THE CUCKOO.

It is supposed by some naturalists that the more immediate cause of the instinct of the cuckoo is that she lays her eggs, not daily, but at intervals of two or three days; so that, if she were to make her own nest and sit on her own eggs, those first laid would have to be left for some time unincubated or there would be eggs and young birds of different ages in the same nest. If this were the case the process of laying and hatching might be inconveniently long, more especially as she migrates at a very

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

early period; and the first hatched young would probably have to be fed by the male alone. But the American cuckoo is in this predicament, for she makes her own nest and has eggs and young successively hatched, all at the same time. It has been both asserted and denied that the American cuckoo occasionally lays her eggs in other birds' nests; but I have lately heard from Dr. Merrill, of Iowa, that he once found in Illinois a young cuckoo, together with a young jay in the nest of a blue jay (Garrulus cristatus); and as both were nearly full feathered, there could be no mistake in their identification. I could also give several instances of various birds which have been known occasionally to lay their eggs in other birds' nests. Now let us suppose that the ancient progenitor of our European cuckoo had the habits of the American cuckoo, and that she occasionally laid an egg in another bird's nest. If the old bird profited by this occasional habit through being enabled to emigrate earlier or through any other cause; or if the young were made more vigorous by advantage being taken of the mistaken instinct of another species than when reared by their own mother, encumbered as she could hardly fail to be by having eggs and young of different ages at the same time, then the old birds or the fostered young would gain an advantage. And analogy would lead us to believe that the young thus reared would be apt to follow by inheritance the occasional and aberrant habit of their mother, and in their turn would be apt to lay their eggs in other birds' nests, and thus be more successful in rearing their voung. By a continued process of this nature. I believe that the strange instinct of our cuckoo has been generated. It has, also recently been ascertained on sufficient evidence, by Adolf Muller, that the cuckoo occasionally lays her eggs on the bare ground, sits on them and feeds her young. This rare event is probably a case of reversion to the long-lost, aboriginal instinct of nidification.

It has been objected that I have not noticed other related instincts and adaptations of structure in the cuckoo, which are spoken of as necessarily co-ordinated. But in all cases, speculation on an instinct known to us only in a single species, is useless, for we have hitherto had no facts to guide us. Until recently the instincts of the European and of the non-parasitic American cuckoo alone were known; now, owing to Mr. Ramsay's observations, we have learned something about three Australian species, which lay their eggs in other birds' nests. The chief points to be referred to are three: first, that the common cuckoo, with rare exceptions, lays only one egg in a nest, so that the large and voracious young bird receives ample food. Secondly, that the eggs are remarkably small, not exceeding those of the skylark--a bird about one-fourth as large as the cuckoo. That the small size of the egg is a real case of adaptation we may infer from the fact of the mon-parasitic American cuckoo laying full-sized eggs. Thirdly, that the young cuckoo, soon after birth, has the

instinct, the strength and a properly shaped back for ejecting its fosterbrothers, which then perish from cold and hunger. This has been boldly called a beneficent arrangement, in order that the young cuckoo may get sufficient food, and that its foster-brothers may perish before they had acquired much feeling!

Turning now to the Australian species: though these birds generally lay only one egg in a nest, it is not rare to find two and even three eggs in the same nest. In the bronze cuckoo the eggs vary greatly in size, from eight to ten lines in length. Now, if it had been of an advantage to this species to have laid eggs even smaller than those now laid, so as to have deceived certain foster-parents, or, as is more probable, to have been hatched within a shorter period (for it is asserted that there is a relation between the size of eggs and the period of their incubation), then there is no difficulty in believing that a race or species might have been formed which would have laid smaller and smaller eggs; for these would have been more safely hatched and reared. Mr. Ramsay remarks that two of the Australian cuckoos, when they lay their eggs in an open nest, manifest a decided preference for nests containing eggs similar in colour to their own. The European species apparently manifests some tendency towards a similar instinct, but not rarely departs from it, as is shown by her laying her dull and pale-coloured eggs in the nest of the hedge-warbler with bright greenish-blue eggs. Had our cuckoo invariably displayed the above instinct, it would assuredly have been added to those which it is assumed must all have been acquired together. The eggs of the Australian bronze cuckoo vary, according to Mr. Ramsay, to an extraordinary degree in colour; so that in this respect, as well as in size, natural selection might have secured and fixed any advantageous variation.

In the case of the European cuckoo, the offspring of the foster-parents are commonly ejected from the nest within three days after the cuckoo is hatched; and as the latter at this age is in a most helpless condition, Mr. Gould was formerly inclined to believe that the act of ejection was performed by the foster-parents themselves. But he has now received a trustworthy account of a young cuckoo which was actually seen, while still blind and not able even to hold up its own head, in the act of ejecting its foster-brothers. One of these was replaced in the nest by the observer, and was again thrown out. With respect to the means by which this strange and odious instinct was acquired, if it were of great importance for the young cuckoo, as is probably the case, to receive as much food as possible soon after birth, I can see no special difficulty in its having gradually acquired, during successive generations, the blind desire, the strength, and structure necessary for the work of ejection; for those cuckoos which had such habits and structure best developed would be the most securely

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

reared. The first step towards the acquisition of the proper instinct might have been mere unintentional restlessness on the part of the young bird, when somewhat advanced in age and strength; the habit having been afterwards improved, and transmitted to an earlier age. I can see no more difficulty in this than in the unhatched young of other birds acquiring the instinct to break through their own shells; or than in young snakes acquiring in their upper jaws, as Owen has remarked, a transitory sharp tooth for cutting through the tough egg-shell. For if each part is liable to individual variations at all ages, and the variations tend to be inherited at a corresponding or earlier age--propositions which cannot be disputed--then the instincts and structure of the young could be slowly modified as surely as those of the adult; and both cases must stand or fall together with the whole theory of natural selection.

Some species of Molothrus, a widely distinct genus of American birds, allied to our starlings, have parasitic habits like those of the cuckoo; and the species present an interesting gradation in the perfection of their instincts. The sexes of Molothrus badius are stated by an excellent observer. Mr. Hudson, sometimes to live promiscuously together in flocks. and sometimes to pair. They either build a nest of their own or seize on one belonging to some other bird, occasionally throwing out the nestlings of the stranger. They either lay their eggs in the nest thus appropriated, or oddly enough build one for themselves on the top of it. They usually sit on their own eggs and rear their own young; but Mr. Hudson says it is probable that they are occasionally parasitic, for he has seen the young of this species following old birds of a distinct kind and clamouring to be fed by them. The parasitic habits of another species of Molothrus, the M. bonariensis, are much more highly developed than those of the last, but are still far from perfect. This bird, as far as it is known, invariably lays its eggs in the nests of strangers: but it is remarkable that several together sometimes commence to build an irregular untidy nest of their own. placed in singular ill-adapted situations, as on the leaves of a large thistle. They never, however, as far as Mr. Hudson has ascertained, complete a nest for themselves. They often lay so many eggs--from fifteen to twenty--in the same foster-nest, that few or none can possibly be hatched. They have, moreover, the extraordinary habit of pecking holes in the eggs, whether of their own species or of their foster parents, which they find in the appropriated nests. They drop also many eggs on the bare ground, which are thus wasted. A third species, the M. pecoris of North America, has acquired instincts as perfect as those of the cuckoo, for it never lays more than one egg in a foster-nest, so that the young bird is securely reared. Mr. Hudson is a strong disbeliever in evolution, but he appears to have been so much struck by the imperfect instincts of the Molothrus bonariensis that he quotes my words, and asks. "Must we consider

these habits, not as especially endowed or created instincts, but as small consequences of one general law, namely, transition?"

Various birds, as has already been remarked, occasionally lay their eggs in the nests of other birds. This habit is not very uncommon with the Gallinaceae, and throws some light on the singular instinct of the ostrich. In this family several hen birds unite and lay first a few eggs in one nest and then in another; and these are hatched by the males. This instinct may probably be accounted for by the fact of the hens laying a large number of eggs, but, as with the cuckoo, at intervals of two or three days. The instinct, however, of the American ostrich, as in the case of the Molothrus bonariensis, has not as yet been perfected; for a surprising number of eggs lie strewed over the plains, so that in one day's hunting I picked up no less than twenty lost and wasted eggs.

Many bees are parasitic, and regularly lay their eggs in the nests of other kinds of bees. This case is more remarkable than that of the cuckoo; for these bees have not only had their instincts but their structure modified in accordance with their parasitic habits; for they do not possess the pollen-collecting apparatus which would have been indispensable if they had stored up food for their own young. Some species of Sphegidae (wasp-like insects) are likewise parasitic; and M. Fabre has lately shown good reason for believing that, although the Tachytes nigra generally makes its own burrow and stores it with paralysed prey for its own larvae, yet that, when this insect finds a burrow already made and stored by another sphex, it takes advantage of the prize, and becomes for the occasion parasitic. In this case, as with that of the Molothrus or cuckoo, I can see no difficulty in natural selection making an occasional habit permanent, if of advantage to the species, and if the insect whose nest and stored food are feloniously appropriated, be not thus exterminated.

SLAVE-MAKING INSTINCT.

This remarkable instinct was first discovered in the Formica (Polyerges) rufescens by Pierre Huber, a better observer even than his celebrated father. This ant is absolutely dependent on its slaves; without their aid, the species would certainly become extinct in a single year. The males and fertile females do no work of any kind, and the workers or sterile females, though most energetic and courageous in capturing slaves, do no other work. They are incapable of making their own nests, or of feeding their own larvae. When the old nest is found inconvenient, and they have to migrate, it is the slaves which determine the migration, and actually carry their masters in their jaws. So utterly helpless are the masters, that when Huber shut up thirty of them without a slave, but with plenty of the food

ORIGIN of SPECIES Chapter VIII

which they like best, and with their larvae and pupae to stimulate them to work, they did nothing; they could not even feed themselves, and many perished of hunger. Huber then introduced a single slave (F. fusca), and she instantly set to work, fed and saved the survivors; made some cells and tended the larvae, and put all to rights. What can be more extraordinary than these well-ascertained facts? If we had not known of any other slave-making ant, it would have been hopeless to speculate how so wonderful an instinct could have been perfected.

Another species, Formica sanguinea, was likewise first discovered by P. Huber to be a slave-making ant. This species is found in the southern parts of England, and its habits have been attended to by Mr. F. Smith, of the British Museum, to whom I am much indebted for information on this and other subjects. Although fully trusting to the statements of Huber and Mr. Smith, I tried to approach the subject in a sceptical frame of mind, as any one may well be excused for doubting the existence of so extraordinary an instinct as that of making slaves. Hence, I will give the observations which I made in some little detail. I opened fourteen nests of F. sanguinea, and found a few slaves in all. Males and fertile females of the slave-species (F. fusca) are found only in their own proper communities, and have never been observed in the nests of F. sanguinea. The slaves are black and not above half the size of their red masters, so that the contrast in their appearance is great. When the nest is slightly disturbed, the slaves occasionally come out, and like their masters are much agitated and defend the nest: when the nest is much disturbed, and the larvae and pupae are exposed, the slaves work energetically together with their masters in carrying them away to a place of safety. Hence, it is clear that the slaves feel quite at home. During the months of June and July, on three successive years, I watched for many hours several nests in Surrey and Sussex, and never saw a slave either leave or enter a nest. As, during these months, the slaves are very few in number. I thought that they might behave differently when more numerous; but Mr. Smith informs me that he has watched the nests at various hours during May, June and August, both in Surrey and Hampshire, and has never seen the slaves, though present in large numbers in August, either leave or enter the nest. Hence, he considers them as strictly household slaves. The masters, on the other hand, may be constantly seen bringing in materials for the nest, and food of all kinds. During the year 1860, however, in the month of July, I came across a community with an unusually large stock of slaves, and I observed a few slaves mingled with their masters leaving the nest, and marching along the same road to a tall Scotch-fir tree, twenty-five vards distant. which they ascended together, probably in search of aphides or cocci. According to Huber, who had ample opportunities for observation, the slaves in Switzerland habitually work with their masters in making the nest, and

11 of 28

ORIGIN of SPECIES Chapter VIII

they alone open and close the doors in the morning and evening; and, as Huber expressly states, their principal office is to search for aphides. This difference in the usual habits of the masters and slaves in the two countries, probably depends merely on the slaves being captured in greater numbers in Switzerland than in England.

One day I fortunately witnessed a migration of F. sanguinea from one nest to another, and it was a most interesting spectacle to behold the masters carefully carrying their slaves in their jaws instead of being carried by them, as in the case of F. rufescens. Another day my attention was struck by about a score of the slave-makers haunting the same spot, and evidently not in search of food; they approached and were vigorously repulsed by an independent community of the slave species (F. fusca); sometimes as many as three of these ants clinging to the legs of the slave-making F. sanguinea. The latter ruthlessly killed their small opponents and carried their dead bodies as food to their nest, twenty-nine yards distant; but they were prevented from getting any pupae to rear as slaves. I then dug up a small parcel of the pupae of F. fusca from another nest, and put them down on a bare spot near the place of combat; they were eagerly seized and carried off by the tyrants, who perhaps fancied that, after all, they had been victorious in their late combat.

At the same time I laid on the same place a small parcel of the pupae of another species, F. flava, with a few of these little yellow ants still clinging to the fragments of their nest. This species is sometimes, though rarely, made into slaves, as has been described by Mr. Smith. Although so small a species, it is very courageous, and I have seen it ferociously attack other ants. In one instance I found to my surprise an independent community of F. flava under a stone beneath a nest of the slave-making F. sanguinea: and when I had accidentally disturbed both nests, the little ants attacked their big neighbours with surprising courage. Now I was curious to ascertain whether F. sanguinea could distinguish the pupae of F. fusca, which they habitually make into slaves, from those of the little and furious F. flava, which they rarely capture, and it was evident that they did at once distinguish them; for we have seen that they eagerly and instantly seized the pupae of F. fusca, whereas they were much terrified when they came across the pupae, or even the earth from the nest, of F. flava, and quickly ran away; but in about a quarter of an hour, shortly after all the little yellow ants had crawled away, they took heart and carried off the pupae.

One evening I visited another community of F. sanguinea, and found a number of these ants returning home and entering their nests, carrying the dead bodies of F. fusca (showing that it was not a migration) and numerous

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

pupae. I traced a long file of ants burdened with booty, for about forty yards back, to a very thick clump of heath, whence I saw the last individual of F. sanguinea emerge, carrying a pupa; but I was not able to find the desolated nest in the thick heath. The nest, however, must have been close at hand, for two or three individuals of F. fusca were rushing about in the greatest agitation, and one was perched motionless with its own pupa in its mouth on the top of a spray of heath, an image of despair over its ravaged home.

Such are the facts, though they did not need confirmation by me, in regard to the wonderful instinct of making slaves. Let it be observed what a contrast the instinctive habits of F. sanguinea present with those of the continental F. rufescens. The latter does not build its own nest, does not determine its own migrations, does not collect food for itself or its young, and cannot even feed itself: it is absolutely dependent on its numerous slaves. Formica sanguinea, on the other hand, possesses much fewer slaves, and in the early part of the summer extremely few. The masters determine when and where a new nest shall be formed, and when they migrate, the masters carry the slaves. Both in Switzerland and England the slaves seem to have the exclusive care of the larvae, and the masters alone go on slave-making expeditions. In Switzerland the slaves and masters work together, making and bringing materials for the nest: both, but chiefly the slaves, tend and milk as it may be called, their aphides; and thus both collect food for the community. In England the masters alone usually leave the nest to collect building materials and food for themselves, their slaves and larvae. So that the masters in this country receive much less service from their slaves than they do in Switzerland.

By what steps the instinct of F. sanguinea originated I will not pretend to conjecture. But as ants which are not slave-makers, will, as I have seen. carry off pupae of other species, if scattered near their nests, it is possible that such pupae originally stored as food might become developed; and the foreign ants thus unintentionally reared would then follow their proper instincts, and do what work they could. If their presence proved useful to the species which had seized them--if it were more advantageous to this species, to capture workers than to procreate them--the habit of collecting pupae, originally for food, might by natural selection be strengthened and rendered permanent for the very different purpose of raising slaves. When the instinct was once acquired, if carried out to a much less extent even than in our British F. sanguinea, which, as we have seen, is less aided by its slaves than the same species in Switzerland. natural selection might increase and modify the instinct--always supposing each modification to be of use to the species--until an ant was formed as abjectly dependent on its slaves as is the Formica rufescens.

13 of 28

ORIGIN of SPECIES Chapter VIII

CELL-MAKING INSTINCT OF THE HIVE-BEE.

I will not here enter on minute details on this subject, but will merely give an outline of the conclusions at which I have arrived. He must be a dull man who can examine the exquisite structure of a comb, so beautifully adapted to its end, without enthusiastic admiration. We hear from mathematicians that bees have practically solved a recondite problem, and have made their cells of the proper shape to hold the greatest possible amount of honey, with the least possible consumption of precious wax in their construction. It has been remarked that a skilful workman, with fitting tools and measures, would find it very difficult to make cells of wax of the true form, though this is effected by a crowd of bees working in a dark hive. Granting whatever instincts you please, it seems at first quite inconceivable how they can make all the necessary angles and planes, or even perceive when they are correctly made. But the difficulty is not nearly so great as at first appears: all this beautiful work can be shown, I think, to follow from a few simple instincts.

I was led to investigate this subject by Mr. Waterhouse, who has shown that the form of the cell stands in close relation to the presence of adjoining cells; and the following view may, perhaps, be considered only as a modification of his theory. Let us look to the great principle of gradation, and see whether Nature does not reveal to us her method of work. At one end of a short series we have humble-bees, which use their old cocoons to hold honey, sometimes adding to them short tubes of wax, and likewise making separate and very irregular rounded cells of wax. At the other end of the series we have the cells of the hive-bee, placed in a double layer: each cell, as is well known, is an hexagonal prism, with the basal edges of its six sides bevelled so as to join an inverted pyramid, of three rhombs. These rhombs have certain angles, and the three which form the pyramidal base of a single cell on one side of the comb, enter into the composition of the bases of three adjoining cells on the opposite side. In the series between the extreme perfection of the cells of the hive-bee and the simplicity of those of the humble-bee, we have the cells of the Mexican Melipona domestica, carefully described and figured by Pierre Huber. The Melipona itself is intermediate in structure between the hive and humble bee, but more nearly related to the latter: it forms a nearly regular waxen comb of cylindrical cells, in which the young are hatched, and, in addition, some large cells of wax for holding honey. These latter cells are nearly spherical and of nearly equal sizes, and are aggregated into an irregular mass. But the important point to notice is, that these cells are always made at that degree of nearness to each other that they would have intersected or broken into each other if the spheres had been completed:

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

but this is never permitted, the bees building perfectly flat walls of wax between the spheres which thus tend to intersect. Hence, each cell consists of an outer spherical portion, and of two, three, or more flat surfaces, according as the cell adjoins two, three or more other cells. When one cell rests on three other cells, which, from the spheres being nearly of the same size, is very frequently and necessarily the case, the three flat surfaces are united into a pyramid; and this pyramid, as Huber has remarked, is manifestly a gross imitation of the three-sided pyramidal base of the cell of the hive-bee. As in the cells of the hive-bee, so here, the three plane surfaces in any one cell necessarily enter into the construction of three adjoining cells. It is obvious that the Melipona saves wax, and what is more important, labour, by this manner of building; for the flat walls between the adjoining cells are not double, but are of the same thickness as the outer spherical portions, and yet each flat portion forms a part of two cells.

Reflecting on this case, it occurred to me that if the Melipona had made its spheres at some given distance from each other, and had made them of equal sizes and had arranged them symmetrically in a double layer, the resulting structure would have been as perfect as the comb of the hive-bee. Accordingly I wrote to Professor Miller, of Cambridge, and this geometer has kindly read over the following statement, drawn up from his information, and tells me that it is strictly correct:-

If a number of equal spheres be described with their centres placed in two parallel layers; with the centre of each sphere at the distance of radius x sqrt(2) or radius x 1.41421 (or at some lesser distance), from the centres of the six surrounding spheres in the same layer; and at the same distance from the centres of the adjoining spheres in the other and parallel layer; then, if planes of intersection between the several spheres in both layers be formed, there will result a double layer of hexagonal prisms united together by pyramidal bases formed of three rhombs; and the rhombs and the sides of the hexagonal prisms will have every angle identically the same with the best measurements which have been made of the cells of the hive-bee. But I hear from Professor Wyman, who has made numerous careful measurements, that the accuracy of the workmanship of the bee has been greatly exaggerated; so much so, that whatever the typical form of the cell may be, it is rarely, if ever, realised.

Hence we may safely conclude that, if we could slightly modify the instincts already possessed by the Melipona, and in themselves not very wonderful, this bee would make a structure as wonderfully perfect as that of the hive-bee. We must suppose the Melipona to have the power of forming her cells truly spherical, and of equal sizes; and this would not be very

surprising, seeing that she already does so to a certain extent, and seeing what perfectly cylindrical burrows many insects make in wood, apparently by turning round on a fixed point. We must suppose the Melipona to arrange her cells in level layers, as she already does her cylindrical cells; and we must further suppose, and this is the greatest difficulty, that she can somehow judge accurately at what distance to stand from her fellow-labourers when several are making their spheres; but she is already so far enabled to judge of distance, that she always describes her spheres so as to intersect to a certain extent; and then she unites the points of intersection by perfectly flat surfaces. By such modifications of instincts which in themselves are not very wonderful-hardly more wonderful than those which guide a bird to make its nest--I believe that the hive-bee has acquired, through natural selection, her inimitable architectural powers.

But this theory can be tested by experiment. Following the example of Mr. Tegetmeier, I separated two combs, and put between them a long, thick, rectangular strip of wax: the bees instantly began to excavate minute circular pits in it: and as they deepened these little pits, they made them wider and wider until they were converted into shallow basins, appearing to the eye perfectly true or parts of a sphere, and of about the diameter of a cell. It was most interesting to observe that, wherever several bees had begun to excavate these basins near together, they had begun their work at such a distance from each other that by the time the basins had acquired the above stated width (i.e. about the width of an ordinary cell), and were in depth about one sixth of the diameter of the sphere of which they formed a part, the rims of the basins intersected or broke into each other. As soon as this occurred, the bees ceased to excavate, and began to build up flat walls of wax on the lines of intersection between the basins, so that each hexagonal prism was built upon the scalloped edge of a smooth basin. instead of on the straight edges of a three-sided pyramid as in the case of ordinary cells.

I then put into the hive, instead of a thick, rectangular piece of wax, a thin and narrow, knife-edged ridge, coloured with vermilion. The bees instantly began on both sides to excavate little basins near to each other, in the same way as before; but the ridge of wax was so thin, that the bottoms of the basins, if they had been excavated to the same depth as in the former experiment, would have broken into each other from the opposite sides. The bees, however, did not suffer this to happen, and they stopped their excavations in due time; so that the basins, as soon as they had been a little deepened, came to have flat bases; and these flat bases, formed by thin little plates of the vermilion wax left ungnawed, were situated, as far as the eye could judge, exactly along the planes of imaginary

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

intersection between the basins on the opposite side of the ridge of wax. In some parts, only small portions, in other parts, large portions of a rhombic plate were thus left between the opposed basins, but the work, from the unnatural state of things, had not been neatly performed. The bees must have worked at very nearly the same rate in circularly gnawing away and deepening the basins on both sides of the ridge of vermilion wax, in order to have thus succeeded in leaving flat plates between the basins, by stopping work at the planes of intersection.

Considering how flexible thin wax is, I do not see that there is any difficulty in the bees, whilst at work on the two sides of a strip of wax, perceiving when they have gnawed the wax away to the proper thinness, and then stopping their work. In ordinary combs it has appeared to me that the bees do not always succeed in working at exactly the same rate from the opposite sides; for I have noticed half-completed rhombs at the base of a just-commenced cell, which were slightly concave on one side, where I suppose that the bees had excavated too quickly, and convex on the opposed side where the bees had worked less quickly. In one well-marked instance, I put the comb back into the hive, and allowed the bees to go on working for a short time, and again examined the cell, and I found that the rhombic plate had been completed, and had become PERFECTLY FLAT: it was absolutely

impossible, from the extreme thinness of the little plate, that they could have effected this by gnawing away the convex side; and I suspect that the bees in such cases stand in the opposed cells and push and bend the ductile and warm wax (which as I have tried is easily done) into its proper intermediate plane, and thus flatten it.

>From the experiment of the ridge of vermilion wax we can see that, if the bees were to build for themselves a thin wall of wax, they could make their cells of the proper shape, by standing at the proper distance from each other, by excavating at the same rate, and by endeavouring to make equal spherical hollows, but never allowing the spheres to break into each other. Now bees, as may be clearly seen by examining the edge of a growing comb. do make a rough, circumferential wall or rim all round the comb; and they gnaw this away from the opposite sides, always working circularly as they deepen each cell. They do not make the whole three-sided pyramidal base of any one cell at the same time, but only that one rhombic plate which stands on the extreme growing margin, or the two plates, as the case may be; and they never complete the upper edges of the rhombic plates, until the hexagonal walls are commenced. Some of these statements differ from those made by the justly celebrated elder Huber, but I am convinced of their accuracy; and if I had space, I could show that they are conformable with mv theorv.

ORIGIN of SPECIES Chapter VIII

Huber's statement, that the very first cell is excavated out of a little parallel-sided wall of wax, is not, as far as I have seen, strictly correct: the first commencement having always been a little hood of wax: but I will not here enter on details. We see how important a part excavation plays in the construction of the cells: but it would be a great error to suppose that the bees cannot build up a rough wall of wax in the proper position--that is, along the plane of intersection between two adjoining spheres. I have several specimens showing clearly that they can do this. Even in the rude circumferential rim or wall of wax round a growing comb, flexures may sometimes be observed, corresponding in position to the planes of the rhombic basal plates of future cells. But the rough wall of wax has in every case to be finished off, by being largely gnawed away on both sides. The manner in which the bees build is curious; they always make the first rough wall from ten to twenty times thicker than the excessively thin finished wall of the cell, which will ultimately be left. We shall understand how they work, by supposing masons first to pile up a broad ridge of cement, and then to begin cutting it away equally on both sides near the ground, till a smooth, very thin wall is left in the middle: the masons always piling up the cut-away cement, and adding fresh cement on the summit of the ridge. We shall thus have a thin wall steadily growing upward but always crowned by a gigantic coping. From all the cells, both those just commenced and those completed, being thus crowned by a strong coping of wax, the bees can cluster and crawl over the comb without injuring the delicate hexagonal walls. These walls, as Professor Miller has kindly ascertained for me, vary greatly in thickness; being, on an average of twelve measurements made near the border of the comb, 1/352 of an inch in thickness; whereas the basal rhomboidal plates are thicker, nearly in the proportion of three to two, having a mean thickness, from twenty-one measurements, of 1/229 of an inch. By the above singular manner of building, strength is continually given to the comb, with the utmost ultimate economy of wax.

It seems at first to add to the difficulty of understanding how the cells are made, that a multitude of bees all work together; one bee after working a short time at one cell going to another, so that, as Huber has stated, a score of individuals work even at the commencement of the first cell. I was able practically to show this fact, by covering the edges of the hexagonal walls of a single cell, or the extreme margin of the circumferential rim of a growing comb, with an extremely thin layer of melted vermilion wax; and I invariably found that the colour was most delicately diffused by the bees-as delicately as a painter could have done it with his brush--by atoms of the coloured wax having been taken from the spot on which it had been placed, and worked into the growing edges of the

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

cells all round. The work of construction seems to be a sort of balance struck between many bees, all instinctively standing at the same relative distance from each other, all trying to sweep equal spheres, and then building up, or leaving ungnawed, the planes of intersection between these spheres. It was really curious to note in cases of difficulty, as when two pieces of comb met at an angle, how often the bees would pull down and rebuild in different ways the same cell, sometimes recurring to a shape which they had at first rejected.

When bees have a place on which they can stand in their proper positions for working--for instance, on a slip of wood, placed directly under the middle of a comb growing downwards, so that the comb has to be built over one face of the slip--in this case the bees can lay the foundations of one wall of a new hexagon, in its strictly proper place, projecting beyond the other completed cells. It suffices that the bees should be enabled to stand at their proper relative distances from each other and from the walls of the last completed cells, and then, by striking imaginary spheres, they can build up a wall intermediate between two adjoining spheres; but, as far as I have seen, they never onaw away and finish off the angles of a cell till a large part both of that cell and of the adjoining cells has been built. This capacity in bees of laying down under certain circumstances a rough wall in its proper place between two just-commenced cells, is important, as it bears on a fact, which seems at first subversive of the foregoing theory; namely, that the cells on the extreme margin of wasp-combs are sometimes strictly hexagonal; but I have not space here to enter on this subject. Nor does there seem to me any great difficulty in a single insect (as in the case of a gueen-wasp) making hexagonal cells, if she were to work alternately on the inside and outside of two or three cells commenced at the same time, always standing at the proper relative distance from the parts of the cells just begun, sweeping spheres or cylinders, and building up intermediate planes.

As natural selection acts only by the accumulation of slight modifications of structure or instinct, each profitable to the individual under its conditions of life, it may reasonably be asked, how a long and graduated succession of modified architectural instincts, all tending towards the present perfect plan of construction, could have profited the progenitors of the hive-bee? I think the answer is not difficult: cells constructed like those of the bee or the wasp gain in strength, and save much in labour and space, and in the materials of which they are constructed. With respect to the formation of wax, it is known that bees are often hard pressed to get sufficient nectar; and I am informed by Mr. Tegetmeier that it has been experimentally proved that from twelve to fifteen pounds of dry sugar are consumed by a hive of bees for the secretion of a pound of wax;

so that a prodictious quantity of fluid nectar must be collected and consumed by the bees in a hive for the secretion of the wax necessary for the construction of their combs. Moreover, many bees have to remain idle for many days during the process of secretion. A large store of honey is indispensable to support a large stock of bees during the winter; and the security of the hive is known mainly to depend on a large number of bees being supported. Hence the saving of wax by largely saving honey, and the time consumed in collecting the honey, must be an important element of success any family of bees. Of course the success of the species may be dependent on the number of its enemies, or parasites, or on guite distinct causes, and so be altogether independent of the quantity of honey which the bees can collect. But let us suppose that this latter circumstance determined, as it probably often has determined, whether a bee allied to our humble-bees could exist in large numbers in any country; and let us further suppose that the community lived through the winter, and consequently required a store of honey: there can in this case be no doubt that it would be an advantage to our imaginary humble-bee if a slight modification of her instincts led her to make her waxen cells near together, so as to intersect a little: for a wall in common even to two adjoining cells would save some little labour and wax. Hence, it would continually be more and more advantageous to our humble-bees, if they were to make their cells more and more regular, nearer together, and aggregated into a mass, like the cells of the Melipona; for in this case a large part of the bounding surface of each cell would serve to bound the adjoining cells, and much labour and wax would be saved. Again, from the same cause. it would be advantageous to the Melipona, if she were to make her cells closer together, and more regular in every way than at present; for then, as we have seen, the spherical surfaces would wholly disappear and be replaced by plane surfaces; and the Melipona would make a comb as perfect as that of the hive-bee. Beyond this stage of perfection in architecture. natural selection could not lead: for the comb of the hive-bee, as far as we can see, is absolutely perfect in economising labour and wax.

Thus, as I believe, the most wonderful of all known instincts, that of the hive-bee, can be explained by natural selection having taken advantage of numerous, successive, slight modifications of simpler instincts; natural selection having, by slow degrees, more and more perfectly led the bees to sweep equal spheres at a given distance from each other in a double layer, and to build up and excavate the wax along the planes of intersection. The bees, of course, no more knowing that they swept their spheres at one particular distance from each other, than they know what are the several angles of the hexagonal prisms and of the basal rhombic plates; the motive power of the process of natural selection having been the construction of cells of due strength and of the proper size and shape for the larvae, this

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

being effected with the greatest possible economy of labour and wax; that individual swarm which thus made the best cells with least labour, and least waste of honey in the secretion of wax, having succeeded best, and having transmitted their newly-acquired economical instincts to new swarms, which in their turn will have had the best chance of succeeding in the struggle for existence.

OBJECTIONS TO THE THEORY OF NATURAL SELECTION AS APPLIED TO INSTINCTS: NEUTER AND STERILE INSECTS.

It has been objected to the foregoing view of the origin of instincts that "the variations of structure and of instinct must have been simultaneous and accurately adjusted to each other, as a modification in the one without an immediate corresponding change in the other would have been fatal." The force of this objection rests entirely on the assumption that the changes in the instincts and structure are abrupt. To take as an illustration the case of the larger titmouse. (Parus major) alluded to in a previous chapter: this bird often holds the seeds of the vew between its feet on a branch, and hammers with its beak till it gets at the kernel. Now what special difficulty would there be in natural selection preserving all the slight individual variations in the shape of the beak, which were better and better adapted to break open the seeds, until a beak was formed, as well constructed for this purpose as that of the nuthatch, at the same time that habit, or compulsion, or spontaneous variations of taste, led the bird to become more and more of a seed-eater? In this case the beak is supposed to be slowly modified by natural selection, subsequently to, but in accordance with, slowly changing habits or taste; but let the feet of the titmouse vary and grow larger from correlation with the beak, or from any other unknown cause, and it is not improbable that such larger feet would lead the bird to climb more and more until it acquired the remarkable climbing instinct and power of the nuthatch. In this case a gradual change of structure is supposed to lead to changed instinctive habits. To take one more case: few instincts are more remarkable than that which leads the swift of the Eastern Islands to make its nest wholly of inspissated saliva. Some birds build their nests of mud. believed to be moistened with saliva: and one of the swifts of North America makes its nest (as I have seen) of sticks applutinated with saliva, and even with flakes of this substance. Is it then very improbable that the natural selection of individual swifts, which secreted more and more saliva, should at last produce a species with instincts leading it to neglect other materials and to make its nest exclusively of inspissated saliva? And so in other cases. It must, however, be admitted that in many instances we cannot conjecture whether it was instinct or structure which first varied.

No doubt many instincts of very difficult explanation could be opposed to the theory of natural selection--cases, in which we cannot see how an instinct could have originated; cases, in which no intermediate gradations are known to exist; cases of instincts of such trifling importance, that they could hardly have been acted on by natural selection; cases of instincts almost identically the same in animals so remote in the scale of nature that we cannot account for their similarity by inheritance from a common progenitor, and consequently must believe that they were independently acquired through natural selection. I will not here enter on these several cases, but will confine myself to one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory. I allude to the neuters or sterile females in insect communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind.

The subject well deserves to be discussed at great length, but I will here take only a single case, that of working or sterile ants. How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; for it can be shown that some insects and other articulate animals in a state of nature occasionally become sterile: and if such insects had been social, and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no especial difficulty in this having been effected through natural selection. But I must pass over this preliminary difficulty. The great difficulty lies in the working ants differing widely from both the males and the fertile females in structure, as in the shape of the thorax, and in being destitute of wings and sometimes of eves, and in instinct. As far as instinct alone is concerned, the wonderful difference in this respect between the workers and the perfect females would have been better exemplified by the hive-bee. If a working ant or other neuter insect had been an ordinary animal, I should have unhesitatingly assumed that all its characters had been slowly acquired through natural selection; namely, by individuals having been born with slight profitable modifications, which were inherited by the offspring, and that these again varied and again were selected, and so onwards. But with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how it is possible to reconcile this case with the theory of natural selection?

First, let it be remembered that we have innumerable instances, both in our

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

domestic productions and in those in a state of nature, of all sorts of differences of inherited structure which are correlated with certain ages and with either sex. We have differences correlated not only with one sex, but with that short period when the reproductive system is active, as in the nuptial plumage of many birds, and in the hooked jaws of the male salmon. We have even slight differences in the horns of different breeds of cattle in relation to an artificially imperfect state of the male sex; for oxen of certain breeds have longer horns than the oxen of other breeds, relatively to the length of the horns in both the bulls and cows of these same breeds. Hence, I can see no great difficulty in any character becoming correlated with the sterile condition of certain members of insect communities; the difficulty lies in understanding how such correlated modifications of structure could have been slowly accumulated by natural selection.

This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end. Breeders of cattle wish the flesh and fat to be well marbled together. An animal thus characterized has been slaughtered, but the breeder has gone with confidence to the same stock and has succeeded. Such faith may be placed in the power of selection that a breed of cattle, always vielding oxen with extraordinarily long horns, could, it is probable, be formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox would ever have propagated its kind. Here is a better and real illustration: According to M. Verlot, some varieties of the double annual stock, from having been long and carefully selected to the right degree, always produce a large proportion of seedlings bearing double and guite sterile flowers, but they likewise yield some single and fertile plants. These latter, by which alone the variety can be propagated, may be compared with the fertile male and female ants, and the double sterile plants with the neuters of the same community. As with the varieties of the stock, so with social insects, selection has been applied to the family, and not to the individual, for the sake of gaining a serviceable end. Hence, we may conclude that slight modifications of structure or of instinct, correlated with the sterile condition of certain members of the community, have proved advantageous: consequently the fertile males and females have flourished. and transmitted to their fertile offspring a tendency to produce sterile members with the same modifications. This process must have been repeated many times, until that prodigious amount of difference between the fertile and sterile females of the same species has been produced which we see in many social insects.

But we have not as yet touched on the acme of the difficulty; namely, the fact that the neuters of several ants differ, not only from the fertile females and males, but from each other, sometimes to an almost incredible degree, and are thus divided into two or even three castes. The castes, moreover, do not generally graduate into each other, but are perfectly well defined; being as distinct from each other as are any two species of the same genus, or rather as any two genera of the same family. Thus, in Eciton, there are working and soldier neuters, with jaws and instincts extraordinarily different: in Cryptocerus, the workers of one caste alone carry a wonderful sort of shield on their heads, the use of which is quite unknown: in the Mexican Myrmecocystus, the workers of one caste never leave the nest; they are fed by the workers of another caste, and they have an enormously developed abdomen which secretes a sort of honey, supplying the place of that excreted by the aphides, or the domestic cattle as they may be called, which our European ants guard and imprison.

It will indeed be thought that I have an overweening confidence in the principle of natural selection, when I do not admit that such wonderful and well-established facts at once annihilate the theory. In the simpler case of neuter insects all of one caste, which, as I believe, have been rendered different from the fertile males and females through natural selection, we may conclude from the analogy of ordinary variations, that the successive, slight, profitable modifications did not first arise in all the neuters in the same nest, but in some few alone; and that by the survival of the communities with females which produced most neuters having the advantageous modification, all the neuters ultimately came to be thus characterized. According to this view we ought occasionally to find in the same nest neuter-insects, presenting gradations of structure; and this we do find, even not rarely, considering how few neuter-insects out of Europe have been carefully examined. Mr. F. Smith has shown that the neuters of several British ants differ surprisingly from each other in size and sometimes in colour; and that the extreme forms can be linked together by individuals taken out of the same nest: I have myself compared perfect gradations of this kind. It sometimes happens that the larger or the smaller sized workers are the most numerous; or that both large and small are numerous, while those of an intermediate size are scanty in numbers. Formica flava has larger and smaller workers, with some few of intermediate size: and, in this species, as Mr. F. Smith has observed, the larger workers have simple eyes (ocelli), which, though small, can be plainly distinguished, whereas the smaller workers have their ocelli rudimentary. Having carefully dissected several specimens of these workers, I can affirm that the eyes are far more rudimentary in the smaller workers than can be accounted for merely by their proportionately lesser size; and I fully believe, though I dare not assert so positively, that the workers of

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

intermediate size have their ocelli in an exactly intermediate condition. So that here we have two bodies of sterile workers in the same nest, differing not only in size, but in their organs of vision, yet connected by some few members in an intermediate condition. I may digress by adding, that if the smaller workers had been the most useful to the community, and those males and females had been continually selected, which produced more and more of the smaller workers, until all the workers were in this condition; we should then have had a species of ant with neuters in nearly the same condition as those of Myrmica. For the workers of Myrmica have not even rudiments of ocelli, though the male and female ants of this genus have well-developed ocelli.

I may give one other case: so confidently did I expect occasionally to find gradations of important structures between the different castes of neuters in the same species, that I gladly availed myself of Mr. F. Smith's offer of numerous specimens from the same nest of the driver ant (Anomma) of West Africa. The reader will perhaps best appreciate the amount of difference in these workers by my giving, not the actual measurements, but a strictly accurate illustration: the difference was the same as if we were to see a set of workmen building a house, of whom many were five feet four inches high, and many sixteen feet high; but we must in addition suppose that the larger workmen had heads four instead of three times as big as those of the smaller men, and jaws nearly five times as big. The jaws, moreover, of the working ants of the several sizes differed wonderfully in shape, and in the form and number of the teeth. But the important fact for us is that, though the workers can be grouped into castes of different sizes, yet they graduate insensibly into each other, as does the widely-different structure of their jaws. I speak confidently on this latter point, as Sir J. Lubbock made drawings for me, with the camera lucida, of the jaws which I dissected from the workers of the several sizes. Mr. Bates, in his interesting "Naturalist on the Amazons," has described analogous cases.

With these facts before me, I believe that natural selection, by acting on the fertile ants or parents, could form a species which should regularly produce neuters, all of large size with one form of jaw, or all of small size with widely different jaws; or lastly, and this is the greatest difficulty, one set of workers of one size and structure, and simultaneously another set of workers of a different size and structure; a graduated series having first been formed, as in the case of the driver ant, and then the extreme forms having been produced in greater and greater numbers, through the survival of the parents which generated them, until none with an intermediate structure were produced. Bio342 Animal Behavior

An analogous explanation has been given by Mr. Wallace, of the equally complex case, of certain Malayan butterflies regularly appearing under two or even three distinct female forms; and by Fritz Muller, of certain Brazilian crustaceans likewise appearing under two widely distinct male forms. But this subject need not here be discussed.

I have now explained how, I believe, the wonderful fact of two distinctly defined castes of sterile workers existing in the same nest, both widely different from each other and from their parents, has originated. We can see how useful their production may have been to a social community of ants, on the same principle that the division of labour is useful to civilised man. Ants, however, work by inherited instincts and by inherited organs or tools, while man works by acquired knowledge and manufactured instruments. But I must confess, that, with all my faith in natural selection, I should never have anticipated that this principle could have been efficient in so high a degree, had not the case of these neuter insects led me to this conclusion. I have, therefore, discussed this case, at some little but wholly insufficient length, in order to show the power of natural selection, and likewise because this is by far the most serious special difficulty which my theory has encountered. The case, also, is very interesting, as it proves that with animals, as with plants, any amount of modification may be effected by the accumulation of numerous, slight, spontaneous variations, which are in any way profitable, without exercise or habit having been brought into play. For peculiar habits, confined to the workers of sterile females, however long they might be followed, could not possibly affect the males and fertile females, which alone leave descendants. I am surprised that no one has advanced this demonstrative case of neuter insects, against the well-known doctrine of inherited habit, as advanced by Lamarck.

SUMMARY.

I have endeavoured in this chapter briefly to show that the mental qualities of our domestic animals vary, and that the variations are inherited. Still more briefly I have attempted to show that instincts vary slightly in a state of nature. No one will dispute that instincts are of the highest importance to each animal. Therefore, there is no real difficulty, under changing conditions of life, in natural selection accumulating to any extent slight modifications of instinct which are in any way useful. In many cases habit or use and disuse have probably come into play. I do not pretend that the facts given in this chapter strengthen in any great degree my theory; but none of the cases of difficulty, to the best of my judgment, annihilate it. On the other hand, the fact that instincts are not always absolutely perfect and are liable to

Bio342 Animal Behavior

ORIGIN of SPECIES Chapter VIII

mistakes; that no instinct can be shown to have been produced for the good of other animals, though animals take advantage of the instincts of others; that the canon in natural history, of "Natura non facit saltum," is applicable to instincts as well as to corporeal structure, and is plainly explicable on the foregoing views, but is otherwise inexplicable--all tend to corroborate the theory of natural selection.

This theory is also strengthened by some few other facts in regard to instincts: as by that common case of closely allied, but distinct, species, when inhabiting distant parts of the world and living under considerably different conditions of life, yet often retaining nearly the same instincts. For instance, we can understand, on the principle of inheritance, how it is that the thrush of tropical South America lines its nest with mud, in the same peculiar manner as does our British thrush; how it is that the Hornbills of Africa and India have the same extraordinary instinct of plastering up and imprisoning the females in a hole in a tree, with only a small hole left in the plaster through which the males feed them and their young when hatched: how it is that the male wrens (Troglodytes) of North America, build "cock-nests," to roost in, like the males of our Kitty-wrens, -- a habit wholly unlike that of any other known bird. Finally, it may not be a logical deduction, but to my imagination it is far more satisfactory to look at such instincts as the young cuckoo ejecting its foster-brothers, ants making slaves, the larvae of ichneumonidae feeding within the live bodies of caterpillars, not as specially endowed or created instincts, but as small consequences of one general law leading to the advancement of all organic beings--namely, multiply, vary, let the strongest live and the weakest die.