Incremental Color Change in an Anomuran Decapod
Hippa pacifica Dana[1]

Adrian M. Wenner[2]

THERE IS no longer much question but that natural selection has a strong influence on the color of animals. To cite one of numerous comparisons which can be made, it is clear that toxic animals often have striking and brilliant color patterns and that nontoxic animals most commonly match their background (e.g., Cott, 1957). In the latter category, primarily nocturnal or burrowing animals may also possess what has come to be known as "protective coloration." For example, beach-hoppers of the genus *Orchestoidea* on the California coast normally come out only at night and in the dark of the moon (Craig, 1971). Nevertheless, the color matching of these animals with their background is quite close (personal observations), as is also the case with their staphylinid predators, *Thinopinus pictus* Leconte (Malkin, 1958). These beachhoppers and predators are gray on the gray sand beaches of Santa Barbara, multicolored on the varied sands at Avila Beach near San Luis Obispo, and white on the light colored beaches at Asilomar near Monterey.

On the California beaches this color matching holds as well for hippid mole crabs (*Emerita analoga* Stimpson). Those which burrow into the dark gray wet sand in Santa Barbara have that color. Members of the same species which live in the darker and greener sand at Willows Anchorage on Santa Cruz Island are unquestionably green tinted and darker by a corresponding amount.

Color matching is even more striking among those hippid mole crabs which occur on the islands in the Caribbean and the Pacific. Hanson (1969) has provided photographs of relatively black *Hippa cubensis* Saussure from black sand beaches and speckled animals from those beaches which were not composed of volcanic black sand. In agreement with that find is a report by Eickstaedt (personal communication) that *H. pacifica* Dana individuals found near Guaymas, Mexico, matched the speckled pebbles among which they lived. A comparison of the ivory-colored sand at Lanikai, Oahu, and the red-brown-colored sand at Kihei, Maui, in the Hawaiian Islands with the *H. pacifica* individuals collected from those beaches provides another such color correspondence.

Thus it would appear that natural selection has operated in determining color in populations even among nocturnal and burrowing animals; but use of the phrase "natural selection" does not implicate a specific mechanism. The experiments by Kettlewell and others (e.g., Kettlewell, 1956; Cain and Sheppard, 1954; Clarke, 1960) have already demonstrated the feasibility of one reasonable interpretation, it is true; and it is clear from such work that natural selection via predation can result in a rather rapid alteration of a geographically restricted population.

For animals which have planktonic forms (e.g., *Emerita*, *Hippa*), however, a selective predation interpretation does not necessarily apply; and Hanson (1969) recognized the difficulty posed by this color matching problem. He called for more laboratory and field testing. Fortunately, Pacific island beaches often have the same advantages as those beaches Hanson studied, and the Hawaiian Islands in particular provide a natural laboratory for such studies. The beaches in these islands vary greatly in color composition, and there can be no mistaking these differences. Some are almost white (i.e., the coral sand beach at Lanikai, Oahu). Others are speckled white and black (i.e., Punaluu, Oahu), red-brown (Kihei, Maui), green olivine in part (South Cape, Hawaii), or black (Punaluu and Kalapana, Hawaii). The usual interpretation of selection via predation (predators eliminating those juveniles of a nonmatch-

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[2] University of California at Santa Barbara, Department of Biological Sciences, Santa Barbara, California 93106.

ing color) does not seem to apply, as this would necessitate large numbers of new individuals arriving from the plankton per unit time and would also require a multiplicity of colors among those arrivals.

But as a general rule the young of animals are apparently scarce in the tropics (Connell, personal communication), a generalization which is true for *Hippa pacifica*. Dr. J. Miller at the Hawaii Institute of Marine Biology has sampled Kaneohe Bay, Oahu, extensively; but an inspection of some of his samples revealed no *Hippa* larvae. The virtual absence of young individuals on the beach (Wenner, in press) further agrees with this generalization.

The second condition does not apply either. The planktonic *Hippa* zoeae are transparent, and recently beached megalopae are translucent white and not multicolored as required by the selective predation model. *Emerita analoga* individuals in the Santa Barbara area have similarly colored zoeae and megalopae (Barnes and Wenner, 1968; Wenner, unpublished data). In that location a gray pigmentation which matches the beach sand color is apparent in the exoskeleton only after these animals have moulted to the juvenile form.

These considerations led me to the conclusion that, although it is clear that natural selection operates with respect to the color of these animals, the exact color matching mechanism has yet to be demonstrated. Discussion of this problem with faculty and students at the University of Hawaii and at the Hawaii Institute of Marine Biology eventually led to six possible interpretations:

1. Natural selection of those young which closely match substrate color (selective predation)
2. Natural selection against those young not able to change color rapidly (selective predation)
3. Rapid chromatophoral color changes
4. Gradual deposition of pigment in the exoskeleton
5. Relatively rapid incorporation of pigment in the new premoult exoskeleton
6. Apparent change of color as a consequence of ingested food.

It also became clear that a simple laboratory test could reveal which of these alternatives agrees most closely with that which occurs in nature.

METHODS

On 1 February 1971, 101 animals collected from the wash zone of the white sand beaches at Lanikai and Kailua, Oahu, were transferred to water tables at the Hawaii Institute of Marine Biology. Two water tables had been prepared earlier such that one had a substrate of white (light ivory) colored coral sand obtained from Sandy Beach near Koko Head and the other had a black "sand" substrate. For the black substrate, I used the fire fountain debris from the several-meter-thick layer under the city of Honolulu. I strained, washed, and seasoned this material in seawater for 3 days before setting up the saltwater tables. The larger particles were sieved out and discarded.

After randomly dividing the animals into two equal groups, I further divided each group into seven plastic colanders in each of the saltwater tables fitted with running seawater. The colanders, partially filled with sand, permitted easy removal from the sand substrate and tallying of animals and moults. Moults, excess food, and any dead animals were removed at each feeding time. Once each week I removed all animals, stirred the sand thoroughly, drained out the water, and then refilled the tables with fresh seawater.

Animals in the white sand substrate matched their background and were almost imperceptible even when only partially buried. Animals in a black substrate, however, provided a striking contrast with the black background (Fig. 1).

About once each 2 days, food (shark meat, cut into one-fourth-cubic-centimeter pieces) was given to each animal which assumed the prefeeding posture (Fig. 1). Occasionally goatfish (*Mulloidichthyes samoensis* Günther) served as a replacement for the shark meat. Almost all animals ate at each feeding time.

RESULTS

Mortality and Moult Rate

Mortality was exceptionally low, particularly during the first month. Only one animal died

FIG. 1. A white animal from a white sand beach partially burrowed in a black substrate, illustrating the sharp contrast possible. This is the prefeeding posture of *Hippa pacifica*. When small crustaceans or pieces of fresh meat contact the sensory hairs on the legs during an outgoing wave wash, the animal grasps the food with these raptorial front legs and moves it into the mouthparts.

FIG. 2. Four animals kept in saltwater tables for a 2-month period at the Hawaii Institute of Marine Biology of the University of Hawaii. All four were originally light-colored animals from a white sand beach. The two darkest underwent at most two moults while living in a black sand substrate; and the two lightest individuals spent the same amount of time in white sand.

during that time, even though 34 had moulted in the black substrate and 25 had moulted in the white sand control. By the end of the second month a total of 11 animals had died in each table; and a grand total of 67 moults had been recovered from the black sand table and 56 from the white sand. From these figures it is also apparent that each animal very likely underwent one moult, with some moulting twice during the 2-month experiment.

White and Black Sand

As far as could be ascertained no animal changed color prior to moulting, a conclusion reinforced by the fact that the first cast moult of each animal in the black sand water table matched the color of the animals in the control (white sand) water table. Those animals which lived in the water table with white sand also showed no appreciable change in color at the time of moulting. Control animals clearly matched the color of other animals just obtained from the parent beach.

Those animals which moulted in a black sand substrate, however, all exhibited some change in color. Fig. 2, as an example, shows a comparison of the two darkest animals from each of the two water tables. Characteristically, animals have both a reticulated pattern and a background color (Lee, 1966b). These two characteristics appear to operate somewhat in-

dependently, and one can find all combinations of possibilities on various beaches. In Fig. 2, for example, the pattern is especially pronounced in the carapace of the two animals on the right; and the background color is almost totally white in the two lightest animals. In the course of a color change, the pattern normally darkened from a very light gray toward a total blackness, but the background color became one of various colors. Animals confined in green and red plastic colanders which had no sand moulted into unmistakenly dull green and dull red animals (background color) at the time of moulting.

In almost all cases, the pattern appeared to darken more readily than did the background color. Background color darkened only within specific areas of the exoskeleton during each moult, whereas other areas showed no change whatever (e.g., Fig. 2).

I then repeated the entire experiment (23 April to 21 June), this time starting with 54 animals in each of the water tables. One important distinction with this repeat, however, was that the darkest animals in each size class were placed in the white sand, thus biasing the experiment aginst the color change possibility.

The results did not differ. All except one animal kept in the dark substrate became as dark or darker during the course of the experiment than the darkest of those animals

kept in the control white sand water table. Of the 50 animals remaining in the black substrate, 18 had become appreciably darker than the darkest of the animals kept in the white sand.

In one of the black colanders three of the animals moulted into brown individuals 9 days after the start of the February experiment. A second moult resulted in these individuals being more similar to the background color than were the previous brown tones. (The brown tones in this one case may not be indicative of anything more than a failure to mobilize pigment beyond a certain amount per unit time [Lee, 1966a]).

Evidence of a Color Change in the Field

The obvious color change in the laboratory under experimental conditions led me to sample animals from a black sand beach, just as Hanson had done earlier (Hanson, 1969). I felt that the animals from such a beach could provide an indication of the extent to which color change could occur and perhaps provide further information on the mechanism of this color change.

The Punaluu black sand beach on the island of Hawaii provided such an opportunity, in that it is an isolated beach with black sand only. Sheer lava cliffs separate this beach from the nearest beach of a different color, and it is hardly conceivable that animals move from beach to beach. At least one can reasonably conclude that any animals caught on the black beach have spent their entire lives there.

A trip to that beach in July 1971 produced striking results. The 16 animals caught with staked-out bait matched their background to a degree not expected on the basis of the laboratory results. A comparison with a group of animals collected from a coral sand beach flecked with a small percentage of black particles and located only 32 km away (Fig. 3) left no doubt that these two groups of animals had each adapted to the substrate color found on their respective beaches.

A closer inspection of the animals from the black sand beach (Fig. 4) provided additional evidence relative to the mechanism of color change in that the change was not total, a result which corresponded with the laboratory
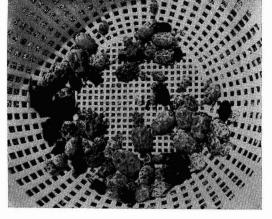

FIG. 3. Black animals from the Punaluu black sand beach on the island of Hawaii compared with a larger number of mole crabs from a nearby speckled sand beach.

results (e.g., Fig. 2). Although the black part was very black, almost every animal had one or more patches of white in the exoskeleton, the amount of white being an inverse function of the size of the animal.

A better appreciation of the lack of total blackness may be derived from an actual measurement of the relative amounts of black and white on the individuals collected. For this purpose, a slide of 15 animals was projected onto a screen and an outline traced both of the entire circumference of each animal and of that part which was totally black in dorsal aspect. By comparing that percentage of the dorsal aspect which was black to the carapace length
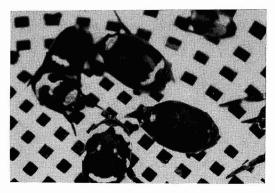

FIG. 4. A close-up view of a few of the animals from the Punaluu black sand beach of Hawaii. The amount of blackness is a function of the size of the animal (see Fig. 5).

of the animal, it could be seen that, for the most part, the percentage of blackness increases rapidly during the early stages of an animal's growth (Fig. 5).

The paucity of very small individuals resulted in the bottom end of the curve being more speculative than the upper part of the curve. It is evident, though, that the animals apparently gain a new area of blackness with each successive moult. A close inspection of the exoskeleton with a binocular dissecting microscope also revealed that this color is pervasive and can be considered an example of extra-chromatophoral pigment deposition in the exoskeleton and epidermis (Hitchcock, 1941; Kleinholz, 1961; Lee, 1966b).

DISCUSSION AND CONCLUSIONS

The Pacific mole crab, *Hippa pacifica,* closely matches the color of the substrate in which it burrows. Although it is clear that natural selection has brought about this close correspondence in color, the exact mechanism has heretofore not been at all clear. Results from
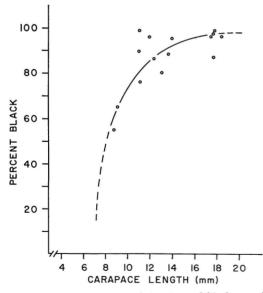

FIG. 5. A comparison of the size and blackness of the 15 black animals visible in Fig. 3. The relative areas of white and black for the individuals obtained from the Punaluu black sand beach of the island of Hawaii show a correspondence with animal size. The line was fitted by inspection (megalopae are not less than about 7 mm carapace length).

observations and experiments have now decreased the number of available alternative explanations.

A mole crab apparently does not move from a beach of one color to one of another color, so there is little selective advantage for a rapid color change (within a few hours) in these animals. The results from laboratory experimentation fell into line with what one might expect in such a circumstance—animals transferred to a darker substrate exhibited no darkening in color before they moulted. The fact that a majority of white animals kept on a black sand substrate did become darker at the time of moulting and not before classifies this color change as morphological rather than physiological. Kleinholz (1961) has already made such a distinction; but, of course, morphological changes would have a physiological basis. Bodenstein (1953) had expressed the same principle earlier when he defined morphological color change as ". . . a quantitative increase or decrease of the amount of pigment."

Mole crabs kept on a red, a green, or a black background became more nearly red, green, or black, respectively, at the time of moulting in the laboratory. This result is especially interesting, in that the animal must somehow recognize the existing disparity between itself and its background color and manufacture the appropriate set of pigments. Lee (1966a) encountered a similar problem in his study of morphological color change in *Idotea montereyensis* (see below).

The fact that animals could become red in the laboratory agrees well with the find that red-brown animals live in the red-brown sands at Kihei, Maui. The small animals in the laboratory experiments also apparently exhibited a greater morphological color change than did the larger animals at the time of moulting (a subjective evaluation). This conjecture leads to the conclusion that the red-brown animals in Kihei could have attained the beach color within a relatively few moults after having arrived as megalopae from the plankton.

If, indeed, megalopae of *Hippa pacifica* which arrive on beaches of various colors are all translucent white in color (and there is not yet any reason to believe otherwise), the interpretation that the color matching of animals

and beaches is brought about by selective predation becomes suspect. From this line of reasoning it is also evident that megalopae arriving on black sand beaches would necessarily exhibit the most radical possible color change.

The data gathered at Punaluu Beach (a black sand beach) on the island of Hawaii suggest that small (young) animals add a larger percentage of black area more quickly than do larger animals. This means that an appreciable color change could occur for juveniles within a very few moults (two to four), a conclusion which agrees with the subjective evaluation obtained from laboratory observations. (There are not yet any available data on the amount of time this might represent in the field.)

The provision of the same diet (shark meat and occasionally meat of other fishes) to both experimental and control animals argues against the possibility that food supply determined postmoult color, a find which agrees with the results obtained by Lee (1966a). In the Hawaiian Islands one of the principal foods for mole crabs is fresh animal material from the inshore waters. Reportedly, Portuguese men-of-war which have washed onto the beach furnish most of this food (Matthews, 1955). In that case the beach would not be a source of pigment for these animals. Certainly the obsidian-like black sand does not enter into the biochemical cycle. Rather, it would appear that these animals mobilize carotenoids and form carotenoproteins (Lee, 1966a), which are then deposited in the newly forming premoult cuticle.

The exact mechanism of pigment production and incorporation in the exoskeleton is far from clear. Brown (1934) studied morphological color changes in the shrimp *Palaemonetes vulgaris* and was the first to assess the relative rates of pigment formation and destruction. He found a 65 percent decrease of pigment in 20 days for shrimps transferred to a white background and a 40 percent increase in the amount of pigment present in 18 days for shrimps partially bleached and kept on a black background. Brown clearly recognized the importance of morphological color change and the incorporation of newly formed pigment in chromatophores. He stated (p. 368): "In reality, the well-adapted shrimps and prawns in nature owe their adaptations at least as much to the differential formation and destruction of pigments within the chromatophores as to the more rapid migration of the already formed pigments."

Hitchcock later encountered the problem of exoskeletal masking of chromatophoral color changes in his studies of color matching in the gulf-weed crab, *Planes minutes* (Hitchcock, 1941). He concluded (p. 28): "In spite of chromatophoral responses, *Planes* is unable to effect color adaptation rapidly, for animals kept all day on white or yellow backgrounds became but slightly lighter than those kept on black" and (p. 29): "Until the diffuse pigment can be elaborated or destroyed, . . . it prevents the changed state of the chromatophores from becoming evident in the general appearance of the animal. This process apparently takes considerable time."

Lee (1966a, b) studied the same problem in greater depth in his investigation of color changes in the marine littoral isopod *Idotea montereyensis,* an animal which feeds on algae and assumes the color of the plant on which it feeds. He is apparently the first to appreciate that an animal might incorporate pigment into the newly forming exoskeleton prior to moulting, and that such a color change might be fully apparent only after moulting. He reported, in part (1966b: 933): "Once the substrate has been changed, the animal first responds by slowly reversing the existing state of contraction or expansion of its chromatophores. Secondly, new pigment is produced, and depending upon the stage in the moult cycle, is either placed in the old cuticle (if this has not yet completely formed) or in a new one underneath the old cuticle. The final step in color change occurs when the animal moults and exhibits its new cuticle, which matches its new substrate."

Herring (1969) repeated Lee's study with a related but pelagic isopod, *Idotea metallica,* and found some important differences in color-changing ability, particularly with respect to the iridescence and biochemistry of the animal he studied.

For *Hippa pacifica* the circumstance appears to be a bit more extreme than that which Hitchcock found for the gulf-weed crab or that which Lee found in isopods. Mole crabs show

no apparent change in color prior to moulting, even if this period extends 2 weeks or more after they have been transferred to a substrate which is darker (or of a different color) than their own body color. The manufacture and incorporation of pigments into the newly developing premoult cuticle first appears in the pattern, but some of the area between pattern lines also becomes filled in with the newly formed pigment. Successive moults lead to a further filling in of the area within the pattern and an ever-closer correspondence in color between animals and substrate.

The dispersion of pigment throughout the matrix of the exoskeleton, as exemplified by the pervasive color in the black animals from a black sand beach, corresponds with Hitchcock's contention that this type of pigmentation is extrachromatophoral. It is also obvious that a large amount of extrachromatophoral pigment would obscure whatever changes might be occurring within the animal or within its chromatophores. In any event, the consequence is a dramatic and apparently sudden color change only at the time of moulting, even though the pigment production and accumulation may have been gradual.

The evidence thus indicates that Pacific mole crabs adapt to the color of their substrate as they grow. Of the several possible interpretations outlined in the introduction as to how this change might come about, the notion of a repeated addition or deletion of a pigmented area at each moult emerges as the most defensible interpretation. In reality this "incremental color change" may be the result of a gradual accumulation of pigment in the animal (i.e., "morphological color change") which becomes incorporated only into the new premoult exoskeleton.

It is also conceivable that this interpretation might fit a number of heretofore unexplained cases of color adaptation, both in crustaceans and in insects. The relatively abrupt nature of the color change and the relatively long amount of time spent in the intermoult phase would weigh against the possibility that this type of color change would be readily noticed.

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