

Response to “Moving on from Kirkpatrick (1994): estimating ‘safety factors’ for flying vertebrates”

Palmer and Dyke (p. 2174) present two main criticisms of Kirkpatrick (Kirkpatrick, 1994). First, they question Kirkpatrick’s measurements of ultimate tensile stress, 125 MPa for bird humeri and 75 MPa for bat humeri. They contrast them with ultimate stresses exceeding 200 MPa for some bird bones other than the humerus, and of 150 MPa for bat bones, recorded by more recent investigators. Though Casinos and Cubo (Casinos and Cubo, 2001) measured ultimate stresses over 200 MPa for some other bird limb bones, their mean for humeri is only 167 MPa, which is still substantially greater than Kirkpatrick’s value. In making these comparisons, Palmer and Dyke are not comparing like with like. Kirkpatrick tested hourglass-shaped specimens in tension, obtaining ultimate tensile stress. The more recent results were obtained by loading intact humeri in bending, so are not ultimate tensile stress but bending strength. Bending strength is generally higher than tensile strength because the outermost layer of a specimen loaded in bending can still withstand increased strain after it has begun to yield. For example, the bending strengths of mammalian long bones have been found to exceed 200 MPa although tensile tests on specimens cut from the bones give tensile strengths of only about 160 MPa [see tables 3.3 and 3.4 in Currey (Currey, 2002)]. This probably explains at least in part the apparent discrepancy between Kirkpatrick’s measurements and those of subsequent authors. In flight, the humeri of birds and bats are loaded in bending, so the appropriate property for calculating safety factors is bending strength, not tensile strength. Palmer and Dyke are right to prefer the strengths derived from bending tests.

Their second criticism is that Kirkpatrick’s estimates of stresses in flight ‘are problematic because of the huge range of values’. His calculated safety factors for birds range from 3.4 to 10.8 (gliding) and 1.1 to 3.3 (hovering). For bats, his ranges are 2.7–5.1 (gliding) and 0.86–1.9 (hovering). Should such wide ranges be considered suspicious? Increasing the strength of a wing bone implies costs; for example, a cost in materials to make a thicker bone and a cost in energy to beat a heavier wing. To find the optimum safety factor, these costs must be balanced against the benefit to fitness of reduced probability of failure. A theory of optimal safety factors along these lines (Alexander, 1981) is unfortunately difficult to apply quantitatively, because we do not know the exchange rates between the currencies involved (materials, energy and fitness), but it suggests strongly that different factors of safety should be expected in flying animals with different ways of life. Lower safety factors may be expected for the wing bones of animals that generally use flapping flight than in those that spend most of their time soaring, because of the cost of flapping heavier wings. Higher factors of safety may be expected in species that fly in cluttered habitats than in those that fly in open country, because of the increased danger of damage by accidental impacts. A higher safety factor may be optimal for birds that fly constantly than for those that spend most of their time on the ground, because of the increased

risk of fatigue failure (Alexander, 1984). Rather than assume that large differences in calculated safety factors of wing bones are due to error, we should ask whether they can be explained by differences in the animals’ habits and environments.

Palmer and Dyke remark that ‘arguably the most illustrative of the limitations’ of Kirkpatrick’s approach is that ‘the ratios between bending stress when hovering and when flying [they mean gliding] were an almost constant factor of three’. This near-constancy should have caused them no alarm. Pennycuik (Pennycuik, 1967) showed that the bending moment arm for the pigeon humerus in hovering was 1.4 times the bending moment for gliding. Combined with Kirkpatrick’s reasonable assumption that lift is generated only during half the hovering wing beat cycle, that implies stresses in hovering 2.8 times those in gliding. If pigeons and other birds have wings designed for optimal spanwise lift distribution, the ratio should be about the same in them all.

In conclusion, Palmer and Dyke seem to be right in their contention that Kirkpatrick’s safety factors are too low. Recalculating them using the more recent measurements of the bending strength of bone instead of his measurements of tensile strength would give safety factors for hovering in the range of about 2 to 7, similar to the range of values that have been measured for leg bones in strenuous terrestrial locomotion (Currey, 2002). Revised values for gliding would be very high, as expected, because the humerus has to withstand much larger loads in other activities. Palmer and Dyke may, however, be wrong to regard the large differences between species, recorded by Kirkpatrick, as symptomatic of error. They may represent adaptations to different environments and ways of life.

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