MODES OF SELECTION

FITNESS

INITIAL NUMBERS

LATER NUMBERS (AFTER SELECTION)

(a) Stabilizing selection (b) Directional selection (c) Disruptive selection
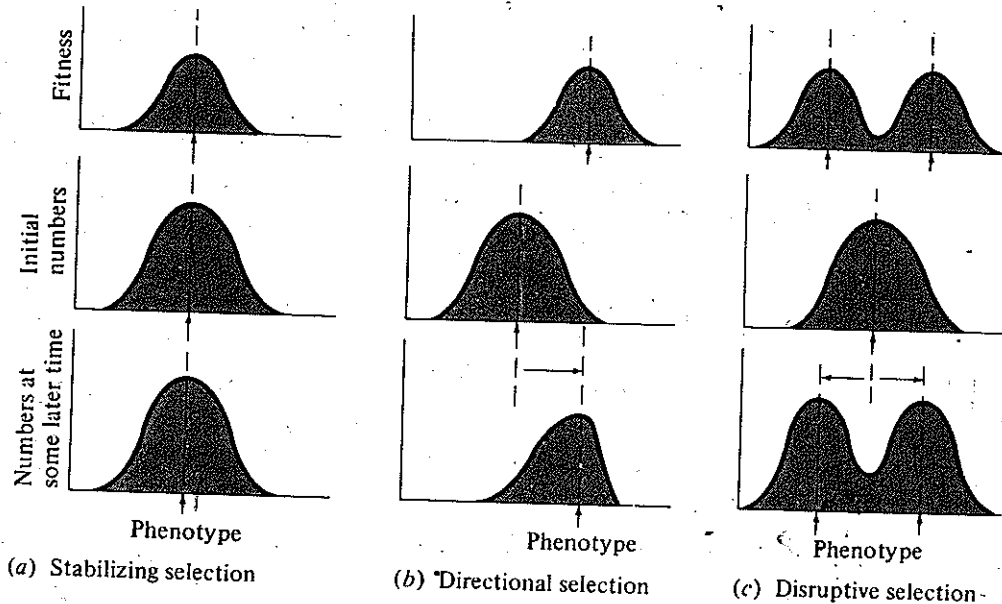
STABILIZING

DIRECTIONAL

DISRUPTIVE

BALANCING SELECTION

Distinguishing Features

1.)

2.)

3.)

Directional Selection

Figure 4.3
Directional selection by fishing on pink salmon, *Onchorhynchus gorbuscha*. The graph shows the decrease in size of pink salmon caught in two rivers in British Columbia since 1950. The decrease has been driven by selective fishing for the large individuals. Two lines are drawn for each river: one for the salmon caught in odd-numbered years, the other for even years. Salmon caught in odd years are consistently heavier, which is presumably related to the 2-year life cycle of the pink salmon.
(5 lb ≈ 2.2 kg.) From Ricker (1981). Redrawn with permission of the Minister of Supply and Services Canada, 1995.

Stabilizing selection

optimal weight infants

All infants
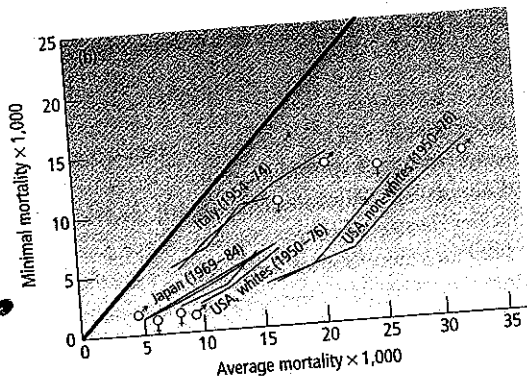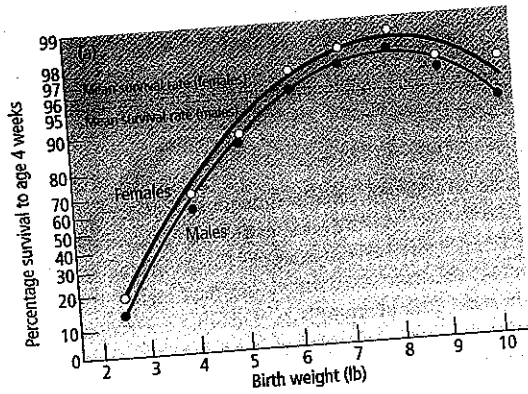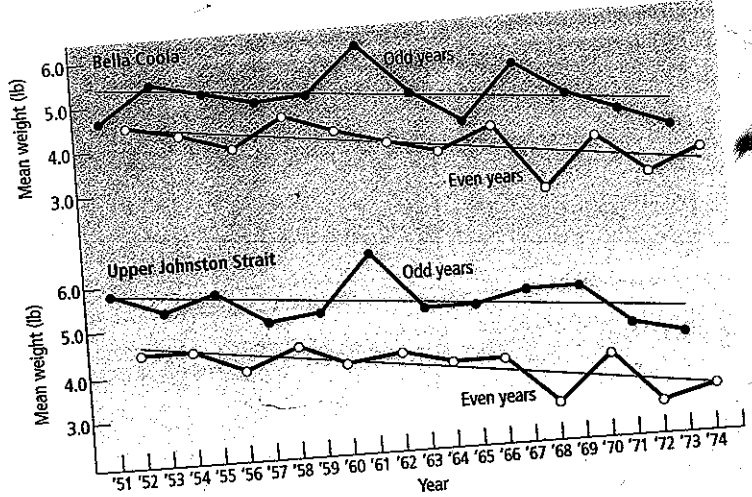
Figure 4.4
(a) The classic pattern of stabilizing selection on human birth weight. Infants weighing 8 lb (3.6 kg) at birth have a higher survival rate than heavier or lighter infants. The graph is based on 13,700 infants born in a hospital in London, UK, from 1935 to 1946. (b) Relaxation of stabilizing selection in wealthy countries in the second half of the twentieth century. The x-axis is the average mortality in a population; the y-axis is the mortality of infants that have the optimal birth weight in the population (and so the minimum mortality achieved in that population). In (a), for example, females have a minimum mortality of about 1.5% and an average mortality of about 4%. When the average equals the minimum, selection has ceased: this corresponds to the 45° line (the "no selection" case in Figure 4.2d would give a point on the 45° line.) Note the way in Italy, Japan, and the USA, they approach the 45° line through time. By the late 1980s the Italian population had reached a point not significantly different from the absence of selection. From Karn & Penrose (1951) and Ulizzi & Manzotti (1988). Redrawn with permission of Cambridge University Press.
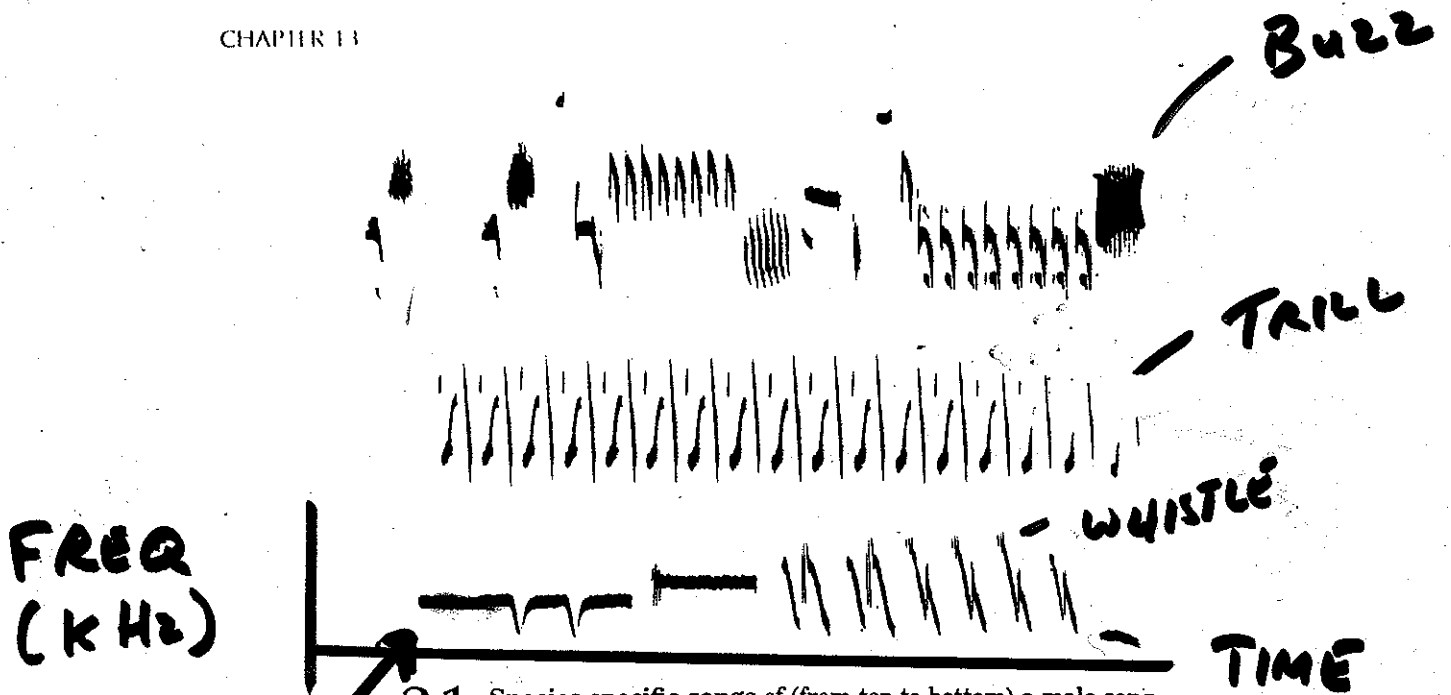
STABILIZING SELECTION

Ex: — CALL FREQUENCIES +
          SPECIES RECOGNITION

BUZZ

TRILL

WHISTLE

FREQ (kHz)

TIME

TONE

21 Species-specific songs of (from top to bottom) a male song sparrow, swamp sparrow, and white-crowned sparrow. Females of different sparrows can use their males' song to identify members of their own species and avoid mating with other species. Courtesy of Peter Marler.

# of Matings

B   A   C   ← SPECIES
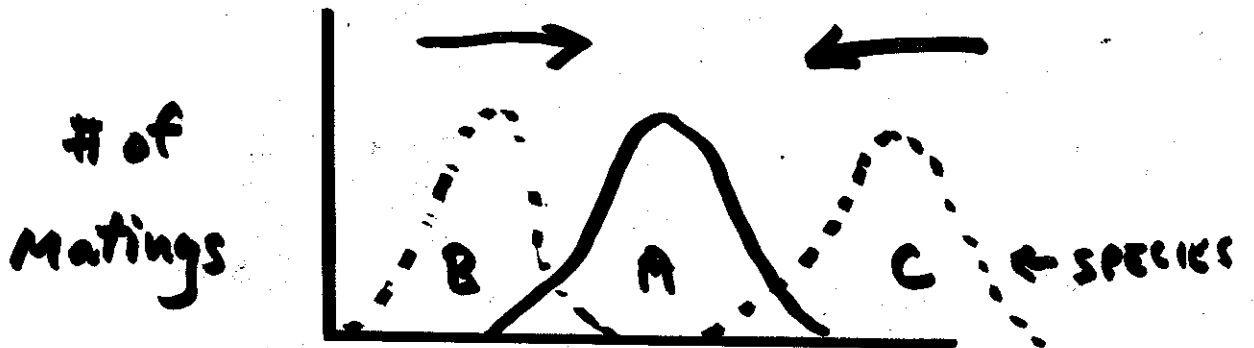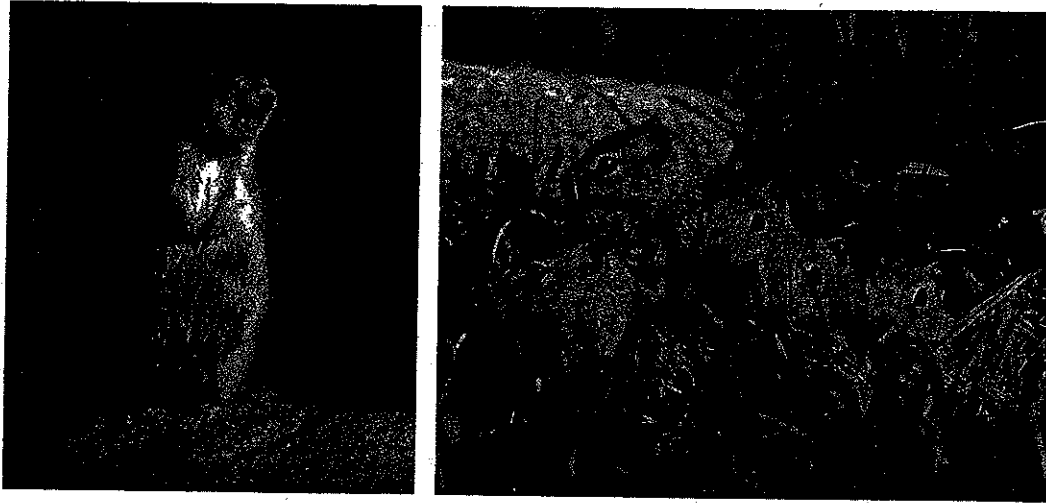
DOM. FREQ. OF MALES CALL

Fig. 11.1 Belding's ground squirrels. (a) Female giving an alarm call. (b) A group of pups at the mouth of a burrow. Photo by © George D. Lepp, Bio-Tech Images.
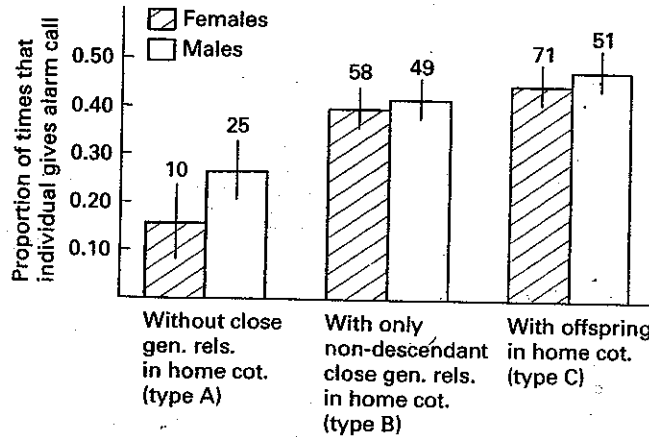
Descendant vs. Nondescendant kin

Fig. 11.2 Alarm calling by black-tailed prairie dogs to a stuffed badger. For both males (white histograms) and females (hatched), there are significant differences between type A and type B individuals and also between type A and type C. There was, however, no significant difference for either sex between type B and type C. Data are means ± 1 SE, with number of different individuals observed indicated. From Hoogland (1983).

A vs. B
A vs. C
───────────
B vs. C

How do animals bias behavior with respect to "r" [handwritten annotation]

Two mechanisms [handwritten annotation]

Female ground squirrels recognize kin partly by learning ...

that unrelated individuals reared together were no more aggressive to one another than true sibs reared together. This suggests, therefore, that individuals learn who are their kin from association in early life.

① *[handwritten]*

Experimental Data 2×2 Factorial Design [handwritten annotation]

(a)

② *[handwritten]*
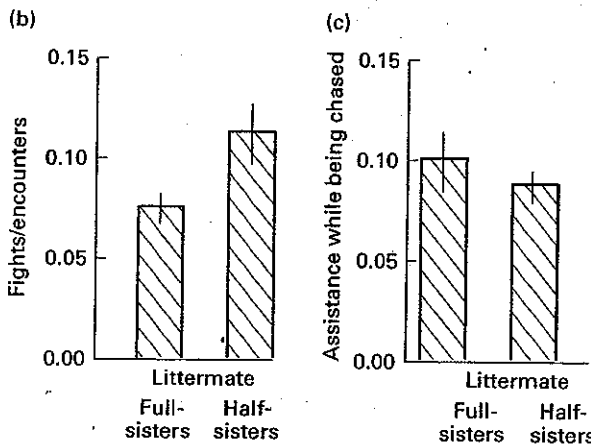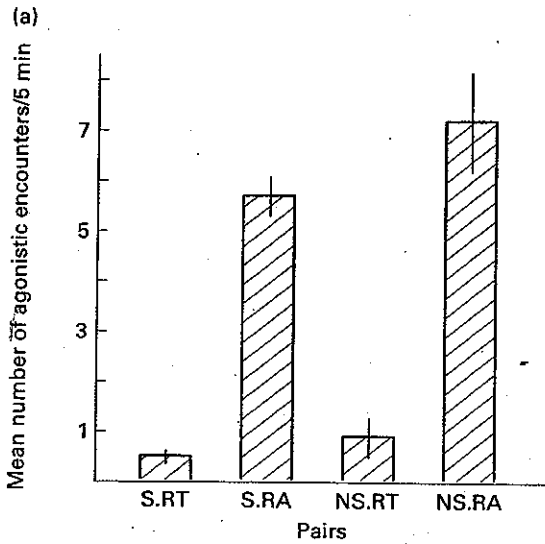
... and par 'phenotype

Observational Data [handwritten annotation]

(b)

(c)

Fig. 11.3 Kin recognition in Belding's ground squirrels. From Holmes and Sherman (1982). (a) Laboratory experiments: mean number (± 1 SE) of agonistic encounters between pairs of yearling Belding's ground squirrels in arena tests. Non-siblings reared together (NS.RT) are no more aggressive than siblings reared together (S.RT). However non-siblings reared apart (NS.RA) are more aggressive than siblings reared apart (S.RA). (b) and (c) Field observations: aggression and co-operation among yearling females which were full or half-sisters (genetic relatedness determined by blood proteins). Full sisters are less aggressive to one another (b), and assist each other more (c).

Evolution of Cooperation Among Non Relative [handwritten]

Unrelated vampire bats feed each other on a reciprocal basis

evaluation [handwritten]

Iteration [handwritten]

B > C [handwritten]

close relatives or between unrelated individuals who were frequent roost-mates. For reciprocity to evolve, the following conditions are needed.

1 *Donors must be able to recognize cheats, and refuse to feed previous recipients who fail to reciprocate.* Wilkinson performed some clever experiments in the laboratory where he formed a group of bats, some individuals (all unrelated) coming from one roost and others (also unrelated) from another roost. In a series of trials, one bat, chosen at random, was removed and kept hungry while all the others had access to blood. The hungry bat was then reintroduced. It was found that 12 of the 13 regurgitations occurred between individuals from the same roost in the field, in other words individuals which were familiar with each other. Furthermore, the starved bats which received blood later reciprocated the donation significantly more often than expected had the exchanges occurred randomly.

2 *Sufficient repeated pairwise interactions so that there are interchanges of roles and therefore net benefits to all donors.* In the field it was found that some unrelated individuals were constant companions in the roosts, sometimes for several years.

3 *The benefit of receiving aid must outweigh the cost of donating it* ($R > S$ in Table 11.4). Figure 11.4 shows that the bats lost weight with increasing time since their last meal. The decelerating curve means that a donation of a small amount of blood by a well-fed individual results in little cost in terms of time moved along the bottom axis towards the threshold of death. However
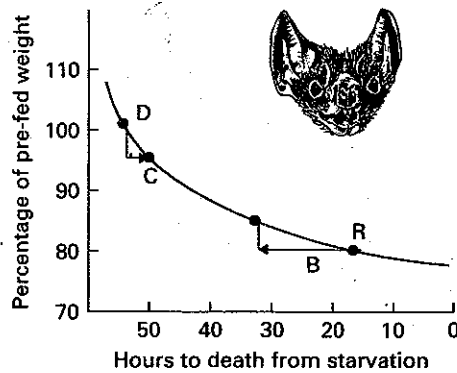

Fig. 11.4 In vampire bats, weight loss after feeding follows a negative exponential decline, with death from starvation occurring at 75 per cent of pre-fed weight at dusk. Therefore a donation of 5 per cent of pre-fed weight when at weight D should cause a donor to lose C hours but will provide B hours to a recipient at weight R. From Wilkinson (1984).

DIRECTIONAL SELECTION

- expt with widow birds
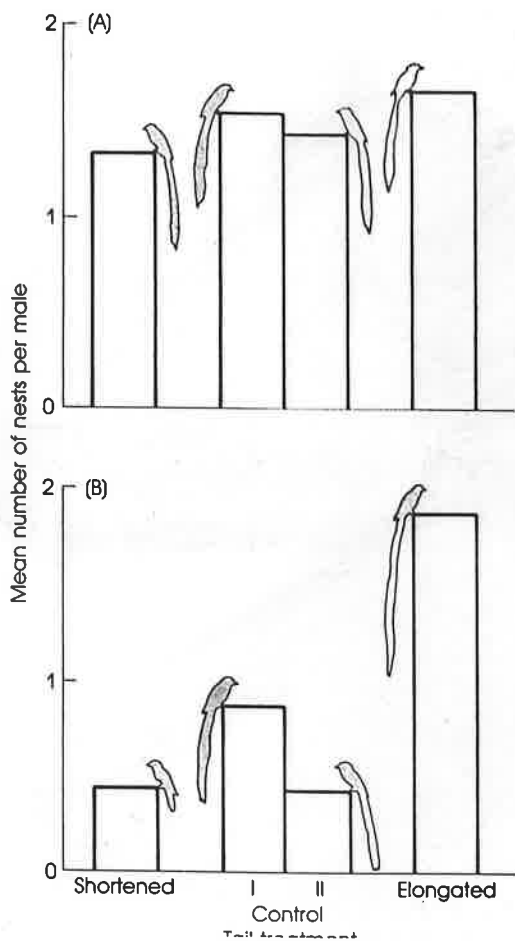
30 Female preference for long-tailed males in the widowbird. (A) The mean number of nests in a territory was the same for four groups of nine males prior to the tail alteration treatment. (The numbers at the base of the bars are the values for individual males.) (B) After the experimental treatments were performed, more nesting females were found in the territories of male widowbirds whose tails had been experimentally lengthened than in the territories of birds whose tail length was shortened or left unchanged. *Source:* Andersson [17].

Disruptive Selection

DISRUPTIVE SELECTION

'Adaptive Landscape'
or
"Fitness Landscape"

Figure 4.5
Disruptive selection in the seedcracking finch *Pyrenestes ostrinus*. (a) Beak size is not distributed in the form of a bell curve; it has large and small forms, but with some blurring between them. The bimodal distribution is only found for beak size. (b) General body size, such as measured by tail size, shows a classic normal distribution. The distributions shown are for males. (c) Fitness shows twin peaks. Notice that the peaks and valleys correspond to the peaks and valleys in the frequency distribution in (a). Fitness was measured by the survival of marked juveniles over the 1983–90 period. Performance was measured as the inverse of the time to crack seeds. (1 in ≈ 25 mm.) Modified from Smith & Girman (2000).
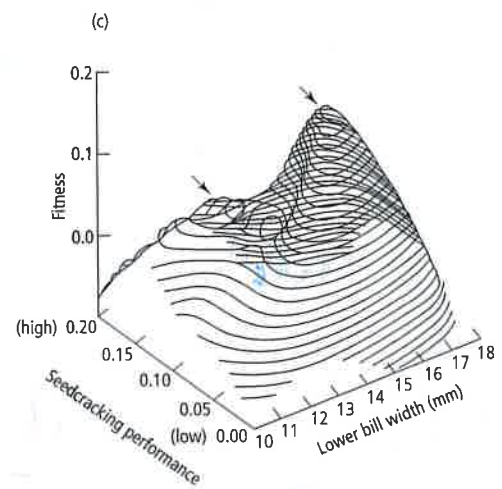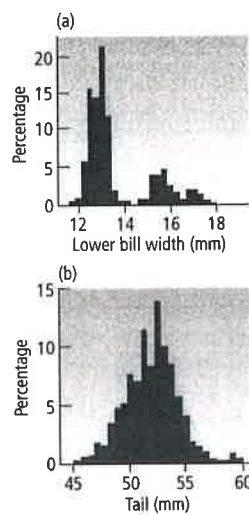
... or disruptive

deliveries (the main cause of lighter babies) and increased frequencies of Cesarian deliveries for babies that are large relative to the mother (the lower survival of heavier babies was mainly due to injury to the baby or the mother during birth). By the 1990s in wealthy countries, the stabilizing selection that had been operating on human birth weight for over a million years had all but disappeared.

The third type of natural selection occurs when both extremes are favored relative to the intermediate types. This is called *disruptive* selection (Figure 4.2c). T.B. Smith has described an example in the African finch *Pyrenestes ostrinus*, informally called the black-bellied seedcracker (Smith & Girman 2000) (see Plate 2, between pp. 68 and 69). The birds are found through much of Central Africa, and specialize on eating sedge seeds. Most populations contain large and small forms that are found in both males and females; this is not an example of sexual dimorphism. As Figure 4.5a illustrates, this is a case in which the character is not clearly either discretely or continuously distributed. The categories of discrete and continuous variation blur into each other, and the beaks of these finches are in the blurry zone. We shall look more at the meaning of continuous variation in Chapter 9, but here we are using the example only to illustrate disruptive selection and it does not much matter whether Figure 4.5a is called discrete or continuous variation.

Several species of sedge occupy the finch's environment, and the sedge seeds vary in how hard they are to crack open. Smith measured how long it took a finch to crack open a seed, depending on the finch's beak size. He also measured fitness, depending on beak size, over a 7-year period. Figure 4.5c summarizes the results and shows two fitness peaks. The twin peaks primarily exist because there are two main species of sedge. One sedge species produces hard seeds, and large finches specialize on it; the other sedge species produces soft seeds and the smaller finches specialize on it. In an evironment with a bimodal resource distribution, natural selection drives the finch population to have a bimodal distribution of beak sizes. Natural selection is then dis-