# COMPARING TWO MODELS OF ALLOREGULATED PREDATORS

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## ABSTRACT

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Two models for the dynamics of predator populations without self-regulation are compared. In both models the relationship between resource density and feeding rate is of the Holling II-type, i.e. increasing towards an asymptotic value. The models differ with respect to the relationship between feeding rate and per capita rate of increase. In one of the models this relation is linear and in the other it is increasing at a diminishing rate. The properties of the two models are discussed and it is suggested that the second is more realistic. Furthermore, the second makes use of fewer parameters.

## INTRODUCTION

### Use of models

Mathematical models can be useful tool in the search for general rules and patterns governing the dynamics of natural populations. The conclusions reached from the analysis of such models are true provided that the assumptions upon which they are based are correct. However, the assumptions are almost certainly not correct and it is difficult to tell to what extent the discrepancies are important. This problem may be circumvented in two ways. The assumptions of models may either be formulated in such general terms that any conclusions drawn may have some importance for our understanding of the real world or we may test the models by comparing predictions from them against patterns observed in the real world. While the models can not be proven, evidence can in this way be provided that supports them. The utility of models in this context is not based on the accuracy of the predictions they make but on the fact that mechanisms

causing a pattern are much more simply observed and studied in a model than in the real world. These considerations focus on the importance of building models upon realistic assumptions and on the utility of models with easily interpretable mechanisms.

*Objectives*

Models of population dynamics in animal communities often consist of sets of differential equations, where each equation describes the rate of change in one population as a function of other conditions within the community. These conditions usually comprise the densities of other populations in the community. If the per capita rate of increase (PCRI) of one population depends upon (among other things) the density of the population itself, then the population is said to be autoregulated or to have intraspecific population regulation. For populations which are not autoregulated the term alloregulated is proposed. In this paper I examine two differential equations for the dynamics of alloregulated predator populations. The equations can be, and have been formulated in several ways by previous authors. In the present paper they are written so as to facilitate comparisons. These comparisons focus on: (a) the biological interpretability of the parameters used; and (b) the extent to which these two models are likely to be realistic.

THE MODELS

Model I has been proposed by Hsu et al. (1978), and a similar model is given by Roughgarden (1979, p. 443). It is given by:

$$dP/dt = P\left(\frac{b_{max}V}{A + V} - d\right) \qquad (1)$$

This is the predator component of the Volterra (1926) model for a predator-prey system, extended to account for a non-linear relationship between prey density and birth rate. The first term in the parenthesis is the birth rate of the predators. This term is zero at a prey density of zero and increases asymptotically towards a maximum ($b_{max}$) as prey density increases to infinity.

Model II, formulated by Tanner (1975) is given by:

$$dP/dt = rP\left(2 - \frac{F_{max} - F_{min}}{F - F_{min}}\right) \qquad (2)$$

The feeding rate ($F$) in this model is depending on prey density according to the Holling (1965) II-type of functional response (Fig. 1):

$$F = \frac{F_{max}V}{B + V} \qquad (3)$$

To facilitate comparisons, model I is here reormulated as follows. I assume that a functional response of the Holling II-type (eq. (3)) applies in this model too and that there is a linear relation between birth rate and feeding rate:

$$b = Fk \tag{4}$$

This model is the same as eq. (1) because combining eqs. (3) and (4) with the tautological relation:

$$dP/dt = P(b - d) \tag{5}$$

gives:

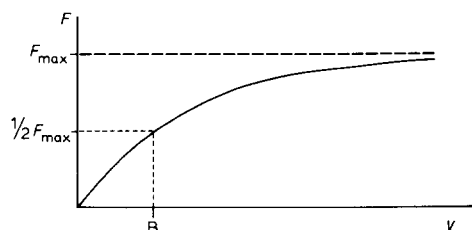$$dP/dt = P(Fk - d) = P\left(\frac{F_{max}Vk}{B + V} - d\right) \tag{6}$$



Fig. 1. Relationship between prey density ($V$) and feeding rate ($F$) of the Holling II-type.

TABLE I

Symbols

| | | |
|---|---|---|
| $A$ | = | Prey density at which a predator realizes half its maximum birth rate |
| $B$ | = | Prey density at which a predator feeds at half its maximum rate |
| $B$ | = | Birth rate |
| $B_{MAX}$ | = | Birth rate when resources are unlimited |
| $D$ | = | Death rate |
| $D_B$ | = | Basal death rate |
| $D_S$ | = | Starvation death rate |
| $F$ | = | Feeding rate (prey units per predator individual) |
| $K$ | = | Constant, relating feeding rate to birth rate |
| $\Lambda$ | = | Prey density at which the predator population is in equilibrium |
| $F_{MAX}$ | = | Maximum feeding rate |
| $F_{MIN}$ | = | Minimum feeding rate, i.e., the feeding rate at which a population goes extinct immediately |
| $P$ | = | Predator density |
| $R =$ | = | Maximum per capita rate of increase |
| $V$ | = | Prey (victim) density |

This is identical to eq. (1) as $k = b_{max}/F_{max}$ (eq. (4) if we assume that $B = A$. The relation between feeding rate $(F)$ and PCRI $((dP/dt)/P)$ is shown in Fig. 2.

Model II assumes that the maximum rate of rate of increase $(r)$ is reached for some finite value of the feeding rate $(F_{max})$ as does model I. PCRI is assumed to increase at a diminishing rate with increasing feeding rate and for small values of feeding rate (approaching $F_{min}$) PCRI is infinitely small
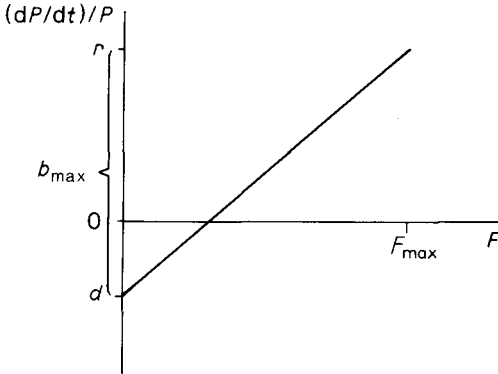


Fig. 2. Relationship between feeding rate $(F)$ and per capita rate of increase according to model I. Abbreviations are explained in Table I.
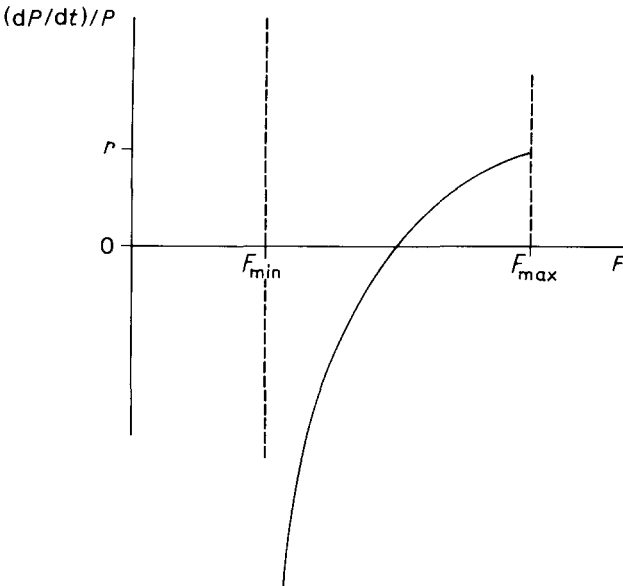


Fig. 3. Relationship between feeding rate $(F)$ and per capita rate of increase according to model II. Abbreviations are explained in Table I.

(large negative value), thus the population becomes extinct immediately. The rate of increase is not defined for feeding rate values below $f_{min}$ (Fig. 3). In model I (eq. (1)) rate of increase is defined for all positive values of the feeding rate and for comparative purposes I assume $f_{min}$ of model II (eq. (2)) to be zero. Furthermore, I believe this to be a realistic value for this kind of model. It is probably possible to obtain still more realism by assuming that there is a minimum value for PCRI, comparable to the death rate of eq. (1). This should be realistic because, however low the feeding rate, no population can decrease in less time than it takes for the individuals to starve to death, a finite time. In the version of model II that is obtained by these modifications, PCRI is defined by eq. (2) for all values of the feeding rate above that which produces a PCRI equal to the assumed minimum value. Below this value, PCRI is constant at the minimum value (Fig. 4).

DISCUSSION

*Parameters and predator efficiency*

Representing the predator population in an isocline diagram (Rosenzweig and MacArthur, 1963) yields a straight vertical line (Fig. 5) for both models.
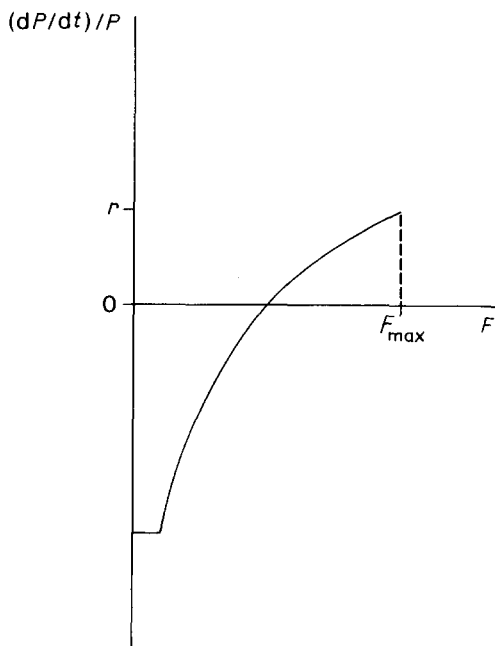


Fig. 4. Relationship between feeding rate and per capita rate of increase according to the adjusted model II.

Above a certain prey density, the predator population increases and below that density it decreases. The 'break-even' density of the prey or resource level has been symbolised with $\lambda$ by Hsu et al. (1978). In model II, $\lambda$ is simply given by:

$$\lambda = B \tag{7}$$

while in model I it is given by:

$$\lambda = A\left(\frac{d}{b - d}\right) \tag{8}$$

The $\lambda$-value has important interpretations. A predator with a low $\lambda$-value can be considered an 'efficient' predator as it is able to maintain a stable population despite a low resource density. Hsu et al. (1978) compared such predators to $K$-selected ones on the $r$–$K$ scale. The $B$-value of eqs. (3) and (7) is the prey density at which the predator reaches half its maximum feeding rate and this is obviously also related to predator 'efficiency'. When interpreting the results of a theoretical analysis, equalling the $B$-value with the $\lambda$-value is likely to be an advantage since this reduces the number of variables. Many variables, as can be incorporated into model I, is desirable only when it is necessary to separate the effects of different components that may contribute to efficiency.

*d-Value of model I*

In most populations, $b_{\mathrm{max}}$ and $r$ should be rather similar since death rate is much less than birth rate under favourable conditions. The $b_{\mathrm{max}}$- and the $r$-value may thus replace each other if one wishes to simulate a system with parameter values from real populations. However, it will most likely be difficult to make estimates of the $d$-value. The $d$-value is a parameter and represents thus a death rate that is constant and is independent of resource level, a situation which is very difficult to imagine for most predator
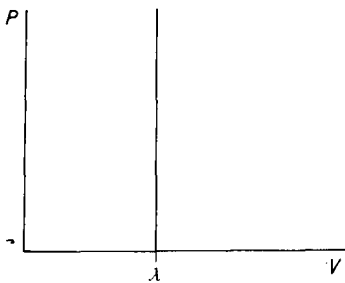


Fig. 5. Predator isocline.

populations. The concept could be 'saved' by assuming $d$ to be the death rate when no resources are available (it would thus be a rather high value) and by defining $b$ as a composite 'birth rate', including both the reduction in death rate at increasing resource levels and the actual birth rate. However, as will be demonstrated in the next section, such a $d$-value results in unrealistic properties of the model. A modification of the model is suggested in the section on further considerations.

### Shape of the feeding rate versus PCRI graph

Interpreting $d$ as the death rate in a population that is devoid of resources leads to rather high values. If the population half-life is 10 days, then $d$ computed on a yearly basis is 12.8; if the half-life is 40 days, then $d$ is 3.2. Of course, an exponential decrease is probably not the best model representing extinction from starvation. Rather, the majority of individuals would probably die a certain number of days after the disappearance of food resources. However, the model may not be too unrealistic since individuals have different resistance towards starvation. Estimates of $r$ range from about 0.2 for large ungulates (Tanner, 1975) to about 4.5 for voles (Leslie and Ranson, 1940). For such values of $d$ and $r$, model I requires that the predator is feeding close to its maximum rate if the population is to be in equilibrium (Fig. 6). Such a requirement seems unrealistic. It also seems unrealistic to assume a linear relation between feeding rate and PCRI at high
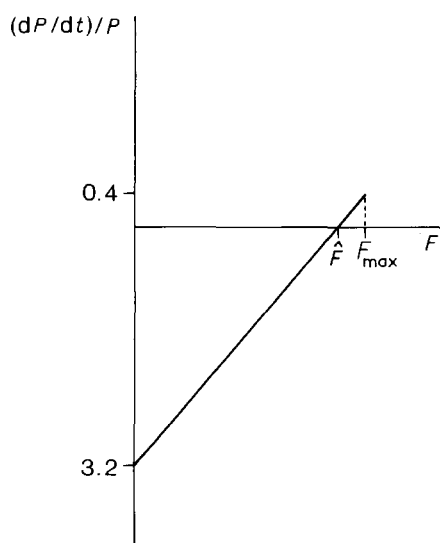


Fig. 6. Relationship between feeding rate and per capita rate of increase with approximately realistic values of death rate and maximum birth rate for a mamal.

feeding rates. Rather, one would expect the 'law of diminishing returns' to apply in this case, as it does in model II (Fig. 4). This is especially true as, for use in the analysis of community dynamics, $F$ (feeding rate) should represent kill rate and include surplus killing, cached food etc. Model II assumes that the population is in equilibrium at a food intake that is exactly half way between the minimum feeding rate (or zero in my simplification) and the maximum feeding rate. This is an inflexible assumption, but probably not too unrealistic. Field data on feral cats (Liberg, 1981, p. 44) support this. Daily food intake was 496 g during a period of food super-abundance while the 'daily food requirement' is 245 g. Furthermore, the maximum feeding rate of a predator is not very well defined, at least less so than the feeding rate at equilibrium. For applications of model II, I suggest that the former rate can be set at twice the latter. The behaviour of model II at low feeding rates is unrealistic unless use is made of the limitation suggested above (Fig. 4). The limitation may complicate mathematical analysis of the model as different relations are used in different intervals. If the model is computer simulated there is no problem, on the contrary, avoiding large negative numbers facilitates the use of the model.

*Further considerations of model I and an extension*

I have so far considered $d$ (death rate in the absence of feeding) to have the nature of an parameter and have included in $b$ all improvements in PCRI due to an increased feeding rate. The term birth rate is not ideal for this variable as it covers not only births in the literal sense. If $b$ should represents births only, $d$ too must be considered a variable. As an extension of model I, I suggest that $d$ may be partitioned into two components. One is the basal death rate ($d_b$), a parameter that represents all deaths that are independant of the feeding rate. The other part is variable and depends on the parameter $d_s$ (starvation death rate, i.e., deaths due to starvation at zero feeding rate) and the feeding rate ($F$). If it is furthermore assumed that there is a limiting feeding rate ($F_{lim}$) above which deaths due to starvation are negligible, then the following model III may be proposed:

$$\mathrm{d}P/\mathrm{d}t = P(b - d)$$
$$d = d_b, \quad F > F_{lim}$$
$$d = d_b + d_s - \frac{d_s F}{F_{lim}}, \quad F < F_{lim} \tag{9}$$

The relationship between feeding rate and PCRI is shown in Fig. 7 and is very simular to that shown by model II (Fig. 4).

Hsu et al. (1978, p. 341) in their use of model I obviously avoided the unrealistic situation represented in Fig. 6 by considering death rate to be a

parameter with the value 0.35 or 0.69 (corresponding to a yearly survival of 0.71 and 0.50, respectively). These values may realistically represent basal death rate for a vertebrate but do not account for starvation. In a pure one-prey model, this is clearly inaccurate but as a model of a field situation it may be a good compromise between realism and simplicity. Deaths primarily due to starvation appear to be rather uncommon among predators. At very low prey densities, predators may survive on alternative prey species or (birds of prey) migrate temporarily. While alternative prey species may not be common enough to permit reproduction of the predators they may prevent starvation. The dynamics of a predator population may under such circumstances be accurately described by the following version of model I:

$$\mathrm{d}P/\mathrm{d}t = P(b - d_b)$$
$$b = Fk$$

(10)

where $d_b$ is a parameter. The relationship between the feeding rate on the *main prey species* and PCRI is given in Fig. 8. The fact that a predator population's PCRI does not decrease drastically at low feeding rates is due to this supplementary feeding on alternative prey species. However, this need not be stated explicitly in the model unless the dynamics of the alternative prey species is under consideration too.
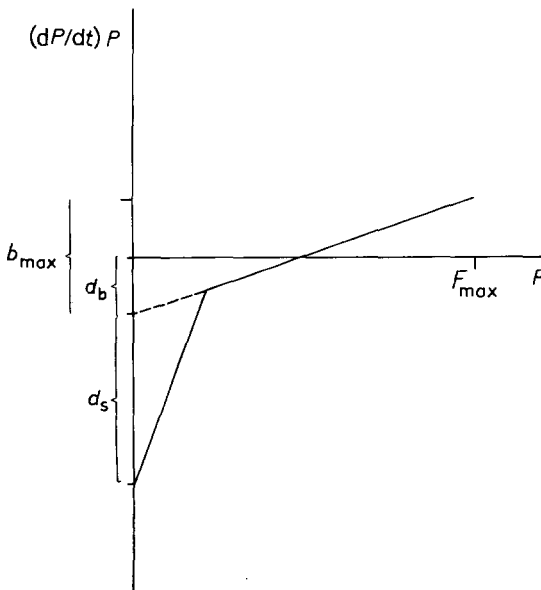


Fig. 7. Relationship between feeding rate and per capita rate of increase according to model III.
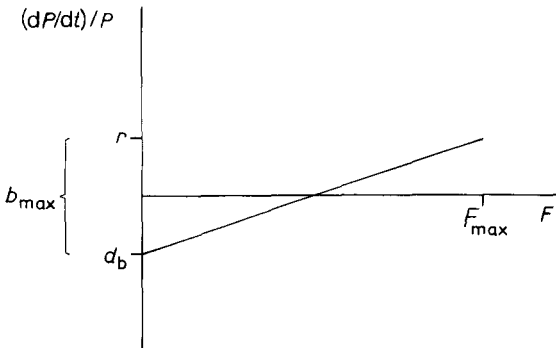
Fig. 8. Relationship between feeding rate on main prey (when alternative prey are available) and per capita rate of increase.

## CONCLUSIONS

The previous discussion should demonstrate that under most circumstances model II is considered to be superior to model I, with regard to the biological interpretability of both its parameters and its structure. However, models such as these are tools whose utility is demonstrated only through their results. It is therefore premature to state here which model should be of most use in all cases. A good model produces conclusions that subsequently are corroborated by field data. If the mechanisms of a model permits biological interpretations, then the model can also be used to interpret observed field phenomena. While either of the discussed models may fulfil these criteria, an awareness of their differences is important when selecting a model for applications.

## ACKNOWLEDGEMENTS

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