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Inside JEB

HOW BIRDS POWER FLIGHT



Ecologists would love to know the metabolic energy requirements that dictate bird behaviours such as flight, but getting a handle on this is challenging.

‘Understanding what determines overall energy requirements is a theme of my lab,’ says Graham Askew from the University of Leeds, UK, and adds, ‘I am trying to get the link between what the muscles are doing and how much energy they use to get a global picture of animal locomotion.’ But very few studies into the energetics of bird flight had systematically scrutinised the problem from the perspective of the mechanical power through to the metabolic energy consumed. Teaming up with graduate student Charlotte Morris, Askew began methodically dissecting out the different components that power bird flight.

First the duo focused on how birds modulate the amount of mechanical power they produce during flight (p.2770). Askew explains that if you plot the mechanical power that a bird produces against its flight speed, you get a U-shaped curve where the power is highest at low speeds (it takes a lot of energy to hover), drops to a minimum at intermediate cruising speeds and rises again at the highest speeds. Curious to know how birds modulate the power output by the main flight muscle, the pectoralis, at different speeds, Morris and Askew trained cockatiels to fly in a wind tunnel at speeds ranging from hovering at 0 m s^{-1} up to a speedy 16 m s^{-1} . Once the birds had got the hang of flying in the wind tunnel, the duo inserted minute ultra-sonic crystals into the birds’ pectoral muscles to measure how much the muscle length changed during each muscular contraction, placed hair-like electrodes adjacent to the sonomicrometry crystals to record the electrical impulses that triggered each contraction and filmed the birds with a high-speed digital camera as they flew.

Analysing the muscle’s electrical activity, Morris and Askew could see that the birds primarily modulated their muscle activation to modulate their power output, increasing

the electrical activity to recruit more muscle fibres at low and high speeds. The duo also noticed that at low speeds, the birds increased the amount of time spent shortening the muscle during each wing beat cycle from 50% to 60%. However, at the highest speeds, the birds increased their mechanical power output by increasing the muscle strain: that is, they increased the relative amount of slide between the actin and myosin filaments to increase the mechanical power output. And when they analysed the movies, Morris and Askew saw that the cockatiels alternated between flapping and gliding at low power intermediate speeds, and switched to flapping continuously when they needed most power at the lowest and highest speeds.

But how much power was the pectoral muscle actually producing as the bird flapped at different speeds? Askew decided to determine the muscle’s power output by measuring the power of isolated bundles of muscle fibres (fascicles) while they contracted. Isolating individual fascicles from the cockatiels’ pectoralis muscles, Morris and Askew stretched and released the muscle fibres in the same way that the muscle filaments had slid past each other as the bird flew while electrically activating the muscle fibres using the electrical impulse pattern that they had recorded during flight. Measuring the force produced by the stimulated muscle fibres, the duo were then able to calculate the power produced by the muscles at various speeds and found that it varied from approximately 120 W kg^{-1} at the high speeds to a minimum of approximately 40 W kg^{-1} at intermediate speeds.

But how did the power estimates based on an aerodynamic model of flight compare with the powers measured from the muscle fascicles (p.2781)? Measuring the position of the bird’s centre of mass and various wing beat parameters from the movies, the duo used coefficients taken from the literature to estimate drag and calculate the bird’s mechanical power output from the aerodynamic model.

But Askew points out that, ‘There has been a build up of a range of different numbers and this is one of the problems with aerodynamic models: what values should you pick for your aerodynamic coefficients and are they appropriate across all flight speeds?’ The duo tested which coefficients produced the best agreement with the powers measured from the flight muscle fascicles and Askew says, ‘We got the best match at low speeds when we used coefficients from the low end of the range and the best match at the high speeds when

we used coefficients from the medium values'. He adds that although estimating mechanical power output based on the bird's flight behaviour is convenient, 'we should be very cautious about the coefficients that we use in aerodynamics models, in particular about using the same coefficients across all flight speeds'.

Finally, Morris and Askew teamed up with Frank Nelson to find out how the mechanical power output measurements related to the metabolic energy consumed by the birds in order to estimate the pectoralis muscle efficiency and the cost of other metabolic systems during flight (p.2788). 'We trained the birds to fly wearing a little mask that we could connect to the respirometry apparatus to withdraw the air that the animal is breathing out and analyse it for the amount of oxygen that the animal is using and carbon dioxide that it is producing to measure their metabolic rates,' explains Askew. Using these values to calculate the birds' metabolic rates as they flew at speeds ranging from 6 to 13 m s⁻¹, the trio then assumed a postural cost of flight – the energy consumed by other flight muscles and the cardiovascular system – of 10% and used this to calculate the pectoral muscle's efficiency. It came out at 7–11%, which seemed quite low given that the efficiency of mammalian muscle has been measured at 10–19%, so the team decided to run the calculation the other way round.

Choosing efficiency values of 19%, they calculated the fraction of the metabolic energy that is being consumed by the pectoralis muscle and found that it could be using between 36 and 54% of the metabolic energy, while choosing a low muscle efficiency of 10% suggested that the pectoralis could use between 69–100% of the metabolic energy, with the remaining energy going to other flight muscles and the respiratory and circulatory systems. 'Our calculations suggest that the postural costs of flight have been under-estimated perhaps because the energy used by flight muscles other than the pectoralis muscles has been ignored,' says Askew.

Having shown that researchers should use some caution when estimating the mechanical and metabolic costs of flight, Askew says, 'Mechanical power calculations are good for general models for understanding how animals might fly, but in terms of coming up with specific predictions I think people need to be quite cautious.' Looking to the future Askew

says, 'We need to fill in some of these gaps and measure flight muscle efficiency,' and adds, 'Getting a handle on the postural costs of flight is more challenging, but probably achievable'.

10.1242/jeb.049114

Morris, C. R. and Askew, G. N. (2010a). The mechanical power output of the pectoralis muscle of cockatiel (*Nymphicus hollandicus*): the *in vivo* muscle length trajectory and activity patterns and their implications for power modulation. *J. Exp. Biol.* **213**, 2770–2780.

Morris, C. R. and Askew, G. N. (2010b). Comparison between mechanical power requirements of flight estimated using an aerodynamic model and *in vitro* muscle performance in the cockatiel (*Nymphicus hollandicus*). *J. Exp. Biol.* **213**, 2781–2787.

Morris, C. R., Nelson, F. E. and Askew, G. N. (2010). The metabolic power requirements of flight and estimations of flight muscle efficiency in the cockatiel (*Nymphicus hollandicus*). *J. Exp. Biol.* **213**, 2788–2796.

DISCOVERING WHICH FORCES DROVE SKELETAL EVOLUTION

When engineers set out to design a new structure, they make it to withstand loads and forces far beyond those experienced on a daily basis. For example, aeroplanes not only have to withstand routine take off and landings but also severe turbulence and other extreme events. In the natural world, natural selection, governed by various functional demands and constraints, has driven the development of a wide range of body forms, all superbly adapted to their individual niches. Åke Norberg from Gothenburg University, Sweden, is intrigued by the forces that shaped locomotor organs, such as the wings of birds or the limbs of mammals. Curious to find out whether bird and mammal bones are designed with respect to the body weight they must bear or the loads experienced during extreme manoeuvres, Norberg and his student, Björn Wetterholm Aldrin, began looking at the proportions of small bird and mammal bones relative to larger creatures' bones (p.2873).

Norberg explains that one way of identifying the selective pressures that moulded animal body shapes is to compare a particular anatomical trait in animals over a wide range of body sizes, plot that trait against body mass to find the rate of change (gradient) of that trait, and see how it matches the predictions of how that trait changes relative to body mass derived from alternative theories. With this in mind, Norberg built a mathematical model of a mammal's leg and a bird's wing to see if he could calculate the rate of change of bone stress in animals ranging from tiny to large

to find out which forces drove their evolution. Based on his models, he explains that among animals that have the same general shape, bone stress will increase with a gradient of 0.33 when bones are loaded by the body weight, but when bones are loaded by maximal manoeuvring muscle forces, the gradient will be 0; that is, bone stress will be the same regardless of animal size. So he decided to use measurements taken from animals and insert them into his models to find out whether, or how, stress experienced by mammal and bird bones might change when loaded by the body weight, or by maximal muscle forces in animals of increasing size.

Thinking first about the bending and twisting forces exerted on mammals' legs ranging from small crouched rodents up to large animals with more upright locomotion postures, Norberg, using measurements taken from animals, found that the gradient for bone stress across a wide range of mammals is 0.11 under loads due to the animal's body weight, rather than 0.33 (expected if animals of different sizes all had essentially the same shape). And when he considered the stress in leg bones at high speed or during manoeuvres, the scaling gradient is 0.17, instead of the expected 0 if animals were the same shape over the entire range of sizes.

Norberg says these values are compromises (0.11 and 0.17 instead of 0.33 and 0), and explains that they are due to the differences in the mammals' postures and leg muscles. He adds that the frequency with which animals experience extreme loads may affect the evolution of bone shape.

Moving on to scaling feather and bone proportions in birds, Norberg used measurements taken from animals, put them into his bird model and found that the gradient is 0.23 when the wing is loaded by body weight and –0.04 when the wing is subject to maximal muscle forces as the bird manoeuvres. This is very close to the gradient of 0 that Norberg expected, and shows that the safety factor against bone breakage during extreme manoeuvres is the same for birds across all size ranges. So wing bone dimensions seem to be adapted to maximal muscle forces rather than to the body weight.

10.1242/jeb.049122

Norberg, R. Å. and Wetterholm Aldrin, B. S. (2010). Scaling for stress similarity and distorted-shape similarity in bending and torsion under maximal muscle forces concurs with geometric similarity among different-sized animals. *J. Exp. Biol.* **213**, 2873–2888.

HEAT DISSIPATION DOES NOT LIMIT HARE MUM'S ENERGY TURNOVER



Most animals face extreme endurance tests during their lives, whether it's surviving cold winters or suckling a family of five. But for most creatures there seems to be an internally set limit to the amount of energy that they can turn over, no matter how extreme the conditions. According to Teresa Valencak and her colleagues from the University of Veterinary Medicine, Austria, there are two possible explanations for this limit. Valencak explains that mammals produce heat as a by-product of metabolism, but overheating is dangerous, so some animals' energy turnovers are limited by the amount of heat that they can dissipate. Alternatively, an animal's energy turnover could be set by other factors, such as the amount of food that they can consume or the amount of energy that they are prepared to invest in the next generation. Knowing that small mammals' and dairy cows' energy turnovers are restricted by the amount of heat they can lose, Valencak, Klaus Hackländer and Thomas Ruf decided to find out what sets a lactating European hare's limit (p. 2832).

Knowing that hare leverets only suckle once a day and are left untended the rest of the time, the trio took hare mums with litters of three leverets, separated the young from their mothers and then kept some mums warm (22°C) while their young were kept in the cold (5°C). Other mums were kept at the same low temperature (5°C) as their young, while a third group of families were kept at 22°C. Reuniting the leverets with their mothers once a day to suckle, the team weighed everything that went into and out of the mums, as well as weighing the leverets before and after they suckled to find out how much milk the mothers produced. The team reasoned that if the hare mums were limited by their ability to dissipate heat, then the warm mums could not turn over more energy to produce enough milk to meet the high energy demands of their cold young, while cold mothers would have no problem suckling their cold leverets. However, if something else was limiting the mothers' energy turnover, then the warm mothers

might be able to produce enough milk to suckle their cold and ravenous young.

Monitoring the mothers' energy budgets over 4 weeks, the team found that the warm hare mums suckling cold young were able to increase their energy intake just as much as the cold mums during the second week of lactation. The warm mums' energy turnover was not restricted by the amount of heat that they can dissipate. Valencak and her colleagues suspect that hare mums actively restrict their energy turnover by limiting their investment in their current litter to maximise their lifetime reproductive success.

10.1242/jeb.049130

Valencak, T. G., Hackländer, K. and Ruf, T. (2010). Peak energy turnover in lactating European hares: a test of the heat dissipation limitation hypothesis. *J. Exp. Biol.* **213**, 2832-2839.

Kathryn Knight
kathryn@biologists.com

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