SHELTER PREFERENCES IN THE ENDEMIC BERMUDIAN HERMIT CRAB, *CALCINUS VERRILLI* (RATHBUN, 1901) (DECAPODA, ANOMURA)\(^1\)

BY

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ABSTRACT

*Calcinus verrilli*, a hermit crab endemic to Bermuda, is unusual in that it inhabits both gastropod tubes (*Vermicularia* spp. and *Dendropoma* spp.) and gastropod shells (*Cerithium litteratum*). It was found in both shelter types, in five marine environments, categorized as intertidal areas, subtidal areas, “boilers”, patch reefs, and rim reefs. We found most males in shells and most females inhabiting tubes. We discovered a size dimorphism, females being larger than males. In the laboratory, when given a choice between shells and tubes, both males and females showed a significant preference for shells. In a Y-maze test of attraction to extracts from tube-forming versus shell-forming gastropods, males showed no discrimination, but females preferred the tube-associated extract. These shelter and size dimorphisms in *C. verrilli* are best explained by intrasexual competition and differences in the ecology of males and females.

RÉSUMÉ

*Calcinus verrilli*, un pagure endémique des Bermudes est particulier par son habitat inhabituel, vivant à la fois dans des tubes (*Vermicularia* spp. et *Dendropoma* spp.) et des coquilles de gastéropodes (*Cerithium litteratum*). Il a été trouvé dans deux types d’abris, dans cinq environnements marins, désignés comme zones intertidales, zones subtidales, “boilers”, plaques récifales et bordures récifales. Nous avons trouvé la plupart des mâles dans les coquilles et la plupart des femelles dans les tubes. Nous avons découvert un dimorphisme de taille, les femelles étant plus grandes que les mâles. Au laboratoire, lorsqu’un choix est offert entre coquilles et tubes, les mâles comme les femelles ont montré une préférence significative pour les coquilles. Dans un test d’attraction aux extraits soit de tubes, soit de coquillages, les mâles n’ont pas montré de différence, mais les femelles ont préféré les extraits associés aux tubes. Ces dimorphismes en matière d’abri et de taille sont le mieux expliqués par la compétition intrasexuelle et les différences dans l’écologie des mâles et des femelles.

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INTRODUCTION

The shell is essential to hermit crab individual fitness as it functions to provide mobility, protection from physical damage and predation, and can influence growth of the inhabitant (Fotheringham, 1976; Spight, 1977). Damaged or ill-fitting shells offer less protection, and can affect the feeding and mating behaviour of the hermits (Childress, 1972). Therefore, the shell is considered to be a limiting resource, which restricts the size of hermit crab populations (Vance, 1972).

In order to obtain an ideal shell, hermit crabs have evolved specialized behaviours that enable them to choose among available shells. These behaviours of hermit crabs have received attention from a number of workers, beginning with the now classic study by Hazlett (1966). Hermit crab shell choice is correlated with a variety of characters, including size, species, quality, and previous familiarity. Each of the shell parameters has been shown to be important for given species of hermit crabs (Reese, 1962; Conover, 1978; Blackstone, 1985; Wilber, 1990).

The majority of investigated species have been ones that utilize non-attached gastropod shells for shelter. However, there are several hermit crab species that use other cavities for protection (see Gherardi, 1996a for a review). These “alternative” shelters are often tubes cemented to the reef, so that the hermit crab cannot move about. Gherardi & Cassidy (1994, 1995) and Gherardi (1996a, b) conducted comprehensive studies of the life history of one such species, Discorsopagurus schmitti (Stevens, 1925). Other studies of “unconventional” hermits have focused on observations of pair formation (Patton & Robertson, 1980) and filter feeding (Markham, 1977; Schuhmacher, 1977; Caine, 1980). However, shell selection per se has not been studied in these species.

Calcinus verrilli (Rathbun, 1901), a species endemic to Bermuda, is unusual in that it occupies vermetid (Markham, 1977) and turritellid tubes, as well as non-attached gastropod shells. The tubes are attached to a variety of different reef substrates, while the gastropod shells allow for mobility. This has interesting implications for shelter selection as shelter choices will dictate feeding modes and reproductive behaviours.

The present study reports on the distribution of C. verrilli throughout Bermuda, and also investigates the shelter preference of C. verrilli in both the field and the laboratory. Our goals were: (1) to determine if there is a preference in the field for inhabiting shells versus tubes, (2) to determine the relationship between hermit crab size and shelter size occupied by hermits in the field, and (3) to determine preferences for shells versus tubes under laboratory conditions.
MATERIALS AND METHODS

This work was carried out in Bermuda from May to September 1999 at the Bermuda Biological Station for Research (BBSR). Since the last comprehensive survey of *Calcinus verrilli* was conducted over 20 years ago, the study began by examining potential new sites and reassessing sites where *C. verrilli* had previously been found (Provenzano, 1960; Markham, 1977). In all, 20 sites were visited and comprehensively searched. Locations were distributed from the east end (Sandys Parish) to the west end (St. George’s Parish) of Bermuda and included intertidal areas, subtidal areas, “boilers”, inshore patch reefs, and offshore rim reefs. Intertidal sites are those where numerous tide pools (depths of < 20 cm) form in depressions at low tide. During high tides, the entire area is submerged under 0.5-1 m of water. Subtidal areas do not usually exceed more than 2 m in depth and are not exposed during low tides. “Boilers,” which have the appearance of miniatolls (diameter of 1-2 m), have a partially exposed surface at low tides (Morris et al., 1997). They are constructed primarily of calcareous red algae, tubes of vermetid gastropods, and *Millepora* sp. (fire coral, hydrozoans). Patch reefs are inshore reefs that can be found anywhere within the shallow lagoons of the Bermuda platform. They do not exceed depths of 3-4 m. The rim reefs are found at the raised edge of the Bermuda platform and extend inwards towards the lagoon, exceeding depths of 9-10 m.

Fourteen of the 20 sites were selected as collecting areas. Depending on the location, wading in tide pools, snorkeling, or SCUBA was required to collect animals. Animals found in tubes were collected with a chisel and hammer; those housed in shells were collected by hand. Individuals were isolated from each other in partitioned plastic containers while in the field and in the laboratory, to ensure that shell exchanges did not occur.

All shelter dimensions were measured to the nearest 0.05 mm using vernier calipers. Shells were measured for length, width, and aperture length and width (Kellogg, 1976), while tubes were measured for opening diameter. All crabs were removed from their shelters in a similar manner: the tip of the shell or the base of the tube was broken with Vice Grip brand pliers, and monofilament fishing line inserted to gently urge the animal out. Shield length (Markham, 1968), measured to the nearest 0.01 mm, and sex were determined with a light microscope and ocular micrometer.

A multiple regression was used to determine the correlation of the four shell measurements, and each was linearly regressed against shield length. The shell dimension of length was chosen for regressions against crab shield length, as it resulted in the highest correlation. Tube diameter was regressed against crab shield length. All animals were given back their original shelters and returned to their
collecting site. For all regressions, data for males and females were calculated separately.

Naive animals were used in preference experiments. Prior to preference experiments, naked crabs (without shelters) were isolated for 24 hours in plastic cylindrical containers (diameter = 10 cm; height = 8 cm) with seawater, sand substrate, and compressed air. Only healthy, intact animals were used in preference experiments.

Visual Preference Experiment

The plastic isolation containers (as described above) were covered with a fiberglass mesh lid and 26 were submerged in a large glass aquarium supplied with a constant flow through of unfiltered seawater from Ferry Reach near the BBSR, and maintained on the local light/dark cycle. Empty turritellid tubes, *Vermicularia knorrii* (Deshayes, 1843) and *Vermicularia spirata* (Philippi, 1836), and gastropod shells, *Cerithium litteratum* (Born, 1778), were obtained by collecting live individuals and sacrificing them with injections of sodium hydroxide so as not to damage the shells. These were washed and rinsed daily for 3-4 weeks prior to being used in the experiment.

In 3 repetitions of the experiment, a total of 60 naked crabs (males: 19; females: 41) were given both a tube and shell, the sizes of which were determined from the equation of the respective regression line. The tube and shell were placed next to each other on the substrate at the centre of the container. Once a shelter type was selected, the individual’s shelter occupancy was recorded every hour for the next 4-6 hours. Each crab was tested once and then returned to its collection site.

Chemical Preference Experiment

A Y-maze was constructed using clear Plexiglas with two arms at a right angle to each other (length = 15 cm each) and with a base (length = 19.5 cm). The width of all the corridors was 6 cm and the depth was 10 cm. The sand substrate was 1 cm deep and covered the bottom of the entire Y-maze. Inflow of non-filtered seawater into both arms was at a constant velocity and outflow was from the stem. An open-topped removable fiberglass mesh cage (5 × 6 × 10 cm) was placed between the stem and two arms to prevent the crab from entering an arm when first introduced.

The snail chemical extracts were prepared with a method similar to that of Orihuela et al. (1992). Removal of the soft parts (whole animal excluding the foot and operculum) of *Cerithium litteratum* and *Vermicularia* spp. from their respective shells was conducted using Vice Grip brand pliers and forceps. These were placed into separate glass vials and frozen. The next day, the frozen tissue was ground, and weighed with an electronic balance to the nearest 0.1 g. Unfiltered seawater was added in a ratio of 1 ml for each 0.1 g of snail tissue. The extract was
removed and kept on ice throughout the day of the experiment. Each day a fresh sample of extract was prepared.

A naked crab that had been isolated for 24 hours was placed into the open-topped mesh cage of the Y-maze. Then, 0.05 ml of each gastropod extract was simultaneously introduced to the far end of a different arm using a pipette. *Cerithium* and *Vermicularia* extract presentation arms were alternated between trials to eliminate any possible directional bias. Thirty seconds after extract introduction, the mesh cage was lifted and the following data recorded: (1) reached end of left arm and extract type, (2) reached end of right arm and extract type, (3) remained in base, (4) remained in the middle of an arm or no movement after 5 minutes. The test was performed on a total of 28 crabs (males: 11; females: 17).

Following each trial, the Y-maze was washed thoroughly with fresh sea water and the substrate was redistributed. Each animal was given the shelter it was originally collected in and returned to its collection site.

Statistical analysis

χ² tests were calculated by hand using a table from Sokal & Rohlf (1987). Regression analyses and Mann-Whitney rank tests were calculated using Sigma Stat software version 2.0 by Jandel. Significant *P*-values were those < 0.05.

RESULTS

Field observations

Field surveys confirmed the observations of Markham (1977) that *Calcinus verrilli* occupies the vermetid tubes of both *Dendropoma corrodens* (D’Orbigny, 1842) and *Dendropoma irregulare* (D’Orbigny, 1842) (most recent conserved names for *Spirogyphus annulatus* and *Spirogyphus irregularis*, respectively (Turgeon et al., 1998)). We also found *C. verrilli* commonly using two turritelid species, *Vermicularia spirata* and *Vermicularia knorrii*, neither of which have previously been reported as hermit shelters. The non-attached gastropod shell species used was almost exclusively *Cerithium litteratum*.

This hermit species was found to inhabit each of the five different reef environments surveyed (table I). Animals in shells primarily inhabited patch and rim reefs, although a small number were found in a subtidal area. Those in *Dendropoma* spp. tubes were found in intertidal areas, the “boilers”, and all rim reefs. The two *Dendropoma* spp. are small (diameter opening: 1.9-4.3 mm), prostrate and tightly coiled. They are embedded into the substrate, so that their openings are flush with the surface of the reef. *Vermicularia* spp. tubes were found in subtidal areas and patch reefs. They are slightly larger than *Dendropoma* spp. (diameter opening: 4.0-7.8 mm), more erect and loosely coiled.
Table I

Locations visited from May to September 1999 and the areas and shelter types occupied by Calcinus verrilli (Rathbun, 1901)

<table>
<thead>
<tr>
<th>Location</th>
<th>Area</th>
<th>Shells?</th>
<th>Tubes?</th>
<th>Method</th>
<th>Collection site?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rocky Bay</td>
<td>I</td>
<td>no</td>
<td>D</td>
<td>wade</td>
<td>yes</td>
</tr>
<tr>
<td>Spittal Pond</td>
<td>I</td>
<td>no</td>
<td>D</td>
<td>wade</td>
<td>yes</td>
</tr>
<tr>
<td>Achilles Bay</td>
<td>S</td>
<td>no</td>
<td>V</td>
<td>snorkel</td>
<td>no</td>
</tr>
<tr>
<td>Bailey’s Bay</td>
<td>S</td>
<td>no</td>
<td>V, D</td>
<td>snorkel</td>
<td>yes</td>
</tr>
<tr>
<td>Fort St. Catherine Beach</td>
<td>S</td>
<td>no</td>
<td>V</td>
<td>snorkel</td>
<td>no</td>
</tr>
<tr>
<td>Gibbets Island</td>
<td>S</td>
<td>C</td>
<td>V</td>
<td>snorkel</td>
<td>yes</td>
</tr>
<tr>
<td>Shelly Bay</td>
<td>S</td>
<td>no</td>
<td>V, D</td>
<td>snorkel</td>
<td>no</td>
</tr>
<tr>
<td>Whalebone Bay</td>
<td>S</td>
<td>no</td>
<td>V</td>
<td>snorkel</td>
<td>no</td>
</tr>
<tr>
<td>Elbow Beach Boiler</td>
<td>B</td>
<td>no</td>
<td>D</td>
<td>snorkel</td>
<td>no</td>
</tr>
<tr>
<td>Church Bay</td>
<td>B, R</td>
<td>C</td>
<td>D</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>Caricomp Seagrass North</td>
<td>P</td>
<td>C</td>
<td>no</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>Crescent Reef 1</td>
<td>P</td>
<td>C</td>
<td>no</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>Crescent Reef 2</td>
<td>P</td>
<td>C</td>
<td>V</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>Tynes Bay East</td>
<td>P</td>
<td>no</td>
<td>V</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>Tynes Bay West</td>
<td>P</td>
<td>no</td>
<td>V</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>Wreck Hill Reef</td>
<td>P</td>
<td>C</td>
<td>no</td>
<td>snorkel</td>
<td>yes</td>
</tr>
<tr>
<td>Grounding Site</td>
<td>R</td>
<td>C</td>
<td>D</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>Hog Reef</td>
<td>R</td>
<td>C</td>
<td>D</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
<tr>
<td>John Smith’s Bay</td>
<td>R</td>
<td>C</td>
<td>D</td>
<td>SCUBA</td>
<td>no</td>
</tr>
<tr>
<td>Twin Reef</td>
<td>R</td>
<td>C</td>
<td>D</td>
<td>SCUBA</td>
<td>yes</td>
</tr>
</tbody>
</table>

Key. — I, intertidal; S, subtidal; B, boiler reef; P, patch reef; R, rim reef; C, Cerithium sp.; D, Dendropoma spp.; V, Vermicularia spp.

Females were found to be significantly larger than males ($P = 0.002$). For both males and females, individuals in shells were significantly larger than those in tubes (males: $P < 0.001$; females: $P = 0.023$). Significantly more males were collected in shells than in tubes ($N = 163$, $\chi^2 = 36.37$, $P \ll 0.001$), while more females were collected in tubes than shells ($N = 227$, $\chi^2 = 60.30$, $P \ll 0.001$).

Regression analyses

Multiple linear regressions showed that the four shell measurements were all highly correlated with one another for both males and females (males: $r = 0.928$, $N = 122$, $P < 0.001$; females: $r = 0.958$, $N = 34$, $P < 0.001$). Significant positive correlations were found between all C. litteratum shell measurements and hermit size for males and females (table II, fig. 1). Positive correlations were also found between tube diameter and hermit size for both Dendropoma spp. and Vermicularia spp. tubes, in both males and females (table II, figs. 2, 3).
Choice Experiments

The sex-related pattern in shelter type in the field was not observed in the visual preference experiment, as both males and females chose shells significantly more than tubes (males: $N = 19$, $\chi^2 = 4.26$, $P < 0.05$; females: $N = 41$, $\chi^2 = 5.49$, ...
Fig. 2. The relationship between hermit crab size (shield length, SL) and *Vermicularia* spp. opening diameter inhabited by males (A) and females (B) of *Calcinus verrilli* (Rathbun, 1901) in the field.
Fig. 3. The relationship between hermit crab size (shield length, SL) and *Dendropoma* spp. opening diameter inhabited by males (A) and females (B) of *Calcinus verrilli* (Rathbun, 1901) in the field.

\[ \text{Diameter} = (0.678 \times \text{SL}) + 1.683 \]

\[ \text{Diameter} = (0.666 \times \text{SL}) + 1.573 \]

\[ P < 0.025 \]. None of the individuals changed their choice in the 4-6 hours following their initial selection. In the chemical preference experiments, which tested distant chemical stimuli, males showed no significant preference for either
TABLE II
Correlation coefficients obtained from linear regressions with hermit crab shield lengths for each category and shell or tube measurement

<table>
<thead>
<tr>
<th>Categories</th>
<th>Measurement</th>
<th>r</th>
<th>df</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males in <em>Cerithium</em> sp.</td>
<td>length*</td>
<td>0.913</td>
<td>121</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>width</td>
<td>0.847</td>
<td>121</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>aperture length</td>
<td>0.799</td>
<td>121</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>aperture width</td>
<td>0.814</td>
<td>121</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Females in <em>Cerithium</em> sp.</td>
<td>length*</td>
<td>0.877</td>
<td>33</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>width</td>
<td>0.797</td>
<td>33</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>aperture length</td>
<td>0.689</td>
<td>33</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>aperture width</td>
<td>0.759</td>
<td>33</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Males in <em>Vermicularia</em> spp.</td>
<td>diameter*</td>
<td>0.844</td>
<td>6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Females in <em>Vermicularia</em> spp.</td>
<td>diameter*</td>
<td>0.644</td>
<td>108</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Males in <em>Dendropoma</em> spp.</td>
<td>diameter*</td>
<td>0.357</td>
<td>40</td>
<td>0.004</td>
</tr>
<tr>
<td>Females in <em>Dendropoma</em> spp.</td>
<td>diameter*</td>
<td>0.430</td>
<td>76</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

r = coefficient of correlation; df = degrees of freedom; * = measurements used to predict shell and tube sizes in choice experiments.

chemical stimulant \((N = 11, \chi^2 = 0.09, P < 0.90)\), while females showed a significant attraction to *Vermicularia* tube extract \((N = 17, \chi^2 = 4.76, P < 0.05)\).

Individuals collected in shells also selected shells in the visual experiment significantly more than tubes \((N = 32, \chi^2 = 7.26, P < 0.01)\). However, those collected in tubes showed no significant discrimination \((N = 29, \chi^2 = 2.79, P < 0.10)\). In the chemical preference experiment there were no significant differences relative to previous shelter type.

DISCUSSION

Hermit crab distribution

The variation in distribution of *Calcinus verrilli* across five different reef environments is best explained by the distribution of the gastropod populations that house them and by other, sympatric species of hermit crabs. *Cerithium litteratum* is considered a subtidal species (Sterrer, 1986), although it is also found in large numbers on the patch and outer reefs. In Bermuda, this shell is heavily utilized by the sympatric hermit crab *Clibanarius tricolor* (Gibbes, 1850) in the subtidal zones, which may outcompete *C. verrilli* for shells, since they are rarely used in those areas by *C. verrilli* (table I). The gastropod’s range extends to deeper waters and it is on the reefs, in the absence of *C. tricolor*, that *C. verrilli* is able to occupy that shell. *Dendropoma* spp. face the open ocean, probably because of the
constant exchange of water bringing food, so they are found in relatively turbulent environments (Sterrer, 1986). The more delicate structure of Vermicularia spp. requires that they inhabit shallow, quiet, undisturbed areas. The use of these two tube-dwellers permits C. verrilli to also inhabit these environments.

Regression analyses

Coefficients of correlation (r) may be taken as indices of shell suitability, because hermit crabs given free choice over time, tend to select shells of a certain size relative to their body size (Markham, 1968). The difference in hermit size correlation between tubes and shells may be because selection pressure for individuals to have a snug-fitting sessile tube may be somewhat less than for a snug-fitting shell, which must be carried. However, individuals in fixed tubes are also less mobile, and consequently have fewer opportunities for finding an ideal sized tube, which would also result in a lower correlation value.

Choice experiments

Although males and females significantly selected shells over tubes in the visual choice experiment, it was not clear whether individuals made a true choice. In many cases, one or the other of the shelters had not been obviously disturbed, so it may be that the individual never investigated both shelter types. None of the study animals ever changed the shelter they initially selected, which suggests that they may not have made a true choice, as other species will usually “try on” several available shells before making a final decision (Hazlett, 1966). Therefore, the experiment using distant chemical stimuli was conducted. In that experiment, we could be certain that each individual was exposed to both stimuli. Female preference, in this case, matched preference observed in the field.

Dimorphism in resource utilization

Several workers have reported a sexual dimorphism in terms of resource utilization among different species of hermit crabs (Blackstone & Joslyn, 1984; Asakura, 1995; Elwood & Kennedy, 1998). In each of these cases males and females preferred shells of different species, or restricted themselves to different size categories of the same shell species. Calcinus verrilli may be the only case thus far of a hermit crab exhibiting sexual dimorphism in resource choice in which one sex prefers loose gastropod shells and the other attached gastropod tubes.

Asakura (1995) suggested a possible hypothesis to explain an observed difference in resource utilization. It relies upon males of the hermit species being significantly larger than their female conspecifics. Larger males, therefore, tend to be better competitors than females, resulting in their ability to acquire greater numbers of available shells and greater numbers of the more preferred shells. This does
not appear to be the case with *C. verrilli* as females are significantly larger than males. The inverse of the same hypothesis, namely that females are out-competing males, is probably not occurring either, since males do not select the type of housing females predominantly use in the field, when given a choice.

A second hypothesis suggests that the housing difference is due to sexual selection (Abrams, 1987). Among solely mobile gastropod-dwelling hermit crabs, successful males must usually be larger than the females they mate with, as reproductive behaviour involves dragging and carrying the female as well as mate guarding (Hazlett, 1966). In *C. verrilli*, the females are functionally sessile and therefore those behaviours cannot be involved in mating. Males do not need to attain a large size for access to females, while females can increase their reproductive output by growing, because they produce more eggs at a larger size (Hazlett, 1981).

Sex related differences in ecological preference do not usually explain the distribution of traditional gastropod dwellers (Abrams, 1987), but in the case of *C. verrilli*, it is very likely. The environments that *C. verrilli* inhabit are extremely diverse, ranging from intertidal areas to offshore reefs. Each sex may have specific adaptations to the different environments. For example, male *C. verrilli* have fewer and stronger spines on the armature of the chelipeds than similarly sized females (Campos & Lemaitre, 1994). Although we do not yet know the function of these, this and other as yet undiscovered dimorphisms may be related to sexual differences in shelter choice and habitat.

Therefore, the hypotheses that best explain the shelter resource dimorphism in *C. verrilli* are: (1) intrasexual selection, which may partially explain the size dimorphism observed, and (2) the drastic differences in ecology, which could confer some advantages which are yet to be discovered.

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