My Brother's Keeper: A Case Study in Evolutionary Biology and Animal Behavior

by
Kari Benson
School of Sciences
Lynchburg College, Lynchburg, VA

Part I—Hypothesis Development

Belding's ground squirrels (*Spermophilus beldingi*) are diurnal rodents. They live in sub-alpine meadows in the far Western United States. Due to the extreme weather, the squirrels hibernate for seven or eight months of the year. The squirrels must enter hibernation with sufficient fat stores to survive this long hibernation. They spend their short active period by initially mating, then eating large quantities of food. They are primarily herbivorous, eating mostly seeds, flowers, and vegetation.

Adult females mate shortly after they emerge from hibernation. After mating, some males disperse to new groups and the others often return to hibernation before the young are born. The females establish territories within the social group and have between three and six pups. The pups emerge from their burrows when three to six weeks old and the juvenile males disperse (leave to join new groups) shortly after. The females typically remain in their natal (birth) group for life.

Paul Sherman (1977) studied Belding's ground squirrel behavior. The squirrels are subject to many dangers. Predators include coyotes, weasels, and raptors. Often, if a squirrel spots a predator, they will stand up on their hind feet and call out an alarm. When others hear the alarm, they quickly retreat to their burrows. Not all squirrels are equally likely to call.

Question

1. Generate some hypotheses to explain why the squirrels call.

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Part II—Alternative Hypotheses and Predictions

What predictions do you have about the frequency of alarm calling for the hypotheses you generated in Part I?

Hypotheses	**Predictions**				
Why do the squirrels call?	**Who benefits?**	**When do they benefit?**	**Should all individuals call?**	**Group/predator response to call?**	**Immediate effect on caller?**

Question

1. How can we discriminate between these competing hypotheses?

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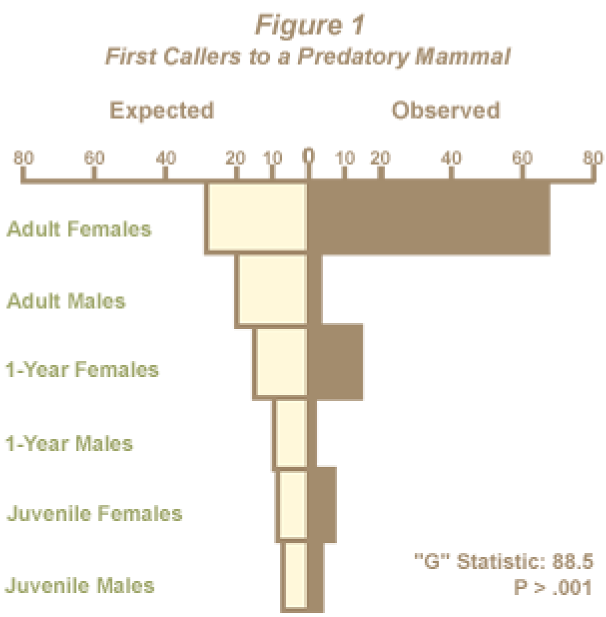
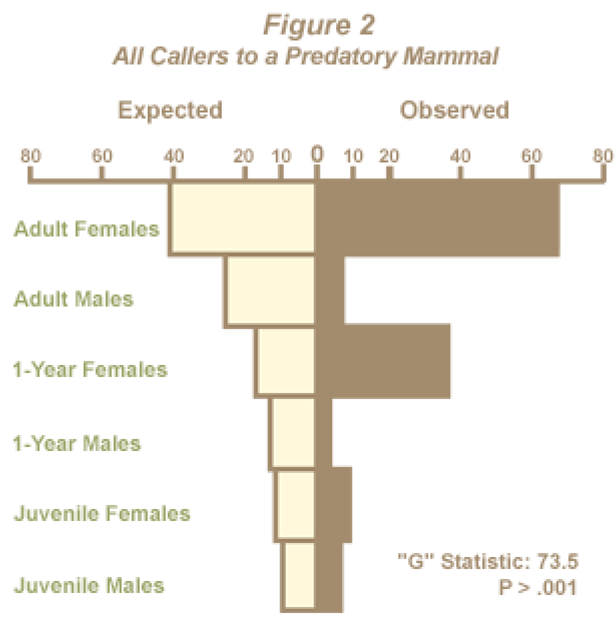
Part III—Experimental Results

Not all squirrels call equally. See the following figures.





Figures represent expected vs. observed frequencies of alarm calls across classes of Belding's ground squirrels drawn from 102 interactions with predators. Adapted from Sherman 1977.

Question

1. What conclusions can you draw from these data?

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Part IV—Sherman's Conclusions

Females call disproportionately more often than predicted by their abundance. Adult females call more often than one-years or juveniles. Males call disproportionately less than predicted by their abundance.

Questions

1. Why might this be?
2. Advanced Questions:
    1. How do these data compare to your predictions?
    2. Why would females call more than males?
    3. How should the proximity of relatives influence whether it is cost-effective to call?
3. Consider the following additional information: females call more readily when they are close to other related individuals. Does this provide further support for the kin selection hypothesis?

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Part V—Kin Recognition Mechanism

The kin selection hypothesis requires that individuals can recognize kin. Sherman's data demonstrate that females are more likely to call when there are kin nearby.

Questions

1. How might individuals recognize kin?
2. Can you provide some ways of testing whether a particular modality (call, smell, taste, etc.) is important in kin recognition?

Image Credit: Photo by Dr. Gwen Bachman, School of Biological Sciences, University of Nebraska-Lincoln. Used with permission. To learn more about Dr. Bachman's research with Belding's ground squirrels, see http://bsweb.unl.edu/emb/bachman/index.html.

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Part VI—Other Squirrels

There is another species of ground squirrel whose males behave differently (Dunford 1977). In this species (*Spermophilus tereticaudus*), males are more likely to alarm call before they leave their natal site, but remain silent after they disperse.

Questions

1. Do these data support your current hypotheses about calling?
2. What predictions would you make if females dispersed and males remained in natal groups?
3. What predictions would you make if neither sex dispersed?
4. Why is it that one sex disperses from each of these groups?

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Part VII—Economics of Kin Selection

Hamilton (1964) proposed a mathematical means of interpreting whether individuals should help kin. The economic analysis incorporates several aspects of the situation.

First, the decision requires that you can recognize (in some way) who is related to you, and (ideally) by how much. In this case, Hamilton measures the percent of DNA that you would share with someone by common descent, which he calls relatedness (*r*). For example, you would share half of your genes with a parent by common descent. Thus, you would have a relatedness of 0.5 with either parent or with a full sibling; you would have a relatedness of 0.25 with a half sibling or a grandchild; and you would have a relatedness of 0.125 with a cousin. (This is why the biologist J. B. S. Haldane purportedly stated that he would die for two of his brothers or eight of his cousins.)

You will need to know the relatedness between the donor and the recipient ($r_{recipient}$) and the relatedness between the donor and their offspring ($r_{offspring}$). Note that ($r_{offspring} = 0.5$) in typical diploid organisms.

Second, you have to know what it will cost you to help. For simplicity, Hamilton measured cost as the number of offspring (corrected for the relatedness) that you won’t have because you helped someone else. This is the cost of helping (*c*).

Third, you have to know how many more offspring your kin can have because you helped; this is the benefit of helping (*b*).

It is adaptive to help if:

$$\frac{B}{C} > \frac{r_{offpsring}}{r_{recipient}}$$

Thus, you can determine for a number of circumstances whether you should help your relative or not.

Example

You share a relatedness of 0.5 with your offspring and the same ($r_{offspring} = 0.5$) with a full sibling (one with whom you share a father and mother). If you can help some nephews, then $r_{recipient} = 0.25$. The benefit in the form of nephews must be greater than twice the cost to your own offspring to be adaptive. That is, for every offspring you cannot have due to helping (this is the cost or *C*), anything more than an additional two nephews (this is the benefit or *B*) would satisfy the inequality. For example, this condition would be satisfied if $B = 2.5$ and $C = 1$.

Example *continued*

Written mathematically, this would look like the following:

$$\frac{2.5}{1} > \frac{0.5}{0.25}$$

This expression is correct. The left hand part of the equation equals 2.5. The right hand part of the equation equals 2. The left exceeds the right, so helping is adaptive through kin selection.

Questions

1. Suppose there were a car wreck and you could only save one person, your best friend or your sibling. Whom would you save?

2. How many siblings would you have to save if helping forced you to give up one child?

3. How many nephews or nieces would you have to help if helping forced you to give up three children?

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Part VIII—Applied Kin Selection

Many recent articles demonstrate that decreased parental attention and increased child abuse are more common in step-children than for offspring that are genetically related to both caregivers (Tobby and Cosmides 1989, Emlen 1997, and Hofferth and Anderson 2001).

Question

1. How does kin selection explain these data?

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