A Semi-Markovian Model for Predator-Prey Interactions

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Summary

In the study of population dynamics, the predator-prey system is recognized as a vitally important aspect in natural population control. One aspect of predator-prey interactions is studied in this paper. The attack cycle of a predator is assumed to consist of four different activities, namely, search, pursuit, handle and eat, and digestion. A semi-Markovian model is proposed to obtain the number of prey devoured by a predator during the activity of a day. The advantages of a new semi-Markovian model to the queueing model developed by Curry and DeMichele (1977) is demonstrated, as the results from the semi-Markovian model are closer to Holling's (1966) experimental data than their results, which were based entirely on Poisson assumptions.

1. Introduction

In the study of population dynamics, the predator-prey system is recognized as a vitally important aspect in natural population control. A number of mathematical descriptions of the population dynamics are proposed in the literature. Notable among them are the contributions of Lotka (1925), Volterra (1926), Stoy (1932), Nicholson and Bailey (1935), and Thompson (1939). Recently, Ivlev (1955), Watt (1959), Holling (1959, 1963), Royama (1971), and Curry and DeMichele (1977) have also presented mathematical descriptions of predator-prey interactions. The predator-prey relationship has been described by the above authors in several different approaches. However, until recently their approaches have been primarily deterministic, with very little attention paid to the real-life uncertainties of the wild. Royama (1971) has written an excellent comparison of some of the mathematical models. In addition, Royama proposes a simulation model in which he considers the random searching of predators and the probability of random encounters. Because the direction and length of each search path are determined by chance, Royama argues that the predator's mind is a kind of Markov chain. He holds to this concept even though the probability distribution of both the direction of the path and length of all paths are stochastically dependent on the location of the prey which are encountered. He did not consider, however, the case when the distribution of prey is nonrandom.

Paloheimo (1971a,b) considers the case of nonrandom distributions of prey. He develops a stochastic model to study the success of a predator's search for a clustered prey. His model gives the distribution of search time to locate the cluster of prey and the joint distribution of

handling time and number caught from each cluster sighted. As the predator resumes its search, the process starts from the beginning. Hence, the predation activity is a type of renewal process, and the total catch by the predator is a cumulative renewal process. The successive renewal points are the times when the predator resumes its search, and the results are obtained by using the limit theorems of renewal theory.

Curry and DeMichele (1977) developed a predator-prey model using queueing theory techniques for the description and synthesis of the system. There are several advantages to this approach, the notable one being that the transient behaviour model could be readily adjusted for the case of non-constant prey populations such as those in multiple predator systems when exploitation is present. In general, the predator's activity time can be split into four components: search time, pursuit time, handling and eating time, and digestion time. In their model, Curry and DeMichele pooled the first three components into a single factor, and the expression obtained for the number of prey caught is analogous to Holling's (1959) disc equation. The model would be more realistic if each component were treated separately, and hence this generalization is considered in this paper.

2. Random Distribution of Prey—Four State Model

In this model the prey species are assumed to be distributed randomly. Holling (1966), in his simulation model "The Functional Response of Invertebrate Predators to Prey Density," considers the act of predation by a predator to be composed of the following activities or states: search, pursuit, handle and eat, and digestion. He assumed that the four states are sequential and he developed equations describing the time spent in each state in terms of the hunger level of the predator. In his report, Holling analyzes the situation for a mantid-fly system, where the mantid (*Hierodula crassa*) is preying on house flies (*Musca domestica*).

Predation can also be considered as a non-sequential process. When we note that the physiological characteristics of predators allow for non-sequential predation, this change becomes logical. The data presented by Holling is transformed to suit the requirements for the present analysis, while maintaining the same values for the physiological parameters, e.g., the weight of the fly, maximum gut capacity of the mantid, threshold hunger level of the mantid, etc. Holling (1966) obtains the results for three different prey densities: (i) high density (0.0143 per cm²), (ii) medium density (0.0045 per cm²), and (iii) low density (0.00114 per cm²).

In this section, the situation is analyzed and the results are compared with those of Curry and DeMichele (1977) and Holling (1966). However, the numerical calculations are shown for only one of the three reported prey densities.

2.1. Probabilistic Features of Attack Cycle

Suppose, at the beginning of the day, the predator starts searching for prey. The hunger level at this time is high, as it is presumed that no attacks were made during the previous night. The hunger continues to rise until the first prey is caught. When the predator is in the searching state, the probability that it will pursue the prey depends on the success of its search. If it succeeds in locating a prey, it pursues the prey. The probability that the predator handles and eats the prey depends on the pursuit success. If the predator fails in pursuit, it again starts searching. Once it eats the prey, it either goes to the searching state, or to digestion state with a fixed probability. Although this fixed probability assumption is not realistic, it is necessary in order to make the mathematics tractable and to get an elegant solution. The complete details of the model are worked out here. A more realistic assump-

tion, however, would be that after the predator eats the prey it either continues searching until hunger is satiated or takes a digestive pause until hunger reaches a threshold level.

Once the predator resumes its search, the whole cycle is repeated a number of times until the feeding period comes to an end. With the above description, the states can be labelled as follows:

S_1 = Searching state, S_3 = handling and eating state, and
S_2 = pursuit state, S_4 = digestion state.

The four different states of the predator during the feeding period are represented schematically in Figure 1. With the assumptions made earlier in this chapter, the predation can be viewed rather simply as a stochastic process. The probability of going from state "i" to state "j" is designated as "p_{ij}" ($i, j, = 1, 2, 3, 4,$).
The matrix of the transition probabilities, according to Figure 1, is

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

The length of stay in each state depends on the physiological condition of the predator and is a random variable whose distribution function in general may depend on the state being occupied, as well as on the next state to which the process is moved. If the parameters involved are assumed to be constant with respect to time as measured from the beginning of the process, this is indeed a Markov chain, because it is implicitly assumed in a Markov chain that a transition is a "must" after a "unit" interval. Because of this restriction, many nondeterministic processes cannot be represented as well as by Markov renewal processes.
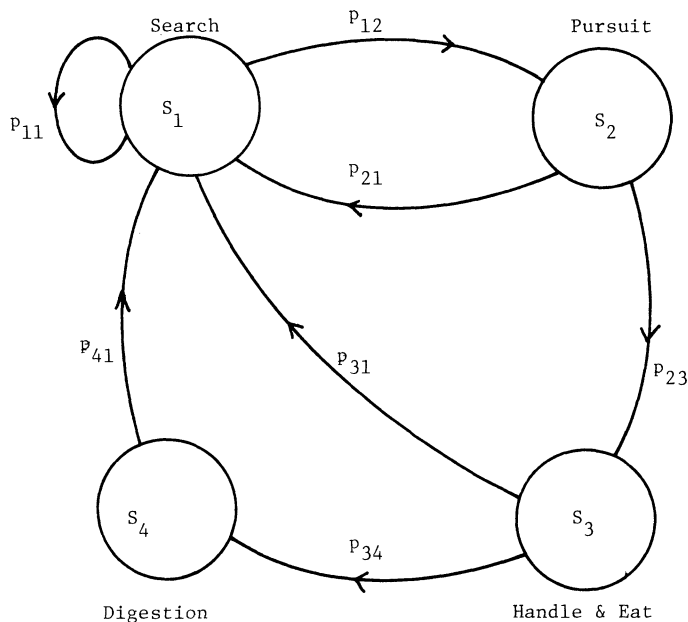

Figure 1
Schematic Diagram of the States of the Predation Process

For example, it will be very unrealistic in the present problem to assume that the predator will stop searching after a unit of time and go to the pursuit state if the predator has not found any prey. In general, the time interval between any two realistic states will be random, and that is why Markov renewal processes are better able to model the true phenomenon. Since a Markov renewal process is a generalization of a Markov chain, all points of interests of a Markov chain and, in addition, several other factors which depend on the random lengths of the intervals between successive states, can be considered. These are studied in relation to this predator-prey problem using the results developed for Markov renewal processes by Kshirsagar and Gupta (1973).

Assuming that the Markov chain underlying the above system is irreducible, aperiodic, and recurrent, and that the observed states $J_0, J_1, J_2, \ldots$ have successive holding times X_0 $(=0), X_1, X_2, \ldots$ in each state, then the M.R.P. makes a transition from state J_{k-1} to state J_k after remaining in J_{k-1} for time X_k. Then by the Markovian property, we know that

$$Pr\{J_n = j, X \le x \,|\, J_0, J_1, J_2, \ldots, J_{n-1} = i\} = Pr\{J_n = j, X_n \le x \,|\, J_{n-1} = i\} = p_{ij}F_{ij}(x),$$
(2.1)

which is the transition distribution function of the M.R.P. If Z_t is the state of the system at time "t", then $Pr\{Z_0 = i\} = a_i(i = 1, 2, \ldots, m)$ is the set of initial probabilities.

Let F_{ij} be the distribution function with means μ_{ij} and second moments $\mu_{ij}^{(2)}$ of sojourn times. The time spent in transition from state "i" to state "j" given that it has come from state "i", may be formulated as shown in Table 1. The matrix of transition distributions is denoted by $Q = \{Q_{ij}\} = \{Q_{ij}(t)\} = \{p_{ij}F_{ij}(t)\}$ (Pyke 1961a,b). In this matrix, the $(i,j)th$ element represents the probability that the predator will pass directly into state "j" within "t" times units after entering state "i". In this formulation, "t" is the sojourn time. From the transition distribution matrix, explicit expressions may be obtained which yield the moments of the number of visits to all the states. If $q(s)$ is the Laplace-Stiltjes transform (L-S.T.) of the Q-matrix, the L-S.T. of the $N_j(t)$, the expected number of visits to state "j" in $(0, t)$ is (Pyke 1961a,b)

$$m(s) = \{I - q(s)\}^{-1}.$$
(2.2)

In this particular case, the matrix $m(s)$ will be

$$z^{-1} \begin{bmatrix} (a + bc + bde + bdfg)/z & b/z & bd/z & bdf/z \\ (c + de + dfg)/z & (bc + bde + bdfg)/z & d(1 - a)/z & (1 - a)df/z \\ (e + fg)/z & (be + bfg)/z & (bde + bdfg)/z & f(1 - a - bc)/z \\ g/z & bg/z & bdg/z & bdfg/z \end{bmatrix}$$

where

$$z = 1 - a - bc - bde - bdfg, \quad a = p_{11}f_{11}(s), \quad b = p_{12}f_{12}(s), \quad c = p_{21}f_{21}(s),$$

$$d = p_{23}f_{23}(s), \quad e = p_{31}f_{31}(s), \quad f = p_{34}f_{34}(s), \quad \text{and} \quad g = p_{41}f_{41}(s),$$

and

$$f_{ij}(s) = \text{L-S.T. of } F_{ij}(t).$$
(2.3)

Assuming that the predation process starts in the searching state (S_1), the expected number of visits to the four states are

$$\text{L-S.T. of } E\{N_1(t)\,|\,Z_0 = S_1\} = m_{11}(s) = (a + bc + bde + bdfg)/(1 - a - bc - bde - bdfg),$$
(2.4)

TABLE 1
Matrix of Transition Distributions

	S_1	S_2	S_3	S_4
S_1	$p_{11}F_{11}(t)$	$p_{12}F_{12}(t)$	0	0
S_2	$p_{21}F_{21}(t)$	0	$p_{23}F_{23}(t)$	
S_3	$p_{31}F_{31}(t)$	0	0	$p_{34}F_{34}(t)$
S_4	$p_{41}F_{41}(t)$	0	0	0

$$\text{L-S.T. of } E\{N_2(t)\,|\,Z_0 = S_1\} = m_{12}(s) = b/(1 - a - bc - bde - bdfg), \tag{2.5}$$

$$\text{L-S.T. of } E\{N_3(t)\,|\,Z_0 = S_1\} = m_{13}(s) = bd/(1 - a - bc - bde - bdfg), \tag{2.6}$$

and

$$\text{L-S.T. of } E\{N_4(t)\,|\,Z_0 = S_1\} = m_{14}(s) = bdf/(1 - a - bc - bde - bdfg). \tag{2.7}$$

The variance of the number of visits to each of these states has also been derived (Kshirsagar and Gupta 1973). All these results are in terms of Laplace transforms and must be inverted in practice. For this the Laplace transform is expanded using Tauberian theorems in powers of the argument s and higher order terms are neglected. The final results are therefore asymptomatic and approximate. They involve only the first and second order moments of the sojourn time distributions.

The L-S.T. of the second factorial moment of the number of visits is given as

$$r(s) = 2m(s)\,_d m(s), \tag{2.8}$$

where $_d m(s) = \text{diag } m(s)$, from which the variances can be readily obtained.

The asymptotic probability distribution of the four states of the model can be obtained from the matrix of transition distributions by Pyke's (1961a,b) methods. Letting p_i ($i = 1, 2, 3, 4$) be the asymptotic probability of S_i ($i = 1, 2, 3, 4$) under this model, these asymptotic probabilities are

$$p_1 = (p_{11}\mu_{11} + p_{12}\mu_{12})/P, \tag{2.9}$$

$$p_2 = p_{12}\{p_{21}\mu_{21} + p_{23}\mu_{23}\}/P, \tag{2.10}$$

$$p_3 = p_{12}p_{23}\{p_{31}\mu_{31} + p_{34}\mu_{34}\}/P, \tag{2.11}$$

and

$$p_4 = p_{12}p_{23}p_{34}\mu_{41}/P, \tag{2.12}$$

where

$$P = p_{11}\mu_{11} + p_{12}\mu_{12} + p_{12}\{p_{21}\mu_{21} + p_{23}\mu_{23}\} + p_{12}p_{23}\{p_{31}\mu_{31} + p_{34}\mu_{34}\} + p_{12}p_{23}p_{34}\mu_{41}. \tag{2.13}$$

That is, the probability that the predator will be in the searching state (S_1) at a given time, after a large number of attack cycles, is

$$(p_{11}\mu_{11} + p_{12}\mu_{12}) \Big/ \sum_{i=1}^{4} p_i, \tag{2.14}$$

and so forth for each of the states of the model.

3. Numerical Results

By utilizing the strike success, pursuit success, and the hunger level data given by Holling (1966), the transition probability matrix is taken as

$$P = \{p_{ij}\} = \begin{bmatrix} 0.3757 & 0.6243 & 0 & 0 \\ 0.4247 & 0 & 0.5753 & 0 \\ 0.9755 & 0 & 0 & 0.0245 \\ 1.0000 & 0 & 0 & 0 \end{bmatrix}.$$

In the matrix shown above the pursuit success is 0.5753; thus, the predator will be in the handling state with probability 0.5753 and in the searching state with probability 0.4247. In the same manner, the other elements of the matrix (p_{ij}) are obtained. Holling (1966) obtains the time spent in the different activities by analyzing the various components in a deterministic manner. However, by considering the stochastic element present in the process, the first two moments can be obtained for all the activities. For example, consider the time spent (TE) in handling and eating the prey. This time varies depending on the initial level of hunger. As long as the hunger level is greater than the weight of prey, then all the prey will be eaten; if the hunger level is less than the weight of the prey, then only enough of the prey will be eaten to lower the hunger level to zero. Hence,

$$TE = KE \cdot W \text{ for } W \leq H1 \text{ and } KE \cdot H1 \text{ for } W > H1, \tag{3.1}$$

where KE = feeding rate (time per unit weight), W = weight of prey, and $H1$ = hunger at the time of prey capture.

In this mantid-fly system,

$$KE = 0.76 \text{ hrs/gm and } W = 0.0245 \text{ gm} .$$

Case (i)

$$W \leq H1, \quad TE = 0.76 \times 0.0245 \times 60 = 1.1172 \text{ minutes for } W \leq H1 .$$

When the weight of prey is less than the hunger level of the predator, all the prey will be eaten. As the maximum gut capacity of the predator is 1 gram equivalent, the probability that the hunger level is greater than the weight of prey = 1.0 − (weight of prey) = 1.0 − 0.0245 = 0.9755.

Case (ii)

$$W > H1, \quad TE = KE \cdot H1 .$$

When the hunger level of the predator is less than the weight of prey, then only enough of the prey will be eaten to lower the hunger level to zero. Average hunger at the time of capture when $W > H1$ is 0.0073 (Holling 1966).

$$TE = 0.76 \times 0.0073 \times 60 = 0.3335 \text{ minutes},$$

$$PR(W > H1) = 1 - Pr(W \leq H1) = 1 - 0.9755 = 0.0245$$

and

$$E(TE) = Pr(W < H1) \times 1.1172 + Pr(W > H1) \times 0.3335$$

$$= 0.9755 \times 1.1172 + 0.0245 \times 0.3335 = 1.098 \text{ minutes}.$$

Second moment of $TE = Pr(W \leq H1) \times 1.1172^2 + Pr(W > H1) \times 0.3335^2 = 1.219$ minutes.

In the same way, the first and second moments for the other sojourn times are

$$
\begin{bmatrix}
11.779,276.76 & 11.779,276.76 & 0,0 & 0,0 \\
0.735,0.992 & 0,0 & 0.735,0.992 & 0,0 \\
1.098,1.219 & 0,0 & 0,0 & 1.098,1.219 \\
22.407,660.70 & 0,0 & 0,0 & 0,0
\end{bmatrix} .
$$

The estimated values are in minutes and the calculations are based on a time period of 16 hours (960 minutes). This can be justified physiologically and mathematically as follows:

(i) The average daylight period per day is 16 hours, during which time the predator will be in the feeding period. Holling's experiments were done using 16 hours of daylight.

(ii) The time period is large enough to enable the asymptotic results of the Markov renewal processes to be applied. The asymptotic M.R.P. time period is $t > \max_j \{m_{jj}^3/v_{jj}^2\}$, $j = 1, 2, \ldots, m$.

Using the data and results presented in the previous sections, the expected number of visits to each state, given the initial state as the searching state, denoted as $N(t)$, and the variances of the number of visits, denoted as $V(t)$, are evaluated as

$$
N(t) = \begin{bmatrix}
74.83 & 46.78 & 26.78 & 0.6554 \\
75.70 & 46.71 & 27.40 & 0.6683 \\
75.69 & 46.69 & 26.82 & 0.6787 \\
74.08 & 45.68 & 26.25 & 0.6400
\end{bmatrix} \text{ and } V(t) = \begin{bmatrix}
66.37 & 40.57 & 23.78 & 0.6351 \\
65.50 & 40.59 & 23.48 & 0.6348 \\
65.60 & 40.59 & 23.78 & 0.6342 \\
63.13 & 40.25 & 23.67 & 0.6353
\end{bmatrix} .
$$

The elements of the first row of the $V(t)$ matrix give the variance of the number of visits to each of the states if the predator starts its activities in state S_1, and so on for all of the rows.

The expected number of transitions in the given time, given that the predator is initially in the searching state, is

$$
F(t) = \{f_{ij}(t)\} = \begin{bmatrix}
28.46 & 46.77 & 0 & 0 \\
19.85 & 0 & 26.88 & 0 \\
26.19 & 0 & 0 & 0.6579 \\
0.6579 & 0 & 0 & 0
\end{bmatrix} ,
$$

and the asymptotic probability distribution of states is

$$[0.9187 \quad 0.0357 \quad 0.0301 \quad 0.0155]^T.$$

It is observable from the matrices $N(T)$ and $V(t)$ that the initial state did not influence the expectation and variance of the number of visits to each of the four states.

4. Analysis of the Results

From the results presented in the previous section, the expected number of handlings made by a predator during a day could be easily obtained. The expected number of successful handlings made is equal to the expected number of visits to the handling and eating state, which is the expected number of prey devoured by the predator. The results for all three prey densities (low, medium, and high) are shown in Table 2. These results are compared with those obtained by Holling (1966) and Curry and DeMichele (1977). It is observable that the results obtained are in agreement with the previous results.

In such a complex model involving so many parameters, comparing the three models at only three points (low, medium and high densities) is not very strong evidence of the

TABLE 2

Comparison of Results of the Three Models For the Total Number of Prey Eaten in a Day

Prey Density	Holling	Curry and DeMichele	M.R.P. Model
Low	13.50	14.80	13.76
Medium	26.50	26.00	26.88
High	33.00	32.10	32.46

superiority of the M.R.P. model. But the object of this paper is to indicate the usefulness and flexibility offered by the M.R.P. model.

5. Conclusions

The predator-prey interaction is a very complex phenomenon. To explain it as a whole is a very difficult task. That is why only individual components of the predator-prey system have been considered in the literature. Curry and DeMichele (1977) used some techniques from queueing theory for this problem, while Royama (1971) uses the assumption of Markovity. A further step in this investigation is, therefore, to make the model slightly more complex by relaxing some of the more restrictive assumptions, thereby giving more flexibility to the model. The advantages of the M.R.P. model to the queueing model employed by Curry and DeMichele (1977) is evident from Table 2, as the results from M.R.P. model are closer to Holling's (1966) experimental results than their results, which were based entirely on Poisson assumptions.

To keep the mathematics tractable, only four states were employed in the embedded Markov chain of the M.R.P. It is possible to extend the state space (Rao 1976) and to assume different distributions for the intervals between the states which is the main purpose and justification of this model extension.

Résumé

Dans l'étude des dynamiques de population, le système prédateur proie est reconnu comme un aspect d'importance vitale dans le contrôle naturel des populations. Dans cet article, on étudie un aspect des intéractions prédateur-proie. On suppose que le cycle d'attaque d'un prédateur est composé de quatre activités différentes, à savoir : recherche, poursuite, prise et repas, et digestion. On propose un modèle semi-markovien pour obtenir le nombre de proies dévorées par un prédateur durant la période d'activité journalière. On démontre les avantages d'un nouveau modèle semi-markovien par rapport au modèle de file d'attente développée par Curry et Demichele (1977), dans la mesure où les résultats du modèle semi-markovien sont plus proches des données expérimentales de Holling (1966) que les leurs qui reposaient entièrement sur l'hypothèse poissonienne.

References

Cox, D. R. (1962). *Renewal Theory.* Methuen, London.

Curry, G. L. and DeMichele, D. W. (1977). Stochastic analysis for the description and synthesis of predator-pray systems. *Canadian Entomologist 109,* 1167–1174.

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomologist 91,* 385–398.

Holling, C. S. (1963). An experimental component analysis of population processes. *Memoirs of Entomological Society of Canada 32,* 22–32.

Holling, C. S. (1966). The functional response of invertebrate predators to prey density. *Memoirs of Entomological Society of Canada 48,* 3–86.

Ivlev, F. S. (1955). *Experimental Ecology of the Feeding Fishes.* Yale University Press, New Haven, Connecticut.

Kshirsagar, A. M. and Gupta, Y. P. (1973). A note on the matrix renewal function. *The Journal of the Australian Mathematical Society 13,* 417–422.

Lotka, A. J. (1925). *Elements of Physical Biology.* Wilkins and Wilkins, Baltimore.

Nicholson, A. J. and Bailey, V. A. (1935). The balance of animal populations, Part I. *Proceedings of Zoological Society,* London.

Paloheimo, J. E. (1971a). On the theory of search. *Biometrika 58,* 61–75.

Paloheimo, J. E. (1971b). A stochastic theory of search: implications for predator-prey situations. *Mathematical Biosciences 12,* 105–132.

Pyke, R. (1961a). Markov renewal processes: definitions and preliminary properties. *Annals of Mathematical Statistics 32,* 1231–42.

Pyke, R. (1961b), Markov renewal properties with finitely many states. *Annals of Mathematical Statistics 32,* 1243–59.

Rao, C. R. (1976). Mathematical models for predator-prey interactions. Unpublished Ph.D. thesis, Texas A & M University, College Station, Texas.

Royama, T. (1971). A comparative study of the models for predation and parasitism. *Researches in Population Ecology, Supplement No. 1,* 1–90.

Stoy, R. H. (1932). Appendix of G. Salt. *Bulletin of Entomological Research 23,* 215–216.

Thompson, W. R. (1939). Biological control and the theories of the interaction of populations. *Parasitology 31,* 299–388.

Volterra, V. (1926). Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Accademia Nazionale Del Lindei, Rome. Classe Di Scienze Fisiche, Matematiche e Naturali. Memorie 6,* 31–133.

Watt, K. E. F. (1959). A mathematical model for the effect of attacked and attacking species on the number attacked. *Canadian Entomologist 91,* 129–144.