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Adaptive Coloration in Texas Fiddler Crabs (Uca)

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Common fiddler crabs (*Uca*) of Texas. A. *Uca subcylindrica* (Stimpson). B. *Uca panacea* Novak and Salmon(courtesy of F.H. Barnwell). C. *Uca spinicarpa* Rathbun. D. *Uca longisignalis* Salmon and Atsaides. E. *Uca rapax* (Smith).

Adaptive Coloration in Texas Fiddler Crabs (*Uca*)

CARL L. THURMAN

Synopsis

Five species of fiddler crabs occupy a variety of intertidal niches along the Texas coast. Each *Uca* is adapted to a specific array of physical factors in the environment. Some aspects of their adaptations are reflected by body color. Interspecific differences in morphological coloration are correlated with camouflage and substrate characteristics. Intraspecific color variation is expressed through neurosecretion-mediated physiological change in cellular pigment distribution. Adaptation to a dark or light colored background reveals different "secondary" chromomotor capabilities for each species. In addition, pigments in melanophores, leucophores and erythrophores exhibit circadian rhythms of dispersion and aggregation.

During a "primary" chromomotor response to light or temperature, chromatophores act as independent effectors without endocrine mediation. Generally, logarithmic changes in luminosity from 12- to 1,000-foot candles disperse chromatophore pigments in species from the *Minuca* subgenus but not members of the *Celuca* subgenus. In the very terrestrial *Celuca*, *U. subcylindrica*, erythrophores and melanophores were observed to aggregate. Since this does not occur in eyestalk-less crabs, the response is augmented by light activating a visual-neurosecretory reflex. Changing temperature stimulated thermoregulatory chromomotor activity in the *Celuca*, *U. panacea* and *U. subcylindrica*, but not the *Minuca*. In *Celuca*, the carapace darkens as temperature decreases and lightens as it increases. Based on these chromatophore studies, the pigmentary systems of the subgenus *Celuca* appear to be predisposed for better short-term thermoregulation than those in the subgenus *Minuca*.

Introduction

The forces affecting the evolution of invertebrate pigmentation are numerous (Burtt, 1979). As pointed out by other contributors to this symposium, coloration plays an important role in (1) communication, (2) camouflage, and (3) thermoregulatory behavior. A large number of studies have addressed the role played by pigmentation in cryptic coloring, inter- and intraspecific communication (e.g. courtship, aposematic and parasematic signaling). In addition, dermal and hypodermal pigments may regulate the absorption of radiation through either behavioral, physical or biochemical changes. Through these modifications, color may control body temperature or rates of evaporative water loss. Thus, pigmentation can have considerable significance where radiation, temperature and moisture are critical factors limiting the distribution of species.

These physical factors appear to have influenced both evolution (Bliss, 1979) and pigmentation in terrestrial crustaceans. In aquatic Crustacea with thick, strongly calcified exoskeletons, body color is conferred by a pigment layer in the integument below the epicuticle (Bagnara and Hadley, 1973; Ghidalia, 1985). If the crustacean possesses a thin, translucent exoskeleton, like the semi-terrestrial fiddler crabs, body color is due to pigments occurring inside the body or in special cells called chromatophores. Regardless of their localization in a layer or a cell, the same pigment compounds are responsible for crustacean color: carotenoids, ommochromes and pterins (Ghidalia, 1985). The distribution of these pigments may be modified to alter body color.

Modifications in the display of a pigment are classified as either morphological or physiological color change (Rao, 1985). The integumental color of a crab is determined by the number, types and distribution of both epidermal and chromatophore pigments. Quantitative changes in these components will lead to a morphological color change. Typically it occurs in response to environmental changes or development and takes place over several days, weeks or months. For example some herbivorous crustaceans may incorporate different carotenoids into their exoskeleton with each molt and growth cycle (Lee, 1966). Altering the number of chromatophores or quantitative changes in cellu-

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lar pigment content or arborescence may contribute to morphological color change (Green, 1964).

Color transformations due to pigment migration within chromatophores are commonly known as physiological color change. During these chromomotor responses (Needham, 1974), colors are displayed or obscured by the respective dispersion or aggregation of chromatophore pigment. Physiological color change may be either slow, predictable and rhythmic, or rapid and spontaneous. Slow chromomotor responses are usually expressed as daily, tidal, lunar or seasonal rhythms (Palmer, 1974). Rapid responses are displayed immediately in response to background color, fluctuating illumination and changes temperature. Some species of fiddler crabs may use rapid physiological color change in courtship (Crane, 1944; 1975).

Physiological color change occurs by one of two basic mechanisms: a "primary" or a "secondary" response. Primary responses are primitive chromatophore changes independent of nerve and hormone control (Brown, 1973). These responses are elicited by illumination or temperature directly stimulating chromatophore pigment migration. The cellular basis of the primary response is unknown (Weber, 1983). Secondary responses occur through indirect routes involving neurosecretory tracts in the eyestalk. The primary response persists in the absence of neurosecretory components while the secondary will not.

Generally, secondary responses are mediated by neurosecretory hormones known as chromatophorotropins (Rao, 1985; Fingerman, 1987). The sinus gland, located in the crustacean eyestalk, is a neurohemal organ engaged in the storage and release of material elaborated by cells in the nervous system. Brown and his associates (Brown and Ederstrom, 1940; Brown and Wulff, 1941; Brown and Klotz, 1947) demonstrated that chromatophore pigment migration is regulated by a dual hormone mechanism. Antagonistic pairs of pigment-dispersing and pigment-aggregating hormones released from the sinus gland regulate chromatophore movements. However, removing the sinus gland-nervous system complex may not block entirely a secondary response. In some natantians, reptatians and stomatopods, a caudal photoreceptor may entrain light-dependent responses by an extraocular pathway (Page and Larimer, 1976; Wilkens and Larimer, 1976). Since pigment-affecting hormones are synthesized in the nervous system, removal of the sinus gland does not prevent the release of hormones from neurosecretory cells located in other parts of the crab (Webb et al., 1954; Fingerman et al., 1967, 1969).

Light intensity, temperature and water loss are important factors influencing the evolution of semiterrestrial crabs (Bliss, 1979). Much of our basic understanding about crustacean color physiology has been developed using the fiddler crab (Fingerman, 1970; 1987; Rao, 1985). Consequently, it appears that color change plays a significant role in the physiological adjustment of semiterrestrial *Uca* to some environmental factors. This discussion will focus on cryptic coloration, circadian rhythms in pigment movement and subgeneric differences in the primary responses of Texas *Uca*. Their color patterns and physiological responses are similar to those expressed by other *Uca* around the world.

An Ecological Perspective for Color

From a recent biogeographic survey (Barnwell and Thurman, 1984), seven species of *Uca* occur in Texas. Two, *Uca minax* (Le Conte) and *Uca vocator* (Herbst), are rare in the region. The five remaining species are frequently encountered in either semiarid, riverine or intertidal areas. Only these common species will be addressed (Plate 7). From a systematic perspective, two species, *Uca longisignalis* Salmon and Atsaides and *Uca rapax* (Smith), are recognized as members of the subgenus *Minuca* according to Crane (1975). Two others, *Uca panacea* Novak and Salmon and and *Uca spinicarpa* Rathbun are considered to be *Celuca*. The fifth species, *Uca subcylindrica* (Stimpson), was recently transferred from the *Minuca* to the *Celuca* subgenus (Barnwell and Thurman, 1984). All species except *U. rapax* are endemic to the western Gulf of Mexico. *Uca rapax* is found throughout the Gulf and distributed into Central and South America.

Climate

Fiddler crabs are inhabitants of the intertidal zone throughout tropical and temperate latitudes. Neotropical species, in particular those from the western Gulf of Mexico, are unique in their adaptation not only to temperate latitudes but also to relatively arid coastal conditions. In terms of climate, the Texas coastline is divided sharply into two distinct zones (Hedgpeth, 1953). Between the Sabine and the Guadalupe rivers along the northern coast, the climate is moist with more than 35 inches of precipitation annually. South of the Guadalupe river, the climate becomes subhumid and semi-arid with less than 25 inches of precipitation per year. Because of low rainfall, few rivers, barrier-islands, and a high transevaporation coefficient, coastal lagoons in the south are often hypersaline (salinity >> 35 o/oo). Along the northern Texas coast the average winter-minimum temperature is about 4.4°C. Fiddler crab populations in this region may be inactive during the winter months. In south Texas, the average winter-minimum rises to near 10°C. During most of the winter, periodic warming periods are not uncommon along the southern coast

and crab activity is often seen during the day. To inhabit this region, intertidal *Uca* must tolerate temperature extremes, high salinity and low humidity (Thurman, 1984; Rabalais and Cameron, 1985).

Intertidal distribution

The ecological distribution of fiddler crabs in the western Gulf of Mexico has been described by Thurman (1982, 1984, 1987). A description of the ecology of *Uca* in the northern Gulf is forthcoming (Thurman, in preparation). A typical distribution of fiddler crabs in a brackish-water habitat is shown in Figure 1. Between the Louisiana border and the Laguna Madre near Corpus Christi, Tex., the shores of embayments and lagoons usually contain *U. longsignalis, U. rapax, U. spinicarpa* and *U. panacea*. The fifth species, *U. subcylindrica*, is ecologically distinct from the others (Figure 2a). It is endemic to hypersaline, brackish, and freshwater niches in semi-arid south Texas. This species expresses a greater degree of terrestriality than other species of *Uca*.

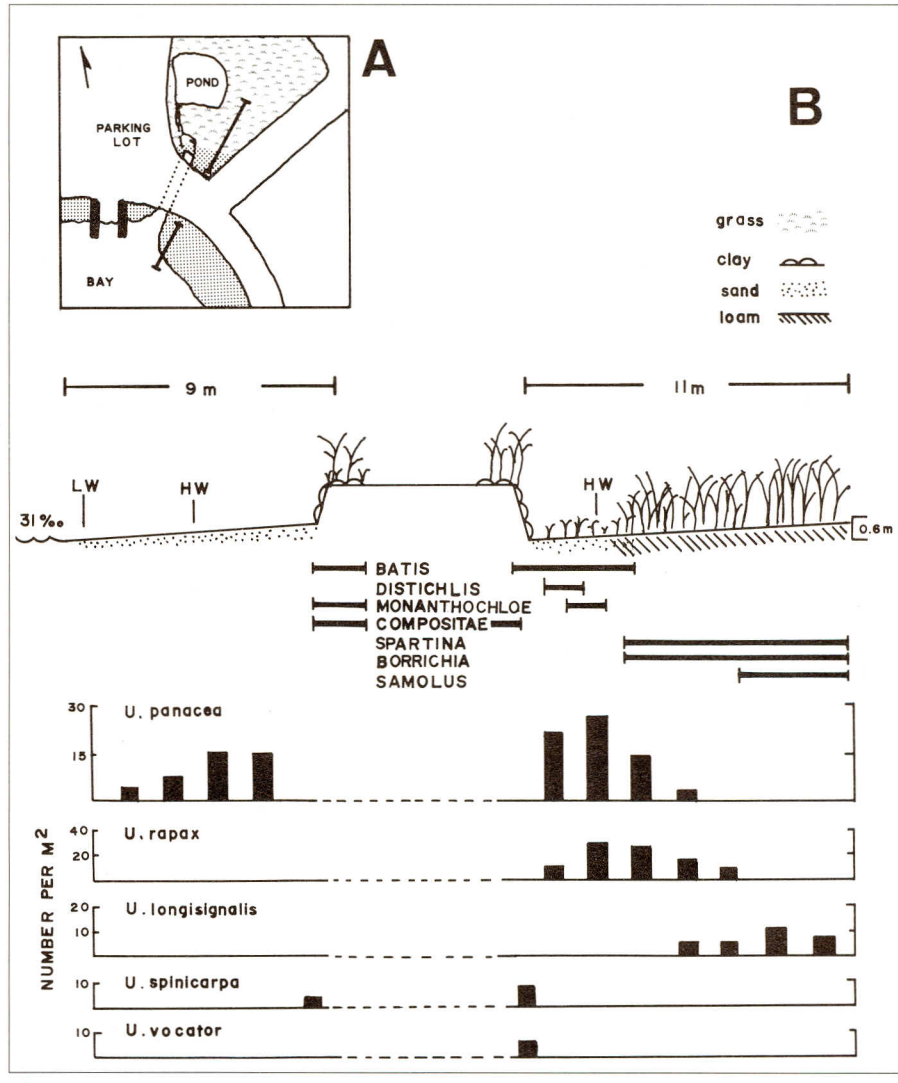

Figure 1. Transect of *Uca* habitat at Ingleside Cove, Tex. (Thurman 1984). A. Overall view of location. B. Transect through marsh. Position of transect in A indicated by bars. LW = low tide water mark. HW = high tide water mark.

Throughout their distributions, each species of *Minuca*, *U. longisignalis* and *U. rapax*, typically inhabits substrates with an average particle diameter of less than 109 μ (Thurman, 1982; 1987). Both live on dark-colored soils with vegetation coverage. Although they are commonly sympatric, *U. longisignalis* is often collected in areas with lower salinity (5 o/oo) than *U. rapax* (Thurman, 1982; 1984). However, due to their ability to osmoregulate over a broad range of salinities (Rabalais and Cameron, 1985), populations of *U. longisignalis* can be euryhaline in their distribution. Although its osmoregulatory abilities have not been assessed, colonies of *U. rapax* are commonly limited to habitats with salinities greater than 15 o/oo. Segregation into two different microhabitats appears to be due to differences in the physiological capabilities of these *Minuca*.

Among the *Celuca*. *U. panacea* typically inhabit exposed, sandy substrates in euryhaline environments (Rao and Fingerman, 1968; Powers, 1975; Thurman, 1984). They are found on intertidal substrates having a mean particle diameter of 112 μ between western Florida and Tabasco, Mexico. *Uca spinicarpa*, on the other hand, occur in habitats with low salinity. Water near or in the crab's burrow has a salinity between 1 and 30 o/oo. They often burrow in clay or loam banks with an average particle diameter greater than 110 μ (Thurman, 1984). These habitats are covered with low but thick vegetation. The third *Celuca*, *U. subcylindrica*, is found near hypersaline and freshwater lagoons in Texas and northeastern Mexico with very low vegetational coverage. Since they possess the ability to burrow exceptionally deep (Figure 2b) and have special larval characteristics, this species can maintain populations in nontidal, isolated lagoons several kilometers from the coast (Thurman, 1984; Neck, 1987). Because of its terrestriality, *U. subcylindrica* is

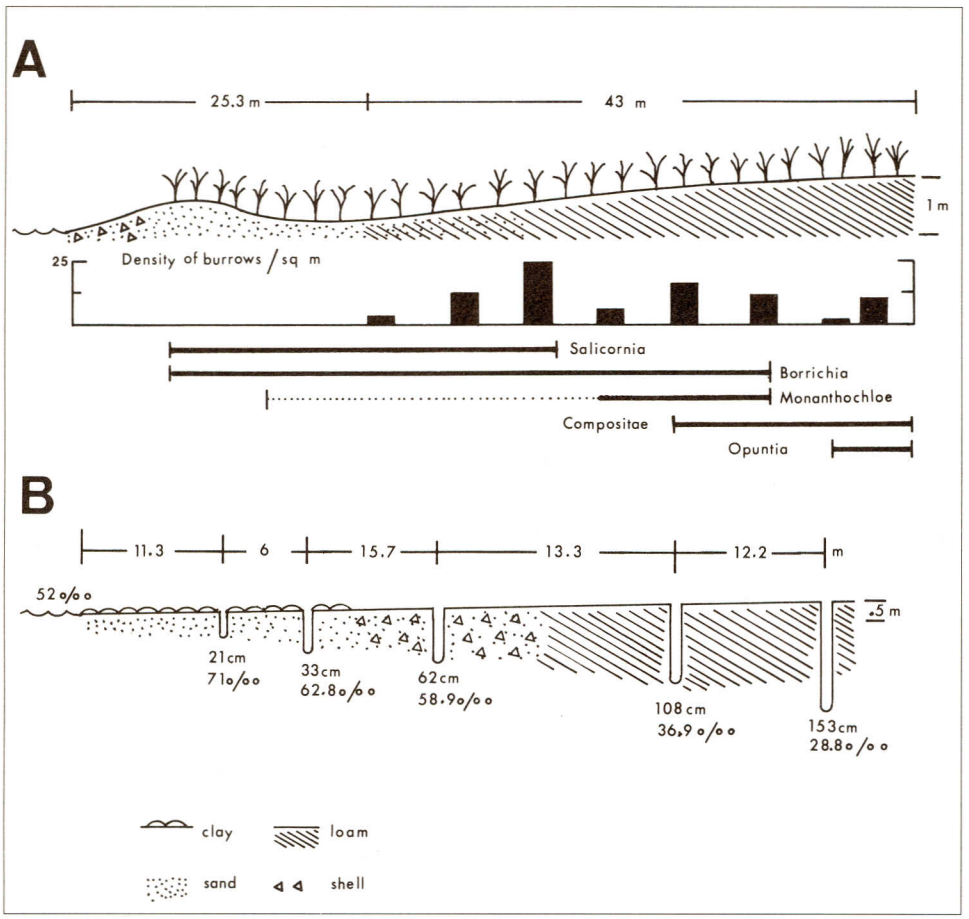

Figure 2. Transect of *Uca subcylindrica* habitat at Laguna Salado, Riviera, Kleberg County, Tex. (Thurman 1984). A. Burrow distribution. B. Burrow depth and salinity profile along transect.

often exposed to high levels of evaporation, insolation, and elevated temperatures (Thurman, 1984).

Environmental rhythms

Cycles of color change in the fiddler crabs usually correlate with specific environmental periodicities such as photoperiod or tidal inundation and ebb (Brown, 1973). Daily solar and temperature cycles appear to be among the more important "zeitgebers." In the western Gulf, these appear more important than tides for regulating fiddler crab activities (Barnwell, 1968a; 1976; Powers, 1975) During summer months, high surface temperatures may restrict crabs to crepuscular and nocturnal activity where as during the winter, daily warming may encourage diurnal crab activity (Thurman, 1984).

Color Variation in *Uca*

Morphological coloration

Usually each species of *Uca* can be identified by its color (Plate 7). However, this sole criterion should not be used to identify a taxon. The general pigmentation of both male and female *Uca subcylindrica* is remarkably constant throughout the range of the species. They possess a gray-mottled carapace with gold, yellow, and orange flecks (Plate 7a). The carapace of an individual crab can vary from pearl-white to tan depending upon its physiological state. The large cheliped of the male is white. Although the ambulatories are heavily setose, they are usually gray or white.

The carapace of *U. panacea* varies from light gray to olive-brown. It is similar in color to *U. pugilator* (Bosc), a close relative from the eastern Gulf (see Rao and Fingerman, 1968; Novak and Salmon, 1974). The H-depression in the mesogastric region is permanently dark (Plate 7b). Unlike *U. pugilator*. *U. panacea* never possess a purple spot in the anterio-mesogastric region. The fingers of the male's large cheliped are white and the outer propodus is orange to purple. Ambulatories are usually colored creamy-tan or brown-black.

The carapace of *U. spinicarpa* is ash-gray mottled with small white, black and brown specks (Plate 7c). Some individuals have a cream-colored carapace. Individuals with green pigmentation on the interocular lobe were collected in Ocean Springs, Miss. (Barnwell and Thurman, 1984). This color variety is rare. The major cheliped has gray to white

fingers; the propodus is yellow to ochre. Walking legs are usually mottled with black, brown and white spots.

Morphological coloration in the *Celuca* correlates closely with edaphic characteristics (Plate 7). First, *U. subcylindrica* inhabit a dry, gray-colored clay. The gray carapace undoubtedly contributes to cryptic coloration. *U. panacea* live on sandy soils with sparse vegetation. The brown-gray body color of this species aids in substrate-matching camouflage. Likewise, *U. spinicarpa* are cryptically colored for inhabiting gray to black-colored clay-loam soils.

Minuca are generally darker in color than *Celuca*. They possess a gray, brown or buff-colored carapace (Crane, 1975). This "broad-fronted" *Minuca* may have a light-colored anterior edge on the carapace (Plate 7d). The most anterior third of the carapace can vary in color from apple-green to blue-green or turquoise (Salmon and Atsaides, 1968). The carapace of the female, in cases, may be void of this bright coloration. Her carapace may be simply brown-black. Fingers of the male's large cheliped are yellowish white with brown to dark-yellow pigment spots on the articulations. The upper carpus and merus are often yellow-green with dark-yellow and brown specks. The ambulatories are black-brown in color.

In *U. rapax* from the western Gulf of Mexico carapace color is invariant over a wide geographic range. Anterio-frontal and orbital regions are creamy-white to rose (Plate 7e). The anterior third of the carapace is blue with purple-red specks. Dactyl and exopodite of the large cheliped are white while the propodus is gray to blue with yellow lining. The ambulatories are always dark.

Coloration in the *Minuca* is also correlated with edaphic characteristics. Both *U. longisignalis* and *U. rapax* possess dark pigmentation on the lower portions of the carapace and legs that provides cryptic coloration in muddy habitats. However, the bright colors around frontal and orbital regions of carapace in both sexes are not correlated with any obvious environmental parameter.

Physiological coloration

Individual variation in body color is achieved by altering chromatophore pigment distribution. Experiments examining physiological color change were conducted with fiddler crabs measuring at least 14 mm across the carapace within 24 hours of their capture. The crabs were kept individually in pans with saltwater under constant temperature (22°C) and illumination (32-foot candles) unless otherwise indicated. The dispersion index or stage of melanophores, leucophores and erythrophores on the anterior merus of the third pereopod was estimated using the method of Hogben and Slome (1931). An index of one (1) describes a chromatophore in which the pigment is completely aggregated; while five (5) indicates one in which pigment is maximally dispersed. To examine the direct effect of illumination and temperature on chromatophore dispersion, the methods of Brown and Sandeen (1948) and Barnwell (1968b) were used. Chromomotor datum is reported as the mean and standard error of dispersion index.

Background adaptation. To chromatically blend with a background, the chromatophores of an organism are physiologically adjusted to adapt its body color to that of the substrate. Optimum physiological color adaptation to a light substrate is the complete dispersion of leucophores and aggregation of melanophores and erythrophores. On the other hand, dark adaptation involves the dispersion of melanophores and erythrophores and a concentration of leucophores. Physiological color change in these cases usually takes about one hour.

The magnitude of the color-change associated with background adaptation was determined for each species of *Uca* by indexing chromatophores on dark- and light-background adapted crabs. Crabs were placed in either a white or black plastic container for one hour to adjust or adapt their body color to a dark (DBA)- or light (LBA)-background under constant conditions. The chromatophores were initially staged at 0900 CST, then once every hour for three hours. Mean dispersion index (±SEM) for black, white and red chromatophores following the adaptation of each species (N = 20) is shown in Figure 3.

Except for erythrophores in *U. longisignalis* (Figure 3b), the chromatophores in all species exhibit dispersion patterns indicating statistically significant background adaptation ($P<0.05$). The difference in average chromatophore stage between black and white background-adapted crabs can be used as a measure of physiological flexibility or capability. The difference in average chromatophore index is minimum in *U. rapax* (1.3 units) and maximum in *U. subcylindrica* (2.6 units). Intermediate physiological capabilities are seen in *U. spinicarpa* (1.7), *U. panacea* (1.9) and *U. longisignalis* (2.1). In general, *Minuca* tend to remain dark when placed on either dark or light substrata. Except for leucophores in *U. longisignalis*, chromatophores of the *Minuca* do not exhibit extensive physiological adjustment to background color. The amplitude of chromatophore background responses is greater in the *Celuca* (Figure 3c,d,e).

Chromatophore rhythms. Chromomotor adjustments for background adaptation are not constant. The fiddler crabs are well known for their circadian rhythms of color change even though their adaptive significance is unknown (Brown, 1973; Webb, 1983). Chromatophore pigment migration in *Minuca* under constant temperature and illumination (LL) for 48

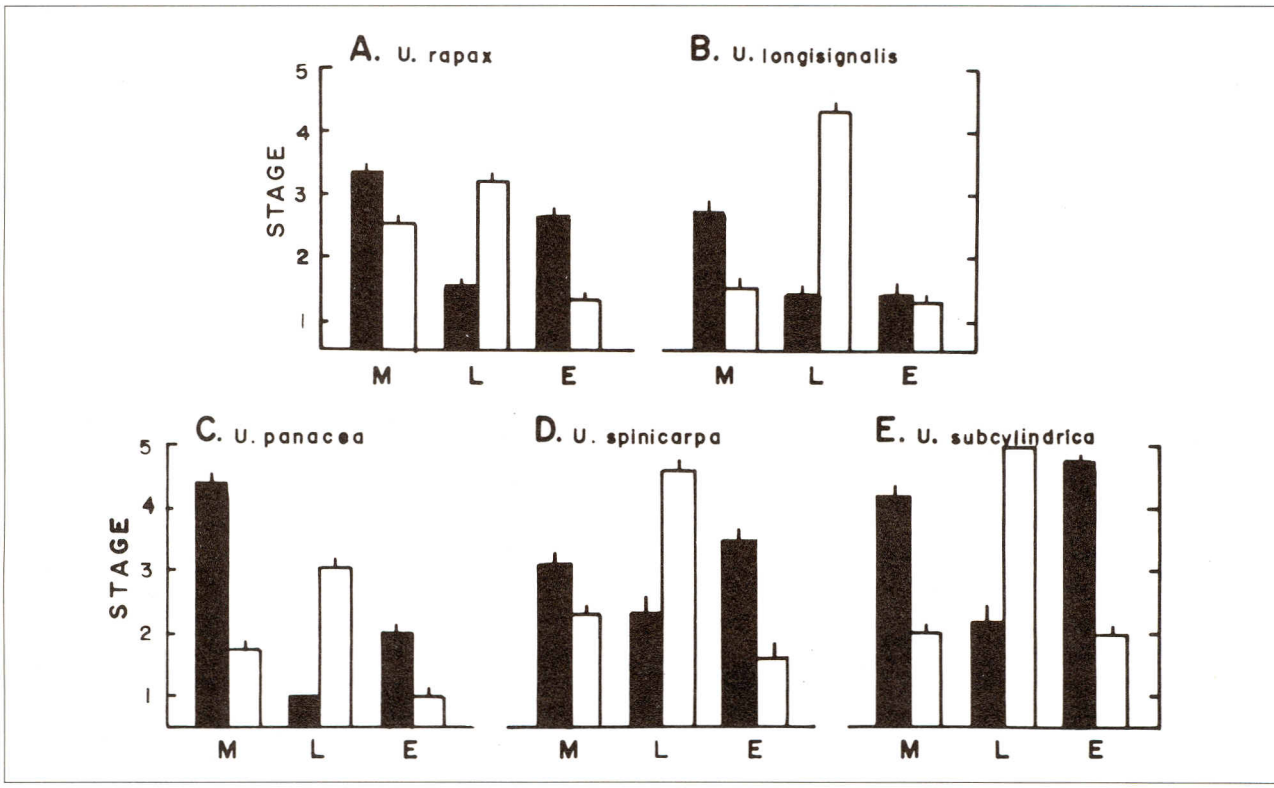

Figure 3. Mean (±SEM) chromomotor response of *Uca* following dark (solid bar) and light (open bar) background adaptation. N = 20 individuals/species. M = melanophore, L = leucophore, E = erythrophore.

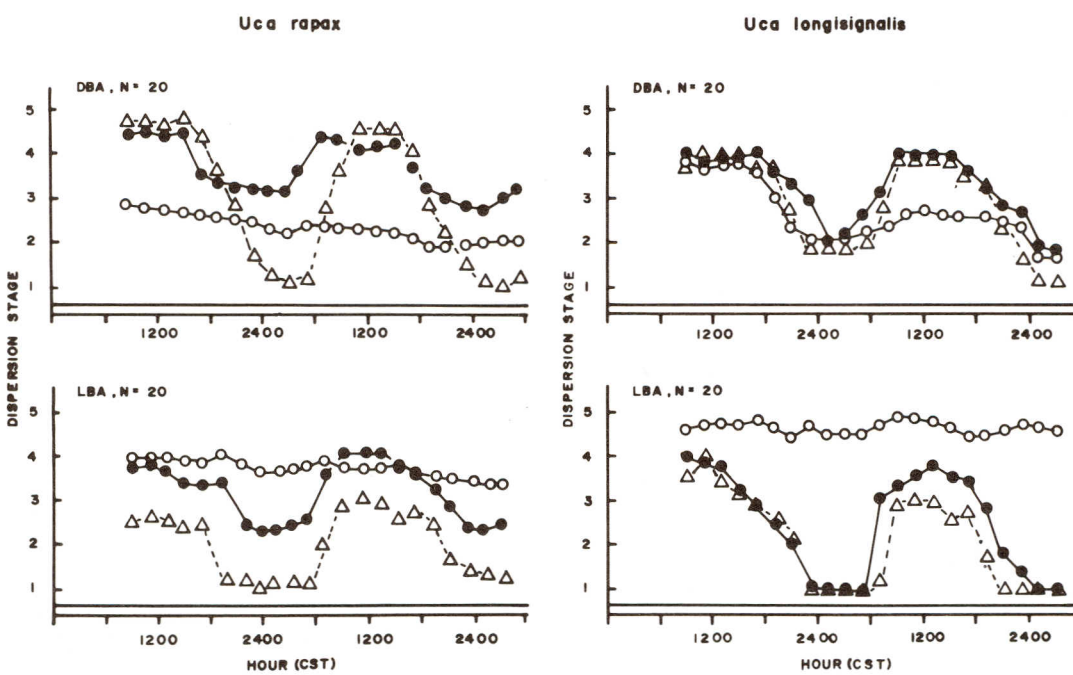

Figure 4. *Minuca* chromomotor rhythms in constant illumination (LL, 32-foot candles). DBA - dark background, LBA - light background. • - melanophores, o - leucophores, Δ - erythrophores.

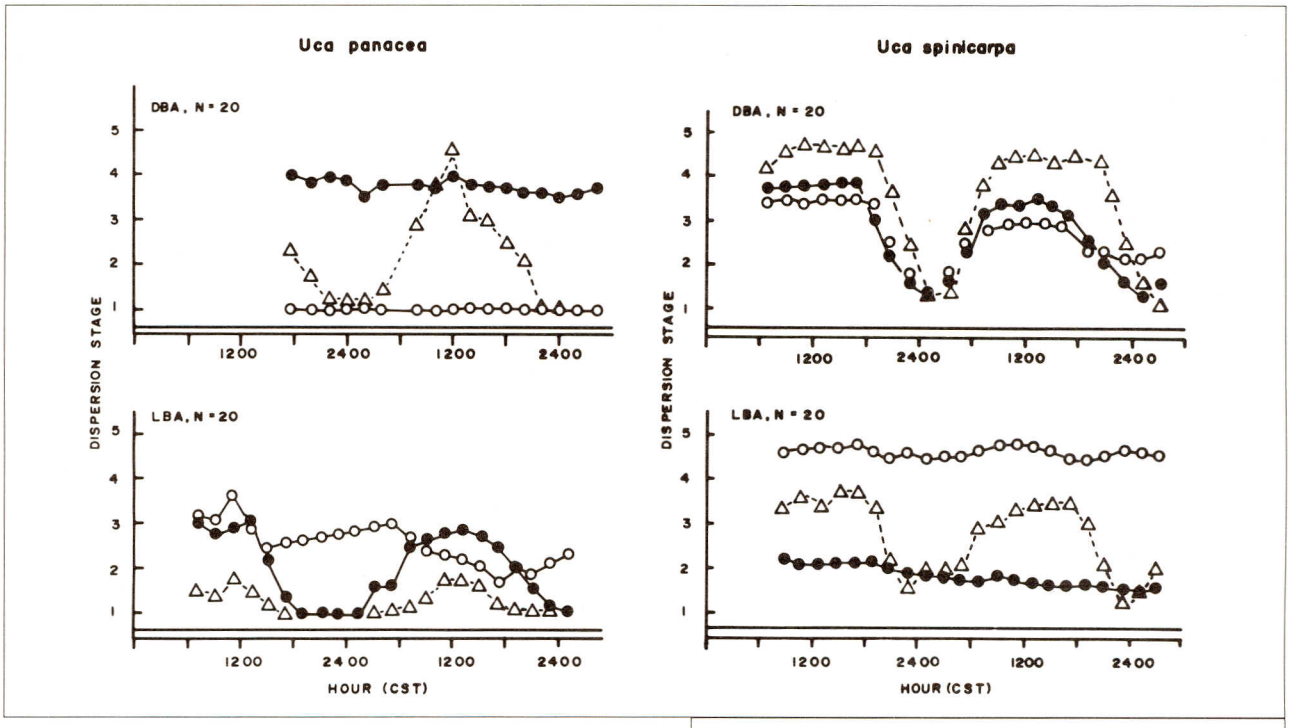

Figure 5. *Celuca* chromomotor rhythms in constant illumination (LL). Symbols same as in Figure 4.

hours is shown in Figure 4 while *Celuca* rhythms are shown in Figures 5 and 6. Both *Minuca* species darken between 0600 and 1800 CST regardless of background. This is due primarily to endogenous black and red chromatophore rhythms. The amplitude of the black pigment cycle is greater in *U. longisignalis* than *U. rapax* (e.g. Figure 4). Although white chromatophores initially exhibit a circadian rhythm during dark background adaptation in *U. longisignalis*, the oscillation dampens. Illumination is reported to inhibit chromatophore rhythms in *U. pugilator. U. pugnax* and *U. thayeri* (Brown, 1950; Brown and Hines, 1952; Barnwell, 1963). Black and red pigment background adaptation in constant illumination is overridden by a circadian rhythm of either chromatophorotropin release or chromatophore responsiveness to regulating hormones.

The *Celuca* chromatophore rhythms under constant conditions are diverse (Figures 5 and 6). Melanophores exhibit circadian rhythms in LBA-ed *U. panacea* and *U. subcylindrica* and DBA-ed *U. spinicarpa*. In general, leucophores adapt. However, a white pigment rhythm is expressed in DBA-ed *U. spinicarpa*. Erythrophores express a circadian rhythm in all species regardless of background.

All chromatophore rhythms under constant conditions are low amplitude in *U. subcylindrica* (Figure 6). Erythrophore and melanophore rhythms are not seen in LBA-ed specimens. In constant darkness (DD), melanophores and erythrophores adapt while leucophores express a circadian rhythm

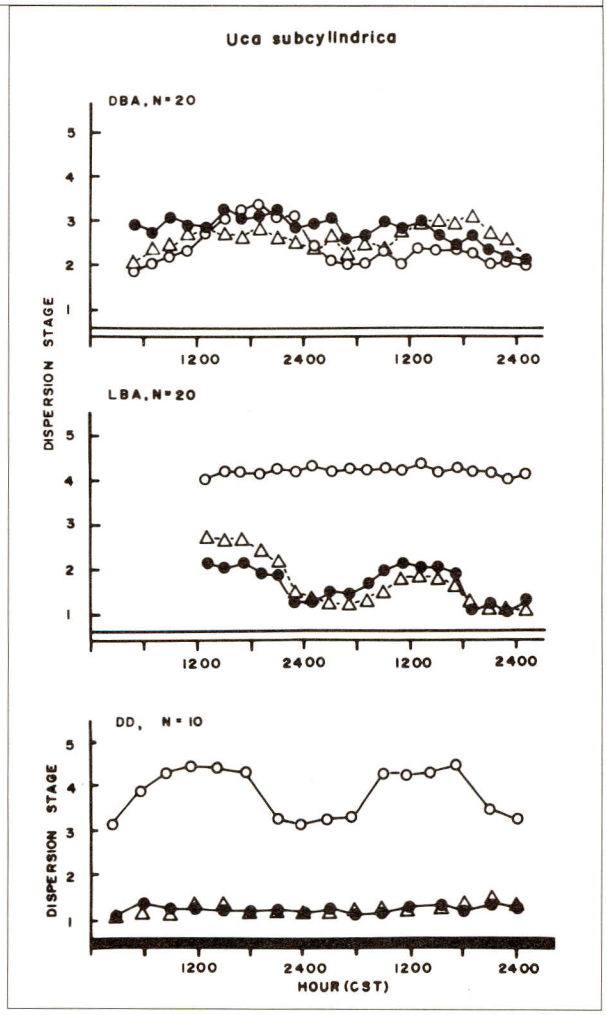

Figure 6. *U. subcylindrica* (*Celuca*) chromomotor rhythms in constant illumination (LL) and darkness (DD). Symbols same as in Figure 4.

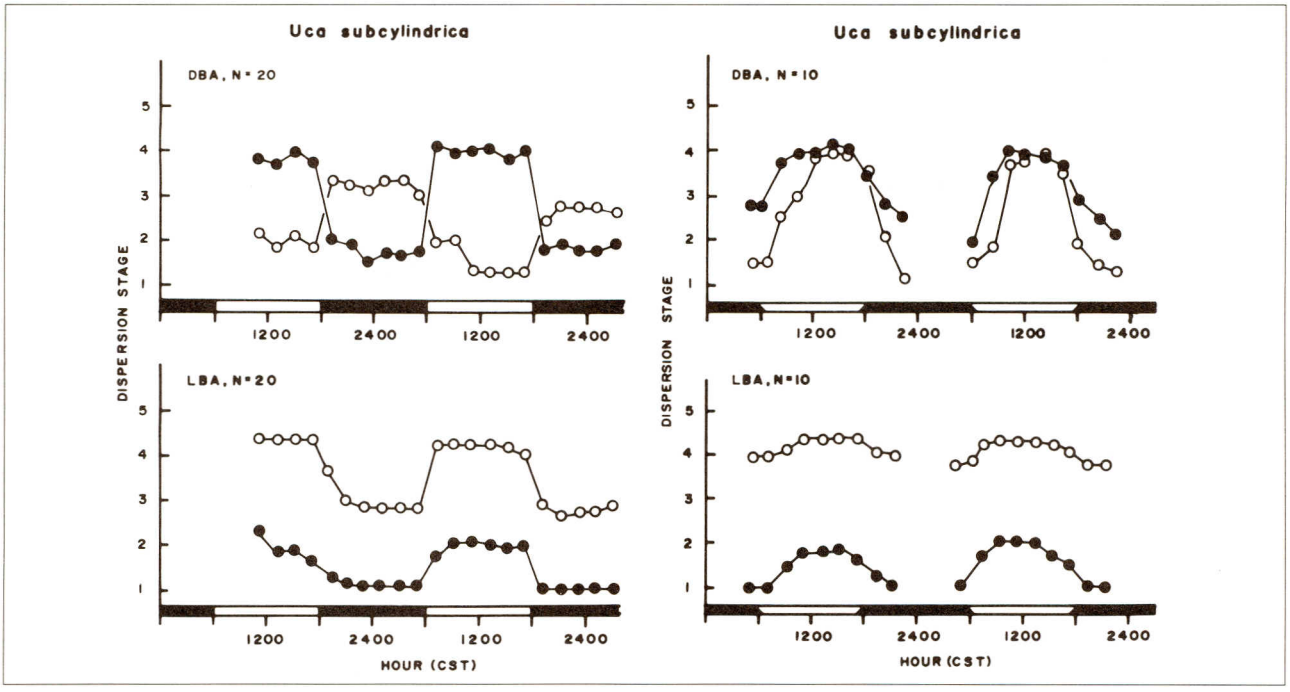

Figure 7. Photoperiod-induced chromomotor disperion in *U. subcylindirca*. Left graph — artificial LD cycle (32-foot candles). Right graph — natural light cycle (= 900-foot candles). Symbols same as Figure 4.

(Figure 6). To examine the effects of photoperiod on color change rhythms, *U. subcylindrica* were exposed to cycles of either natural (NL) or artificial (LD) illumination (Figure 7). DBA-ed crabs experiencing LD cycles darkened during illumination and lightened in the dark. In LBA-ed crabs, the leucophore rhythm was phase-shifted 180 degrees to produce white pigment dispersion during the photoperiod. Under indirect natural illumination (app. 900-foot candles), melanophores and leucophores disperse and aggregate in synchrony.

From these experiments, several conclusions can be drawn about color change physiology in *U. subcylindrica*. First, the expression of periodic color change is influenced by light intensity and substrate color. Constant illumination inhibits the expression of chromatophore rhythms (Figure 6). Second, periodic illumination encourages the expression of color change rhythms. Leucophore rhythms are expressed in constant darkness and natural illumination. Leucophore dispersion in DBA-ed crabs experiencing NL-cycles indicates the photoperiod response may override background adaptation in this species. Third, in these experiments natural illumination was 28 times more intense than the artificial light. The dispersion of leucophores in DBA-ed crabs could be due to a strong primary response to illumination.

Primary responses to illumination. A primary chromatophore response requires the direct dispersion of pigments with increased illumination. In secondary chromatophore responses, pigment migration is mediated visually through a neurosecretory reflex. For this albedo or background response, the eye measures, simultanously, the intensity of incident light from above and reflected light from below. Neurosecretory activity is regulated by visual assessments. Light backgrounds have high albedo while dark backgrounds have low. Due to albedo and neurosecretory coupling, black and red chromatophores will have greater dispersion on a dark than a light background. Leucophores will have greater dispersion on a light than a dark background. Since the reflectance of a light background is greater at any given illumination intensity, a strictly primary response produces a greater degree of pigment dispersion on a light than on a dark back-ground. In many species, the primary response may be antagonized by the secondary.

To examine illumination and albedo responses in the fiddler crabs, a variety of light intensities was achieved by placing a light bulb (60 or 100 watt) or G.E. flood lamp at various distances from crabs adapted to either a dark or light background. Light intensities at the level of the crabs was estimated with a G.E. color-cosine corrected light meter to be 1,000, 320, 120, 32 and 12-foot candles. White containers reflected 40 percent of the incident light while black reflected 14 percent. The chromatophores on each crab were staged after one hour under a particular illumination. The crabs were then rotated to another bath for an hour until they had experienced all five light intensities. The experiments were carried out twice during the day

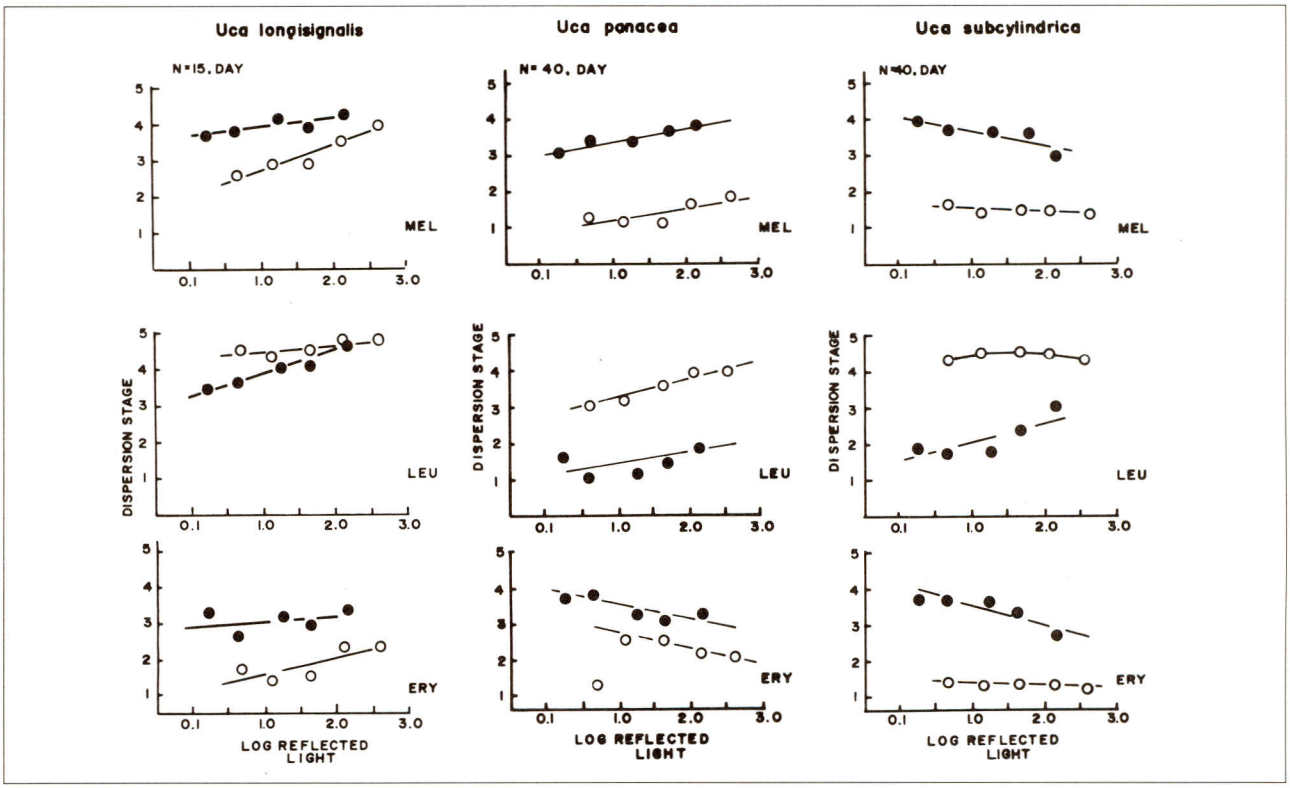

Figure 8. Relation between reflected light intensity and chromatophore dispersion in *Uca*. • - DBA, o - LBA. Mel = melanophores, Leu = leucophores and Ery = erythrophores.

(0900 and 1400 CST) and night (2100 and 0200 CST). Bath temperatures were maintained at 21° ± 1°C. Figure 8 illustrates the relationship between reflected light and pigment dispersion in three species of fiddler crabs: *U. longisignalis*. *U. panacea* and *U. subcylindrica*. Due to the similarity between day and night reactions, only the results of daily studies are shown.

The albedo or secondary response is clearly evident in the chromatophores in all three species (Figure 8). Red and black chromatophores are always more dispersed on a dark than a light background. The opposite is always true for leucophores. In *U. longisignalis*, the albedo response is susceptible to the primary illumination response. As light intensity increases, melanophores, leucophores and erythrophores disperse to augment the albedo response. However, the ability of the primary response to override background adaptation prevents *U. longisignalis* from chromatically adapting to light backgrounds under high intensity illumination. That is, the light-background adapted crab becomes black due to the primary chromomotor effects.

Similar results are seen in *U. panacea* (Figure 8). The primary response is seen in the chromomotor behavior of black as well as white pigment. Unlike the other chromatophore systems, the albedo response of the erythrophores antagonizes the primary response. Consequently, red chromatophores concentrate with increasing illumination. The net chromatic effect of the albedo and primary responses in *U. panacea* produces a pale crab under high intensity illumination on either light or dark substrates.

In *U. subcylindrica*, a strong albedo-mediated antagonism of the primary response occurs in both melanophores and erythrophores (Figure 8). The primary response augments the albedo response of the leucophores. The net effect of the chromomotor system is to produce a white crab on a black background under high intensity illumination. This response is enhanced in *U. subcylindrica* over *U. panacea* or *U. longisignalis*.

The illumination responses of the *Celuca* appear better controlled than those in the *Minuca*. In *U. longisignalis*, primary responses can override the albedo response. As a result, the crab darkens as illumination intensity is increased. In the *Celuca*. the secondary response is better developed and antagonizes the light-mediated dispersion of black and red pigments. Consequently, the crabs do not darken under high intensity illumination. The melanophores and erythrophores of *Uca subcylindrica* possess the most efficient albedo response. This secondary response inverts the primary response in black and red pigment cells.

To test the strength of the primary chromomotor

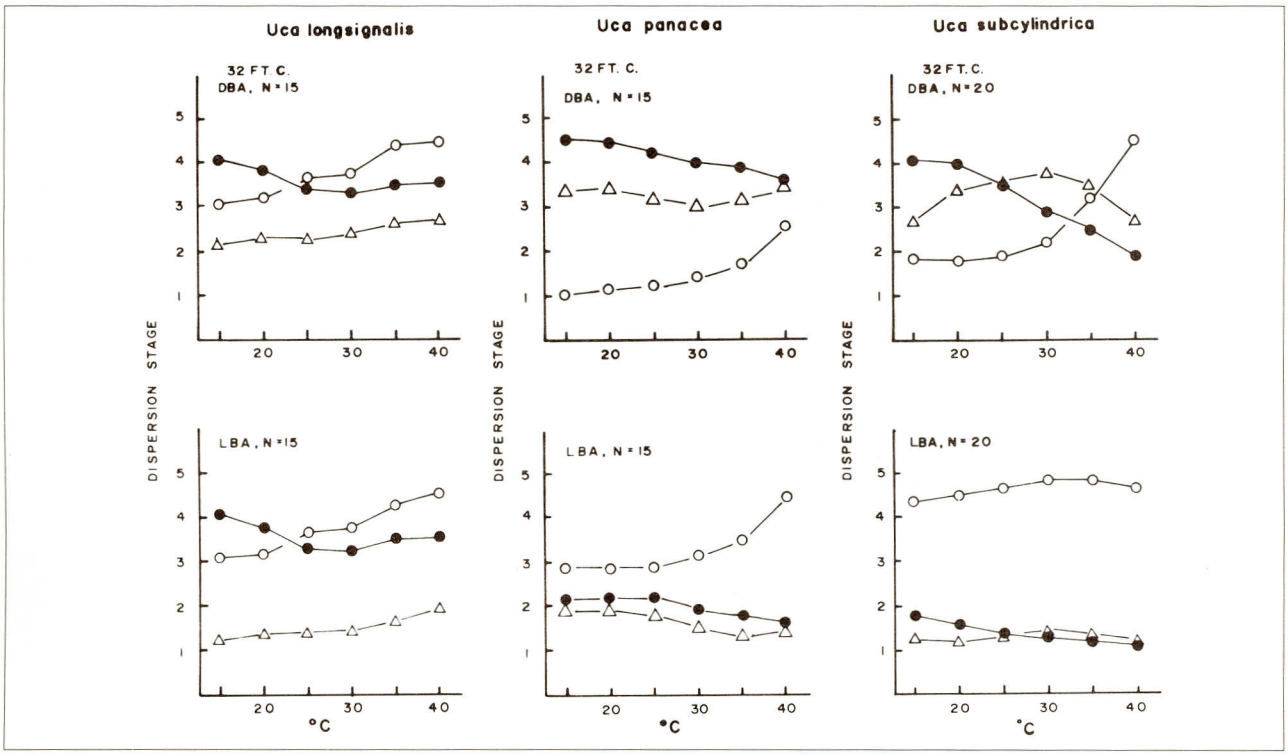

Figure 9. The response of *Uca* chromatophores to temperature. Symbols same as Figure 4.

response, eyestalk-less *U. subcylindrica* were subjected to increasing illumination intensity. Melanophores and erythrophores aggregated while the leucophores dispersed to near maximum following eyestalk ablation. None of the chromatophores exhibited a primary response. Consequently, the aggregation of black and red chromatophores with elevated illumination in *U. subcylindrica* is mediated completely by the neuroendocrine system. In addition to evolving an exceptional albedo response, it has ameliorated itself from the direct reaction to light. Since color may be related to body temperature, this chromomotor behavior can be interpreted as evidence for thermoregulation.

Primary response to temperature. Another factor influencing physiological color change is temperature. In addition to altering chromomotor activity, extreme temperature alters hormone secretion from the sinus gland and nervous system (Fingerman et al., 1969). Consequently, changes in the dispersion of chromatophores induced by temperature may be secondary rather than primary responses to stress. *Uca longisignalis*, *U. panacea* and *U. subcylindrica* were held under constant illumination and subsequently exposed to six different temperatures between 15°C and 40°C. After an hour at each temperature, black, white and red chromatophores were indexed. The experiments were carried out twice between 0800 and 1600 CST on the same crabs.

The pigments of the *Minuca*, *U. longisignalis*, exhibit little in the way of a thermoregulatory response to temperature (Figure 9). The reactions of melanophores and leucophores are virtually identical regardless of dark or light background. Temperature promotes the dispersion of leucophores and erythrophores and the concentration of melanophores. The crab darkens slightly at low temperature while blanching a little at high temperatures.

In the *Celuca*, *U. panacea*, the erythrophore response to temperature is minimal (Figure 9). Melanophores concentrate as temperature increases for crabs on both black and white backgrounds. The leucophores in both DBA-ed and LBA-ed crabs disperse with elevated temperature.

Since LBA-ed crabs adjust their chromatophores to a maximum extreme, thermal regulation is obvious only in DBA-ed *U. subcylindrica* (Figure 9). At low temperatures, the albedo response keeps the DBA-ed crabs dark. As temperature increases, the crabs blanch. Both erythrophores and melanophores concentrate significantly while leucophores disperse at elevated temperatures. At 40°C, the crabs are pearl-white on a black background. In this species, the thermal response overrides the albedo response at high temperatures.

In general, the pigments of *Celuca*, *U. panacea* and *U. subcylindrica* exhibit greater thermoregulatory behavior than those of the *Minuca*. Under elevated illumination, dark chromatophores in *Celuca* may contract rather than dispersing (e.g. Figure 8). Dark-background adapted *Celuca* abandon the al-

bedo response to enhance their pale color at elevated temperatures (e.g. Figure 9). Blanching under high temperature and light intensity presumably increases body reflectance and decreases absorption of solar radiation (Wilkens and Fingerman, 1965; Coohill *et al*, 1970). In the case of *U. longisignalis* with its strong primary response, only slight changes in the dispersion of the chromatophores are observed as temperature is elevated. The chromatophores appear to contribute little toward thermoregulation.

Discussion

Body color in the fiddler crabs results from the combined effects of morphological (chromogenic) and physiological (chromomotor) processes. Morphological pigmentation is generally stable over long periods of time. Chromogenic variation results from changes in development or the environment occurring over a period of weeks, months or years. Physiological color change occurs in minutes or hours due to alteration in the distribution of pigments within chromatophores. Chromogenic and chromomotor mechanisms have evolved to satisfy both long-term ecological and short-term physiological needs, respectively.

Of the two, our understanding about morphological coloration is the most limited. The genetic and nutritional factors regulating morphological pigmentation are essentially unknown. Comparing representatives from two subgenera indicates that the *Minuca* are more variable in morphological coloration than the *Celuca* (Plate 7). Except for the anterior carapace, major body portions of the *Minuca* are usually drab. The dark-brown to black coloring of walking legs and lower carapace blend well with dark, muddy environments. This apparently confers cryptic coloration to these marshland inhabitants.

However, the anterior portion of the carapace in male *Minuca* may be brightly colored. It is difficult to see how this bright color could serve a cryptic function. Perhaps it is involved in species recognition. In the "narrower-fronted" *U. rapax*, the pink and blue anterior carapace does not vary along the Texas coast. In one estuary, *U. longisignalis* may possess carapaces colors ranging from solid brown to bright turquoise. Usually crabs with a brown or dark-green carapace are collected in low salinity while those with brighter green and turquoise are found in more brackish habitats. *Uca longisignalis* is related to the North American "broad-fronted" species *U. minax* and *U. pugnax* (Barnwell and Thurman, 1984). The colors of the Gulf species are reminiscent of those seen on anterior portions of the carapace in *U. pugnax* from the Atlantic coast, which ranges from green to blue or turquoise (Crane, 1975). Since there are no green chromatophores, dietary and/or genetic differences may account for this pigment polymorphism in the *Minuca*.

In general, the morphological color of the Texas *Celuca* are somewhat lighter than that of the *Minuca* (Plate 7). Members of the subgenus usually inhabit light-color substrates in tidal or supratidal zones. Excepting *U. spinicarpa*. the lower carapace and walking legs are lighter than those of the *Minuca*. In addition, the anterior carapace lacks the bright pigments seen in the other subgenus. *Uca panacea* from the western Gulf of Mexico never possess a tan-white carapace like *U. pugilator* from the eastern United States. The carapace of *U. panacea* is usually gray, brown or dark-tan matching the color of the beach sands in the western Gulf. This distinction is evident even in areas of sympatry between the two species (Rao and Fingerman, 1968). The mottled brown and tan colors of both *U. subcylindrica* and *U. spinicarpa* appear typical for most *Celuca* according to Crane's assessment (1975). The general morphological coloration of these *Celuca* make them less conspicuous on the gray or black soils they inhabit. Like the *Minuca*, the morphological color of *Celuca* correlates with substrate. For long-term ecological adaptation, their coloration is probably determined either by genetic selection or diet.

On the other hand, physiological color change or chromomotor physiology has been studied in a large number of crustaceans. Color change in the fiddler crabs was first reported in *U. pugnax* and *U. pugilator* by Megusar (1912) and Abramowitz (1937). Since then, our knowledge concerning chromatophore physiology has developed into a sophisticated biochemical and biophysical science (Thurman, 1988). Chromomotor processes affect short-term adaptation through rapid physiological adjustments. This review summarizes chromatophore (1) endogenous rhythms, (2) thermal reactions, and (3) illumination responses in *Uca*.

The cyclic physiological process(es) driving periodic color change overrides background adaptation in some chromatophore systems. Counting the *Uca* species discussed here, rhythms of color change have been described in 15 species (Table 1). Details of these rhythms differ among species. In view of the ecological diversity exhibited by the genus, this variety may correlated with the habitat difference of each species (e.g. Barnwell, 1976). Generally, rhythms are considered to be either circadian or tidal depending upon their characteristics. For the most part, circadian rhythms have been well documented. Daily rhythms of black pigment dispersion have been recorded in all species except *U. thayeri* (Table 1). Erythrophore rhythms do not occur in *U. thayeri* , *U. mordax* or *U. pugnax*. Although leucophore rhythms are common among to all species, they may be expressed only in constant

Table 1. Chromatophore rhythms in *Uca*.

Subgenus, Species	Reference	Locale	Lighting	Cell	Rhythm	
					Circadian	Tidal
Uca						
U. maracoani	Barnwell, 1963	Brazil	NL/LL	M	X	?
			LL	E	X	-
Boboruca						
U. thayeri	Barnwell, 1963	Brazil	NL/LL	M	-	-
			LL	E	-	-
Minuca						
U. mordax	Barnwell, 1963	Brazil	NL/LL	M	X	?
			NL/LL	E	-	-
U. pugnax	Brown and Webb, 1949; Brown *et al*, 1953; Barnwell, 1968b)	Mass	DD/LL	M	X	X
			DD	L	X	X
			LL	E	-	-
U. longisignalis	Fingerman *et al*, 1958	Miss/Texas	DD/LL	M	X	?
			LL	L	X	-
			LL	E	X	-
U. zacae	Barnwell, 1968b	Costa Rica	LL	M	X	-
			LL	L	X	-
U. rapax	Barnwell, 1963; Delft, 1968	Brazil, Curacao, Texas	NL/DD/LL	M	X	?
			LL	L	X	-
			NL/DD/LL	E	X	-
U. herradurensis	Barnwell, 1968b	Costa Rica	LL	M	X	-
			LL	L	X	-
			LL	E	X	-
Celuca						
U. pugilator	Brown and Webb, 1948; Brown, 1950; Webb, 1983	Mass	DD/LD	M	X	-
			DD	L	X	-
			DD	E	X	-
U. panacea	Fingerman, 1956; Fingerman *et al*, 1958; Fingerman and Yamamoto, 1967; Rao *et al*, 1967	Miss/Fla	DD/LL	M	X	?
			DD	L	X	-
			LL	E	X	-
U. crenulata	Bates, 1966	W. Mexico	NL	M	X	?
			DD	E	X	?
U. spinicarpa	Fingerman, 1956	Miss/Texas	DD/LL	M	X	?
			LL	L	X	-
			LL	E	X	-
U. uruguayensis	Martin *et al*, 1959	Brazil	NL/LD	M	X	-
			LD	L	X	-
			LL	E	X	-
U. annulipes	Nagabhushanam, 1963; 1964; Rao and Nagabhushanam, 1967	India	DD	M	X	-
			DD	L	X	-
			DD	E	X	-
U. subcylindrica		Texas	NL/LL/LD/DD	M	X	-
			NL/LL/LD/DD	L	X	-
			NL/LL/LD/DD	E	X	-

NL—natural illumination, LL—constant light, LD—light/dark cycle, DD—darkness. M—melanophore, L—leucophore, E—erythrophore. X—present, - — absent, ?—possibly present.

darkness. Since melanophores and erythrophores are often incomplete in their adjustment to a background, their daily rhythms may be seen under constant but low intensity illumination. Higher intensities of light may inhibit rhythmic expression through either primary or albedo reflexes (Brown and Webb, 1949; Brown and Hines, 1952). Low amplitude daily chromomotor rhythms are seen in *U. thayeri* and *U. subcylindrica*. However, rhythmic expressions for *U. subcylindrica* are promoted by DD, LD or NL lighting regimens. Circadian chromatophore rhythms are synchronized with each other regardess of pigment content or species. Generally, they exhibit peak dispersion during the day and aggregation at night.

The presence of tidal rhythms has not been reported as frequently in the *Uca*. Although circatidal rhythms have been attributed to at least seven species, they remain to be confirmed in all but *U. pugnax*. Since tides are unpredictable along the Texas coast where *Uca* live, it is not surprising that overt tidal rhythms are not readily apparent in their chromatophore behavior. Tidal rhythms of both color change and locomotor activity have been observed in *U. pugnax* and *U. maracoani* (Brown et al, 1953; Barnwell, 1963; 1966). Although considered intertidal (Crane, 1967), there are no reports of tidal locomotor or chromatophore rhythms in *U. rapax*. When kept in the dark for 30 days, a circadian melanophore rhythm develops in *U. rapax* which has a 24.8 h period (Delft, 1968). However, it is not clear that this "free-running" rhythm is correlated with the local tides (e.g. Barnwell, 1976). Strong daily rhythms of locomotor activity have been observed in *U. longisignalis, U. minax, U. pugnax, U. pugilator*, and *U. mordax*. Tidal rhythms of locomotor activity are known in *U. minax, U. pugilator*, and *U. pugnax* (Barnwell, 1963; 1966; 1968a,b). Each of the five Texas species expresses daily rather than tidal rhythm of color change.

In addition to the rhythms, the direct effects of light and temperature can modify neurosecretion-mediated chromatophore movement. In those species with limited physiological regulation, environmental factors control pigment dispersion. In other species, an internal mechanism regulates color change conferring independence from the environment. Primary responses have been observed in four *Minuca* and four *Celuca* species. In general, the *Minuca* exhibit strong primary responses that conflict with thermoregulation. *Celuca* exhibit greater physiological control over chromatophore activity. Some members of this subgenus may manipulate body color in a limited attempt to become homeothermic.

Celuca frequently show unusual adaptations for extreme semi-terrestrial life (Crane, 1975: p 219). They often live in open sandy or muddy habitats surviving high temperatures and severe desiccation. The chromomotor systems of four *Celuca* exhibit responses to light and temperature that are interpreted as thermoregulatory (Brown and Sandeen, 1948; Barnwell, 1968b). Several investigators have examined primary chromatophore activity in *Celuca*. The responses of *U. pugilator* in the laboratory were first reported by Brown and Sandeen (1948). Wilkens and Fingerman (1965) examined the role played by color change, evaporation and burrow-retreating behavior in the thermoregulation of the crab. In addition to the present study, the responses of *U. panacea* to illumination have been analyzed by Fingerman and Yamamoto (1967) and Rao and Fingerman (1968). Nagabhushanam (1963; 1964) and Rao and Nagabhushanam (1967) found chromatophore dispersion in the tropical species *U. annulipes* to be influenced temperature and light. *Uca subcylindrica*, another member of the subgenus, posseses chromomotor reponses to light and temperature that physiologically facilitate thermal regulation.

In general, responses to light are regulated better in *Celuca* than *Minuca* (Figure 8). The primary response of *Minuca* chromatophores enhances adaptation to dark, muddy backgrounds. In addition to *U. longisignalis* in the present study, the dispersion of dark chromatophores by a primary reflex has been documented in *U. pugnax* and *U. g. herradurensis* by Barnwell (1968b). When exposed to elevated light, light background-adapted (LBA-ed) *Minuca* become conspicuously dark. In *Celuca*, the primary response of melanophores and erythrophores but not leucophores is antagonized by the neurosecretory system. This behavior is apparent in the temperate species *U. panacea*, *U. pugilator* and *U. subcylindrica* but lacking in the tropical form *U. annulipes*. Temperate species lighten even on dark substrata. Increasing light intensity to high levels will eventually disperse melanophores and erythrophores in *U. pugilator* and *U. annulipes*. Using eyestalk-less crabs, a strong primary response has been found in melanophores of *U. annulipes, U. pugilator* and *U. panacea*. (Brown and Sandeen, 1948; Nagabhushanam, 1963; Rao and Fingerman, 1968). Black pigment dispersion in eyed-crabs proceeds at illumination intensities too low to stimulate melanophores in eyestalk-less *U. pugilator* (Coohill and Fingerman, 1976). This light-dependent behavior is lacking altogether in eyestalkless *U. subcylindrica*. Unlike the *Minuca*, chromomotor behavior in the *Celuca* is mediated internally to a greater degree by neurosecretion and chromatic cell physiology than by external environmental factors.

Within the *Celuca*, hormonal control of melanophore responses is more completely developed in *U. panacea* and *U. subcylindrica* than in *U. pugilator*. *U. subcylindrica* have apparently abandoned the

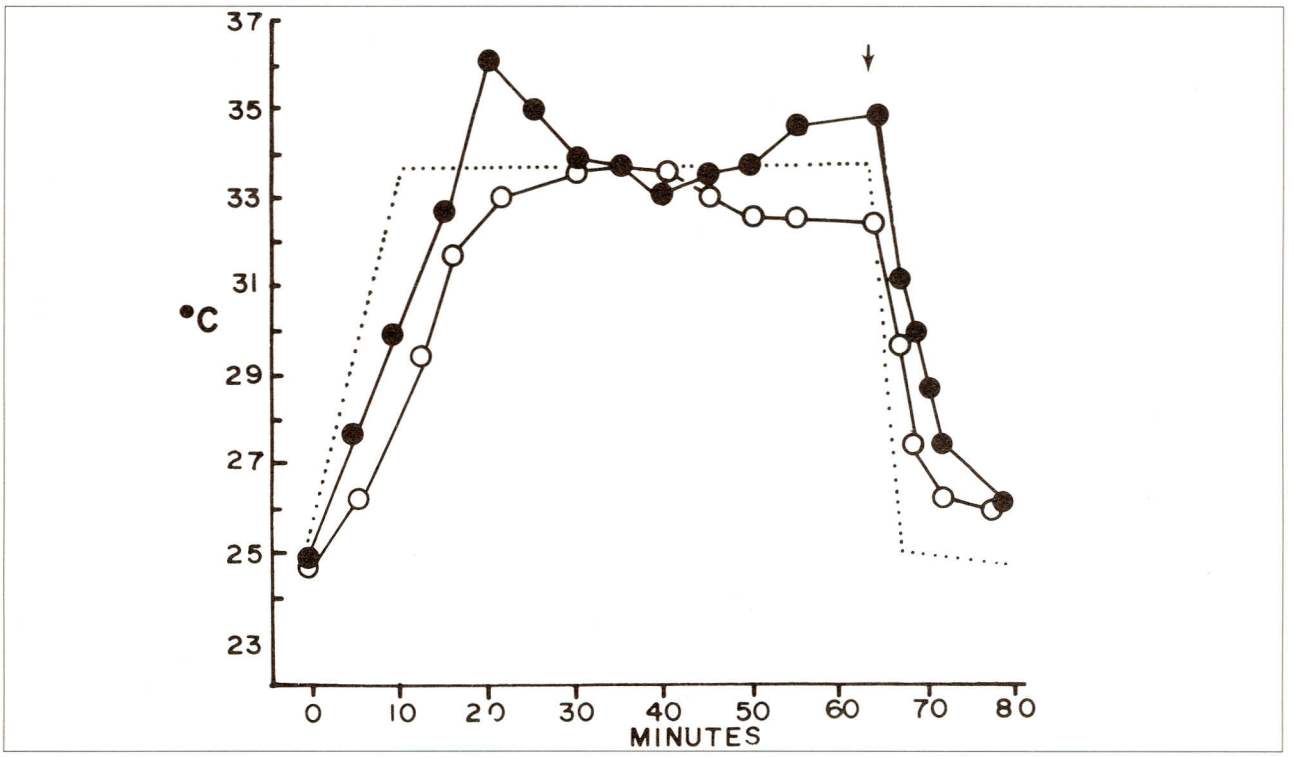

Figure 10. Branchial chamber temperature of DBA and LBA *U. subcylindrica* in sunlight. • - DBA, o - LBA, ... - box temperatures. Arrow - moved into shade.

primary illumination response for internal neurosecrtory control over the black and red chromophores. Both pigment cells may contract with increased illumination. This is apparently mediated by factors released from the sinus gland in the eyestalk. A similar trend is seen in the red pigment of *U. panacea*. From this perspective, the *Celuca* species may be ranked according to their control over the primary illumination response: *U. subcylindrica* > *U. panacea* > *U. pugilator* > *U. annulipes*.

Chromatophore dispersion with elevated temperature also appears to be better controlled in *Celuca* than *Minuca*. As ambient temperature is increased, leucophores disperse in all species. However, the dark chromatophores of the *Minuca* also disperse. In the two tropical species, *U. g. herradurensis* and *U. zacae* (Barnwell, 1968b), increasing temperature increased melanophore and erythrophore dispersion. In this case, temperature stimulates the albedo response. The apparent lack of a thermoregulatory response may be correlated to the narrow range of environmental temperatures confronting these species. Although the chromatophores of *U. pugnax* from the temperate latitudes respond in a thermoregulatory fashion, the amplitude of the reaction is small (Barnwell, 1968b). Smith and Miller (1973) found that color change in another *Minuca*, *U. rapax*, contributed a minimum to thermoregulation. In the present study, the chromatophores of *U. longisignalis* respond minimally to thermal changes. The paling of *Minuca* at high temperatures is antagonized by a strong, inflexible, albedo response cancelling any thermoregulatory benefits of blanching. Under these conditions, the *Minuca* tend to remain a black-body absorbing heat.

In the *Celuca*, red and black chromatophores tend to aggregate with elevated temperature. This is best illustrated in dark-background adapted *U. subcylindrica*. As temperature is increased, the background respond is reduced as black and red chromatophores aggregate. Leucophores expand to shade internal organs from insolation and increase reflectance. Paling of the carapace in sunlight can lower corporal temperature 2°C below that of a dark crab (Wilkens and Fingerman, 1965). The thermal role associated with chromomotor blanching can be demonstrated in *U. subcylindrica* (Figure 10). Crabs were placed in high humidity, transparent, containers and copper-constantan thermocouples were inserted into their branchial chambers as described by Wilkens and Fingerman (1965). The crab that adjusted its body color to the dark background initially gained body temperature more rapidly than the one on the white substrate. However, the dark adapted crab began to blanch after 20 minutes. Its body temperature fell to equal that of the white adapted crab in 10 minutes. Afterwards, the corporal temperature rose above that of the chamber as well as the white crab. A change in body coloration may bestow some thermoregulatory capability to

U. subcylindrica at elevated temperatures for a short period of time.

To colonize terrestrial habitats, *Uca* have evolved adaptations to: (1) avoid ionic and osmotic stress, (2) survive thermal extremes and (3) assure reproductive success. Undoubtedly, color has played an important role in the adaptation of aquatic crabs to habitats with high temperature and little water. Both morphological and physiological color change mechanisms appear to contribute to the ecological success of the genus. In south Texas where the environment is hostile to marine organisms, both *Minuca* and *Celuca* are common along the nontidal coast. In terms of thermal regulation, the *Celuca* to possess better color-mediated capabilities than the *Minuca*. Based on a comparison to other species around the world, these subgeneric differences may be determined by phylogeny. The *Celuca* are far more adaptable in extreme habitats and express considerable plasticity in their chromomotor responses.

Physiological coloration does not appear to confer a thermoregulatory advantage to *Uca* of the *Minuca* subgenus. Both *U. longisignalis* and *U. subcylindrica* are very terrestrial species endemic to the western Gulf of Mexico. *Uca longisignalis* has been found to be a better ionic/osmotic regulator than *U. subcylindrica* (Rabalais and Cameron, 1985). Assuming other homeostatic mechanisms equal, the strong primary and albedo response may contribute to the inability of the *Minuca* to inhabit hot, dry exposed habitats. The *Minuca* tenaceously hold to the albedo response preventing dark background-adapted crabs from increasing their reflectance by blanching. This reduces the ability of their pigments to aid in thermoregulation. Since the crabs remain dark even on light substrates, this could be a liability under intense insolation and heat.

Uca subcylindrica, a *Celuca*, has evolved unusual reproductive and developmental strategies, desiccation tolerance and behavioral patterns that make it distinct from other members of the genus (Rabalais and Cameron, 1983; Thurman, 1984). Adaptive coloration may contribute, in part, to their unique distribution in the harsh supratidal habitats of the western Gulf of Mexico. Flexible chromomotor capabilities may represent a physiological advantage evolved in the *Celuca* but not the *Minuca*.

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