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The effects of shell size and coil orientation on reproduction in female hermit crabs, *Clibanarius vittatus*

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Abstract

We investigated the effects of shell coil orientation and shell size on reproduction in field populations of the hermit crab, *Clibanarius vittatus*. Females were collected in the intertidal in Beaufort, NC. Shell parameters were measured and size (cephalothorax length) and reproductive status were determined for 70 females occupying *Busycon* shells. Crabs were categorized as berried (eggs on the pleopods), mature ovaries, or non-reproductive (no eggs). For berried females, the number of eggs was recorded. By offering a separate group of females access to empty shells, it was possible to calculate optimal shell size and the deficit in shell size for field-collected animals.

Females that were berried were in shells closer to the optimal shell size than females with mature ovaries, both for shell weight and shell volume. And females with mature ovaries were in shells that were closer to the optimal size than females that were non-reproductive. For both categories of females without eggs on the pleopods, the majority of females were in shells that were too big (in weight and internal volume). While the percentage of berried females did not differ between dextral (*Busycon carica*) and sinistral (*Busycon sinistrum*) shells, the non-reproductive females had a much smaller deficit in volume in sinistral shells compared to dextral shells. For berried females, there was no relationship between the magnitude of their shell deficit and the number of eggs carried. Our results suggest that reproduction is inhibited when females occupy shells sufficiently greater than the optimal shell size.

Keywords: *Clibanarius vittatus*; Hermit crab; Reproduction; Shell coil orientation; Shell volume; Shell weight

1. Introduction

The availability of resources influences the reproductive status of female animals in a variety of species. Food availability can determine both whether females reproduce in a given season (Scott and Fore,

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1995; Gill and Rissman, 1997) and the number of offspring produced (Balashov, 1972; Carlotti and Hirche, 1997). In other species, nesting sites can be a limiting resource that determines reproductive status (Pöysä and Pöysä, 2002; Kokko et al., 2004). In the case of hermit crabs, a critical resource for all individuals is a gastropod shell of the appropriate size.

Having a shell of the appropriate size for a given size of hermit crab influences a wide array of ecological parameters in hermit crabs (Hazlett, 1981; Rittschof et al., 1995). Having the wrong-shaped shell for male hermit crabs can negatively affect the chances of males obtaining copulation (Hazlett, 1989a; Hazlett and Baron, 1989). Field surveys indicated that when individuals of *Clibanarius tricolor* were under stronger interspecific competitive pressures for shells, female egg production suffered (Bach et al., 1976). Childress (1972) found a reduced clutch size in *C. albidigitus* if females were in shells that were either too small or too large and this pattern was suggested for *C. tricolor* (Fotheringham, 1980). Bertness (1981) reported that non-berried females in three species in Panamanian hermit crabs occupied heavier shells than berried females. Occupying a shell that is too heavy results in using more energy as measured by either oxygen consumption (Herreid and Full, 1986) or by higher blood lactate levels (Briffa and Elwood, pers. comm.).

Clibanarius vittatus is a common intertidal species that occurs from Brazil to North Carolina. The patterns of reproductive behavior of this species have been described and the existence of a female sex pheromone demonstrated (Hazlett, 1996a). When exposed to cues indicating elevated predation risk, female *C. vittatus* cease reproductive activities temporarily while males continue to engage in precopulatory behavior (Hazlett and Rittschof, 2000). While observing reproductive behavior in the course of a separate study it appeared that females in shells that were especially large for the crab occupying that shell were not courted as frequently as females in better fitting shells. This appeared to be the case particularly for occupation of shells in the genus *Busycon* that were heavily encrusted with epibionts such as oysters, crepidula, and barnacles. These epibionts added weight, reduced internal volume when growing in the shell aperture, and often extended the linear dimensions of the original shell.

Another important factor potentially affecting reproduction of hermit crabs occupying *Busycon* shells is the coil orientation of the shell, dextral compared to sinistral. The vast majority of gastropod shells have a dextral coil orientation and the asymmetric abdomen of hermit crabs fits best in dextral shells (Agassiz, 1875). Approximately 60% of the *Busycon* shells occupied by larger *C. vittatus* in the study area are sinistral.

In this study we addressed the question of how shell characteristics affected reproduction in *C. vittatus*. Epibionts were much more common on shells in the genus *Busycon*, thus we restricted our study to crabs in those shells. In particular, we examined whether the number of eggs a given size female extrudes and whether a female extrudes any eggs at all are influenced by (1) shell coil orientation and/or (2) shell size (weight and volume).

2. Materials and methods

This study was conducted at the Duke University Marine Laboratory in Beaufort NC in early June, 2004, which is near the end of the mating season at this latitude (Hazlett, 1996a). Individuals of *C. vittatus* occupying *Busycon* shells were collected in the intertidal around Pivers and Carrot Islands, near the Duke Marine Laboratory. A total of 70 female *C. vitattus* were used. Of these 48 were in *Busycon sinistrum* (=*contrarium*) (Porter and Houser, 1994) (sinistral coil) and 22 were in *Busycon carica* (dextral coil). Females were removed from their field-occupied shells by drilling a hole in the apex of the shell and inducing them to come out of their shells using tactile stimulation from a flexible plastic rod. Female cephalothorax length was measured with calipers and reproductive status was recorded. Females were categorized as (a) berried (eggs on the pleopods), (b) mature ovaries (eggs were visible inside the abdomen but none on the pleopods), or (c) non-reproductive (ovary not visible and no eggs on the pleopods). In the case of berried females, the eggs were removed and preserved for later counts.

The number of eggs on each berried female was estimated by removing a sub-sample (approximately 20% of the total), blotting dry, and weighing the subsample. The rest of the egg mass was also blotted dry and weighed. The eggs in the sub-sample were