

13.6 Ecological influences on the form of a species are shown by the phenomenon of character displacement

Ecological competition can influence the form of a species (as we mentioned, theoretically, in Section 13.2.3 above). The range of a morphological character, such as beak size, within a species may be limited because the extreme forms suffer competition from neighboring species. In this section we shall look at some evidence for the influence of ecological competition on species. The clearest evidence is provided by *character displacement*.

Two species may differ more in places where they coexist than elsewhere

Character displacement can arise in the following conditions. Two closely related species exist — species that may be ecological competitors. The two species must have a special kind of geographic distribution: it must be the case that both species are present in some places, but only one of the species is present at other places. That is, the two species must have partly overlapping ranges. Character displacement means that individuals of the two species differ more if they are sampled from a place where both species are present (*sympatry*, same place) than do individuals sampled from places where only one of the species is present (*allopatry*, other place). In these terms, character displacement means that sympatric populations of two species differ more than do allopatric populations of the same two species.

Character displacement is difficult to detect because it requires two competing species to have partly overlapping ranges. Many pairs of species either have completely separate ranges, or ranges that are very similar; in either case, it is impossible to study character displacement.

Two salamander species are an example

An example of character displacement comes from two species of salamander, *Plethodon cinereus* and *P. hoffmani*. *P. cinereus* lives throughout much of northeastern USA, except for parts of Pennsylvania and Virginia, whereas *P. hoffmani* lives in parts of Pennsylvania where *P. cinereus* is absent. The two species also live together, sympatrically, in a small region of overlap in Pennsylvania. The two species differ in the shape of their heads and jaws: *P. hoffmani* has a jaw that is relatively weak but can be closed fast and *P. cinereus* has a stronger jaw but is slow to snap it shut. *P. hoffmani* is better adapted to eat large prey items, which are caught by immediately closing the mouth on them, whereas *P. cinereus* is better adapted to eat smaller prey, which are eaten by pressing them between the tongue and teeth.

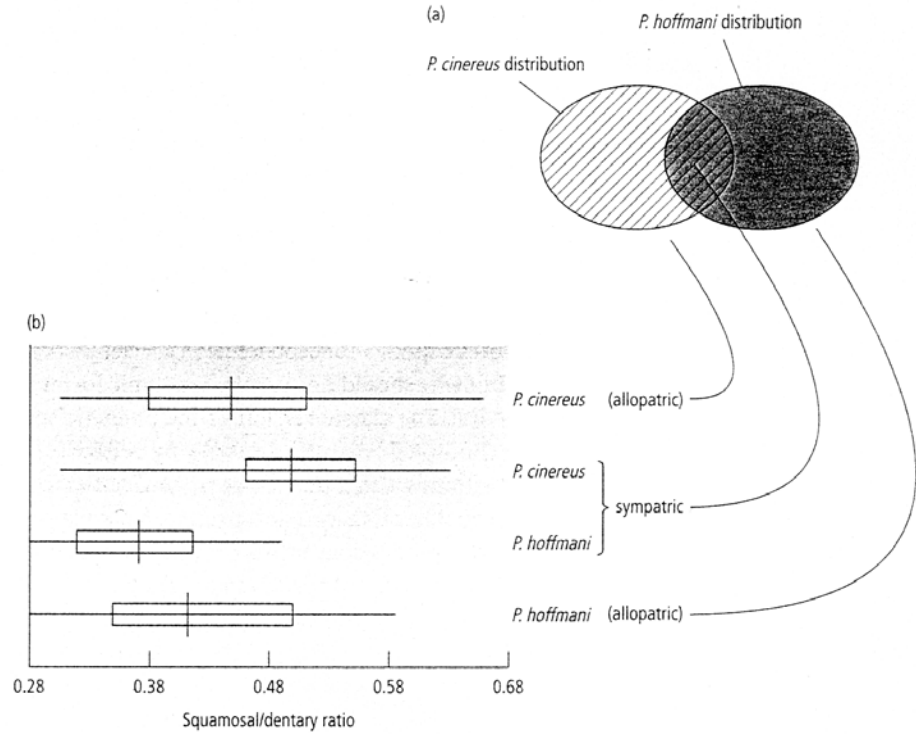
Figure 13.7 shows that the two species differ more in locations where both species are present, that is they show character displacement. The standard interpretation of character displacement is that, where only one species is present, it is released from competition with the other species and it evolves to exploit resources that would be taken by its competitor if it were present. All the allopatric populations evolve to have a similar array of forms. Where both species are present (in sympatry), each species evolves to exploit the resources that it is better adapted to. Competition forces each species to become more specialized. Character displacement shows how ecological competition results in a discrete array of forms within each species.

It is hard to show that character displacement is caused by competition

However, it takes rigorous research to show conclusively that a result such as Figure 13.7 is really caused by ecological competition. Taper & Case (1992), Losos (2000), and Schluter (2000) discuss six criteria that a full study would need to satisfy. For instance,

Figure 13.7

Character displacement in North American salamanders. (a) Character displacement can only be studied in two species with partly overlapping ranges, such that in some places both species are present (sympatry) and in other places only one species is present (allopatry). (b) Where only one of the species of *Plethodon cinereus* or *P. hoffmani* is found (allopatric populations) the form of the species is similar. Where both species are found together (sympatric populations) they differ more. (c) Measurements were made of the skull form, which is related to diet. Redrawn, by permission of the publisher, from Adams & Rohlf (2000).



the pattern could be caused by differences in resources, for example if the insect prey differed between sites, or it could be caused by chance. Adams & Rohlf (2000) came close to ruling out all the alternatives to competition: they met five of the six criteria in their study of the salamanders *P. hoffmani* and *P. cinereus*. These salamanders are about the best example we have of character displacement, and its explanation by ecological competition.