

## COMPETITION

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### Literature Review

by

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**Abstract:** *As a scientific term the word «competition» has been used to cover a variety of phenomena, having different meanings in animal ecology, genetics and evolution. According to Darwin and other latest biologists natural selection and competition are synonymous. Several other authors give a broader meaning in the term by including predation in it. Opposed to the confusion caused by this broad meaning of competition, another group of researchers tried to restrict it by avoiding to include predation in it.*

*From Darwin to the latest researchers the distinction between interspecific and intraspecific competition has been accepted. Active and passive types of competition, disoperative and cooperative, scramble and contest, exploitative and interference, are some kinds of competition met in biological literature.*

*Competition can be studied by the compositionist method which is a community approach, the reductionist method through experimental manipulation and by observations in the field. Theoretical models of competition have been designed by Lotka-Volterra, Svårdson and others who based their mathematical models on a series of assumptions, often biologically unrealistic.*

*We have evidence from nature that competition occurs through the competitive exclusion principle. Active avoidance of interspecific competition implies that competition has occurred sometime in the past and the species concerned have adapted to one another's presence. Congeneric species may coexist by differential spatial utilization of the environment. Overdispersion, territoriality and studies on «incomplete biotas» are indicative of competition. Character displacement and ecological release through nich expansion also give evidence about competition.*

#### Definition

Competition has been a familiar term in the vocabulary of biologists, ecologists and evolutionists for more than a century.

In dictionary usage «competition» is viewed as «the act of seeking for something for which others are also contending», or «a common struggle for the same object» (Webster's, 1964). The word derived from Latin, which had the verb *competere* and the noun *competit-or, -oris*. According to the Latin lexicographer Duñcan (1854) the prime meaning of *competere* was «to ask or sue for the same thing that another does». As a scientific term, the word «competition» has been used to cover a variety of phenomena, or has come to have different meanings in animal ecology, genetics and evolution (Birch, 1957). Some of these meanings are so ambiguous that the word has largely lost its usefulness as a scientific term. The result is confusion and misunderstanding in some of the writings in these fields.

Darwin in 1859, in «The Origin of Species», explained the «struggle for existence» regarding competition as one of the components of this struggle. He suggested, «As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera». Some biologists regard the struggle for existence, as Darwin used the term, or its outcome -natural selection- and competition as synonymous. According to Elton (1946), «competition is used not merely for direct antagonism or struggle for space etc., but as an objective description (in the same way that 'natural selection' or 'the struggle for existence' are only shorthand terms) of the interplay of longevity and fertility factors of all kinds favouring one species at the expense of another». Schmalhausen (1949) used the same broad meaning of competition and suggested that, «it includes the struggle of organisms against harmful physical (climate) and biologic (predator, parasites) factors in order to protect their own lives and those of their progeny...» His interpretation of competition is that it is density independent. This use of competition is found in the writings of geneticists and evolutionists more than in those of ecologists (Birch, 1957).

Some authors include «predation» in their meaning of competition. Birch (1957) defined predation as «the use of one animal as the main source of food of another». The following quotation from Nicholson (1933) illustrates this meaning of competition: «The reactions of natural enemies to population changes of their hosts must be regarded as a form of competition...» His criterion of competition is that the chances of survival decrease as density increases. In this sense, competition is a

density dependent factor. Crombie (1947) justified predator-prey interactions being regarded as a form of competition on the grounds that sometimes, as in the laboratory and field examples of interspecies and intraspecies interrelationships, one competitor for food or space may eat another.

Another example that illustrates the diversity of phenomena which are covered by competition is the «cooperative competition» by Allee et al. (1949). Their notion arose from laboratory observation that sea-urchin sperms had longer life the more crowded they were. Longer life is regarded by them as a beneficial effect arising from competition for space. Milne (1961) regarded cooperative competition as a contradiction in terms.

Clements and Shelford, in 1939, tried to give competition a single strict meaning. According to them, «The process of competition may be defined inclusively as a more or less active demand in excess of the immediate supply of material or condition on the part of two or more organisms». Their definition is accompanied by remarks where they emphasized «the common demand upon a limited supply». Clements and Shelford did not make a distinction in their remarks between intraspecific and interspecific competition. However, Park (1954) considered this definition as for both unispecific and multispecific competition. The same author analysed Clements' and Shelford's definition in detail and concluded that competition has an «exploitation» and an «interference» component. And he added that «although these (components) may be quite different processes, they must often -indeed typically- affect each other».

Elton and Miller (1954) distinguished competition into that between members of the same species (intraspecific) and that between populations of different species (interspecies). They defined competition by its results, as following: «Interspecific competition, in the more limited and correct use of the notion, refers to the situations in which one species affects the population of another by a process of interference i.e. by reducing the reproductive efficiency or increasing the mortality of its competition. Or both species may be acting in such a way on each other».

Birch (1957) on an extensive study upon the meaning of competition suggested that in biological writings the term should be restricted to one strict meaning, which he redefined: «Competition occurs when a number of animals (of the same or of different species) utilize common

resources, the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or another in the process». Birch's conclusion was that «competition for inadequate resources results in reduction of birth rate and/or increase of mortality rate».

Another rather broad definition of competition was given by Odum (1959): «Competition refers to the interaction of two organisms striving for the same thing». Regarding interspecific relations, Odum recognized eight types of interactions between populations of two species which are neutralism, competition, mutualism, protocoperation, commensalism, amensalism, parasitism and predation. He considered competition as the only one of the eight interactions in which both populations are adversely affected. Odum believed that the supply does not have to be limited and, in a way, he included natural selection by predation within its meaning of competition.

In opposition to Odum's broad meaning of competition, Milne (1961) proposed a single strict definition for use in ecology, genetics and evolution, covering both intraspecies and interspecies relations: «Competition is the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing, when that supply is not sufficient for both (or all)».

MacArthur (1972) proposed again a broad definition of competition which is likely to lead the investigator to the world of predator-prey interactions: «Two species are competing if an increase in either one harms the other».

A combination of Milne's (1961) and Birch's (1957) definitions is given by Grant (1978). This definition can be considered restricted as well as more complete, covering all aspects of competition: «Two species do compete when a resource they both require is in short supply. And they may do this either by using up all of that resource, or the share of the resource that each wants to the detriment of the other; or they may get in each other's way in the process of harvesting that resource».

### Kinds of competition

Various kinds of competition have been distinguished in the literature. The distinction between intraspecific and interspecific competition is generally accepted, as the former occurs between members of the same species and the latter between populations of different spe-

cies. From Darwin (1859) to the latest researchers it has been emphasized that intraspecific competition is more intense than interspecific competition.

Schmalhausen (1949) wrote about «active» and «passive» competition: «In its active form individual competition corresponds to the unusual concept of competition for means of subsistence and for propagation... In its passive form, it includes the struggle of organisms against harmful physical and biological factors».

Allee et al. (1949) distinguished between disoperative and cooperative competition with their peculiar definition.

A distinction is made by Nicholson (1954) on whether the resource is consumed when it is used (for example food) calling it «scramble» competition, or is not consumed (for example nesting sites) as «contest» competition.

Park (1954) in his analysis of competition referred to two components. «Exploitation» which is the resource utilization and is explicit in the definition, and «interference» which is usually aggressive and is implicit. For exploitation Park wrote: «In the favorable environment there is undoubtedly heavy exploitation of the limited resources». About interference he said that «Populations compete for limited resources through mutual interference, which differentially affects multiplication and survival as a consequence of species co-association». Park preferred to use the term to encompass both components.

A considerable literature gives evidence of exploitation and interference competition. Wilson (1975) referred to interference competition as a mechanism of agonistic interaction in the use of space, and to exploitation as a more peaceful process of competition. Miller (1967) wrote that, «interference is the method in which one species inhibits another species' access to a resource through territoriality, aggression etc.» He pointed out that for interference competition to occur there must be some form of intraspecific communicatory mechanism, such as territoriality, that has been extended to interspecific interactions. Miller (1969) also observed that interference is immediately effective due to the agonistic component since it occurs even before the resource becomes limited. On the contrary, exploitation may have to continue for several generations before the actual limiting condition occurs. Consequently, the results of interference competition are more visible to the researcher in a typical short term study while exploitation may not be detected as a competitive process (Jaeger, 1974).

## Study of competition

There are basically two ways of studying competition. Through observations in the field and through experimental manipulation (Grant, 1978). The first approach is the observational or community approach and it is compositionist. The community approach deals with the analysis of patterns of coexistence and resource partitioning of animals; it provides indirect evidence that interspecific competition has been an important factor in the past. Elton (1946) with an analysis of the genus/species composition of plant and animal communities came to conclusions on inter and intraspecific competition occurring in nature. Brown (1973) analysed the patterns of coexistence of small mammals to get information on the importance of interspecific competition in the past. This method has been extensively used to answer evolutionary questions of community structure and function that implicate interspecific competition (Grant, 1978). The weaknesses of the method are that it is indirect and inferential, as well as subject to interpretational bias. The greatest value of the analysis of patterns of coexistence is that it may suggest competition hypotheses to be tested experimentally.

We can have more direct evidence of competition in the field through observations of interference interactions between animals. These may be valuable on a short term study of competition (see interference competition, above).

The second approach, to study competition by experimental manipulation is the reductionist method. Gause (1934) was one of the first to investigate competition in the laboratory. His classic early experiments on protozoa verified competitive exclusion. He grew cultures of two species of *Paramecium* in isolation and in mixed cultures under carefully controlled environmental conditions and showed how one of the species would prevail eventually over the other. An effect of environment on the outcome of competition was demonstrated by Park (1954). Working with two species of flour beetles, he showed that, depending upon conditions of temperature and humidity, both species persist indefinitely when each is husbanded only by itself. When interspecies competition is added to the ecosystem, with coassociation of the two species, one species always wins, and the other one always is selectively eliminated (Park, 1954). Connell (1961) has done extensive experimental work in the field and described mechanisms by which competition and exclusion are effected. In his study of the interactions

between two species of sessile, intertidal barnacles, Connell showed that the distribution of one species was limited to the uppermost region of the intertidal zone, because below that region it was physically crowded out of the limited available space by a second species.

Grant (1972) conducted nine sets of enclosure experiments, between the years 1957 to 1971, to show interspecific competition between small mammals experimentally. His enclosures were in the field, where he watched the effects of the presence of the two species in coexistence, versus the effects of each species living separately. Since then, many researchers have used enclosure experiments in the field to estimate interspecific competition. The shortcoming of experiments with enclosures is that control over the animals and their environment is gained at the expense of realism. The enclosure walls restrict movements and other social interactions of the animals; the piece of land they enclose is thus more similar to an island than to a sample of mainland (Grant, 1972).

The two approaches in the study of competition are rather complementary and not competitive and are required, wherever they can be applied, to answer evolutionary as well as ecological questions on competition.

#### Theoretical models of competition

Competition was placed on a fairly firm, if greatly oversimplified, theoretical basis nearly 50 years ago by Lotka (1925) and Volterra (1926). Their equations describing competition have strongly influenced the development of modern ecological theory and illustrate a mathematical model of an important ecological phenomenon (Pianka, 1978).

The Lotka-Volterra competition equations are a modification of the Verhulst-Pearl logistic equation and they share its assumptions.

$$\frac{dN_1}{dt} = r_1 N_1 \left( \frac{K - N_1 - a_{12} N_2}{K_1} \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

Where:  $N_1$  and  $N_2$  are the two competing species

$K_1$  and  $K_2$  the carrying capacities in the absence of one another.

$r_1$  and  $r_2$  are the maximal instantaneous rates of increase per head.

$a_{12}$  and  $a_{21}$  are competition coefficients.

$a_{12}$  is a characteristic of species 2 which measures its competitive inhibition in the species 1 population.

$a_{21}$  is a similar characteristic of species 1 that measures its inhibitory effects on species 2.

Implicit in the Lotka-Volterra competition equations are a number of assumptions: Maximal rates of increase, competition coefficients and carrying capacities are all assumed to be constant; they do not vary with population densities, community composition or anything else. The two species are not allowed to diverge; so, the environment is assumed to be completely homogenous. In real populations, rates of increase, competitive abilities, and carrying capacities do vary from individual to individual with population density, community composition, and in space and time. Finally, a heterogenous environment may allow real competitors to evolve divergent resource utilization patterns and to reduce interspecific competitive inhibition (Pianka, 1978). The numerous biologically unrealistic assumptions reveal the inadequacy of competition theory.

Svärdson (1949) published a model of interspecific and intraspecific competition. It was designed to represent some bird situations he studied but with small modification can be applied to mammals and other taxa (Grant, 1978). Generalized, the model says that, 1) when intraspecific demand upon resources increases, perhaps as a result of an increase in population number, an increasing variety of resources will be exploited, but 2) expansion of resource use will be counteracted by interspecific competition for the resources newly exploited. In the model the opposing tendencies are intraspecific and interspecific competitive effects, which are proportional to densities. The Svärdson model is still a useful conceptual framework for viewing competitive processes in mammals (Grant, 1978).

#### Evidence from nature

A variety of observations and studies suggest that competition does indeed occur regularly in nature and that it has been an important factor in molding the ecologies of many species of plants and animals.

Ecologists have several different sorts of evidence, suggesting that



competition either has occurred or is occurring in natural populations. Active avoidance of interspecific competition in itself implies that competition has occurred sometime in the past and that the species concerned have adapted to one another's presence.

In some cases, closely related species may exclude each other from local habitats by direct, aggressive interference. Then, the competitive exclusion principle occurs which Gause (1935) suggested: «Two species cannot indefinitely coexist if they occupy the same niche». In other cases, congeneric species may coexist by exploiting different habitats (differential spatial utilization of the environment), or by having different patterns of temporal activity and thus, avoiding interspecific competition. There are numerous examples in nature of ecologically similar animals which show differences in time of activity, in the use of space and in dietary separation (Pianka, 1978). Nevertheless, there is available evidence which indicates that species may coexist through competing, until some critical level of dietary or some other resource overlap occurs (Jaeger, 1974).

Overdispersion in general, and territoriality in particular, are indicative of competition, in that they reduce its intensity; both intraspecific and interspecific competition have led to territorial behavior (Pianka, 1978). Grant (1978) emphasized the role of competition as an immediate ecological process that influences local distribution and abundance in rodents.

The phenomenon of «character displacement» is also evidence that competition occurs in nature. Sometimes, two widely ranging species are ecologically more similar in allopatry than they are in sympatry. «Character displacement» may be either morphological or behavioral and is thought to have occurred in some lizards, snails, birds, mammals and insects (Brown, 1978).

Another type of evidence for competition comes from studies on «incomplete» biotas, such as islands, where all the usual species are not present. Those species which invade such areas often expand their niche and exploit new habitats and resources that are normally exploited by other species on areas with more complete faunas. This type of niche expansion under reduced interspecific competition has been termed «ecological release» (Pianka, 1978). It is interesting to speculate that the exceptionally high densities of birds (MacArthur, 1972) and lizards on some oceanic islands compared to similar habitats on nearby continents, is attributable in part to the absence of distantly related compe-

titors, such as mammals, amphibians and arthropods (Brown, 1978).

Finally, observations involving the taxonomic composition of communities have been used as evidence of competition between species. Elton's (1946) analysis of plant and animal communities suggested that competitive exclusion occurs more often among congeneric species than it does in more distantly related ones. However, recent evidence (Brown, 1978) suggested that small mammals compete significantly with distantly related taxa of vertebrates and invertebrates. Such interactions may have important consequences for the structure and function of natural ecosystems.

I would like to end up this paper with Brown's (1978) statement that, «one of the most challenging problems is to distinguish between these patterns caused by competition acting right now as a dynamic force that maintains the organization of communities and those resulting from competition acting as an evolutionary force that has shaped communities, such that coexisting species have evolved differences in resource utilization to minimize contemporary competition».

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## ΠΕΡΙΛΗΨΗ

### ΑΝΤΑΓΩΝΙΣΜΟΣ

ὁπὸ

ΜΥΡΤΟΥΣ ΠΥΡΟΒΕΤΣΗ-ΒΑΣΙΛΕΙΑΔΟΥ

(*Ἐργαστήριο Ζωολογίας Παν/μίου Θεσ/νίκης*)

Ἡ λέξι ἀνταγωνισμὸς ἔχει χρησιμοποιηθεῖ στὴ βιολογία σὰν ἐπισημονικὸς ὄρος, καλύπτοντας ποικίλα φαινόμενα καὶ ἔχοντας διαφορετικὴ ἐρμηνεία στὴν οἰκολογία ζώων, γενετικὴ καὶ ἐξέλιξη. Σύμφωνα μὲ τὸν Δαρβίνο καὶ ἄλλους μεταγενέστερους βιολόγους οἱ ὄροι: «φυσικὴ ἐπιλογή» καὶ «βιολογικὸς ἀνταγωνισμὸς» εἶναι συνώνυμοι. Ἄλλοι ἐπιστήμονες ἔχουν δώσει μιὰ εὐρύτερη ἔννοια στὸν ὄρο, συμπεριλαμβάνοντας τὴν θήρευση —predation— τῶν ζώων στὴν ἐρμηνεία τῆς. Μιὰ ἄλλη ὁμάδα ἐρευνητῶν, ἀντίθετοι μὲ τὴ σύγχυση ποὺ προκάλεσε ἡ διεύρυνση τῆς ἔννοιας ἀνταγωνισμὸς, προσπάθησαν νὰ τὴν περιορίσουν, ἀποφεύγοντας νὰ περιλάβουν τὴν θήρευση στὴν ἐρμηνεία τῆς.

Ἡ διάκριση ἀνάμεσα σὲ ἀνταγωνισμὸ μεταξὺ τῶν εἰδῶν καὶ ἀνάμεσα σὲ ἄτομα τοῦ ἴδιου εἴδους ἔχει γίνεαι ἀποδεκτὴ ἀπὸ τὸν Δαρβίνο ὡς τοὺς πῶς σύγχρονους ἐρευνητές. «Ἐνεργητικὸς» καὶ «παθητικὸς» ἀνταγωνισμὸς, «συνεργατικὸς» καὶ «ἀνταγωνιστικὸς», «διεκδικητικὸς» καὶ «διαγωνιστικὸς», «γιὰ ἐκμετάλευση» ἢ «ἐπέμβαση», εἶναι μερικὰ εἶδη ἀνταγωνισμοῦ ποὺ συναντοῦμε στὴ βιολογικὴ βιβλιογραφία.

Ὁ βιολογικὸς ἀνταγωνισμὸς μπορεῖ νὰ μελετηθεῖ α) μὲ τὴ συνθετικὴ μέθοδο ποὺ εἶναι ἡ ἐρευνητικὴ προσέγγιση στὴ βαθμίδα τῆς κοινωνίας, β) τὴν ἀφαιρετικὴ μέθοδο μὲ πειραματικὸ χειρισμὸ καὶ γ) μὲ παρατηρήσεις στὴ φύση.

Οἱ Lotka- Volterra, Svårdson καὶ ἄλλοι βιολόγοι ἔχουν σχεδιάσει θεωρητικὰ μοντέλα γιὰ τὸν ἀνταγωνισμὸ, βασιζόντας τοὺς μαθηματικούς τους ὑπολογισμούς σὲ μιὰ σειρά σημαντικῶν προϋποθέσεων ποὺ συχνὰ εἶναι βιολογικὰ μὴ πραγματικές.

Ἐνδειξὴ ἀπὸ τὴ φύση ὅτι συμβαίνει βιολογικὸς ἀνταγωνισμὸς μᾶς πα-

ρέχει «ή άρχή τοῦ άνταγωνιστικοῦ άποκλεισμοῦ» (competitive exclusion principle)». Η ένεργή άποφυγή άνταγωνισμοῦ μεταξύ δύο ή περισσοτέρων ειδών σημαίνει ότι στο παρελθόν υπήρχε έντονος άνταγωνισμός μεταξύ τους και εξέλικτικά τά είδη προσαρμόστηκαν σε είρηνική συνύπαρξη. Συγγενή είδη μπορεί νά συνυπάρχουν στον ίδιο τόπο με «διαφορετική μερική, έκμετάλευση» τοῦ περιβάλλοντος. Τά φαινόμενα τής διασποράς τών ειδών, τής κτήσης έδάφους άπό τά ζώα (territoriality) και έρευνες πού έγιναν σε «άτελεις βιοκοινωνίες» μάς δίνουν ένδείξεις για τόν άνταγωνισμό. Η «μετατόπιση χαρακτῆρα» και «ή οικολογική χαλάρωση» με διεύρυνση τοῦ οικολογικοῦ θώκου (τής θέσης τοῦ οργανισμοῦ μέσα στον βιο-οικολογικό χῶρο) είναι επίσης ένδεικτικά τοῦ άνταγωνισμοῦ.