SUMMARY

Introduction

Cephalopods (including squid, cuttlefish and octopus) have the most sophisticated color changing ability in animal kingdom. Their skin colors and patterns, textures, postures and locomotion are under neural control directly from brain, which enables them to rapidly change their appearance, which is often termed as “body pattern”, and express diverse body patterns. Cuttlefish are known to use this ability in various behavioral contexts, such as, defense, mating and foraging. Especially, they are known to use diverse body patterns for defense.

Because they change their body patterns so intricately, how they use their ability for defense is still not no fully understood. The function of body patterns for defense could be divided into two major types: primary and secondary defense. There are a large number of studies of primary defense (i.e., camouflage), which have documented that cuttlefish change their color patterns according to surrounding visual backgrounds. However, several previous studies have also documented that cuttlefish express diverse patterns even in the same background. On the other hand, there are only a little studies for secondary defense. They are also not fully understood. Recently, several studies have demonstrated that *Sepia officinalis* use different body pattern according to the species of predators. However, that cuttlefish continuously change their body patterns against the same predator. Why they use diverse

body patterns against the same stimuli has little been studied. The purpose of this study is to understand how cuttlefish use diverse body patterns for defense. Firstly, I examined the diversity in their body patterns in response to the same background. Secondly, examined the diversity in their body patterns in response to the same predator by using a model predator. Finally, using an animated predator, I examined diversity in their body patterns in response to the same predator in different backgrounds.

Materials and methods

In chapter 1, I maintained 16 *S. pharaonis* in the same tank. I recorded their behavior for 24 h with a video mounted above the tank. From the recorded-video, we assessed the camouflage patterns of each individual every 5 min to examine the diversity in camouflage patterns in each individual. We also examined whether there are consistent individual differences in camouflage patterns of *S. pharaonis*.

In chapter 2, I made a model that resembles a real predator (*Lethrinus nebulosus*) as predator stimulus. I moved the model predator in three different trajectories and presented to 48 *S. pharaonis* placed inside an experimental tank. I examined the relationship between the movements of the model predator and body patterns that *S. pharaonis* expressed.

In chapter 3, I made a three-dimensional computer graphics (3DCG) of teleost fish that resembles a real predator (*Lethrinus nebulosus*). Using this 3DCG, I

made animations that an animated predator approached an observer in two different trajectories including the trajectory that the predator passed through above the observer and the trajectory that the predator approaches directly to the observer. I examined the effect of the movements of a predator and surrounding backgrounds on the body patterns that cuttlefish expressed. I presented the animation of approaching predator to 17 *S. pharaonis* on different backgrounds such as white-black checkerboard and uniform grey background.

Results

In chapter 1, all individuals expressed multiple camouflage patterns (i.e., disruptive, mottle and uniform pattern) in the same visual background, but there were consistent individual differences in disruptive and uniform patterns.

In chapter 2, cuttlefish expressed diverse body patterns in response to the model predator. I classified these body patterns into seven main categories. Predator-prey distance and the trajectory of the model predator significantly affected the body patterns of cuttlefish.

In chapter 3, cuttlefish showed jetting against the animation of directly approaching predator and expressed various body patterns, such as all dark pattern and eyespots pattern, which are the same body patterns as those expressed against real predators. Cuttlefish tended to express all dark pattern on the checkerboard background, whereas they tended to express eyespots on the uniform grey background in response to the animation of the approaching

predator.

Discussion

Sepia pharaonis expressed diverse camouflage patterns in the same background. This may function as impeding predators to make a searching image of cuttlefish. Another possibility is that because cuttlefish are predated upon by various species of predators, which have different visual systems and hunting strategies, and effective camouflage patterns differ even in the same background.

Cuttlefish changed their body patterns in response to predator-prey distance and the trajectory of the model predator. This suggests that cuttlefish change their body patterns according to the level of predation risk and the view-point of predators. Furthermore, cuttlefish expressed different body patterns in response to the animation of the approaching predator according to the surrounding backgrounds. These results suggest that *S. pharaonis* has an excellent ability to evaluate the surrounding environment, and select and express the appropriate body pattern from a diverse repertoire of body patterns.