

THE ANALYSIS OF A CONCRETE CASE OF INTERGRADATION  
BETWEEN TWO SUBSPECIES<sup>1</sup>

BY FRANCIS B. SUMNER

SCRIPPS INSTITUTION OF OCEANOGRAPHY OF THE UNIVERSITY OF CALIFORNIA

Communicated January 5, 1929

The subdivisions of a species which are known as subspecies or geographic races commonly occupy distinct but adjoining territories, and intergrade with one another along a zone of varying width, lying between these. It may be assumed that two contiguous races of this sort are commonly very closely related to one another, as compared with any two species taken at random. In cases where one of these related forms occupies a much larger and more typical land area than the other, and where it exhibits much more nearly the average characters of the genus, we may reasonably suspect it of being ancestral to its neighbor, particularly if the latter is a highly aberrant form, occupying a restricted and peculiar type of environment.

The intensive study of one concrete example of subspecific intergradation was undertaken by the author in 1927. On a previous trip to the southeastern states during the summer of 1924, I found what appeared to be an extremely promising case for an investigation of this sort.<sup>2</sup> A rather widely distributed mouse, *Peromyscus polionotus polionotus* (Wagner), having color characters fairly typical for the genus, is represented in the coastal region of northwestern Florida and southern Alabama by a quite distinct race (*P. p. albifrons* Osgood), differing from it strikingly in color and some other characters. On an island reef, skirting this part of the Florida coast, is a third race, *leucocephalus* Howell,<sup>3</sup> having paler coloration and more extensive white areas than any other wild mouse with which I am acquainted. This island, as well as the beaches and dunes of the mainland, consist of extremely white sand, covered to only a limited extent by vegetation.

The interior race, *polionotus*, and the coastal race, *albifrons*, although of strikingly different appearance, had been described as subspecies, rather than distinct species, because it was assumed that *somewhere* their ranges met and that intergradation occurred. Up to the fall of 1927, however, a belt of unexplored territory, over a hundred miles in width, intervened between the known ranges of these two forms.

The interest of this case was enhanced by the probable phylogenetic relationship between the two races in question. For the subspecies *polionotus*, in view both of its geographic range and of its distinguishing characters, may be regarded as representing the ancestral stock from which

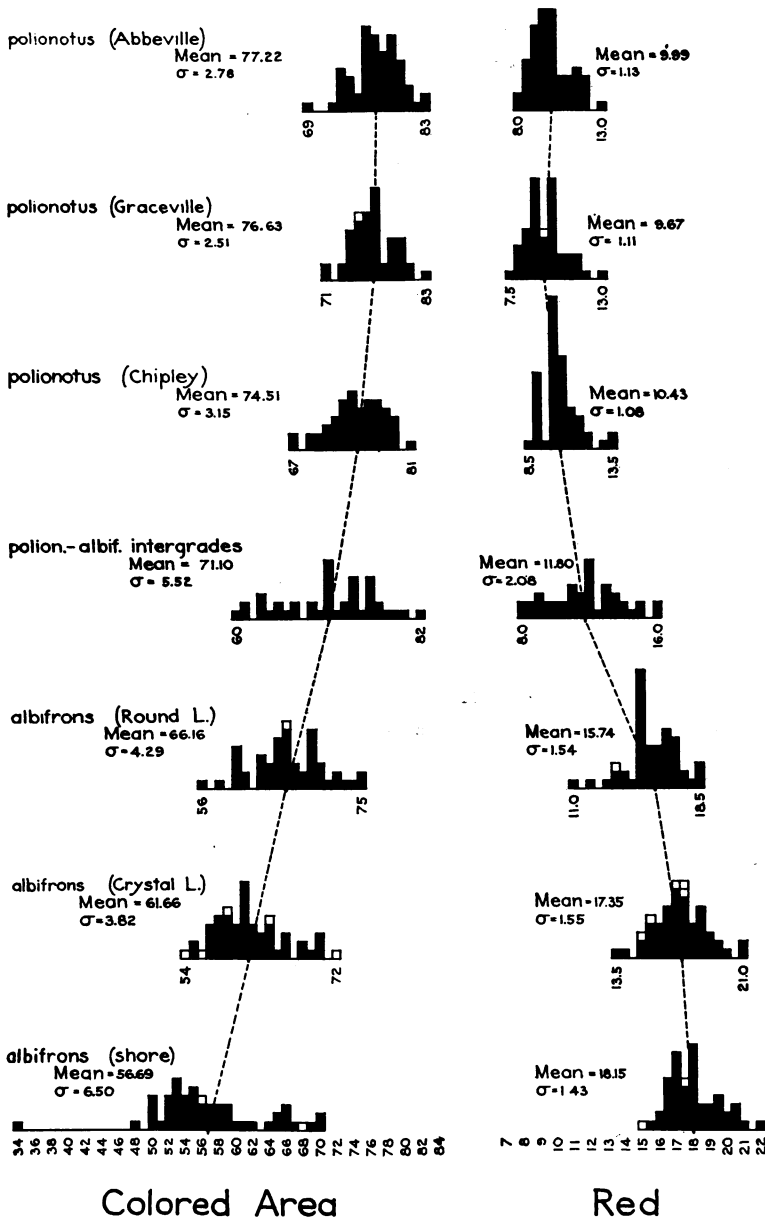


FIGURE 1

Distribution of values for "colored area" and "red," at each of the seven chief collecting stations. The broken lines connect the means of the series. Each square represents an individual. The unshaded squares represent a few individuals, which, for certain reasons, are not included in the regular series, upon which the averages are based.

*albifrons* immediately sprang. The latter, on the other hand, possesses in a high degree certain peculiarities which have been described in the case of a number of other beach-dwelling types. It seemed possible, therefore, that somewhere in this region the steps might still be discernible through which one geographic race gave rise to another very distinct one.

The present paper is based upon the study of some 400 specimens which were trapped alive by the writer, with the assistance of Mr. J. J. Karol. During September and October, 1927, we trapped at seven chief stations and a few minor ones, situated along a very irregular line, extending from the gulf coast of Florida, near St. Andrews Bay, to the vicinity of Abbeville, in southeastern Alabama. Specimens had previously been collected from the two terminal points of this line by A. H. Howell, but the condition of the intervening population was entirely conjectural.

It was already evident to us, in the field, that specimens trapped close to the gulf shore, were, on the average, paler than those from other points; likewise that there was a gradient of increasing pigmentation as we passed inland, to the northward. Despite these differences, it seemed fair, however, to regard all specimens, up to a point about forty miles from the coast, as being referable to the subspecies *albifrons*. This form possesses a pale, buff pelage, of much the same shade as many of the rodents of our southwestern deserts. Unlike most of the latter, however, the hairs of the ventral white area in *albifrons* are white to their very bases, the dorsal stripe of pigmented hair on the tail is commonly vestigial or lacking, and the dorsal surface of the snout is frequently white. This last is particularly true of the dune-dwelling representatives of the subspecies.

At a point about forty miles from the coast, this pale race was found to give place rather abruptly to one which was far more typical of the genus *Peromyscus*. This was readily recognized as *P. polionotus polionotus*. The latter is a much darker race, quite comparable in appearance with our more familiar white-footed mice of other regions. The dorsal tail stripe is fully developed, and the hair of the ventral area is white at the tips only, being dark at the base. Various regions of the naked skin are likewise more heavily pigmented.

The "area of intergradation" between these two subspecies, at least in the territory explored, was found to be surprisingly narrow. We trapped large and relatively uniform collections of *albifrons* and *polionotus*, respectively, at points not more than ten miles apart, and it is likely that these distances could have been greatly diminished. The population of the intervening area was found to resemble *polionotus* much more nearly than *albifrons*. The majority of specimens appeared to be quite indistinguishable from "true" *polionotus*, although trapped only two or three miles from a region infested by *albifrons*. Other specimens were obviously

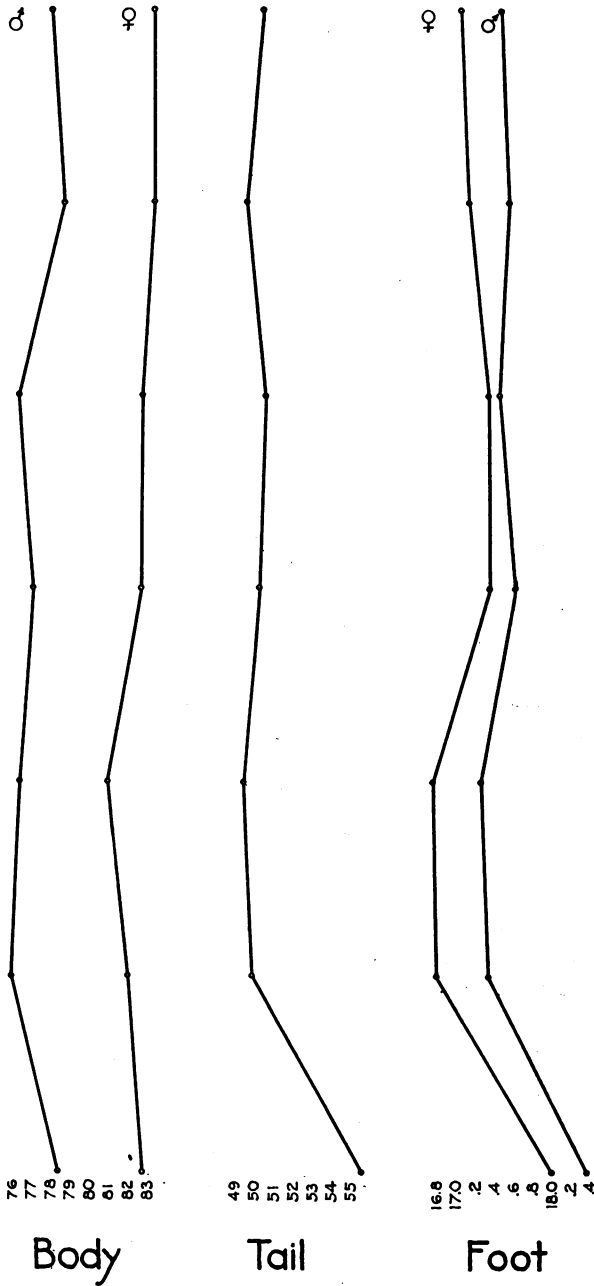


FIGURE 2

Graphs showing the mean values for linear measurements of body (head plus trunk), tail, and foot length, respectively, for each of the seven chief collections. The values for tail and foot have been "corrected" (see text). The seven collecting stations are arranged in the same order as in figure 1.

intermediate between the two races, while a small minority would have passed for the darker specimens of *albifrons*.

This abrupt transition which was found between one subspecies and the other was surprising in view of the lack of any evident barrier, geographic or ecological, between the ranges of the two forms. And it was doubly so when one considered the fact, which had already been determined experimentally, that these forms are perfectly fertile *inter se*, and give rise to fertile hybrids.

The mice from this expedition were nearly all kept for 9 to 11 months in captivity before killing, and were consequently fully mature when they were measured and skinned. The methods employed throughout the *Peromyscus* studies, and the nature of the characters measured have been recently discussed in detail,<sup>4</sup> and need receive only brief mention here.

*Tail-length* and likewise *foot-length* have here been reduced to a common standard, the values given being those most probable for a body-length of 80 mm. (Computed, of course, by means of the regression coefficient.) "*Colored area of pelage*" represents the percentage of the total pelage occupied by hairs which are pigmented to their tips (thus visible superficially). "*Red*" is the reading obtained through the red color-filter of the Ives Tint Photometer. It is used here merely as an index of the relative paleness or darkness of the hair. "*Pigmentation of ventral hair*" designates the condition of the basal zone of the hairs on this region of the body. Pigment may here be lacking ("0"), or present in full measure ("2"), or only a trace may be present ("1"). The figure for *tail stripe* indicates the length of the dorsal stripe, stated as a percentage of the total length of the visible part of the tail.

Figures 1 and 2 present the distribution frequencies, as well as the means and standard deviations, for five of these characters, in the seven chief local collections, comprising about 50 specimens each. In figure 3 are plotted the mean values of certain pigmental characters, in relation to distance from the coast.<sup>5</sup>

From these graphs, collectively, the following general conclusions may be drawn:

1. In regard to the four pigmental characters here considered, there is a striking degree of parallelism in the geographic relations shown. The condition as regards "red" is by no means an exception, as one might infer, since it is *low* values which indicate *heavy* pigmentation and *high* values which represent *light* pigmentation. To be comparable with the others, this curve should be inverted.

In all cases, there is evident a gradient of varying steepness, from the coast to a point 39 miles in the interior. There is then a very abrupt change within the space of a few miles, the extent of this change, in three

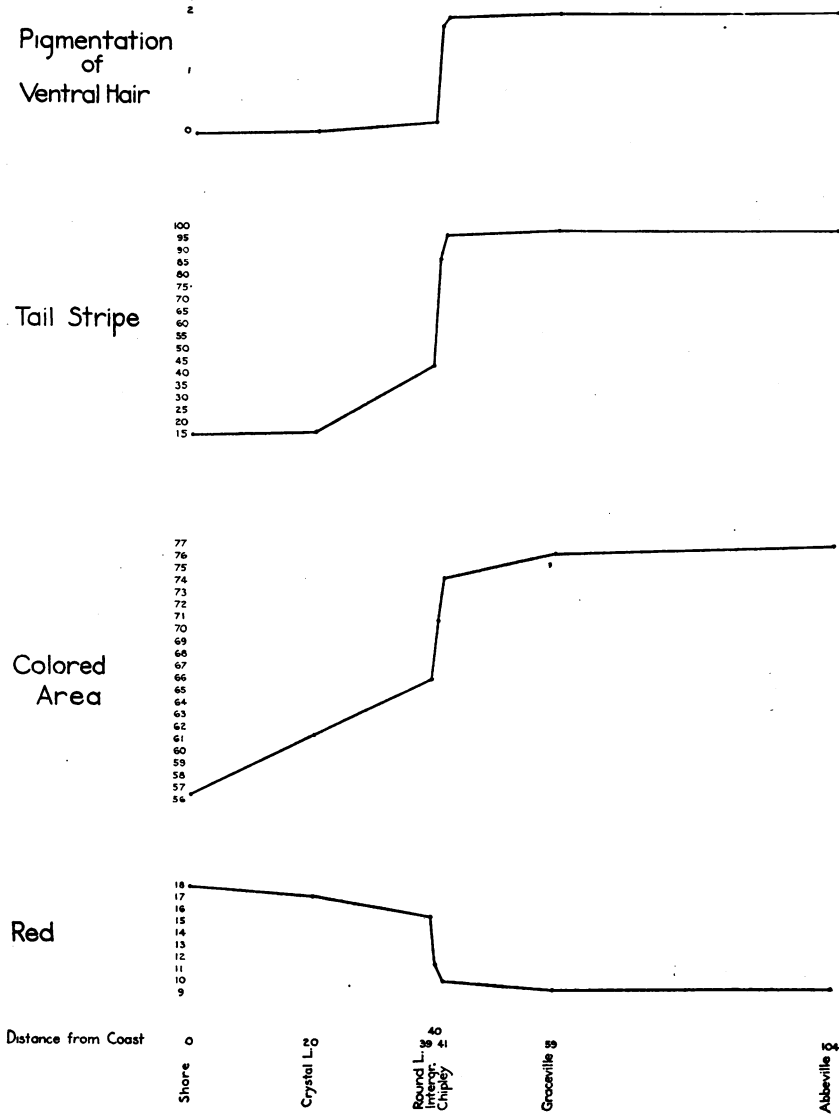


FIGURE 3

Graphs showing mean values for four pigmental characters, in each of the seven collections. In this figure, unlike the others, the stations are plotted with reference to their actual distances from the coast. (Note that these distances represent, in each case, the distance from the *nearest point* on the coast. Since the stations do not lie in a single straight line, this procedure appears to reduce the distance between certain stations.)

cases out of four, being greater than in both of the other segments of the line, taken together. This is followed by a resumption of the original gradient, which, however, is here feeble, and disappears, in all cases but one, between the last two stations. Otherwise stated, *polionotus* displays a much higher constancy within its range than does *albifrons*.

2. Both the graphs for "colored area" and "red," and the standard deviations, computed for these two characters, indicate a considerably lower range of variability for *polionotus* than for *albifrons*. This is in harmony with the last fact mentioned in the preceding paragraph.

3. The group of "intergrades," as might have been expected, shows a higher variability than either of the "pure" races, though its standard deviation for "pigmented area" is exceeded by that of the coast collection of *albifrons* (largely due to a single highly aberrant individual).

4. When we consider the length of tail and foot, a wholly new situation presents itself. It was already known<sup>6</sup> that *albifrons* from coastal points had considerably longer feet and tails than *polionotus*. But the collections of 1927 showed that no such gradient exists as is observed in the case of pigmental characters. The length of both of these members appears to fall off abruptly as we pass to the first inland station, only twenty miles from the shore, and thereafter it undergoes but slight diminution. For both characters, indeed, the minimum length is reached within the range of *albifrons*, a slight initial increase being encountered as we pass to that of *polionotus*.

5. Racial differences in body-length are probably non-significant.

Most students of terrestrial vertebrates will probably agree that the general picture presented by this series of local populations is far from being unique.<sup>7</sup> It is exceptional only in the extent of the divergence shown within a very limited territory, and in the completeness of our knowledge of the case, due to intensive collecting and subsequent analysis of the material. The difficulties which beset an interpretation of this and similar cases, in terms of evolutionary history, are still formidable. I think, however, that we have enough evidence in the present instance to warrant us in making a few tentative suggestions.

Before thus proceeding, it will be well to consider a few facts relative to the genetic status of the characters distinguishing these races. The reader should be reminded that these various racial differences have been definitely proved to be hereditary, at least in certain other species of the genus. The races remain practically unmodified even after a considerable number of generations in a changed environment.<sup>8</sup>

For the present series, I have limited, though fairly decisive, evidence that the most important differences between these local collections are genetic. Finally, even individual differences within a race, in respect to some of these characters, have been shown to be in part hereditary.<sup>9</sup>

Regarding the "behavior" of these subspecific differences in heredity, it may be said that while no single character difference has been detected which acts as if dependent upon a single pair of mendelian factors, I now have abundant and striking evidence of segregation, at least as regards color characters. In even such a wide cross as that between *polionotus* and *leucocephalus*, we find that specimens which reach or surpass the mean value of one or the other parent race, in respect to the extensity of the pigmented area, appear in a quite limited series of  $F_2$  hybrids.

The computation of coefficients of correlation among these various characters, for each of our local collections separately, confirms certain conclusions which have already been reported, for this and related species,<sup>10</sup> but which may once more be profitably summarized. (1) Pigmental characters, as a rule, are at least moderately correlated with one another within the race (mean correlation between "red" and "colored area" is here  $-0.363$ ). (2) Tail-length and foot-length are moderately correlated, even when the effect of diverse body size has been eliminated. (3) No certain correlation between the length of tail or foot (or of any other body part) and any pigmental character has been discovered.

Data derived both from geographic variation and intra-racial correlation make it plain, therefore, that certain characters commonly vary quite independently of one another, despite instances of simultaneous change along the same environmental gradient. It has likewise been pointed out that the length of these body parts is more subject to erratic and unexplainable local influences and to the transitory effects of environment than are characters related to pigmentation.<sup>11</sup> It seems reasonable, therefore, that we should attach more importance to pigmental characters than to tail or foot-length in considering the probable course of evolution in the present races.

Let us now return to the task of interpreting the relations shown in this cross-section through the ranges of two contiguous subspecies. Firstly, we can hardly escape the conclusion that environment, directly or indirectly, has played some all-important part in the production of these differences. For each of the racial differences here considered appears to depend upon a number of mendelian unit factors, and the process of mutation, unassisted, seems inadequate to account for this piling up of factorial changes *in the same direction*.

Granting this basic fact, we next face the question: How can a continuous environmental gradient bring about such relatively abrupt change in a population as that which is encountered in passing from the range of *polionotus* to that of *albifrons*?

The picture presented in figure 3 suggests rather forcibly that we have to do with one of those critical points in an environmental gradient, at which the individual adjustability of a given race or species seems to reach



its limit. One thinks at once of the analogous situation presented by the familiar "life zones" of our students of distribution. Critical points in the environment do occur, and faunal and floral associations are known to succeed one another in many cases, with considerable abruptness. In the present instance, it would not be unreasonable to suppose that there are fundamental physiological differences, distinguishing these two races, which are quite as pronounced as the visible ones of color and proportions. If one concentrates his attention on these graphs, and abandons himself to an exclusively physico-chemical point of view, it is likely that the foregoing interpretation will assume a high degree of probability. And indeed it has much in its favor. There are, however, serious complications.

In the absence of exact knowledge on this question, the only probable environmental gradients which suggest themselves here are those of temperature and humidity. But the pigmental differences in our present series are not such as we are accustomed to associate with the climatic gradients which here exist. One of the most certain generalizations from distributional studies of mammals and birds is the association of dark pigmentation with high atmospheric humidity. In the present instance, however, our color gradient shows a reverse relation to the customary one, at least, if we may assume a decrease in atmospheric humidity as we pass inland. In any case, the humidity throughout the entire range of *albifrons* probably compares well with that of the ranges of even some of our darker races on the Pacific Coast.

On the other hand, there are strong reasons for believing that extensive depigmentation may result from life upon a background of pale sand. Reference has already been made to the extraordinary pallor of the subspecies *leucocephalus*, in which complete isolation upon a reef of pure white sand, very sparsely clad with vegetation, has entailed an unparalleled degree of modification. Less striking examples have been reported from a number of other beaches where conditions are not so extreme.<sup>12</sup> In the absence of direct evidence, the most plausible hypothesis to account for these changes seems to be that of protective coloration, achieved through the differential survival of paler variants.<sup>13</sup> This is less easy to admit, doubtless, in the case of a nocturnal animal like *Peromyscus*, and it must be borne in mind that the palest of these animals is very far from white. But any appeal to the physical effects of light, direct or reflected, would involve even greater difficulties.

However, we become once more involved in difficulties as soon as we endeavor to apply the protective coloration hypothesis here in detail. It is not obvious why such a highly depigmented condition should occur so far inland, where there are no white beaches or dunes, and where the soil is largely concealed by vegetation. Nevertheless, throughout the entire range of *albifrons* the process of depigmentation has been carried

farther than in any of our desert races of *Peromyscus*, despite the much smaller proportion of bare sand and gravel in the habitat of the former.<sup>14</sup>

Once more, we have left unexplained one of the most striking features in the distribution of these two races, namely, the fact that the boundary between their ranges is so sharp, in spite of their mutual fertility. The simplest explanation of this circumstance would be to assume that our two races became differentiated in localities more remote from one another, and that they subsequently (and rather recently) came into contact. But of this there is no evidence whatever, and there are other circumstances which render such an explanation improbable.

In the present preliminary communication, it is impossible to enter into all the complexities of this situation. A more complete report of these investigations will be published shortly. It must be admitted, however, that the data now at our disposal do not permit us to choose with any confidence among the several alternative interpretations of these facts. As regards the causes which are responsible either for the extent of the respective territories occupied by our two races, or for the abrupt transition between their ranges, we must defer judgment.

However, it can hardly be said that the conclusions herein reached are altogether negative. It has been shown that *albifrons* in all probability arose from *polionotus* (or a common ancestor closely similar to this), in adaptation to life upon a background of extremely pale sand. And it has been possible to portray the probable steps through which the former, highly modified, race arose from the latter. The quality and magnitude of the germinal changes involved in one actual case of evolution are thus to some extent revealed by this analysis, and considerable additional light is thrown upon these changes by the genetic data to be reported shortly.

<sup>1</sup> These studies were conducted under the joint auspices of the Scripps Institution of Oceanography and the Carnegie Institution of Washington.

<sup>2</sup> Sumner, F. B., *J. Mammalogy*, 7, 1926, 149-184.

<sup>3</sup> Howell, A. H., *Ibid.*, 1, 1920, 237-240.

<sup>4</sup> Sumner, F. B., *Ibid.*, 8, 1927, 177-206.

<sup>5</sup> Cf. Cockerell, T. D. A., *Science*, N. S., 23, 1906, 145, whose diagram, representing a purely hypothetical case, presents considerable similarity to my own.

<sup>6</sup> *J. Mammalogy*, 7, 1926, 149-184.

<sup>7</sup> Cf. case of *Neotoma*, discussed by Grinnell and Swarth, *Univ. Calif. Publ. Zool.*, 10, 1913, 197-417 (particularly figs. A,B,C).

<sup>8</sup> Sumner, F. B., *Amer. Nat.*, 58, 1924, 481-505.

<sup>9</sup> Sumner, F. B., *Ibid.*, 52, 1918, 290-301. (Also abundant unpublished data.)

<sup>10</sup> Sumner, F. B., *J. Exp. Zool.*, 30, 1920, 369-402; *J. Mammalogy*, 7, 1926, 149-184.

<sup>11</sup> Sumner, F. B., *Amer. Nat.*, 51, 1917, 173-185.

<sup>12</sup> Jameson, H. L., *J. Linn. Soc. (Zool.)*, 26, 1898, 465-473; Bangs, O., *Proc. New Eng. Zool. Club*, 4, 1905, 14-15; Osgood, W. H., *N. Am. Fauna*, U. S. Dept. Agric., 28, 1909, 285 pp. (particularly 66, 121); Allen, G. M., *Am. Nat.*, 48, 1914, 467-484; *J. Mammalogy*, 1, 1920, 235; Sumner, F. B., *Am. Nat.*, 51, 1917, 173-185; *J. Mammalogy*, 7, 1926, 149-184.

<sup>13</sup> In admitting the probability that selection, in this case, has operated primarily upon a visible character, color, I am adopting a viewpoint somewhat different from that expressed by me only recently (Carnegie Institution Yearbook for 1928).

<sup>14</sup> Cf. Sumner, F. B., *Ecology*, 6, 1925, 352-371, where evidence has been presented for believing that the primary cause of the depigmentation of desert animals has been the climatic factor, though the need for concealment (through selection) has probably accelerated the process in certain cases.

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### NOTE ON C. S. PEIRCE'S EXPERIMENTAL DISCUSSION OF THE LAW OF ERRORS

BY EDWIN B. WILSON AND MARGARET M. HILFERTY

DEPARTMENT OF VITAL STATISTICS, HARVARD SCHOOL OF PUBLIC HEALTH

Read before the Academy November 19, 1928

Incident to the preparation of the official biography of C. S. Peirce for this Academy the senior author came across Peirce's experimental discussion of the law of errors<sup>1</sup> wherein the conclusion was that the normal law was, on the whole, verified. This is in accord with the dictum of Poincaré<sup>2</sup> that everybody believes in the law of errors: the mathematicians because they think it empirically demonstrated by experimenters and the experimenters because they think the mathematicians have proved it *a priori*. The series of observations given by Peirce is long, consisting of about 500 records each day for 24 different days of the time elapsed between the making of a sharp sound and the record of reception of the sound by an observer. According to our previous experience such long series of observations generally reveal marked departures from the normal law, and it seems interesting to examine this material of Peirce's from the point of view of the modern theory of frequency functions.<sup>3</sup> Accordingly we have entered in the tables, (1) the median with its standard deviation, (2) the mean with its standard deviation, (3) the semi-interquartile range, (4) two-thirds of the standard deviation, (5) the ratio of probable error as defined by the semi-interquartile range to the probable error as defined by two-thirds or more accurately 0.6745 of the standard deviation, (6) the arithmetic mean error about the median as origin, (7) the number of negative errors greater than  $3\sigma$  and the number of positive errors of similar magnitude and their sum, (8) the number of observations within  $0.25\sigma$  of the mean and the number expected according to the normal law, (9) the percentage excess of the observed over the expected number, (10) the second moment  $\mu_2$  and its standard deviation, (11) the third moment  $\mu_3$  and its standard deviation, (12) the Pearsonian constant  $\sqrt{\beta_1} = \mu_3/\sigma^3$