Moving on from Kirkpatrick (1994): estimating 'safety factors' for flying vertebrates

The most cited work (by far) to provide safety factor estimates for the wing bones of flying vertebrates is inaccurate. Kirkpatrick (Kirkpatrick, 1994) presented extremely low measurements for the material properties of wing bones and anomalous estimates of applied loading that deflate estimated safety factors to around half those reported by subsequent workers. He also did not discuss the limitations of a calculation methodology that resulted in a huge range of estimated values with unreliable means.

In engineering, a 'safety factor' is a multiplier applied to stresses calculated in the design phase to allow for uncertainties in loading, material properties, manufacturing tolerances and material degradation. The magnitude of a safety factor depends on the consequence of failure and the degree of certainty to which loads, material properties and the operational environment are known (Juvinall and Marshek, 1991; Hansson, 2009). In this context a safety factor is a 'forward-looking' design tool, used to ensure that a design will be capable of resisting the loads that it will encounter during its lifetime.

In contrast, the concept of a 'safety factor' in biology is the opposite: retrospective. Biologists use these multipliers to look at existing structures and estimate how close they might come to failure when loaded.

Three different methods have been applied in biological research to obtain the applied loading in structures. The first relies on direct calculation of loads and estimation of stresses from knowledge of structural section and material properties (Kirkpatrick, 1994); the second utilises indirect measurement of loads *via* techniques such as force platforms [e.g. pp. 45–73 of Biewener (Biewener, 1992)]; and the third requires application of strain gauges *in vivo* [pp. 124–147 of Biewener (Biewener, 1992)] (Biewener and Dial, 1995; Blob and Biewener, 1999). Of the three approaches, the calculation method is likely to be the least accurate while *in vivo* measurements are potentially the most accurate.

Kirkpatrick (Kirkpatrick, 1994) used the calculation method with 11 bird and seven bat species. He estimated applied bending moments from calculated lift forces during gliding and hovering flight and made estimates of bone stresses from which safety factors were calculated. There are two significant problems with this study.

First, to obtain material properties, Kirkpatrick (Kirkpatrick, 1994) tested small samples of bone, recording a mean ultimate tensile stress of 125 MPa for bird humeri and 75 MPa for bats. We now know these results are extremely low when compared with subsequent studies: Swartz and colleagues (Swartz et al., 1992) recorded 150 MPa for bats while Currey (Currey, 2004) and Casinos and Cubo (Casinos and Cubo, 2001) recorded values >200 MPa for birds. These differences reduce the safety factors of Kirkpatrick (Kirkpatrick, 1994) by almost a half when compared with results using material properties recorded by subsequent workers.

Second, Kirkpatrick's (Kirkpatrick, 1994) estimates of stresses due to bending are problematic because of the wide range of reported values. For birds the mean was 21 MPa with a range (±1 s.d.) of 13–29 MPa and for bats the mean was 19.6 MPa with a range of 15–25 MPa. Kirkpatrick (Kirkpatrick, 1994) did not discuss this huge range.

We question the validity of such wide distributions for flying animals: mass reduction is vital to performance and consequently the main load-bearing bones would be expected to be consistently close to maximum stress. In any case, what behavioural differences could explain Kirkpatrick's finding that the humerus of a Clapper Rail is three times more highly stressed when gliding than that of an American Kestrel, or that the humerus of a gull is twice as stressed as that of a shearwater?

Reviewing Kirkpatrick's (Kirkpatrick's, 1994) datasets, we found no significant differences between the calculated mean stresses for bats and birds, also unexpected given the large differences between the ultimate tensile strengths of their bones and the very different nature of the two taxa. Finally, and arguably most illustrative of the limitations of the calculation approach for generating safety factors, the ratios between bending stress when hovering and when flying were an almost constant factor of three (mean 2.99, s.d. 0.16 for birds). Such extreme consistency is much more likely to be an artefact of the calculation procedure than a reflection of behavioural reality across a wide range of bird and bat species. We also find it very difficult to reconcile the magnitude of this ratio with the conclusion of Biewener and Dial (Biewener and Dial, 1995) that for pigeons, '[measured] strains did not vary by more than 60% over the full range of flight behaviour recorded' – behaviour that included hovering.

Perhaps as a result of the methodological anomalies there is one case where Kirkpatrick's (Kirkpatrick, 1994) calculations lead to a safety factor of less than one and several where the safety factor is only a little more than one. Kirkpatrick (Kirkpatrick, 1994) did not discuss the implications of these implausible results, only concluding, on the basis of mean values, that, 'the mean safety factor against failure due to bending in gliding flight was 6.63 for birds and 3.99 for bats. In hovering, the mean safety factors against failure due to bending were 2.22 for birds and 1.41 for bats.'

Why did Kirkpatrick (Kirkpatrick, 1994) not comment on these extreme values for safety factors when they imply that the species in question would break their bones when engaged in hovering flight. For this reason alone, we recommend that the estimates provided by Kirkpatrick (Kirkpatrick, 1994) are treated with extreme caution.

In conclusion, the calculation approach employed by Kirkpatrick (Kirkpatrick, 1994) is probably erroneous and led to over-estimation of applied dynamic loads, which when combined with under-estimations for ultimate tensile strength resulted in predicted safety factors that were much lower than reality. Our argument is confirmed by results of more recent studies that use direct measurement approaches and predict safety factors at yield for bird and bat wing bones of rarely less than three, and more commonly between four and six, under all flight conditions.

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