

What's in a niche? I. The usefulness of prey-size spectra.

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ABSTRACT: The crucial importance of the trophic dimension has been recognized since the beginnings of niche theory. Knowledge of the trophic roles of the species in each ecosystem is pivotal to our understanding of its structure and function. For both practical and theoretical reasons, this paper proposes using trophic niche descriptions which do not include estimates either of the prey species availability or the influence of competitors. However, it proposes to include descriptions of the prey organisms, allowing ordering, rather than relying only on taxonomic categories.

In recent years, the simplification of ecosystem description allowed by partitioning into size groups of the components has led to important insights about system function. While overall energy and mass flows can be estimated purely on the basis of predator size, information about the trophic niche is required for interpretation of impacts of predators on particular components of the biomass spectrum or, conversely, the ability of given components to support production at a higher level. In many systems, prey size has been often recognized as being at least as important as prey species in prey selection, and size, as one of the simplest descriptors, provides a way to order the species. The spectrum of prey sizes and numbers eaten can be both a simple and a useful way to conceptualize the trophic niche, and standard statistical measures of the width of the prey size spectrum can thus be used as a niche width index. Two such, the coefficient of variation of prey sizes ("CVH") and the standard deviation of logarithmically-transformed prey sizes ("SLH") are proposed. Several studies have demonstrated that a size-based trophic niche metric provides a bridge between foraging and size-aggregated ecosystem models. This paper examines some of the difficulties as well as benefits of doing so.

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INTRODUCTION: WHY TROPHIC NICHES?

From the early days of niche theory, there have been two dominant concepts of niches: the temporal/spatial niche of Grinnell (1917, 1924), which culminated in the "Hutchinsonian" hypervolume (Hutchinson, 1957)- where the population lives- and the "Eltonian" niche (Elton, 1927 and many others)- what resources it uses. These have been described by Whittaker *et al.* (1973) as "habitats" and "niches", and by Leibold (1995) as "requirement niches" and "impact niches", respectively. As generally used by animal ecologists, the Eltonian niche has been taken as equivalent to a trophic niche, and it is in that sense that I will discuss it here. The histories of these concepts have been detailed elsewhere (*e.g.* MacArthur, 1968; Vandermeer, 1972; Leibold, 1995; Wang, 1995) and so will not be pursued here. However, note that Hutchinsonian (temporal/spatial) niches must refer to species or populations (Colwell & Futuyma, 1971), while a trophic niche can be described for an individual organism (*e.g.* Arlettaz *et al.*, 1997). Whereas practical application of the Hutchinsonian niche has proven difficult (Green, 1971), the trophic niche has been a useful concept (*e.g.* Werner, 1979), both because diet is one of the more easily quantified aspects of the predator's lifestyle, and because predation is its principal mode of interaction with most other species. The limits to population growth are often referred to a theoretical

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Evolutionary Theory 12: 1-22 (October, 1999)

The editors thank two referees for help in evaluating this paper.

carrying capacity of the environment. However, as organisms are seldom too crowded to actually be fitted in to their environment, the actual limiter is more likely to be predation or food rather than any aspect of space *per se*. This is equivalent to saying that the trophic dimension of the niche is of overriding importance- as was recognized by Elton (1927). Hutchinson (1959) remarked that "food relations appear as one of the most important aspects of the system of animate nature", and Hespenehede (1973) stated that food was "perhaps the critical niche dimension". Indeed, Matsuno (1995) feels that on the basis of stability criteria, predation must be the major driver of evolution. Even when considering the trophic axis as only one of the Hutchinsonian dimensions (e.g. Green, 1971), Grinnell (1904) and most later authors (e.g. Ross, 1986) have agreed that it is one of the most important. Green (1971) concluded that "...Elton's...concept of the niche as trophically defined tends to hold for even what would seem, a priori, to be physically rather than biologically accommodated communities." In 1997 alone, I have seen more than 40 trophic niche breadth studies; the total number published is undoubtedly much greater. Although interest in theoretical aspects may have declined in recent years (Leibold, 1995), use by field biologists is strong and even growing.

In this paper, I shall argue that trophic niche indices need not include descriptions of the environment in which the predator lives, nor of possible partitioning of the environment by competitors, but should include descriptions of the prey species themselves. I shall discuss drawbacks of taxon-based niche breadth indices and the theoretical and practical advantages of size-based statistical niche breadth indices.

For the purposes of this paper, I shall designate as "predators" all organisms being considered as consumers, whether carnivores or not, and as "prey" all those organisms which they consume, whether animal or plant.

WHAT INFORMATION SHOULD COMPRISE A TROPHIC NICHE DESCRIPTION?

1). **The question of incorporating resource availability:** Many authors feel that a niche description should include information about the predator's environment, and hence the degree of selection it exercises (e.g. Schoener, 1974a; Petraitis, 1979; Feinsinger *et al.*, 1981; Smith, 1982; Hansen *et al.*, 1994). Boyd (1976) and Lehman (1976) noted that a passive device such as a filter will produce different prey spectra depending on the available environmental prey size distribution. There are clearly many advantages to including selection among resources in niche descriptions, and given an unambiguous way to do so, indices incorporating it could greatly enrich our understanding. However, there are several problems with attempts to incorporate prey availability into most feeding (trophic) niche estimations:

a). How can potential prey be identified? We can assume with intuitive certainty that a bear is not within the list of potential prey of a sparrow, nor is a porpoise likely to be a prey of a herring- nor of a sparrow, but we really only "know" these things because we have never seen them on a list of recovered prey. Probably the largest body of prey species or size data has been published on predators that eat things which are smaller than they are (Warren and Lawton, 1987; Cohen *et al.*, 1993), but in fact many, including most parasites- arguably the most abundant predators (Price, 1977; Rohde, 1993)- and insect parasitoids (J.H. Lawton, pers. comm.), can be said to eat things larger. Hespenehede (1973) has suggested that the overall relationship of predator-to-prey sizes is virtually a continuum over a very wide range (e.g. see his Figure 1). However, very large prey are apt to be unrecognized in many predators' diets because they are ingested only in small pieces, and very small prey are often overlooked or underestimated because of differential digestion (Pearre, 1974).

b). Even if we feel we know what the potential prey organisms are, their numerical abundance in our environmental samples probably does not well reflect their availability to the predator.

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i). Our ability to sample the environment almost certainly differs from that of the animal we are studying: a plankton net, or a pitfall trap, or a shotgun, has its own sampling characteristics and biases, and none can sample all sizes and morphologies of potential prey with equal efficiency (Root, 1967; Pearre, 1974; Perrin, 1982; Yom-Tov & Wool, 1997; see also Pearre, 1999). Perrin (1982), in his study of Barn Owls *Tyto alba*, sampled their mammalian prey with two types of traps. These yielded different estimates of the proportions of the available small mammal populations: to which should the Barn Owl diets be compared? Pardieck and Waide (1992) sampled birds with mist nets of two mesh sizes, obtaining differing mean sizes and size distributions. Potter *et al.* (1983) sampled in an Australian estuary with three types of fishing gear. Each yielded a different species composition, mean fish size, and size distribution. If one wished to include prey availability in the niche breadth of a predator in either of these situations, which prey abundance estimate should one use? Gibb (1954) noted that "It is always difficult, and often impossible, to measure the availability of food to birds in the field", and concluded that "...the numerical abundance of food in the habitat may bear no close relationship to its availability...to the bird." Edwards (1968) attempted to estimate abundances of commercial fish species in the northwest Atlantic. Despite a massive sampling program involving analyses of the performances of many types of gear, he stated that "It is virtually impossible to get precise values for either availability or vulnerability."

ii). The problem of vulnerability has been extensively investigated in aquatic habitats. Most pelagic fish depend on vision for hunting, and many prey zooplankton species typically migrate away from the surface waters during daylight in order to be less conspicuous to them (Hardy & Gunther, 1935; also Pearre, 1979 and references therein). If the fish detects them less efficiently as the light level decreases, but our plankton nets catch them equally well at all light levels- or as in some cases, less well in brighter light, how do we meaningfully assess their availability to the fish? There has also been considerable experimental investigation on how fish detect prey in light (see O'Brien, 1987 and references therein). Large, or otherwise conspicuous prey (color, movement, etc.) are detected further away than are small, inconspicuous ones. Thus fish search larger volumes for large prey than they do for small ones, and this effect also varies with both fish size and species. How can we allow for these differences in assessing the prey available to the predator?

iii). There is no convention for deciding what parts of an predator's behavior are included in its selection mechanism. If a mobile predator feeds only within a small part of its overall range, are the "available prey" only those within that patch at that time, or are they all suitable prey in the range? Three vertically migrating chaetognath species (non-sight hunting) appeared to be feeding very selectively when abundances of prey zooplankton, which were also vertically migrating, were estimated from the entire water column (Pearre, 1974). However, minimization of residuals from overall prey composition compared to those collected from the water column enabled estimation of the time and depth of feeding of each species: this was checked against estimates of prey digestive state. Based on these local abundances, much of the apparent selectivity disappeared. But should we include the predator's choice of feeding times and places- and hence of prey availabilities- as part of its prey selection strategy? If not, what do we do when we do not know where and when the predator fed, *e.g.* in analysis of pellet or scat data from a raptor or mammalian carnivore?

iv). Similarly, what aspects of a prey's defenses should affect the estimate of its availability? Arguably, neither size nor bad taste should be considered to do so (but see Root, 1967), but what of camouflage or escape speed? A prey organism which moves out of the predator's detection field may be less "available" than one which does not. In the example above, most of the residual "selection", after accounting for time and place of feeding (above), was removed when experimentally determined escape radii were used to adjust the local raw prey abundances (Pearre, 1974).

These sampling problems are very intractable, and sometimes affect even carefully controlled

laboratory situations. **If it is likely, for any reason, that estimates of prey availability are biased or incorrect, niche breadth estimates incorporating such faulty data will also be biased, and clearly less reliable than those independent of them** (e.g. see Dickman, 1986).

c). If we could somehow overcome these objections, we are still left with a philosophical question of why the environment should be part of the niche description *per se*? An index which compares prey ingestion to estimated prey availability essentially incorporates prey selection. But prey selection is often examined independent of trophic niches (e.g. Pearre, 1974, 1982a), which itself implies that they are separable concepts.

This might be only a semantic problem: Schoener (1968) proposed referring to overlap values comparing diets to available prey as "density specialization". Perhaps we should simply designate niche indices which include environmental information as "inclusive", "relative" or "comparative" indices and those which do not as "restricted" or "absolute" indices. These terms should not be confused with "fundamental" and "realized" niches as used by Hutchinson (1957) and other authors. For present purposes I will define a trophic niche as "absolute", and equivalent to a "prey utilization spectrum" (Levins, 1968). That is, a trophic niche, as I am using the term, is the spectrum (types and numbers) of prey and prey classes actually used by the predator population, but not their abundance, availability, or use by competitors in the environment.

By this definition a trophic niche is ideally the result of coevolution by the organism and its surroundings (Van Valen, 1983; Marrow *et al.*, 1992). Prey selection ability, in this usage, itself becomes an adaptation to the spectrum of food ordinarily available. Successful introduced predators must be pre-adapted to a spectrum of available prey similar to that in the habitat into which they are inserted. In engineering terms, the predator's total morphological, physiological and behavioral apparatus is here considered a single "black box"- i.e. a device of unspecified internal mechanism which acts on a known or unknown input to produce some output. This black box is adapted, among other things, to obtain an adequate diet from its particular environment- including its environment's normal variability (Krzysik, 1979). The absolute trophic niche of an organism is then the output of the system, regardless of the inputs or mechanisms, and can be regarded as an emergent property of the organism (S.R. Kerr, pers. comm.). This is equivalent to stating that "Electivity ...would not be regarded as an active process, but as a passive result of a mechanical feeding system" (Boyd, 1976), termed "mechanical grazing" by Gilbert & Bogdan (1984). However, I here expand that concept to include all systems and behavior for choosing prey, even including 'choosing' where to live or the seasons in which to live there, as part of the same mechanism. A trophic niche dominated by a single prey species might be the result either of non-selective predation in an environment dominated by that species, or of a high degree of selection by a predator living where that prey species is rare. Schoener (1969) anticipated this in defining a "specialist" predator as one which excels at processing a narrow range of prey- not necessarily one in which a narrow range is found.

Comparative indices may still be valuable descriptors in laboratory experiments and comparative field studies in which the prey collection methods are standardized. However, although an obviously secondary consideration, the usefulness of a niche index will be greater if it allows comparisons among more types of diet data. Absolute niche indices can usually be estimated from data gathered for comparative ones (i.e. with estimates of prey availability), but never vice-versa.

2). **The effects of competitors:** Cohen *et al.* (1990) suggested that a trophic niche index should account for higher dimensions of the trophic niche itself. Species live in a complex matrix of interspecies interactions, and all of these affect each other's resource use. On the other hand, two animals may share the same prey size range but not compete because one is diurnal and the other nocturnal (but see Jakšić, 1982), or they may forage in different patches (Schoener, 1968). Cohen *et al.* (1990) suggested that the dimensionality should be determined by the number of competitor species, i.e.

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the number of species having significant "niche overlap" with the species under consideration. While this is intellectually appealing, it presents practical difficulties analogous to those of including environmental prey abundances:

- a). Estimates of trophic niche overlap will depend on whether the diet is considered in terms of prey size or prey taxa (e.g. Salvidio, 1992).
- b). The degree of overlap also depends on the level of taxonomic identification (Greene & Jaksic, 1983) or the scale of division of the resource axis (Schoener, 1968). Schoener points out that too fine division can lead to elimination of all overlap. Thus, estimates of the niche dimensionality will depend on the way in which the data were collected.
- c). Likewise, the degree of niche overlap also varies with the overlap index chosen (Linton et al., 1981).
- d). How can a potential competitor be identified? An owl, for example, may prey on birds, small mammals, and large insects. Are its competitors other owls (nocturnal), other nocturnal predators, owls and hawks (diurnal), owls, hawks, cats and foxes (bird eaters), owls, hawks, foxes, cats and snakes (bird and small mammal eaters), or perhaps all those plus shrews, spiders and mantids (insect eaters)? Do they all compete with parasites? Do they compete with humans?
- e). Although characteristic feeding in different patches could often take two species out of competition, temporal division of the same resource only does so if the resource can be considered self-limiting and self-renewing within a time frame short compared to the temporal division. It is doubtful, for instance, that the owl and hawk example would qualify (their prey species often overlap: see Jaksic, 1982, and references therein), nor would the example (above) of vertically-migrating chaetognaths feeding on vertically-migrating prey (Pearre, 1974). However, seasonally migrant birds or fishes, or seasonally abundant herbivorous insects or zooplankters probably would. Between these extremes the decision would probably (and unfortunately) vary with the investigator.
- f). The requirement to consider such dimensionality would make virtually impossible the quantitative comparison of trophic niches between species with niches of different dimensionality, or between populations of the same species in different parts of the world.
- g). This analysis requires simultaneous estimation of many diet spectra, and at this time probably is of more interest for theoretical analysis of food web structure (e.g. Cohen et al., 1990) than for practical analysis of field data. However, unlike the problems of including availability, this concept could nonetheless become viable with formal standardization of index type, degree of identification and prey specification, and definitions of time and site differentiation. Despite the practical difficulties in application, it is an exciting idea and has the potential to add richness of understanding to ecosystem analysis.

3). **Indices concerned with neither resource availability nor competitors:** Based on an informal survey of recent trophic niche literature, very few studies do account for prey availability (less than 3% of trophic niche studies published in 1992-97). No studies were found which included higher dimensions due to competitors, but this concept is newer and may gain acceptance in the future. The indices most commonly used to describe trophic niches are undoubtedly the two discussed by Levins (1968: as "Levins" and "Shannon-Weaver" indices) and their normalized derivatives. Probably the next most popular is the Brillouin index (Pielou, 1975). These are all based only on enumeration of species of prey found in the diets, and so are "absolute" by the usage above. Note that "species" as used here need not be (although it usually is) a taxonomic species: it is just as easy to use other taxa (e.g. genera or orders: Greene & Jaksic, 1983) or groups based on some other characteristic such as color, size, or ecological requirements (Ehrlich & Holm, 1962; Schoener, 1968).

TAXON-BASED NICHE METRICS vs. SIZE-BASED ONES:

Advantages to taxon-basing: The most common way to describe trophic niches is in terms of the numbers of each taxonomic species of prey consumed (a "cardinal" index in Cousins' (1991) terminology). This approach is appealing for several reasons:

1). It is frequently the easiest: the raw numbers of each identified prey type can be used in some niche metric such as those above; no measurements need be taken, nor estimates of reconstructed fresh prey size made.

2). It is often the best way to examine certain biological interactions: one can look for preferences for particular species, consider the effects of an outbreak of that species on the predator's population, or evaluate a predator's impact on a prey species population, or through it on a competitor (Greene and Jakšić, 1983).

3). Several authors (e.g. Smith & Marti, 1976; Herrera & Jakšić, 1980; Jakšić *et al.*, 1982; Greene & Jakšić, 1983; Marti *et al.*, 1993a,b) have used this type of index estimated separately on species and on a higher taxonomic level to differentiate "species diversity" from "trophic diversity", with the latter assumed to indicate versatility in foraging methods.

Disadvantages of taxon-basing: However, taxa as categories have perhaps overwhelming theoretical and practical disadvantages:

1). **Choice of taxonomies:** The way in which species are defined obviously has a great effect on niches estimated using them. As Greenwood (1997) points out, there are a number of logical taxonomies, and the choice of which to use can vary with both circumstance and fashion.

a). **Biological vs. phylogenetic species:** There is an imminent crisis in terminology among taxonomists. The traditional method of classification defines species largely on the basis of presumed reproductive isolation (Mayr, 1942), and higher taxa on phenotypic characters of their constituent groups (Lee, 1996). Phylogenetic species and higher taxa (sometimes termed "evolutionary" classification) are instead based on cladistic interpretations of relatedness (Cracraft, 1983; de Queiroz & Gauthier, 1990; Lee, 1996; Greenwood, 1997). According to Snow (1997) this would result in perhaps a doubling of the number of recognized bird species. Taxon-based niches converted to phylogenetic terminology would thus often differ from traditionally-based ones, and converting many older studies might be impossible.

b). **Ecological association:** This refers to the way in which species are distributed relative to other organisms in the environment, including effects of their own foraging types and competition. It reflects Ehrlich & Holm's (1962) suggestion of a "taxonomy" based on ecological requirements: Bird species A and B are seed-eaters, and will often be found in the same places, while C is an insectivore. Is it as significant to find A and B together in the prey of a raptor as A and C? Is it as significant to find five fish species and a bird as to find six fish (or bird) species?

2). **Choice of taxonomic level:** The higher the taxon used, the easier it is to enumerate, but the lower the number of available categories.

a). If one study has prey enumerated to species, and another on the same predator has prey enumerated only to phylum, the estimated niches will be quite different (Petraitis, 1979; Greene & Jakšić, 1983). Usually there are some prey which cannot be identified further than, say, genus. Some authors attempt to even out such problems by reporting predation only to genus level. However, a predator which selects only one species in a genus probably has a narrower niche than one that takes all species in the genus. Would a predator which eats all the species in a genus have the same niche breadth in area "A" where there is only one species in the genus as in area "B" where there are 10? In a survey of eight studies of sympatric predator species, Greene and Jakšić (1983) found that when the

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prey are classified only by order, the estimated Levins Niches were always smaller and overlapped less than when the same prey were identified to species (see above).

b). For the same reason, different taxonomic levels should not be mixed in the same study (but see "(3)", below). Unfortunately, mammalogists frequently identify all mammal prey to genus or species, while grouping avian prey as "birds". Ornithologists do the opposite, and both usually will group insects in a single taxon, or at best identify them to order (e.g. "Coleoptera"; see Schoener, 1968; Greene and Jakšić, 1983; Marti *et al.*, 1993). Many studies report prey which were not fully identifiable: should these be counted as separate species, or orders, or just ignored?

c). Clearly more information is added by considering higher taxa as well. The niche of some animal which eats 5 species of insects, 5 of birds, and 5 of mammals must be different from that of one which eats only 15 species of birds. This overlaps the problem of ecological association (above), and this type of information is seldom incorporated with information on lower taxa. Pielou (1975) discussed means of integrating different taxonomic levels into the Shannon or Brillouin indices. Warwick & Clarke (1995) have proposed use of weighting factors for different taxonomic levels, such that two species in different genera would contribute less to total diversity than two in different families, etc. They adopted standard weighting factors based on the number of steps up the "Linnaean" taxonomic scale which separates the species, and range from 1 (species of the same genus) to 6 (different phyla). These weighting factors were included in an index analogous to the Shannon-Weaver diversity index.

3). **Taxonomic relatedness:** However, even with our most sincere efforts to report all prey to equivalent taxonomic level- do we really know, in an ecological sense, what "equivalent" taxa are (e.g. see Vane-Wright *et al.*, 1991; Harper & Hawksworth, 1994)? While species themselves are clearly different categories, we get on less certain ground when we group them into higher taxa. Are differences between bird families the same "taxonomic distances" as between mammal or insect families? Is an Order among fish equivalent to one among molluscs or insects? The introduction of new taxonomic levels such as Grades, Divisions, Tribes, and Sections, as well as the prefixes "infra-", "sub-", and "super-" to the traditional taxa in the past 50 or so years, accompanied by the frequent reassignment of some taxonomic groups to different levels (Classes to Super-classes, Orders to Infraorders, etc.), argues strongly that they are not. We think we know that species are less distinct within genera than between, but some families are larger than others. Even if we could assume that all species in one phylum (or even in a family) were the same taxonomic distance from each other, species in one phylum are unlikely to be the same distance from each other as those in another phylum (Cousins, 1991). As an example, the Phylum Chaetognatha contains only about 200 species in very few genera, and these species, and possibly even most genera are considerably more homogeneous in both morphological and ecological characteristics and are on average probably taxonomically closer to each other than are species of the Class Insecta (about 750,000 species) or even of the Order Coleoptera (about 300,000 species).

The cladistic solution (Vane-Wright *et al.*, 1991) would replace the type proposed by Warwick & Clarke (1995) by one in which the weightings reflected the differences in branch lengths of the cladogram including all of the prey species. Cladistic taxonomies can be constructed in several ways (E.G. Merinfeld, pers. comm.). One, of course, is molecular taxonomy: ultimately, the resemblance of two species' genotypes may give us the best answer to their relatedness, but definitive results are still in the future (Raff *et al.*, 1994). As Warwick & Clarke (1995) note, "Detailed, fully resolved cladograms are not available for most groups of organisms." Roy & Foote (1997) put it even more forcefully: "Not only are robust phylogenies currently unavailable for most large clades, but the number of equally supported, alternative topologies increases with the number of taxa analyzed." However, even if we had such data, the phenotypic comparison- what the predator sees- and ecological association- where

the predator feeds- will probably remain more relevant than genetic relatedness in determining trophic niches.

Numerical phenology is another attempt to resolve this problem, with species catalogued, sorted, and grouped by morphological features. The degree of difference on a multidimensional scale is then used to generate a numerical estimate of relatedness (Sneath & Sokal, 1973). This is a promising approach, but of course the numerical index keeps changing as more phenotypic features are added. Furthermore, as Roy & Foote (1997) note, "...we are far from having a meaningful set of traits that can be measured for all the known phyla...". One would be lucky indeed to find relatedness data of any type already compiled on the species one happened to find in a particular predator's diet. However, **these considerations eventually must be addressed if we wish to assert that it is between-taxon differences in prey which are important to the predator, and hence to its trophic niche.**

Hutchinson (1957) noted that for a set-theoretic niche description, "It is assumed that all environmental variables can be linearly ordered." While many other environmental variables such as temperature, elevation, pH, salinity etc. are simply orderable, prey species usually are not. Prey species might be ordered in a number of ways (Cousins, 1991): for instance, by abundance per species in the environment or the predator's diet, or by cladistic or phenotypic distances (see above), *e.g.* from the most abundant, or perhaps from the predator's own species. Krzysik (1979) suggested that "The most tractable niche dimension, and therefore the one most used for theoretical models of resource allocation and species packing, is food size." Size provides a system of ordering, which can be considered a simply-measured, well-documented, relatively unambiguous element (axis) of phenotypic distance (Roughgarden, 1972; Cohen *et al.*, 1993; Roy & Foote, 1997).

PREY-SIZE BASED NICHE INDICES: Approaches:

Although it is probably seldom the only consideration, a number of authors have concluded that prey size is a more important criterion for prey selection than is species (*e.g.* McCormick, 1969 (hydromedusae); Rothaupt, 1990, and Hansen *et al.*, 1997 (rotifers); Moens and Vincx, 1997 (nematodes); Hansen, 1991 (opisthobranch molluscs); Boyd, 1976 (herbivorous copepods); Yen, 1985 (carnivorous copepods); Lawton, 1970, and Hall & Pritchard, 1975 (insect larvae); Gibbons & Stuart, 1994 (chaetognaths); Keast, 1985 (freshwater fish); Quast, 1968, Mattson, 1981, and James, 1987 (marine fish); Krzysik, 1979 (salamanders); Schoener, 1967, 1974b; Schoener & Gorman, 1968, and Pianka, 1977 (lizards); Root, 1967, and Hespenheide, 1971 (insectivorous birds); Wheelwright, 1985 (frugivorous birds); Remsen, 1990, and Reynolds & Hinge, 1996 (kingfishers); Hulseman, 1981, Camphuysen, 1994, and Walter & Becker, 1997 (seabirds); Rosenzweig, 1966 (Carnivora); Martuscelli, 1995 (bird-eating bats): see also discussion in Hespenheide (1973)). Indeed, this result is predicted by optimal foraging models (Lehman, 1976; Cousins, 1991), and Werner & Gilliam (1984) state that "Size has a predominant effect on an animal's ...susceptibility to natural enemies." There are two ways to incorporate information about prey size into a trophic niche index, either of which will form an "ordinal" index (Cousins, 1991). The less usual is to estimate one of the taxon-based indices (above) with biomass groups of prey, *i.e.* using the proportion of total estimated ingested biomass attributable to a particular prey species instead of the numerical proportion (Herrera, 1974; Krzysik, 1979; Jedrzejewski *et al.*, 1994; Vitt & Carvalho, 1995). This attempts to describe a trophic niche by its nutritional value to the predator, but without distinguishing between gross and net energy inputs. Also, as many predators do not consume the whole of large prey, the weighting may overrepresent the nutritional contributions of these taxa.

The other approach is to use size classes of the prey (instead of total biomass) as "species" in one of the niche indices (*e.g.* Barbault & Maury, 1981: Shannon Index on prey volumes; Remsen, 1990:

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Levins Index on prey lengths). This assumes that useful information about the ecosystem can be obtained by simplification of species to size groups. Aggregation of ecosystem components into size groups, which was suggested by Elton in 1927 but little utilized for many years, has proven to be a very powerful tool for analysis of many systems and system models (Kerr, 1974; Platt & Denman, 1978; Werner & Gilliam, 1984; Dickie *et al.*, 1987; Cohen *et al.*, 1990; Cohen *et al.* 1993, Thiebaut & Dickie, 1993, Blackburn & Lawton, 1994; Silvert, 1984, 1996; Peters *et al.*, 1996). A major proportion of physiological parameters of animals scales as simple functions of size (Peters, 1983). Werner & Gilliam (1984), noting that "Body size is... one of the most important attributes of an organism from an ecological and evolutionary point of view," observed that "size-selective predation can be a primary organizing force in some communities." Peters *et al.* (1996) modelled ingestion, growth, respiration, defecation, and excretion all as simple functions of body mass throughout the animal kingdom, and Silvert (1996) noted that "Size structure is now widely used as an investigative and diagnostic tool in ecological research".

Ecosystem effects of prey size selection by predators have been investigated by Brooks & Dodson (1965), Rosenzweig (1966), Schoener (1968), Kerr (1971), Werner (1979), Werner and Gilliam (1984), and a number of later authors. Brooks & Dodson (1965) proposed that in the absence of fish predation, zooplankton would be dominated by large forms because they were able to obtain and utilize energy more efficiently than small ones (the "size-efficiency hypothesis"). Rosenzweig (1966) showed by means of prey size spectra that sympatric Carnivora partitioned prey resources on the basis of size. Schoener (1968) examined resource (diet + microhabitat) partitioning in a community of *Anolis* lizards. He estimated trophic overlaps between pairs of predator species using both prey sizes and prey taxa. He found that habitat overlaps were inversely related to those based on prey size (providing a niche separation to permit coexistence), though they were positively related to overlaps based on prey taxa. Werner (1979) combined estimated prey-size optima and predator morphology to explain habitat niche divergence in three species of centrarchiid fish. Pearre (1986) found by prey-size based niche analysis that small fish had access to equal or larger prey biomass pools than did larger ones, contradicting one of the key assumptions of the size-efficiency hypothesis (Brooks and Dodson, 1965). However, Pepin & Penney (1998) report that the size-based niches of larval fish increase as they grow. Kerr (1974) and Warren and Lawton (1987) used prey/predator size relationships to explain the size-frequency distributions of aquatic organisms and invertebrates. Pearre and Maass (1998) compared size-based trophic niche estimates with normalized Levins and Shannon-Weaver indices for diets of the cat *Felis catus*, and found that the size-based index was more responsive to environmental influences than was either of the others.

Investigation of the influence of prey size on feeding efficiency and growth perhaps dates from Dahl (1926). Theoretical and experimental investigation was done by Paloheimo and Dickie (1966), Kerr (1971), and Emlen (1973). Werner (1974) and Werner and Hall (1974) extended this into estimation of benefit/cost curves, which became one of the cornerstones of optimal foraging theory (Pike *et al.*, 1977). Trophic structure, of course, governs energy pathways through all ecosystems (*e.g.* Cohen, 1994). It ultimately determines the number of species in an ecosystem (Paine, 1966), and whether small or large organisms are the principal energy consumers (Blackburn & Lawton, 1994). These are essentially trophic niche questions, and add some urgency to the already fascinating riddles of the interactions of predators and their prey. Given its utility for simply ordering species, prey size seems a logical and useful choice on which to construct a trophic niche index. It also provides a framework within which to discuss questions of "niche position" and "within-" *vs.* "between-phenotype" niche components (Roughgarden, 1972), all problematic concepts in taxon-based indices (*e.g.*, see Krzysik, 1979).

Finally, reports of prey often are given only as prey sizes. While it is relatively straightforward

to convert prey species to mean sizes, conversion in the other direction is seldom possible. Therefore, size-based niche indices give the opportunity to use both types of data, greatly expanding the number of comparisons possible from literature data (see: **The question of incorporating resource availability**, above).

EVOLUTION OF A SIZE-BASED TROPHIC NICHE INDEX:

Elton (1927: p.59) observed: "There are very definite limits, both upper and lower, to the size of food which a carnivorous animal can eat. It cannot catch and destroy animals *above* a certain size, because it is not strong or skilful enough....a carnivore cannot subsist on animals *below* a certain size, because it becomes impossible at a certain point to catch enough in a given time to supply its needs." Although we now tend to couch the discussion in terms of "benefit/cost ratios", these size constraints turn out to hold for most animals, carnivorous or not (e.g. see Hansen *et al.*, 1994). There are many mechanisms by which these size limits are enforced- see Hansen *et al.*, 1994, for an introduction- but their existence, and the implication of some optimal size between them, suggests that a simple statistical descriptor of the intervening distribution would serve as a niche estimator. Some older studies have used the range of prey sizes to describe the niche, but range as a statistic is not a generally useful niche measure (Schoener, 1968; Pearre, 1986; Roy & Foote, 1997). A number of studies have found that in general the distribution of prey size frequencies approximates a normal (Ursin, 1973; Roughgarden, 1972, 1974, 1979; Case, 1979; Wheelwright, 1985) or, more commonly, a lognormal distribution (Williams *et al.*, 1961; Hespenheide, 1971; MacArthur, 1972; Alevizon, 1975; Werner & Hall, 1974; Pearre, 1980b, 1982b; Case, 1981; Peters, 1983; Vézina, 1985; c.f. McAlister, 1879). The use of normal or lognormal prey size spectra in trophic ecology is not new: these have been referred to as "prey utilization functions" or "prey-size resource axes" by Levins (1968), Schoener (1974a), and Roughgarden (1972, 1974, 1979); see also Schoener's comments on MacArthur's (1972) use of the term. A number of authors have made use of statistical descriptors of prey size distributions to estimate trophic niches; for brevity these are listed in Table I, showing the combination of prey dimensionality, statistical descriptor, and distributional assumptions used.

On the assumption that prey sizes should be either normal or lognormal (as argued above), in a previous paper (Pearre, 1986) I used two such: the coefficient of variation of prey sizes ("CVH": the standard deviation of the distribution divided by its mean, which assumes a normal distribution), and the standard deviation of the logarithm of prey sizes, "SLH", which of course assumes a lognormal distribution ("H" enters the nomenclature as a general designation of a prey or "Herbivore" species). These can both be characterized as "ratio" or "relative" measures (Lewontin, 1966; MacArthur, 1972; Pearre, 1986), and thus incorporate Ursin's (1973) suggestion that, to a predator, "...half as big' and 'twice as big' differ by the same amount from 'just fine'." Hespenheide (1971) and Maiorana (1978) suggested that this might be accomplished if the predator recognized proportionate rather than absolute size differences (c.f. Yezerinac *et al.*, 1992). Schoener (1968) applied the same reasoning to the selection of lognormally-distributed perch diameters by lizards. This might be thought of as a predator's-eye version of the Weber-Fechner Law (e.g. see Galton, 1879), which states that the minimal perceptible difference between the physical magnitudes of stimuli is a constant fraction of one of them. In the real world it is often difficult to properly characterize the distribution of a biological data collection, and few will fit any hypothetical curve well. A decision only between normality and lognormality can be simply resolved by examination of the skewness and kurtosis of the estimated fit (Schoener & Janzen, 1968; Hespenheide, 1971), but more powerful methods are available if the fit is considered crucial (Gingerich, 1995). Note that the choice of dimensionality (see **Appendix**) affects not only the estimated niche width but also the shape of the distribution and the niche position (the modal or "optimal" (*sensu* Elton, 1927)

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Table 1: Statistical functions, dimensionality, and assumptions of prey size distributions adopted to estimate width of prey-size spectra: Authors and dates.

Statistic:	<u>VARIANCE:</u>	<u>STANDARD DEVIATION:</u>	<u>COEFFICIENT OF VARIATION:</u>
Dimensionality:			
<u>1-DIMENSIONAL:</u> length/ width/ ESD:			
Distributional assumption:			
<u>Normal:</u>		Roughgarden, 1972 (2 s.d.)	Baker, 1977 Krzysik, 1979 Case, 1979 Pearre, 1986
<u>Lognormal:</u>	Hespenheide, 1971	Krzysik, 1979 Case, 1981 Pearre, 1986 Jenkins, 1987 Munk, 1992 Munk & Nielsen, 1994 Munk, 1997 Pepin & Penney, 1997 Pearre & Maass, 1998	
<u>2-DIMENSIONAL:</u> area:			
Distributional assumption:			
<u>Normal:</u>	Yoshiyama, 1980		
<u>3-DIMENSIONAL:</u> mass/ volume:			
Distributional assumption:			
<u>Normal:</u>	Roughgarden, 1974 Ross, 1977		Ross, 1977 Golani, 1994
<u>Lognormal:</u>		Alevizon, 1975 (2 s.d.) Werner and Hall, 1977 Krzysik, 1979	
	Werner, 1979 Vézina, 1985		

prey size). The higher the order of the dimension, the further the mean prey size will be shifted towards the right and the larger the standard deviation (Case, 1981). Also, while spectra based on prey numbers or proportionate numbers might be normal or strongly skewed to the right, the same data expressed as biomasses (mass or volume per organism x number per size class, e.g. Herrera, 1974; Krzysik, 1979; Jedrzejewski et al., 1994; Vitt & Carvalho, 1995) will usually appear skewed to the left, and so inappropriate for logarithmic transformation. As with the choice of dimensionality, the choice of a linear

or logarithmic prey scale affects the estimated niche position, or mean prey size (Schoener, 1968). Note also that a normal distribution, or even the portion covered by its standard deviation could, on occasion, extend into negative "prey sizes", which is a quite practical argument for use of the lognormal distribution (Galton, 1879).

The use of variances (Roughgarden 1974, 1979) is computationally convenient, as it allows simple summation of the niches of different population groups contributing to the overall niche of the population (Roughgarden's "within phenotype" components). However, standard deviations (see Table I), seem more intuitive because they have the dimensions of the sizes of prey examined. SLH has the dimensions of the log-transformed prey size data, and will thus vary with both the units of measurement and the logarithmic base chosen, while CVH is dimensionless (Pearre, 1986). CVH and SLH differ, of course, in their distributional assumptions, but they covaried tightly ($p < 0.001$) in real data sets on fish predators (Pearre, 1986). Use of CVH may be necessary when the investigator wishes to compare his trophic data with others presented, as is common, simply as estimates of prey size mean and variance (Pearre, 1986). However, Wright (1968) and Lewontin (1966) suggested equations for approximate interconversion.

As noted above, the Levins and Shannon-Weaver niche indices are sometimes used with size categories instead of biological taxa (e.g. Remsen, 1990). If every prey species is of a different mean size, the numerical value of one of these indices estimated this way is of course identical to that based on taxa. However, a size-based index can incorporate information on the spectrum of sizes utilized within each prey species as well as between-species means. In another study (Pearre, 1999), I will compare size-based trophic niche widths as estimated by both untransformed and normalized Levins' and Shannon's indices, with the two statistical indices (CVH and SLH, as above) through a range of simulated conditions and in some examples of real data.

LIMITATIONS:

1). Rodríguez & Magnan (1993) examined the community structure of macrobenthos in three lakes through various seasons of two years. They noted that the taxon-based approach yielded different results from a size-based one, and commented that "Taxon-based analyses highlighted the differences... (while)...size-based analyses underscored the similarity..." The same tendency can be expected in size-vs. taxon-based trophic niches. Schoener (1968) found that in the diets of a lizard community "...great taxonomic overlap invariably implies great size overlap, but great size similarity can also be found for pairs whose prey taxa are very different." Hespeneheide (1971) noted that insectivorous bird species had uniform niche breadths (variances of logarithm of prey size), though differing in mean size taken. Werner (1979) noted that the log scale variances of cost curves for three sympatric centrarchiids of different mean sizes were very similar, despite their use of different prey types. Macpherson (1981) found that prey size distributions overlapped more than prey type distributions in 26 demersal fish species. Pearre (1986) found that the size-based trophic niche breadths of various fish species were notable for their similarity over a wide range of fish sizes and types. Whether this similarity is good or bad depends, of course, on the questions being asked. This difference between the functions of the two niche concepts does, however, argue that taxon-based trophic niches, despite their theoretical problems (above) may also still find uses.

2). Size-based niche metrics do not directly address the question of breadth of use of different major taxa (e.g. Greene & Jaksic, 1983). However, because closely-related taxa (e.g. species) are more apt to be similar-sized than are higher taxa, much of the between-major taxa information is probably captured automatically by the size-based approach. Neither size-based nor taxon-based metrics directly

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address the problem of ecological association: perhaps this is less difficult with taxon-based indices (see Warwick & Clarke, 1995).

3). It is sometimes difficult to ascertain the proper estimate of prey item size, for instance in considering grasses eaten by ungulates, benthic algae grazed by marine snails, swarms of krill engulfed by whales, or prey of pack-hunting predators (e.g. Creel & Creel, 1995).

4). Even when supplied with mean sizes of prey (say, as prey species mean masses), there is certain to have been within-species variability which properly should contribute to overall prey-size diversity. Because of this, unless we are supplied with data on each individual prey item, the estimated niche breadth will always be an underestimate of the true niche breadth- the limiting case, of course, being prey of a monophagous predator (e.g. see Conover & Lalli, 1972). The true values should be approached asymptotically as more prey size classes are added, or more information about the distribution within each class. This problem will be further addressed in Pearre (1999).

5). All of the trophic-niche indices under consideration, including those based on prey size, may be subject to biases due to pooling or aggregation of the prey data (Leger & Didrichsons, 1994). Relatively few field studies report data on individual predators, though this is more common in laboratory investigations (but see Arlettaz *et al.*, 1997). Thus, it is usually difficult to estimate between-individual differences in prey use within a population, and also likely that some members of the population will have contributed more to the pooled data than others. If summing samples of different sizes from different years or locations, this bias may be reduced by using proportions of the prey species instead of the recorded numbers, but doing so makes it impossible to assign meaningful degrees of freedom to the error variance terms.

CONCLUSIONS:

Attempts to incorporate environmental availability of prey into trophic niche indices seem unwise, for both theoretical and practical reasons. Incorporation of multiple niche dimensions also seems impractical, though it may yield to standardized procedures. Indeed, few trophic niche estimates reported in recent literature attempt to do either of these. Ordinal indices seem superior in principle to cardinal ones, because of higher information content (Cousins, 1991) and usefulness in set-theoretic niche description (Hutchinson, 1957). However, cardinal (e.g. taxon-based) indices may still be useful for some purposes.

Among possible ways in which to order prey species data, prey size is a simple and robust prey descriptor, and the spectra of prey sizes in predator diets tend to have the general form of normal or, more usually, log-normal distributions. If this is so, simple statistics characterizing such spectra may be used as trophic niche indices.

DEDICATION: This paper is based on a presentation made at a special symposium held in honor of Peter J. Wangersky at Dalhousie University, Halifax, N.S., in July 1994, a year after his formal retirement from the Department of Oceanography at Dalhousie University. Pete's professional interests have spanned population dynamics, seawater chemistry, geochemistry, chemical oceanography and biological oceanography and in all of these fields he has made very substantial contributions. Pete also holds two patents for scientific apparatus, but throughout this very productive career, his first concern has been the welfare of his many students. By any index, Pete's niche has been very broad.

ACKNOWLEDGEMENTS: Many of the ideas stem from "lunch and philosophy" discussions with Peter Wangersky in his laboratory. I would also like to thank E.G. Merinfeld, R.J. Conover, and G.C. Harding

for advice and suggestions for improvement, and for stimulating discussions of the ideas presented here. I am especially grateful to G.C. Harding, J.H. Sharp, J.H. Lawton, P.S. Petraitis, and several anonymous reviewers for critical and helpful reviews of earlier versions of the manuscript; R.J. Conover provided a timely and extremely helpful review of this version. This work was supported by a grant from the Natural Sciences and Engineering Research Council of Canada.

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APPENDIX:

The first consideration in using any size-based criterion is how to designate size, and the first decision must be the choice between one, two or three dimensions. One-dimensional options are length, width (or thickness), or a synthetic dimension such as "equivalent spherical diameter" (ESD). The two two-dimensional choices are projected area or surface area. The three-dimensional metric, volume, is generally taken to be equivalent to mass on the assumption of unit density. The choice between these depends largely on the questions one wishes to ask: one-dimensional representations or the two-dimensional projected area might reflect the predator's view of the predation event: e.g. the ability of the predator to detect the prey and/or the prey to escape (reflecting the cost of prey capture). Length and projected area are related to the prey's visibility: length is also generally proportional to its escape speed. Width or thickness is probably better related to its ability to be swallowed by the predator (Wiborg, 1948; Krzysik, 1979; Pearre, 1980a,b; Hulseman, 1981; Kane, 1984; Wheelwright, 1985), and ESD must be seen as a compromise, but derived from volume (Sheldon et al., 1972).

The two-dimensional surface area and the volume (or mass) are proportional to the benefit to the predator. Surface area is often seen as an indicator of metabolic processes, and has been related to an organism's position in the trophic web (Tenney & Tenney, 1970; Brodie, 1975; Harding, 1977; Kamenir & Khaylov, 1987), as has mass or volume (Elton, 1927; Sheldon et al., 1972; Kerr, 1974; Platt & Denman, 1978; Dickie et al., 1987).

If the investigator is interested in energy transfers, mass or volume may be an appropriate currency, assuming that whole prey are ingested. Although the energy density varies between organisms, energy is generally taken to be roughly proportional to mass. A more appropriate unit is dry mass, or, even better ash-free dry mass (often called "organic weight") if necessary conversions are available. If specific energy values are available for the prey organisms in question, this of course represents the best

currency of all, and the analysis could be carried through in these units. To the best of my knowledge, no theoretical statistical distribution for these has been proposed, but an assumption of lognormality is probably a good starting point.

If the investigator is most interested in prey consumption as a predation phenomenon as opposed, for instance, to an energy transfer, the equivalent spherical diameter (ESD) is probably the most useful prey size measure (Hansen *et al.*, 1994). Differences in prey shape and predation mechanics make any other one-dimensional ("linear") dimension useful only within restricted prey and/or predator groups. Also, environmental biomass spectra are often expressed in terms of either ESD or mass, which makes ESD useful for examining predation impacts.