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RESEARCH ARTICLE

The elaborate plumage in peacocks is not such a drag

Graham N. Askew*

ABSTRACT
One of the classic examples of an exaggerated sexually selected trait is the elaborate plumage that forms the train in male peafowl *Pavo cristatus* (peacock). Such ornaments are thought to reduce locomotor performance as a result of their weight and aerodynamic drag, but this cost is unknown. Here, the effect that the train has on take-off flight in peacocks was quantified as the sum of the rates of change of the potential and kinetic energies of the body (P_{CoM}) in birds with trains and following the train's removal. There was no significant difference between P_{CoM} in birds with and without a train. The train incurs drag during take-off; however, while this produces a twofold increase in parasite drag, parasite power only accounts for 0.1% of the total aerodynamic power. The train represented 6.9% of body weight and is expected to increase induced power. The absence of a detectable effect on take-off performance does not necessarily mean that there is no cost associated with possessing such ornate plumage; rather, it suggests that given the variation in take-off performance per se, the magnitude of any effect of the train has little meaningful functional relevance.

KEY WORDS: Sexual selection, *Pavo cristatus*, Flight, Peafowl, Take-off, Performance

INTRODUCTION
Sexual selection may favour the evolution of extravagant secondary sexual characteristics that are important in mate choice and confer reproductive benefits (Darwin, 1871). There are several theories about the origin and maintenance of such sexual traits, but central to 'handicap' and 'good genes' models of sexual selection is the assumption that such ornaments incur a cost (Zahavi, 1975; Andersson, 1994). It is hypothesised that exaggerated sexually selected traits negatively affect organismal performance (e.g. endurance or escape response) by directly (e.g. through increased predation risk) or indirectly (e.g. through increased metabolic energy expenditure) incurring costs (Kotiaho, 2001). However, while the sexual trait has a negative affect on organismal performance, it is an indicator of overall superior genetic quality and therefore has a net positive effect on fitness [e.g. fecundity or offspring success (Petrie, 1994; Rowe and Houle, 1996; Möller and Alatalo, 1999; Hale et al., 2009; Husak and Swallow, 2011)]. Examples of such traits are found throughout nature, and include the ornate plumage exhibited in the males of some bird species [e.g. long-tailed widowbirds, *Euplectes* sp. (Andersson, 1982); peafowl, *Pavo* sp. (Petrie, 1994); and paradise whydas, *Vidua* sp. (Alatalo et al., 1988)]. It has been suggested that these structures may impair flight performance (Balmford et al., 1993). However, empirical evidence quantifying the costs associated with sexually selected traits is generally lacking (Kotiaho, 2001). Demonstrating whether sexually selected traits do

incur a cost is necessary to test current theories in evolutionary biology.

Arguably one of the most iconic examples of sexual selection is the extravagant plumage that forms the train in male peafowl (peacocks; *Pavo cristatus* Linnaeus 1758), which is thought to have evolved as a result of female preference to mate with males possessing more elaborate trains (Darwin, 1871; Petrie et al., 1991; Petrie and Halliday, 1994; Loyau et al., 2005). Possessing a more elaborate train reflects male health status (Loyau et al., 2005), and may confer reproductive benefits (Petrie, 1994). Take-off flight is an important means of avoiding predators and the ability to take-off at high speeds and at a steep angle of ascent demands a very high power output (Askew and Marsh, 2002) and may have a direct influence on an individual's survival (Cresswell, 1993; Witter et al., 1994). Peafowl spend most of their time on the ground or roosting in trees; in adult males, flight only accounts for 0.12% of their daily activity (Harikrishnan et al., 2010). While being capable of sustained flight (Hoyo et al., 1994), peafowl primarily use flight to access roost sites and to evade mammalian predators, such as leopards *Panthera pardus fusca* (Mondal et al., 2011). Possessing elaborate plumage with high aerodynamic drag and/or weight could negatively affect take-off flight performance and consequently could have a direct influence on an individual's survival (Witter et al., 1994).

The aim of this experiment was to determine whether possessing elaborate plumage during the breeding season adversely affects take-off flight performance in peacocks. High-speed videogrammetry was used to capture the wing and body kinematics of flights in birds possessing the train and following removal of the train. Take-off performance was quantified as the sum of the rates of change of the potential and kinetic energies of the body. In addition, wind tunnel tests were carried out to determine the aerodynamic forces on the train in order to estimate the drag it incurs during take-off flights. It was hypothesised that the train would increase the parasite drag of the bird's body during flights, and this, together with the additional weight, would impair take-off performance.

RESULTS
The morphological data for the birds are given in Table 1. Birds with trains performed 4.6±0.7 flights and birds without trains performed 4.8±0.9 flights.

Take-off performance
The velocity of the bird at take-off and the flight velocity of the peafowl at the end of the second wingstroke were not significantly different between the two treatments (Table 2). The overall velocity decreased during the flight; the rate of loss of kinetic energy was similar across the two treatments (Table 2). The rate of change of potential energy was not significantly different between the two conditions (Table 2). Note that in all birds the rate of increase in potential energy far exceeded the rate of loss of kinetic energy; hence, net positive mechanical power is required from the flight muscles to move the centre of mass of the body (CoM) of the bird.

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Table 1. Morphological data for peafowl *Pavo cristatus*

Variable	
Body mass (kg)	4.66±0.14
Pectoralis muscle mass (kg)	0.58±0.02
Supracoracoideus muscle mass (kg)	0.16±0.01
Train mass (kg)	0.32±0.05
Wing length (m)	0.54±0.02
Wing area (m²)	0.18±0.02

Reported values are means ± s.e.m. for five individuals. Body mass includes the mass of the train. For each muscle, the reported mass is the total for both sides of the animal; wing variables are for a single wing.

The total mass-specific power of the centre of mass of the body (P_{CoM}; calculated relative to pectoralis muscle mass) was not significantly different between birds with and without trains (train P_{CoM}=222.6±43.3 W kg^{-1}; no train P_{CoM}=210.0±25.5 W kg^{-1}; t_4=0.41, ns; Fig. 1A,C, Table 2).

Aerodynamic forces on the peafowl train

The drag on the train increased linearly with increasing air velocity for each angle and was highest at steeper angles (Fig. 2). At the mean flight velocity for birds (4 m s^{-1}) possessing a train, the drag on the train ranged from 0.12 N (level) to 0.15 N (−10 deg): during take-off, the train was held at an angle of between 0 and −10 deg relative to the angle of elevation of the flight trajectory of the bird. A small vertical lift force was produced when the train was held at angles below the horizontal (0.04 N at a train angle of −10 deg at 4 m s^{-1}). This was less than 0.08% of body weight and was ignored in the calculation of induced power.

Aerodynamic power

The total power requirement of take-off (P_{aero}) was not significantly different between the two conditions (train P_{aero}=414.1±31.2 W kg^{-1}; no train P_{aero}=393.3±27.1 W kg^{-1}; t_4=0.55, ns; Fig. 1B, Table 2). Parasite drag was significantly higher in birds with a train compared with birds following the train's removal (Table 2). Profile power and the power required to generate the induced velocity were not significantly different between the two conditions (Table 2).

DISCUSSION

The train of male peafowl is one of the most elaborate sexually selected structures found in nature. It is hypothesised that such

structures incur a cost (Andersson, 1994), e.g. by reducing locomotor performance, and could have functional ecological consequences such as increased predation risk (Witter et al., 1994). However, contrary to this prediction, here it is shown that possessing a train does not significantly reduce flight take-off performance (Fig. 1A,C). P_{CoM} was not significantly different in birds possessing trains compared with those birds from which the train had been removed. There was no significant difference in P_{aero} between the two treatments, suggesting that birds with trains were not maintaining take-off performance (P_{CoM}) simply by increasing the mechanical power output of the flight muscles (P_{aero}).

The drag on the train depends on flight velocity and the angle at which it is held relative to the flight trajectory of the bird (Fig. 2) (see also Evans and Thomas, 1992). At the flight velocities and relative train angles used during take-off (4.1±0.2 m s^{-1}), the drag on the train was only 0.12–0.15 N. This results in a significant, twofold increase in parasite power, but as parasite power only represents 0.1% of the total aerodynamic power requirements, the effects of the drag of the train on flight performance are trivial. The train represents 6.9% of the bird's body mass. Increasing body mass is expected to increase induced power (through increases in thrust and induced velocity), and therefore to decrease flight performance via a reduction in P_{CoM}. However, this effect was not detected. Diurnal mass gains of 5.3% in great tits have also been shown to have no significant effect on escape flight performance (Macleod, 2006). Together, these findings suggest that although added mass must affect the induced power requirements, the magnitude of the effect has little meaningful functional relevance (given the high variability in individual take-off performance per se; Table 2, Fig. 1A) (Macleod, 2006). There are several other examples of sexually selected traits having rather subtle effects on bird locomotor performance. In Anna's hummingbirds (*Calypte anna*) and scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*), artificial manipulations of the tail by the addition of feathers from a different bird species or the removal of the tail feathers demonstrate that elaborate tail ornaments can have relatively small effects on flight performance by reducing maximum speed (by 3%) and increasing metabolic cost (by 11%, but only at the highest speeds, which represent 1–7% of the birds' flight behaviour) (Clark and Dudley, 2009), and by reducing hawking efficiency (Evans and Thomas, 1992). The vertical display flights performed by collared doves (*Streptopelia decaocto*) have been estimated to incur a relatively low metabolic cost (~5% of basal metabolic rate) (Usherwood, 2008).

Table 2. Take-off performance and aerodynamic power requirements in peafowl *Pavo cristatus* with and without a train

	Train	No train	
V_0 (m s^{-1})	4.3±0.2	4.4±0.2	t_4=−1.01, ns
V_2 (m s^{-1})	4.2±0.2	4.1±0.3	t_4=0.38, ns
d$E_{K,ext}$/dt (W kg^{-1})	−9.7±19.7	−33.4±9.5	t_4=1.69, ns
dE_P/dt (W kg^{-1})	232.3±29.2	243.5±21.3	t_4=−0.45, ns
P_{CoM}=(d$E_{K,ext}$/dt)+(dE_P/dt) (W kg^{-1})	222.6±43.3	210.0±25.5	t_4=0.41, ns
P'_{ind} (W kg^{-1})	182.0±37.7	172.3±14.7	t_4=0.32, ns
P_{pro} (W kg^{-1})	9.2±2.7	11.5±4.3	t_4=−0.69, ns
P_{par} (W kg^{-1})	0.4±0.05	0.2±0.03	t_4=−2.63, P=0.013
P_{aero}=P_{CoM}+P'_{ind}+P_{pro}+P_{par} (W kg^{-1})	414.3±31.2	393.3±27.1	t_4=0.55, ns

V_0 is the velocity of the bird at take-off; V_2 is the velocity of the peafowl at the end of the second wing stroke; d$E_{K,ext}$/dt is the rate of change of kinetic energy of the centre of mass (CoM); dE_P/dt is the rate of change of potential energy of the CoM; P_{CoM} is the total power of the CoM, calculated as the sum of the rate of change of potential and kinetic energy; P'_{ind} is the component of induced power required to generate the induced velocity per se, calculated as the difference between the induced velocity and P_{CoM}; P_{pro} is the profile power; P_{par} is the parasite power; P_{aero} is the total power requirement of take-off calculated as the sum of P_{CoM}, P'_{ind}, P_{pro} and P_{par} (following Askew et al., 2001).
Reported values are means ± s.e.m. for five individuals. For each individual, the flight with the highest P_{CoM} for each of the two treatments was selected for statistical comparisons. All powers are expressed relative to pectoralis muscle mass and are averages of the maximal flight for each individual studied.
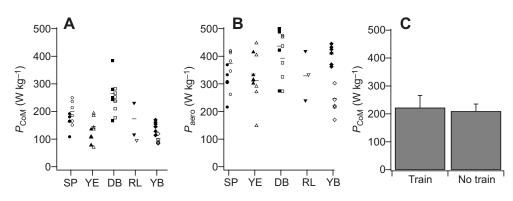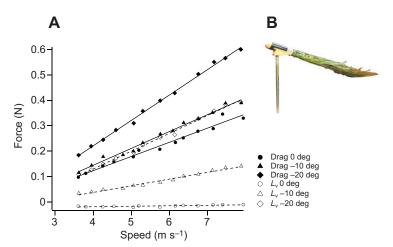
Fig. 1. The effects of possessing a train on the performance and power requirements of take-off in male peafowl. (A) Inter-individual variation (bird identification denoted as: SP, YE, DB, RL, YB) in take-off flight performance (power of the centre of mass of the body, P_{CoM}) relative to pectoralis muscle mass. Filled symbols are data for birds with a train and open symbols represent individuals from which the train has been removed. Horizontal lines indicate the mean value for each individual. (B) Inter-individual variation in total aerodynamic power requirements during take-off flight (P_{aero}; bird identification and symbol notation as in A). (C) Maximal take-off flight performance (P_{CoM}) across all individuals; data are presented as means (±s.e.m.) of the maximal flight performed by each individual.

Not all flights performed were maximal, as indicated by the range of values measured for the total aerodynamic power requirements of take-off (P_{aero}; Fig. 1B). The flights were performed in a flight arena with which the birds were familiar, using captive-bred birds. These are conditions that could potentially compromise performance. If flights were submaximal performance, it would be feasible for a bird encumbered by some handicap to maintain take-off performance (P_{CoM}) by increasing the mechanical power output of the flight muscles (P_{aero}) and the conclusion about the absence of a significant effect on locomotor performance could be doubted. The maximal P_{aero} recorded across individuals was similar and averaged $403.7 \pm 19.8 \, \text{W kg}^{-1}$. Whether these flights were maximal is not known; however, the total power is close to the maximal power reported in other species [$395 \, \text{W kg}^{-1}$ in magpie, $350 \, \text{W kg}^{-1}$ in grey jay (Jackson and Dial, 2011); $390 \, \text{W kg}^{-1}$ in blue breasted quail (Askew et al., 2001)]. The work output from the muscles ($66 \, \text{J kg}^{-1}$) is also close to the total mechanical work required from the muscles during take-off flights in common raven [$48 \, \text{J kg}^{-1}$ (Jackson and Dial, 2011)] and Harris hawks [$56 \, \text{J kg}^{-1}$ (Askew et al., 2001)], and close to the maximum work skeletal muscles are predicted to be capable of generating (Peplowski and Marsh, 1997). Together, the high power output and work generated by the flight muscles suggest that the flights obtained for each individual were likely very close to maximal, and performed with a similar level of effort.

The absence of a detectable effect of the male peafowl train on flight take-off performance does not necessarily mean that there is no

cost to possessing a train: there are other potential costs. It could affect the bird's moment of inertia, which could affect flight control and stability. The train could impair running performance and increase the metabolic cost of carrying the additional mass during terrestrial locomotion (Marsh et al., 2006). There is also the cost of feather production during the seasonal growth of the train. The cost of feather production, C_f, is estimated to be $54.9 \, \text{kJ g}^{-1}$ dry feathers [following Lindstrom et al. (Lindstrom et al., 1993) and using an estimate of basal metabolic rate from Lasiewski and Dawson (Lasiewski and Dawson, 1967)]. The mass of the train in this study was $320 \, \text{g}$, giving an estimated cost of producing the train of $17.5 \, \text{MJ}$. The train is produced over ~6 months (M. Caunce, personal communication), such that the train production costs are estimated to be $96.3 \, \text{kJ day}^{-1}$, representing ~10% of basal metabolic rate [$947 \, \text{kJ day}^{-1}$ (Lasiewski and Dawson, 1967)] and 3% of field metabolic rate [$2805 \, \text{kJ day}^{-1}$, estimated from a scaling equation for Galliformes (Nagy et al., 1999)]. None of these potential costs are mutually exclusive and all could individually be relatively subtle and difficult to detect: the ultimate fitness costs could be the result of the cumulative effect of each of these factors on locomotor performance.

Conclusions

The peacock's train is often cited as a classic example of a 'costly' product of sexual selection. However, here it is demonstrated that possessing a train does not detrimentally affect take-off flight performance. This is partly due to the low drag of the train and its

Fig. 2. The aerodynamic forces on a peafowl train at a range of air velocities and angles. (A) The angle of the train in relation to the free-stream airflow is equivalent to its angle relative to the flight trajectory of the peafowl during take-off. The vertical component of the lift force (L_v) represents the contribution of the train to weight support. For comparison, the mean weight of the peafowl in this study was $45.7 \pm 1.4 \, \text{N}$. (B) A peafowl train mounted in the wind tunnel for aerodynamic force measurements (mounted at an angle of $-20 \, \text{deg}$ relative to the airflow at an air velocity of $3.95 \, \text{m s}^{-1}$).

consequent trivial effects on take-off power. These results do not necessarily mean there are no costs associated with possessing an ornate train; rather, any such costs are small with limited meaningful functional significance to take-off performance.

MATERIALS AND METHODS
Animals and flight recordings
Five mature, adult male Indian peafowl (*P. cristatus*) were obtained from a UK population of captive-bred birds.

Flight arena and filming set-up
A flight arena (1.7×4.3×4.6 m, width×length×height) was constructed from galvanised steel scaffolding covered with galvanised steel chicken wire netting (50 mm hexagonal sections). Two wooden perches were placed within the flight chamber (separated by a total distance of 3.5 m and by a vertical distance of 2.7 m). The peafowl were flown within the flight arena and recorded using two synchronised digital high-speed video cameras (Troubleshooter, Fastec Imaging, San Diego, CA, USA) operating at 125 frames s^{-1} and shuttered at 0.8 ms and mounted on tripods. The flight arena volume was calibrated using the direct linear transformation method (Hedrick, 2008). Peafowl were stimulated to fly from the lower to the higher perch (usually by clapping or rattling a stick on the perch) in an effort to elicit a maximal response. The flight was recorded using a centre trigger mode that recorded a sequence of images both before and after the trigger, thereby capturing the flight in its entirety. There were two experimental conditions: flights were recorded in birds possessing the train and following removal of the train. The train was removed by cutting through the calamus (shaft) of the feathers close to the body using secateurs, either 2 or 5 days after the recording of the flights in which the birds had trains. The flights in birds from which the train had been removed were recorded on the same day that the train was removed. However, birds were given time to become accustomed to the missing train, prior to recording.

Kinematic and aerodynamic analysis of flight
All recordings were initially assessed to determine which flights to analyse. Flights were analysed if the bird flew between the two perches without colliding with the sides of the flight arena. From the two synchronised video images, the estimated CoM (taken as the centre of the body), the positions of the wing base and wing tip in the extreme upstroke and downstroke positions, and the base and tip of the train were manually tracked using an *x*, *y*, *z* coordinate system (where *x* and *y* are orthogonal coordinates in the horizontal plane, and *z* is the vertical coordinate) relative to a fixed origin (Askew et al., 2001; Morris and Askew, 2010; Wakeling and Ellington, 1997) using customised software (Hedrick, 2008). Flights were digitised from the instant the bird became airborne to the start of the third downstroke. All of the power generated during this period can be attributed to the flight muscles as the hindlimbs are not in contact with the ground. The coordinates of the CoM of the bird were plotted with respect to time for each flight and a quadratic equation was fitted to the data. The velocities were calculated by differentiating the quadratic equation in each axis dimension with respect to time [following the methods reported elsewhere (Askew et al., 2001; Wakeling and Ellington, 1997)]. The overall velocity (*v*) of the bird was calculated as follows:

$$v = \sqrt{\left(\dot{x}^2 + \dot{y}^2 + \dot{z}^2\right)} . \tag{1}$$

Take-off performance was quantified by calculating the rates of change of the potential energy (dE_P/dt) and kinetic energy (d$E_{K,ext}$/dt) of the CoM (Askew et al., 2001):

$$\frac{dE_P}{dt} = M_b \boldsymbol{g}\dot{z} , \tag{2}$$

$$\frac{dE_{K,ext}}{dt} = \frac{M_b}{2}\left(\frac{v_{max}^2 + v_{min}^2}{\Delta t}\right), \tag{3}$$

where M_b is body mass, v_{max} and v_{min} are the maximum and minimum velocity, respectively, $\boldsymbol{g}$ is gravitational acceleration and Δt is the flight

duration. In flights in which the bird decelerated, the rate of change of kinetic energy was defined as being negative. P_{CoM} was calculated as the sum of the rate of change of potential and kinetic energy (Eqns 1 and 2):

$$P_{CoM} = \frac{dE_P}{dt} + \frac{dE_{K,ext}}{dt} . \tag{4}$$

To allow the total effort of take-off to be assessed, it was necessary to estimate the total power requirements of take-off (P_{aero}). An aerodynamic model was used to calculate the induced (P_{ind}), profile (P_{pro}) and parasite power (P_{par}) components of flight, the sum of which equals P_{aero} (following Askew et al., 2001; Morris and Askew, 2010; Wakeling and Ellington, 1997).

P_{ind} was calculated as the product of the velocity through the actuator disc (*w*) and net thrust (*T*). The induced power factor (*k*) was included in this equation to correct for tip losses and non-uniformity in the wake (Wakeling and Ellington, 1997); it was assumed that *k*=1.2:

$$P_{ind} = T(kw - v\sin\alpha') , \tag{5}$$

where –α′ is the angle at which the velocity vector is inclined to the actuator disc (Wakeling and Ellington, 1997). The total thrust (*T*) was calculated as:

$$T = M_b\left(a - \boldsymbol{g}\right), \tag{6}$$

where *a* is body acceleration and $\boldsymbol{g}$ is gravitational acceleration (taken as −9.81 m s^{-2}). P'_{ind} is the component of induced power required to generate the induced velocity itself (Askew et al., 2001) and was calculated from the difference between P_{ind} and P_{CoM}.

w was calculated using classic actuator disc theory (Wakeling and Ellington, 1997). Induced velocity was determined by solving Eqn 7 for *w*:

$$w^4 - 2vw^3\sin\left(\alpha'\right) + v^2w^2 - \left(\frac{T}{2\rho D}\right)^2 = 0 , \tag{7}$$

where *D* is the area of the actuator disc:

$$D = \phi l_w^2 , \tag{8}$$

where l_w is extended wing length during the downstroke and ϕ is wing stroke amplitude.

Parasite power resulting from drag on the body (Pennycuick, 1975) was calculated as:

$$P_{par} = \frac{1}{2}\rho S_b C_{D,par}v^3 + F_t v , \tag{9}$$

where ρ is air density, S_b is body frontal area [calculated following Pennycuick et al. (Pennycuick et al., 1988)], $C_{D,par}$ is the parasite drag coefficient, taken to be 0.13 (Rayner, 1999) and F_t is the drag force on the train (where present) at the velocity *v* (see 'Wind tunnel tests', below).

The profile power (P_{pro}) required to overcome the drag on the wings during the downstroke was calculated as:

$$P_{pro} = \rho v_R^3 S_w C_{D,pro} , \tag{10}$$

where S_w is wing area, $C_{D,pro}$ is the profile drag coefficient and v_R is the resultant velocity of the wing at the estimated wing's centre of lift (taken to be 2/3l_w) (after Pennycuick, 1967):

$$v_R = \sqrt{\left(\dot{x} + \frac{4}{3}\phi l_w n\cos\beta\right)^2 + \left(w + \dot{z} - \frac{4}{3}\phi l_w n\sin\beta\right)^2} , \tag{11}$$

where *n* is wing beat frequency and β is the angle of the stroke plane relative to the horizontal. The profile drag coefficient $C_{D,pro}$ was taken to be 0.02 (Rayner, 1979).

For each individual, the flight with the highest P_{CoM} for the two treatments was selected for statistical comparisons, as any potential differences in performance are most likely to be apparent during maximal effort flights.

Morphological measurements
Following the flights, animals were killed using an overdose of sodium pentobarbital injected into the brachial vein. The outstretched wings were photographed in order to determine wing area and wing length. The pectoralis and supracoracoideus muscles were dissected and their masses determined. The mass of the train was also determined. All power

components were expressed relative to the total pectoralis muscle mass, determined post-mortem.

Wind tunnel tests

The train was secured inside a hollow cylindrical tube (170 mm long×68 mm outer diameter) with a hemispherical nose profile, which held the train in a manner that reproduced the in-flight train morphology. The cylinder was mounted on a six-component under-floor balance (Aerotech ATE Ltd, UK) via a 20 mm diameter cylindrical shaft that passed through a clearance hole in the floor of the wind tunnel (see Johl et al., 2004). Tests were performed with the train mounted at angles of 0, −10 and −20 deg at free-stream velocities (v) of 3.6–8 m s^{-1}, encompassing the range of speeds and angles (relative to the path of motion of the bird) observed during take-off. Equivalent force measurements were also made on the cylinder and mount, and these values were subtracted from the force measurements made with the train in place. All force measurements were sampled at 300 Hz and averaged over 20 s to obtain a mean.

Comparative and statistical analyses

Reported values are means ± s.e.m. for the five individuals. Flight performance variables and aerodynamic power components were analysed using paired t-tests with significance levels adjusted using the Bonferroni–Holm correction for multiple comparisons.

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