

## Spite

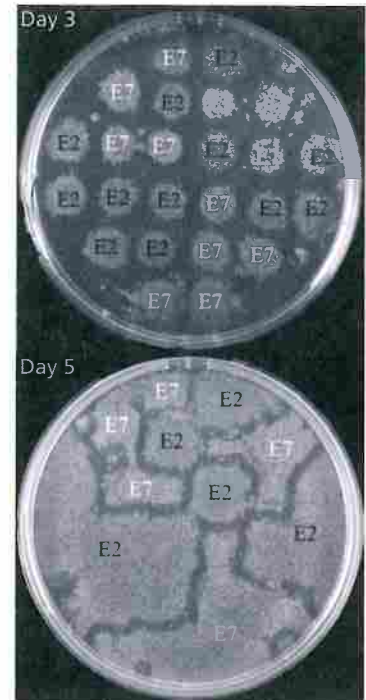
Most bacteria make proteins, called bacteriocins, that are lethal to other members of the same species (Riley and Wertz 2002; Riley et al. 2003). The makers of a given bacteriocin are either immune to their own poison because they lack the poison's molecular target or resistant because they make an antidote. **Figure 12.6** shows a nutrient plate seeded with *E. coli* from two strains (Majeed et al. 2011). One strain makes a bacteriocin called colicin E2; the other makes colicin E7. Note that by day 5, many E2 colonies have merged, as have many E7 colonies. Blocks of E2 versus E7, however, are separated by bacteria-free bands. Any bacterial cell straying into these border zones is killed by the other strain's toxin.

Because bacteriocins require energy and materials to make, strains that produce them grow somewhat more slowly than otherwise identical strains that do not (Inglis et al. 2011). Furthermore, many strains that make bacteriocins release the toxins by rupturing their cell walls and spilling their contents to the outside (Riley and Wertz 2002; Morales-Soto and Forst 2011). By making and releasing bacteriocins, a bacterial cell therefore reduces its direct fitness. And because the weapons are lethal, a bacterial cell that constructs and deploys them reduces the direct fitness of susceptible recipient cells. Bacteriocin production thus meets our definition of spite (Gardner et al. 2004; West and Gardner 2010).

To investigate whether spiteful interactions among bacteria occur in nature, Hadas Hawlena and colleagues (2010) isolated 36 strains of the bacterium *Xenorhabdus bovienii* from two soil samples taken from an Illinois forest. *X. bovienii* is a lethal insect pathogen transmitted by nematode worms. The first 18 strains came from the first soil sample, while the remaining 18 strains came from the second sample. The locations of the two samples were separated by a distance of just four meters. Hawlena and colleagues tried all 1,260 pairwise combinations in which one bacterial strain served as actor (bacteriocin donor) and a different strain served as recipient (bacteriocin recipient). For each trial, the researchers induced cells of the actor strain to make bacteriocins, prepared a cell-free extract of their contents, and tested its ability to inhibit the growth of the recipient strain.

**Figure 12.7** summarizes the remarkably consistent results. No strain inhibited any other strain from its own soil sample. And every strain from each sample inhibited all the strains from the other sample. Additional tests supported the researchers' interpretation that the inhibition was due to bacteriocins. That naturally occurring *X. bovienii* can make costly poisons that are deadly to members of the same species living just a few meters away suggests that wild bacteria indeed behave spitefully toward each other.

Like altruism, the evolution of spite is difficult to understand. Heritable behaviors causing fitness loss for the actor should disappear from populations. However, bacteriocin production and other examples show that spite occurs (Gardner and West 2006; Gardner et al. 2007). In the next section, we see that one of the explanations biologists have developed to explain altruism can also explain spite.



**Figure 12.6** Two strains of *E. coli* that make mutually lethal bacteriocins From Majeed et al. (2011).

		Recipient	
		Sample 1 strain	Sample 2 strain
Actor	Sample 1 strain	No inhibition	Inhibition
	Sample 2 strain	Inhibition	No inhibition

**Figure 12.7** Mutual spite among naturally occurring bacterial strains found in soil samples collected just 4 meters apart After Hawlena et al. (2010).

## 12.2 Kin Selection and Costly Behavior

Altruism is a central paradox of Darwinism. An allele that results in behavior benefiting other individuals at the expense of the allele's bearer would seem destined for elimination by natural selection. Charles Darwin (1859, p. 236) viewed the apparent existence of altruism as a "special difficulty, which at first appeared to

me insuperable, and actually fatal to my whole theory.” But he glimpsed a resolution. Selection could favor traits that result in decreased direct fitness if they increase the survival and reproductive success of close relatives. This crucial insight had to wait over a hundred years to be formalized and widely applied.

### Inclusive Fitness

In 1964, William D. Hamilton devised a genetic model showing how an allele causing altruistic behavior can spread (Hamilton 1964a). His crucial insight was that an individual is seldom the sole repository of his or her genes. Copies occur in other individuals too, most predictably in kin. This means that the behavior of an individual toward others can influence the success of the actor’s genes. A key parameter in Hamilton’s model is the **relatedness**,  $r$ , of the actor and recipient. Biologists use somewhat different definitions of relatedness in different contexts, but by all definitions  $r$  is a measure of the genetic similarity between individuals.

Using his model, Hamilton derived a condition, called **Hamilton’s rule**, under which altruism will increase in frequency:

$$Br - C > 0$$

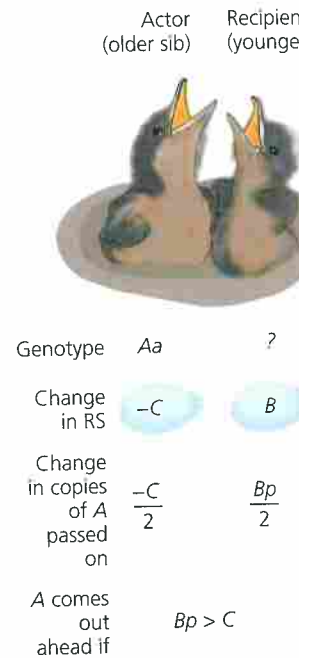
where  $B$  is the benefit to the recipient and  $C$  is the cost to the actor. Both  $B$  and  $C$  are measured in units of surviving offspring. This simple inequality indicates that altruism is more likely to spread when the benefits to the recipient are great, the cost to the actor is low, and the participants are closely related.

A simple derivation of Hamilton’s rule, from John Maynard Smith (1998), appears in **Figure 12.8**. Imagine a rare dominant allele,  $A$ , in a large randomly mating population of birds that always lays two eggs. Because the allele is rare, nearly all copies are in heterozygotes.  $A$ ’s only influence on phenotype, relative to  $a$ , is that when it finds itself in an older sibling,  $A$  causes its carrier to beg less aggressively for food the parents bring to the nest. This diminishes the older sibling’s prospects, ultimately reducing the number of eggs it can expect to produce over its lifetime by  $C$ . Because half the eggs lost would have carried a copy of  $A$ , the altruistic behavior reduces the number of copies transmitted by  $\frac{C}{2}$ . The younger sibling, however, is better fed. Its prospects rise, ultimately increasing the number of eggs it can expect to produce over its lifetime by  $B$ . This increases the number of copies of  $A$  transmitted by  $\frac{Bp}{2}$ , where  $p$  is the probability that allele  $A$  occurs in the younger sibling. Note that  $A$  has a net gain in copies transmitted if  $Bp > C$ .

To estimate  $p$ , note that because  $A$  is rare, it will occur in the younger sibling only if one or the other of the younger sibling’s gene copies is **identical by descent** to the copy of  $A$  in the older sibling. The probability that a gene copy sampled from one individual is identical by descent to a gene copy present in another individual is a commonly used definition of relatedness. A method for calculating relatedness this way is described in **Computing Consequences 12.1**.

The condition for  $A$  to increase in frequency is thus  $Br > C$ , which is Hamilton’s rule. If the birds are monogamous, so that the chicks in a clutch are always full sibs,  $r$  is  $\frac{1}{2}$ . The older chick will value the survival and reproduction of its sibling at half the worth of its own. If they are half-sibs,  $r$  is  $\frac{1}{4}$ . The older chick will value the fitness of its sibling at a quarter the worth of its own.

More general derivations of Hamilton’s rule—requiring fewer assumptions about, among other things, the number, frequency, and dominance of the genes involved—are possible (Grafen 1985; Gardner et al. 2011). The essence of all derivations is the inclusion of two components of an individual’s genetic



**Figure 12.8** A simple derivation of Hamilton’s rule text for explanation. RS is reproductive success. After Mayr Smith (1998).

Personally costly behavior evolve if the benefit to kin is sufficiently high.



## COMPUTING CONSEQUENCES 12.1

## Calculating relatedness as the probability of identity by descent

Calculating the probability of identity by descent requires a pedigree including the actor and the recipient. Starting with the actor, all genealogical paths are traced through the pedigree to the recipient. For example, half-siblings share one parent and have one genealogical path with two steps, as shown in **Figure 12.9a**. Parents give half their genes to each offspring, so the probability that genes are identical by descent in each step is  $\frac{1}{2}$ . Put another way, the probability that a particular allele was passed from parent to actor is  $\frac{1}{2}$ . The probability that the same allele was transmitted from parent to recipient is  $\frac{1}{2}$ . The probability that this same allele was transmitted to both the actor and the recipient (making the alleles in actor and recipient identical by descent) is the product of these two independent probabilities, or  $\frac{1}{4}$ .

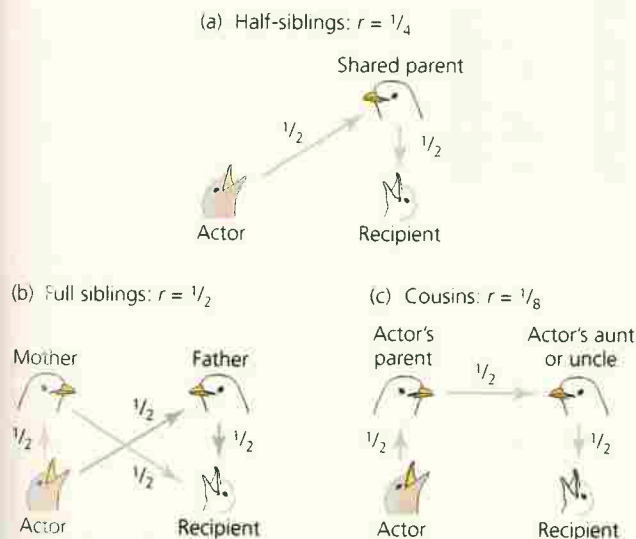
Full siblings, on the other hand, share genes inherited from both parents. To calculate relatedness when actor and recipient are full siblings, we have to add the probabilities that genes are identical by descent through each genealogical path in the pedigree. In this case, we add the probability that genes are identical by descent through the mother to the probability that they are identical by descent through the father (see **Figure 12.9b**). This is  $\frac{1}{4} + \frac{1}{4} = \frac{1}{2}$ .

Using this method gives the following coefficients:

- First cousins,  $\frac{1}{8}$  (**Figure 12.9c**)
- Parent to offspring,  $\frac{1}{2}$
- Grandparent to grandchild,  $\frac{1}{4}$
- Aunt or uncle to niece or nephew,  $\frac{1}{4}$

The analyses we have just performed work for autosomal loci in sexual organisms and assume that no inbreeding has occurred. If the population is inbred, then the probabilities will be higher. But when studying populations in the field, investigators usually have no data on inbreeding and have to assume that individuals are completely outbred. On this basis, estimates of relatedness that are reported in the literature should be considered minimum estimates. Another uncertainty in calculating relatedness comes in assigning paternity in pedigrees. As we indicated elsewhere (**Chapter 10**), extrapair copulations are common in many species. If paternity is assigned on the basis of male–female pairing relationships and extrapair copulations go undetected, estimates of relatedness may be inflated.

When constructing genealogies is impractical, relatedness can be estimated from genetic data (Queller and Goodnight 1989). Microsatellites and other marker loci have proven useful for estimating relatedness in a wide variety of social insects (e.g., Peters et al. 1999).



**Figure 12.9** Computing relatedness with pedigrees

The arrows describe paths by which genes can be identical by descent. After Trivers (1985).

contribution to future generations. **Direct fitness** results from reproduction an individual achieves on its own, without help from related individuals. **Indirect fitness** results from additional reproduction by relatives that is made possible by the individual's actions. The sum of its direct and indirect fitness is an individual's **inclusive fitness** (West et al. 2007b). Natural selection leading to the spread of alleles that increase the indirect component of fitness is called **kin selection**.

**Fitness** has both direct and indirect components. **Inclusive fitness** is the sum of both.

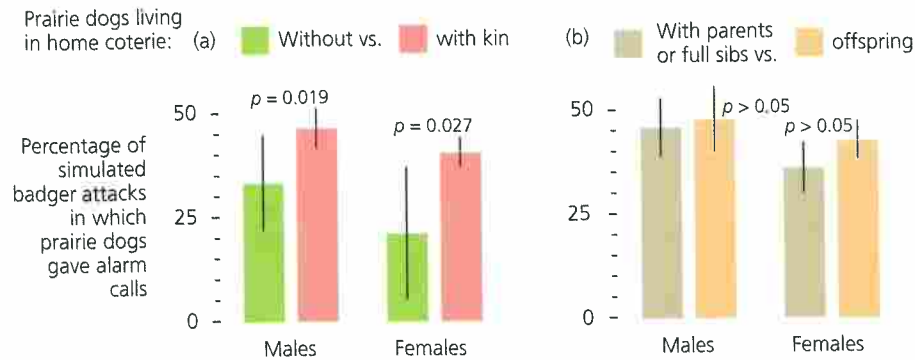
## Alarm Calling in Black-Tailed Prairie Dogs

To see the power of kin selection in explaining the evolution of altruism, we go first to the Black Hills of South Dakota, where John Hoogland (1983, 1994, 1995) studied black-tailed prairie dogs (*Cynomys ludovicianus*). Prairie dogs are large squirrels that live in family groups called coteries. Each coterie holds a territory within a prairie dog town. Females typically remain in their birth coterie for life, whereas males disperse at maturity. Prairie dogs are prey to badgers, bobcats, coyotes, eagles, and falcons, and spend as much as half of their aboveground time standing watch. When it spies a predator, a prairie dog often sounds the alarm with the high-pitched bark that gave the species its common name (Figure 12.10).

Despite logging over 50,000 person-hours watching individually marked prairie dogs in a town in South Dakota, Hoogland and his assistants were unable to document for certain whether prairie dog alarms are selfish or altruistic. Hoogland suspected that they are altruistic, however, and sought to determine whether the prairie dogs' calling behavior was consistent with the hypothesis that it evolved as a result of kin selection. Hoogland simulated predator attacks by having an assistant pull a stuffed badger through a prairie dog town on a sled while watching to see who gave alarm calls and who just dove for cover.



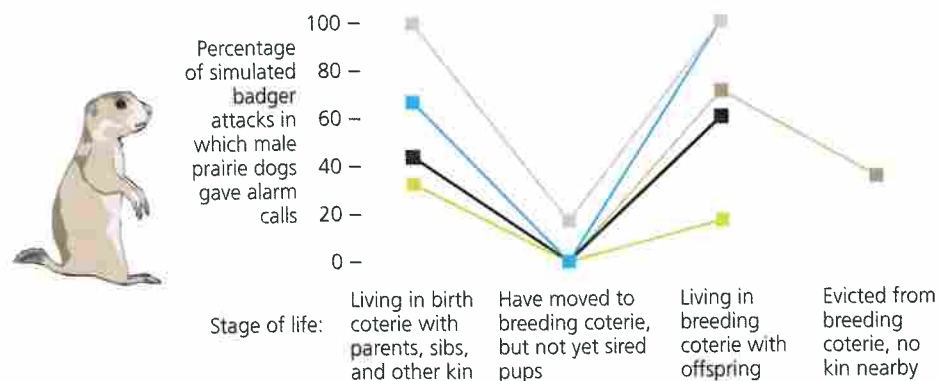
**Figure 12.10** A black-tailed prairie dog barks an alarm



**Figure 12.11** Black-tailed prairie dogs give alarms under circumstances predicted by kin selection theory (a) Rates of alarm calling by prairie dogs without versus with kin nearby (b) Rates of alarm calling by males and females living with non-offspring kin versus offspring. Redrawn from Hoogland (1995).

Both male and female prairie dogs are more likely to give alarm calls if their coterie includes genetic kin (Figure 12.11a). These calls are not simply a form of parental care: Individuals give calls nearly as often when the kin they live with are parents and siblings as when they are offspring (Figure 12.11b). Hoogland was even able to follow individual males across different stages of life, and saw them modify their rate of calling with changes in their proximity to kin (Figure 12.12).

Hoogland's data show that apparently altruistic alarm calls are not dispensed randomly. They are nepotistic. Self-sacrifice is directed at close relatives and thus



**Figure 12.12** Male black-tailed prairie dogs change their alarm-calling behavior when their living situation changes. This graph plots the rate of alarm calling by five individual males at different stages of life. The males increased or decreased their rate of calling according to whether kin was nearby. Redrawn from Hoogland (1995).

Prairie dogs are more likely to give alarm calls when close relatives are nearby.

should result in indirect fitness gains. We turn next to a study in which researchers were able to quantify the costs, benefits, and indirect fitness gains more precisely.

### Measuring Costs and Benefits for Adoptive Mother Squirrels

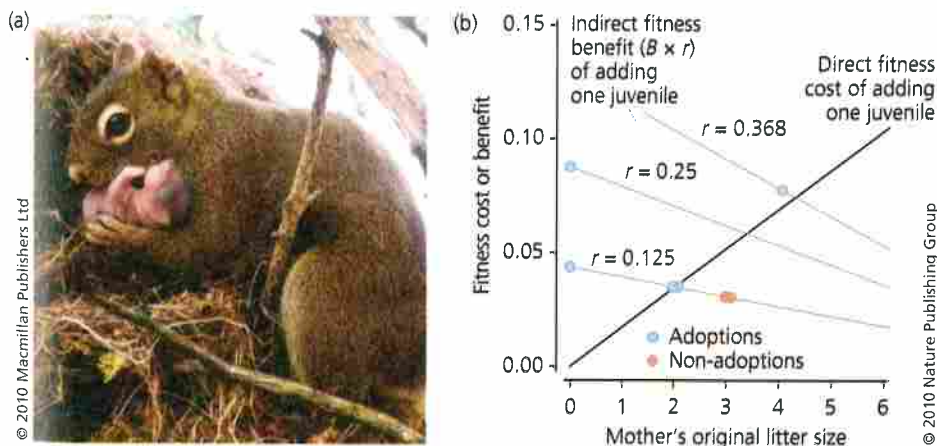
Stan Boutin and colleagues have followed a population of North American red squirrels (*Tamiasciurus hudsonicus*) near Kluane Lake, Canada, since 1987 (Boutin et al. 2006; McAdam et al. 2007). Each squirrel defends a feeding territory that, except when mothers are caring for kittens, it occupies alone. During spring and summer the researchers livetrapped and tag the squirrels, monitor reproduction by the females, and track the growth and survival of their litters. From 1989 through 2008, the scientists gathered data on the survival and reproductive success of 6,793 juveniles from 2,230 litters birthed by 1,101 mothers (Gorrell et al. 2010).

This sample includes 34 litters orphaned during lactation, from which a kitten could have been adopted and nursed to weaning by one or more lactating females nearby (Figure 12.13a). For seven of the litters, a genetic relative was among the available adoptive mothers. A kitten was adopted from five of these litters, always by the relative. For the other 27 litters, there were no relatives among the available adoptive mothers. No kittens were adopted from any of these. The association between kinship and adoption is consistent with Hamilton's rule. But the data allow a deeper look at why some related females adopted and others did not.

Because they knew how the size of a litter affects the probability that any given kitten will survive, Jamieson Gorrell and colleagues (2010) could estimate the direct fitness cost to a potential adoptive mother of adding a kitten to her litter. This cost is shown by the black line in Figure 12.13b. Adding a kitten reduces the chance that each of her existing offspring will survive (Humphries and Boutin 2000), so the mother's direct fitness cost increases with her original litter size.

And because Gorrell and colleagues had maternal genealogies for all the squirrels in their population—and some data from genetic tests—they were able to estimate the indirect fitness benefit to a potential adoptive mother of caring for a related kitten. This indirect benefit, shown by the gray lines in Figure 12.13b, is the probability that the adopted kitten will survive, which falls as a function of litter size, multiplied by the relatedness between the kitten and the mother. The figure includes three lines that cover the estimated values of  $r$  for each of the seven litters that might have been adopted by a relative. In five cases,  $r$  was at least 0.125, equivalent to the relationship between first cousins. In one case,  $r$  was at least 0.25, equivalent to half-siblings. In the remaining case,  $r$  was 0.368.

Female red squirrels adopt related kittens when the result is a net gain in the mother's inclusive fitness.



**Figure 12.13 Inclusive fitness and adoption in red squirrels**

(a) A female red squirrel moving a juvenile from one nest to another.

(b) Estimates of terms in Hamilton's rule for five adoptions and two non-adoptions by kin. From Gorrell et al. (2010).

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