

SELECTION FOR MATING BARRIERS BETWEEN POPULATIONS OF UNEQUAL SIZE

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ABSTRACT: Natural selection for reproductive isolation is stronger in smaller populations than in larger ones, when populations of unequal size undergo such selection. This can explain asymmetrical patterns of reproductive isolation and can help to explain divergence of peripheral isolates which survive long enough to be observed.

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Wallace (1889) suggested that natural selection would favor the accumulation of mating barriers between incipient species, because any such barrier would increase individual fitness by reducing gamete wastage on maladapted hybrids. In particular, selection should favor mating barriers that prevent the wastage of female gametes, since fitness is not greatly reduced by the wastage of male gametes in most organisms. Inappropriate matings do not diminish the future reproductive success of males as severely as it does that of females. In plants, prezygotic, post-pollination barriers against hybridization are of no benefit to the pollinating parent, but they may prevent the wastage of ovules.

Ordinarily one might expect the evolution of such barriers against hybrid fertilization to arise in both of two incipient species subject to potential hybridization. If there is a great disparity in population size between the two incipient species, however, the intensity of natural selection for prezygotic mating barriers will be correspondingly asymmetric, and only the smaller of the two populations may evolve such a defense.

Consider two parapatric (i.e., contiguous or slightly overlapping) incipient species of population sizes A and a respectively, where A is much greater than a . Such a situation must occur most often when the larger population is a widespread, ancestral species and the second, smaller population is a peripheral isolate derived from the first. Suppose that each population is well adapted to its particular habitat, and/or has developed a coadapted gene complex such that hybrids between the two have a reduced fitness by amount s . Suppose furthermore that potential gene flow between the two is reciprocal, so that in each generation an absolute number m of potential fertilizations involve microgametes of the first population and megagametes of the second, and also an absolute number m of potential fertilizations involve the reciprocal combination. The absolute wastage of female gametes suffered by each of the two populations, in the absence of mating barriers, is ms . However, the reduction in mean fitness in each population is proportional to the reciprocal of the population size: i.e., ms/A and ms/a in the two populations respectively. Thus the reduction in mean fitness due to hybridization is much greater in the smaller population.

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⁺Deceased, 1983. This is a less-than-final draft, dated late 1979, found among King's papers. The abstract and reference were supplied by the editor.

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Any tendency of the female to reject inappropriate male gametes (e.g., behavioral acceptance in animals or barriers to pollination or pollen-tube growth in plants) will be selected for in either population, if the mating barrier has no cost or deleterious effect; but the strength of selection will be greater in the smaller population. Specifically, a new allele that prevented a proportion b of inappropriate fertilizations would have a selective advantage of bms/A or bms/a in the two populations. If there is a physiological, developmental or behavioral cost associated with a given mating barrier, it may be selected for only in the smaller population. In other words, if the physiological disadvantage of the mating barrier allele were c , the net advantages in the two populations would be $bms/A - c$ and $bms/a - c$ respectively. The first of these terms might often be insignificant or even negative while the second is substantial and positive, because of the relatively greater effect of hybridization on the smaller population.

Thus we might explain the observation that mating barriers between large ancestral populations and smaller derived populations are often asymmetrical, such that females of the derived species more often reject males of the ancestral species than females of the ancestral species reject males of the derived. In plants, we might expect that hybridization in which the derived species is the pollinator would be more successful than those in which the derived species is the seed plant. Most derived incipient species are at least initially small relative to the ancestral group, and the evolution of mating barriers is most critical at this stage; the initial asymmetry of the mating barriers might often persist even when derived group has fully speciated and may have become numerous and widespread.

The differential survival of groups is also an important factor in the long-term evolution of barriers to gene exchange. The usual fate of incipient species, especially of those that arise as small, derived, peripheral isolates, is probably extinction or resorption into the parental population. In most cases mating barriers may not have arisen. The persistence of such isolates will certainly be enhanced by the presence of mating barriers, postzygotic as well as prezygotic, when they do occur. Thus at any one point in time the majority of extant isolates may display such barriers, while the parent populations may not. Similarly, past derived population isolates that have successfully evolved fertilization barriers against microgametes of the parental population are more likely to have survived and to have fully speciated than any that have not.

LITERATURE CITED

Wallace, A.R. 1889. Darwinism. London: Macmillan. 494 pp.

[Editor's note: King' MS had 1879 as the year, but I have found no such relevant publication and suspect it was a misprint. The asymmetry of selection calls to mind, from a different perspective, the compilospecies concept of Harlan and de Wet 1963, Evolution 17: 497-501.]

Comment by a Referee:

Though simplistic, this statement considers speciation in parapatric populations of unequal size. What Dr. King predicted regarding the behavior of ancestral versus derived populations is unlike that of Kanishiro (1980: see Giddings and Templeton, 1983), but like that of Watanabe and Kawanishi (1979). I believe both viewpoints are likely to prove more often incorrect than "documentable," and that reproductive isolating mechanisms largely evolve, at least initially, as byproducts of selection -- of assorted types - for other entities. Speciation, after all, need not involve discrete founder events (as Dr. King did indeed note).

Giddings, L. and A. Templeton. 1983. Behavioral phylogenies and the direction of evolution. Science 220: 3772-3778.

This article contains all requisite references though flawed in its conclusions.

Kanishiro, K.Y. Evolution 34, 437 (1980).

Watanabe, T.K. and M. Kawanishi. Science 205, 906 (1979).

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To continue this multilog, I do not find the theoretical arguments (e.g. Paterson 1978; S. Afr. J. Sci. 74: 369-371) against selection for pre-mating reproductive isolation to be persuasive. These predict the extinction of the smaller population. Dispersal into the overlap zone from the major populations outside can in principle, though, provide an indefinite influx of each "pure" species. Regulation of density, especially of the less common species, acts similarly when there is reproductive excess, as commonly occurs. These are qualitative arguments, so their domain of truth is not clear in relation to the other ecological and genetic influences, but I doubt that the domains are narrow. My experimental investigation of the general subject (1963, Heredity 18: 205-214) produced a third result, introgression. It is in any event unfortunate that geneticists so often ignore the ecology of the populations they study; as here, it may critically affect their own results.

- L.M. Van Valen

