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A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method

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A modification of the graphical Costello method is proposed for the analysis of stomach contents data. The new method allows prey importance, feeding strategy and the inter- and intra-individual components of niche width to be explored using graphical presentation. The analysis is based on a two-dimensional representation of prey-specific abundance and frequency of occurrence of the different prey types in the diet. The paper describes the new method and the parameters therein, and also present some examples of the utilization of the method. The method may be particularly well-suited for the examination of predictions made from optimal foraging, competition and niche theories.

Key words: diet analysis; graphical method; feeding strategy; prey importance; niche width components.

INTRODUCTION

Diet analysis is of importance in studies of predation, competition, trophodynamics and food webs. In field studies, analysis of stomach contents is often the only available means of accessing information of feeding ecology, and a vast number of publications considering stomach contents data exist. For fish, two measurements are often used in the description of the diet based on stomach contents; the frequency of occurrence and the relative abundance of the different prey (Hynes, 1950; Hyslop, 1980; Mohan & Sankaran, 1988). The frequency of occurrence of a given prey type is defined as the number of stomachs in which that prey occurs, expressed as a frequency of the total number of stomachs in which prey are present. The relative abundance of a prey (or contribution to the stomach contents) is defined as the percentage of total stomach contents (volume, weight or numbers) in all predators comprised by that given prey. In mathematical terms, the percentage occurrence ($\%F_i$) and the percentage abundance ($\%A_i$) of prey type i can be described by the equations:

$$\%F_i=(N_i/N)\times 100 \tag{1}$$

$$\%A_i=(\Sigma S_i/\Sigma S_t)\times 100 \tag{2}$$

where N_i is the number of predators with prey i in their stomach, N is the total number of predators with stomach contents, S_i the stomach content (volume, weight or number) composed by prey i, and S_t the total stomach content of all stomachs in the entire sample.

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The feeding strategy of predators has been given increased attention over the last few decades through developments in optimal foraging theory (e.g. Kamil *et al.*, 1987). A central aspect of feeding strategy, the generalist-specialist dichotomy, is also of major importance to niche theory (Pianka, 1988). A generalist predator has a broad dietary niche width, whereas the food niche of a specialist is narrow. However, it is important to distinguish between the niches of the different individuals and that of the whole population (Putman & Wratten, 1984). A population with a narrow niche must necessarily be composed of individuals with narrow and specialized niches. A population with a broad niche may, on the other hand, consist of individuals with either narrow or wide niches, or a combination of both. In this relationship, two separate components have been identified as contributing to a population's total niche width. First, each individual shows variation in its own resource use (the within-phenotype component, WPC), and second, there is variation in resource use among individuals (the between-phenotype component, BPC) (Roughgarden, 1972, 1974; Giller, 1984; Pianka, 1988; Wootton, 1990). The sum of the two components combines to form the total niche width (Giller, 1984). A population with a high between-phenotype component to the niche width would consist of specialized individuals with little or no overlap in resource use, whereas a population with a high within-phenotype component would be composed of generalists, each exploiting a wide range of overlapping resources (Giller, 1984; Pianka, 1988).

The assessment of feeding strategy and phenotype contribution to niche width is of central importance in the evaluation of predictions made by both optimal foraging, competition and niche theory. Nevertheless, in most field studies of feeding ecology, the presentation of results has been restricted to descriptions of the diet, without any further analysis of the feeding strategy and niche width components of the predator. Costello (1990), however, proposed a graphical method for analysis of predator feeding strategy, based on percentage occurrence and abundance of the prey. The rationale of Costello's method is promising, but unfortunately the method does have some problems. In the present paper we propose a modification of the Costello method. We also outline possible interpretations related to predator feeding strategy and the inter- and intra-individual components of niche width that can be inferred from the new graphical analysis, and give some examples of the utilization of the method.

THE COSTELLO METHOD

Costello's (1990) analysis is based on a two-dimensional representation, where each point represents the frequency of occurrence and the abundance of a prey taxon (Fig. 1). Costello suggested that the two diagonals of the plot represent prey importance (dominant–rare) and predator feeding strategy (specialization–generalized). Prey points close to 100% occurrence and 100% abundance represent the dominant prey taxa. Points clustered close to 100% occurrence and 1% abundance are considered to be indicative of a generalized diet, and points close to 1% occurrence and 100% abundance are indicative of a specialization on certain taxa by some predators. These interpretations may, however, be criticized. Data points indicative of generalized diet are not strictly confined to the

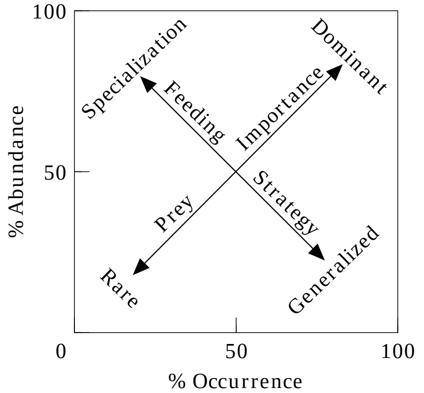

FIG. 1. The explanatory diagram for the Costello (1990) method.

lower right of the diagram, but may be distributed along the entire x-axis (Tokeshi, 1991; Costello, pers. comm.). Further, the sum of percent abundances of prey must be exactly 100. Hence it is not possible that several prey points will be clustered in the upper left of the diagram. This is clearly illustrated by the hypothetical example presented by Costello (1990, Fig. 2): two data points are located in the specialization corner, but concurrently the sum of the percent abundances of prey taxa from this predator population exceeds 250. In practice, using the Costello plot, prey points will rarely be located on the specialization side of the feeding strategy axis. This is also exemplified by examination of the data presented by Costello *et al.* (1991). When the method was used in the study of the two-spot goby, *Gobiusculus flavescens* (Fabricius), all points were found to be located along or below the prey importance diagonal.

THE NEW APPROACH

In an attempt to overcome the problems inherent in the Costello method, we suggest that a new parameter; *the prey-specific abundance* (P_i), is incorporated into the graphical representation of dietary composition. Prey-specific abundance is defined as the percentage a prey taxon comprises of all prey items in only those predators in which the actual prey occurs, or in mathematical terms:

$$P_i = (\Sigma S_i / \Sigma S_{t_i}) \times 100 \tag{3}$$

where P_i is the prey-specific abundance of prey i, S_i the stomach content (volume, weight or number) comprised of prey i, and S_{t_i} the total stomach content in only those predators with prey i in their stomach.

In the new graphical presentation, the prey-specific abundance is plotted against the frequency of occurrence on a two-dimensional graph [Fig. 2(a)]. This resembles the Costello plot, but prey-specific abundance (P_i) is used instead of percentage abundance (A_i). The product of prey-specific abundance and frequency of occurrence (expressed in fraction rather than in percent) equals the prey abundance, provided that the average amount of stomach contents is independent of the prey categories consumed, or that the amount of food in each stomach is standardized to equality (i.e. to 100%) before abundance estimates are

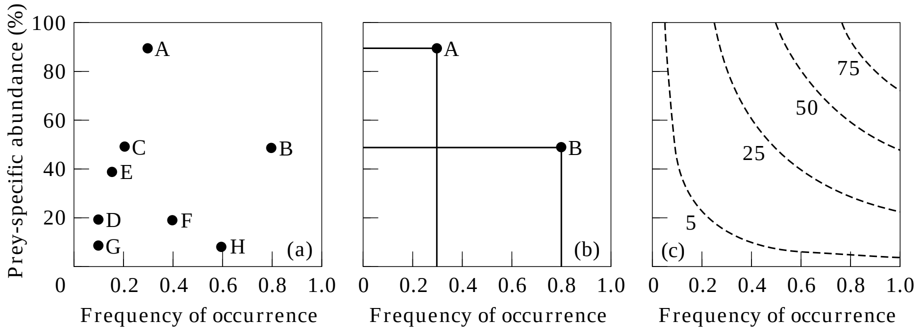

FIG. 2. The feeding strategy diagram: prey-specific abundance plotted against frequency of occurrence of prey in the diet of the predator. (a) A hypothetical example (A, B, C etc. represent different prey types). (b) Percent abundance of prey type A and B indicated by enclosed areas. (c) Isolines representing different values of prey abundances.

made. Therefore, for each point on the graph, the prey abundance is represented by the area enclosed by all the co-ordinates of the two axes [Fig. 2(b)]. The sum of the areas for all prey types, will equal the total area of the diagram (=100% abundance). Furthermore, any combination of prey-specific abundance and frequency of occurrence equals a certain prey abundance, and different values of prey abundance can be represented by isopleths on the graph [Fig. 2(c)].

INTERPRETATION OF THE DIAGRAM

Information about prey importance and feeding strategy of the predator can be obtained by examination of distributions of points along the diagonals and axes of the diagram (Fig. 3). The percent abundance, increasing along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey at the upper, and rare or unimportant prey at the lower end. It should, however, be emphasized that prey importance (or abundance) is not represented by a linear increase along the diagonal, but rather as a function of prey-specific abundance and frequency of occurrence [cf. Fig. 2(c)].

The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization (Fig. 3). The predators have specialized on prey types positioned in the upper part of the graph, whereas prey positioned in the lower part have been eaten more occasionally (generalization). Prey points located at the upper left of the diagram would be indicative of specialization of individual predators, and those in the upper right would represent specialization of the predator population. Observations located to the upper right of the diagram (population specialization) must necessarily be restricted to a single or a few points, reflecting a predator population with a narrow niche width [Fig. 3(b)]. If there are no prey points in the upper right of the diagram, and all prey points are located along or below the diagonal from the upper left to the lower right, the predator population will have a broad niche width.

Prey points positioned in either the upper left or the lower right corner represent prey types that make the same overall contributions to the population diet [cf. Fig. 2(c)], but they are indicative of totally different feeding strategies of

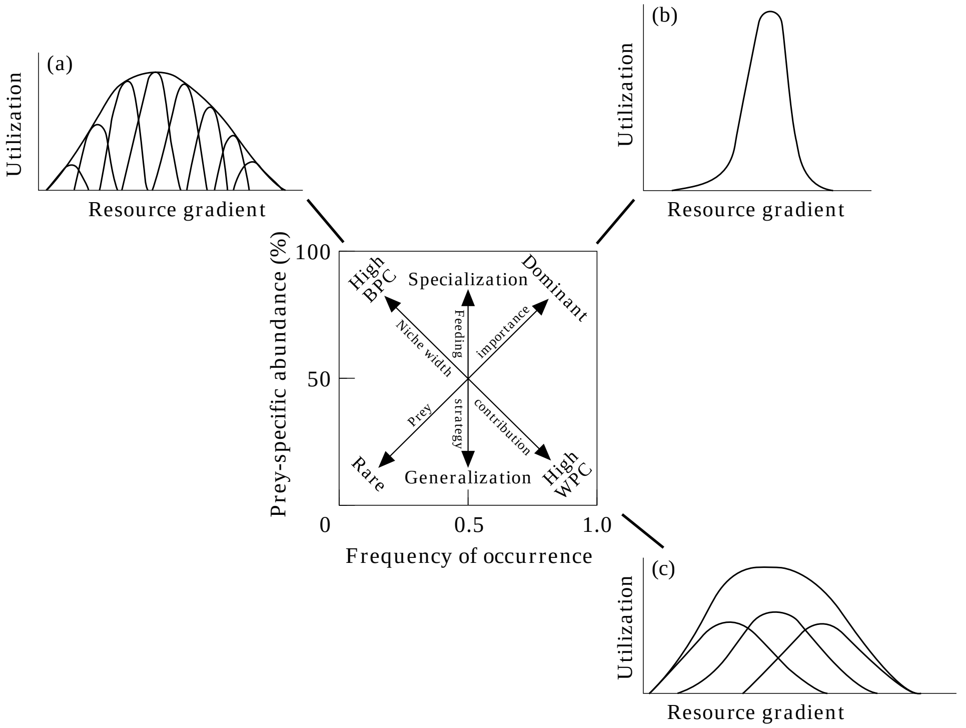

FIG. 3. Explanatory diagram (centre) for interpretation of feeding strategy, niche width contribution and prey importance from the proposed method, together with characteristic niche utilization curves. (a) High between-phenotype component to niche width, (b) narrow niche width and (c) high within-phenotype component.

the individual predators. Prey with high specific abundance and low occurrence (upper left) will have been consumed by a few individuals displaying specialization, whereas prey with a low specific abundance and a high occurrence (lower right) will have been eaten occasionally by most individuals. These differences in feeding strategy are related to the between- and within-phenotype contributions to the niche width. In a population with a high between-phenotype component, different individuals specialize on different resource types [Fig. 3(a)], whereas in populations with a high within-phenotype component, most of the individuals utilize many resource types simultaneously [Fig. 3(c)] (Giller, 1984; Pianka, 1988; Wootton, 1990). In the feeding strategy diagram, these two situations are represented by the lower right and upper left-hand corners, respectively (Fig. 3). The distribution pattern of prey points along this diagonal is, thus, indicative of the contributions of between- and within-phenotype components to the niche width.

A HYPOTHETICAL EXAMPLE

Consider two hypothetical populations, from each of which 100 individuals have been sampled. The diets of both populations are found to be equal, being restricted to the same five prey types (a, b, c, d and e), and with an abundance of

20% for all five categories. However, in the sample from population I, all five prey types are present in the stomachs of all individuals, and their mean contribution to the stomach content is equal (i.e. 20%). In the sample from population II, five groups of 20 individuals each have eaten only one of the prey types (either a, b, c, d or e), excluding all the other four. Thus, in population I, the frequency of occurrence of each prey type is 100% (or 1·0) and the prey-specific abundance 20%, whereas in population II, each prey type has a frequency of occurrence of 20% (or 0·2) and a prey-specific abundance of 100%. In the feeding strategy diagram for population I, the five prey points will be located in the lower right corner, indicating a generalized feeding strategy among the predator individuals, and a high within-phenotype contribution to the niche width. In population II, on the other hand, all prey points will be located in the upper left corner, demonstrating a strong specialization among the individual predators and a high between-phenotype contribution to the niche width. Therefore, although each prey type has the same overall contribution to the total diet of the two populations, the feeding strategy is totally different in the two situations.

SOME CASE STUDY EXAMPLES

To illustrate the application of the new method further, data from some of our field studies of stomach contents of fish have been analysed (Fig. 4). The first example [Fig. 4(a)] demonstrates a situation in which there was a high between-phenotype contribution to the niche width, with most of the prey points positioned towards the upper left corner of the graph. Individual predators had specialized on different prey types, and each food category had been consumed by only a limited fraction of the predators. The second case [Fig. 4(b)] illustrates a relatively high within-phenotype component, with points positioned towards the lower right part of the graph. The most important prey taxa had been eaten by more than half of the fish, but their average contribution to the stomach contents of these fishes was low, indicating a generalized feeding strategy. The niche widths in these two examples were relatively wide [5·05 and 4·60, respectively; Levins index, B (Levins, 1968)]. The third example [Fig. 4(c)] shows a population specialization towards one single prey type. All individuals had been feeding on the dominant prey taxon, but small proportions of other prey types were included occasionally in the diet of some individuals. There were neither high within- nor between-phenotype contributions to the niche width, and the niche width was narrow ($B=1{\cdot}07$). The last example [Fig. 4(d)] demonstrates a more mixed feeding strategy, with varying degrees of specialization and generalization on different prey types ($B=4{\cdot}55$).

Although three of the examples [Fig. 4(a), (b) and (d)] represent situations where the niche width indices were similar, the resource use patterns of these three populations were very different, ranging from strong individual specialization [Fig. 4(a)] to a generalized feeding by the individuals [Fig. 4(b)]. These differences in feeding strategy, which are ecologically very important, would not be possible to interpret from the commonly applied diet indices from descriptions based on prey abundance or frequency of occurrence, or from a diet analysis using the Costello plot. The proposed method thus enhances the ecological insight that may be derived from stomach contents data.

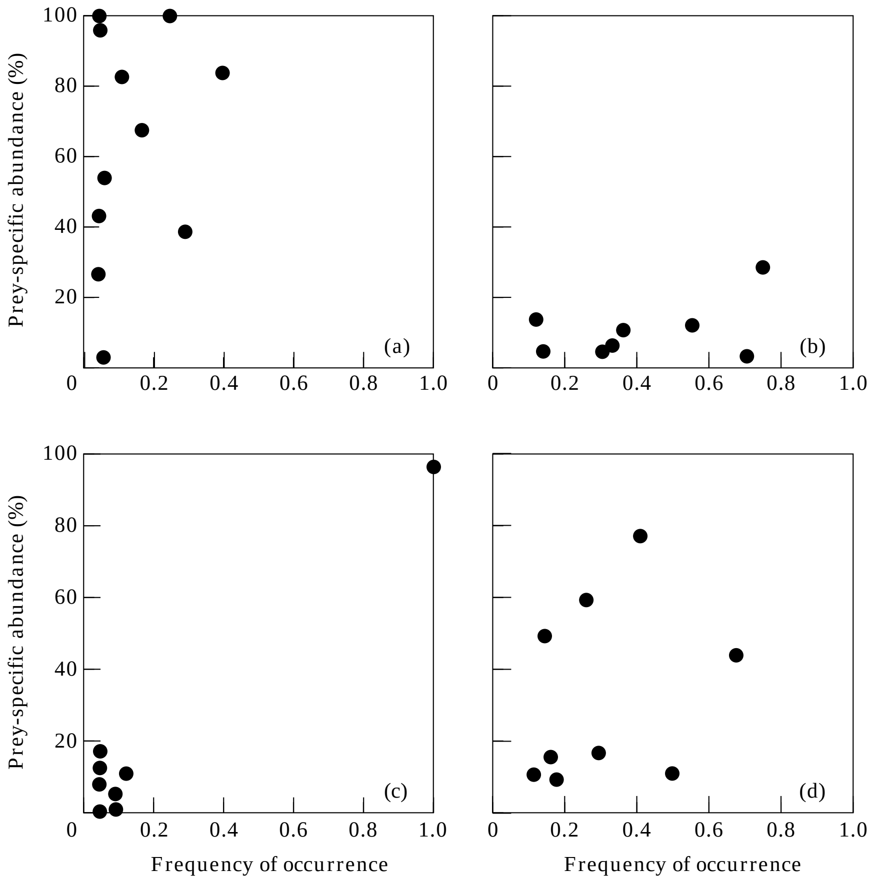

FIG. 4. Case examples of feeding strategy plots. (a) Arctic charr *Salvelinus alpinus* L., from Lake Takvatn, October 1980 ($n=79$); (b) Atlantic salmon *Salmo salar* L., parr from Reisa River, May 1990 ($n=59$); (c) Arctic charr from Lake Takvatn, June 1989 ($n=54$); and (d) whitefish *Coregonus lavaretus* (L.) from Lake Stuorajavri, September 1987 ($n=51$). The points represent different prey types. See Fig. 3 for interpretation of the results.

CONCLUDING REMARKS

The described method enables the analysis of feeding strategies and niche width components of natural populations. The contributions of between- and within-phenotype components to niche width can be inferred from examination of the outlined graphical plot. Further, information about feeding strategies in terms of specialization and generalization, both at the individual and population level, can also be extracted. Thus the method allows stomach contents data from field studies to be used analytically, and not solely in a descriptive context. Such analyses may be particularly well-suited for the examination of predictions made from optimal foraging, competition and niche theories.

Finally, it is of note that within a predator population, the feeding strategy towards a certain prey category may be mixed. Some individuals may specialize on this particular prey type, whereas others consume it more occasionally. In the feeding strategy plot, the prey-specific abundances are represented as mean values only. Additional information may reside in frequency distributions of the prey abundances of each individual predator. These distributions could, therefore, preferably also be taken into consideration when the feeding strategy plot is employed. It should also be emphasized that the application of the method must be based on a sufficient number of observations, and that individuals with only small remains of stomach contents should not be included in the analysis, as this may lead to an over-estimation of slowly digested prey types.

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