THE ASSESSMENT OF PREFERENCE

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SUMMARY

(1) Of the eight methods of measuring preference used in the past, only the widely used index C of, for example, Murdoch (1969) (method 4), the indices α and β of Manly, Miller & Cook (1972) (method 7) and the second index proposed by Jacobs (1974) (method 8) do not have major drawbacks.

(2) Methods 4 and 8 are only suitable when the exploitation of prey is a negligible factor. In such situations, Index 8 is most sensitive to slight preference and Index 4 to great preference. Since Method 4 is best adapted to graphical display, it is the more useful approach.

(3) Where exploitation is not negligible, Method 7 provides a suitable index (β) which should be used.

(4) The predictive approach of the two-prey functional response models although involving extra experiments, yields more information (e.g. Figs 2(b) and 3(a)) and should be used in conjunction with the descriptive index β.

INTRODUCTION

Predators, when offered a choice between two or more prey types, will often show a preference for one of them. This results in more of that prey type being eaten than would be expected on the basis of their respective densities. In any predator–prey population model involving more than one prey type, it is therefore of importance to be able to assess and hence predict a predator's preference towards the various prey types. In the first part of this paper various methods of assessing preference used in the past are examined. It will be seen that some of these are unsuitable, while others do not differ from previous methods. The inter-relationships and similarities of these approaches are shown. In the second section the adaptation of functional response models to two-prey interactions and their use in predicting preference are described. These results are related to the methods described in the first section, and recommendations are made on the most suitable approaches to use.

We shall consider the simplest of multi-prey systems: where there is a single predator species and two prey types (I and II). More prey types may often be present, and some indices of preference can incorporate these. When this is not possible, a suitable approach is to pool all prey except type I into the type II category and treat as a predator and two prey interaction. Although these remarks are made with predator-prey interactions in mind, they also apply directly, or with slight modifications, to host-parasitoid interactions.

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REVIEW OF METHODS PREVIOUSLY USED

In the following review, eight methods of assessing preference are considered in turn. In the interpretation of these methods, the following basic symbols are used:

N_e, N_e' —the numbers of prey types I and II eaten,

N, N' —the numbers of prey types I and II initially present,

S_e —the total number of prey eaten; for the two-prey situation, $S_e = N_e + N_e'$,

S —the total number of prey initially present; for the two-prey interaction, $S = N + N'$.

Further symbols are introduced and defined as necessary.

Although these symbols are defined as actual numbers, N_e, N_e' and S_e can also be considered as rates of consumption, and N, N' and S as densities. It will become apparent that for all except the first method below, the time elements of the consumption rates and the area or volume elements of the prey densities will cancel out. Similarly these symbols can be considered in terms of biomass instead of numbers.

In comparing the suitability of different methods, the following factors are considered.

(i) The scales of the resultant index. It is preferable for both negative and positive preference to have finite scales symmetrical about zero.

(ii) The adaptability of the method to include more than two prey types. Alternatively, as mentioned above, this can be achieved by pooling all except prey type I into the prey type II category.

(iii) Whether maximum index values are attainable at all combinations of prey densities.

Generally, it would seem that the fulfilment of (ii) is mutually incompatible with the fulfilment of (iii).

It will be seen that in most of the following methods the prey densities are assumed to remain constant. However, unless prey are replaced as they are eaten, the prey densities will decrease, and hence, unless the prey are eaten in the proportions at which they are present, the relative densities of the prey types will change and the descriptive equations will not be suitable. Only if the numbers of prey present are large, and the number eaten relatively small, will this exploitation effect be relatively unimportant. Otherwise, it should be considered when selecting a suitable analytical method.

Method 1

Scott (1920) measured the preference shown by mackeral using the term N_e/N, the ratio of the rate of consumption of a prey type to the density at which it is present. The former was measured as numbers per unit of time (dimension T^{-1}), whilst the latter was measured as numbers per unit area (dimension L^{-2}), resulting in an index of dimensions $L^{-2}T^{-1}$. No measure of the total food eaten or available is incorporated in this index, and so it cannot give any real estimate of preference. This measure does not seem to have been used since.

Method 2

By comparing the proportion of a predator's diet consisting of a given prey type with the proportion of the available prey which were of that type, Savage (1931) obtained a measure of preference. Thus, the preference for prey type I is defined as:

$$\text{Index } 2 = \frac{N_e/S_e}{N/S}. \tag{1}$$

Negative preference (i.e. preference for prey type II) will cause the value of this index to vary from one to zero, while positive preference will result in a range of from one to infinity. Clearly more than one prey type can be included. However, it can be seen that the maximum index value attainable depends upon the relative densities of the prey types. For example, if five each of prey types I and II are present, greatest preference for type I occurs when all of type I are eaten and none of type II; this results in a maximum value for Index 2 of 2·0 (i.e. (5/5)/(5/10)). On the other hand, if two of type I and eight of type II are present, the maximum value of Index 2 is 5·0 (i.e. (2/2)/(2/10)).

Three Russian workers all independently rediscovered this index in 1939 (Ivlev 1961). It has since been used by Menge (1972) and discussed by Jacobs (1974) who refers to it as the Forage Ratio.

Method 3

Larsen (1936) used the reciprocal of Index 2:

$$\text{Index } 3 = \frac{N/S}{N_e/S_e} \tag{2}$$

The resultant scales are the converse of those obtained for Index 2, resulting in the further disadvantage that as preference increases, the value of the index decreases.

Method 4

This is the most widely used index, and it has been independently proposed at least five times.

Cain and Sheppard published a series of papers (e.g. Cain & Sheppard 1950) on the selection of colours and patterns of the snail, *Cepaea nemoralis* L., by predatory birds such as thrushes. In presenting their data, they did not formalize an index as such, but did compare the ratio of the number of each prey type in the diet with the ratio in the environment, to obtain a measure of preference. In effect,

$$\text{Index } 4 = \frac{N_e/N_e'}{N/N'}. \tag{3}$$

Kettlewell (e.g. 1956) presented his results on predator selection of the peppered moth, *Biston betularia* L., in a similar manner.

Tinbergen (1960), studying predation by small insectivorous birds in the field, approached this problem from a slightly different angle. He defined a model which, for two prey types, takes the form,

$$\frac{N_e}{S_e} = \frac{rN}{rN + r'N'} \tag{4}$$

where r and r' are the 'risk indices' of the two prey types. The risk index is defined as the instantaneous rate of capture per prey individual: N_e/NT where T is the total time considered. Rearranging eqn (4) gives

$$\frac{r}{r'} = \frac{N_e/N_e'}{N/N'} = \text{Index } 4. \tag{5}$$

Murdoch (1969) formally defined this relationship in the form

$$\frac{N_e}{N_e'} = C\frac{N}{N'} \tag{6}$$

where C is equivalent to Index 4.

Elton & Greenwood (1970) suggested a mathematically derived description of preference and switching. In the absence of switching, this model is of the form

$$\frac{N_e}{N_e'} = \frac{N}{N'} \cdot \frac{v}{v'} \tag{7}$$

where v and v' are the visibilities of the two species to the predator. As used, the ratio v/v' is equivalent to the ratio r/r' derived from Tinbergen's model, and hence is the same as Index 4.

Jacobs (1974) proposed two new indices of preference. The first of these he defined as

$$Q = \frac{m_A}{m_B} \tag{8}$$

where m_A and m_B are the mortality rates of the two prey types. Changing to the symbols used here, Jacobs showed that transforming eqn (8) gives

$$Q = \frac{N_e/S_e(1 - N/S)}{N/S(1 - N_e/S_e)}. \tag{9}$$

Substituting for S and S_e and rearranging reveals this again to be the same as Index 4.

This index has the same unwieldy scales as that introduced by Savage (Index 2)—one to zero for negative preference and one to infinity for positive preference. However, Jacobs (1974) has pointed out that, by using the logarithm of the index, symmetrical scales for negative and positive preference can be obtained. The actual prey densities do not affect the maximum attainable value of this index. Extra prey types cannot be incorporated without pooling them in the type II category.

Method 5

Ivlev (1961) developed a more sophisticated index, which compares the relative proportions of prey eaten, taking the form

$$\text{Index } 5 = \frac{N_e/S_e - N/S}{N_e/S_e + N/S}. \tag{10}$$

The value of this index will vary from zero to minus one for increasing negative preference, and from zero to plus one for increasing positive preference. Such a scale is much easier to use and comprehend than those resulting from the previous methods. Due to this finite scale, Index 5 is more sensitive to slight preference than those indices with infinite scales. However, as Landenberger (1968) and Jacobs (1974) have pointed out, the maximum (or minimum) value attainable for Index 5 depends upon the relative prey densities (cf. Method 2). For example, if five of each prey type were present, maximum preference for type I would result in a value for Index 5 of 0.33 (i.e. $(1 - 0.5)/(1 + 0.5)$); whereas, if two of prey type I and eight of type II were present, this would lead to a value of 0.67 (i.e. $(1 - 0.2)/(1 + 0.2)$). Thus, preference values calculated using this index for different prey densities are not directly comparable. The proportion of the maximum

attainable value for each combination of prey densities could be compared (Jacobs 1974), but this is too cumbersome to be practical. This method does, however, have the advantage that more than two prey types can be included.

Method 6

A less well known model of preference was proposed by Rapport & Turner (1970), based on the use of 'standard prey densities'. This term they defined as the minimum density of prey at which the predator can obtain its food requirements. To measure food requirements, the most feasible approach is to take the upper asymptote of a functional response. However, since it is at this point that the consumption of prey changes very little with large changes of prey density, estimation of the standard density will be subject to large errors. This drawback seems unavoidable. The 'no-preference' model assumes that, when two prey types are present at half their standard densities, the predator obtains half its food requirements from each:

$$\mu = (\mu' + \mu'')/2 \tag{11}$$

where μ is the total consumption, and μ' and μ'' are the consumptions of prey types I and II at their standard densities. When preference occurs, eqn (11) can be written as

$$\mu = (p'\mu' + p''\mu'')/2 \tag{12}$$

where the parameters p' and p'' are stated to 'have an obvious interpretation', presumably the ratio of the observed consumption to the expected consumption. They continue by defining the preference for prey type I to type II, p_{12}, as the difference between p' and p''. Since, due to the use of standard densities, p' and p'' will vary from zero to two and sum to two, the value of p_{12} will vary from zero to minus two for negative preference and from zero to plus two for positive preference. Although this model can be expanded to include more than two types of prey, the difficulties caused by its structure and interpretation render it an unsuitable alternative. This approach has been used by Rapport, Berger & Reid (1972) studying the food preference of *Stentor coeruleus* Ehrenberg, but it does not seem to have been used elsewhere.

Method 7

This method, suggested by Manly, Miller & Cook (1972) is the only one which allows for the exploitation of prey during the course of the experiment. The importance of exploitation, as outlined in the introduction to this section, is that the prey densities change as prey are eaten. Clearly, if no preference is shown, the changes will be in proportion to the initial prey densities, and the exploitation will not affect the ratio or proportions of the prey types. However, once the predator shows preference towards one prey type, the ratio (or proportions) of the prey types will change, and the descriptive equations (e.g. eqn (3)) will no longer be applicable. Manly, Miller & Cook (1972) derive an index α, similar to Index 4, which allows for exploitation. They postulated the instantaneous relationship

$$P_1 = \frac{n_e}{s_e} = \frac{n}{(n + \alpha' n')} \tag{13}$$

where P_1 is the probability of the next prey found being of type I, α' is the preference for prey type II, and n_e, s_e, n and n' are the instantaneous values of N_e, S_e, N and N'. This rearranges to give the instantaneous version of Index 4:

$$\alpha = \frac{1}{\alpha'} = \frac{n_e/n_e'}{n/n'} . \tag{14}$$

This means that when exploitation is negligible (or prey are replaced as they are eaten), α and α' are equivalent to Index 4. From the instantaneous relationship (eqn (13)), the authors derive a complex probabilistic solution for α' which allows for exploitation. By simplification, they obtain a good approximation of this which is suitable for use when the total prey density is large; this is of the form

$$\alpha' = \frac{\ln(N'/N_e')}{\ln(N/N_e)} \tag{15}$$

which means that α' can be evaluated as the ratio of the proportionate mortalities of the two prey types expressed as natural logarithms, i.e. the k values (Haldane 1949; Varley & Gradwell 1960).

$$\alpha' = \frac{\ln(N_e/N)}{\ln(N_e'/N')} = \frac{k_I}{k_{II}} . \tag{16}$$

Apart from allowing for exploitation, the index α behaves similarly to Index 4 (C).

The authors go on to point out that when the two prey types are present at equal densities, simplification of eqn (13) leads to

$$\frac{N}{(N + \alpha'N')} = \frac{1}{(1 + \alpha)} = \beta \tag{17}$$

where β, the probability of the next prey eaten being of type I, provides an alternative measure of preference. This index β has a scale from zero to one with a value of 0·5 for no preference, values of greater than 0·5 for positive preference, and values of less than 0·5 for negative preference (i.e. preference for prey type II). This rescaled form of the index β is, therefore, suitable for use when exploitation occurs.

Method 8

Jacobs (1974) proposed two indices of preference. The first of these has been considered under Method 4; the second was based upon that of Ivlev (Method 5). In the symbols used here, it can be shown to be equivalent to

$$\text{Index } 8 = \frac{N_e/N_e' - N/N'}{N_e/N_e' + N/N'} . \tag{18}$$

This index, like Index 5, varies from zero to minus one for negative preference, and from zero to plus one for positive preference. Unlike Index 5, however, its maximum attainable values are not defined by the relative prey densities, being minus one and plus one at all combinations. On the other hand extra prey types cannot be incorporated without pooling prey classes.

Thus, it can be seen that, of the methods used in the past, only Methods 4, 7 and 8 do not have major drawbacks, and of these only Method 7 allows for exploitation.

Therefore, when exploitation is negligible, Methods 4 and 7 are suitable. Method 4 is the most widespread, and is used by Cain & Sheppard (1950) and Kettlewell (1956). It was formally defined as an index by Murdoch (1969), and has also been introduced and defined in various forms by Tinbergen (1960), Elton & Greenwood (1970) and Jacobs (1974). By taking logarithms, a symmetrical scale can be obtained. Alternatively, the

index can be transformed to a form analogous to the index β described in Method 7 (i.e. $C' = 1/(1 + C)$), and this provides finite symmetrical scales. Method 8 proposed by Jacobs (1974) also provides a suitable index with finite symmetrical scales. Comparing the logarithm of Index 4 with Index 8, Jacobs (1974) pointed out that Index 8 is more sensitive when preference is slight, whilst the logarithm of Index 4 is more sensitive when preference is great. This also holds true when considering the untransformed value of Index 4.

The index α of Manly, Miller & Cook (1972) (Method 7) is based upon the instantaneous relationship described by Method 4 and, in the transformed form (β) provides the only index with finite symmetrical scales which allows for exploitation.

PREDICTING PREFERENCE FROM FUNCTIONAL RESPONSE MODELS

All the approaches considered in the last section were concerned with the measurement of preference. In this section functional response models are used to predict preference, and the resultant relationships compared with those described above. Murdoch (1969) hinted at such an approach since, in proposing his model of preference (eqn (6)), he suggested that an appropriate predation model could be used as a null hypothesis. In this section two such null hypotheses are derived.

The first null hypothesis is derived from the disc equation of Holling (1959b)

$$N_e = \frac{aNT}{1 + aT_hN} \tag{19}$$

where, as before, N_e is the number of prey eaten and N is the number of prey present, while a is the instantaneous rate of discovery, T is the total time available and T_h is the time taken by the predator to handle each prey. This, as pointed out by Murdoch (1973) and Lawton, Beddington & Bonser (1974), can be adapted for two prey types to give

$$N_e = aNT/(1 + aT_hN + a'T_h'N')$$
$$N_e' = a'N'T/(1 + a'T_h'N' + aT_hN) \tag{20}$$

where the primed symbols refer to a second prey type. Dividing the equation for N_e by that for N_e' gives

$$\frac{N_e}{N_e'} = \frac{a\ N}{a'\ N'}. \tag{21}$$

It should be noted that Murdoch's eqns (2) and (3) (Murdoch 1973) are given incorrectly and should match eqns (20) and (21) above. Equation (21) is analogous to the situation described by Method 4 above. Therefore, if exploitation is negligible, or prey are replaced as they are eaten, Index 4 can be used, and defined as the ratio of the search efficiencies for the two prey types (a/a'). The similarity of this definition to the preference models of Tinbergen (1960) and of Elton & Greenwood (1970) is evident. It can be seen that the risk index of Tinbergen (r) and the visibility of Elton & Greenwood (v) correspond to the instantaneous rate of discovery of Holling (a). Indeed, the definition of the risk index of Tinbergen ($r = N_e/NT$) is the same as that of the instantaneous rate of discovery.

Since, in predator-prey interactions, it is often the case that exploitation is not negligible or prey are not replaced as they are eaten, the disc equation is often unsuitable (Royama 1971; Rogers 1972). In such cases the random predator equation of Rogers (1972) is suitable, namely:

$$N_e = N[1 - \exp(-a(T - T_h N_e))] \tag{22}$$

This can readily be adapted to the two prey situation (Lawton, Beddington & Bonser 1974), giving

$$N_e = N[1 - \exp(-a(T - T_h N_e - T_h' N_e'))]$$

$$N_e' = N'[1 - \exp(-a'(T - T_h' N_e' - T_h N_e))]. \tag{23}$$

Dividing the equation for N_e by that for N_e' now gives

$$\frac{N_e}{N_e'} = \frac{1 - \exp(-aT_s)}{1 - \exp(-a'T_s)} \frac{N}{N'} = \gamma \frac{N}{N'} \tag{24}$$

where T_s, the time available for searching, is given by $(T - T_h N_e - T_h' N_e')$. The definition of the preference term (γ) is now a complex variable dependent upon T_s, which itself depends upon the numbers of each prey type eaten, the handling times and the total time available, in addition to the search efficiencies. The preference term (γ) cannot be estimated directly, but eqns (23) can be used to predict actual consumption of prey, and hence the ratio N_e/N_e' when both prey types are present.

It follows from eqn (24) that if the handling times are relatively low (compared with the total time) then there is little difference from the no exploitation model. However, as the relative handling times increase (particularly that of the preferred prey), the effects of preference are reduced, as is the value of the preference term (γ).

This model can be used to describe preference experiments where exploitation occurs, and provides an alternative approach to that of Manly, Miller & Cook (1972) (Method 7).

DISCUSSION

Brief consideration will now be given to the methods of graphical display of preference. This will be followed by a description of the use of two-prey functional response models to describe and predict preference, illustrated with data from Fernando (1977).

Murdoch (1969) suggested two methods for the graphical display of preference. In the first of these, the ratio of the prey types eaten is plotted against the ratio at which they are present (i.e. illustrating eqn (6)). This method, illustrated by Fig. 1(a), means that constant preference will take the form of a straight line relationship where a slope of one indicates no preference, a slope of greater than one positive preference, and a slope of less than one negative preference. The main drawback to this figure is that the scales are infinite. The second method suggested is to plot the proportion (or percentage) of prey type 1 within the diet against the proportion (or percentage) present, as is shown in Fig. 1(b). This results in finite scales, but constant preference is now indicated by a curvilinear relationship. Either method can be used, but perhaps the second yields a more useful figure, and it will be used here.

These two figures are suitable when the total prey density is constant for all combinations of prey densities considered. To use these figures when this is not so, assumes that preference is defined by the ratio of prey types available, and is unaffected by the total prey density. Often, this assumption will not hold true, as was shown, for example, by Ivlev (1961). Thus, a more complete, albeit more complex, figure can be obtained by plotting N_e and N_e' against the two dimensions of N and N', to yield a three dimensional
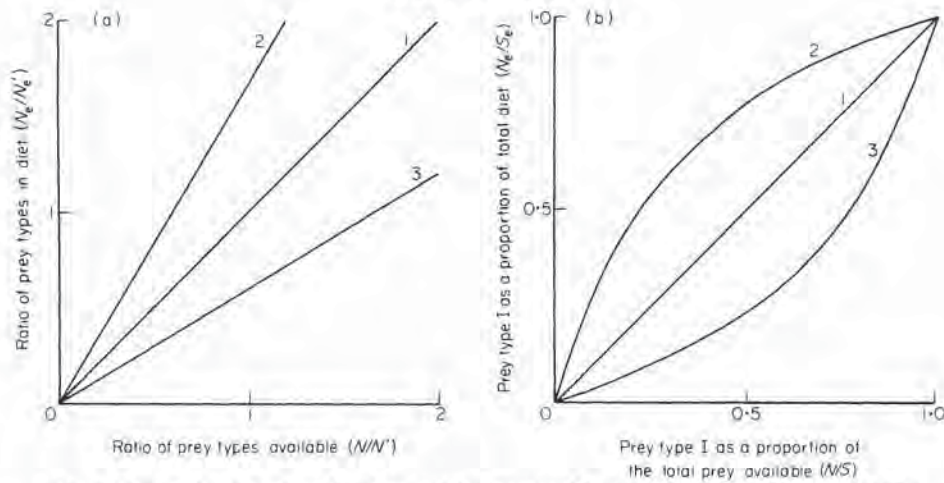
FIG. 1. The graphical display of preference. (a) The ratio of the two prey types in the diet (N_e/N_e') plotted against the ratio at which they are initially present (N/N'), (b) the proportion of the diet consisting of prey type I (N_e/S_e) plotted against the proportion of the initially available prey which are type I (N/S). The lines show (1) no preference, (2) preference for prey type I (positive preference) and (3) preference for prey type II (negative preference).

figure, as is shown by the predictive figure of Lawton, Beddington & Bonser (1974, Fig. 3).

The discussion of two-prey functional response models in the last section suggests two lines of approach. The first is exemplified by the work of Lawton, Beddington & Bonser (1974) on the predation of penultimate instar larvae of the damselfly *Ischnura elegans* (Lind.) upon the two cladocerans, *Daphnia obtusa* Kurz and *Simocephalus vetulus* (O. F. Müller). The authors obtained data of the predation shown at a range of combinations of prey densities of the two prey types. To these data, they fitted the two-prey random predator equations (eqns (23)), using multiple regression on linearized forms of eqns (23); alternatively, a least squares best fit technique would have been more appropriate. Comparing these abstracted parameters with those obtained for the individual functional responses, they found differences associated with some evidence of switching. An alternative approach, used in Cock (1977), uses eqns (23) to predict predation and preference, and compares the observed results with those predicted. It incorporates the following steps:

(i) Perform functional response experiments for each prey type individually.

(ii) Describe these functional responses with a suitable model. For the normal, Holling type II response (Holling 1959a) the random predator equation (eqn (22)) is most suitable, but clearly for sigmoid, dome-shaped or complex responses some other model would be necessary (Hassell, Lawton & Beddington 1976, 1977; Hassell 1978).

(iii) Combine these two functional response equations to describe the two-prey interaction (e.g. as eqns (23)). Use the parameters of the individual functional responses to predict predation when both prey types are present. These equations can be used to generate the three dimensional figure of N_e and $N_e' \times N \times N'$ or, as is more often the case, a section through such a figure.

(iv) Examine predation over a range of combinations of densities of the two prey types and compare this with the predicted predation.

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(v) The simpler figure of the proportion of prey type I within the diet plotted against the proportion present can be examined, and the observed preference compared with that predicted.

The null hypothesis of this approach assumes that the searching behaviour of the predator remains constant in the presence of either prey type individually and both types together. It follows that the parameters for the individual prey type functional responses can be used to predict predation, and hence preference, when both types are present. Deviations from this prediction would be caused by a change in one of the searching parameters due to either a change in search strategy, or the selection and/or rejection of disproportionate numbers of prey.

Data from Fernando (1977) are used to demonstrate this approach. The first example (Fig. 2) is the preference shown by deutonymphs of the mite *Phytoseiulus persimilis* Athias-Henriot when offered a choice of larvae and deutonymphs of the glasshouse red
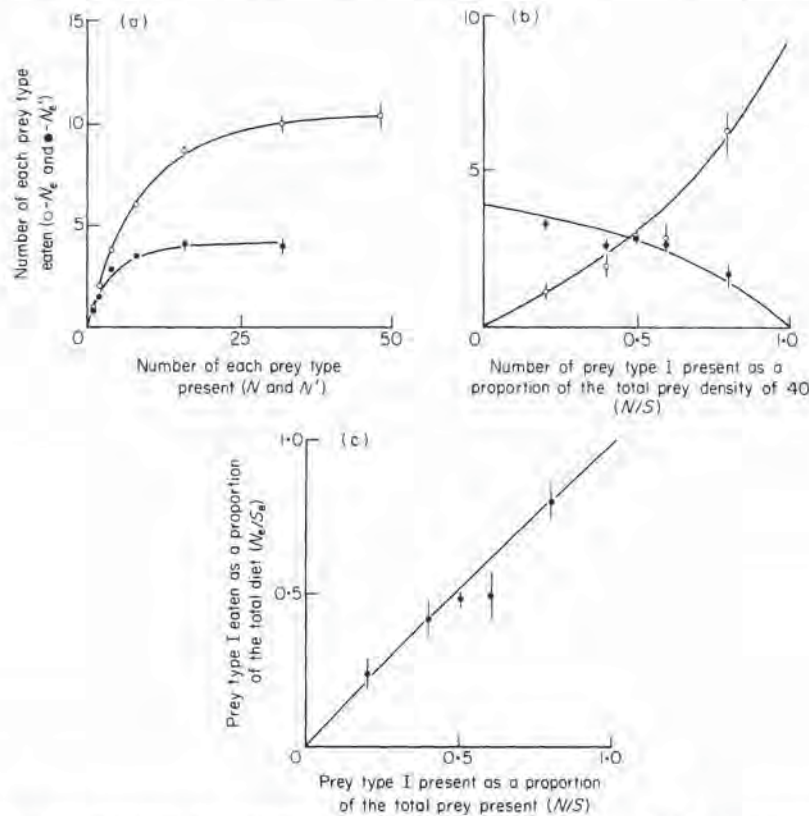

FIG. 2. The predation of deutonymph *Phytoseiulus persimilis* upon larvae and deutonymphs of *Tetranychus urticae*. (a) Functional responses of deutonymph *Phytoseiulus persimilis* to larvae (o) and deutonymphs (•) fitted with the random predator equation by the least squares best fit to the functional response (Cock 1977) with the parameters $a = 0.138/h$, $T_h = 2.17h$, $a' = 0.128/h$, $T_h = 5.69h$. (b) Predation of deutonymph *P. persimilis* upon larvae (o) and deutonymphs (•) of *Tetranychus urticae*, when both are present together. The lines show the predictions of eqns (23) using the parameters obtained from (a). (c) The proportion of larvae in the diet of *Phytoseiulus persimilis* plotted against the proportion initially present. The solid line shows the predicted proportion in the diet based upon the predation predicted for (b). Data from Fernando (1977). Points plotted with the standard error of the mean.

spider mite, *Tetranychus urticae* Koch. Figure 2(a) shows the functional responses to larvae and deutonymphs individually. Both responses are Holling type II functional responses and are well described by the random predator equation (eqn (22)). The abstracted parameters of these individual functional responses (a, T_h, a', T_h') are used in eqns (23) to predict the consumption of prey when both stages are present together (solid lines, Fig. 2(b)). It can be seen that the predicted predation is a good fit to that observed. Finally, since the total prey density is held constant for all prey combinations, the predicted and observed proportions that the larvae make up of the diet are plotted against the proportion they make of the total initial prey density (Fig. 2(c)). It can be seen that negligible preference is observed, while the prediction, which describes the data well shows a very slight preference for larvae. Thus, the searching behaviour of deutonymph *Phytoseiulus persimilis* remains constant in the presence of larvae alone, deutonymphs alone, and both together.
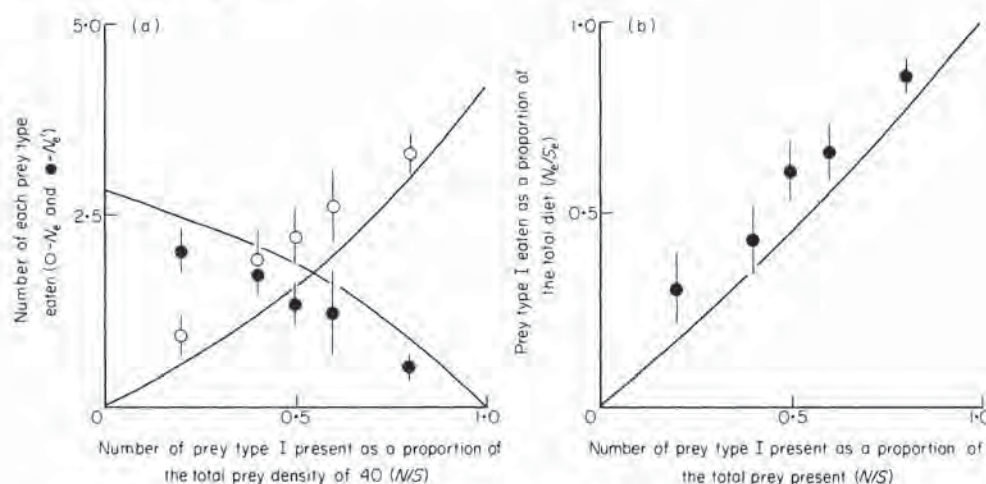

FIG. 3. The predation of protonymph *Phytoseiulus persimilis* upon eggs and deutonymphs of *Tetranychus urticae*. The functional responses to the two prey stages are described by the random predator equation with parameters of $a = 0.093/h$, $T_h = 4.91h$, $a' = 0.122/h$, $T_h' = 5.69h$. (a) Predation of protonymph *Phytoseiulus persimilis* upon eggs (o) and deutonymphs (•) of *Tetranychus urticae* when both are present together. The lines show the predictions of eqns (23) using the parameters obtained for the individual functional responses. (b) The proportion of the diet consisting of eggs plotted against the proportion of the initially available prey which were eggs. The line shows the prediction based upon the predation predicted for (a). Data from Fernando (1977). Points plotted with the standard error of the mean.

The second example (Fig. 3) shows the predation of protonymph *P. persimilis* upon eggs and deutonymphs of *T. urticae*. Here, the functional responses were fitted with the random predator equation and the abstracted parameters substituted in eqns (23) to calculate the expected predation in Fig. 3(a). It can be seen that more eggs and fewer deutonymphs than expected are eaten. Hence, Fig. 3(b), analagous to Fig. 2(c) of the last example, can be derived. This figure shows that, although constant searching behaviour would lead to a slight preference for deutonymph prey (Fig. 2(b), •), the predators actually show a preference for eggs. This implies either some change in the searching behaviour which favours the finding of eggs, or that the rate of successful encounter changes for eggs or deutonymphs or both.

ACKNOWLEDGMENTS

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