


Unique arm-flapping behavior of the pharaoh cuttlefish, *Sepia pharaonis*: putative mimicry of a hermit crab

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Abstract Cephalopods are able to control their arms sophisticatedly and use them for various behaviors, such as camouflage, startling predators and hunting prey. Here, we report a previously undescribed arm-flapping behavior of the pharaoh cuttlefish, *Sepia pharaonis*, observed in captivity. *S. pharaonis* raised the first pair of arms and wrinkled the parts near the distal end, where the skin color was darkened. Additionally, *S. pharaonis* spread the second and third pairs of arms and bent them as if they were jointed, and flapped the distal ends. *S. pharaonis* showed this behavior in two different situations: after being introduced into a large space, and during hunting. We discuss the putative functions of this behavior, including possible mimicry of a hermit crab, considering the situations in which the behavior was observed.

Keywords Color changing · Camouflage · Masquerade · Flamboyant display · Luring

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Introduction

Coleoid cephalopods (cuttlefish, squids and octopuses) are molluscs as well as being bivalves and gastropods, but they have two remarkable characteristics. Firstly, they have the most highly developed nervous systems among invertebrates, which are comparable to those of vertebrates (Packard 1972; Hochner 2012; Vitti 2013). They show various learning abilities such as associative learning, conditional discrimination and observational learning (Darmaillacq et al. 2014). Secondly, within the animal kingdom, cephalopods have the most sophisticated ability to change their appearance (Hanlon and Messenger 1988, 1996; Messenger 2001; Hanlon 2007). Their body coloration, pattern, skin texture and posture are under the direct control of the brain, which enables them to change their appearance in milliseconds (Barbosa et al. 2008; Mäthger et al. 2008; Allen et al. 2009; Barbosa et al. 2012).

Using these characteristics, cephalopods are able to adaptively change their appearance according to different situations. Especially, they are extremely adept at camouflage. They are able to change their appearance to match their color, contrast and pattern to their surroundings to avoid being detected by predators (Chiao and Hanlon 2001; Mäthger et al. 2007; Chiao et al. 2010; Akkaynak et al. 2013), and imitate inanimate three-dimensional structures, such as rocks, seaweed and algae to avoid being recognized as prey by predators (Moynihan and Rodaniche 1982; Hanlon and Messenger 1988; Buresch et al. 2011; Barbosa et al. 2012). Previous studies have also reported that several octopuses are able to mimic the appearance and behavior of other animals (Norman et al. 2001).

Cephalopods change their appearance not only for camouflage. They often spread their arms against approaching predators (i.e., flamboyant display), which is

considered a means of startling or frightening them (Hanlon and Messenger 1996). Additionally, there are several anecdotal reports that squids and cuttlefish use their arms for luring prey (Hanlon and Messenger 1996).

In the present paper, we describe a novel arm-flapping behavior of the pharaoh cuttlefish, *Sepia pharaonis*, observed in two different situations. We briefly discuss its putative function based on the situations where the behavior was observed.

Materials and methods

Situation 1: arm-flapping behavior observed in a large tank

Observations in 2011

Eggs of *S. pharaonis* were collected from the coastal waters of Okinawajima Island in May 2011 and were transported to the Department of Chemistry, Biology and Marine Sciences of the University of the Ryukyus. In November and December 2011, forty-eight individuals were transported to Sesoko Station, at the Tropical Biosphere Research Center, University of the Ryukyus. These cuttlefish were maintained in six round tubs [110-L volume (300-mm height, 700-mm diameter)], with eight individuals in each tank. The first time we observed the unusual arm moving behavior was when cuttlefish were transferred to a large circular tank [10,000-L volume (1.1-m height, 3.0-m diameter)] for the purpose of conducting other experiments. We observed three of 48 cuttlefish flapping their arms intensely, which had not been observed while the cuttlefish were kept in the small maintenance tanks. Therefore, after the experiments had finished, we transferred eight cuttlefish [206–211 days old; 88.1-mm mean mantle length (ML)] simultaneously to the large circular tank again to observe the behavior in December 2011. We submerged a video camera (HD HERO; GoPro) at the bottom of the experimental tank and recorded the behavior of the cuttlefish. Observations were conducted for 5 days after the cuttlefish had been transferred to the tank.

Observations in 2013

Eggs of *S. pharaonis* were collected from the coastal waters of Okinawajima Island in April and May 2013 and were transported to the Department of Chemistry, Biology and Marine Sciences at the University of the Ryukyus. Cuttlefish were reared in rectangular tanks [90-L volume (400-mm length, 600-mm width, 400-mm height)]. We introduced eight cuttlefish (234 days old; 139.8-mm mean ML) into a larger tank [1500-L volume (1800-mm length,

1800-mm width, 500-mm height)] in December 2013. We recorded behavior of the cuttlefish with a video camera (HERO3 + Black Edition; GoPro) submerged at the bottom of the tank for 1 h immediately after they were transferred to the tank.

The total recording time of the behavior of cuttlefish was 404 min. We counted the occurrences of the behavior shown by *S. pharaonis* (i.e., intense flapping of arms; see “Results”) and measured the duration of each behavior. When the behavior was continuously performed for more than 5 s, we considered the behavior had occurred. When the interval between a previous and subsequent display of the behavior was longer than 10 s, we counted the two events as separate occurrences.

Situation 2: arm-flapping behavior observed while hunting prey

The cuttlefish were derived from the same egg masses collected in 2013 and reared under the same conditions as described above. We conducted experiments to examine the development of the hunting ability of *S. pharaonis*. A total of 34 individuals was used in the experiments: 42–47 days old ($n = 6$), 74–79 days old ($n = 8$), 104–109 days old ($n = 8$), 134–139 days old ($n = 8$), and 164–169 days old ($n = 4$). Cuttlefish were individually introduced into an experimental tank [60-L volume (400-mm length, 600-mm width, 250-mm height)], and presented with ten small live fish (tropical damselfish, *Chrysiptera cyanea*) simultaneously as prey. We recorded the hunting behavior of each cuttlefish for 2 h using a video camera (HDR-CX560V and HDR-CX630V; Sony) mounted above the experimental tank.

During the experiments, we unexpectedly observed cuttlefish showing arm-flapping behavior similar to that in situation 1, although the size of the experimental tank did not differ from that of the rearing tank. We measured the duration of this arm-flapping behavior according to the definition described above, calculated the mean duration of the behavior, and compared the total number of prey animals captured between the cuttlefish that did and did not display this arm-flapping behavior. We also counted the number of tentacular strikes, which is a behavior used to capture prey, and tested whether the arm-flapping behavior exhibited until immediately before the tentacular strike affected the success ratio of the following strike. We also examined the relationship between the total duration of the arm-flapping and the total number of tentacular strikes. All statistical analyses were performed using R version 3.2.1 (R Core Team 2015). We excluded the data of one individual (i.e., 104–109 days old) from the analysis because the prey animals were apparently weakened so that this cuttlefish was able to capture them easily.

Results

Situation 1: arm-flapping behavior observed in a large tank

We observed the following arm-flapping behavior in 21 and 16 cases in 2011 and 2013, respectively. *S. pharaonis* manipulated each pair of its arms differently (Fig. 1). The first pair of arms was raised together vertically (Fig. 2a). The parts near the distal end of the first arms were rounded, and the skin color of these parts was darkened (Fig. 2a). The second and third pairs of arms were separated and extended (see S1 Electronic Supplementary Material), often being bent as if jointed, and were flapped independently (see S2 Electronic Supplementary Material). The fourth pair of arms did not show any characteristic movement and were positioned as usual. The mean duration of the behavior was 36.2 s (± 34.3 SD) and 20.9 s (± 18.4 SD) in 2011 and 2013, respectively. Cuttlefish displayed this behavior both when moving around (see S1 Electronic Supplementary Material) and when staying in the same place (see S2 Electronic Supplementary Material). Even when cuttlefish moved around while displaying this behavior, they remained close to the bottom of the tank and hardly swam in the water column. The color patterns of the dorsal mantle during the behavior were not consistent. During the behavior, cuttlefish often lightened their skin, in a flickering manner, around their eyes and at the base of their arms.

Situation 2: arm-flapping behavior observed while hunting prey

Sixteen of 33 individuals showed the arm-flapping behavior described above at least once during the experiments



Fig. 1 The arm-flapping behavior of *Sepia pharaonis* observed in a large, open tank

(Fig. 3). The total duration of this behavior in each individual was 2183.0 s (± 1778.7 SD), and the mean duration of the behavior was 242.9 s (± 492.6 SD), which was significantly longer than in situation 1 (Wilcoxon rank sum tests, 2011, $W = 326.5$, $P < 0.001$, 2013; $W = 742.5$, $P < 0.001$). Cuttlefish that displayed the arm-flapping behavior captured a significantly larger number of prey fish (4.0 ± 2.5 SD) than those that did not display this behavior (1.9 ± 1.1 SD) (Wilcoxon rank sum test, $W = 199.0$, $P < 0.05$). We observed a total of 298 tentacular strikes. In 98 cases of these, cuttlefish exhibited the arm-flapping behavior until immediately before the strike. The success ratio of a strike with and without the arm-flapping behavior was 26.5% (26 out of 98) and 38.5% (77 out of 200), respectively, but there was no significant difference between them (χ^2 -test, $\chi^2 = 3.65$, $df = 1$, $P > 0.05$). There was a positive correlation between the total duration of the arm-flapping and the number of tentacular strikes of each individual (Spearman's rank correlation, $r = 0.71$, $P < 0.001$, $n = 33$). Cuttlefish actively approached prey animals while exhibiting this behavior yet the prey fish seemed to pay little attention to the cuttlefish.

Discussion

In cephalopods, several behavior patterns that are characterized by the spread of their arms have been reported previously (Hanlon and Messenger 1996). Although *S. pharaonis* also shows typical arm-spreading behaviors (personal observation), the behavior we describe in the present study differs from previously described arm-spreading behaviors, because *S. pharaonis* was observed here not only to spread its arms but also to flap them intensely. Hanlon and Messenger (1996) reported that *Sepia latimanus* raises the first pair of arms and twirls the second pair. This behavior is apparently similar to the behavior we observed here; however, *S. latimanus* waves the first pair of arms side to side and darkens the second pair of arms, whereas *S. pharaonis* did not do this in the behavior observed in the present study. Thus, we consider that the present behavior is different from that described in *S. latimanus*.

Several functions have been suggested for behaviors using the arms in cephalopods: masquerade, flamboyant display and luring. With regard to the function of the behavior we describe in the present study, masquerade is unlikely since the present behavior is characterized by conspicuous flapping movements of the arms, which would disrupt the effectiveness of camouflage. A flamboyant function is also unlikely because this display is only exhibited when the predator is imminent (Hanlon and Messenger 1996), whereas there were no predator stimuli

Fig. 2 *S. pharaonis* exhibiting arm-flapping behavior. **a** A frame from the digital video taken from the side, and **b** from above. The first pair of arms are raised vertically and partly colored. The second and third pairs of arms are bent down, as if they were jointed

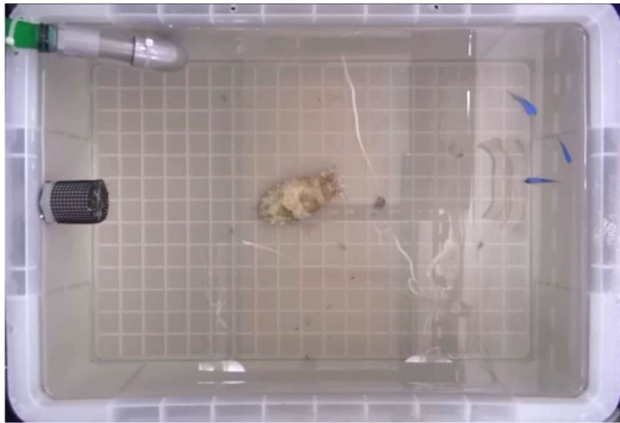
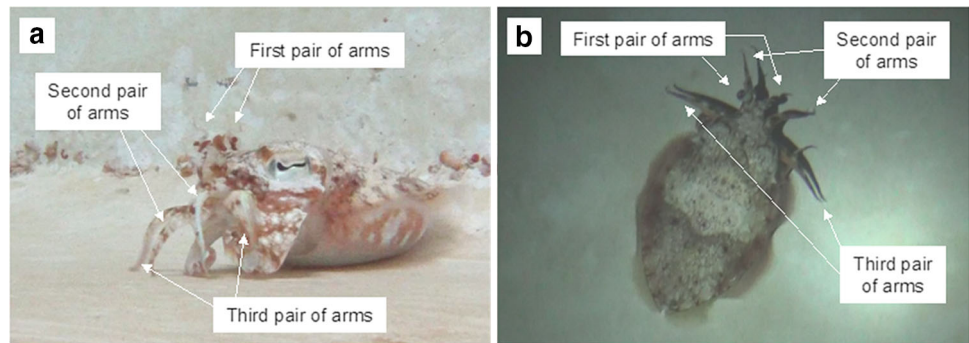


Fig. 3 The arm-flapping behavior of *S. pharaonis* observed during hunting

during our observation. It is possible that the present behavior functions as luring because 16 out of 33 cuttlefish showed the behavior during hunting. In fact, the cuttlefish that displayed the mimetic behavior captured twofold the number of prey fish. However, prey animals did not seem to be attracted to the cuttlefish, and cuttlefish actively approached prey animals. Experimental verification is necessary to conclude the luring function of this behavior by *S. pharaonis*.

Another possibility is that the present behavior functions as mimicry. The color and posture of the first pair of arms resembled the eyes of a crustacean, and the movement of their second and third pairs of arms resembled a crustacean moving its appendages. The dorsal mantle of the cuttlefish would correspond to the gastropod shell of a hermit crab. Several previous studies have reported that octopuses are able to impersonate other animals (Hanlon et al. 1999; Hochberg et al. 2006; Huffard 2007; Hanlon et al. 2008; Krajewski et al. 2009; Hanlon et al. 2010). A mimic octopus, *Thaumoctopus mimicus*, is the most well-known example of this, and has been suggested to impersonate various venomous animals, such as a poisonous sole, sea snake and lionfish (Norman et al. 2001). In addition, Warnke et al. (2012) have reported that the stumpy-spined

cuttlefish, *Sepia bandensis*, seems to move like a snail. Since cuttlefish are soft bodied and vulnerable to predation (Hanlon and Messenger 1996), mimicking hermit crabs, which have a hard shell to protect them against predators, presumably would be beneficial to some degree for the cuttlefish. In addition, hermit crabs are generally scavengers and filter feeders (Angel 2000) and not active hunters. Thus, mimicking hermit crabs would help cuttlefish to approach their prey more closely, inside the range of their tentacles (Messenger 1968). Nonetheless, the arm-flapping behavior exhibited until immediately before the tentacular strike did not increase the success ratio of the following strike in the present study. We studied the arm-flapping behavior in the simple visual environment of an experimental tank, which lacked substrates, structural objects and other animals including possible model species (i.e., hermit crab). It is thus necessary to examine the effect of the arm-flapping behavior under natural conditions. Unfortunately, few field studies of *S. pharaonis* have been conducted (Minton et al. 2001), and its behavior, habitat and life history in the wild are poorly understood. Thus, we are currently unable to identify the species that *S. pharaonis* may mimic. Future research in the wild as well as experimental studies are necessary to verify the validity of the above mimicry hypothesis and increase our understanding of the function of the described behavior.

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