March 19, 2009 5/5 Craig McFarlane 6850806

A Markov Chain Model of Predator Prey Interactions uh?

Predator prey interactions appear the represent a simple system. There is a decrease in the number of prey as they are eaten by predators and an increase in the number of predators as they acquire energy. The converse relationship is true as well, fewer prey means that not all of the predators will have enough food to eat and the population of predators will decline. However, it becomes apparent that there are a large number of factors that need to be accounted for. This includes but is not limited to: the rate at which prey is caught, the number of prey that each predator requires, density of predators and prey, how long it takes to find prey and the interaction between those factors. There have been many attempts to characterize these relationships using deterministic equations (eg Lotka-Volterra equations or Nicholson-Bailey) but these do not take into account the stochastic nature of the real world. This model attempts to predict how much energy and time is expended in each state of hunting.

The current model incorporates stochastic processes into predator prey interactions and attempts to predict behavioural outcomes and to incorporate as many of the above factors as possible. The process is then broken down into four different states that each represent an aspect of prey acquisition. The four states are searching, pursuit, handling and eating, and digestion. The time that is spent in each of these states can be used to predict functional responses. These are based on the searching and handling time as a response to prey density. There are three functional responses: type II, most common, occurs when an increase in prey density decreases searching time until a plateau occurs when the predator is satiated and cannot increase its feeding rate. In the type III response, a plateau is still reached, but search time is very high at low prey density and feeding rate is very low.

Each of these states incorporates a number of factors. The searching phase incorporates how often prey are encountered, the efficiency of finding prey, and the paths chosen to find prey. Density of prey is particularly important, especially if the distribution of prey is uneven. This is likely to be the case because few prey species have territorial distributions and will often be found in areas where resources are abundant. A second important factor that this model incorporates is the hunger of the animal; this will affect the probability of shifting to the searching state. Holling (1966) also lists ten other factors that will play a role in predation but a balance must be struck between representing reality and developing a model with sufficient explanatory powers.

Previous authors have argued that search paths are randomly chosen and could be represented by a Markov Chain. Once searching leads to the detection of prey (e.g. scent or sight) the predator transitions to the pursuit state. The detection of prey will occur at a rate that is proportional to the density of prey. Regardless of the efficiency of the predator, the general results should hold. The predator begins in the first state, S_1 (e.g. the beginning of a day for a diurnal predator). The model also assumes that the transition from eating to either searching or digestion occurs with a fixed probability. If the prey is large enough to satiate the predator then they will enter the digestion phase, if it is not, the predator will resume searching until enough prey items are consumed. It is important to recognize that predators will not necessarily move through the states in a linear fashion, for example, if the prey captured does not satiate the predator, they will go back into the searching state rather than entering the digestion phase of the model. The non-sequential nature of this model extends the work of Holling (1966) where it was assumed that the progression through each state was linear. The model also assumes that the process is a strict Markov chain, that is. The probability of moving to another state can be represented by the transition matrix

$$P = \{p_{ij}\} = \begin{bmatrix} p_{11} & p_{12} & 0 & 0 \\ p_{21} & 0 & p_{23} & 0 \\ p_{31} & 0 & 0 & p_{34} \\ p_{41} & 0 & 0 & 0 \end{bmatrix}$$

where p_{ij} is the probability of going from state i to j and $i,j = \{1,2,3,4\}$. By the general Markov property, given states $J_0, J_1, J_2, \ldots$ and times $X_0, X_1, X_2, \ldots$ in each state, the probability of moving from state J_{n-1} to J_n is given by

$$Pr\{J_n = j, X_n \leq x \mid J_{n-1} = i\} = p_{ij} F_{ij}(x) \qquad (1)$$

where F_{ij} is the distribution function with mean μ_{ij} and p_{ij} is as above. If t is defined as the sojourn time and *i* and *j* are as above the matrix of transition probabilities is

$$Q = \{Q_{ij}\} = \{p_{ij} F_{ij}(t)\} \tag{2}$$

Since the process is a Markov chain,

$$Q = \begin{bmatrix} p_{11}\lambda_{11}e^{-\lambda_{11}t} & p_{12}\lambda_{12}e^{-\lambda_{12}t} & 0 & 0 \\ p_{21}\lambda_{21}e^{-\lambda_{21}t} & 0 & p_{23}\lambda_{23}e^{-\lambda_{23}t} & 0 \\ p_{31}\lambda_{31}e^{-\lambda_{31}t} & 0 & 0 & p_{34}\lambda_{34}e^{-\lambda_{34}t} \\ p_{41}\lambda_{41}e^{-\lambda_{41}t} & 0 & 0 & 0 \end{bmatrix} \tag{3}$$

By example, the expected number of visits of remaining in the first state, S_1, in the initial state, $Z_0 = S_1$ is

In your report, you will have to explain a little more how these quantities are obtained.

$$E\{N_1(t) | Z_0 = S_1\} = E\{Q_{11}\} = p_{11}E\{\lambda_1 e^{\lambda_1 t}\} = \frac{p_{11}}{\lambda_{11}} \tag{4}$$

and the variance of the expected value is

$$Var\{Q_{11}\} = \frac{p_{11}}{{\lambda_{11}}^2} \tag{5}$$

The rest of the expected number of visits are calculated similarly and result in the matrix

$$N(t) = \begin{bmatrix} \frac{p_{11}}{\lambda_{11}} & \frac{p_{12}}{\lambda_{12}} & 0 & 0 \\ \frac{p_{21}}{\lambda_{21}} & 0 & \frac{p_{23}}{\lambda_{23}} & 0 \\ \frac{p_{31}}{\lambda_{31}} & 0 & 0 & \frac{p_{34}}{\lambda_{34}} \\ \frac{p_{41}}{\lambda_{41}} & 0 & 0 & 0 \end{bmatrix} \tag{6}$$

and

$$Var(t) = \begin{bmatrix} \frac{p_{11}}{{\lambda_{11}}^2} & \frac{p_{12}}{{\lambda_{12}}^2} & 0 & 0 \\ \frac{p_{21}}{{\lambda_{21}}^2} & 0 & \frac{p_{23}}{{\lambda_{23}}^2} & 0 \\ \frac{p_{31}}{{\lambda_{31}}^2} & 0 & 0 & \frac{p_{34}}{{\lambda_{34}}^2} \\ \frac{p_{41}}{{\lambda_{41}}^2} & 0 & 0 & 0 \end{bmatrix} \tag{7}$$

The asymptotic probability can be calculated from the expected number of visit. If p_k where k = {1,2,3,4} is the asymptotic probability of S_k for k = {1,2,3,4} then

$$p_k = \frac{\sum_{i=1}^{4} p_{ik}}{\sum_{i=1}^{4}\sum_{j=1}^{4} Q_{ij}} \quad (8)$$

where $p_{ik} \in P$ and $Q_{ij} \in Q$. This allows us to predict the probability of being in one state as a proportion of the total time. For example, the probability of being in S_1 at a given time is

$$\frac{(p_{11}\mu_{11} + p_{12}\mu_{12})}{\sum_{i=1}^{4} p_i} \quad (9)$$

The remaining probabilities can be calculated in a similar manner.

This model allows us to predict how a predator will spend its time as a function of predator density. It would be expected that changes in density will affect the transition distributions (Q, eq. 3), a lower density would increase the probability of finding a predator in the searching state. This will affect the expected number of visits to each state as well, changing the form of the matrix N(t) (eq. 6). The assumption of a strict Markov chain with an exponential transition distribution makes the model less realistic but I expect it to perform well regardless.