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'Notes on the colors of West Coast mammals.'

In considering problems in the domain of evolution, it is necessary to recognize the frequently slighted fact that natural selection is never creative, but simply selective in its workings. Every modification in an organism must have some more fundamental factor to originate it, upon which natural selection may subsequently act. Whether we recognize with Spencer the Lamarckian factors of use and disuse, or follow Weismann and Wallace in excluding the inheritance of acquired characters, we must agree in positing individual, and what, for lack of a more significant name, has been called fortuitous variation, as propensities of organic beings, without which natural selection would be impossible. But it still remains to be accounted for why the tendency to vary is directed along definite lines, and the answers commonly given to this question seem insufficient to explain it.

Taking a concrete example of this from west coast mammals, the black-headed ground squirrel of Lower California (*Spermophilus grammurus atricapillus*) belongs to the same group as *S. grammurus beecheyi*, of central California, into which variety it shades by insensible gradations. It is distinguished from the latter roughly by the darker color of the back, especially of the anterior parts, which in typical specimens are black. From characteristic localities the black is very constant, and so strongly marked as to make a strikingly distinct species were there no intergradations in other regions. Now some shade of brown or gray was in all probability the original color of this species, judging both from the fact that these colors are naturally more primitive than black, that the black races are more local than the lighter ones, and that the young are much paler than the adult. It then becomes proper to ask how this black color has been derived.

Mr. Walter E. Bryant, who discovered the race, says that it is

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usually found in a region of black volcanic rock, so that its colors have been assumed for protective reasons, in order to conform with the general color of its environment. The explanation seems perfectly simple—individual variation upon which natural selection has worked; or rather, as Lloyd Morgan has well shown,* natural elimination. But it must again be asked: what has directed the variation along a certain line? This question has been well discussed in a recent book by Schurman, entitled the "Ethical Import of Darwinism," and I think that any who may peruse its pages will admit its force. Suppose we have a mixture of light and dark ground squirrels, and the light ones, being more conspicuous by contrast with a dark background, are killed off. Why, then, should even a part of the descendants of those remaining be darker than the darkest of their parents? I am not referring to fortuitous variation which produces "sports," the characters of which may be inherited and produce a new species, but to that comparatively slight individual variation which is always present. We can well understand how a particular kind of food might possibly influence a color, but this color would not, except by the merest accident, bear any relation to the color of the environment, and consequently could not result in a protectively marked race. The whole subject reduces itself to this: Is it possible for any character, however slight it may be, not produced by use and disuse or the direct action of environment, and which was not present in some ancestor, either near or remote, to appear in an offspring?

In the case of our Lower Californian ground squirrel, it may be assumed, what there is every reason to believe is the case, that its ancestors from remote times have been some shade of brown or gray, but never black. Use and disuse is, of course, entirely out of the question in regard to color, while it is evident that no possible direct action of the environment, either food or climate, could produce black. Where then did the black come from? In an article on the Factors of Evolution† Prof. Jos. Le Conte makes a suggestion, which we may find of use in answering this question. He says: "In sexual generation, on the contrary, the characters of two diverse individuals are funded in a common offspring; and

*Animal Life and Intelligence, p. 79.
†Monist, i, p. 323.

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the same continuing through successive generations, it is evident that the inheritance in each individual offspring is infinitely multiple. Now the tendency to variation in offspring is in proportion to the multiplicity of the inheritance; for among the infinite number of slightly different characters, as it were offered for inheritance in every generation, some individuals will inherit more of one and some more of another character. In a word, sexual generation, by multiple inheritance, tends to variation of offspring and thus furnishes material for natural selection." This passage might seem to have a slight teleological flavor, as if this difference in sex were instituted in order that we might have a greater amount of variability, whereas the author simply means to imply, it seems to me, that a greater amount of variability is incident to this difference between the sexes. However, this suggestion of Prof Le Conte's merely shows us how a difference in the sexes may increase the material upon which natural selection may work, but does not show how new material may be created. Just here it is of importance to take note of two of the laws of heredity as stated by Haeckel:* "A third law of conservative transmission may be called the law of sexual transmission, according to which each sex transmits to the descendants of the same sex peculiarities which are not inherited by the descendants of the other sex. * * * A fourth law of transmission, which has here to be mentioned, in a certain sense contradicts the last, and limits it, viz: the law of mixed or mutual (amphigonous) transmission. This law tells us that every organic individual produced in a sexual way receives qualities from both parents, from the father as well as from the mother."

In examining the series of *Spermophilus grammurus atricapillus* it is found that there is quite a well marked average difference between the sexes in regard to color, the males being so much darker than the females that I was enabled to separate the specimens of the two sexes, making but one error, when a very dark female was placed in the series with the males. It is now necessary, before continuing, to call attention to one more fact, stated by Geddes & Thomson,† that: "A review of the animal kingdom, or a perusal of Darwin's pages will amply confirm the conclusion that on an

*History of Creation, i, pp. 209-210.
†Evolution of Sex, p. 15.

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average the females incline to passivity, the males to activity." This katabolic condition of the male in contradistiction to the anabolic state of the female, has been used by Wallace to explain the bright colors of male birds, and while it does not seem to me that we are justified in following him to the extent of excluding sexual selection, a fair consideration of his arguments seems to show that this excess of vitality in the male has at least furnished the material upon which sexual selection may act.

And now to return to our spermophiles once more. It has been seen that according to one of the laws of heredity there is always more or less difference between the sexes. In the case in point this difference manifests itself, among other ways, in the tendency on the part of the male to be slightly darker than the female, which may be explained by the katabolic state of the male inducing a surplus of energy which is expended in a darker pigment. Accordingly, however dark the female may average, we may expect the male to maintain a tolerably constant ratio of shade to the female. In order to facilitate the explanation, suppose that a certain amount of black has been introduced and see if it can be understood how it could be added to. Owing to the katabolism of the male the ratio between the shades of the two sexes will maintain an average constancy. Suppose, in the evolution of the race, it has reached a point where the color is brindled, a mixture of black, brown and white, but in which the dark colors are in the ascendant. Something like the following proportions of color would then exist in a fairly typical pair:

	MALE.	FEMALE.
Brown…………………..	10	20
Black……………………	60	40
White……………………	30	40

According to Haeckel's law of mixed or mutual transmission, and more important still, according to many observed cases, a combination of all the characters of the two sexes may produce an average between them. And it is perfectly reasonable to suppose in the case in point, that out of a large number of pairs possessing the average proportion of colors given in the table above, a few of the female offspring would be found to possess a medium between the colors of the two sexes of their parents. In these females the proportion of colors would be about as follows: Brown 15, black 50, and white 35. These darker females being more in harmony with

their environment would escape destruction, while those in whom the lighter colors preponderated would naturally be eliminated. Moreover these darker females would naturally pair with the darker males, there being many facts to indicate that, other things being equal, like mates with like. The paler males also would be eliminated so that there would be more dark males to choose from. It is at any rate not unreasonable to suppose that these darker females would pair with mates at least not paler than the average shade of the male. This would give us a generation in which the proportions would be something like the following:

	MALES.	FEMALES.
Brown………………..	10	15
Black…………………	60	50
White………………..	30	35

In other words, the tendency of natural selection would be, if no other factor were at work, to make the female approach the color of the male, for the females which did come the nearest to the shade of the male would be the best protected and consequently survive. But the fact must not be lost sight of that the katabolism of the male in this species induces it to expend its surplus energy in an excess of pigment over that of the female. There would thus be a tendency to maintain the average proportion between the two sexes. Therefore, other things being equal, the average color of the males of the third generation would be shown as follows:

	1st GENERATION.				MALE OF		FEMALE OF
	MALE.		FEMALE.		3D GENERATION.		2D GENERATION.
Brown	10	:	20	::	x	:	15
Black	60	:	40	::	x	:	50
White	30	:	40	::	x	:	35

In which case the average male of the third generation would have colors in the proportion of brown 7.5, black 75, and white 26.25, which shows a great increase in the proportion of black. Of course, owing to the great number and complexity of the limiting and modifying conditions in a state of nature no such rapid change in color would be possible, but on the contrary the change would be infinitely gradual. All I have attempted to show is that when the male takes the lead in a variation, if it be a modification which is of equal use to both sexes, there will be a tendency for the female to follow the male, but, in following its mate, owing to the difference in metabolism between the two sexes, to keep pushing it in advance

along the line of greatest advantage to the species. This tendency might be termed the Law of Sexual Intensification. It can by no means be considered a universal law, but it might be found useful in explaining more fully many cases of bright or dark colors in birds and mammals. And the cases to which it would apply would not be simply those in which the male was more intensely colored than the female. There must be a limit to the development of every color—a point at which it reaches its maximum of intensity. When the male has reached this goal, if the color be of general utility to the species, the tendency of the characters of one sex to cross over to the other will in time cause the female to assume a color identical with that of her mate.

The black hare (*Lepus insularis*) found by Mr. Bryant on Espiritu Santo bland, in the Gulf of California, is a case very similar to the one above considered. Mr. Bryant says that it also is found in a region of black volcanic rock where its colors are completely protective, and that the only time when specimens could be secured was when they came down on the light sand of the shore where they were very conspicuous. In this animal, however, the evolution is very complete. Being an insular form it has been completely isolated, and the black has extended over the entire upper parts of the body. In the small series available for examination there is no appreciable difference between the sexes, and it is probable that the female has overtaken the male as previously explained.

On the sandy mainland and adjacent sandy islands, a very pale form of Lepus occurs, which may in the light of more ample material be found to be a separate variety. This suggests the question of how to account for the paler forms of the genus, for a law of intensification could be of no service in such a case. The direct action of the environment seems to be the most reasonable hypothesis, although of course it would be no longer tenable if the non-inheritance of acquired characters should be proved. Examples of the remarkable bleaching power of sunlight are common. Animals living in a sandy or desert region constantly exposed to the sun's rays would become somewhat bleached. Those individuals which were the most affected, or were affected so that their colors were most in harmony with their environment, would have the greatest chances of survival, and, granting that acquired characters can be inherited, would be the parents of a paler colored race. Thus in

this case, also, natural selection would be the secondary cause, the variations being directed in a certain channel by the immediate action of environment.

Dr. Harrison Allen has published a paper on the "Distribution of Color Marks of the Mammalia,"* in which he attributes many of the markings of mammals to excess of nourishment near the surface in particular areas, and attempts to correlate them with the presence of nerve terminals, masses of muscle, etc. This is an interesting and important line of investigation, and his theory appears to have much plausibility in it, but I am unable to find a single fact in regard to the markings of west coast mammals which lends any particular support to the theory, and it would seem that its applicability should be a very general one if it had any force whatever. That there are some deep-seated mechanical causes at work, however, in the production of many of the characteristic patterns or regions of color marks seems highly probable, to say the least.

There are few groups in the animal kingdom in which brilliant color is so conspicuously absent as among mammals. This fact can be accounted for in two ways: by the greater need for protection incident to a terrestrial life, and by the fact that the majority of mammals are more or less nocturnal in their habits. Brilliant colors would therefore be of no use, but on the contrary would be positively harmful. There is another class of colors to which Wallace has called particular attention, and which are very frequently present among mammals, viz: recognition markings. Mr. J. E. Todd,† apparently without having consulted Wallace on the subject, arrived at about the same theory in regard to this class of colors. He calls them directive colors, and by their aid attempts to account for nearly all the special markings of mammals and birds. It appears to me that both he and Wallace attribute too much to this factor, although it is doubtless of great importance and of wide application. Supposing that natural selection has been the means of producing these recognition marks, it must not be forgotten that here, as in the example first considered, there must be some creative and directive force behind it. But could natural selection have had a hand in bringing about these recognition markings? Wallace,‡ in discussing the

*Proc. Acad. Nat. Sci. Phil., 1888.
†American Naturalist, xxii, 1888, pp. 201-207.
‡Darwinism, p. 218.

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subject, calls attention to the white upturned tail of a rabbit, so conspicuous when the animal is retreating from an enemy. He says:

"For the rabbit is usua1ly a crepuscular animal, feeding soon after sunset or on moonlight nights. When disturbed or alarmed it makes for its burrow, and the white upturned tails of those in front serve as guides and signals to those more remote from home, to the young and the feeble; and thus each following the one or two before it, all are able with the least possible delay to regain a place of comparative safety. The apparent danger, therefore, becomes a most important means of security."

It will be well to inquire right here whether natural selection can ever be socialistic or communistic in its operation. It seems inevitable that only from a teleological point of view can it be conceived as such. If some overlooking power can be imagined doing the selecting, it might be supposed that it would direct matters so that the strong might aid the weak, but this is in direct opposition to the doctrine of the survival of the fittest, which has for its motto: "Each one for himself," etc. The rabbit having the most conspicuous white upturned tail would be individually at a great disadvantage in the struggle for existence, for, while he might be of very material assistance in leading his less conspicuously marked associates out of danger, he would himself be at a positive disadvantage, and the variation, it would seem, could hardly be favored by natural selection. Having no theory to offer in the place of the pre-existing one, I am loath to call attention to this difficulty, but the wonder is that it has so long escaped notice.

There is every reason to suppose that these markings were originated to facilitate the recognition of individuals, but if such is the case it seems to require a new explanation. There are two quite distinct classes of recognition markings, which neither Wallace nor Todd have differentiated. The first class includes those markings which enable individuals of the same species to recognize their fellows and thus escape from a common danger or combine against a common enemy. For these markings we may borrow the name given by Todd for recognition markings in general, viz: directive coloration. The other class includes all markings which enable one species to distinguish its own kind from allied species. These markings might be appropriately called discriminative markings. The validity of this second class is in a large measure dependent

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upon the tenability of the theory of physiological selection, about which scientists have not yet reached any unanimity, fascinating and plausible as it certainly appears. If incipient species are sterile when crossed, then any markings which would enable the individuals readily to distinguish their own kind from the allied form would be an advantage, and it would seem that natural selection would encourage it. We are here stopped again by the question: What if the two incipient species did cross and the result prove to be infertile? Would this be a disadvantage to the individuals concerned, or to the race in general? Clearly to the race and not to the particular individuals. But if this be the case, how could natural selection favor these markings any more than it could the ones previously considered?

There are some interesting examples of recognition markings among west coast mammals, one of the most striking being the antelope squirrel (*Tamias leucurus*), to which Dr. C. Hart Merriam has already called attention.* Following are his words: "The antelope squirrel and its geographical races afford striking illustrations of the exhibition of two principles of color adaptations combined in the same individual. When at rest the animal is seldom seen, its color and markings being in complete harmony with its surroundings, in obedience to the law of *protective* coloration. But the instant it starts to run, the tail is elevated and its conspicuous white under-side is turned towards the observer, forcing itself upon the eye whether on the lookout for it or not." This is clearly a case of directive coloration, and I am at a loss to consider in what other manner this marking could be construed. Any one who has seen a party of these little chipmunks skurrying away across the desert with their white tails elevated must admit that so conspicuous a marking can only be explained as a means for enabling the laggards and stragglers to travel with the main body of the party away from danger. Harris' chipmunk (*Tamias harrisi*) resembles the preceding species very closely, the only conspicuous difference being that it has the under surface of the tail black instead of white. Having never seen this species alive, it is impossible for me to say how conspicuous this black under tail would be in a state of nature, but it certainly cannot be as conspicuous as the white tail. This

*North American Fauna, No. 3, p. 52.

may well be considered as an example of discriminative marking. The two species are found in neighboring districts and without doubt had a common ancestor. If some of the individuals at any time became sexually isolated from the remainder, the differentiation in the color of the under side of the tail, becoming light in one species and dark in the other, would have materially increased the prosperity of both races. Directive coloration might have been brought to bear upon them at a later stage and accentuated the two shades in order to facilitate recognition by their own kind. It must be borne in mind, however, that natural selection seems incapable of having effected these changes, assuming the validity of the theory that they are recognition markings.

Prof. Todd has called attention to other uses to which recognition markings might be put. Most important of these are such markings as enable individuals to recognize one another in the darkness of their dens or by night. Such markings as these would be of practical use in the domestic intercourse between families and in the care of the young. These markings would be in no way of use in escaping from danger or in distinguishing one species from an allied form; and indeed differ so much in their use from those which have been previously considered as to warrant their being made a separate class, which might appropriately be called socialistic markings. Prof. Todd mentions a number of examples of this class, including among others the skunk, which properly belongs in another division which will be considered later. The markings on the head of the yellow-bellied marmot (*Arctomys flaviventer*) consisting of a white ring around the muzzle, in distinct contrast to the ground color, would serve to indicate in the dark the position of the head, which would be a great advantage in the social life of the animal in its burrow. The black and white patches on the head and the rings on the tail of the racoon (*Procyon lotor*) would serve the same purpose of recognition in the dark, as would also the conspicuous white spot above the eye and the long, ringed tail of the civet cat (*Bassaris astuta*).

Whether or not the lateral and dorsal streaks of *Tamias* and *Sciurus* can be accounted for in the same manner cannot be answered with as much confidence.

It seems difficult to account for the conspicuous black lateral streak of *Sciurus hudsonius douglassi* in any way except as a recognition marking, possibly to mark the position of the body, but why it should

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be of more use in this species than in *Sciurus fossor*, for instance, is not easy to understand. There is another and more serious difficulty in the way of thus explaining it. Mr. J. A. Allen has shown in his article "Seasonal Variations in Color in *Sciurus hudsonius*,"* that the black stripe in this species becomes indistinct or obliterated in winter pelage, and the same is in all probability the case with the variety in question. Whether the black streak were of use as a recognition marking or as a sexual mark it would be of greatest importance during the breeding season at which time it is wanting.

There are many markings in this group which are difficult to explain. Thus, *Sciurus fossor*, of the Sierra Nevada Mountains, and *S. fossor nigripes*, of the Coast Range, are not strikingly different, except that in the latter the hind feet are darker than the back (apparently at all seasons either black or dark brownish), while in the former the feet are lighter than the back (silvery or whitish gray). What influence could have produced this modification is not easily seen, for it could hardly have any utility as a recognition mark, nor could it have been produced by the direct action of the environment.

In the genus *Tamias* we have, as Mr. Allen has observed,† a striking example of a plastic group which has spread from a common center in comparatively recent times, and rapidly differentiated. There can be little doubt that the streaks so characteristic of the group are of some utility, for otherwise natural selection would have a tendency to obliterate them. In a few forms this has been done, possibly for protection in open districts. The most obvious use of these markings, it would seem, would be for recognition in the darkness of the burrow, in which situation they would greatly facilitate in locating the position of the body of one individual to its mate. In forms in which the streaking has attained the maximum of intensity a broad white line on each side is bordered by black, which relieves it so well that in the dark all that is visible of the animal is the white stripe down each side of the back. The white patch on the back of the ear might also facilitate recognition in the dark, and be classed with the socialistic markings. In accounting for the great number of variations in the group, Dr. Allen says:‡ "From

*Bull. Am. Mus. Nat. Hist., iii, No. 1, pp. 41-44.
†Bull. Am. Mus. Nat. Hist., iii, No. I, pp. 45-116.
‡l. c., p. 53.

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the extreme susceptibility of this plastic group to the influences of environment, it is one of the most instructive and fascinating groups among North American mammals. * * * * Probably a more striking illustration of evolution by environment cannot be cited." Certain it is, that in the Eastern States, where the physiographic conditions are tolerably uniform, the species remains constant, while in the west (particularly in California) where there is much physiographic diversity, we find an extraordinary number of forms. It is very doubtful, however, that the direct action of the environment has produced all, or even a large part of these changes. As long as a correlation can be established between light varieties with dry districts and dark varieties with rainy districts, it seems perfectly reasonable to suppose that the changes have been effected directly by the environment; but in a large number of cases such a correlation does not appear to exist; in which event the change must be attributed to the indirect effect of environment. When the species first began to migrate from its primitive home it would find itself placed in many different situations. Wherever the character of the country was materially different from its previous abode, a change in food and to some extent in habits, occurred. This would have a tendency to modify the color in various ways. For example: if the animal lived in a cold or rainy climate it would be confined to its burrow a comparatively large portion of the time, and any intensification of the socialistic markings would be of great advantage. If, on the contrary, it lived in a warm, sunny region, it would be in the open air a large portion of the time, and protective coloration would be of greatest utility to the species, in which event the streaks would tend to become obscure or obliterated. This is merely an instance of the many ways in which environment might act indirectly. Having thus produced two races in adjacent regions, let us suppose that from some reason (persistence of bad weather, for example) one form migrates into the territory of the other. Difference in food, etc., granting the truth of the theory of physiological selection, have made the two races sterile when crossed, so that any accentuation of the slight differences already produced would favor the prosperity of both races. Accordingly, the markings originally of use as socialistic marks would become discriminative. Thus it is seen how complex the factors may be which operate in the production of even trivial changes. Simple explanations, in which a single factor is

made to explain all, are very alluring, but are apt to be superficial from their very simplicity.

The skunks were excluded from the class of animals having colors for purposes of recognition. True the marked contrast of black and white is decidedly conspicuous. In the dark, particularly, they are the most conspicuous colors which could be devised; but note the very radical difference in their use from any recognition markings. Recognition markings are of use, not to the ones possessing them, but to their fellows; the markings of the skunk are of use to the individual as a warning for other animals to avoid it.

A large number of our mammals have colors probably not very different from their primitive hue. Wallace has shown that color is a normal product of organization. He says:* “If we consider that in order to produce white all the rays which fall upon an object must be reflected in nearly the same proportions as they exist in solar light—whereas, if rays of any one or more kinds are absorbed or neutralized, the resultant reflected light will be colored; and that this color may be infinitely varied according to the proportions in which different rays are reflected or absorbed—we should expect that white would be, as it really is, comparatively rare and exceptional in nature.” “Now the various brown, earthy, ashy, and other neutral tints are those which would be most easily produced, because they are due to an irregular mixture of many kinds of rays.”† It is these neutral tints which are predominant among mammals, and in many cases they would seem to require no further explanation. Color does not seem to enter into the life of our smaller rodents, or of bats, for instance. Being nocturnal in their habits their sense of sight has probably but little capacity to distinguish between different colors, and their habits are such that no very accurate protective shades are required, other than some dull neutral tint. Certain species which may sometimes move about on the desert by day, as *Dipodomys*, assume a color on the back almost identical with the sand, and with a white superciliary stripe for a recognition mark, but such forms are the exception rather than the rule. It seems highly probable that the absence of conspicuous colors among mammals as a class is to be explained by the lack of

*Natural Selection, new ed., p. 359.
†l. c., pp. 300-361.

development in them of the color sense. Sexual selection would then be directed in other channels, while the colors would be left either neutral or of some practical utility—either for protection, recognition or warning—but would seldom have any aesthetic significance as among birds.

The following classification of the colors of mammals follows mainly that of Poulton,* which has the merit of being natural and simple, grouping them according to their uses:

I. APTETIC COLORS (deceitful).
  1. Cryptic colors—Protective and aggressive resemblance.
    a. General protective resemblance.
    b. General aggressive resemblance.

II. SEMATIC COLORS—Warning and signalling.
  1. Aposematic colors—Warning colors.
  2. Episematic colors—Recognition marks.
    a. Directive.
    b. Discriminative.
    c. Socialistic.

The Mammals of the Pacific Coast may be roughly classified under the above headings, as follows:

GENERAL PROTECTIVE RESEMBLANCE. By far the largest class including all the neutral colored species, as the bats, most rodents, etc., and such as harmonize with unusual surroundings, as *Lepus insularis* and *Spermophilus grammurus atricapillus*.

GENERAL AGRESSIVE RESEMBLANCE. The *Felidæ, Canis latrans*, etc.

WARNING COLORS. *Mephitis* and *Spilogale*.

DIRECTIVE RECOGNITION MARKS. *Tamias leucurus, Lupus sylvaticus, Antilocapra americana.*

DISCRIMINATIVE RECOGNITION MARKS. Many species of *Tamias* probably; black wedge of *Spermophilus grammurus douglassii*, possibly, and many other related species inhabiting adjacent territory.

SOCIALISTIC RECOGNITION MARKS. *Arctomys flaviventer, Tamias, Sciurus?, Procyon lotor, Bassaris astuta.*

*The Colors of Animals, 338.