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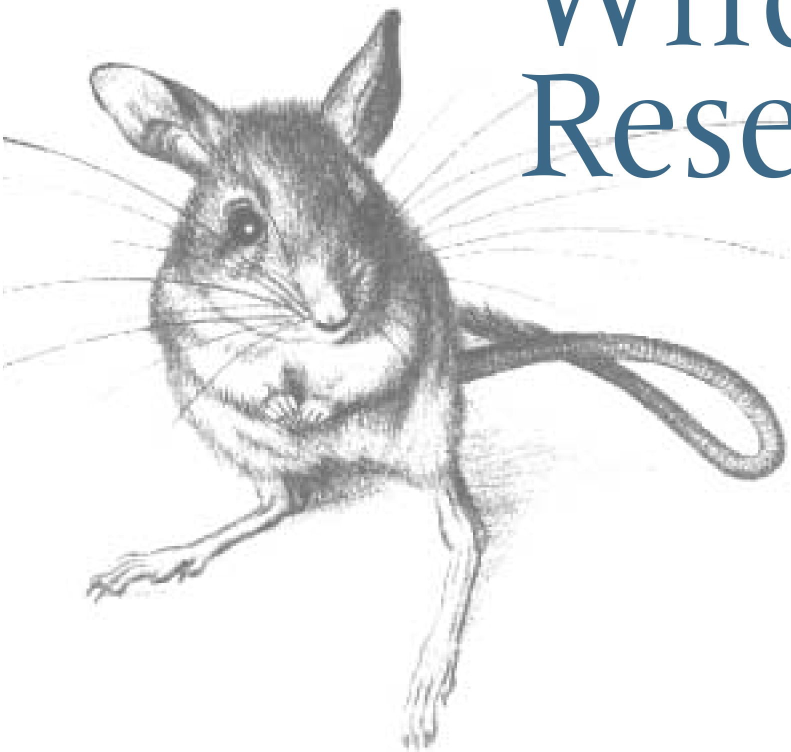

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The index of relative importance: an alternative approach to reducing bias in descriptive studies of animal diets

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Abstract. The Index of Relative Importance (IRI) is a composite measure that reduces bias in descriptions of animal dietary data. The two papers introducing the IRI in 1971 had been cited a total of 214 times by the end of 2001 and proposed as a standard methodology. However, 180 of these citations concerned the description of the diets of fish, indicating that the IRI is not well known outside fisheries biology. This illustrates how the interests of researchers in a narrow range of taxa may restrict the application of a useful technique to particular groups of animals. Here we apply the IRI to dietary data from one mammal species, two bird species and two species of geckoes to illustrate its applicability to a wide range of taxa. We believe the approach should be considered seriously by terrestrial ecologists concerned about the biases inherent in single-index approaches to describing animal diets.

Introduction

> The ideal system … [of diet analysis] is one that combines the good points of both the numerical and volumetric methods – a system which, as a matter of record, counts individuals as far as possible, or at least in enough instances to assure the inclusion of typical cases, and which further estimates the proportion of all relevant items by bulk. (McAtee 1912, p. 464)

> Measurements of numbers, volume and frequency of occurrence used traditionally in evaluating stomach contents of fish fall short of depicting true relative value. Numerous small organisms overshadow the importance of a few large ones. Differential digestive values distort volumetric measurements. Frequency of occurrence tabulations are sensitive to sampling error. An ideal representative value would probably be one which integrates each of the above plus one for nutrition. (Pinkas *et al.* 1971, p.9)

Few ecologists would dispute that feeding and food selection are key ecological processes (e.g. Stephens and Krebs 1986; Pimm *et al.* 1991; Sih *et al.* 1998). However, there has been intense discussion on the relative merits of the different techniques used to describe or quantify animal diets (see McAtee 1912, 1936; Mohr 1935, 1936 for early controversies; and Hynes 1950; Hyslop 1980; Litvaitus *et al.* 1996; Cortes 1997; Liao *et al.* 2001 for more recent reviews). Stomach contents may be collected by *post mortem* dissection (Recchia and Read 1989; Martin *et al.* 1996), by inducing vomiting (Radke and Fydendall 1974; Prys-Jones *et al.* 1974; Gales and Burton 1988), or by stomach pumping or flushing (Legler and Sullivan 1979; Randall and Davison 1981; Gales 1987). Alternatively, droppings may be collected (Tullis *et al.* 1982; Dickman 1995). Such samples are commonly analysed by counting the frequency of each food type found (numerical percentage), determining the relative volume of each food type (volumetric percentage), or by recording the percentage of samples containing each food type (frequency percentage).

Each method has limitations and biases. Counting particular food items may ascribe a false importance to small foods occurring at high frequency but not forming much of the volume or mass of the diet. Volumetric estimates may be biased towards large prey eaten infrequently, or that predominate in the samples because they are digested slowly. Recording the frequency of individuals feeding on each prey type does not solve these problems. Foods eaten by many individuals but in small numbers or small volumes will have a high frequency of occurrence, but may not be highly important in the diet (see Pinkas *et al.* 1971 for a more detailed discussion of the merits and demerits of each approach). Methods combining two measures have been proposed (Hynes 1950; Berg 1979; Webb *et al.* 1982). However, many studies continue to use only one method (e.g. Dickman 1995), or two or more simultaneously but without any attempt to combine them in a single index (e.g. Wooller and Calver 1981).

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Pinkas (1971) proposed, and Pinkas *et al.* (1971) first applied, an index of relative importance (IRI) to combine all three measures into a single estimate of the relative importance of food types. Although they conceded that the index included no component for the nutritional value of foods and might '… fall short of some theoretical ideal' (Pinkas *et al.*1971, p. 9), the papers have been highly successful. Between 1971 and the end of 2001 they had been cited 214 times overall (Institute for Scientific Information 1971 ff.). There were 180 citations in studies of fish diets, 9 citations in studies of bird diets, 10 in studies of mammal diets, 3 in studies of reptile or amphibian diets and 6 in studies of invertebrate diets. We were unable to locate the original papers for a further six citations and hence cannot ascribe them with certainty to any of these categories. Nevertheless, it seems clear that the IRI is widely applied by fisheries biologists, although its potential appears less well known to ecologists studying other vertebrates.

Here, we illustrate the application of IRI methodology to descriptions of the diet of a mammal (the house cat, *Felis catus*), two species of birds (the straw-necked ibis, *Threskiornis spinicollis*, and the barn owl, *Tyto alba*) and two species of reptiles (the geckoes *Diplodactylus assimilis* and *D. stenodactylus*). In each case, we compare the rankings of prey importance produced by the numerical percentage, volumetric percentage and frequency of occurrence percentage, thereby highlighting the biases and values of each method. We also compare the IRIs for the two gecko species, illustrating how rank correlation coefficients can be used to compare the relative order of importance for different foods eaten by different predators. These examples may alert ecologists other than fisheries biologists to the value and potential of the IRI in describing diets.

Methods

Collection and analysis of diet samples

For each predator, food remains in each scat, stomach or pellet sample were assessed by volumetric percentage, numerical percentage and occurrence percentage. Volumes were estimated by eye for all predators except the straw-necked ibis, for which they were measured with a graduated cylinder. Numerical percentages were calculated according to the method of Calver and Wooller (1982), while occurrence percentages were derived from the number of predators feeding on a particular prey type divided by the number of predators in the sample. Except where indicated below, the data have not been published previously.

The cat data are from cat scats collected from Ethabuka Station, Simpson Desert, south-west Queensland, Australia in 1991 (23°46′S, 138°28′E). A full description of the site is given in Dickman *et al.* (1993). Scat samples were collected from tracks and open areas on dune sides and dune tops, placed individually into paper envelopes and air-dried. They were later pulled apart and examined under low power. Hairs were identified using methods in Brunner and Coman (1974). All reference material including mammal hairs, lizards, frogs and invertebrates was collected on site. The gecko data are from scats collected from pitfall-trapped geckoes at Bungalbin Hill, Goldfields, Western Australia between 1986 and 1989 (30°16′S, 119°46′E). The site is described in Dickman *et al.* (1995). Scats were collected from traps or, more usually, directly from animals during handling. They were preserved in 70% ethanol, then examined under low-power and high-power microscopes after teasing apart on a Petri dish. Prey remains were identified by comparison to reference specimens collected in the field. The ibis data are stomach contents retrieved from 18 moribund nestlings between four and seven weeks old. They came from a breeding colony located near Capel, south-west Western Australia in 1993 (33°38′S, 115°33′E). Stomach contents were retrieved immediately after euthanasia, preserved in 70% ethanol and subsequently sorted using a dissecting microscope. Prey were identified by reference to Calver and Wooller (1982) and included references. A more detailed version of this summary data set appears in Hart *et al.* (1998). The barn owl data are from pellets collected from roosts at Boullanger Island, off the Western Australian coast (30°16′S, 119°46′E). The site is described in Dickman *et al.* (1991), where a subset of the data is also presented. Pellets were processed in the same manner as the cat scats.

Statistical analysis

Spearman's rank correlation coefficients were used to test whether similar prey rankings were obtained using the volumetric percentage, numerical percentage and occurrence percentage techniques for each predator. Three comparisons were made for each predator (volumetric percentage *v.* numerical percentage, volumetric percentage *v.* frequency percentage, and numerical percentage *v.* frequency percentage). Therefore we used the Bonferroni correction of $\alpha = 0.017$ for each test to reduce the possibility of Type I error because of the multiple hypotheses.

The IRI for each predator was calculated using the formula:

$$IRI = (N + V)F,$$

where N = numerical percentage, V = volumetric percentage, and F = frequency of occurrence percentage (Pinkas *et al.* 1971). Martin *et al.* (1996) substituted mass for volume in this formula. IRI values are suitable only for ranking the relative importance of food types for one animal species and cannot be compared directly between one predator species and another, or between two groups of the same species (e.g. different age classes or sexes, or animals from different locations). However, rank correlation coefficients can be used to test the null hypothesis of varied prey rankings in different species or groups of predators against the alternative that prey rankings are similar (Martin *et al.* 1996). The relative IRI rankings for prey categories taken by the two geckoes were compared using Spearman's rank correlation coefficient, with $\alpha = 0.05$.

Results

Descriptions of the diet of each predator by volumetric percentage, numerical percentage, occurrence percentage and IRI are shown in Tables 1–5. Results of the Spearman's rank correlations between different measures taken for the same species are shown in Table 6. In most cases, the different measures produced similar rankings of the importance of prey taxa. However, in the case of *Diplodactylus stenodactylus* volumetric percentage and numerical percentage did not correlate significantly, while in the case of the barn owl volumetric percentage did not correlate significantly with either numerical percentage or occurrence percentage.

Table 1. Foods of feral cats based on analysis of 181 prey items identified from 50 scats collected in the Simpson Desert, 1991
See text for details of measures

Prey	Number	Percentage volume	Percentage number	Percentage frequency	IRI
Mammals					
Rattus villosissimus	14	24.5	7.7	28	902.6
Notomys sp./*Pseudomys* spp.	33	47.6	18.2	58	3818.3
Dasycercus sp.	2	0.6	1.1	4	6.8
Sminthopsis spp.	5	4.7	2.8	10	74.6
Ningaui sp.	3	0.5	1.7	6	12.9
Reptiles					
Dragon	5	3.5	2.8	8	50.1
Skink	16	5.8	8.8	20	292.8
Gecko	5	2.6	2.8	6	32.2
Other lizard	2	0.9	1.1	4	8.0
Snake	3	0.7	1.7	6	14.1
Other taxa					
Frog	2	0.2	1.1	4	5.2
Bird	7	3.0	3.9	14	96.1
Invertebrate	28	1.3	15.5	30	503.1
Plant	41	3.1	22.7	36	927.1
Scavenged	4	0.3	2.2	8	20.1
Other	11	0.7	6.1	22	149.1

Table 2. Foods of the gecko *Diplodactylus assimilis* based on analysis of 52 prey items identified from 21 scats collected in Western Australia, 1986–89
See text for details of measures

Prey	Number	Percentage volume	Percentage number	Percentage frequency	IRI
Grasshopper	9	26.0	17.3	38.1	1649.8
Ant	4	0.7	7.7	9.5	79.9
Termite	5	0.7	9.6	4.8	49.1
Beetle	8	19.5	15.4	28.6	996.7
Cockroach	2	2.1	3.8	9.5	56.6
Mantid	5	14.8	9.6	23.8	581.3
Moth	4	13.1	7.7	19.0	396.0
Fly	2	2.4	3.8	9.5	59.5
Homoptera	1	2.6	1.9	4.8	21.5
Heteroptera	1	1.2	1.9	4.8	14.9
Spider	5	8.1	9.6	19.0	337.4
Scorpion	1	0.5	1.9	4.8	11.5
Larvae	2	5.5	5.8	14.3	161.0
Other	3	2.9	3.8	9.5	64.2

The IRI rankings for the prey types of the two gecko species did not correlate significantly ($r_{s(12)} = 0.51$, $P = 0.06$). Grasshoppers, beetles and mantids were ranked highly for *Diplodactylus assimilis*, whereas beetles, spiders and homopterans were ranked most highly for *D. stenodactylus*.

Discussion

Implicit in the concept of IRI is the notion that the importance of different foods in the diet is defined solely in terms of their frequency, number and bulk, rather than any nutritional or other importance. This should be satisfactory for most descriptive studies of diets, where the IRI protects against bias that might result if only one of the component measures was used. However, the IRI is inadequate for foraging models using energy as a currency if the energy per unit mass relationship differs markedly between foods, or where the nutrient content of foods is in question (see discussions in Studier *et al.* 1991; Keeler and Studier 1992; Brooks *et al.* 1996).

MacDonald and Green (1983) criticised the IRI on the basis of redundancy of component variables, principal components analysis revealing for their data that all three

Table 3. Foods of the gecko *Diplodactylus stenodactylis* based on analysis of 50 prey items identified from 20 scats collected in Western Australia, 1986–89

See text for details of measures

Prey	Number	Percentage volume	Percentage number	Percentage frequency	IRI
Grasshopper	2	3.5	4.0	10.0	75.0
Ant	3	0.5	6.0	5.0	32.5
Termite	11	1.0	22.0	5.0	115.0
Beetle	11	31.5	22.0	45.0	2407.5
Cockroach	1	2.0	2.0	5.0	20.0
Mantid	2	4.5	4.0	10.0	85.0
Moth	3	9.8	6.0	15.0	236.3
Fly	1	1.2	2.0	5.0	16.2
Homoptera	4	11.2	8.0	20.0	385.0
Spider	9	29.2	18.0	40.0	1890.0
Scorpion	1	1.2	2.0	5.0	16.2
Larvae	1	3.8	2.0	5.0	28.8
Other	1	0.5	2.0	5.0	12.5

Table 4. Foods of nestling straw-necked ibis, based on 1240 prey items collected from the stomachs of 18 nestlings

Birds were collected at Capel, Western Australia, in 1993. See text for details of measures. These data are also used in Hart *et al.* (1998)

Prey	Number	Percentage volume	Percentage number	Percentage frequency	IRI
Lepidoptera larvae	553	44.1	45.2	61.1	5456.2
Scarab beetle 1	17	0.9	1.4	50.0	115.0
Scarab beetle 2	104	9.1	8.5	94.4	1661.4
Scarab beetle 3	146	4.5	11.9	50.0	820.0
Ground beetle	120	3.1	9.8	50.0	645.0
Beetle larvae	8	0.4	0.6	22.2	22.2
Unknown beetle	30	0.5	2.4	38.8	112.5
Mayfly larva	9	0.5	0.7	11.1	13.3
Leech	24	0.6	2.0	11.1	28.9
Centipede	2	0.4	0.2	5.6	3.4
Fly	4	0.1	0.3	5.6	2.2
Fly larva	2	0.1	0.2	5.6	1.7
Earwig	28	0.8	2.3	27.8	86.2
Cricket	3	0.2	0.2	11.1	4.4
Cockroach	1	0.1	0.1	5.6	1.1
Wolf spider	17	0.8	1.4	27.8	61.2
Gastropod	94	4.8	7.8	27.8	350.3
Crustacean	18	26.0	1.5	11.1	305.2
Unknown pupae	44	2.4	3.6	16.7	100.2

variables were highly correlated. They advised researchers to check for such redundancy in pilot samples and only use all three variables or the IRI in the final study if correlations were low. However, their analysis was based on 217 prey types across five fish species. With such a large range of prey it seems reasonable that many prey types would be represented only in traces. Therefore, consideration of all prey types in the analysis would be likely to show high correlations, even though the rankings of the most important 10 prey or less may have been different. Whether or not this is a problem will depend on the aims of studies. In two of the five species considered in this paper, the component measures did not all rank the prey taxa similarly and different conclusions would be drawn depending on which component was used.

Alternative composite indices have been proposed (Mohan and Sankuran 1988), although they are likely to encounter similar problems of correlations between

Table 5. Foods of the barn owl based on analysis of 424 prey items identified from 151 pellets collected at Boullanger Island, off Western Australia, in 1986

See text for details of measures. These data, except % frequency, are also used in Dickman *et al.* (1991)

Prey	Percentage mass	Percentage number	Percentage frequency	IRI
Mammals				
Mus domesticus	81.8	83.0	97.0	15985.6
Sminthopsis sp.	6.6	4.5	11.9	132.1
Parantechinus apicalis	1.1	1.4	4.0	10.0
Rattus fuscipes	0.3	0.2	0.7	0.4
Birds				
Petrel spp.	3.6	1.6	4.0	20.8
Neophema petrophila	0.6	0.2	0.7	0.6
Rallus philippensis	0.6	0.2	0.7	0.6
Unidentified birds	6.4	4.7	11.9	132.1
Unidentified reptiles	0.3	0.5	1.3	1.0
Insects				
Grasshoppers	0.3	2.1	5.3	12.7
Beetles	0.3	1.6	3.3	6.3
Plant matter				
Grass	0.1	0.5	1.3	0.8
Seeds	0.1	0.5	1.3	0.8

Table 6. Results of Spearman rank correlation coefficients comparing volumetric percentage, numerical percentage and frequency percentage as indices of prey importance for each of six predators

Significance levels are set at 0.017 because of the multiple comparisons. Significant results are marked with an asterisk

Predator	Percentage volume *v.* percentage number	Percentage volume *v.* percentage frequency	Percentage number *v.* percentage frequency
Feral cat	$R_{s(14)} = 0.71, P = 0.002$*	$R_{s(14)} = 0.67, P = 0.005$*	$R_{s(14)} = 0.97, P < 0.001$*
Diplodactylis assimilis	$R_{s(12)} = 0.64, P = 0.013$*	$R_{s(12)} = 0.91, P < 0.001$*	$R_{s(12)} = 0.79, P < 0.001$*
D. stenodactylus	$R_{s(12)} = 0.46, P = 0.116$	$R_{s(12)} = 0.90, P < 0.001$*	$R_{s(12)} = 0.79, P < 0.001$*
Straw-necked ibis	$R_{s(17)} = 0.86, P < 0.001$*	$R_{s(17)} = 0.75, P < 0.001$*	$R_{s(17)} = 0.83, P < 0.001$*
Barn owl	$R_{s(12)} = 0.59, P = 0.035$	$R_{s(12)} = 0.63, P = 0.021$	$R_{s(12)} = 0.98, P < 0.001$*

component measures. Moreno-Amich (1996) used mean percentage mass ('the sample average of the percentage of the weight of the item with respect to the weight of the gut contents'); it was claimed that this correlated closely with the IRI, while not weighting occurrence more heavily than number or volume, as occurs in the IRI.

However, neither criticism nor the availability of other options has dented the popularity of the IRI. Tavares-Cromar and Williams (1996, p. 93) specifically defended the IRI, arguing that it reduced the inherent bias in the single use of each of its components, which was '… especially important when the prey items ingested are of different sizes and represent many prey types'. A further advantage of the IRI is that if all three of its components are recorded, there will be easier comparability with studies that have perhaps used only one measure, and there may be greater opportunities for meta-analyses (Gurevitch and Hedges 1993). Two recent reviews of dietary assessments in fisheries biology both recommended the IRI as a valuable alternative to single-index measures, while expressing it as a percentage facilitated comparisons between different samples (Cortes 1997; Liao *et al.* 2001). The IRI is most appropriate for simple descriptions of diets and basic comparisons. More sophisticated statistical approaches are available for analysing large data sets or when specific *a priori* hypotheses about diets are to be tested (e.g. Luo and Fox 1996; Platell and Potter 1998; Gill and Morgan 1998). Furthermore, the IRI might not be ideal if comparisons between the frequency with which prey items occur in the diet and in the environment are to be compared.

We claim no originality for the IRI or its applications in this paper. However, the natural tendency of researchers to read mainly within their specialisation appears to have restricted awareness of the IRI. We hope that by discussing the IRI in a forum used by a broad spectrum of wildlife biologists its potential and limitations may become more widely known, rather than being largely the preserve of fisheries biologists.

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