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GRAPHICAL ANALYSIS OF PREDATOR FEEDING STRATEGY AND PREY IMPORTANCE

Comment from Mutsunori Tokeshi

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Patterns of feeding represent one of the important aspects in the general ecology of any animal species. From an analysis of stomach contents, two simple measures are commonly derived to describe the dietary patterns of a predator population, particularly fishes (Hynes 1950; Windell & Bowen 1978). For the predator species, the frequency of occurrence (F) is defined as the number of individuals feeding on a particular prey type, expressed as the proportion of all individuals in the population of the predator. The proportional abundance of prey (P) is the proportion of each prey-type among all the prey-types consumed by all the predators in the population, measured in terms of the number of prey items, prey volume or prey biomass. Using these two measures of F and P, Costello (1990) has proposed a graphical method for analysing predator (fish) feeding strategy and prey importance. Because the issues of dietary analysis have a wide implication not only for studies on fish but also for all other animals, such a proposal deserves a careful consideration and appraisal, especially if ecological insights are to be sought from dietary patterns (e.g. specialist versus generalist predators, cf. Begon et al. 1986). This comment briefly describes some problems associated with graphical presentation and analysis, and suggests a better, alternative approach.

Costello (1990) has drawn diagonal axes on a two-dimensional graph of relative occurrence (F) and abundance (P), (Fig. 1a), and suggests that one axis represents feeding strategy (specialized – generalized) and the other axis represents prey importance (dominant – rare). Consider first the feeding strategy axis. There are two extreme cases of a "generalist" predator. Suppose that a sample of 10 specimens is taken, where each specimen has consumed an equal amount of each of ten different prey-types. Each prey-type will then be represented by $F=1.0$ and $P=0.1$. This

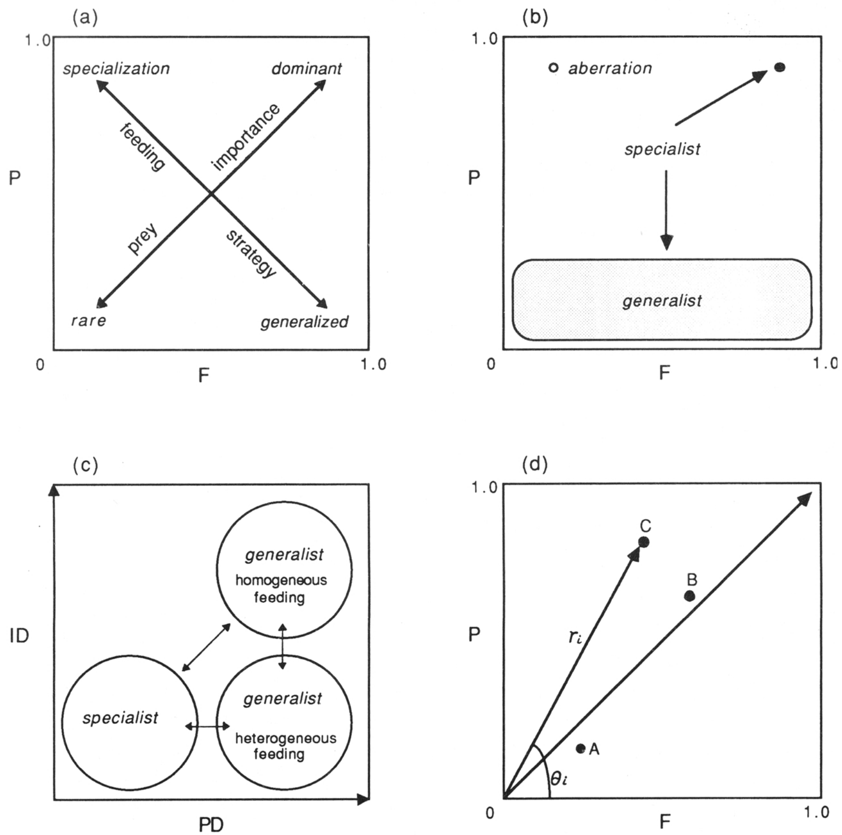

FIG. 1. Graphical analysis of dietary data. (a), Costello's (1990) diagonal scheme of feeding strategy and prey importance on the F (frequency of occurrence) versus P (proportional abundance of prey) graph. (b), expected patterns of generalist and specialist (see the text). (c), mean individual feeding diversity (ID) plotted against population feeding diversity (PD) and the general patterns of specialist/generalist and homogeneous/heterogeneous feeding. (d), method of quantifying prey importance based on the diagonal prey importance axis. Further explanation in the text.

example conforms to the proposed scheme. In contrast, suppose that each specimen has consumed a single prey-type, but the prey-type is different in each of the 10 sampled predators. In this case each prey-type will be represented by F=0.1 and P=0.1 and consequently the data points would all plot in the bottom left-corner of Fig. 1a. In reality, data points for most "generalist" predators would spread across the F axis in the bottom portion of the P axis, as illustrated in Fig. 1b.

Furthermore the situation referred to as "specialization" (low F, high P) in Fig. 1a does not conform to a common notion of specialized feeding. Rather, a specialist should be associated with high values of both F and P. The combination of low F and high P represents a predator population where a small proportion consumes a disproportionately large amount of a particular prey-type, while the majority feed on small quantities of numerous prey-types. This is more likely to be an aberration (e.g. a small sample size; a few very large predators mixed with small ones; unsuitable sample handling; regurgitation of stomach contents, etc.) rather than a real population pattern for most predator species. For a specialist predator an expected pattern would be where one data point is located towards the top right-corner of the graph (i.e. a specialized prey item) while other (limited number of) points are scattered in the "generalist" area along the F axis (Fig. 1b). Therefore the graph of P/F does not neatly segregate specialists from generalists. If the feeding strategy axis in Fig. 1a does not represent all possible circumstances, it follows that any conclusions made about distinctions between heterogeneous or homogeneous feeding by a particular predator population, or species, are without a logical foundation.

If one wishes to graphically represent the specialist/generalist paradigm, it is probably more meaningful to plot mean individual feeding diversity (ID), an indication of how diverse a diet a predator individual on average takes, against population feeding diversity (PD), the diversity of prey-types consumed by the predator population as a whole, using any existing diversity index (Fig. 1c). If the Shannon function is chosen:

$$\mathrm{ID} = \frac{\sum_{j=1}^{N} \left(-\sum_{i=1}^{n} P_{ij} \log_e P_{ij} \right)}{N}$$

and

$$\mathrm{PD} = -\sum_{i=1}^{n} P_i \log_e P_i$$

where N is the total number of predator individuals and n is the total number of prey-types; P_{ij} is the proportion of prey-type i in the jth predator individual and P_i is the proportion of prey-type i in the entire predator population. A population with low ID and low PD corresponds to a specialist, whereas one with high ID and high PD corresponds to a generalist with a homogeneous feeding regime. The combination of low ID and high PD indicates a generalist with a heterogeneous feeding regime, while high ID and low PD is considered to be a rare occurrence. This scheme will allow the presentation of ontogenetic/seasonal/spatial change in feeding patterns of a predator population and also facilitates interspecific comparisons, in a clearer way than that achieved by plotting P/F.

The prey importance axis of Fig. 1a conforms to a general feeling among ecologists that prey-types with high values of F and P are more important to the predator (leaving aside a discussion of what is exactly meant by "importance"). However, although a plot of P/F readily enables visual comparisons to be made for different sets of data, the conceptual representation of an axis by itself is inadequate for a quantitative analysis. Consider, for example, data points for prey-types A, B and C shown in Fig. 1d. If these are plotted on Fig. 1a it is easy to recognize that B (and C) is more important than A, but there is little qualitative difference between B and C on the basis of the proposed prey importance axis. The difference can be quantified, however, by estimating two variables; the distance of a point from the origin, $r_i(=[F_i^2 + P_i^2]^{0.5})$, and its vector angle, $\theta_i(=\tan^{-1}[P_i/F_i]$, (Fig. 1d). A prey is considered to be more important if it is associated with larger r_i and smaller angular departure from the vector of the diagonal axis, i.e. if the value of $|\theta_i - \pi/4|$ is small. It is therefore possible to propose a measure of prey importance, PI:

$$\mathrm{PI} = r_i \left[1 - \frac{|\theta_i - \pi/4|}{\pi/4}\right]$$

where θ_i is given in radians. This can be converted to a proportional value either against the theoretical maximum of PI $(=[F_{max}^2 + P_{max}^2]^{0.5} = \sqrt{2},\ \theta = \pi/4)$ or against the sum of PIs for all the prey-types (n). In the former case the adjusted prey importance index is:

$$\mathrm{PI}_\alpha = r_i \Upsilon_i / \sqrt{2}$$

In the latter case:

$$\mathrm{PI}_\beta = \frac{r_i \Upsilon_i}{\sum_{i=1}^{n} r_i \Upsilon_i}$$

where $\Upsilon_i = 1 - |\theta_i - \pi/4| / (\pi/4)$. It should be noted here that PI_β is identical to the Weighted Resultant Index (WRI) of Mohan & Sankaran (1988). Obviously, PI_α and PI_β,(= WRI), are more rigorous expressions of the idea of prey importance than is a graphical diagonal axis.

It is therefore apparent that the simple graphical method of data analysis illustrated by Fig. 1a adds little to a better understanding of the dietary ecology of predator species. This does not, however, mean that F and P are useless measures. On the contrary, they have been and will be used to summarize dietary data for fish and other animals (e.g. Hildrew & Townsend 1976; Hildrew et al. 1985). Where it is desirable to combine estimates of F and P in order to make inferences about feeding strategies and prey importance, the alternative methods suggested here provide a more logical basis on which to analyze dietary data obtained from routine surveys of fish and invertebrates.

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