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NATURAL SELECTION AND ALTERNATIVE HYPOTHESES.

Animal Coloration: an Account of the Principal Facts and Theories relating to the Colours and Markings of Animals. By F. E. Beddard, M.A., F.R.S. (Swan Sonnenschein & Co.)

THE theory of natural selection has been pre-eminent for over thirty years as the most generally accepted explanation of organic evolution. It has, and has had throughout, many critics; but its position is strengthened by the fact that these critics invariably accept the principle as accounting for something, while most of them make it clear that they reject all other proposed substitutes, except those for which they are individually responsible. Sometimes the attempt to formulate an alternative hypothesis, or to apply it to the facts of nature, breaks down as soon as it is undertaken. A curious instance of this is to be found in Semper's "Animal Life," which begins with very large anticipations:—all the "popular cant" of the Darwinian is to be "put out of court as useless"; a selective explanation can never be a real one, but for the latter we are to consult the subsequent pages. But as case after case is examined, the author is constrained to admit that his real explanation is not forthcoming, and that, although he never will think much of selection, it is the only cause he has to offer. Semper would appear to have written his preface before he considered the materials from which he proposed to write his book.

Mr. Beddard's work does not open in this ambitious manner, but he is far bolder in offering alternatives to natural selection, and in applying them. Further consideration would probably have brought him to Semper's admission, at least as regards many of his suggestions. Indeed, the number of these suggestions, and the confidence with which they are brought forward, are clearly due to haste and want of sufficient reflection, which also leave their mark upon the scheme of the volume and the number of contradictory statements to be found in it. Nor is this to be wondered at when the amount and variety of work which the author accomplishes is borne in mind. But the result will be to confuse the beginner and the untrained student. Principles which are supposed to be refuted in one part, are subsequently introduced with considerable enthusiasm as the heads of the main sections of the work, and are later on again treated with scant courtesy. In fact some readers will rightly infer that the author is a profound sceptic as to the value of the scheme he nevertheless adopts. Others may perhaps be led to suppose, by the arrangement of the book, that the author is sceptical of his own scepticism. Even the very fairness of the author in giving the arguments in favour of views he rejects, will be, such is the system pursued, a cause of confusion to a reader. These sources of difficulty are not only apparent in the general scheme; particular explanations are disputed in one part, and adopted a little further on without a word of explanation.

The chief value of the book lies in the fact that it is straightforward, and speaks out on points of great difficulty and dispute. Arguments of which echoes have been already heard, perhaps, in the report of some conversation which is supposed to have taken place, or which have been crudely stated in the publications of unknown writers, are here met with in a form in which they can be dealt with. For thus stating the opinions which are vaguely supposed to be held, perhaps vaguely held, by others, every Darwinian owes a debt of gratitude to the author.

The main aim and purpose of the book would appear to be a criticism of natural selection as applied to the explanation of the colours of animals, and the proposal of alternative explanations.

Some of the difficulties which the author finds in the theory of natural selection appear to follow from his conception of the process itself. Thus, on p. 12, he speaks of polymorphic species appearing in two or more well-marked forms, and of those extreme cases of variation known to entomologists as "varieties," and concludes, "In fact, if colouring were really constant for a given species, there would be no chance for natural selection"; thus implying that natural selection depends upon such pronounced divergences, instead of upon those minute differences which distinguish the individuals of every species. He then continues, "Supposing that a marked variety occurs in a wild species, there is, first of all, a considerable chance against its reaching maturity; secondly, there is a considerable chance against its finding a mate; thirdly, the hereditary influences on both sides are against the perpetuation of the variety. These appear to be more potent causes of the comparative fixity of colours in wild animals than the unfitness of the varieties to live." It has already been pointed out that the "marked variety" is of little importance for natural selection as compared with the individual difference. But if the objections urged were valid there would appear to be little chance of a "marked variety" existing in any numbers and persisting from generation to generation, side by side with the normal form: and yet numbers do persist. As to the first of the alleged objections, the chances are against *every* individual, but not equally so, if there be anything in natural selection. So far from this objection being valid, it is but the expression of a fact upon which natural selection rests, the fact that many more individuals of every species are born into the world than can by any possibility survive. Were this not so all selection would cease. The second difficulty certainly does not apply to minute individual differences which occur in vast numbers. To take the simplest case, let us suppose that the individuals of a species are divided, as regards any character, into two equal groups—the one above, the other below the mean. It is clear that each individual would stand as good a chance of mating within the limits of its own group as within those of the other. The third objection does not appear to me to hold in the case of "marked varieties" any more than with individual differences. The total hereditary influence of the varying side, allowing even considerable force for atavism, is certainly in favour of the variation. Furthermore, experience shows us that among the offspring will be some that vary even further than their parent. Those

who accept the Darwinian principle do not expect heredity to achieve more than this—to offer the materials which can be accumulated by natural selection.

Interesting as is the study of such "marked variations" and the statistics of their occurrence in nature, the great principle of natural selection, whether applied to the evolution of animal colouring or to any other character, is not greatly affected thereby, but rather demands such exact numerical investigations as those published by Galton upon man, by Wallace upon various animals, by Weldon upon *Crangon*, and by Lloyd Morgan upon bats.

Another objection to the natural selection argument is given on p. 25, and it too turns on the author's conception of the mode in which this principle operates. Recapitulating Weismann's argument that longitudinal stripes have been replaced by oblique ones in certain larvæ, on account of the more perfect concealment afforded by the latter, he points out that some species "have, on the contrary, remained at a stage of coloration which is, *ex hypothesi*, disadvantageous." The longitudinal striping was never disadvantageous, but only relatively less advantageous, in certain species, and under certain conditions. The failure of a species to take this line of evolution may have been due to many causes, the development of other modes of defence, the nature of its peculiar environment, or may be solely due to the kind of selection exercised by its foes.

The author sees far-reaching conclusions against the principle of natural selection in the admission that pigment as a cause of colour was originally non-significant, and is so still in many cases (colours of certain lower forms, colours of blood, fat, &c.). He argues (pp. 68-70) that as colour did not arise by natural selection, it must be a normal product of the organization, and its disappearance in cave-dwelling forms cannot be due to the cessation of selection, but must follow as the direct effect of surroundings, although he does not even hint at the mode in which such effects are supposed to be wrought. But these conclusions are by no means warranted by the original admission. The first appearance of pigment in the skin of the ancestor of a group of species which are now coloured was certainly a normal product of the organization; but the fact that this variation subsequently spread over all the individuals of the ancestral species, and of those to which it gave rise, will be claimed by Darwinians as the result of selection. And so strong are the tendencies of variation in other directions that partially or completely albino races can be produced by man in a relatively short period of time, while such individuals are far from uncommon in nature in spite of selection. The facts support the opposite conclusion that the absence of colour from the skin would be the normal result of organization for the average individual, were it not for the strong and continuous action of selection. There are other instances of the disappearance of colour in addition to that which has occurred in caves, and in some of these the conclusion appears inevitable. The whiteness of birds' eggs laid in dark holes certainly cannot be traced to the direct action of surroundings, any more than the colour of eggs laid in open nests; and natural selection being prevented by man, the colour is disappearing from the eggs of the domestic fowl, just as it is lost in other species when prevented by darkness.

It is certainly true that colour "must be there before it can be acted upon, and modified in this or that direction according to the needs of the animal." But this objection, which has been familiar since the earliest days of natural selection, is less formidable than it appears to be. Colour must have been present in the skin of some individual ancestor certainly, but its *existence*, as well as its modification, in the normal individual of the species is to be explained by selection.

It is hardly necessary to point out that this argument does not apply to colours which still remain non-significant and are excluded from selection; but these are precisely the colours which are unaffected by the changes of environment alluded to above; the blood of cave-dwelling vertebrates remains red like that of others; the yolk of eggs laid in holes does not differ in appearance from that of those laid in open nests.

A similar argument as to seasonal change of colour in arctic animals may be answered in the same manner.

The author's difficulties appear to arise in part from his inadequate conceptions of the struggle for existence. Speaking of certain night-feeding caterpillars, he says (p 102): "It may be suggested that they prefer to feed early in the evening, when their colours, if conspicuous, would be readily seen. If this is so, it does not much matter, for the birds would—the bulk of them at any rate—have gone to roost." Or speaking of *Mimnonectes*, an Amphipod crustacean which bears a remarkable likeness to a *Medusa* well defended by stings, he objects to attribute any significance to so wonderful and detailed a superficial resemblance, because "a school of whales or a shoal of pelagic fish, rushing through the water and devouring all before them, could hardly be supposed to stop and analyze carefully the advantages or disadvantages of selecting or rejecting a given animal as food." On p. 115 he remarks: "If Mr. Poulton is right in assigning a protective value to the bright-coloured wings of butterflies, 'as a conspicuous mark easily seized by an enemy, and yet readily tearing without much injury to the insect,' it seems unnecessary to pay much attention to the supposed utility of protective colours, such as are shown by the *Kallima* or the Green Hairstreak."

The author scoffs at natural selection as an "easy" road to an explanation, as "the very simple hypothesis of a need for resemblance to the environment": it may at any rate be maintained that this method of meeting it is very far from profound.

It is only possible to give a very brief account of the causes which the author would propose to substitute for natural selection. The merits of each proposal lie in its application, and the consideration of this means a discussion of each particular case.

In support of the "effects of food upon colour," a number of examples are quoted, many of which are so inherently improbable and so imperfectly supported by details, that it is impossible to accept them as evidence. I am very far from disputing that changes of colour may be directly produced by certain foods, although the significance of such changes in the evolution of animal colouring is a very different matter. When the author proceeds to

apply this principle he falls into errors which a little consideration would have avoided. Thus, on p. 21, the following sentence occurs:—"Seeing that pigment has been proved in so many cases to be alterable by changes in the food, it is not surprising to find that as a rule the colours of larvæ are totally different from those of the adult form;" implying that the difference of diet accounts for the difference of colour,—a conviction stated even more strongly on the next page. It is quite sufficient answer to this hasty conclusion to point out that the colours of the imago are just as dependent on the larval food as the larval colours themselves, and that they have made their appearance long before the imago has had the opportunity of feeding. Again, in speaking of the "strong superficial likeness" of the Drone-fly (*Eristalis tenax*) to a bee, the author hints at likeness of food as a possible explanation (p. 232). "It is an interesting fact, in connection with the resemblance between this fly and a hive bee, that it feeds upon pollen and honey. This fact *may* have some significance in relation to the effects of food upon form and coloration." But the form and coloration of *Eristalis* depend upon the food absorbed by its "rat-tailed" larva, living in putrid mud, under conditions utterly unlike those of the larval bee.

Under the consideration of light as a cause of colour an extremely bad piece of reasoning is adopted from Werneburg (p. 62), who argues that light has an important influence on the formation of pigment during the pupal period. By selecting favourable instances and describing them with an enthusiasm which borders on inaccuracy (*e.g.*, speaking of *U. sambucaria* as "bright yellow") and by neglecting all others, he makes it appear that there is something to be said for this view.

In the section on "Variable Protective Resemblance in Chrysalids," the results of recent work are given very inaccurately; the golden colour of pupæ is explained as due to "thin films of air or some gas," and it is even suggested that "intense light may cause some gas to be given off in greater abundance." But it was shown years ago that the appearance is due to some lowly refractile liquid, and, in fact, alcohol answers the purpose very well indeed. Gases do not appear to have the power of entering the intervals between the cuticular lamellæ, perhaps because the latter come together and obliterate the chinks on the evaporation of the fluid. Again, it is stated that "the pupa was also made to assume a light colour upon one half and a dark colour upon the other." As a matter of fact the invariable failure of the pupa to do this formed the basis of some of the principal conclusions reached. It was also surely unnecessary to quote an ignorant assumption of Eimer's on the subject—an assumption which was not even original, and has been disposed of long ago.

In favour of the effects of climate reliance is placed on Scudder's conclusion that melanism is only found in the butterflies south of New York, albinism only to the north (p. 55). And yet in Europe melanism is especially prevalent among the northern moths, from which we may infer that the American observations, however they are to be explained, are not direct effects of climate.

He suggests that the blackness of a lizard on one of the Canaries may be due to moisture; but these islands are about as dry as small oceanic islands can be. All the lizards seen by the present writer in Teneriffe and Grand Canary, some three or four species, were dark in colour and harmonized with the tint of the dark dry volcanic rocks on which they were seen, and among which they almost invariably escaped when pursued.

One suggestion is very remarkable. After giving reasons why he does not consider that the resemblance of *Volucella* to humble-bees, &c., is to be explained as a case of aggressive mimicry, the author suggests (p. 228), "If wasps and bees have the same unintelligible liking for keeping pets that another group of Hymenoptera—the ants—have, the whole series of facts may prove to have a very different meaning, but one which is not quite in accord with the theory of mimicry on the part of the *Volucella*." The keeping of pets by ants is so very far from being unintelligible in some of the most important cases (*Aphides*, Lycænid larvæ, &c.) that we may fairly expect an explanation in other instances. But even if the author's suggestion were valid it would still fail to account for the very point at issue—the great superficial resemblance of *Volucella* to Hymenoptera.

On p. 92 he is quite prepared entirely to dispose of all advantages in the struggle for existence in favour of fertility; this alone is enough to prevent extermination. Speaking of the wonderful disguise of Geometer larvæ (and if this be not the result of selection it must be admitted that the principle fails indeed) he says, "In the meantime the excessive fertility of the parent moths appears to be a sufficient guarantee against extinction, apart from any subsidiary advantage to be gained by colour protection." It is sufficient reply to this statement to point out that the fertility of these small-bodied moths is very far from excessive when judged from an insect standard; that if the larvæ are offered to any insect-eating animals they are when detected, devoured with the greatest avidity, but that if offered motionless on their natural food-plant they are often passed over; that insect-eating animals, especially when r earing their young, are by no means fed to repletion, so as deliberately to refuse the food they evidently relish.

It is very confusing after this candid avowal to read a few pages further on (p. 97), "On the whole, it seems more profitable to a caterpillar to adopt protective resemblance to its surroundings as a means of escaping its foes; at any rate, this is what actually occurs. 'The main purpose in life of a caterpillar,' says Mr. Scudder, 'next to feeding, is *not to be seen*.'"

Many quite irresponsible suggestions, which it would have been wiser to have withheld unless accompanied by at least some evidence, are made or adopted from other writers. Of this nature are the remarks of Leydig on the colours of *Helix nemoralis*, and the author's suggestion that the dark variety of the female Silver-washed Fritillary may be due to the moisture of wooded districts.

Of some of the author's suggestions we may use his own words, and say, "This explanation has an air of reasonableness, which might lead to the inference that it had been amply tested by actual experiment" (p. 64). Others however, including some which have been quoted here, certainly appear to lack this "air of reasonableness."

The author is especially candid and straightforward in bringing forward the evidence in favour of an explanation he is about to attack. After thus fairly showing the strength of the opposed position, he proceeds to reject it for reasons which will strike the instructed and uninstructed reader alike as singularly inadequate. Examples of this method occur continually throughout the volume. As an example may be selected his treatment of the opinion that the light of phosphorescent organs enables certain deep-sea animals to see. He admits the existence of eyes, the prevalence of phosphorescence, the intensity of the light emitted, the existence of "lens-like transparent bodies serving to concentrate the rays of light," the fitness of the light to illuminate the prevalent colours. In spite of all these facts the author believes that all deep-sea colours are unseen and meaningless for the following remarkable reason:—"The presence of well-developed eyes, or the total absence of these structures, are, as has been explained, intelligible on the theory of abyssal light; not so the existence of eyes in an intermediate condition. The inevitable conclusion, therefore, from these facts appears to be that the brilliant and varied coloration of deep sea animals is totally devoid of meaning; they cannot be of advantage for protective purposes, or as warning colours, for the simple and sufficient reason that they are not seen" (p. 37). The author carries this conclusion to its logical end, and, pointing to the resemblance of deep-sea forms to their shallow-water allies, and the existence of protective resemblances in both, he maintains that "if natural selection has been the cause in the one case, it ought to be in the other. . . . . The question therefore is pressing: need natural selection be responsible for the coloration of the shallow-water forms?" (p. 38). A somewhat large conclusion to base on the fact that the eyes of certain deep-sea animals are in process of degeneration! The author admits that the *absence* of eyes is no argument for his views; and yet, in every such instance, a gradual process of degeneration has been passed through. He gives us no reasons for rejecting the opinion that the cases upon which he bases such startling conclusions are merely tending in the same direction; indeed, elsewhere (p. 11) he insists on the probability that such biological changes are still progressing. It is indeed most probable that light is far from widespread or intense on the floor of the ocean, and that, therefore, eyes to be of use must be unusually efficient, while, unless absolutely necessary, they are likely to disappear. We meet, in fact, with a case somewhat parallel to that of beetles on oceanic islands in tempestuous zones, where selection operates in opposite directions—towards unusual powers of flight, when flight is a necessity, and towards the total loss of any such capacity when it is unnecessary. Thus, among deep-sea fish we find eyes of immense relative size, as well as those which are degenerate. And the phosphorescent organs of certain fish (*Ceratias*) appear to emit a light which is invisible to the degenerate eyes of the possessor, but serves to attract other and better endowed fish upon which the *Ceratias* feeds. The frequency of this degeneration among the deep-sea Crustacea, which impressed the writer so profoundly, may very probably be due to conditions of life which render vision less necessary for them than for many other groups, and this is especially probable since many shallow-water genera are sightless, as is abundantly shown in the book itself (p. 36).

On pages 115, 116, the author adopts Prof. Weldon's objection to the usually received interpretation of the whiteness of certain eggs, and the under-sides of fish, porpoises, &c., which are seen from below, on the ground that snow-flakes appear almost black when seen from beneath against the bright sky. The original suggestion is due to neither Mr. Wallace nor to the present writer, but to Erasmus Darwin, writing very nearly one hundred years ago. The objection entirely misunderstands the hypothesis, at any rate so far as the eggs are concerned. If an egg, lay exactly over one of the interstices in the nest, it would, of course, shut out the sky altogether, and when viewed from some distance through the opening would appear dark like the nest itself. There would be no question of its appearing against a back-ground of sky. As a matter of fact, no such continuous back-ground can be seen through the nest at all. Minute bright points are seen through the interstices of the nest, and those of the leaves and branches above and below it. The hypothesis in question suggests that part of the bright white side of an egg, viewed obliquely from below through an interstice, may be mistaken for one of these bright points. The hypothesis may be erroneous, but it is not to be set on one side by a criticism which fails to understand it. In the case of the fish, the question is complicated by the absorption of light by the layer of water.

The reader who finds that the above-quoted criticism is held to be destructive by the author, may be excused strong language when he meets with the following sentence only seven pages further on:—"Among pelagic fish it is common to find the upper surface dark-coloured and the lower surface white, so that the animal is inconspicuous when seen either from above or below."

The chapter on Warning Coloration is one of the most valuable parts of the book, for in it we meet with a solid contribution to the subject in the form of some interesting experiments conducted by the author upon the animals in the Zoological Gardens. Many of the results are of extreme interest, and are a further proof of the difficulty of the investigation, and the great care with which it must be conducted if the conclusions are to be depended upon. It has been already suggested that some of the results may be perhaps explained by the fact that the insect-eating animals chosen for experiment are restricted to a very monotonous or very scarce insect diet. In some rather extensive experiments made by the present writer upon a marmoset, it appeared that the animal possesses a most keen appreciation of the meaning of warning characters, but the individual in question was accustomed to be fed on a very varied diet. The discussion of the details given in this chapter cannot now be attempted, but it may be safely affirmed that there is nothing which is fatal to the theory of warning colours, when we admit, as we are of course bound to do, that even unpalatable animals have their special enemies, and that the enemies of palatable animals are not indefinitely numerous.

Further criticism of the arguments is rendered impossible on the present occasion by the exigencies of space. Certain obvious misstatements call for correction, such as

the description of the jet black larva of the Peacock Butterfly as "dusky greenish" (p. 21), the assertion that the present writer discovered uric acid in the excreta of Vanessid imagos (p. 41), the implication that leaf-mining larvæ eat only the deeper tissues of the leaf instead of everything between the upper and lower cuticle (p. 63), the description of "red eye-like markings upon the blue underwings" of the Eyed Hawk Moth (p. 134), in which red and blue should of course be transposed.

The book is well printed, misprints such as "Tortorix" for "Tortrix" (83), "freshly-moulded" for "freshly-moulted" (67), "distinction" for "distinctive" (185) being fortunately uncommon.

The coloured plates are good, although it would have been a pleasure to see the wings of one of the resting *Volucellæ* in Plate IV. folded one over the other in a very characteristic attitude. The antennæ of the *Kallima* shown at rest in Plate II. would have been concealed, and the same applies to the figures of the Buff-tip and Lappet Moths. The worst figure is that of the Bee Hawk Moth on p. 245, in which an entirely wrong notion of the opaque border to the wings is conveyed. The source of the figures is not mentioned.

EDWARD B. POULTON.

SUNSHINE.

Sunshine. By Amy Johnson, L.L.A. (London Macmillan and Co., and New York, 1892.)

THIS book is likely to puzzle any one who may by chance pick it up and glance casually over the pages, more especially if he should happen to first open it towards the end and find two chapters headed "Tommy's Dream," concluding with a conversational account of how "the nurse puts baby into a bath, generally too hot or too cold, and scrubs away as if he were a wooden doll. Poor baby's skin is red all over, and he screams with pain," &c. On the other hand, in the early part of the book, several familiar figures, such as pictures of ice flowers, or diagrams of the action of simple lenses, of total reflection, of the rainbow, &c., show that "Sunshine" is, in spite of the nursery episode, in reality connected with physical science. As a matter of fact the authoress has taken a number of easy experiments and every-day observations, and has amplified and explained them in a simple and often very charming manner, adopting for the purpose the conversational form as between herself, called teacher, and, judging by the number of Christian names of the children addressed, a host of youngsters.

The conversational style is out of fashion just now, but no objection can be taken on that account. What is of far more importance is the general effect produced upon the mind of the child. The writer of this notice well remembers how the attempt was made to beguile him into being interested in conversations between a horridly precocious child Willie and his papa. Willie always said the right thing, and always made the right mistakes, so that much instruction was to be gathered from the answers and corrections of his papa. The writer, no doubt, did acquire some general information; perhaps he did not resent the attempted deception, but he is sure that he would like to have punched Willie's head, or to have made him suffer in some way that is pleasing to the boyish imagination. In the present instance the risk of arousing open hostility on the part of children who may receive instruction from the pages of "Sunshine" is largely reduced by the fact that the conversation is very one-sided; the children are made to say very little in these talks—they are not quite lectures, but more lectures than conversations. Whether "teacher" says too much, or in the attempt to appeal to the imagination rather than the reasoning faculties of her audience rambles too far afield, is a question of taste. Many parts of the book demand the highest praise, though in some the authoress seems to have gone beyond reasonable bounds. For instance, after a most clear and excellent illustration of the method by which the distance of the moon from the earth is determined, in which the children are made to find by folding paper how far it is from the table to a ball hanging up in the room, the imagination of the reader is stimulated as follows:—

"At the beginning of our 'talk' about the moon, I tried to impress upon you what old travellers you were. Do you remember how far you have been each year? (585,000,000 miles.) And you, Tom, are——?" "Seven." "What age are you, Percy?" "Eight." "And you, Minnie?" "Nearly eight." "You shall work that sum out for me on your slates. We will neglect the travelling since last birthday. Multiply 585,000,000 by 8, Percy. Four thousand six hundred and eighty millions of miles, you say. Have you felt any pain or sickness? Are you willing then to accompany me for a little 'out' to call on our next neighbour, the moon? It is only 240,000 miles, and would take us a little over three hours and a half at earth's usual rate of travelling. Do you think your mothers would trust you with me if I guaranteed to bring you safely back again? Most of you say 'Yes.' What is it that Ethel is saying to you, Lucy?" "She wants to know if we are really going, or if it's 'only pretending.'" "That is a question which Ethel must decide for herself. Those who are going with us must be ready in time, or they will be left behind. Before we make a journey it is usual to consider, not merely the distance, but a few other matters also, such as—'What to take with us,' 'How long we shall be away,' 'Where we can get lodgings,' 'Whether we should take shawls, umbrellas, &c.,' and so many other considerations, that I am afraid we can't go to-day. Make all inquiries at home, and let me know how many of you are prepared to go."

As has been stated, the imagination rather than the reason is being constantly appealed to, and for the purpose the most picturesque language is employed. Perhaps the most striking example is to be found in a chapter headed, "The Mill with Stained Glass Windows." A beam of sunlight is made to pass through a condenser and into a slit. Then slips of coloured glass, red, green, and violet, are placed edge to edge over the slit, and the red-green-violet line of light is looked at through a scratch in a piece of smoked glass. The resulting diffraction phenomenon is the mill with stained glass windows. The upper story with violet windows has a greater number closer together than the second story with the green windows, and there is the same difference between this