Food imprinting and visual generalization in embryos and newly hatched cuttlefish, *Sepia officinalis*

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Juvenile cuttlefish spontaneously prefer shrimp to crabs. This preference can be changed by early visual learning during embryonic and postembryonic life and has been related to a form of food imprinting. Nevertheless, it is unknown whether generalization occurs in conjunction with this early learning process. We found that inexperienced hatchling cuttlefish preferred 'black' to 'white crab' for their first meal, the black ink envelope of cuttlefish eggs did not prevent embryos discriminating between black and white crabs and embryonic or postembryonic visual familiarization to 'white crabs' induced a subsequent visual preference for 'white crabs' over 'black crabs' in the hatchling's first meal. Finally, juvenile cuttlefish previously pre- or postnatally exposed to 'white crabs' preferred 'black crabs' to shrimp, indicating for the first time that prey generalization occurs as early as the embryonic stages in cuttlefish. Such cognitive abilities could confer important adaptive advantages in processing information about prey likely to be available in the egg-laying environment at hatching and in the course of juvenile dispersal.

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Perinatal learning is of considerable ecological significance. Young or even embryonic animals may detect and learn features of their environment to shape their early behaviours. This specific kind of early learning, imprinting, was one of the first phenomena tackled by the field of ethology. Since Lorenz (1937) first described imprinting, extensive developmental studies of social preference have been performed in young animals. Filial imprinting is a learning process underlying the formation in young animals of an attachment to, and a preference for, a parent, parent-surrogate or sibling (Bolhuis 1991). Although Lorenz claimed that imprinting had to occur during a critical period and was irreversible, subsequent studies have shown that imprinting preferences can be reversed, and that the critical period is not as strict as previously thought (Bolhuis 1991). Imprinting does not imply a simple stimulus–response association, but rather a representation of the stimulus that can then be used flexibly (Bolhuis 1999). Distinct from filial imprinting, sexual imprinting is involved in the formation of mating preferences that are expressed later in life. In males, initial attachment to the mother is later generalized to choose a sexual partner (Immelman 1972). Generalization is the evaluation of stimuli for similarity on one or more perceptual scales to elicit appropriate responses (Ghirlanda & Enquist 2003). Chicks imprinting to a template generalize (Jaynes 1956, 1958; Cofoid & Honig 1961) within a perceptual scale and respond positively to novel objects sharing features with the imprinted one (e.g. shape, colour). This stimulus generalization in imprinting has consequences not only in the later choice of a sexual partner, but also on filial attachment towards different objects. Imprinting has also been associated with food preferences. Burghardt & Hess (1966) first reported that young snapping turtles, *Chelydra serpentina*, exhibit a strong preference for the first food experienced, and that this preference could be established after only one meal (Burghardt 1967). Although this preference was initially characterized as food imprinting, ingesting the first meal may be perceived as a reward, making food preference a result of an associative-learning process distinct from imprinting (Punzo 2002). Since generalization occurs in the context of filial and sexual imprinting, it could be that this process also occurs in the context of food imprinting to aid in the sorting of potential prey.

In young domestic chicks, *Gallus gallus domesticus*, the formation of filial preferences involves at least two processes: a learning process through which chicks come to recognize the features of certain stimuli to which they are exposed and a predisposition to

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approach stimuli resembling conspecifics (Johnson et al. 1992). More than a predisposition, chicks also show a natural preference for brightness that is so stable that it cannot be eliminated by incubating, hatching and rearing in the dark (Zolman & Lattin 1972). Such natural or so-called innate preferences have also been demonstrated in pollinators: honeybee, *Apis mellifera*, workers have a natural colour preference that can be extinguished by training (Giurfa et al. 1995). This combination of innate preference and learning may demonstrate ubiquitous cognitive processes that control foraging behaviour in pollinators and possibly all insects.

The cuttlefish, *Sepia officinalis*, is a sophisticated marine invertebrate that is able to hunt very early in life. Early juveniles are active predators feeding on different types of prey, including fishes and crustaceans, crabs and shrimp (von Boletzky 1983; Dickel et al. 1997). Darmaillacq et al. (2006a) demonstrated that an early visual exposure to prey modifies the food preference of newly hatched cuttlefish for its first meal, several days after hatching. In a two-way choice test (crabs versus shrimp), a 'naïve' cuttlefish preferred shrimp for its first meal, whereas a cuttlefish that had previously seen crabs preferred crabs. This early familiarization has been referred to as food imprinting (Darmaillacq et al. 2006b) since the behaviour includes all characteristics of imprinting. Namely, this familiarization to crab must occur during a sensitive period that ends a few hours after hatching, the learned preference for crabs is persistent, the preference overrides direct food experience with shrimp, and there is no reinforcement during learning (i.e. during the familiarization crabs are not captured). This preference for crabs can also be induced via visual familiarization to crabs during the last stages of embryonic development (Darmaillacq et al. 2008). Any flexibility, however, in learned preferences arising from food imprinting is still uncharacterized. Can generalization occur around these preferences? There is evidence that adult *Octopus* generalize stimuli during visual conditioning: Muntz (1962, 1965) demonstrated that *Octopus* generalize between two squares on the basis of their size. Whether cuttlefish also generalize among stimuli during imprinting is unknown. Cuttlefish are able to discriminate between shrimp and crabs (above), but in those experiments the size of the crabs, *Carcinus maenas*, was controlled (carapace width 2–4 mm). Other characteristics of the prey phenotype may be relevant in imprinting: the human brain clearly classes different groups of young *C. maenas* on the basis of the brightness of their carapace. The first aim of our study was to determine whether hatchlings show a spontaneous preference for a specific crab group and, if so, whether this spontaneous preference can be changed by prior familiarization with a nonpreferred group (experiment 1). The second aim was to determine whether cuttlefish generalize a learned crab group with an unfamiliar one (experiment 2). Experiment 2 was conducted with juvenile cuttlefish, with familiarization to crabs occurring both prehatching and posthatching to determine whether there is an effect of hatching on visual generalization.

METHODS

Cuttlefish lack paralarval or larval stages (von Boletzky 2003), and juveniles have the same morphological traits as adults. Basic behaviours are fully developed upon hatching. As the hatchlings do not receive any parental care (Richard 1971), they must quickly learn to identify prey, shelters and predators. For the present study, *S. officinalis* eggs were obtained from egg clusters that were originally collected from cuttlefish traps, checked daily at low tide, in the vicinity of Luc-sur-Mer, Normandy, France. When performed by competent technicians, this trapping method is by far the least stressful method of collection. Eggs were kept in a 1500-litre tank at the Centre de Recherches en Environnement Côtier (CREC), Luc-sur-Mer, France. Eggs initially laid in clusters were separated to ensure optimal developmental conditions and were placed in strainers floating in laboratory tanks. The tanks were supplied with flowing, oxygenated natural sea water maintained at $19 \pm 1\,^{\circ}\mathrm{C}$ (mean $\pm$ SD) under ambient daylight conditions. All experiments comply fully with current laws in France.

Crabs and shrimp were collected daily in the field at low tides from locations where female cuttlefish naturally lay their eggs. Small shrimp of suitable size (*Crangon crangon*, 5–10 mm length) were captured with specially designed soft nets in small pools and kept in a circular tank, 30 cm in diameter and 10 cm deep, in the laboratory. Small *C. maenas* were taken by hand from under rocks and kept in the laboratory in half-submerged boxes with empty shells, pebbles and shelters (15 × 20 cm) to provide both marine and terrestrial resting spots. All animals were collected by authorized scientific technicians and researchers. After experiments, the cuttlefish were released into the sea at low tide in small sandy pools in which prey were abundant. The crabs and the shrimp used as prey were used after the experiments to feed other cuttlefish reared in the laboratory.

Todd et al. (2005) distinguished eight different phenotypes of *C. maenas*, on the basis of the brightness of the patterns on their carapace. Two of these were used in the present experiments: small crabs with a dull brown carapace ('black crabs') and small crabs with white spots covering at least half of the carapace surface (Fig. 1, 'white crabs'). These crabs were then sorted by size (3–5 mm carapace width). As seen in Todd et al. (2005) and from our own observations of specimens under a binocular microscope, the crabs were identical in behaviour and morphology except for the brightness of their carapace.

Familiarization Protocols

For prehatching familiarization experiments, a square box made of black PVC (50 × 50 cm and 12 cm high) was divided into 25 cases (10 × 10 × 10 cm) that were used as individual compartments to isolate eggs. In each case, the floor was pierced in the middle (2 cm in diameter); this hole was surrounded by a glass box in which one
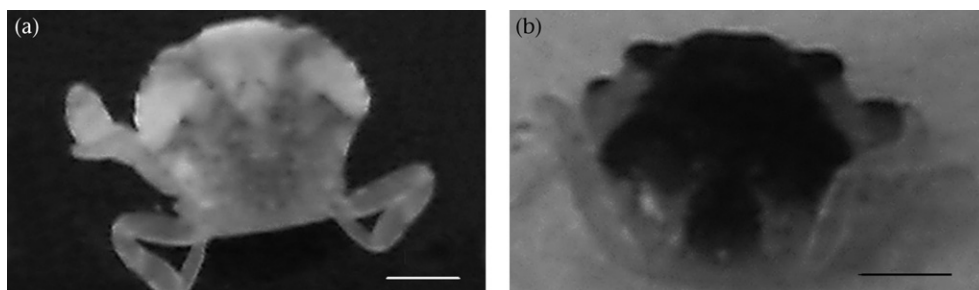

Figure 1. Photographs of the (a) 'white' and (b) 'black' phenotypes of *Carcinus maenas*. Both crabs are 3 mm wide. (Scale: line = 1 mm).

egg was suspended by a nylon string attached to a small net enclosing the glass box (Fig. 2). The view from the egg would therefore include the crabs. When animals hatched, cuttlefish fell through the hole and lost visual contact with the crabs. Five white crabs (WC; carapace width 3–5 mm) were placed in the visual field of each egg for at least 7 days prior to hatching. Eggs from control groups (C_1, $N = 25$; C_3, $N = 25$) were isolated in the same apparatus but without crabs. After hatching, cuttlefish were gently moved into black PVC tanks ('rearing tanks', 7×8 cm and 8 cm high) for 7 days before subsequent testing.

For posthatching familiarization experiments, eggs were put in plastic strainers floating in tanks until hatching. Since hatching occurs at night (Paulij et al. 1991), hatched cuttlefish were collected every morning at 0600 hours (Day 0) and moved to posthatching 'familiarization tanks' of black PVC (7×4 cm and 8 cm high). These hatchlings were then visually exposed to five white crabs for 2 h (see Darmaillacq et al. 2006a). After exposure, juveniles were gently moved to 'rearing tanks' for 7 days before subsequent testing. Eggs from control groups (C_2, $N = 15$; $C_{2'}$, $N = 30$; C_4, $N = 10$) were isolated in the same apparatus after hatching but without crabs.

Cuttlefish were not fed until testing 7 days after exposure since they hatch with yolk reserves that last for several days (von Boletzky 1975, 2003; Dickel et al. 1997). The number of cuttlefish hatched in each group may differ from the initial number of eggs, since some eggs failed to hatch and some cuttlefish died after hatching (see Results).

Preference Testing

On day 7, all juveniles from both experimental groups (experiments 1 and 2) were tested individually in test arenas to examine their preferences for two types of prey (crabs/shrimp or crabs/crabs) depending on the experiment (for details see Darmaillacq et al. 2004). The apparatus consisted of a rectangular arena ending in two separate adjacent compartments, made with light-grey PVC, in which each of the two types of prey were enclosed. Five live prey were placed in each compartment to create a constantly moving visual stimulus to elicit natural attack behaviour by the hatchlings. Prey were separated from the rest of the arena by a glass partition that did not affect light polarization. The glass also prevented the cuttlefish from perceiving chemical and mechanical cues from the prey. The arm containing each prey type was switched randomly from trial to trial to eliminate the possibility of a choice based on a natural position preference. The prey were hidden behind a sliding PVC door and one cuttlefish was

placed in a Perspex cylinder at the centre of the arena, equidistant from the two types of prey. After a 5 min acclimation period, the sliding door was opened rapidly so that all prey appeared at the same time. The cuttlefish was released from the cylinder as soon as it had detected the prey and moved towards it. The first prey item chosen was recorded. Trials lasted a maximum of 5 min after acclimation or until a prey type was chosen, whichever came first. Each individual was tested only once, unless the subject failed to attack within 5 min of the test; in this case prey were hidden again and the cuttlefish was tested on the next day.

Experiment 1 (Table 1) tested whether a prehatching (WC_1 group, $N = 25$) or a posthatching (WC_2 group, $N = 30$) exposure to 'white crabs' can induce a preference for this crab phenotype when tested 7 days after hatching. In the control group (C_1), cuttlefish eggs had no visual exposure to crabs ($N = 25$) pre- or posthatching. On day 7, the preference of cuttlefish from all groups (WC and C) for 'white crabs' or 'black crabs' was tested in the choice arena. To determine whether the darkness of the background influences their prey preference, control juveniles were tested either in a light-grey PVC test tank (C_2 group, $N = 15$) or in a black PVC test tank ($C_{2'}$ group, $N = 30$).

Experiment 2 (Table 1) was designed to test whether cuttlefish previously familiarized to 'white crabs' before hatching (WC_3 group, $N = 25$) or after hatching (WC_4 group, $N = 25$) would have a preference for an unfamiliar crab phenotype (i.e. 'black crab', generalization) over shrimp compared to cuttlefish without any previous prey exposure. In experiments 1 and 2, some cuttlefish died or failed to hatch (see Results).

Data were analysed with nonparametric tests using StatXact 7 (Cytel Software, Cambridge, MA, U.S.A.) with two-tailed tests. For statistical analysis, we considered only the cuttlefish that made a choice. The preference for one type of prey over the other type presented within groups was analysed with a chi-square exact test with an alpha risk of 5%. The Fisher's exact test was used to examine whether prey preferences differed between groups with an alpha risk of 5%.

RESULTS

Experiment 1: Familiar versus Unfamiliar Crabs

Eight eggs in the WC_1 group and four in the C_1 group failed to hatch. Two WC_1 cuttlefish died soon after hatching. During testing 7 days posthatching, control (C_1) cuttlefish exhibited a significant preference for 'black crabs' over 'white crabs' (16 versus 5 choices, respectively; $\chi_1^2 = 5.76$, $N = 21$, $P = 0.003$; Fig. 3a), whereas WC_1 cuttlefish significantly preferred 'white crabs' (12 versus 3 choices; $\chi_1^2 = 5.34$, $N = 15$, $P = 0.035$; Fig. 3a). The choice distributions
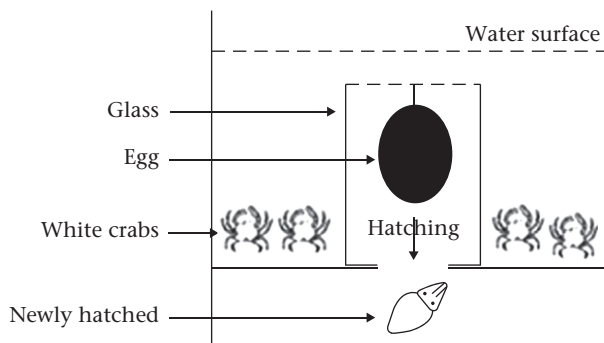

Figure 2. Schematic representation of the apparatus (not drawn to scale) used to familiarize embryos to 'white crabs'. Each egg was exposed to five 'white crabs'. After hatching, the cuttlefish fell through the central hole, ensuring that it was no longer visually exposed to the prey.

Table 1
Exposure experience and choice test for each experimental group

Group	Exposure period	Prey type	Test
Experiment 1			
WC_1	Prehatching	White crabs	White vs black crabs
C_1	None	None	White vs black crabs
WC_2	Posthatching	White crabs	White vs black crabs
C_2	None	None	White vs black crabs
$C_{2'}$	None	None	White vs black crabs
Experiment 2			
WC_3	Prehatching	White crabs	Black crabs vs shrimp
C_3	None	None	Black crabs vs shrimp
WC_4	Posthatching	White crabs	Black crabs vs shrimp
C_4	None	None	Black crabs vs shrimp

All cuttlefish were tested in a grey PVC apparatus except for the cuttlefish of the $C_{2'}$ group, which were tested with prey in a black PVC apparatus.
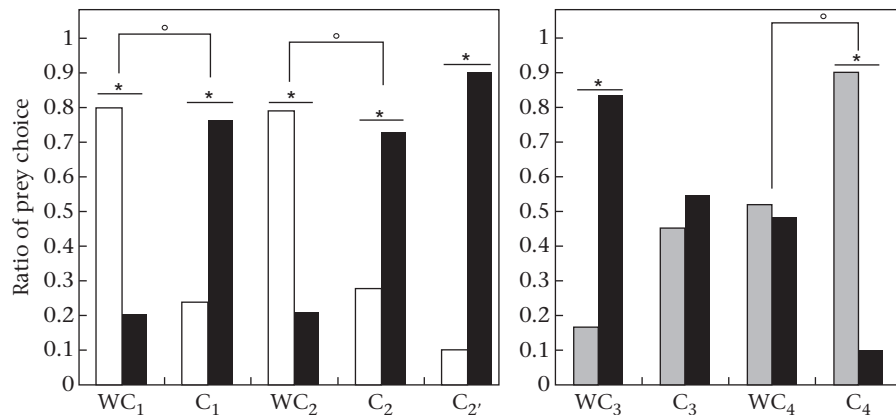
Figure 3. (a) Preferences for 'white crabs' (white bars) and 'black crabs' (black bars) exhibited by 7-day-old naïve cuttlefish (C_1, $N = 21$; C_2, $N = 29$), or cuttlefish previously exposed visually to 'white crabs' during embryonic stages (WC_1, $N = 15$), or just after hatching (WC_2, $N = 24$) in a light-grey PVC apparatus, or naïve cuttlefish ($C_{2'}$, $N = 10$) tested in a black PVC apparatus. (b) Preferences for shrimp (grey bars) and 'black crabs' (black bars) exhibited by 7-day-old cuttlefish previously exposed visually to 'white crabs' during embryonic stages (WC_3, $N = 18$), or just after hatching (WC_4, $N = 25$), or with no prey exposure (C_3, $N = 11$; C_4, $N = 10$). *Significant prey preference within groups (chi-square exact test: $P < 0.05$) and °significant difference in prey choice between groups (Fisher's exact test: $P < 0.05$).

differed significantly between the two groups (Fisher's exact test: $P < 0.001$).

Six eggs in the WC_2 group, one in the control C_2 and three in the $C_{2'}$ group failed to hatch. Two cuttlefish from the $C_{2'}$ group died shortly after hatching. Cuttlefish that were familiarized to 'white crabs' (WC_2) after hatching attacked significantly more 'white crabs' than 'black crabs' (19 versus 5 choices, respectively; $\chi_1^2 = 8.17$, $N = 24$, $P = 0.004$; Fig. 3a). The choice distributions differed significantly between WC_2 and C_2 groups (Fisher's exact test: $P = 0.0002$). Lastly, cuttlefish from C_2 and $C_{2'}$ groups attacked significantly more 'black crabs' than 'white crabs' whatever the grey level of the background (respectively, C_2 group: 21 versus 8 choices; $\chi_1^2 = 5.82$, $N = 29$, $P = 0.02$; $C_{2'}$ group: 9 versus 1 choices; $\chi_1^2 = 6.4$, $N = 10$, $P < 0.01$; Fig. 3a).

Experiment 2: Unfamiliar Crab versus Shrimp

Seven eggs in the WC_3 group and 14 in the C_4 group failed to hatch. C_3 cuttlefish did not show a significant preference for shrimp or 'black crabs' (5 versus 6 choices, respectively; $\chi_1^2 = 0.09$, $N = 11$, $P = 0.763$; Fig. 3b), whereas WC_3 cuttlefish exhibited a significant preference for 'black crabs' over shrimp (15 versus 3 choices; $\chi_1^2 = 8$, $N = 18$, $P = 0.007$; Fig. 3b). Cuttlefish in the C_4 group (without previous crab familiarization) attacked shrimp more often than 'black crabs' (9 versus 1 time, respectively; $\chi_1^2 = 6.4$, $N = 10$, $P < 0.01$; Fig. 3b). Cuttlefish from WC_4 (with posthatching familiarization to white crab) attacked shrimp as often as 'black crabs' (13 versus 12 choices, respectively; $\chi_1^2 = 0.04$, $N = 25$, $P = 0.84$; Fig. 3b). The distributions of choice differed significantly between the two groups (Fisher's exact test: $P < 0.05$).

DISCUSSION

The first aim of this study was to examine whether a spontaneous preference for a given crab phenotype could be changed by early visual experience (experiment 1). When faced with a choice between 'white crabs' and 'black crabs', cuttlefish with no prior crab exposure (C_2 and $C_{2'}$) showed a spontaneous preference for the darker phenotype, whatever the contrast between the prey and the background (Fig. 3a). This observation is consistent with previous reports that showed that octopuses naturally prefer dark items to pale ones in a visual discrimination task (reviewed in Boal 1996). It has been suggested that phenotypic variation of young *C. maenas*

crabs is related to habitat. The carapace pattern of young crabs matches the background to generate camouflage, which may confer an advantage against visual predation (Hogarth 1978; Bedini 2002). 'Black crabs' generally live in algal fields, while patterned 'white crabs' live on mussel beds (Todd et al. 2005). In the English Channel cuttlefish eggs are usually laid on algae (von Boletzky 1983) where 'black crabs' are abundant. The 'innate' preference of cuttlefish hatchlings for darker prey may therefore be adaptive in their natural habitat. In experiment 1, cuttlefish preferred the prey type to which they had been familiarized before and right after hatching (Fig. 3a). This clearly demonstrates that the black-inked egg envelope does not prevent cuttlefish embryos from visually discriminating between 'white crabs' and 'black crabs'. Darmaillacq et al. (2008) have shown that embryonic visual familiarization induces subsequent food preference in hatchlings in favour of the prey items to which they had been exposed. Our results confirm and reinforce this observation: learning of specific features of prey such as carapace brightness manifests in subsequent hunting behaviour. Since this crab phenotype varies as a function of habitat (Todd et al. 2005), familiarization in ovo would be a highly adaptive response to variation in spawning grounds (e.g. when eggs are laid on mussel beds instead of algae). Even while still in the egg, cuttlefish could bias initial crab preference by visual familiarization with the most abundant crab phenotype in its location (e.g. 'white crabs' on mussel beds).

The second aim of this study was to examine whether cuttlefish could generalize their learned preference for a given crab phenotype to an unfamiliar crab phenotype (experiment 2). Cuttlefish previously familiarized to 'white crabs' before and immediately after hatching preferred 'black crabs' to shrimp, their naturally preferred prey (Fig. 3b). Thus cuttlefish hatchlings are able to transfer a learned preference for one crab phenotype (here 'white crab') to a new phenotype ('black crab'). These two prey items share common features (motion, size and morphology), but differ in their brightness. Young cuttlefish, however, must have learned different characteristics of the crabs than their brightness. Our results demonstrate a typical case of visual generalization (Cofoid & Honig 1961) in hatchlings. This directly relates to imprinting: Lorenz (1937) proposed that, in birds, generalization of preference in adulthood builds a base for subsequent learning. Imprinting generalization also occurs in early life (Bolhuis & Horn 1992). Darmaillacq et al. (2006b) described criteria of early familiarization to crabs in *Sepia*: a sensitive period, the persistence of the

preference, the absence of reinforcement, and different neural substrates than those in associative learning (see also Dickel et al. 1997, 1998, 2006). By demonstrating generalization processes in hatchlings here, we confirm that early visual exposure to crabs in young cuttlefish results in food imprinting. Surprisingly, cuttlefish from the C_4 control group showed a spontaneous preference for shrimp over crabs (Fig. 3b), which is consistent with previous reports (Wells 1958; Darmaillacq et al. 2004, 2006a), although cuttlefish from the C_3 group did not exhibit this preference (Fig. 3b). Unlike the C_4 group in which eggs were kept in clusters, eggs from the C_3 group were isolated individually during the last stages of embryonic development. This result suggests that an initial preference for shrimp is not 'innate' as previously thought (Darmaillacq et al. 2004, 2006a, b) but may depend on the conditions of embryonic development (Guibé et al. 2010). This result further underscores the importance of the visual environment during the embryonic development on future prey preference.

Taken together, these observations suggest that the ability to generalize among visual stimuli may have an important adaptive value: early diet selection may utilize food item generalization to reduce energy and time devoted to information processing (Ginane & Dumont 2006). Generalizing among initial prey preferences would allow a young cuttlefish to diversify its diet while dispersing away from the laying site without the increased cost associated with trial-and-error learning (Dickel et al. 2006). The ability to generalize food items would be particularly beneficial for hatchlings exposed to numerous predation threats during foraging by reducing the energy spent in identifying and choosing food items.

Juvenile and adult cuttlefish sort prey items using different prey capture strategies; cuttlefish dart forward and strike with their tentacles to catch a shrimp or a fish, but smother crabs by approaching and capturing from the back (Messenger 1968). In predator species, the cost of learning different tactics predicts that sorting food items should begin to operate very early in development, as soon as the animal is able to forage (Santos et al. 2001). Dickel et al. (2006) emphasized the importance of learning processes early in life in cuttlefish to refine their predatory behaviour. We have demonstrated here that cuttlefish embryos and hatchlings visually generalize among crabs, which are captured in similar ways. Sorting prey items therefore begins early in cuttlefish, even during embryonic development. Embryonic and hatchling cuttlefish exhibit complex learning and cognition, including visual generalization of prey items.

Acknowledgments

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