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INTEGRATIVE MODELS OF
POISONING VERTEBRATE PESTS

J. Hone

School of Applied Science, Canberra College of Advanced
Education, Belconnen, ACT, Australia

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J. HONE, School of Applied Science, Canberra College of Advanced Education, Belconnen, ACT, Australia 2616.

ABSTRACT: Strategies for the control of vertebrate pest are identified using mathematical models of poisoning. The models integrate aspects of foraging ecology and toxicology in a probabilistic framework. The structure, assumptions and control implications of the models are presented. Variables (control parameters) influencing the probability that a pest animal dies in a poison programme are identified and classified according to their degree of operator control. Control strategies suggested by the models are identified, and practical means of applying them are discussed. The models suggest that the probability that an animal dies is a function of 15 to 17 control parameters, of which operators have direct control over a maximum of 4: poisoned bait abundance, poison bait dispersion, the time over which poisoned bait is available, and poison concentration.

INTRODUCTION

Many methods are used to control the damage or abundance of vertebrate pests. Poisoning is one of the oldest methods, with a recorded history going back to classical Greece. Today poisoning is used against many vertebrate pests around the world, such as rodents, birds, and large mammals.

The evaluation of poisoning has concentrated on either laboratory or field testing of and acceptability and toxicity to, target and nontarget species. Many of the current field practices have evolved from a combination of rigorous experiments and field experience. Not all the practices have been exhaustively tested because it is virtually impossible to do so. Experiments to evaluate three poisons, in each of three bait types with four delivery systems, in four seasons of the year become too large to conduct in the field. An alternative approach to evaluating poisoning is to develop theoretical models based on relevant field and laboratory data and evaluate the effects of different poisoning strategies. Mathematical models can be used to indicate the response of pests to different control inputs, and to describe how the control inputs interrelate.

The principal use of mathematical models in pest control is to provide guidelines for evaluating alternative control strategies (Conway 1977, Conway and Comins 1979). If the values of model parameters can be estimated then the models may also be of great predictive value. This paper is concerned with the development of models of strategic rather than predictive value. The models are developed from theoretical and empirical backgrounds in vertebrate pest control, and aspects of theoretical and applied ecology. The integration of principles from these diverse scientific fields reveals some unusual and useful patterns.

There have been surprisingly few attempts to integrate the many patterns and processes in poisoning vertebrate pests, identify control strategies and express the results in a mathematical form or model. Gentry (1971) developed a mathematical model of rat eradication programs. The model was based on a series of simultaneous integral equations, which describe changes in the number of rats of different ages. Natural changes in abundance were described, and the effects of sterilization and poisoning examined. Batcheler (1982) developed a simple probability model to estimate the number of random bait encounters required to kill a pest. This was based on the toxic loading and piece-weight distribution of baits. Modelling has been used more extensively for evaluating chemical and other control of invertebrate pests such as cattle tick (Sutherst et al. 1979).

The aim of this paper is to describe strategies suggested by four mathematical models of poisoning vertebrate pests.

Models

The models are formulated for short time periods so that natural births, deaths, immigration and emigration are approximately zero. An attempt has been made to remove from a poisoning program many minor features and describe the essential, central elements. Population parameters such as age, breeding status, sex ratio, and weather are treated as sources of random variation. The models relate to typical vertebrate pest poison programs such as those using poisonous bait stations, throw-packs, or poisoned bait trials.

Probabilistic models are developed which estimate the probability of an animal dying in a poisoning program. The probabilistic approach reflects underlying uncertainty in describing the effects of all factors and interactions that may determine how many, or what percentage of a vertebrate pest population is killed by poisoning.

The models are based on several principles. Firstly, that the total number of animals in a population (N) is equal to the sum of the number of animals that find and eat the poisoned bait (NE), that find and do not eat the poisoned bait (NDE), and that do not find the poisoned bait (NDF).

$$N = NE + NDE + NDF \quad (1)$$

where NE, NDE or $NDF \geq 0$

Secondly, the number of animals that find and eat the poisoned bait (NE) comprises two groups: those that eat the poisoned bait and die (NED) and those that eat the poisoned bait and do not die (NEd) (Hone 1983).

$$NE = NED + NEd \quad (2)$$

Thirdly, the number of animals that eat the poisoned bait and die (NED) is equal to the product of the number of animals (N) and the probability of an animal dying (p).

$$NED = p N \quad (3)$$

The fourth principle is that the probability (p) of an animal dying is the product of the probability of an animal eating the poisoned bait (P(E)) and the probability of dying given that it has eaten the poisoned bait (P(D/E)).

$$p = P(E) \times P(D/E) \quad (4)$$

The modelling process now concentrates on estimating the probabilities P(E) and P(D/E).

Models are developed for differing ecological and control situations (Table 1). The determinants of which model is appropriate are bait dispersion and the search pattern of the vertebrate pest(s). Models based on random search by a pest use different forms of the functional response relationship commonly described for predator-prey (Hassell 1981) and plant-herbivore interactions (Caughley and Lawton 1981).

Table 1: Ecological components of probability models of poisoning vertebrate pests for differing bait dispersion and pest search patterns. The notation in the table indicates that the probability of an animal dying (p) is partly a function of that enclosed by the brackets.

Pest search pattern	Poisoned bait dispersion	
	Random	Clumped
Random	$p = f(\text{Functional response Type III})$	$p = f(\text{Functional response Type II})$
Non-random	$p = f(\text{Optimal foraging})$	$p = f(\text{Optimal foraging})$

The functional response describes the relationship between bait (food) intake and bait (food) abundance. In poisoning programs when bait is provided ad libitum this response is still relevant as it is simply a special situation described by the functional response relationship. As animal search patterns are often nonrandom, other models are developed based on such searching, and these models use aspects of optimal foraging theory (Charnov 1976 a, b, Caraco and Pull 1 am 1984).

Discussions of functional response and optimal foraging models in the literature usually assume that once an animal found food it ate the food. The models developed here do not assume this, but generate a probability that an animal eats bait, P(E), and describe what influences that probability. Hence the models are more general than that developed by Batcheler (1982) in which random search and a linear relationship between bait abundance and bait intake were assumed. The models are simpler than that developed for mantid feeding by Charnov (1976a), as vertebrate pests feed on stationary not mobile prey (bait).

Poisoning vertebrate pests most commonly involves distributing poison bait in clumps and the pests feeding in a nonrandom manner. Such a situation is described in model (iv). The other models are described for comparative purposes. Surprisingly the control strategies suggested by each model are very similar.

(i) Random bait dispersion and random search pattern.

The probability that an animal eats the poisoned bait is assumed to be a positive saturation function of the number of times an animal finds the bait (t) and a function of behavioral interference or facilitation between animals that find the bait (α). In a simple case:

$$P(E) = \left(\frac{k_1 t}{x_1 + t} \right) \alpha \quad \text{for } t \geq 1 \quad (5)$$

$$0 \leq k_1 \leq 1$$

$$x_1 \geq 0$$

where k_1 is the maximum probability or value of $P(E)$, and x_1 is the number of times required to have k_1 at half its maximum value. Equation (5) is a saturation equation as t increases. Animals showing neophobia such as some rats (Shorten 1954, Barnett 1958) and some rabbits (*Oryctolagus cuniculus*) (Rowley 1963, Oliver et al. 1982) will have $k_1 = 0$ and hence $P(E) = 0$. The coefficient α equals 1 when animals do not interact, $\alpha > 1$ represents behavioral interference between animals such that others decrease the probability, and $0 \leq \alpha < 1$ represents social facilitation, where other animals increase the probability that an individual eats the poisoned bait. The value of α is assumed to be related to the weight (W) of each animal, such that larger animals experience less interference from others, and less social facilitation. This relationship is not formalized here, but will be examined elsewhere.

The probability that an animal ingests a lethal dose of poison given that it has eaten the bait ($P(D/E)$) is a positive saturation function of the dose of poison bait ingested (f) / weight of animal (W). This is based on the classic dose-response relationship when the dose is expressed on an arithmetic scale (Snyder 1984). A simple equation for this is:

$$P(D/E) = \frac{a \left(\frac{f}{W} \right)}{\left(\frac{f}{W} \right) + b} \quad (6)$$

$$= \frac{a f}{f + bW}$$

where $0 \leq a \leq 1$ and $b > 0$. The maximum probability is a , and when $a = P(D/E) = 1.0$ then b is the dose/weight at which the probability ($P(D/E)$) is 1/2; the LD_{50} .

The weight of poisoned bait eaten (f) is the sum of the weight of bait (food) eaten (W_b) and the weight of poison eaten (W_p).

$$f = W_b + W_p \quad (7)$$

The weight of bait eaten (W_b) is assumed to be a positive saturation function of the weight of poison bait available (\bar{x}), bait dispersion (i), a function of behavioral interference or facilitation among animals that find the bait (β), and the time bait is available (T).

$$W_b = \left(\frac{k_e \bar{x}^i T}{1 + (k_2 t_1 \bar{x} + k_3 t_2 AF)^i} \right)^\beta \quad \text{for } k \geq 0 \quad (8)$$

where k_2 is the maximum weight (kg) of bait that can be eaten, AF is the weight of alternate food, t_1 is the handling time for each bait unit, t_2 is the handling time for each alternate food unit, k_3 is a coefficient and $\beta = 1$ when there is no interference between animals. When $0 < \beta < 1$ other animals decrease an individual's intake, and when $\beta > 1$ other animals facilitate greater bait intake. Hence this incorporates the effect of social rank (Brown 1975). The value of β is, as for α , a function of body weight (W).

The part of equation (8) in the outer brackets is the multispecies equivalent of the functional response of a predator or herbivore to changes in prey abundance (Lawton et al. 1974). Real (1979) showed that random prey dispersion generated a Type III response, which occurs when $i > 1$, so this was added to the basic model. Other types of functional responses (Marten 1973) are not described here but may be incorporated later. Similarly the two-prey equivalent of the Rogers (1972) random predator equation (Lawton et al. 1974) is not discussed, other than the note that it is relevant when feeding significantly reduces bait abundance (\bar{x}).

The maximum weight of bait eaten by an animal (k_2) is assumed to be linearly related to its maintenance energy requirements, which is related to body weight (Kirkwood 1983) as:

$$k_2 = d W^{0.75} \quad (9)$$

where d is a coefficient such that $d > 0$.

The weight of poison eaten (W) is related to the concentration of poison (C) in the poisoned bait.

$$C = \frac{W_p}{W_p + W_b} \quad (10)$$

Rearranging equation (10) gives:

$$W_p = \left(\frac{C}{1 - C} \right) W_b \quad (11)$$

Substituting for K_2 in equation (9) into equation (8), then modified equation (8) and equation (11) into equation (7), and equation (7) into equation (6) gives:

$$P(D/E) = \frac{a(dW^{0.75}\bar{x}^i T)^\beta}{(dW^{0.75}\bar{x}^i T)^\beta + b(1 + (dW^{0.75}t_1\bar{x} + k_3t_2AF)^i)^\beta W(1 - C)} \quad (12)$$

We now have estimates of $P(E)$ (equation (5)) and $P(D/E)$ (equation (12)). Substituting for each in equation (4) gives:

$$p = \left(\frac{k_1 t}{x_1 + t} \right)^\alpha \times \frac{a(dW^{0.75}\bar{x}^i T)^\beta}{(dW^{0.75}\bar{x}^i T)^\beta + b(1 + (dW^{0.75}t_1\bar{x} + k_3t_2AF)^i)^\beta W(1 - C)}$$

Equation (13) indicates that the probability that an animal dies is a function of 17 control parameters. As equation (13) includes two terms each with divisions, then the value of p will be determined by the relative value of parameters in the numerator and denominator of each term, rather than the absolute value of each parameter.

The strategic planning options are defined by the above relationships (Table 2). However, of all 17 parameters operators have direct control over only \bar{x} (bait density), i (degrees of bait randomness or clumping), C (poison concentration) and T (time bait is available). By prebaiting (also called free-feeding) operators attempt to increase t (number of times an animal finds the bait) to increase the probability of dying. Rowley (1958) reported an increase in the number of rabbits feeding on bait, with days since start of free-feeding, indicating an increase in the probability of eating bait ($P(E)$). Rowley (1958) also noted the social effect of feeding on the bait, corresponding in this model to social facilitation ($0 < \alpha < 1$) increasing the probability of eating. Krebs et al. (1972) reported a similar effect of group foraging on the behavior of captive great tits (Parus major). Operators have partial control over behavioral interactions (α and β) by careful design of poison sites.

Table 2. Control parameters that influence the probability of an animal dying in a poisoning program, based on a model for random bait dispersion and random pest search pattern. Control strategies suggested by the model to increase the probability and a subjective assessment of the degree of operator control over each control parameter are also listed. Strategies for other bait dispersion, search pattern combinations are outlined in the text.

No.	Control parameter	Control strategy	Degree of operator control
1	k_1	Maximum value of $P(E)$	Limited
2	t	Times animal finds bait	Partial
3	x_1	Coefficient	None
4	α	Behavioral interactions	Partial
5	a	Maximum value of $P(D/E)$	Limited
6	d	Coefficient	None
7	W	Animal weight	Limited
8	\bar{x}	Poisoned bait abundance	Direct
9	i	Poisoned bait dispersion	Direct
10	T	Time bait available	Direct
11	β	Behavioral interactions	Partial
12	b	Susceptibility to poison	Limited
13	t_1	Handling time of bait	Limited
14	k_3	Coefficient	None
15	t_2	Handling time of other food	None
16	AF	Alternate food abundance	Limited
17	C	Poison concentration	Direct

There is limited or no control over the average value of each other parameter. By strategic timing of poisoning, the amount of alternate food available (AF) and animal weight (W) can be decreased. Managing poison resistance, can decrease the LD_{50} (b).

(ii) Clumped bait dispersion and random search pattern.

With clumped bait dispersion the above model (equation (13)) is altered, but only by setting $i = 1.0$. This generates a Type II functional response (Real 1979) and simplifies the model slightly. This corresponds to the situation of extreme clumping, where all the bait is in one location. The control options are the same as for the previous model. In both models the response to an increase or decrease of a control parameter will be a curvilinear change in the value of p .

(iii) Random bait dispersion and nonrandom search.

Many models of foraging by a predator have been developed to describe how a predator forages when it responds to food abundance and depletes its own food supply. Such foraging is equivalent to nonrandom search by an animal. Mathematical description of this foraging usually assumes prey occur in patches with the patches randomly distributed. Pulliam (1974) developed a foraging model for random distribution of prey and systematic searching by the foraging animal. This will form the basis of the discussion here. Similar equations were described by Charnov (1976a), Belovsky (1984) and Persson (1985). The stopping rates are not discussed here other than to recognize they are a basic mechanism of nonrandom search.

The model developed by Pulliam (1974), described the number of prey eaten per-unit-time when two prey types were available. These correspond to the bait and alternative food which is invariably present. Pulliam's equation (9) when translated to familiar terminology and including the effect of behavior (β) is:

$$W_b + W_{AF} = \left(\frac{(\bar{x} + AF)T}{1 + t_1\bar{x} + t_2AF} \right)^\beta \quad (14)$$

where W_{AF} is the weight of alternate food eaten per-unit-time, AF is the weight of alternate food available, t_1 is the handling time for each alternate food unit, and T is the time bait is available. This equation is very similar to the functional response in equation (8)--both are positive saturation equations. Differences between the equations will be discussed elsewhere.

Rearranging equation (14), and substituting as before, into equation (6) gives:

$$P(D/E) = \frac{a((\bar{x} + AF)T)^\beta - aW_{AF}(1 + t_1\bar{x} + t_2AF)^\beta}{((\bar{x} + AF)T)^\beta - (1 + t_1\bar{x} + t_2AF)^\beta(W_{AF} + bW(1 - C))} \quad (16)$$

We now have estimates of $P(D/E)$ (equation (16)) and $P(E)$ (equation (5)), so substituting for each in equation (4) gives:

$$P = \left(\frac{k_1 t}{x_1 + t} \right)^\alpha \times \frac{a((\bar{x} + AF)T)^\beta - aW_{AF}(1 + t_1\bar{x} + t_2AF)^\beta}{((\bar{x} + AF)T)^\beta - (1 + t_1\bar{x} + t_2AF)^\beta(W_{AF} + bW(1 - C))} \quad (17)$$

Equation (17) shows that the probability that an animal dies is a function of 16 parameters. The strategic planning options are as listed in Table 1, with the exceptions of increasing the coefficient d , and bait dispersion i . A new strategy is to decrease the value of the weight of alternate food eaten (W_{AF}), though this is under limited operator control. Of all parameters only bait density (\bar{x}), poison concentration (C) and the time bait is available (T) are under direct operator control.

Pulliam (1974) also developed a model for clumped prey distribution. It is not used in the next section, as it assumed that once an animal found a clump it consumed all prey in the clump before going to the next clump. Clearly this violates the marginal value theorem of Charnov (1976b), or other stopping rules (Iwasa et al. 1981, Green 1984).

(iv) Clumped bait dispersion and nonrandom search.

Most situations of poisoning vertebrate pests involve poisoned bait distributed in clumps, and pest animals searching for it, with a nonrandom search pattern.

Caraco and Pulliam (1984) outlined a model for a group of n animals exploiting food in a patchy environment. Extending the model by including alternative food the average amount of food (poisoned bait and alternate food) consumed by individuals ($W_b + W_{AF}$) in the group in a patch is given by

$$W_b + W_{AF} = \frac{\bar{x} + AF}{n} (1 - e^{-hnT}) \quad (18)$$

where $\bar{x} + AF$ is the initial food abundance in a patch (= weight of poisoned bait offered + alternate food), h is a coefficient, T is the time in the patch (= time at a bait station), $e = 2.718$ and n is the number of animals that eat the bait.

Caraco and Pulliam (1984) described the situation where no interference occurred between animals feeding in a patch, i.e., $\beta = 1$ where:

$$W_b + W_{AF} = \frac{\bar{x} + AF}{n^\beta} (1 - e^{-hn^\beta T}) \quad (19)$$

Behavioral interference occurs when $\beta > 1$, and when $\sigma < \beta < 1$ social facilitation occurs.

Further, they assumed that when one individual had located a food patch, other members of the group immediately congregated there and started feeding. This is equivalent to the limiting value of 0 for α , because of the social facilitation.

Caraco and Pulliam (1984) assumed $P(E) = 1.0$; however, in the more general case here we will not be so restrictive. An estimate of $P(E)$ is given by equation (5). An estimate of $P(D/E)$ is given by equation (6), however, f is now estimated from equation (19).

Substituting for f from equation (19) into equation (6) gives:

$$P(D/E) = \frac{a(\bar{x} + AF)(1 - e^{-hn^\beta T}) - aW_{AF}n^\beta \left(\frac{1}{T-C}\right)}{(\bar{x} + AF)(1 - e^{-hn^\beta T}) - n^\beta W_{AF} \left(\frac{1}{T-C}\right) + bW} \quad (20)$$

Substituting for $P(E)$ and $P(D/E)$ in equation (4) gives:

$$p = \left(\frac{k_1 t}{x_1 + t} \right)^\alpha \times \frac{a(\bar{x} + AF)(1 - e^{-hn^\beta T}) - aW_{AF}n^\beta \left(\frac{1}{T-C}\right)}{(\bar{x} + AF)(1 - e^{-hn^\beta T}) - n^\beta W_{AF} \left(\frac{1}{T-C}\right) + bW} \quad (21)$$

Equation (21) indicates that the probability that an animal dies is a function of 15 parameters. This is only slightly simpler than the models above for random search (Equation 13). The control strategy options are again similar to those outlined in Table 1, with several exceptions and additions. The exceptions are changes to d , i , t_1 , k_3 or t_2 as they do not appear in equation (21). Two new variables are included: a coefficient h and the number of pest animals that eat the poisoned bait n . In both cases the control strategy is to increase the parameter which is under limited or no operator control.

Caraco and Pulliam (1984) showed that when feeding interference within a group of n foragers did not occur ($\beta = 1$) and animals foraged optimally, the rate of food intake was the same for individuals whether they were in a group or not. Also they showed the variance on daily intake per individual was n times greater for solitary than group foragers. Clark and Mangel (1984) also reported a model that predicted a reduction in the variation in individuals feeding when in a flock. Since feeding interference is unlikely to be nonexistent, these interesting results may not be of general application, but they identify an interesting area for applied research. When feeding interference occurs, an increased variance in food intake could be expected and would have important practical consequences. Conway (1981) described a model developed by Comins, which showed the consequences of each pest receiving an equal pesticide dose or an unequal dose. The latter situation increased the proportion of the population subject to a low dose and hence to higher selection for pesticide resistance. In our example feeding interference could be the mechanism producing the same result because of the increased variability in poison intake. This possibility has not been widely discussed in managing resistance to anticoagulant pesticides in rodents or other species.

CONCLUSION

Many strategic planning options for poisoning vertebrate pests have been described. The planning options for different ecological situations are very similar. Some options are currently used, such as varying the poison concentration, and amount, location, and temporal availability of poisoned bait. Other options have had limited or no use, such as using small baits to decrease handling (eating) time per-bait-unit, poisoning when there is limited alternative food, and designing bait packets or stations to decrease behavioral interference between animals.

The modelling shows how many control parameters interact in complex, usually nonlinear relationships. The models provide a theoretical framework for explaining why particular events occur when poisoning vertebrate pests. Aspects of foraging ecology are suggested as a useful area for applied pest research. Demographic characteristics (e.g., age and sex) of pest populations influence poisoning kills in several ways, especially as determinants of pest body weight, which directly influence food intake, behavior and poison susceptibility. Pest species with a large variation in body weight, such as large mammals, should have more variable responses to poisoning than small mammals. As a consequence they may develop greater pesticide resistance independent of any contribution from different breeding rates.

The models outlined describe some of the essential features of poisoning programs and reveal interesting relationships between various factors influencing the probability that an animal is killed. The models are more than an analogy but less than a facsimile of poisoning vertebrate pests. The strategic planning uses of the models are obvious, and some agreement exists with laboratory and field data. Further development will refine the strategic and predictive applications of these models.

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