The Supposed Effects of the Color Tone of the Background Upon the Coat Color of Mammals

FRANCIS B. SUMNER AND HARRY S. SWARTH

Reprinted from Journal of Mammalogy, Vol. 5, No. 2, May, 1924

Reprinted from JOURNAL OF MAMMOLOGY
Vol. 5, No. 2, May, 1924, pp. 81-113.

THE SUPPOSED EFFECTS OF THE COLOR TONE OF THE BACKGROUND UPON THE COAT COLOR OF MAMMALS

BY FRANCIS B. SUMNER AND HARRY S. SWARTH

[*Plates 6–12*]

The existence of a general correlation between atmospheric humidity and the depth of color of birds, mammals and some other groups of animals has become a commonplace in biological literature. It is plain, however, that the mere existence of such a correlation tells us nothing of the causal agencies at work in the production of the results in question. Thus, in the present instance, it is possible that the effects of humidity upon pigmentation are very indirect. Those who accept the more extreme mendelian-mutation picture of organic evolution will naturally doubt the likelihood of any cumulative effect of environmental conditions upon a race of organisms, whether these conditions are conceived of as acting immediately upon the germ-plasm or indirectly through the cells of the body. Such persons will be disposed to attribute the undoubted correlation just mentioned to the survival of variations (mutations) which are purely random in origin, so far as the environment is concerned. As in all cases of natural selection, the basis of survival must be conceived of in terms of adaptation, or utility in the broad sense.

So far as we know, two chief explanations of the marked color differences between desert and coast-dwelling birds and mammals have been suggested which are based upon the supposed utility of these characters. The more obvious of these explanations is the hypothesis that we have to do with the familiar phenomenon of protective coloration. This interpretation of the facts derives support from the undoubted existence of protectively colored animals, belonging to a wide range of natural groups and occupying a great diversity of habitats. Indeed, the applicability of this principle to the ground-dwelling animals of desert regions will perhaps seem self-evident to most persons who have had much experience in observing them. And conversely, the protective value of a darker colored plumage or pelage against a more somber background will seem to be inherently probable. It is scarcely necessary to point out, however, that the fact that these animals are well concealed by their harmonious coloration is of itself no proof that this shade was developed because of its protective value.

Another attempt to explain these color characters on the basis of utility may be founded on the assumption that the differences of pigmentation, while of no value in themselves, are the visible expression of constitutional (physiological) differences which adapt the animals to different climatic conditions. It is these underlying constitutional peculiarities, rather than color *per se*, which may be supposed to furnish the basis for selection. The possibility of such an origin of the pigmental distinction among our various geographic races cannot be denied. Indeed, it has a considerable measure of plausibility, despite the entire lack of direct evidence in its favor.

It is not our object in this paper to discuss the last named interpretation of the pigmental differences under consideration. No data at hand seem to be decisive between this view and that of the direct effect of environmental conditions, without the influence of selection. Our present concern is with the hypothesis of protective coloration.

The latter hypothesis, as applied to the prevailing hues of desert mammals, has already been discussed by one of us.[1] Various reasons have been given for doubting the supposed dependence of the degree of pigmentation upon the optical properties of the background. While it is unnecessary to repeat all of these arguments here, it is desirable to state briefly the evidence derived from the special field studies which were described in the earlier paper. About fifty skins from mice which were trapped upon a very dark lava-field in the Mojave Desert, were compared with an equal number from a point about fifty miles distant, in a region of pale, non-volcanic rock, but having closely similar climatic conditions. The mean color values for the two series were found to be almost exactly the same.

[1] Sumner: Desert and Lava-Dwelling Mice and the Problem of Protective Coloration in Mammals. Journal of Mammalogy, May, 1921.

Several things must be emphasized in connection with this result. In the first place the species (*Peromyscus crinitus stephensi*) is one which is known to be restricted in habitat to rocky regions. This point was specially tested by trapping upon sandy areas of the desert, immediately surrounding the lava field. *P. crinitus* was not found to stray far from the lava. Thus the vast level tracts of sandy desert doubtless act as fairly effective barriers between the colonies inhabiting the various scattered areas of rock. It is probable that the *Peromyscus* population of this lava field is self-perpetuating, and that it is recruited but slightly from non-volcanic areas. Yet here we find a very pale species of mouse to be present in considerable abundance. This fact certainly lends no support to the assumption of any very rigid selection on the basis of color. A race which has maintained itself in large numbers for probably hundreds of years cannot be conspicuously ill adapted to its environment.

These findings were not in agreement with the statements of several prominent mammalogists who have been disposed to credit areas of lava with a pronounced modifying influence upon the pelage color of rodents. Definite assertions to this effect have been cited in the earlier paper and need not be repeated here.

The general applicability of these earlier negative conclusions of the senior author has been challenged by various correspondents, including some of those who were responsible for the claims which had been called in question. Stress has been laid by these persons upon the fact (fully recognized in the published report) that the lava field in question was of limited extent, and that it was likewise very recent geologically speaking.[2] In any case, it must be conceded that such negative findings as these cannot be offered as conclusive evidence against the accuracy of positive assertions on the part of other naturalists.

It was urged by several critics that the most favorable locality in which to test this problem of alleged lava influence was the neighborhood of San Francisco Mountain in Arizona. Here, we were told, the volcanic area is vastly more extensive, as well as far more ancient,

[2] Mr. N. H. Darton, of the United States Geological Survey, to whom the question of the age of this lava field was submitted, writes that, whereas "no quantitative data as to time are available, ... 500 years might be a reasonable guess and 1,000 years an outside limit." See also Guidebook of The Western United States, Part C, Santa Fe Route, Bull. 613, U. S. Geological Survey (page 158, plate XL).

geologically speaking. Here, it was, likewise, that Merriam, Bailey and Goldman had reported actual cases of modification in several different groups of rodents.

Despite the seemingly narrow scope of such an investigation, a somewhat intensive study of the San Francisco Mountain situation seemed warranted by the broader biological bearings of the chief problem involved. By the aid of funds contributed through the generosity of Mr. E. W. Scripps, an expedition was sent into this region in the fall of 1922, under the joint auspices of the Scripps Institution for Biological Research and the Museum of Vertebrate Zoölogy, both departments of the University of California. The party consisted of the two authors, together with Mr. R. R. Huestis, assistant and graduate student in the Scripps Institution. Following the return of Mr. Huestis to La Jolla, Mr. Carr H. Schwarz, of Flagstaff, Arizona, was employed as a temporary assistant.

After some reconnoitering, a base was established on September 5, at Dead Man Flat, on the high plateau northeast of San Francisco Mountain, and but a few miles from its base. The collection and preparation of specimens was carried on until November 12, when the senior author (the last in the field) discontinued operations.

We wish here to record our indebtedness to Messrs. Vernon Bailey and E. A. Goldman, of the United States Biological Survey, for helpful suggestions and information which contributed to the success of our labors. Mr. Goldman has likewise been good enough to examine some of our rodent specimens, belonging to several genera, with reference to their specific and subspecific identity, and to secure for us the loan of the type specimens of several of these subspecies.

Necessary data, regarding local conditions, ecological, topographical and meteorological, were placed at our disposal through the courtesy of various Forest Service officials, particularly Mr. G. A. Pearson of the Fort Valley Experiment Station and Mr. E. G. Miller, supervisor of the Coconino National Forest. Mr. Pearson has been good enough to inspect those pages of our manuscript relating to local ecological conditions.

Our hearty thanks are due to Dr. H. M. Hall, of the Carnegie Institution, for identifying a considerable collection of plant specimens, representing the more abundant species occurring at our various trapping stations, as well as for revising our lists of plant species. We must also record our indebtedness to Prof. A. C. Lawson, of the University of California, for information regarding rock samples from various

points in the region, and to Mr. H. H. Robinson, superintendent of the Connecticut Geological and Natural History Survey, for further information regarding the geology of the region visited.

Finally, it is a pleasure to acknowledge the never-failing helpfulness of Mr. and Mrs. W. J. Osborn, of Dead Man Flat, who contributed in many ways to our enjoyment, as well as to the successful outcome of our visit to this region.

Before proceeding with a detailed account of our operations and our results, it may be well to state in a few words the outcome of our labors. We were able, pretty promptly, to confirm the accounts of those authors who had reported the existence of races of rodents in the volcanic area surrounding San Francisco Mountain which were distinctly darker than those which were trapped in the adjacent Desert of the Little Colorado. Indeed, our evidence in this respect is based upon much larger series of specimens than have hitherto been collected in this region, and relates to species which have not been included among the illustrative cases. On the other hand, the evidence to us seems pretty conclusive that the volcanic soil of the San Francisco Mountain plateau has not been a factor in the production of these color differences. In general the rodents of this region are not particularly dark in comparison with mountain or forest dwelling races from other parts of the southwest. They are only dark in comparison with the characteristically pale forms from the desert areas. Furthermore, we have what seems to be rather crucial evidence bearing against the alleged effect of the volcanic soil and rock formations, at least in this region. The data upon which these conclusions rest will be discussed at some length in the ensuing pages.

ACCOUNT OF THE REGION VISITED[3]

The San Francisco Mountains form a group of volcanic peaks and ridges which rise from the elevated plateau of northern Arizona to a maximum altitude of nearly 13,000 feet. The plateau region here varies in elevation from 6,000 to 8,000 feet. The entire "volcanic field," comprising the mountains and adjacent eruptive material, covers, according to Robinson, an area of over 2,000 square miles.

[3] Those who wish a more detailed account of the biological and geological features of this region should consult the works of Merriam (Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado, Arizona. North American Fauna, No. 3, Government Printing Office, 1890), and Robinson (The San Franciscan Volcanic Field, Arizona. U. S. Geological Survey, Professional Paper 76, 1913).

It was in this region, as is well known, that C. Hart Merriam first worked out the details of his life zone conception. Within this quite restricted area, he found represented all zones from the Lower Sonoran to the Alpine-Arctic, inclusive. Indeed the most casual inspection of this territory reveals the existence of some form of zonation, whether or not one accepts the general validity of any particular classification.

It is not, however, our purpose to discuss the life zones of this region except in so far as they relate to the problem at hand. The rodents which Merriam and others have supposed to be affected by the background of volcanic soil are all denizens of the piñon-juniper (Upper Sonoran) zone. Our own collecting operations—so far as they relate to this problem—were therefore confined to this zone and to the succeeding Lower Sonoran of the Little Colorado Desert. The ensuing remarks regarding the character of the volcanic territory refer, accordingly, to those portions which lie within the Upper Sonoran zone. The conditions at a greater altitude have not been carefully examined by us. It is worth stating, however, that, so far as we have observed, areas of bare volcanic rock and exposed dark colored soil seem to be no more prevalent in the yellow pine (Transition) zone than among the piñons and junipers lower down.

The eruptions which brought to the surface the volcanic materials of this region are assigned by Robinson to three distinct periods, lasting altogether from late Pliocene to recent times. During the last of these periods, cinder cones were formed and lava ejected which are estimated to cover about 1200 square miles. This period of eruption is attributed, for the most part, to the late Quarternary. From the degree of disintegration to which most of the lava of this region has been subjected, as well as the depth of the soil deposits which overlie it in many places, it is obvious that the volcanic activities represented in the San Francisco Mountain region are, as a whole, very much older than those which were responsible for the formation of the Mount Pisgah field in the Mojave Desert (p. 82). The most recent activities, occurring at the close of the third period, were limited to the formation of a few cones and lava fields, occupying an insignificant part of the entire area.[4]

Merriam likewise points out that San Francisco Mountain itself cannot be of more recent origin than the glacial period, since "its summit is inhabited by species of animals and plants which could not have

[4] After referring to the fact that the latest cones and flows are older than the pine trees growing in their vicinity, Robinson writes: "This would make them not less than 300 years old. Not improbably they may be as much as 1,000 years old."

reached it since the recession" of the ice. Thus the requirements of those who have insisted that the volcanic territory investigated should be both ancient and extensive are fully realized in the present case.

On the other hand one may readily derive a false impression from previous references to conditions within this territory, in their bearing upon the protective coloration hypothesis. While it is true that there are still a few square miles of dark, fresh looking lava (figure 2), which is not as yet covered, to any great extent, by soil or vegetation, this is not true of by far the greater part of the San Francisco Mountain region. Most of this area has long since been covered by soil, and upon the latter now flourish trees and shrubs, along with more or less abundant grass and other herbaceous plants. As a result of extensive journeying throughout this territory, and careful scrutiny from various elevated points, we must insist that the prevailing color tone of the ground, as thus seen, is not dark but pale. As partial exceptions to this statement are the summits and to some extent the slopes of the numerous cinder-cones, along with the relatively small areas of bare lava, referred to above. But the greater part of the level and gently sloping surfaces throughout this region display the pale gray hue of the rabbit-brush (*Chrysothamnus*) or the still paler straw color of the (usually dry) grass.[5] (Figures 4, 5.)

The foregoing statement applies strictly only to oblique views of the ground surface, and especially when the latter is seen from a distance. Under such conditions the bare patches of soil are overtopped by the vegetation, and are thus nearly or quite concealed from view. It must be admitted that a somewhat different impression is obtained when one views the ground surface from above and at short range. As is commonly the case in semi-arid regions, the vegetation does not form a continuous covering, but occurs in clumps, separated by areas of bare ground. In the region under discussion, both the clumps of vegetation and the intervening bare patches are of small size, ranging from a few inches to a few feet across, while the uncovered surfaces are commonly of less extent than the areas of turf (figures 10, 11). In sections which are occupied predominantly by rabbit-brush, this preponderance of vegetation is still more marked.

[5] Needless to say, the coniferous trees are of a decidedly dark hue, but these could hardly be supposed to influence the color of ground-dwelling animals. Moreover, the trees are commonly rather widely scattered, and they are nearly or quite absent throughout extensive "flats" or "parks," which occupy much of the Upper Sonoran territory in this region.

The exposed ground surface varies greatly throughout the region in question. Much of it consists of fine soil, of perhaps medium hue, but dark reds and browns are of rather frequent occurrence. Typically, the bare ground is covered by volcanic "cinders" or scoriæ, these ranging in color from pale brown to nearly black.[6] Tracts of wide extent may, indeed, be found, in which these scoriæ give a decidedly dark aspect to the bare portions of the ground (figure 3). It is such areas as these which Merriam and others have probably had in mind in their discussions of the darkening effect of volcanic soil upon rodents. So far as our observations have gone, however, these tracts of noticeably dark soil form but a small proportion of the total area of the San Francisco Mountain region. Furthermore, it must be emphasized that even here the closely spaced clumps of turf are decidedly pale in hue. In semi-arid regions such as this, the grass is green for only a small part of the year, and the green is seldom vivid. If it is true that a darkly colored rodent would be better concealed than a pale one, if resting on the bare ground, it is equally true that a pale rodent would be better concealed than a dark one, against a background of turf. (See figures 10, 11.)

Northeast of San Francisco Mountain (figure 1), the land slopes gradually from the base (about 8000 feet altitude) to the bed of the Little Colorado River (4000 feet). Following the road from Flagstaff to Tuba, in the Navajo Reservation, one descends the 3000 feet, from the belt of yellow pine to the Little Colorado in the course of a journey of about 35 miles. The passage from the yellow pine (Transition) zone to the zone of piñons and junipers (Upper Sonoran) seems, in general, to be fairly abrupt. On the other hand, the boundary between the piñon-juniper belt and the desert is far less obvious. The coniferous trees end, it is true, rather abruptly, but the succeeding territory, for many miles, is occupied by grassland, rather than desert proper. Extreme xerophytic conditions are not reached until one approaches within a few miles of the Little Colorado.[7] Thus the river, at least in this part of its course, lies much closer to the western than the eastern border of the desert. This fact must be borne in mind in interpreting certain facts of distribution.

[6] This layer of "cinders" is due to wind action. The entire soil is permeated by these volcanic pebbles, which are left behind when the lighter ingredients are blown away by the heavy gales of the region. Cultivated land if left untilled, soon reverts to its original appearance, owing to this action of the wind.

[7] Merriam uses the word "desert" rather loosely in this connection, including here the grassland area as far up as the piñon zone.

In spite of scattered outcroppings of dark volcanic rock, extending to, and even beyond, the Little Colorado, the prevailing rock formations of the Painted Desert[8] are non-volcanic. The most conspicuous rock of the region is a red sandstone, the weathering of which has given rise to extensive tracts of loose drifting sand, of a decidedly reddish hue.[9] At other points, the sand commonly has the more familiar buff tone of of our southwestern desert country, while throughout large areas the surface is covered with a layer of pebbles and rock fragments, which on the whole are likewise pale. As is usual in desert regions, the vegetation is sparse and widely scattered, leaving the greater part of the ground surface uncovered. Indeed there are extensive areas of shifting sand dunes, which are nearly or quite devoid of vegetation (figures 6–9).

In order to indicate to some extent the life conditions under which the animals of this region dwell, we here offer some rather meagre data relating to the meteorology and the flora of the localities in which we trapped. It is stated by Robinson that the mean temperature of the Little Colorado Valley is about 56°F., the average absolute maximum being 100°–105° and the minimum 0°. The mean annual rainfall is said by the same writer to be "less than 5 inches," while "in some years practically no rain falls in that area." These statements are based upon United States Weather Bureau records for Holbrook, Arizona.

At Tuba (4,500 feet), near which much of our desert trapping was done, the mean annual rainfall for a period of 23 years was 6.90 inches, according to United States Weather Bureau records. That bureau likewise informs us that the mean annual temperature at Tuba was 54.4° for this same period. The average of the annual maxima was 101° (12 years), that of the annual minima being 8°.

In the neighborhood of San Francisco Mountain, on the other hand, the mean annual temperatures are considerably lower and the rainfall much higher. Unfortunately, no data are available for Dead Man Flat and neighboring territory on the northeast side of the mountain. At Flagstaff on the opposite side of the mountain and at a slightly greater altitude, the temperature averages 44.5° (29 years), the average annual maximum being 89° and the average annual minimum −14°. The

[8] Here used synonymously with Desert of the Little Colorado.

[9] Mr. H. H. Robinson contributes the following note: "The red formation west of the Little Colorado is called the 'Moencopie', of Lower Triassic age. It is briefly described as chocolate-red and banded arenaceous shales and sandstones. The formation in the neighborhood of Tuba City is the Navajo sandstone of Jurassic age, described as light-red, massive, cross-bedded, fine and variegated sandstone."

mean annual rainfall at Flagstaff for this same period was 22.80 inches. It is quite certain, however, that the rainfall to the north and east of San Francisco Mountain is considerably lower than this, even at corresponding altitudes. Judging from general appearances, Mr. G. A. Pearson[10] offers an estimate of 15 inches for the annual rainfall of Dead Man Flat.

It is obvious to the visitor both that the rainfall is much lower and the percentage of sunshine much higher in the Painted Desert than in the more elevated land at the base of the mountains. We have on numerous occasions looked down upon the brilliantly lighted desert from our headquarters at Dead Man Flat, while heavy showers and overcast skies prevailed all about us in the upland region.

To the botanist it is likely that tables of the prevailing plants which occur in the localities under comparison will suggest a much more vivid picture of local climatic differences than these meagre meteorological data. The lists which are presented herewith make no pretense to even approximate completeness. Only the more conspicuous or abundant plants which were observed in a given locality were listed or preserved for subsequent identification.[11] In general, trees and shrubs were more likely to be noticed than herbaceous plants and annuals. Many fairly common species were deliberately omitted from the list, and many others were doubtless overlooked.

In listing these plants, the same grouping of localities will be employed as in the case of the trapping stations. Stations have been grouped together which represent the same type of locality—so far as the present problem is concerned—although these may have been ten or more miles distant from one another.

1. *Volcanic Areas in the Piñon-Juniper Zone* (Collections from a number of rather widely scattered points)

Pinaceæ
- Pinus edulis Engelmann

Cupressaceæ
- Juniperus utahensis (Engelmann) Lemmon
- Juniperus monosperma Engelmann

Gnetaceæ
- Ephedra viridis Coville

Gramineæ
- Aristida californica Thurber

---

[10] In a letter to one of us.

[11] We again take pleasure in acknowledging the services of Dr. H. M. Hall, who identified most of these species, or confirmed identifications made in the field.

Bouteloua gracilis (H.B.K.) Lagasca
Bouteloua aristidoides (H.B.K.) Watson
Pleuraphis rigida Thurber
Liliaceæ
Yucca angustissima Engelmann
Chenopodiaceæ
Atriplex canescens (Pursh) Nuttall
Salsola kali Linnæus
Berberidaceæ
Berberis fremonti Torrey (probably)
Rosaceæ
Fallugia paradoxa (Don) Endlicher
Leguminosæ
Lotus wrightii (Gray) Greene
Astragalus diphysus Gray
Anacardiaceæ
Rhus trilobata Nuttall
Cactaceæ
Opuntia (at least two species)
Compositæ
Brickellia californica Torrey and Gray
Gutierrezia lucida Greene
Chrysothamnus nauseosus speciosus (Nuttall) Hall
Chrysothamnus nauseosus glareosus (Jones) Hall
Psilostrophe cooperi (Gray) Greene
Pericome caudata Gray
Senecio spartioides Torrey and Gray
Tetradymia canescens De Candolle

2. *Limestone Area in the Piñon-Juniper Zone* (Collection made within a single very restricted area)
Pinaceæ
Pinus edulis Engelmann
Cupressaceæ
Juniperus utahensis (Engelmann) Lemmon
Gramineæ
(Grasses not saved for identification)
Chenopodiaceæ
Atriplex canescens (Pursh) Nuttall
Compositæ
Senecio spartioides Torrey and Gray
Chrysothamnus nauseosus consimilis (Greene) Hall
Chrysothamnus stenophyllus (Gray) Greene

3. *Rocky Gorge of Little Colorado and Adjacent Desert Areas*
Gnetaceæ
Ephedra californica Watson
Gramineæ
Sporobolus airoides Torrey

Liliaceæ
  Yucca angustissima Engelmann (or Y. glauca Nuttall)
Salicaceæ
  Populus fremonti Watson
Chenopodiaceæ
  Atriplex canescens (Pursh) Nuttall
  Atriplex obovata Moquin
Capparidaceæ
  Cleomella longipes Torrey
Rosaceæ
  Fallugia paradoxa (Don) Endlicher
  Prunus fasciculata (Torrey) Gray
Leguminosæ
  Parryella filifolia Torrey and Gray
  Prosopis juliflora glandulosa (Torrey) Cockerell
Oleaceæ
  Fraxinus coriacea Watson
  Adelia neomexicana (Gray) Kuntze
Labiatæ
  Hedeoma incana Gray
Compositæ
  Dicoria canescens Torrey and Gray
  Chrysothamnus nauseosus glareosus (Jones) Hall
  Isocoma acradenia Greene

4. Little Colorado Desert, in Vicinity of Tuba (Including species from border of a creek (starred) as well as those from open desert)
Gnetaceæ
  Ephedra viridis Coville
  Ephedra californica Watson
Gramineæ
  *Phragmites communis Trinius
Liliaceæ
  Yucca angustissima Engelmann (or Y. glauca Nuttall)
Salicaceæ
  *Salix sp.
Polygonaceæ
  Eriogonum sp.
Chenopodiaceæ
  Atriplex canescens (Pursh) Nuttall
  Atriplex confertifolia (Torrey) Watson
  Sarcobatus vermiculatus Torrey
  Suaeda moquini (Torrey) Greene
  Salsola kali Linnæus
Amaranthaceæ
  *Amaranthus retroflexus Linnæus
Ranunculaceæ
  *Clematis ligusticifolia Nuttall
Capparidaceæ

Cleomella longipes Torrey
Leguminosæ
*Melilotus alba Lamarck
Anacardiaceæ
Rhus trilobata Nuttall
Loasaceæ
*Mentzelia multiflora Gray
Cactaceæ
Opuntia (at least 2 species)
Oleaceæ
*Adelia neomexicana (Gray) Kuntze
Labiatæ
Hedeoma sp. (same as in list 3?)
Solanaceæ
Datura meteloides De Candolle
Compositæ
Gutierrezia lucida Greene
Chrysothamnus nauseosus consimilis (Greene) Hall
Chrysothamnus nauseosus graveolens (Nuttall) Piper
Chrysothamnus stenophyllus (Gray) Greene
Isocoma acradenia Greene
*Solidago occidentalis Nuttall
*Aster hesperius Gray
*Helianthus annuus Linnæus
Artemisia filifolia Torrey
Senecio spartioides Torrey and Gray
Senecio douglasi De Candolle
*Carduus sp.

METHODS AND MATERIAL

A large majority of the specimens dealt with in the present report were caught in live-traps of the "Delusion" type. A considerable number, however, were caught in spring-traps of the sort commonly used for rats and mice. A few of the squirrels were shot. Since it is not the object of the present paper to give a general report upon the collections obtained in the course of this trip, no inventory of specimens will be given here.[12] It may be said, however, that over 1200 "mice" (in the broad sense of the term) were caught in the live traps, comprising 12 species and at least 15 subspecies, while about 225 rodents, belonging to 21 species and subspecies, were caught in spring traps or shot. By no means all of these, however, were measured or saved as specimens.

[12] These comprised large numbers of birds and some reptiles, as well as mammals.

An automobile "touring-car," remodeled to serve as a truck, was an indispensable part of our equipment. When it is stated that our trapping stations were widely scattered, and that collections were made from localities as far as sixty miles from our base, the need of rapid transportation will be appreciated. The living part of our catch was brought back to our headquarters in specially constructed chests, the animals being killed, measured and skinned at our convenience.[13] Indeed, a considerable number of the specimens were sent alive to La Jolla, where they were skinned later. Such as were plainly immature were kept for some months before skinning.

The quantitative data presented in the following pages are based almost entirely upon specimens which had been caught in the live-traps. These were measured by the senior author, according to methods already briefly described.[14] For use in the instrumental color determinations, flat skins were prepared in the manner which has been followed in previous studies. An important part of this technique consists in the thorough removal of grease by means of benzine.[15]

The color determinations were conducted, as in the past, with the aid of the Hess-Ives Tint Photometer. The procedure employed in the use of this instrument has been discussed briefly in two previous papers,[16] and no further account will be offered at the present time. A more adequate discussion of this instrument and its uses in biological research is contemplated for publication in the near future.

It should be stated at this point, however, that the conclusions reached in the present paper are not based entirely upon strictly quantitative data, derived from the study of flat skins. The considerable number of filled "study skins" have supplemented the latter in a valuable way, while many specimens were examined in the field which were not skinned at all.

[13] The advantages of using live-traps for catching certain species of rodents are very great, but we cannot dwell upon this point here.

[14] American Naturalist, April-May, 1918.

[15] Under laboratory conditions, each skin is subjected to a uniform degree of tension by means of a series of eight radially arranged weights and pulleys, after which it is pinned to a block of wood and allowed to dry for about ten days before cleaning. For various reasons, this stretching-frame has not been used in the field. Here the skins are stretched slightly by hand, while being pinned to the drying blocks. Under desert conditions in summer, a mouse skin may lose much of its elasticity by the time that it has been removed from the body.

[16] Journal of Mammalogy, May, 1921, (pp. 77, 84); Journal of Experimental Zoology, Oct., 1922, (foot-notes on pp. 289, 294).

As already indicated in the foregoing lists of plants, our trapping stations have been grouped into four series (figure 1). The first group comprised stations in Dead Man Flat and all other points in the Piñon-Juniper zone, where the soil and rock formations were volcanic. These stations lay at altitudes between 6,000 and 7,000 feet, the majority being not far from 6,500 feet.[17] The greater part of the specimens were taken on open, level ground, incompletely covered by scattered clumps of turf and rabbit-brush. The most successful catches were made in the immediate vicinity of cultivated land. On several occasions the number of specimens taken in the live-traps in a single night nearly or quite equalled the total number of traps set. In this first series of stations are likewise comprised a few localities on the summits and slopes of cinder-cones, and one rather extensive field of fairly fresh lava (figure 2).

The second region to be considered actually comprised but a single trapping station. This lay in a northwesterly direction, at a distance of about thirty miles from Dead Man Flat, on the southern margin of T 28 N, R 5 E. It had closely the same altitude as the former locality, but was situated in a very different geological formation. This point was selected because of its bearing on the question whether the color of the soil has played any part in bringing about the differences of coat color between the desert and upland races of rodents. The exposed rock of this region was the Kaibab Limestone. The trapping station was removed eight to ten miles from the nearest conspicuous outcropping of volcanic material, and further yet from any extensive areas of this sort. The specimens were trapped, for the most part, in open flats, bordered by dense growths of piñons and junipers, and incompletely covered, as elsewhere, by scattered clumps of grass and rabbit brush. The soil, in many places, was strewn with fragments of very light colored limestone and chert (figures 14, 15), though not otherwise conspicuously pale.

The third group of trapping stations was in the vicinity of the Little Colorado River. Part of the specimens were taken in rocky gorges connecting with the main canyon of the river, not far from the bridge on the Tuba road (Cameron Post Office). The remainder were trapped in a quite different sort of territory, in the open desert, four to six miles east of the river.

[17] Most of the trapping in the volcanic area was carried on at Dead Man Flat, within the township T 24 N, R 8 E. Two other townships in this region, T 25 N, R 8 E and T 26 N, R 7 E were also visited for trapping purposes. The latter contains a relatively recent lava field, a few square miles in extent.

The last series of stations were located in the neighborhood of Tuba City, the western agency of the Navajo Indian Reservation. This settlement lies northeast of the aforementioned bridge, and about 20 miles, in an air line, from the nearest point of the river. Its altitude is about 4500 feet. It is largely a region of loose, reddish sand, and, excepting in the neighborhood of creeks or irrigation canals, the vegetation is of a typically xerophytic character. Two trips of several days each were made to this region, and abundant specimens were trapped. The record catch of 165 mice, taken in 100 traps in a single night, was made on the border of an irrigated tract, cultivated by Indians.

The following table indicates the species and subspecies of rodents which have been studied by us, in relation to the problem of color modification. The number of individuals trapped (or shot) is likewise included, as well as the number which were preserved as specimens, both in the form of flat skins and of study-skins of the more usual type. It should not be necessary to state that care was taken to avoid selection on the basis of color, in choosing the specimens for skinning. Practically all available individuals of these species were skinned, except in the case of *Peromyscus*, the numbers of which were too great to allow of this. Immature specimens and those with damaged pelts were rejected,[18] otherwise the specimens were chosen entirely at random.

	TYPE OF LOCALITY	NUMBER TAKEN	NUMBER SKINNED
Citellus spilosoma obsidianus	Volcanic	9	9
Perognathus flavus fuliginosus	Volcanic	19	19
Perognathus flavus bimaculatus	Desert, near Little Colorado River	20	20
Onychomys leucogaster fuliginosus	Volcanic	55	55
Onychomys leucogaster fuliginosus	Limestone	3	3
Onychomys leucogaster melanophrys	Desert, mainly near Tuba	41	39
Peromyscus maniculatus rufinus	Volcanic	600(±)	131
Peromyscus maniculatus rufinus	Limestone	88	45
Peromyscus maniculatus rufinus (or *sonoriensis?*)	Desert, mainly near Tuba	200(+)	100

[18] This is strictly true only of specimens in the juvenile pelage. We have thus far discovered no certain way of distinguishing the first post-juvenile pelage from later, and more truly "mature" ones, so that our material doubtless includes a certain proportion in the former stage. The differences between the second and later pelages are, however, commonly small in comparison with the racial differences among these mice, and in any case we have excluded the possibility of any "systematic error" due to this cause (see p. 106).

The *Citellus*, *Perognathus* and *Onychomys* represent the three species cited by Merriam (Biological Survey of the San Francisco Mountain Region) as illustrating the modification of mammalian coat color by a background of volcanic soil. Our most extensive series of skins, however, belongs to a species (*Peromyscus maniculatus*) which was not referred to by Merriam in this connection, but which has yielded results of high interest.

Another mouse, *Reithrodontomys megalotis megalotis*, should be mentioned in passing, although, owing to the small number of specimens, it has not been included in the above table. About 20 specimens were trapped in the volcanic region and 15 in the vicinity of Tuba. Of these, 10 and 7 specimens respectively were prepared as study skins. A larger number would have been prepared, had the color differences between the two series been recognized in the field.

One of the commonest mice of the region was *Peromyscus truei truei*. We early began the preparation of a considerable series of skins of this species, in the hope of being able to make an instructive comparison. But *P. truei* was not trapped in sufficient numbers in the more typical portions of the Painted Desert. Specimens from the rocky gorges in the vicinity of the Little Colorado show no significant differences from those trapped at Dead Man Flat and vicinity.

The attempt was also made to collect sufficient numbers of *Peromyscus crinitus* (here represented by the subspecies *auripectus*), the species which was earlier discussed in relation to the lava field in the Mojave Desert. *P. crinitus auripectus* was fairly common in the canyon region of the Little Colorado, but was not taken at Tuba. It was likewise not trapped on Dead Man Flat or vicinity. Of the four specimens which were taken upon a lava field about 12 miles from the latter point (about 6000 feet elevation) it happens that one is noticeably darker than any adult skin in the series of 33 from the neighborhood of the Little Colorado. The remaining three are close to the average of the latter, however, and it is plain that no conclusions are warranted from the material at hand.

ANALYSIS OF THE DATA

1. *Citellus spilosoma obsidianus*[19]

This subspecies of ground-squirrel was described by Merriam from two specimens taken in "the disintegrated lava soil of the cedar belt . . . . northeast of San Francisco Mountain." It was said to exhibit "the darkest phase of coloration yet observed in the species" and was cited, along with certain other "striking illustrations of the law of color adaptation." "*Spermophilus spilosoma obsidianus*", as he then called it, was contrasted on the one hand with the lighter colored *S. s. pratensis*, which was said to inhabit "the grassy openings or parks of the pine belt," and on the other with the yet paler "*Spermophilus cryptospilotus*" of the Painted Desert.

Nine specimens of *Citellus spilosoma obsidianus* were obtained by us from Dead Man Flat. These were prepared as study skins, so that instrumental analysis is out of question. No specimens were taken of the two paler forms described by Merriam. While these squirrels from the piñon-juniper belt vary widely among themselves both in respect to color and to the distinctness of their markings, it may be freely granted that they are all of a considerably darker hue than most ground squirrels from the desert. They are not, however, exceptionally dark, when compared with various mountain or coast-dwelling forms, from regions in which the soil is not volcanic. Reference to museum series of California ground-squirrels shows that the color of our *Citellus* from Dead Man Flat may be matched fairly well by *C. beecheyi beecheyi*, *C. beecheyi fisheri* (particularly specimens from the San Jacinto Mountains), and *C. douglasii*. Indeed, the latter species is much darker than this San Francisco Mountain form, and has an almost jet-black patch on the back, which the latter lacks entirely.

[19] Mr. Goldman informs us that he regards *C. s. obsidianus* and *C. s. pratensis* as synonymous, and that he plans to include both of them under the latter name, this having priority. We have here followed Merriam in employing the name *obsidianus* for the specimens from the piñon-juniper belt, though with no thought of disputing Goldman's opinion as to the identity of the two forms.

We have compared our nine skins of "*obsidianus*" with the type and six topotypes, collected by Merriam and Bailey in 1889. On the whole the latter are plainly redder and somewhat darker than our specimens, but we cannot feel sure that the older material has not undergone a change of color in the course of time. It is significant that the skin, as well as the hair, of these earlier specimens shows a reddish-brown hue, in strong contrast to that of our own material.

If it be objected that the comparison is here made with a quite distinct species, one may fairly reply that this comparison is quite relevant to a discussion of the protective coloration hypothesis. Our contention is that the darker color of San Francisco Mountain ground-squirrels, in comparison with those of the desert, cannot be attributed to the volcanic nature of the soil, nor to any other factors in the color tone of the background. The cases just cited tend to support the view that this is merely one instance, among innumerable others, of the general correlation between body color and atmospheric humidity or rainfall.

2. *Perognathus flavus fuliginosus* and *P. flavus bimaculatus*

Merriam's "*Perognathus fuliginosus*" was based on a single "immature specimen . . . . captured in the cedar and piñon zone on the black lava or 'malpais' northeast of the mountain." It was said to be "modified in the same manner and for the same reason as *Onychomys fuliginosus*," another of Merriam's instances of a protectively colored rodent.

Goldman[20] has likewise described a dark subspecies of pocket-mouse, *Perognathus apache cleomophila* from the vicinity of Winona, a station about fifteen miles east of Flagstaff. Of this he writes: "The dark coloration of the upper parts harmonizes well with that of the decomposed lava or cinders of its local habitat and contrasts correspondingly with that of *P. a. apache* and the lighter sands it inhabits."

We obtained 19 specimens of *Perognathus flavus fuliginosus* from Dead Man Flat and vicinity and 20 specimens of *P. f. bimaculatus* from the Painted Desert, chiefly from the open sandy section some miles from the Little Colorado River. These figures indicate the scarcity of this species in comparison with various other mice of the region.

A very casual inspection suffices to show the marked differences of color tone between these two subspecies. Whereas in both races the dorsal region of the pelage is abundantly sprinkled with black hairs, that of the upland form is much the darker of the two, being in extreme cases nearly black along the mid-dorsal line. Figure 12 shows the lightest and (nearly) the darkest of the flat skins from each of these races. It should be stated that these differences are shown much less strikingly by photographs than by the skins themselves. The mean

[20] Proceedings of the Biological Society of Washington, May 16, 1918.

color values, in terms of "black," "white" and "color"[21] are indicated by the following table, which is based upon the limited number of adult flat skins available for the purpose. Two juvenile flat skins belonging to the "volcanic" series are correspondingly dark, while the considerable number of "study skins" from adult specimens of the latter further emphasize the distinctness of these two races. So far as available specimens are concerned, it may be said that the two series do not overlap one another at all in respect to color characters. The "volcanic" race is consistently darker and less highly colored.

Perognathus flavus (adult)

	VOLCANIC (9)	DESERT (18)
Black	87.3	78.8
White	7.7	10.9
Color	5.0	10.3

General reasons have already been given for doubting the alleged effect of the volcanic soil in bringing about the dark color of its rodent inhabitants. As regards the present species, it may be said that, in some specimens at least, the "protection" has been *greatly overdone*, the dorsal surface of the animals being much darker than the average soil color of the region, and darker than any except the blackest of the cinders.[22] It is, moreover, of interest to point out that two other subspecies of *Perognathus flavus*, *P. f. mexicanus* and *P. f. perniger*, show this same tendency toward a darkening of the pelage. Of the former subspecies, Osgood[23] writes that "many are almost as dark as *fuliginosus*." There is nothing in Osgood's text to indicate that these were collected in volcanic areas, though Mr. Goldman states that "the

[21] For reasons which we shall not justify here, the difference between the highest color-screen reading (red) and 100 per cent is regarded as the percentage of "black," the lowest reading (blue-violet) is regarded as indicating the percentage of "white," while the remainder is credited to (free) "color." The ratio between the figures for "free" red and green (after deducting the amounts regarded as contributing to the composition of the white light present) constitutes the "Red: Green ratio" which is referred to below. It is a rough index of the spectral position of the "free" color. No exact value for the latter is given by the readings and this, indeed, is not required for present purposes.

[22] This statement has been checked by comparison with actual samples of these materials.

[23] Revision of the Pocket-Mice of the Genus Perognathus. North American Fauna no. 18, U. S. Department of Agriculture, 1900.

soils in the higher part of the Mexican table land are rather dark in color." *P. f. perniger* occurs in South Dakota, on "rather heavy soil," Mr. Bailey states.

3. *Onychomys leucogaster fuliginosus, and O. l. melanophrys*

Four specimens of an *Onychomys* were described by Merriam from the vicinity of San Francisco Mountain, and referred to a new species, *O. fuliginosus*. Three of these were said to have been taken on lava beds at Black Tank (12 to 15 miles north of Dead Man Flat). Of this form Merriam writes that "its dark, almost blackish, coloration, unique in the genus, is in as complete accord with the prevailing color of the decomposed lava and 'malpais' soil on which it lives as the pallid-cinnamon tints of its congener of the Painted Desert are with its environment." Merriam regards it as certain that the dark, upland form was differentiated in very recent times from the desert race, which presumably entered the Painted Desert, after the excavation of the latter, by way of the Colorado River.

Here again, we were able, very promptly, to confirm Merriam's statement as to the marked differences of color between the desert and the upland races. The latter animals, to be sure, were not found to be phenomenally dark as Merriam's small series seemed to indicate, but rather of a general color-tone widely prevalent among rodents from non-desert regions.[24] The former, on the other hand, are not only exceptionally pale, even for a desert race, but are highly colored as well. So far as comparison with any single "standard" color is possible, the lateral regions of the pelts of our collection seem to be intermediate between Ridgway's "cinnamon" and "cinnamon buff." The dorsal region, as usual, contains a larger proportion of black hairs.[25]

In figure 13, are shown our darkest and palest adult flat skins of each of these subspecies. It will be seen that there is no overlapping of the two series. Furthermore, the difference in hair pigment is almost as clearly shown on the ventral as on the dorsal side. In general, there is a considerable slaty zone at the basal ends of the ventral hairs

[24] Through the kindness of Mr. Goldman, we have been able to examine three of Merriam's original specimens. The type, a fully adult specimen, appears to be darker than the darkest of our adults, but this may be due to the greasy condition of the fur. The other two are immature.

[25] For more detailed comparisons between these subspecies, see Hollister: A Systematic Account of the Grasshopper Mice, Proceedings U. S. National Museum, vol. 47, 1914, pp. 427–489.

in *fuliginosus* while this is much less developed, and may in places be quite lacking in the desert race. For this reason the ventral pelage of the latter looks intensely white, while that of the former has a slightly grayish appearance.

The differences in the coat color of these two races are shown in a quantitative way in the following tables.

Onychomys leucogaster (adult)

	VOLCANIC (8)	DESERT (24)	LIMESTONE (1)
Black	82.5	70.5	78.5
White	9.8	13.6	11.0
Color	7.7	15.9	10.5

Onychomys leucogaster (immature)

	VOLCANIC (17)	DESERT (7)	LIMESTONE (2)
Black	84.9	74.4	81.7
White	9.7	14.3	11.3
Color	5.4	11.3	7.0

In the tables are likewise given the figures for three specimens of this species which were taken at the trapping station in the limestone territory. Of these three specimens, one of the immature individuals gives readings which are very close to the average values for the immature specimens from the volcanic country. The other two are paler, though both are considerably nearer the means for the volcanic series than the means for the desert series. In the aggregate, the three "limestone" specimens lie about twice as close to the former as the latter, and it seems proper, therefore, to assign them to "*fuliginosus*," rather than to "*melanophrys*." On the other hand, it must be admitted that their condition is to some extent intermediate, though this fact may have no significance.

Two immature specimens of this species were taken in the Painted Desert, near the Little Colorado. These are likewise somewhat intermediate between the Tuba and Dead Man series, but, in the present case they lie closer to the former than to the latter.

In respect to one other character besides coat color the upland and the desert races of *Onychomys* are found to differ widely from one another. The width of the dorsal tail stripe (considered as a percentage of the circumference of the tail) gives us a mean value of 44.2 for the former and 32.8 for the latter. These figures are based upon 25 and 24 specimens respectively.[26] The difference is here nearly equal to that between *Peromyscus maniculatus rubidus* and *P. m. sonoriensis*, belonging to the northern California coast and to the Mojave Desert, respectively.

On the other hand these races of *Onychomys* show no difference in respect to the pigmentation of the hind foot. Every foot which was examined was assigned to the "0" grade of pigmentation,[27] with the exception of a single specimen, belonging to the volcanic series, which showed a low grade of pigmentation ("1").

As in the case of the species previously considered, there seems to be no good reason for attributing the differences between these two subspecies of *Onychomys* to differences in the color of the soil. The doubtful nature of the "protection" afforded by the color of *fuliginosus* against a mixed background of pale turf and dark soil, has been already discussed (p. 87 and figures 10, 11).

As a further reason for questioning the origin of the dark color of *O. l. fuliginosus* as a protective adaptation may be mentioned the fact that both species of *Onychomys*, *O. leucogaster* and *O. torridus*, contain subspecies nearly or quite as dark as *fuliginosus*. In some of these cases, at least, the color-tone of the background can hardly be invoked as an explanation.

4. Peromyscus maniculatus rufinus and P. m. sonoriensis (?)

Merriam described as a new subspecies "*Hesperomys leucopus rufinus*," from San Francisco Mountain, at an altitude of 9,000 feet, and lists 24 specimens from this mountain, without further specifications as to locality. He also lists 10 specimens of "*Hesperomys leucopus sonoriensis*" from the "Painted Desert," although it is evident from the text that 7 of these were taken from lava beds near "Black Tank," far above the desert proper. He makes no comparison between these two races in respect to color, which may readily be accounted for, in view of the relatively slight differences here shown and the small size of Merriam's series.

We have no desire to involve ourselves in any discussion of the sub-

[26] The tail stripe presented too indefinite an outline in many of the desert specimens to allow of its being measured.

[27] See Sumner, Journal of Experimental Zoölogy, April, 1920.

specific position of the mice here to be considered by us.[28] That they all belong to the more inclusive species known as *Peromyscus maniculatus* is beyond doubt. Our present task is to compare collections made at our four groups of trapping stations with one another and, incidentally, with certain races from more distant points. For the purposes at hand, the nomenclature used is quite immaterial.

The specimens from the volcanic districts in the piñon-juniper zone are appreciably smaller, on the average, than those taken in the vicinity of Tuba. The two collections (each including numerous immature, though not juvenile, specimens) average 86.5 and 90.0 millimeters in body length (body + head), respectively, these figures being based upon 131 and 99 individuals.[29] This difference in length is further indicated by the fact that 11 of the Tuba series reach a length of over 95 millimeters, while only one of the volcanic series reaches this length, despite the larger numbers comprised. Except for this difference in mean size, the significant differences which we have observed between these two races all relate to the pigmentation of the hair and skin.[30]

Unlike the cases of *Perognathus* and *Onychomys*, which have been discussed above, the differences between these local collections of *Peromyscus* are shown only by a comparison of considerable numbers. Many specimens from the volcanic district are as pale as average specimens from the desert, while a few from the desert are very nearly as dark as the darkest from the volcanic district. Each series presents a wide range of variability. Nevertheless, the mean differences between these two races, in respect to a number of pigmental characters, while small, are of absolutely certain significance. In only one case among those listed ("color") is the difference statistically doubtful. The other quotients $\frac{\text{(difference)}}{\text{probable error}}$ range from 4 to 17.5 in magnitude.

[28] Osgood (Revision of the Mice of the American Genus Peromyscus) assigns to *sonoriensis* the 11 specimens from the Painted Desert which were examined by him, and to *rufinus* the 28 specimens from San Francisco Mountain.

[29] All specimens smaller than 80 millimeters in body length have been excluded from these computations.

[30] Of course this difference in body-size involves corresponding size-differences of all the parts, but these absolute differences are not what are here referred to. When the lengths of the various appendages are reduced to a standard body-length of 90 millimeters (Sumner, Journal of Experimental Zoology, April, 1920), the differences are slight or non-significant.

Peromyscus maniculatus

	VOLCANIC (110)	TUBA (75)	DIFFERENCE (VOLCANIC AND TUBA)	LIMESTONE (43)
Black	83.2±0.13	80.7±0.23	2.5 ±0.26	82.8±0.17
White	8.7±0.07	10.8±0.10	2.1 ±0.12	9.2±0.08
Color	8.1±0.09	8.5±0.18	0.4 ±0.20	8.0±0.12
Red:Green ratio	2.99±0.02	2.85±0.02	0.14±0.028	2.95±0.03
Tail stripe*	28.9±0.22	27.1±0.23	1.8 ±0.32	27.1±0.28
Foot pigmentation*	1.48±0.05	1.22±0.04	0.26±0.064	1.37±0.08

* The figures for these characters are based upon larger numbers of individuals than those for hair color. The numbers in this case are 131, 99, and 57, respectively, for the three series.

Since the three components "black," "white" and "color" in every case total 100 per cent, they are not, of course, independent variables. The more black is present, for example, the less white and color. On the other hand, the red: green ratio is not correlated in the least with the darkness or paleness of the skin. It is of interest to point out the small though significant difference between these ratios for the "volcanic" and "desert" series. This corresponds to the fact that even a naked-eye comparison of these series seems to show a larger proportion of *reddish* skins among the former and a larger proportion of *yellowish* ones among the latter. The last circumstance is quite independent of the difference in shade, due to differing proportions of black. It is interesting to note that these same differences, both in respect to shade and to color, have been found to obtain between *P. m. sonoriensis* and some other races, especially *P. m. rubidus*, in California.

The difference in the mean width of the tail stripe is so small that it was not detected until the measurements were averaged. It appears, however, to be a real one, being about 5½ times its probable error. This difference, likewise is of the same sort (though less in degree) as that between desert and non-desert races in California.

Another difference to be noted is that in respect to the pigmentation of the hind foot. This difference likewise appears to be statistically significant, being four times its probable error. Here again, we are dealing with one of the characters which distinguish *P. m. sonoriensis* from the darker races *gambeli* and *rubidus*. It must be admitted, however, that in the Arizona case we can not be at all certain that this difference between our mountain and desert series has any biological significance. Foot pigmentation is found to be in a considerable degree correlated with body length (perhaps due to changes with age). When due allowance is made for this factor, the difference between these races is so far diminished that we cannot be sure it is not accidental.

It must, however, be pointed out in this connection that none of the other pigmental differences here considered can be due to possible differences in the mean size or age of the series. No correlation whatever has been detected between body length and the relative width of the tail stripe. While the same cannot be said of body length and coat-color[31] steps have been taken to eliminate this possible source of error. To test this point the mice of each of our two chief races ("Tuba" and "Volcanic") were divided into groups of approximately the same body length, and the mean of the character in question (e.g. "black") was determined for each of the size groups. Thus the comparisons between the two races could be limited to groups of individuals of approximately the same size. While it is not worth while to encumber this report by figures or graphs, illustrating these relations in detail, we are able to say that such a treatment of our material leaves unaffected the differences between these two races in respect to coat color.

One of the important features of the foregoing table is the comparison which it permits between the limestone series and the two major series considered in these studies. Eighty-eight specimens of *P. m. rufinus* were trapped in this last region, of which 57 were measured, and 45 skinned.[32]

Examining these last figures in detail we find that the limestone series averages slightly paler than the volcanic one, though the difference is not of probable significance. On the other hand, the former series is undoubtedly darker than the desert one. On the whole, it seems fair to say that, in respect to color, the limestone mice belong to the upland

[31] Coat color is known to change with age, at least during the earlier months of life. For this or some other reason, it has been found that certain series of mice show an inverse correlation between body length and the percentage of black in the hair. Such a correlation seems to hold in the case of the *P. m. rufinus*, belonging to our "volcanic" race.

[32] A larger series, representing this critical locality, would have been desirable. On the occasion of our first trip to the limestone district, we were seeking primarily for *Perognathus* and *Onychomys*. Since it was not at that time realized that *Peromyscus* showed any local differences throughout the entire region, few specimens were saved. A later visit was made in November, after severe winter weather had commenced. These weather conditions unfortunately made it necessary for us to abandon field work rather hurriedly.

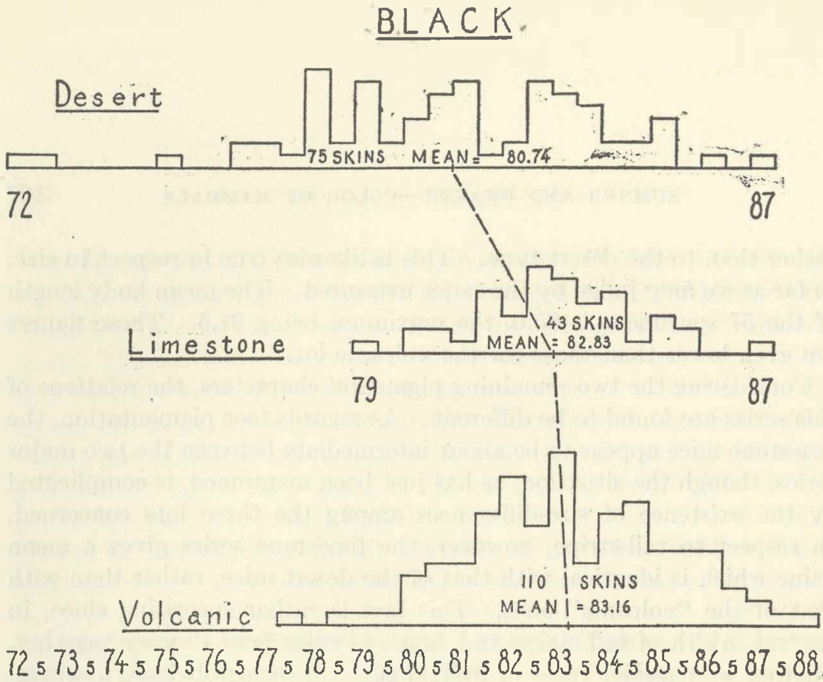
rather than to the desert type. This is likewise true in respect to size, so far as we may judge by the series measured. The mean body length of the 57 specimens is 85.0, the maximum being 91.5. These figures are even lower than those for the volcanic lot.

Considering the two remaining pigmental characters, the relations of this series are found to be different. As regards foot pigmentation, the limestone mice appear to be about intermediate between the two major series, though the situation, as has just been mentioned, is complicated by the existence of size-differences among the three lots concerned. In respect to tail-stripe, however, the limestone series gives a mean value which is identical with that of the desert mice, rather than with that of the "volcanic" ones. This fact is rather surprising since, in general, width of tail stripe and depth of color tend to vary together, whether we consider races or individuals. It seems obvious, however, that this character has but a remote bearing on the protective coloration hypothesis.

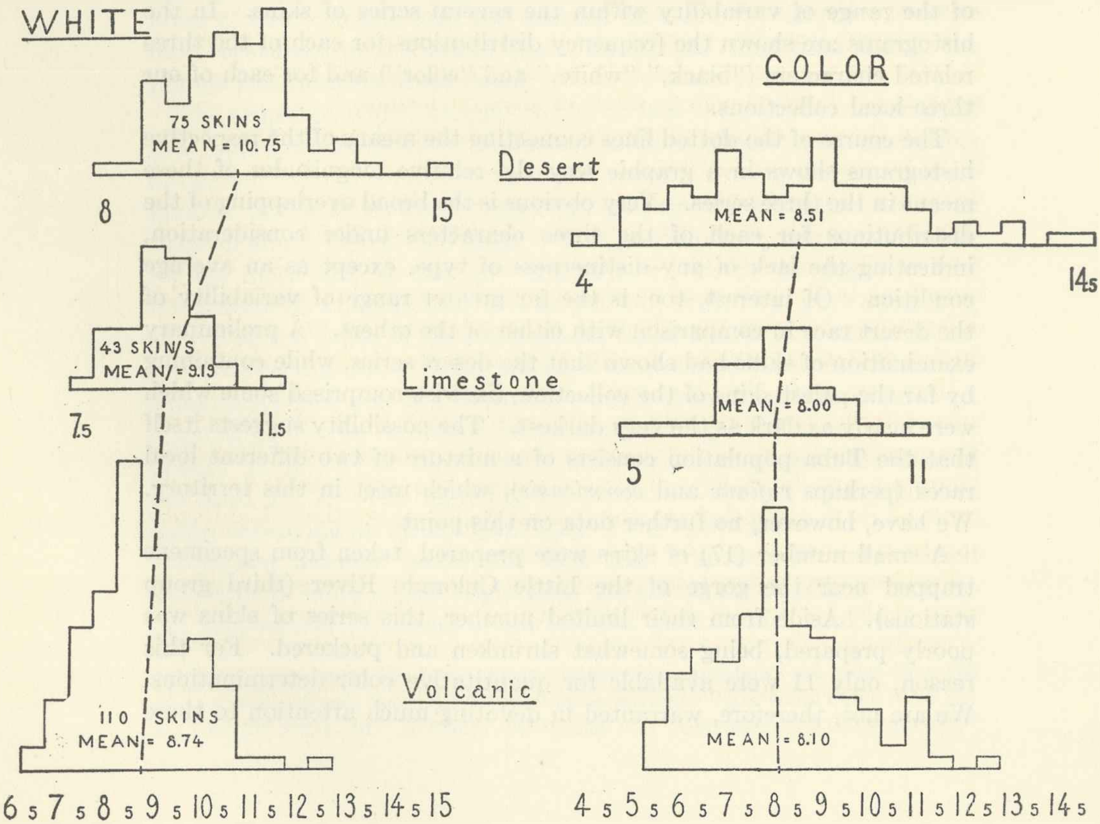
The foregoing table deals only with mean values, and gives no idea of the range of variability within the several series of skins. In the histograms are shown the frequency distributions for each of the three related characters ("black," "white," and "color") and for each of our three local collections.

The course of the dotted lines connecting the means of the respective histograms shows in a graphic way the relative magnitudes of these means in the three series. Very obvious is the broad overlapping of the distributions for each of the three characters under consideration, indicating the lack of any distinctness of type, except as an average condition. Of interest, too, is the far greater range of variability of the desert race in comparison with either of the others. A preliminary examination of skins had shown that the desert series, while containing by far the palest skins of the collection, likewise comprised some which were nearly as dark as the very darkest. The possibility suggests itself that the Tuba population consists of a mixture of two different local races (perhaps *rufinus* and *sonoriensis*), which meet in this territory. We have, however, no further data on this point.

A small number (17) of skins were prepared, taken from specimens trapped near the gorge of the Little Colorado River (third group stations). Aside from their limited number, this series of skins was poorly prepared, being somewhat shrunken and puckered. For this reason, only 11 were available for quantitative color determinations. We are not, therefore, warranted in devoting much attention to these



HISTOGRAMS, SHOWING PERCENTAGES OF "BLACK" FOR EACH OF THE THREE PRINCIPAL SERIES OF PEROMYSCUS MANICULATUS, DISCUSSED IN THIS REPORT



HISTOGRAMS, SHOWING PERCENTAGES OF "WHITE" AND "COLOR," FOR PEROMYSCUS MANICULATUS mice, nor in basing any conclusions of importance upon them. It need only be said that on the average they are intermediate in shade between the "volcanic" series and that taken at Tuba, a point considerably nearer the heart of the Painted Desert. No particularly pale specimens are included in this small series, the lowest value for "black" being 80 per cent, as compared with 72 per cent in the Tuba lot.

To recapitulate the evidence derived from *Peromyscus maniculatus*, we may say that the upland mice (whether from volcanic or limestone territory) average somewhat smaller than the desert ones (at least those of the Tuba lot), and that they average somewhat darker than the latter in respect to coat color. Mice from the volcanic territory likewise have a slightly broader average tail stripe, and slightly darker feet than those from the Tuba district.

The limestone series, while very slightly paler than the volcanic series, agrees with the latter in being significantly darker than the desert race. In respect to tail stripe, on the other hand, the limestone mice agree with those from the desert.

Specimens from the vicinity of the Little Colorado River appear to be intermediate in coat color between desert and upland forms, but the series is not large enough to allow of any conclusions.

As in the case of the rodents previously discussed, there would seem to be no reason for attributing the slightly darker hue of the upland deer-mice to any influence of the color tone of the ground upon which they live. Aside from the general considerations which were dealt with in our discussion of the local environment, we have in this case something in the nature of an experimental "control" permitting us to differentiate between the effects of meteorological and soil conditions. Such a control is furnished by our series from the limestone district.

Here, too, as in the other cases, it should be borne in mind that the upland forms are dark only in comparison with those of the desert. The specimens of *P. m. rufinus* from the neighborhood of San Francisco Mountain are, in reality, of almost exactly the same shade as specimens of *P. m. gambeli* from the coastal region of southern California and from Calistoga, at the head of Napa Valley.[33]

Furthermore, it must be pointed out that the upland and desert races of the portions of Arizona visited by us differ far less in respect to nearly all these pigmental characters than do *gambeli* and *sonoriensis*,

[33] This applies strictly only to the percentage of "black." The proportions of "white" and "color" are somewhat different in the three cases mentioned.

from climatically contrasted regions of southern California. The following table gives the values for these same characters in the two latter races.

Peromyscus maniculatus gambeli and P. m. sonoriensis (Southern California)

	LA JOLLA (COAST)	VICTORVILLE (DESERT)
Black	83.47±0.23	78.06±0.24
White	9.70±0.13	11.00±0.12
Color	6.83±0.16	10.94±0.18
Red:Green ratio	2.96±0.04	2.94±0.03
Tail stripe	32.31±0.26	28.12±0.24
Foot pigmentation	1.88±0.09	0.90±0.07

If differences in pigmentation are due to differences in the colortone of the background, we should hardly expect these to be so much greater in the case of the two California races than in the case of the two Arizona ones. The relations are more in harmony with the known fact that the differences in climatic conditions are far greater between the California stations under consideration than between the Arizona ones.[34]

In this connection it must be insisted that *Peromyscus*, as well as *Onychomys* and *Perognathus*, are almost exclusively nocturnal in their habits. The following test affords striking evidence of this fact. One hundred live traps were baited and set on Dead Man Flat shortly before noon (10:30 to 12:30). They were inspected at the close of the afternoon (4:45 to 5:55,—the sun set about 5:30). Not a single trap was found to contain a mouse. On the following morning, these 100 traps contained exactly 100 mice, 95 of which were *Peromyscus maniculatus rufinus*, the others being *Reithrodontomys*.

While it is not claimed that nocturnal animals have no need whatever for protective coloration, the need would seem to be far less urgent than in the case of diurnal ones.

[34] It may well be that the much greater *distance* between the contrasted stations in California has played a part in the matter. Were atmospheric humidity the only factor concerned we should expect the La Jolla mice to be far *darker* than those from Dead Man Flat. But no such strict proportionality in the effects of this factor are claimed to exist.

5. *Reithrodontomys megalotis megalotis*.[35]

Seven study skins of this species from the neighborhood of Tuba City were compared with 10 from Dead Man Flat. The former, as a series, are paler than the latter, not only as regards the general hue of the dorsal and ventral surfaces of the body, but likewise as regards the color of the snout region and the dorsal surfaces of the feet. Such a distinction in color-tone could not, it is true, be maintained for every specimen of one series in comparison with every specimen of the other. But it holds for the two series in the aggregate, and the difference was commented upon independently by five different observers. Even more pronounced than this difference in the average shade of the pelage is a difference in the distribution of the light and dark hairs. In the upland form the pelage presents a more homogeneous color-tone.

The small number of specimens[36] renders the result of such a comparison inconclusive, but it is quite in keeping with the relations just described for *Peromyscus maniculatus*.

SUMMARY AND CONCLUSIONS

1. We are able to confirm the statements of Merriam, Bailey and Goldman that certain rodents of the volcanic region surrounding San Francisco Mountain, Arizona, are darker than their nearest relatives in the Desert of the Little Colorado (Painted Desert), not many miles distant.

2. With regard to both *Onychomys leucogaster* and *Perognathus flavus*, the two local subspecies are so widely distinct that there is little or no overlapping of their ranges of variation, in respect to coat color. In *Onychomys* the difference relates to the width of the tail stripe, as well as to the color of the pelage.

3. *Citellus spilosoma obsidianus*, the remaining one of the three rodents mentioned by Merriam as being specially adapted to a dark background of volcanic soil, is represented in our collections by nine specimens. We did not, however, obtain specimens of the paler subspecies reported by Merriam as inhabiting nearby non-volcanic areas.

4. Two very limited series of the harvest-mouse (*Reithrodontomys megalotis megalotis*) exhibited local differences, comparable with those shown by the *Peromyscus* next to be discussed.

[35] Mr. Goldman assigns all of our specimens to this subspecies.

[36] Many more were trapped, but few were skinned, owing to our first impression that these two local races agreed very closely in shade.

5. Considerable collections of skins of *Peromyscus maniculatus* reveal the existence of a small but significant mean difference between specimens taken in the volcanic regions of the piñon-juniper belt (6,000–7,000 feet) and a point in the Painted Desert, about 50 miles distant and 2,000 feet lower in altitude. The upland race is darker and slightly redder on the average than the desert race, as well as being somewhat smaller. Likewise the dorsal tail stripe is somewhat broader in the former, and the feet more deeply pigmented.

6. In order to test the question whether this difference has been due to the adaptation of the upland race to a background of particularly dark soil, a control series of mice of the last named species was trapped in a limestone region, at the same elevation as the volcanic territory, but about ten miles removed from the nearest outflow of volcanic material. The "limestone" series of mice were found to be very nearly, though not quite, as dark as the "volcanic" series. The situation here is quite in harmony with that described by the senior author in relation to the species *Peromyscus crinitus*, from volcanic and non-volcanic regions of the Mojave Desert.

7. A further reason for doubting the alleged influence of the color-tone of the background upon the coat-color of these rodents lies in the fact that the ground surface is, in reality, not exceptionally dark throughout much of this volcanic region, while the soil everywhere (except in very limited fields of exposed lava) is partially covered by clumps of turf and low shrubs (mainly *Chrysothamnus*). Since both of these last are commonly of a pale hue, they give to most of this territory a predominantly light colored aspect, rather than a dark colored one, when viewed from a short distance.

8. Pointing to the same conclusion is the fact that these darker rodents of the upland districts are only dark in comparison with related forms from the neighboring deserts. They are not particularly dark when compared with other mountain and coast-dwelling races. This is true, at least, of the species of *Peromyscus*, *Onychomys* and *Citellus*, here considered. It is perhaps not true of one species of *Perognathus* (*P. flavus*) which is admittedly dark—darker, probably, than most of the bare ground in the region which it inhabits. We must, however, call attention here to the existence of other dark subspecies of *Perognathus flavus*, which have been described from regions not known to be volcanic.

9. For these and other reasons, it seems to us more likely that climatic factors, rather than the optical properties of the background, are

responsible for the differences of color between rodents from San Francisco Mountain and the Desert of the Little Colorado. Of these various factors it seems probable that atmospheric humidity (including rainfall, which must affect the humidity of the air within the burrows) is the most important. As to how this factor acts—whether directly or indirectly—we have no knowledge at present. In any case, it doubtless acts in conjunction with other unknown factors in the production of these differences of pigmentation. The protective coloration hypothesis, while having a wide applicability in nature, does not seem to account satisfactorily for the color differences between desert dwelling mammals and the denizens of more humid climates.

Scripps Institution, La Jolla, Calif., and Museum of Vertebrate Zoology, Berkeley, Calif.

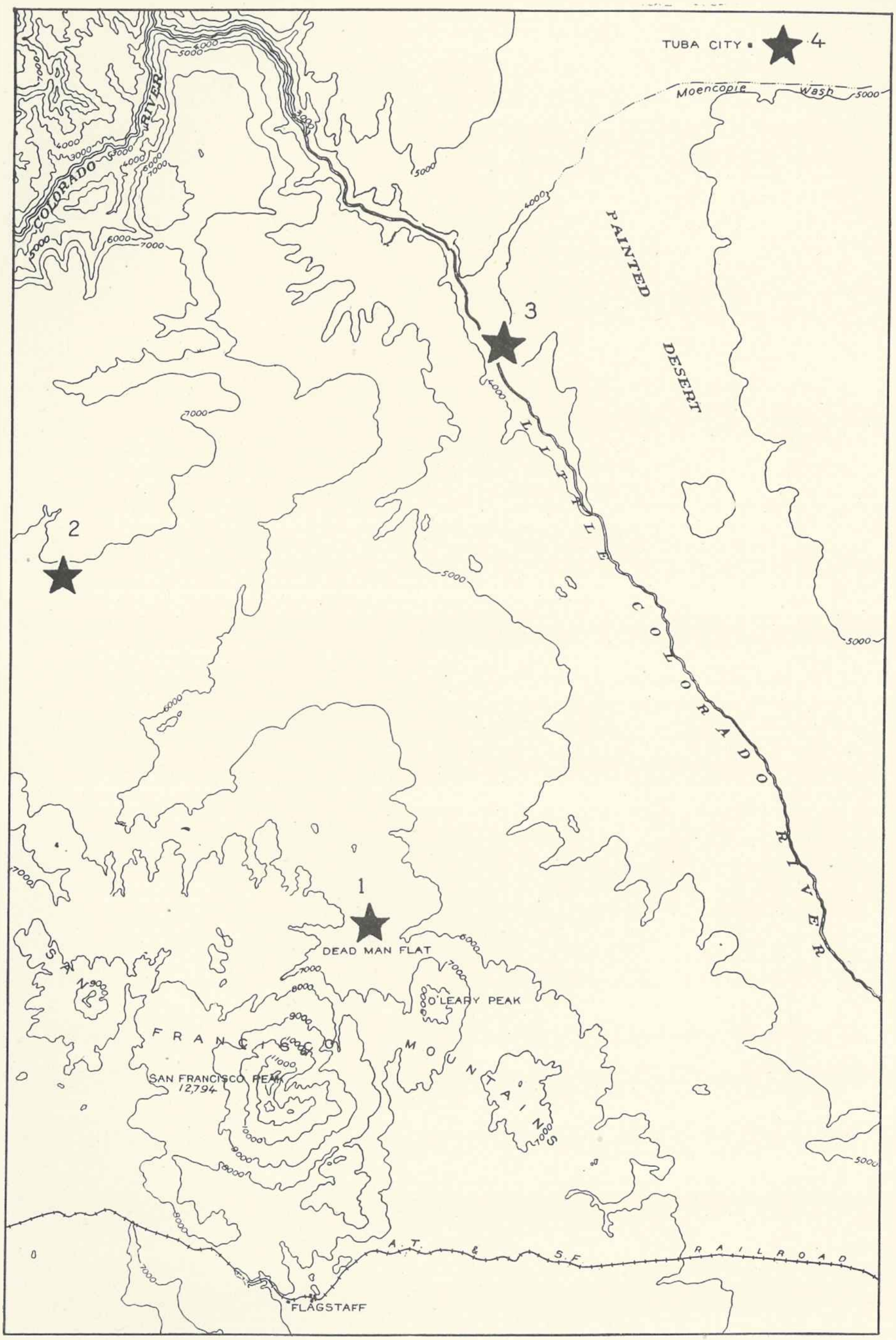
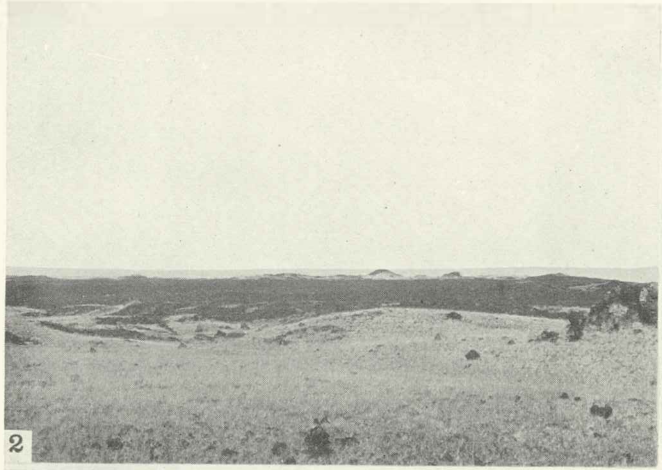
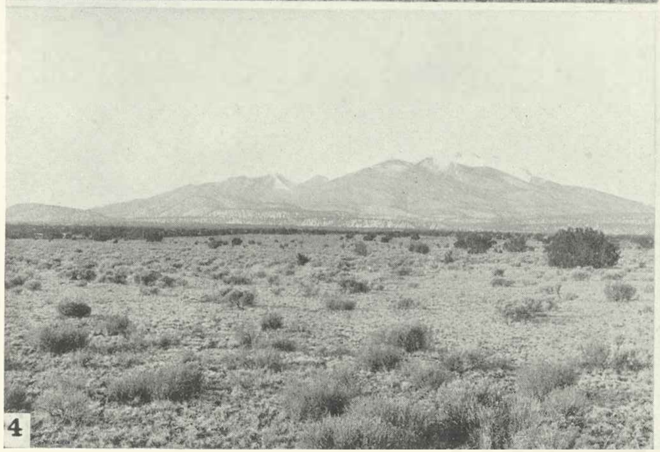


Fig. 1. Map showing region discussed in present paper, based upon U. S. Geological Survey quadrangles "San Francisco Mt." and "Echo Cliffs." Stars indicate approximate position of principal areas in which rodents were collected. (1) Dead Man Flat, representing volcanic territory in piñon-juniper zone; (2) the limestone station; (3) stations in vicinity of Little Colorado River; (4) stations near Tuba City.

(Sumner and Swarth: Color of Mammals)





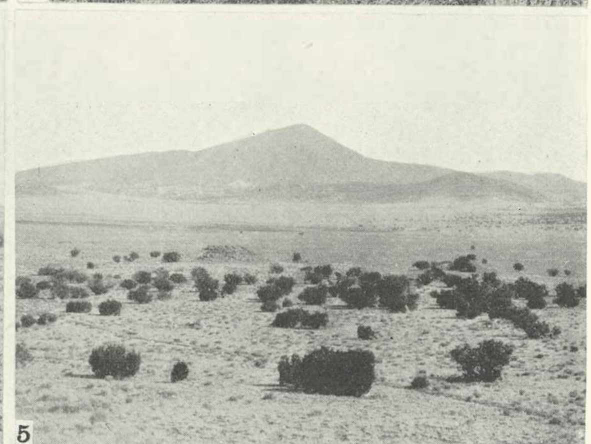


Fig. 2. Edge of lava field (T 26 N, R 7 E), not far from "Black Tank" of Merriam's San Francisco Mountain report. Fig. 3. Area covered with exceptionally dark volcanic "cinders" and having ground comparatively little concealed by turf and shrubs. Fig. 4. Dead Man Flat, showing turf and brush, covering greater part of ground surface. This is more typical of condition within volcanic area. (San Francisco Mountain in the background.) Fig. 5. Another view of Dead Man Flat, from a slight elevation.

(Sumner and Swarth: Color of Mammals)

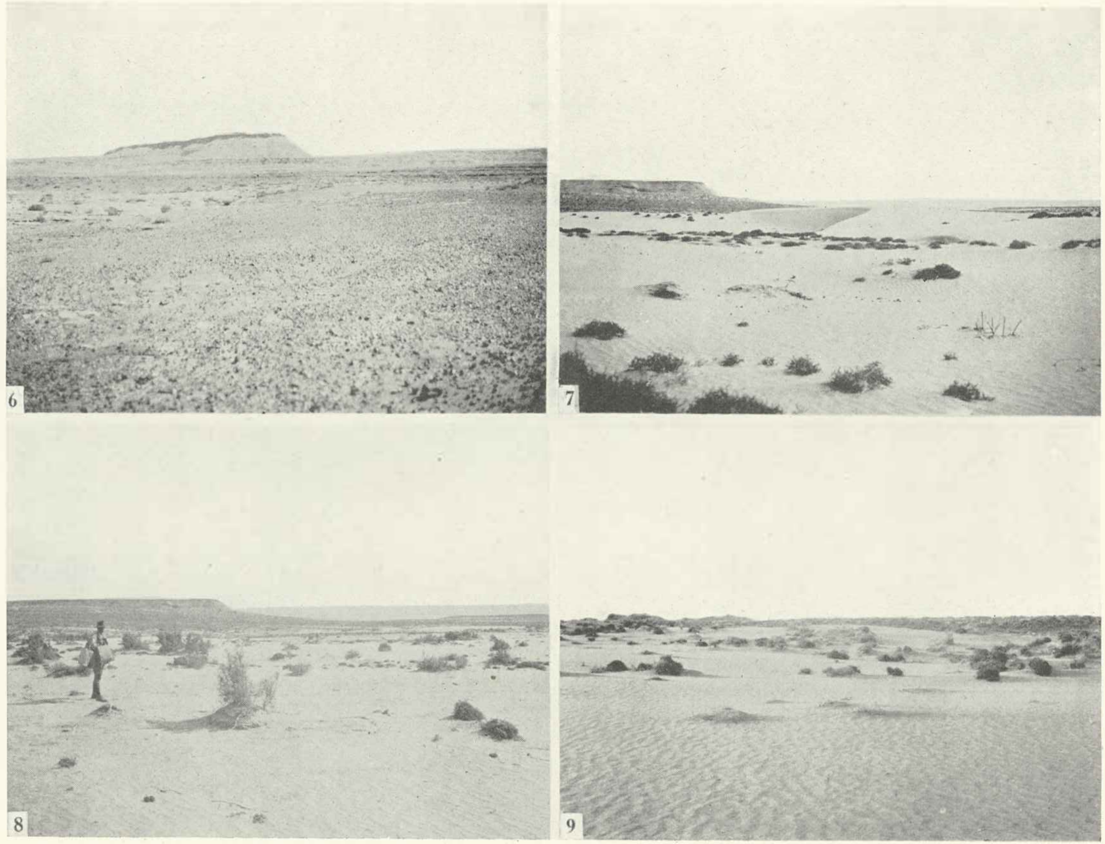
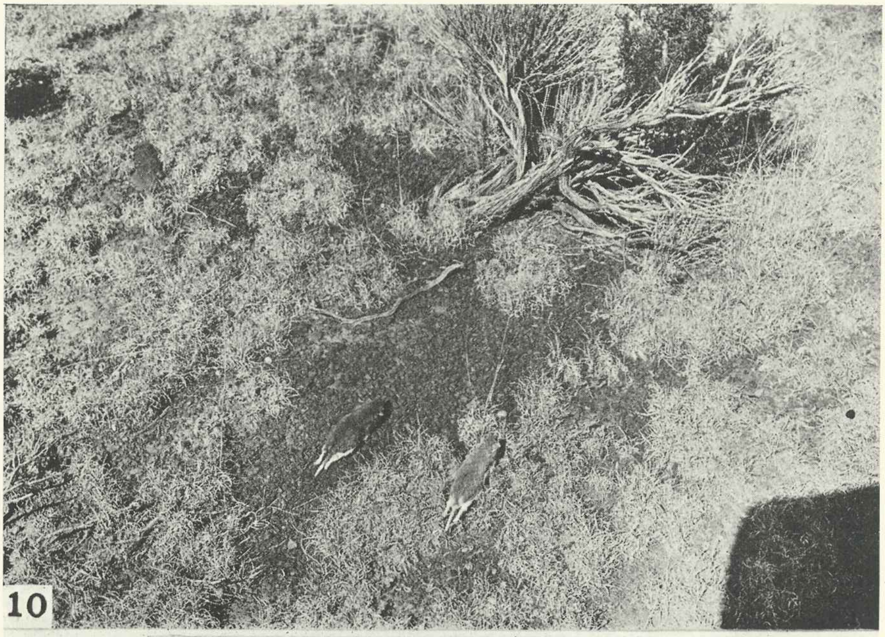
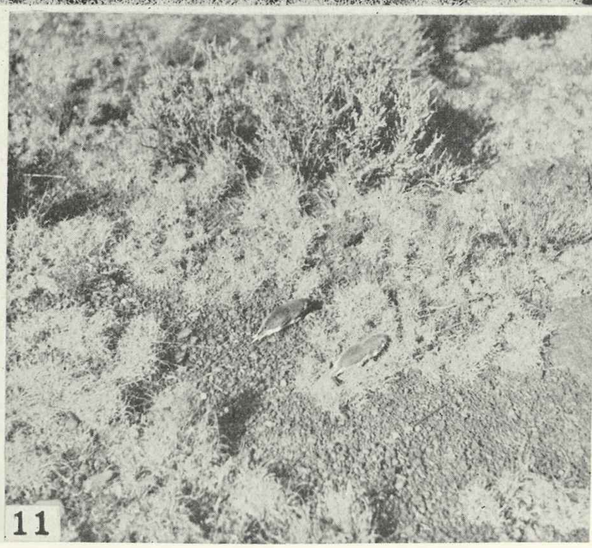


Fig. 6. Desert of the Little Colorado (Painted Desert),—an area in which surface is covered with coarse gravel. Figs. 7, 8, 9. Painted Desert, near Tuba,—region of drifting sand and widely scattered vegetation.

(Sumner and Swarth: Color of Mammals)





Figs. 10, 11. Skins of *Onychomys leucogaster fuliginosus* and *O. l. melanophrys*, against a mixed background of volcanic cinders and pale, straw-colored turf. The color-tone of *melanophrys* seems to harmonize as well with the latter background as *fuliginosus* does with the former. (For the purpose of these photographs areas were selected having more than average proportions of dark cinders.)

(Sumner and Swarth: Color of Mammals)

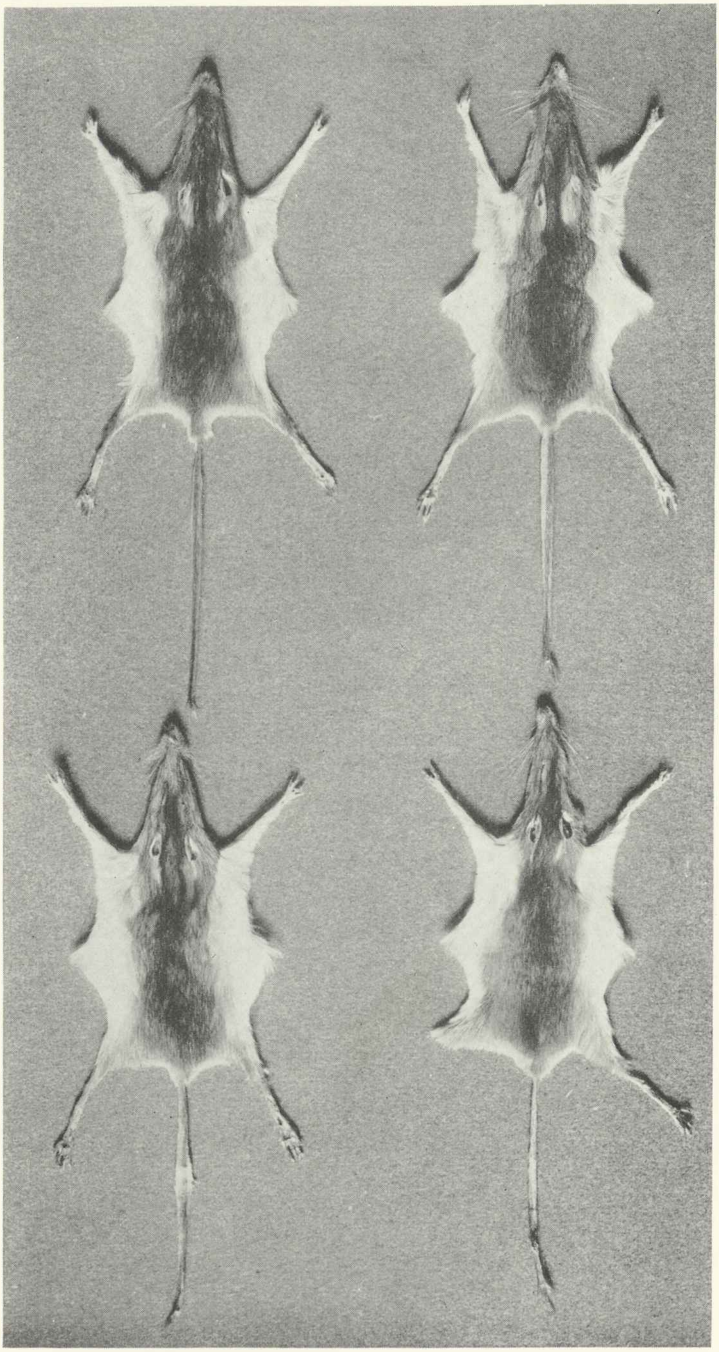


Fig. 12. The darkest (except one) and palest flat skins of *Perognathus flavus fuliginosus* (above), and the darkest and palest skins of *P. f. bimaculatus* (below). The darkest skin of *fuliginosus* is considerably darker than that here shown, but has not been figured owing to poor preservation.

(Sumner and Swarth: Color of Mammals)

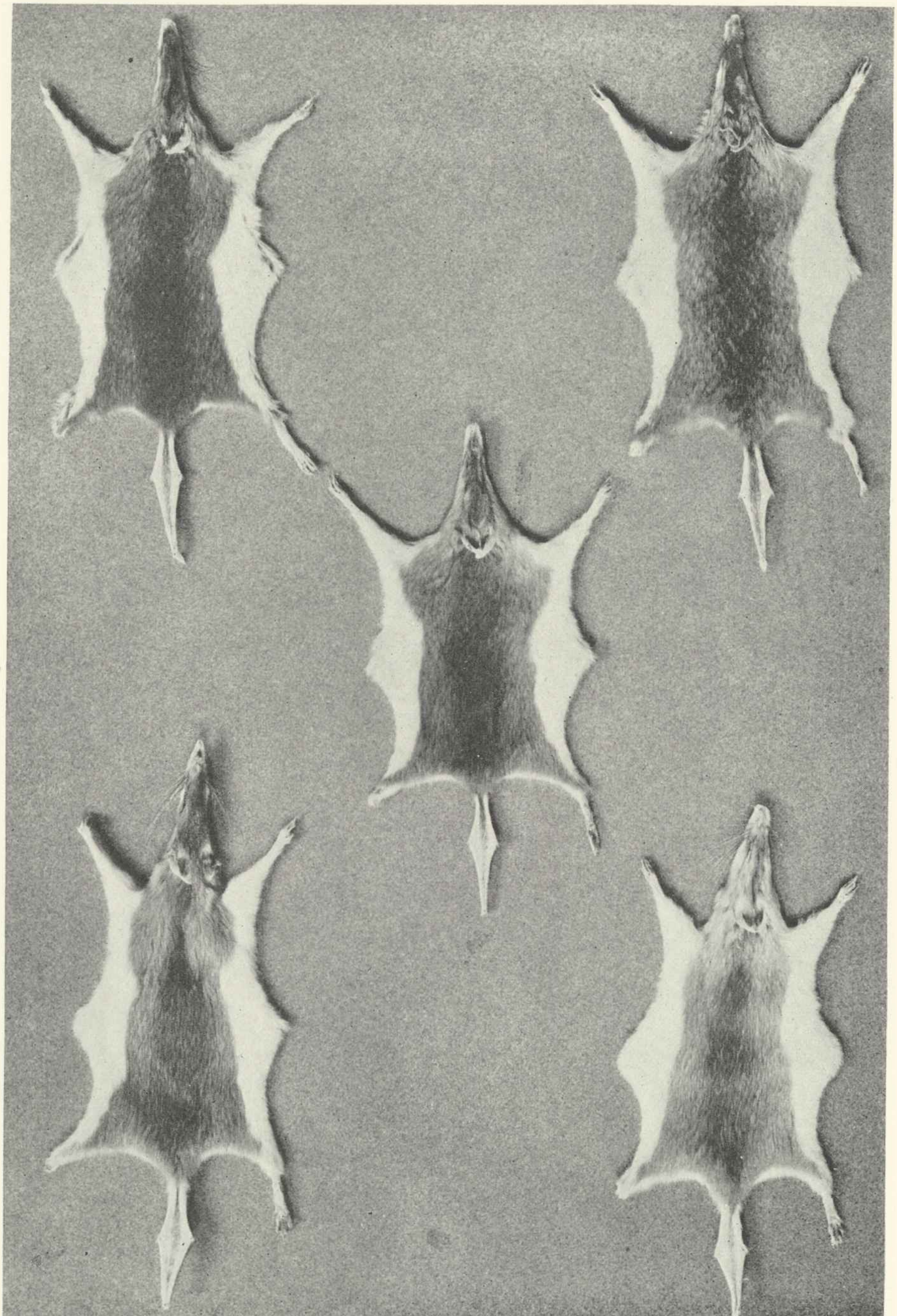
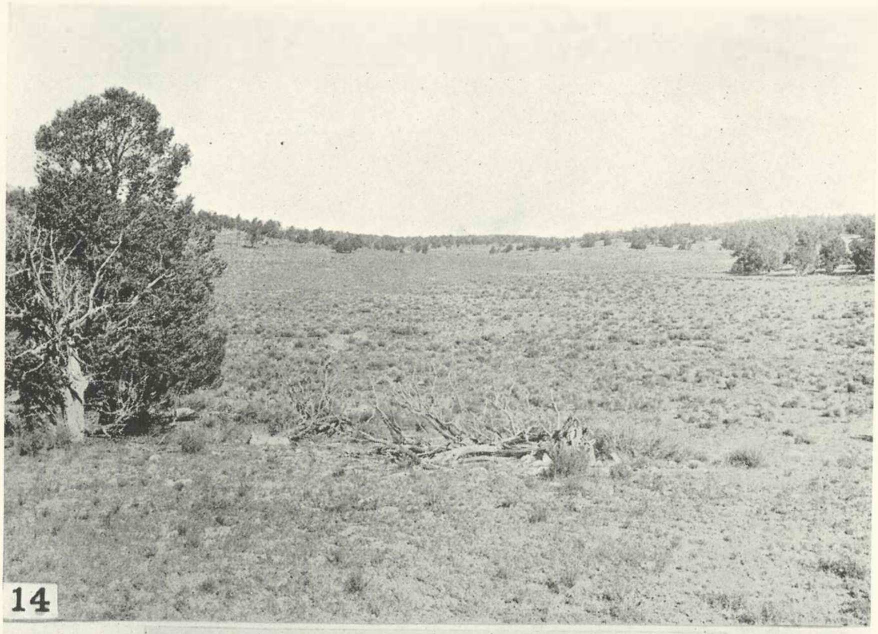


Fig. 13. Above: darkest and palest flat skins of *Onychomys leucogaster fuliginosus* from Dead Man Flat. Center: single mature skin of same subspecies from limestone region. Below: darkest and palest *O. l. melanophrys* from vicinity of Tuba City.

(Sumner and Swarth: Color of Mammals)



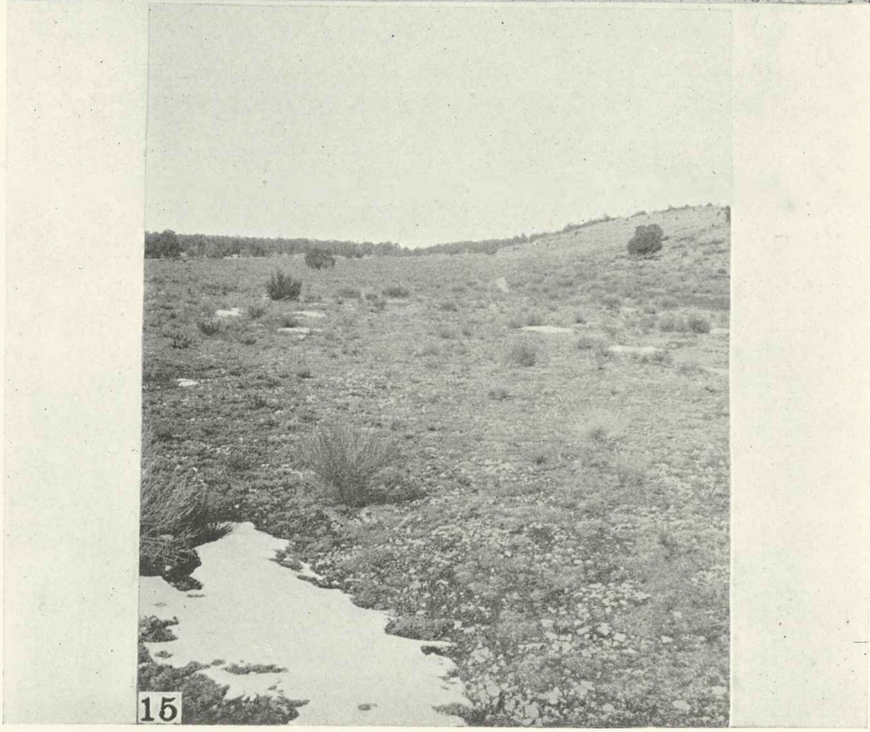


Fig. 14. Region of Kaibab limestone. Open "flat" or "park," surrounded by piñon-juniper forest. (The "limestone" series of mice were trapped here.) Fig. 15. (See figure 14.) The larger white areas are snow, the smaller ones are due to pale rock fragments.

(Sumner and Swarth: Color of Mammals)