



**FIGURE 21.19.** Alleles that are harmful to the individuals that carry them can nevertheless increase, provided that they benefit others who carry the same allele. In this example, the wild-type individuals (*black*) produce an average of one offspring each by their own efforts (*gray arrows*). Individuals that carry an “altruistic” allele (*red*) produce no offspring by their own efforts, but cause their immediate neighbors to produce an average of three extra offspring in total (*red arrows*). Thus, isolated “red” individuals (a) produce no offspring, but those in a cluster of the “altruist” alleles benefit (e.g., b): On average, the cluster of six individuals carrying the new allele produce 2.4 offspring each. Some wild-type individuals also benefit (e.g., c), but this does not directly affect the rate of increase of a rare “altruist” allele. In terms of Hamilton’s rule,  $C = 1$  (the reduction in number of offspring produced by the altruist’s own efforts),  $B = 3$  (the net increase in neighbors’ fitness), and so the allele will increase if at least  $R = 1/3$  of neighbors carry the “altruist” allele.