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Size and sex bias in air-exposure behavior during low tide of the intertidal hermit crab *Clibanarius virescens* (Krauss, 1843) (Decapoda: Anomura: Diogenidae)

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ABSTRACT

Many species of the hermit crab *Clibanarius* (Diogenidae) live on rocky shores of tropical and warm temperate regions. Some of these species are known to climb out from tidal pools onto rock surfaces exposed to air during low tide. The ecological significance of this behavior, however, remains unclear. We investigated the differences between air-exposed and non-air-exposed *Clibanarius virescens* (Krauss, 1843) in relation to their body size, sex, and infestation by three species of parasitic bopyrid isopods. Our generalized additive model (GAM) analyses showed a significant effect of the “smoothing factor” of the interaction between body size and sex for the occurrences of the “air-exposure behavior.” The presence of the ectoparasitic isopods did not affect the air-exposure behavior. Females of *C. virescens* showed a more distinct trend than in males, whereas air-exposure in both sexes had a peak in approximately 3.0–4.0 mm shield size (comparatively larger size in females, and middle-size in males) and decreased after this size range. Intraspecific and/or interspecific competition for shells may be intense in hermit crabs of this size range because of size overlap, and the individuals that carry suitable shells may avoid such competition by actively escaping from tide pools at low tide.

Key Words: bopyrid isopods, intertidal rocky shore, posing behavior, generalized additive model

Hermit crabs that live on rocky shores are usually found in tidal pools during low tide to avoid heat and desiccation. Some species of diogenid hermit crabs are nevertheless known to actively climb out from these pools onto rocky surfaces, becoming exposed to air during low tide. This behavior has been reported in *Calcinus laevimanus* (Randall, 1840) and several species of *Clibanarius* Dana, 1852, including *C. corallines* (H. Milne Edwards, 1848), *C. erythropus* (Hilgendorf, 1879), *C. taeniatus* (H. Milne Edwards, 1848), *C. virescens*, and *C. vittatus* (Bosc, 1802) (Reese, 1969; Rittschof *et al.*, 1995; Dunbar, 2001; Pérez-Miguel *et al.*, 2015). When exhibiting this behavior, hermit crabs adopt a specific posture, in which the shell aperture points upward (Supplementary material video S1) (Reese, 1969; Dunbar, 2001; Pérez-Miguel *et al.*, 2015). This behavior has been mentioned by many researchers using different terminologies (e.g., “air-exposure behavior,” “posing behavior,” or “sunbathing behavior”) (Reese, 1969; Dunbar, 2001; Pérez-Miguel *et al.*, 2015). We have opted to use “air-exposure behavior” as it best describes the behavior.

Dunbar (2001) compared the shell usage pattern of *C. taeniatus* and *C. virescens* between air-exposed and non-air-exposed individuals in Keppel Bay, Queensland, Australia, and

found differences, with the shell of three gastropods, *Planaxis sulcatus* (Born, 1778), *Clypeomorus petrosa* (W. Wood, 1828), and *Cronia* sp., were more frequently used by air-exposed hermit crabs than the others. Dunbar (2001), however, did not focus on the size and sex of air-exposed and non-air-exposed individuals despite the significant effects of both attributes on the shell-use patterns of *C. virescens* (Imazu & Asakura, 1994). Such observations, then, may suggest that the occurrence of the air-exposed-behavior is biased in particular size classes or a particular sex of hermit crabs.

Bopyrid isopods often cause serious damage to host hermit crabs, including external modification and reduced growth and reproductive ability (McDermott, 2002; McDermott *et al.*, 2010). *Clibanarius virescens* is infested by bopyrid isopods, including *Asymmetrione asymmetrica* (Shiino, 1933) parasitic in the host's left branchial chamber, *Eremitione clibanaricola* (Shiino, 1933) in the right branchial chamber, or *Pseudostegias setoensis* Shiino, 1933 on the abdomen (Shiino, 1933; Saito, 2002). Air-exposure in *C. virescens* could reduce infestation by these parasites. Dunbar (2001) investigated the effect of the air-exposure behavior on the infestation by *P. setoensis* in *C. taeniatus* and *C. virescens*, but found no

significant differences in infestation between air-exposed and non-air-exposed crabs.

We investigated differences between air-exposed and non-air-exposed *C. virescens* in terms of their size, sex, and infestation by parasitic isopods in an effort to understand the biological significance of this behavior in the hermit crab.

Individuals of *C. virescens* were collected by hand on rocky shores along the coast of Banshyo Cape, Shirahama, Nishimuro, Wakayama, in warm temperate Japan (Supplementary material Fig. S2A). The quantitative sampling was conducted using a 50 × 50 cm quadrat at the lowest tidal time on 10–12 April 2019 and 6 and 18 July 2019, which reflected non-reproductive and reproductive season, respectively, of *C. virescens* in temperate Japan (Imazu & Asakura, 1994). The quadrats used to collect non-air-exposed individuals were placed on the bottom of tidal pools at 1 m intervals along the maximum diameter of the pools. The quadrats used to collect air-exposed individuals were placed the same interval on the rock surface just above the water edge of the tidal pool (see Supplementary material Fig. S2B–D). Additional data of each sampling site (e.g., weather, water/air temperature, location, and size of the tidal pool) is provided in Supplementary material Table S3. The length of the carapace shield of crabs was used as an index of body size and was measured using calipers (minimum range 0.01 mm) (Supplementary material Table S4); the sex and the presence of parasitic isopods were also recorded.

To determine the factors that could be associated with the air-exposure behavior, the generalized additive modeling (GAM) (Hastie & Tibshirani, 1986) with a binomial error distribution was conducted on the samples of April (model 1) and July (model 2), respectively. The response variable was binary data regarding the presence/absence of air-exposure behavior (non-air-exposed = 0, air-exposed = 1), and each of the following five factors was incorporated as factorial explanatory variables: 1) the smoothing shield length, S(SL), 2) smoothing interaction of shield length and sex, S(SL x SEX) (SEX; female = 1, male = 2), and the presence/absence of each ectoparasitic isopod: 3) *A. asymmetrica*, 4) *E. clibanaricola*, and 5) *P. setoensis* (for each species, without parasite = 0, with parasite = 1). Although we collected ovigerous and no ovigerous females on July, there was no significant effect of brooding on the occurrence of air-exposed females during this month (models 3 and 4; Supplementary material Table S5).

We therefore pooled the data as “female” and then examined the effects of the five variables on the air-exposed females in July. In all four models, we did not consider any interaction between shield length (SL) and each parasite due to the absence of any significant effects ($P > 0.28$). GAM modeling was conducted using the mgcv function of R ver. 3.6.1 (R Development Core Team, 2019), and all statistical analyses were also performed on R ver. 3.6.1.

A total of 740 individuals of *C. virescens* were collected, including 256 air-exposed individuals (80 non-ovigerous females and 49 males on April; 42 non-ovigerous females, 45 ovigerous females, and 40 males on July) and 484 non-air-exposed individuals (94 non-ovigerous females and 49 males on April; 78 non-ovigerous females, 16 ovigerous females and 120 males on July) (Supplementary material Table S4).

In the GAM analysis, the factor S (SL x SEX) had a significant effect on both model 1 and 2 (Table 1). It suggests, regardless of the season body size is the predictable factor of air-exposure behavior but with a different trend between males and females. In both sexes, the frequency of the air-exposure behavior differed depending on the size ranges, with the peak in approximately 3.0–4.0 mm shield length, and then decreasing in the larger individuals (Fig. 1). Females, however, showed a well-defined peak compared with males in both April and July (Fig. 1). Because females are generally smaller than males (Imazu & Asakura, 1994), this size range represents a large size in females but medium size in males. Taken together, this behavior may, therefore, be more significant for females than in males in the same size range.

The infestations of the three isopods were very low in both months, 0–5.3 % in *A. asymmetrica*, 0–19.2 % in *E. clibanaricola*, and 0–3.3 % in *P. setoensis* (Supplementary material Table S6). The results of GAM analysis indicate that the presence of the three parasitic isopods is not associated with the occurrence of air-exposure behavior (Table 1). It is possible, however, that the low infestation of bopyrids might be not enough for this analysis.

Rittschof *et al.* (1995) suggested that the presence of *C. vittatus* on mud-sand and oyster reef substrates during low tide is an adaptation in the larger individuals in order to avoid shell competitions when they carried a suitable shell. Size-biased air exposure in *C. virescens* may also help avoid inter/intraspecific competitions for shell resource during low tide. We collected seven species of

Table 1. Results of a generalized additive model (GAM) with a binomial-error distribution. “S” indicates that the factor was treated as the smoothing factor in the model; SL, shield length. The possible effect of three bopyrid parasites was also investigated.

Factors	Approximate significance of smooth terms				Parametric coefficients			
	edf	Ref. df	Chi-square	P	Estimate	Standard error	z	P
Model 1								
Whether <i>Clibanarius virescens</i> engaged in “air-exposure behavior” or not (N = 399, April 2019)								
S(SL)	1.00	1.001	0.24	P = 0.62	–	–	–	–
S(SL x SEX)	7.95	10.92	41.70	P < 0.0001	–	–	–	–
<i>Asymmetrione asymmetrica</i>	–	–	–	–	–33.09	2.37E + 07	0	P = 1.00
<i>Eremitione clibanaricola</i>	–	–	–	–	–0.15	0.53	–0.29	P = 0.77
<i>Pseudostegias setoensis</i>	–	–	–	–	–0.45	1.00	–0.45	P = 0.65
Intercept	–	–	–	–	–0.81	0.13	–6.22	P < 0.0001
Model 2								
Whether <i>Clibanarius virescens</i> engaged in “air-exposure behavior” or not (N = 341, July 2019)								
S(SL)	1.83	2.16	4.44	P = 0.13	–	–	–	–
S(SL x SEX)	3.32	4.71	14.04	P < 0.05	–	–	–	–
<i>Asymmetrione asymmetrica</i>	–	–	–	–	–1.13	3.88E + 07	0	P = 1.00
<i>Eremitione clibanaricola</i>	–	–	–	–	–43.53	0.46	–1.48	P = 0.14
<i>Pseudostegias setoensis</i>	–	–	–	–	–0.54	1.17	–0.97	P = 0.33
Intercept	–	–	–	–	–0.68	0.14	–3.91	P < 0.0001

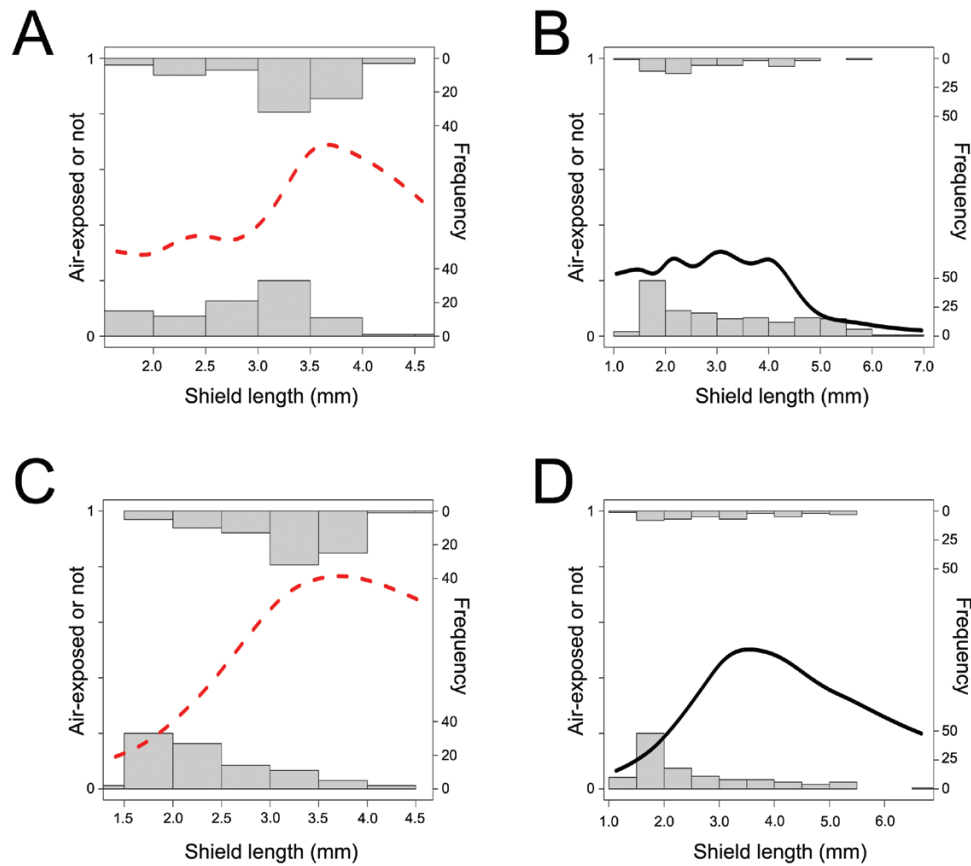


Figure 1. Frequencies of air-exposure behavior in relation to size (measured by the carapace-shield length) and sex. Females (**A**) and males (**B**) collected in April 2019; females (**C**) and males (**D**) collected in July 2019. The values were obtained using a generalized additive model (GAM) with a binomial error distribution. Histograms indicate the size distribution in air-exposed (upper) or non-air-exposed (lower) individuals. Values of 0 and 1 represent non-air-exposure or air-exposure, respectively.

other hermit crabs sympatric with *C. virescens* in tidal pools (*Pagurus decimbranchiae* Komai & Osawa, 2001; $N = 3$, mean \pm SD = 1.93 ± 0.53 mm shield length; *P. filholi* (De Man, 1887), $N = 175$, mean \pm SD = 2.13 ± 0.75 mm; *P. lanuginosus* De Haan, 1849, $N = 1$, 2.83 mm; *P. minutus* Hess, 1865, $N = 31$, mean \pm SD = 2.21 ± 0.44 mm; *Clibanarius* sp., $N = 1$, 1.3 mm; *Diogenes* sp., $N = 11$, mean \pm SD = 2.04 ± 0.35 mm; *Paguristes ortmanni* Miyake, 1978, $N = 1$, 2.96 mm). Given that interspecific as well as intraspecific shell fights are common (Hazlett, 1967; Turra & Denadai, 2004), such presence of multiple species in a tidal pool might act a potential threat over shells.

Air-exposure behavior, especially in females, could be involved in avoiding intersexual shell-competition, because females are often subordinate to males due to poorer competitive ability in several intertidal hermit crabs (Yoshino & Goshima, 2002; Briffa & Dallaway, 2007). In *P. filholi*, for example, a male attacker more easily succeeded in shell exchange with a female defender than with a male defender (Yoshino & Goshima, 2002). Given that the loser must expose its own abdomen during shell exchange, ovigerous females may show a higher avoidance of shell fights to protect eggs. Moreover, even if females are not ovigerous, air-exposed as avoidance of shell fights may be important to increase the reproductive success because egg productivity is affected by the species of shells and their quality (Elwood et al. 1995). The mature (i.e., relatively larger) females of *C. virescens*, therefore, may frequently engage in the air-exposure behavior regardless of the season, when they keep a preferable, or high-quality, shell from potential competitors.

Air exposure in *C. virescens* may not function in parasite avoidance, at least as shown herein. Although the life cycles of *A. asymmetrica*, *E. clibanaricola*, and *P. setoensis* have not yet been fully elucidated, the larvae of the bopyrid *Athelges paguri* (Rathke, 1843) settle on the cephalothoraxes of megalopae of hermit crabs, their definitive hosts (Pike, 1961; McDermott et al., 2010). The larvae of our three bopyrids may, therefore, also settle on the megalopae or juvenile/young *C. virescens*. If so, air exposure is not an appropriate tactic to avoid infection because air-exposed crabs (3.0–4.0 mm) are expected to be mature rather than immature, based on the size of ovigerous females (Supplementary material Table S4). While our study deals only with ectoparasites, various endoparasites are also known to infect hermit crabs, including fecampiid flatworms, trematodes, acanthocephalans, and rhizocephalan barnacles (McDermott et al., 2010).

We showed that there were size biases in 3.0–4.0 mm air-exposed individuals of *C. virescens* in both sexes, with a distinct trend in females than in males. The avoidance of shell competition is a probable factor involved in the selection of this behavior, although there are other hypothesis that might explain the selective advantage of the air-exposure behavior, such as the reduction of movement to use more energy for growth and the avoidance of shell fights (Rittschof et al., 1995), as well as shell care or cleaning (Pérez-Miguel et al., 2015). Further operational experiments with different conditions such as the varying density of conspecific and/or heterospecific hermit crabs, or a situation with/without of snail-shell epibioties, are needed to elucidate the ecological significance of this behavior.

SUPPLEMENTARY MATERIAL

Supplementary material available at *Journal of Crustacean Biology* online.

S1 Video. Air-exposure behavior in *Clibanarius virescens* (recorded on 30 September 2019).

S2 Figure. Sampling sites and sampling methods.

S3 Table. Environmental condition of tidal pools investigated and total number of *Clibanarius virescens* collected from each tidal pool.

S4 Table. Shield length in air-exposed and non-air-exposed individuals of *Clibanarius virescens*.

S5 Table. Results of the Wald test for the occurrence of air-exposure behavior in *Clibanarius virescens* using a generalized additive model (GAM).

S6 Table. Prevalence of parasitic bopyrid isopods on *Clibanarius virescens*.

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