Seasonal changes in body color of *Mictyris guinotae* (Brachyura: Mictyridae)

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**Abstract.**— The body color of the soldier crab, *Mictyris guinotae*, varies from a pale blue to a dark ink-blue. We describe the composition of black and blue body color forms in animals obtained during a year-long collection effort. Body color showed clear seasonal changes; almost all crabs were black between April and September (non-breeding season) and blue between late November and February (breeding season). Larger black crabs, \( > 7 \) mm in carapace length, first showed blue coloration in October, suggesting that color change is associated with sexual maturity. Some newly molted black individuals with white exuviae were found inside the burrow in March. The timing of the color change from blue to black was later in females because ovigerous females are unable to molt. Black body color during summer months may mitigate the harmful effects of ultraviolet radiation and provide visual crypsis from predators during activity on the surface of sand flats.

**Key words:** Iriomote Island, morphological color change, reversible color change, soldier crab

**Introduction**

Animals in a wide range of taxonomic groups are capable of color change. Camouflage is often a primary function of this ability. Color change can be very rapid, in seconds, or relatively slow, in hours to months, and may include changes induced by developmental plasticity. Slow change is likely more common than rapid change but is less studied (Duarte, 2017). The adaptive significance of color changes in the Brachyura, a highly colorful group of arthropods, has received relatively little attention. Color changes may assist in thermoregulation, crypsis, camouflage, and interspecific (social and sexual communication) and intraspecific signaling (aposematism) (Umbers *et al.*, 2014; Caro, 2018).

The soldier crab, *Mictyris guinotae* Davie, Shih & Chan, 2010, is a member of the family Mictyridae, and is found only in the Ryukyu Islands, Japan. The species is the only mictyrid crab distributed on the islands (Davie *et al.*, 2010). The crabs inhabit intertidal sand or muddy sand substrate of inner bays and estuaries and represent the dominant species in the estuarine crab community (Irie *et al.*, 2005; Kawaida *et al.*, 2017). Individuals of this species vary in body color from pale blue to a darker blue-gray to a dark ink-blue. Color variation is seasonal and might be related to maturity (Davie *et al.*, 2010); however, no quantitative data are available. Thus, we analyzed seasonal changes in body color and population dynamics of the soldier crab to clarify relationships among body color changes, season, and sexual maturity. We discuss functions and mechanisms of color change in *M. guinotae* using data from a year-long collection effort.

**Materials and Methods**

**Materials**

Individual soldier crab, *Mictyris guinotae,*
remains in non-permanent burrows during high tide. When low tide exposes their habitat, they feed microorganisms and organic materials from surface sediment and sediment within the top few centimeters below the surface. Subsurface-feeding crabs make the roof-like structure of sediment scooped up with chelipeds and first and second ambulatory legs (Takeda & Murai, 2004). Smaller and nocturnal crabs emerge and feed separately on the surface of waterlogged sand near the waterline, where subsurface feeding is not possible. During daytime low tides, larger surface-feeding crabs congregate in dense masses and feed in droves, walking toward the water with frequent short stops to feed. These crabs stay along the shoreline as it moves with the tide (Yamaguchi, 1976; Takeda & Murai, 2004).

Methods

*Mictyris guinotae* specimens were collected from exposed bare sand flats during low tide in the Urauchi River on the northern coast of Iriomote Island, Okinawa, Japan (24°24′N, 123°46′E) between June 2010 and May 2011.

From June to November, and in April and May, during the daytime low tide, crab sampling was performed twice monthly (November) or monthly (other months) 300 m upstream from the mouth of the river. Five 0.5 × 0.5-m quadrats were established within three areas (near shoreline, landward, and the area between them) with a width of 6 m inside, and burrowing crabs in each quadrat were collected using a 1-mm sieve after excavating the sediment to a depth of 30 cm; *M. guinotae* burrows can reach 30 cm below the sediment surface (Jinno et al., unpublished data).

From December to March, during the nighttime low tide, crab samples were collected two to six times per month on sand flats 400 m upstream from the river mouth. Crabs wandering on the sediment surface near the shoreline and landward areas were identified and collected by hand. After collecting wandering crabs in the landward area, when no crabs appeared on the surface, sediment was excavated and any crabs found were collected without using the sieve. Each collection effort continued until the total number of individual animals collected exceeded 500.

After species identification, body color (black or blue, Fig. 1), carapace length (CL, nearest 0.1 mm), sex (identified by the shape of the first gonopods), and numbers of ovigerous or non-ovigerous females were recorded.

![Fig. 1. Live color patterns of *Mictyris guinotae*. Black (a) and blue (b) forms of crabs collected from the Urauchi River, Iriomote Island.](image-url)
The body color of *Mictyris guinotae* showed clear seasonal changes (Fig. 2). Between June and September, the population displayed the black form only. The proportion of the blue form abruptly increased in October, and body color of all individuals had changed from black to blue by December. Ovigerous females in the blue form were observed from December to late February. Blue individuals began to change to black beginning in February, and most individuals became black by April or May. During this period, some newly molted black individuals with white exuviae were found inside the burrow (Fig. 3). In contrast, no newly molted crabs in the soft-shelled blue form were collected. This pattern of temporal color change was the same for both sexes, but percentages were different in March. The proportion of blue individuals was still high for females, and indicating that the timing of color change from blue to black occurred later.

Body color for larger black males and females with CL $> 7$ mm first became blue in
October, and some small individuals were still black in November (Fig. 4). In contrast, the timing of the change from blue to black did not differ with body size. Ovigerous females in the blue form \((n = 577)\), collected between December and March, showed CL gradually shifting to smaller sizes, i.e., 11.06 ± 1.08 mm (mean ± standard deviation) in December, 10.03 ± 1.22 mm in early January, 9.59 ± 1.31 mm in late January, 8.61 ± 0.90 mm in early February,
8.63 ± 1.06 mm in late February, and 7.5 mm (n = 1) in March.

Discussion

Body color of soldier crabs change seasonally, with almost all individuals being black from April to September, blue from December to February, and back to black again in March. Smaller crabs became blue later than did larger individuals. The CL of ovigerous females in the blue form gradually decreased in the breeding season, i.e., larger and older females, >1 yr, begin to bear eggs early in the breeding season, while smaller and young females in their first breeding season, incubate later (Nakasone & Akamine, 1981). The period of emergence of blue individuals appears to correspond to the breeding season (Nakasone & Akamine, 1981; Kosuge & Kohno, 2010), suggesting that body color change is associated with sexual maturity. In March, body color changed from blue to black as crabs began molting, and by April almost all individuals returned to black. In March, about 80% of males but only about 20% of the females were black, displaying differences in the timing of color changes. Presumably, egg-bearing behavior underlies this difference, since ovigerous females are unable to molt. Post-molting crabs were frequent after the end of the breeding season, consistent with observation for Mictyris brevidactylus in Taiwan (Shih, 1995). Reversible body color change in this latter species is morphological rather than physiological and occurs over a relatively long period (Umbers et al., 2014).

Fiddler crab coloration lightens and darkens after a 30 min exposure to high (40°C) and low (15°C) temperature, respectively, reflecting a thermoregulatory function (Kronstadt et al., 2013). Color changes in Mictyris guinotae show the reverse pattern. Coloration of M. guinotae thus lightened and darkened in the winter and spring–autumn, respectively. Thermoregulation is not an explanation for body color change in M. guinotae.

Melanin in the carapace absorbs ultraviolet (UV) radiation and seasonal changes in carapace darkness may thwart the harmful effects of UV radiation when crabs forage in the intertidal zone during daylight hours (Darnell, 2012). Soldier crabs emerge on the surface of sandy mud or sand flats both during the day and night, but nighttime surface activity is only seen between December and March, when nighttime tide levels do not decrease as much as seen during spring neap tides, where tide flats are exposed (Jinno et al., unpublished data). Black individuals emerge between spring and fall seasons when surface activity occurs during daylight hours because tide flats are not exposed at night. The amount of UV radiation exposure thus increases and black coloration may mitigate its harmful effects.

Black body color on sandy mud and sand flats may provide visual crypsis from shorebirds that rely on vision to detect and prey on mictyrid crabs (Zharikov & Skilleter, 2004), surface sediments in the estuary black, matching the color of the crabs. Fourteen avian species from families of Charadriidae and Scolopacidae use tide flats in estuaries in the western part of Iriomote Island, including the Urauchi River as feeding grounds. The top four dominant shorebird species were observed taking 40–60% of their prey on the tide flats as M. guinotae (Mizutani et al., unpublished data). The most abundant species, the Kentish plover, Charadrius alexandrinus, feeds on macrobenthos on the sediment surface by pecking during both daytime and nighttime hours (Kuwae, 2007). This species uses the estuary as overwintering habitat. Three species of sandpipers use the area as a stopover during migration, and numbers of individuals increase in either spring or autumn (Mizutani et al., 2010). Thus, predation pressure by shorebirds might be lower in summer and higher in winter. In winter, crabs change to blue, and adult females and juvenile crabs spend most of their time inside
their burrows and rarely appear on the sediment surface (Takeda, 2005). However, large blue males do emerge onto the flats during the daytime and form feeding droves (Fig. S1), and this diurnal feeding pattern do not change with body color changes. These observations suggest that black body color may have no substantial benefit for predation avoidance. Further studies are needed to clarify any crypsis effect provided by body color.

On the contrary, conspicuous blue color in winter may be a warning for shorebirds. Under rearing conditions, an individual of the Whimbrel, *Numenius phaeopus*, the third of the dominant shorebirds at the study site, preferred to feed on Macrophthalmid crabs. This bird consumed $>200$ crabs day$^{-1}$, but seldom targeted *M. guinotae* (A. Mizutani, personal observation). Blue *M. guinotae* could produce repellent substances and alter seasonal feeding preference by shore birds.

Color vision and claw coloration are involved in mate choice by fiddler crabs that exhibit courtship behavior on the sediment surface during the daytime (Detto, 2007). Male and female *M. guinotae* copulate in the female’s burrow based on an observation of one mating pair (Yamaguchi, 1976). During the reproductive season, males and females mainly feed on and below the sediment surface, respectively. Tunnels made by females may provide a visual signal to males on the surface for the presence of females. Males may enter burrows because females are not active on the sediment surface and remain in tunnels during the night in the breeding season (Takeda, 2005). Since female soldier crabs choose their mates in their burrows, body coloration may not play a role in their reproductive behavior.

The results of the present study suggest that morphological change in body color of *M. guinotae* is due to endogenous pigmentation rhythms associated with maturity. The black form in summer may provide UV protection and camouflage. This study only describes phenomena, and mechanisms for changes in carapace color from black to blue, UV protection of black body color, and impact of body color on predation all need further investigation. Body color variation and ontogenetic changes have been reported in other mictyrid crabs (McNeill, 1926; Unno, 2008; Unno & Semeniuk, 2011; Davie et al., 2010, 2013); future work should investigate whether seasonal reversible color changes are common with respect to surface activity and feeding droves during daylight hours. This monophyletic group, a family consisting of a single genus, may be ideal for assessing such phenotypic plasticity.

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