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Original papers

How to analyse prey preference when prey density varies? A new method to discriminate between effects of gut fullness and prey type composition

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Summary. State-dependent changes in prey preference are among the phenomena to be expected in studies of predator behaviour. For example, the rate of attack on each prey type is well known to be affected by the state of satiation, the dynamics of which is often assumed to parallel that of gut fullness. An interesting question is whether satiation alone is the determinant of the attack rate or whether the particular mixture of prey types in the predator's direct environment has an additional influence by itself. To detect examples of the latter type the predictive method proposed by Cock (1978) may be useful. In the present paper the predictive tool is a model built on the assumption that gut fullness is the sole internal state variable determining the attack rate. It is provided with parameter estimates from observations in monocultures of each type and then used to predict predation in mixtures of prey types. When measured predation on these prey types differs from what is predicted, the model may be too simple in various respects, one of which is that predators change prey preference in response to their own sample estimates of the densities of each prey type and their (innate or sample) estimate of the profitability of each prey type in terms of reproductive success. Thus, the lack of fit of the model poses a challenging problem, for to explain it one must identify underlying causes, such as differences in prey quality with respect to scarce nutrients or noxious chemicals that need to be detoxified or rendered harmless in other ways. The predictive approach is illustrated by analysis of preference of predatory mites (*Phytoseiulus persimilis* Athias-Henriot and *Typhlodromus occidentalis* Nesbitt) with respect to various stages of development of their prey, the two-spotted spider mite (*Tetranychus urticae* Koch). The results show that the relation between attack rate and gut fullness might well explain prey stage preference of predatory mites when the prey stages are presented together rather than each alone. In another paper by Dicke et al. (1989) marked deviations between predicted and measured diet are reported when the predatory mite, *Typhlodromus pyri* Scheuten, was offered a choice between two prey species, i.e. apple rust mites and (larvae of) European red spider mites. The underlying causes are to be revealed by further research, the impetus of which is born out by use of the method proposed by Cock (1978) and extended in this paper.

Key words: Prey preference – Predation – Behaviour – Acari Phytoseiidae

There are several ways to analyse prey preference of predators. One approach is to assess how dietary composition changes with relative density of each prey type and/or total prey density in the environment. This requires a well defined measure of preference, the desirable properties of which are discussed at length by Cock (1978) and Lechowicz (1982). This measure should not itself change with prey density (nor with prey depletion) and it should vary only as a consequence of behavioural changes of the predator (apart from behavioural changes of the prey, a possibility which cannot be ruled out without additional observations). Chesson (1983) showed that these requirements are met by an index of prey preference due to Manly et al. (1972) and further extended by Manly (1974) and Chesson (1978). An advantage of using Manly's index is that it can be used to predict consumer preference in situations other than the ones in which the index was originally estimated. These predictions are based on the assumption that predator behaviour does not change with changes in prey type supply. The predicted values can thus be used as a null-hypothesis against which actual experimental values can be compared. Examples of this method can be found in Scott and Murdoch (1983), Chesson (1981), Lechowicz (1982) and Heisey (1985).

An important shortcoming of the Manly-Chesson approach is that the index can be estimated only from predation experiments in mixtures of at least two prey types and that its value depends on the number of prey types included. An alternative approach is to use a predation model, the parameters of which are measured in experiments with one prey type present and to use these estimates in another version of the predation model extended to predict predation on each prey type in a mixture of prey types. Thus, the approach is in fact to test the null hypothesis that predator and prey do not change their behaviour as a result of the prey types being presented together. It was independently proposed by Rabbinge (1976) with much inspiration coming from De Wit's analysis of competition between plants by use of replacement series (De Wit 1963; De Wit and Goudriaan 1978) and Cock (1978) who modified a descriptive method proposed by Lawton et al. (1974) into a predictive method. Examples can be found in De Wit and Goudriaan (1978), who used De Wit's yield equation (valid only under conditions of constant prey density), Akre and Johnson (1979) who used Holling's disc equation (under the same condition as the former), and Cock (1978), Fernando and Hassell (1980) and Colton (1987), who used Rogers' variant of the Holling disc equation (valid also under condi-

tions of prey depletion). Useful comments on estimating the parameters are given by Juliano and Williams (1987).

All above-mentioned predation models have in common that they are determined by two parameters, that these parameters do not depend on prey density and that the multi-prey extensions of these models follow from specific rules such as set by the predator's time budget. Thus, when predicted and measured predation in prey mixtures differ, one or more of the assumptions underlying the model do not hold, the challenge being to identify what's wrong. In this way predation models can be used to detect the unexpected, rather than to mimic reality. To do this a stepwise approach is required starting from the simplest possible model and followed by simple and relevant extensions of this model until the predictions are not rejected anymore by experimental tests.

An advantage of Holling's disc model compared to e.g. De Wit's yield equation is that it has a clear mechanistic interpretation in terms of the predator's time budget. However, when used as a descriptive rather than mechanistic model the parameters found by a curve fitting procedure usually appear to have unrealistic values especially for predators. For example, Fernando and Hassell (1980) found that the curve fitting procedure applied to predation on spider-mite eggs by a predatory mite resulted in ca. 75 min as an estimate of the time spent handling, whereas the actual time spent per prey was equal to ca. 5 min. This difference may arise because predators reach full satiation far before the time spent handling comprises a significant part of the predator's time consuming activities. Satiation should then significantly affect the attack rate and this is exactly what is supported by a large body of empirical evidence (Curio 1976). Thus, satiation should either be standardised in prey preference analysis or the analysis should be based on a predation model extended to include satiation as a state variable. The first solution is not always possible or practicable, e.g. when the mean and variance of the time needed to catch prey are large. Hence, there are good reasons to extend predation models to include a state dependent variable, to estimate its parameters in experiments with one prey type present and to predict and compare predation rates in prey type mixtures. Deviations from the predictions may – among others – constitute an indication that behaviour has changed as a result of the prey types being presented together, rather than due to an effect on the satiation level. Clearly, the specific rule determining predation on each prey type is completely different from that in Holling's disc equation. Rather than rules set by the time budget, it is now the satiation level that sets the values of the attack rates on each prey type. This level in turn is the result of prey consumption and gut clearance. This predation process can be modelled by analogy with solved problems in queueing theory, as recognized first by Taylor (1976) and Curry and DeMichele (1977); in their view, prey mites in the predator's gut could be regarded as a line of customers waiting to be served by a service facility, i.e. waiting to be digested by the predator. By analogy with gut capacity the line of customers has a maximum length; attack rate, ingestion and gut emptying are conceived as customers joining and leaving the line depending on the length of the line and the service rate. This Markov-type model is extended by Sabelis (1981, 1985, 1986) to include partial prey consumption and predation in mixtures of prey types. In an important series of papers Metz and Van Batenburg (1985a, b),

Metz and Diekmann (1986) and Metz, Sabelis and Kuchlein (1988) formulated the full continuous version of the model, studied the asymptotic behaviour and provided some very useful approximations.

In the first part of this paper the model will be discussed and its assumptions will be examined. In the second part estimates of the model parameters are presented for the case of an acarine predator-prey system, whereas the remainder of the paper is devoted to validation of the model as an integral part of a method to analyse prey preference. The acarine predator-prey system concerns predatory mites (Acarina: Phytoseiidae) and various stages of development of a phytophagous prey mite (Acarina: Tetranychidae). It is chosen because there is convincing evidence that satiation is an important determinant of the attack rate (Sabelis 1981, 1985, 1986), and because previous attempts at analyzing prey-stage preference resulted in rejection of a two-prey version of Holling's disc equation (or rather Rogers' variant of it) (Cock 1978; Fernando and Hassell 1980).

A finite state markov model of predation in prey mixtures

Imagine a large population of identical predators in a large prey colony. They search at random and without mutual interference. Searching is now and then interrupted by resting and cleaning or by attacking and handling prey. The time required for these activities is subject to stochastic variation, but on average depends on the satiation level the dynamics of which is assumed to be related to the food content of the predator's gut. At full satiation predators will not attack, feed or harm prey, but as time proceeds food will be digested, resorbed and egested causing the degree of gut filling (and thus satiation) to decrease and the motivation for capturing prey to increase. Thus, given the discrete nature of feeding events and the stochasticity of searching periods each predator goes through a unique time series of satiation levels. The state of the individual is therefore bound to cycle, but this does not necessarily apply to the population mean as will be discussed below.

To bring mathematical treatment within the realm of queueing theory (or stochastic theory of birth-death processes) (Gross and Harris 1974) three simplifying assumptions must be made. Firstly, assume that the amount of food in prey (w) or in gut (s) consists of small, but discrete units of size u (Note that this assumption is implicit to any experimental analysis of feeding-state dependent behaviour). Secondly, assume that feeding represents a single gulp of food (Note that this is reasonable when the time constant of ingestion is small compared to the time constant of gut emptying, as in the mite example below). Thirdly, assume that the total time spent handling prey is small compared to the total time available for searching (Note that this assumption requires specific understanding of the system under consideration; it is generally valid for the mites in the example below).

Let w , the food content of the prey, consist of h food units of size u and let s , the food content of the gut, consist of n food units where n ranges from 0 (empty gut) to N (at full satiation m). Then, the resulting state space consists of integers from 0 to N where N equals the integer part of m/u . Transitions from one state to the other are either upward due to prey capture and ingestion or downward due to digestion, resorption and egestion. The upward tran-

sitions are from n to $n+h$, if all prey are of the same type and contain h food units. These transitions occur at a rate $\sigma(n)$, the rate of prey capture which depends on the satiation level (n or s). The downward transitions are set equal to one food unit, e.g. from n to $n-1$. These transitions occur at a rate $\rho(n)$, the rate of gut emptying which also depends on the satiation level (n or s). This rate is such that the mean time needed to make a transition in absence of any prey capture exactly equals the time the deterministically decreasing satiation needs to cross the same distance. This was supposed to give the best approximation to the real continuous process for sufficiently small u . Let the holding time of any state be exponentially distributed with the sum of the outward transition rates as a parameter. The inverse of this parameter then equals the mean of the exponential distribution. Therefore, the rate of gut emptying from n to $n-1$ (as well as un to $un-u$) can be obtained from:

$$\rho(n) = r_G / \ln(n/(n-1)) \quad \text{for } n = 2, 3, \dots, N$$

where r_G is the relative rate of gut emptying (t^{-1}). For $n=1$ an approximate value of $\rho(n)$ was used by taking n slightly larger than 1; for $n=0$, $\rho(n)$ was set equal to zero by convention.

Given the upward and downward transition rates the differential equations for $p(n)$, the probability that a predator is in state n , consist of three transition terms, i.e. (1) outwards (from n), (2) downwards (from $n+1$ to n) and (3) upwards (from $n-h$ to n):

$$\begin{aligned} \frac{dp(n)}{dt} &= -(\underbrace{\rho(n) + \sigma(n)}_{(1)}) p(n) + \underbrace{\rho(n+1) p(n+1)}_{(2)} + \underbrace{\sigma(n-h) p(n-h)}_{(3)} \end{aligned}$$

for $n = 1, 2, \dots, N-1$ and with $p(n-h) = 0$ for $n-h \leq 0$

For $n=0$ the equation reduces to:

$$\frac{dp(0)}{dt} = -\sigma(0) p(0) + \rho(1) p(1)$$

Because the time spent handling a prey is short, ingestion is fast and the food content of a prey may exceed one food unit, predators at less than h food units from full satiation N will consume only part of their prey. In all these cases upward transitions will end at N (instead of $n+h$). Hence the differential equation for $p(N)$ has a term representing all possible ways to end at N from $n \geq N-h$:

$$\frac{dp(N)}{dt} = -\rho(N) p(N) + \sum_{i=N-h}^{N-1} \sigma(i) p(i)$$

This system of differential equations governs the changes in $p(n)$, the probability distribution of predators over the (discretized) satiation axis. When the transition rates are constant, $p(n)$ will converge to a steady state distribution, as proven by Heijmans (1984). Under this condition $\hat{p}(n)$ can be found by selecting an arbitrary starting value for $p(0)$, solving $p(1)$ from $p'(0)=0$, $p(2)$ from $p'(1)=0$ and so on, and finally by rescaling the $p(n)$ values such that they sum to unity. The mean rate of predation F can now be found from:

$$F = \sum_{i=0}^N \sigma(i) \hat{p}(i)$$

This completes the description of the finite state Markov model of predation on one prey type. Sabelis (1986) extended this model to include more prey types. For two prey types with different rates of being captured (σ_1 and σ_2) and different food contents (h_1 and h_2) the differential equations are:

$$\begin{aligned} \frac{dp(0)}{dt} &= -(\sigma_1(0) + \sigma_2(0)) p(0) + \rho(1) p(1) \\ \frac{dp(n)}{dt} &= -(\sigma_1(n) + \sigma_2(n) + \rho(n)) p(n) + \rho(n+1) p(n+1) \\ &\quad + \sigma_1(n-h_1) p(n-h_1) + \sigma_2(n-h_2) p(n-h_2) \\ &\quad \text{for } n = 1, 2, \dots, N-1 \\ \frac{dp(N)}{dt} &= -\rho(N) p(N) + \sum_{i=N-h_1}^{N-1} \sigma_1(i) p(i) \\ &\quad + \sum_{i=N-h_2}^{N-1} \sigma_2(i) p(i) \end{aligned}$$

By setting these differential equations equal to zero and starting with an arbitrary value of $p(0)$ values of $p(1)$, $p(2)$, ..., $p(N)$ can be obtained which after rescaling such that all $p(n)$ sum to unity give an estimate of the steady state distribution $\hat{p}(n)$ over the state space. The mean rate of predation on prey type 1 (F_1) and on prey type 2 (F_2) can now be calculated from:

$$F_1 = \sum_{i=0}^N \sigma_1(i) \hat{p}(i) \quad \text{and} \quad F_2 = \sum_{i=0}^N \sigma_2(i) \hat{p}(i)$$

and the expected mean satiation level of the predator population equals:

$$E(n) = \sum_{i=0}^N i \hat{p}(i)$$

This completes the description of the finite state Markov model of predation on two prey types. Extensions for multiple prey types readily follow.

It may be questioned why the satiation-axis is discretized from the start in model building. This is done partly because estimates of the state-specific parameters cannot be obtained without defining upper and lower limits of satiation levels. Of course, one may still wonder how the discrete approximation compares to its full continuous equivalent. A full continuous model framed in partial differential equations is given by Metz and Van Batenburg (1985a, b). These equations, however, can be solved only by numerical means in which the satiation-axis is divided in discrete compartments anyway. Hence, it is decided to skip the intermediate 'posh' mathematics and to go directly from the biology to a discrete, approximating Markov model.

Estimates of the model parameters

To illustrate the method of prey preference analysis a predator-prey system of plant inhabiting mites was chosen. Females of two species of predatory mites (Acarina: Phytoseiidae), *Phytoseiulus persimilis* Athias-Henriot and *Typhlodromus occidentalis* Nesbitt, were studied to assess the relation between their satiation level (n or s) and their rate of prey

capture ($\sigma(n)$) in monocultures of various developmental stages of the two-spotted spider mite, *Tetranychus urticae* Koch. All experiments were started with young female predators at full satiation, i.e. 3 to 6 days old since final moult and sampled just after a feeding event under conditions of ample prey-egg supply. These predators were then starved for a predetermined period (20°C; 70% RH) and subsequently placed on a leaf with much prey for observation of behaviour (20°C; 70% RH). Dynamic changes in satiation level were calculated from the time series of ingestion events using estimates of available food per prey (w or h), gut capacity (m or N) and the relative rate of gut emptying (r_G and thus $\rho(n)$). Calculated satiation levels were then related to observed predatory behaviour. It is important to stress that this behavioural experiment was done in spider mite colonies formed in a natural way, i.e. with all possible cues relevant to prey searching (web, faeces, leaf damage due to feeding by spider mites, other information conveying chemicals and structures) and with all possible attributes and opportunities for prey defense (e.g. web) except that the mites cannot escape by dropping themselves because the leaf was positioned upside down on wet cotton wool. Leaves were taken from rose plants (cv Sonia).

Ingestible food per prey

An estimate of w (or h) was obtained by measurement of the weight increase due to feeding on a prey. Interruption of feeding at various time intervals showed that ingestion followed the negative exponential, $1 - \exp(-r_1 t_F)$, where r_1 is the ingestion constant (t^{-1}) and t_F is the feeding time. Estimates of r_1 are 1.8 min^{-1} for prey eggs and 0.05 min^{-1} for prey females, which is exceedingly large compared to the relative rate of gut emptying being ca. 2 day^{-1} at 20°C as will be shown below. Hence it is justified to conceive ingestion as a single gulp of food per prey.

Estimates of the amount of food ingested per prey stage are given in Table 1. These show that (1) w increases with stage of development until the deutonymph stage, that (2) w differs little between deutonymph and adult female, that (3) adult females contain much more food than ingested by one predator alone and that (4) females of *P. persimilis* ingest more food from the larger prey stages than do females

Table 1. Estimates of w , the amount of food ingested per prey stage (*Tetranychus urticae* Koch) by female predators that were deprived of food for 2 days starting in satiated state

Prey stage	w (μg) ^a	
	<i>P. persimilis</i>	<i>T. occidentalis</i>
Egg	1.0	1.0
Larva	—	1.1
Protonymph	—	2.2
Deutonymph (female)	7.3	2.9
Adult male	2.4	—
Adult female	7.8	2.8
Adult female ^b	17.1	—

^a Difference in weight of a single (but see ^b) predator before and after feeding. This weight increase was measured for 15 to 30 (but see ^b) predators by use of a Cahn Electrobalance. Standard errors did not exceed $0.1 \mu\text{g}$

^b Total weight increase of three hungry predators after feeding on a single prey female (only one observation)

Table 2. Estimates of the parameters in the mass balance equation for females of two species of predatory mites feeding on two-spotted spider mites (*T. urticae*)

Parameter	<i>P. persimilis</i>	<i>T. occidentalis</i>
$m = \max(s)$ (μg) ^a	8.1	3.3
s^* (μg) ^b	7.8	3.1
c_B ($\text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$) ^c	0.036	0.039
B (μg) ^d	7.1	2.3
c_O ($\text{egg day}^{-1} \text{ } ^\circ\text{C}^{-1}$) ^e	0.300	0.247
E (μg) ^f	4.7	1.9
c_E ($\text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$) ^g	0.014	0.011
c_A ($\text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$) ^h	0.213	0.184
c_G ($\text{day}^{-1} \text{ } ^\circ\text{C}^{-1}$) ^h	0.227	0.195
W (μg) ⁱ	25.5	9.9
W_D (μg) ^j	5.9	2.6

^a Weight increase of females after ca. 1 h *ad lib* feeding; females were starved for two days preceding the experiment and then weighed before and after feeding by use of a Cahn Electrobalance; $n = 25\text{--}38$ (see ^k)

^b Tentative estimate of the steady state satiation level

^c Estimate obtained from the decrease in female weight during the second day of a starvation period (started with females in a satiated state) where weight loss due to defaecation is negligible; $r_B = -\ln(Q)$, where $Q = (W_{t=1} - W_D)/(W_{t=2} - W_D)$ (see ^g, ^h); r_B was measured at $T = 20^\circ\text{C}$ and c_B was calculated assuming $r_B = c_B(T - 11)$; $n = 20$

^d $B = W - W_D - E - s^*$ is an estimate of the body mass that may be lost due to transpiration, respiration and secretion

^e c_O was estimated from oviposition rates of young females at various constant temperatures (15°C , 20°C , $25\text{--}26^\circ\text{C}$, $29\text{--}30^\circ\text{C}$, 32°C). For *T. occidentalis* r_O does not continue to rise linearly above 30°C ; $n = 25\text{--}35$

^f Predator eggs were collected within 2 hours since deposition and then weighed by use of a Cahn electrobalance; $n = 40\text{--}50$

^g r_E was measured by counting the number of faecal droplets and estimating their volume at one temperature only (20°C); c_E was calculated assuming $r_E = c_E(T - 11)$; $n = 10$

^h c_A was calculated from the mass balance equation and c_G equals the sum of c_A and c_E

ⁱ Weight W was measured only for females carrying a full sized egg in their opisthosoma (directly visible because body wall of predatory mites is transparent) ($n = 22$)

^j Dry weight W_D was measured by weighing females that died due to starvation and dried out for at least one day; $n = 10\text{--}20$

^k n = number of replicates per treatment

of *T. occidentalis* (Note that the relative difference is the same as the relative difference in total weight of these predators; see Table 2). These data show the importance of partial prey consumption. Evidently, ingestion is limited by gut capacity; the amount of food ingested per prey is equal to the minimum of the available amount of food per prey and the food deficit of the gut ($N - n$ or $m - s$).

Gut emptying

The relative rate of gut emptying r_G can be estimated directly by measuring weight increase after feeding to full satiation following starvation periods of increasing length (starting from predators at full satiation). Assuming that weight increase indicates food deficit of the gut these measurements were in support of a negative exponential decrease of the food content of the gut, and thus $s_t = m \exp(-r_G t)$ with $r_G = 1.84 \text{ day}^{-1}$ and $m = 8.1 \mu\text{g}$ for *P. persimilis* (no data for *T. occidentalis*). This method may be biased, however, be-

cause (1) it is difficult to define full satiation in terms of behavioural observations (criterion here: 10 successive predator-prey contacts without any attempt to attack and feed), because (2) a resorption 'leak' is inevitable, and because (3) manipulations needed to weigh the mites may disturb their behaviour. Therefore, r_G was also estimated indirectly from a simplified mass balance equation for a female predator under conditions of ample prey supply:

$$r_A s^* = r_B B + r_O E \quad \text{and} \quad r_G = r_A + r_E$$

r_A = the relative rate of food absorption from the gut (day^{-1})

r_B = the relative rate of weight loss by trans- and respiration (day^{-1})

r_E = the relative rate of egestion (day^{-1})

r_O = the rate of oviposition (eggs/day)

s^* = steady state value of the food content of the gut (near m) (μg)

B = body mass that may be lost by trans- and respiration (μg)

E = the weight of a 'fresh' egg of the predator (μg)

Females of predatory mites invest most of the ingested food into egg biomass; they are capable of producing egg biomass per day to an amount equal to their own body weight. Hence because r_O is linearly related to temperature with slope c_O and intercept close to 11°C (found by extrapolation from the linear trajectory!), all relative rates indicated by r were assumed to follow a linear relation with the same intercept (11°C) but slopes c to be measured. This leads to the following formulas for estimating r_G :

(1) $r_G = c_G(T - 11)$ with T = temperature ($^\circ\text{C}$),

(2) $c_G = c_A + c_E$ with c_E in Table 2,

(3) $c_A = (c_B B + c_O E)/s^*$ with c_B , c_O , B and E in Table 2 and

(4) $s^* = m \exp(-r_G t^*) \approx m(1 - \frac{1}{2} r_G t^*)$ with m in Table 2, t^* = mean time interval between successive prey captures under steady state conditions and at high prey density.

Note that s^* also depends on r_G , the parameter to be estimated; solving for r_G therefore requires an iterative procedure. The results are given in Table 2. For *P. persimilis* the estimate of r_G at 20°C is 2.07 day^{-1} which is quite close to the estimate obtained from the direct method discussed above. For *T. occidentalis* r_G at 20°C is 1.75 day^{-1} according to the indirect method based on the mass balance equation.

Rate of prey capture

For inactive prey stages the rate of predator-prey encounter is equal to the product of (1) prey density, (2) the width of the searching path (which – assuming prey and predator detect each other by contact only – equals the sum of the diameters of predator and prey), (3) the walking speed of the predator, (4) the fraction of time spent walking by the predator, (5) a reduction factor due to recrossing sites previously depleted of prey and (6) a reduction factor due to the fact that in the web predator and prey may pass over and under each other without contact even though their projections on the surface plane coincide. For active prey stages the rate of predator-prey encounter is equal to the sum of three product terms each of which applies to a different combination of predator and prey activity. Assuming

that predator and prey activity are independent and have a uniform probability distribution these product terms have component 3 and 4 replaced by (1) $(1 - a_s) a_p v_p$, (2) $(1 - a_p) a_s v_s$ and (3) $a_p a_s v_r$, where a is the activity, v is the walking speed, subscripts p and s stand for predatory mite and spider mite and v_r is the expected value of the resultant walking speed which according to Skellam (1958) is approximately equal to $(v_p^2 + v_s^2)^{\frac{1}{2}}$ under random walk assumptions. For active prey the recrossing factor (component 5) can be neglected when their walking movements result in homogeneous mixing of the prey population.

In principle each of the three product terms of the rate of encounter have prey density in common and the remaining components may either depend on the feeding state of the predator or that of the prey. However, both effects can be safely neglected under the conditions relevant to this paper; host plant leaves were never in the deteriorated condition where effects on prey activity are known to occur, and the prey densities considered were never low enough to bring the predatory mites in a state of increased searching activity (time intervals between captures always less than a day). Hence, the rate of predator-prey encounter is equal to the product of a rate constant C in cm^2/day and prey density D in prey/cm^2 . Experimentally established values of C are given in Table 3. These C -values increase with the stage of development of the spider mites mainly due to the increase in diameter of the prey stages and to some extent also due to an increase in their walking speed and activity. The consistent difference between the two species of predatory mites is caused by a difference in walking activity.

To obtain the rate of prey capture the rate of encounter should be multiplied by the capture success ratio R . This ratio represents the fraction of successful attacks following predator-prey encounters. Experimentally established values of R are given in Table 4. It appears that R strongly

Table 3. Estimates of C , the rate constant of encounter between female predatory mites and various developmental stages of the two-spotted spider mite (*Tetranychus urticae* Koch) on a webbed rose leaf (20°C ; 70% RH). Estimates apply to predators that feed on prey within a day since achieving a satiated state (i.e. their gut fullness exceeds 10% of gut capacity)

Prey stage	C (cm^2/day)	
	<i>P. persimilis</i>	<i>T. occidentalis</i>
Egg ^a	6.4	19.4
Larva ^b	8.0	23.7
Protonymph ^b	9.1	26.8
Deutonymph ^b (female ^c)	11.2	30.0
Adult male	11.7	33.0
Female in preoviposition phase	11.8	33.1
Female in oviposition phase	12.8	34.8

^a Recrossing areas previously freed of immobile prey stages, such as eggs and moulting stages, leads to a reduction of C unrelated to the change in overall prey density. For example, tortuous walk of predatory mites on a webbed leaf results in a 20% reduction of C due to local scale effects of predation. For mobile prey stages this reduction is of little importance due to reinvasion of local areas previously exploited

^b For moulting stages C values are equal to 70–80% times C of the preceding active stages (but see also ^a)

^c C values of male deutonymphs hardly differ from protonymphs

Table 4. Capture success ratio (%) of females of *P. persimilis* (A) and *T. occidentalis* (B) in relation to their gut fullness (%) and the stage of development of their prey, the two-spotted spider mite *T. urticae*. Each ratio is calculated from 200 to 400 predator-prey contacts and near gut capacity from ca. 1000 predator-prey contacts

Prey	Gut fullness (100 s/m)											
	0-5	5-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-95	95-100
A												
Egg	93.3	98.3	89.8	90.1	88.4	85.0	85.0	81.3	78.0	48.2	30.9	7.4
Larva	—	84.0	88.2	83.0	84.6	85.5	84.1	77.9	70.1	42.4	14.3	4.5
Protonymph	—	89.7	85.7	86.7	83.3	85.2	82.9	74.6	64.6	33.8	9.8	2.5
Deutonymph (female)	—	73.0	66.4	57.0	63.2	55.8	60.3	41.2	44.8	22.9	1.2	0.0
Adult male	—	69.0	72.5	66.5	64.0	61.0	72.1	54.2	48.3	29.2	8.7	1.1
Adult female	79.6	83.0	83.7	75.2	71.2	64.0	51.9	34.7	24.0	18.5	1.5	0.0
B												
Egg	55.8	93.6	85.4	27.3	21.7	15.2	10.3	8.3	4.7	2.2	0.7	0.3
Larva	—	88.3	73.8	23.7	16.6	18.8	5.4	3.3	3.0	1.2	0.4	0.1
Protonymph	—	75.0	59.4	16.2	15.4	12.1	3.1	2.2	1.1	1.0	0.2	0.0
Deutonymph (female)	—	65.1	6.2	5.6	1.2	0.8	1.1	0.6	1.0	1.0	0.0	0.1
Adult male	—	85.2	4.9	6.4	1.5	3.1	1.1	1.2	0.3	0.6	0.6	0.0
Adult female	5.7	11.2	1.2	0.7	0.5	0.6	0.3	0.3	0.0	0.4	0.0	0.0

depends on the developmental stage of the spider mites, on the species of predatory mites and on their satiation level. Given prey density, the rate of prey capture can be calculated for any satiation level from Tables 3 and 4 by use of the following simple equation:

$$\sigma_i(n) = D_i C_i R_i(n)$$

where the subscript *i* denotes the prey stage under consideration. Were the predator to stay at level *n*, then the inverse of $\sigma(n)$ represents the mean time spent searching between two consecutive prey captures. A more appropriate estimate of the mean time interval between feeding events would be to sum the mean searching time and the mean handling time:

$$\sigma'_i(n) = (t_s + t_{H_i})^{-1} \quad \text{where} \quad t_s^{-1} = \sigma_i(n)$$

This formula is a reasonable approximation when the total time spent handling is small and when handling does not preclude attacks on other prey that happen to pass by. The first assumption holds in that total handling time does not exceed 10% of the total time available. Evidence in support of the second assumption is provided by the observation of Sandness and McMurtry (1972), that predatory mites may stop feeding when disturbed by contact with another prey and that this event may be followed by an attack on the disturber. These responses, however, are quite rare because usually predators approach satiation early in a feeding period and are therefore less motivated to attack prey passing by during the rest of the feeding period. Mean values of the handling time of hungry and satiated predators are given in Table 5. These data show that hungry predators take more time to handle a prey than satiated predators, and that it takes more time to handle large prey stages than it takes to handle small ones.

In conclusion it is clear that developmental stages of spider mites differ in the amount of ingestible food and in the risk of being captured by predatory mites, that females of the two species of predatory mites differ in gut capacity, rate of gut emptying and rate of prey capture, and that their rate of prey capture depends on satiation

level. It may be questioned whether the food content of the gut is the only state variable determining the hunger drive of the predator. This may be too simple a hypothesis to account for all hunger related behaviour (Dethier 1976). To put it in the form of a testable hypothesis: Does a certain level of gut fullness induce the same searching behaviour whether it is achieved just after food ingestion or through gut emptying? The answer is yes, but as may be expected exceptions are known. For example, severe starvation for more than 2 days at 20° C can lead to irreversible loss of strength or increased aggressiveness for a few hours, even after the gut was filled to capacity. Despite these noteworthy exceptions satiation seems to be an unambiguous indicator of the motivational state of the predator provided the time intervals between prey captures do not exceed 2 days (Sabelis 1981). This is not to say that there is only one state variable, but rather that gut fullness is a good indicator in case there are more state variables together determining the motivational state.

Table 5. Time spent feeding and handling by females of two species of predatory mites in relation to the stage of development of their prey, the two-spotted spider mite *T. urticae*

Prey stage	Handling time (min) ^a			
	<i>P. persimilis</i>		<i>T. occidentalis</i>	
	Hungry ^b	Satiated ^c	Hungry ^b	Satiated ^c
Egg	6.2	3.2	10.8	6.2
Larva	15.6	8.7	16.1	9.3
Protonymph	18.7	8.6	18.3	12.3
Deutonymph (female)	36.2	27.8	30.8	14.4
Adult male	32.7	15.9	33.4	25.6
Adult female	36.8	28.2	45.6	19.1

^a Means calculated from 40 to 110 observations

^b Predators were starved to 1 day starting from a satiated state (20° C, 70% RH)

^c Predators, reared under ample prey supply, had fed on at least one prey egg within the 4 hours preceding the handling period to be measured

Validation of the finite state Markov model

To validate the performance of the Markov model predictions of the predation rate were compared with measurements in experiments with either a single type of prey present or with a mixture of prey types. The first series of predation experiments was done with females of *P. persimilis* as predator and two prey stages, eggs and females of the two-spotted spider mite, *T. urticae*. To prevent egg deposition prey females were used that were in the preoviposition phase. The following features of the experimental procedure are relevant here:

(1) *the experimental arena* consisted of a leaf disc with 3.7 cm diameter; it was punched out of the centre of a rose leaf (*Rosa canensis*; cv Sonia); the disc was positioned upside down on water soaked cotton wool in a Petri dish; the water barrier surrounding the disc was to prevent the mites from escaping;

(2) *prey egg density at the start* of the experiment was established by releasing spider-mite females in the oviposition phase in adequate numbers on the day before and by removing these females and the surplus of eggs just before the predation experiment; the spider-mite females were carefully removed by goading them with a needle so as to drive them to the edge of the disc whereupon they were removed by use of a brush; the surplus of eggs were removed by puncturing them with a thin needle; these methods ensured that damage to the web structure was kept to a minimum;

(3) *initial density of prey females* was established by releasing the desired number of prey females on the leaf disc ca. half a day before the experiment; these females had moulted only a few hours before transfer to the disc; hence, they were definitely in the preoviposition phase for at least 1.5 days;

(4) *mixtures of prey eggs and prey females* were established in essentially the same way, but the preoviposition females were not released until a few hours before the experiment started; the densities of each prey stage were chosen so as to obtain approximately the same amount of ingestible food (ca. 16–20 μg) per cm^2 webbed leaf area;

(5) *prey densities* were chosen within the range of densities observed on greenhouse roses in absence of predators, i.e. between 0 and 60 eggs per cm^2 webbed leaf area (ca. 40 eggs on average) and between 0 and 6 females per cm^2 webbed leaf area (ca. 4 females on average);

(6) *the condition of the predator* was standardized by using young females whose last moult had occurred 3–8 days previously and by allowing them an adaptation period of 8 to 12 h prior to the actual predation experiment; in this period the predator was placed on a leaf disc with prey at exactly the same density and stage composition as in the subsequent predation experiment; in this way the predators were allowed to enter steady state conditions before measurements were made; after the adaptation period the predators were transferred on an excised part of the leaf disc to a new disc with prey density at the initial standard level;

(7) *the experimental period* was set at 10 h; if the predator dispersed from the disc into the water before elapse of the 10 h period, the replicate was discarded from further analysis because the exact moment of departure was not known;

(8) *constancy of prey density* could not be ensured by replacement of the prey killed, but the decrease of prey density was kept within acceptable limits by selecting a sufficiently

short experimental period and a sufficiently large size of the disc (and webbed leaf area); would the predator consume prey eggs at a maximum rate of 1 per hour and prey females at one per 3 h, even then would the decrease in overall prey density not have exceeded 1 unit of prey egg density or 0.33 unit of prey female density given the 10 cm^2 leaf disc and the 10 h period;

(9) *the number of prey killed* was obtained from counts of the number of live prey and, as a cross check, also from direct counts of the number of prey remnants; the latter method was not always feasible because remnants of predator-consumed eggs may not be accurately distinguished from eggs punctured by the needle (in order to get rid of the surplus); in case some of the mobile prey were found drowned in the water these records were not included in the calculation of the number of prey consumed by the predator; correction of the results for influence of abiotic mortality was not necessary being negligible in all the control experiments carried out;

(10) *the number of replicates* of each experiment was invariably equal to 20; this was achieved by continued experimentation until the fixed number of replicates was obtained;

(11) *environmental conditions* were identical to those present during the behavioural observations, i.e. 20°C, 70–75% RH and continuous light.

This completes the description of the experimental procedure of the first series of experiments. The second series was set up in a very similar way except that another species of predator was used (*T. occidentalis*), that the experimental period was doubled (20 h) and that the temperature was slightly higher (21°C). The third series differed from the second only in that densities of the two prey types offered simultaneously were made equal (rather than keeping total amount of food offered at a more or less constant value, as done in the other two experiments).

It should be stressed that the experimental procedure used here differs largely from methods used by other authors. Hence, straightforward comparison of results may be problematic and it is therefore useful to point out some salient properties that are shared by the experiments discussed in this paper, but that need scrutiny before justifying comparison with results obtained by other authors:

(1) predation was measured under steady state conditions using predators standardized with respect to sex, age, ovipositional and feeding history;

(2) females of the prey, *T. urticae*, were used to deposit eggs on the leaf discs, thereby causing feeding damage to the leaf and leaving web, faeces, pheromones etc. behind; alternative prey stages were transferred to leaf discs treated in this way;

(3) in case the alternative prey stages were adult females, care was taken to prevent them from laying eggs by selecting females in the preoviposition phase.

Experiments published so far usually differ in one or more of these aspects.

The results of the three experiments referred to above are presented in Tables 6, 7 and 8, together with steady state calculations of the mean predation rate and the mean gut fullness by use of the finite state Markov model. Apparently, there is little difference between measured and predicted rate of predation in monocultures of prey as well as mixed cultures of prey, deviations being well within two times the standard error of the mean predation rate established by experiment. Hence, there is no good reason to

Table 6. Predation rate of females of *P. persimilis* in mono- and mixed cultures of eggs and non-gravid females of the two-spotted spider mite, *T. urticae*

Density (prey/cm ²)		Measured Predation rate (prey/10 h)		Predicted Predation rate (prey/10 h)		Predicted Gut fullness (%)
Eggs	Females	Eggs ^a	Females ^{ab}	Eggs	Females	
2	–	3.15 (0.24)	–	3.48	–	51
10	–	6.50 (0.26)	–	6.64	–	89
20	–	8.30 (0.52)	–	7.74	–	93
40	–	9.65 (0.41)	–	9.23	–	95
–	0.5	–	0.80 (0.11)	–	0.92	60
–	1	–	1.05 (0.08)	–	1.31	69
–	2	–	2.00 (0.14)	–	1.81	76
–	4	–	2.10 (0.12)	–	2.43	82
5	1.5	4.90 (0.27)	0.65 (0.15)	4.40	0.89	85
10	1	6.50 (0.31)	0.60 (0.19)	6.15	0.39	90
15	0.5	7.15 (0.22)	0.05 (0.05)	7.08	0.14	92

^a Mean and standard error between brackets; 20 replicates per experiment^b Young adult females in the preoviposition phase**Table 7.** Predation rate of females of *T. occidentalis* in mono- and mixed cultures of eggs and larvae of the two-spotted spider mite, *T. urticae*

Density (prey/cm ²)		Measured Predation rate (prey/20 h)		Predicted Predation rate (prey/20 h)		Predicted Gut fullness (%)
Eggs	Larvae	Eggs ^a	Larvae ^a	Eggs	Larvae	
5	–	4.3 (0.32)	–	3.94	–	70
15	–	5.15 (0.35)	–	5.39	–	84
40	–	7.05 (0.30)	–	7.35	–	89
–	5	–	3.35 (0.15)	–	3.45	70
–	10	–	4.3 (0.23)	–	4.16	77
–	20	–	5.3 (0.22)	–	5.10	83
5	10	1.9 (0.12)	3.35 (0.20)	2.03	2.98	82
10	5	3.9 (0.20)	1.35 (0.18)	3.74	1.47	83

^a Mean and standard error between brackets; 20 replicates per experiment**Table 8.** Predation rate of females of *T. occidentalis* in mixed cultures of eggs and alternative stages of the two-spotted spider mite, *T. urticae*. Density of eggs and density of alternative stages were equal to 5 per cm² leaf area

Alternative prey: Development stage	Measured Predation rate (prey/20 h)		Predicted Predation rate (prey/20 h)		Predicted Gut fullness (%)
	Eggs ^a	Alternative stage ^a	Eggs	Alternative stage	
Larva	2.6 (0.15)	1.9 (0.16)	2.53	2.00	79
Protonymph	2.8 (0.19)	1.4 (0.17)	2.70	1.39	78
Deutonymph (female)	2.95 (0.15)	1.1 (0.18)	3.27	0.93	75
Adult male	3.35 (0.22)	0.85 (0.15)	3.15	0.92	75
Adult female in preoviposition phase	3.85 (0.19)	0.15 (0.08)	3.63	0.38	72

^a Mean and standard error between brackets; 20 replicates per experiment

assume that prey stage composition has an effect on prey preference, other than through its effect on satiation. The results clearly show that it is possible to predict predation in prey mixtures from parameter estimates based on observations of predator behaviour in prey monocultures and their relation to the satiation level. Yet in theory, there may still be changes in behaviour compensating each other's effect on diet composition. Hence, the agreement between

measured and predicted diet is not a definite proof of the absence of behavioural changes due to the predator experiencing two prey stages together. Such a proof would require additional observations of predatory behaviour in prey mixtures. These observations were not done extensively because preliminary work did not provide any clue as to the possibility of compensatory changes.

Tables 6–8 also provide estimates of mean gut fullness

by use of the Markov model. These suggest that gut fullness is unlikely to be the same in prey stage mixtures despite measures taken to standardize food supply, such as in terms of total food weight (Table 6; ca. 18 µg food in prey mixtures) or in terms of prey numbers (Table 8; 5 of each prey type per cm²). These standardisations tend to be effective only when the prey stages differ little in food content and predation risk, as is the case for eggs and larvae of *T. urticae* (Table 7). Thus, given that not only $R_i(n)$, the success ratio, but also $R_i(n)/R_j(n)$ ($i \neq j$) depends on gut fullness (check Table 4), and given that the food content largely differs between the prey stages, differences in gut fullness and relative prey preference are to be expected when prey mixtures vary. Fernando and Hassell (1980) also analysed preference of *P. persimilis* in relation to different developmental stages of *T. urticae*. They used the 'random predator' equation with two parameters, i.e. catch rate and handling time (Rogers 1971; Royama 1972), to describe the functional response to prey density in monocultures of prey stages. These were then used to predict diet composition in mixtures of prey stages. As this predation model does not take the feeding state of the predator into account, the measured diet in prey stage mixtures is likely to be different from the predicted diet, because at least part of the discrepancies result from ignoring the effects of the predator's feeding state on the attack rate. This may explain why Fernando and Hassell (1980) found marked deviations from their predictions indicating that there is some change in predator searching behaviour arising from two prey types being presented together. The preference analyses presented in this paper suggest that these changes in searching behaviour may be the result of changed feeding states rather than of changes in prey stage preference *per se*.

When diet predictions fail

Changes in prey preference may become manifest by use of the method advocated by Cock (1978) and extended by Sabelis (1986; this paper). However, even if observations on predatory behaviour under supply of a single prey type fail to explain the predator's diet in prey mixtures, it would still be premature to infer a change in prey preference as a result of the prey types being presented together. This is because a change in any of the model's parameters may be related to properties of the prey or to properties of the predator or to both. To see this consider first the rate constant of encounter C_i which clearly depends on walking activity of both prey and predator. Thus a failure to predict the diet in prey mixtures may result from changes in prey behaviour alone. However, this possibility can be ruled out quite easily by additional observations in prey type mixtures. Failures to predict may also result from increased walking activity of the predator. Such a kinetic response leads to proportionally equivalent increases of C_i for all prey types and, through its effect on satiation, this may lead to a shift in prey preference that does not necessarily contradict the observations on predatory behaviour made on leaves with a single type of prey. A more direct change through C_i can only occur by differential enlargement of the distance of prey type detection (although this could also result from one type of prey causing increased conspicuousness of the other). A second parameter to be considered when diet prediction fails is the success rate after predator-prey contact (or detection), $R_i(n)$. This parameter is also

influenced by properties of prey and predator and additional behavioural analysis is thus required to elucidate how much can be attributed to the prey and how much to the predator. As a third possibility, handling time should be mentioned. This parameter may also be the result of prey and predator related properties. Yet in the mite example above, it seems exceedingly unlikely to be a major cause of a deviating prediction (even if handling time would change due to the prey types being together). Finally, food quality and food conversion could be factors underlying a difference between predicted and measured diet. The parameters determining these components, however, do not allow a clear distinction between predator-related and prey-related properties.

Thus, in case diet prediction fails, careful analysis is required to trace the causes and to determine whether they can be attributed to the prey or predator or to both. The logical next question is *why* it is more profitable to change prey preference (profit in terms of reproductive success). Under the assumptions of the Markov model fitness is maximized when the rate of food absorption (from gut into haemolymph) equals $r_A m$. Thus, given that handling time is short relative to the intercatch time interval, it makes sense that predatory mites consume both prey stages when presented together and that they attack them as vigorously as they do when presented alone. Had prey preference changed, however, then one may expect a shift towards consumption of the more profitable prey type or the more profitable prey mixture (e.g. in the case of complementary food quality of prey types). Thus prey quality is likely to be the ultimate cause of any behavioural change with respect to prey selection. The analysis of prey quality is therefore a major task to understand the adaptiveness of foraging decisions.

Some first examples of failures to predict predation in mixtures of prey types are available. Dicke et al. (1988; 1989) applied the method of prey preference advocated by Cock (1978) and Sabelis (1986; this paper) to the case of prey *species* selection by predatory mites. They found large deviations between measured and predicted consumption of apple rust mites and (larvae of) European red mites by females of two species of predatory mites: *Typhlodromus pyri* Scheuten and *Amblyseius potentillae* (Garman). An interesting possibility discussed by these authors is that differential prey quality may arise from prey-specific concentrations of nutrients, such as carotenoids that are essential for diapause induction. The predictive method of prey preference analysis may thus provide a useful tool in detecting shifts in prey selection and may help to formulate new questions as to the proximate and ultimate causes of these shifts.

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