ADDITIONAL OBSERVATIONS

—ON—

SEXUAL SELECTION

—IN—

SPIDERS OF THE FAMILY ATTIDÆ,

WITH SOME REMARKS

—ON—

MR. WALLACE'S THEORY OF SEXUAL ORNAMENTATION,

—BY—

GEORGE W. AND ELIZABETH G. PECKHAM.

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ADDITIONAL OBSERVATIONS ON SEXUAL SELECTION IN SPIDERS OF THE FAMILY ATTIDÆ.

GEORGE W. AND ELIZABETH G. PECKHAM.

In the species of Attidæ whose mating habits we have heretofore described, the adornments displayed by the male in courtship have consisted of bright color on the cephalothorax or abdomen, colored hairs on the clypeus, tufts or ridges of hair over the face, modifications of the color or form of the first pair of legs, or modifications of the falces. We have had for some time in our collection three species, all belonging to the same genus, whose males showed a peculiar enlargement of the third leg; thus in Habrocestum peregrinum the patella is enlarged and somewhat triangular in shape, with an apophysis, of variable length, projecting over the tibia, while the anterior face of the patella has a black spot on a white ground. The third leg of the male of Habrocestum cœcatum has a similar, but less striking, enlargement of the patella; and in an as yet undescribed species, Habrocestum howardii, the patella has the same modification.

The general appearance of this structure, together with the fact that it was limited to the males, and was very variable, suggested that it was one of those sexual adornments which are useful in gaining the favor of the female. Had it occurred on the first leg we should have felt reasonably sure that this was its function; but it seemed improbable that a modification of the third leg could be displayed with advantage during courtship, and we were therefore considerably in doubt as to its meaning.

On the first day of June of the present year we were so fortunate as to discover on a hot, stony hillside (on ground, by the way, that we had worked industriously for ten years) large numbers of males and females of a new species of Habrocestum, having a modification of the third leg (Fig. 1) very similar to that

of Habrocestum peregrinum, but carried to a much higher degree. As it was their mating season, we had now a welcome opportunity of seeing what use the active little male, which is further beautified by having his first legs of a delicate light green color, with a fringe of white hairs along the outer side, makes of this adornment in paying his addresses to the female.* The display was witnessed not only by ourselves, but by Mr. Wm. M. Wheeler, who made several sketches on the spot.

Fig. 1.—Third leg of new species of Habrocestum (from nature).

When they are put into a mating-box together, the male notices the female at a distance of from six to eight inches, and rapidly approaches her. When within three or four inches,

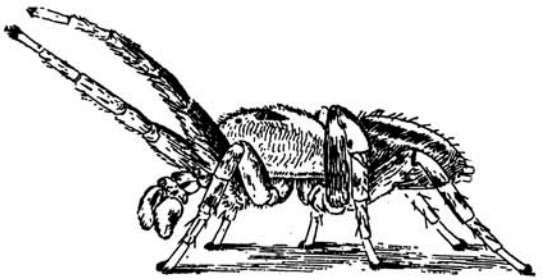


Fig. 2.—New Habrocestum, showing position of first and third legs of male in courtship (from nature).

he begins to move from side to side, with his handsome first legs pointed downward and somewhat outward, his palpi extended parallel with them, and his third legs raised above the first and second in such a way as to show the apophyses on the patellæ. Frequently, in these preliminary movements, he bends the ends of the first legs inward—the bend being at the tibia—so as to put them into the form of a diamond, meanwhile moving the palpi rapidly up and down. As he ap-

*To show how a species may appear and disappear within a short time, we may mention that while on June 1st we found eleven males and six females in an hour, one week later four and a half hours' hunting on the same spot gave us only one male and no emales.

proaches the female, she all the time eying him most intently, he raises the first pair of legs, swaying them backward and forward, still keeping the third pair well up, seeming as eager to display them as the first pair (Fig 2). In this way he approaches to within about two inches, when she rushes at him and he retreats. The whole performance is repeated. When he gets to within an inch of her, he lifts the first legs nearly at right angles with the body, giving them a bowed position, with the tips approaching each other, so that each leg describes a semicircle, while the palpi are held firmly together in front. Up to this time he has held the body well above the ground, but now he lowers it by spreading out the second and fourth pairs, at the same time bringing the tips of the third pair nearer the body and arching the legs over the posterior part of the cephalothorax in such a way that the proximal ends of the tibiæ nearly meet (Fig. 3). As he stands in this position the female, who is watching him eagerly, has the front surface of the apophysis plainly in view over the dorsal surface of the cephalothorax, and his face and clypeus are also well exposed (Fig, 4). Now he approaches her very slowly, with a sort of creeping movement. When almost near enough to touch her he begins a very complicated movement with the first pair of legs. Directing them obliquely forward, he again and again rotates each leg around an imaginary point just beyond the tip; when they are at the lowest point of the circle he suddenly snaps the tarsus and metatarsus upward, stiffening and raising the leg and thus exposing more completely its under surface. While this is going on with the first pair, he is continu-

Fig. 3.—New Habrocestum, showing front view of male when approaching female (from nature).

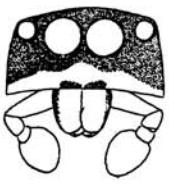


Fig. 4.—Face of new Habrocestum, showing ornamentation (from nature).

ally jerking the third pair up higher over his back, as though unable to get them into a satisfactory position, and the abdomen is kept twitching. At one time he carried on these movements within one-sixth of an inch of the female for six minutes, and at another time for five minutes; then she dashed at him and it all started over again.

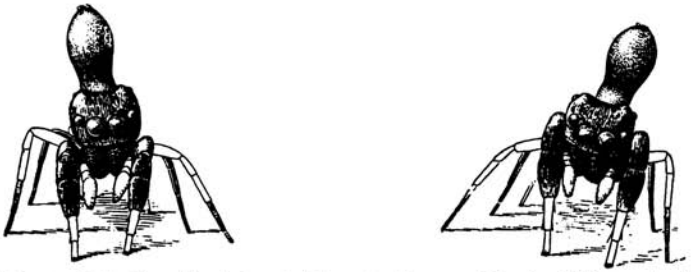
This display indicates that the enlargement of the third leg is useful in pleasing the female during courtship. In all probability the similar formations in peregrinum, cœcatum and howardii serve the same purpose.

At the same time that we discovered the new Habrocestum, we found, for the first time in this neighborhood, some examples of A. leopardus Hentz. The male of this species is very striking, from the fact that his clypeus is of a lovely turquoise blue—a most unusual color among spiders, where the blues are almost invariably metallic and iridescent. The male of leopardus is also adorned by having the space above the first row of eyes, extending to the second row, covered with brick-red hairs. He matures, as is usual in spiders, before the female. His courtship is as follows:

On seeing the female, which he does when eight or ten inches away, he approaches her slowly; when within three or four inches he begins to sway from side to side by bending all the legs on one side and extending the opposite ones, and then reversing the process, at the same time advancing. The palpi are stretched out sideways, thus exposing the blue clypeus. As he moves, the female eyes him attentively and seems to be interested in his display. When quite near her he raises the first legs and holds them perpendicularly upward, and then, as he comes closer, lowers them so as to touch her. This seems to frighten her, and she runs off. The whole performance is repeated six or eight times before she finally yields, either to his boldness and persistence, as Mr. Wallace would have it, or to the combination of these qualities with grace and beauty.

Sometime ago we published an account of the mating habits of Synageles picata, not, however, giving any figures. Having captured some fresh males and females early in the

present season, we first repeated our experiments with them in order to verify our former results, and then sent them to the



Figs. 5 and 5½.—Synageles picata. Positions of male approaching female (from nature).

well-known arachnologist, Mr. J. H. Emerton, who made from life the following sketches. To render them more intelligible, we repeat the account of the love-dance given in our former paper. *

"These are ant-like spiders. The most important sexual difference is the greater thickness of the first legs of the male. These are flattened on the anterior surface and are of a brightly

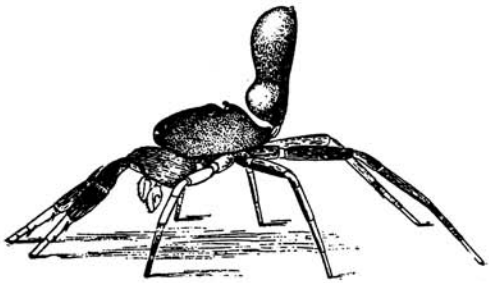


Fig. 6.—Synageles picata. Male as he appears from the side when approaching female (from nature).

iridescent steel-blue color. Unlike most of the *Attid* males this species keeps all his feet on the ground during his courtship: raising himself on the tips of the posterior six, he slightly inclines his head downward by bending his front legs, their convex surface being always turned forward. His abdomen is lifted vertically so that it is at a right angle to the plane of the cephalothorax. In this position he sways from side to side (Figs.

* Occasional Papers of the Wisconsin Nat. Hist. Soc., p. 43.

5 and 5½). After a moment he drops the abdomen, runs a few steps nearer the female, and then tips his body and begins to sway again (Fig. 6). Now he runs in one direction, now in another, pausing every few moments to rock from side to side and to bend his brilliant legs so that she may look full at them. We were much impressed by the fact that the attitudes taken by the males served perfectly to show off their fine points to the female. We had never known the male of this species until the day that we caught this one and put him into the mating-box, and it was while studying his courtship that we noticed how he differed from the female in his iridescent first legs. He could not have chosen a better position than the one he took to make a display. We had six females in the box, and we saw him mate with all of them."

The rule for the male *Attus*, when dancing before the female, is either to raise or stretch out the first legs, the apparent object being to display the colored hairs and other appendages with which they may be ornamented, as in the Icius mitratus, or to take an imposing attitude, as in Philæus militaris; or else to lower these legs so that they may not interfere with a view of the ornamented face or clypeus, as in Dendryphantes capitatus. In Synageles picata we are struck by the entirely unique position of the male, and, moreover, by the fact that this position is the only one which would serve to display his principal sexual adornment. If the legs were raised, outstretched, or held close to the ground, the effect of the flattened and iridescent anterior surface would be lost. This is a good example of what we have again and again observed in the courtship of the Attidæ—that whatever fine points of color or structure the male possesses, his actions before the female display them to the very best advantage; indeed, he *seems* to have a strong consciousness of every advantage, and to sedulously strive to bring it to the notice and impress its beauty upon the mind of the female to whom he is paying his addresses.* The females, on the other hand, are

*We do not say that, in our opinion, he *is* conscious of his strong points. It is quite conceivable that the tendency to perform the antics may have developed along with the beauties which they serve to display without any idea of their existence dawning in the mind of the spider.

as "uncertain, coy, and hard to please" as the males are eager. Both Dr. McCook and Mr. Emerton have remarked that the female, in mating, seemed to do nothing but run away, and this often does seem to be her only idea at the beginning of the courtship. After a little, however, her attention is caught, and she lingers for a moment before turning away, and, as the affair progresses, she becomes excited and watches the male with absorbing interest, only turning to flee when he comes close to her.

It may be well to say in this connection that any one who wishes to make a study of the mating habits of spiders should have a considerable knowledge of their haunts, their habits and of the time at which each species matures. The spiders should be taken just at the point of reaching maturity, as after that period their interest in the matter is only lukewarm, and although they may make some display it is but a feeble suggestion of their eager and excited action at an earlier time. Moreover, the observer must be prepared to draw largely upon his stock of patience, as some of the best dancers do not show what they can do just at first. For example, Habrocestum splendens will sometimes remain sulky and sullen for hours in the box with females, but when he is well warmed up to an interest in them (this is not altogether figurative, as it is often necessary to put the box in the hot sunshine) he becomes perfectly wild with excitement.

In a former paper we set forth some facts and arguments in favor of Darwin's theory of sexual selection, considering at the same time Mr. Wallace's counter-theory by which he attempts to explain the superior beauty of the male in many species of birds and insects. Since then, in his extremely interesting and suggestive work on Darwinism, Mr. Wallace has summed up his former views on this subject, supplementing them with additional arguments. Having here brought forward some new facts in regard to the courtship of spiders, we take this opportunity of re-considering the theory that Mr. Wallace would substitute for the one offered by Darwin.

THE THREE PARTS OF MR. WALLACE'S THEORY.

It is of primary importance to see what evidence Mr. Wallace brings forward in support of the proposition which forms

the whole foundation of his theory that the more brilliant and intense color of the male is due to his greater vigor and activity, and higher vitality. This proposition is a complex one, holding within it three implications which must be proved before its acceptance can be demanded—first, that male animals have higher vitality than females; second, that those males that have the highest vitality have also the most brilliant and intense colors; and third, that the superior ornamentation of these males is due to their activity.

FIRST PART: RELATIVE VITALITY OF MALES AND FEMALES.

Mr. Wallace does not say, in so many words, that males have higher vitality than females; he assumes this to be so universally acknowledged as to need no proof. Thus he says: "The very frequent superiority of the male bird or insect in brightness or intensity of color, even when the general coloration is the same in both sexes, now seems to me to be, primarily, due to the greater vigor and activity and the higher vitality of the male." * And again: "The more vivid colors and more developed plumage of the males, I am now inclined to think, may be wholly due to their greater vital energy." † In view of the fact that a contrary opinion has been generally held (Darwin, in "Origin of Species," says that the vitality of the two sexes is probably about equal), we object to the assumption of Mr. Wallace, and shall endeavor to show that in all probability the female, at least among birds and spiders, has as high vitality as the male.

Before we can discuss this point we must ask, What are the criteria of high vitality?

Mr. Pocock, in a review of our former paper on this subject, objects to our using activity and pugnacity as the only tests of vitality. As a matter of fact, these are the only ones put forward by Mr. Wallace; and, so far as the question is one of relative vitality among males, we are unable to suggest any that are better. When it comes to determining the relative vitality of males and females, we must also take into account the

* Tropical Nature, p. 193.
† *Ibid.*, p. 213

reproductive processes. Here the demand upon the female is obviously heavy. Even in birds and insects, where the embyro develops outside the body of the parent, the numerous eggs must be formed and stored with highly nutritious material, and there seems no room for doubt that in these relations the female evinces an amount of vital power that at least equals that ofthe male.

How does she compare with him in pugnacity and activity? Of birds we cannot speak with much authority, but it seems fair to say that in the construction of the nest, in feeding and rearing the young and in supplying her individual needs, the female shows as much activity as the male, while she exceeds him in the anxious vigilance with which she watches over her young and the vigor with which she defends them from the enemies which constantly menace their safety. As to spiders, we have no hesitation in saying that the females are both more active and more pugnacious than the males.

In "Darwinism" Mr. Wallace supports his position by the following quotation—not of facts, but of opinion—from the eminent arachnologist, Rev. O. P. Cambridge:

"I myself doubt that particular application of the Darwinian theory which attributes male peculiarities of form, structure, color and ornament to female appetency or predilection. There is, it seems to me, undoubtedly something in the male organism of a special and sexual nature which, of its own vital force, develops the remarkable male peculiarities so commonly seen, and of no imaginable use to that sex. In as far as these peculiarities show a great vital power, they point out to us the finest and strongest individuals of the sex, and show us which of them would most certainly appropriate to themselves the best and greatest number of females, and leave behind them the strongest and greatest number of progeny. And here would come in, as it appears to me, the proper application of Darwin's theory of natural selection, for the possessors of greatest vital power being those most frequently produced and reproduced, the external signs of it would go on developing in an ever-increasing exaggeration, only to be checked where it became really detrimental in some respect or other to the individual."

We oppose to this opinion of Mr. Cambridge, most of whose work has been done in systematic arachnology, that of the Rev. Henry McCook, who has devoted many years to a study of the habits of spiders, and who must be considered an important witness on a point to which he has given especial attention. We ourselves had supposed that in the sedentary group the male spiders were more active and vigorous than the females until converted to the contrary opinion by his argument. He says:

"Blackwall and Mr. C. Spense Bate reported to Darwin that the males of spiders are very active and more erratic in their habits than those of females. This appears to be a general opinion among arachnologists, upon what ground as to the matter of activity I am not able to perceive. One, of course, is compelled to ask what is meant by activity and inactivity as applied to spiders. Certainly the words must be regarded as relative terms. There is a sense in which the females of sedentary spiders are not as active as the females of the wandering groups. They may not, indeed, be able to make way over the ground and among herbage with the same facility that marks the Saltigrades, Laterigrades, and Citigrades; but the activity in spinning work of the average female Orbweaver is simply enormous. One who has watched the method by which the great round webs of our common indigenous species are spun, will certainly agree that the operator is one of the most active of creatures in that department of work, at least. The rapidity with which the threads are woven, the unceasing play of the hind legs in pulling out the thread, and the striding of the other limbs around the circle, together with the active exercise of the remaining organs, are evidences of immense vigor and activity. The fact that such a large and intricate web as Epeira spins can be wrought out in the course of half an hour or forty minutes, is proof enough of this activity. These snares will be reproduced several times a day if necessary, and the reproduction continues day after day throughout the life-time of the aranead.

"So also the same vitality of the female Orbweaver appears

in the construction of nests, which is not an inconsiderable work, involving no slight exercise of strength, as well as of ingenuity, as any one will see by turning to the chapter upon Nesting Habits, of this work, Chapter XVII, Volume I.

"Again, this activity appears in the capture of prey. If any one will take his stand before an average orbweb of almost any common species, say Epeira strix or Epeira scolpetaria, or Argiope cophinaria, at a season when flies and other insects abound, and in a site where they are plenty, he will be surprised at the intense activity displayed in the capture of insects. One after another these victims are seized, swathed, dragged to the hub or den to be devoured, and that with a display of vigor in capturing, in swathing, in cutting out the captive, and repairing the web, which must strike the most casual observer. The feast will be left a number of times to seize and truss up in like manner other victims who happen to strike the snare, and on each successive capture the same tremendous rush and energy of action will be noticed.

"I scarcely know a limit to the voracity of these Orbweaving spiders when full opportunity is given them to feed upon their natural prey; and I can certainly appeal to any one who has observed the actions referred to whether the whole demeanor of the aranead is not such as to impress him with the sense of a vast store of vitality and an almost exhaustless activity. Taking, then, the spinning work, and the ordinary action in capturing prey by means of nets as the standard, it cannot be affirmed with truthfulness that female Orbweavers are inactive, or that they suffer in respect of this element from comparison either with the wandering tribes or with the males of their own species.

"I might go further and say that when a female Orbweaver is placed upon the leaves of a plant, or even upon the ground among the grasses, she will display an amount of activity in getting from leaf to leaf, and limb to limb, and from point to point, which is surprising in a creature whose habits are so generally sedentary. I have often been amazed at the rapidity and facility with which the largest Orbweavers, as

Argiope cophinaria and arygraspis, could make the circuit of a bush, or travel over a plane surface.

"As to the males of Orbweavers, generally, it is certainly not in accordance with my observations that they are more active than the females. On the contrary, I am disposed to think them rather lethargic and sluggish fellows. I am aware that it has been said, in corroboration of the theory that the female is more inactive than the male, that she will hang to the hub of her orb, or remain motionless within her tent, for hours and perhaps even days. It is true; but that action is quite as characteristic of the male as of the female. I have seen the males of Cophinaria, in attendance upon a female, hanging upon the outer courts of their lady love's snare, apparently entirely inactive, for as much as two or three or four days in succession. They are very patient in their waiting, and make few movements during the courting period.

"So also it may be said that those Orbweaver males, which spin webs that are as perfect after their kind as those of the female, show precisely the same degree of patience in managing their snares and watching for the advent of insects as is shown by the female.

"If we turn now to the wandering groups, and make comparison between the males and females of the species of these tribes, I am certain that it will be found that the females are as active as, or even more active than, the males. During certain seasons of the year, as, for example, when they are carrying their cocoons, they do indeed prepare for themselves a little cave or silken cell wherein they live until their young are hatched. But during that period, even, the Lycosids may be found running around upon the rocks and over the fields, dragging their egg-bag after them. When the young are hatched, it is not uncommon to observe the mother wandering over the fields with all her offspring piled upon her abdomen and the lower part of the cephalothorax—a strange, and, to most beholders, a horrible sight, since the ordinary observer is not apt to associate the uncouth vision with the beautiful maternal devotion which the spider thus shows, and which has its

analogue in the human mother bearing her child in her arms or carrying it upon her bosom. Moreover, the excavating and fitting up these subterranean homes is a strong proof of a decidedly industrious character, and the act requires the exercise of great vigor, which, of course, is exclusively by the female.

"As a matter of fact, therefore, I am compelled to think that among all wandering groups, the difference between the activity of male and female is certainly not in favor of the former. Whatever conclusions, therefore, are drawn from the belief that the male is possessed of greater activity and vital force than the female, must, in my judgment, be regarded as erroneous. That he is more erratic in certain species, is true." *

In "Natural Selection" Mr. Wallace has brought out certain facts which are inconsistent with his present view. If the frequent superiority in the ornamentation of male birds arises from the fact that they have higher vitality than the females, how is it that in many families (including 1,200 species, or about one-seventh of all known birds †) we find the two sexes alike ornamented with brilliant colors and accessory plumes, which quite equal in beauty those of the male in those species where one sex alone is decorated? These facts while comprehensible under his earlier supposition (that color is normal, and in these species is not kept down by natural selection since they build covered nests), find no explanation in his later theory of the higher vitality of the males.

And, again, how shall we explain the fact that we often find the males in birds, insects and spiders as plainly colored as their mates, and this, too, when the habits of the two groups, the one plainly and the other brightly colored, are entirely similar?

Mr. Pocock allows us to make the following quotation (from a letter of his) which bears on this subject, as showing that there is no relation between the activity of the males and their color:

"The following case, with regard to which I can speak as an expert, seems to me to be rather against Mr. Wallace.

* American Spiders and their Spinning Work, Volume II, pp. 70-72.

† On Natural Selection, p. 244.

Throughout the great group of Myriapoda, of which hundreds of specimens from all localities have passed through my hands, there is not a single case, so far as I know, of the sexes differing in color. And yet, many of the species, both of Diplopoda and Chilopoda, are very beautifully colored. Now, there is no scope in this group for the action of sexual selection, because if not entirely without eyes, none of the species (except perhaps Sentigera) can see to any appreciable extent. But if Wallace's generalization with regard to the greater vigor of the male be true, we should expect to find the males more beautiful than the females, quite irrespective of powers of vision. And that the males are more vigorous, at least in some cases, is shown by the fact that the males of two South African species of Spirostreptus, that I have in captivity, certainly excel the females in activity and amorousness—the last quality being, I should think, an unquestionable criterion of vital force. But these males only differ from the females in primary sexual features."

SECOND PART OF MR. WALLACE'S THEORY: CORRELATION OF HIGH VITALITY AND BRIGHT COLOR AMONG MALES.

The second point in Mr. Wallace's proposition is that those males that have the highest vitality have the most brilliant color. In "Tropical Nature" there are named six species of humming-birds in which there is a combination of unusual activity and pugnacity with brilliant color. Since there are four hundred and twenty-six species of humming-birds, a large proportion of which are brightly colored, this number is certainly very low. There are also adduced five cases of birds where the females are brighter than the males, in which "the males take charge of and incubate the eggs while the females are almost always larger and more pugnacious than the males." * Furthermore, Mr. Wallace, in "Darwinism," speaks of the ornamental plumes that arise not only in birds of paradise, but

*Tropical Nature, p. 212.

also in many humming-birds and in some sun-birds and honey suckers, all of which are remarkable for their activity.

This is surely a very small amount of evidence for so wide a generalization. The weak spot in the argument, however, is not that Mr. Wallace gives but few instances of this combination of color with activity, for he might easily have multiplied them; but that he takes no notice of the numerous cases which are completely at variance with his theory. A fair consideration of these cases shows that there is no relation whatever between bright color and activity. Look, on the one hand, at the numerous groups of birds that are not especially active and yet are gorgeously decorated with colored plumes, crests and ruffs, and on the other at the still larger number that have scarcely any ornamental plumage and yet are endowed with enormous strength and activity. In the former class we find the gaudy parrots, including several hundred species, among which are the cockatoos, with their enormous crests; the clumsy barbets, with their sky-blue, green, yellow and crimson plumage; the slow, majestic, crowned pigeon, the crested hoopoos, the short-legged and clumsy hornbills; the brilliant todies, some of which are so inactive that they may be caught with the hand; the sluggish, stupid jacamars, whose brilliant, metallic, golden-green breasts rival those of the humming-birds; the magnificently colored toucans, which, although they can move with considerable agility among the branches, are heavy and awkward in flight; the dull, stupid puff-birds, which are often gaily colored, and the extremely sluggish and stupid gapers, which are adorned with the most brilliant and conspicuous tints; while the latter class would include the hawks, eagles and falcons, which occasionally have crests, but are lacking in bright color, and are certainly not remarkable for ornamental plumage; the gulls, terns, albatrosses and petrels, and, most remarkable of all, the swallows. In this group, of about one hundred species, we find an activity that is unequalled in the whole order of birds. They fly with astonishing velocity, often passing and repassing a railroad train going at full speed; they scarcely ever perch to rest; their temperature is the highest known

among birds (111½), they are, moreover, widely distributed and numerous in individuals; indeed, we find in them the fulfillment of every condition specified by Wallace for the development of high color and ornamental plumage, and yet they are entirely lacking in these attributes.

In speaking of accessory plumes, Mr. Wallace says that in many cases they can have no use, "but must be rather injurious than beneficial in the bird's ordinary life. The fact that they have been developed to so great an extent in a few species is an indication of such perfect adaptation to the conditions of existence, such complete success in the battle for life, that there is, in the adult male at all events, a surplus of strength, vitality and growth-power which is able to expend itself in this way without injury. That such is the case is shown by the great abundance of most of the species which possess these wonderful superfluities of plumage." *

Now, remembering that brilliant color and accessory plumes are classed together by Mr. Wallace as arising from identical causes and under identical conditions,† look at the family of pittas, which are adorned with brilliant and strongly contrasted colors. In regard to this group Leonhard Stejneger writes:

"The rich blues and crimsons, the delicate greens, yellows and purples, the velvety black and pure white (three of which tints at least generally adorn each species) remind one of the tanagers of South America; and, in fact, these two groups are almost the only ones which have no one characteristic tint or style of dress, but whose different species seem free to adorn themselves with the brightest hues from Nature's laboratory. There is, however, this difference, that whereas the tanagers are a dominant group, abounding in genera, species and individuals, over a very wide area, and presenting to our view much variety of form and almost every possible combination of colors, the pittas are a small and probably decreasing genus, with but

* Darwinism, p. 293.
† *Ibid*, p. 291.

slight modifications of form, and alike poor in species and in individuals." *

In regard to spiders the argument fails entirely. Not only are the plainly colored females more active and pugnacious than the males, but the sedentary Orbweavers are incomparably more gorgeous in color than the quick-running ground spiders.

Among the Attidæ, where sexual color is most common, perhaps the most brilliant of all the males is Habrocestum splendens, which has the body of a splendid iridescent red. According to the theory before us, this should be an especially lively species. The fact is, however, that splendens is the most sluggish and retiring spider that we know of. Even where half a dozen males are brought together each one spins himself a thick cover of silk, under which he hides. Here he remains for days at a time, not even coming out to eat and drink. In the presence of the female, to be sure, he is capable of the liveliest action, but at other times he holds himself hidden and absolutely quiet.

THIRD PART OF MR. WALLACE'S THEORY: ACTIVITY THE CAUSE OF COLOR AND ACCESSORY PLUMES.

Let us now look at activity as a cause of ornamentation.

As Mr. Wallace left his theory in "Tropical Nature" it did not explain the distribution of the sexual colors of the males, and their frequent appearance in certain definite parts of the body. It might be granted that he had made clear the origin of color in general, but not the sexual ornamentation of the males. This question is taken up in "Darwinism."

In view of all Mr. Darwin's work in this connection we are surprised at his opening assertion that female selection does not account for the fact that these ornamental appendages appear in a few definite parts of the body, and that "we require some cause to initiate the development in one part rather than in another." No one has taken greater pains to prove, nor has any one presented in so masterly a way as Mr. Wallace himself

* Standard Natural History, edited by J. S. Kingsley, Vol. IV., p. 467.

the immense mass of facts going to show that "individual variability is a general character of all common and widespread species of animals or plants; and, further, that this variability extends, so far as we know, to every part and organ, whether external or internal." *

If this be true, what is the difficulty in supposing that the females have selected one ornamental variation rather than another, and that, as the generations passed, this process being cumulative, all the sexual color and ornament that we find in nature have resulted? This supposition would at least explain the facts. It is expressly to make clear why the ornamentation appears so frequently in certain tracts of the body that the supporters of female selection have brought forward the innumerable instances of male display, and, at the risk of being tedious, have pointed out that the ornaments are always well in view of the female, and presumably for her benefit.

When Mr. Wallace denied that the choice of the female was influenced by ornamentation (not because this would not explain the facts, but because he disbelieved in any such predilection on her part), he was left without any explanation of the very important fact that color and ornament in birds, insects and spiders almost always appear in certain parts of the body.

The explanation which he now offers (which was suggested to him by the theory of Mr. Tylor) is that color and accessory plumes are situated on surfaces where muscular and nervous development is considerable and where functions change; and that this is in fact the cause of the ornamentation and determines its distribution. He asserts that the development of color and feather is proportional to that of muscle and nerve, and if he can establish this conjunction he will go a long way towards substituting his own theory for that of female choice.

In so complex a subject it is necessary, even at the risk of being wearisome, to analyze the steps of the argument into their simplest terms; and the more so because the force and charm of Mr. Wallace's style sometimes carry the reader too

* Darwinism, p. 81.

far. The point to be proved is that there is a concomitant variation between color, plumes and other sexual ornaments and the functional development of the surfaces upon which they are found. We are investigating a question of cause and effect, and we are to prove that in places where there is great functional activity, the cause, there is found sexual ornamentation, the effect. Mr. Wallace's way of stating the relation is a little different. He gives instances of the development of plumes from certain well-nourished parts, showing that in some cases these ornaments arise from the most powerful muscles of the body, and near the spot at which the activity of the muscle is at its maximum; and he implies that sexual ornaments always arise from such muscular and well-nourished parts. We even understand him to believe that there is a quantitative proportion between the muscular development and the ornamentation. To quote his own words:

"The view that color has arisen over surfaces where muscular and nervous development is considerable, and the fact that it appears especially upon the accessory or highly developed plumes, leads us to inquire whether the same cause has not primarily determined the development of these plumes. The immense tuft of golden plumage in the best known birds of paradise (Paradisea apoda and P. minor) springs from a very small area on the side of the breast. Mr. Frank E. Beddard, who has kindly examined a specimen for me, says that 'this area lies upon the pectoral muscles, and near to the point where the fibres of the muscle converge towards their attachment to the humerus. The plumes arise, therefore, close to the most powerful muscle of the body, and near to where the activities of that muscle would be at a maximum. Furthermore, the area of attachment of the plumes is just above the point where the arteries and nerves for the supply of the pectoral muscles, and neighboring regions, leave the interior of the body. The area of attachment of the plume is, also, as you say in your letter, just above the junction of the caracoid and sternum.' Ornamental plumes of considerable size rise from the same part in many other species of paradise birds, sometimes extending

laterally in front, so as to form breast shields. They also occur in many humming-birds, and in some sun-birds and honey-suckers; and in all these cases there is a wonderful amount of activity and rapid movement, indicating a surplus of vitality, which is able to manifest itself in the development of these accessory plumes.

"In a quite distinct set of birds, the gallinaceæ, we find the ornamental plumage usually arising from very different parts, in the form of elongated tail-feathers or tail-coverts, and of ruffs or hackles from the neck. Here the wings are comparatively little used, the most constant activities depending on the legs, since the gallinaceæ are pre-eminently walking, running and scratching birds.* Now the magnificent train of the peacock—the grandest development of accessory plumes in this order—springs from an oval or circular area, about three inches in diameter, just above the base of the tail, and therefore situated over the lower part of the spinal column near the insertion of the powerful muscles which move the hind limbs and elevate the tail. The very frequent presence of neck-ruffs or breast-shields in the males of birds with accessory plumes may be partly due to selection, because they must serve as a protection in their mutual combats, just as does the lion's or the horse's mane. The enormously lengthened plumes of the bird of paradise and of the peacock can, however, have no such use, but must be rather injurious than beneficial in the bird's ordinary life. * * * * If we have found a *vera causa* for the ornamental appendages of birds and other animals in a surplus of vital energy, leading to abnormal growths in those parts of the integument where muscular and nervous action are greatest, the continuous development of these appendages will result from the ordinary action of natural selection in preserving the most healthy and vigorous individuals, and the still further selective agency of sexual struggle in giving to the strongest and most energetic the parentage of the next generation."

* Eight out of fifteen species of birds of paradise, although they are flying, not running, birds, have elongated and ornamental tail-feathers.

Accessory Plumes of Birds of Paradise Frequently Arise from Parts where Muscular Development is Inconsiderable.

In view of the vital importance of this supposition to the argument before us, the very life of the argument depending upon its validity, let us examine carefully the evidence upon which it is based. Do we find that all highly colored and decorated birds agree in a proportion between the ornamentation and the nervous and muscular development of those parts of the integument from which the ornaments arise? The examples given by Mr. Wallace are not only few in number, but seem to us to be misleading in character, since we find in the very groups that he cites much more numerous instances which go to prove the exact opposite. Look, for example, at the birds of paradise. It is true, as he states, that in P. apoda and P. minor the immense tuft of plumage springs from near the great pectoral muscle, where muscular activity is at a maximum; but to show that there is no causal relation between the muscular activity and the plumes, we need only examine closely the whole group of paradise birds, where we shall find that these ornaments arise wherever they can be made useful for display, and often from parts where there is no marked muscular development.

Thus the Great Bird of Paradise (P. apoda) has two elongated tail-feathers (34 inches long).

The Red Bird of Paradise (P. rubra) has two elongated tail-feathers (about 22 inches long), "which always attract attention as the most conspicuous and extraordinary feature of the species" (Malay Archipelago, p. 558). On the forehead, where the muscular development is at its minimum, is a richly colored double-crest. There are also tufts from the breast.

The next species, the King Bird of Paradise (P. regia), besides the breast-tufts, has "another ornament still more extraordinary" (Malay Archipelago, p. 560); the two middle tail-feathers are modified into very slender, wire-like shafts, which, at their extremity, are enlarged and colored emerald green.

We next come to the Magnificent Bird of Paradise (Diphyl-

lodes speciosa), where we find no well developed breast plumes, but two rich mantles that spring from the dorsum, one from the nape and the other just back of it; these are the marked feature in the bird. The tail has two elongated middle feathers.

In Wilson's Bird (D. wilsoni) there are breast plumes, but the most highly developed feathers spring from the back, between the wings. There are also tail ornaments.

The Superb Bird of Paradise (Lophorina atra) is one of the most beautiful birds of this wonderful group. Although it has the breast-shield, a still more extraordinary ornament springs from the back of the neck—a shield of similar form to that on the breast, but much larger (Malay Archipelago, p. 564).

The Six-shafted Bird of Paradise (Parotia sexpennis) has immense tufts of soft feathers on each side of the breast. From the side of the head spring six wonderful feathers, reaching nearly as far back as the end of the tail, which, in this species, is not elongated.

The Standard Wing (Semioptera wallacei) has, besides the metallic-green gorget from the breast, an altogether unique ornament in the form of four long white plumes, which spring from the carpus of the wing, a place where there is very little muscular development. It has no tail modification.

In the Long-billed Birds of Paradise, one, the Twelve-wired Paradise Bird (Seleucides alba) has its wonderful plumes from the sides of the breast; while another, the Long-tailed (Epimachus magnus) has, besides its chief ornament, that from the breast, "a magnificent tail, more than two feet long, glossed on the upper surface with the most intense opalescent blue" (Malay Archipelago, p. 569).

The Scale-breasted Paradise Bird (Epimachus magnificus) has breast plumes and also two broad middle tail-feathers.

The Prince Albert's Bird (Ptiloris alberti) has well developed plumes from the under side of the body.

The Paradise Pie (Astrapia nigra) has a very long tail, but its chief ornament is from the back part of the head and neck. All the plumage around the head is lengthened and erectile,

and when it is spread out the bird is very beautiful, and is hardly surpassed by any of the Birds of Paradise.

The Carunculated Paradise Pie (Paradigalla carunculata) has neither marked plumes nor ruff.

The Paradise Oriole (Sericulus aureus) is chiefly characterized by a quantity of feathers of an intense glossy orange color which cover its neck down to the middle of the back.

Two of the Rifle Birds we know nothing of.

Thus we see that while eleven out of the fifteen paradise birds have plumes arising near the pectoral muscle, the whole fifteen have plumes arising from other places—tail, upper and under surface of body, head and neck; and that while nine out of the fifteen have their most important ornament on the breast, six have their finest plumes on some other part of the body. The conclusion is inevitable that there is no causal relation between muscular development and ornamentation. Indeed, so far as these birds are concerned, it seems to us that Mr. Wallace's earlier opinion is best, and as he so clearly sums up the evidence we quote him in full:

"The successive stages of development of the colors and plumage of the birds of paradise are very interesting, from the striking manner in which they accord with the theory of their having been produced by the simple action of variation, and the cumulative power of selection, by the females, of those male birds which were more than usually ornamental. Variations of *color* are of all others the most frequent and the most striking, and are most easily modified and accumulated by man's selection of them. We should expect, therefore, that the sexual differences of *color* would be those most early accumulated and fixed, and would therefore appear soonest in the young birds; and this is exactly what occurs in the paradise birds. Of all variations in the *form* of birds' feathers, none are so frequent as those in the head and tail. These occur more or less in every family of birds, and are easily produced in many domesticated varieties, while unusual developments of the feathers of the body are rare in the whole class of birds, and have seldom or never occurred in domesticated species. In accordance with

these facts, we find the scale-formed plumes of the throat, the crests of the head, and the long cirrhi of the tail, all fully developed before the plumes which spring from the side of the body begin to make their appearance. If, on the other hand, the male paradise birds have not acquired their distinctive plumage by successive variations, but have been as they are now from the moment they first appeared on the earth, this succession becomes at least unintelligible to us, for we can see no reason why the changes should not take place simultaneously, or in a reverse order to that in which they actually occur."*

The Ornamental Plumes of the Gallinaceæ are not Confined to the Area of the Most Powerful Muscles.

To answer Mr. Wallace's argumeut from the gallinaceæ it should be necessary only to present a number of cases of running birds with sexual colors and plumes which are found on other parts of the body than the area of the muscles which move the hind limbs and elevate the tail. The proposition being that where there is great muscular activity there is surplus vitality, which is disposed of in the formation of ornamental plumage, we must show that ornamental plumage frequently arises from parts of the body which have no especial muscular activity.

We have such a case in the Argus Pheasant, which is as highly decorated as the peacock and is as truly a gallinaceous bird, but which has its chief ornament in a different place. The two elongated tail-feathers are insignificant when compared with the enormous expanse and exquisite marking of the wings, the unwieldy size of which almost deprives the male bird of flight. In "The Geographical Distribution of Animals" Mr. Wallace, in speaking of this bird, says: "It is interesting to note, that during the display of the plumage the bird's head is concealed by the wings from a spectator in front, and, contrary to what usually obtains among pheasants, the head is entirely unadorned, having neither crest nor a particle of vivid color,—

* Malay Archipelago, p. 559.

a remarkable confirmation of Mr. Darwin's views that gayly colored plumes are developed in the male bird for the purpose of attractive display in the breeding season." *

In the gallinaceæ of North America there are some thirty species of partridges and grouse, in which the tail is short or only moderately long—not longer than the wing. In fourteen species there are head and neck plumes, which are, evidently, not protective. To show that these cannot be due to the superior vitality of the male, we may mention that in six of these species, plumes are found on the top of the head in both sexes.

The Distribution of Accessory Plumes in Humming-Birds Refutes Mr. Wallace's Theory.

The pectoral muscles reach their highest development in the humming-birds, the diurnal birds of prey and the swallows, and we may, therefore, fairly use these groups to test Mr. Wallace's explanation of breast plumes. In the swallows and birds of prey we find no such appendages, in spite of their further claim to them, on the ground of great vigor and activity. As to the humming-birds, we find in the genus Aglæactis six species with more or less developed breast-plumes, which are also found in nine other species, scattered through different genera—in all, only fifteen species out of four hundred and twenty-six; while we find in fifty-six species the lengthened and modified tail-feathers, which, according† to Mr. Wallace's view, should be peculiar to the gallinaceæ.

Again there are elongated feathers from the throat or from the side of the neck in thirty-five species,‡ while seventeen have crests from the top of the head, and seventeen, downy puffs from the tarsi.

From this very brief survey of the family we see that, contrary to what we should expect from Mr. Wallace's theory,

* Volume I, p. 339.

† Loddigesia mirabilis has the tail about three times as long as the body. Similar modifications are found in the genera Sappho, Cynanthus, Lesbia, Steganura, Discura, Gouldia, *et al.*

‡ Among the most remarkable of this wonderful family are the nine species of coquettes (Lophornis), which have elongated feathers, with metallic tips, springing from the sides of the neck; some have also beautiful crests.

although the breast muscles are the seat of the highest activity, breast plumes are the least frequent of all the forms of ornamental plumage.

We may fairly say, then, that the humming-birds completely refute the proposition that there is any relation between the development of color and accessory plumes and "surfaces where muscular and nervous development is considerable." If the facts prove anything, it is that color and plumes appear on all those parts of the body that are in view when the bird is on the wing. This conclusion is irreconcilable with Mr. Wallace's theory, but is quite in accord with that of Darwin, since the humming-bird, in his display before the female, circles about, rising and falling in the air in such a way that all his beauties are well shown. Another important point in this connection is that the courtship colors of the male are not found on the long wing feathers. Professor Newton remarks, in his article on humming-birds,* that "the flight feathers are almost invariably dusky; the rapidity of their movement would perhaps render any display of color ineffective." Mr. Poulton says that in birds and insects we distinguish two kinds of flight; in one it is produced by an excessively swift vibration of the wings, in the other by a relatively slow, flapping movement. In the former, including the humming-birds and the majority of insects, the wings are quite invisible, owing to their rapid motion; in the latter, including the majority of birds and butterflies and many moths, they can be easily seen. We find, as a general rule, that the colors distinctive of sex are displayed on the wings in the latter group, but are absent from the wings in the former. Facilities for female observation are thus afforded by the distribution of color." †

Relation Between Sexual Ornaments and Highly Nourished Surfaces in Spiders.

It is no less true in spiders than in birds that sexual ornaments are found where they can best be used in display, and

*Enc. Brit., Vol. XII, p. 358.

† Colors of Animals, p. 332.

that their appearance is by no means confined to those areas that have high muscular development.

If it be admitted that there is no causal relation between high muscular and nervous development and brilliant ornamentation in either birds or spiders, Mr. Wallace is left with only a very incomplete theory of sexual ornamentation, since, without Tyler's hypothesis, the really important point—*i. e.* the limitation of the ornaments to a few definite parts of the body—is unexplained. Whether the evidence which he offers is enough to prove the relation we leave the reader to decide. For ourselves, when we consider the mass of evidence offered by Mr. Darwin in support of his theory and contrast it with the small amount offered by Mr. Wallace, we are impressed anew with the high value of facts as compared with opinions.

OBJECTION TO MR. WALLACE'S THEORY.

Even if Mr. Wallace were able to prove the propositions upon which he founds his theory, his view would still be open to the strong objection that under it the bright colors and ornaments of the males are mere by-products, meaningless and useless, belonging, in fact, to Poulton's non-significant group. He states, in more than one place, his belief that the possession of ornamental appendages and bright colors in the male is not an important character functionally.* Are, then, all these sexual peculiarities in birds and spiders, plumes, colors, leg-modifications and enlargements and ornamentation of the falces, to be put into the same category as the color of the bile? If they have any use, we must suppose that it is that of pleasing the female, and that they have arisen through female selection.

In his review of Mr. Poulton's work on Colors of Animals, Mr. Wallace demurs to the use of the term *æsthetic* in connection with these creatures. We take it that all would agree that the word is unfortunate if any one understands that it is used in its higher sense. Perhaps Allen's suggestion, that we

*Tropical Nature, pp. 199 and 210. In the latter place he states his opinion that they may be slightly injurious; and in Darwinism he says that the plumes of the birds of paradise and the peacock must be injurious rather than beneficial.

substitute *conspicuousness** for beauty, might help to make the matter clearer; but when Darwin spoke of sexual selection as the cause of these modifications (and we do not doubt that Mr. Poulton so understands it) he attributed to the female only a low kind of pleasure when she saw the color which she connected with the male of her own species, or was pleased by the song of one bird more than by that of another; just about the amount of pleasure that insects have in visiting flowers. It seems to us that in this review far too much stress is laid upon the term æsthetic, implying that so high a faculty is inconceivable in these low organisms. Mr. Wallace, himself, admits as highly probable that the female is "pleased or excited" by the display, and this pleasure or excitement is a fair definition of what Mr. Poulton means by his æsthetic sense.

While Mr. Wallace is very loath to admit the existence of emotional states in the female he is by no means so in the case of the male. On the question of the state of consciousness of the males during courtship he speaks of the display "under the influence of jealousy or sexual excitement. * * * * The males, in their rivalry with each other, *would see what plumes were most effective; and each would endeavor to excel his enemy* as far as voluntary exertion would enable him." † If the males have so complex an emotion as jealously, and further, if they are conscious of the value of the plumes, may it not be asked why the female is unable to "see what plumes are most effective?" The mental state in the male is without meaning unless we suppose the female to be affected and pleased.

MR. WALLACE'S OBJECTIONS TO DARWIN'S THEORY.

Mr. Wallace, besides suggesting a substitute for the theory of female selection, has criticised, with much ingenuity, the arguments that have been offered in its support. His most important objection is that there is little or no evidence that the female pays any attention to the antics of the male, and that there is positively no evidence that she is influenced in her choice of any male by his color or ornaments. In regard to the

* Color Sense, p. 157.

† Tropical Nature, p. 210. The italics are ours.

first point, Mr. Wallace admits the display, and says that the female is probably pleased or excited by it, but he thinks that the males act as much from an internal impulse to motion and exertion as from any desire to please their mates. Why, then, do they not perform their antics when alone, as much as when in the presence of the female? He also thinks that while the female does exercise a choice in the selection of her mate, she is influenced, not by superior color or ornament, but by vigor and liveliness. Although we object to his dismissing the color as entirely meaningless, we fully agree with him that the female is strongly influenced by the agility of the male. Where both sexes are dull colored this is all that he has to depend upon to render himself attractive to her. Thus, as he has himself noted, "Goatsuckers, geese, carrion vultures and many other birds of plain plumage have been observed to dance, spread their wings or tails, and perform strange love-antics," and the same proposition holds true among spiders.

Owing to the habits of birds and insects the particulars of their love-making are very difficult to obtain, but in spiders we have positive evidence that in all the species of Attidæ that we have thus far been able to obtain under proper conditions for study, the female watches the love-antics of the male with great attention. Mr. Pocock has suggested that the attitude of observant interest on the part of the female spider might be taken to indicate that she was preparing to spring upon her mate and devour him; or that it might simply mean that she was warily guarding herself from his approach. Neither of these suppositions is admissible. In some species the male is not attacked by the female, and when she does wish, as frequently happens, either to avoid or to destroy him, her attitude is totally different. In the former case she turns about and runs rapidly away, or suspends herself by a thread of web. In the second, there is a contraction of all the muscles, the legs are drawn together, and in this crouching position she creeps slowly toward him, as she might if he were a fly, only with something more malignant in her aspect. When she takes this stand the male incontinently flees. When, on the con-

trary, the female is interested in the male display, she seems perfectly absorbed in watching him, the muscles are all relaxed, unconscious of herself she directs her glance now here, now there, as he moves about; as he continues his mad antics, her appearance gives every indication of pleasurable excitement, and as he comes closer and closer, she yields herself to the impulses which he has awakened in her, and, as in *pulex*, joins in his dance and whirls around and around as though intoxicated. We claim, then, to have completely answered Mr. Wallace's first objection. As to the second point, it is true that we have no direct proof that the females select the more beautiful males. In the nature of things, such proof is almost, if not quite, impossible to get; but indirect evidence we have in abundance. Thus we have shown that many male spiders have varied ornaments and brilliant color. That these are only developed when they become sexually mature, before which time the males resemble their plainly attired mates. That these secondary characters are extremely variable and are always so placed as to be useful in attracting the attention of the female, and, in point of fact, are so used. As we have shown, in a former part of this paper, that Mr. Tylor's explanation of this remarkable distribution of color and ornament has little, or we might almost say, no evidence at all in its support, the way is left open for the only other explanation of these facts thus far offered, namely, the one that asserts that the female has been the important factor in determining both the ornamentation and its location, Natural Selection controlling the process, and in many cases allowing only a minimum of sexual difference.

While it may be admitted that the vigor of the male plays some part in deciding the choice of the female, it seems to us impossible to admit that it is the important factor, since it would leave entirely unexplained all the facts of display. This would not count for so much in the case of birds, since the peculiarities of their display are difficult to observe, and in some instances the assertion that the movements are meaning-

less is incapable of disproof.* Fortunately, in the case of spiders the facts are quite different. The spider has four pairs of legs, and all are equally available for display or locomotion, and since all the movements are slow and on the ground they are entirely open to observation and study, and we are thus in a position to decide by facts whether their activity is simply an outlet for superfluous energy, and therefore meaningless, or whether there is a purpose in it. If the purpose of the antics is only to let off energy, then we should expect one pair to be flourished around quite as often as another, and that the pair flourished should as frequently be one that was not ornamented as one that was; and, moreover, their movements ought not to be of such a nature as to display the color or ornament more frequently than the law of chance would explain. If the spider almost always moves the ornamented legs, and in such a way, too, as to bring out their beauty, it would seem to us, to say the least, highly improbable that the dance of the spider was merely a meaningless overflow of surplus energy. Such an explanation leaves much that needs explanation. The facts are, that the best foot is put forward; and this is just what Darwin's theory requires and explains. Under Mr. Wallace's view the facts are inexplicable. The better to show that these movements are not simply meaningless outlets of high vigor, we illustrate the several positions by figures taken from nature (Figs. 7–12). The figures would seem to prove that the legs that are ornamented or contrasted in color are also the legs that are usually flourished; that where none of the legs have special ornament, then all are used; or, as sometimes happens, when an unornamented leg is used the movements are of such a character as to display some ornament that would otherwise have been more or less hidden from the female. Mr. Wallace, in his review† of Mr. Poulton's recent work on Color, remarks, in this connection, that in the case of the black variety of Astia vittata "there is not a particle of proof that the black color was the cause of the selection rather than the 'superior'

* The absence of color on the flight feathers of humming-birds, along with other facts, shows that even in this class there is a good deal of evidence on the other side.

† Nature, July 24th, 1890, p. 290.

Fig. 7.—Icius mitratus. Male displaying his fringed legs before female.

Fig. 8.—Astia vittata, var. Niger. Male striking an imposing attitude before female.

Fig. 9.—Dendryphantes capitatus. Male lowering his first legs to display his ornamented face to the female.

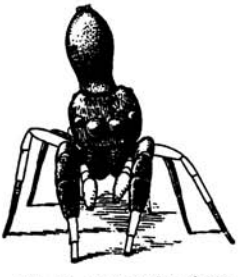


Fig. 10.—Sygnageles picata. Male displaying his iridescent first legs before female.

Fig. 11.—New species of Habrocestum. Male taking an attitude, before female, which displays his ornamented first legs and the apophyses on his third legs.

Fig. 12.—Saitis pulex. Male using all his legs to display before female.

liveliness which all breeders of animals believe to be the most attractive characteristic a male can possess." If liveliness, *per se*, is the most important factor, what has produced the differences that exist in the modes of display in the two varieties? The black form raises the first legs high in the air; the red form, while frequently taking the same position, has another attitude peculiar to itself, in which the body is dropped to the ground and the first and second pairs of legs are lowered and so placed that the tips touch in front. Mere overflow of energy might as well be let off by way of the movements of the black form as by those of the red. Niger certainly gains an advantage from his superior liveliness and persistence in chasing the female, but why does he never attempt to mate with her until he has spent some time in posturing before her? And what is the meaning of the three tufts of hair which stand erect on his head? According to Mr. Wallace's theory they should spring from the leg muscles. Certainly in no part of the body is there less muscular activity than at their point of origin. All these minute details are insignificant when looked at alone, but taken along with all the other facts, they seem to us to completely refute the supposition that all the different movements—so generally related to the ornamentation of the several parts—are meaningless, and due to an excess of vitality.

The final criticism offered by Mr. Wallace is, that supposing female selection to be a fact, the action of natural selection would render it entirely ineffective since there would be no chance that the ornamental variation would appear in just those individuals which were the fittest to survive from their perfect adaptation to the conditions of life, and that this inefficiency would be most complete in insects where immense numbers perish in the egg, larva and pupa stages. This point has been so forcibly and conclusively answered by Mr. Poulton that we cannot do better than to quote his argument on the subject. He says:* "Every one will admit that such a process as this has been vigorously checked by the far more important process of natural selection. But it does not therefore follow, as

*The Colors of Animals, p. 307.

Mr. Wallace argues, that 'the effect of female preference will be neutralized by Natural Selection.' It must be remembered that such preferences can only decide between males which have already successfully run the gauntlet of by far the greatest dangers which beset the higher animals, the dangers of youth. Natural Selection has already pronounced a satisfactory verdict upon the vast majority of animals which have reached maturity. The male which has only just passed this test, and is nevertheless accepted because of some superior attraction, will soon succumb and will leave far less offspring than one of equal or perhaps inferior attractions, which is fitted to live for the natural term of its life. Furthermore, the offspring of the former will stand a greater chance of failure than those of the latter. Natural Selection is a qualifying examination which must be passed by all candidates for honors: Sexual Selection is an honors examination in which many who have passed the previous examination will be rejected. But the conditions for qualifying are more rigid than in any existing system; for the candidates who have barely qualified, or have qualified by some piece of luck, or have failed to keep up the necessary standard in afterlife, will in the end be excluded from the advantages of any honors they may have gained. Mr. Wallace states that 'the action of Natural Selection does not indeed disprove the existence of female selection of ornament as ornament, but it renders it entirely ineffective.' This opinion can hardly be maintained if we believe that such preferences lead to the failure, comparative or complete, of the plainer or less graceful males, although the equal in other respects of their more successful rivals. Each of these two processes will check the other: Natural Selection will ensure that the males which succeed because of their beauty are among the fittest; Sexual Selection will ensure that the males which succeed on account of their 'fitness' are among the most beautiful."

SUMMARY.

Mr. Wallace's theory, then, rests on a number of unproved propositions, and since one depends on the other the argument

is no stronger than the weakest link in the chain. If males have greater vitality than females, and if the males that have the greatest vitality have also the greatest ornamentation; and, further, if the superior ornamentation of these males is due to their greater activity, then the great vitality is the cause of high color. We have found the weak point in his argument was the small amount of evidence that he was able to offer in support of each of the three propositions, so that the successive steps in the argument grew weaker and weaker. Indeed, it seemed to us that although many of his arguments were strikingly ingenious, they all appeared to rest on very slender evidence, or to admit of another interpretation. Even yet he had not explained the distribution of the color over certain limited areas of the body, and he was obliged to adopt the exceedingly unsatisfactory hypothesis of Mr. Tylor that color and ornament are a sort of by-product from the surfaces where there is a great deal of activity. The most weighty objection to this view is the almost entire lack of evidence in its support; perhaps it is as great an objection that it places so many striking and apparently important structures in the category of useless organs.* "Tropical Nature" was published, and Mr. Wallace argued at great length and with much ability in favor of his views of sexual color, during Darwin's life, and it is of the highest interest to learn what impression this reasoning had made upon his mind. We close with a quotation from a paper read at a meeting of the Zoological Society only a few hours before his death:

"I may, perhaps, be here permitted to say that, after having carefully weighed, to the best of my ability, the various arguments which have been advanced against the principle of sexual selection, I remain firmly convinced of its truth."

* We do not deny that some specific characters may be useless, but the demand that Mr. Wallace's theory makes in this direction seems to us extravagant and beyond the limits of reasonable probability.