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# Spontaneous alternation in marine crabs: Invasive versus native species

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ABSTRACT

Organisms ranging from paramecia to humans tend to explore places that have been least recently explored, which is referred to as spontaneous alternation. Although organisms rely on different sources of information in alternating between places, the emergent behavioral pattern is likely advantageous during exploration and foraging. Under this rationale, continuous spontaneous alternation performance of the invasive green crab, *Carcinus maenas* was assessed and compared with the native blue crab, *Callinectes sapidus* in a plus-maze submerged in seawater. For the first time spontaneous alternation behavior was demonstrated in Crustacea (i.e., *C. maenas*) and significant interspecific differences in alternation performance were observed between the invasive versus the native species. *Carcinus maneas* exhibited a pronouncedly higher spontaneous alternation performance than *C. sapidus*. *Carcinus maneas* on average alternated at levels higher than chance, which was not the case for *C. sapidus*. These observations point to an additional behavioral mechanism that might result in the competitive success of green crabs over blue crabs in areas where they co-occur. Most of the subjects exhibited asymptotic alternation performance from the onset; there was no improvement in their performance over the course of the experimental session. This finding implies the innate nature of this behavioral policy.


## 1. Introduction

Spontaneous alternation is the behavioral pattern emerging from an organism's tendency to explore places that have been least recently visited without any reinforcement mediation. This means that the organism has not been trained through reinforcement (e.g., it is not escaping an aversive state nor is it receiving a reward) to exhibit this behavioral pattern (Richman et al., 1986). Spontaneous alternation has been demonstrated in several organisms ranging from paramecia and flatworms (Aderman and Dawson, 1970; Harvey and Bovell, 2006) to rats and humans (Still, 1966; Schultz, 1964). Different processes have been proposed to underlie this pattern, including reactive inhibition (Hull, 1951), curiosity and response to novelty (Dember, 1956), and spatial working memory (e.g., Stefani and Gold, 2001). It is thought that different phyla rely on different cues in exhibiting this pattern. Some invertebrates have been shown to rely on body turn whereas vertebrates employ directional and/or odor cues (for a review see Richman et al., 1986). Irrespective of the possible underlying mechanism(s), spontaneous alternation appears to be innate and the behavior may be beneficial during exploration and foraging (Estates and Schoeffler, 1955; Dember and Earl, 1957). For example, this pattern might increase the likelihood of discovering an unexploited resource, especially in heterogeneous environments with patchy prey distributions. Based on this rationale, we compared the spontaneous alternation performance of two Portunid (F. Portunidae) crabs: the invasive European green crab (*Carcinus maenas* [Linnaeus, 1758]) and the native, swimming blue crab (*Callinectes sapidus* Rathbun, 1896).

Native to the Atlantic coast of Europe, the green crab has proven to be a highly successful invader worldwide with established populations on both coasts of North America (e.g., Ropes, 1967; Cohen et al., 1995; Carlton and Cohen, 2003). Its success has in part, been attributed to its ability to tolerate a wide range of temperatures and salinities (Eriksson et al., 1975), as well as exposure to air (Crothers, 1968). Moreover, it is a highly effective predator on a wide variety of benthic invertebrates (e.g., Ropes, 1967; Taylor, 2005), and life history traits such as high fecundity, long planktonic larval stage, and fast growth have also facilitated its global expansion (Roman and Palumbi, 2004). Once established, the green crab has become the dominant intertidal crab in some areas, affecting the abundance, size structure, and defense response of native species (Ropes, 1967; Cohen et al., 1995; Tyrell and Harris, 1999; Yamada et al., 2005). In bays and estuaries on the east coast of the United States green crabs may be a major competitor with the ecologically and commercially important blue crab (Roudez et al., 2007) as they broadly overlap in habitat utilization and diet (Williams, 1984). Thus, recent research has focused on examining potential competitive

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interactions between these two species (e.g., DeRivera et al., 2005; Henry, 2005; MacDonald et al., 2007). This led us to compare these species in a continuous spontaneous alternation paradigm using a plus-maze submerged in seawater.

The objectives of the present research were to determine (1) if spontaneous alternation behavior is exhibited by two species of portunid crabs; (2) whether there are interspecific differences (i.e., invasive versus native species) in their spontaneous alternation performance; and (3) if spontaneous alternation performance for individual subjects improved over the course of an experimental session, by which we aimed to address the innateness of this behavioral policy (not learned via recent experience).

## 2. Materials and methods

### 2.1. Subjects

A total of 19 *C. maenas* (carapace width = 5.50, ±0.15 cm SE) and 18 *C. sapidus* (carapace width = 11.70 ± 0.73 cm SE) were obtained from Tuckerton, New Jersey in August/September 2008 and transported in coolers to the Institute of Marine and Coastal Sciences (IMCS) in New Brunswick for experiments. Carapace length was measured from tip to tip of the longest lateral spines. Green crabs were all adult females (catches at this time consisted of only females) and blue crabs were an even mixture of adult males and females. Blue crabs did not exhibit significant differences in spontaneous alternation performance between the sexes, $t(14) = 0.06$, $p = 0.95$ (female mean = 0.30; male mean = 0.30). Crabs were housed individually in minnow traps (to prevent agonistic interactions) partly submerged, in temperature controlled running seawater tables (salinity = ∼32; temperature = ∼20 °C) at a 12 h light: 12 h dark photoperiod. They were fed with local mussels (*Geukensia demissa*) every 2 days. Testing for spontaneous alternation performance was conducted in a separate light controlled room, fed with seawater that was maintained at the same temperature and salinity as the seawater tables where crabs were maintained. Crabs were kept for 5–7 days prior to conducting experiments to give them time to adjust to their new surroundings. The carapace of each crab was also marked with a small amount of "white out" to aid in viewing crabs under the dimly lit experimental conditions.

### 2.2. Apparatus

A glass plus-maze was built in house (arm length: 31.0 cm, arm width: 13.0 cm, arm height: 25.5 cm) and placed at one end of a fiberglass seawater table (length: 141.0 cm, width: 91.0 cm, height: 14.0 cm) (Fig. 1). Five cylindrical objects of different size (diameters ∼4–12 cm) and color (i.e., white, grey, and black) were placed around the plus-maze (Fig. 1) to potentially aid crabs in spatial navigation. Identical pieces of wood (3 cm × 1 cm cube) were secured at the end of each maze arm, and a white waterproof flooring was placed in the last 1/3 of each arm (10 cm from the end of each arm). The wood provided some structure within the maze, whereas the white flooring indicated, under dim lit conditions, the "threshold" individual crabs had to cross in order for us to score each of the arm entries as an arm choice (described below). The seawater table and thus the plus-maze were filled with water to a depth of 13 cm for each experimental session.

### 2.3. Procedure

For each session, the subject was gently placed in the center, open area of the plus-maze (Fig. 1) and its movements within the maze were recorded for 63 min (to ensure 60 min of observation in the absence of the experimenter) under dimly lit conditions using a digital video camera (Sony DCR-SR42) and a PC. Following placement of the subject in the maze, the experimenter promptly left the room. After each session, the water was flushed and renewed to a large extent for the next subject. Crabs were released back to their natural habitat upon completion of the study.

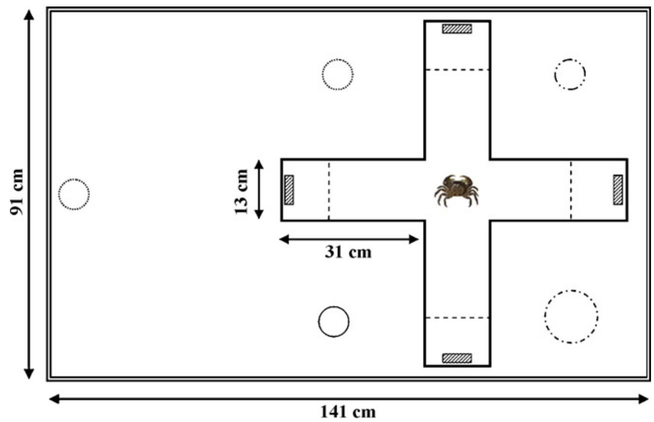


**Fig. 1.** Diagram of the plus-maze and its position in the seawater table. Circles indicate the placement of the objects relative to maze arms, shaded rectangles = identical pieces of wood secured at the end of each maze arm, crab = the area where the crab was placed at the start of each experimental session, and dashed line = the threshold a crab needed to cross with at least half of its body in order to score an arm entry as an "arm choice".

### 2.4. Data analysis

#### 2.4.1. Scoring

The subject was considered to have made an arm choice (an arm entry) when at least half of its body passed the threshold (1/3 of the arm length—see apparatus). Each choice was noted and time stamped. Consistent with the scoring regimes used in studies of continuous spontaneous alternation and because of the difficulty in defining an immediate repeated arm choice, repeated entries of the same arm were not included in the data analysis (also see Anisman, 1975; Kokkinidis and Anisman, 1976; McNay and Gold, 2001; Lennartz, 2008). Alternation performance was assessed within overlapping runs of five choices. If the subject chose four different arms within five consecutive choices, that sequence was scored as a successful alternation (1) else it was scored as an unsuccessful one (0). The overall alternation performance of each subject was the ratio of successful alternations to the number of all possible alternations ($n - 4$, where $n$ is the total number of arm choices). For instance, assume that a crab made the following scored choices: A-C-B-A-D-C-D-C-A-B, where it had 4 out of 6 possible alternations (111001), thus scored (4/6 = 0.67). Subjects making fewer than 10 arm choices were not included in the data analysis, so three green crabs and two blue crabs were excluded (green crabs $n = 16$; blue crabs $n = 16$).

Alternation performance scores were compared with chance level which was calculated by the following method: a subject's first arm choice was always novel (4/4). Since we did not consider immediate repeated choices, its second arm choice was also always novel (3/3). On the third arm choice a subject had a 2/3 probability of choosing an arm that was not its first choice (note that repeated choices were not considered). If the subject had a novel third choice, on the fourth choice it had 1/3 probability of choosing an arm that was novel/not chosen as its first or second choice. At this point, the subject did not need another choice to have chosen four different arms. Thus, partial probability of choosing four different arms here is (4/4)(3/3)(2/3)(1/3)(1) = 0.22. The subject however, could have made a mistake on its third choice but could still choose all four arms within five choices, where