Pearson New International Edition

Ecology: The Experimental Analysis of Distribution and Abundance

Charles J. Krebs

Sixth Edition

ALWAYS LEARNING

PEARSON

Pearson New International Edition

Ecology: The Experimental Analysis
of Distribution and Abundance
Charles J. Krebs
Sixth Edition

PEARSON

Table 1 Criteria for establishing the occurrence of interspecific competition, listed according to the strength of the evidence for its occurrence in natural populations.

Criteria	Strength of evidence
1. Observed checkerboard patterns of distribution consistent with predictions	Weak
2. Species overlap in resource use	↓
3. Intraspecific competition occurs	Suggestive
4. Resource use by one species reduces availability to another species	↓
5. One or more species is negatively affected	Convincing
6. Alternative process hypotheses are not consistent with patterns	

SOURCE: Wiens (1989), p. 17.

are plentiful. Occasionally a "crunch" occurs, a period of scarcity in which competition does occur. This may happen only once every five or ten years, or even less frequently, implying that competition may be difficult to detect in most short-term studies.

Evolution of Competitive Ability

If two species are competing for a resource that is in short supply, both would benefit by evolving differences that reduce competition. The benefit involved is a higher average population size for each species, and presumably a reduced possibility of extinction. But in many cases it will be impossible to evolve differences that reduce competition. Consider, for example, food size as a limiting resource. If species A evolves such that it uses smaller food items than species B, it still may encounter a third species, C, that also feeds on small-sized food. Thus species may be constrained by a web of other possible competitors, such that the option of evolving to avoid competition is not always feasible. If a species cannot avoid competition, it must evolve competitive ability. Competitive ability is one element of the more general problem of the evolution of life history strategies.

Ecologists have used two general approaches to the general question of the evolution of competitive ability as an element in life history strategies. Animal ecologists have utilized the theory of *r*-selection and *K*-selection first proposed by MacArthur and Wilson (1967), while plant ecologists have utilized a related theory of plant strategies, the *C-S-R* model developed by Grime (1979).

Theory of *r*-Selection and *K*-Selection

The idea of competitive ability in animals is an ecological concept that is intuitively clear but difficult to define, and to understand how competitive ability might evolve we need to look at life history strategies more broadly. To understand life history evolution, we can begin with the Lotka-Volterra equations for competition, which are based on the logistic curve for each competing species. Two parameters characterize the logistic curve of each competing species: *r* (rate of increase) and *K* (saturation density). We can characterize organisms by the relative importance of *r* and *K* in their life cycles.

In some stable environments, organisms exist near the asymptotic density (*K*) for much of the year, and these organisms are subject to *K*-selection. In other unstable or unpredictable habitats the same organisms may rarely approach the asymptotic density but instead remain on the rising portion of the curve for most of the year; these organisms are subjected to ***r*-selection**. MacArthur and Wilson (1967) defined *r*-selection and *K*-selection to be density-dependent natural selection. As a population initially colonized an empty habitat, *r*-selection would predominate for a time, but ultimately the population would come under *K*-selection.

Species that are *r*-selected seldom suffer much pressure from interspecific competition, and hence they evolve no mechanisms for strong competitive ability (**Table 2**). Species that are *K*-selected exist under both intraspecific and interspecific competitive pressures. The pressures of *K*-selection should thus push organisms to use their resources more efficiently.

If *K*-selection is a complete description of competitive ability, we should be able to predict the outcome

Table 2 Characteristics of *r*-selected species and *K*-selected species. Many species will have characteristics intermediate between these two extreme life history strategies.

r-selected life history	*K*-selected life history
Small-sized organisms	Large-sized organisms
Many small reproductive units (seeds, spores, offspring)	Few larger reproductive units
Little energy used per reproductive unit	Much energy used to produce one reproductive unit
Early maturity	Late maturity and often parental care
Short expectation of life	Long life expectancy
Single reproductive episode (semelparous)	Many reproductive episodes (iteroparous)
Type 3 survival curve (Figure 6)	Type 1 or 2 survival curve

of competition in laboratory situations by knowing the K values for the two competing species. We cannot do this, however, because of the third parameter in the Lotka-Volterra equations for competition—the competition coefficients α and β. Species can evolve competitive ability by the process of α-selection (Gill 1974). Any mechanism that prevents a competitor from gaining access to limiting resources will increase α (or β) and thereby improve competitive ability. Most types of interference competition fall into this category. Territorial behavior in mammals and birds, and allelopathic chemicals in plants, are two examples of interference attributes that keep competing species from using resources.

One major evolutionary problem with α-selection is that the strategy of interference often affects members of the same species as well as members of competing species, such that competitive ability is achieved only at the expense of a reduction in the species' own values of r and K. An example is a shrub that produces chemicals that retard the germination and growth of competing plants but that also induces autointoxication after several years (Rice 1984). An individual's negative effects on members of its own species present no evolutionary problem so long as the affected individuals do not include the individual itself or its kin.

Alpha-selection for interference attributes can also operate when organisms are at low density. In animals, the evolution of a broad array of aggressive behaviors has been crucial in substituting ability in mock combat for ability to utilize resources in competition in many situations (MacArthur 1972), and we can recognize an idealized evolutionary gradient:

$$\begin{array}{ll}\text{Low density} - & \text{colonization and growth } (r \text{ selection}) \\ & \qquad\qquad\downarrow \\ \text{High density} - & \text{resource competition } (K \text{ selection}) \\ & \qquad\qquad\downarrow \\ \text{High density} - & \text{interference mechanisms } (\alpha \text{ selection}) \\ & \text{prevent resource competition}\end{array}$$

Populations may exist at all points along this evolutionary gradient because competition for limiting resources is only one source of evolutionary pressure that molds the life cycles of plants and animals (Roff 1992).

Grime's Theory of Plant Strategies

Vascular plants face two broad categories of factors that affect their growth and reproduction. One category includes shortages of resources such as light, water, or nitrogen; temperature stresses; and other physical-chemical limitations. This category Grime (1979) called stress. A second category includes all the factors classified as disturbances, including grazing, diseases, wind storms, frost, erosion, and fire. Grime examined the four possible combinations of these two categories and recognized that, for one combination, no strategy was possible:

	Intensity of stress	
Intensity of disturbance	**Low**	**High**
Low	Competitive (*K*) strategy	Stress-tolerant strategy
High	Ruderal (weed or *r*) strategy	None possible

If stress and disturbance are too severe, no plant can survive. Grime (1979) suggested that the other three strategies formed the primary focus of plant evolution, and that individual plant species have tended to adopt one of these three life history models.

The three strategies can be diagrammed as a triangle (**Figure 20**), which emphasizes that these three strategies represent trade-offs in life history traits. A plant cannot be good at all three strategies but must trade off one set of traits against another (Wilson and Lee 2000). Competitive plants show characteristics of *K*-selection—dense leaf canopies, rapid growth rates, low levels of seed production, and relatively short life spans—and many perennial herbs, shrubs, and trees show these characteristics. Stress-tolerant plants often have small leaves, slow growth rates, evergreen leaves, low seed production, and long life spans. Ruderals are weeds that thrive on disturbance; they exhibit small size, rapid growth, are often annual plants, and devote much of their resources to seed production. Ruderals are the *r*-strategists of the plant world.

The evolution of competitive ability, although viewed differently by botanists and zoologists, has achieved a convergence of ideas. Both *r*- and *K*-selection theory and Grime's theory describe well the trade-offs organisms must face in evolutionary time. Organisms cannot become good at everything, and adaptations are always a compromise between conflicting goals.

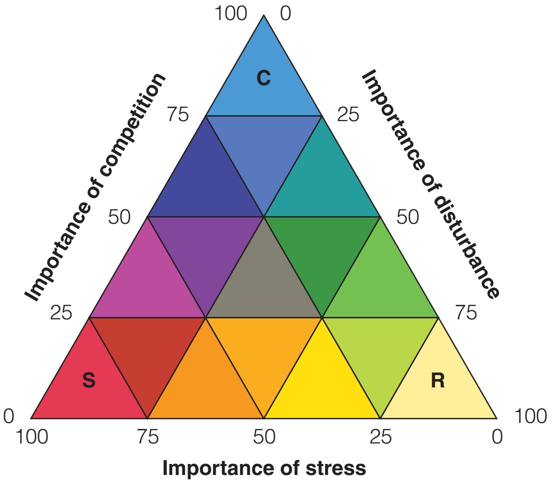

Figure 20 Grime's triangle model of plant life history strategies. Plant attributes evolve within this life history space depending on the relative importance of three factors: competition (*C*), stress (*S*), and disturbance (represented by *R*, for ruderal or weed strategy). It is for these factors that this model is also called the *C-S-R* model. (Modified from Grime 1979.)

Westoby's Leaf-Height-Seed Theory of Plant Strategies

One problem with the C-S-R triangle theory of Grime (1979) is that it has been difficult to place a particular species at a point within the triangle by measuring some ecological traits. Mark Westoby (1998) proposed an alternative scheme of plant strategies that is empirically based on three measures of plants that can be readily taken in the field. The three axes of Westoby's scheme are:

- Specific leaf area—the light-capturing area deployed by the plant per unit of dry mass allocated to leaves
- Height of the plant canopy at maturity
- Seed mass

Both plant height and seed mass are readily measured for plants. Specific leaf area is somewhat more difficult to conceptualize. It measures the light-catching area deployed by a plant, and is analogous to the expected rate of return on investment. A high specific leaf area allows the plant to obtain a shorter payback time on a gram of leaf matter invested in a leaf. A plant species employing a low specific leaf area achieves a longer life span through higher structural strength and sometimes by way of defensive chemicals such as tannins.

Plants may produce many small seeds or fewer large seeds, and we expect ruderal or *r*-selected species of plants to produce many small seeds and competitive or

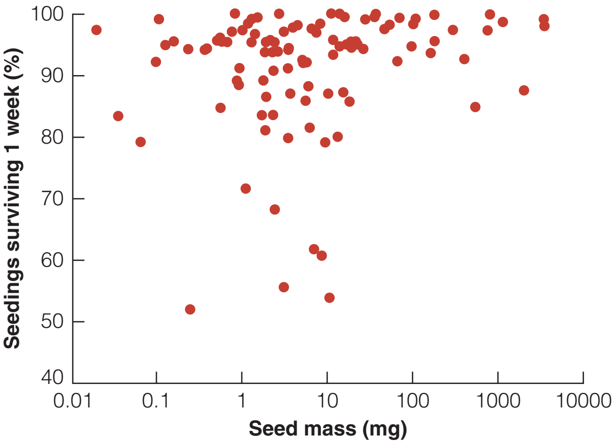

Figure 21 Percentage of plant seedlings surviving the first week after germination in relation to seed size. Data for 112 species from tropical to temperate habitats were used. Seed mass is on a logarithmic scale. There is a significant positive relation, indicating that larger seeds are more likely to survive the first week after emergence, but there is wide scatter from different species, so that not all small seeds survive poorly. (Data from Moles and Westoby 2004.)

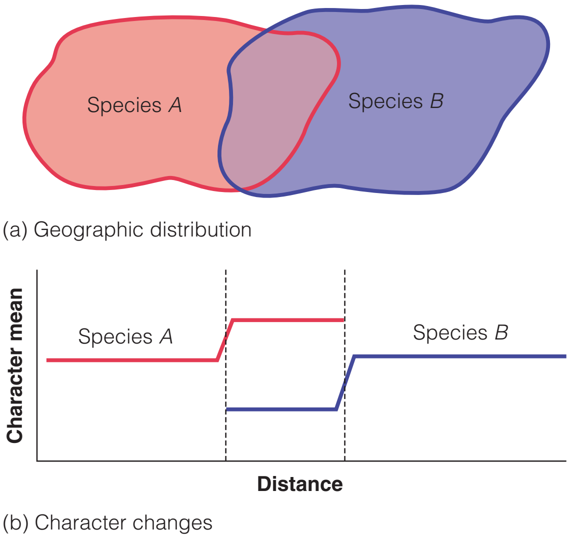

Figure 22 Schematic view of character displacement arising from interspecific competition in the zone of overlap of two species. The character measured must be one that is critical in competition between the species. This scheme is inferred as an explanation of the observations illustrated in Figure 23.

K-selected plants to produce fewer smaller seeds. If seed survival was constant over all seed sizes, we would predict that small seed producers would win out. But this clearly does not happen, and one hypothesis is that large-seeded species make up for their low seed production by increased survival during seedling establishment. There is no relationship between seed mass and survival to the newly emerged seedling stage, but survival to one week of age is higher in plant species with larger seeds (**Figure 21**). Moles and Westoby (2004) concluded that this survival advantage of larger seeds was not large enough to permit larger-seeded species to outcompete smaller-seeded plants unless larger-seeded species had a longer reproductive life span. There is a clear trade-off between a plant producing many small seeds, each with a lower chance of establishment, and producing fewer larger seeds, each with a high chance of successful establishment (Westoby et al. 2002). However, the exact quantitative trade-offs need to be measured more carefully to decide which of these strategies will be favored by natural selection in a particular competitive environment.

Character Displacement

One evolutionary consequence of competition between two species has been the divergence of the species in areas where they occur together. This sort of divergence is called **character displacement** (**Figure 22**) and can arise for two reasons. Because two closely related species must maintain reproductive isolation, some differences between them may evolve that reinforce reproductive barriers. In other cases, interspecific competition causes divergence in critical niche dimensions. Character displacement is an important ecological hypothesis because it assumes that species too similar to one another could not coexist without diverging due to interspecific competition. Observations of character displacement are thus consistent with the predictions of Gause's hypothesis.

Character displacement is often inferred from studies in areas where the two species occur together and where they occur alone. **Figure 23** gives a classic example of character displacement from Darwin's finches on the Galápagos Islands. Before we conclude that this example is a good illustration of evolutionary changes in competing populations, we must satisfy six criteria (Schluter and McPhail 1992):

1. The pattern observed could not have occurred by chance.
2. The observed phenotypic differences should have a genetic basis.
3. The trait differences should result from actual evolutionary changes.
4. The morphological differences should reflect differences in resource use.

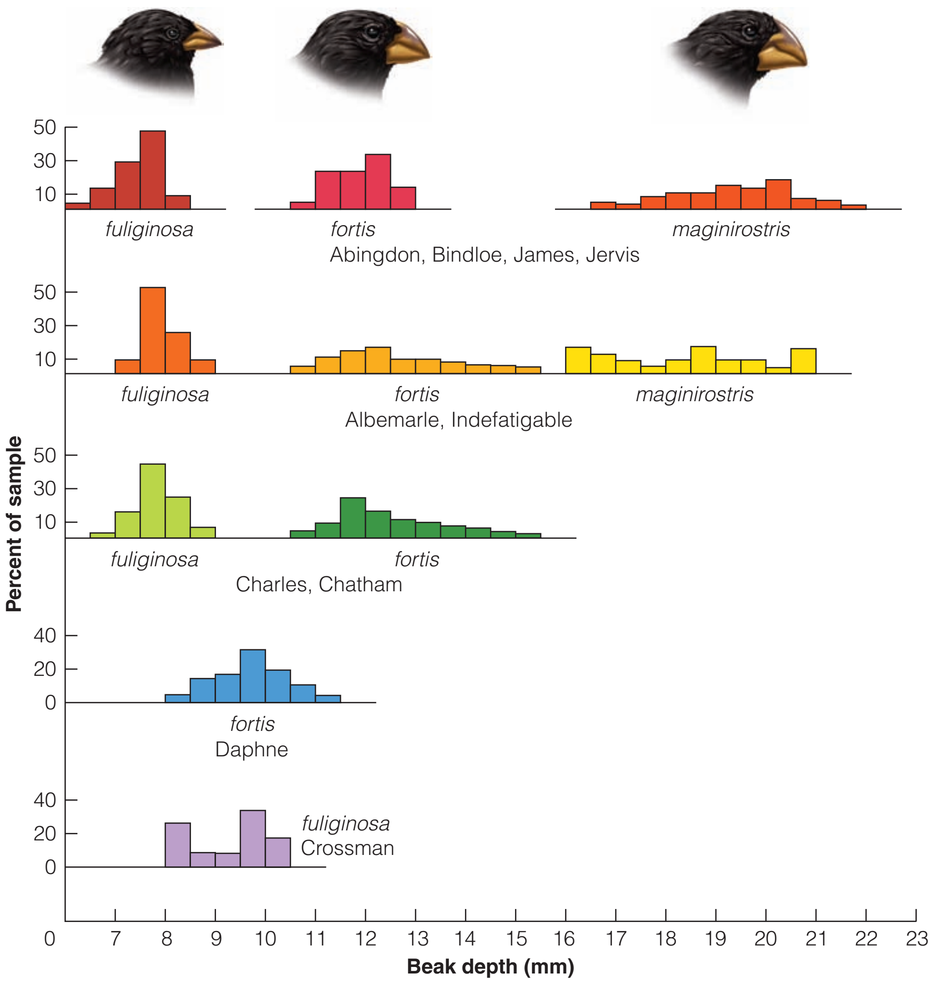

Figure 23 Character displacement in beak size in Darwin's finches from the Galápagos Islands. Beak depths are given for *Geospiza fortis* and *G. fuliginosa* on islands where these two species occur together (upper three sets of islands) and alone (lower two islands). *Geospiza magnirostris* is a large finch that occurs on some islands. (After Lack 1947.)

5. The sites of sympatry and allopatry should not differ greatly in environmental factors that affect the phenotype.
6. There must be independent evidence for competition between the species.

For Darwin's finches, all these criteria are satisfied (Grant and Grant 2006). The change in beak size in *Geospiza fortis* in isolation on Daphne Island, for example, is much greater than one would predict from observed variation on any of the other islands. Beak characters in *G. fortis* have a very high heritability (offspring resemble parents), which suggests that the variation in beak depth in *Geospiza* shown in Figure 23 is largely genetic in origin. There is good observational evidence of competition for food in Darwin's finches.

Many examples of character displacement in the feeding morphology of carnivores have been measured. One example comes from three closely related small carnivorous marsupials that live on Tasmania—the spotted-tailed quoll (*Dasyurus maculatus*), the eastern quoll (*Dasyurus viverrinus*), and the Tasmanian devil (*Sarcophilus laniarius*). Because these carnivores are sexually dimorphic (males are about twice the size of females), the sexes must be considered separately. **Figure 24** shows the even spacing of body mass in these three carnivores that is consistent with the hypothesis of character displacement in the past (Jones 1997).

There are now many cases in which character displacement has been conclusively demonstrated (Dayan and Simberloff 2005). These cases all attest to the important role of interspecific competition in the evolution of species traits.

Apparent Competition and Indirect Effects

Competition between species is usually thought of in terms of two species directly interacting over limited resources. But organisms of different species may interact

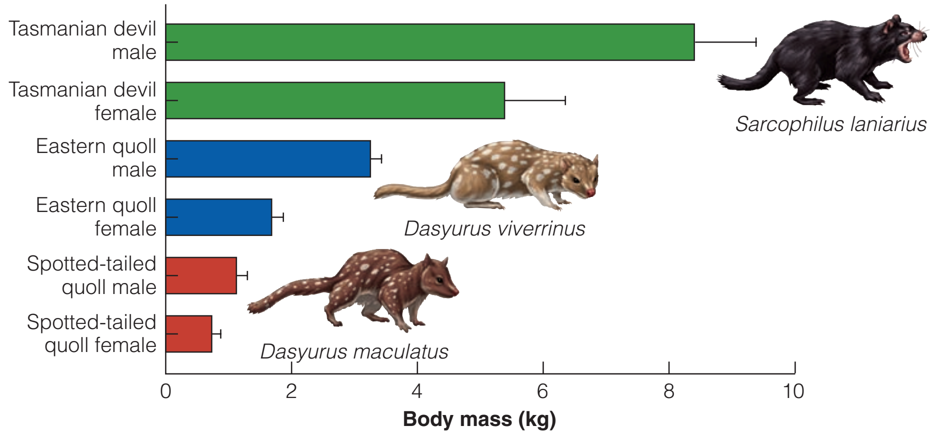

Figure 24 Character displacement in body size in the carnivorous marsupials of Tasmania. There is a regular progression of body sizes that is reflected in their hunting behavior and prey eaten, and this character displacement is most readily explained by interspecific competition for food in the past. (Data from Jones 1997.)

directly or indirectly (**Figure 25**). Interference competition occurs by direct effects in which, for example, two species of birds vie for access to tree holes for nesting. Exploitative competition involves indirect effects because the two species have no interactions with each other but interact only through a third species or a shared resource. For example, if buffalo and grasshoppers eat the same grass, exploitative competition may occur even though buffalo have nothing directly to do with grasshoppers. Indirect effects are often surprising and can take on a variety of forms (Abrams 1987). Holt (1977) pointed out how indirect effects could produce apparent competition. Consider two herbivores, such as rabbits and pheasants, that do not eat any of the same foods or compete for any essential resources. If these two species have a common predator, an increase in the abundance of rabbits could increase the abundance of the predator, which might then eat more pheasants and reduce their numbers. In systems like this, one could easily be fooled into thinking that two species were competing because when one increased in numbers, the other decreased, and vice versa. The important idea here is that we should try to understand the mechanisms behind interactions between species and not simply describe how numbers may go up or down without knowing why.

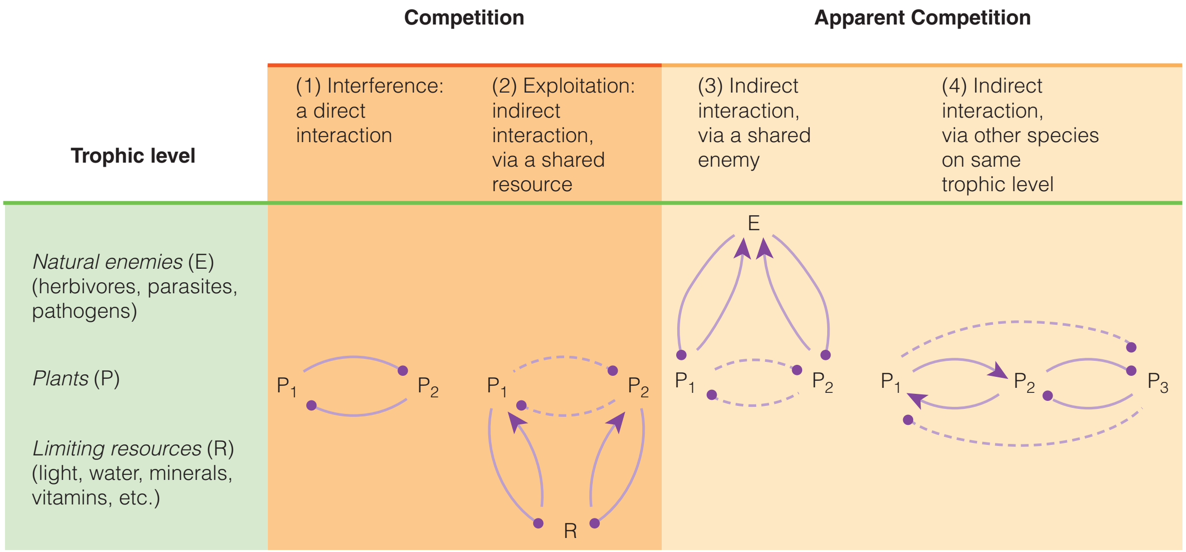

Figure 25 Illustration of possible pathways of interspecific competition, in this case for plants. Solid lines are direct interactions, dashed lines are indirect ones. An arrowhead indicates a positive effect, a circle indicates a negative effect. A similar type of interaction scheme can be applied to animals. Species can affect the abundance of other species without direct interactions. (After Connell 1990.)