CORRELATION OF FLIGHT-MUSCLE SIZE AND BODY MASS IN COOPER'S HAWKS: A NATURAL ANALOGUE OF POWER TRAINING

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Muscle hypertrophy in response to increased load (e.g. power training) is well documented in laboratory animals and in man (see, for example, Thorstensson, 1976; Gonyea, Ericson & Bonde-Peterson, 1977), but this phenomenon has not been quantitatively linked to changes in the use of muscles by wild animals. In free-living animals, and sometimes even in those used in laboratory studies, predicting the stress placed on an individual muscle is difficult. Thus, evaluating a compensatory response in relation to a change in muscle use is also difficult. The flight muscles of birds, however, represent a system in which changes in muscle size can be quantitatively compared to the power output required for flight. We describe here a correlation of flight-muscle mass with body mass in Cooper's hawks (*Accipiter cooperii*). We believe this correlation represents a natural analogue of power training. The variation in muscle mass between individuals can be directly related to differences in the power requirements for flight caused by differences in body mass.

In sharp contrast to the provision of power during terrestrial locomotion, which involves a large number of muscles, power for flight in birds is derived primarily from two muscles. The pectoralis muscle powers the downstroke and the supracoracoideus muscle powers the upstroke. With few exceptions, notably the hummingbirds, the upstroke in birds provides little or no aerodynamic power (Lighthill, 1977), so that virtually all the power for flight is produced by the pair of large pectoralis muscles. The differential role of the antagonistic muscles is reflected in their relative size, with the mass of the pectoralis muscle averaging 10 times the mass of the supracoracoideus muscle (Greenewalt, 1962).

Within a given species (and sex) most of the morphological and kinematic parameters which influence the power required to fly are relatively fixed. These parameters include wing length, wing area, stroke angle, and wing-beat frequency (Lighthill, 1977). However, body mass, another major determinant of the power requirements for flight, may vary greatly during the adult life of an individual bird. Much of this variation is due to changes in the amount of stored fat. For example, fat reserves

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increase markedly before migratory flights in many species (Berthold, 1975), whil■ other species undergo a winter fattening cycle (see, for example, Carey et al. 1978). These increases in mass will increase the power requirements for flight and thus increase the power output required from the pectoralis muscle.

In 1953 one of us (R.W.S.) instituted a programme of data collection on *Accipiter* hawks received by the University of Michigan Museum of Zoology. The birds used were obtained from a variety of sources and include birds that were shot, trapped, killed by automobiles, or killed by flying into windows. No bird was killed specifically for this study. Data from this long-term study form the basis for the present analysis. Birds that had died in captivity or were obviously emaciated were excluded. It should be noted especially that the lightest female included in the analysis (Fig. 1) was a free-flying individual. Body mass and pectoralis muscle mass were obtained by weighing to the nearest gram and 0·1 gram, respectively, on a single-beam, double-pan balance. Wing arc is the length of the flattened wing from the wrist to the tip of the longest primary measured with a millimetre ruler. Wing semi-span is essentially the total length of one wing from the body to the tip of the extended wing. This latter measurement was obtained with the ruler on tracings of the wing. Wing area was obtained by polar planimetry from the same tracings and is the area of one wing only. Sex was determined by examination of the gonads, and age by plumage differences.

Body mass varies substantially in our sample of Cooper's hawks from Michigan (Table 1). Reflected in our sample is the well-known sexual dimorphism found in the genus *Accipiter* (Storer, 1966). Female Cooper's hawks average 56% larger in body mass than males and almost proportionally larger in the linear dimensions and area of the wing. Laws of geometrical similarity indicate that mass ∝ [linear dimensions]³ ∝[area]³/². In our sample females are 47% larger in [linear dimensions]³ and ~ 47% larger in [area]³/². Unlike the average differences between the sexes, body mass within each sex is not correlated with the dimensions of the wing ($P > 0·20$; $|r| < 0·22$). Thus, superimposed on a relatively small amount of variability in structural size within each sex, as indicated by wing dimensions (c.v., s.d./mean, < 4%), is a larger component of unrelated variability in body mass (c.v. > 13%). Immature and adult birds were not statistically different in any of the measured parameters (Student's t test; $P > 0·15$; 9 immature and 11 adult males, 14 immature and 9 adult females). The age-related differences in size noted by Mueller, Berger & Allez

Table 1. *Body mass, muscle masses, and wing dimensions of Cooper's hawks. Data are presented as the mean ± S.E.M. The range is given in parentheses followed by the sample size.*

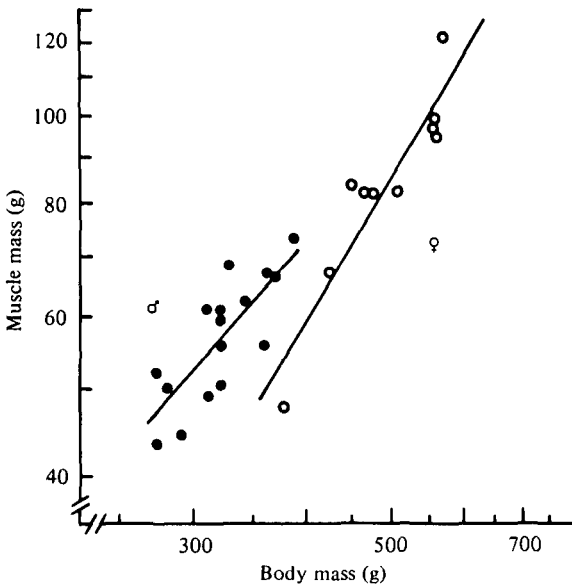| Body mass (g)	Pectoralis muscle mass (g)	Wing arc (cm)	Wing semispan (cm)	Wing area (cm²)
		Males		
326±9·31	57·4±2·2	23·6±0·07	31·4±0·19	398±3·63
(271–431, n = 21)	(43·6–73·0, n = 16)	(22·7–24·2, n = 21)	(29·1–32·7, n = 21)	(360–427, n = 21)
		Females		
510±15·9	85·2±6·2	26·8±0·11	35·7±0·24	514±4·47
(379–736, n = 22)	(47·4–121·2, n = 10)	(25·8–28·2, n = 24)	(32·9–37·9, n = 24)	(475–572, n = 24)

Fig. 1. The mass of the pectoralis muscles (both sides) of Cooper's hawks as a function of the body mass. $\bigcirc = \female$; $\bullet = \male$. Both scales are logarithmic. Solid lines are simple linear regressions. Regression equations are for males: $\log P = 1.13 \log M - 1.08$; for females: $\log P = 1.67 \log M - 2.565$; where P = pectoralis mass and M = body mass.

(1979) for the related sharp-shinned hawk (*Accipiter striatus velox*) are very slight and would likely be undetected in our small samples. Such slight differences are of little significance in the calculations of flight power considered below.

Variation in body mass in raptors has not been well studied. However, several species add fat in the winter months at temperate latitudes (this study; Piechocki, 1970; Henny & VanCamp, 1979). The addition of fat in the winter is not a consistent population-wide phenomenon, but instead is manifested as an increased variance in body mass. For example, male Cooper's hawks in Michigan range from 271 to 431 g in November–March and only from 271 to 313 g in April–October (winter *vs.* summer, Mann–Whitney, $U = 12.5$, $P < 0.025$; $n_1, n_2 = 13, 6$). Presumably during the winter, when prey availability is unpredictable, birds add fat when prey is abundant and deplete this reserve during times of low prey availability.

The mass of the pectoralis muscle varies directly with the body mass in both male and female Cooper's hawks (Fig. 1; $r = 0.80$, $P = 0.0002$ for males; $r = 0.91$, $P = 0.0002$ for females). Within each sex the muscle mass is not correlated with wing dimensions ($P > 0.08$); however, as might be expected, the average difference in muscle size between males and females is proportional to these indicators of body size (pectoral mass of females averages 48% larger than that of males). To determine if the major components of the muscles were changing differentially, muscles from 7 birds were freeze-dried to constant mass, fat extracted with petroleum ether in a Soxhlet apparatus, and finally re-dried in an oven at ~ 90 °C. They consisted of 24.85 ± 0.52% lean dry mass, 73.12 ± 0.49% H_2O, and 2.03 ± 0.19% fat. This

composition was independent of muscle size, with muscles ranging in wet mass fro█ 25 to 61 g (one side).

We suggest that the increase in muscle mass with increasing body mass is related to the power requirements for flight. Hunting success in Cooper's hawks depends heavily on a substantial power reserve over the minimum power requirements for flight. This reserve allows the quick accelerations in dense cover which characterize *Accipter* hunting techniques (Brown & Amadon, 1968), as well as allowing these predators to carry prey which may equal them in body mass (Storer, 1966). If these birds are to maintain their level of flight performance as they gain weight, they must increase the power output available from their flight muscles. Because the hawk's wing morphology remains constant with increasing body mass, only two possibilities exist for augmenting the maximum power output from the pectoralis muscles: (1) increasing the wing-stroke frequency (f) and/or (2) increasing the size of the muscles. Comparative data suggest that f is relatively constant with species (Greenewalt, 1975). Our own observations on accipiters indicate that the variation in f among individuals is insufficient to compensate for the predicted variation in flight power, although we cannot conclusively rule out this possibility.

Is the observed increment in muscle mass sufficient to compensate for the increase in flight power as body mass increases? If we assume that the relative proportions of myofibrils and mitochondria remain the same and that fibre length does not change (as is the case during muscle hypertrophy in the catbird *Dumetella carolinensis*; Marsh, 1979), then the cross-sectional area of myofibrils will be directly proportional to the muscle mass. Thus, at a fixed f and stroke angle, the power output available from the muscles should also be proportional to muscle mass. Simple linear regressions of log pectoralis mass versus log body mass yield slopes of 1·13 for males and 1·67 for females (Fig. 1). (These slopes are not significantly different from one another.) Aerodynamic theory predicts that the power requirements for flight will be proportional to approximately the 1·5 power of body mass (Pennycuick, 1975). The slopes calculated from regression analyses are not significantly different from this value, and thus indicate that the increase in muscle size with increasing body mass could totally compensate for the increment in power requirements for flight. Also consistent with theoretical predictions are the relative masses of the pectoralis muscles of males and females of similar body mass. As pointed out above, the average muscle mass of females is larger than that of males, as expected from the overall sexual dimorphism; however, in the range of overlap in body mass the males have larger pectoral muscles (Fig. 1). For example, for a male and a female both weighing 380 g, the regression equations (Fig. 1) predict a muscle mass of 68·6 g for the male and 54·4 g for the female, a ratio of 1·26:1. A similar ratio, 1·21:1, is predicted in the power requirements for flight of males compared to females of the same body mass. The difference in power requirements is due to the smaller wing span of the male. Thus based on these scaling arguments, the magnitude of the variation in muscle mass can entirely compensate for the predicted variation in flight power.

In this context a numerical comparison of estimates of power requirements and power availability is useful in judging the importance of the hypertrophy of the flight muscles. In Fig. 2 we compare the calculated curves of flight power versus
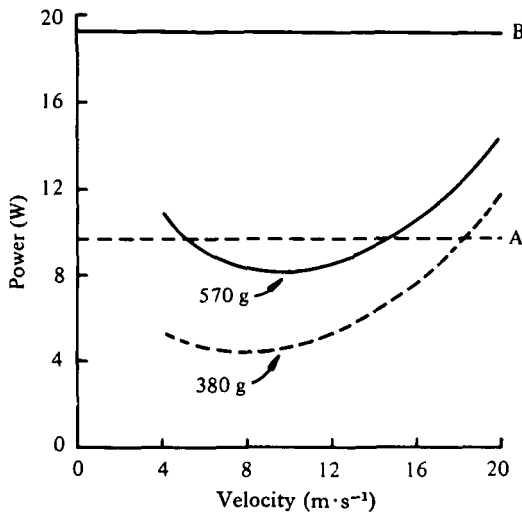
Fig. 2. The curves show the predicted power requirements for flight (see text) for female Cooper's hawks weighing 380 and 570 g. Lines A and B indicate the predicted maximum sustainable power output (see text) from the flight muscles of the 380 and 570 g bird, respectively. Note that if a 380 g hawk were to gain mass without an increase in muscle mass, its flight capabilities would be severely compromised.

forward velocity of a light (380 g) and a heavy (570 g) female Cooper's hawk, with the same average wing span of 0·87 m. The curves are based on the formulae of Penny-cuick (1975), and represent only the mechanical power required from the flight muscles. Also shown are the predicted maximum sustainable power outputs based on the size and contraction frequency of the pectoralis muscle (Weis-Fogh & Alexander, 1977) with muscle masses of 54 g and 107 g for the light and the heavy female, respectively. We measured f on Cooper's hawks captured during a banding operation in northern Michigan. Measurements were made from cine films photographed at 32 frames·s⁻¹. Cooper's hawks had fs ranging from 4·0 to 5·5 beats·s⁻¹. Birds were capable of increasing f to 7–8 beats·s⁻¹. when accelerating during take-off. We estimate a maximum specific power available of approximately 180 W/kg muscle. Note that for both birds (Fig. 2) the power available exceeds the power required by a similar relative amount, with ratios of the power available to the minimum power required of 2·21:1 and 2·36:1 for the light and the heavy female, respectively. These calculations are consistent with the existence of a substantial power reserve in these hawks and also point to the quantitative importance of the correlation of muscle mass with body mass.

The stress placed on the flight muscles of an animal engaged in powered flight will increase with increasing body mass. Obviously, the degree of muscle hypertrophy in response to this stress will depend not only on the change in load, but also on the amount and types of flight activity undertaken, the time period over which the stress is applied, morphological constraints on the amount of muscle mass that can be carried, and the capacity of the muscle to respond to the stress. Data available on several other species of birds suggest that the correlation of the mass of the pectoralis

muscle with body mass may be a general phenomenon. We have collected data ◼
sharp-shinned hawks (*Accipiter striatus velox*) and on pied-billed grebes (*Podilymbu̶s̶*
podiceps) which show the same degree of compensatory hypertrophy of the flight
muscles as in Cooper's hawks. The same trends can also be detected in data on flight-
muscle mass of Canada geese (*Branta canadensis*) during the course of the yearly cycle
(Raveling, 1979). Additionally, small passerines which undergo extensive pre-migra-
tory fattening show evidence of the same phenomenon although the relative changes
are more modest (Fry, Ferguson-Lees & Dowsett, 1972; Marsh, 1979). These animals
provide a cogent example of the responsiveness of vertebrate skeletal muscle to
changes in load. The resulting adaptive hypertrophy matches the size of the muscles
to the changing energetic demands.

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