advice and support during the course of our work.
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Reflexive Selection: A Possible Answer to an Old Puzzle

Abstract. With the color vision and learning abilities of birds and teleosts now proved, it appears possible that the hitherto puzzling massive variation in color and pattern of certain species, distributed through at least five phyla, is not the result of the mere free play of mutation but represents a protective variation and is the product of what may be called reflexive selection.

Animal species in which variation in color and pattern is so great that virtually no two individuals look alike have long presented an evolutionary puzzle. For such species it is impossible to designate one form as "wild-type" and others as mutants. In marked contrast stand most species with their rigorous uniformity, as, for example, the common eastern robin, *Turdus migratorius*, in which every individual among countless thousands will show a white spot on each outer corner of the tail when in flight. In contrast also are the commonly recognized polymorphic species such as the eastern gray squirrel, *Sciurus carolinensis*, with its two color phases, or the well-studied ladybird beetle, *Adalia bipunctata*, and *Drosophila pseudoobscura*, where only a limited number of forms occur and do not necessarily coexist in time and place.

The kind of variation discussed here is well exemplified by the common North Atlantic brittlestar, *Ophiopholis aculeata*, among echinoderms, and the little coquina or butterfly clam, *Donax variabilis*, among mollusks. In *Ophiopholis* the variation in color and pattern occurs on both the body disc and on the arms. The colors range from reds and purples to browns, near blacks, light yellows, deep yellows, oranges, and pinks. The disc may be some solid color with or without a conspicuous colored border. Instead of a continuous border there may be a large colored spot on the disc at the base of each arm. Or the disc itself may show a single central spot or group of spots with or without a colored border or peripheral spots. The disc may bear a large five-pointed star, or it may be mottled or finely speckled. Every combination and permutation of these designs and colors, and many more besides, can be found. The variation of colors and patterns on the arms is as great as it is on the disc and is independent of the design on the disc. The not surprising result is that out of hundreds of individuals collected at low tide in about an inch of water in a single cove on the coast of Maine it is not possible to find two exactly alike (see Fig. 1).

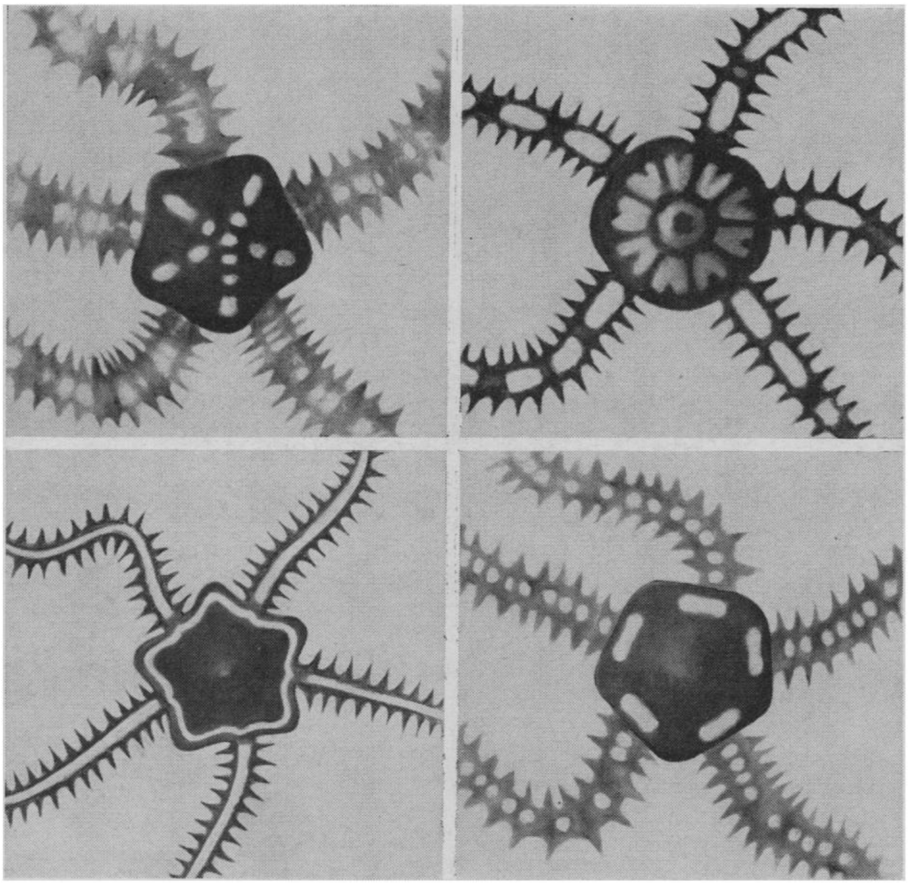

Fig. 1. Four individuals of the same species of brittlestar, *Ophiopholis aculeata*, showing variation in pattern.

In *Donax* the shells range from white to yellow, orange, green, pale blue, lavendar, deep purple, red, pink, and brown. These colors, or lack of color, are sometimes uniform over the entire shell but are usually combined in various ways and the colors themselves are found in concentric rings following the growth lines of the shell and as bands of color radiating out from the umbones so that a plaid-like effect is produced. The statistical possibilities for variation are again enormous, and diligent search through hundreds of individuals is required to find two that are the same.

Massive diversity of this kind is usually dismissed as the result of the free play of meaningless mutation in the absence of selection on the assumption that the colors and patterns have a selection value of approximately zero, being neither positive or negative in effect. Even in the familiar cases of polymorphism mentioned earlier there is "little or nothing," according to E. B. Ford (*1*), "to show what are the advantages that are opposed to one another" in maintaining the condition.

However, in the case of massive variation the possibility presents itself that it is the variation as such which is adaptive, giving a measure of protection against predators. *Donax variabilis*, for example, lives in enormous numbers on beaches from Maryland to Texas, migrating daily with the surf up and down the beach (*2*) where it is eaten by various species of sandpipers (*3*). Brittlestars are known to be eaten by teleosts and are probably eaten by birds also (*4*). Birds and teleosts are now known to possess color vision as well as the ability to learn (*5*). Consequently, if all brittlestars or all coquina clams bore the same color and pattern, it would be possible for their predators to learn to distinguish them quickly by these signs. However, the virtually endless variation makes it impossible for a sandpiper to learn that all "pebbles" of any particular appearance are probably little clams for the very good reason that no two clams have the same appearance. The situation is somewhat analogous to making a code by randomizing the components.

A similar explanation would hold good for the massive variation in the brittlestars and in such other species showing it as *Cerianthus americanus* (*6*) among coelenterates, the Bermuda *Sabella* and the Woods Hole *Hydroides* among tubiculous polychaetes, and *Acridium arenosum* and possibly other grasshoppers (locusts) among insects (*7*).

The type of selection postulated for massive polymorphism does not easily fit into the familiar categories as stabilizing, directional, or disruptive (*8*). It is not disruptive selection, at least in any ordinary sense, since it does not break the population into two or more incipient new species. Perhaps it should be regarded as a special form of stabilizing selection which produces not uniformity but continual diversity. This seems a contradiction in terms. At the same time it does not seem to be "balancing selection" (*9*) where, for example, heterozygotes producing sickle cell anemia, or the MN blood group, are maintained because the heterozygote is superior to the homozygote by conferring resistance to a specific disease or in some other way. The term *reflexive selection* suggests itself because it is the variation per se which is adaptive, and the frequency of any one type is determined by a feedback relationship with all the other types.

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Transpiration Rate Reduction in Plants with Atrazine

Abstract. When treated with atrazine, a herbicide that acts as an inhibitor of photosynthesis, both tolerant and susceptible plants showed a reduction in transpiration rate. This occurred within 1 to 3 hours of application and usually reduced transpiration by 50 percent or more after about 6 hours.

Atrazine (2-chloro-4-ethylamino-6-isopropylamino-*s*-triazine) has gained widespread use as a herbicide, especially for the control of annual weeds and quackgrass (*Agropyron repens*) in corn. Recently, we noticed an interesting plant response to atrazine. Young plants showed a dramatic reduction in transpiration rate soon after treatment. In solution culture this took place within 1 to 2 hours. This effect seems to correspond in time to the effect of simazine (2-chloro-4,6-bis-ethylamino-*s*-triazine) on photosynthesis which was observed by Ashton *et al.* (*1*), who found a drastic reduction in $C^{14}O_2$ fixation in red kidney bean leaves within 3 hours after they placed the roots in a 1 ppm solution of simazine. The first visible evidence of damage by the herbicide to susceptible plants did not occur until about 3 days after treatment under the conditions of our experiments. The reduction in transpiration rate was established in plants grown in soil, as well as in solution culture, and occurred in a wide variety of crop plants.

Our experiments were conducted under controlled light (2500 ft-ca) and temperature (light 76°F, dark 65°F) conditions in a controlled environment room with a light period of 15 hours. Measurements of transpiration rate were made with a modification of the potometer described by Grobbelaar (*2*). In experiments involving soil the method of weighing pots was used.

In most experiments with the potometer, treatment was accomplished by replacing the distilled water with previously prepared solutions of atrazine. Foliar sprays with suspensions ranging from 14 ppm to 12,000 ppm, in which the leaves were thoroughly wetted, all gave significant reductions within 6 hours. In the case of soil experiments atrazine was applied in water solution.

Figure 1 shows the transpiration response of corn, a species known to be very tolerant of atrazine, and of soybeans, a susceptible species. The difference in magnitude of response is not necessarily due to the difference in susceptibility of the two crops. Maximum reduction of transpiration ranged from 44 percent of the normal rate in corn to 67 percent in soybeans. In canning peas a significant reduction occurred within 1 hour after treatment. Maximum reductions were generally obtained 4 to 6 hours after treatment.

In order to estimate the degree of stomatal closure after treatment with atrazine, the leaves were infiltrated with gentian violet in absolute ethanol after a method described by Williams (*3*). The leaves of control plants showed much greater injection of the dye than leaves of treated plants. This difference indicated that the reduction of transpiration rate resulted from decreased stomatal aperture. This was further substantiated by determining the water content of leaves 6 hours after the plants had been treated with atrazine. Leaves of treated plants showed no decrease in moisture content. This would indicate that inhibition of water uptake occurred at the stomata. If water movement were blocked further down the plant, loss of water from leaves would have proceeded until wilting occurred.

Shaw and Maclachlan showed that $C^{14}O_2$ was fixed by guard cells (*4*). This gave considerable support to a long-held idea that the guard cells are capable of photosynthesis. Heath proposed that the most important function of photosynthesis in the guard cells is not the production of osmotically active materials, but the removal of carbon dioxide (*5*). Shaw found that the guard cells in white areas of variegated leaves

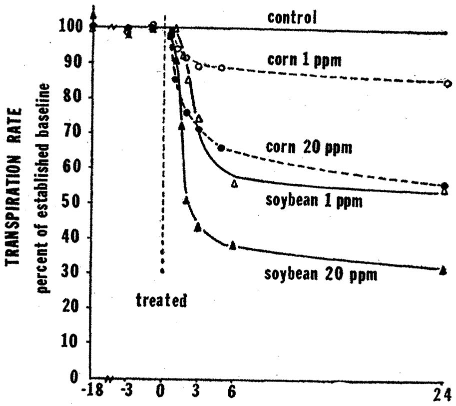

Fig. 1. Transpiration rate of soybeans and corn before and after treatment with 1 and 20 ppm of atrazine. The rates are presented as a percentage of the baseline established prior to treatment. The control was defined as 100 percent, and all observations were adjusted according to the absolute transpiration rate of the control plants.