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A reassessment of the effect of body mass upon flight speed and predation risk in birds

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ABSTRACT

A number of theoretical studies have predicted that avian predation risk is mass dependent. Models of bird flight predict that increased mass will reduce flight velocity, making birds more vulnerable to predation. Empirical studies supporting this have demonstrated a significant relationship between mass and routine flight velocity (when birds are not alarmed). Studies investigating the effects of mass upon flight velocity when birds are alarmed, however, tend to show that the mass/velocity relationship is less marked. We found a real difference in the relationship between mass and flight velocity in zebra finches, *Taeniopyga guttata*, when comparing flights of alarmed and unalarmed birds. Despite the strong mass/routine velocity relationship already shown for zebra finches, mass tended to be a poor predictor of the flight velocity of alarmed birds within the natural weight range of the species. This difference appeared to be partly due to alarmed birds increasing their velocity more when heavy than when light, in comparison to their respective predicted routine flight velocities for their weights. As a result, mass/velocity regression slopes tended to be more shallow for alarmed birds. Consequently, increases in body mass within the natural weight range of a bird, may have less effect on the flight velocities of alarmed birds than they do on routine flight velocities. We therefore recommend caution in the use of weight as a predictor of predation risk in birds without examining its effects upon the flight velocity of alarmed birds. We suggest some explanations for the differences in the mass/velocity relationship between the flights of alarmed and unalarmed birds.

In avian prey species, predation must be considered as one of the most powerful selective forces in the evolution of behavioural and morphological characteristics. It has been suggested that predation risk in birds is mass dependent, through its effect on flight performance. Certain aspects of flight performance, especially parameters that increase the time taken to reach cover, such as take-off speed, flight velocity and manoeuvrability, are vital in the escape response repertoire of prey species, in particular for small ground-feeding birds. Attacks on small birds are most effective if the prey can be surprised and caught whilst still on the ground, as once airborne a small bird's chances of being caught are much lower (Temeles 1985). Predators generally attain speed through diving. Prey species in turn attempt to outclimb pursuing predators as the chances of capture are much reduced if they can stay above the predator (Howland 1974). Cresswell (1993), for example, found that redshanks, *Tringa totanus*, suffered an 8% capture rate if they were in flight when attacked by sparrowhawks, *Accipiter nisus*, compared with a 91% capture rate if they remained on the ground. In addition, many species of small birds form flocks when feeding and benefit from dilution, confusion and selfish herd effects (Grier & Burk 1992). Such coordinated behaviour makes it essential for individuals to be able to take off and manoeuvre rapidly, as stragglers will be at a greater risk of predation from both aerial and ground-dwelling predators (Hamilton 1971; Davis 1975; Kenward 1978).

Theoretical work on animal flight has for a long time suggested a link between body mass and take-off performance. Hartman (1961) suggested that take-off ability was determined by the flight muscle ratio (the ratio of flight muscle mass to total body mass). Pennycuick (1969) suggested that maximum lift production was inversely proportional to the square root of wing loading. There is also indirect empirical evidence of mass having an effect upon avian predation risk, such as a reduction in mass or fat storage in relation to an increase in perceived predation risk (Grant 1965; Blem 1976; Gosler et al. 1995; Lilliendahl 1997). Direct studies on the effects of mass upon flight performance have, however, been somewhat

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