THE RELATION OF SOME OBSERVATIONS UPON PREDATION TO THEORIES OF PROTECTIVE COLORATION

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The colors of animals often harmonize with the colors of their environment. Many attempts have been made to explain this fact, of which the theory of protective coloration is most widely accepted today. This explains the resemblance of the colors of animals to those of their environment by saying that such coloration either assists animals to escape enemies or to catch prey. Although the theory tries to tell why organisms are so colored, it does not say how these colors may have been achieved. Additional theories have been offered as an answer to this question; of these, all but one have been rejected by most students.

This theory explains protective coloration (as we shall refer to this general subject) as the result of the natural selection of genetic mutations. The operation of this process is well described in the words of Shull ("Evolution," McGraw-Hill, 1936, p. 166). "Predaceous animals are supposed to pass by those individuals whose mutations lead them to be less conspicuous, or more like some uninteresting object, and to concentrate their attacks on the ones which they readily perceive. Accumulation of these concealing or deceptive mutations as rapidly as the latter occur should lead to what has been called protective resemblance. This concept thus rests heavily on escape from enemies as one of the great necessities of life."

Consideration of these two correlated theories brought up the following questions which this paper attempts to answer. Under what conditions would the identity of an animal be concealed? What methods are used by raptorial birds to hunt prey and what methods are used by prey to escape enemies? Do the methods employed fulfill the conditions under which protective coloration would be effective? What probability do the answers to the above questions give to the actuality of protective coloration and its origin through natural selection, at least as far as the animals studied are concerned?

Before continuing, the matter of the anthropomorphic basis of the theory of protective coloration should be discussed. This is the assumption that the animals studied have a sense of sight very similar to our own. If this is not assumed, the theory possesses no credibility at all, for a color that to us appears to be harmonious with its surroundings may not appear so to another species and we have no criteria upon which to base the theory. Evidence either favoring or discouraging this assumption is at present too fragmentary to approach actuality; we must therefore arbitrarily decide for ourselves whether we favor this view or not. As a denial of the point would leave no basis for the theory of protective coloration, and as many people do favor such a theory, the author feels justified in interpreting the included animal behavior, as far as vision is concerned, in the light of human experience. This should be borne in mind.

We return to the question of the effective conditions for protective coloration. Reflection shows that creatures would be deceived by protective coloration when such colors cause the identity of an organism to be misinterpreted. If the properties characteristic of a particular form were also characteristic of its background, the whole would appear as a homogeneous unit to an observer. This homogeneity would break down, however, as soon as other properties were introduced that would be recognized as peculiar to the animal—distinctive characteristics that the animal possessed, but that

its environment did not. By far the most important of these is the property of motion. A moving animal is easily recognized as such against its background. This matter will be considered in detail later on.

The answer to the first question, therefore, is that the identity of an animal is concealed when the animal does not show any characteristic feature by which it may be distinguished.

This brings us to the problem of ascertaining the methods of attack and defense employed by various organisms, the solution to which is to be derived from the evidence of field studies. These studies, of my own, were confined to bird predators, chiefly hawks, and their prey. Most of the observations were made in the spring of 1937 in connection with a course in vertebrate zoology given by Joseph Grinnell, of the California Museum of Vertebrate Zoology, Berkeley. The work was done chiefly on Tomales Point, Marin County, California, and in the hills back of Berkeley. A scattering of notes from other places and of other dates also has been used. The organisms studied are described under two group headings: Those that hunt and those that are hunted. Only those facts, ascertained by actual observation of one or more cases and that appear to be of general application to the problems involved, will be described. The work was aided by the use of a pair of eight-power binoculars.

PREDATORS

Western Red-tailed Hawk. *Buteo borealis calurus*. These hawks were observed to hunt mostly by perching upon a suitable bush, post or tree that was elevated above its surroundings and commanded a good view. Sometimes birds were seen to be soaring high in the air acting as though they were hunting. The sedentary hunters usually faced down hill, or else into the wind, if it was blowing, and often had their backs to the sun.

Once perched, they maintained a close watch over the vicinity as indicated by head movements and their general attitude. A good place may be held for five hours or longer, although the individual perch may be shifted from time to time. The activity of individuals was determined by numerous factors, including the presence of prey. Hawks were seen to fix their attention upon a particular spot, or prepare to leave their post and then relax, or to sail swiftly out and strike, or to perform any variety of movements which indicated all degrees of interest in food animals, from merely watching to actual catching of them.

Hawks were to me, as observer, conspicuous upon their perches, especially when the sun shone on their white breasts. This did not appear to interfere with their hunting, for they often struck at animals within a few feet of them. Further, I was surprised at the distance to which hawks sometimes flew to strike. One hawk did this at an estimated 175 yards; others at distances well over 100 yards. This would indicate that, even if a motionless hawk were visible as such to small animals, the hawk would be able to see them farther than they could see it.

Two Red-tailed Hawks were observed diving almost directly toward me with closed wings. In both cases they were difficult to see and their forward motion hard to judge, not, as Thayer ("Concealing Coloration in the Animal Kingdom," Macmillan, 1909, pp. 10 ff) would have it, because of the barring on their ventral surfaces, for this was not visible, but because in head-on view they were extremely thin and their line of movement offered no points of reference to surrounding objects. This same phenomenon was observed in the dive of a Sharp-shinned Hawk (see below). Two other hawks were especially noted as examples of a far from unique situation. These appeared as dark

shapes against the sky while diving toward the ground. No coloration whatever could be detected.

Several times Red-tailed Hawks were seen to strike into the grass with their feet and then to stamp vigorously about the place, which indicates that though their prey may be partially hidden by the grass and hence hard to see, yet it may be sought after and taken. To quote from my notes a favorable case that supports this conclusion: "I saw him just after he landed and he moved his feet actively and bent his head down. He raised his head and I saw a small mammal swinging by its tail from his beak. White underparts, dark above, size of a mouse. . . . At place where mouse was caught was a runway through the grass, continuing as a covered path into a dead iris patch. Several drops of blood were to be seen near the edge of the patch and a few loose iris stems with fur on them. From the looks of things the hawk grabbed the mouse while it was under the iris. . . ."

At this same place many White-crowned Sparrows were feeding and moving about, showing that the hawk had discriminated between the two types of organisms. While quantitative data at present are lacking, my observations indicate that much more prey is seen and struck at than is captured. This point is interesting, but hardly can be used to support or deny any of the hypotheses in this paper.

The Accipiters. *Accipiter cooperii* and *A. velox*. Differentiation between these species in the field is often uncertain and for this reason the two are considered here as representing one type of predator. No doubt there are differences in their behavior, but these should not be significant in the present connection.

A hunting accipiter either perched well concealed in the foliage of a tree or bush and from there attacked unwary animals, or flew rapidly along, taking advantage of intervening objects to conceal itself, and attempted to fall upon its prey before the latter could escape. Observations showed the accipiters to be more active than Red-tailed Hawks, seldom remaining long at one station, but rather, moving from place to place, carefully searching each area. This may have been a consequence of the game they hunted, which is in general more active than that of the red-tails and thus could have been detected sooner.

A hawk that perched near the author on the edge of a wood overlooking an open area came there through the trees, possibly to avoid being seen by birds that would give an alarm. The hawk actively looked over the open land before it, even looked over its shoulder into the woods behind it, and once watched something intently in a gully. After eight minutes it flew out of sight. Whether or not the bird was conscious of using the woods to conceal its approach, small birds are acute at seeing these hawks flying over the countryside and have been heard to utter cries of alarm even though their enemy was well over 100 yards away and obviously not hunting them.

Once a hawk, probably a Sharp-shinned, dove toward the writer, intent upon a flock of White-crowned Sparrows close at hand. As in the case of diving red-tails, it was moving head first with its wings close to its body and was hard to see. Again, lack of perspective was responsible for this deception and not ventral coloration, which could not be seen.

Miss Elizabeth Over and Miss Lillian Halstrom were eye witnesses of a successful attack upon two juncos, and the author is indebted to them for the use of their notes on the subject. The two birds were clearly taken by surprise, the hawk diving very quickly from a near-by tree to seize one before it was able to fly off. From this and other observations, it seems that the victims are usually taken by surprise, the effectiveness of which may be aided by the swiftness of the hawks.

Sparrow Hawk. *Falco sparverius*. In the Tomales Point area the Sparrow Hawk chiefly takes insects. These were hunted by a bird's perching on rock piles or posts in open fields or by hovering at a varying distance above the ground and watching the terrain below. When an insect or other food was seen, the bird dropped gracefully down and seized it, often diving head first with partially closed wings. One bird was seen to flutter over an area of bunch grass about twenty feet up and then to drop with outspread wings, checking and controlling its flight as though to land at a desired spot. However, when it did land, it did not appear to catch anything. Such action may be interpreted in favor of the hypothesis that barred wings act as a camouflage (Thayer, *op. cit.*, p. 80). However, as Sparrow Hawks hunt in the open, their background in such cases is the open sky, not a criss-cross of branches, and conjecture is the only evidence upon which it could be claimed that ventral barring was protective (or "concealing") under these conditions.

Duck Hawk. *Falco peregrinus*. A favorite hunting trick of this bird was to fly to a considerable height above a suitable place and from there to watch for game moving below it. These falcons possess keen eyesight and remarkable powers of flight. These faculties enable them to fall with great swiftness upon unsuspecting birds half a mile or more away. When such an attack is launched, the falcon moves like an arrow and the only escape open to its victim is that it dive under water or dodge. There is little chance that the coloration of the Duck Hawk aids it in hunting. If seen while far away, it appears as a speck against the sky; more closely, as a blurred dark shape, moving with a speed demanding instant action, occupying too much of the visual field to be hard to see.

Apparently these falcons kill both moving and stationary birds, either by knocking them down or by seizing them bodily. The author has heard eyewitness stories of Duck Hawks seizing wooden decoys and of one killing and then retrieving a swimming duck. A flock of Ruddy Ducks were passing over the water close to the writer's boat when a falcon seized one and bore it to a beach.

Duck Hawks were often seen hunting in the evening, watching the bay surface from the air, with the setting sun at their backs. This is a trick well known to wartime aviators, but whether the hawk employed it intentionally or not is hard to say. A clam digger told me that he had seen them hanging in the deep shadows of a hill adjacent to the estuary and watching the water from there. Again the question of intent is not answered.

Marsh Hawk. *Circus hudsonius*. Marsh Hawks characteristically hunt by flying over open country quite close to the ground, often only five to ten feet up, and watching below them for suitable prey. Sometimes a hawk appears to follow a definite beat, passing at intervals over the same stretch of territory. When food is seen, the "harrier" drops and tries to seize it, apparently depending upon the suddenness of its appearance to catch the victim off guard.

A male Marsh Hawk, flying about five feet above the ground over some brush, checked its flight and extended its legs over a bush as though it saw something. Immediately it alighted on the bush and looked about. Suddenly it jumped to the ground on the far side of the bush; then back to the top. Then it hopped into the air and dove at the bush with its legs extended, only to repeat the same action at another point. Finally it drove down hard into the center of the bush and came up with a small rabbit, which was carried squealing over a gully to the ground.

Bent (U. S. Nat. Mus., Bull. 167, 1937, p. 87) records that: "Eugene S. Rolfe (1897) noted the following interesting attempt to secure a meal: 'Many times I have watched the Marsh Hawk sailing low and keenly scanning the ground on the open prairie, and suddenly pouncing down and quickly ascending again with an empty mouse

nest in its talons, and on one occasion I followed behind for fully 2 [sic] miles and in that distance it picked up and dropped seven of these empty nests. On examination, they proved to be simply wads of fine dried grasses, and it was easy to see that if these had all chanced to be occupied by families of young mice, the foray of that particular hawk would have been most fruitful in the destruction of these small pests.' "

These two instances show that the Marsh Hawk is capable of complex reactions when hunting and that its sight must be keen in order to detect mouse nests while moving through the air.

The dichromatic plumages of the adult sexes (plus the less contrasting, but distinct, plumage of juveniles) show that in this species coloration can hardly be a factor involved in the capture of prey. Here are two quite different color patterns existing under identical conditions of hunting. If one is concealing, the other must also be so, even though they are in contrast to each other. This being so, success in hunting appears not to be affected by the color of the birds. The case is similar to that seen in the color phases of the Arctic fox and other animals.

Great Blue Heron. *Ardea herodias*. Great Blue Herons regularly come inland to the grassy hills on Tomales Point and hunt gophers, mice and other creatures. The author has not actually seen gophers caught, but has talked to ranchers who have. However, the following things have been noted by him. Herons were found to be standing in places where fresh gopher diggings were present and where the grass appeared too short to support meadow mice. At such a place, a heron was seen to watch one spot intently and to stalk forward, now swiftly, now slowly, just as though a gopher were being hunted.

In such hunting, the advantage would be the heron's, which only has to see a slight movement of earth or the briefest appearance of the gopher to become alert. There is evidence to indicate that gophers disregard motionless animals. The heron's method of hunting is similar to that of the various hawks, in that it watches for its prey to expose itself and then tries to fall upon it before escape is possible.

Owls. Observations on owls that were hunting are not extensive. However, a few were made that are of interest. A Great Horned Owl (*Bubo virginianus*) was seen at night perched upon a telephone pole, silhouetted against the sky. He was there when first seen and remained for at least ten minutes. This behavior suggests that of Red-tailed Hawks and Sparrow Hawks when hunting.

Both Great Horned and Barn owls have been seen flying at night. In every case they were silhouetted against the sky, even at times when the moon was shining. In view of this, the fact that Great Horned Owls of the desert are lighter in color than those of the coast can hardly be explained by the theory of concealing or protective coloration, at least as far as food getting is involved. There is no chance for color variations to be detected in black silhouettes.

Barn Owls have been attracted by the author's squeaking like a mouse, but this does not necessarily mean that they hunt by ear as well as by sight, for even small birds and deer will be attracted in a similar way.

PREY

We now turn to the animals that comprise the bulk of the food of the predators. How do they escape their enemies?

Cottontail and Brush Rabbits. *Sylvilagus audubonii* and *S. bachmani*. These species are considered together because of the writer's inability to distinguish them easily in the field. Many observations show that these two species of rabbit rely upon their ability to dash into cover for protection from their enemies. Their general pattern of behavior

is to feed in grassy places, often several feet from the nearest brush. When feeding, they are constantly alert as shown by their reactions to indications of possible danger.

In all cases, rabbits that were really alarmed made an instantaneous dash for cover, and in no case did they resort to "freezing." Freezing, often mentioned in many connections, deserves special comment. The writer has noticed in hunting with bow and arrow, and at other times as well, that a rabbit, not quite certain as to his intent, will sit very still in the attitude called freezing. However, when really alarmed by too close an approach, a sudden movement, or a striking arrow, freezing is supplanted by instant motion toward the nearest brush. These observations indicate that freezing is in reality the stopping of normal activities in order to ascertain the extent of an uncertain danger and to prepare for flight should it become desirable.

The reliance these animals place upon running to cover was further emphasized by observations upon individuals unaware of the writer's presence. These rabbits were busily feeding and when not in motion were often hard to see due to their protective coloration. However, they seldom remained stationary for more than a minute or two, with the result that they were identified easily as small mammals whenever they moved. Any hawk watching the area in which they were feeding would have had no difficulty in detecting them. The rabbits themselves placed no reliance upon freezing as a protective device when alarmed. Invariably, they ran for cover. Among other things, the alarm notes of various species of birds were enough to cause an instantaneous movement into the brush.

The coloration of any one rabbit was not always constant to the eye, but varied with the animal's position in relation to the sun, shade, color of background, and other physical factors. This shows that slight genetic differences in coat color would often be hard to distinguish in the field.

Jack Rabbit. *Lepus californicus*. Jack rabbits depend for escape from predators upon their speed, which is developed to such a degree that, unlike the other two species of rabbit, they will usually attempt to outrun their enemies rather than seek safety in cover. Often when lying in their forms, these rabbits are impossible to see unless or until they rush out. Although such hiding will protect the creatures from a man, it can not be employed against avian enemies that may be hunting the area. Sooner or later the rabbits must move about and feed, which at once makes them conspicuous to any hawk that is patiently watching the region.

As is the case for many kinds of wild game, jack rabbits can be closely approached by a man by exercising every faculty necessary to insure a silent, slow advance, even though the hunter may sometimes be partially or wholly exposed. This and the fact that these and other animals often do not notice motionless humans even when in full view, show that moving predators are more easily recognized than stationary ones.

The following field notes of mine may have some bearing upon Thayer's "Law of Concealing Coloration": "While walking at dusk, I saw a jack rabbit crouched on the edge of some brush in a plowed field and was struck by the way in which he stood out from his surroundings. A short time later, I saw another which was similarly contrasted, this time in natural surroundings. He ran, starting two others that I had not seen. All three soon stopped; one was plainly visible, but the other two were hard to see. The one that was visible was facing so that his flank received the full strength of the fading light. I could not definitely see how the other two were facing, but they appeared to be in the shadow of a hill. From these observations, it seems that Thayer's Law is not effective when the light strikes the animal from the side, as was the case of the two visible rabbits. (In these the light underparts were to be seen clearly.) This result is

natural to expect from the working of the law." This observation may have a direct bearing upon early morning and evening hunting in that animals are more easily seen at such times. However, such a possibility is at present only a matter of conjecture.

California Ground Squirrel. *Citellus beecheyi.* The reactions of the ground squirrel to danger may be said to be stereotyped, so similar are they in different individuals. The animals feed at varying distances from their holes, and, at the slightest alarm, dash headlong back to them. Once the safety of the burrow is gained, the squirrel's actions are conditioned by the type and intensity of danger that threatens and he either vanishes into the earth or remains partly exposed until he considers it safe to begin feeding again. As his main enemy is the Red-tailed Hawk, it is important that he become aware of this foe before it can cut off his retreat.

Pocket Gopher. *Thomomys bottae.* Gophers live underground but tunnel to the surface in order that they can come out to feed upon the surface vegetation. If alarmed when out of their burrows, they often shoot backwards into their holes so fast that they appear to be drawn by strings. Gophers (and moles also) may create quite a disturbance while excavating earth and yet not be visible themselves. Such operations should be as visible to a waiting heron as they are to man. Dawson (Birds Calif., vol. 4, 1923, p. 1890) says that herons often transfix fish with their beaks, intimating a spear-like action; so it is plausible that gophers could be similarly treated even though covered by a few inches of loose earth. This remains to be seen, but in any case it is apparent that the bird could locate its prey without even seeing it and be in readiness to seize it when it came out.

Cameron (Auk, vol. 31, 1914, p. 159) gives direct evidence of such action in the case of the Ferruginous Rough-legged Hawk. He quotes Sullivan: "I have watched the hawks often through glasses in our alfalfa field after the first crop has been taken off. The pocket gophers get pretty busy tunneling, and pushing all the loose, damp earth up in piles on the surface. The hawks fly slowly over the field until they discover a fresh pile of damp earth. Here they will alight softly, and wait for the gopher to push close to the surface. They will then spread their wings, and, rising a few feet in the air, come down stiff-legged into the loose earth, when the gopher is transfixed and brought out. I have seen them eat the gopher where caught, and at other times carry it away."

Once, while I was sitting motionless in a meadow, a gopher appeared in a hole not two feet away. It was there for some time, often exposing its body down to its shoulders and could have been struck by a heron or hawk. It did not appear disturbed by my presence. This slight evidence indicates that a stationary predator would have been similarly treated.

Fresh gopher hills are easily seen in their undisturbed surroundings from quite a distance and could well serve as an indicator of possible food to interested predators (for example, Ferruginous Rough-legs). With fresh mounds and actual digging operations serving as secondary clues to the presence of gophers, their danger lies in coming up at a time when an enemy is watching for them. Under such conditions, coloration (with the possible exception of violent contrasts) would make little difference to the animal's security; for ample opportunity would be given the hunter to see it when it moved into view.

Mice and Rats. Inasmuch as notes on various species of rats and mice are not plentiful, they will be considered together. Meadow mice (*Microtus californicus*) are numerous over the entire area studied. Often while I have been hunting other game, and moving very quietly, they have been started in the grass. Invariably the mouse appeared as a dark brown streak flashing into the nearest cover along its runway. This suggests a

similarity in behavior to the small rabbits, but further statements than this would be pure conjecture.

Three wood rats (*Neotoma fuscipes*) observed in an abandoned cabin at night invariably hid in holes or under debris when alarmed, their plan of escape again being to seek cover. Deer mice (*Peromyscus*) act in the same manner.

One overcast day, the author and his brother accidentally walked into a colony of Point Reyes jumping mice (*Zapus orarius*). They were in dry, dense grass on a steep slope and at least seven or eight were started in a fifty yard radius. These gave two or three leaps and vanished into holes in the earth. Again their idea was to get away and hide.

The small evidence at hand suggests that, in general, rats and mice, when frightened, behave in a manner similar to that of the other mammals which have been studied more carefully.

Waterfowl. This name includes in this instance the species chiefly attacked by Duck Hawks. A grebe (species uncertain) was seen to escape the stoop of a Duck Hawk by diving from full flight straight into water ten feet below. An old hunter at Point Arena, Humboldt County, California, said that old time duck shooters never killed the Duck Hawks that frequented nearby lagoons, for these birds forced ducks down onto the water where they risked being shot to avoid the falcons. Accounts in various ornithological books support the fact that ducks frequently escape their enemy by hastily landing upon any body of water that may be available. Probably some birds are able to escape by dodging, but the author has not happened upon any evidence for this.

In any case, a duck's real danger lies in not seeing the falcon until too late to avoid its blow, however this may be done. This was the case with the Ruddy Ducks previously mentioned. The birds, skimming over the water, were apparently not aware of the hawk until he seized one and carried it off.

Miscellaneous Birds. The following notes were selected because of the relation which they bear to the hunting methods of accipiters. White-crowned Sparrows, when scared by a hawk, did not freeze, but flew in a body to the nearest cover. This same reaction is true of Golden-crowned Sparrows, juncos, and many other small birds. Whenever an accipiter is seen, the birds at once begin a distressed chipping which is taken up by all in the vicinity, and causes even rabbits to take cover. The birds are adept at seeing hawks at distances well beyond any chance of an unpleasant encounter. This means that the only way a hawk can catch small birds is to take them by surprise before they can reach safety. This implies that the hawk must see them first, before they are aware of its presence and when they are moving about feeding, thus rendering their protective colors ineffective.

DISCUSSION

Basic similarities are revealed by comparing the hunting methods of various predators. The first of these is their common necessity, that of finding prey. As far as present facts show, this is accomplished in essentially the same way by all the birds studied. Every species of hunter makes an ambush of some type and watches for animals to expose themselves by moving about. The high-flying of the Duck Hawk, the hidden perch of the accipiter, the rock pile of the Red-tailed Hawk, are all modifications of this general scheme. Even the active Marsh Hawk, suddenly appearing over some clump of brush, employs but another modification of the general plan.

Not only does this "watchful waiting" cause an unsuspecting animal to give itself away by moving about, but it also allows the hunter the best possible chance to catch it. There is sufficient evidence to demonstrate that the birds studied possess the ability

to withhold their attack until a suitable moment arrives. This is shown by the variety of actions performed when prey is in sight: By the ability of some birds to discriminate between uncatchable and catchable prey, as in the case of a Red-tailed Hawk not molesting sparrows but seizing a mouse beside them; by the mouse nest investigations of Marsh Hawks; and by other activities elsewhere discussed. Obviously, a hawk's chances for success are greatly increased if it chooses the best moment for attack.

Hawks are aided in their work by a remarkable eyesight that enables them to watch unseen from places sometimes conspicuous, far beyond the vision of their intended prey. The predators here studied, then, universally use the method of watching for their food from "ambush," which allows the prey to reveal itself in moving about and gives the hunters more chance to launch a successful attack and to take their prey by surprise.

The animals that are hunted have, in turn, a general method of escape that is adapted to the habits of their enemies. They maintain a constant vigilance and, when threatened, spring into action, either dodging or dashing to cover. No other method would be effective against an enemy that keeps hidden until prey is carefully marked and then falls swiftly upon it, knowing its exact position. To remain motionless would be fatal; all the victim can do to escape being struck down is to run. As in the case of the hawks, various modifications of this general plan are executed: The cotton-tail rabbit takes to the brush, ducks dive under water, and gophers and ground squirrels hide in their burrows in the face of danger.

A fact observed on Tomales Point, but best expressed by Brewster ("October Farm," Harvard Univ. Press, 1936, p. 108), supports the generalizations just laid down. "Of one thing I am convinced, viz., that nearly if not all our birds of prey including the Shrike lack *persistence* in the chase . . . ." If surprise is as fundamental a necessity to success as it seems, there is reason not to expect hawks long to follow up an attack that failed at its onset.

Furthermore, the conclusion of McAtee (Smiths. Inst., Misc. Coll., vol. 85, no. 7, 1932, p. 144) that food species are taken in proportion to their numbers irrespective of protective coloration agrees with the fact that predatory birds hunt by watching a given area for food. With this the case, one would expect the more numerous species to be seen moving about, and thus subject themselves to attack more often than the less numerous ones, and therefore to be caught more frequently.

To summarize, the answer to the question concerning methods of escape and capture for all the species observed is this: A predator watches promising terrain and soon sees any animal in it that moves. Waiting for a suitable moment, and knowing exactly where the animal is, the hunter attacks, taking it by surprise. The prey, if it sees its enemy in time, tries to escape by dodging or taking to cover. This seems a general relationship, at least in the animals studied.

It may now be asked if the colors of animals, blending as they do with those of the environment, are of any significance in such a scheme. In other words, are the conditions under which protective coloration would be effective fulfilled in nature? First will be considered the relation of motion to the problem. Admittedly, the colors of many animals are such as to render them inconspicuous in their natural environment when they do not move. This can be verified by anyone who has watched and hunted animals at all and is, in fact, the main basis of the theory of protective coloration. However, as soon as the animal moves about, it assumes a new property and one sharply distinct from those of its otherwise similar environment. This is easily proven in several ways, some of which are as follows: First, by the rapidity with which we see a creature, previously overlooked, when it flies or runs; second, by the certainty with which we identify a

stationary object as living the moment it moves; third, by the difficulty we have in seeing, for instance, a small bird in a tree during a wind that causes the leaves to move.

We now come to a very important point: The characteristic movement of an animal seen against a still background shows with no doubt that it is a *living organism* irrespective of its color. Observations on many kinds of animals also prove this in several ways. Moving birds can be identified as living creatures of a certain size at distances far exceeding those at which their specific coloration can be made out. When hunting birds and mammals, they are easily located when seen moving, even though concealed or shaded so that their true colors are not determinable. Rabbits dashing away in moonlight are of a far different color than they would be in the day, yet they are easily seen.

Now to correlate these facts about motion with those of the mechanism of predation. Movement, as has been shown, is the only property needed to identify any of the organisms studied as alive. When moving, an animal can be seen though its colors cannot, its size can often be determined, and it can be detected where otherwise it would have been overlooked. A hawk, owl or heron patiently watching a certain territory would sooner or later be able to see any animals present as these unsuspectingly went about feeding or attending to other affairs. There would be no way for the creatures to avoid this consequence except not to move, there would be no reason not to move unless danger threatened, no danger would be detected as long as the enemy remained concealed.

Under such circumstances, a predator need only have patience to wait and to watch (which is what was done by all the predators I studied), to be assured of seeing any suitable prey living within its field of vision, no matter what its color. With conditions like this, the author cannot believe that color plays a part in the detection of prey, at least insofar as the types of animals studied are concerned.

Once seen, however, prey must be caught. Can color be important in this connection? The enemy has its eye upon its quarry, knows exactly where it is, and attacks with the intent of going to it and seizing it. The closer the bird approaches its prey, the larger the prey becomes in proportion to the landscape and therefore the more conspicuous it is. By the time they are near together the victim is of relatively large size; a rabbit, for instance, would be to a Red-tailed Hawk as a medium-sized dog would be to a man. If at this time the animal fails to run, the hawk has merely to seize it; if it does run, the hawk should be as well able to see it as a man could a dog under such circumstances. With this the case, color again seems not to play a part in the outcome of such an attack.

As to predators, there are many facts that are incompatible with the idea that variations in color in any way affect their success in hunting. Some of these are: The contrast in markings between sexes of the same species (as in the Marsh Hawk), the impossibility of seeing the under parts (or dorsal for that matter) of diving hawks, the difficulty of accurately determining the colors of birds seen against the sky or in motion, the hunting over open country by hawks ventrally marked to resemble twig patterns, the conspicuousness of white-breasted hawks not appearing to alarm their prey, the impossibility of determining colors at night, and the great variety of specific patterns that could all be called "aggressive." Once more, the evidence is against the probability that coloration is significant in raptorial affairs.

Because the behavior of predators and prey toward each other apparently nullifies any protective value of the colors of animals, natural selection does not seem to be the process that has developed harmonious coloration in the case of the animals studied. In order for natural selection to operate, color should be a significant factor in predation through aiding some animals and hindering others. This does not appear to happen; therefore, no selection should take place.

There are some matters that at first glance seem to contradict the above statements. The young of numerous animals possess the ability to lie motionless when threatened by enemies; their colors resemble those of their environment in a general way and would appear to protect them from being seen. However, granting that in this case, where specific use is made of "freezing," protective coloration actually works, can we grant further that natural selection evolved such coloration? The author thinks not, for several reasons. There is such a variety of patterns that are protective and these often resemble each other so much that they are not to be differentiated in the field. It appears unlikely that selection could have been the agent that developed these patterns. A more logical action of selection would be, in accordance with the views of this paper, between young that moved and young that did not move, rather than between slight differences of pattern.

The argument has been advanced that, as a black object moving against a black background is harder to see than a white object against the same background, animals which are more protectively colored should be harder to see moving than those which are less so. In such a case, selection would work toward more efficient protective coloration. This would be true were these all the factors; but, in nature, there are others involved.

In the first place, a contrast between some individuals and their environment must occur before selection can take place. In nature such contrasts are seldom seen, either among individuals of the same region or, more importantly, between closely related taxonomic groups. The numerous racial differences that even a zoologist must have right at his hand to distinguish, exemplify the type of difference that actually occurs. A great stretch of the imagination would be required to say that these differences were the products of the type of selection described above. Furthermore, studies in genetics show that a complexity of genes is involved in coat colors generally and that theoretically the gene mutations that are of significance in evolution are usually those of small degree. This does not support the idea that nature provides genetic differences in coat color of magnitude sufficient for them to be acted upon by selection.

Then, in the second place, the method of watching an area soon reveals anything moving in it. Add to this the facts about genetic differences just discussed and the evidence shows the argument using black and white contrasts does not have its parallel in nature.

A matter worth mentioning before passing to the conclusion of this paper is the idea that the selection of slight differences will over a long period of time have effect upon the characters of a species. While this may be so for some genetic characters, it does not seem so in the case of coloration. Slight differences in coloration have here been shown to be non-essential in predation with regard to present cases. Therefore there is no reason to believe that they would be essential over a length of time, which merely serves to augment the number of non-essential cases.

As the evidence all indicates that the theory of natural selection cannot explain why the colors of animals harmonize with those of their environments, another explanation must be sought. The most obvious one is that the external colors of animals are the by-products of their physiological processes and that the resemblance of these colors to their environment is either coincidental or due to causes far more subtle than the theory of natural selection proposes. The similarity in coloration often seen among species living in a common environment, such as a desert or a humid coastal area, does not go contrariwise to the idea of "physiological by-products." These similarities in pigmentation could be the result of parallel adjustments in various physiological mech-

anisms to the same general conditions, no matter how such adjustments were evolved. This is purely conjectural, but the possibility of its being true should not be overlooked until some definite evidence to the contrary is discovered.

An alternative idea is that, while single mutations of the genes affecting coat color may not be of a size to be influenced by selection, these mutations may accumulate and develop a color pattern then of sufficient contrast to come under such an influence. However, if it is granted that mutations can accumulate in such a fashion, this itself could explain the differentiation of specific color patterns and therefore there is no need to invoke the theory of natural selection.

SUMMARY

1. The most widely accepted theories explaining the fact of harmonious coloration are outlined.
2. Four questions are asked:
   a. Under what conditions would the identity of an animal be concealed?
   b. What methods are used by raptorial birds to hunt prey and what methods are used by prey to escape enemies?
   c. Do the methods employed fulfill the conditions under which protective coloration would be effective?
   d. What probability do the answers to the above questions give to the actuality of protective coloration and its origin through natural selection, at least as far as the animals studied are concerned?
3. Question (a) was answered as follows: The identity of an animal is concealed when it does not show any characteristic features.
4. The answer to question (b) was obtained from field observations upon a variety of raptorial birds and their most usual prey. The predators studied universally watched for their food from "ambush," different methods being employed by each species. This allows prey to reveal itself by moving about and greatly increases the chance of a successful attack. The various species of prey, in turn, all maintained a constant vigilance and all sought safety by dashing to cover or dodging. Thus the relationship between predators and prey is based upon two general methods of attack and escape.
5. In answer to question (c) it was pointed out that the movement of an animal seen against a still background identified it as a living organism, irrespective of its color at the time. This fact, correlated with the general method of predatory attack, makes it difficult to believe that color plays a part in the detection of prey, at least as far as the type of animals studied is concerned. Many facts were also shown to militate against color being important to prey in the detection of predators.
6. Because color does not appear to play a significant rôle in predation, it is not probable that the coloration of animals is actually protective (or aggressive). In the face of this, the theory of the origin of such coloration through natural selection does not appear to be compatible with the facts.
7. Some matters have been discussed that at first seem to contradict the above ideas.
8. The possibility was suggested that the external colors of animals are by-products of their physiological activities, and that the resemblance of these colors to their environment is due either to coincidence or to causes far more subtle than the theory of natural selection proposes.

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