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SHORT COMMUNICATION

MAXIMUM LOAD-LIFTING AND INDUCED POWER OUTPUT OF HARRIS' HAWKS ARE GENERAL FUNCTIONS OF FLIGHT MUSCLE MASS

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Pennycuick *et al.* (1989) recently reported results of an experiment in which climbing rate and load-lifting ability were measured for two trained Harris' hawks (*Parabuteo unicinctus* Audubon) flying with various amounts of experimentally applied loads. These data were used to estimate climbing power, maximum aerodynamic power output, and performance consequences of loads in the form of radiotracking equipment.

Measuring the rate of gain of potential energy (which is presumably equal to maximum induced power output in level flight) is highly advantageous, since it uses empirical observations of the rate of work and involves considerably fewer assumptions than do previous estimates of maximum induced power output. However, Pennycuick *et al.* (1989) neglected to relate their results to previous measurements of maximum load-lifting, and thereby overlooked the generality of their result. The purpose of this note is to show that maximum load-lifting by Harris' hawks is consistent with results from a wide variety of birds, bats and insects, and that maximum induced power output from Harris' hawks and other flying animals can be estimated from flight muscle mass and wing length.

Marden (1987) showed that maximum load-lifting among a diverse sample of birds, bats and insects was an isometric function of total flight muscle mass, with little interspecific variation (r^2=0.99). This result was not predicted by previous data or theory, and to date had not been confirmed with independent measurements from other studies. Because the largest animal used in Marden's study was a pigeon (0.267 kg), results from Harris' hawks (0.920 kg) also permit a further test of the isometry of maximum lift production.

Estimates of maximum load-lifting and of flight muscle mass from Harris' hawks are necessary to compare their performance with that of other flying animals. Pennycuick *et al.* (1989) determined that Harris' hawks were able to gain altitude while carrying 1.4 kg, but not while carrying 1.55 kg. Thus, their maximum load was somewhere between these two masses, and can be approximated as 1.475 kg (the midway point). This is the same approximation used by Marden (1987), where

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maximum loads were estimated as midway between the largest load lifted and the smallest load not lifted.

To determine flight muscle mass of Harris' hawks, Pennycuick *et al.* (1989) used an estimate of 17 % of body mass, which is the percentage of body mass comprising the pectoralis muscles in a Cooper's hawk (*Accipiter cooperii*; Marsh and Storer, 1981). However, an estimate of total flight muscle mass (pectoralis, supracoracoideus and wing muscles) is needed to make comparisons with birds from Marden (1987). Total flight muscle mass has been measured for four species of buteonid hawks (Hartman, 1961; red-shouldered, broad-winged, roadside and black hawks), and the ratio of flight muscle mass to total body mass in those species was not highly variable, averaging 0.220 (s.d.=0.006). Thus, a 0.920 kg Harris' hawk must have had about 0.202 kg of flight muscle. Using these estimates for maximum load and flight muscle mass (1.475 and 0.202 kg, respectively), performance of Harris' hawks can be compared to measurements from other birds.

Maximum loads lifted by Harris' hawks fell close to the prediction based on measurements from other birds (Fig. 1); a regression including the Harris' hawk value remains isometric (slope=1.011; 95 % confidence interval=1.08–0.94), with a high coefficient of determination (r^2=0.993), and differs little from the regression based solely on previously measured birds (Table 1). Thus, the Harris' hawk result provides an independent verification of the tight, isometric relationship between flight muscle mass and maximum load-lifting, and extends the range of body size over which this relationship has been demonstrated.

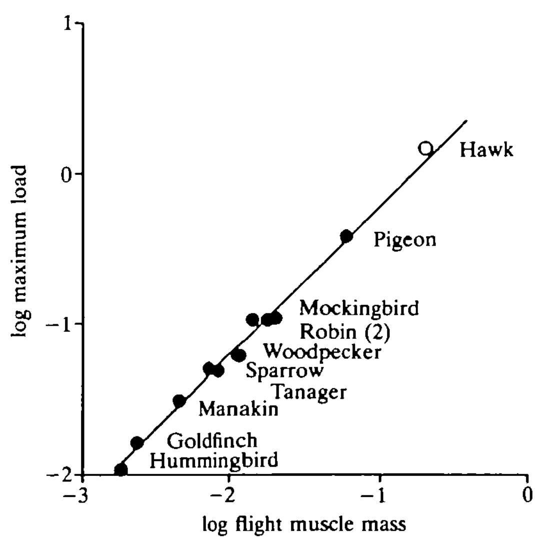

Fig. 1. Regression based on previous data (line and closed circles; Marden, 1987) relating load-lifting (measured in kg) to flight muscle mass (in kg) in birds. The open circle shows result for Harris' hawks from Pennycuick *et al.* (1989).

Table 1. *Coefficients of regression equations (log–log transformed) relating maximum loads (kg) lifted by birds to their flight muscle mass (kg)*

Data	Slope	Intercept	r^2
Old	0.980	0.761	0.987
New	1.011	0.828	0.993

The coefficients labelled 'old' were derived from data in Marden (1987). Coefficents labelled 'new' include those data with Pennycuick *et al.*'s (1989) measurements from Harris' hawks.

Maximum induced power output can be estimated for animals whose maximum lift force and wing length are known by using the actuator-disk equation from helicopter aerodynamic theory (Hoff, 1919; Weis-Fogh, 1972; Alexander, 1983):

$$P_i = (L^3/2\rho\pi r^2)^{1/2},$$

where P_i is induced power (W), L is lift (N), ρ is air density (kg m^{-3}), and r is wing semi-span (span/2; m). The units of the right-hand side of the equation convert to Watts (i.e. kg m^2 s^{-3}). Using this equation with the measured maximum lift force of 14.46 N for Harris' hawks, and assuming a wing length 0.50 m (Robbins *et al.* 1966), yields an estimate of maximum induced power output of 39.7 W, which is very close to Pennycuick *et al.*'s empirically derived 40–46 W. This result demonstrates that it is possible to predict maximum P_i from measurements of maximum lift and wing length. Furthermore, applying the helicopter equation to

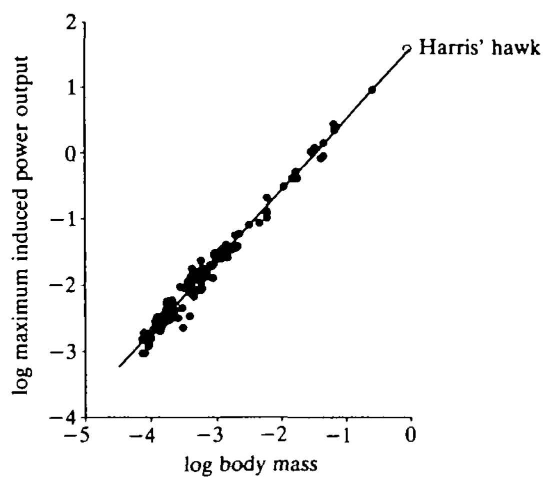

Fig. 2. Scaling of estimated maximum induced power output. Data points (solid circles) and regression line (y=1.076x+1.58) were derived from measurements of maximum lift and wing semi-span from all conventional-wingbeat animals in Marden (1987). The measured power output of Harris' hawks (open circle; Pennycuick *et al.* 1989) is closely predicted by this scaling relationship. Power output is measured in Watts, body mass in kg.

Marden's (1987) data for lift and wing semi-span from a wide variety of birds, bats and insects shows that the scaling of estimated P_i with body mass also predicts the measured maximum P_i of Harris' hawks (Fig. 2).

In summary, Pennycuick *et al.*'s (1989) measurement of maximum load-lifting ability of Harris' hawks corroborates previous measurements from other animals. Their measurement of maximum short-burst (i.e. anaerobic) induced power output agrees closely with the value predicted by using maximum lift and wing length in the equation from helicopter theory, and with the value predicted from the scaling of P_i estimates derived from measurements of maximum lift and wing length in other animals. Therefore, since maximum lift force is a tight, isometric function of flight muscle mass, measurements of flight muscle mass and wing length are all that is needed to predict maximum induced power output for all flying animals.

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