# Chains of opportunity: a Markov model for acquisition of reusable resources

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## Summary

A vacancy chain is a unique type of resource acquisition process composed of an interconnected series of events in which the gaining of a particular resource unit by one individual depends directly on prior acquisition events by other individuals. Taken from the sociological literature, vacancy chains may also describe the distribution of many types of animal resources such as burrows, dwellings and shelters. Using data on hermit crabs, we present a Markov model simulating a vacancy chain process, and test the model against field data. Our results show that a simple Markov model adequately describes shell acquisition in hermit crabs, and that models combining shell size and crude estimates of quality fit the data extremely well. We illustrate in detail how to generate vacancy chain models from ecological data, how to determine the number and size of organisms gaining new resource units from resource introductions of specific sizes, and how to statistically evaluate the accuracy of Markov models. Not recognizing the presence of a vacancy chain system may lead to serious errors in estimating resource dynamics and therefore in demographic and competition models based on those dynamics. Finally, we suggest some ways in which vacancy chain models can aid studies of competition, population dynamics, life histories, and conservation in species using this type of resource acquisition process.

*Keywords*: Markov model, demography, resource allocation, *Pagurus longicarpus*, vacancy chains.

## Introduction

Vacancy chain models describe the movement of resource units through a population of users in a manner different from the models ordinarily used by ecologists. Rather than treating resource acquisition as the product of a number of independent events (as, for instance, do models of 'scramble' competition, vacancy chain models describe resource acquisition as a series of interconnected events, where the acquisition of a resource unit by one individual depends on prior acquisition events by other individuals. Taken from the human sociological literature, the most often used analogy is that of job mobility up a corporate ladder. A vacancy created, say by the firing of the president, is filled by the vice president, and this recently vacated spot is filled by an executive at the next lowest position, and so on. The initial vacancy moves down the user chain as individuals move up the corporate hierarchy and fill the opening created above them. Vacancy chain models organize the consequences of resource introductions by determining the

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probability that any given individual will gain a new resource via the chain created by the initial introduction.

In systems where resources are distributed by vacancy chains, an initial resource introduction allows a succession of individuals (often differing in some attribute such as status or size) to gain new units as the vacancy flows through a population of users. Resource allocation in these systems has different implications than in systems where access to resources is controlled by pairwise interactions between individuals or contests occurring simultaneously among all participants (i.e. interference and exploitative competition). This is most clearly seen when analysing the demographic consequences of resource introductions. Since higher quality resources (e.g. better jobs) initiate a series of resource switches, a chain of individuals acquire new resources, whereas in a non-vacancy chain system only a single individual benefits from the resource introduction. This has important implications for size- or state-based competitive models, since the effects of resource supply rates at one level trickle down to affect lower levels. This process may go undetected if vacancy chains happen quickly relative to the intervals between sampling the resource base. Because of these trickle down effects, resource acquisition through vacancy chains also has differing implications for models of population growth and biomass increase.

The vacancy chain approach has been used to model a variety of phenomena in human resource systems (e.g. White, 1970; Stewman, 1986). Recently Chase *et al.* (1988) and Chase and DeWitt (1988) have demonstrated that vacancy chains describe shell acquisition in populations of the hermit crab *Pagurus longicarpus*, and Chase (1991) has provided a general review of the vacancy chain literature that finds some striking similarities among human and hermit crab vacancy chain systems. Many other resources used by animals have the qualities required for distribution via vacancy chains (Chase *et al.*, 1988), e.g. refugia, burrows and other dwellings.

This paper describes methods for applying the vacancy chain model in ecological contexts. Our derivations adapt methods from the sociological literature to provide information and predictions specifically tailored to ecological systems. We develop a first order Markov model to fit observational data and test the robustness of the model. Since we assume no previous knowledge of Markov models, our treatment should confer upon most workers the ability to apply vacancy chain models to their own systems. Taking our data on hermit crabs, we then use the model to illustrate how to predict the demographic impact of resource introductions upon a population of users and also how to examine broad patterns of resource selection. We provide a treatment of the mathematical assumptions of the model which is sufficiently detailed to give researchers the means to assess the suitability of other systems for vacancy chain modelling. Finally, we suggest how the results of vacancy chain modelling can be used to examine some questions in life history evolution and conservation biology.

*The Markov model*

Imagine an animal that utilizes a resource with the following properties: the resource is reusable; resource units differ in some attribute indicative of quality, so that each unit can be assigned to a state (class) based on that attribute; animals have a recurrent need for resources and continually seek out new resource units of a higher quality than that presently utilized.

An appropriate system is hermit crabs occupying gastropod shells. These shells are reusable and may be assigned to size categories, so that a resource state corresponds to a particular size range of shells; and as individual crabs grow, they must periodically find larger shells to inhabit.

Imagine that an unutilized (vacant) resource unit of state *i* is introduced into a population of users, and that an individual currently occupying a resource unit in state *j* takes the vacant unit. The vacancy has flowed from state *i* to *j*, while the individual has made the opposite move from a resource unit in *j* to a unit in *i*. An individual may not move until a vacancy is created. Vacancies

are causal, moves of individuals are resultant. At this point the vacancy resides in a resource unit in state $j$, which then may be taken by another individual, and so forth. Thus, introduction of a single resource unit sparks a series of resource acquisition events as the vacancy flows through a population of users.

The states described above are termed transient states, since they are occupied temporarily by a vacancy, as the chain moves towards termination. The vacancy chain ends with the movement of the vacancy to a state which does not in turn liberate a vacant resource unit. Vacancies making this move may be said to have moved into an absorption state. In general this will occur when the vacancy goes to a resource unit that is then lost to the system or otherwise destroyed, or when an individual currently without a resource unit acquires the vacant unit.

Imagine now that we repeatedly introduce resource units into a system and observe vacancy movements, including movements to the absorption state. The observed moves can be summarized in a matrix where $a_{ij}$ is the number of vacancy movements from resource units in state $i$ to units in $j$. Note that this is an asymmetrical $m \times s$ matrix since vacancies can move to, but not from, the absorption state. This matrix can then be transformed to a matrix of maximum likelihood estimates, $T$, where every element $t_{ij}$ is the probability of a vacancy moving from $i$ to $j$, such that: $\Sigma_{j=1}^{s} t_{ij} = 1$, for all values of $i$ (Billingsley, 1961). This corresponds to normalizing each element in $T$ by dividing by the appropriate row sum, or: $t_{ij} = a_{ij}/\Sigma_{j=1}^{s} a_{ij}$, over all values of $i$. $T$ is called the transition matrix, and forms the basis for predicting the characteristics of the vacancy chain process.

Several important assumptions come into play regarding the generation of this matrix. First, the probabilities are presumed to be governed by a first order process, that is, $t_{ij}$ is dependent only on the resource states $i$ and $j$, and is blind to previous vacancy moves. Second, unlike many ecological Markov models, vacancy chains are imbedded Markov models (White, 1970; Kemeny and Snell, 1976; Heyman and Sobel, 1984). Such models do not treat time as an explicit parameter. This requires that transitions must be measured over an ecologically relevant time frame, and that the resource base remains relatively static. Violation of either criterion would produce transition probabilities that are time dependent within the observation period due to changing biological or physical conditions. Finally, it should be well understood that our model is unaffected by the resource selection behaviour of individual animals. The model does not track individual choices but follows vacancies as they move through a population of users. While individual biases for certain types of resource may determine who moves, the model considers the average, aggregate consequences of vacancy movement.

The transition matrix is used to predict the average vacancy chain length – the number of moves in an average chain beginning with the first move from the initial resource unit and ending with the final move to absorption. This is referred to as the multiplier effect (ME), and is contingent upon the state of the initial vacant resource. Since vacancy movements generally imply a corresponding acquisition event, the ME also estimates the number of animals acquiring new units. The move to absorption may not result in a resource acquisition event, and consequently we must distinguish between ME, and the animal ME – the number of animals acquiring new resources.

Let $Q$ be an $m \times m$ submatrix of $T$, which includes only transitions among the various transient (non-absorbing) states. The fundamental matrix $N$ is calculated as

$$N = (I - Q)^{-1} \qquad (1)$$

where $I$ is an $m \times m$ identity matrix. Each element $n_{ij}$ equals the expected number of times a vacancy starting out in $i$ will be in resource units in state $j$ before it is absorbed. Derivations of the calculation for the fundamental matrix can be found in any standard textbook of Markov chains with absorption states (e.g. Kemeny *et al.*, 1966; Roberts, 1976).

Let $ME_i$ equal the expected chain length resulting from a vacancy initially in state $i$, $ME_i = \Sigma^s_{j=1}$ $n_{ij}$, which is simply a sum of the expected number of times a vacancy starting in state $i$ will be in various resource states on the way to absorption. Thus, if 1 is a column vector of 1's,

$$n = N1 \tag{2}$$

where $n$ is a column vector of $ME_i$'s. The variances of these expected chain lengths are calculated as

$$\sigma^2 = (2N - I)n - n^2 \tag{3}$$

Recall that there may be several different absorption states which may have different implications for the animal $ME$. In some cases the final move to absorption will result in an animal acquiring a resource unit, while others may not. If the chain is absorbed by an animal without a resource unit (a 'naked' animal) taking the final resource unit, the animal $ME = ME$. If the last unit is abandoned or destroyed, the vacancy is considered to make one last move outside the system, without a corresponding acquisition event by an animal. Therefore in this case the animal $ME = ME - 1$. The Markov model can be refined to give probabilities for absorption in each different absorption state as a function of the state of the initial vacancy. Mathematically

$$B = NR \tag{4}$$

where $R$ is an $m \times a$ submatrix of the transition matrix $T$, where $a$ is the number of different absorption states. $R$ contains only the transition probabilities into the absorption states. The matrix $B$ gives the probability of being absorbed in each absorption state, as a function of the initial vacancy state. The average animal $ME_i$ is calculated as

$$\text{Animal } ME_i = (p_{ni} * ME_i) + [(1-p_{ni}) * (ME_i-1)] = P_{ni} + ME_i-1 \tag{5}$$

where $p_{ni}$ is the probability of absorption via a naked animal, and $1-p_{ni}$ is the corresponding probability of absorption by all states that lead to resource loss (i.e. abandonment or destruction), for a chain starting in state $i$.

It is quite easy to provide specific predictions concerning the numbers of individuals moving from resource units of one state to those of other states. One must first calculate a from–to matrix for each starting state, which shows the expected number of times a vacancy will move from one particular state to another. This information will be contingent on the state of the initial vacancy. Let $M_i$ be the from–to matrix for a chain started in state $i$. Each element in $M_i$, $m_{i(j,k)} = n_{ij} * t_{jk}$. Thus the element $m_{i(j,k)}$ is the product of the number of times a chain starting in state $i$ will be in state $j$ (before absorption) and the probability that a vacancy in $j$ will move to state $k$. In matrix form

$$M_i = D_i * T \tag{6}$$

where $D_i$ is a diagonal matrix of elements from the $i$th row of the fundamental matrix. In order to calculate the aggregate effects of a number of resource introductions, the matrix $M_i$ must be scalar multiplied by the number of resource units in state $i$ that initiated vacancy chains. Recall that since vacancies are causal, $M_i$ is a from–to matrix for vacancies, and the transpose of $M_i$ is the corresponding matrix for the from–to movements of animals.

## Modelling vacancy chains in hermit crabs

### Methods and results

*Animals, observations, and measuring techniques.* The methods for observing vacancy chains and for measuring shells and crabs are described at greater length by Chase *et al.* (1988). We carried

out our observations in a large tidal pool at West Meadow Beach, Stony Brook, New York on Long Island Sound using the hermit crab *Pagurus longicarpus*. Crab density was high in this pool (14.6 ± 6.7 SD crabs per 0.1 m²). Our observations were made from about 1 h before to 1 h after mean low tide from June to September 1984 and 1985. Observation periods were 45 min long.

In the local area in which we made our observations *Pagurus longicarpus* commonly occupies the shells of four species of snails: *Littorina littorea, Ilaynassa obsoleta, Urosalpinx cinerea*, and *Nassarius trivittatus*. In order to initiate a vacancy chain we dropped a starting shell into the pool and then collected the crab which took the starting shell, the crab taking the first crab's old shell, and so on until the observation period terminated. At the end of the observation period we collected the empty shell abandoned by the last crab taking part in the chain. Occasionally, a 'naked' crab, one without a shell, would take the shell left by the previous crab, and so that chain would terminate before the end of the observation period leaving no empty shell. We initiated chains using a total of six shell types, two size classes each of *L. littorea* and *I. obsoleta*, and one each of *U. cinerea* and *N. trivittatus*. The mean width, length, and dry weights of each class of starting shells are given by Chase *et al.* (1988).

We removed crabs from their shells by brief immersion in warm (50°C) tap water, weighed them, and measured the lengths of their shields (hard portion of the carapace) using a digitizer. Shells were rinsed in fresh water, dried for several days at 50°C, and then measured and weighed. Crabs were provided with new shells and released.

*The number of categories.* The first step in developing a Markov model to fit vacancy chain data is to consider the number of states that a vacancy can inhabit before it is absorbed (the chain ends). In past modelling for human vacancy chains the number of states used has usually been between three and five (White, 1970; Stewman, 1975; Brown, 1975; Sands and Bower, 1976). The choice of the number of states balances two conflicting considerations. As mentioned above, all the resource units in a specific state are considered to be alike in that a vacancy moving from any one unit is expected to have the same probability distribution of going to the other states, staying within the state, or being absorbed. Enough states have to be used to separate resource units into categories in which vacancies behave similarly, and in general, more categories produce more homogeneous states. However, the upper limit to the number of states will be determined by the number of observed vacancy movements (i.e. resource switches). A common rule of thumb is that one should have about ten observations for each probability estimated. We had observed about 570 moves in our work with *P. longicarpus* and thus were limited to models with no more than about seven transient states and one absorbing state. Our first model had five transient states, and a second one had all seven states.

*State boundaries.* In modelling human vacancy chains, researchers, not surprisingly, have grouped resource units into states based on what can be thought of as size or rank measures of the resource units. We used a size attribute, dry weight, to group shells into states for our first model of vacancy chains in crabs. The problem is that a size dimension for resource units is usually a continuous variable but the Markov model assumes a relatively small number of discrete states. Unfortunately no rigorous statistical techniques have been developed, as far as we are aware, for deciding where boundaries should be drawn between states. Indications are that this is a very difficult statistical problem.

In developing the first model for the crabs, we followed the successful example of the modellers of human vacancy chains and used a combination of exploratory data analyses and our knowledge of the system gained through past observation and research. One of the most helpful exploratory techniques was to plot the shell weights at successive positions in a chain for each of the six classes of starting shells. We found natural gaps among the weights of shells in the second

position of each chain. These gaps were usually coincident in two or more of the plots, indicating that there may be non-arbitrary state boundaries. This is not unexpected given that the four shell species differed in their size distributions and ranges. (Rosenzweig, 1986 gives a formula to determine particularly large gaps in distribution of proportions; this formula could be used to separate shells into different states if all the shell sizes at a specific link in a set of vacancy chains were plotted as proportions of the largest shell size at that link.) We used the gaps in shell size distributions as the basis upon which to divide the shells into the following five states: >2.000 g, 2.000 to 1.201 g, 1.200 to 0.701 g, 0.700 to 0.301 g, and 0.300 g or less (state 1 shells are the largest and state 5 the smallest). In our models we used two absorption states, one representing abandoned shells, and the other representing shells which were taken by a shell-less animal.

If the distribution of objects in state space is uniform, then boundaries are largely arbitrary, and only considerations of sample sizes are relevant to boundary formation. In the absence of state boundaries defined by the resource base, an appropriate alternative approach is to equalize the number of transitions into each state. The number of states should reflect constraints on sample sizes discussed above.

We also developed a second Markov model using both shell quality and shell weight to group shells into seven transient states. We reasoned that while large shells are rare, small shells are more abundant and likely to represent more of a 'buyer's market' for the crabs. Thus individuals might be less constrained to take smaller shells and more likely to abandon poor quality small shells. Since we began all chains with shells in perfect condition, our model would over-estimate the multiplier effect (ME) of small shells if poorer ones are abandoned. In our second model we kept states 1 to 3 as they had been in the first model but split states 4 and 5 into separate categories for good and bad shells.

We assessed shell quality on a four point scale. Shells of quality 1 had no physical blemishes such as holes or missing chips; those of quality 2 had one or two very small holes (less than 1 mm diameter); those of quality 3 up to two or three small holes (from about 2 to 4 mm diameter); and those of quality 4 several larger holes, large areas peeled back from the shell margin, and/or the opening largely blocked by *Crepedula planar*. In the estimated transition matrix of this model shells of quality 1 and 2 are combined as 'good' shells and those of quality 3 and 4 as 'bad' shells. Only the transitions for shells of states 4 and 5 have been so split into those for good and bad shells; transitions for shells of states 1 to 3 remain as in the previous model.

*Forming the transition matrix.* The next step in forming the model is to estimate the probabilities of a vacancy moving within a state, going from one state to another, or being absorbed. Combining the observations from all types of starting shells and using the state boundaries given above, this matrix for the five state model is shown in Table 1. In order to get this matrix, we randomly split our data into two halves. The first half yielded the matrix of observed transition frequencies (Table 1), and the second provided empirical estimates of the vacancy chain parameters with which to compare the predictions of the Markov model. In general, vacancies flowed from larger to smaller shells with fairly large numbers of within state transitions for the smaller states.

The probability of absorption varied with shell size. Vacancies in state 1 shells were only rarely absorbed; only once in the 21 transitions was a shell abandoned. In contrast, vacancies in smaller shells were more likely to be absorbed, e.g. 30 of 59 state 5 shells were abandoned and two were taken by crabs without shells.

The frequency counts in Table 1 were used to calculate the maximum likelihood estimate of the Markov transition matrix by normalizing the counts by the row sums. This leads to the estimated transition matrix $T$ shown in Table 2.

Table 1. Frequencies of transitions for the five state model with two absorption states; $n$ = absorption by a naked crab, $a$ = absorption by abandonment.

| Original state | State of destination | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | 1 | 2 | 3 | 4 | 5 | $n$ | $a$ | Total |
| 1 | 2 | 7 | 9 | 2 | 0 | 0 | 1 | 21 |
| 2 | 0 | 3 | 19 | 17 | 1 | 0 | 2 | 42 |
| 3 | 0 | 2 | 20 | 11 | 10 | 4 | 23 | 70 |
| 4 | 0 | 0 | 10 | 26 | 26 | 6 | 24 | 92 |
| 5 | 0 | 0 | 0 | 5 | 22 | 2 | 30 | 59 |

Table 2. Normalized transition frequency matrix $T$ for the five state model with $n$ = absorption by a naked crab and $a$ = absorption by abandonment.

| Original state | State of destination | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | 1 | 2 | 3 | 4 | 5 | $n$ | $a$ |
| 1 | 0.0952 | 0.3333 | 0.4286 | 0.0952 | 0.0000 | 0.0000 | 0.0476 |
| 2 | 0.0000 | 0.0714 | 0.4524 | 0.4048 | 0.0238 | 0.0000 | 0.0476 |
| 3 | 0.0000 | 0.0286 | 0.2857 | 0.1571 | 0.1429 | 0.0571 | 0.3286 |
| 4 | 0.0000 | 0.0000 | 0.1087 | 0.2826 | 0.2826 | 0.0652 | 0.2609 |
| 5 | 0.0000 | 0.0000 | 0.0000 | 0.0847 | 0.3729 | 0.0339 | 0.5085 |

*Calculating expected chain length.* Using Equations 1 and 2, we calculated the expected chain lengths, the average multiplier effects (*ME*'s), for both the five and the seven state models. The fundamental matrix $N$ for the five-state model is shown in Table 3.

Table 4 compares the observed and expected chain lengths (*ME*'s) for chains started in the five states of the first model. While we started no chains with shells in state 5, the model still predicts the *ME* for this state. Chains started in other states often moved to state 5 shells, thus we can use these transition probabilities to estimate the *ME* resulting from initiating a chain with shells of this type.

The observed mean chain lengths can be compared to the expected mean chain lengths in terms of associated z-scores (Table 4), standardized normal deviates (Sokal and Rohlf, 1981). These differences are quite small; none are statistically significant. Although this is a remarkably good

Table 3. Fundamental matrix of the five state model.

| Original state | State of destination | | | | |
| --- | --- | --- | --- | --- | --- |
| | 1 | 2 | 3 | 4 | 5 |
| 1 | 1.105 | 0.429 | 1.039 | 0.682 | 0.560 |
| 2 | 0.000 | 1.103 | 0.832 | 0.878 | 0.627 |
| 3 | 0.000 | 0.046 | 1.492 | 0.415 | 0.529 |
| 4 | 0.000 | 0.007 | 0.239 | 1.539 | 0.758 |
| 5 | 0.000 | 0.001 | 0.032 | 0.208 | 1.697 |

Table 4. Observed and predicted chain lengths and z-scores for chains begun in various states for the five state model.

| Original state | Observed length | Predicted length | z-score |
|---|---|---|---|
| 1 | 3.556 | 3.815 | −0.1332 |
| 2 | 3.323 | 3.440 | −0.0640 |
| 3 | 2.667 | 2.482 | 0.1026 |
| 4 | 2.567 | 2.533 | 0.0247 |
| 5 | – | 2.101 | – |

Table 5. Predicted and observed chain lengths and z-scores for the seven state model using shell quality. Good shells of a particular size category are indicated by 'g' and bad shells by 'b'.

| Original state | Observed length | Predicted length | z-score |
|---|---|---|---|
| 1 | 3.541 | 3.540 | 0.0005 |
| 2 | 3.229 | 3.156 | 0.0419 |
| 3 | 2.542 | 2.474 | 0.0403 |
| 4g | 2.797 | 2.893 | −0.0062 |
| 4b | – | 1.893 | – |
| 5g | – | 2.030 | – |
| 5b | – | 1.690 | – |

fit between the observations and the model, the seven state model, including shell quality, provided a better description of the vacancy chain dynamics.

Expected and observed lengths for the seven state model are presented in Table 5. Sample size considerations dictated that this data set could not be split as in the previous five state model, so we were forced to use the same data to generate both the chain length predictions as well as the observed chain lengths. We observed no chains beginning in states 4b, 5g, and 5b. As expected, splitting tended to reduce chain length due to the likely abandonment of small, poor quality (4b and 5b) shells. In the four out of seven states in which we have observations the fit of this model is excellent: z-scores are lower than in the original five state model.

When, as in our model, there is more than one absorption state, the crab $ME$, the average number of crabs obtaining new shells in the chains, will depend on which absorption state terminates the chain. The naked crab absorption state is ecologically different from absorption

Table 6. Probability that a chain will end in a particular absorption state, by original state.

| Original state | Absorption state | |
|---|---|---|
| | Naked crab | Abandoned shell |
| 1 | 0.123 | 0.877 |
| 2 | 0.126 | 0.874 |
| 3 | 0.130 | 0.870 |
| 4 | 0.139 | 0.861 |
| 5 | 0.073 | 0.927 |

due to an abandoned shell; only in the former will the move into the absorption state supply an animal with a new shell. Using these two absorption states, and Equation 4, we calculated the probability that a chain would end in a particular absorption state as a function of the original state. The results are presented in Table 6 for the five state model. In general, chains begun in all states are equally likely to end with abandoned shells since many chains, regardless of starting state, eventually move down to small, low quality shells.

Using Tables 3 and 6, and Equation 5, we predicted the animal *ME*'s. Since the model accurately predicts the (vacancy) ME's, it should also accurately predict the animal *ME*'s. This is indeed the case, as these values demonstrate: animal $ME_1$ = 2.94 (2.61 observed); $ME_2$ = 2.57 (2.52 observed); $ME_3$ = 1.61 (1.75 observed); $ME_4$ = 1.67 (1.81 observed); $ME_5$ = 1.01 (no chains observed).

*From–to movements of crabs.* Table 7 shows the matrix of predicted from–to movements for vacancies for one chain starting in state 1 of the five state model with two absorbing states using Equation 6, and Table 8 compares the total predicted and observed from–to movements for crabs

Table 7. From–to matrix for one vacancy starting in a state 1 shell for the five state model with two absorbing states (naked crabs and abandoned shells).

| From state | To state | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | *n* | *a* |
| 1 | 0.105 | 0.368 | 0.474 | 0.105 | 0.000 | 0.000 | 0.053 |
| 2 | 0.000 | 0.031 | 0.194 | 0.174 | 0.010 | 0.000 | 0.020 |
| 3 | 0.000 | 0.030 | 0.297 | 0.163 | 0.148 | 0.059 | 0.341 |
| 4 | 0.000 | 0.000 | 0.074 | 0.193 | 0.193 | 0.044 | 0.178 |
| 5 | 0.000 | 0.000 | 0.000 | 0.048 | 0.209 | 0.019 | 0.285 |

Table 8. Grand from–to matrix for the mobility of crabs to new shells in the five state model with two absorbing states: 'naked' crabs (indicated by state n) and abandoned shells. Observed data are given in parentheses beneath each prediction. In the data set used for observations, 18 chains started in state 1 shells, 31 in state 2 shells, 12 in state 3 shells, 33 in state 4 shells, and none in state 5 shells.

| From state | To state | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| 1 | 1.9 | 0 | 0 | 0 | 0 |
| | (1) | (1) | (0) | (0) | (0) |
| 2 | 6.6 | 3.0 | 2.0 | 0 | 0 |
| | (6) | (8) | (4) | (3) | (1) |
| 3 | 8.5 | 19.3 | 20.1 | 10.4 | 0 |
| | (8) | (18) | (16) | (9) | (2) |
| 4 | 1.9 | 17.3 | 11.0 | 26.9 | 5.1 |
| | (3) | (16) | (16) | (34) | (4) |
| 5 | 0 | 1.0 | 10.0 | 26.9 | 22.6 |
| | (0) | (2) | (9) | (20) | (9) |
| n | 0 | 0 | 4.0 | 6.2 | 2.1 |
| | (0) | (0) | (4) | (9) | (2) |

in our study. The reader should keep in mind that Table 8, in contrst to all other previous tables, shows the movements of crabs rather than vacancies. In order to get these predictions, the basic from–to matrices for vacancies for one chain in each starting state was scalar multiplied by the number of chains observed in that state, the resulting matrices added together, and then transposed as indicated above in the Methods section. No values are shown for movements involving the abandoned state (a shell not taken) since only vacancies and not crabs can make those movements.

The comparison of predicted and observed from-to movements for crabs is a more conservative test than the comparison between predicted and observed chain lengths. Here we are examining the model by inspection of 30 different, detailed estimates rather than the five more aggregate parameters used in comparing chain length. In addition, only relatively small numbers of chains starting in some of the states, e.g. state 3, are available on which to base these comparisons, or none, in the case of state 5. The small numbers can of course lead to considerable sampling error, nevertheless, the great majority of the predicted and observed values are close; 80% deviate by 3.0 crabs or less. Most of the large deviations involve the movements of crabs from state 4 and 5 shells, and we expect that these deviations might be caused by the fact that good and bad shells of these sizes are lumped together in this five state model.

## Discussion

In systems in which resource units are distributed throughout vacancy chains, the interdependent nature of resource allocation requires use of Markov models in order to describe and predict the dynamics of resource distribution. If the type of resource allocation in such a system is misidentified, then any conclusions about the system itself, as well as any other conclusions based upon other models incorporating this misidentification, will likely be inaccurate. For instance, a traditional competitive model applied to a vacancy chain system will not detect resource units trickling down from individuals in one state to those in another, and may thus incorrectly estimate the limiting nature of resources or competition intensity within various classes of individuals.

We have used our work with hermit crabs to illustrate how to incorporate data into a simple Markov model and to show some of the basic information and predictions that this model can provide. These techniques are easily adaptable to vacancy chain data in other hermit crab systems or other species getting resources in this way (copies of the computer programs used for the calculations in this paper are available from the third author upon request).

Our results indicate that our model estimates very closely the empirical measures of crab mobility to new shells. Estimates of vacancy $ME$'s were close to the empirical observations, with the highly accurate predictions of the five state model further improved by the seven state model in which smaller shells were distinguished by quality. The model predictions appear to be quite robust. For example, changing state boundaries by +30% of the intial state boundaries in our five state model results in an $ME$ change of less than 10%, averaged across all states. This implies that state boundary location may be somewhat arbitrarily determined, especially when the sole quantity of interest is maximum $ME$. We have never observed the $ME$ of the largest resource state change by more than 6–7%, even with a 35% change in boundary location. This also implies that, if desired, state boundaries may be set to target a specific size class without undue perturbation to the rest of the model's predictions.

The crab $ME$'s are easily derived from the vacancy $ME$'s and absorption probabilities and provide an estimate of the number of individuals receiving new resource units as a consequence

of a single resource unit introduction of any specific type. Our predictions indicated that on average, for every initial shell added to our system, between one and nearly three crabs would gain new shells. In cases with crab $ME$'s greater than one, one crab would take the initial unit and the others would take shells trickling down to them from previous individuals in the chain. Our models can be extended to predict the general, aggregate consequences of a set of resource unit introductions for a population of users. Using the example of hermit crabs, if a researcher has either empirical or theoretical estimates of the number and shell sizes of gastropods killed by predators (e.g. Wilber and Herrnkind, 1982; 1984); then he/she could estimate the total number of crabs moving to new shells (number of shells in state $i$ introduced times crab $ME_i$).

Detailed predictions of crab movements are provided by the from–to matrices. Our results here also demonstrated the close fit between the model's predictions and empirical data. Even though the model did well in this extremely conservative test, its predictions would have probably been improved if we had observed enough chains so that smaller shells could have been distinguished by quality.

This extremely detailed information concerning new and old shell sizes for crabs gaining new resource units can be used to predict fitness consequences resulting from the introduction of a specified set of new resource units. Because the sizes of crabs are correlated with their shell sizes, a from–to matrix can be used to estimate the numbers and sizes of crabs moving to new shells of particular sizes, contingent upon resource introduction. If field or laboratory data were available to indicate associated fitness changes, e.g. the growth or predation rates for individuals of various sizes moving into new shells of various sizes, then estimates such as aggregate biomass increases or aggregate predation losses could be made for a population of crabs, given particular resource introductions.

Combining fitness data with estimates of individual mobility derived from from–to matrices can also be a valuable method for examining the evolution of life-history tactics. This approach may allow one to predict the location of bottlenecks in resource supply rates which can have an impact on the timing of reproductive events. For instance, Table 7 indicates that many vacancies jump from state 1 to state 3 shells, implying that many animals inhabiting state 3 shells may be of sufficient size to utilize state 1 shells. These individuals must wait to acquire larger resources, and may therefore start reproductive activities at a smaller than optimal size, rather than risking death before a larger shell becomes available.

Furthermore, males and females may show a variety of differences because of sex-specific functions relating reproductive output to size. These functions may interact with resource supply rates so that each sex experiences bottlenecks at different sizes. Alternatively, males and females may evolve different resource acquisition strategies to reduce chances of being caught in a bottleneck. These strategies could hypothetically manifest themselves as individual decisions to acquire a larger than necessary resource if it becomes available, thus producing resource transitions spanning several states. Examining sex-specific from–to matrices may reveal patterns consistent with these hypotheses, which would then be open to subsequent investigation. In addition, Stewman's (1986) methods examining the rates at which individuals move from resource units in one state to another would be helpful in examining life-history tactics and possible differences for males and females.

These predictions of the size and number of individuals gaining new resource units from specific sets of resource introductions are also valuable information for size-based competitive models (e.g. Abrams, 1987), or conservation efforts in systems with resource distribution through vacancy chains. Since in vacancy chain systems, a resource introduction at one point in time and space has impacts upon other individuals at different points in time and space, it is absolutely vital in these systems to understand how resources trickle down from one class of individuals to

another. For example, if we were interested in hermit crab conservation, Table 3 indicates that state 1 resource introductions have little impact on crabs inhabiting state 2 shells even though they do trickle down extensively to crabs in state 3 shells. If crabs inhabiting state 2 shells were specifically targeted, it is clear that additional state 2 resources would be required, just adding state 1 shells would be insufficient. On the other hand, if state 3 crabs were targeted, then adding state 1 shells would be almost as beneficial as direct additions of state 3 shells, and this would have the advantage of supplying new shells to individuals in state 1. A practical and economically important example in which this type of analysis might apply occurs in the Gulf of Mexico where fishermen use artificial shelters appropriate to individual size to enhance spiny lobster productivity (Eggleston, personal communication).

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