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THE ANIMAL NICHE: A FORMALIZED FUNCTIONAL DEFINITION AND ITS USE IN CLASSIFYING NICHES

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Abstract. A formalized functional definition of niche is given using an extension of the standard definition of a mathematical relation. The niche is conceived as a relation between species and environment; previously published mathematical definitions of both these concepts are incorporated and described briefly, together with examples. The new definition of niche may be used to classify animal niches. It is unlikely, because of the lack of an associated identity operator, to be of use in further mathematical development, however, because of its simple form it lends itself to use by field ecologists.

Introduction

In a thoughtful and interesting article Alley (1982) discusses the concept of niche in ecology and stresses the necessity for a functional definition. The concept of an 'empty' niche is severely criticised. Alley suggests that a variety of levels of analysis are necessary, ranging from "Elton's goal of partitioning organisms into 'professional' classes (such as scavengers and parasites) - to - a detailed examination of ecological relations -".

In the present article I give a formalized functional definition of the concept of niche in animal ecology, using the formalization technique introduced by Woodger (1937, 1939, 1952) who wrote "In considering the relation of mathematics to biology we must distinguish between the process of applying existing mathematics to biology and the less familiar process of letting biological statements suggest new mathematical ones". Woodger's work was difficult for biologists to read and understand; its inaccessibility has resulted in the method being less widely known among biologists and biomathematicians than one might expect. An exception is a formalized system for evolutionary theory which was constructed by Williams (1970) following Woodger's ideas but using more modern notation. In my work on formalized theory of ecology of which this paper forms a part I have complied with the following: (i) close contact is kept with field workers, (ii) the difficult and cumbersome notation of Whitehead and Russell (1925) which was used by Woodger is replaced by more modern notation interspersed with enough natural language to convey meaning without losing too much rigour, (iii) intermediate theoretical results are checked immediately against data from a wide range of appropriate biological organisms.

The *modus operandi* for the total study is to construct a new branch of pure mathematics specifically for ecology. Thus mathematics is conceived to be a formalized language, containing sentences. Russell (1953) wrote "Pure mathematics consists entirely of assertions to the effect that, if such and such a proposition is true of *anything*, then such and such another proposition is true of that thing". The techniques for the construction are derived from standard works in mathematical logic such as Church (1956). In this article the niche is treated as a relation between an animal species and the objects in the environment of the members of that species. The niche definition uses an extension of the Wiener-Kuratowski definition of relation (Kuratowski and Mostowski, 1976). The mathematical definitions of environment and species are dealt with in Niven (1987a, 1988e). The niche definition was foreshadowed in Niven (1982).

The formalization method in biomathematics should be contrasted with the method of mathematical modelling familiar to many ecologists. Models are often poor predictors, at least partly because the mathematics we use has foundations derived from the physical, not biological, sciences. Thus the theory of differential equations used in animal population dynamics by for example May (1974) was developed initially to deal with Newtonian physics and the n-dimensional Euclidean geometry used by Hutchinson (1957) as a model for the concept of niche has at the foundational level primitive terms like 'point' which is derived from ideas about physical space.

In this paper first I present an interpretation of the five primitive (undefined) terms 'An', 'Off', 'Hab', 'H' and 'ξ', all of which are derived from ideas within the biological sciences. I shall then briefly repeat the mathematical definitions of environment and species given in full elsewhere and use them to define the animal niche, illustrating all three definitions with examples. I shall show how the niche definition may be used for the classification of a niche in some practical cases. I then comment on some consequences of using the definition, in particular its relevance to the principle of competitive exclusion. A list of symbols is given in the Appendix.

The primitive terms AN, OFF, HAB, H and ξ

In any formalized system such as a branch of mathematics it is necessary to include certain undefined words or phrases called 'primitive terms'. It is not possible to construct a branch of mathematics in which all terms are defined. The primitive terms are then used in definitions. Axioms are assumed sentences containing the primitive terms and the definitions and the rules of deduction of the system enable us to evolve theorems from the axioms. The following interpretations apply:

'An' stands for 'animal', meaning individuals of the Kindom Animalia of Margulis and Schwartz (1982). By 'An (χ)' I mean that χ is an animal.

'Off' stands for 'offspring'. This primitive term is sometimes sub-indexed by 't' or 'δt' which indicates the time of birth or the time interval during which the offspring is born. So 'χ Off $_{\delta t}$ y' means that χ is born to y during the interval δt.

'Hab' stands for 'habitat'. The term is derived from Elton (1966) and refers to the place in which the ecologist confidently expects to find the animal of interest. It may also be sub-indexed by 't' or 'δt'. By 'B Hab a' I mean that the place 'B' is a habitat of 'a', where 'a' is specified to be an animal i.e. An (a). B may be a specific pond, paddock, field, forest, continent, ocean or small region of ocean and so on. It may even be an entire planet. When necessary a region of the atmosphere is included, or a certain depth of soil. In this paper B is always a specific place, not a class of places.

'H' is the survival and reproduction primitive of the system. It is derived from 'an animal's chance to survive and multiply' in Andrewartha and Birch (1954). H (χ) is a positive real number which is a non-decreasing function of:

(i) the expectation of life of χ at birth or on entering its present stage of the life cycle, and

(ii) the probability that χ will have an offspring.

'H' may be sub-indexed by 't' or 'δt'. Unlike the notion of 'fitness' in evolutionary theory, 'H' refers to the present generation only, not a sequence of generations.

'ξ' is the interaction primitive of the system. By '$\xi\chi$y' I mean that an interaction occurs between χ and y evoking immediately in y some physical, physiological or behavioural response or a change of position and no other object (other than χ) reduces or enhances this effect of χ on y, i.e. χ affects y directly. Judgement as to whether the response is significant is to be made by the ecologist. For instance if an animal 'y' gazes at some object 'χ', a tree say, this is a response of 'y' to the tree and doubtless some sort of physiological process is evoked. A response of this type would often be regarded by the ecologist as trivial, and ignored. Like 'Off', 'Hab' and 'H' the interaction primitive may be sub-indexed by 't' or 'δt'.

The inclusion of 'H' as a primitive term implies that the formalized system is stochastic at a foundational level. 'ξ', which is incorporated in all definitions, ensures that the system is totally interactive. The time-dependence of 'Off', 'Hab', 'H' and 'ξ' implies that the system is dynamic.

Environment

A symbolic definition of an animal's environment was published by Niven in 1980. The environment was defined as a structured set of objects which were functionally related to the subject animal. An improved formulation was published by Niven (1982) and used by Andrewartha and Birch (1984) to classify objects in the environment; these authors derived, from the mathematical definition, a useful diagram called an 'envirogram' which displays objects in the environment in their correct logical place. The definition is for one animal at a particular time; the envirogram is for many animals at different times and is used as a practical tool for the field ecologist. The formulation of the definition which was used by Andrewartha and Birch is not easy to manipulate; for this reason I have since developed a simpler formulation which is suitable for teaching undergraduates and facilitates very precise classification of objects in the environment by non-mathematicians (Niven, 1987a).

The structured set of objects which constitute the environment of an individual animal at some particular time is divided into two subsets called the 'centrum' and the 'web'. The centrum is further subdivided into 'resources', 'mates', 'predators' and 'malentities'. Each of these four subsets is defined by a mathematical sentence containing a conditional; in ordinary English the centrum contains *potential* resources, mates etc; this device means that an object which is not at that time in the animal's immediate vicinity may still be defined as a resource or other element of the animal's environment. The web consists of an infinite structured set of 'modifiers'. Zero-order modifiers are elements of the centrum and first-order modifiers modify these elements. Second-order modifiers modify objects which are first-order modifiers and so on. The conditional form of defining sentence is used throughout.

For subject animal 'a' the definitions of a resource, mate, predator and malentity are:

$$\mathrm{r\ Res}_{t}\ \mathrm{a} =_{\mathrm{df}} [\{\mathrm{H}_{t}(\mathrm{a}) > \mathrm{H}_{t-}(\mathrm{a})\} \mid \xi_{t}\,\mathrm{ra}]\ \&$$

$$[\mathrm{An}(\mathrm{r}) \supset \{\mathrm{H}_{t}(\mathrm{r}) \leq \mathrm{H}_{t-}(\mathrm{r})\} \mid \xi_{t}\,\mathrm{ra}]$$

$$\mathrm{m\ Mat}_{t}\ \mathrm{a} =_{\mathrm{df}} \mathrm{Prob}\ [(\exists \mathrm{x})(\mathrm{x\ Off}_{t+\beta}\ \mathrm{a}\ \&$$

$$\mathrm{x\ Off}_{t+\beta}\ \mathrm{m}) \mid \xi_{t}\,\mathrm{ma}] > 0$$

$$\mathrm{p\ Pred}_{t}\ \mathrm{a} =_{\mathrm{df}} [\{\mathrm{H}_{t}(\mathrm{a}) < \mathrm{H}_{t-}(\mathrm{a})\{\ \&$$

$$\{H_t(p) > H_{t-}(p)\} \mid \xi_t\, pa]$$

$$c\ \mathrm{Mal}_t\, a =_{df} [\{H_t(a) < H_{t-}(a)\} \mid \xi_t\, ca]\ \&$$

$$[\mathrm{An}(c) \supset \{H_t(c) \leq H_{t-}(c)\} \mid \xi_t\, ca]$$

The interval of time 'β' in the definition of a mate is the gestation time. A predator must be an animal.

The centrum is the set of objects which are resources, mates, predators or malentities. Formally:

$$C_t\, a =_{df} \{x\colon x\ \mathrm{Res}_t\, a\ \mathrm{V}\ x\ \mathrm{Mat}_t\, a\ \mathrm{V}\ x\ \mathrm{Pred}_t\, a\ \mathrm{V}\ x\ \mathrm{Mal}_t\, a\}.$$

In the web the modifiers of order greater than zero are divided into two sets called 'positive' and 'negative' modifiers, depending on whether their presence or absence causes the lower order modifier to appear in the system. Formally:

$$w\ \mathrm{Mod}_t^{+(n+1)}a =_{df} (\exists x)\ [\{x\ \mathrm{Mod}_t^n\, a \mid (\xi_t\, wx\ \mathrm{V}\ \xi_t\, wy)\}\ \&$$

$$\{\sim x\ \mathrm{Mod}_t^n a \mid (\xi_t\, wx\ \mathrm{V}\ \xi_t\, wy)\}]$$

$$w\ \mathrm{Mod}_t^{-(n+1)}a =_{df} (\exists x)\ [\{x\ \mathrm{Mod}_t^n a \mid \sim(\xi_t\, wx\ \mathrm{V}\ \xi_t\, wy)\}\ \&$$

$$\{\sim x\ \mathrm{Mod}_t^n a \mid (\xi_t\, wx\ \mathrm{V}\ \xi_t\, wy)\}$$

$n = 0, 1, 2\ldots$; y is either 'a' or a modifier of order $<n$; $\mathrm{Mod}_t^n a =_{df} \mathrm{Mod}_t^{+n} a\ \mathrm{V}\ \mathrm{Mod}_t^{-n} a$.

The total environment of the subject animal is the union of the centrum and the web in which the structure of the four subsets of the centrum and their attached modifier chains is preserved.

The following examples from the ecology of the Atlantic fulmar *(Fulmarus glacialis)* are taken from Fisher (1952). Large numbers of these fulmars used to attend whale flensing, in the days when whales were hunted. They disregarded the men and gorged whale blubber and oil. Thus blubber is classified as a resource of a subject adult fulmar:

H (fulmar) is increased $|\xi$ (blubber) (fulmar).

Fulmars are attracted to glacier run-off streams in order to feed on planktonic creatures. Occasionally, Fisher records, some are killed by ice-falls. We classify a particular (loose) block of ice as a malentity:

H (fulmar) is decreased $|\xi$ (ice) (fulmar).

A different kind of resource is observed when we consider the breeding habits of the bird. A female fulmar prospects for and chooses a nesting site, usually a ledge on a high cliff, when still a non-breeding juvenile. The bird may occupy the site for over four years before laying eggs there. A suitable ledge is clearly a necessity for a subject female fulmar to breed and thus a resource:

H (fulmar) is increased $\mid \xi$ (ledge) (fulmar).

An adult male fulmar is classified as a mate of the subject female:

An offspring of both individuals will be produced with probability greater than zero $\mid \xi$ (male fulmar) (subject female).

The ledge, as a nesting site, is also a positive first-order modifier:

($\exists$ male fulmar) such that
(male fulmar) Mat (subject female) $\mid \xi$ (nesting site) (subject female)
and
$\sim$(male fulmar) Mat (subject female) $\mid \sim \xi$ (nesting site) (subject female),

that is, unless the ledge is available, the female will not lay her eggs and so the male cannot be a mate.

When threatened a fulmar will vomit or spit foul-smelling stomach-oil, not directly at the intruder but simply in the direction in which it is looking at the time. A baby fulmar not yet out of its shell has been observed to vomit through a small chink when disturbed by the observer. The glaucous gull *(Larus hyperboreus)* will readily eat fulmar eggs and fledglings if the parents are away from the nest. The gull is classified as a predator in the environment of a subject fledgling fulmar:

H (fledgling) is decreased and H (gull) is increased $\mid \xi$ (gull) (fledgling).

The fledgling, in turn, is classified as a resource in the environment of a subject gull:

H (gull) is increased and H (fledgling) is decreased $\mid \xi$ (fledgling) (gull).

Notice that in this case the term 'H (fledgling) is decreased' is included in the defining sentence, in contrast to the two previous examples of resources in which the resource was not an animal.

The stomach-oil emitted by a subject fledgling fulmar when disturbed by a gull is a negative first-order modifier:

($\exists$ gull) such that (gull) Pred (fledgling) $\mid \sim \xi$ (stomach-oil) (gull) and
$\sim$ (gull) Pred (fledgling) $|\xi$ (stomach-oil) (gull).

The fledgling is modifying its own environment by producing the stomach-oil; it is a positive second-order modifier:

($\exists$ stomach-oil) such that
(stomach-oil) Mod^1 (fledgling) $|\xi$ (fledgling) (fledgling)
and $\sim$ (stomach-oil) Mod^1 (fledgling) $|\sim\xi$ (fledgling)
(fledgling).

Here we assume that the fledgling is interacting with itself in the sense of the primitive term ξ to produce the stomach-oil. The parent bird which protects the fledgling from the gull is a negative first-order modifier:

($\exists$ gull) such that (gull) Pred (fledgling) $|\sim\xi$ (parent)
(fledgling)
and $\sim$ (gull) Pred (fledgling) $|\xi$ (parent) (fledgling).

It is the case here that both the parent and the fledgling are acting to protect the fledgling against the predacious gull, but the fledgling acts via an intermediate object (the stomach-oil) whereas the parent acts directly on the predator, hence the classifications are different.

Other examples, taken from the ecology of animals ranging from a sponge to a non-human primate, are given in Niven (1987a, 1988a, b, c, d, Niven and Stewart 1987). The definition is unsuited to human beings, since the cultural and psychological factors which are of such importance to humans are not sufficiently stressed in the defining sentences of an animal's environment.

Species

In a series of articles Paterson and his colleagues have developed a non-mathematical definition of an animal species (Paterson, 1980; Paterson 1981, Paterson 1985, Paterson and Macnamara 1984, Lambert and Paterson 1985). Paterson's definition is dependent on the notion of specific-mate-recognition necessarily occurring in a particular habitat and arose via a careful consideration of evolutionary concepts. A mathematical definition based on Paterson's work is given in Niven (1989). The animal species S_a at the time 't' which includes a subject animal 'a' is the set as follows:

$$S_a =_{df} \{x : x = a \; V x \; \mathrm{Mat}_t a \; V x \; \mathrm{Mat}_t \mathrm{Mat}_t a \,|\, \mathrm{An}\ (a)\ \&$$

$$\mathrm{An}\ (x)\ \&\ B\ \mathrm{Hab}_t\ (x\ \&\ a)\}.$$

For hermaphroditic animals the terms 'x $\mathrm{Mat}_t\mathrm{Mat}_t$a' is redundant. The sub-index 't' may be replaced by 'δt' if, for example, we wish to include juvenile animals which will become (potential) mates of 'a' during the interval of time δt.

As examples, first consider the case of chimpanzees *(Pan troglodytes)* and, to begin with, choose the Gombe National Park in East Africa to be the habitat 'B'. Since female chimpanzees have marked sexual cycles the sub-index 'δt' should replace 't' in this case in order to ensure that all the animals are included (Lemmon and Allen, 1978; Tutin and McGrew, 1973; van Lawick-Goodall, 1971). Then if we choose as our initial animal 'a' some mature female chimpanzee we have that the species S_a is the set of objects x where either x is a (potential) mate of 'a' or a mate of a mate of 'a' during the time interval 'δt', given that 'a' is an animal and the 'x's' are all animals and that 'a' and all the 'x's' are in the Gombe National Park. In order to include all the animals normally thought of as being of species *Pan troglodytes* we simply extend 'B' to include the Mhale mountains and other suitable areas. It is not necessary for the theory that these areas are connected.

If now we are working with the hermaphroditic earthworm *Lumbricus terrestris* (Edwards and Lofty 1972) then the mate of our initial subject worm is simply another mature adult and it is unnecessary to consider the mates of its mates.

In the case of a perpetually self-mating animal the definition reduces to just the animal 'a' which is in habitat 'B'; thus the definition is not suitable for animals which reproduce parthenogenetically. In the case of an animal which has only daughters for several generations, followed by normal bisexual reproduction for one or two generations the mathematical definition covers only the latter case.

Paterson deals with animals in the wild state. If the biologist should so desire the habitat 'B' in the mathematical definition could be some artificial place, such as a cage in a zoo, thus leading to the classification of animals such as lions and tigers, dogs and jackals, or mallard and pintail ducks, being defined as being of the same species. However these are very peculiar cases and, although they are logically valid, they seem unlikely to be of any practical use. Another peculiar and artificial case is that of artificial insemination. The mathematical definition can be 'forced' to cover this case by making both the habitat 'B' and the time interval 'δt' large enough to include both parents.

It does not follow from the formal definition that either the parents or offspring of the animal 'a' are elements of the set S_a. Thus mutations resulting in some change of mate recognition in at least one pair of offspring may well result in a different species.

Unlike the definition of 'environment' the mathematical definition of 'species' is valid also for humans. The inclusion of the probabilistic sentence used to define 'mate' implies that the definition of 'species' is stochastic.

The definition of the animal niche

The animal niche is the relation of that animal (species) to the environment of individuals of the species. Roughly speaking, the niche gives us some idea of the place of the species in the biotic milieu; it provides information about the status of the species in the community. It is sometimes useful to think of the niche as the 'profession' of the species (Elton 1927, Andrewartha and Birch 1984). So the niche is to do with the animal's functional relations with some of the objects in the environment.

When we observe a particular species of animal we usually find that all members of the species eat much the same kind of food, have more-or-less the same enemies and so on. In fact we expect all the adults of the same sex to have the same (potential) resources, mates, predators and malentities and apart from modifying one another's environments as competitors or predators, the same modifiers. In practical ecology it is not feasible to examine all possible objects in an animal's environment and some intuitive selection has to be made by the ecologist of those objects which seem to be the most important (Dennison and Hodkinson 1984).

A relation is formally defined in mathematics as a class of ordered pairs (Kuratowski and Mostowski 1976). Rather than speak of modifiers of order zero and greater ecologists prefer the terms 'centrum' and 'web' (Andrewartha and Birch 1984) so it is convenient to specify the niche as a class of triplets instead of pairs. Thus the niche of animal species S is defined as a class of one or more ordered triplets as follows:

(i) The first member of a triplet is an animal species.
(ii) One of the triplets has S as first member.
(iii) The second member of each triplet is either empty or an ordered set of objects in the centrum of the animals belonging to the first element.
(iv) Objects in the i-th place of the second member are all of the same kind *i.e.* they belong to the same well-defined class of objects; furthermore they are all resources or all mates or all predators or all malentities.
(v) The third member of each triplet is either empty or an ordered set of objects in the web of the animals belonging to the first element.
(vi) Objects in the i-th place of the third member are all of the same kind *i.e.* they belong to the same well-defined class of objects; furthermore they are all of the same modifier order.
(vii) At least one of the second or third elements is not empty.
(viii) A zero-order niche is one in which all third elements are empty.
(ix) An n-th-order niche contains n-th order modifiers in the third element of each triplet and does not contain modifiers of order greater than n.
(x) A simple niche contains only one modifier in the third element of each triplet; multiple niches contain more than one.

Examples of animal niches

1. The first example is taken from Elton (1927). Consider the arctic fox which subsists on eggs of guillemots but in winter relies partly on remains of seals killed by polar bears. The eggs and remains of dead seals are resources. The guillemots and polar bears, as providers of resources, are first-order modifiers. The associated ordered triplet is:

<arctic fox; guillemot eggs, seal remains; guillemots, polar bears>.

Now consider the African spotted hyaena which eats ostrich eggs and also the remains of zebras killed by lions. The eggs and zebra remains are resources and the ostriches and lions first-order modifiers. The triplet is:

<spotted hyaena; ostrich eggs, zebra remains; ostriches, lions>.

Elton clearly considers the two species to belong to the same niche and indeed we may write the two triplets with objects occupying the same places in the second and third elements being: (a) eggs, (b) carcasses, (c) birds and (d) large predators. Thus we have a niche containing two ordered triplets:

<arctic; guillemot, seal; guillemots, polar bears>
fox eggs remains

<spotted; ostrich, zebra; ostriches, lions>
hyaena eggs remains

Since the modifiers are all of first order and there are two of them in each triplet the niche is a first-order double niche. Notice that there are two distinct habitats. We may refer to this niche as either 'the niche of the arctic fox' or 'the niche of the spotted hyaena'.

2. Now consider a second example from the same source. This is the niche of animals which eat ticks off other animals. Three species are included by Elton: (i) The African oxpecker, which sits on the back of wild African ungulates, picks off the ticks and eats them, (ii) the English starling which eats ticks off sheep and (iii) the scarlet land crab which takes ticks from the great aquatic lizard. So the niche is the class:

<oxpecker; ticks; ungulates>
<starling; ticks; sheep>
<crab; ticks; lizards>

The second elements in the ordered triplets are all ticks which are resources of animals in the first elements and the third elements are all vertebrates which are first-order modifiers. Thus the niche is a first-order simple niche.

Elton contrasts this niche with that of the African cattle egret which follows buffalo or other ungulates in order to catch and eat grasshoppers. The modifier chain for a subject egret is:

buffalo → kinetic energy → grasshopper → egret

since without the buffalo that particular energy package does not come into existence and without the movement the grasshopper is not a resource. The corresponding niche triplet is:

<egret; grasshoppers; kinetic energy, buffalos>.

Since a second-order modifier appears in the third element and there are two modifiers named the niche is a second-order double niche. It contrasts sharply with the previous case by including the energy component which shifts the buffalo into a higher order of modifiers.

3. We now turn to a study of Wolf spiders by Vogel (1972). The two species *Pardosa falcifera* and *P. sternalis* are often found in the same place, however *P. falcifera* is very much more dependent on cover such as fallen leaves which serve to protect the spiders from predators, like birds. In Cochise County, Arizona, a marked change in conditions at Lake Cienaga from a lush green marsh in 1963 to a nearly dry overgrazed pasture in 1970 showed how dependent *P. falcifera* is on cover. In 1963 one collection of the spiders contained twenty-three times as many *P. falcifera* as *P. sternalis.* In contrast a collection made in the same place in 1970 contained thirty-six times as many *P. sternalis* as *P. falcifera.* The exact mechanism is unknown; it was observed, however, that these spiders have a 'territory sphere' surrounding them, into which they do not allow another spider to enter. We shall assume here that both species are subject to predation by the same predatory birds, that both would use cover readily available in the habitat, but that *P. falcifera* is able to drive *P. sternalis* away from cover, whereas *P. falcifera* by its own actions is able to use the cover to protect itself against the predators. Thus for both species the cover is a first-order modifier of predators. *P. falcifera* is a second-order modifier of cover in its own environment and also a second-order modifier of cover in the environment of *P. sternalis.* The two ordered triplets are:

<*P. falcifera*; predatory birds; cover, *P. falcifera*>
<*P. sternalis*; predatory birds; cover, *P. falcifera*>

Since there are two modifiers in each third element and the second of these is of second order the niche is a second-order double niche. In contrast to Elton's examples the two species are found in the same habitat.

4. The predatory bark beetles *Olophrum piceum* and *Lathrobium brunnipes* have both been found in a wood near Liverpool, England, according to Dennision and Hodkinson (1983). *O. piceum* feeds on Collembola and *L. brunnipes* on mites. The two triplets are:

<*O. piceum*; Collembola; —>
<*L. brunnipes*; mites; —>

Both second elements contain resources which are arthropods and both third elements are empty. The niche is therefore of zero order. The habitat is the same for both species.

5. The marine copepods *Calanus* and *Eucalanus* were observed by Boyd and Smith (1980) at a station in the Peruvian upwelling system. *Eucalanus* were sometimes found in water below the surface layers which had very low oxygen concentration. These layers were avoided by *Calanus*. The copepods are detritus feeders; *Calanus* fed both day and night in a fairly even pattern but *Eucalanus* moved near the surface at night and reduced its feeding intensity. Clearly water with low oxygen concentration (WLO) is a malentity and detritus a resource for both species. Both species modify their food by moving to suit the feeding requirements; they are thus first-order modifiers of resources in their own environment. If we work over a period of time long enough to accommodate the migrations, say twenty-four hours, then the two triplets are:

<*Eucalanus*; WLO, detritus; *Eucalanus*>
<*Calanus*; WLO, detritus; *Calanus*>

The niche is a first-order simple niche.
If we wish to show up the difference in the night-time position then we reduce the time period to, say, the twelve hours of darkness and introduce the objects 'water with low detritus concentration' (WLD) and 'water with high detritus concentration' (WHD). These objects, which provide resources at the required levels, are then first-order modifiers. The animals are first-order modifiers in their own environments, since they locate themselves in the preferred places. For convenience we leave out the malentities WLO. Then the two triplets are:

<*Eucalanus*; detritus; WLD, *Eucalanus*>
<*Calanus*; detritus; WHD, *Calanus*>

We have now written down a second-order double niche for the same species in the same habitat, but using a different time interval. This example clarifies two points (i) the environment classification and therefore the niche classification are both critically dependent on the time chosen by the observer and (ii) the observer's choice of object (high or low detritus layers) and the accuracy and completeness of the natural history (*e.g.* night-time behaviour of *Eucalanus*) are also critically important when classifying a niche.

6. The waterfleas *Daphnia magna, D. pulex* and *D. longispina* were found together in a freshwater rock pool in an archipelago near the Gulf of Finland by Ranta (1979). The animals are filter feeders and unable to select food particles so the size of the ingested particles is controlled by the density of the filtering combs and the width of the carapace crevice. These measurements relate to the body length. The maximum body lengths of the three species observed were:

D. magna 5.0 mm; *D. pulex* 3.5 mm;
D. longispina 2.5 mm.

If we classify particles as large, medium or small then the three sorts of particles will be resources for the three species, the animals themselves acting as first-order modifiers of these resources. The corresponding niche triplets are:

<*D. magna*; large particles; *D. magna*>
<*D. pulex*; medium particles; *D. pulex*>
<*D. longispina*; small particles; *D. longispina*>

The niche is a first-order simple niche.

The principle of competitive exclusion

In the context of this paper the Principle of Competitive Exclusion is that the second and third elements of any one triplet are unique to the species. It would seem to be very likely that if a large number of objects are named in the triplet then the principle would be true. One has only to imagine two n-th order triplets for which the second and third elements were identical but the species of the first elements different; for n large enough it seems highly likely that we could find a pair of (n + 1) th-order modifiers which differ from one another.

However the Principle clearly does not hold for zero-order niches. Consider as a counter-example No. 3 above on Wolf spiders. A zero-order niche would be:

<*P. falcifera*; predatory birds; —>
<*P. sternalis*; predatory birds; —>

Thus when invoking the Principle we should be careful to state precisely what order of niche is being studied. Between the limiting cases of zero-order and n-th order for n large there is a grey area in which the Principle may or may not hold.

Discussion

The untutored peasant, gazing bucolically at a frog and a bird, may dismiss as fanciful and unnecessary the Latin nomenclature of modern animal taxonomy. In contrast the trained zoologist is well aware of the necessity for such classification. In science in general and ecology in particular classification is essential. The main practical use of the mathematical definition of niche given in this paper is that a method of classifying niches is provided which is both well-defined and simple to write down.

On the theoretical side defining the niche as a functional relation between animals and their environment matches Elton's original concept and answers Alley's severe criticism. However we may well ask whether the niche concept is likely to lead to further development of a mathematical basis for ecology and here the answer is at present an unqualified negative for the following reason. In any useful branch of pure mathematics an axiom asserting the existence of an identity operator is essential. An example of an identity operator is the multiplication by the unit in ordinary arithmetic. This operation on any number yields that same number as the answer; the identity operator sends a number back to itself. The identity operator for new ecological mathematics is readily available; it is the mathematical object '$E^{-1}E$' where by '$E^{-1}B$' we mean the animal whose (formalized) environment is B and by 'Ea' we mean the environment of the animal 'a'. The uniqueness of an animal's environment (Niven 1983) leads naturally to the axiom. In ordinary English we may say "The animal whose environment is the environment of animal 'a' is in fact that same animal 'a' ". This axiom applies immediately when we construct new mathematics for animal communities and, by extension, for ecosystems, the latter assuming that an equivalent to 'environment of an animal' will be found for plants and modules when the formalization of plant and module ecology is undertaken (Niven 1988e). Unfortunately we cannot extend the uniqueness of the environment of an individual animal to a set of animals such as a species. Consider as an example three frogs of the same species F_1, F_2, and F_3 sitting next to each other. F_2 and F_3 appear in F_1's environment as first-order modifiers of food and other objects. Similarly F_1 and F_3 are in F_2's environment and F_1 and F_2 in F_3's environment. In order to obtain a set of objects, a pseudo-environment, say, which is unique to the set $\{F_1, F_2, F_3\}$ we need to exclude certain objects. Including the frog F_4 further complicates the situation. So the construction of a biologically meaningful mathematical object which will send the set of frogs back to itself is certainly very difficult and may well be impossible. Without an axiom asserting the existence of an identity operator we are left with the prospect of handling ecological mathematics in which a unique inverse does not exist. Such branches of pure mathematics are difficult to handle in practice and are unlikely to be useful in scientific work.

Nevertheless the concept of niche may well continue to be useful in field ecology. As McIntosh (1982) writes "(the question now is) how similar can (species) be and still coexist?" In the cases in which suitable metrics exist, such as the particle sizes of example 6 above on *Daphnia* spp., well-tried methods of statistical univariate and multivariate analysis may be used to ascertain the separation of the triplets. Such methods of niche separation are already in wide use (McIntosh 1982, 1985; Whittaker and Levin, 1975). However it should be noted that not all field workers agree that the niche is a useful concept. For example Johnson (1984) writes "One of the problems facing a niche analyst is that niche differences can nearly always be found, provided that enough niche parameters are examined". Johnson investigated the coexistence of two flycatchers in the Nigerian rain forest, between which, in spite of their close proximity, competition appeared to be absent. He writes "If niches are at least partially genetically... determined, then the occasional high niche overlap is an unremarkable certainty".

The niche is a dynamic concept. In the present formalization the time-dependence of the environment is provided by the primitive terms. This time-dependence is, therefore, incorporated in the definition of niche. Similarly the defined niche is stochastic at a foundational level.

The mathematical definition of species used in the niche definition is habitat-dependent. (In practice we usually work with the museum concept of species which is not). However the mathematical definition of environment is independent of habitat. In ordinary English we refer to *potential* resources, *potential* mates, *potential* predators, *potential* malentities and *potential* modifiers. Thus it is strictly correct to specify a triplet in which the first element (the species) is restricted to a particular habitat, but the objects of the second and third elements are not restricted to the same habitat.

The original concept of niche as described by Elton included animals only; this is clearly an unnecessary restriction. Elton's concept, however, also enabled us to compare species in several quite different habitats and this flexibility has been incorporated into the formalization since it may well prove suggestive to write down several triplets which refer to a variety of habitats. The exercise could point the way to further study on important objects which have been observed in one place but missed in another.

It should be noted that according to the definition it is not possible to have an empty niche. The question as to how many niches might exist does not seem to be profitable. Presumably a clever genetic engineer could tailor a new species to almost any given subset of the objects in a habitat and so the number of possible niches within a given habitat, although not infinite, is certainly very large.

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APPENDIX

$>$	greater than
$<$	less than
$\leq$	less than or equal to
x_t	x at time t
x_{t-}	x just before time t
$A \mid B$	A given that B
$\sim$	negation
ϵ	element of
$\supset$	The subjunctive conditional; read '$x \supset y$' "if x then y".
$=_{df}$	Definition; read '$x =_{df} y$' "x is interchangeable with y" or "x is equal by definition to y".
&	Conjunction; read 'A & B' "A and B".
V	Disjunction; read 'A V B' "A or B" (or both).
$\exists$	The existential quantifier; read '$\exists x$' "there is at least one x (such that)...".