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*The American Naturalist*, Vol. 51, No. 610. (Oct., 1917), pp. 577-595.

Stable URL:

*The American Naturalist* is currently published by The University of Chicago Press.

## THE MUTATION THEORY AND THE SPECIES-CONCEPT[1]

### R. R. GATES

IN the early days of natural history, when the conceptions of special creation held sway, it was supposed that any one could determine species who was capable of observing the differences between existing forms. Linnæus crystallized this sentiment into the dictum that there are as many species as were created in the beginning, implying that any one with sufficient powers of discrimination could determine exactly how many species there were in each group. But with the introduction of the theory of evolution, species came to be viewed more and more as dynamic entities, and questions of origin have entered progressively into the species-concept. The latter has grown continually more complex, and yet Darwin's anticipation that systematists would cease to discuss how many Rubi there were in Britain or how many Crataegi in North America, has not been realized.

On the contrary, with this increase in the complexity of the conception of species, the extreme views as to what constitutes a species have become more and more divergent, until the "lumpers" and "splitters" among systematists usually differ radically in their interpretation of the species in a given genus. This diversity of opinion among systematists has been partly a direct result of our increasing knowledge of the complexity of species, de-

[1] Presented at the Pacific Coast meeting of the American Association for the Advancement of Science at San Diego, August, 1916.

rived from studies of variation and geographical dis-
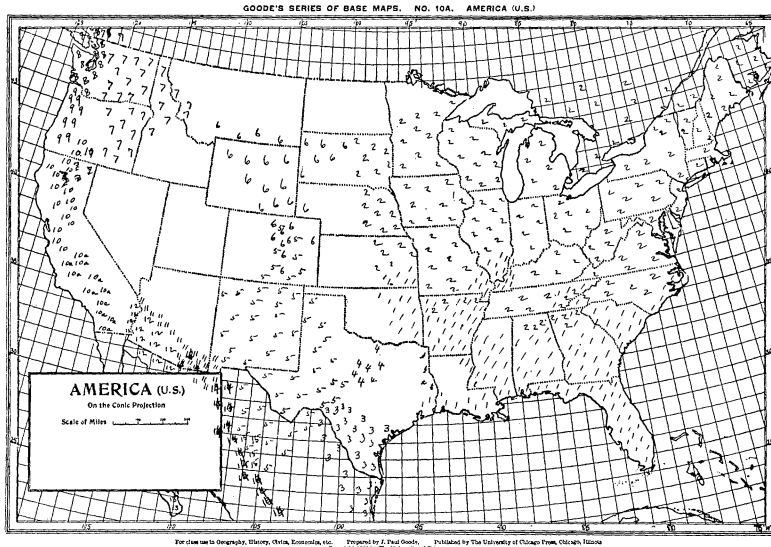tribution and from the experimental study of evolution.



FIG. 1

*Key to Map*

1. *Otus asio asio* (Linn.) Ridgway (= *floridanus*).
2. *Otus asio naevius* (Gmel.) Ridgway.
3.          *mccallii* (Cassin) Ridgway.
4.          *hasbroucki* Ridgway.
5.          *aikeni* (Brewster) Ridgway.
6.          *maxwelliae* (Ridg.) Ridg.
7.          *macfarlanei* (Brewster) Ridgway.
8.          *kennicottii* (Elliot) Ridgway.
9.          *brewsteri* Ridgway.
10.         *bendirei* (Brewster) Ridgway.
10a.        *quercinus* Grinnell.
11.         *cineraceus* (Ridg.) Ridg.
12.         *gilmani* Swarth.
13.         *xantusi* (Brewster) Ridg.
14. *Otus trichopsis* (Wagler) Ridg.
15. *Otus vinaceus* (Brewster) Ridg.

If we look for a moment first at the complexities which
have been added to the original simple concept of species,
we find all grades and kinds of difference within the
species itself, such as subspecies, varieties, forms and
races, ending finally in the differences between single in-
dividuals. Some of these conceptions as ordinarily used
are also related to geographical distribution. To them

must be added from experimental work the conceptions of mutants, Mendelian units, phænotypes and genotypes, and pure lines differing only in the position of their modal condition and requiring statistical analysis for their demonstration.

With such an array of apparently (though not really) conflicting concepts before him, it is small wonder that the systematist is inclined to cast them all aside and describe his species according to his own ideas of what they are and how they have originated. Nevertheless, for him as for the experimentalist the question What is a species? is more or less colored, if not determined by the question What is its origin? How did it appear? It might be said that the systematist should pay no attention to origins at all, merely describing what he sees. Some systematists doubtless adopt this plan. But obviously, for an understanding of the characters and relationships of species all possible facts and conceptions bearing on their origin should be considered, and in this way systematics may ultimately hope to become something more than a purely descriptive science.

If we examine the ideas which form the background of thought of the systematist in his work of constructing species, we find almost invariably that they are based entirely upon the Darwinian conception of natural selection by the gradual accumulation of slight individual differences. We are then concerned to ask, Is the systematist justified in assuming that all specific and varietal differences have originated in one way? I can find no reason in logic or philosophy why this should be the case; and for ourselves, we believe there is no single method of species formation, but we think the conclusion will ultimately be reached that the methods of species formation are multiform, though certain of them are doubtless more widespread and important than others. Among the more important factors in speciation which we wish to consider here should therefore be mentioned (1) local adaptation of races through natural selection or by direct response

to environment, (2) mutations occurring more or less independently of the environment and not necessarily of adaptive value, (3) orthogenesis, whatever that may imply. These are by no means mutually exclusive, and we can see no reason why all, and others as well which we have not time to consider, should not have been at work producing the result we call organic evolution.

It is not difficult to find, particularly among birds and mammals, instances of specific variation giving rise to local geographic races which are apparently the result of response on the part of the organism to local conditions. Again, it is easy, particularly among plants, to find varieties, species and even genera which have arisen apparently through sudden mutations and without anything in the nature of adaptational response. Finally, paleontology teems with apparent cases of orthogenetic phylogeny which are not at present clearly explainable in terms of natural selection or mutations. Before examining concrete cases which come under each of these categories let us diverge for a moment to consider the effect which natural selection as a theory has had upon biological conceptions.

We see at once that the philosophical conception of continuity took an extraordinary hold on the minds of biologists. Largely as a result of the great influence of Darwin, towards the end of the nineteenth century continuity in the origin of species became almost a fetish, and all efforts were directed to showing how every character whatsoever might have originated through the selection of a series of gradually intergrading infinitesimal steps. Yet it is more than doubtful if Darwin himself would ever have been led into such an extreme position. Biological philosophy has thus been ridden with the conception that if a character could be shown to have arisen in a gradual, piecemeal fashion its origin was thereby explained or accounted for, even though natural selection could not be shown to have operated in its development. On the other hand, the appearance of a character sud-

denly, at one step, was considered practically equivalent
to its creation by a miracle, and the type of argument in-
volving this view is still not infrequently leveled against
the mutation theory.

But where lies the necessity for assuming that either
continuity or discontinuity is universal? Surely the
matter is one to be determined by direct observation, and
not by *a priori* argument. The continuity concept of
origins appears not to have influenced other sciences to
the extent it has biology. True, Lyell first introduced it
by developing the doctrine of uniformitarianism in geol-
ogy. Nevertheless the geologist has continued to deal
with large and relatively catastrophic effects occurring
at irregular intervals, such as landslides, floods, earth-
quakes and volcanic eruptions. The phenomena of ge-
ological history are then continuous only in a limited
sense.

Similarly, no chemist supposes it necessary to think
that, for example, carbon and silicon were gradually dif-
ferentiated from some previous substance which pos-
sessed certain qualities of both. On the contrary he sees
his atoms built of definite units, the electrons, combined
in various ways and numbers to give a variety of prod-
ucts, the elements, which are for the most part stable
from the first. Hence, while perhaps little can be gained
for the biologist by reasoning from analogy with other
sciences, yet we at least realize that concepts of discon-
tinuity are quite as widespread in science at large as are
those of continuity, and that the origin of a character is
not explained merely by breaking it up into infinitesimal
steps through which it may not have passed at all.

Let us consider now some concrete instances. And here
we shall select chiefly cases of discontinuity, since we are
considering especially the bearing of the mutation theory
on the conception of species. In examining species and
genera of plants and animals, we find very often, par-
ticularly in plants, characters which almost certainly had
a discontinuous origin. Perhaps the majority of generic

characters in higher plants have originated in this way. Such morphological generic characters are found in numbers wherever one turns. They indicate a great variety of marked changes, in addition to those involving alteration in number of parts; they most often concern the flower structure, on which generic differences usually depend; and in many cases at least they can not reasonably be supposed to be of any special value to the plant.

If we turn to the lily family and compare the well-known North American genera, *Smilacina* and *Maianthemum*, we find the following differences:

| *Smilacina* | *Maianthemum* |
|---|---|
| Perianth segments 6 | Perianth segments 4 |
| Stamens 6 | Stamens 4 |
| Ovary 3-celled | Ovary 2-celled |
| Style short and thick | Style about as long as the ovary |
| Stigma 3-grooved or 3-lobed | Stigma 2-lobed or 2-cleft |
| Leaves oblong or lanceolate | Leaves usually cordate at base |

These generic differences are almost entirely in the number of parts in the flower. Otherwise, in foliage and habit *Maianthemum* might be considered a reduced boreal subgenus of *Smilacina*. Can it be doubted that *Maianthemum* originated from the ancestors of certain species of *Smilacina* through a mutation, in which the flowers changed suddenly from the hexamerous to the tetramerous condition? All these changes in flower-parts would then have occurred at one stroke. It can not well be imagined that they passed through a series of gradual transition stages which have since been lost. When one remembers the almost universal occurrence of 3-parted flowers in Monocotyledons, this change becomes all the more striking. The whole order Cruciferæ, among Dicotyledons, must have originated in the same way, through a sudden change from pentamery to tetramery.

If we examine the species of *Maianthemum* and their varieties we find evidence that similar processes of discontinuous variation are going on at the present time. The genus contains three species, *M. canadense* in Amer-

ica, *M. bifolium* in Europe and *M. dilatatum* in western America and northwestern Asia. *M. canadense* differs from *M. bifolium* chiefly in leaf-shape and in being typically glabrous. The pubescence probably was lost at one stroke, just as numerous glabrous varieties arise. Another step is sufficient to account for the alteration in leaf-form, so that two steps are ample for the transition from one species to the other. *M. dilatatum* resembles *M. bifolium* except for its relatively gigantic size and the fact that it is glabrous like *M. canadense*. Again two definite steps are sufficient to account for its origin.

Turning now to the geographic variations of *M. canadense* particularly as regards pubescence, a detailed study shows that over the greater part of its extensive range it is absolutely glabrous, but that pubescence has appeared especially in two localized parts of its range. A heavily hirsute variety *interius* Fernald, occurs in the Black Hills of South Dakota, an exceedingly arid region on or near the western extremity of the range of the species. This variety is apparently restricted in its distribution to the arid portion of western South Dakota, and the most reasonable interpretation appears to be that it has originated here through a marked variation, and has thus enabled the species to extend its range into this arid region. Further east, chiefly in Minnesota and Wisconsin, a semi-pubescent form occurs, and this may be the form from which the much more marked hirsute variety arose. The evidence, when closely examined, favors then a discontinuous rather than a continuous manner of origin of this heavily pubescent condition. The condition itself is nevertheless an adaptation, enabling the plant to survive in extreme conditions of aridity.

The monotypic genus *Kruhsea* is related to *Streptopus* in much the same way that *Maianthemum* is related to *Smilacina*. It was originally described in the "Flora Rossica" by Ledebour as *Smilacina streptopoides* from eastern Siberia. His name indicates his idea of its relationships. Baker afterwards, from plants without flowers

collected in Oregon, described what has proved to be the
same form under the provisional name *Streptopus brevi-
pes.* *Kruhsea streptopoides* then, although it agrees
with *Streptopus* in foliage and in fruit and seed char-
acters, differs remarkably in its flowers. They are very
small, the perianth nearly rotate, dark purple; the sta-
mens altered; and in the absence of a style the discoid
stigma rests directly on the ovary. It is possible that
connecting forms between *Kruhsea* and *Streptopus* may
yet be found in Siberia, but at any rate the differences
between these two genera can not be reasonably sup-
posed to have arisen through natural selection. *Kruhsea*
appears to have originated through a few definite ger-
minal changes and to have since been perpetuated by
heredity.

Another pair of genera which is of much interest in
this connection is *Platystemon* and *Platystigma,* two Cali-
fornian genera of the Papaveraceæ. Both occur abun-
dantly as spring flowers, occupying similar habitats.
Their main differences are as follows:

| *Platystemon* | *Platystigma* |
|---|---|
| Stamens numerous | Stamens 6–12 |
| Filaments broad and flattened | Filaments narrower, flattened or filiform |
| Carpels 6–20, forming a compound ovary, which in fruit breaks up by constrictions into 1-seeded joints | Carpels 3, forming a 1-celled, 3-valved or terete ovary which in fruit forms a 3-valved dehiscent capsule |

These genera are almost exactly alike in habit, foliage,
pubescence, color of flowers and general form of the sta-
mens. They differ chiefly in the pistils, and these differ-
ences only become conspicuous as the seed capsules
mature. *Platystemon* has acquired numerous carpels
which are connivent or coherent in a circle. In develop-
ing, the carpels separate and their free margins cohere
with each other. Each carpel then becomes torulose by
constrictions between the seeds. How shall we account
for the origin of such a condition except through a marked

variation, which is perpetuated by heredity and not because the plant has any advantage or disadvantage in life compared with *Platystigma*. Only one species of *Platystemon* (*P. californicus* Benth.) and two of *Platystigma* have been generally recognized, although Greene[2] has described some 50 species based on minor differences.

Another significant difference between *Platystemon* and *Platystigma* is in the variations of the petals. In *Platystemon* the number varies from 6 to 10 or more, and all the petals of a flower or a plant vary together in color from dark yellow through light yellow to white. In *Platystigma,* on the other hand, the number of petals appears to be uniformly six, and the outer three vary in color independently of the (alternate) inner three. Thus in *Platystigma lineare* Benth. (which Greene calls *Hesperomecon pulchellum*) the outer petals may be dark yellow, or with a more or less extensive wedge-shaped dark yellow mark at the tip, while the inner petals are light yellow or white.[3]

The peculiarity in the carpels of *Platystemon* acquires added interest from the fact that, as Lindley pointed out,[4] it is by no means unique, but contraction of the sides of the carpels, forming a torulose structure, has occurred equally and must have originated independently in *Hypecoum* of the Papaveraceæ, in such genera as the radishes among Cruciferæ, in *Ornithopus* among the Leguminosæ, and in other families. We may look upon this condition as apparently the result of parallel mutation in different families, independent of utility; and countless other cases of a similar kind occur among higher plants.

From the few instances I have cited, which could be added to indefinitely, and from the abundant evidence of marked variations which we have from experiment, the

[2] Greene, E. L., 1903, "*Platystemon* and its Allies," *Pittonia,* 5: 139–194.

[3] A figure of *P. lineare* in *Bot. Reg.,* T. 1954 (1837), from the Russian River, Cal., shows the petals alternately yellow and white.

Another interesting point, to which Mrs. K. Brandegee has directed my attention, is the abundant occurrence of tiny plants bearing a single minute flower, intermingled with the larger plants.

[4] *Bot. Reg.,* T. 1679 (1834).

conclusion seems clear that many marked morphological characters in plants have arisen independently of function and without the aid of natural selection. This conclusion is all the more probable because form is so much more loosely tied to function in plants than in animals. In many plants it makes little or no difference what is the shape of the leaf so far as its chlorophyllian function is concerned, nor what is the shape of the anthers so long as they produce pollen.

Another matter, which I have touched upon elsewhere,[5] is the geographic relationships of the most closely related species of plants. It appears that Jordan's well-known law that the most nearly related species occupy adjacent areas, although widely applicable especially to the subspecies of mammals and birds, is by no means so generally true in regard to plants. But we shall come to this point again.

Referring now to animals, the North American screech owls afford an interesting case in which two kinds of variability can be clearly contrasted as regards their geographic relationships. These two types of variations are (1) those in which apparently continuous or nearly continuous variations occur progressively over certain geographical areas, with no two forms occupying the same area, and (2) those in which two or more sharply marked forms occupy the same area.

The accompanying map, compiled largely from Ridgway's data,[6] shows the distribution of the various sub-

[5] Gates, R. R., 1916, "On Pairs of Species," *Bot. Gazette,* 61: 177–212. Figs. 12.

[6] Ridgway, Robert, 1914, "The Birds of North and Middle America," *Bull. U. S. Nat. Mus.,* No. 50, Part VI, pp. 882, pls. 36.

Ridgway says (p. 683): "In the main, geographic variations [in *Otus*] are more or less marked and constant; but occasionally specimens occur in a given area which are with difficulty, if at all, distinguishable from the form inhabiting another—sometimes distant—geographic area." He further comments on the fact that, while *O. choliba* in South America is remarkably uniform over a vast area, *O. asio* shows great change of coloration within relatively short distances, indicating an organization sensitive to slight changes in the physical environment.

species of *Otus Asio* Stephens (formerly known as *Megascops asio* Kaup) over the North American continent. While such a map is only approximately accurate, it shows that in general only one subspecies occupies a given geographic area.[7] There are, however, certain excep-tions. Thus in Central Colorado *Otus asio aikeni* and *Otus asio maxwelliæ* both occur, the former finding here its northern limit from Texas and Mexico, the latter the southern limit of its range from Montana. It is stated, however,[8] that they occur in Colorado chiefly at different altitudes, *maxwelliæ* up to 6,000 ft. and *aikeni* from 5,000 to 9,000 ft. This is the reverse of what might be expected, since *aikeni* is the more southern form. But Mr. Aiken states[9] that at Colorado Springs *maxwelliæ* occurs only in winter and *aikeni* only in summer, indicating a slight migration. Again, *gilmani* and *cineraceus*—the latter somewhat darker with coarser pencilings and averaging slightly larger in size—both occur in southwestern Ari-zona, but, according to Swarth,[10] although both birds may occasionally be taken in the same locality, this is only in winter when *cineraceus* comes down from the higher alti-tudes to the different life zone of the hot Lower Sonoran valleys occupied by *gilmani*.

The differences between these various subspecies are chiefly in density of coloration and in size.[11] Thus *Otus asio nævius* is larger than *Otus asio asio* and is also lighter in coloration, with more white on the under parts. The subspecies *mccallii* in Texas and northern Mexico is in-termediate between these in size, but is paler than either

[7] It may be pointed out that there is sometimes discernible a tendency for systematists to call a form a subspecies or a species according to whether or not it is the only form in a given area, thus making the geographical rela-tions of the form their criterion, rather than the degree of its distinctness.

[8] Cooke, W. W., 1897, "The Birds of Colorado," Bull. No. 37, Agric. Expt. Sta., Fort Collins, Colo., p. 78.

[9] Cooke, W. W., 1898, "Further Notes on the Birds of Colorado," Bull. No. 44, Agric. Expt. Station, Fort Collins, Colo., p. 160.

[10] Swarth, H. S., 1916, "The Sahuaro Screech Owl as a Recognizable Race," *Condor*, 18: 163–165.

[11] I am indebted to Dr. Grinnell for permission to examine series of speci-mens in the Museum of Vertebrate Zoology of the University of California.

and more coarsely mottled. *Hasbroucki,* very limited in
known range (see map), is decidedly larger and darker
than *mccallii,* with much less buffy gray above and
broader transverse bars. *Maxwelliæ,* another northern
form, is decidedly larger but paler than *aikeni.* It is the
palest of all in color, with more extensive pure white than
even *nævius.* West of *maxwelliæ,* in Washington and
Oregon, is *macfarlanei,* which is larger and very much
darker, almost agreeing in coloration with *bendirei* of
California.

The Pacific coast forms comprise an interesting series
running down the coast, beginning with *kennicottii,* which
occurs from Sitka through British Columbia to the south-
ern border of Washington State. It is very large like
*macfarlanei,* but much darker, and browner rather than
gray. The remaining subspecies extending down the
coast region and into the desert become progressively
paler and smaller. Thus *brewsteri* in Oregon is smaller
and less brownish than *kennicottii.* In California occurs
*bendirei* which is lighter again and smaller. Grinnell[12]
has segregated from *bendirei* in the more arid region of
southern California another form under the subspecific
name *quercinus,* considered to be paler dorsally and with
less or no ferruginous markings around the head. But I
confess that this difference, if it exists as a constant dis-
tinction, is too fine for me to appreciate. On the contrary,
specimens of *bendirei* from Palo Alto appeared to me
somewhat lighter on the breast than a series from Pasa-
dena. Whether or not this very close form is distinguish-
able from *bendirei,* the next in the series are *cineraceus,*
*gilmani* and *xantusi,* becoming progressively lighter with
finer vermiculations, the two former in southern Arizona
and *xantusi* confined to the tip of the peninsula of Lower
California, smaller and with the toes less feathered.

Thus the subspecies appear to be arranged progres-
sively in passing from one geographic area to another,
and there is little overlapping. But this conception of

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[12] Grinnell, J., 1915, ''A New Subspecies of Screech Owl from Califor-
nia,'' *Auk,* 32: 59–60.

gradual and progressive change can be overdone when it is attempted to correlate the alterations observed with climatic or other environmental features. Thus the progressive lightening in color from *kennicottii* to *xantusi*, first by lightening and restriction of the brown until it practically all disappears and then by paling and diminution of the gray, is believed to be associated with the decreasing moisture in the northern part of the range and the increasing aridity in the south. There are of course many well-known cases of paler races of birds and mammals occupying desert areas. Yet it is not clear that the coastal region of Oregon, where the less dense brown *brewsteri* occurs, is any less humid than the corresponding part of Washington where *kennicotti* is found. Similarly *xantusi* on the peninsula of Lower California can not be supposed to exist in a drier habitat than *gilmani* or *cineraceus*. Of course in none of these cases is it known just what feature in the environment acts as the critical factor nor how the race responds to it. The experimental studies of Tower[13] and others show that a race may respond in the same way (*i. e.*, by showing the same variations) to different environmental stimuli or in different ways to the same stimulus. But studies of this character are still too few to furnish a basis for interpreting these reactions on the part of species of the higher animals. The experiments being carried on by Sumner[14] with the white-footed mouse, *Peromyscus maniculatus* may be expected to throw further light on this important question of the origin of local subspecies.

Again, it is not certain that such races as *kennicottii*, *brewsteri* and *bendirei* form an absolutely graded series with all intermediates. On the contrary there appears to be some evidence that although their boundaries are contiguous there are definite though small steps from one to

[13] Tower, W. L., 1906, ''An Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*,'' Carnegie Inst. Publ. 48, pp. 320, figs. 31, pls. 30.

[14] Sumner, F. B., 1915, ''Genetic Studies of Several Geographic Races of California Deer-mice,'' AM. NAT., 49: 688–701, with map.

the other. This may conceivably be explained through the principle of invasion and reinvasion. Grinnell,[15] who is doing so much towards a detailed knowledge of the Pacific coast fauna, has considered this principle and also the part played by barriers in the development of geographic subspecies or races, in connection with the discussion of many specific cases of distribution in birds and mammals. Walter P. Taylor,[16] in a recent study of the western beavers, concludes in agreement with others, that migration, geographic isolation with adaptation to local ecological niches, and final reinvasion of earlier-occupied localities, will account for the origin and present distribution of geographic subspecies such as we have been considering. This explanation seems as likely as any other at the present time, but it is beyond the purpose of the present paper to discuss these aspects of speciation in birds and mammals. The intention is rather to show that the problems involved are entirely different from those concerned with another type of variability to be mentioned in a moment. It may be pointed out, however, that although the theory of reinvasion as developed involves the conception of races isolated in certain geographic areas becoming gradually modified through environmental stress and fixed before the reinvasion takes place; that there is at the present time no definite evidence that fixation actually takes place gradually, in this way or in any other way. If intermediates between the various geographic subspecies do not occur, this may be because definite though small steps in variation are taken from one race to the other, which would do away with the necessity for assuming a long period of isolation during which the gradual development and fixation of the race

15 Grinnell, Joseph, 1914, "An Account of the Mammals and Birds of the Lower Colorado Valley, with Especial Reference to the Distributional Problems Presented." *Univ. Calif. Publ. Zool.*, 12: 51–294, 9 figs., pls. 3–13, and other papers.

16 Taylor, Walter P., 1916, "The Status of the Beavers of Western North America, with a Consideration of the Factors in Their Speciation," *Univ. Calif. Publ. Zool.*, 12: 413–495.

occurred. However, the process does appear to be gradual at least in comparison with the other type of variability, which is fundamentally different in its geographic relations.

The second type of variability in *Otus asio* to which I have reference, consists in the occurrence of gray and reddish or rufous phases of coloration in the same area of distribution. Thus all the eastern subspecies, *asio, nævius, mccallii* and *hasbroucki,* produce both gray and red birds. These phases are sharply marked, and intermediates rarely occur. Hasbrouck[17] attempted an explanation of this dichromatic condition, but some of his conclusions were justly criticized by Allen.[18] The gray phase occurs more commonly in Florida and in the northern part of the range of *nævius,*[19] while the red phase occurs commonly in the Central Atlantic states, perhaps to the exclusion of the gray in some localities. The red phase is unknown in the western forms of *Otus asio.* Nevertheless grayish and rufescent phases of the small *O. flammeolus,* which is found in the mountains of western America from British Columbia to Mexico, occur in this region. The red phase is found also in *O. trichopsis* (see map). Similarly, brown and rufous phases are found in *O. choliba* which extends over a large part of South America, and also in the Central and South American species *O. cassini, O. guatamalæ, O. barbarus* and *O. vermiculatus.*

Owls belonging to other genera also exhibit two phases. For example *Bubo virginianus (Asio magellanicus),*[20] the single species of *Bubo* occurring in all North and South America, with many geographic varieties, shows dichromatism in various parts of its range. The same is apparently true of various Old World owls.

[17] Hasbrouck, E. M., 1893, ''Evolution and Dichromatism in the Genus *Megascops,*'' AMER. NAT., 27: 521–533, 638–649, 4 maps.

[18] A(llen), J. A., 1893, *Auk,* 10: 347–351.

[19] Oberholser, H. C., 1904, ''A Revision of the American Great Horned Owls,'' *Proc. U. S. Nat. Mus.,* 27: 177–192.

[20] The red phase is stated by Allen to be rare in Maine.

Dichromatism is then, both geographically and systematically, a widespread phenomenon in owls. The red phase appears to be quite independent of geographic locality in its origin. Hasbrouck attempted to show with regard to *Otus asio* that the red phase had arisen gradually from the gray, which it was slowly supplanting in certain areas. He believed that the grays inhabited regions of greater humidity (Florida, northern range of *nævius*) and the reds the drier interior, yet grays occur in Florida and reds are found, though uncommonly, in Maine. He also reported reds as occurring exclusively in the relatively humid Mississippi valley. But, as Allen pointed out, any such correlation with climatic or environmental factors hopelessly breaks down because both types are found indiscriminately over at least the greater part of the eastern range. All writers agree that the two types of plumage are independent of age, sex or season, and that in many localities at least both occur together and freely interbreed. Hasbrouck states, however, that gray males far outnumber red males, while red females outnumber gray females 4:1. Confirmation of this point is to be desired, as it suggests sex-linkage of the red condition. It is further stated that on the continent of Europe the red owls are said always to be females and the grays males.

All young birds of *Otus asio* are gray in the down, the red first appearing in the feathers. Observations go to show that red birds mated with red may give (1) all red offspring, (2) all gray, or (3) both red and gray. When one parent is red and the other gray, the same three results may follow. Further, Hasbrouck claims that gray × gray gives always only gray young. This is probably true, but since the result is based on observation of only six matings of this kind in regions where reds occur, it is much to be desired that further observations on this point should be recorded.

The obvious hypothesis to explain these facts is that the red phase appeared as a mutation from the gray, and

that it is inherited as a simple Mendelian dominant character. The results of the various matings between red and gray would then be as stated above, according to whether the red parent were homozygous or heterozygous, but the offspring from red × red should seldom be all gray, since this would be only a chance result when both parents were heterozygous. It is not impossible, however, since the screech owls usually have only three or four young in a nest, or sometimes only two.

Since the red phase occurs in various species as well as subspecies it is not improbable that it has originated through independent variations in different species. In any case the geographic ranges of the red phases show that, having appeared as variations, they are inherited without any conspicuous advantage or disadvantage in competition with the gray. The present frequency of the reds in certain areas and their infrequency in others may be merely an indication of the localities where the original mutations took place, and from which as centers they have gradually spread.

Although the western forms have no red phase, yet *Otus asio kennicottii* exhibits in addition to its usual tawny-brown phase a relatively rare gray phase. This fact is indeed an argument favoring the assumption that the brown phase of *Kennicottii* also arose at one step and has since nearly supplanted the original gray form.

If now we compare the two types of variability that I have described in *Otus asio,* we find them sharply contrasted in several respects: (1) the former is clearly related to geographical distribution, a single race occurring in each locality: the latter has no such relation, but two forms may occur interchangeably in the same place; (2) the former is essentially continuous as a form of variation, the latter markedly discontinuous; (3) the former appears to be related to environmental (climatic) conditions, the latter apparently bears no such relation. As regards their evolutionary significance, there can be little doubt that the former or apparently continuous type of

variations is more important in this case, for they appear
to have given rise to the geographic subspecies now recog-
nized, and, moreover, the specific differences in the genus
are merely an exaggeration or intensification of the kinds
of difference shown by these subspecies. It seems evi-
dent, then, that the differentiation which has gone on in
the evolution of the genus *Otus* is for the most part of the
kind exemplified by the small differences now existing be-
tween geographic races or subspecies occupying different
areas.

The same thing is true of many other birds and mam-
mals, but this condition is by no means universal even in
these groups of animals. On the contrary, it is not diffi-
cult to find instances in which the discontinuous type of
variation, independent of environment or function, has
been the main factor in speciation. I will merely mention
the case of the North American flickers, *Colaptes auratus*
and *C. cafer,* set forth by Bateson,[21] since the latter is a
Californian bird. These species differ remarkably in
their color markings, the most conspicuous differences
being (1) yellow or red quills, (2) a black or a red malar
strip in the males, (3) the presence or absence of a scarlet
nuchal crescent in males and females. *C. auratus* pos-
sesses the first of each pair of characters and *C. cafer* the
second. *C. auratus* extends from Alaska diagonally across
Canada and the United States to Texas and eastward to
the Atlantic, while *C. cafer* occurs in its pure form from
Oregon through Utah, California and Arizona into
Mexico. Each possesses 3 or 4 geographical subspecies.
Where the ranges of the species overlap over a large area
a mixed population of forms occurs which is usually in-
terpreted as a series of complex hybrids, but this will
bear further study. It is clear, however, as Bateson
points out, that the differences in range of the species
can not be associated with any constant environmental
difference in the habitats, and that the species can not
have differentiated from this mixed population of inter-

[21] Bateson, W., 1913, ''Problems of Genetics,'' Yale Univ. Press, p. 146.

mediate forms. However these species originated, they can not be reasonably supposed to have developed through gradual adaptation, but the color differences probably play no more part in the economy of the species than is the case with the red and gray phases of the screech owls. Something in the germinal organization of *Colaptes* doubtless determines the definiteness of its color patterns, and it is probable that each element of the pattern was changed by a marked step rather than through a series of gradual stages. This view is strengthened by the fact that a third species, *C. chrysoides* in Lower California, is essentially a *cafer* with yellow instead of red quills.

Thus even in birds our second type of variation, nonadaptational and not related to local conditions, is apparently an important factor in speciation, although in *Colaptes* too geographical races occur as well. In distribution also these species do not follow the rule for geographic subspecies, for they overlap over large areas. The fact that each species has its own geographic subspecies shows that the origin of these species antedates the development of their geographic varieties.

I have endeavored to show that in plant and animal species there are two distinct types of variability, having different geographical relations. The one is discontinuous, independent of environmental or functional influence, and has given rise to many specific and generic characters, notably in plants but also in higher animals. The other is continuous and apparently represents the results of the stress of the environment on the species in its dispersal, leading to the gradual differentiation of local races or subspecies whose peculiarities are ultimately intensified and fixed. The latter type of speciation is notably exemplified in birds and mammals, organisms in which, unlike plants, the individuals can migrate from place to place and so substitute for a stress resulting from overpopulation an environmental stress caused by a new set of climatic or physiographic conditions.