Introduction To
ATTACK AND DEFENSE: BEHAVIORAL ECOLOGY OF PREDATORS AND THEIR PREY

ENDEMICS AND EPIDEMICS OF SHIBBOLETHS AND OTHER THINGS CAUSING CHAOS

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> "When I use a word," Humpty Dumpty said, in rather a scornful tone, "it means just what I choose it to mean—neither more nor less."
>
> "The question is," said Alice, "whether you **can** make words mean so many different things."
>
> "The question is," said Humpty Dumpty, "which is to be master—that's all."
>
> Lewis Carroll (1872)

Classical biological control is a set of activities in which non-native predators, parasites, parasitoids, competitors or pathogens, are introduced into an area for the control of pests, especially immigrant pests. The language of classical biological control is that of ecology, which uses words of classical (Greek and Latin) origin because these can be assigned precise meanings. The precision of the meanings allows for conciseness and accuracy of expression, or such is the intention. Unfortunately, the meanings of a group of words describing the origins of predators etc. and pests alike are anything but precise. Their definitions are chaotic in several dictionaries. Therefore we take an etymological voyage to the origins of the words **precinctive, autochthonous, indigenous, epidemic, endemic, adventive, introduced,** and **immigrant** to see how they have been used, and we illustrate this voyage by citations from the literature. Then we show the relationships of the five words that we deem most useful in describing origins, and we redefine the words **adventive, immigrant,** and **introduced.**

AN ETYMOLOGICAL VOYAGE

Precinctive (from Latin praecinctus, *present participle of* praecingere, *to gird, encircle)*

David Sharp rose to eminence as a describer of insects, many of them predatory, in the final quarter of the last century. His works include contributions on the faunas of Britain, the Amazon basin, New Zealand, Central America, Japan, and Hawaii. In the last of these works (Sharp 1900: 91), faced with need of a word under which to group organisms restricted in distribution to Hawaii, he chose and defined the word **precinctive**: "I use the word **precinctive** . . . in the sense of 'confined to the area under discussion' . .. **'Precinctive** forms' means therefore forms that are confined to the area

specified." The word was adopted by Bequaert (1940: 266) and others: "Of a total of 42 recorded species [of Antillean Tabanidae], 33 (or nearly 80%) are precinctive and 26 (or 60 per cent) are restricted to a single island".

Autochthonous (*from Greek* autochthon = *sprung from the land itself*)

Browne (1646: 274) "There was never any **Autochthon**, or man arising from the earth but Adam." Gardiner (1804) "If the English have this great predilection for **autoohthonous** bread and butter". Anon. (1860) "Most of them [the Red Indians], of course, believe themselves to be **autochthonous**; but the Chippewas and one or two others retain, or till lately retained, the tradition of a migration from over the sea." Torre-Bueno (1937) **"autochthonous**, native or aboriginal; used for those species which are considered to have arisen as a part of the native or aboriginal fauna or flora, as contrasted with those which are considered to have immigrated from outside regions ([after] Tillyard [1926])." Mackerras (1970: 191) "An **autochthonous** group is one that evolved within the country".

Indigenous (*from Latin* indigenus = *native*)

Browne (*in* Pseudoxia epidemica 1646: 325) "and although in many parts thereof it be confessed there bee at present swarmes of Negroes serving under the Spaniard, yet were they all transported from Africa, since the discovery of Columbus, and are not indigenous or proper natives of America." Williams (1809: 85) "GINSENG was formerly esteemed a plant **indigenous** only to China and Tartary." Buckle (1857: 118) "Indeed, of those cruel diseases now existing in Europe, scarcely one is **indigenous**; and the worst of them were imported from tropical countries in and after the first century of the Christian era." Lyell (1875: 419) "The insects of Madeira, the Salvages, and the Canaries, unlike the birds, exhibit a large proportion of **indigenous** species".

Epidemic (*from Greek* epi = *on and* demos = *population, through Late Latin* epidemia *and French* épidémique)

Lodge (1603: B2b) "Popular and **epidemick** have one and the same signification; that is to say, a sicknesse common unto all people, or to the moste part of them." Malthus (1803: 330) "The endemick and **epidemick** diseases in Scotland, fall chiefly, as is usual, on the poor." Southwood & Comins (1976: 963) "The model is used to describe field-data on endemic and **epidemic** populations of aphids and eucalyptus psyllids and to correlate experience in biological control situations." **Epidemic** has a long history of use as a descriptor of populations and is used to describe population explosions, in contrast to the endemic condition.

Endemic (*from Greek* en = *in and* demos = *population*, through French endémique)

Larousse (1972) lists 2 French synonyms (*chronique, permanent*) and 4 antonyms (*cyclique, épidémique, momentané*, and *passager*) of *endémique*, and defines the French word *endémicité* (endemicity) as the endemic state of a disease. Lodqe (1603: B2) "And such sicknesses as are these, are called **Endemiques**, provintiall or regionall infirmities, yet for all that they are not to be accounted pestilentiall or contagious." Hickeringill (1705: 42) "For which I need not beg credit, since there is no country disease (as at Virginia and Surinam) **endemically** raging throughout the Isle". Malthus (1803, above, under epidemick). Buckle (1857: 118) "For evidence of the extra-European origin of European diseases, some of which, such as the small-pox, have passed from epidemics

into **endemics.**" Smith (1869: 77) "Hence famines are periodical or **endemic** in Hindostan." Cameron (1870: 149) "The **endemical** disorder passing rapidly into epidemical." Southwood & Comins (1976) "The predator can reduce all populations below the release point to extinction, so there is no lower equilibrium or **endemic** level." OAD (1980) "Yellow fever was **endemic** in parts of South America. The last American epidemic of this disease occurred in New Orleans in 1905." Price (1984) "When the effect of enemies is disrupted or environmental conditions become particularly favorable for reproduction, the population escapes the stabilizing influence of enemies . . . and increases to epidemic proportions. . . However, shortage of food and disease may lead to massive mortality and low natality causing the population to crash to . . . **endemic** levels." Church (1989) "In a country where problems are **endemic**". **Endemic** has a long history of use as a descriptor of populations and is the antonym of epidemic. It implies nothing about native origin [yellow fever is **endemic** to parts of South America but is believed to be indigenous to Africa].

Second and third meanings of endemic

Darwin (1872: 178) "Although in oceanic islands the species are few in number, the proportion of **endemic** kinds (i.e. those found nowhere else in the world) is often extremely large." Dallas (1872: 311) "**ENDEMIC**.—Peculiar to a given locality". By coincidence, Carroll's "Through the looking-glass. . ." also was published in 1872. Mackerras (1970: 192) "An **endemic** (or **precinctive**) group".

However, Lyell (1875) and Darwin (1876), who were contemporaries and colleagues, used the word **endemic** elsewhere, without definition. Lyell (1875: 413) "General inferences to be deduced from the **endemic**, and other species of animals and plants in the Atlantic Islands." Darwin (1876: 415) "Bees . . . visit many exotic flowers as readily as the **endemic** kinds". These uses of **endemic** apparently were interpreted by some as "Of plants or animals; Having their ordinary habitat in a certain country; opposed to exotic" [= indigenous] (OED 1971), and "belonging or native to a particular region or country" [= indigenous] (Webster 1986), and Ehrlich & Roughgarden (1987: 619) defined **endemic** as "Native to a particular region" [= indigenous].

Only two meanings were defined by Allaby (1977), the ecological meaning, "Of pests or disease-producing species. The normal population level of a species which occurs continuously in a given area", and a biogeographical meaning, "General. Confined to a given region and having originated there."

A fourth meaning of endemic

Wallner (1987) "on the other hand, **endemic** or rare species approximate stable equilibrium. In this review '**endemic**' refers to insects that are either rare or uncommonly abundant and therefore seldom, if ever, occur at densities sufficient for them to be considered pests." The expression **endemic species** is used, but such species are so-named according to their population level, regardless of whether they are indigenous or adventive.

Adventive (*from Latin* advenire = *to arrive*)

Bacon (1605: 137) "Upon the first of these, the considerations of the origin of the soul, whether it be native or **adventive**". Pemberton (1964: 695) "Since a few hundred more have been added to the endemic [= precinctive] list we can assume that the **adventive** species, including harmful, beneficial and indifferent species number well over 2,000."

A related word, adventitious, is used in biology, especially botany, to describe structures occurring in other than their customary position, e.g., the adventitious roots which arise from branches of some *Ficus* species.

Immigrant (from Latin immigrantem, *present participle of* immigrare, *one who or that which migrates into a country as a settler)*

Belknap (1792: 6) "There is another deviation from the strict letter of the English dictionaries; which is found extremely convenient in our discourses on population . . . the verb IMMIGRATE and the nouns IMMIGRANT and IMMIGRATION are used without scruple in some parts of this volume." Kendall (1809: 252) "*Immigrant* is perhaps the only new word, of which the circumstances of the United States has [sic] in any degree demanded the addition to the English language."

Introduced (species or other taxa introduced deliberately by man)

Sailer (1978) used the expressions **introduced**, exotic and immigrant virtually interchangably, but here we restrict the expression **introduced**, following Zimmerman (1948: 64) "the word introduced should be reserved for those species which have been purposely imported".

A Rationalization

The words **indigenous** and **autochthonous** are synonyms and mean native. **Indigenous** has been used more widely in biology, so for that reason is preferable to **autochthonous**. We prefer **indigenous** to **native** as a biological term because the latter has subsidiary meanings in English. The third meaning of **endemic** is as a synonym of **indigenous**, but we can find no excuse for this misconception.

Epidemic and **endemic** were employed as antonyms almost 400 years ago and they have retained this sense in epidemiology and ecology to mean outbreak and non-outbreak population levels respectively. The biogeographio meaning of "**endemic**", apparently first employed or at least popularized by Darwin (1872), is unfortunate. Brodie's (1856: 26) words are pertinent: "There are epidemics of opinion as well as of disease, and they prevail at least as much among the well-educated as among the uneducated classes of society." The opinion of persons concerned with distribution of species seems to be to continue Darwin's usage despite existence of a more valid alternative (**precinctive**) and despite prior and continuous usage of **endemic** as an antonym of **epidemic** by persons concerned with populations of organisms. Sharp's (1900) statements are explicit: "I use the word **precinctive** in preference to endemic or peculiar—both of which are in common use—in the sense of 'confined to the area under discussion.' The word endemic has been objected to on the grounds that its definition does not indicate geographical restriction, and that it is actually used in medicine to signify constant, but not necessarily exclusive, presence in a locality." We conceive **precinctive** to be a subclass of **indigenous**, and we prefer not to use **endemic** in this sense.

Wallner's (1987) use of the word **endemic** is a logical extension of the epidemiological/ecological use. We doubt that it will be popularized until Darwin's (1872) sense of **endemic** is replaced widely by **precinctive**.

It is clear that **adventive** has the broadest sense among the words used to denote non-indigenous organisms. Our definitions are: **Adventive** species are those which have arrived in a previously-unoccupied area, whether of their own volition or through the inadvertent or deliberate agency of man. They include the 2 subclasses **immigrant** and **introduced. Immigrant** species are adventive species which arrived without the deliberate agency of man, even though they may have been transported accidentally by man.

The word suggests to us an active movement which is the complement of the passive movement implied by the word **introduced. Introduced** species are adventive species which have been introduced by the deliberate agency of man. Among them are to be included those introduced for biological control purposes, together with those introduced for other purposes (e.g., crop plants, farm animals, and ornamental plants). We exclude those organisms which Sailer (1978) called "accidentally introduced" because we consider them immigrants.

More is known about current and former distributions of *Homo sapiens* L. than about any other species, so we can employ these as examples to demonstrate use of the vocabulary. Man as a species is not indigenous to the Americas, but is adventive and, more specifically, is an immigrant. At an infra-subspecific level, we recognise several waves of immigration. Some immigrants (Amerindians [including Chippewas] and Eskimos) are considered by sociologists to be indigenous to North America because immigration occurred >10,000 yrs BP, whereas no other group is considered indigenous. Eskimos populated Arctic areas of Asia and North America, so were not and are not precinctive to Arctic America. However, Amerindians evolved in and thus became precinctive to the Americas (it is arguable whether they can still be considered precinctive because a few have migrated to other continents). The time frame of these immigrations spans >10,000 years. Descendants of even the earliest European immigrants still are considered immigrants.

Ideally, we should apply the same criteria to all species. The criteria are formulated below as a dichotomous key.

For any species (or other taxon) of organism occurring in a specified area:

1 It achieved its current taxonomic identity elsewhere (it was formerly absent but is now present) ..... **adventive** 2

1′ It achieved its current taxonomic status here (and has been present virtually continuously since then) ..... **indigenous** 3

For an **adventive** species (or other taxon):

2 It was introduced deliberately by man ..... **introduced**

2′ It was not introduced deliberately by man ..... **immigrant**

For an **indigenous** species (or other taxon):

3 It is known from no other area ..... **precinctive**

3′ It is known from other areas ..... **indigenous but not precinctive**

It is reasonably simple to distinguish between alternatives in couplet 2 (**introduced** vs **immigrant**) and in couplet 3 (**precinctive** vs **indigenous but not precinctive**). However, the parenthetic time frame in couplet 1 (**adventive** vs **indigenous**) is uncertain.

The ability to distinguish very recent immigrants is of practical value in economic entomology, because some of these immigrants are, or are likely to become, pests. Whitehead & Wheeler (1990) suggested that **indigenous** species should be distinguished from **immigrant** species through records of former absence and current presence of the putative immigrants in the area of interest (this criterion is placed in parentheses in couplet 1 of the key above) Most records for invertebrates are associated with presence or absence of preserved specimens in museums. For the most part such specimens can at best help us decide whether an organism immigrated or was present continuously during the last few decades of human history.

There are two avenues to extend the record further into the past. The fossil record, although scanty, has demonstrated the presence of some invertebrate species in the distant past though it is better adapted for demonstrating presence rather than absence. Probable immigration can be inferred from cladistic studies.

To take examples from Florida mosquitoes, *Aedes albopictus* (Skuse) is an **immigrant**, and a recent one, with its arrival well-documented. *Aedes aegypti* (L.) likewise is an **immigrant**, believed to have originated in Africa, and probably has been present

in Florida for some hundreds of years (at or soon after Spanish settlement), long before humans began to catalog the mosquito fauna. *Toxorhynchites amboinensis* (Doleschall) was **introduced** into Florida for biological control purposes. All 3 species are **adventive**. The two *Wyeomyia* species whose larvae develop in the leaf axils of bromeliads of the genus *Tillandsia* in southern Florida cause more thought. Both occur also in the Greater Antilles (and one in eastern Mexico), so they are not precinctive to Florida (and neither are *Tillandsia utriculata* L. and *Tillandsia fasciculata* Swartz, the 2 plants providing principal habitat for their larvae). It is likely that both *Wyeomyia* were **immigrant** to Florida in prehistoric times, and perhaps immigration by their conspecifics from the Greater Antilles still occurs in hurricane winds. However, their evolutionary biogeography is unstudied, so by default we consider them **indigenous** at least for the present. We do not know of any mosquito species **precinctive** to Florida.

This Symposium

This tenth Behavioral Ecology Symposium is entitled "Attack and Defense: Behavioral Ecology of Predators and Their Prey." It continues the theme of the ninth symposium, which was entitled "Attack and Defense: Behavioral Ecology of Parasites and Parasitoids and Their Hosts." In our introduction to the ninth symposium (Frank & McCoy 1989), we asked how the contributions fit in with predictions that have been made about the immediate future courses of behavioral ecological research in general (Krebs 1985) and of behavioral ecological research on insects in particular (Burk 1988). The answer clearly was that the contributions fit in well, and it seems approprate to ask the same questions for the contributions to this thematically-similar tenth symposium.

Before we can answer the question, however, we will need to reiterate the predictions. Krebs (1985) predicted five paths of behavioral ecological research: (1) life history and population dynamics in relation to behavioral ecology, (2) mating systems, (3) parasites and sexual selection, (4) learning, and (5) the genetic basis of behavior. Likewise, Burk (1988) predicted five paths for research specifically on insects: (1) sexual selection, (2) resource competition among females, (3) learning, (4) orientation and movement, and (5) communication. The salient difference between the two lists is the emphasis upon studies of orientation, movement, and communication in insects.

It is interesting to note, then, that four of the five contributions to the tenth symposium deal in some manner with orientation, movement, and/or communication. John Linley's contribution details the movements employed by species of *Toxorhynchites* to effect the capture of subsurface prey. His exhaustive analysis reveals an unimagined melange of movements necessary for successful prey capture, rivaling in complexity those documented for many larger, much more visible predators. Jim Lloyd's contribution suggests that the sometimes puzzling "sexual signals" of fireflies may be hard to interpret because they have evolved under constraints beyond simple efficacy of attraction of potential mates. He posits that these signals also reflect strong selection imposed by predation and, therefore, that they are not solely species-isolating mechanisms. Multiplicity of selective pressures also is central to Dave Pearson's contribution. He questions the common assumption that prey have only single anti-predator characters, and presents six theories, based upon his work with tiger beetles, to explain the evolution of multiple anti-predator characters. He shows how various types of movements, orientations, signals, and other mechanisms work in concert to deter predation upon tiger beetles. Finally, Brian Witz catalogues some of the recent literature on predator-prey interactions, and places the studies into categories of taxonomy of participants and type of interaction. Many of the categories of interaction he erects are based upon directed movements of prey species toward predators, or upon some sort of signalling

by prey species to predators. He suggests that the frequency with which taxa and types of interactions are studied often is not the same as their proportional representations in nature.

Jon Allen's contribution is quite distinct from the other four. He explores the "phase-locked," "quasiperiodic," and "chaotic" behaviors of predator-prey models in relation to the functional response, and finds unexpected and complex switching among these behaviors. He also finds that some types of functional response produce more complexity than do others. He notes that his models ignore genetics, arrangements of individuals in space, and other real complications, but suggests that inclusion of these complicating factors is not likely to reduce the complexity he has uncovered. Allen discussed some contributions of genetics and arrangement of individuals in space to parasitoid-host models in the ninth Behavioral Ecology Symposium.

Endnotes

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THE PREDATORY BEHAVIOR OF *TOXORHYNCHITES AMBOINENSIS* AND *TX. BREVIPALPIS* LARVAE (DIPTERA: CULICIDAE) IN RESPONSE TO SUBSURFACE PREY

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ABSTRACT

Time lapse video recordings and high speed cinematography were used to provide a description and analysis of the predatory behavior of *Toxorhynchites amboinensis* and *Tx. brevipalpis* larvae. Only behavior in response to subsurface prey was examined with emphasis on the bending response, in which larvae turn towards approaching prey, and the strike, which effects prey capture. Bending was a very common response and occurred when prey was positioned in any direction relative to the larva's body. *Toxorhynchites brevipalpis* was more responsive than *Tx. amboinensis; Tx. brevipalpis* larvae bent more rapidly, towards more distant prey, and through angles representing larger proportions of the prey angle. Bend angle increased with increasing prey angle, but as a proportion of prey angle, bend angle increased as prey angle decreased. Bend angle was little affected by prey distance. Movement during being was smooth and continuous. Each bend consisted of a brief accelerative and longer decelerative phase, with average bending rates varying greatly depending on prey angle and distance. Average bending rate increased with decreasing prey distance, the rate of increase being especially rapid as prey approached close to the body. Prey capture during strikes was accomplished in 0.012-0.024 s, and the entire strike completed in 0.060-0.076 s. Only the lateral palatal brushes were used to capture prey. Immediately after capture, prey was seized by the mandibles and released by the palatal brushes, which played no further role in holding or manipulating food.

For descriptive convenience, 3 types of strike were recognized, frontal with head extension, lateral with head extension, and lateral without head extension. These 3 form part of a continuous series. Frontal strikes involved little or no lateral turning towards prey and involved dramatic forward extension of the head, accompanied by opening and closing of the palatal brushes. Head extension was accomplished by sudden increase in the larva's internal pressure resulting from rapid contraction of circular muscles primarily in abdominal segments 1 and 2. Lateral strikes always involved some degree of turning towards prey, and also some degree of head extension when prey was