Box 9.2 Calculating phylogenetically independent contrasts

Here we use an example from Garland and Adoph (1994) to illustrate the calculation of independent contrasts from a phylogeny (see also: Felsenstein 1985; Martins and Garland 1991; Garland et al. 1999). Figure 9.15 shows the phylogeny we will use. It shows the relationships among polar bears, grizzly bears, and black bears, and gives the body mass and home range of each. We will calculate independent contrasts for both traits among the bears. The steps are as follows:

1. Calculate the contrasts for pairs of sibling species at the tips of the phylogeny. In our three-species tree, there is just one pair of sibling species in which both species reside at the tips: polar bears and grizzly bears. The polar bear–grizzly bear contrast for body mass is:

$$265 - 251 = 14$$

The polar bear–grizzly bear contrast for home range is:

$$116 - 83 = 33$$

2. Prune each contrasted pair from the tree, and estimate the trait values for their common ancestor by taking the weighted average of the descendants' phenotypes. When calculating the weighted average, weight each species by the reciprocal of the branch length leading to it from the common ancestor. In our example, we are pruning polar bears and grizzlies from the tree and estimating the body mass and home range of their common ancestor A. The branch lengths from A to its descendants are both two units long. Thus, the weighted average for body mass is:

$$\text{Body mass of species A} = \frac{\left(\frac{1}{2}\right)265 + \left(\frac{1}{2}\right)251}{\left(\frac{1}{2}\right) + \left(\frac{1}{2}\right)} = 258$$

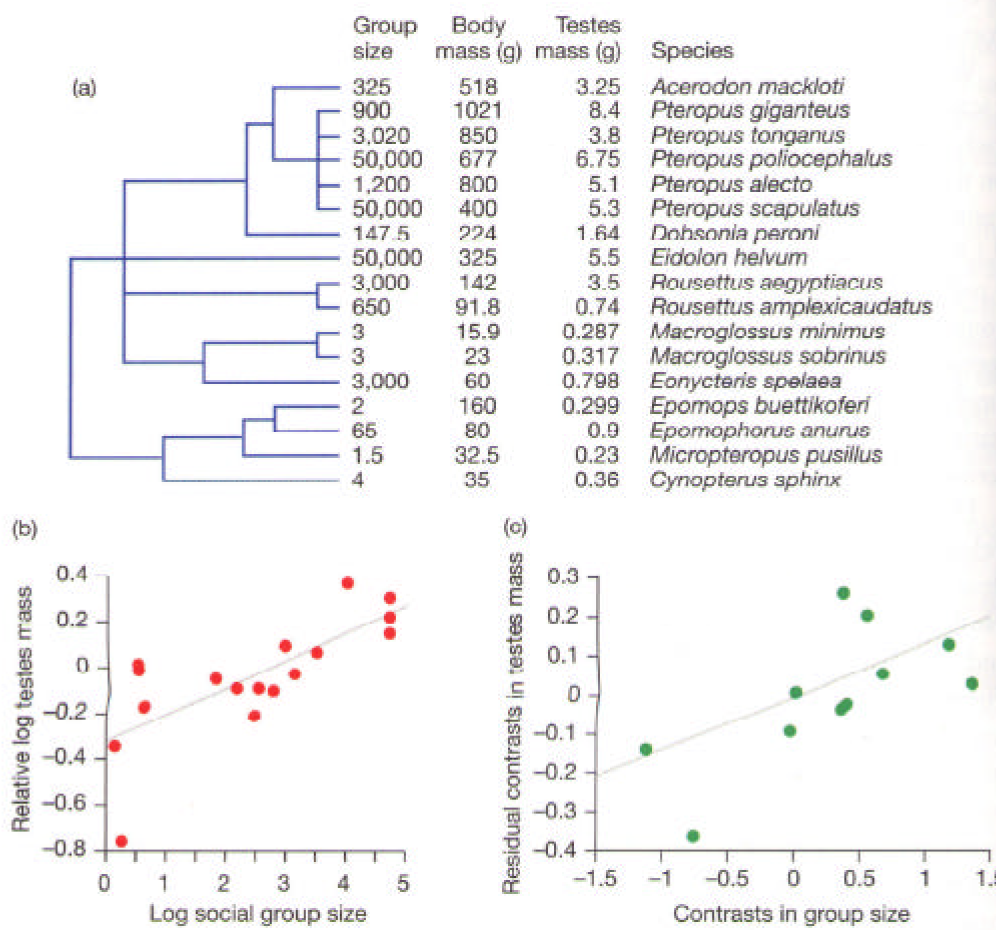
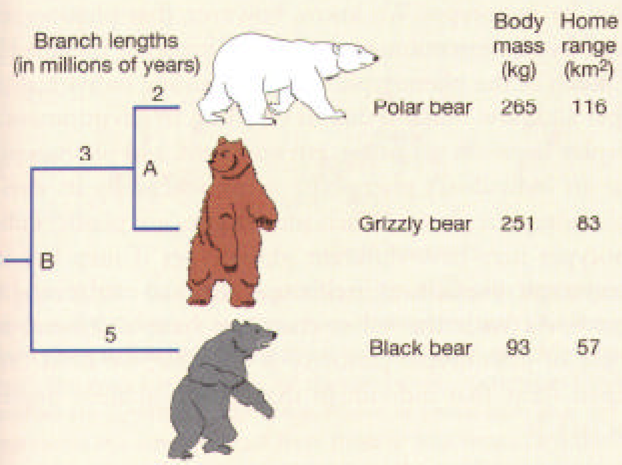


Figure 9.14 Correlated evolution of group size and testes size in fruit bats and flying foxes (a) A phylogeny for 17 species of bats, showing roost group size, body mass, and testes mass for each species. (b) The correlation between relative testes size and roost group size among the 17 species shown in the phylogeny, uncorrected for the influence of phylogenetic history. (c) Independent contrasts for relative testes size versus group size. The points on this graph show that when a bat species evolved larger (or smaller) group sizes than its sister species, it also tended to evolve larger (or smaller) testes ($P = 0.027$). From Hosken (1998).

Box 9.2 (Continued)



Contrast	Value for body mass	Standard deviation	Standardized contrast
Polar – Grizzly	265 – 251 = 14	2	7
A - Black bear	258 – 93 = 165	3	55

Contrast	Value for home range	Standard deviation	Standardized contrast
Polar – Grizzly	116 – 83 = 33	2	16.5
A - Black bear	99.5 – 57 = 42.5	3	14.17

Figure 9.15 An example showing how the data are adjusted when calculating phylogenetically independent contrasts From Garland and Adolph (1994).

The weighted average for home range is:

$$\text{Home range of species A} = \frac{\left(\frac{1}{2}\right)116 + \left(\frac{1}{2}\right)83}{\left(\frac{1}{2}\right) + \left(\frac{1}{2}\right)} = 99.5$$

3. Lengthen the branch leading to the common ancestor of each pruned pair by adding to it the product of the branch lengths from the common ancestor to its descendants, divided by their sum. In our example, we are lengthening the branch leading to species A. The new branch length is:

$$3 + \frac{2 \times 2}{2 + 2} = 4$$

4. Continue down the tree calculating contrasts, estimating the phenotypes of the common ancestors, and lengthening the branches leading to the common ancestors. In our example, the only remaining contrast is between species A and black bears. We do not need to estimate the phenotype of species B, or lengthen the branch leading to it, because species B is at the root of our tree. The species A–black bear contrast for body mass is:

$$258 - 93 = 165$$

The species A–black bear contrast for home range is:

$$99.5 - 57 = 42.5$$

5. Divide each contrast by its standard deviation to yield the standardized contrasts. The standard deviation for a contrast is the square root of the sum of its (adjusted) branch lengths. The standard deviation for the polar bear–grizzly bear contrast is:

$$\sqrt{2 + 2} = 2$$

The standard deviation for the species A–black bear contrast is:

$$\sqrt{4 + 5} = 3$$

The standardized contrasts for our example are given in Figure 9.15.

Once we have calculated the standardized contrasts, we can use them to prepare a scatterplot and to perform traditional statistical tests.

We have now considered three methods evolutionary biologists use to evaluate hypotheses about adaptation. In the next two sections of the chapter, we turn to complexities in organismal form and function that are active areas of current research. In the examples we discuss, researchers use experiments, observational studies, and the comparative method to investigate hypotheses about phenotypic plasticity (Section 9.5), and trade-offs and constraints on adaptation (Section 9.6).

When formulating and testing hypotheses about adaptation, biologists must keep in mind that organisms, and the lives they live, are complex.

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