Vacancy Chains Provide Aggregate Benefits To *Coenobita clypeatus* Hermit Crabs

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Abstract

Vacancy chain theory describes a unique mechanism for the sequential distribution of animal resources across multiple individuals. This theory applies to any resources, such as shelters or nest sites, that are discrete, reusable, and limited in use to single individuals or groups at one time. Hermit crabs rely on gastropod shells for shelter, and a single vacant shell can initiate a chain of sequential shell switches that distributes new resources across many individuals. Using the terrestrial hermit crab *Coenobita clypeatus*, we examined the previously untested theoretical prediction that this process will yield trickle-down resource benefits to vacancy chain participants (aggregate benefits). In laboratory experiments, we measured improvements in shell quality when a single vacant shell was provided to groups of eight crabs. We found that crabs participating in vacancy chains (averaging 3.2 individuals) gained significant reductions in their shell crowding. In addition, vacancy chains terminated early when experimental groups included a single crab occupying a damaged shell, because damaged vacancies always remained unoccupied. Hermit crabs in damaged shells were more likely to win resource contests for high quality shells against size-matched hermit crabs in crowded shells. Finally, field additions of many new shells to an island population of *C. clypeatus* hermit crabs reduced average shell crowding for crabs of all sizes, possibly from propagation of benefits through vacancy chains. These results provide empirical support for the theoretical prediction that vacancy chains should provide benefits distributed across many vacancy chain participants. Since shelter-based vacancy chains likely occur in other animals, additional studies of vacancy chain processes should provide new insights into resource acquisition behaviors in diverse animal groups.

Introduction

Many different animals rely on resources that are discrete, reusable and limited in their use to a single individual/group at a time; some examples include hermit crabs sheltering in gastropod shells, anemone-dwelling clownfish and cavity-nesting birds. Vacancy chain theory was developed in social science research to describe how vacancies involving discrete, reusable resources such as apartments or jobs will propagate in human populations (White 1970; Chase 1991; Friman 2004). When a single individual acquires a new resource, the vacancy created by this move then cascades through the system in a series of inter-related events. Vacancy chain processes and associated behaviors are thus likely to be important mechanisms influencing shelter-based resource distribution in diverse animal groups.

Experimental studies of animal vacancy chains have thus far been restricted to hermit crabs (Chase & DeWitt 1988; Chase et al. 1988; Chase 1991; Weissburg et al. 1991; Osorno et al. 1998). Both marine and terrestrial hermit crabs rely on gastropod shells for shelters that provide protection from predation (Bertness 1981a,b; Kuhlmann 1992; Angel 2000) and desiccation (Taylor 1981; Brodie 1999). These shells represent discrete, reusable resources and hermit crabs require new shells as they grow (reviewed by Hazlett 1981; Reese 1962). In hermit crab vacancy chains, a single vacant shell triggers a chain of sequential shell vacancies that can distribute new resources across many individuals. A fundamentally important yet untested prediction of vacancy chain theory is that this process should provide benefits to many individuals through the acquisition of new physical resources or social positions (termed aggregate benefits, Chase 1991). Hermit crabs provide an ideal model system for testing this prediction.

Shell assessment and shell-fighting behaviors have been particularly well-studied in marine hermit crabs (reviewed by Hazlett 1981; Elwood & Neil 1992; Hazlett & Rittschof 1997; Elwood & Briffa 2001). When single hermit crabs are allowed to interact with one or more empty shells, they assess several aspects of shell quality, including damage (physical integrity of the gastropod shell), crowding (how well a shell fits a particular hermit crab), shell weight, and shell internal volume (e.g. Scully 1979; Elwood & Stewart 1985; McClintock 1985; Herreid & Full 1986; Wilber 1990; Pechenik & Lewis 2000; Rotjan et al. 2004; Gherardi 2006). Hermit crabs avoid damaged shells because these lead to increased mortality via predation and desiccation (Vance 1972; Bertness 1981a,b; Bertness & Cunningham 1981; Pechenik et al. 2001). High shell crowding (when crabs are unable to fully retract into their shells) similarly increases crabs' susceptibility to predators, and is associated with reduced growth and reproduction (Fotheringham 1976; Angel 2000).

Hermit crab agonistic and shell fight behavior have been characterized based primarily on an experimental paradigm that examines interactions between pairs of hermit crabs with or without a vacant shell (but see Gherardi 2006). In this context, several factors have been identified that determine the likelihood that hermit crabs will initiate, escalate and win contests for better shells; these factors include relative fighting ability (body size or physiological condition) and relative shell quality (Hazlett 1978, 1981; Dowds & Elwood 1983; Hazlett 1996;

Briffa & Elwood 2002; Gherardi 2006, Elwood et al. 2006; Tricarico & Gherardi 2006, 2007; Tricarico et al. 2008). However, much less is known concerning shell acquisition behaviors employed by hermit crabs within the social context of larger groups. Large aggregations have been described in several species, including the mangrove hermit crab, *Clibanarius laevimanus* (Gherardi & Vannini 1993; Gherardi et al. 1994). Many marine and terrestrial hermit crabs are attracted to odors from dead gastropods or conspecifics (McLean 1974; Rittschof 1980; Rittschof et al. 1992; Small & Thacker 1994; Thacker 1994; Tricarico & Gherardi 2006). Although vacancy chains have been previously described within these aggregations, the central prediction that this process yields aggregate benefits to vacancy chain participants has not yet been examined.

In this study, we used the terrestrial hermit crab *C. clypeatus* to experimentally test whether the addition of a single new resource will result in shell quality improvements that are distributed across many individuals. First, we created vacancy chains in the laboratory and examined potential benefits by measuring changes in shell fit for vacancy chain participants. In these experiments, we also examined how shell damage, an ecologically relevant dimension of resource quality for hermit crabs, affected vacancy propagation in order to test the prediction that the terminal vacancy will represent the least desirable resource. We also determined which aspect of shell quality (damage vs. crowding) better predicted who wins when identically sized hermit crabs competed for high-quality shell resources. Finally, to determine whether laboratory results might generalize to field populations, we conducted a field experiment in which we added new shell resources to an island hermit crab population and measured changes in *C. clypeatus* shell fit and damage over time.

Materials and Methods

Study Site

This work was conducted in February and August 2006 at Carrie Bow Cay (16º48′N and 88º05′W), a 0.77-acre island located on the Belizean barrier reef. This island houses the Smithsonian Caribbean Coral Reef Ecosystems field station and a large population of tropical land hermit crabs, *C. clypeatus*. Natural food sources for *C. clypeatus* at this site include palm flowers (Palmaceae) and drift seeds; hermit crabs commonly feed on sea coconut endocarp (*Manicaria saccaifera*). At this site, *C. clypeatus* inhabit shells from

diverse gastropod species, the most common of which are: *Cittarium pica, Nerita versicolor, N. peloronta, N. tesselata, Cerithiopsis greeni, Batillaria minima, Natica canrena* and *Polinices lacteus*. Some hermit crabs were also found in alternative housing, including calcified marine polychaete tubes and metal and plastic debris, suggesting limited availability of suitable shells for this *C. clypeatus* population.

Measuring Shell Quality

For laboratory and field studies, we assessed the quality of hermit crab occupied shells along two dimensions of resource quality: shell damage and shell crowding. Although some marine hermit crabs show preferences for shells of particular gastropod species (reviewed by Elwood & Neil 1992), field observations suggest that numerous species may be suitable for these terrestrial hermit crabs. We visually assessed shell damage as a categorical variable that was based on the presence of aperture damage, apex damage, and/or erosion of the shell. Shells were categorized as intact (no damage), low, medium or high damage (shells showing one, two, or three different types of damage, respectively).

Many different quantitative measures (e.g. Abrams 1978; Taylor 1981; McClintock 1985) and qualitative measures (e.g. Elwood & Stewart 1985; Angel 2000; Rotjan et al. 2004; Gherardi 2006; Tricarico & Gherardi 2006) of shell crowding/shell adequacy have been employed in previous studies. Here, we used a non-invasive and reproducible assessment of shell crowding for each hermit crab by counting the number of exposed appendages. Once crabs were fully retracted into their shells (accomplished by repeatedly tapping the major cheliped), shell crowding was measured by counting the total number of exposed appendages, which included: individual segments of each cheliped excluding the major chela, which is used to block the shell aperture (total of five possible segments), individual segments of the second and third pereopods (total of 20 possible segments, five for each of four legs), plus the abdomen, eyes, and antennules. In our sample of *C. clypeatus* crabs, this shell crowding measure ranged from 0 appendages exposed (major chela effectively blocked the shell aperture) to 19 appendages exposed (including exposure of some pereopod segments, eyes, antennules and abdomen exposure through shell hole). This quantitative method of measuring shell crowding is based on the ecologically relevant degree to which a hermit crab's body parts are exposed to potential predators and competitors, and in this respect parallels several qualitative measures previously developed (Abrams 1978; Taylor 1981). Other shell adequacy measures based on shell or aperture lengths (e.g. Vance 1972; Rittschof et al. 1992; Pechenik & Lewis 2000; Rotjan et al. 2004; Gherardi 2006) are not appropriate when crabs naturally inhabit shells of so many different gastropod species.

Laboratory Study: Aggregate Benefits from Vacancy Chains

We experimentally examined vacancy chain propagation and the potential for aggregate benefits in laboratory trials with *C. clypeatus* hermit crabs. Vacancy chains are typically studied by introducing a new vacancy (in this case, an unoccupied shell) into a system, then following this vacancy as it moves through the system until the chain terminates (Chase & DeWitt 1988; Chase et al. 1988; Chase 1991; Friman 2004). To create these initial vacancies, we used shells of a novel gastropod species (commercially available *Turbo marmoratus* shells; Cyber Island Shops, Kissimmee, FL, USA) to avoid potential bias due to crabs' previous experiences with the vacant shell type. These trials also allowed us to estimate the chain multiplier effect (Chase et al. 1988), which is the total number of individuals getting new resources when a single new resource is added to a group.

For these trials, we collected crabs from the field and placed them in groups of eight crabs in five gallon (30 cm diameter) plastic containers under natural light conditions with a layer of sand, food *ad libitum* and fresh water. Within each group, we chose crabs of increasing size to give a gradient of cheliped widths ranging from 5.5 to 15.8 mm (cheliped width is linearly related to body weight in *C. clypeatus*; Morrison & Spiller 2006). This was done to facilitate vacancy chain formation, because vacancy chains in other hermit crabs have been shown to move from larger to smaller crabs (Chase & DeWitt 1988; Chase et al. 1988). We assessed shell quality by scoring initial shell crowding for each crab (as described above), and then we individually marked each crab's major cheliped and shell with a silver Sharpie® marker (Sanford Corp., Oak Brook IL, USA). Once groups were established, we added one new *T. marmoratus* shell that was appropriately sized for the largest crab (preliminary trials were conducted to ensure that the largest crab would initiate the chain by moving into the vacant shell), and then left crabs undisturbed for 24 h. In control groups of eight size-sorted hermit crabs lacking a

vacant shell, no shell switches occurred over 24 h; similarly, no switches were observed when experimental crabs were held in groups prior to each shell addition.

We conducted six trials in which all crabs started in intact shells (involving 48 crabs, as each crab was used only once). In addition, we conducted another set of five trials to examine how shell damage might affect the propagation of vacancy chains, and to test the prediction that damaged shells, which may be the least desirable resource, would become the terminal vacancy in the chain. In the damaged-shell trials, a crab occupying a highly damaged shell was included in the middle of the size range (either position 3 or 4) for each group of eight crabs (total of 40 crabs, again each crab used only once). These hermit crabs were collected in shells with major aperture damage, apex damage, and/or holes that exposed the crab's abdomen or cephalothorax.

At the end of each trial, we determined how many crabs had switched into new shells, and measured the change in shell crowding for each of these crabs. Within damaged and intact treatments, we pooled data across all trials because we were interested in testing the aggregate benefit accruing to all vacancy chain participants. We used paired t-tests to examine the null hypothesis that there was no overall change in shell crowding measured before and after trials for each vacancy chain participant.

Resource Competition between Hermit Crabs in Crowded vs. Damaged Shells

In our laboratory vacancy chain experiments, we observed that *C. clypeatus* hermit crabs with either damaged shells or high shell crowding more often participated in vacancy chains compared to other crabs. Therefore, we conducted an experiment designed to examine whether hermit crabs in damaged shells would outcompete size-matched crowded hermit crabs when they competed for a new, high-quality shell that we provided. We size-matched hermit crabs by cheliped width and set up pairs (n = 13 pairs) consisting of one uncrowded crab occupying a highly damaged shell and one crowded crab occupying an intact shell (shell crowding score >10). Hermit crabs and shells were individually marked and placed in 22 × 23-cm plastic containers with a layer of sand, fresh water and hermit crab food (typically cooked rice) *ad libitum*. Once pairs were established, we added one high-quality, novel shell (commercial *Turbo brunneus*) appropriately sized for each pair. After 24 h during which crabs were left undisturbed,

we recorded which crab had acquired the new shell, and which shell remained unoccupied; the latter was considered to be the least desirable resource. We used an exact binomial test to examine whether *C. clypeatus* hermit crabs with high shell crowding vs. damaged shells were equally likely to win the high-quality shell.

Field Study: Changes in Resource Quality after Shell Addition

To see if our laboratory vacancy chain results translated into changes in resource quality at the population level, we measured *C. clypeatus* shell damage and crowding before and following the addition of new shell resources to the population. In February 2006, we measured shell quality for a sample of 348 *C. clypeatus* collected at dusk, when these nocturnal hermit crabs become active. We also measured crab size based on the maximum width of the major cheliped, and categorized crabs as either small (<10 mm), medium (10–19.9 mm) or large (>20 mm). In other terrestrial hermit crabs, larger individuals show greater shell limitation (Abrams 1978). To examine whether use of damaged shells differed across *C. clypeatus* size categories, we used 3 × 4 contingency table analysis to examine the association between crab size (small, medium or large) and shell damage (four levels as described above).

We also conducted a mark-recapture study to estimate *C. clypeatus* population size and frequency of shell switching in February 2006. On a single night, we collected crabs (n = 154) of various sizes, marked their shells and chelipeds with the same number, and released them. Crabs (n = 324) were collected again after 48 h, and we estimated the total population size of *C. clypeatus* on the island based on the percentage of marked crabs that we recaptured. The hermit crab population on this island appeared well-mixed, as marked crabs released in a central location were subsequently recaptured at island edges. We also used these recaptured crabs to determine the frequency of shell-switching, detected if we found numbered crabs that did not match their shell number.

After establishing these initial patterns of shell resource use by *C. clypeatus*, we experimentally added new, undamaged shell resources at several different strata (sizes) to test the hypothesis that these additional resources would generate vacancy chains whose propagation would eventually lead to improved shell quality for many *C. clypeatus* hermit crabs. For these resource additions, we again used

commercially available shells that we verified were suitable for *C. clypeatus* in preliminary experiments. We attempted to match the observed crab size distribution by adding at a single central location new shells as follows: five shells (*C. pica*) suitably sized for large hermit crabs, 20 shells (*T. marmoratus* and *T. brunneus*) suitable for medium-sized crabs and 100 shells (*Turbo argyrostomus*) suitable for small crabs.

In August 2006, 6 mo after these experimental shell additions, we again collected *C. clypeatus* hermit crabs (n = 265) to assess whether shell resource quality had changed. We originally intended to measure changes in shell quality (shell crowding and damage) for individual hermit crabs that had been previously marked. Unfortunately, by 6 mo all crabs' marks had become illegible or disappeared, although shell marks were still clearly visible. Therefore, we measured shell quality for a new sample of *C. clypeatus* taken from the same population. We relied on comparing randomly sampled crabs taken from the same population before and after shell additions because no suitable spatial control was possible, but these results could potentially also be influenced by non-experimental changes in shell availability. Mean shell crowding was compared for small, medium and large crabs between February and August 2006 using two-way ANOVA with Bonferroni multiple comparisons. Differences in the proportions of hermit crabs in each size class using damaged vs. intact shells were examined using 2×2 contingency tables with likelihood ratio (G) tests of homogeneity of proportions.

Results

Laboratory Study: Aggregate Benefits from Vacancy Chains

When a single new shell resource was added at the top of the size gradient for experimental groups of hermit crabs (all starting in intact shells), vacancy chains occurred in all trials. These vacancy chains involved an average of 3.2 crabs (this crab multiplier effect ranged from 2 to 5 crabs) that moved into different shells. Among these hermit crabs that participated in vacancy chains, the majority (17 of 19 crabs, or 89%) gained significant reductions in shell crowding (Fig. 1a, mean difference = −5.5 ± 1.0 exposed appendages, paired t = −5.52, df = 18, p < 0.0001).

In damage treatments with groups that included a single hermit crab in a damaged shell, the average crab multiplier effect was 2.8 crabs (range 1–4
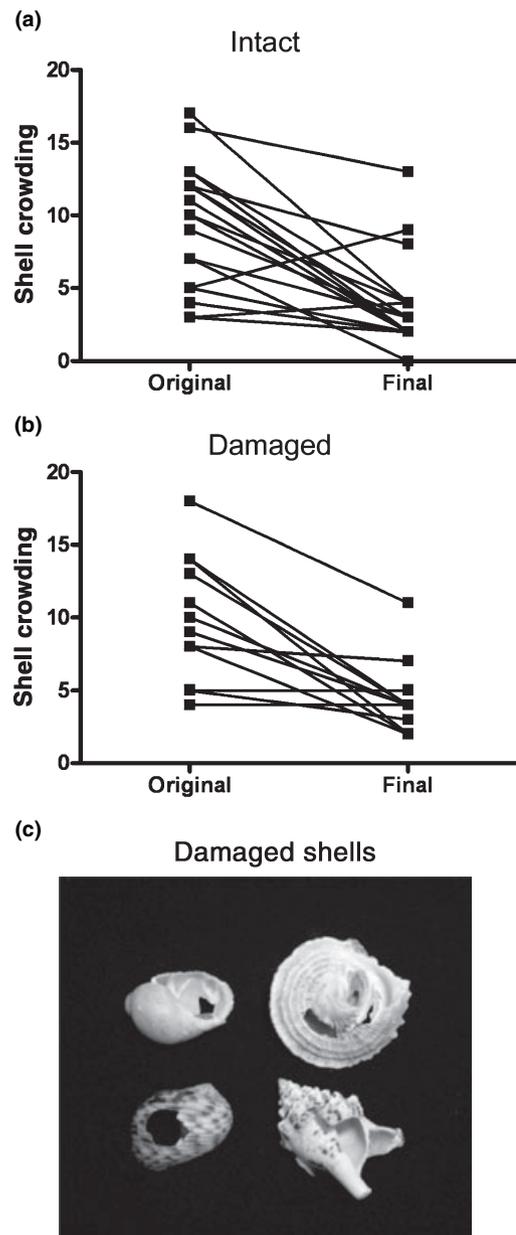
(a)

Intact

(b)

Damaged

(c)

Damaged shells

Fig. 1: Experimental vacancy chains in *Coenobita clypeatus* hermit crabs: (a) Changes in shell crowding for individual vacancy chain participants in the Intact treatment, in which all hermit crabs started in intact shells (lines represent changes in shell crowding for 19 vacancy chain participants), (b) Changes in shell crowding for individual vacancy chain participants in the Damaged treatment, in which one mid-sized crab started in a damaged shell (lines represent changes in shell crowding for 14 vacancy chain participants), and (c) Damaged gastropod shells formerly occupied by *C. clypeatus* hermit crabs that terminated experimental vacancy chains once they were abandoned.

crabs). Again, crabs that participated in vacancy chains gained significant reductions in their shell crowding (Fig. 1b, mean difference = −5.1 ± 1.1

exposed appendages, paired t = −4.78, df = 13, p = 0.0004). In four out of five trials, once the damaged shell was vacated, the vacancy chain was terminated (Fig. 1c).

Resource Competition between Hermit Crabs in Crowded vs. Damaged Shells

When size-matched pairs of *C. clypeatus* hermit crabs in either highly damaged or highly crowded shells were allowed to compete for a vacant, high-quality shell resource, hermit crabs with damaged shells won in 10 out of 13 trials. This outcome occurred significantly more often than would be expected by chance if both crabs were equally likely to acquire the new shell (exact binomial test: p = 0.0349). In all of these trials, the damaged shell remained unoccupied once it was vacated, indicating that it was less desirable to the remaining hermit crab than its own highly crowded shell. In the three remaining trials, the crab that was initially crowded won the new shell; in one case a protracted shell fight lasting approx. 48 h ensued in which the losing hermit crab (occupying a highly damaged shell) attacked and attempted to forcibly evict the winner from the new shell. Thus, *C. clypeatus* hermit crabs in damaged shells were more likely to win than highly crowded crabs when matched in resource competition for high-quality shells.

Field Study: Changes in Resource Quality after Shell Addition

Coenobita clypeatus hermit crabs that were surveyed in February 2006 (total of 348 crabs) often occupied damaged gastropod shells, with shell use patterns differing across crab sizes (Table 1). A higher percentage of medium-sized crabs were found in damaged shells compared to either small or large crabs (February only in Table 1; 3×4 contingency table test of homogeneity of proportions: G = 22.513, df = 6, p = 0.001). As reported in other locations throughout the Caribbean, large *C. clypeatus* crabs at this site were most commonly found in *C. pica* (West Indian top) shells, which are thick-walled (reviewed by Robertson 2003) and appear resistant to breakage. Shell crowding measured in February 2006 also differed significantly across crab sizes [Fig. 2; ANOVA: $F_{(2,244)} = 101.09$, p < 0.0001], with medium and large crabs showing greater shell crowding relative to small ones.

Based on mark-recapture results, the population of *C. clypeatus* hermit crabs present on Carrie Bow

Table 1: Relative frequencies of *Coenobita clypeatus* hermit crabs (small, medium and large) occupying gastropod shells in different damage categories (see text for size and damage category descriptions) at two time points: before (February 2006) and 6 mo after (August 2006) new shell resources were added to the population

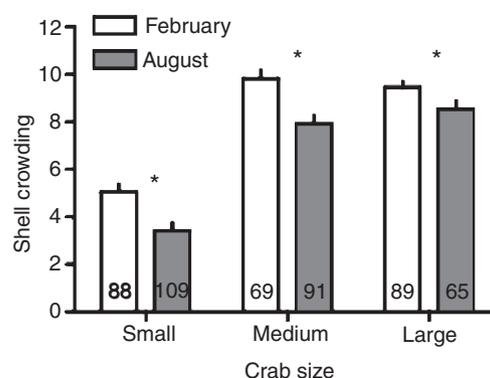| | % Intact | % Damaged shells | | | |
		Low	Medium	High	n
Small hermit crabs					
February	52.6	33.3	7.9	6.1	114
August	54.1	29.4	11.0	5.5	109
Medium hermit crabs					
February	34.8	40.0	19.1	6.1	115
August	39.6	37.4	8.8	14.3	91
Large hermit crabs					
February	54.8	29.6	11.3	4.3	115
August	43.1	38.5	12.3	6.1	65

Fig. 2: Shell crowding (mean ± 1 SE) based on number of exposed appendages for *C. clypeatus* hermit crabs before (February 2006) and 6 mo after (August 2006) new shell resources were added to the population. Hermit crabs sampled on a single night were later grouped into three size classes (sample sizes within bars). Asterisks indicate significant differences between timepoints by Bonferroni-adjusted multiple comparisons.

Cay was estimated as approximately 1084 crabs, or 0.35 crabs/m². Forty-nine marked crabs were recaptured after 48 h, and all of these crabs had cheliped numbers that matched their shells, indicating that no shell switches had occurred. Within 24 h after addition of 125 new shells to the resource base, we observed *C. clypeatus* queuing up in decreasing size order and exchanging shells in a vacancy chain process (illustrated in Fig. 3).

In August 2006, 6 mo after shell additions, *C. clypeatus* shell crowding (Fig. 2) and damage (Table 1) was resurveyed at the same location. Overall, shell crowding in this population was reduced following shell addition (two-way ANOVA, Table 2).

Fig. 3: An aggregation of the terrestrial hermit crab *C. clypeatus* queuing up prior to switching shells in a vacancy chain.

Table 2: Statistical results from a two-way ANOVA examining differences in shell crowding among three size classes of *Coenobita clypeatus* hermit crabs before and after the addition of new shell resources to the population

Source	SS	df	F-value	p-value
Time (month)	273.79	1	26.34	<0.0001
Crab size (S, M, L)	2633.48	2	126.66	<0.0001
Time × size	20.01	2	0.9622	0.3827
Error	5249.88	505		

S, small; M, medium; L, large.

Reductions in shell crowding were evident within each hermit crab size class (Fig. 2; Bonferroni-adjusted comparisons, all $p < 0.036$). However, there were no significant differences in the proportion of hermit crabs occupying intact shells between time points (Table 1: 2×2 tests of homogeneity for small crabs, $G = 0.05$, df = 1, $p = 0.8228$; for medium crabs, $G = 0.4973$, df = 1, $p = 0.4807$; for large crabs, $G = 2.2817$, df = 1, $p = 0.1309$).

Discussion

This study makes several substantive contributions to our understanding of vacancy chains, a process controlling the distribution of many different material resources and social positions that are discrete, reusable and restricted to a single user at a time (Chase 1991). For humans, such resources include jobs, houses, and cars (White 1970; Haveman & Cohen 1994; Friman 2004). In animals, vacancy chains based on shelters or territories may be quite common; some likely examples include snapping shrimp associated with sea anemones, blennies inhabiting rock holes, and red-cockaded woodpeckers utilizing nest cavities built in long-leaf pines by (Chase & DeWitt 1988; Walters 1990). Although vacancy chain concepts might therefore be broadly applicable to many animal resources, such processes have been studied only in humans and hermit crabs. Experimental studies of shell vacancy chains have previously been conducted only within single tide-pools for marine hermit crabs (Chase & DeWitt 1988; Chase et al. 1988; Chase 1991; Weissburg et al. 1991), although the occurrence of vacancy chains has been reported in many other marine (McLean 1974; Rittschof 1980; Rittschof et al. 1992) and terrestrial (Small & Thacker 1994; Osorno et al. 1998) hermit crabs.

To our knowledge, this is the first study to empirically test and verify a central prediction of vacancy chain theory (Chase & DeWitt 1988; Chase 1991), which is that aggregate benefits should accrue to multiple individuals following the addition of a single new resource unit. In laboratory vacancy chains, nearly all *C. clypeatus* hermit crabs that participated in experimental vacancy chains benefited by significantly reducing their shell crowding (an average of approximately five fewer appendage segments exposed). In hermit crabs, reduced shell crowding is likely to translate directly into fitness benefits. Marine hermit crabs that are unable to fully retract into their shells are more susceptible to both predation and desiccation (Taylor 1981; Angel 2000), and have lower growth rates and reproductive output (Fotheringham 1976; Angel 2000). In addition, our laboratory results suggest that the population-wide reduction in shell crowding that we observed for *C. clypeatus* hermit crabs 6 mo after the addition of new shells may have been due to propagation of benefits through multiple vacancy chains. However,

it is also possible that such differences were caused by seasonal patterns of juvenile recruitment or shell availability, and controlled field studies involving replicate island populations would be required to confirm that changes were due to experimental shell additions.

In addition, this work provides the first characterization of vacancy chains in terrestrial hermit crabs under controlled conditions. Our results agree with previous observations that vacancy chains progress from higher to lower social and economic rankings (Chase et al. 1988), as in hermit crabs they progress from larger to smaller crabs (Chase & DeWitt 1988). In laboratory experiments, we found that an average of 3.2 crabs switched shells in vacancy chains initiated by addition of a single vacant shell. This hermit crab multiplier effect is consistent with previous estimates of multiplier effects between 2 and 3 in vacancy chains involving jobs and houses in humans, and of 2.5 for vacancy chains in marine hermit crabs (Chase & DeWitt 1988; Chase et al. 1988).

Damaged gastropods shells were found to terminate the propagation of vacancy chains in laboratory experiments. Shell damage is ecologically relevant, as our field surveys showed that many *C. clypeatus* hermit crabs in all size classes occupied damaged shells. Previous studies have shown that marine hermit crabs avoid occupying damaged shells (Wilber 1990; Pechenik & Lewis 2000; Rotjan et al. 2004), and shell damage increases crabs' mortality risk from predation and desiccation (Vance 1972; Bertness 1981a,b; Bertness & Cunningham 1981). Our demonstration that damaged shells disrupt vacancy chains suggests such damage may have far-reaching effects on the dynamics of resource distribution that extend beyond the behavioral avoidance shown by individual crabs. In resource contests for a vacant high-quality shell, size-matched *C. clypeatus* hermit crabs in damaged shells were significantly more likely to win than highly crowded crabs. Although behaviors were not quantified during these shell contests, these results imply that shell damage provides strong motivation in fights for a new, higher-quality shell. These results are consistent with previous work showing that hermit crabs avoid damaged shells, even if they must compromise on shell fit (Wilber 1990; Pechenik & Lewis 2000), and that hermit crabs inhabiting damaged shells have high motivation to switch (Scully 1979; McClintock 1985). Previous experiments found that shell crowding increases aggressive behavior during shell fights (Gherardi 2006; Tricarico & Gherardi

2007), and our results suggest that hermit crabs in damaged shells are even more aggressive. Thus, during vacancy chain interactions hermit crabs in damaged shells may be capable of gaining better positions when they interact with similarly sized opponents.

Finally, this work implies that future behavioral studies of resource acquisition by hermit crabs need to take social context into account. Although hermit crab shell assessment and shell competition have been well-studied (reviewed by Hazlett 1981; Elwood & Neil 1992; Elwood & Briffa 2001), most of this work has been limited to experimental paradigms involving single individuals or pairs (but see Gherardi 2006; Tricarico & Gherardi 2006). In contrast, little is known about shell assessment and decision-making behaviors that generate the size-sorted queues that often precede shell exchange in hermit crab vacancy chains (Fig. 3). The importance of vacancy chains as a process for shell acquisition by hermit crabs suggests that it will be worthwhile to carefully examine behavioral dynamics within the context of larger social groups.

In conclusion, vacancy chain theory has the potential to provide new insights into resource acquisition behaviors and patterns of resource distribution in a wide range of organisms. Studies of vacancy chain processes in additional groups should provide a fascinating area for future research.

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