Social context of shell acquisition in Coenobita clypeatus hermit crabs

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Vacancy chains involve unique patterns of resource acquisition behaviors that determine how reusable resources are distributed through animal populations. Shell vacancy chains have been described for several hermit crab species, both terrestrial and marine, but little is known about the ecological and behavioral dynamics of shell choice in social versus solitary contexts. Here, we present a novel conceptual framework that differentiates 2 types of shell vacancy chain in hermit crabs and discuss fundamentally distinct predictions concerning the behavioral and ecological costs and benefits associated with synchronous versus asynchronous vacancy chains. In laboratory studies of the terrestrial hermit crab Coenobita clypeatus, we found support for the prediction that social context alters shell acquisition behaviors. Field observations demonstrated that both synchronous and asynchronous vacancy chains are common and revealed previously undescribed waiting and piggybacking behaviors that appear to facilitate synchronous vacancy chains. Additionally, simulation results from an agent-based model showed that population density and waiting behaviors can both influence the likelihood of synchronous vacancy chains. Together, these results indicate that better understanding of hermit crab resource acquisition requires studying social behaviors, including vacancy chain formation. Key words: agent-based modeling, NETLOGO, resource acquisition, shell crowding, shell fit, shelter-based vacancy chain, social behavior, vacancy chains. [Behav Ecol 21:639–646 (2010)]

Vacancy chain theory was originally developed in social science research to describe how vacancies involving discrete, reusable, and limited resources such as apartments or jobs propagate through human populations (White 1970; Chase 1991; Friman 2004). When a single individual gets a new resource, the vacancy thus created can propagate down the socioeconomic order through a series of interdependent events, with the result that many individuals can benefit through the acquisition of new physical resources or social positions. Similar shelter-based vacancy chains are likely to take place in many animal groups that use discrete, reusable resources that are limited to occupancy by a single individual or group at a time; some examples include shell-inhabiting hermit crabs, anemone-dwelling clownfish, and cavity-nesting birds.

Hermit crabs provide an ideal model system for testing predictions of vacancy chain theory as they require gastropod shells for shelter and must regularly obtain new shells as they grow (reviewed by Briffa and Mowles 2008). In hermit crab vacancy chains, a single vacant shell triggers a sequential chain of crabs switching into newly vacated shells (Chase 1991; Weissburg et al. 1991). Such vacancy chains have been documented in both terrestrial (Small and Thacker 1994; Osorno et al. 1998; Lewis and Rotjan 2009) and marine hermit crabs (McLean 1974; Rittschof 1980; Chase and DeWitt 1988; Chase et al. 1988; Rittschof et al. 1992). In addition, a recent study of the terrestrial hermit crab Coenobita clypeatus verified a key theoretical prediction that such vacancy chains provide aggregate benefits that are distributed across many vacancy chain participants (Lewis and Rotjan 2009). However, little is known concerning the behavioral mechanisms that lead to shell va-

cancy chains in hermit crabs, and the ecological factors influencing vacancy chain formation remain poorly understood.

To better understand animal vacancy chains, here we provide a conceptual framework that distinguishes 2 categories of hermit crab vacancy chain, synchronous and asynchronous, which differ in their behavioral and ecological costs and benefits (Table 1). These 2 types of vacancy chains are both social and stand in direct contrast to solitary shell interactions involving a single crab and a single shell. Most research on shell-switching behavior to date has occurred in a solitary context, but examining shell behavior in a social context is critical to understanding hermit crab behavior in the wild. Synchronous vacancy chains occur after several crabs adjacent to an available vacant shell have queued in decreasing size order; as soon as the largest crab switches into the vacant shell, a rapid series of sequential shell switches takes place. In asynchronous vacancy chains, in contrast, individual crabs encountering a suitable vacant shell will switch and later their discarded shells will be discovered and occupied by other crabs. Thus, asynchronous vacancy chains do not involve social interactions or queue formation, and sequential shell switches take place over considerably longer time periods. In both cases, vacancy chains are terminated when the last shell discarded is of such low quality (too small or damaged) that all crabs reject it.

Synchronous and asynchronous vacancy chains are predicted to have fundamentally different behavioral and ecological benefits and costs (Table 1). Because participants in asynchronous vacancy chains experience low rates of interference competition, they are predicted to benefit from unlimited opportunity to investigate any vacant shells they might encounter and should also be able to directly compare their original with new shell quality by switching back and forth. Asynchronous vacancy chains are predicted to carry a cost because individual crabs should have a low probability of finding a vacant shell that meets their specific size and quality

Table 1

A conceptual model detailing the benefits and costs of solitary versus social shell acquisition. Benefits of one are necessarily costs to another, representing a zero sum game. Illustrations by M. Flynn
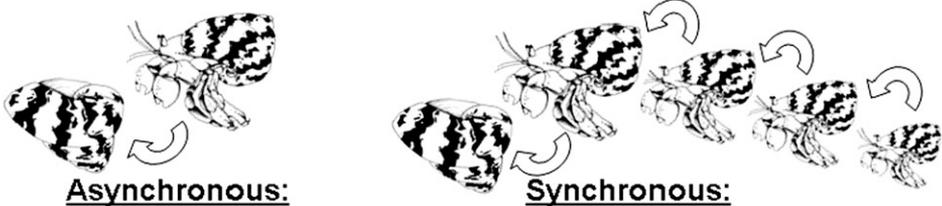
Asynchronous:	Synchronous:
- Low potential for finding an optimal shell (only two shells available)	-Greater potential for finding an optimal shell (more shells available)
- Easily reversible shell switching (no risk of shell stranding)	- Greater potential to get stranded in a sub-optimal shell (shell reversals more difficult)
-No risk of injury from conspecific agonistic encounters	- Conspecific competition requires time and energy; creates risk of injury
-Decreased vulnerability to predators (low profile)	- Increased vulnerability to predators (large crab aggregations)

requirements. In contrast, participants in synchronous vacancy chains should benefit from the wide size range of shells that become available as the vacancy propagates through the chain. Predicted costs of synchronous vacancy chains include a higher risk of injury due to agonistic interactions with conspecifics and a greater predation risk associated with large aggregations. Thus, these 2 distinct types of vacancy chain are predicted to generate very different patterns of resource use and assessment behavior. In addition, within any hermit crab population, the frequency with which new shells are acquired through these distinct processes is likely to depend on several factors, including crab population density, the spatial distribution of shell resources, and predation risk.

In this study, we investigated several aspects of vacancy chain behavior in the terrestrial hermit crab *C. clypeatus*. First, we conducted laboratory experiments to test the prediction that a group social context alters shell investigation behavior and resource acquisition by hermit crabs compared with solitary situations. Second, we monitored the frequency of synchronous and asynchronous vacancy chains in a field population after the addition of vacant shells and described some novel behaviors that precede synchronous vacancy chains. Finally, using an agent-based simulation model we investigated how population density and hermit crab behavior (wait time) both affect the relative frequency of synchronous and asynchronous vacancy chains.

MATERIALS AND METHODS

Study site

This work was conducted in March 2008 at Carrie Bow Cay (lat 16 48#N and long 88 05#W), a 0.77-acre island located on the Belizean barrier reef. This island houses the Smithsonian Caribbean Coral Reef Ecosystems field station, and *C. clypeatus* occurs here at an estimated population density of 0.35 m^{22} (Lewis and Rotjan 2009).

Shell investigation and acquisition behaviors

Shell investigation and acquisition behaviors by solitary hermit crabs have been particularly well studied (reviewed by Hazlett 1981; Elwood and Neil 1992). Solitary hermit crabs "investigate" vacant shells by examining the shell exterior using their antennae, chelipeds, and walking legs and by inserting their chelipeds into the shell aperture. "Shell switching" takes place when the crab holds the new shell with the aperture facing upward and releasing its abdominal grip on the old shell, rapidly swings its abdomen over to occupy the new shell. Solitary crabs often retain hold of their original shell and "reversals" occur when a crab moves back and forth between shells before finally choosing one.

Hermit crab agonistic behavior has previously been described based mainly on interactions between 2 crabs; detailed descriptions exist for several marine species (e.g., Dowds and Elwood 1983; Briffa and Elwood 2000a, 2000b, 2002, 2007; Tricarico and Gherardi 2006), as well as for the terrestrial hermit crab *C. clypeatus* (Hazlett 1966). However, very few studies have examined shell acquisition within the context of larger social groups (Gherardi 2006). Previous descriptions of hermit crab vacancy chains have noted "queuing" behavior (Rittschof et al. 1992 called these "scrums"), which we define as the formation of one or more size-ordered, linear arrays of hermit crabs in which the largest crab in each line is grasping an empty shell, and each successively smaller crab grasps from behind the shell of the preceding crab. We define a similar behavior, "piggybacking," whereby 2 or more crabs line up (not necessarily in order by size) by grasping the shell of another crab from behind. Piggybacking does not involve a vacant shell, and the lead crab often continues walking with the attached crabs trailing behind it.

Shell acquisition behaviors by solitary hermit crabs versus groups

In laboratory experiments, we compared shell acquisition behaviors of solitary hermit crabs with those shown by groups of crabs. To measure shell assessment and choice by solitary

crabs (n ¼ 14), we placed single randomly assigned crabs (cheliped widths ranging from 0.9 to 1.15 cm) housed in their original shells in a 700-cm^2 container with sand. Each crab was given 5 intact vacant shells Turbo marmoratus to investigate (Cyber Island Shops, Kissimmee, FL). We used shells of a novel gastropod species to avoid possible confounding effects of different shell types. To measure shell acquisition behaviors by crabs in groups, in each container we placed 5 crabs chosen to differ by approximately 0.2 cm in cheliped width (cheliped widths ranged from to 0.4 to 1.8 cm); based on previous studies, we knew this procedure would facilitate vacancy chain formation (Lewis and Rotjan 2009). A single vacant T. marmoratus shell that was appropriately sized for the largest crab (determined in preliminary experiments) was added to each group (n ¼ 15 trials). The following behaviors were recorded continuously for 30 min in both solitary and group treatments: number and duration of shell investigations, number of shell switches and reversals, latency between shell investigation and shell switch, and the number of piggybacks observed. In group trials, we also scored whether synchronous or asynchronous vacancy chains occurred.

We compared shell investigation and acquisition behaviors shown by solitary hermit crabs versus crabs in groups using separate variances t-tests as data met the normality assumption; for each group trial, the number of shell investigations, switches, and reversals were divided by 5 to yield frequencies of behaviors per crab. Shell investigation durations and latencies from the beginning of an investigation to shell switching were calculated for each investigation and were pooled across trials to examine solitary versus group differences. Within group trials, we also compared behaviors between crabs that participated in synchronous vacancy chains and those that participated in asynchronous vacancy chains using separate variances t-tests. All statistical analyses were conducted using SYSTAT 11 (Chicago, IL, USA).

Vacancy chain dynamics in the field

To investigate the proportion of synchronous versus asynchronous vacancy chains that might occur in natural populations of nocturnally active C. clypeatus, we marked 20 locations dispersed around the island. At each station, we set out a single vacant shell at dusk; these consisted of 11 large T. sparverius shells (aperture length 6–7.5 cm) and 9 medium T. stenogyrus shells (aperture length 3–4.5 cm). We monitored these stations periodically for 24 h, and at each observation, we recorded the number of hermit crabs within 50 cm of the vacant shell. Periodic observations likely underestimated the frequencies of these behaviors but were chosen in order to simultaneously assess 20 stations. We also noted the following behaviors: shell investigation, number of queues (and number of participants), number of piggybacks, whether any shell switches had occurred (evident by the original vacant shell being replaced with a discarded shell), and whether a synchronous vacancy chain occurred. Over the 24-h period, multiple vacancy chains of different types could occur at each station.

Simulation model: effects of population density and waiting behavior on vacancy chain dynamics

Population density is likely to be a key factor affecting vacancy chain dynamics, and C. clypeatus population densities are known to vary 1000-fold across different islands (Morrison and Spiller 2006). Also, our field observations revealed a novel crab behavior that involves waiting near vacant, too large shells (see RESULTS below), and this behavior also has the potential to affect vacancy chains. To investigate how population density and waiting behavior affect the relative frequency of asynchronous and synchronous vacancy chains, we used an agent-based model implemented in NetLogo version 4.0.2

(http://ccl.northwestern.edu/netlogo/). Agent-based stochastic models are designed to examine emergent behaviors (here, vacancy chains) given a few simple agent properties (e.g., size and speed) and interaction rules between agents (e.g., when to switch shells).

In our model, an initial population of crabs was generated with crab sizes randomly selected from a negative exponential distribution ranging from 1 to 100 arbitrary size units. Each crab initially occupied a shell that was too small, with randomly assigned fit decrements that could be up to 50 arbitrary units. Crabs were allowed to explore a simulated habitat space that was 50 3 50 units^2 with both vertical and horizontal wrapping (without this toroidal geometry, crabs would accumulate at the "sealed" edges), interacting and exchanging shells (as described below) for 500 time steps to equilibrate the population. Crabs were programmed to move through this habitat at speeds proportional to their size and could alter their travel direction by up to 50 degrees between each time step; this allowed crabs to travel in a consistent direction, but over time most crabs explored the entire habitat. After 500 time steps, a vacant shell that was appropriately sized for the largest crab in the population was added at the center of the habitat and the simulation continued for an additional 1000 time steps.

We established rules for shell switches that realistically reflected hermit crab behavior. When 2 crabs encountered each other (defined as being within one spatial unit), a shell exchange occurred only if all the following conditions were satisfied: 1) the larger crab would improve its shell fit by switching shells, 2) the size difference between the 2 crabs exceeded a threshold of 5 size units, and 3) the smaller crab was not in an optimally fitting shell. These conditions represent natural interactions in which larger crabs can forcibly acquire shells from smaller conspecifics in poorly fitting shells. Crabs encountering a vacant shell switched only if they gained improved shell fit.

We conducted 100 model runs at each combination of 2 parameters: population density (8 levels from 10 to 900 crabs) and maximum waiting times (2 levels). For maximum waiting times of 250, if the vacant shell was too large for a particular crab (the absolute difference between the crab size and the new shell was greater than the absolute difference between its size and current shell), it waited near the vacant shell for 250 time steps before it began moving again; after waiting, crabs were prevented from waiting by any nearby shells for 5 time steps to prevent crabs returning and waiting by the same shell again. For maximum waiting times of 0, crabs continually move and never pause near empty shells.

For each model run, we tracked the following output variables: the number of asynchronous vacancy chains created by the vacant shell (defined as a crab switching into the shell, then its discarded shell remaining unoccupied for at least 1 time step), the number of synchronous vacancy chains (multiple crabs switching in the same or sequential turns), and the number of crabs involved in each synchronous chain (vacancy chain length). Our agent-based model is available in the Supplementary Material for this manuscript.

RESULTS

Shell acquisition behaviors in solitary hermit crabs versus groups

We found that social context influenced shell acquisition by C. clypeatus as solitary crabs investigated empty shells significantly more often than crabs in groups (Figure 1A; 2 sample t ¼ 4.45, degrees of freedom [df] ¼ 14.5, P ¼ 0.0005). Similarly, there was a trend toward more frequent shell switching by solitary crabs, though this difference was not significant (Figure 1D; t ¼ 1.92, df ¼ 18, P ¼ 0.0712). The duration of
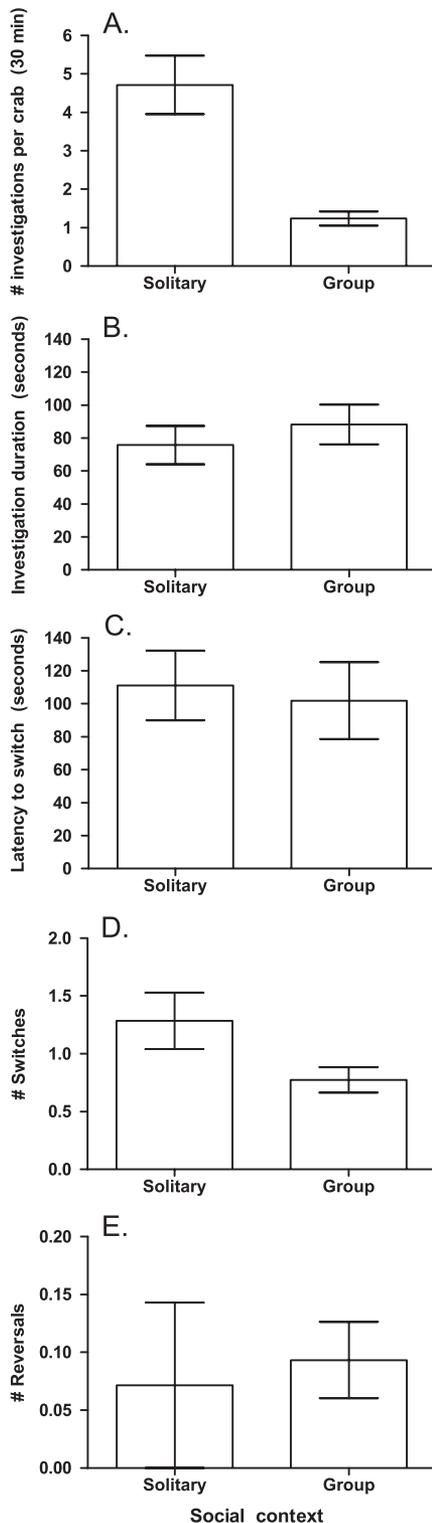
Figure 1
Comparison of *Coenobita clypeatus* behaviors (measured over 30-min observation periods) in laboratory studies of solitary (1 crab, 5 shells) versus group (5 crabs, 1 shell) social contexts: (A) number of shell investigations per crab, (B) duration of each shell investigation, (C) latency from initial contact with vacant shell to shell switch, (D) number of shell switches, and (E) number of shell reversals (see MATERIALS AND METHODS for behavior descriptions), which describe the number of reversed shell switch decisions. For (A), (D), and (E), experimental values were divided by 5 to yield frequencies of behavior per crab in order to enable a direct, per crab comparison with solitary social context experiments. (B) and (C) were directly comparable on a per investigation basis.

Figure 2
Social behavior in *Coenobita clypeatus* hermit crabs: size-sorted queue with largest hermit crab (top) grasping a vacant shell. Such queuing behavior precedes synchronous vacancy chains.

shell investigations remained the same regardless of social context (Figure 1B; t ¼ 0.75, df ¼ 171.6, P ¼ 0.4576), as did the latency to switch (Figure 1C; t ¼ 0 ¼ 2 0.30, df ¼ 57.1, P ¼ 0.7691). Hermit crabs did not show many shell reversals in either social context (Figure 1E), and shell reversals did not differ between treatments (t ¼ 2 0.28, df ¼ 18.4, P ¼ 0.7839). One distinctive behavior shown by group crabs was piggyback-ing, in which one crab approached another from behind and climbed up onto its shell even as the first crab continued walking. Piggybacking behavior involving up to 5 crabs was observed in the group trials.

Vacancy chains occurred in 13 of the 15 trials with groups of crabs, and on average, 3.9 crabs switched into different shells. Synchronous vacancy chains occurred in 2 of these trials (Figure 2), whereas 7 showed asynchronous vacancy chains, and in 4 trials both types of vacancy chain occurred. In these trials, we compared shell acquisition behaviors that occurred during synchronous versus asynchronous vacancy chains (Figure 3). Crabs that participated in asynchronous vacancy chains behaved similarly to solitary crabs as they showed a higher frequency of shell investigation compared with crabs in synchronous chains (Figure 3A; t ¼ 3.327, df ¼ 8, P ¼ 0.0104). Number of shell switches did not differ between the 2 types of vacancy chain (Figure 3B; t ¼ 1.840, df ¼ 8, P ¼ 0.1031). Crabs in asynchronous vacancy chains exhibited piggybacking behavior marginally more often (Figure 3C; t ¼ 2.264, df ¼ 8, P ¼ 0.0534).

Vacancy chain dynamics in the field

Across the 20 stations at which vacant shells were provided, we observed a total of 16 shell vacancy chains over 24 h. Vacancy
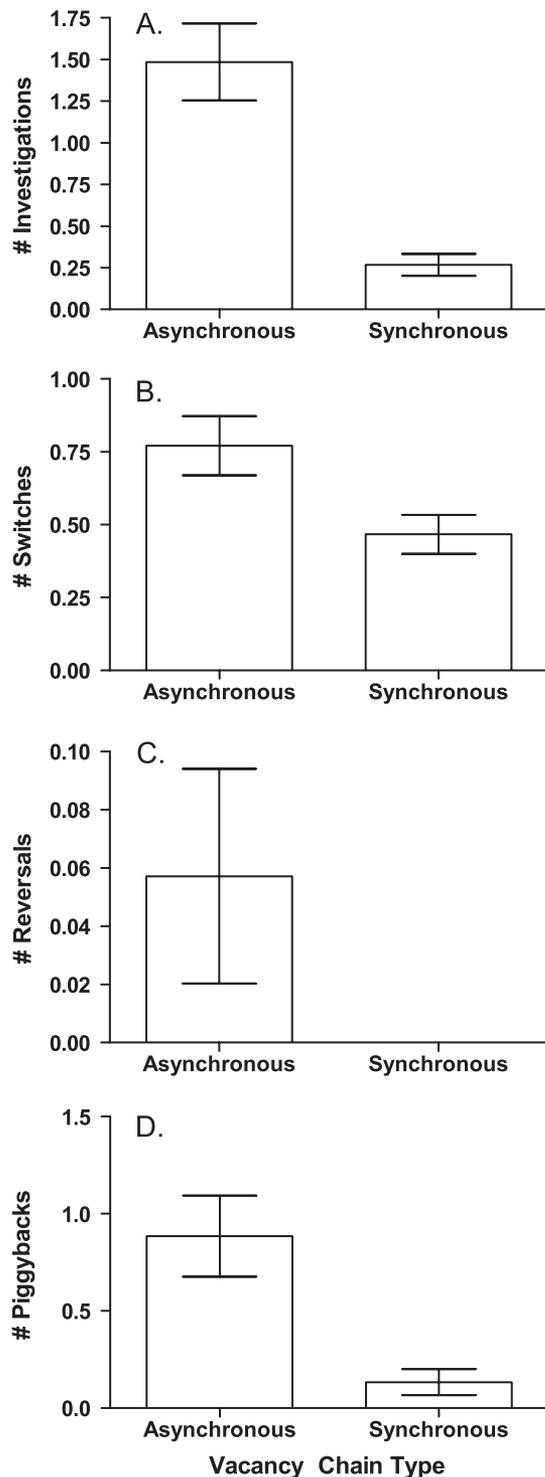
Figure 3
Comparison of *Coenobita clypeatus* behaviors during asynchronous and synchronous vacancy chains in group trials (30-min observation periods). For each chain type, we recorded (A) number of shell investigations per crab, (B) number of shell switches, (C) number of shell switch reversals, and (D) the number of piggyback events (see MATERIALS AND METHODS for behavior descriptions).

chains were observed at all 9 stations started with medium-sized vacant shells, consisting of 7 synchronous and 6 asynchronous vacancy chains. At 44% (4 of 9) of these stations, both chain types were observed over the 24-h period. Vacancy chains were

observed at 3 of the 11 (27%) stations started with large vacant shells, consisting of 1 synchronous and 2 asynchronous vacancy chains. At the remaining large-shell stations, no shell switching was observed, likely due to the lower abundance of appropriately sized *C. clypeatus* in this population.

These field observations also revealed 3 unique shell acquisition behaviors that *C. clypeatus* hermit crabs exhibited only in social contexts and which appeared to be associated with shell vacancy chains. The first is a novel behavior that we term "waiting": after investigation of a vacant shell that was too large, hermit crabs would remain near (within 50 cm) the shell rather than moving away immediately: crab waiting times ranged from several minutes to . 1 h, and up to 20 waiters at a time were present near the empty shell. Crabs exhibited waiting behavior at 55% (6 of 11) of stations with large vacant shells and at 100% (9 of 9) of stations with medium vacant shells. Waiters were observed at all stations where synchronous vacancy chains eventually occurred.

Piggybacking behavior, in which 2 or more crabs form a line with each crab grasping the shell of another crab from behind, was observed at 78% (7 of 9) stations with large vacant shells and at 18% (2 of 11) with medium vacant shells. These piggyback lines formed when several waiting crabs accumulated near a vacant shell that was too large for any of the crabs present. Individual crabs frequently moved in and out of such lines and appeared to jockey for position by aggressive cheliped pushing (described by Hazlett 1966). Thus, behavioral interactions during piggybacking may help establish a dominance hierarchy and may eventually lead to queues (lines of crabs leading away from a vacant shell in decreasing size order, with each crab holding onto the preceding crab's shell). Piggyback lines often transformed into queues after the arrival of crabs that were appropriately sized for the vacant shell. Queues were observed at 6 stations, and these contained between 2 and 8 crabs. In all queues, the largest crab grasped the aperture of the vacant shell, followed by a line of crabs of decreasing sizes.

At some stations, multiple (2 or 3) queues formed, each leading away from the vacant shell, which we term "tug-of-war" dynamics. Multiple queues appeared to form when there were many similarly sized waiters, and crabs in these multiple queues appeared engaged in a tug-of-war for control of the vacant shell. The smallest crabs positioned at the end of each queue frequently switched back and forth between these multiple queues. Within 4–24 h of when we first set out empty shells, all 6 stations with queues led to synchronous vacancy chains. In each case, immediately after the largest crab had switched into the vacant shell, the crab holding onto its shell also switched, and so on until the smallest crab in the queue had discarded its shell.

Simulation model: effects of population density and waiting behavior on vacancy chain dynamics

Model results indicate that population density had a marked effect not only on the number of times crabs switched into vacant shells but also affected the predominant type of vacancy chain (Figure 4). Vacancy chain lengths increased with population density as any newly vacated shells were more likely to be encountered by a model crab of the appropriate size. At the highest level of population density, nearly 50% of switches into vacant shells occurred in synchronous vacancy chains that routinely had 6 crab participants, and occasionally had up to 10 participants.

When the maximum waiting time was reduced from 250 to 0 time steps, the total number of crabs changing shells per simulation decreased slightly (Figure 4B) and that the vast majority of switches in nonwaiting populations became asynchronous (Figure 4C).

A.

B.

C.
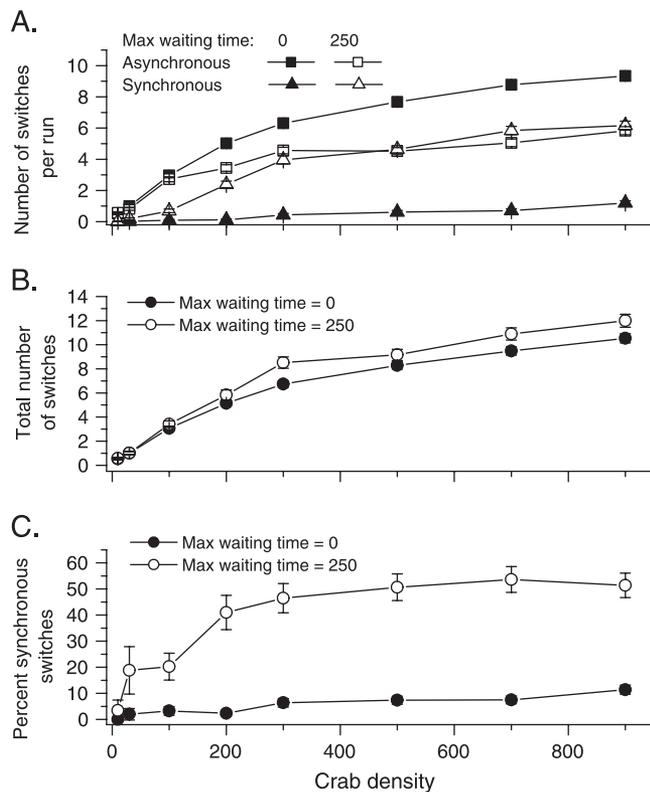
Figure 4

Hermit crab vacancy chain dynamics modeled with NetLogo (means ± standard error for n ¼ 100 simulation runs at each parameter combination). (A) Number of asynchronous (squares) and synchronous (triangles) shell switches by model crabs as a function of crab population density and maximum waiting times (0 or 250 time steps; see text for description). (B,C) Total number of switches (B) and percentage of all shell switches that took place in vacancy chains (C) as a function of crab population density and maximum wait time.

DISCUSSION

Vacancy chains involve unique patterns of resource acquisition behaviors that determine how reusable resources are distributed through animal populations. Shell vacancy chains have now been described for several hermit crab species (McLean 1974; Rittschof 1980; Chase and DeWitt 1988; Chase et al. 1988; Rittschof et al. 1992; Small and Thacker 1994; Osorno et al. 1998; Lewis and Rotjan 2009), and it has been demonstrated that a single vacant shell can trigger a sequential chain of vacancies that effectively distributes resource benefits across many individuals (Lewis and Rotjan 2009). Here, we present a novel theoretical framework that differentiates 2 types of shell vacancy chains in hermit crabs and that leads to fundamentally distinct predictions concerning the behavioral and ecological costs and benefits associated with synchronous and asynchronous vacancy chains. In laboratory studies of the terrestrial hermit crab *C. clypeatus*, we found support for the prediction that social context alters shell acquisition behaviors. Field observations demonstrated that both synchronous and asynchronous vacancy chains are common and revealed previously undescribed behaviors that appear to facilitate synchronous vacancy chains. Simulation results from an agent-based model confirmed the importance of waiting behavior in promoting synchronous vacancy chains and showed that higher population densities increase the likelihood of syn-

chronous vacancy chains. Together, these results contribute important new elements to vacancy chain theory and begin to establish some important behavioral and ecological differences between synchronous and asynchronous vacancy chains.

Shell investigation and acquisition is likely to take place in a highly social context in many hermit crabs (Table 1 and Figure 2). Large crab aggregations have been described in several species, including the mangrove hermit crab, *Clibanarius laevimanus* (Gherardi and Vannini 1993; Gherardi et al. 1994). Furthermore, many marine and terrestrial hermit crabs form aggregations in response to odors from dead gastropods or conspecifics, both of which represent a potential shell source (McLean 1974; Rittschof 1980; Rittschof et al. 1992; Thacker 1994; Small and Thacker 1994; Tricarico and Gherardi 2006). It has been suggested that hermit crab aggregations function as "shell exchange markets" (Gherardi and Vannini 1993). Despite this, most previous work describing shell investigation by hermit crabs has focused on behaviors exhibited by single hermit crabs, or sometimes pairs, as they investigate a vacant shell. However, our results demonstrate that social context has a major influence on shell investigation and acquisition behaviors shown by *C. clypeatus* hermit crabs. In laboratory comparisons of solitary versus grouped crabs, we found significantly higher frequency of shell investigations by solitary crabs compared with those in groups (Figure 1A). As predicted, crabs participating in asynchronous vacancy chains also investigated shells more often compared with those in synchronous vacancy chains (Figure 3A). Our prediction that solitary crabs as well as crabs in asynchronous vacancy chains would engage in more shell-choice reversals was not supported (Figures 1E and 3C); it is possible that the ample range of shell sizes that we provided to solitary crabs obviated the need for shell reversals. Similarly, our laboratory experiments show that shell investigation duration and latency to switch did not differ between solitary and group shell acquisition contexts. Consistent with the vast literature on shell investigation in a solitary context, we found that investigation duration was highly variable (in solitary contexts, ranging from 3 to 429 s). Given the wide variance in investigation time, it is perhaps unsurprising that investigation duration and latency did not differ with social context, though it is noteworthy that investigations ranged from 1 to 859 s in a group context, almost double that of solitary. Piggybacking behavior, approaching from behind and climbing onto the shells of other ambulatory crabs, may be a form of external shell investigation for an already-occupied shell, which would be absent in a solitary context. However, piggybacking as a form of shell investigation has yet to be experimentally tested.

Our field study also supports the idea that shell acquisition in *C. clypeatus* hermit crabs is often highly social. When we added vacant shells to a field population, we observed behaviors that facilitated intraspecific behavioral interactions. After investigating a vacant shell that was too large, some hermit crabs waited near the shell for periods up to 24 h. After 2 or more waiters had accumulated near a vacant shell, they engaged in piggybacking behavior, which may allow initiating crabs to gage the strength of other crabs as well as shell size and exterior quality. Newly arriving crabs used cheliped pushing to jockey for position in these piggyback lines. Over time, these waiting and piggybacking behaviors may facilitate the formation of queues, which are linear arrays of size-sorted crabs leading away from a vacant shell (Figure 2). These queues frequently led to synchronous vacancy chains: immediately after the largest crab had switched into the vacant shell, a rapid cascade of sequential shell switches by each queued crab followed until the smallest crab in the queue had discarded its shell. In the field, we also occasionally observed 2 or 3 tug-of-war queues radiating out from a single vacant shell, with the largest crabs in each queue struggling to gain control of the

vacant shell. Such tug-of-wars between multiple queues appeared to inhibit vacancy chains as in some cases this situation lasted up to 4 h without any crabs moving into the vacant shell. These findings indicate that the formation of hermit crab queues and other linear dominance hierarchies involves more complex social interactions than previously thought (Chase et al. 2002).

When new resources are added to populations, numerous factors will determine the relative frequencies of synchronous and asynchronous vacancy chains. In hermit crabs, such factors include population density and whether crabs exhibit waiting behavior. The agent-based simulation model presented here provides a powerful tool to investigate how these factors affect vacancy chain dynamics. This model allowed us to add a single reusable resource unit to a population and track how many individuals subsequently gained new resources. When the maximum waiting time was reduced shell switches were predominantly asynchronous, whereas increases in wait time subsequently increased the proportion of synchronous chains. This suggests that waiting allows for a higher number of crabs to benefit from a single, introduced shell resource. Importantly, these results demonstrate that synchronous switching does not arise significantly from several appropriately sized crabs simultaneously arriving at the shell but rather as a consequence of smaller crabs waiting.

Our model results support the expectation that higher population densities lead to more crabs switching into newly vacated shells, based on increased rates of shell encounter. In addition, higher population densities lead to increased likelihood that resources will be distributed through the population via synchronous rather than asynchronous vacancy chains. These results suggest that natural variations in hermit crab population density, such as those observed across Bahamian islands by Morrison and Spiller (2006), are likely to strongly alter vacancy chain dynamics.

Vacancy chain theory applies to any system where critical resources are discrete, limited, and reusable (White 1970; Chase 1991; Friman 2004). In previous studies, vacancy chains have been applied to humans, as well as hermit crabs both marine (McLean 1974; Rittschof 1980; Chase and DeWitt 1988; Chase et al. 1988; Rittschof et al. 1992) and terrestrial (Small and Thacker 1994; Osorno et al. 1998; Lewis and Rotjan 2009). It has also been suggested that vacancy chains could be applicable for stomatopods, anemone shrimp, red-cockeaded woodpeckers, robot task allocation, and other systems (e.g., Chase et al. 2002; Dahl et al. 2003; Persky and Felsenstein 2008; Lewis and Rotjan 2009). However, the distinction between synchronous and asynchronous vacancy chains has not yet been applied to any of these other systems. Though asynchronous vacancy chains are likely to be the dominant chain type given the stochastic nature of resource availability, synchronous vacancy chains can occur in systems beyond hermit crabs; for example, the human housing market (e.g., Emmi and Magnusson 1995a, 1995b; Dieleman 2001; Persky and Felsenstein 2008; Turner 2008). In many Boston, MA neighborhoods, there is an extremely competitive apartment rental market dominated by college students. Synchronous vacancy chains happen annually on 1 September "move-out day" as many students move in and out of apartments with annual leases tied to academic schedules, thus creating a massive housing shift taking place on a single day. Applicable to the ownership market as well, the smooth purchase of a new home often hinges on a series of contingency clauses, whereby the seller (who is also usually a buyer), and so on, all try to close on the same day so that the risk of homelessness is diminished. In an asynchronous housing situation, houses often remain empty for a period or the new owners remain renting for a period such that synchronized closing dates are not critical. Our conceptual model highlights fundamentally different predictions, with different behavioral and ecological costs and benefits, between synchronous and asynchronous vacancy chains. Additional work is needed to experimentally test these predictions and to ascertain the relative importance of resource distribution via these 2 vacancy chain types in other animal systems.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco .oxfordjournals.org/

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