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Combining the use of accelerometry and GPS to measure free-flight performance in homing pigeons (Columbia livia)

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Combining the use of Accelerometry and GPS to Measure Free-Flight Performance in Homing Pigeons (*Columba livia*)

by

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ABSTRACT

Miniature accelerometer data loggers, in combination with GPS tags, were deployed on homing pigeons during 11 km flights along the Menai Strait, Bangor, North Wales in order to use new technology to assess the flight performance of free-ranging birds. The GPS data was used to calculate position and ground speed during the flights and the latter was converted to estimated airspeed using anemometer readings located on the local Britannia Bridge. The accelerometer data was used to calculate wing beat frequency (WBF) and a number of other variables, such as vectorial dynamic body acceleration (VeDBA), mean acceleration in the y-axis (static y) and a term called fraction positive (the proportion of time per wing beat spent accelerating the body above average g force). Relationship between these variables and airspeed were investigated along with the potential effects of pigeons carrying added mass or flying in different environmental conditions, such as strong tailwinds, low winds or strong headwinds.

Integration of the raw Y and Z-axis accelerations were used to calculate power in the body of the bird (using *Power = Mass x Acceleration x Velocity*), assuming no net change in velocity over the section of integrated data. This indicated that the power detected by the accelerometer could be as little as approximately 3% of the total flight biomechanical costs, at a wing beat frequency of around 7 Hz. However, VeDBA_{YZ}^2 was very highly linearly correlated ($R^2 = 0.947$) with the integrated raw yz-accelerations and, therefore, an excellent predictor for power in the body of a pigeon. This relaltionship should also be applicable to other flying animals. Double integration of the z-axis

accelerations and assuming sinusoidal accelerations and motion of the body gives an estimate of dorsal body displacement.

Pigeons that were released individually flew with relatively low wing beat frequencies (L-WBF, < 6 Hz), low airspeeds (14.89 m s^{-1}) and low values of VeDBA^2 (1.17 m s^{-2}) during the flights back to the loft. Pigeons released as a flock on average flew with relatively high airspeeds ($>20 \text{ m s}^{-1}$) and usually with high wing beat frequencies (H-WBF, > 6 Hz). However, some birds occasionally broke from the back of the flock and flew more slowly and with L-WBF. Values of VeDBA^2 and fraction positive tended to be positively correlated with WBF.

When birds were released in a flock, airspeed was not found to vary systematically with wind speed or direction on different days but to be fairly consistent around a mean value of 20.9m s^{-1} (range 17.8m s^{-1} to 23.9m s^{-1}). $\text{VeDBA}_{\text{YZ}}^2$ was shown to be well correlated with airspeed ($\rho = 0.703$) and this suggested that power in the body was, indeed, a reasonable indicator of the overall biomechanical flight costs. WBF showed a slightly less predictable response. It was possible to categorise the birds as slow or fast returning birds, particularly in the flight into the strong headwind, with $\text{VeDBA}_{\text{YZ}}^2$, wing beat frequency and fraction positive generally much lower for the slowest group of birds on the day. Wing beat frequency tended to be consistently correlated within-individuals across days, but there was a considerable amount of variation in $\text{VeDBA}_{\text{YZ}}^2$ for a given value of wing beat frequency between individuals, indicating the difficulties in making average assessments of flight performance.

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Abbreviations and Symbols

$\Delta\lambda$ – Difference between longitudinal measurements

$\Delta\sigma$ – Angular distance

ρ – Density of air or correlation co-efficient

φ – Latitude

$-\Phi$ to $+\Phi$ - Angular excursion angle of the wing relative to the body

B - Body

CaO_2 – Amount of oxygen in arterial blood

$C\overline{V}\,O_2$ – Amount of oxygen in venous blood

DLW – Doubly labelled water

DOP – Dilution of precision

E_b – Energy in body

f or WBF – Wing beat frequency

f_H – Heart rate

g – Acceleration due to gravity

GPS – Global positioning systems

H-WBF – High wing beat frequency

L-WBF – Low wing beat frequency

m – Mass

m_b – Mass of body

m_w – Mass of wings

ODBA – Overall Dynamic Body Acceleration

OS – Ordnance Survey

P_b – Power required by body

PDBA – Partial Dynamic Body Acceleration

Pint – Integrated power in the body

S – Wing area

V – Air velocity

VeDBA – Vector Dynamic Body Acceleration

VeDBA$_{YZ}$ - Vector Dynamic Body Acceleration in the Y and Z axes

V_{MP} – Minimum power speed

V_{MR} – Maximum range speed

$\dot{V}$ O$_2$ – Oxygen consumption rate

$\dot{V}$ s – Stroke volume

ω – Angular frequency of wing beats

W – Wings

z_b – Vertical displacement of body

$\dot{z}_b$ - Vertical velocity of body

z_w – Vertical displacement of wing

$\dot{z}_w$ – Vertical velocity of wing

CHAPTER I - General Introduction

Birds and bird flight have always captivated humans, scientists and the general public alike. For some this fascination stems from their evolution from dinosaurs, for others it is their remarkable versatility that has led them to colonising every continent on Earth, but for many it is their ability to fly. Flapping flight is extremely energetically demanding (Rayner, 2001) and the fact that some species are capable of making migrations of thousands of miles is remarkable (Hendenström, 2002). At the other extreme, some species are only capable of short bursts of flight whilst others have lost the ability to fly completely (reviewed by McNab, 1994). This diversity makes birds, their anatomy, physiology, metabolism and behaviour intriguing topics for research.

Early work on avian flight can be traced back to the 1860's and 1870's. For example Hutton (1873) observed and described the detailed wing movements of flying black-backed gulls (*Larus dominicanus*), although societies as far back as the ancient Greeks tried to address the question of how do birds fly? (see Videler, 2005). The creation of aeroplanes meant that natural flyers were studied extensively during the early parts of the 20th century and for this reason bird flight proved to be a popular research topic during the inter-war periods (e.g. Idrac, 1925; Bunnell, 1930; Cooke, 1933). Post-war technological progress was utilised by natural historians with many using photography to produce 'stills' of moving bird wings whilst flapping (e.g. Brown, 1948). Theoretical and mathematical modelling than began to come into the mainstream from the 1960's onwards, with C.J. Pennycuick and J.M.V. Rayner at the forefront of this growing research field. Their aerodynamic models are still the basis of many flight experiments (Pennycuick, 1998; Rayner, 2001). Pennycuick (1998) created an analogy between the three legs of a tripod and the three research disciplines frequently used to study bird flight ('physics, physiology and strategy'), stating that as with a tripod, all three aspects of investigation are required to make informed, stable conclusions.

Areas for flight research range from take-off and hovering flight, to mechanics and aerodynamics, to energetics and flight performance (e.g. Tucker, 1971; Rayner, 1982; Marden, 1987; Pennycuick et al., 1989; Hedenström and Alerstam, 1995; Tobalske and Dial, 1996; Askew et al., 2001; Tobalske, 2007; Berg and Biewener, 2010). However, much of what we know about avian flight biology has been established through theoretical and modelling work, along with the use of laboratory experiments and wind tunnels. More recently improvements in electronic technology, such as the invention of miniature global positioning systems (GPS) and light-level geolocators (e.g. Bächler et al., 2010; Catry et al., 2010; Egevang et al., 2010) have played a major part in the rapid acquisition of high-resolution data of free-living or free-ranging animals. Similarly, the development of miniaturised data loggers incorporating additional physical and physiological parameters (such as temperature, pressure, accelerometry and heart rate) has made it possible to address some of the aerodynamic predictions in truly free-flying birds, rather than be solely dependent on the constraints of wind tunnel and laboratory studies (e.g. Gagliardo et al., 2007; Weimerskirch et al., 2009; Gagliardo et al., 2011).

It is fair to say that the use of GPS has become widespread since the turn of the 21st century to monitor flight paths, with ever more complex and lighter designs being manufactured (see section 1.2.3). This type of work gives an increased insight into the daily lives of animals without causing them unnecessary disturbance from humans (although the negative impacts of fitting animals with loggers should be considered, see section 1.2.1). Due to logger size and weight, early work concentrated on large pelagic seabirds such as the wandering albatross (*Diomedea exulans*) (Weimerskirch et al., 2002; Fritz et al., 2003) and the Cape gannet (*Morus capensis*) (Grémillet et al., 2004). This early work centring around GPS monitoring gave an unprecedented and fascinating in-depth insight into foraging patterns and behaviours. Early scientists who pioneered and persevered with GPS technology have made it possible for modern-day biologists to use such loggers to investigate flight performance as it is extremely difficult to monitor free-flying birds accurately without these devices.

The main aim of this thesis was to explore how the flight patterns, behaviour and energetics of free-flying homing pigeons (*Columba livia*) can be assessed using miniature GPS and accelerometer data loggers. Consideration is given to how accelerometry in particular may be used to determine specific flight behaviours and to provide an indication of how much energy and relative effort the pigeon is consuming during flight. Flight performance is assessed with respect to the potential effects of environmental factors such as wind strength and direction, body morphology (such as differences in natural body mass or experimental manipulation of carried mass), and individual behavioural differences such as homing motivation and flight speed. The species of choice is the homing pigeon (*Columba livia*) because they can be easily trained to carry biologgers while returning to a home loft from release sites at various locations, thus allowing flight in relatively natural surroundings.

1.1 Theoretical basis of flight performance in pigeons

There are several components to the aerodynamics of bird flight, including drag, thrust and lift, which closely link bird morphology to flight performance (Pennycuick, 1968a). The relative wing span and area per unit body mass are considered to be particularly important, along with the individual style and kinematics of the wing. Compared to man-made systems, birds such as pigeons are considered to have rather limited flight capabilities, e.g. high co-efficients of body and wing profile drag and a mediocre lift to drag ratio (Pennycuick, 1968a). Nevertheless, pigeons are excellent avian generalists and are able to fly in a wide variety of situations due to their powerful morphology (low aspect ratio, large flight muscles, large hearts etc) and ability to create enough thrust to generate relatively fast forward flight (Rayner, 1979). Theoretical models have been used extensively to predict and investigate the relationship between the interlinked factors of flight mechanics and aerodynamics and describe how a bird should behave if it is to fly effectively and strategically.

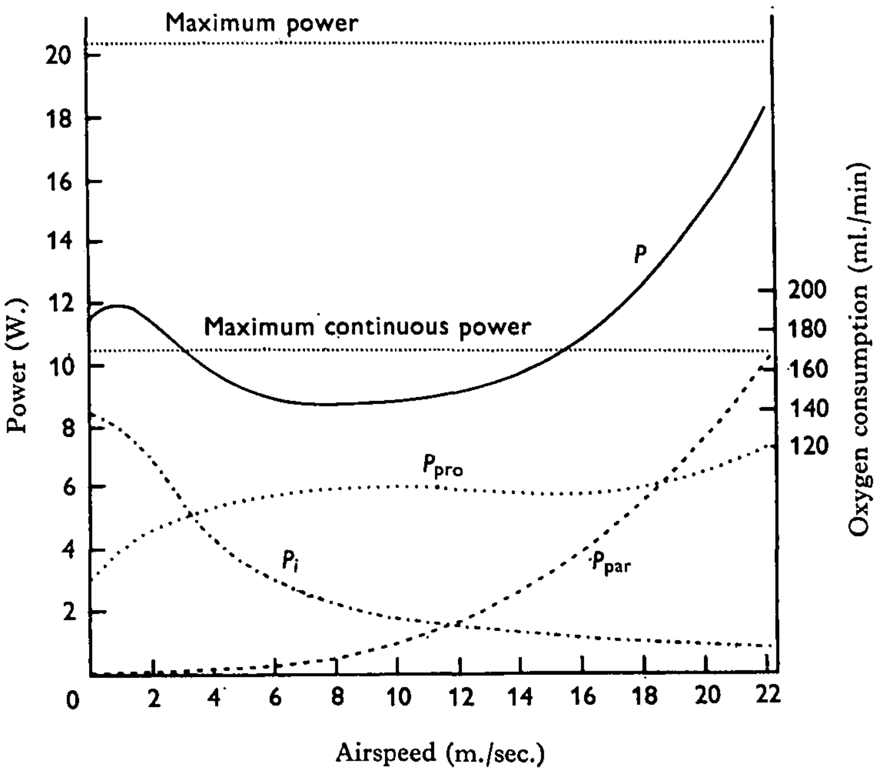


Fig. 1.1 Power (W) requirements plotted against speed (ms^{-1}) for the pigeon (*Columba livia*); *Pi is* induced power, Ppro is profile power, Ppar is parasite power, *P* is total power. The continuous line represents the U shaped curve. Taken from Pennycuick (1968a).

From the U-shaped curve plotted for pigeons by Pennycuick (1968a, Figure 1.1) it is possible to see that the power required for flight should be greatest during slow and fast speeds, with the minimum power needed for speeds in between these extremes. In general, as flight speed increases, induced power (required to increase the velocity of the air over the wings and support the weight of the bird) decreases whilst parasite and profile power (required to provide thrust to overcome drag) increases, although Rayner and Pennycuick's models handle profile power slightly differently (Pennycuick 1968a; Rayner 1979). This overall power curve displays two distinct speeds, one where power required is at an absolute minimum (V_{MP}) and the other where overall or total flight costs per unit distance are minimal and the range of travel is maximised (V_{MR}). Flying at speeds above or below the minimum power speed is more demanding than remaining at V_{MP}, thus, the latter ensures that the bird can remain in flight for the greatest amount of time (Pennycuick, 1969a). The power required for horizontal flight above V_{MP} increases with velocity primarily as there is an increase in air resistance and, therefore, drag and this causes profile and parasite power to increase (Rayner, 1999).

Horizontal flight even at V_{MP} still requires quite a large amount of power and can be up to 10 to 20 times basal metabolic rate in larger species (Butler 1991; Bishop, 1999; Rayner, 1999). However, due to the necessity of birds having to flap their wings to generate both lift and thrust, along with the complex kinematic movements and structure of feathers, it is difficult to predict power curves for species with the accuracy that has been attributed to aeronautical engineering (Pennycuick, 1998). For example, in Fig. 1.1 the flight power predicted for the pigeon does not directly match up to empirical measurements of metabolic power. Gessaman and Nagy (1988) show that pigeons can sustain flight speeds of at least 20 m s^{-1} (at around 21 W kg^{-1}) compared to Pennycuick's 1968 estimate of 16 m s^{-1} for aerobic top speed (at around 30 W kg^{-1}). However, more recent default values for Pennycuick's model do alter these predictions (Section 1.1.1. and Chapter III).

In theory, it might be expected that most species of birds should chose to fly faster than their V_{MP}, as their overall energy expenditure and flight time can be reduced with only a slight requirement of increased power per unit time (Pennycuick, 1997). Thus, V_{MR} is the most economic speed, particularly if they must travel a long way, e.g. on migration. However, for some species with relatively limited aerobic ability, the advantage of flying faster can become outweighed by the extra power required even before V_{MR} is achieved (Pennycuick, 1997), while some species, such as the homing pigeon, seem to have such excellent aerobic capacity that they may be capable of flying well above their predicted V_{MR} for many hours (Gessaman and Nagy, 1988). The actual rate of chemical energy turnover (metabolic power) required by birds is much higher than the mechanical power for flight, partly because additional metabolic power is also used throughout the body and not just in the metabolism of flight muscles (Pennycuick, 1998). For example, it is typically estimated that the metabolic costs of breathing and circulating the blood could be as much as 5% each of the overall costs of locomotion.

The other major consideration, however, is that the flight muscles may vary in their efficiency in converting stored chemical energy (adenosine triphosphate) into usable mechanical energy (Rayner, 1988; Kvist et al., 2001; Bishop, 2005), with the rest liberated as heat. Indeed, some authors believe that the efficiency of the flight muscles is even constant within an individual bird, and can vary between species, or with body mass, or flight speed (Rayner, 1988). For example, in a recent study it was suggested that the mechanochemical conversion efficiency increased by 4.3% in cockatiels (*Nymphicus hollandicus*) as their flight speed increased from 8 m s^{-1} to 13 m s^{-1} (Morris et al., 2010), with a range between 6.9% and 11.2%. The potential scaling of flight muscle efficiency introduces another very significant level of uncertainty into the study of both metabolic and biomechanical costs of flight (Bishop, 2005) but, at least for pigeons, the default value for flight muscle efficiency has been taken as around 23% (Pennycuick, 1968a) and this value will be used in this thesis.

1.1.1 Drag

There are three components to drag in a gliding bird – induced drag which is the drag incurred by accelerating the air to support the birds' weight when airborne, plus profile drag from the movement of the wings and parasite drag from the cross-sectional area and shape of the body (Pennycuick et al., 1992). Drag is an important aspect of bird flight energetics, particularly at higher velocities and a bird must generate enough thrust to balance all the created drag by accelerating air backwards (Videler, 2005). However, gliding birds are quite capable of supporting their body weight, but the forward thrust required to overcome drag (profile and parasite) when transferring to horizontal flight can only be created when the bird flaps its wings (Rayner, 1985).

Again, there has been some degree of debate and uncertainty regarding the exact value of the body drag coefficient for parasite power (Pennycuick et al., 1996; Hedenström and Liechti, 2001). This discrepancy has been highlighted, for example, when relatively high values for drag were obtained from frozen specimens placed in a wind tunnel (Pennycuick et al., 1988), whilst lower values appeared to be more appropriate for living birds with more streamlined bodies than so-called 'bluff bodies' (Pennycuick et al., 1996). As a result, it was suggested that the default value for the body drag co-efficient should be assumed to be 0.05 to 0.1 replacing the previous default values of between 0.25-0.40 (Pennycuick et al., 1996). However, this has been questioned as values of between 0.17-0.77 (mean of 0.37) have since been estimated in free-flying but "diving" or rapidly descending birds (Hedenström and Liechti, 2001), which seemed to confirm the 'older' estimates for the drag co-efficient. Conversely, when birds such as the swallow (*Hirundo rustica*) are flown in a wind tunnel, their effective drag co-efficient (when compared to predicted but modelled results) appear too high, possibly because their rather erratic flight behaviour (such as movements of the head and tail) could create additional drag (Pennycuick et al., 2000). To some extent, birds may also be capable of altering the amounts of drag experienced on different areas of their wings by changing their wing shape, most notably by flexing the carpo-metacarpal region, as shown by a Harris' hawk (*Parabuteo unicinctus*) perched within a wind tunnel (Pennycuick et al., 1992). Thus, uncertainties in the values for parasite and profile drag, may provide a limit to the accuracy of predictions for the modelled biomechanical costs of flight. In this thesis, the more recent body drag coefficient of 0.1 is used for modelling pigeon flight (Chapter III) as, counter to the observations of Hedenström and Liechti (2001), this value appears to provide more realistic values for estimated mechanical flight costs of homing pigeons.

1.1.2 Wing beat frequency

By using field observations, Pennycuick (1990) was able to present a mathematical model to determine the wing beat frequency of a bird derived from its morphological characteristics:

$$f = 1.08(m^{1/3}g^{1/2}b^{-1}S^{-1/4}\rho^{-1/3}) \tag{1.1}$$

where, f is wing beat frequency, m is mass, g is acceleration due to gravity, b is wing span, S is wing area and ρ is the density of air. As the density of air decreases with altitude, flying higher will increase an individuals' minimum power flight speed and wing beat frequency whilst decreasing its overall flight time, but this will increase biomechanical costs as well as put more demand upon its heart and circulation causing it to work harder and require more power (Pennycuick and Battley, 2003). Assuming that measurements are identical to the methods used by Pennycuick (1990), it should be possible to use this equation to accurately predict wing beat frequency for other species, especially as it was based on data from extremely diverse species. Pennycuick revised this equation in 1996 as he found that wing beat frequency was underestimated in species with higher wing beat frequencies. The equation derived by Pennycuick (1996):

$$f = m^{3/8} g^{1/2} b^{-23/24} S^{-1/3} \rho^{-3/8} \qquad (1.2)$$

shows that as body mass increases, so too does wing beat frequency. In a more recent study, using equation 2, Pennycuick (Pennycuick, 2001) was able to predict wing beat frequency and by using this formula it was possible to calculate with good accuracy the wing beat frequency of species that flew using either flap-gliding or solely flapping flight. Morphological measurements taken from the experimental pigeons were averaged to create values for an ‘average’ pigeon from the flock. Using equation 1 (Pennycuick, 1990) the average wing beat frequency should be approximately 7.26Hz. Similarly by using equation 2 (Pennycuick, 1996), it should be roughly 6.35Hz. Using Figure 3.10 (Chapter III) it is possible to see that the average wing beat frequency during steady flight was around 6.8Hz, while during take-off it was 7.7Hz. These values are reasonably similar to those derived from Pennycuick’s equations and suggest that for pigeons, at least, these formulae can be used to generally link morphology to wing beat frequency.

1.2 Biologgers

'Biologging' is the term used to refer to devices affixed to animals to collect data about the individual or the environment in which it is living (Rutz and Hays, 2009). For many years scientists have attached data logging equipment to animals (for example, Wilson et al., 1997; Tremblay et al., 2003). This method has several advantages as it enables data to be collected in free-ranging animals and gives a better insight into natural behaviours, rather then those affected by the artificial situation induced by captivity. These methods also reduce human disturbance and handling (Gauthier-Clerc and Le Maho, 2001).

Historically, a large number of tags have often been fitted to marine vertebrates, such as Adélie penguins (Culik et al., 1994), seabirds (reviewed by Wilson et al., 2002 and cited references) and loggerhead sea turtles (*Caretta caretta*) (Schofield et al., 2007). Data loggers have been used to record diving depth and time spent underwater, temperature, heart rate (e.g. Wilson et al., 1995; Hochscheid et al., 1999; Quintana et al., 2007) and satellite tracking (e.g. Butler et al., 1998). The main advantage of marine vertebrates is that they are generally quite large and, at least for those species that are aquatic, some of the weight of the devices can be reduced via buoyancy. Such an approach has greatly increased our understanding of both behavioural and physiological responses of animals in the field as well as helping scientists to monitor environmental changes. However, there are several issues associated with the attachment and use of data loggers on free-ranging animals.

1.2.1 Considerations on the use of biologgers

One notable draw back of the use of biologgers is the fact that these devices may need to be attached for long periods of time and could interfere with the normal behaviours or normal routines of the animal carrying the logger. Whilst the attachment of such devices to animals can improve understanding regarding their ecology (Wilson and Wilson, 1989; Wilson and McMahon 2006), care must be taken to consider the possible negative effects this may have on the individual animal. Biologgers used to be relatively large and bulky and could be difficult to fit and secure to the animals. It has been shown by several authors (for example Wilson et al., 1986; Culik et al., 1994; Ropert-Coudert et al., 2000; Bowlin et al., 2010) that animals are affected by the wearing of loggers. Wilson et al. (2002) therefore suggest that scientists should only use the technology if the individual performs "normal" behaviour.

Trials have been conducted to discover the best possible way in which to attach such loggers to animals to minimise disruption to their lives. For example, Adélie penguins (*Pygoscelis adeliae*) were found to swim slower when fitted with a biologger, particularly if fitted to the middle of the back, although they expended the same power as birds without biologgers, possibly due to larger drag co-efficients (Culik et al., 1994). Similarly, a major concern to flight investigations is the increased drag resulting from the wearing of loggers on the back between the wings, and to this end, scientists have recently begun advocating a move towards leg-loop attachments, rather than thoracic body harness, to reduce drag (Bowlin et al., 2010). Studies have also compared internally and externally fitted loggers on Adélie penguins (Culik and Wilson, 1991). Both methods of attachment had some detrimental effects on the penguins. However, penguins fitted with external loggers had to use more power when swimming, although they did swim faster than those fitted with internal loggers. It may also be important that the logger is affixed correctly (Wilson et al., 2008) and securely and where possible is camouflaged against the animals' body (Wilson and McMahon, 2006). This will help lessen the risk of predation (Hawking, 2004) and can help reduce the amount of time spent excessively grooming (Wilson et al., 1990).

1.2.2 Design of biologgers

An animal swimming in water can be likened to one flying in air as both are fluid mediums and both activities incur drag. Loggers fitted onto swimming animals will disrupt the flow of water over the individual and because of this the faster the animal swims the greater the increase in drag and greater thrust must be produced to overcome this extra drag (Bannasch et al., 1994). By altering the shape of loggers (from a basic box to a wedge; maximum dimensions 12x5.7x3.3cm) attached to model penguins (gentoo (*Pygoscelis papua*) and chinstrap (*P. antarctica*) in a water tank, drag was substantially reduced by approximately 65% (Bannasch et al., 1994). Similarly investigations have studied the optimal logger shape to be used on a flying bird by comparing various shapes and sizes (e.g. Obrecht et al. 1988). Longer, thinner devices (85.7x40.0x31.8mm) with curved ends reduce drag the most when fitted on wingless bird bodies in wind tunnels (Obrecht et al., 1988). Homing pigeons wearing just such a body harness, with and without added mass attached, flew home significantly slower (Gessaman and Nagy, 1988), highlighting that even the design of the harness must be carefully assessed. With 5% added mass, the pigeons produced significantly more carbon dioxide, indicating that the additional weight and drag forced the birds to work harder and for longer during flight (also see Chapter IV).

As technology is continually developing, data loggers are becoming smaller, lighter and more sophisticated and current developments are aimed at reducing any negative impacts on the individuals wearing them, so as to interfere less with their day-to-day activities.

1.2.3 GPS (global positioning systems)

Animal tracking, and specifically bird tracking, has been utilised in research for several decades. Early work centred upon following individuals in small aeroplanes (e.g. Griffin, 1943; Hitchcock, 1955) to the use of radio tracking; following birds in light aircraft (e.g. Michener and Walcott, 1966, 1967), or on the ground (e.g. Schmidt-Koenig and Walcott, 1978). These latter experiments required that small transmitters be affixed to the birds, but were unable to record data and the individual had to be constantly monitored.

Jouventin and Weimerskirch (1990) were the first authors to effectively satellite track birds using ARGOS-based tags. They focussed their study upon the wandering albatross (*Diomedea exulans*) which can cover several thousand kilometres when foraging (Weimerskirch and Jouventin, 1987), which would have been impossible using the older methods of pursuit monitoring. By the year 2000 the use of the more accurate global positioning system (GPS) was becoming popular. von Hünerbein et al. (2000) were successful in manufacturing a relatively small GPS data logger (33g) which could be used on small birds (greater than body mass 500g), whilst Steiner et al. (2000) had also developed a separate GPS logger (35g) that was also able to be used on pigeons. By 2004, the

GPS loggers used by Biro et al. (2004) weighed between 24g and 28g. Rose et al. (2005) fitted feral pigeons with GPS loggers weighing between 29g and 36g and stated that there were no adverse effects to the birds after being fitted with, and carrying the equipment. Guilford et al. (2008) modified designs by von Hünerbein et al. (2000) and Steiner et al. (2000) to create an even lighter GPS device (weighing approximately 17g) that could be fitted to Manx Shearwaters (*Puffinus puffinus*). These are still too large for many bird species but future improvements down to around 5g are realistic.

Other, less accurate technologies, such as the use of daylight monitoring to estimate longitude and latitude have enabled much smaller species to be monitored on long distance flights. For example, Egevang et al. (2010) fitted micro-geolocating loggers (weighing less than 2g) to Arctic terns (S*terna paradisaea*) to monitor light levels and day length which are used to map their long-distance migration.

1.2.4 Accelerometry

The use of accelerometers to monitor behaviour and potentially energetics is a rapidly developing field. Accelerometers can be useful for measuring both dynamic movements and static body position (Shepard et al., 2008b) and, when incorporated into dataloggers, can make it possible to determine the long term behaviours of individuals even when they are out of sight. Static acceleration can be used to indicate the angle and, therefore, posture, of the individual to the gravitational field of the earth as it is a measure of the accelerometer’s incline (Shepard et al., 2008b). Dynamic acceleration represents the movement of an individual due to a change in speed (Shepard et al., 2008b).

For example, using solely the static acceleration Shepard et al. (2008b) could discriminate between a Magellanic penguin (*Spheniscus magellanicus*) standing upright and lying down, a Eurasian badger (*Meles meles*) lying on its back and on its side, and a leatherback turtle (*Dermochelys coriacea*) changing position, rotating on its front on to its shell. Similarly by detailed monitoring of Imperial cormorants (*Phalacrocorax atriceps*) using accelerometry it was possible to determine the differences between the various forms of locomotion (walking, flying, diving) and stationary postures (standing, sitting, floating) and define a flow diagram to recognise these distinct separate behaviours (Gómez Laich et al., 2008).

Behavioural research has often centred upon observing individuals, which is both time consuming and has associated problems, such as the animals disappearing out of sight (Sakamoto et al., 2009). Ethograms are created to provide a specific list of the full behavioural repertoire performed by a particular species (Lehner, 1987); however it is often necessary to observe a species at great length to create a full ethogram. With the aid of detailed accelerometry data it has become possible to produce comprehensive ethograms although previous understanding of the studied species is still required (Sakamoto et al., 2009).

Tri-axial accelerometry uses three transducers which are placed orthogonally. This enables acceleration to be measured in all three planes (Wilson et al, 2008; see Chapter III for detailed description of accelerometers). One of the first studies to employ this use of the technology to differentiate between behaviours performed by a non-human species was by Yoda et al. (2001) who studied Adélie penguins (*Pygoscelis adeliae*). Since then, species as diverse as cattle (Robert et al., 2009), sockeye salmon (*Oncorhynchus nerka*)

(Clark et al., 2010), green turtles (*Chelonia mydas*) (Yasuda and Arai, 2009), raptors: Harris' hawk (*Parabuteo unicinctus*), tawny eagle (*Aquila rapax*) and Griffon vulture (*Gyps fulvus*) (Halsey et al., 2009b) and, of course, humans (*Homo sapiens*) (Godfrey et al., 2008) have been fitted with accelerometers to monitor their movements. Patterns of average dynamic body acceleration (DBA) can also be directly correlated with measures of energy consumption or power output, for example, using measures such as vectoral dynamic body acceleration (VeDBA) or overall dynamic body acceleration (ODBA), which have provided strong correlations with energy consumption during terrestrial locomotion (e.g. Halsey et al., 2008; Halsey et al., 2009c) (Section 1.3.3).

1.3 Methods for measuring energy expenditure in the field

Two popular methods have traditionally been used to determine energy expenditure in free-flying birds: the doubly labelled water (DLW) technique or the determination of heart rate (Wilson et al., 2006). Both of these techniques have associated advantages and disadvantages (for review, see Butler et al., 2004 and cited references), but are generally useful as proxies for measuring energy expenditure. Heart rate is directly linked to convection of blood around the body and can be directly correlated with oxygen consumption, whereas doubly labelled water indirectly measures the production of carbon dioxide (Butler et al., 2004) and can be converted to the rate of oxygen consumption using the respiratory coefficient. A few species of birds have also be trained to fly in wind tunnels while wearing masks, enabling direct measurement of gas exchange (Butler, 1991) to be directly compared with DLW and heart rate measurements.

Much of the information on the physiological responses to bird flight comes from such techniques.

1.3.1 Heart rate

The heart rate of an animal is often measured as it can give an indication of the metabolic rate of the individual (Froget et al., 2001). The use of heart rate loggers allows for long periods of monitoring (Froget et al., 2001) and such loggers are able to record other behavioural, physiological and environmental variables (Butler et al., 2004). Unfortunately, these loggers can be fairly expensive, may require skilled surgical implantation and removal and at times the technology can be unreliable (Butler et al., 2004). Additionally, a major problem with this technique it that for every new species studied, different calibration equations need calculating (Froget et al., 2001; Butler et al., 2004) and the detailed association between the heart rate and oxygen consumption of an animal depends upon the physiological conditions of the individual and how active it is (Froget et al., 2001).

The Fick equation can be used to demonstrate the potential relationship between oxygen consumption and heart rate (see Green et al., 2001):

$$\dot{V}\mathrm{o}_2 = f_\mathrm{h} \text{ x } V_\mathrm{s} \text{ x } (C_\mathrm{a}\mathrm{o}_2 - C_{\bar{\mathrm{v}}}\mathrm{o}_2) \tag{1.3}$$

where $\dot{V}\mathrm{o}_2$ represents oxygen consumption rate, f_H represents heart rate, V_s represents stroke volume, $C_\mathrm{a}\mathrm{o}_2$ represents the amount of oxygen in arterial blood and $C_{\bar{\mathrm{v}}}\mathrm{o}_2$ represents the amount of oxygen in venous blood. When V_s $(C_\mathrm{a}\mathrm{o}_2 - C_{\bar{\mathrm{v}}}\mathrm{o}_2)$ remains constant or alters systematically, the relationship between $\dot{V}\mathrm{o}_2$ and f_h will be linear (Butler et al., 1992). Using heart rate to estimate metabolic rate has been shown to be a method that is as precise as any other technique, such as doubly labelled water (Bevan et al., 1994).

1.3.2 Doubly labelled water (DLW)

Doubly labelled water estimates the production of carbon dioxide (Butler et al., 2004) calculated using the differences between the removal rates of isotopes of hydrogen and oxygen from the body (Speakman, 1993). As oxygen can exit the body in the form of either carbon dioxide or water, it moves through faster than hydrogen (which exits solely through water) and, therefore, the differences between these elimination rates can be used to estimate carbon dioxide production (Speakman, 1998). Unfortunately, this method requires the experimental subject to be captured, have body fluid samples taken, injected with isotopes of oxygen and hydrogen ($H_2{}^{18}O$ with one of ${}^2H_2O$ or ${}^3H_2O$); then the individual must be re-captured and samples of body fluids taken again before the animal can be released (Hawkins et al., 2000). Samples must then be analysed in a mass-spectrometer to determine the relative quantity of the various isotopes.

1.3.3 Overall dynamic body acceleration (ODBA)

Overall dynamic body acceleration (ODBA) is a very recent concept that can also be used as a proxy to describe energy expenditure by an individual (e.g. Halsey et al., 2009a). This idea was pioneered by Wilson et al. (2006) and has been tested on a number of species (e.g. imperial cormorants (*Phalacrocorax atriceps*), Wilson et al., 2006; humans (*Homo sapiens*), Halsey et al., 2008; koalas (*Phascolarctos cinereus*), Ropert-Coudert et al., 2009; cane toads (*Bufo marinus*), Halsey and White, 2010; Magellanic penguins (*Spheniscus *magellanicus*), Wilson et al., 2010). Locomotion and movement account for a large amount of energy usage in mammals and birds (e.g. Schmidt-Nielsen, 1972) and because of this Wilson et al. (2008) suggested that ODBA could be a useful method to analyse the energy budgets of different animals. When an animal is moving, it must use energy to contract its muscles and in turn this causes the body and limbs to accelerate and decelerate and, therefore, overall summation of acceleration can be used to indicate energy expenditure (Halsey et al., 2009a).

1.3.4 Comparisons between these techniques

The measurement of heart rate often involves some surgical procedures with invasive implantation of equipment (e.g. Hawkins et al., 2000), which can be viewed as a detrimental to welfare. If data loggers are used, rather than radio transmitters, then this also means that results are not available for many months. However, the use of heart rate is able to estimate energy costs for specific behaviours and movements with high temporal resolution whereas DLW is only able to give an average measurement over a pre-defined time period (usually many hours to days) and not for particular activities (Boyd et al., 1995), while the amount of time required for the study is reliant upon the half life of the $H_2{}^{18}O$. The heart rate technique to determine metabolic rate has generally to be applied to a group and not just for one individual (Bevan et al., 1994) and for every species monitored, species-specific calibrations need to be made (Froget et al., 2001).

Wilson et al. (2006) compared these two methods against the use of 3D-accelerometry on two species of cormorant (*Phalacrocorax carbo* and *P.*

atriceps), by measuring oxygen consumption and carbon dioxide production alongside calculated ODBA values. They discovered a positive linear correlation between ODBA and oxygen consumption and ODBA and the production of carbon dioxide, suggesting that ODBA gives a useful alternative to other more invasive techniques of measuring energy expenditure. Single or double axis accelerometry can also be useful, as a significant correlation existed between partial dynamic body acceleration ($PDBA_{y,z}$) and oxygen consumption in hammerhead sharks (*Sphyrna lewini*) swimming in a respirometer (Gleiss et al., 2010). The relationship between ODBA and oxygen consumption appeared to be generally highly correlated within species, but there was variation between species (Halsey et al., 2009c). In large species oxygen consumption increases rapidly compared to rises in acceleration, suggesting that body mass has to be taken into account when making comparisons between species (Halsey et al., 2009c). Additionally, when height and body mass were included in analyses, ODBA gave better predictions for oxygen consumption in humans (*Homo sapiens*) (Halsey et al., 2008). Indeed, to calculate power, acceleration only provides one factor whilst other components need to be taken into account, such as mass to calculate force and distance moved to calculate work (Gleiss et al., 2011).

Using $PDBA_{xz}$ values it was possible to predict oxygen consumption of domestic hens (*Gallus gallus*) walking on a treadmill and when engaged in other less active behaviours (Green et al., 2009). For relatively inactive chickens the better predictor of energy expenditure was the heart rate method, but for more active individuals, body acceleration was a more accurate technique (Green et al., 2009).

Both the use of heart rate and accelerometry require specific calibration relationships to be generated for each species and possibly different modes of locomotion. The relationship calculated between heart rate and oxygen consumption in walking geese was unable to accurately estimate oxygen consumption during flight for the same birds as the relationship differs in the two activities as heart rate rises (Nolet et al. 1992; Ward et al., 2002). This suggested that each major activity might need to be monitored separately as although oxygen consumption and heart rate are correlated, the degree of correlation might depend on the particular behaviour performed. In the case of birds, this is probably because there is a complete separation of fore and hind limbs in birds so the cardiovascular system has evolved to allow the flight muscles to consume large amounts of oxygen, whilst only a quarter of the amount of oxygen is consumed during running compared to flying (Ward et al., 2002).

One of the earliest pieces of research examining energy expenditure during flight in homing pigeons using the doubly labelled water technique was conducted by LeFebvre (1964) who found that pigeons expended at least eight times more energy during flights of several hundred miles, that when at rest. Pigeons were also utilised by several other research groups investigating energy expenditure during flight in wind tunnels (e.g. Butler et al., 1977; Rothe et al., 1987; Peters et al., 2005). The studies yielded rather variable results (see chapter III) with the study of Peters et al. (2005) showing that pigeons flying at 18.4 m s^{-1} in a wind tunnel increased their oxygen consumption by 17.4 times compared to resting values (Peters et al., 2005).

While the use of accelerometry to measure energy consumption has some of the same calibration issues associated with heart rate, it is less invasive and easier to apply to the study of free-ranging birds. However, there are currently very few studies published on flight. Halsey et al. (2009b) investigated flight in raptors (Harris' hawk (*Parabuteo unicinctus*), tawny eagle (*Aquila rapax*) and Griffon vulture (*Gyps fulvus*)) using accelerometry and was able to distinguish between periods of flapping and gliding and flying up and down hill using calculated ODBA values. The current project will extend this approach and exploit the use of dynamic body acceleration (DBA) to study the flight behaviour and performance of free-ranging pigeons.

1.4 The effect of mass on flight performance in birds

1.4.1 Theoretical considerations and aerodynamic predictions

Over the last twenty years the emphasis within a large area of avian research has focussed upon collected data from monitoring recorders fitted to birds. The long-standing rule of thumb is that such loggers should never weigh more than 5% of the individual animal's body mass which was reinforced by work undertaken during the 1980's by Caccamise and Hedin (1985) and Gessaman and Nagy (1988). To this day it is often recommended that these limits should not be broken but this often leads to the assumption that individuals can continue behaving as normal when carrying an extra 5% of body mass (Gessaman and Nagy, 1988; Barron et al., 2010). Furthermore externally fitted loggers also increase the drag experienced during flight which can be responsible for a reduction in the flight range of a bird, similarly to an individual carrying additional mass (Bowlin et al., 2010).

Larger species of birds will have bigger wings than smaller species but the area of the wing does not increase directly in proportion to the mass. For a given shape, wing area should scale allometrically, approximately as mass$^{0.67}$, so that wing loading will scale as mass$^{-0.33}$. Because of this, larger species of birds need to generate a larger amount of lift for a given area of wing by increasing the flow of air over the aerodynamic surfaces. This will raise their minimum flight speed, where speed is proportional to body mass$^{0.17}$ and the power for flight is proportional to body mass$^{1.17}$ (Hughes and Rayner, 1991). If they normally fly faster than their minimum flight speed, then they might respond by lowering speed and/or increasing their wing beat frequency or other flight wing kinematics to compensate. However, looking at the response of additional mass upon an individual bird, where the wing size remains unaltered, the minimum flight speed is predicted to increase as a function of body mass$^{0.50}$ and the power required increases as a function of body mass$^{1.50}$ (Hughes and Rayner, 1991).

During the mid-1980's affixing radio transmitters and other data monitoring loggers onto birds began to increase in popularity. For this reason it became apparent that the implications upon flight biology had to be considered (e.g. Caccamise and Hedin, 1985). It has been suggested that the effect of the mass of a logger on the bird's flight abilities could be estimated depending upon the resulting reduction in the 'surplus power' available due to the additional load (Caccamise and Hedin, 1985, Figure 1.2). Surplus power was defined as the difference between the power required to fly at the maximum range speed (V_{MR}) and the amount of overall power that is available for use. Pennycuick (1969) argues that the muscle-specific power from the flight muscles declines with increasing body size, essentially due to decline in wing beat frequency (assuming fixed values for stress and strain in the muscles) and that this leads to a scaling of mass$^{0.67}$ for the power available for flight. Similarly, Bishop (1997) suggests that maintaining flight aerobically is also more difficult in larger birds as the mass-specific oxygen available decreases with increasing body mass, at around mass$^{0.82}$. Hence, the general consensus is that surplus power reduces as body mass increases; if a fixed percentage of body mass is used, surplus power will be reduced more for a larger bird than a smaller individual (Caccamise and Hedin, 1985).

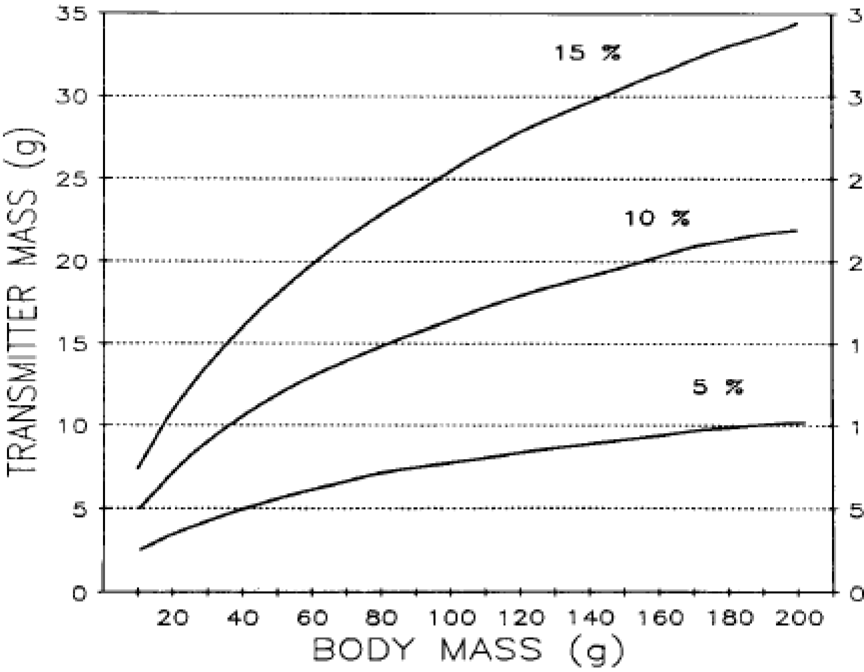


Fig. 1.2: Each of the lines on the graph represent either a 5%, 10% or 15% reduction in surplus power (see text for definition) for the association of body mass and transmitter mass; taken from Caccamise and Hedin (1985).

From Figure 1.2 it is possible to see that for species with a small body mass each of the three curves increase rapidly before flattening which is due to the large amount of surplus power associated with smaller birds and, therefore, these smaller species can carry a larger proportion of their own body when compared to larger ones (Caccamise and Hedin, 1985). If a fixed percentage of body mass is added to an individual, the surplus power is reduced relatively more for larger species than smaller ones, so the addition of a fixed percentage of body mass does not lead to an even result between species (Caccamise and Hedin, 1985). Theoretical predictions are all well and good and do give an excellent basis to both design experiments and interpret their results. However, it must be remembered that, until they are tested, they remain predictions and whilst they do assume that individuals perform optimally in real-life situations they may not necessarily do so. However, optimality is subjective to the individual observer as animals may choose to optimise different aspects, such as time, energy, predation risk or a combination of various factors.

1.4.2 Experimental work on the carrying of artificial mass

Working with long-eared bats (*Plecotus auritus*), Hughes and Rayner (1991) found, apparently in contrast to aerodynamic theory, that flight speed decreased as mass increased (by up to 58% of body mass) but, as expected, wing beat frequency increased (by approximately 23%). These experiments can be quite difficult to interpret. One suggestion is that these bats, when unloaded, are flying above their minimum power speed (V_{MP}) because when loaded they chose to fly slower than when unloaded. If under normal conditions they were flying at V_{MP}, then in order to minimise power they should fly faster than before. This would still cost slightly more energy than before but would represent the new V_{MP}. As wing beat frequency did increase, this is consistent with an increase in overall flight costs, but the reduction in flight speed when loaded does suggest that they were reducing flight speed from a previously greater than V_{MP} speed.

High performance homing pigeons fitted with a load of either 2.5% or 5% of body mass showed a dramatic decrease in flight performance using the doubly labelled water technique (Gessaman and Nagy, 1988). Over 90km the pigeons took a similar amount of time to complete the flight irrespective of the difference in the weight of the loads, but were slower than controls by between 25 to 28%, indicating that it was primarily drag as opposed to weight which caused these results. Indeed, even the harness alone slowed the birds by 15%. Over a much longer distance (320km) the birds' flight performance was even more severely compromised by the harness and package, flying significantly slower (greater than 31%) and producing significantly more carbon dioxide (between 41 and 52% higher per hour) than control birds (Gessaman and Nagy, 1988). However, when taken in context with more recent studies, the results of this work appear somewhat perplexing, as they suggest that flight costs scale approximately as mass^6, rather than the theoretical value of $\text{mass}^{1.5}$. Of course, some of this could be as a direct result of the increased drag, when placing a 1cm diameter tube on the back of the bird, but it is still hard to explain. Conversely, a similar experiment conducted on tippler pigeons flying around a loft, showed no significant difference in energy consumption when carrying additional mass but did apparently increase water loss by 57-100% (Gessaman et al. 1991).

The original results of Gessaman and Nagy (1988) seem even more excessive when compared to recent wind tunnel studies by Kvist et al. (2001) and Schmidt-Wellenburg et al. (2007 and 2008) which report a sub-linear increase in the body mass exponent ($\text{mass}^{0.35}$ and $\text{mass}^{0.5}$, respectively). Some possible explanations for this result might be, that the pigeons flew with an uncomfortable leather harnesses, that the birds flew for very long periods which might have incorporated a flawed measurement of air speed, route taken and estimates of flight time budgets, and that the costs of free-flying might be different to those recorded during captive wind tunnel flights (Gessaman and Nagy, 1988).

1.4.2.1 The energetics of take-off and load lifting during hovering

As it is experimentally more tractable to study take-off, hovering and relatively short flights, rather than long distance and free-ranging situations, some of the most detailed experimental manipulations in the effects of natural and added mass have only involved take-off or hovering.

Due to their exceptional ability to hover at wild flowers and artificial feeders, hummingbirds have also been the subject of a number of studies. In the study of Wells (1993), during hovering at imitation flowers of different sizes, wing amplitude was reduced at wider diameter flowers but wing beat frequency increased in compensation. However, as added loads were experimentally increased (up to 30% body mass) wing beat frequency remained constant but the amplitude of each beat increased by approximately 20% in broad-tailed (*Selasphorus platycercus Swainson*) and rufous hummingbirds (S. r*ufus Gmelin*) (Wells, 1993). Thus, wing kinematics was found to be flexible and capable of adjusting to different situations. At the same time, oxygen consumption increased slightly and, in the case of the added mass experiments, a 10% increase in added mass lead to a 5.7% increase in flight costs. This is the equivalent of a mass exponent of mass$^{0.58}$, which is similar to those of Schmidt-Wellenburg et al. (2007 and 2008), assuming that this performance is aerobically sustainable and did not require any anaerobic metabolism.

Marden (1987) studied the load-lifting ability of a variety of insects, bats and birds in a study of their maximal flight performance. He showed that total flight muscle mass was a good predictor of maximum take-off ability. Indeed, the maximum load-lifting ability or all these flying animals was an isometric function of total flight muscle mass and successfully predicted the later work on Harris' hawks (*Parabuteo unicinctus*) by Pennycuick et al. (1989) via extrapolation (Marden 1990). However, for non-hummingbird species (see below) it may be possible to predict a reasonable value for the maximum induced power output capability of birds from knowledge of the total flight muscle mass.

Chai et al. (1997) developed a novel approach to investigating the amount of added mass an individual bird could lift. Briefly small weights were threaded equidistant apart onto a piece of string that had a loop at one end that fitted over the head of the bird. Thus, as the bird took off the weights would also be lifted and when the bird had reached its maximum capacity it was possible to calculate the weight it had lifted by the number of weights that had been raised (Chai and Millard, 1997; Dillon and Dudley, 2004; Altshuler et al., 2010). However, this technique ends with the birds failing to sustain their hovering and so will definitely include anaerobic power production.

Altshuler et al. (2010) studied many different species of hummingbird and found that on average the birds were able to lift almost three times their own body weight (approximately 277%) but only for very brief periods. As expected, lifting capacity declined with altitude (Altshuler et al., 2010) but, by increasing wing size and amplitude of beats as altitude increases, the minimum power needed for hummingbirds to be able to hover remains similar (Altschuler et al., 2004). However, these studies suggested that within family scaling of hummingbirds may require more negative muscle mass specific load-lifting allometry. Larger species of hummingbird were shown to lift almost twice their own body mass, whereas smaller species were only capable of lifting just about their own body weight; however, they were able to do so for a longer period of time than the heavier birds (Chai and Millard, 1997). This suggests that hummingbirds have an increased muscle mass-specific anaerobic capacity as they increase in size, in common with the general trend for birds and mammals.

1.4.2.2 Flight energetics and behaviour over short flights

A number of studies have either flown birds along corridors or short flight ways or encouraged birds to fly between perches over relatively short distances. These flights could contain an unknown amount of anaerobic fuelled activity and also incorporate a relatively large component of ascending and descending flight stages (with very little true horizontal flight). These latter flights might be termed “ballistic” and may be difficult to compare to longer, horizontal flights and may have more in common with take-off studies. Nudds and Bryant (2002) studied the energy expenditure of zebra finches (*Taeniopygia guttata*) flying between two perches 5.46m apart, along a flight corridor. Their energy expenditure did not appear to increase with increasing loads, although to compensate for the extra weight they did reduce their take-off speed and over the course of the experiment reduced their own individual body mass (Nudds and Bryant, 2002). It is extremely difficult to interpret the results of such a study which utilises the DLW technique on such short duration flights. Given the inherently high variation in this technique (usually around 30% error around the mean), the statistical power to detect small shifts in experimental manipulation of energy expenditure is very poor. Blood samples have to be taken after a few days of encouraging the birds to fly between the perches, so a small shift in energy consumption would not be easily distinguishable from the general background. Thus, it is highly likely that this technique and the experimental design were not sensitive enough to detect small variations in energy expenditure. However, take-off speed was reduced with additional load and there was also a reduction in individual body mass during the experiment (which would have also adversely confounded the DLW energy measurements), indicating that an increase in flight costs would be expected immediately following the application of the additional loads using a more suitable experimental approach.

Results from the study of cockatiels (*Nyphicus hollandicus*), by Hambly et al. (2004), suggest that birds tested over short distances may implement different flight techniques depending upon the amount of additional mass that they are forced to carry. For example, flight speed of cockatiels decreased by up to approximately 7.5% when they carried additional weights of 5%, 10% and 15% of their own body weight but when 20% weights were added, flight speed slightly increased (Hambly et al., 2004). Wing beat frequency did increase with increasing weight (although only statistically significantly with 20% loading) whilst time spent in both the up and down beat decreased (Hambly et al., 2004). Similar to the zebra finch (*Taeniopygia guttata*) study, these flights were only of a few seconds in length, conducted over a two minute period as the cockatiels flew between two perches positioned 20m apart. Once again, the behavioural responses to being loaded (such as increased wing beat frequency, amplitude and speed changes) were not apparently mirrored by energetic changes as measured by the ^{13}C bicarbonate technique. This latter method of analysing energy expenditure has not been fully validated for use in flight (C. Bishop, per. comm.) and so its accuracy and precision in this type of experimental design is unknown.

It was suggested that these birds adapted to increasing mass by altering their behaviour (Nudds and Bryant, 2002; Hambly et al., 2004) and, thus, avoided potential increases in flight costs. While this may be a valid factor to consider, it is complicated by the fact that neither of the techniques used by these authors (DLW and ^{13}C-labelled bicarbonate) were probably not subtle enough to detect small energetic changes during these short and unsustained types of flights. Other pieces of research (e.g. Schmidt-Wellenburg et al., 2008, see below) have indicated that birds do experience increased flight costs when loaded even when using the DLW technique, although these flights were much longer in duration

1.4.2.3 Energy expenditure using wind tunnel flights

In rose coloured starlings (*Sturnus roseus*) flying for a number of hours in a wind tunnel, energy expenditure (as measured by DLW) increased with increasing artificial load, however, this increase was well below that predicted by aerodynamic theory (Schmidt-Wellenburg et al., 2008). Energy expenditure increased as a function of body mass$^{0.507}$, whilst wing beat frequency also increased (by almost 7%) when the birds were forced to carry an additional load weighing approximately 7% of their body mass (Schmidt-Wellenburg et al., 2008). Again, using DLW, barn swallows (*Hirundo rustica*) allowed to gain and loose mass naturally, and flown in a wind tunnel, increased their energy expenditure as a function of natural body mass$^{0.58}$, whilst wing beat frequency increased as a function of body mass$^{0.38}$ (Schmidt-Wellenburg et al., 2007). Finally, another study using DLW, showed that for red knots (*Calidris canutus*) flying in a wind tunnel, power increased proportionally by body mass$^{0.35}$, although measures of wing beat frequency were not recorded (Kvist et al., 2001). The latter study only includes data taken from 4 individual birds and has a very large degree of uncertainty around the mean value but the result seems to be in general agreement with that of the previous experiments.

Pennycuick et al. (2000) suggested that wind tunnel flights of a swallow (*Hirundo rustica*) might lead to increased flight cost estimates (based on body acceleration and wind kinematic measurements) compared to those predicted from his aerodynamic model, partly due to the fact that the swallows did not fly in the wind tunnel with a truly steady and minimum-drag configuration. In reality, they are constantly manoeuvring and altering position within the working section. However, in the above wind tunnel experiments (Kvist et al., 2001; Schmidt-Wellenburg et al., 2007, 2008), there is no particular reason to question that the intra-species body mass exponents for these three species appears to be substantially less than the value of mass$^{1.5}$, as predicted with modelling work (Hughes and Rayner, 1991). In addition, the loaded hummingbirds (broad-tailed, *Selasphorus platycercus Swainson* and rufous, *S. rufus Gmelin*) (Wells, 1993) also indicated a value of mass$^{<1.0}$ for the intra-individual scaling of carrying additional mass.

These results suggest that theoretical values for the body mass exponents may over estimate the allometric scaling of the additional costs of flying with additional mass. Alternatively, the mechanochemical conversion efficiency of the flight muscles may increase with body mass (Kvist et al. 2001). Similarly, when looking at minimal flight costs between different species, there is a tendency for the theoretical exponents for body mass of mass$^{1.16\text{-}1.17}$ (Pennycuick, 1975; Rayner, 1990) to be greater than those determined from empirical metabolic studies or from physiological modelling of cardiac function (Bishop, 2005). Again, there is a general view that this observation may support an overall inter-species scaling for the mechanochemical conversion efficiency, with smaller animals operating with high wing beat frequencies and, consequently, a lower value for muscle mass-specific work (Bishop 2005). Indeed, some authors suggest that the mechanochemical conversion efficiency may even change with respect to flight velocity (Ward et al. 2001).

1.4.2.4 Flight kinematics measured over short distances

Behavioural and kinematic research into the capability of various birds of prey to carry additional mass has been undertaken using kestrels (*Falco tinnunculus*) (Videler et al., 1988a, b) and Harris' hawks (*Parabuteo unicinctus*) (Pennycuick et al., 1989), whilst Marden (1987) studied various species of flying animals. These experiments concentrated on take-off (Marden, 1987), climbing after take-off and short horizontal flights of 50m (Pennycuick et al., 1989) or relatively longer flights along a windless corridor, either 50m, 125m or 142m long (Videler et al., 1988a, b).

As mentioned above, the rate of climb after take-off of Harris' hawks (*Parabuteo unicinctus*) decreased with added mass, with a slight increase in wing beat frequency (although actual values were not published; Pennycuick et al., 1989). The more comprehensive study of Marden (1987) also showed a general reduction in take-off speed and angle of ascent for many species, including insects and bats, which indicate that under normal (unweighted) conditions birds probably take-off and climb fairly close to their maximum capacity. A similar assumption was made by Hedenström et al. (1992) studying climbing flight.

As the added weight on the kestrels (*Falco tinnunculus*) increased, similarly to bats (Hughes and Rayner, 1991) there was a corresponding decrease in flight speed (nearer V_{MP} than V_{MR}), with an increase in wing beat frequency, although the individual spent longer in the down stroke in each beat (Videler et al., 1988a, b). When weights were added to the kestrels representing 33% of their body mass it was assumed that there was an increased energy output which was thought to be near the upper threshold of aerobic exercise, whilst gliding distance also had to be reduced to avoid excessive descent (Videler et al., 1988b). Thus, these results are consistent with the idea of flying greater than V_{MP} during normal unloaded flights, thus giving scope for slower speeds when loaded. By flying nearer V_{MP} when carrying additional mass, the studies by Videler et al. (1988a, b) and Pennycuick et al. (1989) are supported by the conclusions of Hughes and Rayner (1991) who were forced to concede that bats were optimising their flight performance, but by minimising their immediate flight power requirements as the best flying option rather than minimising the costs of locomotion overall.

1.5 The effect of airspeed and wind on flight performance in birds

1.5.1 Types of flight

Different species of birds use different types of flight, such as hovering, gliding and flapping flight and variations on these techniques, such as flap-gliding or flap-bounding (Videler, 2005). Flapping is often the main method of locomotion, however some species have developed the ability to intersperse flapping with periods of gliding in an attempt to conserve energy as flapping flight is extremely energetically costly (Videler, 2005). Utilising gliding allows larger species such as vultures, albatrosses and petrels to use the power of prevailing winds to reduce their energy costs by reducing flapping (e.g. Pennycuick, 1971a, 1982; Sachs, 2005). Pigeons, however, rely mainly upon flapping flight interspersed with periods of gliding (Tobalske and Dial, 1996). In fact, they have been re-classified as ‘flap-gliders’ (Tobalske, 2001) and whilst not engaging solely in gliding flight they will still be affected by the strength and direction of prevailing winds.

The direction of wind can both hinder and aid flight performance in birds. Although strong winds can be hazardous to migrating birds as they can force individuals off course (Able, 1970), bird flight at certain altitudes under favourable wind conditions, can reduce flight time and overall energy expenditure (Green, 2004). Flight in general is energetically costly (Pelletier et al., 2008) but birds can use the wind direction to their advantage by allowing themselves to be blown along (Alerstam, 1979). However, this may cause them to be blown off course, thus resulting in more energetically costly flight to try to regain their original route. This could even cause the birds to become disorientated (Bingman et al., 1982).

Many studies have focussed on the effects of wind, however, these are usually focused on migratory birds (e.g. Åkesson and Hedenström, 2000; Erni et al., 2005) or on wind tunnel work (e.g. Lindström et al., 2000; Park et al., 2001; Hedenström et al., 2006). Migration studies have tended to revolve around the necessary wind conditions needed for birds to either begin migration or depart from a stopover site (e.g. Dänhardt and Lindström, 2001; Schaub et al., 2004).

1.5.2 The effects of wind on bird flight

The use of tailwinds can significantly reduce the energy required for migrating birds (Butler et al., 1997) by decreasing the cost of transport (energy per unit distance) and slight tail winds can lead to high numbers of individuals taking to the skies (Zehnder et al., 2001). For example, there is a tendency for red knots (*Calidris canutus*) and bar-tailed godwits (*Limosa lapponica*) to depart for migration in weak tailwinds (Battley, 1997), whilst flocks of bristle-thighed curlews (*Numenius tahitiensis*) can abort attempts to initiate migration when there were unfavourable wind conditions (Marks and Redmond, 1994). The birds will take-off but soon return to the original location. In the autumn, nocturnally migrating birds are least likely to depart for migration when there were strong head or cross winds and instead choose to leave when head or cross winds are weaker (Erni et al., 2002). Re-capture studies conducted by Saino et al. (2010) support these observations because the studies suggested that migrants were less likely to depart in head or cross winds, as there were fewer recoveries in these conditions.

When hunting in windy conditions, falcons are capable of displaying extreme plasticity and are able to alter their flight behaviour as required (Hedenström et al., 1999). Eleonora’s falcon (*Falco eleonorae*) show different flight strategies to cope with on-shore and off-shore winds. During off-shore winds, the birds displayed flapping flight. However, on-shore breezes provided the falcons with lift created by the local topography due to the presence of cliffs which allowed them to soar and gain altitude before beginning flapping flight (Hedenström et al., 1999). Moreover, energy expenditure has been shown to increase in foraging black-legged kittiwakes (*Rissa tridactyla*) in strong winds, possibly due to the increase in time spent engaged in flapping flight as opposed to gliding in such conditions (Gabrielsen et al., 1987). Collectively these examples demonstrate that windy conditions do not always mean a saving of energy and can require some considerable energy loss as the birds use flapping flight to stay stationary or fly against the wind direction.

1.5.3 Use of wind tunnels for bird flight studies

Wind tunnels have been extensively used over the last hundred years to assist research into the mechanisms and energetics of bird flight (Rayner, 1994) Wind tunnels have the advantage over studies on free-flying birds because they enable scientists to collect detailed flight data under controlled conditions (Parrott, 1970). The idea behind a wind tunnel is fairly straightforward: wind is created and blown back past a bird which is flying into the wind. The bird remains still in relation to the ground as the flight speed equals the wind speed (Pennycuick, 1968b). The most sophisticated wind tunnel for bird flight studies can be found at Lund University, Sweden (Pennycuick et al. 1997). This wind tunnel incorporates features that minimise turbulence, which usually receives little consideration in the design of other wind tunnels. Wind tunnels have been used to assess metabolism (e.g. Lindström et al., 1999; Ward et al., 2004), the use of body-mounted loggers (e.g. Obrecht et al., 1988), aerodynamics (e.g. Pennycuick, 1968b; Tucker and Parrot, 1970; Tobalske et al., 2009) and even the olfactory ability of birds (e.g. Cunningham et al., 2006).

Despite the usefulness of wind tunnels in examining bird flight under controlled conditions, there are a number of issues which have to be taken into consideration. For instance, it is often difficult to train the birds to fly in these artificial environments. Birds do not tend to show natural flying behaviour within wind tunnels and results can often not be repeatable in a wild environment. Starlings, *Sturnus vulgaris,* for example, are particularly affected by wind tunnels as shown by Torre-Bueno and LaRochelle (1978) who found that only five of one hundred starlings would fly as required. It is also possible that the costs associated with free-flight may be underestimated as shown in barn swallows (*Hirundo rustica*) and house martins (*Delichon urbica*) (Liechti and Bruderer, 2002).

Due to the agility of some species, such as hirundines, individuals can create their own flight pattern inside a wind tunnel with no generalised style being apparent (Bruderer et al., 2001). Such species did not display steady cycles of flapping interspersed with short resting periods which is unlike other passerine species (Bruderer et al., 2001). This suggests that experiments within a wind tunnel have to take into account, intra-species as well as inter-species variation, and this can create difficulties when attempting to make generalised conclusions regarding flight performance. For example, it was impossible for a teal (*Anas crecca*) to fly at the minimum power speed as expected from empirical calculations, and even though the thrush nightingale (*Luscinia luscinia*) was able to fly at its minimum power speed, it did so unwillingly (Pennycuick et al., 1996). It is possible that these observations are a result of flying in the wind tunnel. However, no direct comparisons were made with free-flying birds in either study, and therefore this conclusion remains to be investigated further. Wind tunnels have in the past been used to estimate values of body drag coefficients by relying on dead birds with no wings to simulate drag. It has now been suggested that the values obtained are higher than those found using live species (Pennycuick et al., 1996). The feet of birds create extra drag when they are outstretched (Pennycuick, 1971b), leading Pennycuick et al. (1996) to suggest that large co-efficients of drag may be found in species with larger feet. In addition, a mismatch has been found between the increase in metabolic power required as flight speed increased in European starlings (*Sturnus vulgaris*) flying in a wind tunnel, and the values expected from aerodynamic models (Ward et al., 2001). This may be because the wind tunnel does not recreate exactly the natural flying environment. It is also possible that the widely held belief that power requirements for flight follow a U-shaped curve is incorrect, as suggested by Dial et al. (1997) in magpies (*Pica pica*) who stated that this model may overvalue the power required to fly at higher speeds.

1.5.4 Wind tunnel studies on pigeons

Pigeons have been used in a number of wind tunnels studies because they are a relatively small but agile species that can be used to study cardiac and respiratory function during flight (e.g. Pennycuick, 1968a; 1968b; Butler et al., 1977; Peters et al., 2005). In addition they have been used to investigate flight performance and in particular, the aerodynamic forces which must be overcome for birds to remain airborne (Pennycuick 1968a, 1968b). Such studies have been used to define many important theoretical equations relating morphology to flight which are constantly used by both theorists and experimental biologists alike. The experiment undertaken by Pennycuick (1968a) provided values for power output, oxygen consumption and the minimum power speed for pigeons. Pennycuick (1968b) investigated gliding flight in the pigeon by photographing birds flying in wind tunnels, and taking simultaneous measurements of various drag components on preserved pigeon bodies. This wind tunnel work has shown that as flight speed increases, pigeons reduce their wing area and span and consequently their aspect ratio. Although the aspect ratio increases induced drag, overall wing profile drag decreases (Pennycuick, 1968b).

Butler et al. (1977) recorded respiratory and cardiovascular data from pigeons flying in wind tunnels. Additionally the authors used free-flying pigeons to record heart and respiratory rate to enable comparisons to be made. These comparisons showed that flight in the wind tunnel was unusual, especially during the take-off phase. Individuals showed a reduced flapping period in the wind tunnel possibly due to the confined space and length of the equipment (Butler et al., 1977). The use of mask respirometry to record metabolic power in a wind tunnel may not be a reliable way of predicting metabolic rates in free-flying birds, mainly because of the artificial flight environment that is created when using a wind tunnel (Ward et al., 2001). This could possibly cause excessive stress due to flying in abnormal surroundings or possibly because the bird has lost the power to determine the length and speed of the flight (Ward et al., 2001); both of which act to give a false representation of the actual metabolic power required for free-flight. In fact, pigeons are difficult to train to fly in wind tunnels. This is demonstrated by two studies: only one of six pigeons performed sufficiently well in an experiment by Pennycuick (1968b) to give usable data when flying in a wind tunnel whilst Butler et al. (1977) only succeeded to train five pigeons out of a total of twelve. Additionally scientists using wind tunnels have to be aware of the boundary effects which could reduce the flight performance of an individual bird (Rayner, 1994).

Peters et al. (2005) also measured cardiorespiratory responses of pigeons flying in wind tunnels. Their study highlighted several different findings from Butler et al. (1977). Peters et al. (2005) recorded lower measurements (such as heart rate and oxygen consumption) in resting pigeons than did Butler et al. (1977) and suggested that this was possibly due to the different methods used to collect the data (mask respirometry, Butler et al. (1997); resting in a familiar environment in darkness, Peters et al. (2005)). The flight values of the rate of oxygen consumption in relation to body mass reported by Peters et al. (2005) were actually greater than those described by Butler et al. (1977) and again it was suggested that differences in the methodology were responsible for this. These two studies highlight the difficulties in repeating experiments and gaining similar results. However it should be remembered when comparing these two studies in particular that they were conducted almost thirty years apart and with the assistance of modern technology it may be that the most recent results possibly give a more accurate insight into the flight performance of pigeons.

Although data has been collected from pigeons flying in wind tunnels, there are clearly problems in getting the birds to fly. Given that there are several constraints in using wind tunnels to study natural flying behaviour, it is important to also examine flight performance in pigeons exposed to various wind directions in their natural environment. Working with free-flying birds also poses its own problems: the birds interact with their surroundings and so can be affected by daily changes in the weather, changes in flock structure and inter-bird conflict (Silk, 2007) as well as the threat from aerial predation (Carere et al., 2009). Additionally it is impossible to follow wild birds for extended periods of time to accurately monitor their flight behaviour (Pelletier et al., 2008). However, if these problems could be over come by the use of the technology described in the current thesis then some of the issues raised by examining pigeon flight in wind tunnels could also be examined in the field.

1.6 Rationale

The general purpose of this thesis was to explore how the flight patterns of free-flying homing pigeons (*Columba livia*) can be assessed using miniature GPS and accelerometer data loggers. Consideration was given to how accelerometry in particular may be used to determine specific flight behaviours and to provide an indication of how much energy and relative effort the pigeon is consuming during flight. Flight performance was assessed with respect to the potential effects of environmental factors such as wind strength, body morphology (such as differences in natural body mass or experimental manipulation of carried mass), or even behavioural parameters such as homing motivation and flight speed.

It is only with recent improvements in both the accuracy and reliability, alongside the miniaturisation, of data recording devices that this methodology is possible without causing large impacts of the bird’s natural behaviours and flight performance. In theory, accelerometry in conjunction with GPS is capable of giving detailed information as to body movements and positional data during a flight, sufficient to inform on aspects of natural flight energetics along with the potential effects of changes to environmental conditions and experimental manipulations.

There is a lack of detailed data regarding the effects of wind direction and strength under semi-controlled conditions upon free-flying birds. Historically this type of research has centred upon the conditions required for wild birds to initiate migration or to utilise thermals for gliding birds etc. Research has also looked into weather conditions for foraging, chick provisioning and nestling survival. Pigeons are a practical species with which to address questions such as the hypothesis of Pennycuick (1978) that birds should try harder in a headwind than in a tailwind. In effect, this is a study of motivation to reach a specific goal, although it may be that captive homing pigeons will not have quite the same drive to fly home that wild migrating birds may have, for example, to reach their breeding grounds. Little research has been conducted into the effects of wind direction by monitoring entire flights of free-flying birds over short distances, and direct comparisons between the effects of wind strength and direction on flight from the same location have not been made. Therefore, accelerometry and GPS dataloggers were used in order to quantify these effects by investigating route choice, flight speeds and body movements of individual birds.

The same approach was also used to enable aspects of an individual's flight performance to be correlated against natural body mass, or against experimental manipulation of carried mass. This could again affect route choice or flight speeds but also flight parameters such as wing beat frequency. Body mass and its relationship to wing morphology, in particular wing loading, is considered an important modulator of individual flight performance as well as an important selective parameter for both intra-specific and inter-specific selection (Rayner, 1988).

1.7 Aims and objectives

The main aim of this thesis was to utilise new technologies to examine the potential for homing pigeons to act as a model species for the study of the flight performance of free-ranging birds. To this end biologgers were used to determine both flight behaviour and aspects of performance during short flights. The biologgers used were GPS to monitor location, and accelerometers to monitor changes in body movement and wing beat frequency, as an indication of effort and energy expenditure during these flights. As this project relied upon new and emerging technology, an entire chapter (Chapter III) has been devoted to describing and explaining the techniques involved in calibrating the accelerometers and deriving useful analysable information from the resulting raw data. The same chapter includes brief information of a typical flight profile of the pigeons in control situations (i.e. low wind conditions) and introduces the terminology used to describe flight patterns throughout the thesis. A separate chapter (Chapter II) describes the methodology common to both experimental chapters. It describes the husbandry of the pigeons in some detail as the welfare of the pigeons was a top priority to ensure that all experiments were carried out on healthy individuals. The chapter also provides an overview of the training schedule used and explains why each step was necessary. A description of the release sites is given along with the location of the loft. The two main experimental chapters, investigate the effects of adding mass (Chapter IV) and the effects of wind direction (Chapter IV) on flight performance in free-ranging pigeons.

1.8 Hypotheses

This thesis aims to address two main questions: (1) how does the addition of artificial mass or differences in nature body mass affect bird flight performance, dynamic body acceleration (DBA) and wing beat frequency?; (2) how does wind speed and direction affect bird flight performance, dynamic body acceleration and wing beat frequency? From theoretical predictions the pigeons should fly faster when loaded to compensate for the predicted increase in their minimum power speed (V_{MP}). Therefore, when fitted with additional mass the birds may also increase their energy output, which should be represented by an increase in DBA and wing beat frequency values. When flying into a head wind, it is predicted that the pigeons should increase their air speed whilst remaining at a lower altitude. Energy output should be greater during these conditions, which should be represented by elevated DBA and wing beat frequency values.

CHAPTER II – Materials and Methodology

Several experiments were carried out during the length of the project to investigate flight performance in free-ranging pigeons either in response to added mass or wind direction. Birds were either flown as a flock (added mass and wind direction) or as individual releases (added mass). The methods used to train birds to return to the loft, as well as to carry added mass are detailed below, along with a description of the release sites. The logging equipment attached to each free-flying bird in order to determine position (GPS) and flight performance (accelerometers) are described as well as the procedures followed before and after each flight. A much more detailed account of the analysis of the data retrieved from the accelerometers is given in the following chapter (Chapter III). The methodology described here is common to both experimental chapters (Chapters IV and V).

2.1 Experimental birds

Homing pigeons (*Columba livia*) were purchased as three week-old fledglings in two separate batches from Louella Pigeon World, Loughborough, UK. Sixty chicks were purchased in the summer of 2007 and a further 30 chicks were purchased in the summer of 2008. Birds from both 2007 and 2008 were used for flight experiments conducted on pigeons flying as a flock during the summer of 2009. Only birds from 2007 were used for individual releases in the added mass experiment carried out in 2008.

On arrival at Bangor University, pigeon chicks were housed in a custom-built pigeon loft located at Treborth Botanic Gardens (OS coordinates SH 551711). The loft was comprised of a long corridor running the entire length of the loft with 10 rooms, which could be partitioned when necessary using sliding doors. The birds only occupied seven rooms, of which four contained 12 perches and three rooms contained 12 nest boxes. The four nest box rooms were 158cm wide by 210cm long, whilst the perch rooms were slightly shorter. For the vast majority of the time the birds had access to all seven rooms. This meant that during the experimental period approximately 60 birds had access to 48 perches and 36 nest boxes. The loft was surrounded by woodland to the rear and sides and grassland directly in front of the loft.

Chicks were trained over the intervening nine months (from purchase to the following March/April) before they were used in flight experiments The main purpose of the training was to enable the birds to successfully locate the home loft from various release locations (Section 2.1.2). Once they were reliably returning home they were then fitted with harnesses and 'dummy' loggers to habituate them to wearing the logging equipment on their backs (Section 2.2.1.3). In addition, some preliminary experiments were conducted on twenty fully trained adult pigeons which were available at the very beginning of the PhD project. Some of the more reliable birds, fully trained adult were also chosen to carry data loggers during the added mass and wind direction studies.

2.1.1. Husbandry of the birds

Feeding took place every day after the loft had been cleaned, apart from days in which flight experiments took place, when feeding commenced after experiments. Food was split between several hoppers (approximately one hopper per ten pigeons), which were cleaned daily after the removal of uneaten food. The food ration was calculated at 25g for each pigeon but this amount was modified according to the appetite of the pigeons on the day of feeding. The type of food supplied varied depending on the age of the birds and the time of year. The main feed used was Versele Laga (Best All-Round, Moulting Sublime and Junior Sublime), although Mariman Breeder-Racer Mix and BJF Stock Bird were also fed to the pigeons. The main ingredients in these feed types were maize and wheat. Some also contained barley, although composition varied between feed types. Additionally ingredients included peas, beans and seeds. Water was refreshed daily and placed into clean drinkers and was available to the birds throughout the day. The pigeons also had ad libitum access to minerals, pick stone (natural mineral supplements) and various types of grit, although calcium grit was removed if the pigeons were receiving a course of Ornicure^{TM}. Cider vinegar was added to the water twice each week to help the birds maintain a slightly acidic gut.

All birds were cared for using a standard daily routine. Each morning birds were thoroughly checked to make sure all birds were healthy. Each day the loft was thoroughly cleaned by the removal of faecal matter from floors, perches and nest boxes. Eggs were also removed to prevent the birds nesting and rearing chicks. Once this was completed the corridor area was sprayed with Virkon^{TM} – a powerful disinfectant used widely within animal husbandry. The rooms within the loft were lightly sprinkled with a chalk powder (combined with a disinfectant) in order to dry the floor as well as making cleaning slightly easier. The birds were then fed and drinking water replaced. Throughout the project a daily record sheet was maintained to track husbandry issues and to record training sessions (Section 2.1.2). Daily records were also kept to record environmental conditions within the loft such as maximum and minimum temperatures and humidity. For this purpose a thermometer measuring to the nearest 0.1°C was used and temperatures fluctuated throughout the year as the loft was neither heated during the winter nor cooled during the summer.

There was an additional deep-cleaning of the loft once a year, which was particularly important if new stock was being brought into the loft. New stock was initially housed in a quarantine area which was used to prevent the birds from mixing and transferring disease. For deep cleaning all the fixtures were removed and washed separately. All floors, walls and ceilings were thoroughly cleaned with disinfectant and dosed in Virkon™ to kill germs and bacteria.

The pigeons were wormed and de-loused regularly with commercially available products and were also vaccinated every year against Pox and Paramyxovirus. Commercially available anti-biotics were also used when necessary, followed by a course of pro-biotic yoghurt to replace the natural gut bacteria. Once each week the birds were given access to a bath with the addition of anti-parasitic bath salts at the start of the month. All the pigeons were weighed (to the nearest g) regularly to check condition. If any of the birds appeared unwell during the daily inspections, the veterinary surgeon was called immediately and weight loss monitored over a period of three days. Unhealthy birds were not flown but kept in the loft and allowed to recover.

2.1.2. Training schedule and description of release sites

The main purpose of the training sessions was to ensure that the birds established the loft as their home and flew back to this site after release at various points north east and south west of Treborth Botanic Garden. As the birds arrived in Bangor as three-week old fledglings they were capable of becoming airborne but were unable to sustain flight for any length of time and were therefore initially unable to fly too far from the loft. The training stage also ensured that the birds were used to being rounded into baskets (constructed and supplied by Boddy and Ridewood) and were habituated to travelling in a vehicle prior to release. Even though the training sessions were labour intensive they were crucial to the success of the project. Unfortunately, the training sessions represented the greatest single loss of pigeons.

In order to encourage the birds to fly from the loft, a specially constructed aviary (168x90x53cm) was built in-house and attached to the loft to be continuous with one of the loft doors. The aviary comprised of a wooden frame with mesh sides and a mesh roof, which was designed to allow the birds the maximum view of their surroundings. When the aviary was attached and the loft door open the chicks were able to venture into an enclosed space but were prevented from escaping. The design was based on the theory that young pigeons need to view the sky as this helps them to develop a mental map of the location of the home loft (Glover and Beaumont, 1999) and possibly develop an olfactory map to guide them home. The chicks were never forced to enter the aviary but were encouraged to do so several times a week –usually the birds simply followed each other into the aviary. Initially a bath was placed into the aviary and once a few birds tentatively entered the aviary to gain access to the bath the others soon followed. Eventually no bath was provided and all the birds entered the aviary of their own accord. After several weeks the aviary was removed and when the loft door was opened the birds were able to venture into the open. The pigeons were then allowed to free-fly around the home area for about 2 weeks. The next stage in the training schedule was to habituate the birds to the baskets (91x45x26cm) that would be used to transport them to release sites north east and south west of the loft. To habituate the birds to the transport basket, the basket was attached to the loft where the aviary had once been located and the pigeons used this door as a means of exiting the loft. Pigeons were ushered calmly and quietly towards the door in order to enter the baskets. This method was successful because it was the least intrusive method for collecting the birds and represented the minimal amount of handling stress. Each basket could be used to transport 15 birds in relative comfort.

Once the birds had been habituated to entering the boxes, they were transported to release sites that were close to the loft (less than one mile). These early release sites were Site A, the University's sports field (OS coordinates SH 546708) approximately 0.6km from the loft and Site B, on local school playing fields (OS coordinates SH 549706) 0.5km from the loft (Fig. 2.1). The purpose of these early flights was to test whether the pigeons returned immediately to the loft once released. Only when the birds returned immediately were they taken further afield. The release site was then extended by approximately 1.1km to Site C across the Menai Strait in a lay-by opposite the loft on Anglesey (OS coordinates SH 543718), which was used to encourage the birds to fly over water. Birds were released form Site C until they returned immediately to the loft. On average this took only two attempts. Average flight time from this site was approximately five minutes. On successful completion of flights from Site C, birds were released from a number of sites to include: Site D at Gallows Point near Beaumaris (OS coordinates SH 598752) at 6.3km from the loft; Site E at Plas Menai (OS coordinates SH 502661) at 7.05km from the loft; and a nearby industrial estate, Site F, (OS coordinates SH 498656) at 7.65km from the loft. Both Plas Menai and the industrial estate are located south west of the loft, while

Site C is located to the north east. These three sites were chosen because of their location along the routes that were eventually used for the flight experiments. The final release sites corresponded to the sites that were used during flight experiments. These were Site G at Penmon, Anglesey (OS coordinates SH 621791) which is 10.5km north east of the loft and Site H at Waterloo Port, Caernarfon (OS coordinates SH 486641) which is 9.5 km south west of the loft. See Figure 2.1 for a map detailing these locations. All these distances were calculated directly from an Ordnance Survey Map (Ordnance Survey Landranger Map 115) and, therefore, represent the distance as the 'crow flies'.

Both of the final release sites used for the experiments described in Chapters IV and V were approximately fifteen to twenty minutes drive from the loft and were almost equidistant from the home loft but were in opposite directions from each other. The loft was halfway between the two locations (Figure 2.1). Both sites were located on the banks of the Menai Strait and both were fairly isolated locations. Release Site F at Penmon was located in a car park for the Anglesey Coastal Path and was popular with dog walkers during the summer months. Owners were politely asked to ensure that their dogs did not disturb the birds. By contrast, the location at Release G at Waterloo Port was situated along a private road and release of the birds from this site attracted little attention apart from the local residents. The location of these two release sites along the Menai Strait was deliberate because the Strait is characterised by near perfect head and tail winds along its banks. This characteristic was utilised in the experiments described in Chapter V which examined the effect of wind direction on pigeon flight. In both sites the birds were released by placing the baskets on sea walls that were 1m above sea level.

Fig. 2.1: Ordnance Survey map indicating the area around the home loft and the various release sites used during the research. Scale: 1cm to 1km.

2.2 Flight methodology

2.2.1 Logging equipment

Once the birds had been trained to enter the transport baskets and to recognise the loft as home they were ready for the flight experiments described in Chapters IV and V. By this time the average age of the remaining birds in the flock was 2.5years. All flight experiments involved the release of pigeons from either Site G or Site H i.e. Penmon on Anglesey and Waterloo Port near Caernarfon. For the experiments all pigeons were fitted with data loggers either a GPS to determine flight path, positional data and speed or an accelerometer device to determine changes in movements of the body (see Fig. 2.2). Unfortunately it was not possible to fit both sets of equipment onto each bird as the weight would have been excessive and would have interfered with the ability of the bird to fly. Each device was held in place by a harness which was developed in-house to hold the data loggers in place but at the same time causing the least inconvenience and hindrance to the birds.

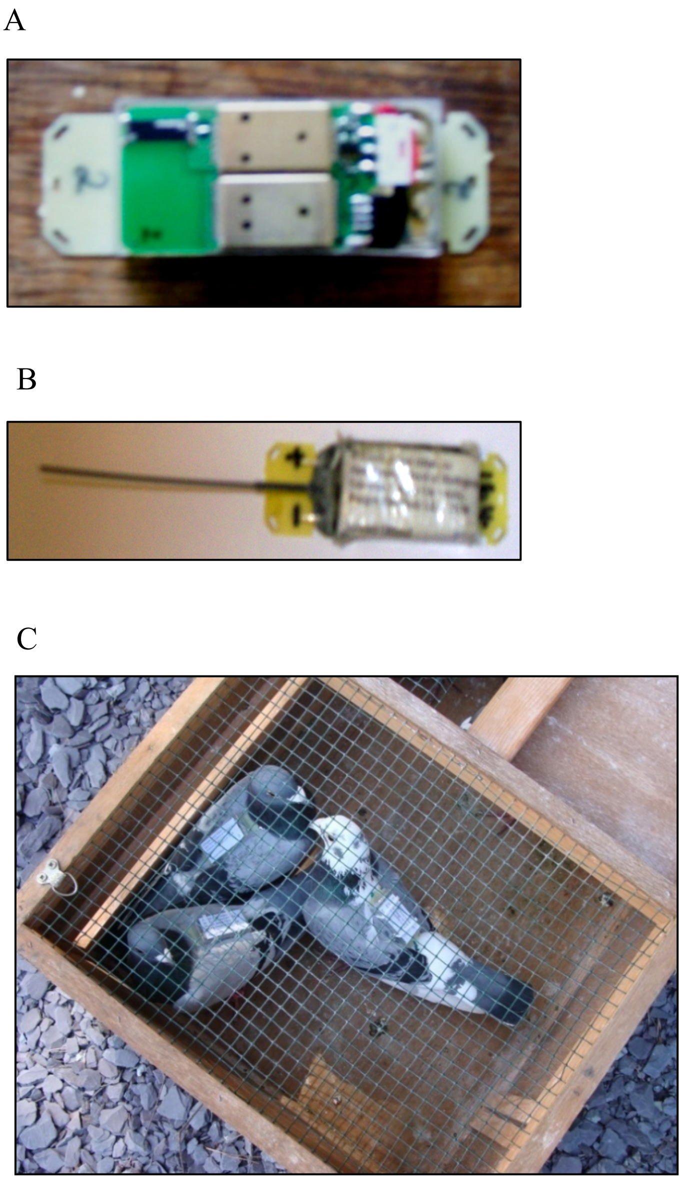


Fig. 2.2: A: Photograph of a GPS logger positioned on a back plate. B: Photograph of an accelerometer mounted on a back plate. C: Photograph of three pigeons fitted with a harness and logger in preparation for an experimental flight.

2.2.1.1. GPS

The GPS devices (Fig. 2.2a) were obtained from Technosmart, Italy and were used to measure positional information, including longitude and latitude, as well as speed. The loggers were able to measure altitude, but occasionally the technology was not always reliable for every flight. Each device weighed either 7 or 12g. Before use the GPS devices were used they taken outside on several different occasions and left on the roof to make contact with up to nine satellites. This allowed them to connect to the satellites faster during the actual flight experiments. Preliminary work showed that failure to follow this routine resulted in the GPS loggers recording position towards the end of each flight.

Advances in technology over the course of this work enabled the purchase of smaller loggers each year. Therefore, several different types of loggers were used in the flight experiments. However, when the same bird was used within an experiment (for example, added mass and no added mass) the same GPS logger was used for consistency. The original GPS loggers had the aerial mounted on the circuit board, however, later versions had a wire antennae that protruded from the device. The original loggers measured 5.0x2.5x1.0cm and weighed 12g and as they consisted of open microelectronics they were encased in a lightweight plastic box (casing and back plate weighed 4g) minimising the possibility of water damage. The second set of GPS loggers were slightly smaller (weighing 7g and measuring 4.0x2.0x1.0cm with an aerial measuring 4.5cm) and the third set of GPS loggers were even smaller (weighing 7g and measuring 3.2x2.0x0.7cm with an aerial measuring 4.5cm). As these new generation loggers still had open microelectronics these were also encased in plastic boxes. All these devices had been designed specifically for use on birds and small mammals by Technosmart, Italy. Additionally a fourth set of GPS loggers (IGotU-120) were purchased. Although they were no smaller than the others, they were considerably cheaper, enabling greater quantities to be bought (weighing 12g and measuring 4.5x2.3x1.0cm; with no wire antennae). Originally these loggers were designed to be sold to backpackers and travellers and were encased in extremely tough plastic. However this casing added extra weight to the bird and so this was removed and the electronics were re-housed as described for the previous loggers. Even though the dimensions of all the loggers were slightly different there were all encased in the same light-weight plastic boxes to ensure that the effects of drag were similar for all birds.

The GPS loggers recorded positional data (altitude, longitude and latitude) as well as data relevant to time (date, time (hours, minutes, and seconds) and speed). Some of the later devices also recorded information relating to DOP (Dilution of Precision) which gives an indication of accuracy of the GPS positional data. A low DOP value was desirable because it meant the satellites were not close together so the angular geometry was stronger. In addition the loggers capable of recording DOP also recorded the number of satellites being used to calculate positional data. Preliminary work confirmed that these loggers were using a high number of satellites and creating a low DOP value. Although the older and the very recent GPS loggers did not record such information, it was assumed that the same satellites are used to calculate positional data and therefore the resulting information was also highly accurate.

All the GPS loggers were capable of recording up to four fixes every second, but for flights they were all set to record once per second. This was termed as ‘continuous’ recording and the battery life in this mode tends to last for approximately five hours for older models, and significantly longer for newer versions. The smallest loggers contained a smaller battery which lasted for approximately three to four hours. This gave plenty of time for the birds to be taken to the release site and for the birds to fly back to the loft. The older GPS loggers were turned on at the loft before departure to the release site as they tended to need longer to record their first fix after being switched on, whereas the newer loggers (with wire antennas and those aimed at travellers) tended to turn on much faster and only needed to be activated at the release location.

2.2.1.2. Accelerometers

Accelerometers were obtained from E-obs Digital Telemetry, Germany (www.e-obs.de) and were built specially for use in the field. A number of the devices were kindly donated by Prof. Martin Wikelski, Max Planck Institute for Ornithology, Germany. The accelerometers were fully encased so that no electronic components were visible and measured 4.5x2.0x0.8cm (with an external aerial measuring 7.7cm) and weighed 9g (Fig. 2.2b). They were activated with the use of a magnet and recording began immediately. For a detailed description of the use of accelerometers, covering calibrations and conversions from the raw data, and potential use in the determination of flight mechanics, see Chapter III.

2.2.1.3 Harness design for attaching data loggers to pigeons

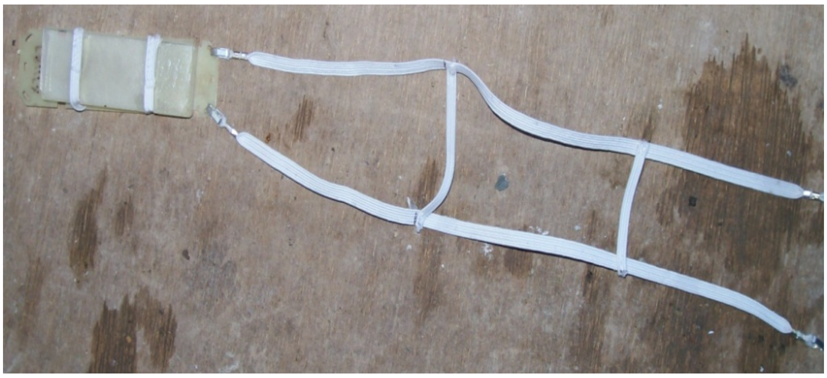
Several exploratory trials were carried out to find the best harness design. The easiest and most effective method which caused the least stress to the pigeons was to mount the GPS or accelerometers on to a separate back plate. The back plate was then fixed to a plate on the bird’s harness using fine garden wire.

The harnesses were made from circuit board and elastic tailored to the specifications of each individual bird and weighed approximately 2.75g. The back plate was made from printed circuit board (7.0x2.2x0.04cm) which was fitted on to the back of each bird. At each corner of the board a metal clip was fitted which holds the elastic in place. Six strand elastic was used because it offered enough strength without being uncomfortable. The two lengths of elastic reached from the back plate over the shoulders of the bird under its body, between its legs and back to the back plate. To add support to the harness, two four strand pieces of elastic were fitted to the six strand elastic across the top and the base of the keel. The pieces of elastic were sewn together to add extra strength. The strands across the body were 6.0cm in width at the top of the keel and 3.0cm in width at the base of the keel (Fig. 2.3). However the lengths of elastic used to hold the back plate in place varied from between 18.5cm to 23.0cm depending on the size of the bird (Fig. 2.4). Occasionally the harnesses broke and fell off the birds (only within the loft and never in flight); in these circumstances, they were repaired and refitted as quickly as possible.

The birds were habituated to wearing their harnesses for several months prior to the commencement of flight experiments. At first the birds often broke the harnesses but they were immediately repaired and refitted. After a short time the birds stopped interfering with the harnesses and they could last for many months without requiring removal. This allowed them time to get used to the harness and also give the birds the opportunity to preen it under their feathers – thus making them as comfortable as possible when flying. Once all the birds had stopped being bothered by the harnesses, small plastic blocks were fitted to the back plates (using elastic loops). These were the exact weight and dimension of the experimental equipment (GPS and accelerometers), as they would become habituated to this extra weight and it could be classified as body weight. Harnesses were worn continually for the duration of the entire experimental period.

A

B



C

Fig.2.3: A: Represents the harnesses used in experiments (not to scale). The grey rectangle is the back plate, the black triangles are the positioning of the metal crimp pins and the grey circles represent the stitched joints for the elastic. B: Photograph of an actual harness. C: Photograph of pigeon wearing the harness – right wing outstretched to show the back plate and the elastic passing over the shoulders and beneath the tail.

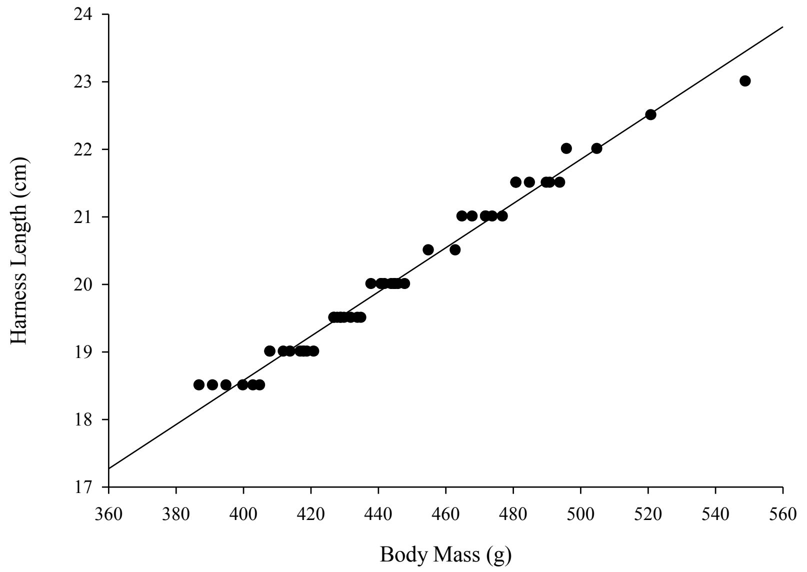


Fig. 2.4: Regression used to calculate harness length (cm) from body mass (g). Note that harness length was increased in 0.5cm increments as birds increased in weight by 15g. R^2 value = 0.9797. Regression equation: $y=0.0327x + 5.4954$. Data represents 53 homing pigeons weighed in June 2009.

2.2.2 Experimental regime

2.2.2.1 Preparation for free-flights

The regime described below was common to all flights. Before any experiment commenced using either GPS or accelerometers, the batteries were always fully charged. This was to ensure that there was enough battery life to cover the time span of the experiment as preliminary work demonstrated that if not fully charged the devices may stop recording data prior to the birds returning home. Batteries were charged from specialist battery chargers using a 12V car battery. Later GPS models were charged via a USB connection to a desktop computer.

2.2.2.2 Preparation of birds for free-flights

The day before each release, the birds were herded into transport baskets (Section 2.1.2). Once in the crates they were removed individually and either a GPS or accelerometer was fitted to their harness (which was worn continuously). They were then returned to the rest of the flock inside the loft. On the day of the release, the birds were again shepherded into the transport crates, removed individually and weighed before being placed back inside the crates ready for transportation. When the entire flock was flown (i.e. non-experimental in addition to experimental birds), the non-experimental birds were fitted with a 'dummy' Perspex block, which created a similar amount of drag for each individual bird to standardise experimental conditions.

The birds were transported to the release site in a van (Ford Connect) which had no rear or side windows so the birds were not able to see outside during transportation and therefore were unable to create a mental map of the outward journey. Once at the release site the crates were immediately removed from the vehicle and the birds allowed to settle for two or three minutes. To allow the release of pigeons individually, the birds were transferred from the transport baskets into smaller boxes (28x34x21cm) for release. Flocks were released straight from the transport baskets. As the GPS loggers took several minutes to record their first measurement, they were turned on 30 minutes prior to release. However, when using newer GPS loggers the waiting time decreased to approximately 10 minutes. As the accelerometers recorded immediately, they were activated a couple of minutes before release. The birds were then given a further couple of minutes to settle again before being released, either as one large flock or individually (dependent upon experiment). Wind speed was measured at the release site using an anemometer (Kestrel 4500) just prior to liberation and additional wind data was obtained from information collected by anemometers on the Britannia Bridge located across the Menai Strait. The anemometer was held above head height for approximately one minute to enable a clear measure of the wind speed to be noted and to take account of occasional gusts. Flights would have been abandoned if the wind speed had been too gusty and unsteady, although this never actually occurred.

2.2.2.3 Care of the birds after free-flights

Once the birds had flown back to the loft, the equipment was removed and replaced with the Perspex block attached to the harness to ensure the birds were completely used to carrying a small weight on their back. The loggers were not removed after every flight as the batteries had enough power for several flights. Instead birds were left with the loggers in place to avoid the increased stress caused by removing and refitting the loggers. In general this amounted to the birds wearing the loggers for no more than five continuous days. No detrimental affects were observed. However, the birds were collected after every flight to ensure the equipment was switched off.

2.3 Morphological measurements

The pigeons were weighed at regular intervals as part of basic husbandry. Additionally this handling also habituated the birds to human contact and handling.

To measure wing area and span, pictures were taken by a digital camera and the images were analysed by Adobe Photoshop and ImageJ. In order to take consistent measurements, the wings of each pigeon were held flattened against a table top edge separately by the same person. The body of the bird was held against the edge of the table to allow the wing to be fully extended and stretched to 90° from the body. This gave a clear view of both the body and the wing. Digital images were used to calculate wing span and wing area. From the calculations of wing area it was possible to determine wing loading for each individual. Preliminary analyses showed a consistent level of symmetry between wings of the same individual and for this reason one wing (right) was analysed and measurements were doubled to form a total wing area/span for the bird.

2.4 Analysis of GPS data

Positional information was recorded every second, which enabled accurate route reconstructions on mapping programmes, specifically, Google Earth Pro. Data was downloaded directly from the loggers using specialised software (older devices, GiPSy; newer devices, @tripPC; which was provided by the manufacturers).When downloading, the older loggers converted data into text files, whereas the newer loggers converted the data into Microsoft Excel. Notepad files were created for both loggers as these were used to visualise the route in Google Earth Pro. Files were created or imported into Microsoft Excel as this was the programme used to analyse the flight data.

The distance the bird flew was calculated using the Haversine Formula:

$$\Delta\sigma = \arctan\left(\frac{\sqrt{(\cos\varphi_f\sin\Delta\lambda)^2 + (\cos\varphi_s\sin\varphi_f - \sin\varphi_s\cos\varphi_f\cos\Delta\lambda)^2}}{\sin\varphi_s\sin\varphi_f + \cos\varphi_s\cos\varphi_f\cos\Delta\lambda}\right) \tag{2.1}$$

where $\Delta\sigma$ represents angular distance, φ_s represents latitude 1, φ_f represents latitude 2, $\Delta\lambda$ represents the difference between the two longitudinal measurements. Before the formula could be applied, the longitude and latitude measurements were converted from decimal degrees and into radians. Once $\Delta\sigma$ had been calculated this value was multiplied by 6371.01 (which represented the radius of the earth) and this resulted in the distance between one set of co-ordinates. These were all summated which resulted in the distance of the flight in total.

The GPS data was used to concentrate on three main measurements: route efficiency, air speed and altitude attained. Route efficiency can be defined as the beeline (or most direct) route back to the loft divided by the actual distance the birds flew. For the purposes of this thesis the amount of distance the birds circled at the release site was not included in this calculation. The flight was split into three sections and where appropriate the mid-third phase of flight was analysed as this should represent steady horizontal flight. Air speeds and total distance flown were calculated (as described above) for the entire flight and the mid-third section. The start and end of flight was not analysed as the birds were ascending or descending and were shown to fly more erratically, such as performing gliding around the home loft area or circling for orientation purposes at the release site.

2.5 Animal welfare

All of the experiments reported in this thesis were carried out without the need for a Home Office Licence. However, every care and attention was paid to the welfare of the pigeons. Routine husbandry of the birds was carried out by appropriately trained animal technicians. In addition, regular visits were made by the Home Office approved veterinary surgeon and the Home Office Inspector.

All the experimental flights conducted in Chapters IV and V were conducted using free-ranging homing pigeons which is important from a welfare point of view. Although the birds were fitted with small data loggers which would unfortunately affect their flight due to increased weight and drag, birds allowed to free-fly are able to make their own decisions regarding flight behaviour (such as speed, distance and route) which would be impossible under laboratory conditions. Free-flight has also provided results from birds flying in natural conditions. However, the disadvantage of allowing birds to free-flight is their exposure to natural predators such as birds of prey.

Unfortunately there were a high number of losses from the first batch of chicks that were purchased in the summer of 2007. There were several reasons for the loss of birds, most of which were related to the free-flying phase of the training schedule. First, the pigeons were attacked on their homeward flights by birds of prey including sparrowhawks (*Accipiter nisus*) and peregrine falcons (*Falco peregrinus*). Both species nest in the local area, and several birds in one flock could be attacked by peregrine flacons. On some occasions two or three birds out of 50 failed to return home and one or two would be injured (showing signs of attack by peregrine falcons). Second, there was a relatively high rate of loss at the very beginning of the training flights when young birds did not return to the loft (on one occasion almost 10% of juveniles were lost in this fashion). The reasons for this are unknown but could have been due to predation and disorientation. In 2007, the birds were relatively strong fliers when they were first released from the loft. It is possible that they ventured too far away and became disorientated and failed to return home. Finally some of the chicks were unhealthy and several subsequently died (roughly 5%). The veterinary surgeon performed several post mortems to try and establish a cause of death but failed to come to an overall diagnosis. The rearing and training of chicks purchased in the summer of 2008 was much less problematic. One reason for this is that young birds were released from the loft at a younger age than the previous year. These birds only ventured short distances before returning home. By the end of the training schedule, only thirty out of the first sixty, and twenty out of the second thirty chicks had survived. This represented a loss of 50% and 33% of total number of pigeon chicks purchased for the project in 2007 and 2008, respectively.

CHAPTER III - Summary

Examples are provided of different variables that can be determined by a 3D-accelerometer deployed on the back of a pigeon once they have been calibrated. Apart from direct readout of accelerometry in m s^{-2} from each axis (x, y and z) various derived variables can be calculated. These include: (1) vectoral dynamic body accelerations (VeDBA) in which a running average value of acceleration is calculated over a suitable number of wing beat cycles (between 6 and 9 in the present study) and then subtracted from each acceleration value to generate the dynamic component in each axis; (2) the average term is called the static component and can be used to indicate general body inclination e.g. along the rostral to caudal direction of pitch (y-axis); (3) the z-axis acceleration can be used to detect wing beat frequency while a new term, fraction positive, is developed to indicate the proportion of time in each flap cycle in which the body is experiencing above average accelerations (or vice versa for fraction negative). Observations show that when wing beat frequency is high there is an approximately 50% split in high verses low accelerations experienced by the body of the bird but when wing beats are slow delivery of the high g accelerations is still fairly rapid in absolute time. As a result the low g accelerations last over a longer period of the flap cycle, perhaps due to increasing the recovery periods following the power stroke.

A review is undertaken of the various studies in which energy consumption during flight has been measured in flying pigeons and a comparison made with respect to the U-shaped power curve predicted by the aerodynamic model of Pennycuick, Flight Program (Version 1.22). An empirical power curve is estimated based on these energetic measurements but to get even a general concept of a potential J-curve (corresponding to relatively high speed flight) the study of Rothe et al. (1987) has to be completely ignored. A model is presented in which the energy required to move the mass of a body along a sinusoidal but "net" horizontal path is calculated so as to illustrate the scale of the potential amount of energy that might be detectable from an accelerometer placed on the back of a bird. It suggests that this might be of the order of only 6% of the total aerodynamic flight costs. Integration of the raw Y and Z is then used to calculate power in the body of the bird directly (using *Power* = *Mass* x *Acceleration* x *Velocity*) and assuming no net change in velocity over the section of integrated data. VeDBA_{YZ}^2 is shown to be very highly linearly correlated ($R^2 = 0.947$) with the integrated raw yz-accelerations and, therefore, an excellent predictor for power in the body of a pigeon. This relationship should also be applicable to other flying animals. Double integration of the z-axis accelerations and, again, assuming sinusoidal accelerations and motion of the body gives an estimate of dorsal body displacements (B).

3.1 Introduction

The aim of this thesis is to explore how the flight patterns of free-flying homing pigeons (*Columba livia*) can be assessed using miniature GPS and accelerometer data loggers. Consideration is given to how accelerometry in particular may be used to determine specific flight behaviours and to provide an indication of how much energy the pigeon is consuming during flight, and how this might be affected by environmental factors such as wind strength, body morphology such as differences in natural body mass or experimental manipulation of carried mass, or even behavioural parameters such as homing motivation and flight speed. With modern technology it is possible to affix small data loggers to individual birds to establish, for example, information relating to position, altitude and ground speed using GPS, or detect wing beat frequency, overall dynamic body accelerations, or even static body orientation, using accelerometers. Taken together these two differing apparatus could provide useful information as to how the above conditions may affect flight in the homing pigeon. Both the strength and the weakness of monitoring the birds' during free-flights is that they are allowed to make their own decisions regarding the flight home, both affecting 3D-routes home and choice of speed.

This chapter aims to illustrate the use of accelerometry from the calibration measures used to explaining the possibility of such devices being able to indicate power consumption, thus providing a less invasive method of estimating energy expenditure when compared to the more traditional methods previously utilised in free-flying birds.

3.2 Accelerometers

Tri-axial accelerometry utilises three transducers placed orthogonally, which enables both static and dynamic acceleration to be measured in all three planes (Wilson et al., 2008). Static acceleration is used to indicate the angle, and therefore posture, of the individual relative to the gravitational field of the earth as it is a measure of the accelerometer's incline (Shepard et al., 2008b). Dynamic acceleration represents the movement of an individual due to a change in speed (Shepard et al., 2008b). Accelerometry is an extremely sensitive technique, for example Shepard et al. (2008b) were able to determine a change of gait in a llama (*Lama glama*), grazing behaviour in herbivores and grooming behaviour in imperial cormorants (*Phalacrocorax atriceps*).

Due to advances in technology throughout the course of this research two consignments of loggers were purchased. Initially the first consignment had less available memory than the second consignment, but these were returned to the manufacturer (E-obs Digital Telemetry, Germany (www.e-obs.de) and updated. Therefore towards the end of the research all the loggers had the same amounts of memory available. There were ten available settings to select from ranging from 10Hz to 1778.28Hz. However these were the frequencies if one axis was activated. If two axes were activated then they recorded half as many data points and if three axes were chosen they recorded as third as many data points (Table 3.1).

Table 3.1: Frequency of data points recorded by the accelerometers at various settings.

Sample Rate	Frequency 1 Axis (Hz)	Frequency 2 Axes (Hz)	Frequency 3 Axes (Hz)
0	10.00	5.00	3.33
1	17.78	8.89	5.93
2	31.62	15.81	10.54
3	56.23	28.12	18.74
4	100.00	50.00	33.33
5	177.83	88.92	59.28
6	316.23	158.12	105.41
7	562.34	281.17	187.45
8	1000.00	500.00	333.33
9	1778.28	889.14	592.76

For the experimental flights all three axes (X, Y and Z) were selected using sample rate 7 (187Hz/axis; see Table 3.1) as it was felt these would give the most accurate measures of overall movements. Preliminary work discovered that at very high frequencies (sample rates 8 and 9) a lot of very detailed data was recorded, however due to the set up of the loggers this was at the expense of quantity; data was only stored in short sections at high resolution. Therefore over short bursts much of the data was often missed as flights were short but in-depth detail was required. For this reason a compromise was reached between quantity and detail and so sample rate 7 was selected. However, only 1.25s out of every 2s had data recorded as unfortunately at this sample rate it was impossible for the loggers to record continuously (from here on referred to as a 'sample collection period' of data). Occasionally there was an extra delay lasting one second before the next 'sample collection period' of data was recorded. The loggers were not designed to record continuously at a high sampling rate. To maximise high resolution recording it was impossible to record data continually. However, even at this sample rate the resolution of the accelerometers was approximately $0.02ms^{-2}$.

3.2.1 Calibration of accelerometers

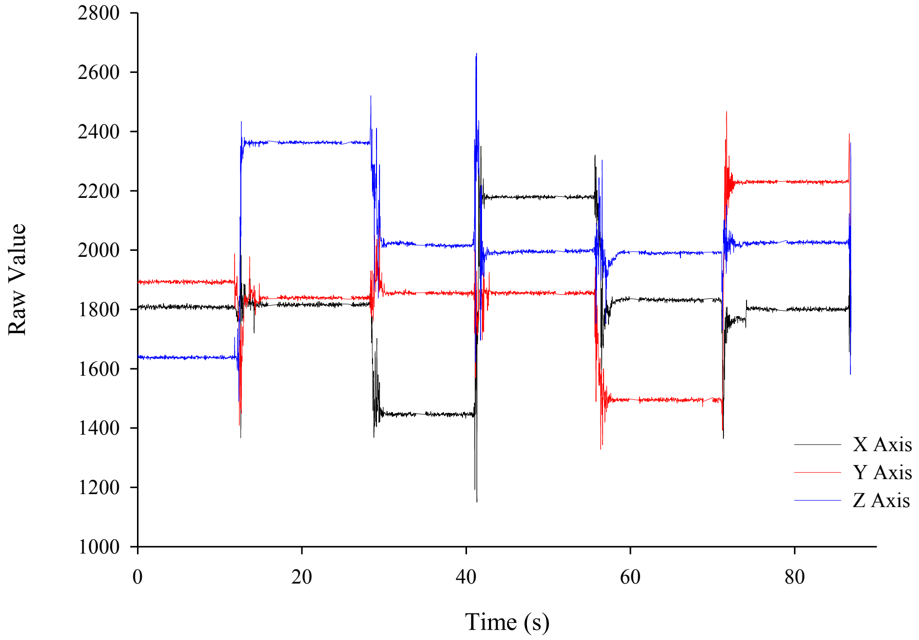


Fig. 3.1: Graphical representation of the raw data when calibrating the accelerometers (logger 338). The raw data points are displayed as a measure of orientation of the logger.

The output from the accelerometers was not in mV but in arbitrary units ranging from 0 to 4095 (12bit unsigned binary values), which are linearly correlated up to the maximum setting of the transducer. The full span of the accelerometer was 4096*0.0027 giving 11.05g*9.81ms^{-2} and a full acceleration range of 108.5ms^{-2}. Leaving the loggers on a flat surface gave calibration values in arbitrary units for either ±1g if set horizontally with respect to gravity, or for 0g if set on their sides. If the sensor read 2048 at 0g then the output range corresponded to ±5.5g. The calibration of the accelerometers is a relatively simple procedure, although each axis on each logger must be calibrated separately. The devices must be positioned for several seconds so that each axis (X, Y and Z) points towards the centre of the earth in both a positive and negative manner. Although the X, Y and Z axes do not follow a right-hand Cartesian co-ordinate system, the system used was left-handed. To calibrate the

Z axis the accelerometer was laid firstly flat on a table and then on its back. As the X and Y axes are parallel to the earth and the Z axis is initially pointing towards the earth (negative gravity) and secondly towards the sky (positive gravity) as the sensor inside the accelerometer records the opposite of gravity. Similarly for the X axis the accelerometer was laid on its left hand side (negative gravity) and then on its right (positive gravity). Finally for the Y axis, the device was placed on the table rear-end down (negative gravity) and then front-end down (positive gravity). Each time the accelerometer was rotated the logger must remain orthogonal to the desk (i.e. 90^o or 180^o). All this calibration data is recorded on each logger which is then downloaded to the computer and graphs can be produced in the raw form (Fig. 3.1) and a smoother form which is easier to read (Fig. 3.2).

As can be seen from Figures 3.1 and 3.2, each axis read zero gravity between roughly 1800 and 2000. When the horizontal line fell below these values negative gravity was represented and above it positive gravity was represented. Zero gravity, and hence the calibration value, was represented by the mean of the values of positive and negative gravity. This gave the calibration value for each axis for each logger for the raw data.

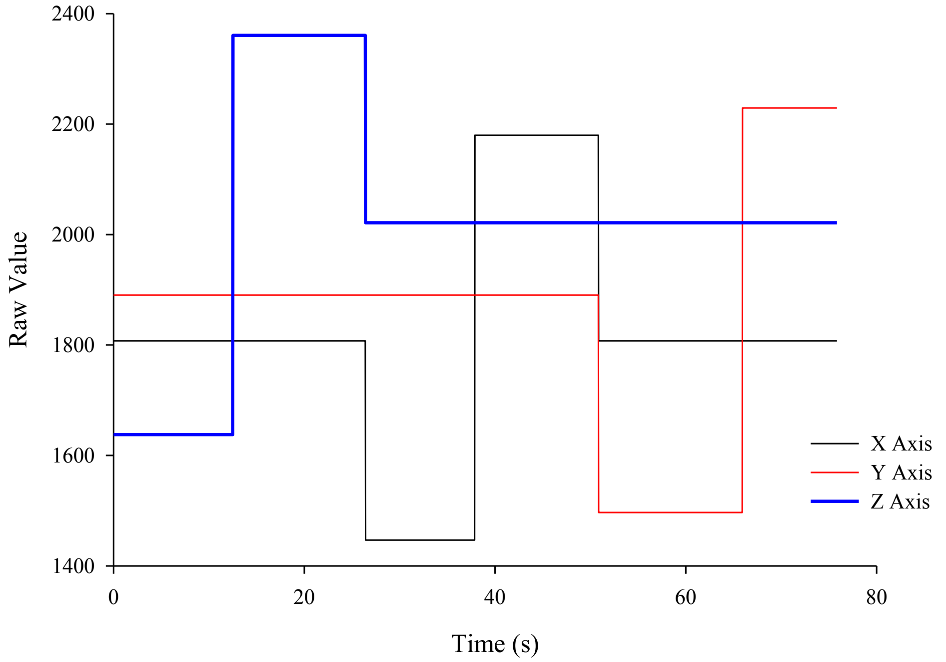


Fig. 3.2: Graphical representation of the calibration for accelerometer 338. Data smoothed to make values clearer.

3.2.2 *Conversion of raw data to values in m s^{-2}*

Once the calibration values were determined for each axis for each logger, they could be used to convert the raw data recorded by the accelerometers into measures of acceleration in ms^{-2}. The acceleration for each axis must be calculated separately (Equation 3.1) by subtracting the calibration value for zero gravity from the raw data value. This new value is then multiplied by 9.81 (acceleration due to gravity) and 0.0027 (which is a constant represented by the accelerometers set to record at ‘low sensitivity’). Raw data from the accelerometer are simply counts of the in-built voltage digitiser, which has an arbitrary voltage scaling. The scaling factor 0.0027 is used to attach units of g to these readings and the factor 9.81 converts g to ms^{-2}. Calibration does not refer to any adjustment of the scaling of the data but rather the 0g offset, which is typically in the range 1800-2000 (raw data measurements).

$$\text{acceleration (ms}^{-2}\text{)} = \text{(raw value – calibrated value at zero g) x 0.0027 x 9.81} \tag{3.1}$$

This constant 0.0027 can be calculated during the calibration Equation (3.2) by dividing the two g span used during the calibration by the mean of the positive one g gravity reading minus the mean of the negative one g gravity reading.

$$\text{constant} = \frac{2\text{ g}}{\text{mean positive gravity-mean negative gravity}} \tag{3.2}$$

As can be seen from Tables 3.2 and 3.3 there is little variation within the calibrations of the ‘original’ loggers. Although all the loggers used had slightly different calibrations (see Tables 3.2 and 3.3) and because of this when doing experiments individual pigeons always wore the same accelerometers to ensure continuity.

Table 3.2: Calibrations for each axis for each accelerometer prior to updating the original loggers (tags 164-170)

Tag No	X Axis	Y Axis	Z Axis
164	1882	1749	2007
165	1901	1814	1965
166	1838	1782	2061
167	1866	1827	1974
168	1916	1769	2025
169	1941	1900	2021
170	1909	1820	2019
338	1813	1863	2000
339	1911	1906	2035
341	1810	1789	1975
342	1786	1866	2011
343	1866	1895	2015
344	1895	1915	1995
361	1869	1878	2041
362	1856	1857	2031

Table 3.3: Calibrations for each axis for each original accelerometer after update (tags 164-170)

Tag No	X Axis	Y Axis	Z Axis
164	1883	1758	2006
165	1902	1819	1966
166	1842	1788	2025
167	1867	1832	1972
168	1919	1768	2024
169	1943	1904	2019
170	1910	1829	2016

3.2.3 Conversion of raw data to create analysable variables

Once the raw data had been converted into a measure of acceleration (units of g or m s^{-2}) (Sections 3.1.1 and 3.1.2) it was possible to convert this acceleration into dynamic body acceleration (DBA). Firstly a running average was then calculated for all data points on each axis separately. Shepard et al. (2008a) calculated static acceleration using a running mean over two seconds for imperial shags (*Phalacrocorax atriceps*). Using similar methods to Shepard et al. (2008a) the running mean was calculated within one sample collection period of data (approximately 1.25s) incorporating around seven wing beats (Figure 3.3). The reasoning behind this was that one sample collection period was 1.25s in length, as the accelerometers were unable to record continually, but this was enough for at least 7 wing beat cycles and, thus, provided a reasonable running mean. This running average was then subtracted from the measure of acceleration, using each point separately to give dynamic acceleration in each axis (A). Static acceleration refers to acceleration due to the earth's gravitational field; dynamic acceleration refers to the movement and hence acceleration of the individual animal (Wilson et al., 2008). These values were then all converted into positive values and summed for each axis to give a value for overall dynamic body acceleration (ODBA).

$$\mathrm{ODBA} = \mathrm{Ax} + \mathrm{Ay} + \mathrm{Az} \tag{3.3}$$

However, an alternative approach is to calculate the true acceleration vector length using Pythagoras' theorem to calculate the vectoral dynamic body acceleration (VeDBA), which is defined as:

$$\mathrm{VeDBA} = \sqrt{\mathrm{A}_x^2 + \mathrm{A}_y^2 + \mathrm{A}_z^2} \tag{3.4}$$

It is argued by Qasem at el. (2012) that where the orientation of the data logger is correctly in line with the axes of the animal, then there is little practical difference between the two methods. However, with regard to future considerations (or modelling) of how body acceleration mass relate to power output of birds during flight it would seem preferable to use VeDBA, as ODBA exaggerates vector length and so gives a mathematically inaccurate measure. During steady flapping flight with symmetrical flapping of the wings, little acceleration was expected to be recorded in the X axis (yawing movements to left and right in the horizontal plane). As anticipated, accelerations recorded on the X axis were lower than the other two and so this axis became fairly redundant. For this reason and in order to simplify the analysis, the decision was taken to only analyse acceleration in the Y (caudal to rostral movements in the horizontal plane) and Z axes (vertical plane or heave), hence the new variable $VeDBA_{YZ}$. Eventually, this variable was squared to become a separate analysable measure, $VeDBA_{YZ}^2$. Later in this chapter (Section 3.5.6) this method is justified by the similarity between this measure and a separate measure of power in the body (P_{int}), as $VeDBA_{YZ}^2$ and P_{int} are strongly linearly correlated. This approach is also mathematically justified in Section 3.5.5.

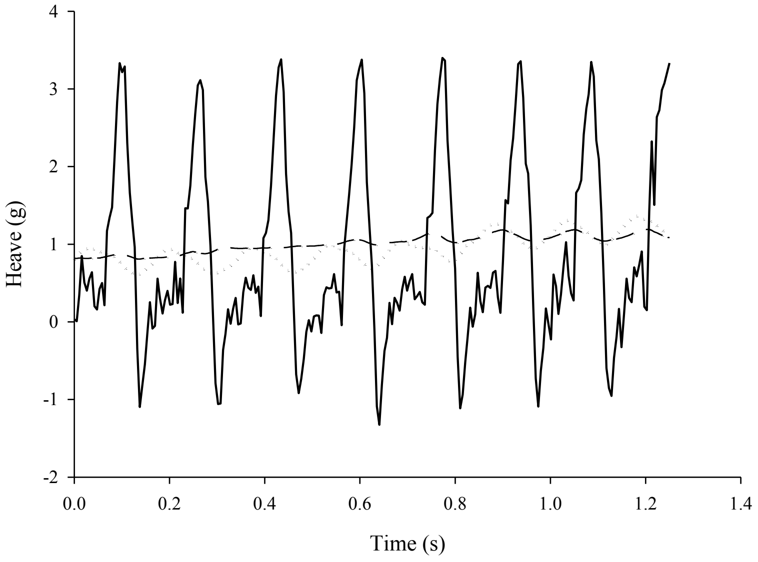


Fig. 3.3: Total acceleration is plotted from a pigeon in flight in the heave axis with the static component being calculated from a running mean of seven wing beats (dashed line; equating to one 'sample collection period' of data) and for comparison from a running mean of three wing beats (dotted line; equating to approximately just less than half a 'sample collection period' of data).

A specialised computer program was developed within the School of Biological Sciences, Bangor University (Pigeons: Vertical Acceleration Analysis, R.J. Spivey) to quickly and accurately analyse large quantities of accelerometry data, with each sample collection period of data analysed separately. This program was used to plot waves from the Z axis to highlight probable wing beats. A decision was made to analyse all entire beats in each sample collection period and these were used to calculate values for DBA (see above for detailed description on calculations involved) as well as wing beat frequency. Therefore, the dynamic data resulted in three variables to analyse; VeDBA, wing beat frequency and fraction negative (the ratio of time that Z axis accelerations are below the mean g averaged over the whole sample collection period, or vice versa for fraction positive), whilst the static data gave an indication of angular change in the body of the individual. For each of these variables the mean values were calculated for the mid third of flight. All these variables were averaged to create one average value for each variable in each sample collection period of data. As the accelerometers recorded at frequencies of over 188Hz each second over three axes, creating averages was the most suitable method to analyse the data.

3.3 Flight profile of one individual

Various terms and phrases have been coined during the course of this research with many being created as new, previously unknown variables, which have been used to describe the flight behaviour of the pigeons. A brief out-line is given here as a reference for the reader so they are aware of what each variable represents. Figures 3.4 to 3.8 outline data taken from the same individual bird during the same flight (no wind conditions from Waterloo Port) during September 2009. This allows the various aspects of flight behaviour to be compared during the same flight. Sections 3.1.2 and 3.1.3 describe how the raw data was converted and analysed for each of the variables.

3.3.1 Vectoral dynamic body acceleration (VeDBA)

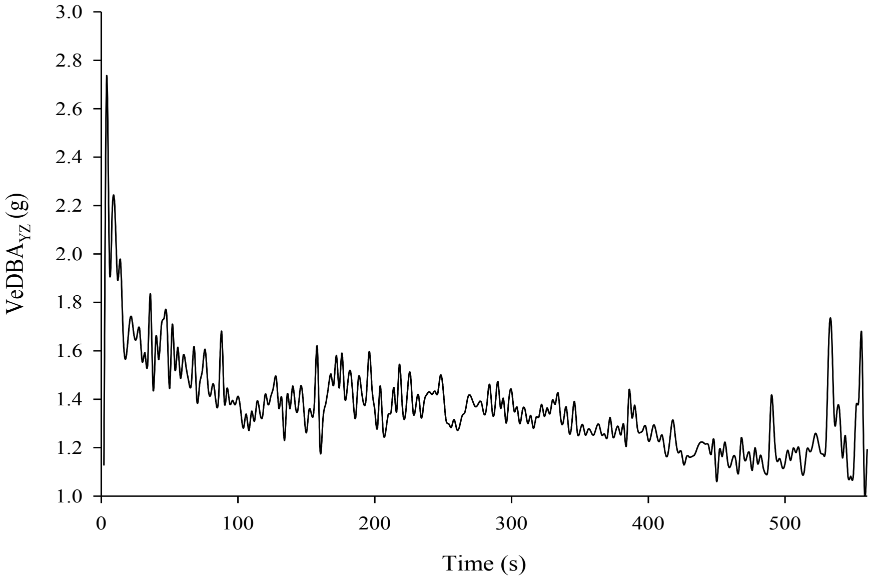


Fig. 3.4: The average vectoral dynamic body acceleration (VeDBA$_{YZ}$) (g) (calculated from four wing beats per sample collection period) from one individual, for an entire flight (Waterloo Port; in no wind conditions).

When an animal is moving, it must use energy to contract its muscles and in turn this causes the body or limbs to accelerate and, therefore, changes in acceleration might be used to indicate energy expenditure (Halsey et al., 2009a). Figure 3.4 shows how the average VeDBA$_{YZ}$ values from one individual change during the course of an entire flight. It is clear that during the first few seconds after take-off VeDBA$_{YZ}$ is at its peak, but as the flight progresses and the bird is making steady progress home, this value declines to around 1.5g. Once the bird has neared the loft VeDBA$_{YZ}$ becomes raised and slightly erratic, probably due to the individual engaging with landing behaviour (gliding, circling and rapid descent).

3.3.2 Wing beat frequency

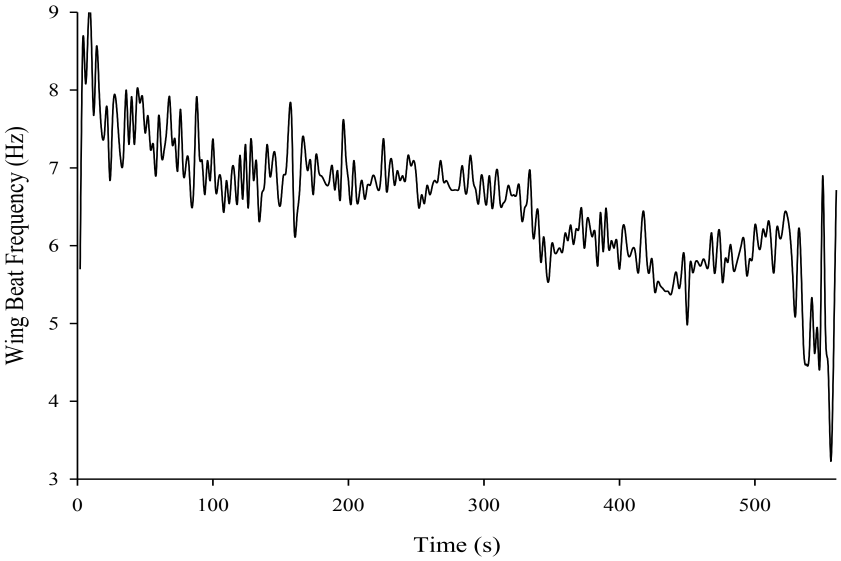


Fig. 3.5: The average wing beat frequency (Hz) from one individual, for an entire flight (Waterloo Port; in no wind conditions).

Wing beat frequency is the number of times a bird flaps its wings each second and is measured in Hertz (Hz). When the flight of one individual (flying in no wind conditions) was investigated (Figure 3.5) it showed that wing beat frequency was initially high, but then settled to an average of 6-7Hz before becoming more changeable at the end of the flight.

3.3.3 Fraction negative

‘Fraction negative’ was a term that was created during the course of this project to represent the proportion of time (s) a bird’s body spends with Z axis acceleration values below the average g for an entire sampling period (around 1.25s). Conversely, ‘fraction positive’ represents the proportion of time a bird’s body spends experiencing accelerations above the average (g). By plotting fraction negative for one individual over the course of a no wind flight (Figure 3.6), it can be seen that initially at take-off the fraction negative is low, meaning that fraction positive is high. This suggests that the bird may spend proportionally more time in the down stroke during this flight period. As the flight progresses and the bird is flying steadily, the fraction negative value is less variable and becomes greater than 0.5, indicating that this individual has longer gaps between applications of work by the wing which result in upward body accelerations. The end of the flight represents a highly different style of flapping with greater variation between the fractions positive and negative.

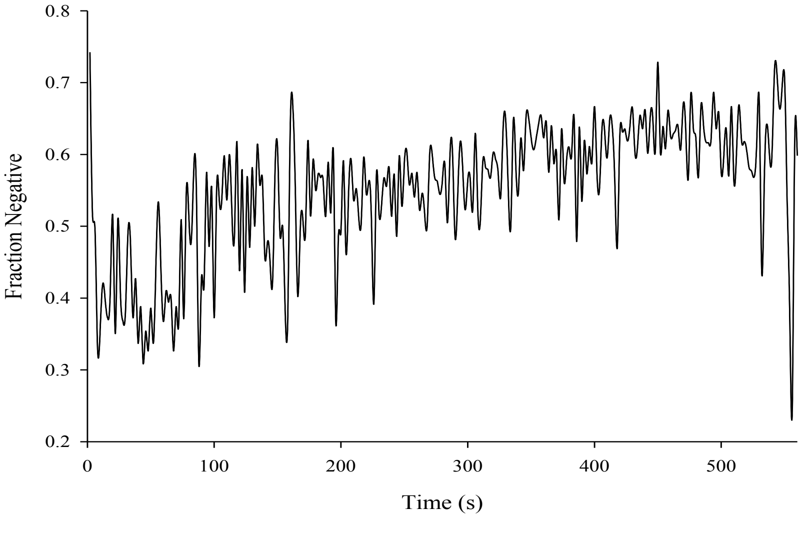


Fig. 3.6: The average ‘fraction negative’ from one individual, for an entire flight (Waterloo Port; in no wind conditions).

3.3.4 Static Y

As mentioned elsewhere (Section 3.1) accelerometers measure both static and dynamic acceleration. For this reason the average values of the static Y axis suggest the posture of the bird ain the rostral to caudal plane (or pitch) and may indicate climbing or descent. From Figure 3.7 which tracks the static Y axis of one individual bird it is possible to see that on average the bird remains fairly stable in a horizontal position with only minor alterations to its posture. However, during the take-off and landing periods, the static Y axis represents greater variability which may indicate the ascending and descending phases required during these episodes of flight.

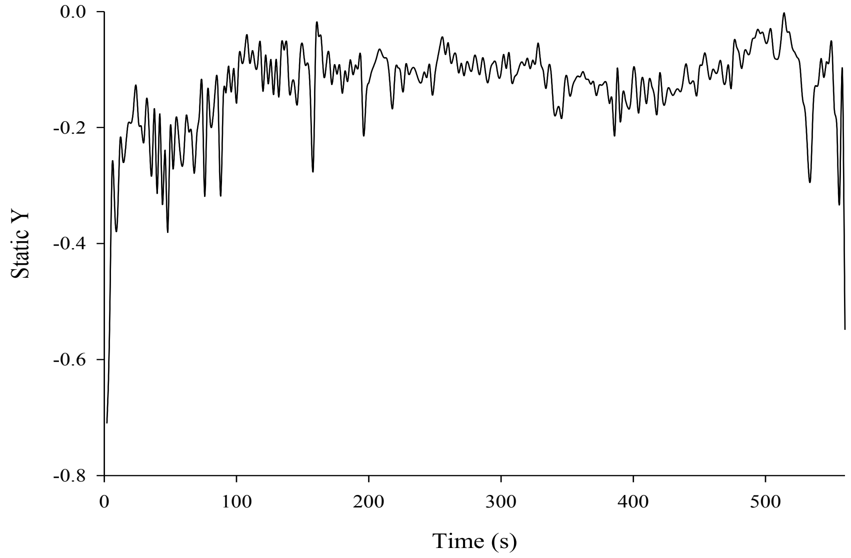


Fig. 3.7: The average static Y from one individual, for an entire flight (Waterloo Port; in no wind conditions).

3.4 Overview of a typical flight

Using the condition 'no wind' (18th September, 2009) it is possible to create and describe typical flight patterns averaged over the flock. From Figures 3.8 to 3.12 it is possible to see that all eleven birds were remarkably well synchronised, with three distinct flight phases, similarly to those described in section 3.2.1 for the individual bird. Firstly, there is a marked increase in the average intensity of the flight behaviour during take-off and the first minute or so of climbing activity, which then becomes steadier and more even during the middle section of near horizontal or gently climbing flight. This increase in flight behaviour as the flight begins can be categorised by an increase in VeDBA value (Fig. 3.8) and wing beat frequency (Fig. 3.9) with a noticeable reduction in fraction negative (therefore a great proportional increase in time engaging in upward acceleration of the bird's body; Fig. 3.10). Static Y (Fig. 3.11) also show discernable differences at the beginning of flight compared to later stages. Similarly, the average ground speed (Fig. 3.12) is also slower at take-off than during later in the flight (although this variable was measured on different birds in the flock).

The final phase is as the bird approaches the home loft and begins to descend before landing where the flight style is extremely erratic. This inconsistency can be seen throughout the measured variables (Figs. 3.8 to 3.12) as VeDBA increases and then sharply falls (Fig. 3.8), wing beat frequency reduces gradually to zero (the point of landing; Fig.3.9) and fraction negative rises and falls several times before reaching zero (Fig. 3.10) to indicate variation in the amplitude of each beat. During this final phase static Y (Fig. 3.11) is extremely variable indicating how the birds' posture is constantly changing as it descends, circles, glides and finally lands. The average ground speed (Fig. 3.12) also decreases sharply and then increases before slowing down again, possibly this hints at a change in flight style from flapping to engaging in more gliding and descending behaviour in preparation for landing.

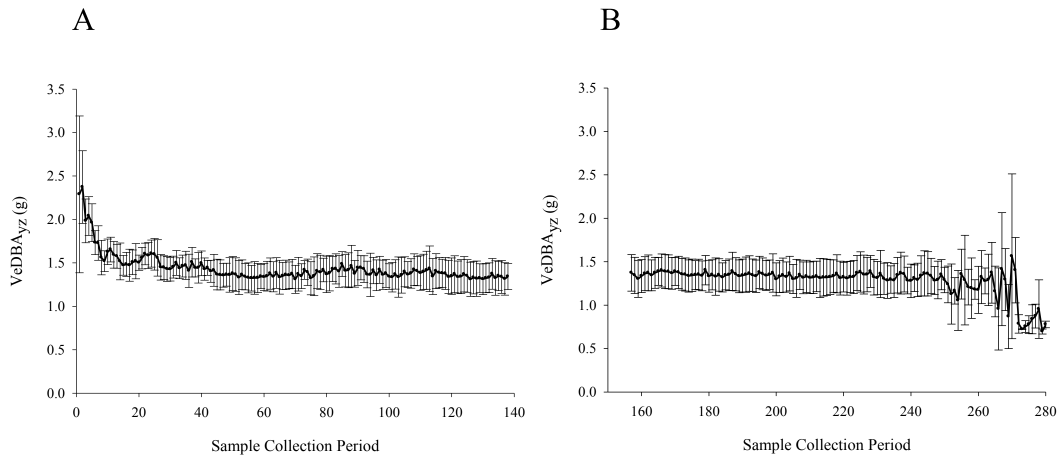


Fig. 3.8: Mean VeDBA$_{YZ}$ (g) from the first half (A), second half (B) of flight; average of 11 birds flying from Waterloo Port in no wind conditions. Error bars represent the standard deviation for each sample collection period.

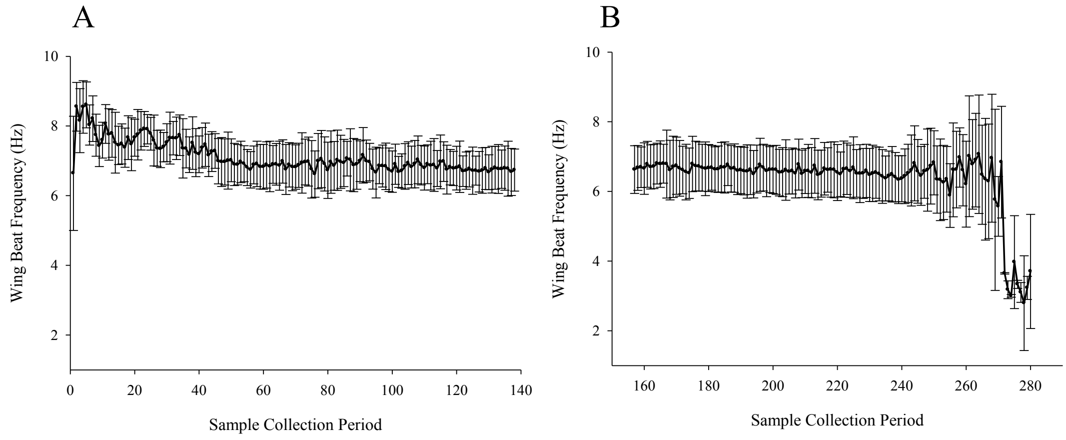


Fig. 3.9: Mean wing beat frequency (Hz) from the first half (A), second half (B) of flight; average of 11 birds flying from Waterloo Port in no wind conditions. Error bars represent the standard deviation for each sample collection period.

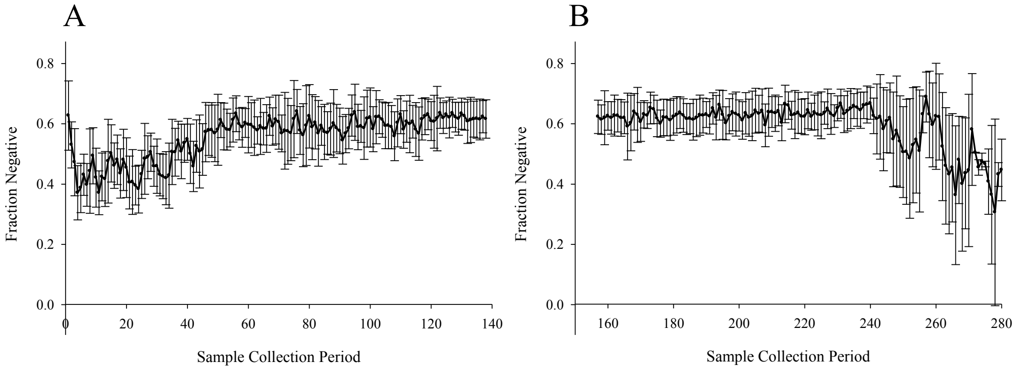


Fig. 3.10: Mean fraction negative from the first half (A), second half (B) of flight; average of 11 birds flying from Waterloo Port in no wind conditions. Error bars represent the standard deviation for each sample collection period.

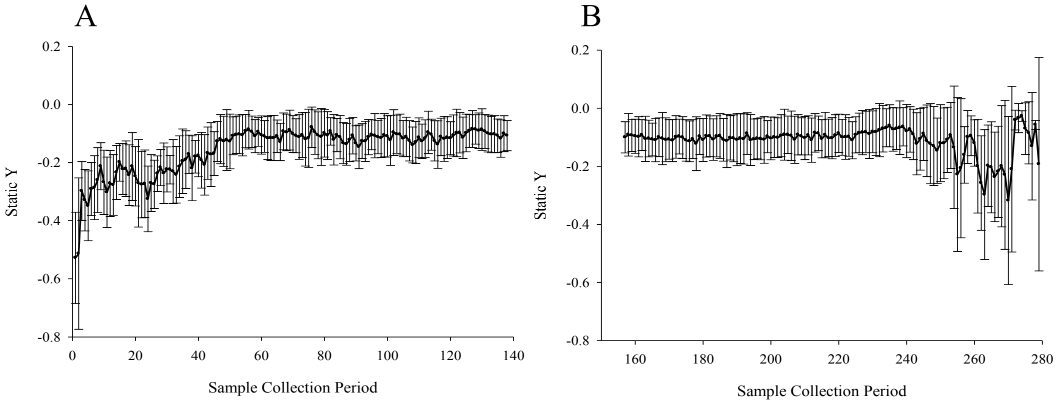


Fig. 3.11: Mean static Y from the first half (A), second half (B) of flight; average of 11 birds flying from Waterloo Port in no wind conditions. Error bars represent the standard deviation for each sample collection period.

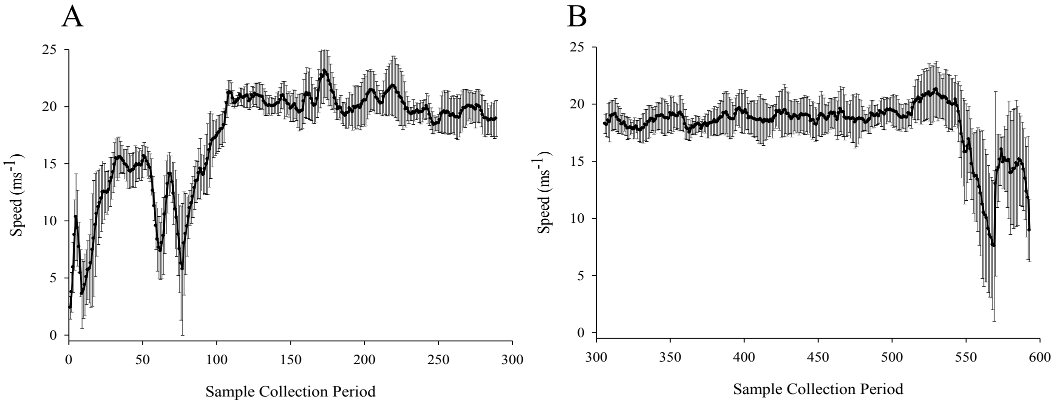


Fig: 3.12: Mean ground speed (ms^{-1}) from the first half (A), second half (B) of flight; average of 7 birds flying from Waterloo Port in no wind conditions. Error bars represent the standard deviation for each second.

By investigating both the flight behaviour of the individual (Figures 3.4 to 3.7) and the flock (Figures 3.8 to 3.12) it was possible to distinguish three phases of flight (as described above). Due to this, the very early (take-off phase) and final (landing phase) sections of flight were not analysed because of their erratic style. Therefore, in particular the mid-third section was analysed where mean values are presented which essentially should represent steady horizontal flight or phases of only moderate climbing and descending flight behaviour. Where the 'whole' flight behaviour of individual birds is investigated the first 10 and final 30 sample collection periods are still removed.

3.4.1 Raw accelerometry data from a typical flight for one individual

The same individual bird used to create Figures 3.4 to 3.7 was used for Figures 3.13 to 3.16. The raw data from the Z (or heave) axis was converted into g (see Sections 3.1.1 and 3.1.2) and was plotted in Figure 3.13, which depicts each wing beat during the entire flight in no wind conditions from Waterloo Port. However, due to the high quantity of data collected during this flight (over 66,000 measurements) it is impossible to show the entire flight in one graph in any detail. For this reason the flight was split into smaller sections to represent the beginning, middle and end of the flight (for description and justification of these phases see Section 3.3) to show in more detail the variation in both the frequency and amplitude of each flap during these three very differing flight phases. Nevertheless, some valuable information can be gleamed from Figure 3.13. It is possible to see that heave is greatest at the beginning and end of flight as the bird is exerting the greatest g as it climbs and descends, whilst during steady flight these values become more stable (see Figs. 3.14, 3.15 and 3.16).

Further examination of the accelerometry allowed a more detailed picture of the flapping style of the pigeons to emerge. As the accelerometers record movement and in a flying animal the vast majority of movement is created by the wings, by plotting data from 10s sample collection periods (Figs. 3.14a, 3.15a and 3.16a) data from one sample collection period (Figs. 3.14b, 3.15b and 3.16b) of the Z axis during take-off, steady flight and the landing phase in no wind conditions (i.e. control conditions before any manipulation) it was possible to visualise how the wing beat frequency and peak acceleration of the flap cycles varies in different sections of flight.

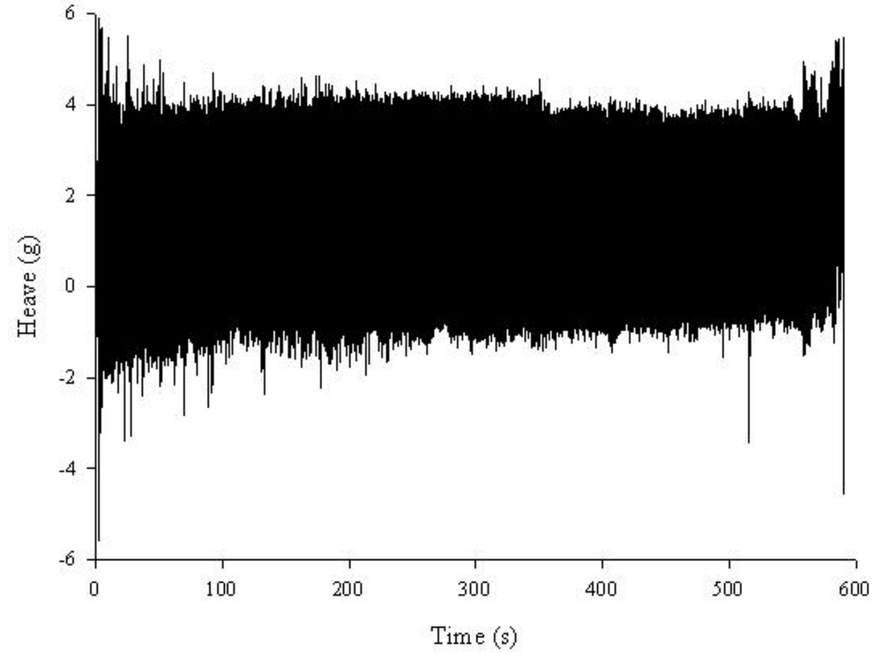


Fig. 3.13: Individual flaps measured by the heave (g) or Z axis for one bird during a no wind flight from Waterloo Port.

A

B

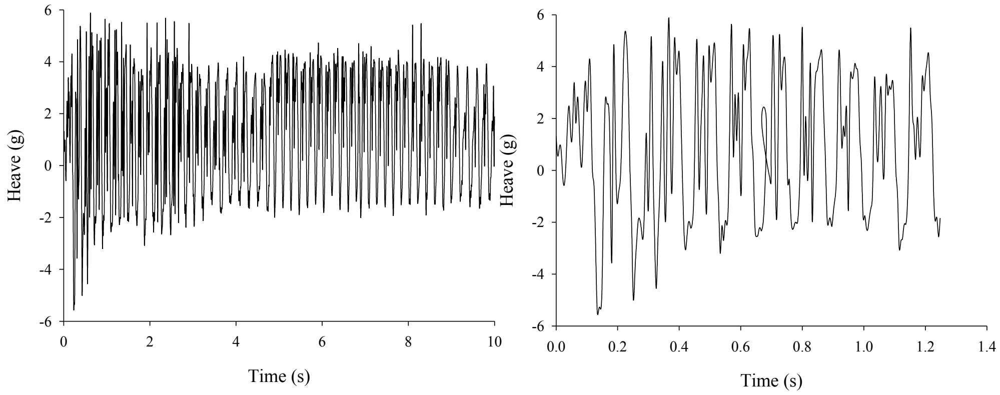


Fig. 3.14: Raw data (g) taken from the Z axis to represent wing movements at take-off for one individual at the start of flight flying from Waterloo Port in no wind conditions; A represents the first 10s of flight, whilst B represents the first sample collection period (1.25s) of flight to aid visualisation of the flaps.

Take-off is an extremely demanding stage of flight; not only has the bird to defy gravity to become airborne but must also climb immediately before it can begin to fly steadily. It is of little surprise, therefore, that when comparing figures 3.14, 3.15 and 3.16, it is possible to see that during the initial take-off period the bird is displaying the most number of wing beats and the strongest flaps during the 1.25s period. There are approximately 11 entire wing beats during the 1.25s snapshot at take-off (Fig. 3.14b) compared with 8 in steady horizontal flight (Fig. 3.15b) and 5 during the descent and landing phase (Fig. 3.16b). Additionally the peak acceleration of each beat also varies with phase of flight. During take-off the birds are flapping in excess of 5g (Fig. 3.14a, b), which decreases to around over 4g during steady flight (Fig. 3.15a, b) and then fluctuated between 4g and 5g in the descent and landing phase (Fig. 3.16a, b).

A B

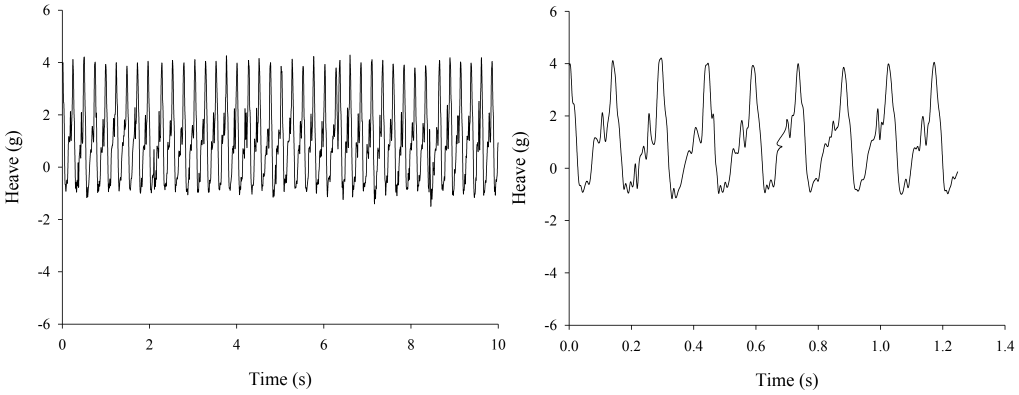


Fig. 3.15: Raw data (g) taken from the Z axis to represent wing movements for one individual during the middle of flight flying from Waterloo Port in no wind conditions; A represents the middle 10s of flight, whilst B represents one sample collection period (1.25s) from the middle of the flight to aid visualisation of the flaps.

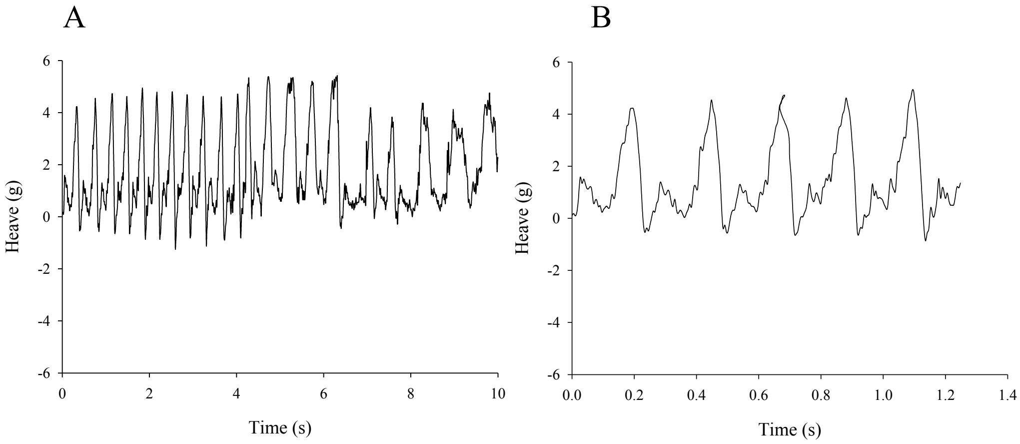


Fig. 3.16: Raw data (g) taken from the Z axis to represent wing movements for one individual at the end of flight flying from Waterloo Port in no wind conditions; A represents the final 10s of flight, whilst B represents one sample collection period (1.25s) from the end of the flight to aid visualisation of the flaps.

3.5 Estimating mechanical and metabolic power during flight

As mentioned in Chapter 1, metabolic power can be estimated using a number of different techniques ranging from mass loss (e.g. Masman and Klaassen, 1987; Kvist et al., 1998), to measurements of oxygen consumption or carbon dioxide production (e.g. Speakman, 1998; Froget et al., 2001), correlation with values for heart rate (see Green et al., 2001) and labelling of bicarbonate ions (e.g. Hambly et al., 2004). The latter has not been used on pigeons but a number of studies have either directly or indirectly measured gas exchange (e.g. Grubb, 1982; Rothe et al., 1987). In addition, various values for heart rate during flight have been published (Butler et al. 1977; Peters et al. 2005) and data exist for heart rates of free-flying homing pigeons (Bishop unpublished), which will be analysed later in this chapter. A few studies have also been undertaken to estimate mechanical and aerodynamic forces generated by the flight muscles and the movements of the wings (e.g. Pennycuick, 1968a; Dial and Biewener, 1993) but when considering a range of forward velocities a prediction for the power verses velocity outputs is usually taken from Pennycuick's aerodynamic model (Pennycuick, 1975). Measures of the overall body accelerations of free-flying birds are still limited (e.g. Halsey et al., 2009b) and have not been reported for pigeons, however, a model will be presented that will estimate the overall power required to move the body of a bird, using parameters measured from pigeons wearing accelerometers and assuming a horizontal but sinusoidal range of motion. This section will summarise the published and unpublished estimates for the power produced and required during the forward flight of pigeons and attempt to provide a new synthesise.

In order to compare measurements or estimates for metabolic power, with those for biomechanical or aerodynamic power it will be necessary to convert between units of gas exchange (ml min^{-1}) to those of mechanical power (W). However, the link between the metabolic power measurements estimating the power input to the flight muscles and the mechanical power output calculations is based on a number of assumptions, including for the apparent mechanochemical conversion efficiency of the muscles (Bishop, 2005). As little is known about the exact value of flight muscle efficiency, a constant value of 0.23 will be used, following the convention of Pennycuick (Pennycuick, 1998). For conversion of the rate of oxygen consumption to Watts and vice versa it is assumed that 4.8kcal is equivalent to l litre of oxygen and that 0.239kcal is equivalent to 1kJ. Thus, 1 litre of oxygen is equivalent to 20.1 kJ, so that 1 ml min^{-1} of oxygen converts to 0.335 W. In addition, again following the convention of Pennycuick (Pennycuick, 1998), measurements of the rate of metabolic energy consumption during exercise will first have a value for resting metabolic rate (Peters et al. 2005) subtracted along with allowing for 10% of the costs to be accounted for by respiratory and cardiac activity.

3.5.1 Studies measuring the rate of gas exchange

Table 3.4 lists estimates for the energy costs of flight based on values from the literature in which either a gas analyser was used, to directly measure the rate of oxygen consumption, or the doubly labelled water (DLW) technique was used, to indirectly estimate the rate of oxygen consumption based on the measurement of carbon dioxide production. To convert to estimates for the rate of oxygen consumption from the rate of carbon dioxide production, a respiratory exchange ratio of 0.7 was assumed. This was based on the observations of Rothe et al. (1987), in which they showed that, while at rest the ratio is usually near 1.0, after around one hour of flight this ratio is approximately 0.7.

Table 3.4: Values for the rate of oxygen consumption (ml kg^{-1} min^{-1}) from published studies, representing pigeons at rest and flying at differing air speeds (ms^{-1}), with the conversion to estimated biomechanical power.

Speed (m s^{-1})	O_2 Consumption (ml min^{-1} kg^{-1})	Mechanical power Wkg^{-1}	Author	Type of Study
0	17.12	1.19	Grubb (1982)	O_2 Consumption
0	17.80	1.23	Peters et al. (2005)	O_2 Consumption
10	200	12.6	Butler et al. (1977)	O_2 Consumption
11-13	295	19.2	Rothe et al. (1987)	O_2 Consumption
16	199	12.5	LeFebvre (1964)	DLW
18.4	310	20.2	Peters et al. (2005)	O_2 Consumption
19.1	244	15.7	Polus (1985)*	Gas Collection
20.56	331	21.7	Gessaman & Nagy (1988)	DLW
?	342	22.5	Gessaman et al. (1991)	DLW
15.65	455	28.86[+]	Gessaman & Nagy1988[$]	DLW

*Cited by Rothe et al. (1987); [$]Birds weighted with leather harness & 2.5% & 5% added mass. [+] n = 7, with outlier bird removed.

Results are in broad agreement at the top end, with maximum sustainable flight costs of between 310 to 340 ml min^{-1} kg^{-1} (20 to 22W). In contrast, differences in flight costs with forward velocity are not particularly clear and nor do they vary systematically between free-flight and wind tunnel experiments. The lowest value reported for the mass-specific rate of oxygen consumption (200 ml min^{-1} kg^{-1}) does coincide with the lowest forward velocity of 10 m s^{-1}. However, it may not be entirely surprising that there is considerable variation in results between the different studies, which utilised various measurement techniques and flight conditions. For example, free flying birds are incorporating a large mixture of manoeuvres, ascents, descents and circling behaviours as well as encountering different environmental conditions, while wind tunnel flight may not be completely natural and representative of steady horizontal flight, especially when the birds have to wear a respirometry mask or have been cannulated for blood sampling.

3.5.2. Data from Pennycuick's Flight Program

Pennycuick's computer program "Flight" is frequently used to provide predictions for the power output of the flight muscles of birds (e.g. Pennycuick, 1997; Pennycuick et al., 1989; Pennycuick and Battley, 2003). Table 3.5 shows estimates for biomechanical and metabolic power, along with predictions for minimum power speeds (V_{MP}) and wing beat frequency (f) during horizontal flight. The predicted values for f are of the order of 7 to 8 Hz and are of a similar magnitude to the actual measured values for the 18thSeptember, 2009 but are not well matched at the individual level.

Interestingly, the fastest airspeeds measured in our pigeons were around 21 to 22 ms^{-1} and at this speed, Pennycuick predicts a rate of oxygen consumption between 340 and 360 ml min^{-1} kg^{-1}, which is similar to the highest values reported in Table 3.4.

Table 3.5: Data obtained from Pennycuick's flight program using morphological measurements from 11 birds flying in no wind conditions 18th September, 2009 (ground and air speed equivalent to 18.95m s^{-1}).

Bird ID	Mass (kg)	Predicted WBF (Hz)	Actual WBF (Hz)	Mechanical Power (W)	O_2 Consumption (ml min^{-1})	Specific Work (Jkg^{-1})
16	0.451	7.53	7.67	6.60	171.0	22.8
44	0.387	7.26	5.88	5.83	99.9	13.8
E27110	0.432	7.07	8.24	5.98	160.0	22.7
X71316	0.405	7.48		6.04	98.7	13.2
Z99889	0.444	7.90		6.55	97.5	12.3
E27130	0.431	8.14		6.95	108.0	13.3
E27269	0.458	8.44	7.66	7.62	112.0	13.2
X71189	0.395	8.63	8.20	6.40	108.0	12.6
X71292	0.512	9.23	7.97	9.80	240.0	26.1
Z94900	0.457	7.50		6.81	98.6	13.1
Z94919	0.473	7.77		7.75	110.0	14.1
Average	0.440	7.87	7.87	6.86	104.0	13.2

3.5.3 Heart rate during free-flight

Hart and Roy (1966) and Butler et al. (1977) reported similar values for the heart rate of homing pigeons during short free-flights, of around 600beats min^{-1}. During wind tunnel flights Butler et al. (1977) recorded average maximum heart rates of 670 beats min^{-1}, while Peters et al. (2005) reported a figure of 663 beats min^{-1}. Heart rates recorded from free-flying homing pigeons from the Bangor Loft (Bishop, unpublished data) reveal values ranging from brief episodes as low as 560 beats min^{-1}, up to maximum values of around 700 beats min^{-1}.

The data of Ward et al. (2002) is the only study to date which has determined the relationship between heart rate (f_{H}) and the rate of oxygen consumption ($\dot{V}\mathrm{O}_2$) of a vertebrate during flight. Their results for barnacle (*Branta leucopsis*) and bar-headed (*Anser indicus*) geese indicate that there is a substantial difference between the relationship obtained while the geese are flying in a wind tunnel and while they are running on a treadmill. For flying geese the relationships were: barnacle geese $\dot{V}\mathrm{O}_2 = 0.0019 f_{\mathrm{H}}^{1.98}$ and bar-headed geese $\dot{V}\mathrm{O}_2 = 0.0013 f_{\mathrm{H}}^{2.08}$. This indicates that the relationship for both species of geese can be reasonably described as a simple square law in which a given percentage change in f_{H} is matched by an equal percentage change in the oxygen pulse (or amount of oxygen consumed per beat). A review of the literature (Bishop & Spivey, 2013) shows that the square law relationship represents the best fit for 24 different species of mammals and birds, when undergoing their primary mode of locomotion (i.e. flying, swimming or running, respectively). Thus, we can make the reasonable assumption that homing pigeons will show a similar relationship during flight and use the results of Peters et al. (2005) to provide a calibration point. This gives a mass-specific relationship for the homing pigeons of $\mathrm{ms}\dot{V}O_2 = 0.0007 f_H^2$.

We can now apply this approach to the heart rate data for a free-ranging pigeon (Bishop, unpublished data) to provide an estimate for changes in energy consumption during flight (Figure 3.17).

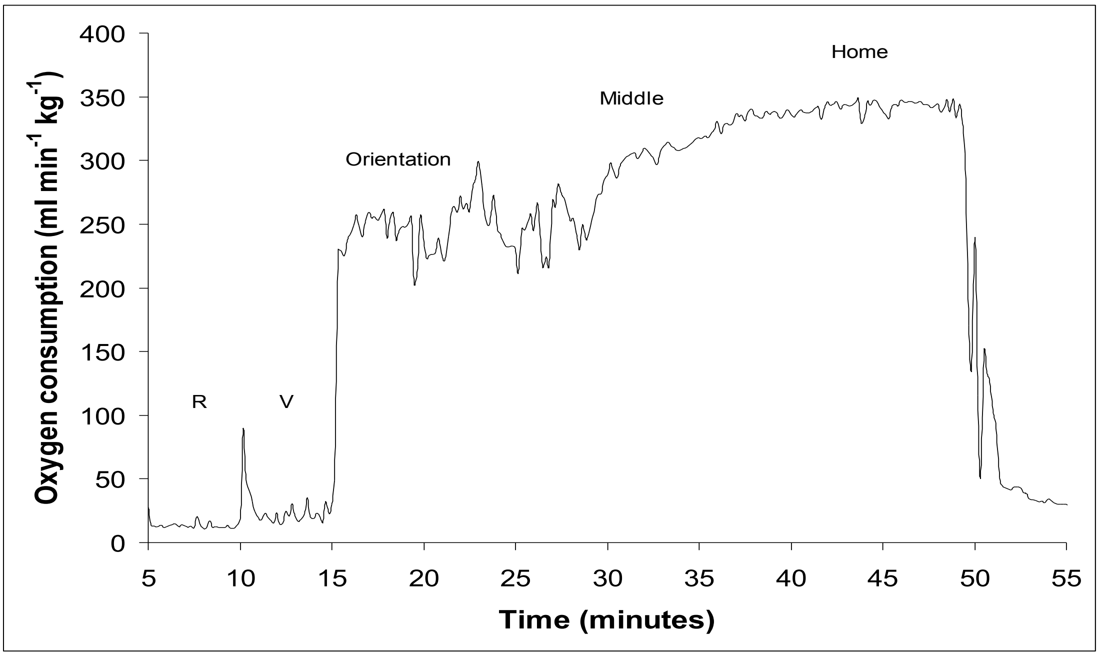


Figure 3.17: Estimated $\mathrm{ms}\dot{V}O_2$ for a single bird flying the 14 miles back from Aberdesach to the Bangor home loft, in a flock of around 40 birds (Bishop, unpublished data). R represents resting during transportation, whilst V represents resting on the sea wall prior to release.

Again, using this approach, the top estimates for oxygen consumption (around 340 ml min^{-1} kg^{-1}) are similar to those recorded from direct respirometry in a wind tunnel, or from free-flying birds using DLW. However, during this flight, the pigeons were not very familiar with the fairly distant release site and spent a long time orientating backwards and forwards and gently circling before breaking for home. During this time, heart rates were mostly between 560 and 610 beats min^{-1} (equivalent to 220 and 260 ml min^{-1} kg^{-1}) and the birds were probably flying relatively slowly. Thus, it would appear to be parsimonious to interpret this result as evidence in support of a U-shaped power curve for *Columba livia*.

3.5.4 Support for a U-shaped power curve in pigeons

Only a few studies of birds during flight have been able to demonstrate a clear U-shaped metabolic or biomechanical power curve, perhaps, in the case of the former because it is difficult for birds to sustain flights at sufficiently low, or sufficiently high, velocities so that the minimum power speed can be statistically validated. The clearest results have been seen in species of parrot e.g. budgerigar (*Melopsittacus undulatus*) (Tucker 1968) and the cockatiel (*Nymphicus hollandicus*) and the turtle dove (*Streptopelia turtur*) (Tobalske et al. 2003), a number of studies have yielded rather flat power curves (Ward et al. 2002), or only so called L-shaped or J-shaped profiles (e.g. Ellington, 1991; Dial et al., 1997). The famous study by Rothe et al. (1987), of pigeons flying at different speeds in a wind tunnel, also claimed to observe a U-shaped power curve, although it contained few data points at very slow speeds.

Figure 3.18 summarises all the data points for indirect and direct measurements and estimates of the rate of oxygen consumption for pigeons, plotted against various flight velocities. Upper and lower boundary lines show the estimated maximum and minimum potential flight costs, based on measurements of heart rate in a free-flying pigeon. A predicted power curve is created based on the average of the 11 individual Bangor pigeons in Table 3.5, using the default model aerodynamic parameters from Pennycuick's Flight program (Version 1.22).

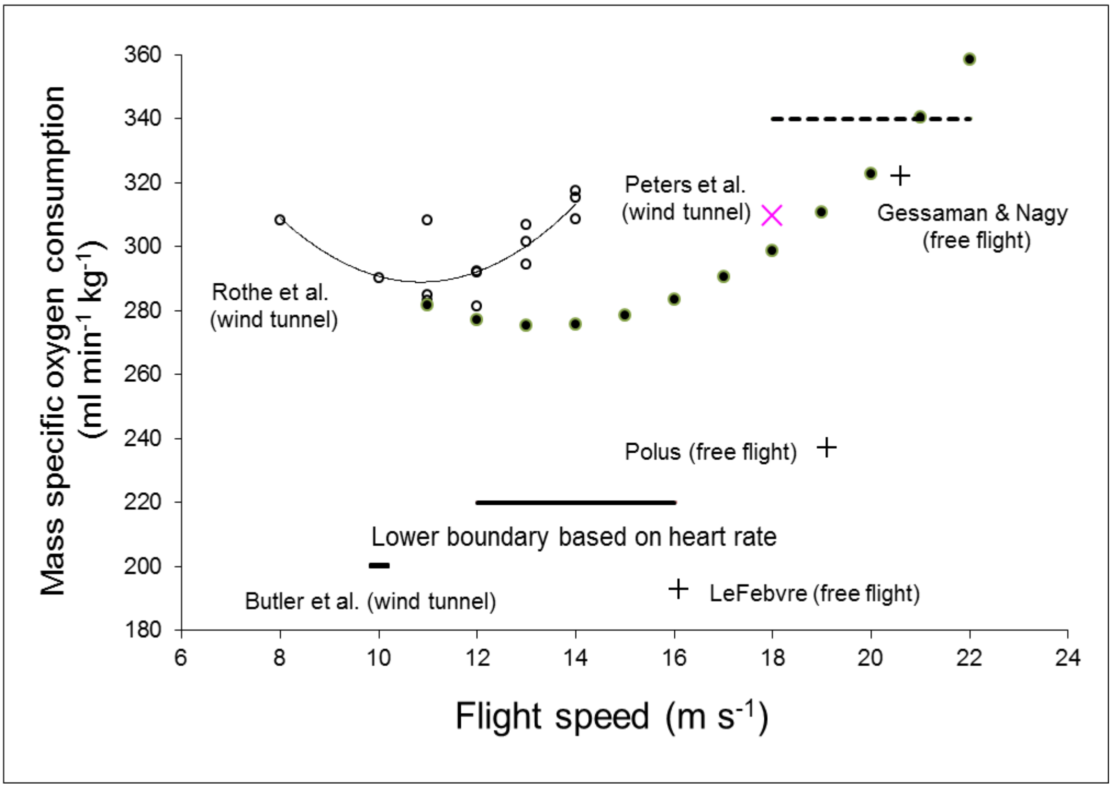


Figure 3.18: Predicted power curve for an average Bangor pigeon created using Pennycuick's Flight program, with inputted data from 11 birds from one flight. Minimum mechanical power = 275 ml min $^{-1}$kg^{-1}, V_{MP} = 13.3ms^{-1}. Exponential regression equation: O_2 consumption = -8.322 + $273.2e^{(1.382x10-10)\text{air speed}}$ + $0.6314e^{0.2249\text{air speed}}$; R^2 = 0.989. Data from the literature (Table 3.4).

With such a diverse assortment of results, experimental designs, techniques and circumstances it is hard to come to a definitive conclusion as to the exact nature of any power curve that might be assigned to the pigeon. However, it is worth pointing out that both the DLW studies of free-flight and the respirometry studies in a wind tunnel leave open the possibility for quite a range in the rate of oxygen consumption during flapping flight, and that this is compatible with the large range in heart rate exhibited by free-flying homing pigeons. At their extremes, there is quite good agreement between the upper and lower boundaries of measurement, although the overall results of Rothe et al. (1987) appear to be inconsistent with a strong U-shape and shifted well to the left of Pennycuick's. The variation in heart rate during free-flight allow for around a 35% reduction in sustained flight costs between maximum and minimum performance, while Pennycuick's recent model only suggests a 19% potential saving and the measurements of Rothe et al. (1987) only show a 10% drop.

Thus, the reasonably large changes of heart rate between different stages of the flight home, along with a tendency for studies to fall into a higher and lower cluster of mass-specific oxygen consumption values, suggest that a U-shaped power curve is realistic for pigeons. This is also supported by the conclusions that parrots and doves also exhibit a clear U-shaped curve (Tobalske et al. 2003). Both Pennycuick (1968a) and Rayner (1979) used their specific aerodynamic models to predict the power curve of a pigeon. A recent version of Pennycuick's model is used to produce the curve in Fig. 3.18, while Rayner's curve produces quite a differently shaped power curve (5 m s^{-1} V_{MP} and an almost linear slope above 10 m s^{-1} speeds), although it requires some knowledge of wing kinematics before calculation. In addition, Rayner's values are unrealistically high (around 18W kg^{-1} for V_{MP} and over 45W kg^{-1} for flight at 20m s^{-1}) compared to the experimental values in Table 3.4 and Fig. 3.18. However, it does show a relatively deep U-shape, with a range of around 2.5-fold between minima and maximum.) A relatively strong U-shape is also seen in the cockatiel and turtle dove (Tobalske et al., 2003).

As a simple approximation, ignoring the data from Rothe et al. (1987), there seems to be some agreement between the heart rate recordings from free-flight of homing pigeons flying at around 20ms^{-1} and the values from Gessaman and Nagy (1988), and these are also not dissimilar to those of Peters et al. (2005) for wind tunnel flights at 18ms^{-1}. Perhaps, the next best study is that of Butler et al. (1977) for wind tunnel flights at 10ms^{-1}, which is in broad agreement with the lower heart rate recordings from free-flight and with the values, but perhaps not with the flight speeds, recorded by LeFebvre (1964) and Polus (1985). By utilising the basic aerodynamic assumption that the power to overcome drag forces on a bird already flying at its V_{MP} and above is dominated by the effect of body and wing drag (e.g. additional costs are proportional to velocity cubed), we can fit a curve between the calibration points provided by Gessaman & Nagy (1988) and Butler et al. (1977) to emulate a simple power curve (Fig. 3.19).

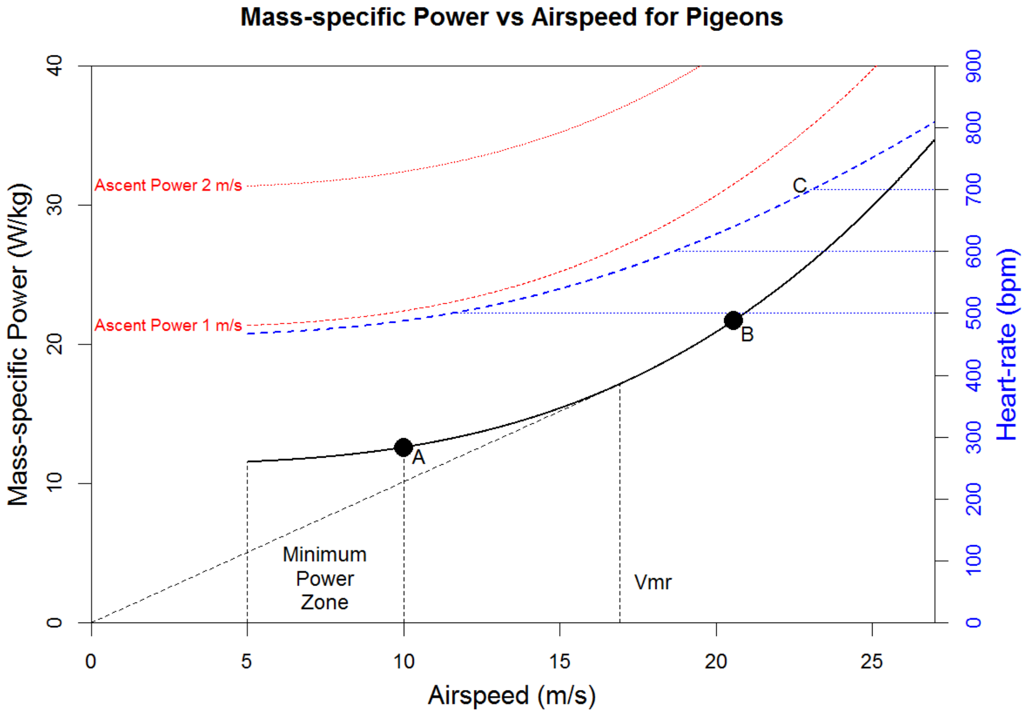


Fig. 3.19: Estimated pigeon power curve (black solid line), based on empirical values of (A) Butler et al. (1977) and (B) Gessaman & Nagy (1988). (C) is the maximum heart rate recorded from free-flying pigeons (Bishop, unpublished data) while a heart rate relationship (blue dashed line) is provided based on a heart rate of 680 beatsmin^{-1} at a speed of 21 ms^{-1} and then assuming

that power is related to heart rate squared (see text). The dotted red lines represent the power curve plus addition of climb power at velocities of 1 and 2 m s^{-1}.

The slope of the line follows the equation:

$$\text{Mass-specific biomechanical power} = 11.42 + 0.001183V^3 \qquad (3.5)$$

Where V = air velocity. While purely empirical, it seems to provide a reasonably realistic curve (compared to either of the theoretical models of Pennycuick or Rayner) with which to compare and contrast the results of both published studies and data acquired from pigeons deployed with data loggers in free-flights.

3.5.5 Accelerometry and modelling the simple harmonic motion of body

In the present study, accelerometers were placed on the back of the bird and recorded the acceleratory movements of the body during different phases of flight. In order to help with interpreting the outputs of the accelerometer it is helpful to consider the energy that would have to be expended in moving the mass of the body. Of course, a lot of energy would also be required to move the wings of the bird and, ultimately, it is the movement of the wings that enable the movements of the body. However, while we can directly measure the movements of the body, we will have to indirectly infer the possible movements of the wing and the components of power that are partitioned between the body and the wing.

A bird is modelled here as three moving masses: two wings of mass (m_w) and a body of mass (m_b) oscillating at the wing beat frequency (f_w). The angular frequency of the wingbeats (ω) = $2\pi f_w$ = 6.283 f_w. It is assumed that the body and wings move sinusoidally in the vertical axis with different potential amplitudes, while the body maintains a fixed altitude within the Earth's gravitational field. The wings also move sinusoidally relative to the body and to the ground. The amplitudes of these motions relative to the ground are B for the body and W for the wings. While a similar analysis can be done with regard to both the body and the wings (for the latter see van den Berg and Rayner (1995), only the movement of the bird’s body will now be considered. The body moves according to:

Vertical displacement of the body $= z_b = B\cos\omega t$ (3.6)

By differentiation we can obtain:

Vertical velocity of the body $= \dot{z}_b = -B\omega\ \sin\omega t$ (3.7)

The energy in the body is the sum of its gravitational potential energy and its kinetic energy:

$$E_b = m_b g\ z_b + m_b\ \dot{z}_b^2/2 \qquad (3.8)$$

Therefore, $E_b = m_b gB\cos\omega t + (m_b B^2\omega^2\sin^2\omega t\ )/2$ (3.9)

The rate of change of energy in the body is:

$$\dot{E}_b = -m_b gB\omega\sin\omega t + \mathrm{m_b B^2 \omega^3}\sin\omega t\cos\omega t \qquad (3.10)$$

which is zero when

$$m_b gB\omega\sin\omega t_* = m_b B^2\omega^3\sin\omega t_*\cos\omega t_* \qquad (3.11)$$

$$\cos\omega t_* = g/B\omega^2 \qquad (3.12)$$

$$t_* = \left(\frac{1}{\omega}\right)\arccos\left(\frac{g}{B\omega^2}\right) \qquad (3.13)$$

It can be shown that the energy in the body is maximal when $t = t_*$ and when $t = \frac{2\pi}{\omega} - t_*$ having the value:

$$E_b^{max} = m_b gB\cos\omega t_* + (m_b B^2\omega^2\sin^2\omega t_*)/2 \qquad (3.14)$$

$$E_b^{max} = m_b gB\cos(\arccos\{\tfrac{g}{B\omega^2}\}) + [m_b B^2\omega^2\sin^2(\arccos\left\{\tfrac{g}{B\omega^2}\right\})]/2 \qquad (3.15)$$

$$E_b^{max} = m_b g B \frac{g}{B\omega^2} + (m_b B^2 \omega^2/2)\left(1 - \frac{g^2}{B^2\omega^4}\right) \tag{3.16}$$

$$E_b^{max} = \frac{m_b g^2}{\omega^2} + \frac{m_b B^2 \omega^2}{2} - \frac{m_b g^2}{2\omega^2} \tag{3.17}$$

$$E_b^{max} = \frac{m_b(g^2 + B^2\omega^4)}{2\omega^2} \tag{3.18}$$

Equation (3.12) follows from (3.13) providing $\sin\omega t \neq 0$ but $\dot{E}_b = 0$ also when $\sin\omega t = 0$. The energy in the body will then be minimal. This occurs when $t = 0$ and $t = \pi/\omega$. The corresponding energies are not equal. At $t = 0$, the energy of the body is:

$$E_b^{min1} = m_b g B \cos 0 + (m_b B^2 \omega^2 \sin^2 0)/2 = m_b g B \tag{3.19}$$

and the energy of the body when $t = \pi/\omega$ is:

$$E_b^{min2} = m_b g B \cos\pi + (m_b B^2 \omega^2 \sin^2 \pi)/2 = -m_b g \tag{3.20}$$

The total energy which the bird must deliver to its body during each wing beat is then:

$$E_b^{beat} = E_b^{max} - E_b^{min1} + E_b^{max} - E_b^{min2} \tag{3.21}$$

$$E_b^{beat} = \frac{m_b(g^2 + B^2\omega^4)}{\omega^2} \tag{3.22}$$

from which the mean power required by the body (P_b) comes to:

$$\langle P_b \rangle = \frac{m_b(g^2 + B^2\omega^4)}{2\pi\omega} \tag{3.23}$$

Example: In the recent study by Peters et al. (2005), homing pigeons flew in a wind tunnel with mean body mass 340g. Thus, it is assumed that actual M_{b} = 0.34 kg – 15% (for the two wings, see below) = 0.289kg. A value of B = 8 mm (based on integration of the accelerometry of the Bangor pigeons in the z-axis) and *f* = 7Hz: then it is estimated that;

P_b = 0.289 (96.236 + 0.000064x 3741966.5)/276.347 = 0.351 W (1.215 W kg^{-1})

Peters et al. (2005) measured the rate of oxygen consumption in pigeons flying in a wind tunnel at 18 ms^{-1} as 310 ml min $^{-1}$kg^{-1}. This is equivalent to 20.2Wkg^{-1} of biomechanical and aerodynamic power, assuming a mechanochemical conversion efficiency of around 0.23 (Pennycuick, 1998). This means that the cost of moving the body against gravity is predicted to be relatively small (about 6% (or a 16th) of the overall costs), even allowing for some additional power required to overcome the parasite drag on the body. Thus, the majority of the power required for flight is incorporated in the energy required to move the wings through the air and to overcome their profile drag. Thus, there is a relatively large amount of power (20.2W – 1.215W = 18.98 W) that may be invisible to an accelerometer placed on the body of the bird, as around 94% of the power required for flight resides in the movement of the wings.

By substituting $\omega = 2\pi f_w$ into equation (3.23) the total power (W) in the body is:

$$\langle P_b \rangle = \frac{m_b(g^2+B^2 16\pi^4 f_w^4)}{4\pi^2 f_w} = \frac{m_b(g^2)}{4\pi^2 f_w} + \frac{m_b(B^2 16\pi^4 f_w^4)}{4\pi^2 f_w} \qquad (3.24)$$

with the mass-specific power (W kg^{-1}) equation as:

$$\langle msP_b \rangle = \frac{(g^2)}{4\pi^2 f_w} + \frac{(B^2 16\pi^4 f_w^4)}{4\pi^2 f_w} = \frac{g^2}{4\pi^2 f_w} + 4\pi^2 B^2 f_w^3 \qquad (3.25)$$

The first part of equation (3.25) consists of a gravity-based term which is inversely proportional to wing beat frequency. It can be simplified to the mass-specific term $2.438/f_w$ and gives values for a pigeon which vary from around 0.49 W kg^{-1} at a flap frequency of 5 Hz to around 0.27 W kg^{-1} at 9 Hz. The second half of equation (3.25) is where the majority of the power in the body resides. We can also simplify the second term slightly to obtain the overall expression:

$$\langle msP_b \rangle = \frac{2.438}{f_w} + 39.48 B^2 f_w^3 \qquad (3.26)$$

Due to the dominance of the second term during typical flight, it is predicted that the total power in the body will be broadly proportional to the cube of the wing beat frequency (f_w^3) and the square of the vertical body displacements (B^2). The inertial power required to flap the wings has a similar form (van den Berg and Rayner, 1995), so it would also be expected that the total power required to fly will be highly sensitive to f_w^3 and B^2, particularly if the latter is directly related to changes in wing amplitude. For values of B = 8mm and f_w = 7 Hz we obtain a mass-specific estimate for power in the body of msP_b = 0.348 + 0.867 = 1.215 W kg^{-1}.

A slightly different analysis of equation (3.25) is achieved by observing that the differential of equation (3.7) is:

Vertical acceleration of the body =

$$\ddot{z}_b = -B\omega^2 \cos\omega t = -4\pi^2 f_w^2 B \cos(2\pi f_w t) \qquad (3.27)$$

For a sinusoidal pattern of movement it can be shown by calculus that the value of the root mean square of acceleration, $a_{rms} = a_{max}/\sqrt{2}$, where a_{max} is half the difference between the peak positive and peak negative accelerations. Since, from equation (3.27), we have that, $a_{max} = 4\pi^2 f_w^2 B$, it follows that:

$$a_{rms} = \sqrt{8}\pi^2 f_w^2 B \tag{3.28}$$

$$a^2{}_{rms} = \sqrt{8}\pi^2 f_w^2 B \tag{3.29}$$

then, by substitution in equation (3.25) we obtain:

$$\langle msP_b \rangle = \frac{2.438}{f_w} + \frac{2a_{rms}^2}{4\pi^2 f_w} = \frac{2.438}{f_w} + \frac{a_{rms}^2}{19.739 f_w} \tag{3.30}$$

Currently, many animal studies have reported excellent correlations between summed measures of acceleration such as ODBA and VeDBA (Halsey et al. 2009b; Gleiss et al. 2010), usually reported in units of g. These are conceptually similar to a_{rms} (in that they are measures of acceleration in some time-averaged sense) and, therefore, could be used as a proxy for a_{rms} in the present sinusoidal-based model. This suggests that use of VeDBA (with units of m s^{-2} and not g), as a substitute for a_{rms} in equation (3.30), could provide reasonable values of P_b. For example, a typical value of VeDBA for pigeons flying with a f_w of around 7 Hz is 1.2 g, equivalent to a mean acceleration of around 12 m s^{-2}. Substitution into equation (3.30) yields the estimate $\langle msP_b \rangle = 0.348 + 1.042 = $ 1.39 W kg^{-1}, very similar to the previous calculation based on $B^2 f_w^3$ of 1.22 W kg^{-1}.

If we consider the use of VeDBA as a proxy for power output when it is not possible to obtain a calibration against a measure such as rate of oxygen consumption, as in the case of the flying pigeons, then consideration of the dimensions shows that VeDBA represents acceleration (m s^{-2}) and does not have the units of power. Therefore, it is unlikely to provide a proportionally meaningful measure. Mass-specific power has the units of m^2 s^{-3}, which are also the units of the terms $B^2 f_w^3$, $\frac{(a_{rms})^2}{f_w}$ and $\frac{(g^2)}{f_w}$. The dimensional analysis, along with the latter terms derived from the sinusoidal model, indicate why VeDBA^2 would be a more appropriate proxy for power in flying animals than VeDBA alone (as currently applied by Bidder et al. (2012); Qasem et al. (2012)), although the model also suggests that this term could also be additionally modulated by f_w.

At the same time equation (3.26) indicates that power in the body can also be reflected by changes in the variables B and f_w, with the former probably correlating strongly with adjustments in wingbeat amplitude, at least during steady horizontal flight. Additionally, this analysis emphasises that, while using a body-mounted accelerometer, we can expect to only capture a small fraction of the overall biomechanical power expended by the pigeons. This in itself may not be a problem, say, if there is a requirement to only gauge the relative effort of the bird. The assumption of linearity between power detected by a body-mounted accelerometer and overall power output has yet to be tested but it may not hold completely true for every type of flight manoeuvre. However, in the absence of strong updrafts, birds can only sustain flight for prolonged periods by beating their wings and it should be possible, in most circumstances, to obtain reliable estimates of at least wing beat frequency and time-averaged acceleration data. Modulation of flap frequency alone should certainly reflect interesting qualitative changes in behaviour, even if not fully quantifiable. It is also likely, however, that birds will generally fly in a manner where a reasonable correlation is apparent between wingbeat amplitude and body displacement, which may well enable body acceleration to be translated into useful estimates of overall biomechanical power output.

3.5.6 Correlating double integration of the YZ-axis against $VeDBA_{YZ}$

Vectoral Dynamic Body Acceleration (VeDBA) has been used by a number of authors to correlated body motions against metabolic energy consumption, usually measured as rate of oxygen consumption. Metabolic rates of energy consumption are available for various studies for pigeons (Butler et al. 1977; Grubb, 1982; Rothe et al., 1987; Peters et al. 2005) but they are either averaged over long periods of time with an associated mean flight speed, or the data was collected at a single specific speed. These can be used as guides but do not provide a continuous range of values useful for detailed calibration of VeDBA. However, the outcome of the sinusoidal model clearly indicates that $VeDBA^2$ would be expected to be a more appropriate proxy for power output and, for this reason it is utilised in this thesis. In addition, while the model was developed by considering only the vertical (z-axis) motion of the bird's body, we have actually incorporated more of the total acceleratory movements of the bird by calculating the vectoral component ($VeDBA_{YZ}^2$) for the z-axis and y-axis motion (i.e including the vertical and forward orientated accelerations). We did not use the side-to-side motion as, in theory, the largely symmetrical flapping of the bird's wings should have limited the expected acceleration power in this orientation and we also suspected that the position of the accelerometer on the back between the wings may have provided some possibility for acceleration artefacts due to physical interference of the wings during intense flight. Thus, $VeDBA_{YZ}^2$ was used as the main proxy for the power in the body of the pigeons.

One approach is to double integrate the accelerometry data for each data time period (of around 1s of analysable data) and make some simplifying assumptions. Power in the body is equal to mass x acceleration x velocity and a mass-specific estimate of power in Watts can be produced by leaving mass as 1 kg. Acceleration is directly measured and an estimate of body velocity in each axis can be obtained by integration, with the assumption that during each sample collection period there is no net change in velocity at the end compared to the start. This may be a reasonably assumption for birds that in steady horizontal flight and with careful selection of data so that whole integers of wing beats are used. During ascent, this method is likely to underestimate the power in the body, with the opposite during descent. However, given that we might expect large changes in wing beat frequency between ascent and descent, it is probably true that some proportion of the extra energy required to perform climbing flight should be visible in the body power.

Fig. 3.20 shows the result of direct integration of the Z-axis and Y-axis to give an estimate for integrated power in the body (P_{int}) in Wkg^{-1} correlated against $VeDBA_{YZ}^2$. $VeDBA_{YZ}$ against P_{int} did not approximate a straight line, whereas $VeDBA_{YZ}^2$ gives an excellent linear relationship.

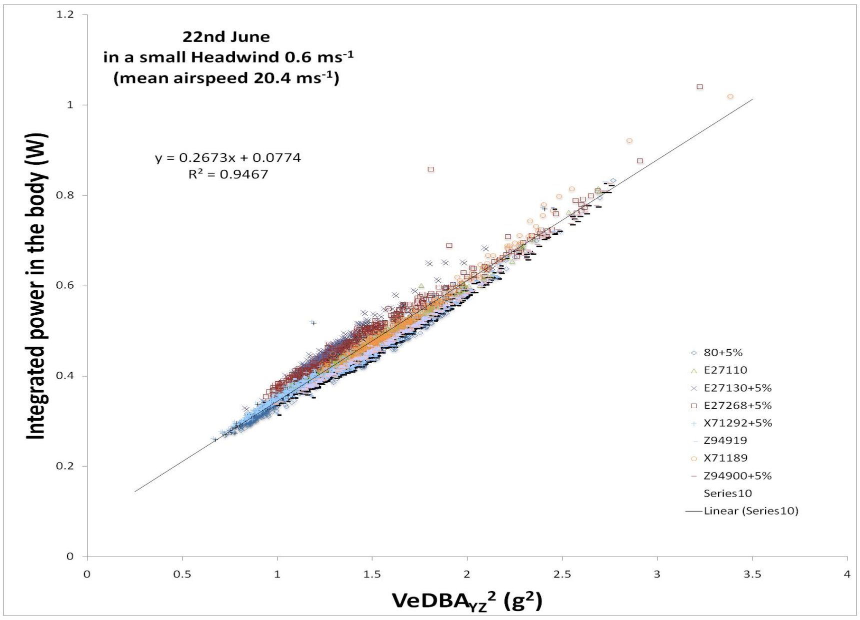


Fig. 3.20: Estimated integrated power in the body (YZ axis) of 9 pigeons flown on the 22nd June 2009 in very low wind condition plotted against VeDBA_{YZ}^2.

This indicates that VeDBA_{YZ}^2 can be used as a very good substitute for relative power in the body of the pigeons, and the relationship with direct integration of the acceleration data can be used to convert to units of Watts, if required. The range of values calculated with direct integration are from around 0.3W up to 0.8W (excluding the first phase of take-off flight). This is about half of the predicted value estimated from the concept of modelling the simple harmonic motion of the body assuming a sinusoidal pattern of motion and acceleration. This may indicate that direct integration of the body accelerations is tending to minimise the energy calculation and/or that birds do not truly have a sinusoidal pattern of accelerations (as can be seen particularly during slow wing beat frequency flights, e.g. Fig. 3.16). In fact, the peak accelerations are delivered quite rapidly and during slow flight occupy much less than half the wing beat cycle.

CHAPTER IV - Summary

In order to study the effects of added mass on flight performance, 17 pigeons were released individually over a period of 4 different days, either with or without 5% added mass. The study used a paired design requiring that each bird did two flights, one as a control and one as an experimental manipulation. All pigeons flew with a relatively low wing beat frequency (L-WBF, < 6 Hz) mode of flight. Mean values for dynamic body acceleration ($VeDBA_{YZ}^2$) were low at $1.17g^2$ as were airspeeds at 14.89 m s^{-1}. An effect of added mass was only detected during the first minute of flight when the birds were climbing, when both $VeDBA_{YZ}^2$ (1.268 verses $1.225g^2$) and wing beat frequency (5.52 verses 5.34 Hz) was slightly greater in the pigeons carrying extra mass.

In a separate experiment, pigeons were released in a flock over a period of two days and provided data from 9 pigeons fitted with accelerometers and 3 fitted with GPS. Again, a paired design was used whereby on one flight the birds were fitted with a lead plate across their chest weighing 5% of the individual's own body mass, and during a second flight the same pigeons wore a control plastic plate of negligible mass. The birds remained as a loose flock for the duration of the flight. Overall, the effect of day had a greater effect than the experimental manipulation with the birds returning far faster on the second flight compared to the first due to a combination of individual behaviour on day one and the presence of a 4.49m s^{-1} tail wind on day two.

Overall the birds grouped into two sets dependent upon their flight characteristics – high wing beat frequency (H-WBF, >6 Hz) and low wing beat frequency (L-WBF, < 6Hz) flyers, which was mirrored by a difference in both $VeDBA_{YZ}^2$ and fraction positive (proportion of time spent accelerating the body

above average g force). On both days, pigeons flew with a high airspeed (> 20 m s^{-1}). Additionally, there was a strong association within individuals for values of wing beat frequency and $VeDBA_{YZ}$ across the two days. There were also significant positive correlations between wing beat frequency and both $VeDBA_{YZ}$ and fraction positive when the birds were wearing 5% additional mass.

4.1 Introduction

At some point in their lives all birds must carry some form of additional mass above their own body weight. This can be in the form of eggs, fuel for migration or for chick provisioning. It is, therefore, vital for the fitness of the individual to be able to cope with certain amounts of extra weight. However, it would be anticipated that there would be an energetic penalty to carrying additional mass during flight (Pennycuick et al., 1989), along with an obvious risk to the bird from being heavier, for example increased chance of predation (e.g. Lima, 1986), possibly due to a reduced take-off and flight performance (Witter and Cuthill, 1993). It is no surprise that much work has been conducted upon the physiological, metabolic and behavioural responses of birds throughout these life stages (e.g. Fransson and Weber, 1997; Jenni and Jenni-Eiermann, 1998; Cottam et al., 2002; Prop et al., 2003). A different approach to this type of work is to artificially increase the mass of a bird by fitting it with extra weights and examining the effect this has on flight performance (e.g. Marden, 1987; Gessaman and Nagy, 1988; Videler et al., 1988a, b; Pennycuick et al., 1989).

Despite these studies, there is little obvious consensus to the additional energetic costs of carrying extra body mass, let alone the behavioural and kinematic affects that various species may exhibit. In theory, pigeons could represent an ideal model species with which to assess the cost of both natural and artificial additional mass on flight, as they naturally fly very much faster than the minimum power speed when homing in flocks and, therefore, may be quite sensitive to mass or drag changes. In this chapter, the body mass of homing pigeons flying over relatively short flights (11 km) was manipulated to investigate whether there was an effect of added mass on their flight speeds, wing beat frequency and body accelerations. A secondary aim was to calculate the effect on power in the body of the pigeons to ascertain if the effect of carrying additional mass was close to the aerodynamic prediction for the mass exponent of $mass^{1.5}$, or more in agreement with the recent studies of less than $mass^{1.0}$ or those of Gessaman & Nagy (1988; i.e. $mass^{6}$).

4.1.1 Effect of mass on flight costs

The long-standing rule of thumb is that such loggers should never weigh more than 5% of the individual animal's body mass which was reinforced by work undertaken during the 1980's by Caccamise and Hedin (1985) and Gessaman and Nagy (1988). To this day it is often recommended that these limits should not be broken but this often leads to the assumption that individuals can continue behaving as normal when carrying an extra 5% of body mass (Gessaman and Nagy, 1988; Barron et al., 2010). Furthermore externally fitted loggers also increase the drag experienced during flight which can be responsible for a reduction in the flight range of a bird, similarly to an individual carrying additional mass (Bowlin et al., 2010).

Looking at the response of additional mass upon an individual bird, where the wing size remains unaltered, the minimum flight speed is predicted to increase as a function of body mass$^{0.50}$ and the power required increases as a function of body mass$^{1.50}$ (Hughes and Rayner, 1991). High performance homing pigeons fitted with a load of either 2.5% or 5% of body mass showed a dramatic decrease in flight performance using the doubly labelled water technique (Gessaman and Nagy, 1988). Over a longer distance (320km) the birds' flight performance was severely compromised by the harness and package, flying significantly slower (greater than 31%) and producing significantly more carbon dioxide (between 41 and 52% higher per hour) than control birds (Gessaman and Nagy, 1988). The results of this work appear somewhat perplexing, as they suggest that flight costs scale approximately as mass^{6}, rather than the theoretical value of mass$^{1.5}$. Conversely, a similar experiment conducted on tippler pigeons flying around a loft, showed no significant difference in energy consumption when carrying additional mass but did apparently increase water loss by 57-100% (Gessaman et al. 1991).

The original results of Gessaman and Nagy (1988) seem even more excessive when compared to recent wind tunnel studies by Kvist et al. (2001), Schmidt-Wellenburg et al. (2007 and 2008) which report a sub-linear increase in the body mass exponent (mass$^{0.35}$ and mass$^{0.5}$, respectively). Some possible explanations for this result might be, that the pigeons flew with an uncomfortable leather harnesses, that the birds flew for very long periods which might have incorporated a flawed measurement of air speed, route taken and estimates of flight time budgets, and that the costs of free-flying might be different to those recorded during captive wind tunnel flights (Gessaman and Nagy, 1988).

In the above wind tunnel experiments (Kvist et al., 2001; Schmidt-Wellenburg et al., 2007, 2008), there is no particular reason to question that the intra-species body mass exponents for these three species appears to be substantially less than the value of mass$^{1.5}$, as predicted with modelling work (Hughes and Rayner, 1991). In addition, hovering hummingbirds carrying added mass (Wells 1993) also indicated a value of mass$^{<1.0}$ for the intra-individual scaling of carrying additional mass.

4.1.2 Effect of mass on flight kinematics

By using field observations, Pennycuick et al. (1996) was able to present a mathematical model, based on his early work in Pennycuick (1990), to determine the wing beat frequency of a bird derived from its morphological characteristics:

$$f = m^{3/8} g^{1/2} b^{-23/24} S^{-1/3} \rho^{-3/8} \tag{4.1}$$

where, f is wing beat frequency, m is mass, g is acceleration due to gravity, b is wing span, S is wing area and ρ is the density of air. It predicts that as body mass increases so too does wing beat frequency, for a given minimum velocity of forward flight.

Behavioural and kinematic research into the capability of various birds of prey to carry additional mass has been undertaken using kestrels (*Falco tinnunculus*) (Videler et al., 1988a, b) and Harris' hawks (*Parabuteo unicinctus*) (Pennycuick et al., 1989), whilst Marden (1987) studied various species of flying animals. These experiments concentrated on take-off (Marden, 1987), climbing after take-off and short horizontal flights of 50m (Pennycuick et al., 1989) or relatively longer flights along a windless corridor, either 50m, 125m or 142m long (Videler et al., 1988a, b).

The rate of climb after take-off of Harris' hawks decreased with added mass, with a slight increase in wing beat frequency (although actual values were not published; Pennycuick et al., 1989). The more comprehensive study of Marden (1987) also showed a general reduction in take-off speed and angle of ascent for many species, including insects and bats, which indicate that under normal (unweighted) conditions birds probably take-off and climb fairly close to their maximum capacity. A similar assumption was made by Hedenström et al. (1992), studying climbing flight in wild migrant species.

As the added weight on the kestrels increased, similarly to bats (Hughes and Rayner, 1991) there was a corresponding decrease in flight speed (nearer V_{MP} than V_{MR}), with an increase in wing beat frequency, although the individual spent longer in the down stroke in each beat (Videler et al., 1988a, b). By flying nearer V_{MP} when carrying additional mass, the studies by Videler et al. (1988a, b) and Pennycuick et al. (1989) are supported by the conclusions of Hughes and Rayner (1991) who were forced to concede that bats were optimising their flight performance, but by minimising their immediate flight power requirements as the best flying option rather than minimising the costs of locomotion overall.

4.2 Aims of the research

The aim of the present chapter was to measure the effect of added mass on various aspects of the flight performance of free-flying homing pigeons when carrying an additional 5% of the individuals' body mass. An accelerometer logger was fitted to each bird to provide measures of wing beat frequency and

$VeDBA^2$ (a proxy for biomechanical power in the bird's body), while a GPS data logger was fitted to different birds in the same flock to record ground speed and position. It was anticipated that when pigeons flew in a flock, that they would try and stay together and, therefore, control for potential effects of flight velocity, so that the pigeons carrying the extra mass would be predicted to have an increased wing beat frequency. It was not known what might happen to $VeDBA^2$. By releasing pigeons individually, it was suspected that birds might fly more slowly when carrying extra mass.

4.3 Methodology

Section 2.2 gives a brief overview of the flight methodology that was followed for all free-flights. However, for the purpose of this experiment the birds were also fitted with either a lead plate (weighing 5% of the individual's body weight) or light-weight plastic control plate across the chest after being weighed on the morning of the release. The plate was fitted close to the crop which is the most natural position for a pigeon to carry additional weight. This possibly would have moved the centre of mass of the individual forward and may have destabilised the bird a little but overall it was decided that this would be the most desirable position to fit the plate. The birds acted as their own controls by wearing the lead plate for one release and the control plate for another release. On each flight half the birds wore the lead plates and the other half wore plastic plates to ensure any day effects would be controlled for.

Birds were flown solely from Penmon (site G, Fig. 2.1) for this particular piece of work to remove possible effects of release site on the results. Penmon was chosen above Waterloo Port due to its location, as releasing the birds from this site resulted in a slightly longer flight path home and forced the birds to cross the Menai Strait.

The same experiment was conducted twice, once in the winter of 2008 to release individuals and once in the summer of 2009 as a flock release. Accelerometry data was analysed as described in Sections 3.3.2 and 3.3.3 using Wbeatsp14 (R. J. Spivey, Bangor University) which incorporated both sampling rates used for the flock and individual releases. The accelerations were so rapid during first few seconds of take-off and so varied and different in sequence during the approach to landing, that for clarity of analysis and interpretation, the first 20 seconds and the last 30 seconds of the flights have been removed. The GPS data analysis has been described elsewhere (Section 2.4) but briefly measurements of speed were recorded directly by the GPS, whereas the distance travelled was calculated from positional data recorded.

The individual flights were undertaken on the 28th and 29th November, 2008 and the 11th and 15th December, 2008 with 17 wearing accelerometry and 15 wearing GPS completing the flights. The flock releases were undertaken on the 22nd and 23rd of June, 2009 on days with no wind (wind speed less than 5mph). Nine birds successfully completed both flights (added mass and control) wearing accelerometry and 3 wearing GPS. Due to each bird acting as its own control, paired analysis of the data was possible which would take into account any individual variation within the flock. During analysis the two flights were not only used to study the effects of added mass but also to examine overall flight performance and individual flight behaviour.

4.3.2 Statistical analysis

Paired t-tests were used to analyse the data, comparing individual flight performance when they were and were not carrying an additional 5% of their own body mass. Pearson's correlations were used to investigate the relationship between morphology and flight performance under these same conditions.

4.4 Results

4.4.1 Overall flight in flock releases 2009

All birds analysed were released as a flock (Table 4.1), comprising of thirteen pigeons wearing GPS and twelve wearing accelerometers (the rest of the birds within the flock wore 'dummy' blocks on their back to represent a similar weight and drag effect). The experiment was conducted over two consecutive days whereby on one day half the individuals wore an additional 5% of their body mass and on the other days wore a control plastic lightweight plate.

When the GPS and accelerometry data was analysed the effect of day can be seen to be greater than the effect of the experimental manipulation, with the majority of the birds flying home quicker on the second day than the first (Fig. 4.5). Using archival data from two anemometers on the towers of Britannia Bridge it was possible to more accurately calculate the prevailing wind speed that the birds might actually have experienced during the flight home on the two experimental days. On the 22nd June, 2009 there was a 1.35mph (0.6m s^{-1}) head wind and on the 23rd June, 2009 there was a (10.10mph) 4.49m s^{-1} tail wind, which explains the increased ground speed and shorter flight time on day 2.

Table 4.1: Experimental design; * represents birds removed from further analysis as they didn't perform to the required standard.

Bird ID	Logger Type	22/06/2009	23/06/2009
Z94919	Accelerometer	Control	5%
Z94900	Accelerometer	5%	Control
X71292	Accelerometer	5%	Control
X71189	Accelerometer	Control	5%
X71035	Accelerometer	Control	5%
E27268	Accelerometer	5%	Control
E27110	Accelerometer	Control	5%
80	Accelerometer	5%	Control
44*	Accelerometer	Control	5%
E27130	Accelerometer	5%	Control
16*	Accelerometer	5%	Control
X71115*	Accelerometer	5%	Control
Z99487	GPS	5%	Control
Z99504	GPS	5%	Control
Z99890	GPS	5%	Control

4.4.1.2 GPS results

When the GPS loggers were retrieved and downloaded to a computer it was clear that many of the devices had malfunctioned. Unfortunately out of thirteen pigeons wearing GPS only three loggers had recorded usable data (Table 4.1). Thankfully all this data was able to be analysed as the three birds appeared to stay with the flock of birds and returned immediately back to the loft after liberation. Whilst it appears that bird Z99890 had a longer flight time than the other two birds wearing GPS (Figs. 4.1 to 4.4) it is clear that the time in which this individual returned home is in keeping with the time of the birds wearing accelerometry (Fig. 4.5) and so was deemed to have performed suitably for further analysis. By chance, these three birds were all control birds on one day (23rd June) and experimental birds the other (22nd June) so that, coupled with the fact that there was a slight tailwind on the second flight, means that these results are dominated by the effect of day rather than of experimental manipulation.

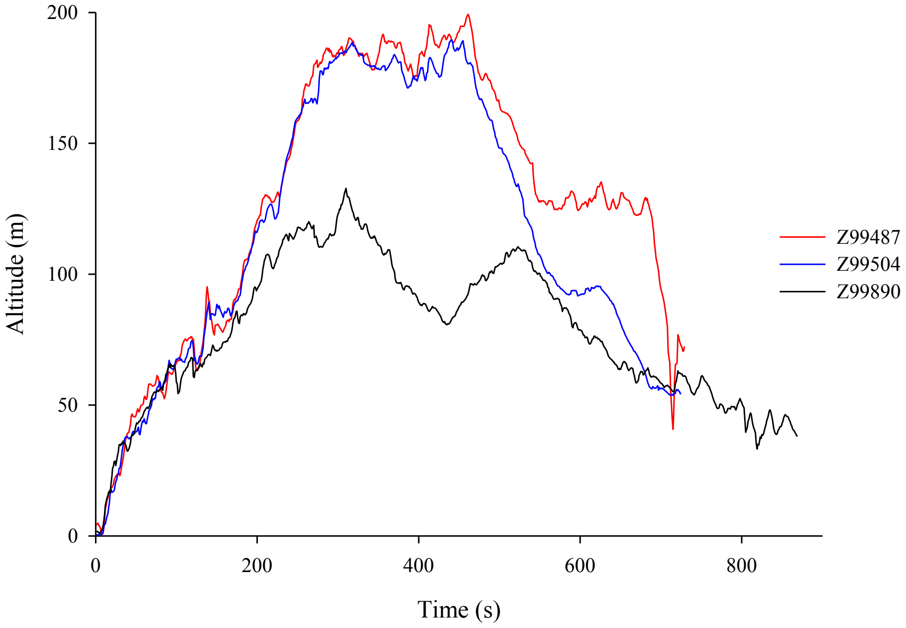


Fig. 4.1: The altitude (m) attained by three individual pigeons fitted with GPS released in a flock over an entire flight on 22rd June, 2009, on a still day (0.6 m s^{-1} headwind).

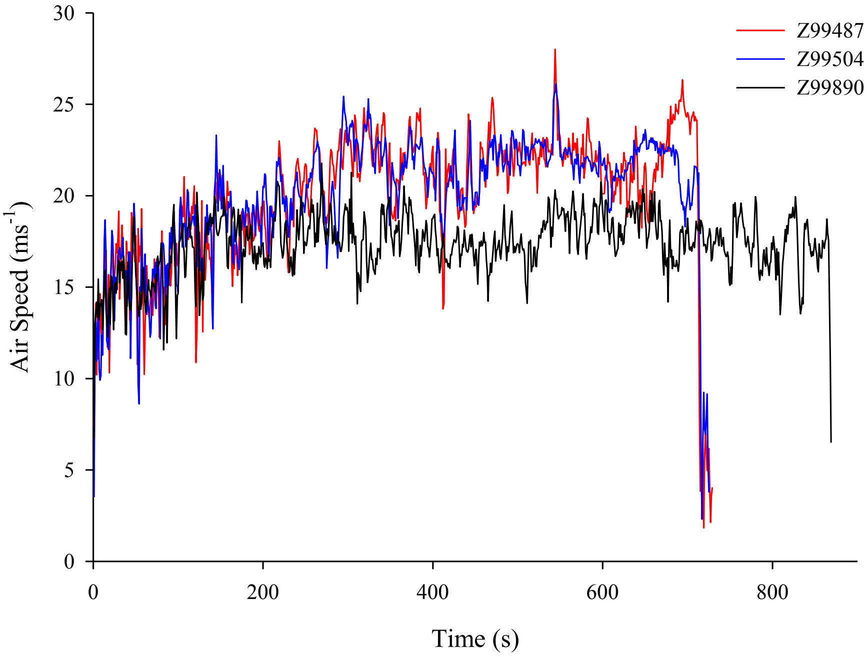


Fig. 4.2: The air speed (ms^{-1}) attained by three individual pigeons fitted with GPS released in a flock over an entire flight on 22rd June, 2009, on a still day (0.6 m s^{-1} headwind).

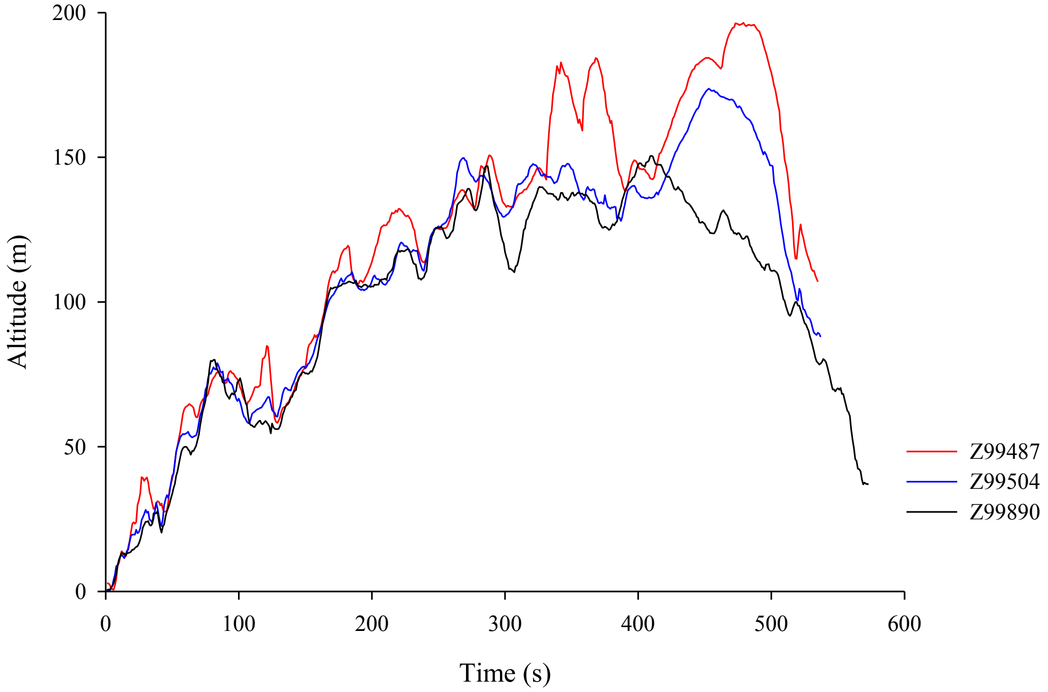


Fig. 4.3: The altitude (m) attained by three individual pigeons fitted with GPS released in a flock over an entire flight on 23rd June, 2009, 2009 in a 4.49 m s-1 tailwind.

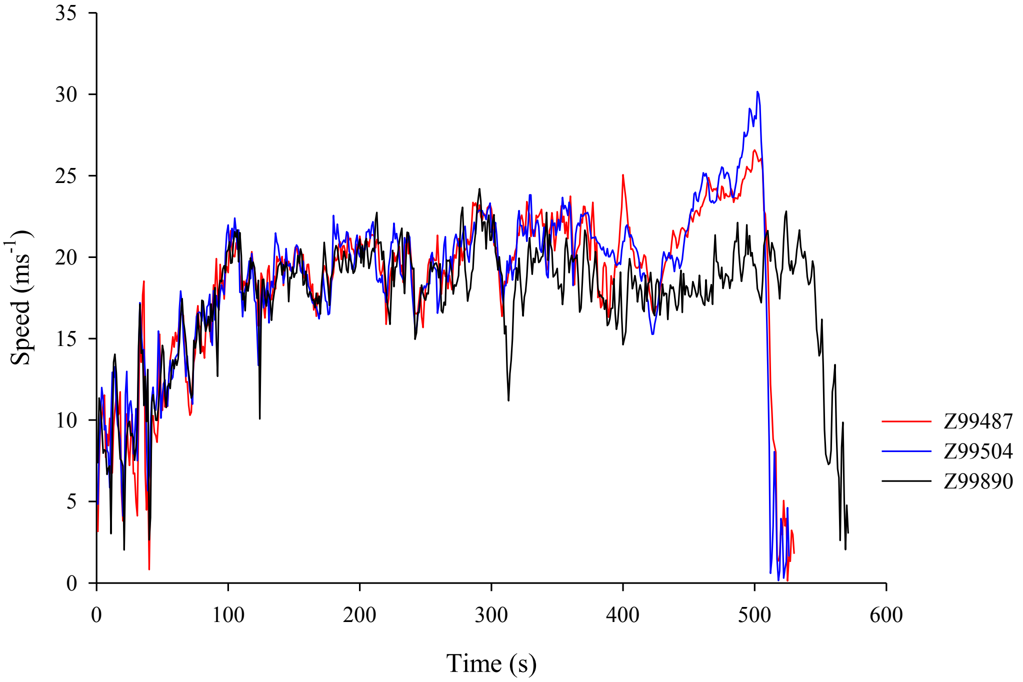


Fig. 4.4: The air speed (ms^{-1}) attained by three individual pigeons fitted with GPS released in a flock over an entire flight on 23rd June, 2009, 2009 in a 4.49 m s^{-1} tailwind.

As the GPS and most of the accelerometry birds returned in a similar time period, and also that the birds flew at similar altitudes (Fig. 4.1 and 4.3) and similar speeds (Fig. 4.2 and 4.4) it is reasonable to assume that both sets of birds probably remained within a loose flock and followed a similar flight profile.

The overall route efficiency proved to be extremely similar in the two flights (0.92 no added mass, 0.93 5% added mass) and thus there was no statistical difference between the flights (paired t-test, t=*, p=1.00, Table 4.2). There were no significant differences between the two experimental manipulations in either air speed (paired t-test, t=2.03, p=0.179, Table 4.2) or altitude (paired, t=-0.24, p=0.832, Table 4.2) of the pigeons over the entire flight. Similarly, when the flight was broken down to just the middle third of the flight, which represents the phase where the birds are flying steadily and with minimal change in altitude, there were no significant differences in the air speed (paired t-test, t=0.20, p=0.859, Table 4.2) or altitude (paired t-test, t=1.00, p=0.421, Table 4.2) of the birds.

Table 4.2: Mean measurements of flight performance followed by the standard deviation as calculated from the GPS data recorded from three individuals. None of the differences are statistically significant (p>0.05).

	Entire Flight			Mid 33% Flight	
	Route Efficiency	Speed (ms^{-1})	Altitude (m)	Speed (ms^{-1})	Altitude (m)
Control	0.92±0.01	17.93±0.53	109.30±10.93	20.04±0.62	130.01±5.29
5% Added Mass	0.93±0.01	19.10±1.52	107.10±26.30	20.23±2.24	153.90±45.5

On the 22nd June, in still air (Fig. 4.1 and 4.2), the birds were released as a flock and generally gained height over the first 90 seconds at an average rate of around 0.7m s^{-1} and a flight speed of 15m s^{-1}, while on the 23rd June, with a tailwind (Fig. 4.3 and 4.4), pigeons climbed at an average of 0.9m s^{-1} and a flight speed of between 10 and 15m s^{-1}. Airspeeds, then generally increased slightly over the next minute or so, before levelling off at around 17 to 18 m s^{-1}. However, on both days, the pigeons were capable of continuing to climb during this second phase. Finally, the highest flight speeds, averaging 20 m s^{-1} are consistently reported once the flight had levelled out.

However, the Britannia Bridge anemometer (BBA) is at 50m above the Menai Strait and located near the loft and, therefore, more representative of the end of the flight. In addition, as the pigeons flew up to 150m above sea level, it is entirely possible that at the beginning of the flights the birds were experiencing a lower actual wind speed than that reported by the BBA, while during the middle of the flight they were experiencing significantly higher wind speeds. Thus, on the 23rd June when there was a 4.5m s^{-1} tailwind the uncertainty around the true airspeeds of the birds is much greater than on the 22nd June when the measured GPS groundspeeds are expected to be within 1m s^{-1} of the actual airspeeds. Given the very similar flight profiles between the two days, the most reliable data is provided by results of the 22nd June.

Referring to the empirical power curve (Fig. 3.19), if we assume that, during the initial climb phase after take-off, the birds were climbing with a minimum forward power output, then would equate to a mass-specific flight power of around 12W + 7W, which is slightly less than the sustainable forward flight measurement of 21.7W (Gessaman & Nagy, 1988). However, during the second phase of ascent, the pigeons then continue to climb at a similar rate while maintaining a higher speed of 18 m s^{-1}, which would have required significantly more thrust. This leads to an estimate for a maximum sustained flight power of around 18W + 7W = 25W. This seems remarkably high and yet, in the paper of Gessaman & Nagy (1988), when the birds were carrying a harness and added mass, their flight was greatly prolonged and their calculated mean sustainable flight power was around 28.9W. While this is hard to reconcile within the context of adding 5% mass in a small tube, when compared to other studies of weighted or naturally fattening birds, it might indicate that well trained homing pigeons are capable of sustaining very high maximum rates of energy metabolism over many hours. The present flights were of much shorter duration and so this analysis may not be unrealistic. Peters et al. (2005) reported a value of 20.2W for pigeons flying in a wind tunnel, which he associated with heart rates of 663 beats/min (heart rate was measured in a separate set of birds to those for oxygen consumption, using an invasive 9.8g blood pressure monitor velcroed to its back). Free-flying pigeons at Bangor have reached heart rates of 700beats/min (Bishop, unpublished data) which would provide an adjusted maximum flight power of 22.5W, based on rate of energy consumption being proportional to heart rate squared (Bishop & Spivey, under review). However, it is possible that relatively small pigeons (0.34kg) flying in a wind tunnel and heavily instrumented, may find it difficult to perform optimally compared to Gessaman & Nagy's larger (0.413kg) and very long distance trained birds. Indeed, Butler et al. (1977) describe how their pigeons could only perform continuous wing beats in their wind tunnel for between 0.5 and 2.5 seconds at a time, which they considered rather unnatural flight performance.

The two fastest birds on the 22nd June, briefly touch on speeds of 24 m s^{-1}, which would require some 28W of flight power according to the power curve in Fig. 3.19, while at the very end of the flight on the 23rd June, the same two birds touch on ground speeds of between 23 and 29 m s^{-1}. While the former are achieved in horizontal flight, the highest speeds on the 23rd June are coincident with descending flight and there must be some uncertainty regarding the tailwind experienced by the birds.

4.4.1.3 Accelerometry results

Fig. 4.5 shows that on the first day the flock appeared to stay only loosely associated and the birds were rather spread out, however, by the second day the flock was strongly joined apart from three individuals (16, 44 and X71115). It was found that these pigeons didn't return immediately after release and landed briefly at various points along the route home. For this reason the data from these birds was not included in generating mean data values or in paired analyses.

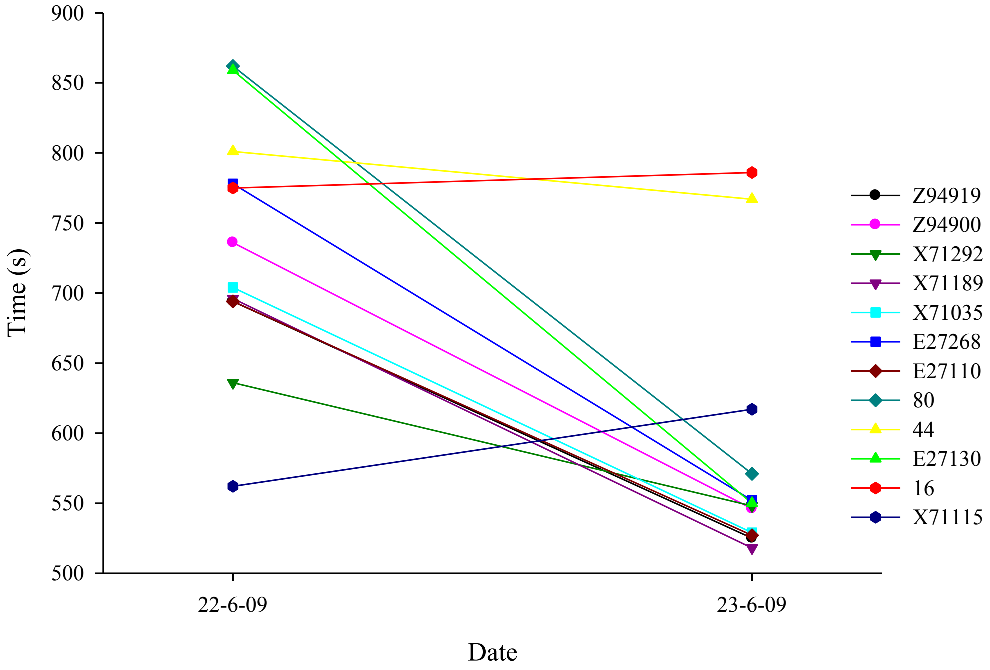


Fig. 4.5: Flight times (s) of 12 individual birds wearing accelerometers released as a flock over two consecutive days wearing 5% added mass or a light-weight plastic control plate.

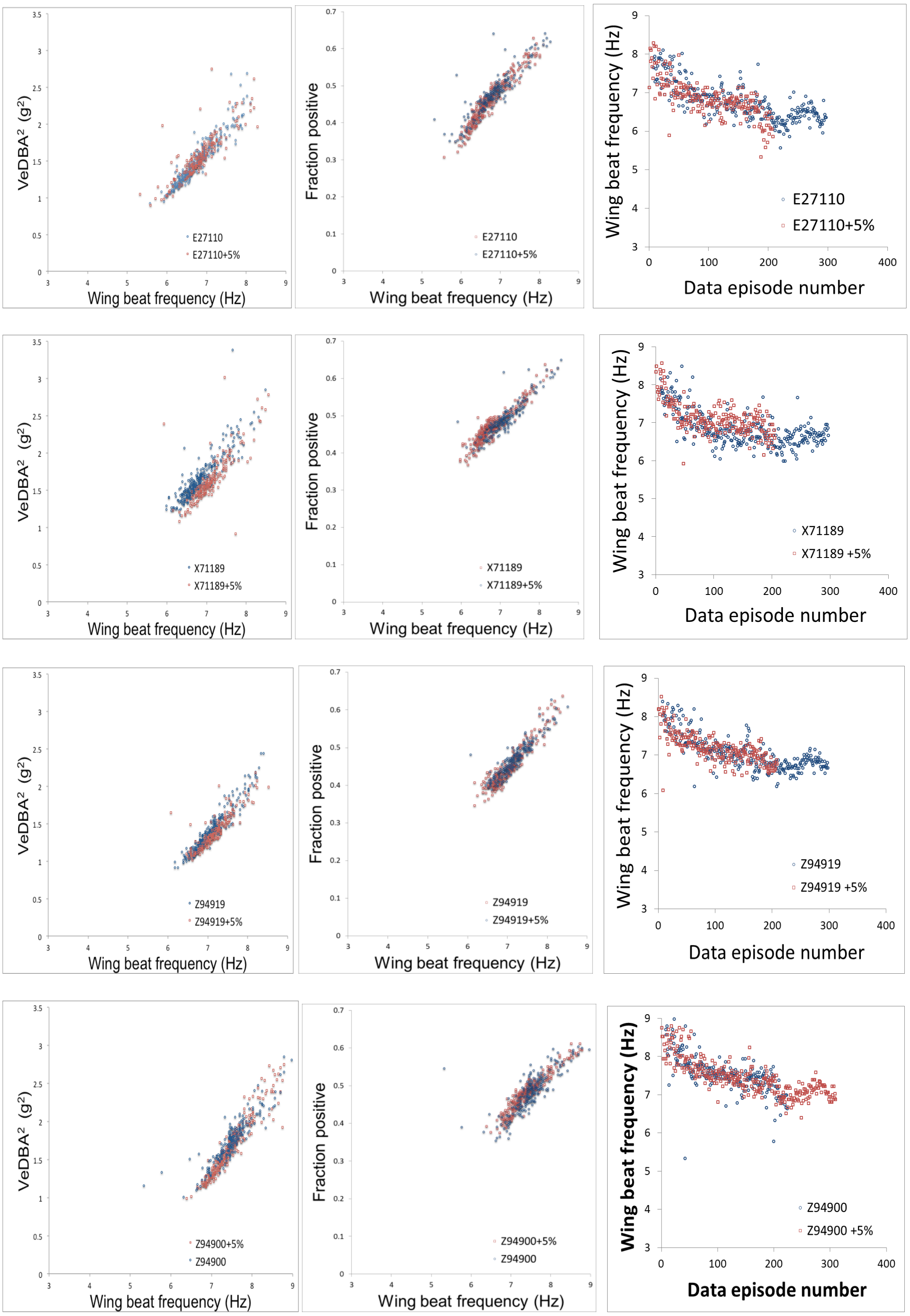


Fig. 4.6a: Shows results for four individual birds flying primarily in a high wing beat frequency mode (see text) on the 22nd June and then again on the 23rd June, either carrying no extra mass (blue) or carrying an added weight of 5% (red). The 23rd of June has a significant tailwind of 4.5 ms^{-1} which accounts for the shorter flight times.

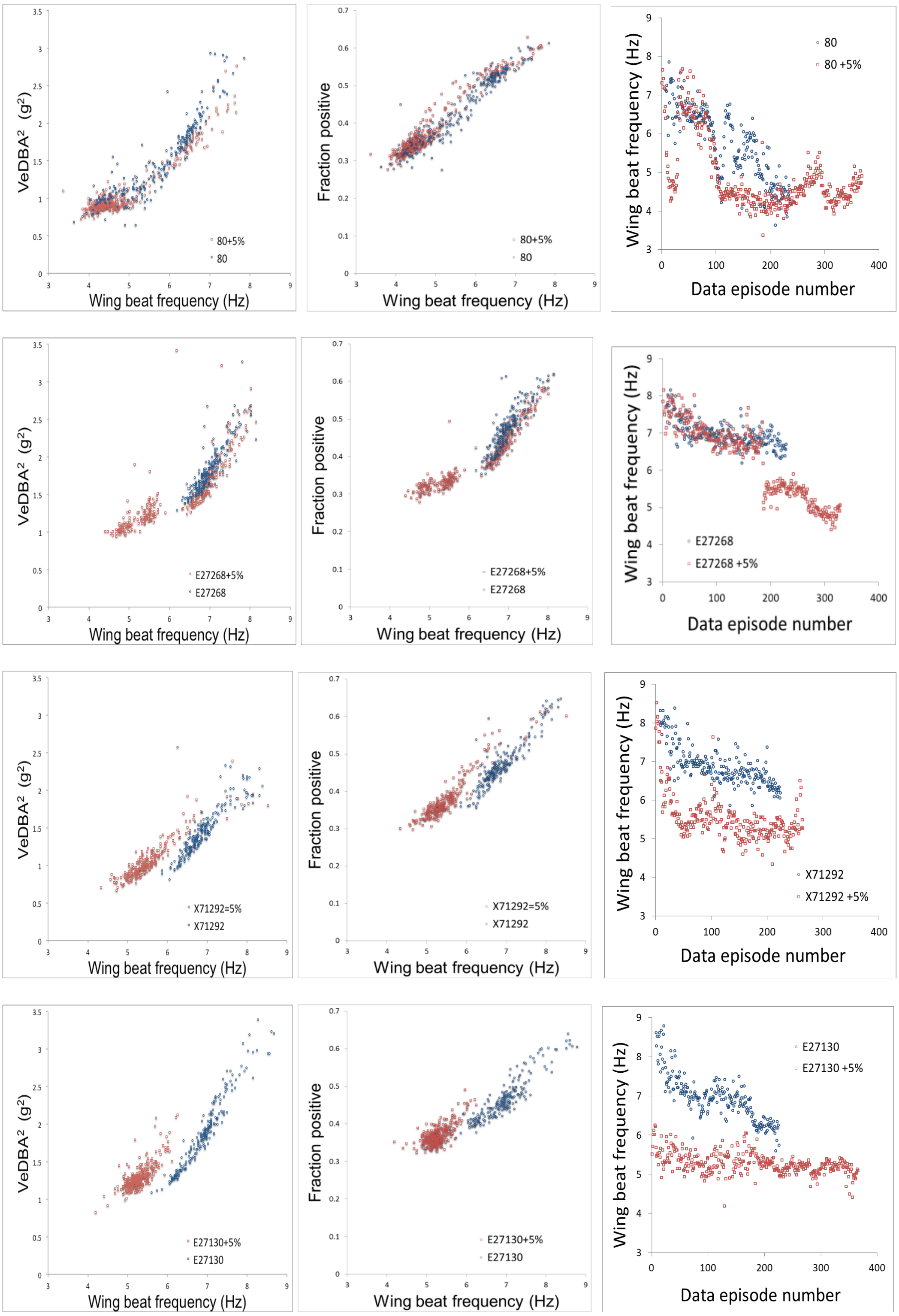


Fig. 4.6b: Shows results for four individual birds flying in a low wing beat frequency mode (see text) for part or all of the flights on the 22nd June and then again on the 23rd June, either carrying no extra mass (blue) or carrying an added weight of 5% (red). The 23rd of June has a significant tailwind of 4.5 ms^{-1} which accounts for the shorter flight times.

Figures 4.6a and 4.6b show the results for VeDBA_{YZ}^2 and Fraction Positive plotted against wing beat frequency (WBF), along with wing beat frequency against sample collection period (around 2 seconds of time for each data period). For all eight birds, there is a strong positive relationship between wing beat frequency and VeDBA_{YZ}^2 and fraction positive. The first four birds (E27110, Z94900, Z94919, X71189) generally show a very similar pattern of relatively high WBF mode flight (greater than 6Hz - H-WBF), with WBF's of around 8 to 8.5 Hz around 20 seconds after take-off and then a gradual reduction over the first 200 seconds of flight (around 100 sample collection periods) down to a value close to 7Hz. Decreases in WBF after this usually range from being very gradual to hardly visible with a value of around 6.5Hz just prior to the approach to landing. As VeDBA_{YZ}^2 and fraction positive are highly correlated with WBF then these changes in flight parameters during the flight are mirrored across the graphs.

The last four birds (80, E27268, E27130, X71292) show a more varied pattern during the flights and particularly between days. All four birds were carrying the 5% added mass on the 22nd June and without the influence of any wind assistance. They appear to have been generally unwilling to keep with the main flock of birds and, at various times, dropped from their H-WBF with respect to both the other monitored pigeons and with respect to their flight the next day on the 23rd June (when they were not carrying any weight). Pigeon 80 appears to be generally unhappy to maintain an H-WBF on either day (and is one of the oldest birds in the colony) but pigeons E27130 and X71292 show a drop of between 1.5 and 2 Hz in WBF on the 22nd compared to the 23rd June. Pigeon E27268 is even more interesting in that the first 6 minutes (180 sample collection periods) of both flights are almost identical with a H-WBF and then within the space of about 10 seconds it switches into a low WBF mode (less than 6Hz - LWBF) of flying for the rest of the flight on the 22nd June. The values for $VeDBA_{YZ}^2$ and fraction positive also mimic, to some degree, the change from a H-WBF to a L-WBF mode of flight. The, values for $VeDBA_{YZ}^2$ drop from around $2.3g^2$ at a WBF of 8Hz to around $0.9g^2$ at a WBF of 5Hz.

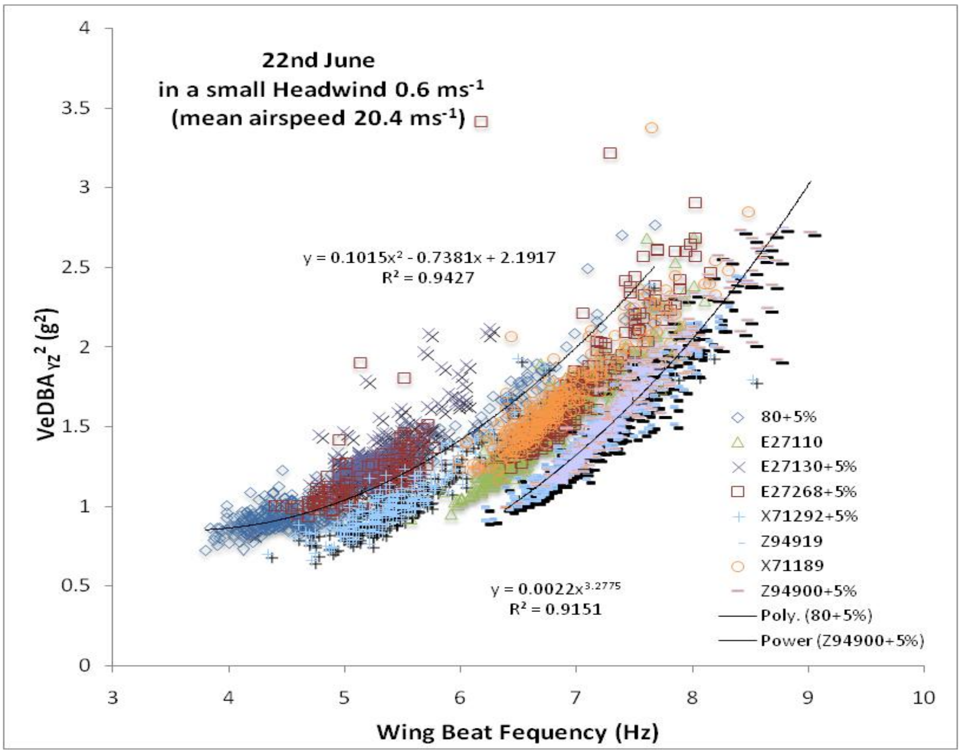


Fig. 4.7: Shows $VeDBA_{YZ}^2$ (g^2) plotted against wing beat frequency (Hz) for 8 birds flown on the 22nd June, on a no wind day ($0.6ms^{-1}$ headwind).

Figure 4.7 shows that, while individual birds show a very strong relationship between $VeDBA_{YZ}^2$ and wing beat frequency, the intercept or coefficient of the relationships do vary between birds. In addition, while the H-WBF mode of flight is quite well described by a power relationship, with exponents typically between fw^2 and fw^3, flights that incorporate lower wing beat frequencies, or the

L-WBF mode, are best fitted with a 2nd or 3rd order polynomial. It has been shown mathematically in Chapter III that power in the body should increase with an increase in wing beat frequency and with the root mean square of acceleration (the latter being related to VeDBA). This is consistent with the empirical result that an increase in wing beat frequency is mirrored by an increase in VeDBA_{YZ}^2 (Fig. 4.7). Thus, it does appear that VeDBA is a good proxy for estimating power in the body of a flying bird.

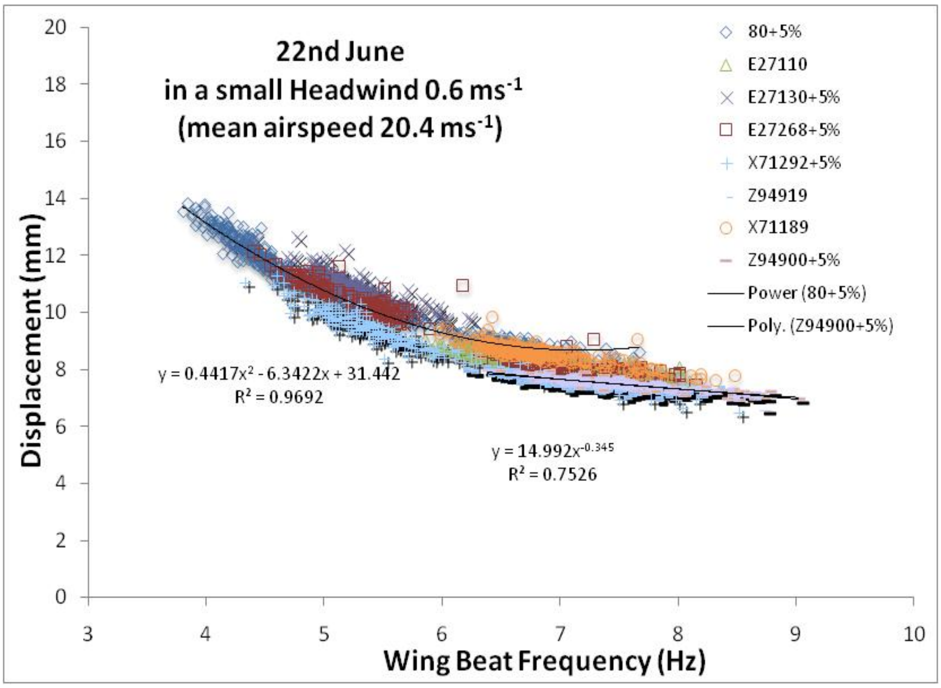


Fig. 4.8: Shows estimates of vertical dorsal body displacement (mm) plotted against wing beat frequency (Hz) for 8 birds flown on the 22nd June, on a no wind day ($0.6 ms^{-1}$ headwind).

Figure 4.8 shows that, individual birds show a strong negative relationship between a decrease in estimates of vertical dorsal body amplitude (based on measurements of VeDBAz) and an increase in WBF. They are reasonably well described by a power relationship, even for birds that are primarily operating with H-WBFs but, again, flights that incorporate a reasonably large range of wing beat frequency can also be fitted with 2nd or 3rd order polynomials.

Mean values of VeDBA$_{YZ}$ (Table 4.3) were lower when the birds were fitted with 5% additional mass compared to when they were flying without this added load (paired t-test, t=2.79, p=0.023*). However the values for fraction negative (paired t-test, t=-1.21, p=0.261) and wing beat frequency (paired t-test, t=2.00, p=0.081) were not statistically different between the two experimental manipulations.

Table 4.3: Mean values followed by the standard deviation of VeDBA$_{YZ}$ (g), fraction negative and wing beat frequency (Hz) (n=9); * represents statistically significant values ($p<0.05$).

	VeDBA$_{YZ}$	Fraction Negative	Wing Beat Frequency
Control	1.232±0.080*	0.555±0.018	6.677±0.508
5% Added Mass	1.147±0.108*	0.579±0.058	6.171±1.001

Correlations were performed between the three main variables analysed from the accelerometers (i.e. VeDBA$_{YZ}$, fraction negative and wing beat frequency) to see if there were repeatable patterns of flight performance occurring with individual birds irrespective of experimental manipulation. There was no significant correlation between VeDBA$_{YZ}$ (Pearson's Correlation, ρ=0.558, p=0.118) or fraction negative (Pearson's Correlation, ρ=-0.008, p=0.984), although the correlation performed on VeDBA$_{YZ}$ between the two conditions yielded a strong trend. However, the correlation of wing beat frequency over the two experiments gave a statistically significant association (Pearson's Correlation, ρ=0.670, p=0.048*, Fig. 4.9).

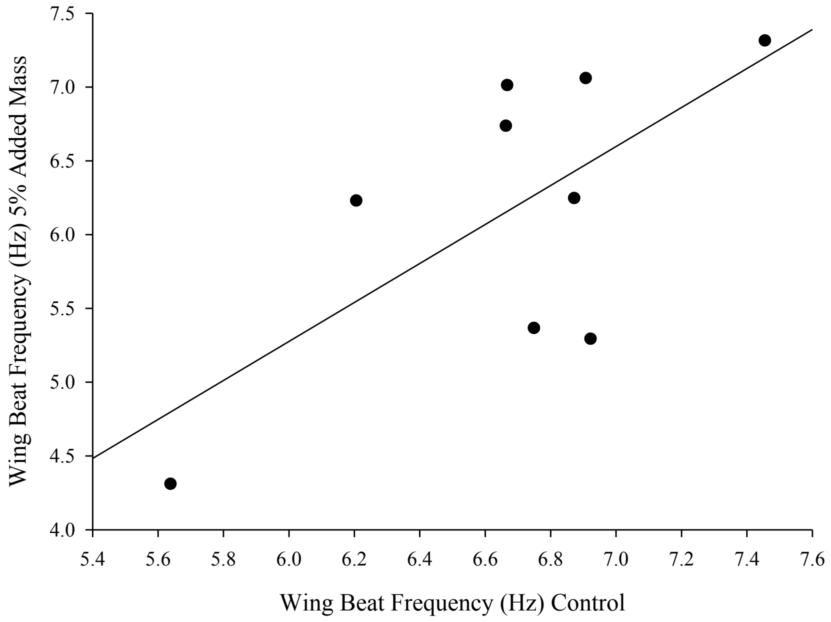


Fig. 4.9: Correlation between the wing beat frequency (Hz) of nine individual pigeons flying with and without wearing an additional 5% of body mass (ρ=0.670, p=0.048*). Regression equation: wing beat frequency 5% added mass = - 2.65 + 1.32 wing beat frequency control.

The relatively strong positive correlations found with wing beat frequency and VeDBA_{YZ} between the two experiments suggest that birds which have a high wing beat frequency and VeDBA_{YZ} values maintain similar patterns across experimental manipulations. For this reason it was thought that performing a correlation between VeDBA_{YZ} and wing beat frequency in the control (Pearson's Correlation, ρ=0.557, p=0.119) and added mass (Pearson's Correlation, ρ=0.834, p=0.005**) experiments would yield strong results. This was clearly found in the added mass experiment and whilst not statistically significant in the control the association was relatively strong (Fig. 4.10).

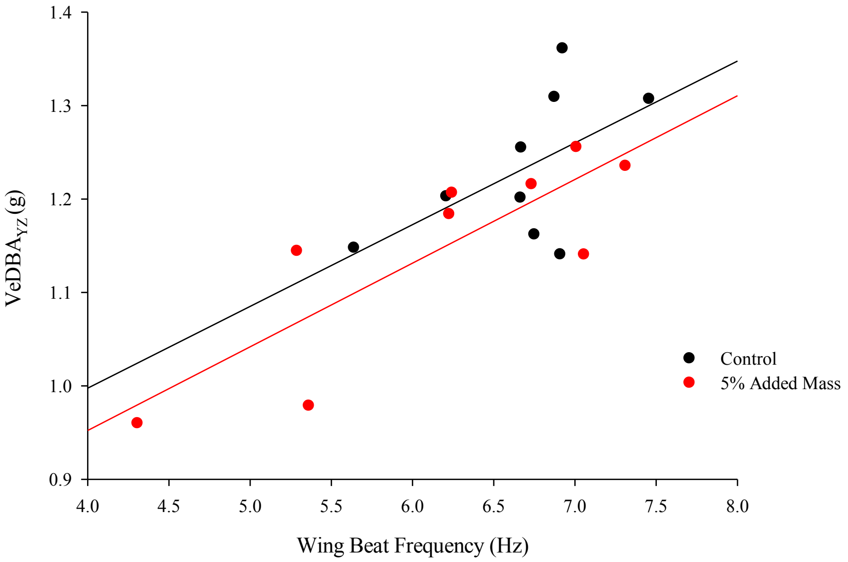


Fig. 4.10: Correlation between wing beat frequency (Hz) and $VeDBA_{YZ}$ (g) when the birds were flying with (ρ=0.834, p=0.005**) and without an additional 5% of body mass (ρ=0.557, p=0.119); Control: $VeDBA_{YZ} = 0.647 + 0.0875WBF$, 5% Added Mass: $VeDBA_{YZ} = 0.594 + 0.0896WBF$

In the control experiment there was no significant correlation between fraction negative and $VeDBA_{YZ}$ (Pearson's Correlation, ρ=-0.543, p=0.131), although the trend was fairly strong, whilst when this analysis was repeated for the added mass experiment the correlation was significant (Pearson's Correlation, ρ=-0.783, p=0.013*; Fig. 4.11).

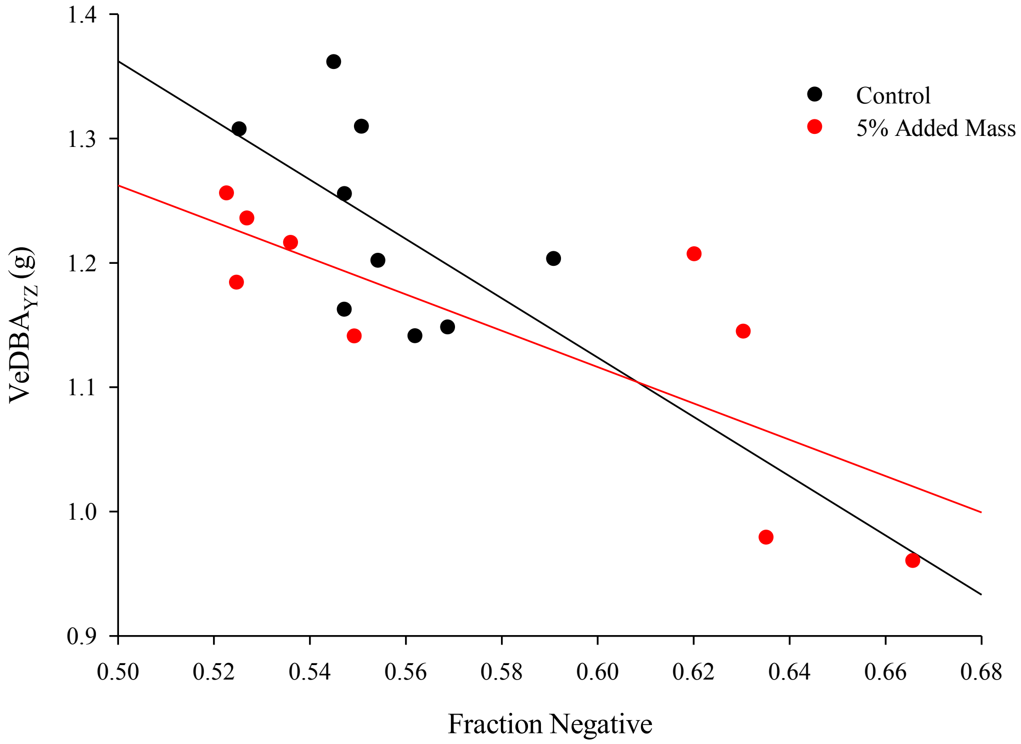


Fig. 4.11: Correlation between fraction negative (FN) and VeDBA$_{YZ}$ (g) when the birds were flying with (ρ=-0.783, p=0.013*) and without an additional 5% of body mass (ρ=-0.543, p=0.131). Control: VeDBA$_{YZ}$ = 2.55 - 2.38FN, 5% Added Mass: VeDBA$_{YZ}$ = 1.99 - 1.FN

Similarly for fraction negative and wing beat frequency in both the control (Pearson's Correlation, ρ=-0.764, p=0.016*) and added mass (Pearson's Correlation, ρ=-0.887, p=0.001**) experiments, there was strong negative significant correlations (Fig. 4.12). Certainly when the birds are carrying an additional 5% of body mass, and to a lesser extent in the control flights, there is a strong correlation between the three parameters analysed (Figs. 4.10 to 4.12).

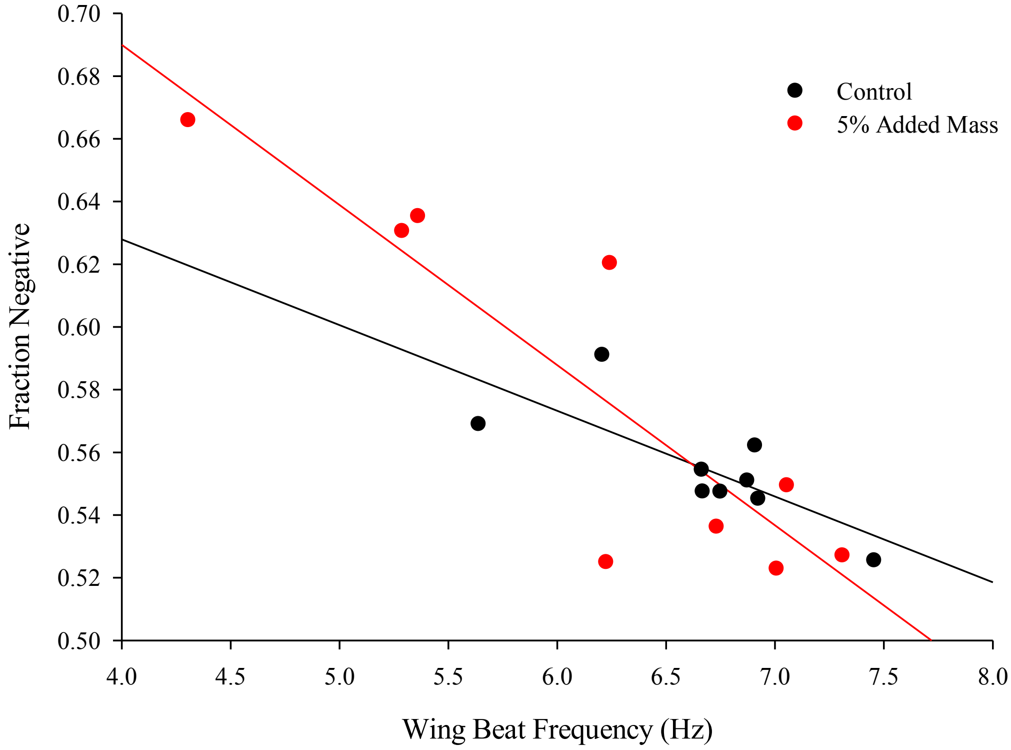


Fig. 4.12: Correlation between wing beat frequency (Hz) and fraction negative (FN) when the birds were flying with (ρ=-0.887, p=0.001**) and without an additional 5% of body mass (ρ=-0.764, p=0.016*). Control: FN = 0.738 - 0.0274WBF, 5% Added Mass: FN = 0.894 - 0.0511WBF

With only three individual birds wearing GPS giving useable results it is difficult to draw overall conclusions as to how the air speed of the pigeons relates to the altitude they flew at when wearing additional mass. It is clear to see from Table 4.4 that all the correlations are very strong although it is only between speed and altitude in the middle third of the added mass flight where the association is statistically significant (Pearson's Correlation, ρ=1.00, p=0.004**).

Table 4.4: Correlations between air speed (m s^{-1}) and altitude (m) for the entire and middle third periods of flight, for both the control and added mass experiments. The test statistic rho (ρ) is given above the value of probability (p); ** represents statistically significant values ($p<0.01$).

		Entire Flight		Mid 33% Flight	
		Speed Control	Speed 5%	Speed Control	Speed 5%
Entire Flight	Altitude Control	0.850 0.354			
	Altitude 5%		0.966 0.167		
Mid 33% Flight	Altitude Control			0.742 0.467	
	Altitude 5%				1.000 0.004**

4.4.1.4 Correlations between morphology and flight performance parameters

As the three flight parameters measured by the accelerometry seemed to be well correlated especially when the birds were carrying additional mass, these parameters were then correlated with body mass to investigate if individual morphology had an effect on flight performance. During the control flights body mass was completely uncorrelated with $VeDBA_{YZ}$ (Pearson's Correlation, $\rho=-0.048$, $p=0.903$), wing beat frequency (Pearson's Correlation, $\rho=0.192$, $p=0.621$) or fraction negative (Pearson's Correlation, $\rho=-0.306$, $p=0.423$). However in the added mass flights the correlations between body mass and these parameters, whilst not statistically significant, were far stronger particularly for $VeDBA_{YZ}$ and fraction negative (Fig. 4.13).

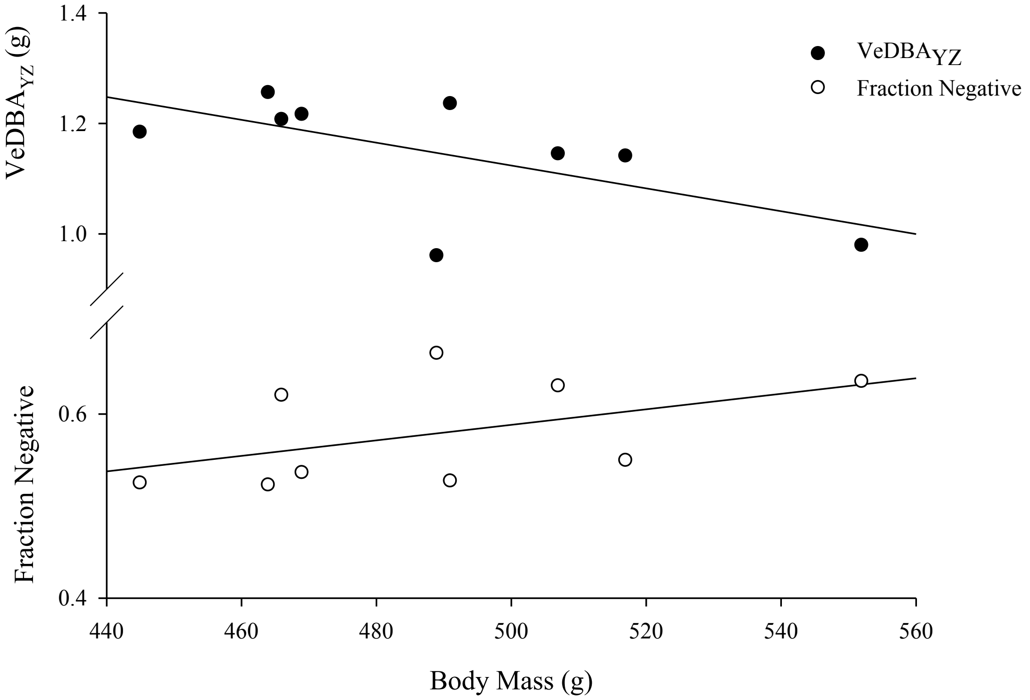


Fig. 4.13: Correlation between body mass (g) and fraction negative (FN) (Pearson's Correlation, ρ=0.479, p=0.192) and VeDBA$_{YZ}$ (g) (Pearson's Correlation, ρ=-0.629, p=0.069) during flight with 5% added mass. FN = 0.167 + 0.000844 body mass, VeDBA$_{YZ}$ = 2.16 - 0.00207 body mass

Body mass and altitude were also had a tendency to be correlated during the entire (Pearson's Correlation, ρ=0.960, p=0.182) and the mid third (Pearson's Correlation, ρ=0.994, p=0.069) of flight of the control flight (Fig. 4.14) and whilst these two results were not statistically significant it is plausible to assume that with a greater number of birds to analyse these would fall into the 5% probability level.

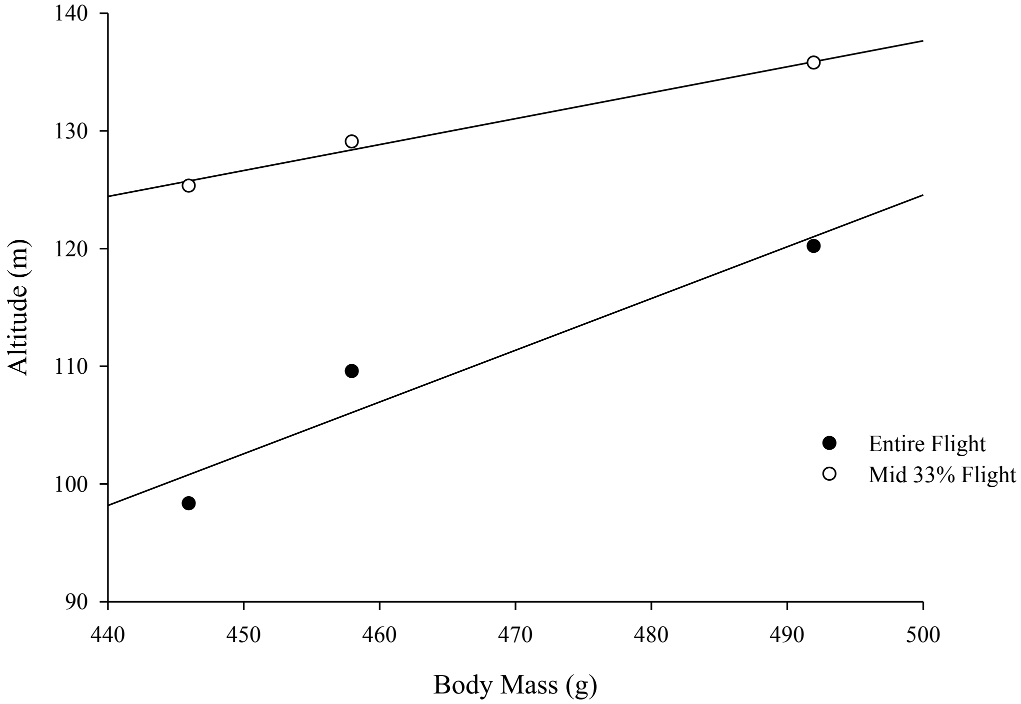


Fig. 4.14: Correlation between body mass (g) and altitude (m) over the entire flight (Pearson's Correlation, ρ=0.960, p=0.182) and the mid 33% flight (Pearson's Correlation, ρ=0.994, p=0.069) in control conditions. Entire flight = -95.2 + 0.440 body mass, Mid 33% flight = 27.4 + 0.221 body mass

4.4.2 Individual releases 2008

Seventeen birds were flown individually over a period of 4 days (28th and 29th November 2008, and the 11th and 15th December 2008) either without added mass or wearing 5% added mass, in a paired design. Average wind conditions were very low on all four days; 2.13m s^{-1} head wind, 0.98m s^{-1} tail wind, 0.52m s^{-1} tailwind and 0.2m s^{-1} head wind, respectively. Fig. 4.17 shows the results for $VeDBA_{YZ}^2$ plotted against wing beat frequency for 11 birds flown on both the 11th and 15th December. The first 5 plots show birds that were faster with the added 5% mass in descending proportionality, while the next 6 plots show birds that got proportionally slower when carrying 5% added mass.

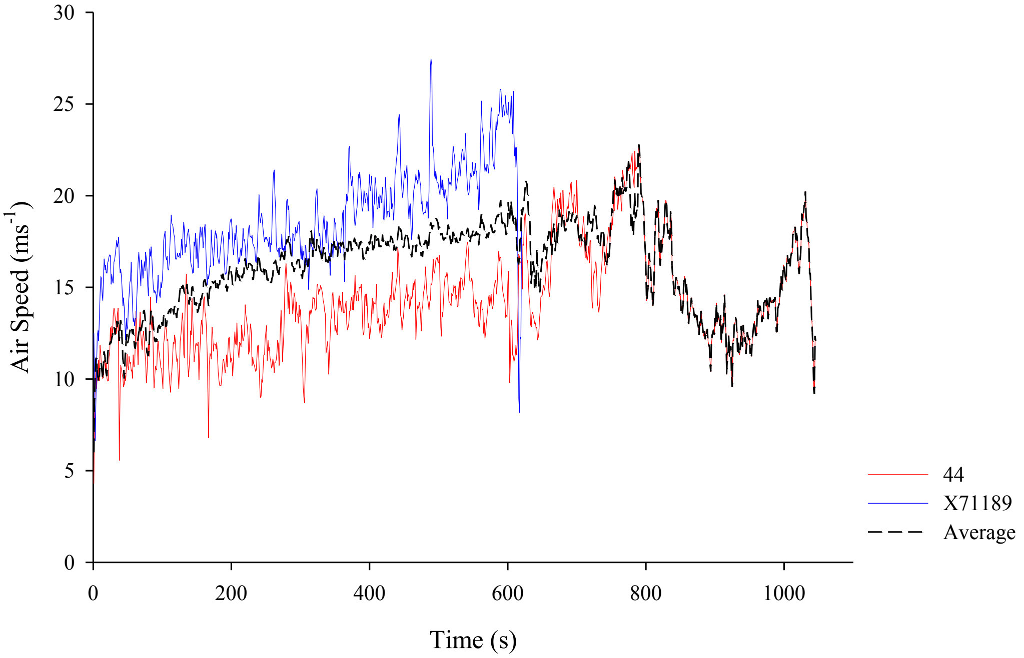


Fig. 4.15: Average air speed (m s^{-1}) alongside the air speed of the fastest and slowest pigeon on the 29th November, 2008.

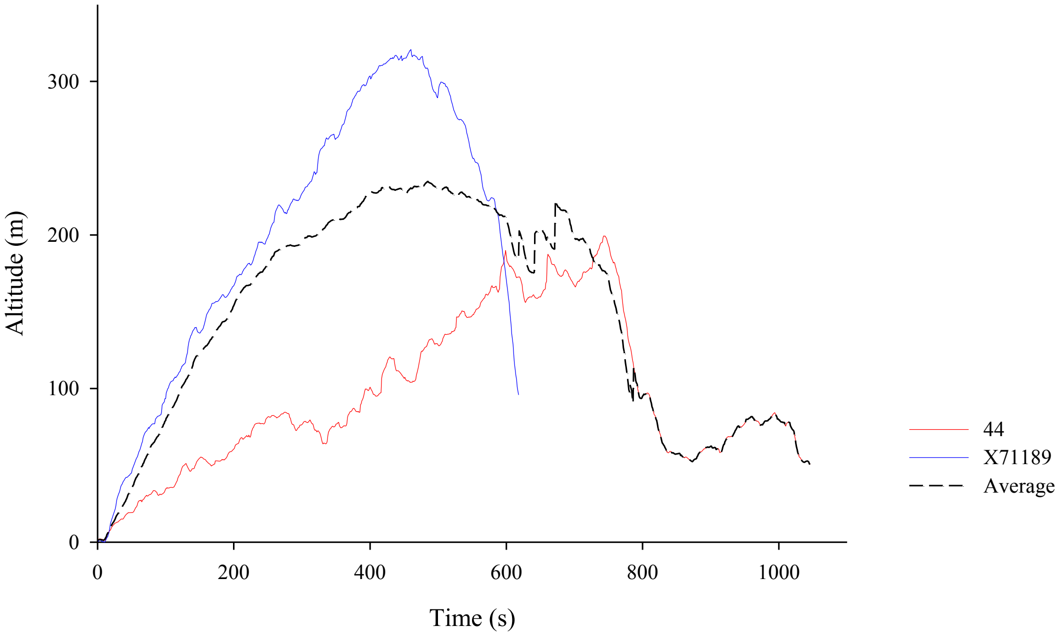


Fig. 4.16: Average altitude (m) alongside the altitude of the highest and lowest flying pigeon on the 29th November, 2008.

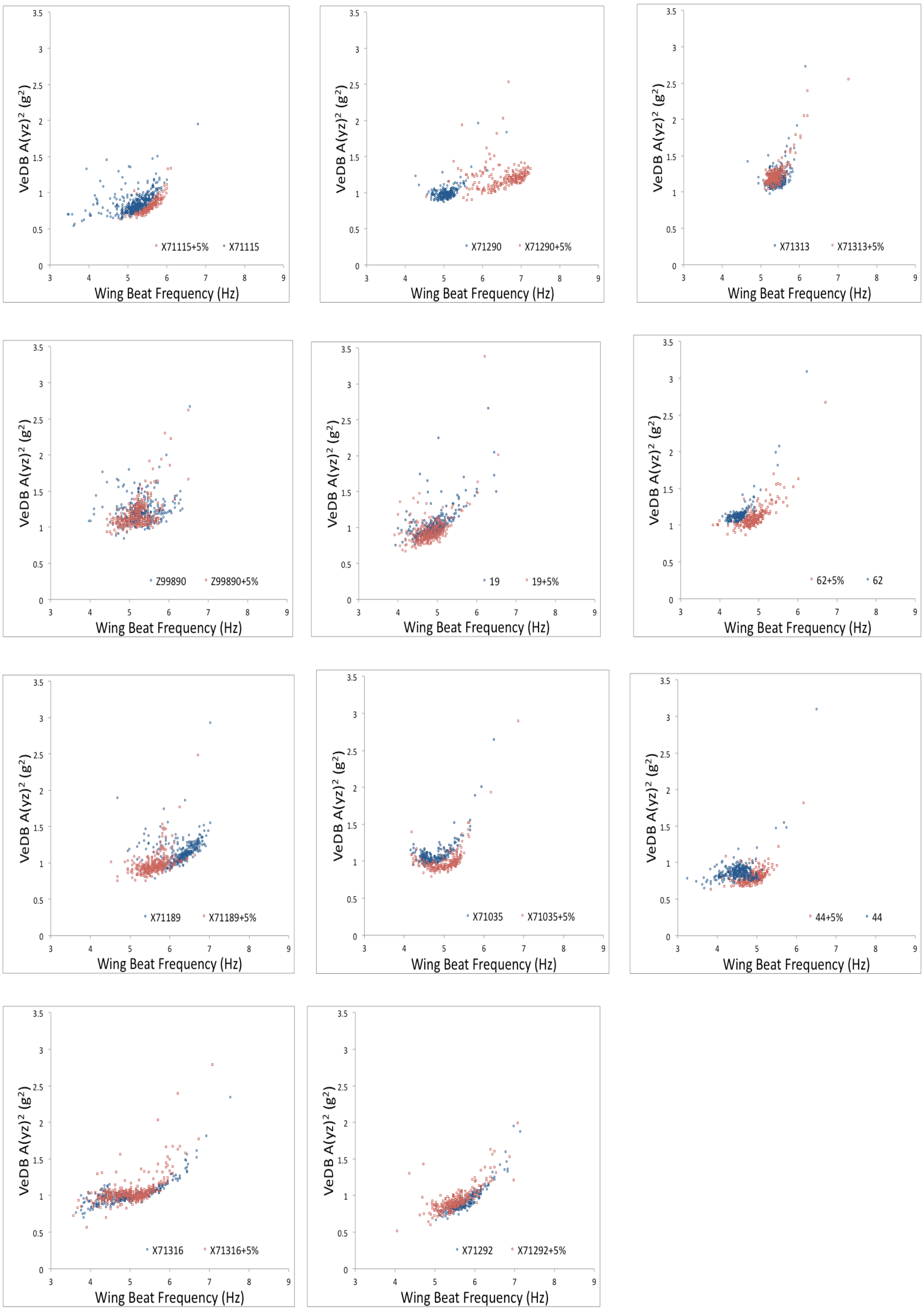


Fig. 4.17: Shows results for 11 individual birds flying on both the 11th and 15th December 2008 (see text), either carrying no extra mass (blue) or carrying an added weight of 5% (red).

The plots in Fig. 4.17, for pigeons released individually, all show a L-WBF mode (< 6 Hz) of flying, similar to the 4 birds in the flock-release experiment plotted in Fig. 4.6b but very different to the 4 pigeons showing a H-WBF mode (greater than 6 Hz) plotted in Fig. 4.6a. Similarly, values for $VeDBA_{YZ}^2$ were low, with a mean of $1.17 \pm 0.02g^2$ during the middle section of the flights, as were mean estimated airspeeds at $14.89ms^{-1}$ over the two days.

There were no significant differences in mean values of VeDBA (paired t-test, $t = -0.68$, $p = 0.507$) and wing beat frequency (paired t-test, $t = 0.43$, $p = 0.670$) during the middle section of the flight. However, during the first minute of flight, during the climbing phase of the flight, both $VeDBA_{YZ}$ ($t = -2.27$, $p = 0.038$*) and wing beat frequency ($t = -2.7$, $p = 0.016$*) were significantly increased (means of 1.268 verses 1.225 and 5.52 verses 5.34, respectively.

4.5 Discussion

4.5.1 General observations and mass effects

In the flock flights, the birds usually show an almost ‘follow-the-leader’ mentality and, thus, it was anticipated that the birds would generally stay together as a group over relatively short flights, as opposed to breaking and flying alone (Dell’Ariccia et al., 2008; Nagy et al., 2010). However, if the birds could not physically maintain the speed at which the flock is flying (or lack sufficient motivation) due to the impediment created by the additional weight, it seems that the flock would not remain as one, as shown during the longer flights reported by Gessaman and Nagy (1988). Even in the relatively short flights of the present study, quite a few of the birds took their time coming home and the flock was not maintained as a single unit. This would appear to be entirely due to the experimental procedure (e.g. handling stress) due to the extra manipulation involved with putting on the weights, when the birds had not flown for a while.

There are other compounding factors to take into account as to why the flock broke, such as the altered centre of mass and the potential for additional drag experienced by individual birds fitted with lead plates and data loggers. However, all birds flying in the flock that were not fitted with data loggers wore an identically shaped and weighed Perspex block which would mirror the additional drag caused to the birds wearing data loggers. Therefore, all birds flying in the flock would have been impeded by a similar amount of drag to minimise the effects of drag on the results. It was impossible to alter all the birds centre of mass as only the birds fitted with the lead plate would be affected by any changes in their centre of mass. Therefore, it remains possible that the results seen may not be solely attributed to the addition of extra weight and may in some part be due to an alteration in the birds' centre of mass. However the differences noted between the birds in the control and the added mass experiment were small and it must be assumed that the addition of 5% mass does not destabilise or impede the birds significantly. Thus, the flock experiments with regard to adding additional mass yielded little statistical results. Indeed, two of the birds flew in an entirely different way on day one, with WBF typically below 6Hz (L-WBF), while on day two they seemed to stay with the flock and flew with WBF typically above 6Hz (H-WBF). Without being able to control for flight velocity, the ability to detect energetic or kinematic difference between the control birds and those with additional weight was going to be extremely unlikely. While the behavioural observation is interesting in itself, it is well known that pigeons are capable of being trained to fly with a reasonable amount of additional mass (Usherwood et al. 2011) and, some of Bangor flock could also do it, so it is most likely that it demonstrates individual attitude and lack of motivation to fly home, rather than a direct effect of flight biomechanics or aerodynamics. Once the birds had left the flock they flew much more slowly.

It has been previously shown that pigeons fly faster in a flock than they do when flying alone (Dell'Ariccia et al., 2008) and this is consistent with both the present flock study and the individual release experiments. In the latter, all the birds flew home slower than when they were released together as flock, regardless of whether they were carrying extra mass or not. Interesting, the birds released individually flew with values of $\mathrm{VeDBA}_{\mathrm{YZ}}$ and wing beat frequency which were similar to the values of the 4 flock released birds once they moved into the L-WBF mode of flight. While we cannot directly know what the precise airspeed of the birds were that broke behind the flock, we can infer that they are likely to be similar to those of the individually released pigeons, given the general similarity in wing beat frequencies, $\mathrm{VeDBA}_{\mathrm{YZ}}$ and flight times. Mean airspeed for over the four days of individual release flights was 15.49 m s^{-1} compared with the mean airspeed of 20.29 m s^{-1} over the two days of flock release flights. Similarly, wing beat frequency was 5.19 Hz for individual pigeons compared to 6.68 Hz while in the flock, while $\mathrm{VeDBA}_{\mathrm{YZ}}^2$ changed from 1.17 g^2 to 1.52 g^2, representing an increase of 30%. Using the relationship between integrated power (W) and $\mathrm{VeDBA}_{\mathrm{YZ}}^2$, presented in Fig.3.20 (Chapter 3) we can estimate the change in power in the body of the pigeons to be from around 0.390 W to 0.484 W, representing an increase of 24.1%. The difference in apparent change in power between the ratio of $\mathrm{VeDBA}_{\mathrm{YZ}}^2$ and that of converting to units of Watts being due to the offset of the relationship as the linear regression does not pass through zero.

Whilst use of accelerometry data loggers is a relatively new technique as far as free-flying birds are concerned, it is rapidly becoming a widely used and popular tool to assist with the recording of behavioural and performance data, particularly with regard to the indirect measurement of energy metabolism using ODBA or the preferred calculation of VeDBA, used in the present study. However, there are few studies that have tried to calibrate either measure against flight energetics or biomechanics of free-flying birds. Wilson et al. (2006) pioneered the use of ODBA specifically to estimate animal energetics and, suggested that cormorants had higher ODBA values when returning from foraging due to the additional weight, compared to when they were leaving on a foraging trip. However, it is not at all clear whether ODBA or, in the present study VeDBA, should go up at all with an increase in added mass. It may be that a small additional mass might have the effect of damping the acceleration of the body if the extra power required can be delivered with, for example, a longer slower downbeat. In the present study, the correlations between natural body mass and flight performance as measured by accelerometry showed no statistically significant results, although there were strong trends with fraction negative and VeDBA_{YZ} in the added mass flight. Mean VeDBA_{YZ} negatively correlated, and fraction negative positively associated with body weight during the mid-third section of the flights. Therefore, heavier birds tended to show lower mean VeDBA_{YZ} values which would be consistent with the hypothesis that their accelerations are actually being damped by the additional mass, whether added artificially or naturally accumulated.

Videler et al. (1988a) demonstrated that when mass was artificially increased, the flight speed of kestrels (*Falco tinnunculus*) decreased. Theory suggests that, as weight increases, the minimum power speed (V_{MP}) should also increase to ensure sufficient lift can be produced according to Norberg (1995). In practice, most birds usually fly above their minimum power speeds so that they have scope to actually reduce their flight speed when weighted and potentially lower their immediate flight costs. Indeed, Videler (1988b) showed that when the kestrels were not fitted with extra mass they flew close to the maximum range speed, but when they carried the extra weight, they flew nearer the predicted minimum power speed. Pennycuick (1968a) calculated the maximum range speed of pigeons to be 16 m s^{-1}, whilst the minimum power speed was calculated as 8-9 m s^{-1}. Thus, when in a flock, it would appear that pigeons probably fly well above their V_{MP} during normal flight, so they could reduce their instantaneous energy expenditure by flying slower. The average air speeds in the present flock flights were around 20 m s^{-1} on both days, which exceeds Pennycuick's original 1968 values but it is possible that pigeons have a relatively high V_{MR}.

Interestingly, Dell'Arriccia et al. (2008) found that pigeons flying alone flew at approximately 14.7ms^{-1}, whereas when the same birds were flown as a flock they flew at approximately 16.9m s^{-1}, which is close to the predicted maximum range speed calculated by Pennycuick (1968a). This is also consistent with the results from the present experiments at Bangor University in which the individually released birds only averaged around 15.4m s^{-1}, while the flock birds more typically flew around 20 m s^{-1}, over our relatively short flight distances. It is interesting to speculate whether the birds that either drop out from the back of the flock, or just fly more slowly as individuals, are choosing to fly at a speed that is more similar to V_{MR} or V_{MP}. There is a 31% increase in speed when flying in the flock, as against the 24% increase in estimated power. Thus, if we assume that the proportional savings recorded for power in the body are directly linearly related to savings in total flight costs, then the pigeons flying in the flock will save around 5% in total energy consumed for the flight back to the loft, indicating that the flock birds are flying slightly closer to V_{MR} than the individual birds. If correct, then it might indicate that individual birds simply prefer to fly well within their maximum capability because it feels easier, rather than that they are making any overall energetic saving.

The lack of many statistically significant differences between the flight performance parameters as measured by the accelerometers during steady horizontal flight when the pigeons were flown as a flock and, individually, may simply reflect the power of the experimental design or, suggest that monitoring acceleration in this manner may not be sensitive enough to pick up the experimental effect. The addition of 5% of an individual's body mass appears not to affect the pigeons' performance to any great extent. This is in contrast to the results from Gessaman and Nagy (1988), who reported an increase of 35% in the energy used during flights of 90km when wearing an additional 5% of body mass compared to controls, although their flight was approximately nine times further than this experiment. However, it is difficult to see how this result could be solely attributed to the addition of the added mass, even if long flights are more sensitive to experimental manipulations. The results of Kvist et al. (2001) and Schmidt-Wellenburg et al. (2007, 2008), predict a less than linear increase in energy consumption with added mass and are completely incompatible with the results of Gessaman and Nagy (1988). The general lack of differences in performance parameters during the middle section of the flight, apart from a

3.74% reduction in fraction negative, supports the conclusion that the birds were only minimally affected over the 11km flight.

Gessaman et al. (1991) could not determine any differences in carbon dioxide production between tippler pigeons fitted with additional 5% of body mass and control birds, although control birds did have longer flight durations and lost water at a slower rate. This may simply reflect the high variability of experimental results involving doubly labelled water (Butler et al., 2004). For example, zebra finches (*Taeniopygia guttata*) performing short flights were shown to increase their energy output by 27% compared to when perching (Nudds and Bryant, 2000). It should be expected that energy expenditure would increase far greater than the 27% reported by Nudds and Bryant (2000) as flying is extremely energetically costly (Alerstam, 1991; Rayner, 2001). Future experiments may show greater differences in flight performance if the weight added is of a larger percentage of body mass. In fact, Dial and Biewener (1993) found that some pigeons were able to take-off with an additional 50% of their body weight, and although when carrying 100% of their body weight the birds were unable to take-off or land they were able to maintain steady flapping flight, although they were performing short flights along a corridor.

4.5.2 Specific flight characteristics and accelerometry.

Data pertaining to GPS speed was only collected from three individuals so the results with regard to the direct experimental manipulation of mass can be ignored. In addition, the effect of the tailwind on the 23rd June resulted in a significant day influence on ground speed relative to the 22nd June, which can only partially be removed by calibration with the anemometer readings from the

BBA. This is because there was almost certainly some stratification of wind speed with altitude, with potentially, almost no wind at the sea-level release site (11km from the BBA) and increasing in speed with increasing altitudes. However, the similarity of the flight times between the 3 GPS pigeons and the rest of the birds in the flock do suggest that their general flight characteristics can be compared with those obtained from the birds wearing accelerometers.

In the present study, the pigeons show a wide range of flight performance, from sustained climbs immediately following take-off, to slightly faster flights while maintaining significant climbs, to fast and slow forward flights and periods of descent. Despite incorporating all these different flight manoeuvres, the current analysis shows a smooth transition in the data of WBF against VeDBA_{YZ}^2 or WBF against B (Fig. 4.7 and 4.8). In theory, the inertial costs of flapping the wing (van den Berg and Rayner 1995) and the energetic costs of moving the body of the bird up and down in a sinusoidal manner (modelled in chapter III) should actually be directly proportional to WBF^3 and amplitude squared (B^2, in the case of the body) (Fig. 4.18a); hence, power in the body of the bird should also be predicted to be proportional to $\text{WBF}^3 \times B^2$ (Fig. 4.18b).

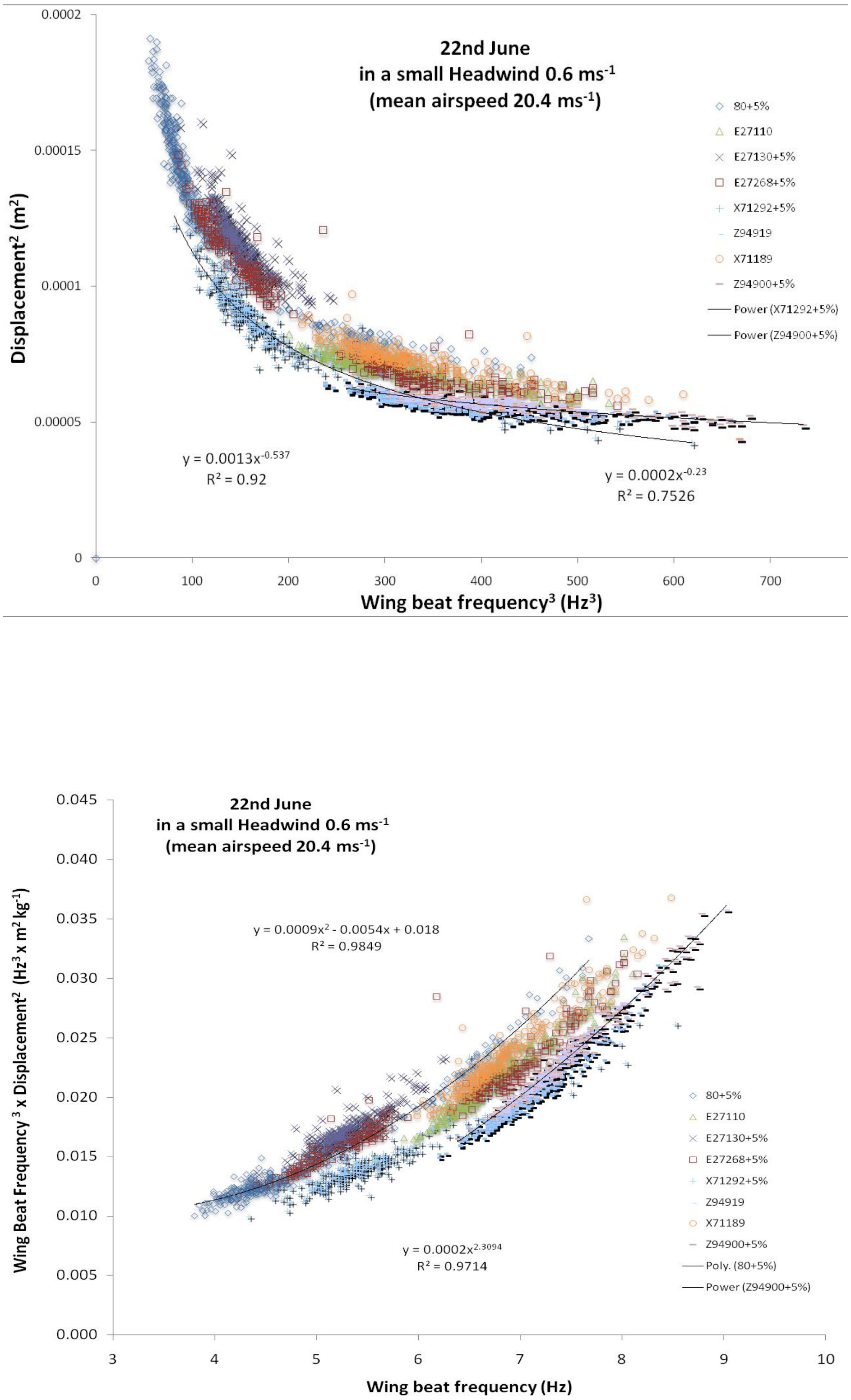


Fig. 4.18a shows estimates of vertical dorsal body displacement squared (m^2) plotted against wing beat frequency cubed (Hz^3); 4.18bB shows WBF^3 x B^2 (Hz^3 x m^2) plotted against WBF (Hz) for 8 birds flown on the 22nd June, on a no wind day (0.6m s^{-1} head wind).

WBF ranging from around 9Hz down to approximately 7Hz are frequently associated with the early few minutes of climbing flight (typically around 0.7m s^{-1}) before transferring to near horizontal flight, more typically incorporating WBF of around 7.5 to 6.5Hz. Fig. 4.18a again demonstrates the smooth, tight but inverse relationship between WBF and B, while Fig. 4.18b specifically illustrates the excellent proxy for power in the body, represented by the product of WBF^3 and B^2 (see Fig. 4.18b). Indeed, while it might be argued that the extra power required to climb against gravity is a different problem to that of the increasing power required to overcoming high body drag at fast forward speeds, in fact, it is not possible to discern any clear transition in the data in either plot which might identify where climbing flight or fast horizontal forward flight is occurring. WBF^3 and B^2 both make remarkably reliable contributions to the detection of overall power in the body and indicate what kind of relative effort the bird is apparently making.

A recent study by Usherwood et al. (2011), studied the circling flight of free-flying homing pigeons while they were instrumented with a 35 g data logger, including tri-axial accelerometer, tri-axial gyroscope and high precision GPS. While circling flight imposed additional dorsal accelerations onto their birds, through modelling and analysis of their data sets, they made specific predictions for both WBF and dorsal amplitude movements (either B or 2 x B?) during steady, straight, level flight. They also make many other observations that are directly relevant to the data collected in the present study, such that some comparisons and contrasts should be made.

Usherwood et al. (2011) predict a U-shaped curve of WBF and velocity, with a flat line between 14 and 18m s^{-1}, followed by a slight increase below and, presumably, above (it is not shown their figures) these limits. In association, they make the prediction that dorsal amplitude of the body will increase at velocities above about 16 m s^{-1}. This is completely unlike our results. Apart from during take-off and immediately afterwards, as the bird gets up to speed (data not shown), the present study shows a tight, inverse relationship between WBF and body displacement (B), as shown in figure 4.18. Usherwood et al. (2011) also make reference to climb power being related to increases in B but their definition of climb power is mixed up with genuinely powered and sustainable climbs during flight, as against their very brief but large changes in vertical velocity while circling and undulating and, almost certainly, while trading height for forward velocity. Yet, in sustained powered circling flight their pigeons increased WBF and decreased B when requiring additional power to overcome increases in weight brought about by higher g forces. The present study suggests, at least at the level of data averaged over 1.25 second periods, that pigeons undergoing sustained powered flight do not obviously discriminate between the resultant power in the body required for circling, or climbing or fast forward flight. In all three cases, they utilise duel positive frequency and inverse amplitude modulation of the body.

CHAPTER V – Summary

Homing pigeons were flown in a flock on nine different days and under varying environmental conditions. In general, airspeed was not found to vary systematically with wind speed or direction but to be fairly consistent around a mean value of 20.9 m s^{-1} (range 17.8 m s^{-1} to 23.9 m s^{-1}). $VeDBA_{YZ}^2$ was shown to be well correlated with airspeed ($\rho = 0.703$), while wing beat frequency showed a less predictable response.

A detailed analysis of three of the most differing wind condition days was performed; strong headwind (7.68m s^{-1}), strong tailwind (5.55m s^{-1}) and slight headwind (1.31m s^{-1}). The flock remained fairly tight during the strong tailwind, slightly less so in the low head wind flight and more spread out, although still loosely together, in the strong headwind flight.

The pigeons flew a less efficient route back to the loft in the strong headwind and at a faster air speed but at a lower altitude than in the strong tailwind. It was possible to categorise the birds as slow or fast returning birds, particularly in the flight into the strong headwind, with $VeDBA_{YZ}^2$, wing beat frequency and fraction positive generally lower for the slowest group of birds on the day. Wing beat frequency tended to be consistently correlated within-individuals across the three days, but there was a considerable amount of variation in $VeDBA_{YZ}^2$ for a given value of wing beat frequency between individuals, indicating the difficulties in making average assessments of flight performance.

5.1 Introduction

Many studies that have focussed on the effects of wind have been in the form of direct observations of the behaviour of migratory birds (e.g. Åkesson and Hedenström, 2000; Erni et al., 2005). During migratory flights, birds may travel many thousands of kilometres and so it may be critical that they are selected to fly when wind conditions are ideal for flight. This is most easily observed either at the beginning of the migration or when birds are departing from a stopover site (e.g. Dänhardt and Lindström, 2001; Schaub et al., 2004). As flight in general is energetically costly per unit time (Pelletier et al., 2008) then the use of tailwinds could significantly reduce the energy required for migrating birds by decreasing the cost of transport (energy per unit distance) through its direct effect on the bird's groundspeed. Potentially, even slight tailwinds could provide a significant advantage (Zehnder et al., 2001) and is consistent with the observation that red knots (*Calidris canutus*) and bar-tailed godwits (*Limosa lapponica*) tend to depart for migration in weak tailwinds (Battley, 1997). Conversely, flocks of bristle-thighed curlews (*Numenius tahitiensis*) may abort attempts to initiate migration when there were unfavourable headwind conditions (Marks and Redmond, 1994). In the autumn, nocturnally migrating birds have been shown to be least likely to depart for migration when there were strong head or crosswinds and instead choose to leave when head or cross winds are weaker (Erni et al., 2002).

Similarly, birds may seek to adjust their altitude of flight in order to catch the most favourable winds as in general, wind speed increases with altitude so the extra costs of climbing flight are compensated by the greatly reduced overall flight time and energy expenditure (Alerstam, 1979; Green, 2004). Of course, strong winds could be potentially hazardous to migrating birds as they could force individuals off course (Able, 1970) and they may be more turbulent and, therefore, add an additional cost to flying (Bowlin and Wikelski, 2008).

Apart from these types of observations there are few theoretical predictions about how birds should change their flight performance with respect to wind direction and strength. The best know is the prediction (Prediction 1 'Effect of wind on maximum range speed') by Pennycuick (1978) that the V_{MR} speed would be affected by relative wind direction such that birds might try harder (increase their airspeed) in a headwind and vice versa in a tailwind. This is due to the fact that the intersect of the tangent of the line that starts from the origin in the U-shaped power curve against airspeed is slightly shifted to the right in a headwind and, thus, making the optimum V_{MR} slightly greater in a headwind (and vice versa). An extreme example of this idea, is illustrated by the fact that energy expenditure has been shown to increase in foraging black-legged kittiwakes (*Rissa tridactyla*) in strong winds, possibly due to the increase in time spent engaged in flapping flight as opposed to gliding in such conditions (Gabrielsen et al., 1987).

5.2 Aims of the research

The aim of the present work was to investigate the effect of wind direction and strength on the flight performance and behaviour of free-flying homing pigeons when they were released as a flock. By flying pigeons on different days and under different wind conditions it was hoped that a pattern would emerge regarding their preferred flight behaviours. Unlike in wind tunnel experiments, the birds would be free to choose their preferred flight speeds and altitudes. An accelerometer logger was fitted to each bird to provide measures of wing beat frequency and VeDBA_{YZ}^2 (a proxy for biomechanical power in the bird's body), while a GPS data logger was fitted to different birds in the same flock to record ground speed and position. It was anticipated that birds might fly at a faster airspeed into a headwind compared to a tailwind, due to the predicted theoretical effect on maximum range speed. This should also be correlated with an increase in wing beat frequency and VeDBA_{YZ}^2 in a headwind. An additional hypothesis was that pigeons might fly higher in a tailwind in order to benefit from the potential for higher wind speeds and, therefore, an increase in their groundspeed, as seen in some migrant birds.

5.3 Methodology

In order to investigate the effects of wind speed on free-flying pigeons, birds were released as a flock from the main release site (Waterloo Port, site H, Fig. 2.1). The Menai Straits runs broadly southwest to northeast and many of the prevailing winds tend to have a similar orientation. As the pigeons appear to like to follow either the edge of the Straits, or the roads that run along its edge, their flight direction is reasonably well constrained and predictable. In general, an attempt was made to release birds on days when there might be either very little (no) wind, or a definite to strong headwind or tailwind. The flock of homing pigeons were flown nine times, on weather conditions that were subsequently confirmed to represent 3 broad categories of 3 tailwinds, 3 low (or no) winds (< 2 m s^{-1}) and three headwinds. The mid-sections of these flights were analysed as a group for wing beat frequency and VeDBA_{YZ}^2 to address the general pattern of flight with respect to the differing wind speeds. Three of these flights, comprising of 11 individuals carrying accelerometers and 7 wearing GPS loggers who successfully provided complete data sets on all three separate days, during a 10 day period in September 2009, were analysed in more detail at the individual level: once in a head wind; once in a tail wind and once when there was no wind. Up to another thirty birds wore 'dummy' loggers and were included to create a relatively large flock. Most of the flights were performed by the same individuals, wearing the same loggers which allowed for a paired analysis. Additionally, those individuals chosen for detailed analysis all flew immediately back to the loft without stopping at any time. Wind direction was initially obtained using a hand-held anemometer and measured at the release site prior to liberation, while subsequent analysis used data accessed from two anemometers located on the 50m towers on the Britannia Bridge (BBA) averaged over each minute of flight. Accelerometer data was analysed as described in sections 3.1.2 and 3.2.3 and the GPS data was analysed as described in section 2.4. When these experiments were conducted it was decided not to fit both types of devices to an individual bird due to size and weight limitations.

5.3.2 Statistical analysis

Two-way ANOVA tests were used to analyse the differences between the three wind conditions (head wind, tail wind and no wind) and post hoc testing was conducted using paired t-test. Differences were deemed significant at the 0.05 level and highly significant at the 0.01 level. Pearson's correlations were used to test for relationships between flight performance and morphological characteristics.

5.4 Results

5.4.1 Overall flights

All birds were released as a flock on all nine days and in a variety of difference wind conditions (Table 5.1), with ground speeds recorded for the mid-sections of the flights ranging from 13.3m s^{-1} up to 25.2m s^{-1}. However, estimated airspeeds, after correcting for prevailing wind speed and direction using data from the Britannia Bridge Anemometers, varied from 17.79ms^{-1} to 23.9m s^{-1} but showed no systematic variation (Fig. 5.1) with respect to the relative net wind speed experienced by the pigeons (range 7.6m s^{-1} headwind to 5.4m s^{-1} tailwind).

Table 5.1: Nine flights with details of average ground speeds, calculated vectoral airspeeds using the Britannia Bridge Anemometers and relative net wind speeds experienced by the pigeons.

Date	Ground speed (m s^{-1})	Pigeon airspeed (m s^{-1})	Relative wind speed experienced by the pigeons (m s^{-1})	
16/09/2009	16.30	23.90	7.60	Head Wind
15/09/2009	14.72	21.13	6.41	Head Wind
10/09/2009	13.27	18.13	4.86	Head Wind
18/09/2009	19.30	20.62	1.32	Slight Head Wind
11/09/2009	16.56	17.79	1.23	Slight Head Wind
10/07/2009	22.31	22.49	0.18	No Wind
06/07/2009	23.13	21.08	-2.05	Tail Wind
15/07/2009	25.22	21.32	-3.90	Tail Wind
25/09/2009	26.87	21.48	-5.39	Tail Wind

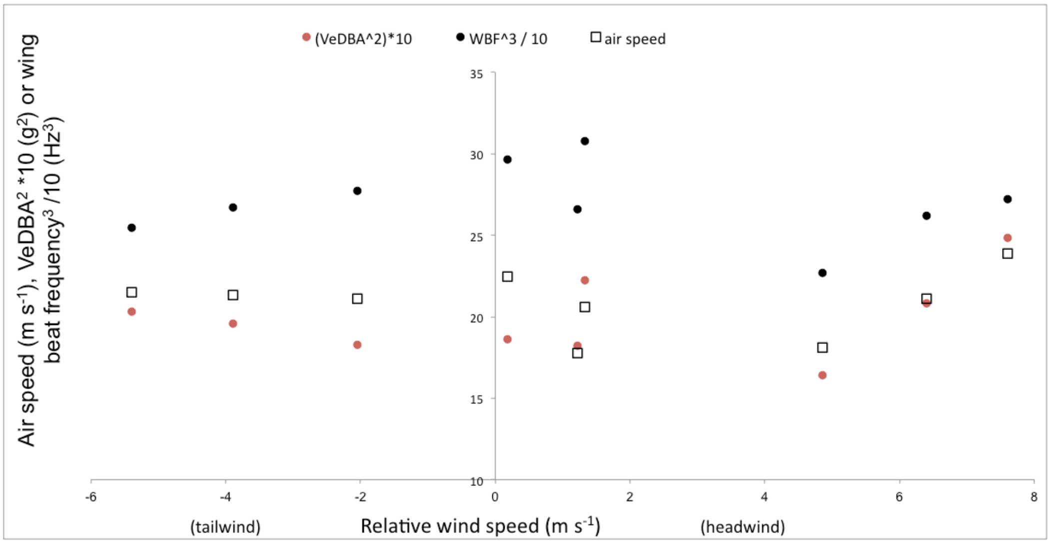


Fig. 5.1: Calculated values for VeDBA_{YZ}^2 x10 (g^2) and wing beat frequency cubed / 10 (Hz^3) along with the estimated vectorial air speed (m s^{-1}) during the mid-section of flights on nine experimental flights on different days, against relative net wind speed (m s^{-1}) for each day.

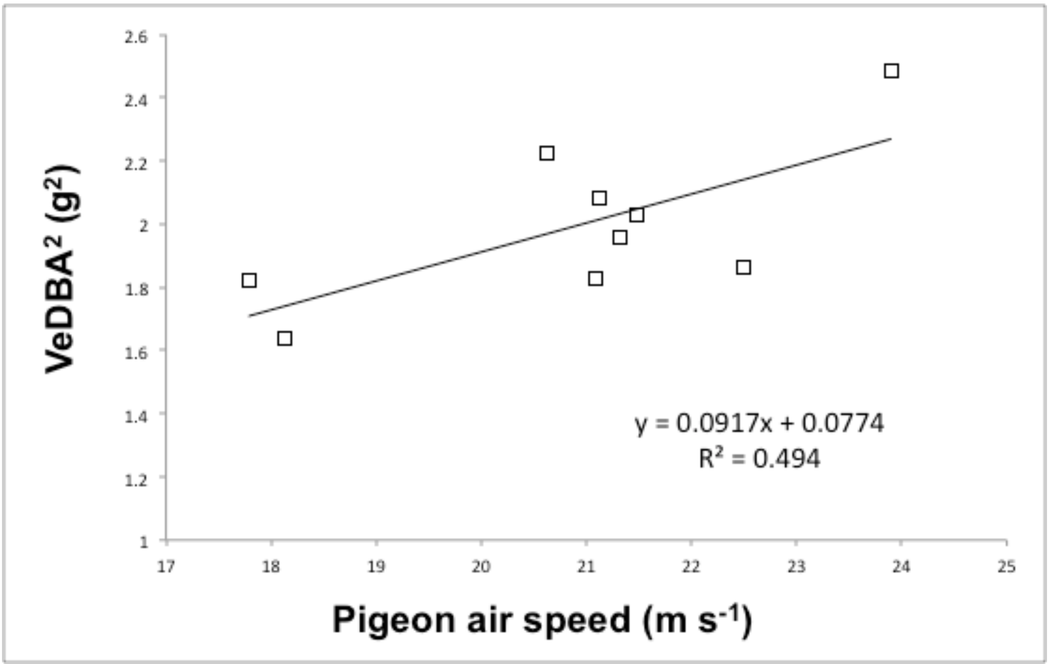


Fig. 5.2: VeDBA_{YZ}^2 (g^2) plotted against vectorial estimated pigeon air speeds (m s^{-1}) for 9 different days of flying in a variety of different wind speed and direction (see Table 5.1).

Values for mean wing beat frequency on different days varied from 6.1 Hz to 6.75Hz but were only poorly correlated with pigeon airspeeds ($\rho = 0.446$).

However, $VeDBA_{YZ}^2$ showed quite a strong correlation with pigeon airspeeds ($\rho = 0.703$, Fig. 5.2).

5.4.2. Three flights in detail

All birds analysed were released as a flock (Table 5.2), comprising of fourteen pigeons wearing GPS and eleven wearing accelerometers and which flew on all three days. On the 16th September 2009 the birds were flying into a strong headwind of $7.68ms^{-1}$; 18th September it was a $1.31ms^{-1}$ headwind; 25th September it was a $5.55ms^{-1}$ tailwind.

Table 5.2: Experimental design; * birds removed from further analysis over the three flights as they didn't perform to the required standard. † GPS that did not record altitude correctly.

Bird ID	Logger Type	16th September, 2009	18th September, 2009	25th September, 2009
16	Accelerometer			
44	Accelerometer			
E27110	Accelerometer			
E27130*	Accelerometer	Left Flock		
E27269	Accelerometer			
X71189	Accelerometer			
X71292	Accelerometer			
X71316	Accelerometer			
Z94919	Accelerometer			
Z94900	Accelerometer			
Z99889*	Accelerometer	Left Flock		
E27262*	GPS		No Data	
Z99487†	GPS	No Altitude Data		
E27244	GPS			
Z99890	GPS			
X71029	GPS			
Z99504	GPS			
X71191†	GPS	No Altitude Data		
E27419*†	GPS		No Data	No Altitude Data
X71035	GPS			

5.4.3 GPS results

As this experiment was conducted at the end of the research period, more reliable GPS loggers had been purchased and consequently out of 14 birds released wearing GPS, suitable data was recorded for five pigeons over the three experimental flights (Table 5.1). Some of the older loggers were used and the majority of these malfunctioned, especially when recording altitude (Z99487, X71191 and E27419), whilst not all of the pigeons returned immediately to the loft on all three days (E27262 and E27419). However, nine pigeons completed both the head wind and tail wind flights whilst seven successfully completed the no wind flight. Further analysis of the GPS data showed that these birds flew at similar altitudes (Figures 5.4, 5.6 and 5.8) and at similar speeds (Figures 5.5, 5.7 and 5.9) over the course of the entire flight, indicating that they most probably remained as a loose flock from liberation to home. Additionally Figure 5.3 shows how similar the flight times of the pigeons were in each of the three wind conditions, whereby in both no wind and a tail wind the flock lands at virtual the same time and in a head wind there is only about 30s between the first and last bird landing. Interestingly, Figure 5.9 shows that the birds flew at a negative air speed soon after take-off and at the end of flight. This is probably accounted for the wind speed briefly dropping and so when the average wind speed was taken into account to calculate air speed during these periods of time it reduced the apparent flight speed to below 0ms^{-1}.

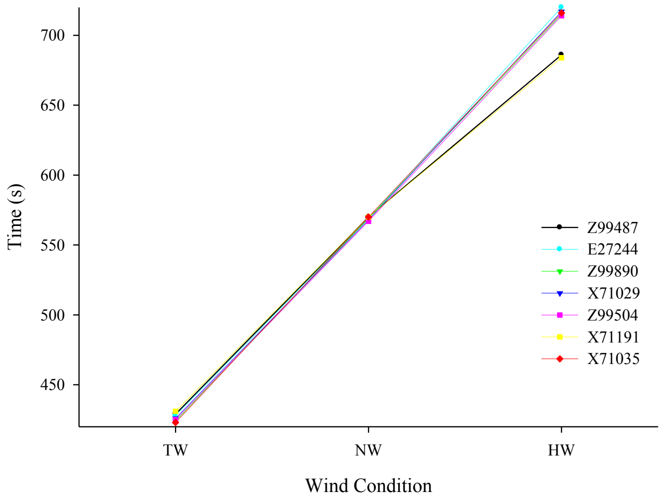


Fig. 5.3: Flight times (s) of seven individual birds wearing GPS released as a flock in three differing wind conditions; tail wind (TW), no wind (NW) and head wind (HW).

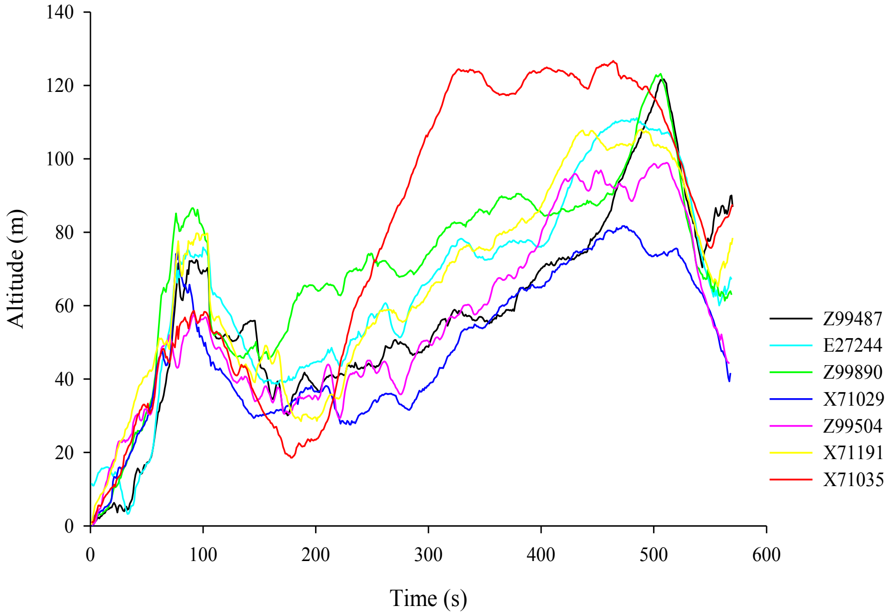


Fig. 5.4: The altitude (m) attained by seven individual pigeons fitted with GPS released in a flock over an entire flight in 'no wind' conditions (18th September, 2009).

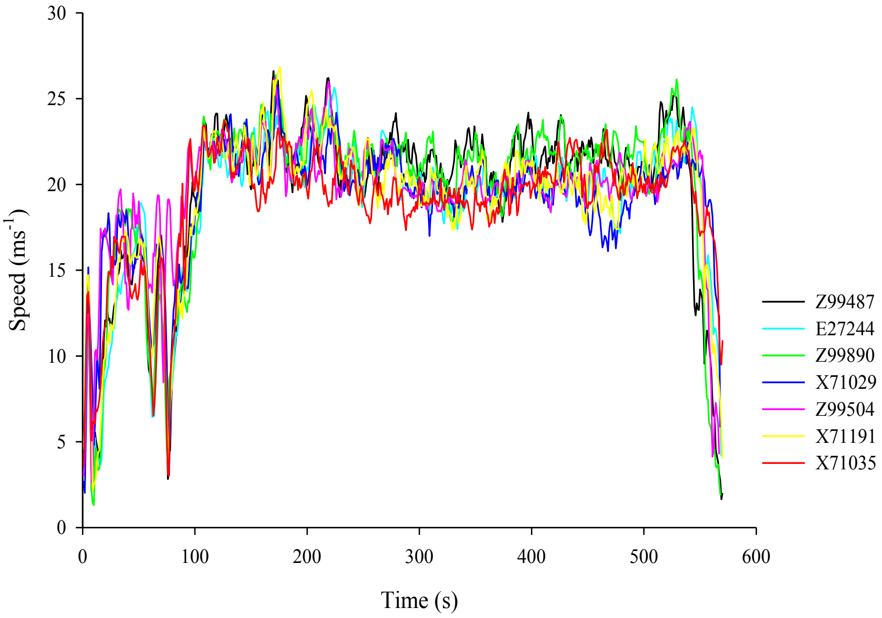


Fig. 5.5: The air speed (ms^{-1}) attained by seven individual pigeons fitted with GPS released in a flock over an entire flight in 'no wind' conditions (18th September, 2009).

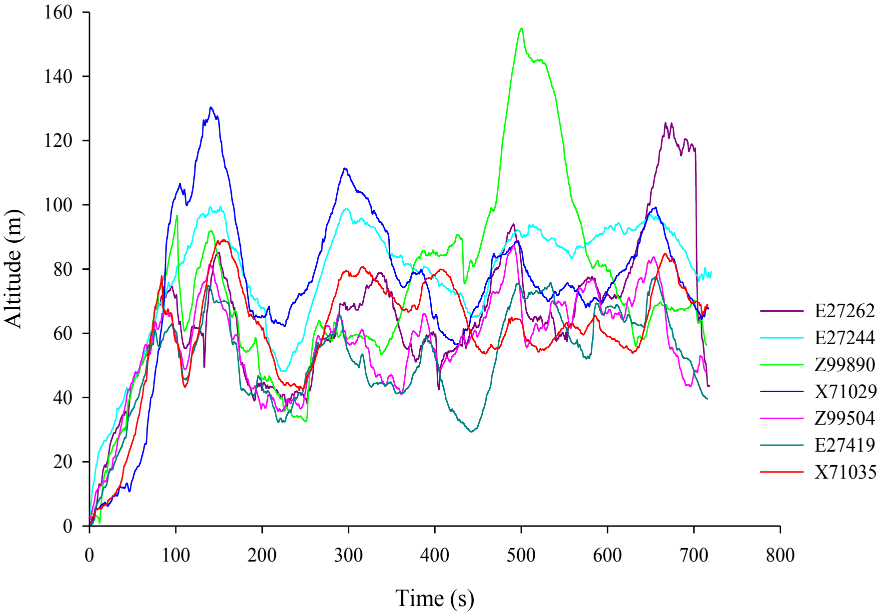


Fig. 5.6: The altitude (m) attained by seven individual pigeons fitted with GPS released in a flock over an entire flight in 'head wind' conditions (16th September, 2009).

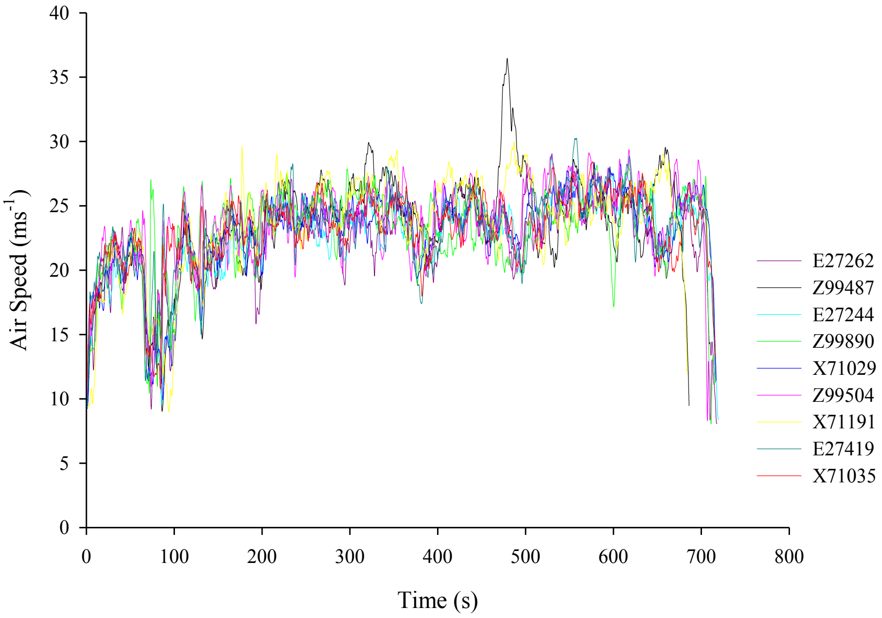


Fig. 5.7: The air speed (ms^{-1}) attained by nine individual pigeons fitted with GPS released in a flock over an entire flight in 'head wind' conditions (16th September, 2009).

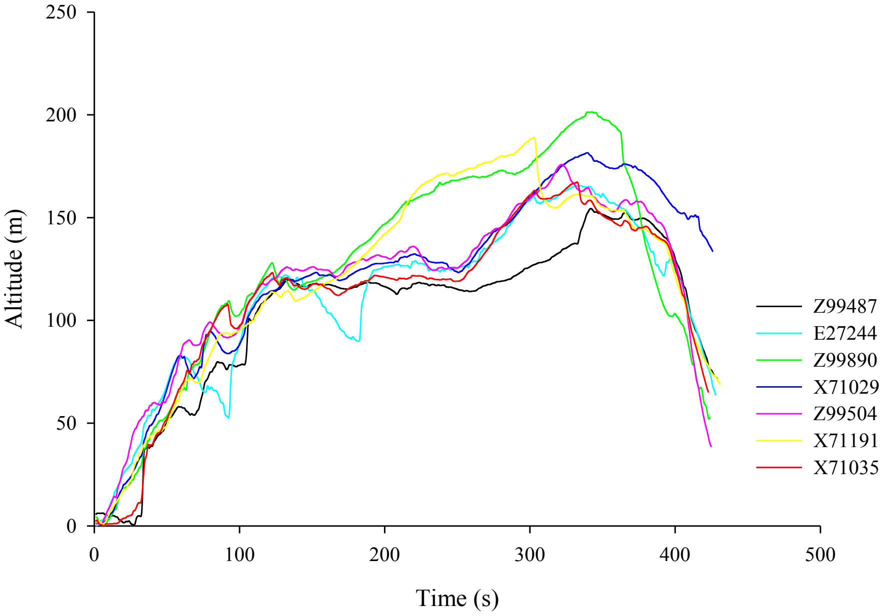


Fig. 5.8: The altitude (m) attained by seven individual pigeons fitted with GPS released in a flock over an entire flight in 'tail wind' conditions (25th September, 2009).

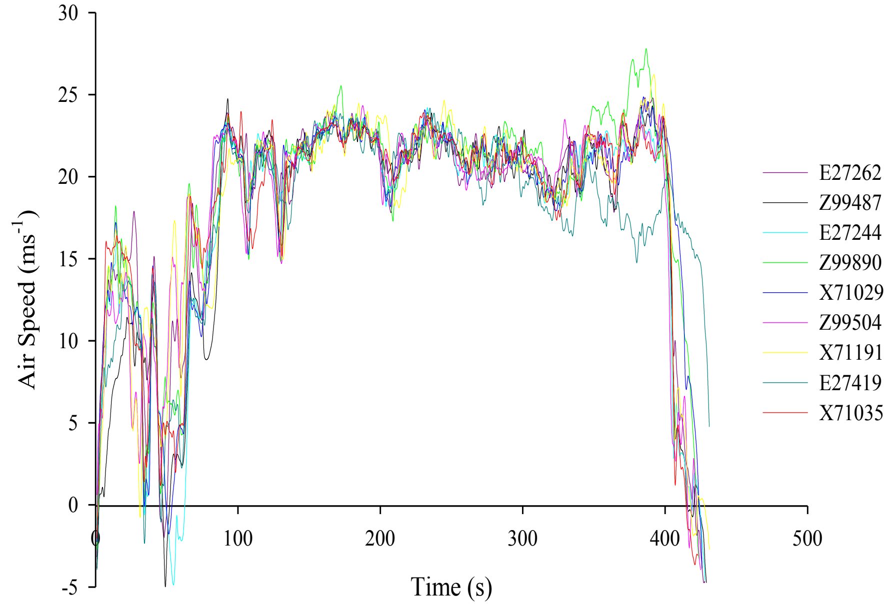


Fig. 5.9: The air speed (ms^{-1}) attained by nine individual pigeons fitted with GPS released in a flock over an entire flight in 'tail wind' conditions (25th September, 2009).

5.4.3.1 Route efficiency

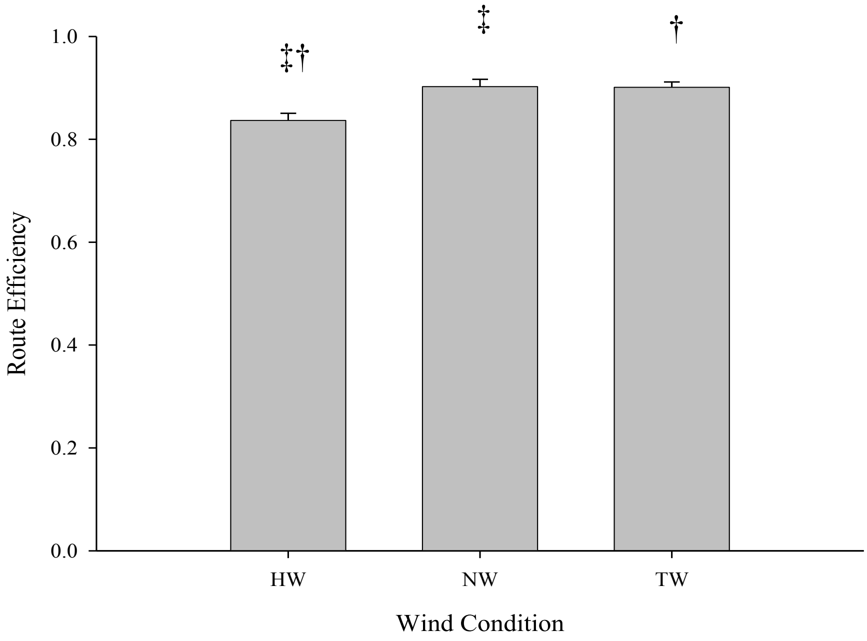
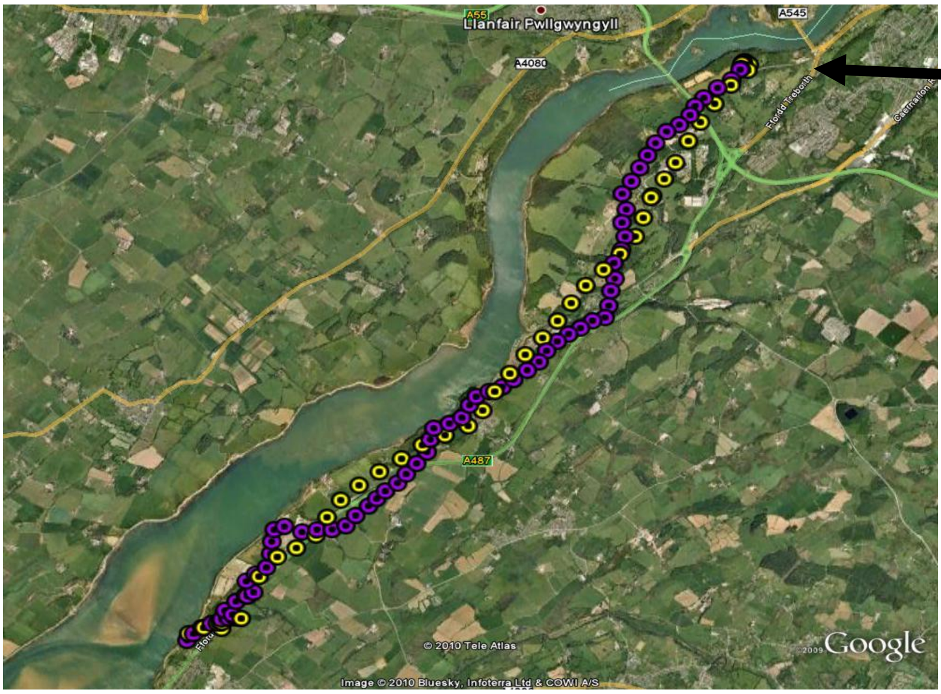


Fig. 5.10: Mean values of route efficiency in each wind condition, head wind (HW), tail wind (TW) and no wind (NW); n=7. Error bars represent the standard deviation of each column and statistical significant differences are labelled above each column ($p<0.001$) with ‡†.

There was a significant difference in the route efficiency of birds across the three wind directions (two-way ANOVA, F=67.95, p<0.001**, Fig. 5.10). Further analysis showed that birds covered more ground and were therefore less efficient in a head wind compared to both a tail wind (paired t-test, t=-10.36, p<0.001**, Figure 5.8) and no wind (paired t-test, t=-11.97, p<0.001**). There was no significant difference between the route efficiency in a tail wind and no wind (paired t-test, t=-0.16, p=0.877). It is clear that the route efficiency is poorer in a strong head wind than in a strong tail wind and this is illustrated in Figure 5.11 where the tracks of the same bird flying in these two differing wind conditions are visualised.



Loft (Treborth Botanic Gardens, SH 551711)

Release Site
(Waterloo Port, SH 486641)

Fig. 5.11: Route taken in a head wind (purple track; 11205m) and in a tail wind (yellow track; 10536m) by the same individual, as visualised using Google Earth Pro (the bee-line route measures approximately 9500m). For simplicity only one fix per ten seconds has been plotted for both tracks.

5.4.3.2 Analysis of overall speed

There was a significant difference in the speed at which the birds flew across the three wind conditions (two-way ANOVA, F=302.86, $p<0.001$**; Fig. 5.12). They flew slower in a tail wind than in either a head wind (paired t-test, t=19.27, $p<0.001$**) or no wind (paired t-test, t=-5.34, p=0.002**), whilst flying slower in no wind than in a head wind (two sample t-test, t=24.74, $p<0.001$**). However there was no significant difference in the air speed between individual pigeons across the three treatment groups (two-way ANOVA, F=1.37, p=0.300; Fig. 5.13). If one individual flew faster in one experimental condition it was more likely to also be one of the fastest individuals in all the wind conditions.

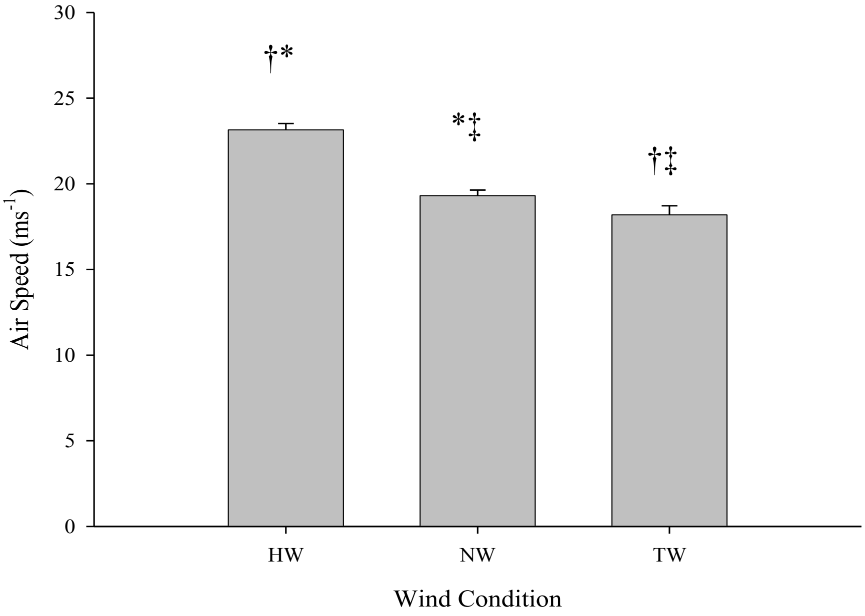


Fig. 5.12: Mean air speed (ms^{-1}) as flown by seven pigeons over the entire flight in a head wind (HW), no wind (NW) and head wind (HW) conditions. Error bars represent the standard deviation of each column, whilst statistically significant differences are labelled above each column ($p<0.001$) are labelled with *† and ($p<0.01$) are labelled ‡.

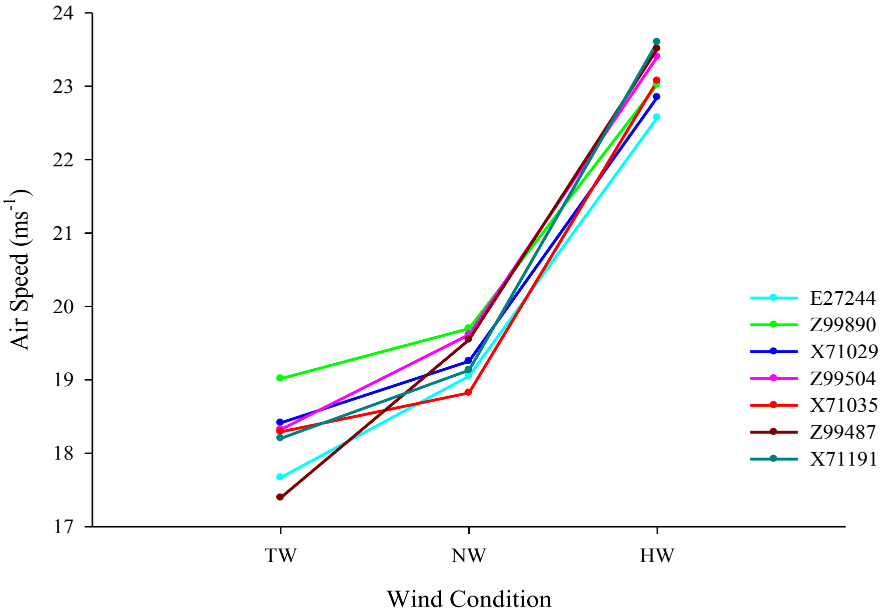


Fig. 5.13: Mean air speed (ms^{-1}) of seven individual pigeons flying in the three wind conditions, tail wind (TW), head wind (HW) and no wind (NW).

5.4.3.3 Analysis of overall altitude

There was a statistically significant difference in the average altitudes the pigeons attained between the three wind conditions (two-way ANOVA, F=45.28, p<0.001**; Fig. 5.14). The birds flew at higher altitudes in a tail wind compared to both a head wind (paired t-test, t=-10.58, p<0.001**) and in no wind conditions (paired t-test, t=-8.02, p<0.001**). However there was no significant difference between the altitudes attained between a head wind and no wind days (paired t-test, t=0.70, p=0.521). There was no statistically significant difference in the altitudes individual birds attained over the three experimental manipulations (two-way ANOVA, F=0.67, p=0.629; Fig.5.15) suggesting that individuals which flew at higher altitudes in one condition didn't necessarily do so in the other two experiments.

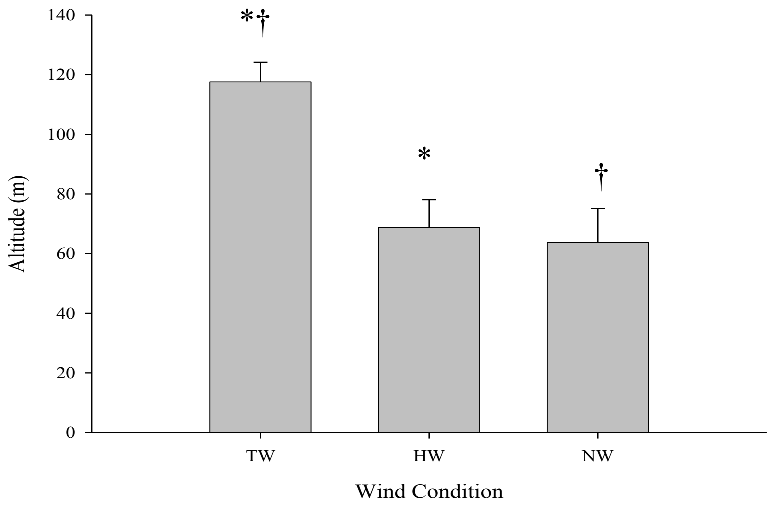


Fig. 5.14: Mean altitude (m) attained by five pigeons over the entire flight in a tail wind (TW), head wind (HW) and in no wind (NW) conditions. Error bars represent the standard deviation of each column, whilst statistically significant differences are labelled above each column (p<0.001) are labelled with *†; assume no statistical difference where no symbols are present.

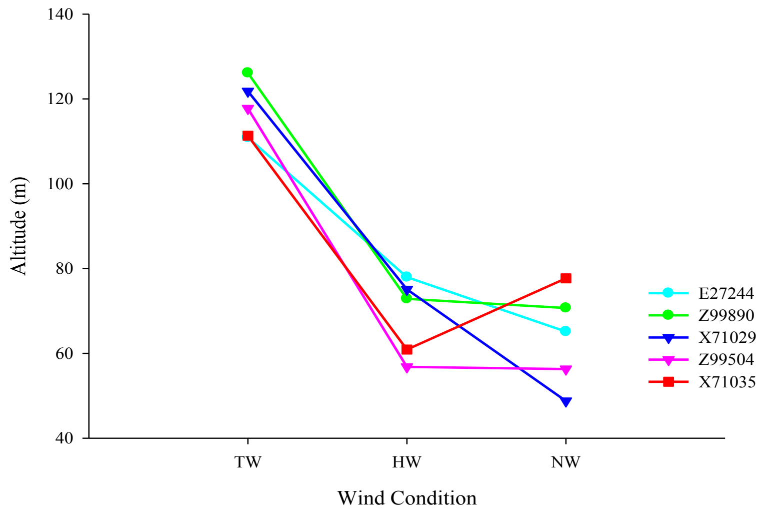


Fig. 5.15: Mean altitude (m) attained by five individual pigeons flying in the three wind conditions, tail wind (TW), head wind (HW) and no wind (NW).

5.4.4 Accelerometry results from steady flight

The time taken to compete the flights over the three days were noted for each individual pigeon that was wearing the accelerometers (Fig. 5.16) by counting the number of data collection periods, as each accounted for 2 seconds of flight (1.25 s data collection and 0.75 s of pause without data). The pigeons showed quite a consistent pattern of relative position for each flight, with some birds at the front most of the time and some returning quite slowly. However, there is a gradual increase in the time between the first bird finishing and the last bird, as the overall flight time increase from the tailwind flight, through the low wind flight to the headwind flight. Two individuals (Z99889 and E27130), in particular, do relatively poorly on the headwind day (Fig. 5.16), such that their data is not included in a mean data values that are created for further analysis, although they are included in individual interpretations of flight performance. As the flight times of the rest of the birds were similar it was assumed that all these individuals must have remained within the flock although longer flights tended to increase the times between the first and last birds home. This was particularly noticeably on the 16th September, when the strong headwind resulted in a much longer flight.

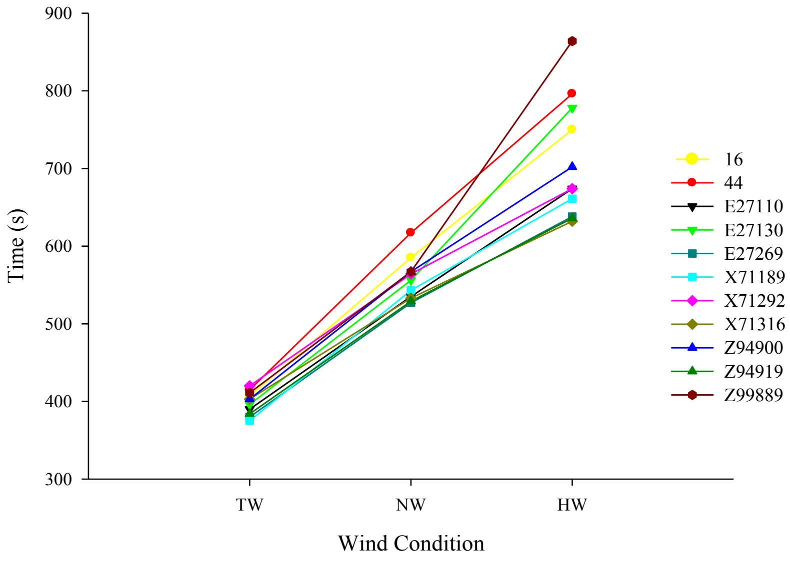


Fig. 5.16: Flight times (s) of 11 individual birds wearing accelerometers released as a flock in three differing wind conditions; tail wind (TW), no wind (NW) and head wind (HW).

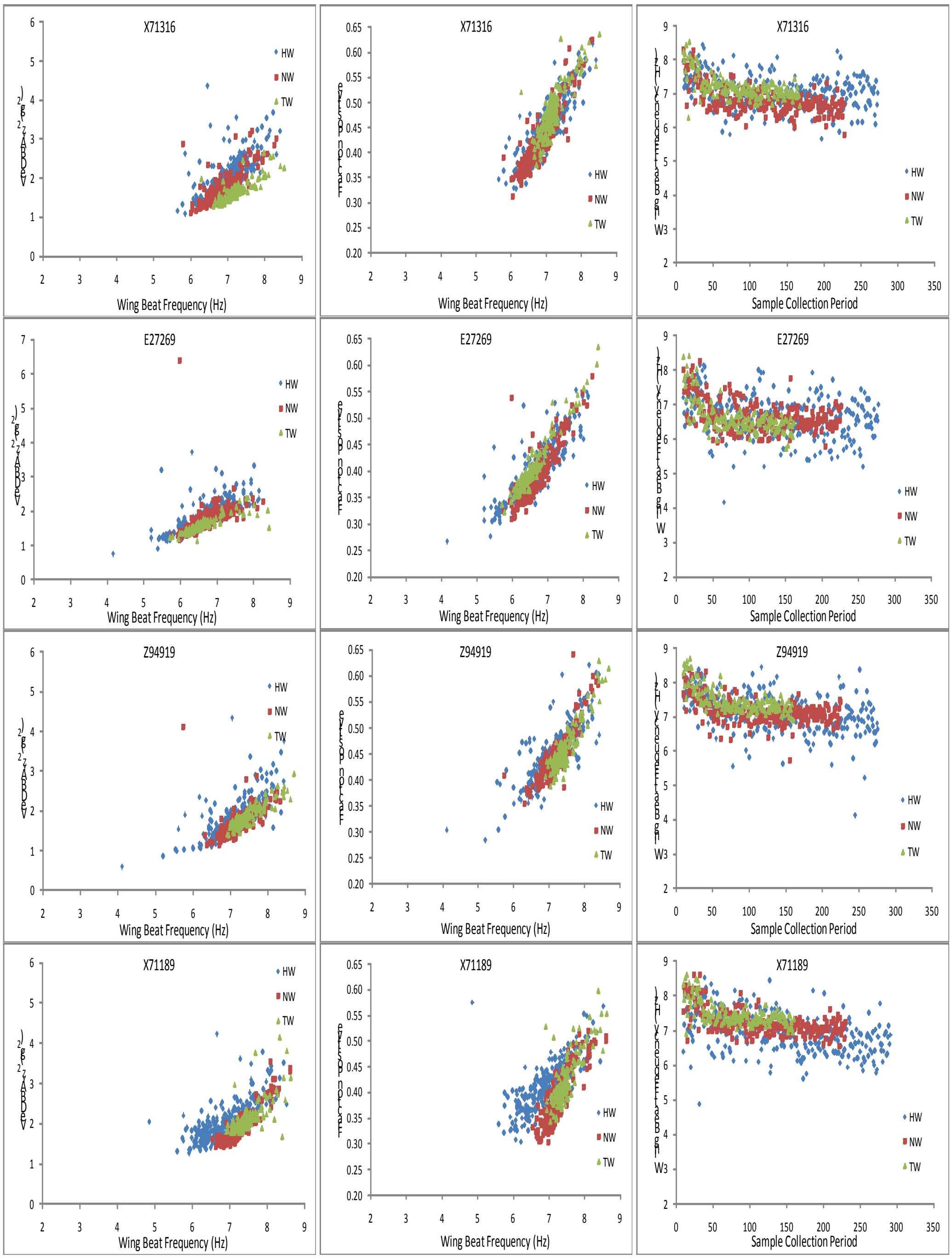


Fig. 5.17a: Shows results for the four fastest individual birds, over the 3 days of flying, in a strong tailwind (green), almost no wind (red) and in a strong headwind (blue). Data shown are for $VeDBA_{YZ}^2$ plotted against wing beat frequency (left column) and wing beat frequency against sample collection period (1.25 s data + 0.75 s pause each) (right column).

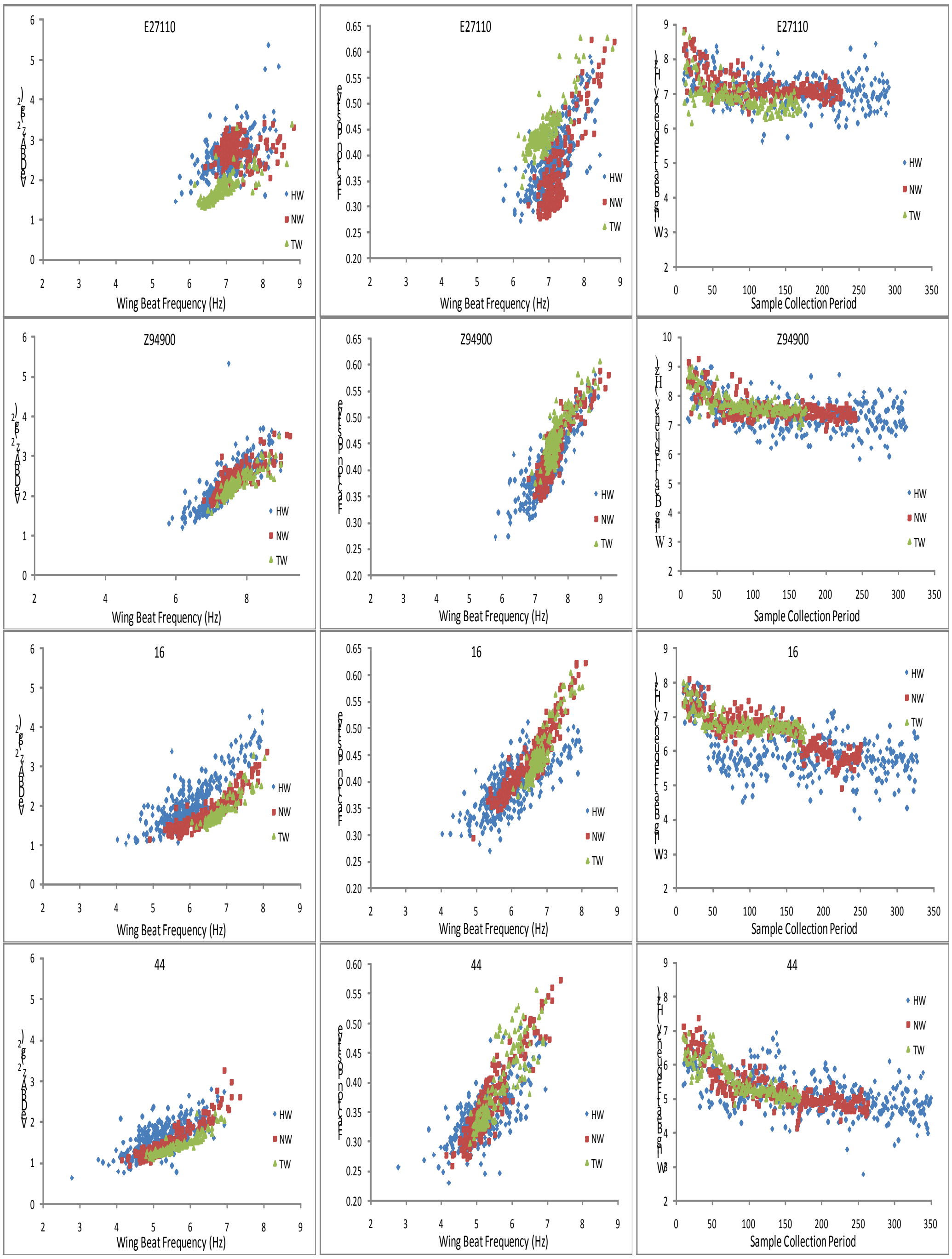


Fig. 5.17b: Shows results for four of the slowest individual birds, over the 3 days of flying, in a strong tailwind (green), almost no wind (red) and in a strong headwind (blue). Data shown are for $VeDBA_{YZ}^2$ plotted against wing beat frequency (left column) and wing beat frequency against sample collection period (1.25 s data + 0.75 s pause each) (right column).

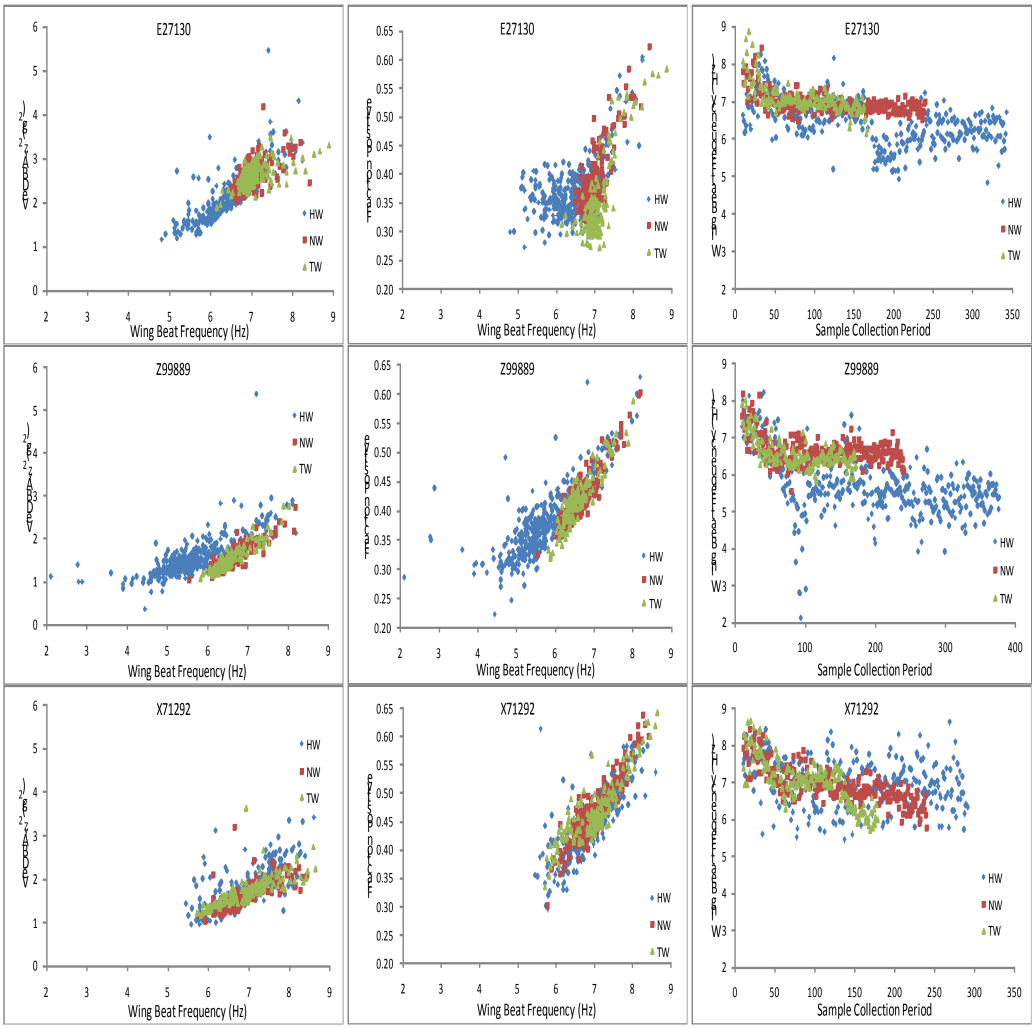


Fig. 5.17c: Shows results for three individual birds who were inconsistent in finishing position, over the 3 days of flying, in a strong tailwind (green), almost no wind (red) and in a strong headwind (blue). Data shown are for $VeDBA_{YZ}^2$ plotted against wing beat frequency (left column) and wing beat frequency against sample collection period (1.25 s data + 0.75 s pause each) (right column).

Figures 5.17a, 5.17b and 5.17c show the results for $VeDBA_{YZ}^2$ plotted against wing beat frequency (WBF), along with wing beat frequency against sample collection period (around 2 seconds of time for each data period). For all eleven birds, there is a strong positive relationship between wing beat frequency (WBF) and $VeDBA_{YZ}^2$.

The four fastest birds tended to be consistent between days in having quite a high WBF which was generally maintained throughout the flights (Fig. 5.17a). The two slowest pigeons across the 3 days (birds 16 and 44 – Fig. 5.16), either maintained relatively low WBF throughout the flights or for a substantial part of the flight, following increased effort during take-off and the first half of the trip (Fig. 5.17b). The two pigeons that flew proportionally more slowly on the head wind day (E27130 and Z99889 – Fig. 5.16) clearly show a large drop in WBF during that particular flight, compared to their low wind and tail wind flights (Fig. 5.17c). Finally, pigeon X71292 showed a reverse pattern to the previous two birds, in that it was in the middle of the flock on the head wind day, was third from the back on the low wind day and was equal last on the tail wind day (Fig. 5.16). Again, its WBF clearly drop by up to 1 Hz during the last third of the tailwind flight, indicating why it dropped to the rear (Fig. 5.17c). Even on the low wind day, there is a drop in WBF close to the end of the flight that may have resulted in its more lowly position.

The values of VeDBA_{YZ}^2 and fraction positive are generally well correlated with wing beat frequency for all birds on a given day and also generally reflect the change in patterns of wing beat frequency over time during the flight of a given pigeon. However, there does not appear to be any obvious absolute lowering of the values for VeDBA_{YZ}^2 or fraction positive between days but rather a tendency for VeDBA_{YZ}^2 to lower in a tailwind for a given value of wing beat frequency

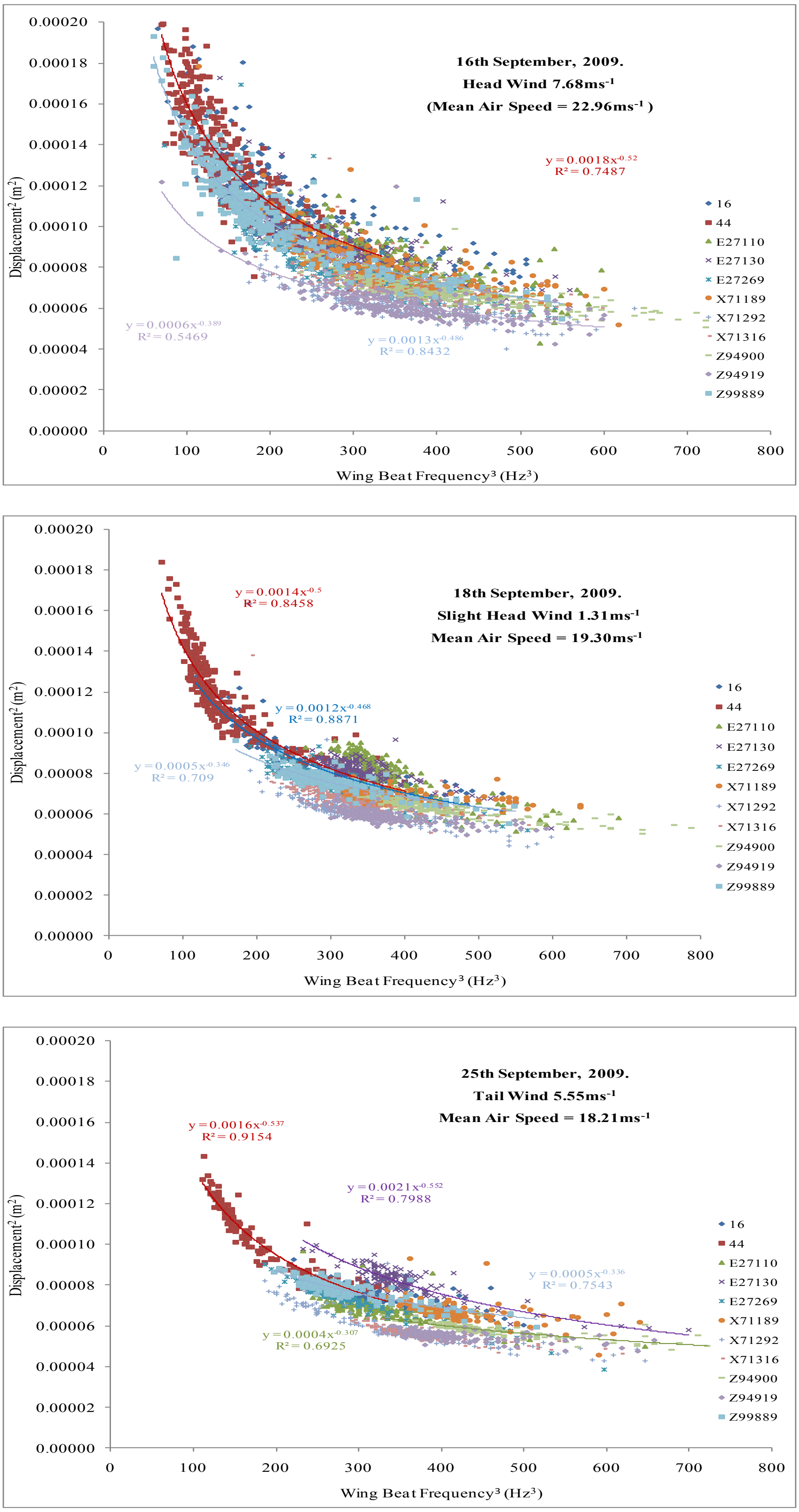


Fig. 5.18: Shows results for all 11 individual pigeons, over the 3 days of flying, in a strong tailwind (A), almost no wind (B) and in a strong headwind (C). Data shown are for displacement squared (B^2; m^2) plotted against wing beat frequency cubed (WBF^3; Hz^3).

Displacement squared (B^2) patterns are similar between the three days for each individual bird (Fig. 5.18), with those birds with the lowest calculated overall flight costs having a lower value of displacement for a given value of WBF (see below). The standard deviation or spread in the displacement figures is also much great on the head wind day then for either the low wind or tail wind day. On the head wind day, where the flight time was much greater, there was a more noticeable split in performance between 4 very slow birds, 6 quite fast birds and Z94900 who was closer to the 6 fast birds than he was to the 4 slow birds (Fig. 5.16). Figure 5.19 shows a plot of wing beat frequency plotted against the sum of WBF^3 and B^2, for the 7 fastest and 4 slowest pigeons.

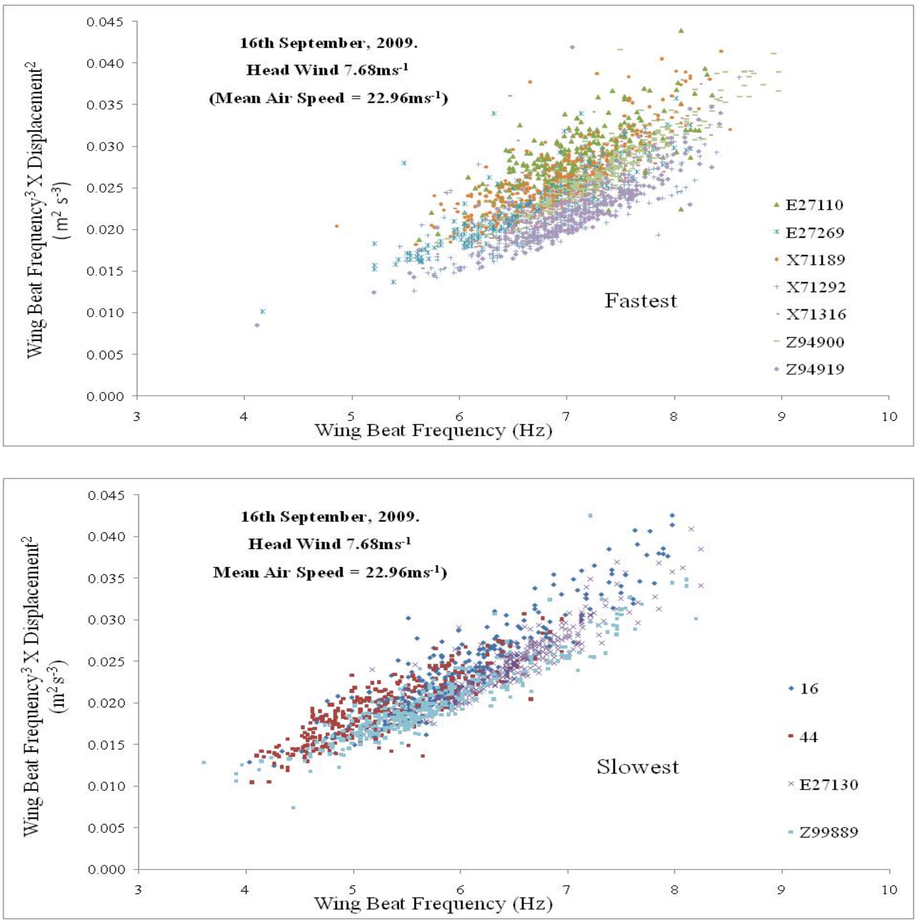


Fig. 5.19: Shows results for the 7 fastest individual pigeons (A) and the 4 slowest (B) on the 16th September flying into a strong headwind. Data shown are for wing beat frequency cubed (WBF^3; Hz^3) times displacement squared (B^2; m^2) plotted against WBF.

There were no significant differences between the values of either fraction negative (two-way ANOVA, F=3.04, p=0.076) or wing beat frequency (two-way ANOVA, F=2.67, p=0.100) in the three wind conditions. $VeDBA_{YZ}$ was greater in a head wind than both a tail wind (paired t-test, t=2.96, p=0.018*) and no wind conditions (paired t-test, t=2.36, p=0.046*). Although there was no difference between $VeDBA_{YZ}$ in no wind and a tail wind (paired t-test, t=0.99, p=0.353) or a head wind.

There was a significant between individual difference in the values of $VeDBA_{YZ}$ (two-way ANOVA, F=6.08, p=0.001**; Fig. 5.20), fraction negative (two-way ANOVA, F=6.79, p=0.001**; Fig. 5.21) and wing beat frequency (two-way ANOVA, F=37.53, p<0.001**; Fig. 5.22) across the three wind conditions.

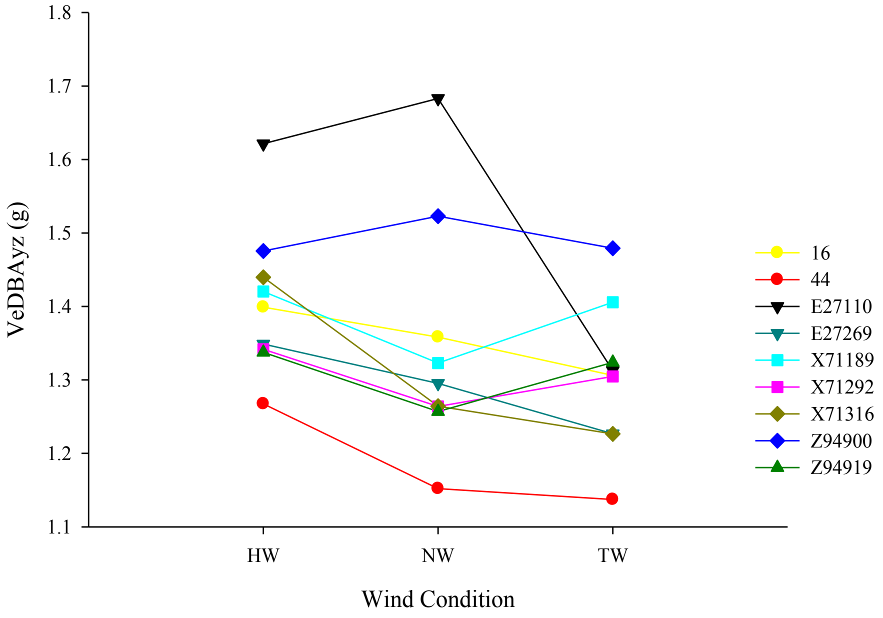


Fig. 5.20: Mean values for $VeDBA_{YZ}$ (g) for nine individual pigeons flying in the three wind conditions, head wind (HW), no wind (NW) and in a tail wind (TW).

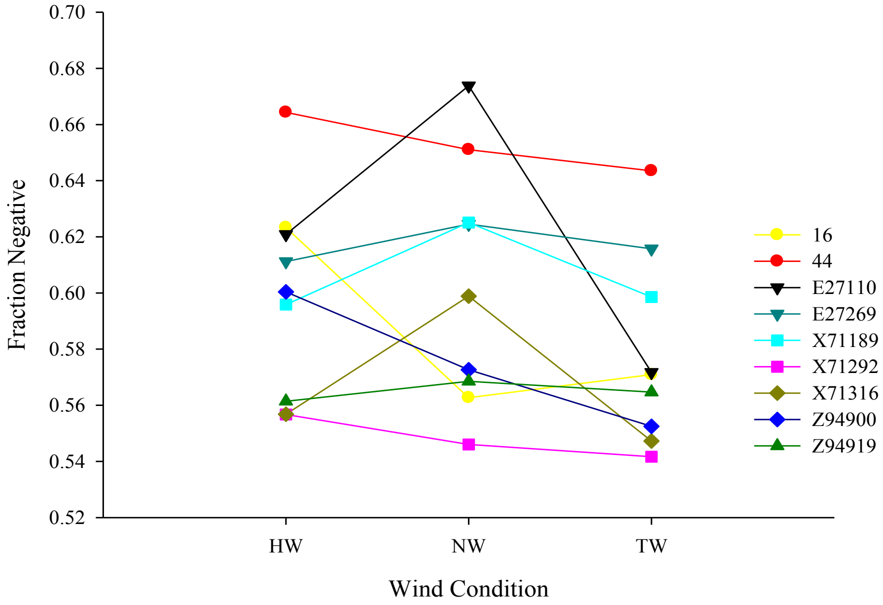


Fig. 5.21: Mean values for fraction negative for nine individual pigeons flying in the three wind conditions, head wind (HW), no wind (NW) and in a tail wind (TW).

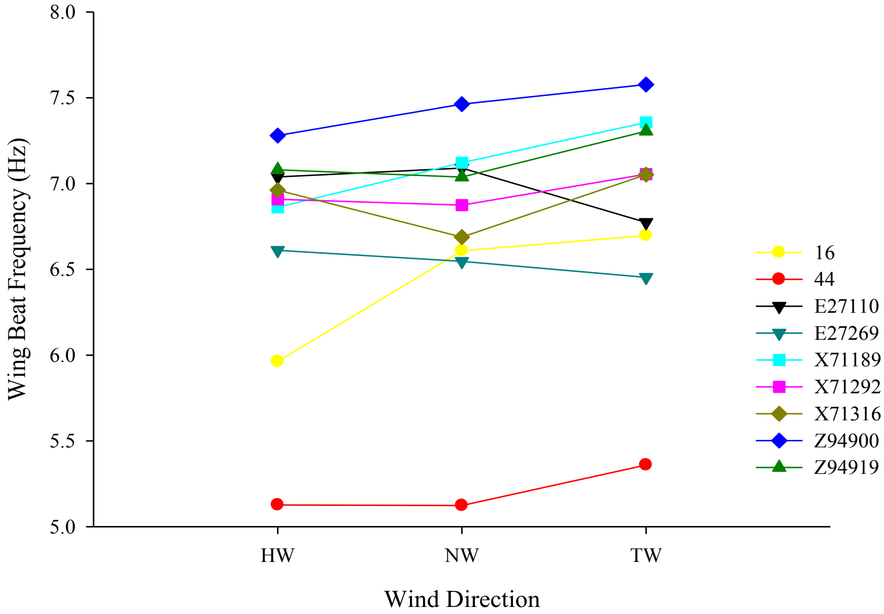


Fig. 5.22: Mean values for wing beat frequency (Hz) for nine individual pigeons flying in the three wind conditions, head wind (HW), no wind (NW) and in a tail wind (TW).

5.4.5 Correlations between flight performance parameters

Correlations were performed to investigate the relationship between the three wind conditions and VeDBA_{YZ}, fraction negative and wing beat frequency from the accelerometry and speed and altitude from the GPS. There were few significant correlations between the wind conditions with either VeDBA_{YZ} or fraction negative (Table 5.3). VeDBA_{YZ} was highly correlated (Pearson's Correlation, $\rho=0.932$, $p<0.001$**) between a head wind and no wind and there was a strong trend between tail wind and head wind (Pearson's Correlation, $\rho=0.472$, $p=0.200$) and no wind (Pearson's Correlation, $\rho=0.557$, 0.119) indicating that individuals maintain a similar VeDBA_{YZ} irrespective of wind condition.

Wing beat frequency was highly significantly positively correlated between head wind and no wind (Pearson's Correlation, $\rho=0.926$, $p<0.001$**; Fig. 5.23), head wind and tail wind (Pearson's Correlation, $\rho=0.898$, $p<0.001$**; Fig. 5.24) and tail wind and no wind (Pearson's Correlation, $\rho=0.951$, $p<0.001$**; Fig. 5.25). This again suggests that individuals maintain a steady flight pattern regardless of wind conditions.

Table 5.3: Correlations between VeDBA$_{YZ}$ (g) and fraction negative (Frac. Neg.) in a head wind (HW), tail wind (TW) and no wind (NW) conditions. The test statistic rho (ρ) is given above the value of probability (p); ** represents statistically significant values (p<0.01), * represents statistically significant values (p<0.05).

	VeDBA$_{YZ}$ HW	VeDBA$_{YZ}$ NW	Frac. Neg. HW	Frac. Neg. NW
VeDBA$_{YZ}$ NW	0.932 <0.001**			
VeDBA$_{YZ}$ TW	0.472 0.200	0.557 0.119		
Frac. Neg. NW			0.612 0.080	
Frac. Neg. TW			0.776 0.014*	0.645 0.061

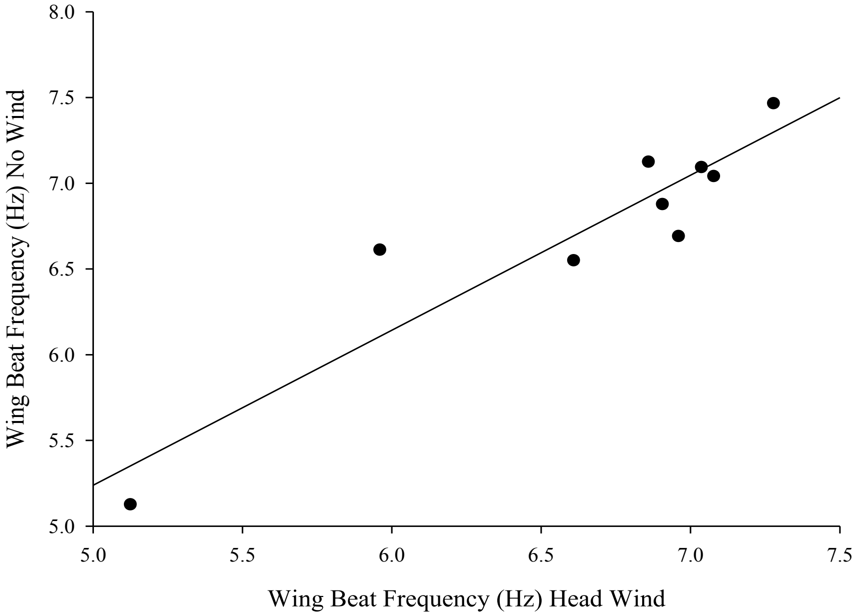


Fig. 5.23: Correlation between the wing beat frequency (Hz) of nine individual pigeons flying in a head wind and in no wind conditions (ρ=0.926, p<0.001**). Regression equation: wing beat frequency no wind = 0.904wing beat frequency head wind + 0.716.

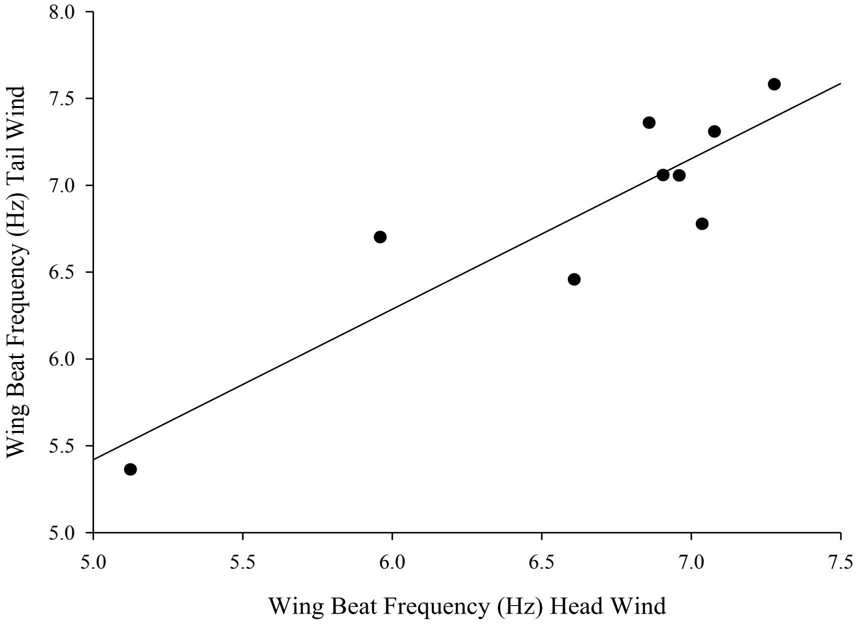


Fig. 5.24: Correlation between the wing beat frequency (Hz) of nine individual pigeons flying in a head wind and a tail wind (ρ=0.898, p<0.001**). Regression equation: wing beat frequency tail wind = 0.867wing beat frequency head wind + 1.086.

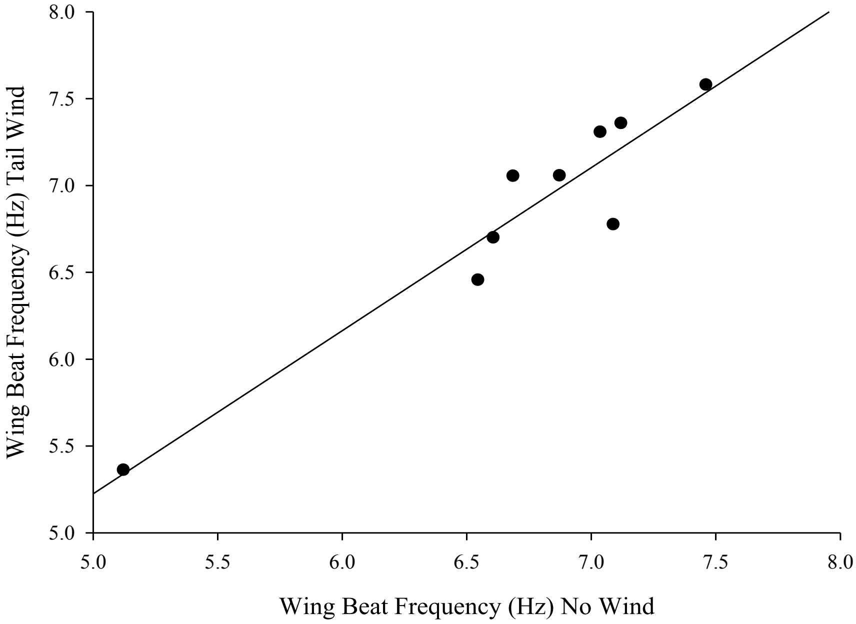


Fig. 5.25: Correlation between the wing beat frequency (Hz) of nine individual pigeons flying in a head wind and a tail wind (ρ=0.951, p<0.001**). Regression equation: wing beat frequency tail wind = 0.939wing beat frequency no wind + 0.528.

There were no significant correlations between altitude in a tail wind (Pearson's Correlation, ρ=0.054, p=0.899) or in no wind conditions (Pearson's Correlation, ρ=-0.405, p=0.367). However, whilst not statistically significant, there was a strong negative association between altitude and speed in a head wind (Pearson's Correlation, ρ=-0.707, p=0.076).

As fraction negative and wing beat frequency are both related to the movement of the wings it was expected that these two variables would show a significant correlation in each wind condition. Indeed these variables were negatively correlated to varying degrees (Fig. 5.26). However fraction negative and $VeDBA_{YZ}$ showed no significant correlations in a head wind (Pearson's Correlation, ρ=-0.043, p=0.912), tail wind (Pearson's Correlation, ρ=-0.516, p=0.155) or in no wind conditions (Pearson's Correlation, ρ=0.270, p=0.482). Although there was no statistically significant correlations between $VeDBA_{YZ}$ and wing beat frequency in a head wind (Pearson's Correlation, ρ=0.559, p=0.118) or in no wind conditions (Pearson's Correlation, ρ=0.611, p=0.080) they were quite strongly positively associated. Whilst in a tail wind $VeDBA_{YZ}$ and wing beat frequency showed a strong positive correlation (Pearson's Correlation, ρ=0.847, p=0.004**; Fig. 5.27).

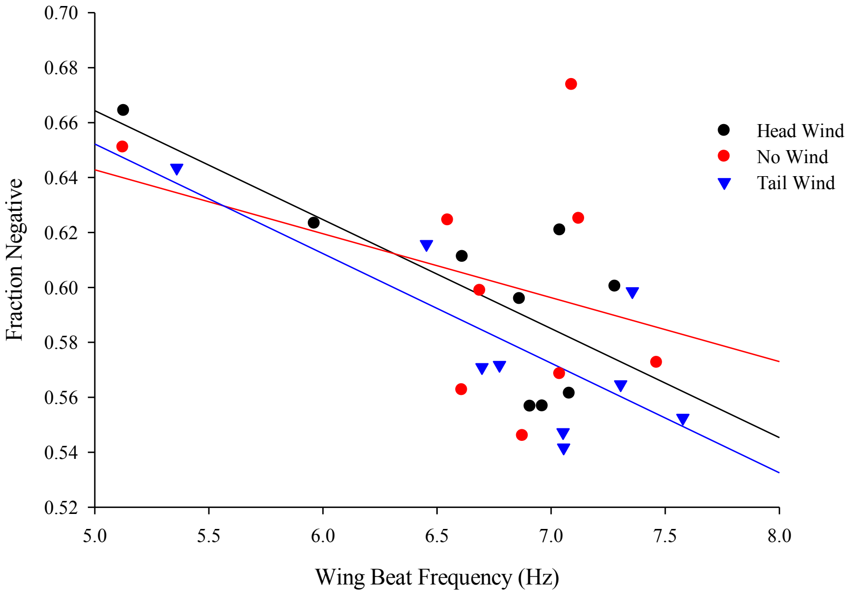


Fig. 5.26: Correlation between wing beat frequency (Hz) and fraction negative (FN) in a head wind ($\rho=-0.749$, $p=0.020$*), no wind ($\rho=-0.356$, $p=0.347$) and a tail wind ($\rho=-0.771$, $p=0.015$*). Regression equations: Head wind: FN = 0.863 - 0.0397WBF, No wind: FN = 0.759 - 0.0233WBF, Tail wind: FN = 0.851 - 0.0399WBF

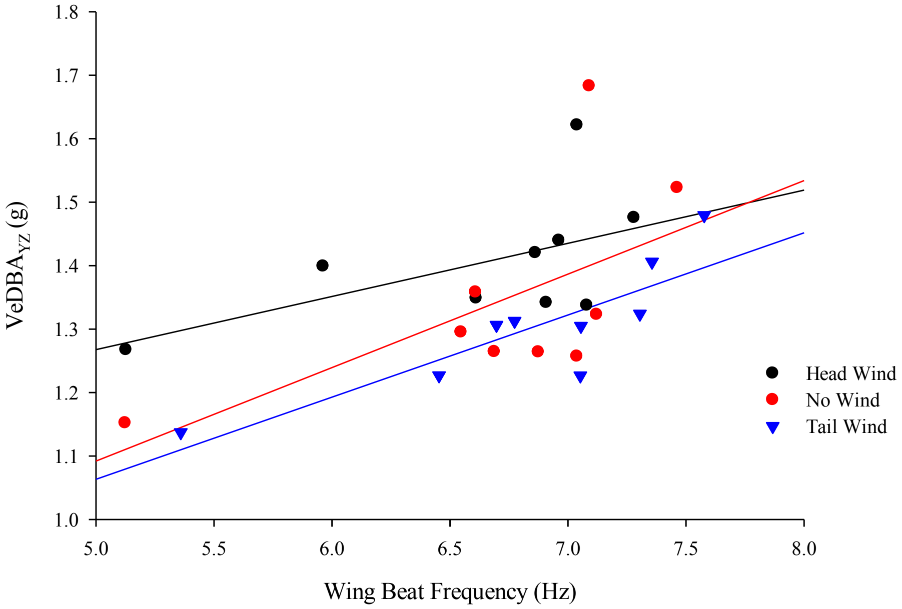


Fig. 5.27: Correlation between wing beat frequency (Hz) and $VeDBA_{YZ}$ in a head wind ($\rho=0.559$, $p=0.118$), no wind ($\rho=0.611$, $p=0.080$) and a tail wind ($\rho=0.847$, $p=0.004$**). Regression equations: Head wind: $VeDBA_{YZ} = 0.849 + 0.084WBF$, No wind: $VeDBA_{YZ} = 0.355 + 0.147WBF$, Tail wind: $VeDBA_{YZ} = 0.416 + 0.129WBF$

From the accelerometry it is clear that to some extent the performance of an individual is repeatable in different wind conditions. A similar approach was applied to the data obtained from the GPS (i.e. altitude and air speed) to determine if, for example, the faster birds in one condition were faster in the others and those that flew at the higher altitudes maintain this flight style. This was proven to not be the case with no significant correlations found between air speed or altitude over the three wind conditions (Table 5.4).

Table 5.4: Correlations between air speed (ms^{-1}) and altitude (m) in a head wind (HW), tail wind (TW) and no wind (NW) conditions. The test statistic rho (ρ) is given above the value of probability (p); no values are statistically significant.

		Air Speed HW	Air Speed NW	Altitude HW	Altitude NW
No Wind	Air Speed	0.324 0.478			
	Altitude			-0.174 0.779	
Tail Wind	Air Speed	-0.111 0.813	0.233 0.615		
	Altitude			0.164 0.756	-0.034 0.943

5.4.6 Correlations between morphology and flight performance parameters

There were no statistically significant correlations between body mass and air speed or altitude in any of the wind conditions (Table 5.5). It is possible that if more birds were available for analysis some of these correlations would be strengthened and would have become statistically significant especially in a head wind where there were strong trends with body mass and both air speed and altitude. Even though it is fairly certain that the birds remained as a flock between liberation and home, altitude was negatively associated with body mass suggesting that the heavier birds remained at lower altitudes in all three wind conditions.

Table 5.5: Correlations between body mass (g) and air speed (ms^{-1}) and altitude (m) in a head wind (HW; n=7), tail wind (TW; n=8) and no wind (NW; n=7) conditions. The test statistic rho (ρ) is given above the value of probability (p); no values are statistically significant.

		Body Mass HW	Body Mass NW	Body Mass TW
Head Wind	Air Speed	0.665 0.103		
	Altitude	-0.661 0.106		
No Wind	Air Speed		0.109 0.816	
	Altitude		-0.325 0.476	
Tail Wind	Air Speed			-0.394 0.334
	Altitude			-0.257 0.539

Neither VeDBA$_{YZ}$ nor wing beat frequency showed any statistically significant, nor strong trends when correlated with body mass (Table 5.6). However when fraction negative was correlated with body mass although it was only in no wind conditions when the association was statistically significant, there were strong trends between these factors in both a head and tail wind (Fig. 5.28). Indeed all these correlations were negative which shows that the heavier birds had lower values for fraction negative which suggests that these individuals spend a larger proportion of each flap cycle with higher than average values of body acceleration. Whilst this association is not statistically significant in every wind condition there is a definite trend on all three days of flight.

Table 5.6: Correlations between body mass (g) and VeDBA$_{YZ}$ (g) and wing beat frequency (WBF) (Hz) in a head wind (HW), tail wind (TW) and no wind (NW) conditions. The test statistic rho (ρ) is given above the value of probability (p); no values are statistically significant.

	Body Mass HW	Body Mass NW	Body Mass TW
VeDBA$_{YZ}$ HW	-0.075		
	0.848		
WBF HW	0.383		
	0.309		
VeDBA$_{YZ}$ NW		0.093	
		0.812	
WBF NW		0.437	
		0.240	
VeDBA$_{YZ}$ TW			0.018
			0.964
WBF TW			0.227
			0.556

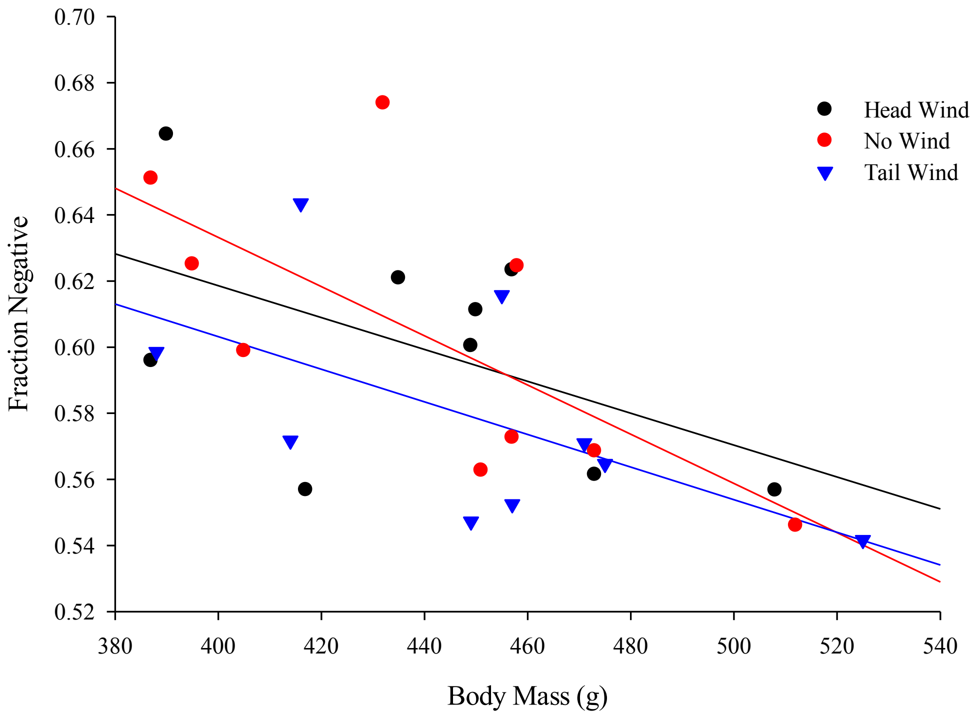


Fig. 5.28: Correlation between body mass (g) and fraction negative (FN) in a head wind (ρ=-0.517, p=0.154), no wind (ρ=-0.690, p=0.040*) and a tail wind (ρ=-0.584, p=0.099). Regression equations: Head wind: FN = 0.812 - 0.000482 body mass, No wind: FN = 0.931 - 0.000745 body mass, Tail wind: FN = 0.801 - 0.000493 body mass

5.5 Discussion

5.5.1 General effects of wind direction and speed

Figure 5.1 showed that the initial hypothesis that birds might have a higher air speed in a headwind as against a low wind or tailwind was not supported. A primary confounding issue here could be that these flights were perhaps not long enough to reveal significant motivational differences, or that they did not involve wild birds where selection may have acted more strongly for birds to be economical in flight. However, there could be many more caveats that are specific to the breeding of homing pigeons, so it cannot really be addressed from the present results.

Looked at overall, the estimated vectoral airspeeds based on the BBA data indicate that airspeed was very uniform in 5 of the 6 flights in low wind and tailwind conditions and typically varied between 21 m s^{-1} and 23 m s^{-1}. The flights in the three headwind conditions were more varied but as they got stronger there was a tendency for the airspeeds to increase. While these flights are too few to distinguish between motivational coincidence or a real effect of increasing headwinds, the mean airspeed in the headwinds is still around 21m s^{-1} and similar to the mean of all nine flights (20.9 m s^{-1}).

Superficially, there is a pattern of variation in wing beat frequency that appears to reflect changes in airspeed but the pattern is not well correlated across all flights and appears to break down particularly when comparing headwinds against tailwind and no wind days. $VeDBA_{YZ}^2$ is much more strongly correlated with airspeed and indicates that it is giving quite a reliable indication of relative overall power during flight, despite only being able to detect the very small amount of total power that is transmitted to the body of the bird. Perhaps, the major factor that has not been considered in this analysis is the effect of altitude on the results. One potential factor could be that the anemometer is at 50m above sea level and is situated near the landing site. The data was not identical from the two anemometers and may be being affected by local conditions associated with each tower. However, as there was no way to differentiate between them, the results from the two meters were simply averaged. On the other hand, wind conditions and direction my not have been identical to the BBA either at the take-off site of the flights and also with varying altitude. At the start, the pigeons were only a few meters above sea level but during many of the flights, some birds climbed over 150m and could have been exposed to high tail or headwinds, respectively. Pigeons that flew higher would also have incurred greater climb power costs but by focussing the analysis on the mid-section of the flights it was hoped to eliminate some of this extra unknown variance in the data. While both wing beat frequency and VeDBA appear to be sensitive to some aspect of climb power, particularly during the first few minutes of flight, it is unclear what proportion of this is in the wing motion rather than in the body of the bird. Nevertheless, $VeDBA^2$ appears to be a good proxy for relative power output during flight (see also chapter IV).

5.5.2 Individual and specific effects of wind direction and speed

It was always assumed that if the pigeons were released as a flock they would remain together throughout the flight and land as a fairly close unit. It is clear from the present work that this assumption, at least as far as the Bangor Loft pigeons are concerned is not as robust as was anticipated. But the question needs to be asked as to what exactly constitutes a flock? On some occasions birds may fly closely together, even using similar airspace and gaining aerodynamic advantage/disadvantage from other members of the flock. At other times birds may be flying within sight of each other but further apart or at different altitudes. When looked at in detail, it is clear that even over the relatively short flights involved in the present experiments (see also chapter IV), there is sufficient individual variation in flight ability and/or motivation to home to complicate experimental design and analysis. Taking simple averages across all pigeons can hide their individual responses and reduce the statistical power of experimental manipulations. Comparing the relative flight positions of birds on the three main experimental days where individual responses were analysed in detail (Fig. 5.16) indicates that, as the length of the flights increases, the flock gradually becomes more dispersed from front to back. This could be a possible direct effect due to the relative wind conditions but almost certainly also includes an indirect effect of the reduced ground speed extending the total flight times. Thus, birds that are generally slower are left further and further behind. It would appear that in the strongest headwind flight there may also have been a greater effort required both due to the apparent higher airspeed and the great degree of change in altitude and direction, which may have affected the "weaker" or less motivated birds to a greater degree but the trend is visible even between the tailwind and no wind day. This is despite the fact that during the tailwind all birds appear to have climbed much higher during the first part of the flight but they still remained tightly bunched. At least on the no wind and headwind days, some of the birds did not maintain their position within the flock and dropped back. If the pigeons had been released further away from the loft in similar conditions it is highly likely that the flock would have completely fallen apart and many of the birds would have returned either individually or in much smaller groups. Thus, it is difficult from these results to accurately compare the wind speeds that each individual pigeon faced during their homeward flight. In general, it would be expected that during a tail wind, birds would gain an advantage to fly at higher altitudes with their increased wind speeds and, conversely, in a head wind it would be more efficient to fly at lower altitudes. This was reflected in the results, as was the fact that the birds flew a more tortuous path home in the head wind flight. The birds appear to skirt close to natural and man-made obstacles such as woodland and large buildings, possibly to use these barriers to gain some sort of aerodynamic benefit or lower air speeds and reduce the energy required to fly into the head wind.

When taking the GPS measurements into account, the birds flew furthest in a head wind and at the fastest air speed, which is reflected by their low flight efficiency in this condition. However, there is no reflection of this in regard to an increased wing beat frequency or fraction negative. The efficiency of the route was calculated by dividing the beeline route (the most direct route back to the loft) by the actual distance covered by the bird. This showed that there was a significant difference in the efficiency of the birds between the conditions, being significantly less efficient in a head wind (0.85), whereas the efficiency in a tail wind and no wind were identical (0.90), illustrated in figure 5.10.

Mean VeDBA_{YZ} values were significantly greater in the headwind and probably reflect the extra effort required by the birds that day to support the increased airspeed to the loft. Other possible contributing factors could be the extra tortuosity of the route home in combination with more changes in altitude, or perhaps the air was in a more turbulent state with the birds flying relatively close to the ground. While in theory, it would seem logical that birds would not be aerodynamically affected by wind direction at such relatively low speeds relative to their typical airspeeds, it is clear from the present data that the mean $VeDBA_{YZ}$ values tended to be smallest during the tailwind and the standard deviation of the mean was significantly lower even than in no wind. Alerstam (1979) suggested that birds might try and drift to some extent with a tailwind and, thus, conserve their energy and Åkesson and Hedenström (2000) showed that birds were more likely to depart on migration on days with tailwinds as opposed to other wind conditions, confirming that these conditions are the most favourable for long flights but this is thought to be due to a direct effect of increased ground speed. Similarly, birds tend to fly at higher altitudes during favourable wind conditions so as take advantage of high speeds (Liechti and Bruderer, 1998; Klaassen et al., 2004) and, from this, it might be expected that in headwinds birds would fly at lower altitudes. This might explain why in the present study (Figs. 5.8 and 5.14) the highest altitudes attained by the pigeons were in the more favourable tail wind condition.

It seems reasonable to take the view that there is less uncertainty in the air speed calculations on the low wind days, such as on the 18th September, under a very slight headwind ($1.31ms^{-1}$). On that day, the pigeons climbed during the first 80s to a maximum height of 70m, at an average climb rate of $0.88ms^{-1}$ and a forward velocity of between 14 and $15ms^{-1}$, before briefly levelling off. As in chapter IV, if we take the view that the energy consumption values of Butler et al. (1977) represent the lowest possible for forward flight, then this level of flight performance is equivalent to a power output of around 12W + 8.6W = 20.6W. They then begin to descend over the next few minutes, while maintaining a speed of 23ms^{-1}, before beginning a gentle ascent of around 0.13ms^{-1} at a forward speed of 19ms^{-1} for over 5 minutes. This would only require an additional climb power of around 1.3W on top of their forward flight costs of between 20 to 21W (Peters et al. 2005; Gessaman & Nagy 1988). If correct, this would suggest that homing pigeons are fairly comfortable at flying with a biomechanical power of around 20W to 22W and that once into the flight, any climbs required are quite gentle and integrated with a small adjustment to forward velocity while keeping the overall flight costs at a similar value. While the very early phases of take-off may utilise anaerobic fibres this cannot be maintained for long so, again, it would appear that the early climb, which is quite steep, is integrated with a much slower forward velocity so that the overall sustainable flight costs are again of the order of 20W to 22W.

Several authors (e.g. Wilson et al., 2006; Halsey et al., 2009c) have linked ODBA with energy expenditure during running in a variety of species, while the present study confirms VeDBA_{YZ}^2 is a good linear proxy of integrated power in the body of the pigeon. It would be expected that this relationship would also apply to other species of flying birds and probably bats. Further, work needs to be conducted to investigate the detailed proportional relationship between VeDBA_{YZ}^2 and the overall cost of flight. However, the fact that VeDBA_{YZ}^2 is well correlated (ρ=0.703) with the air speed of the pigeons suggests that it may also be well correlated with total energy expenditure. The present study also indicates that VeDBA_{YZ}^2 is sensitive to the intense climbing flight during the early phase of the flight but that the pigeons may trade off forward speed against gentle climbs later during the flights so that they are not easily detectable as a distinct behaviour. It is not clear how VeDBA_{YZ}^2 should respond to added mass (Gleiss et al., 2011) but an attempt was made to address the issue in this thesis (see also chapter IV). There is a tendency for heavy birds flying within flocks to have lower VeDBA_{YZ} values when carrying additional mass. Similarly, mean VeDBA_{YZ} values are generally lower in the added mass flight compared to the control. It is not likely that this indicates that energy consumption is reduced in these weighted pigeons but rather that the body accelerations have been damped and that potentially greater energetic outputs by the wings are not coming across to the body. Measurements of heart rate in pigeons showed a small but significant increase in those birds wearing extra mass when flying within a flock (paired analysis; Bishop, unpublished data).

Overall, there was little difference in mean values of air speed, VeDBA_{YZ}^2, wing beat frequency or fraction negative between the different wind conditions. This shows that irrespective of the wind direction and strength, on average, the birds tended to fly with a similar, perhaps optimal, level of energy output and wing beat kinematics. Mean wing beat frequency was recorded at just under 7Hz (range: 6.1Hz in a head wind to 6.75Hz in a tail wind) during the mid-sections of flight. These are similar to values obtained by Pennycuick (1968a), Butler et al. (1977) and Dial (1992) using pigeons flying in wind tunnels. By altering the air speeds in the wind tunnel Pennycuick (1968a) measured a wider range of wing beat frequency (approximately 5.5-6.9Hz), the former being similar to the values recorded for free-flying pigeons breaking off the back of the flock or when released as individuals. However, it is not clear if the air speed to wing beat ratios recorded in the wind tunnels can be directly related to the air speed wing beat relationships of free-flying birds in this experiment.

This present work emphasises that there is a great deal of individual variation between pigeons in their flight performance and motivation to return to the loft. This highlights the difficulties involved in designing manipulations to address specific aerodynamic questions without very careful experimental design. The present work has shown that some excellent results can be achieved but care must be taken to assess results at the individual level. Accelerometry can clearly add to our knowledge of bird flight biomechanics and behaviour but there may be a need to further develop analytical tools to take account of the complex acceleration patterns generated by the wings acting on the body. In addition, while differences in acceleration profiles seemed quite consistent within individuals, absolute values varied between individuals for a given wing beat frequency.

5.6 General conclusion

The overriding aim of this thesis was to determine how body-mounted accelerometers could be used to investigate the effects of wind speed and direction on bird flight performance, along with the influence of natural and added mass. To that effect, various measurements of flight behaviour were recorded using GPS and accelerometer data loggers. A further specific aim was to discover if dynamic body acceleration (in the form of VeDBA) could be used as a proxy for the overall power output of flying birds. This work has shown that although VeDBA is a likely correlate for power in the body, VeDBA_{YZ}^2 appears to be a more accurate substitute for representing power output (Fig 3.20) both from an empirical and mathematical view point. As in horizontal flight there is little acceleration in the X-axis, this axis did not need to be accounted for in the calculation of DBA. Although it would require further investigation, it is highly likely that other modes of locomotion, which are visible in two axes, do not need all three axes computing to highlight power in the body.

It is clear from the two main experiments undertaken that the assumption that pigeons remain as a tight flock between liberation and home is highly time dependent, and this finding highlights an important caveat in any future research focussing on flock flight. However by comparing between individual and flock releases it is clear that birds within a flock tend to fly faster, with higher wing beat frequencies, VeDBA_{YZ}^2 and fraction positive values. This may be due to a greater motivational effect to remain with the flock that is simply not present when pigeons are flying alone.

The heavier birds tended to display lower mean values of VeDBA_{YZ}, which suggests that their acceleration is dampened by the additional mass. This is in contrast to the results of Wilson et al. (2006) who suggested that imperial cormorants (*Phalacrocorax atriceps*) displayed greater values of ODBA when laden after a foraging trip. The results of the present pigeon study suggests that something other than additional mass was creating the higher ODBA values found in the cormorant study, most likely an increased air speed.

The pigeons flew at their highest air speed and their highest value of VeDBA_{YZ}^2 in the strongest head wind, while there was also a good overall correlation between airspeed and VeDBA_{YZ}^2, again suggesting that VeDBA_{YZ}^2 is a suitable proxy for power output in flying birds. This study has also highlighted the significant degree of individual variation displayed within a flock of homing pigeons, which are the same strain, cared for in the same manner and of a similar age and flight experience. Thus, individual could be categorised as fast or slow returning birds and these two types of pigeons show markedly different flight styles.

It is clear that the pigeons were comfortably able to carry an additional 5% of their own body mass, in contrast to the work of Gessaman and Nagy (1988). Future studies may like to repeat this work with heavier loads to determine at what point extra mass compromises flight performance significantly. However, when performing free-flying experiments, care must be taken to ensure that the pigeons are not hampered too much and, thus, making them more liable for predation or reluctant to return home.

It has been suggested that DBA (in this case represented by VeDBA) could be a revolutionary technique to determine energy expenditure without having to rely on invasive surgery or cumbersome equipment, which is obviously advantageous to the focal individual and scientist alike. The principle behind this suggestion is that movement requires energy (Wilson et al., 2006) and, as DBA is based around movement (Gleiss et al., 2011), it should be a suitable proxy for energy expenditure. From the results presented within this thesis it is clear that there is a very real potential for the application of accelerometry to the investigation of bird flight energetics and performance. This is a very significant step forward and has the potential to significantly alter the methods in which energy expenditure and power output are measured in the study of free-ranging animal locomotion.

References

ABLE, K.P. (1970) A radar study of the altitude of nocturnal passerine migration. *Bird Banding,* **41**(4):282-290.

ÅKESSON, S. and HEDENSTRÖM, A. (2000) Wind selectivity of migratory flight departures in birds. *Behavioural Ecology and Sociobiology,* **47:**140-144.

ÅKESSON, S., WALINDER, G., KARLSSON, L. and EHNBOM, S. (2002) Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. *Journal of Avian Biology,* **33:**349-357.

ALERSTAM, T. (1979) Optimal use of wind by migrating birds: combined drift and overcompensation. *Journal of Theoretical Biology,* **79:**341-353.

ALERSTAM, T. (1991) Bird flight and optimal migration. *Trends in Ecology and Evolution,* **6**(7):210-215.

ALLEN, F.H. (1939) Effect of wind on flight speed. *The Auk,* **56**(3):291-303.

ALTSHULER, D.L., DUDLEY, R., HEREDIA, S.M. and McGUIRE, J.A. (2010) Allometry of hummingbird lifting performance. *Journal of Experimental Biology,* **213:**725-734.

ALTSHULER, D.L., DUDLEY, R. and McGUIRE, J.A. (2004) Resolution of a paradox: Hummingbird flight at high elevation does not come without a cost. *Proceedings of the National Academy of Sciences USA,* **101**(51):17731-17736.

ASKEW, G.N., MARSH, R.L. and ELLINGTON, C.P. (2001) The mechanical power output of the flight muscles of blue-breasted quail (*Coturnix chinensis*) during take-off. *Journal of Experimental Biology,* **204:**3601-3619.

BÄCHLER, E., HAHN, S., SCHAUB, M., ARLETTAZ, R., JENNI, L., FOX, J.W., AFANASYEV, V. and LIECHTI, F. (2010) Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS One,* **5**(3):e9566. doi:10.1371/journal.pone.0009566

BANNASCH, R., WILSON, R.P. and CULIK, B. (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental Biology,* **194:**83-96.

BARRON, D.G., BRAWN, J.D. and WEATHERHEAD, P.J. (2010) Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution,* **1:**180-187.

BATTLEY, P.F. (1997) The northward migration of arctic waders in New Zealand: departure behaviour, timing and possible migration routes of red knots and bar-tailed godwits from Farewell Spit, North-West Nelson. *Emu,* **97:**108-120.

BERG, A.M. and BIEWENER, A.A. (2010) Wing and body kinematics at takeoff and landing flight in the pigeon (*Columba livia*). *Journal of Experimental Biology,* **213:**1651-1658.

BEVAN, R.M., WOAKES, A.J., BUTLER, P.J. and BOYD, I.L. (1994) The use of heart rate to estimate oxygen consumption of free-ranging black-browed albatrosses *Diomedea melanophrys. Journal of Experimental Biology,* **193:**119-137.

BIDDER, O.R., QASEM, L.A. and WILSON, R.P. (2012) On higher ground: How well can dynamic body acceleration determine speed in variable terrain? *PLoS ONE* **7**(11):e50556 doi:10.1371/journal.pone.0050556.

BINGMAN, V.P., ABLE, K.P. and KERLINGER, P. (1982) Wind drift, compensation, and the use of landmarks by nocturnal bird migrants. *Animal Behaviour,* **30**:49-53.

BISHOP, C.M. (1997) Heart mass and the maximum cardiac output of birds and mammals: implications for estimating the maximum aerobic power input of flying animals. *Philosophical Transactions of the Royal Society of London, B,* **352:**447-456.

BISHOP, C.M. (1999) The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter. *Proceedings of the Royal Society of London, B,* **266:**2275-2281.

BISHOP, C.M. (2005) Circulatory variables and the flight performance of birds. *Journal of Experimental Biology,* **208:**1695-1708.

BISHOP, C. M. and SPIVEY, R. J. (2013) Integration of exercise response and allometric scaling in endotherms. *Journal of Theoretical Biology,* **323:**11-19.

BOWLIN, M. S. and WIKELSKI, M. (2008) Pointed wings, low wing loading and clam air reduce migratory flight costs in song birds. *PLoS ONE* **3**(5): e2154.

BOWLIN, M.S., HENNINGSSON, P., MUIJRES, F.T., VLEUGELS, R.H.E., LIECHTI, F. and HEDENSTRÖM, A. (2010) The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods in Ecology and Evolution,* **1**(4):398-402.

BOYD, I.L., WOAKES, A.J., BUTLER, P.J., DAVIS, R.W. and WILLIAMS, T.M. (1995) Validation of heart rate and doubly labelled water as measures of metabolic rate during swimming in California Sea Lions. *Functional Ecology,* **9:**151-160.

BROWN, R.H.J. (1948) The flight of birds: the flapping cycle of the pigeon. *Journal of Experimental Biology,* **25**(4):322-333.

BRUDERER, L., LIECHTI, F. and BILO, D. (2001) Flexibility in flight behaviour of barn swallows (*Hirundo rustica*) and house martins (*Delichon urbica*) tested in a wind tunnel. *Journal of Experimental Biology,* **204:**1473-1484.

BUNNELL, S. (1930) Aeronautics of bird flight. *The Condor*, **32**(6):269-287.

BUTLER, P.J. (1991) Exercise in Birds. *Journal of Experimental Biology,* **160:**233-262.

BUTLER, P.J., GREEN, J.A., BOYD, I.L. and SPEAKMAN, J.R. (2004) Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Functional Ecology,* **18:**168-183.

BUTLER, P.J., WEST, N.H. and JONES, D.R. (1977) Respiratory and cardiovascular responses of the pigeon to sustained, level flight in a wind-tunnel. *Journal of Experimental Biology,* **71:**7-26.

BUTLER, R.W., WILLIAMS, T.D., WARNOCK, N. and BISHOP, M.A. (1997) Wind assistance: a requirement for migration of shore birds? *The Auk,* **114**(3):456-466.

BUTLER, P.J., WOAKES, A.J. and BISHOP, C.M. (1998) Behaviour and physiology of Svalbard Barnacle Geese *Branta leucopsis* during their autumn migration. *Journal of Avian Biology,* **29:**536-545.

BUTLER, P.J., WOAKES, A.J., BOYD, I.L. and KANATOUS, S. (1992) Relationship between heart rate and oxygen consumption during steady-state swimming in California sea lions. *Journal of Experimental Biology,* **170:**35-42.

CACCAMISE, D.F. and HEDIN, R.S. (1985) An aerodynamic basis for selecting transmitter loads in birds. *The Wilson Bulletin,* **97**(3):306-318.

CARERE, C., MONTANINO, S., MORESCHINI, F., ZORATTO, F., CHIAROTTI, F., SANTUCCI, D. and ALLEVA, E. (2009) Aerial flocking patterns of wintering starlings, *Sturnus vulgaris*, under different predation risk. *Animal Behaviour,* **77**(1):101-107.

CATRY, I., DIAS, M.P., CATRY, T., AFANASYEV, V., FOX, J., FRANCO, A.M.A. and SUTHERLAND, W.J. (2011) Individual variation in migratory movements and winter behaviour of Iberian Lesser Kestrels *Falco naumanni* revealed by geolocators. *Ibis,* **153**(1):154-164.

CHAI, P., CHEN, J.S.C. and DUDLEY, R. (1997) Transient hovering performance of hummingbirds under conditions of maximal loading. *Journal of Experimental Biology,* **200:**921-929.

CHAI, P. and MILLARD, D. (1997) Flight and size constraints: hovering performance of large hummingbirds under maximal loading. *Journal of Experimental Biology,* **200:**2757-2763.

CLARK, T.D., SANDBLOM, E., HINCH, S.G., PATTERSON, D.A., FRAPPELL, P.B. and FARRELL, A.P. (2010) Simultaneous biologging of heart rate and acceleration, and their relationships with energy expenditure in free-swimming sockeye salmon (*Oncorhynchus nerka*). *Journal of Comparative Physiology B,* **180:**673-684.

COOKE, M.T. (1933) Speed of bird flight. *The Auk,* **50**(3):309-316.

COTTAM, M., HOUSTON, D., LOBLEY, G. and HAMILTON, I. (2002) The use of muscle protein for egg production in the Zebra Finch *Taeniopygia guttata. Ibis,* **144:**210-217.

CULIK, B.M., BANNASCH, R. and WILSON, R.P. (1994) External devices on penguins: how important is shape? *Marine Biology,* **118:**353-357.

CULIK, B. and WILSON, R.P. (1991) Swimming energetics and performance of instrumented Adélie penguins (*Pygoscelis adeliae*). *Journal of Experimental Biology,* **158:**355-368.

CULLEN, J.M. (1954) The diurnal rhythm of birds in the Arctic summer. *Ibis,* **96**(1):31-46.

CUNNINGHAM, G.B., van BUSKIRK, R.W., HODGES, M.J., WEIMERSKIRCH, H. and NEVITT, G.A. (2006) Behavioural responses of blue petrel chicks (*Halobaena caerulea*) to food-related and novel odours in a simple wind tunnel. *Antarctic Science,* **18**(3):345-352.

CUTTS, C.J. and SPEAKMAN, J.R. (1994) Energy savings in formation flight of pink-footed geese. *Journal of Experimental Biology,* **189:**251-261.

DÄNHARDT, J. and LINDSTRÖM, A. (2001) Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Animal Behaviour,* **62:**235-243.

DELL'ARICCIA, G., DELL'OMO, G., WOLFER, D.P. and LIPP, H.-P. (2008) Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. *Animal Behaviour,* **76:**1165-1172

DIAL, K.P. (1992) Avian forelimb muscles and nonsteady flight: can birds fly without using the muscles in their wings? *The Auk,* **109**(4):874-885.

DIAL, K.P. and BIEWENER, A.A. (1993) Pectoralis force and power output during different modes of flight in pigeons (*Columba livia*). *Journal of Experimental Biology,* **176:**31-54.

DIAL, K.P., BIEWENER, A.A., TOBALSKE, B.W. and WARRICK, D.R. (1997) Mechanical power output of bird flight. *Nature,* **390:**67-70.

DIAL, K.P., KAPLAN, S.R. and GOSLOW, G.E. Jr. (1988) A Functional analysis of the primary upstroke and downstroke muscles in the domestic pigeon (*Columba livia*) during flight. *Journal of Experimental Biology,* **134:**1-16.

DILLON, M.E. and DUDLEY, R. (2004) Allometry of maximum vertical force production during hovering flight of neotropical orchid bees (Apidae: Euglossini). *Journal of Experimental Biology,* **207:**417-425.

EGEVANG, C., STENHOUSE, I.J., PHILLIPS, R.A., PETERSEN, A., FOX, J.W. and SILK, J.R.D. (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences USA,* **107**(5):2078-2081.

ELLINGTON, C.P. (1991) Limitations on animal flight performance. *Journal of Experimental Biology,* **160:**71-91.

ERNI, B., LIECHTI, F. and BRUDERER, B. (2005) The role of wind in passerine autumn migration between Europe and Africa. *Behavioural Ecology,* **16:**732-740.

ERNI, B., LIECHTI, F., UNDERHILL, L.G. and BRUDERER, B. (2002) Wind and rain govern the intensity of nocturnal bird migration in central Europe – a log-linear regression analysis. *Ardea,* **90**(1):155-166.

FRANSSON, T. and WEBER, T.P. (1997) Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. *Behavioural Ecology and Sociobiology,* **41:**75-80.

FRITZ, H., SAID, S. and WEIMERSKIRCH, H. (2003) Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society of London B,* **270:**1143-1148.

FROGET, G., BUTLER, P.J., HANDRICH, Y. and WOAKES, A.J. (2001) Heart rate as an indicator of oxygen consumption: influence of body condition in the King penguin. *Journal of Experimental Biology,* **204:**2133-2144.

GABRIELSEN, G.W., MEHLUM, F. and NAGY, K.A. (1987) Daily energy expenditure and utilization of free-ranging black-legged kittiwakes. *The Condor,* **89**(1):126-132.

GAGLIARDO, A., FILANNINO, C., IOALÈ, P., PECCHIA, T., WIKELSKI, M. and VALLORTIGARA, G. (2011) Olfactory lateralization in homing pigeons: a GPS study on birds released with unilateral olfactory inputs. *Journal of Experimental Biology,* **214:**593-598.

GAGLIARDO, A., IOALÈ, P., SAVINI, M., LIPP, H.-P. and DELL'OMO, G. (2007) Finding home: the final step of the pigeons' homing process studied with a GPS data logger. *Journal of Experimental Biology,* **210:**1132-1138.

GATES, W.H. (1933) Hailstone damage to birds. *Science,* **78**(2021):263-264.

GAUTHIER-CLERC, M. and LE MAHO, Y. (2001) Beyond bird marking with rings. *Ardea,* **89**(Special Issue):221-230.

GESSAMAN, J.A. and NAGY, K.A. (1988) Transmitter loads affect the flight speed and metabolism of homing pigeons. *The Condor,* **90**(3):662-668.

GESSAMAN, J.A., WORKMAN, G.W. and FULLER, M.R. (1991) Flight performance, energetics and water turnover of tippler pigeons with a harness and dorsal load. *The Condor,* **93:**546-554.

GLEISS, A.C., DALE, J.J., HOLLAND, K.N. and WILSON, R.P. (2010) Accelerating estimates of activity-specific metabolic rate in fishes: Testing the applicability of acceleration data-loggers. *Journal of Experimental Marine Biology and Ecology,* **385:**85-91.

GLEISS, A.C., WILSON, R.P. and SHEPARD, E.L.C. (2011) Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution,* **2:**23-33.

GLOVER, D. and BEAUMONT, M. (1999) *Racing Pigeons.* UK: Crowood Press Ltd.

GODFREY, A., CONWAY, R., MEAGHER, D. and ÓLAIGHIN, G. (2008) Direct measurement of human movement by accelerometry. *Medical Engineering and Physics,* **30:**1364-1386.

GÓMEZ LAICH, A., WILSON, R.P., QUINTANA, F. and SHEPARD, E.L.C. (2008) Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research,* **10:**29-37.

GREEN, M. (2004) Flying with the wind – spring migration of Arctic-breeding waders and geese over south Sweden. *Ardea,* **92**(2):145-160.

GREEN, J.A., BUTLER, P.J., WOAKES, A.J., BOYD, I.L. and HOLDER, R.L. (2001) Heart rate and rate of oxygen consumption of exercising macaroni penguins. *Journal of Experimental Biology,* **204:**673-684.

GREEN, J.A., HALSEY, L.G., WILSON, R.P. and FRAPPELL, P.B. (2009) Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *Journal of Experimental Biology,* **212:**471-482.

GRÉMILLET, D., DELL'OMO, G., RYAN, P.G., PETERS, G., ROPERT-COUDERT, Y. and WEEKS, S.J. (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Marine Ecology Progress Series,* **268:**265-279.

GRIFFIN, D.R. (1943) Homing experiments with herring gulls and common terns. *Bird Banding,* **14**(1/2):7-33

GRUBB, B.R. (1982) Cardiac output and stroke volume in exercising ducks and pigeons. *Journal of Applied Physiology,* **53**(1):207-211.

GUILFORD, T.C., MEADE, J., FREEMAN, R., BIRO, D., EVANS, T., BONADONNA, F., BOYLE, D., ROBERTS, S. and PERRINS, C.M. (2008) GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis,* **150:**462-473.

HALSEY, L.G., GREEN, J.A., WLSON, R.P. and FRAPPELL, P.B. (2009a) Accelerometry to estimate energy expenditure during activity: best practice with data loggers. *Physiological and Biochemical Zoology,* **82**(4):396-404.

HALSEY, L.G., PORTUGAL, S.J., SMITH, J.A., MURN, C.P. and WILSON, R.P. (2009b) Recording raptor behaviour on the wing via accelerometry. *Journal of Field Ornithology,* **80**(2):171-177.

HALSEY, L.G., SHEPARD, E.L.C., HULSTON, C.J., VENABLES, M.C., WHITE, C.R., JEUKENDRUP, A.E. and WILSON, R.P. (2008) Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: tests with an easy model species, *Homo sapiens. Zoology,* **111:**231-241.

HALSEY, L.G., SHEPARD, E.L.C., QUINTANA, F., GÓMEZ LAICH, A., GREEN, J.A. and WILSON, R.P. (2009c) The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology A,* **152:**197-202.

HALSEY, L.G. and WHITE, C.R. (2010) Measuring energetics and behaviour using accelerometry in Cane Toads *Bufo marinus. PLoS One,* **5**(4):e10170. doi: 10.1271/journal.pone.0010170.

HAMBLY, C., HARPER, E.J. and SPEAKMAN, J.R. (2004) The energy cost of loaded flight is substantially lower than expected due to alterations in flight kinematics. *Journal of Experimental Biology,* **207:**3969-3976.

HART, J.S. and ROY, O.Z. (1966) Respiratory and cardiac responses to flight in pigeons. *Physiological Zoology,* **39**(4):291-306.

HAWKING, P. (2004) Bio-logging and animal welfare: practical refinements. *Memoirs of the National Institute for Polar Research, Special Issue,* **58:**58-68.

HAWKINS, P.A.J., BUTLER, P.J., WOAKES, A.J. and SPEAKMAN, J.R. (2000) Estimation of the rate of oxygen consumption of the common eider duck (*Somateria mollissima*), with some measurement of heart rate during voluntary dives. *Journal of Experimental Biology,* **203:**2819-2832.

HENDENSTRÖM, A. (2002) Aerodynamics, evolution and ecology of avian flight. *Trends in Ecology and Evolution*, **17**(9):415-422.

HEDENSTRÖM, A. and ALERSTAM, T. (1992) Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *Journal of Experimental Biology,* **164:**19-38.

HEDENSTRÖM, A. and ALERSTAM, T. (1995) Optimal flight speeds of birds. *Philosophical Transactions of the Royal Society of London B,* **348:**471-487.

HEDENSTRÖM, A. and LIECHTI, F. (2001) Field estimates of body drag coefficient on the basis of dives in passerine birds. *Journal of Experimental Biology,* **204:**1167-1175.

HEDENSTRÖM, A., ROSÉN, M., ÅKESSON, S. and SPINA, F. (1999) Flight performance during hunting excursions in Eleonora's falcon Falco eleonorae. *Journal of Experimental Biology,* **202:**2029-2039.

HEDENSTRÖM, A., ROSÉN, M. and SPEDDING, G.R. (2006) Vortex wakes generated by robins *Erithacus rubecula* during free flight in a wind tunnel. *Journal of the Royal Society Interface,* **3:**263-276.

HITCHCOCK, H.B. (1955) Flights and orientation of pigeons. *The Auk,* **72**(4):355-373.

HOCHSCHEID, S., GODLEY, B.J., BRODERICK, A.C. and WILSON, R.P. (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas. Marine Ecology Progress Series,* **185:**101-112.

HUGHES, P.M. and RAYNER, J.M.V. (1991) Addition of artificial loads to long-eared bats Plecotus auritus: handicapping flight performance. *Journal of Experimental Biology,* **161:**285-298.

HUTTON, F.W. (1873) On the flight of the black-backed gull (*Larus dominicanus*). *Transactions and Proceedings of the Royal Society of New Zealand,* **5:**140-144.

IDRAC, P. (1925) Experimental study on the “soaring” of albatrosses. *Nature,* **115**(2893):532.

JENNI, L. and JENNI-EIERMANN, S. (1998) Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology,* **29:**521-528.

JOUVENTIN, P. and WEIMERSKIRCH, H. (1990) Satellite tracking of Wandering albatrosses. *Nature,* **343:**746-748.

KLAASSEN, M., BEEKMAN, J.H., KONTIOKORPI, J., MULDER, R.J.W. and NOLET, B.A. (2004) Migrating swans profit from favourable changes in wind conditions at low altitudes. *Journal of Ornithology,* **145:**142-151.

KULLBERG, C., HOUSTON, D.C. and METCALF, N.B. (2002) Impaired flight ability – a cost of reproduction in female blue tits. *Behavioural Ecology,* **13:**575-579.

KULLBERG, C., JAKOBSSON, S. and FRANSSON, T. (1998) Predator-induced take-off strategy in great tits (*Parus major*). *Proceedings of the Royal Society of London B,* **265:**1659-1664.

KULLBERG, C., JAKOBSSON, S. KABY, U. and LIND, J. (2005) Impaired flight ability prior to egg-laying: a cost of being a capital breeder. *Functional Ecology,* **19:**98-101.

KVIST, A., KLAASSEN, M. and LINDSTRÖM, Å. (1998) Energy expenditure in relation to flight speed: what is the power of mass loss rate estimates? *Journal of Avian Biology,* **29**(4):485-498.

KVIST, A., LINDSTRÖM, A., GREEN, M., PIERSMA, T. and VISSER, G.H. (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature,* **413:**730-731.

LEFEBVRE, E.A. (1964) The use of D_2O^{18} for measuring energy metabolism in Columba livia at rest and in flight. *The Auk,* **81:**403-416.

LEHNER, P.N. (1987) Design and execution of animal behavior research: an overview. *Journal of Animal Science,* **65:**1213-1219.

LIECHTI, F. and BRUDERER, B. (1998) The relevance of wind for optimal migration theory. *Journal of Avian Biology,* **29:**561-568.

LIECHTI, F. and BRUDERER, L. (2002) Wingbeat frequency of barn swallows and house martins: a comparison between free flight and wind tunnel experiments. *Journal of Experimental Biology,* **205:**2461-2467.

LIMA, S.L. (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology,* **67**(2):377-385.

LINDSTRÖM, Å., KLAASSEN, M. and KVIST, A. (1999) Variation in energy intake and basal metabolic rate of a bird migrating in a wind tunnel. *Functional Ecology,* **13:**352-359.

LINDSTRÖM, Å., KVIST, A., PIERSMA, T., DEKINGA, A. and DIETZ, M.W. (2000) Avian pectoral muscle size rapidly tracks body mass changes during free flight, fasting and fuelling. *Journal of Experimental Biology,* **203:**913-919.

MARDEN, J.H. (1987) Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology,* **130:**235-258.

MARDEN, J.H. (1990) Maximum load-lifting and induced power output of Harris' hawks are general functions of flight muscle mass. *Journal of Experimental Biology,* **149:**511-514.

MARKS, J.S. and REDMOND, R.L. (1994) Migration of bristle-thighed curlews on Laysan Island: timing, behavior and estimated flight range. *The Condor,* **96:**316-330.

MASMAN, D. and KLAASSEN, M. (1987) Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). *The Auk,* **104:**603-616.

McNAB, B.K. (1994) Energy conservation and the evolution of flightlessness in birds. *The American Naturalist,* **144**(4):628-642.

MICHENER, M.C. and WALCOTT, C. (1966) Navigation of single homing pigeons: airplane observations by radio tracking. *Science,* **154:**410-413.

MICHENER, M.C. and WALCOTT, C. (1967) Homing of single pigeons – analysis of tracks. *Journal of Experimental Biology,* **47:**99-131.

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*). *Journal of Experimental Biology,* **213:**2788-2796.

NAGY, M., ÁKOS, Z., BIRO, D. and VICSEK, T. (2010) Hierarchical group dynamics in pigeon flocks. *Nature,* **464:**890-894.

NOLET, B.A., BUTLER, P.J., MASMAN, D. and WOAKES, A.J. (1992) Estimation of daily energy expenditure from heart rate and doubly labeled water in exercising geese. *Physiological Zoology,* **65**(6):1188-1216.

NORBERG, U.M. (1995) How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology,* **9:**48-54.

NUDDS, R.L. and BRYANT, D.M. (2002) Consequences of load carrying by birds during short flights are found to be behavioral and not energetic. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology,* **283:**249-256.

OBRECHT, H.H. III, PENNYCUICK, C.J. and FULLER, M.R. (1988) Wind tunnel experiments to assess the effect of back-mounted radio transmitters on bird body drag. *Journal of Experimental Biology,* **135:**263-273.

PARK, K.J., ROSÉN, M. and HEDENSTRÖM, A. (2001) Flight kinematics of the barn swallow (*Hirundo rustica*) over a wide range of speeds in a wind tunnel. *Journal of Experimental Biology,* **204:**2741-2750.

PARROTT, G.C. (1970) Aerodynamics of gliding flight of a black vulture Coragyps *atratus. Journal of Experimental Biology,* **53:**363-374.

PELLETIER, D., GUILLEMETTE, M., GRANDBOIS, J-M. and BUTLER, P.J. (2008) To fly or not to fly: high flight costs in a large sea duck do not imply an expensive lifestyle. *Proceedings of the Royal Society B,* **275**(1647):2117-2124.

PENNYCUICK, C.J. (1968a) Power requirements for horizontal flight in the pigeon *Columba livia. Journal of Experimental Biology,* **49:**527-555.

PENNYCUICK, C.J. (1968b) A wind-tunnel study of gliding flight in the pigeon *Columba livia. Journal of Experimental Biology,* **49:**509-526.

PENNYCUICK, C.J. (1969) The mechanics of bird migration. *Ibis,* **111:**525-556.

PENNYCUICK, C.J. (1971a) Gliding flight of the white backed vulture *Gyps africanus. Journal of Experimental Biology,* **55:**13-38.

PENNYCUICK, C.J. (1971b) Control of gliding angle in Rüppell's Griffon vulture *Gyps rüppellii. Journal of Experimental Biology,* **55:**39-46.

PENNYCUICK, C.J. (1975) Mechanics of Flight. In: *Avian Biology,* volume 5, edited by Donald S. Farner and James R. King. Academic Press Inc.: United Kingdom.

PENNYCUICK, C.J. (1978) Fifteen testable predictions about bird flight. *Oikos,* **30:**165-176.

PENNYCUICK, C.J. (1982) The flight of petrels and albatrosses (Procellariiformes), observed in south Georgia and its vicinity. *Philosophical Transactions of the Royal Society of London B,* **300:**75-106.

PENNYCUICK, C.J. (1990) Predicting wingbeat frequency and wavelength of birds. *Journal of Experimental Biology,* **150:**171-185.

PENNYCUICK, C.J. (1996) Wingbeat frequency of birds in steady cruising flight: new data and improved predictions. *Journal of Experimental Biology,* **199:**1613-1618.

PENNYCUICK, C.J. (1997) Actual and 'optimum' flight speeds: field data reassessed. *Journal of Experimental Biology,* **200:**2355-2361.

PENNYCUICK, C.J. (1998) Towards an optimal strategy for bird flight research. *Journal of Avian Biology,* **29:**449-457.

PENNYCUICK, C.J. (2001) Speeds and wingbeat frequencies of migrating birds compared with calculated benchmarks. *Journal of Experimental Biology,* **204:**3283-3294.

PENNYCUICK, C.J., ALERSTAM, T. and HEDENSTRÖM, A. (1997) A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *Journal of Experimental Biology,* **200:**1441-1449.

PENNYCUICK, C.J. and BATTLEY, P.F. (2003) Burning the engine: a time-marching computation of fat and protein consumption in a 5420km non-stop flight by great knots, *Calidris tenuirostris. Oikos,* **103:**323-332.

PENNYCUICK, C.J., FULLER, M.R. and McALLISTER, L. (1989) Climbing performance of Harris' hawks (*Parabuteo unicinctus*) with added load: implications for muscle mechanics and for radiotracking. *Journal of Experimental Biology,* **142:**17-29.

PENNYCUICK, C.J., HEDENSTRÖM, A. and ROSÉN, M. (2000) Horizontal flight of a swallow (*Hirundo rustica*) observed in a wind tunnel, with a new method for directly measuring mechanical power. *Journal of Experimental Biology,* **203:**1755-1765.

PENNYCUICK, C.J., HEINE, C.E., KIRKPATRICK, S.J. and FULLER, M.R. (1992) The profile drag of a hawk's wing, measured by wake sampling in a wind tunnel. *Journal of Experimental Biology,* **165:**1-19.

PENNYCUICK, C.J., KLAASSEN, M., KVIST, A. and LINDSTRÖM, A. (1996) Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *Journal of Experimental Biology,* **199:**2757-2765.

PENNYCUICK, C.J., OBRECHT, H.H. III, and FULLER, M.R. (1988) Empirical estimates of body drag of large waterfowl and raptors. *Journal of Experimental Biology,* **135:**253-264.

PETERS, G.W., STEINER, D.A., RIGONI, J.A., MASCILLI, A.D., SCHNEPP, R.W. and THOMAS, S.P. (2005) Cardiorespiratory adjustments of homing pigeons to steady wind tunnel flight. *Journal of Experimental Biology,* **208:**3109-3120.

PROP, J., BLACK, J.M. and SHIMMINGS, P. (2003) Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos,* **103:**403-414.

QASEM, L., CARDEW, A., WILSON, A., GRIFFITHS, I., HALSEY, L.G., SHEPARD, E.L.C., GLEISS, A.C. and WILSON, R.P. (2012) Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE,* **7**(2):e31187. Doi: 10.1371/journal.pone.0031187

QUINTANA, F., WILSON, R.P. and YORIO, P. (2007) Dive depth and plumage air in wettable birds: the extraordinary case of the imperial cormorant. *Marine Ecology Progress Series,* **334:**299-310.

RAYNER, J.M.V. (1979) A new approach to animal flight mechanics. *Journal of Experimental Biology,* **80:**17-54.

RAYNER, J.M.V. (1982) Avian flight energetics. *Annual Review of Physiology,* **44:**109-119.

RAYNER, J.M.V. (1985) Bounding and undulating flight in birds. *Journal of Theoretical Biology,* **117:**47-77.

RAYNER, J.M.V. (1988) Form and function in avian flight. *Current Ornithology,* **5:**1-77.

RAYNER, J.M.V. (1990) The mechanics of flight and bird migration performance. In: *Bird Migration Physiology and Ecophysiology,* edited by E. Gwinner. Springer-Verlag: Germany.

RAYNER, J.M.V. (1991) On the aerodynamics of animal flight in ground effect. *Philosophical Transactions of the Royal Society London B,* **334:**119-128.

RAYNER, J.M.V. (1994) Aerodynamic corrections for the flight of birds and bats in wind tunnels. *Journal of Zoology London,* **234:**537-563.

RAYNER, J.M.V. (1999) Estimating power curves of flying vertebrates. *Journal of Experimental Biology,* **202:**3449-3461.

RAYNER, J.M.V. (2001) Fat and formation in flight. *Nature,* **413:**685-686.

ROBERT, B., WHITE, B.J., RENTER, D.G. and LARSON, R.L. (2009) Evaluation of three-dimensional accelerometers to monitor and classify behaviour patterns in cattle. *Computers and Electronics in Agriculture,* **67:**80-84.

ROPERT-COUDERT, Y., BOST, C.-A., HANDRICH, Y., BEVAN, R.M., BUTLER, P.J., WOAKES, A.J. and LE MAHO, Y. (2000) Impact of externally attached loggers on the diving behaviour of the King penguin. *Physiological and Biochemical Zoology,* **73**(4):438-445.

ROPERT-COUDERT, Y., BROOKS, L., YAMAMOTO, M. and KATO, A. (2009) ECG response of koalas to tourists proximity: a preliminary study. *PLoS One,* **4**(10):e7378. doi: 10.1371/journal.pone.0007378.

ROPERT-COUDERT, Y., KATO, A., WILSON, R.P. and CANNELL, B. (2006) Foraging strategies and prey encounter rate of free-ranging little penguins. *Marine Biology,* **149:**139-148.

ROPERT-COUDERT, Y. and WILSON, R.P. (2004) Subjectivity in bio-logging science: do logged data mislead? *Memoirs of the National Institute for Polar Research, Special Issue,* **58:**23-33.

ROSE, E., NAGEL, P. and HAAG-WACKERNAGEL, D. (2005) Suitability of using the global positioning system (GPS) for studying Feral Pigeons *Columba livia* in the urban habitat. *Bird Study,* **52:**145-152.

ROTHE, H.-J., BIESEL, W. and NACHTIGALL, W. (1987) Pigeon flight in a wind tunnel; gas exchange and power requirements. *Journal of Comparative Physiology B,* **157:**99-109.

RUTZ, C. and HAYS, G.C. (2009) New frontiers in biologging science. *Biology Letters,* **5:**289-292.

SACHS, G. (2005) Minimum shear wind strength required for dynamic soaring of albatrosses. *Ibis,* **147:**1-10.

SAINO, N., RUBOLINI, D., von HARDENBERG, J., AMBROSINI, R., PROVENZALE, A., ROMANO, M. and SPINA, F. (2010) Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds. *Functional Ecology,* **24:**658-669.

SAKAMOTO, K.Q., SATO, K., ISHIZUKA, M., WATANUKI, Y., TAKAHASHI, A., DAUNT, F. and WANLESS, S. (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS One,* **4**(4):e5379. doi:10.1371/journal.pone.0005379

SCHAUB, M., LIECHTI, F. and JENNI, L. (2004) Departure of migrating European robins, *Erithacus rubecula,* from a stopover site in relation to wind and rain. *Animal Behaviour,* **67:**229-237.

SCHMIDT-KOENIG, K. and WALCOTT, C. (1978) Tracks of pigeons homing with frosted lenses. *Animal Behaviour,* **26:**480-486.

SCHMIDT-NIELSEN, K. (1972) Locomotion: energy cost of swimming, flying, and running. *Science,* **177:**222-228.

SCHMIDT-WELLENBURG, C.A., BIEBACH, H., DANN, S. and VISSER, G.H. (2007) Energy expenditure and wing beat frequency in relation to body mass in free flying Barn Swallows (*Hirundo rustica*). *Journal of Comparative Physiology B,* **177:**327-337.

SCHMIDT-WELLENBURG, C.A., ENGEL, S. and VISSER, G.H. (2008) Energy expenditure during flight in relation to body mass: effects of natural increases in mass and artificial load in Rose Coloured Starlings. *Journal of Comparative Physiology B,* **178:**767-777.

SCHOFIELD, G., BISHOP, C.M., MacLEAN, G., BROWN, P., BAKER, M., KATSELIDIS, K.A., DIMOPOULOS, P., PANTIS, J.D. and HAYS, G.C. (2007) Novel GPS tracking of sea turtles as a tool for conservation management. *Journal of Experimental Marine Biology and Ecology,* **347:**58-68.

SHEPARD, E.L.C., WILSON, R.P., HALSEY, L.G., QUINTANA, F., GÓMEZ LAICH, A., GLEISS, A.C., LIEBSCH, N., MYERS, A.E. and NORMAN, B. (2008a) Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology,* **4:**235-241.

SHEPARD, E.L.C, WILSON, R.P., QUINTANA, F., GÓMEZ LAICH, A., LIEBSCH, N., ALBAREDA, D.A., HALSEY, L.G., GLEISS, A., MORGAN, D.T., MYERS, A.E., NEWMAN, C. and MACDONALD, D.W. (2008b) Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research,* **10:**47-60.

SILK, J.B. (2007) Animal behavior: conflict management is for the birds. *Current Biology,* **17**(2):R50-R51.

SPAAR, R. and BRUDERER, B. (1996) Soaring migration of Steppe eagles *Aquila nipalensis* in southern Israel: flight behaviour under various wind and thermal conditions. *Journal of Avian Biology,* **27:**289-301.

SPEAKMAN, J.R. (1993) How should we calculate CO_2 production in doubly labelled water studies of animals? *Functional Ecology,* **7**(6):746-750.

SPEAKMAN, J.R. (1998) The history and theory of the doubly labeled water technique. *American Journal of Clinical Nutrition,* **68**(sup):932-938.

STEINER, I., BÜRGI, C., WERFFELI, S., DELL'OMO, G., VALENTI, P., TRÖSTER, G., WOLFER, D.P. and LIPP, H.-P. (2000) A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiology and Behaviour,* **71:**589-596.

TOBALSKE, B.W. (2001) Morphology, velocity and intermittent flight in birds. *American Zoologist,* **41:**177-187.

TOBALSKE, B.W. (2007) Biomechanics of bird flight. *Journal of Experimental Biology,* **210:**3135-3146.

TOBALSKE, B.W. and DIAL, K.P. (1996) Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *Journal of Experimental Biology,* **199:**263-280.

TOBALSKE, B.W. and DIAL, K.P. (2000) Effects of body size on take-off flight performance in the Phasianidae (Aves). *Journal of Experimental Biology,* **203:**3319-3332.

TOBALSKE, B.W., HEARN, J.W.D. and WARRICK, D.R. (2009) Aerodynamics of intermittent bounds in flying birds. *Experiments in Fluids,* **46:**963-973.

TOBALSKE, B.W., HEDRICK, T.L. and BIEWENER, A.A. (2003) Wing kinematics of avian flight across speeds. *Journal of Avian Biology,* **34**(2):177-184.

TORRE-BUENO, J.R. and LAROCHELLE, J. (1978) The metabolic cost of flight in unrestrained birds. *Journal of Experimental Biology,* **75:**223-229.

TREMBLAY, Y., CHEREL, Y. OREMUS, M., TVERAA, T. and CHASTEL, O. (2003) Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *Journal of Experimental Biology,* **206:**1929-1940.

TUCKER, V.A. (1968) Respiratory exchange and evaporative water loss in the flying budgerigar. *Journal of Experimental Biology,* **48:**67-87.

TUCKER, V.A. (1971) Flight energetics in birds. *American Zoologist,* **11:**115-124.

TUCKER, V.A., and PARROTT, G.C. (1970) Aerodynamics of gliding flight in a falcon and other birds. *Journal of Experimental Biology,* **52:**345-367.

USHERWOOD, J.R., STAVROU, M., LOWE, J.C., ROSKILLY, K. and WILSON, A.M. (2011) Flying in a flock comes at a cost in pigeons. *Nature,* **474:**494-497.

van den BERG, C. and RAYNER, J.M.V. (1995) The moment of inertia of bird wings and the inertial power requirement for flapping flight. *Journal of Experimental Biology,* **198:**1655-1664.

VIDELER, J.J. (2005) *Avian Flight.* United Kingdom: Oxford University Press.

VIDELER, J.J., GROENEWEGEN, A., GNODDE, M. and VOSSEBELT, G. (1988a) Indoor flight experiments with trained kestrels. The effect of added weight on flapping flight kinematics. *Journal of Experimental Biology,* **134:**185-199.

VIDELER, J.J., VOSSEBELT, G., GNODDE, M. and GROENEWEGEN, A. (1988b) Indoor flight experiments with trained kestrels. Flight strategies in still air with and without added weight. *Journal of Experimental Biology,* **134:**173-183.

von HÜNERBEIN, K., HAMANN, H.-J., RÜTER, E. and WILTSCHKO, W. (2000) A GPS-based system for recording the flight paths of birds. *Naturwissenschaften,* **87:**278-279.

WARD, S., BISHOP, C.M., WOAKES, A.J. and BUTLER, P.J. (2002) Heart rate and the rate of oxygen consumption of flying and walking barnacle geese (*Branta leucopsis*) and bar-headed geese (*Anser indicus*). *Journal of Experimental Biology,* **205:**3347-3356.

WARD, S., MÖLLER, U., RAYNER, J.M.V., JACKSON, D.M., BILO, D., NACHTIGALL, W. and SPEAKMAN, J.R. (2001) Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris. Journal of Experimental Biology,* **204:**3311-3322.

WARD, S., MÖLLER, U., RAYNER, J.M.V., JACKSON, D.M., NACHTIGALL, W. and SPEAKMAN, J.R. (2004) Metabolic power of European starlings *Sturnus vulgaris* during flight in a wind tunnel, estimated from heat transfer modelling, doubly labelled water and mask respirometry. *Journal of Experimental Biology,* **207:**4291-4298.

WEIMERSKIRCH, H., BONADONNA, F., BAILLEUL, F., MABILLE, G., DELL'OMO, G. and LIPP, H.-P. (2002) GPS tracking of foraging albatrosses. *Science,* **295:**1259.

WEIMERSKIRCH, H. and JOUVENTIN, P. (1987) Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Islands, causes and consequences of the population decline. *Oikos,* **49:**315-322.

WEIMERSKIRCH, H., LE CORRE, M., GADENNE, H., PINAUD, D., KATO, A., ROPERT-COUDERT, Y. and BOST, C.-A. (2009) Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. *Oecologia,* **161:**637-649.

WEIMERSKIRCH, H. and ROBERTSON, G. (1994) Satellite tracking of light-mantled sooty albatrosses. *Polar Biology,* **14:**123-126.

WELLS, D.J. (1993) Ecological correlates of hovering flight of hummingbirds. *Journal of Experimental Biology,* **178:**59-70.

WILSON, R.P., GRANT, W.S. and DUFFY, D.C. (1986) Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology,* **67**(4):1091-1093.

WILSON, R.P., GRÉMILLET, D., SYDER, J., KIERSPEL, M.A.M., GARTHE, S., WEIMERSKIRCH, H., SCHÄFER-NETH, C., SCOLARO, J.A., BOST, C.-A., PLÖTZ, J. and NEL, D. (2002) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series,* **228:**241-261.

WILSON, R.P. and McMAHON, C.R. (2006) Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment,* **4**(3):147-154.

WILSON, R.P., PÜTZ, K., CHARRASSIN, J.-B. and LAGE, J. (1995) Artifacts arising from sampling interval in dive depth studies of marine endotherms. *Polar Biology,* **15:**575-581.

WILSON, R.P., PÜTZ, K., PETERS, G., CULIK, B., SCOLARO, J.A., CHARRASSIN, J.-B. and ROPERT-COUDERT, Y. (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin,* **25**(1):101-106.

WILSON, R.P., SHEPARD, E.L.C., GÓMEZ LAICH, A., FRERE, E. and QUINTANA, F. (2010) Pedalling downhill and freewheeling up; a penguin perspective on foraging. *Aquatic Biology,* **8:**193-202.

WILSON, R.P., SHEPARD, E.L.C. and LIEBSCH, N. (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research,* **4:**123-137.

WILSON, R.P., SPAIRANI, H.J., CORIA, N.R., CULIK, B.M. and ADELUNG, D. (1990) Packages for attachment to seabirds: what color do Adélie penguins dislike least? *Journal of Wildlife Management,* **54**(3):447-451.

WILSON, R.P., WHITE, C.R., QUINTANA, F., HALSEY, L.G., LIEBSCH, N., MARTIN, G.R. and BUTLER, P.J. (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology,* **75:**1081-1090.

WILSON, R.P. and WILSON, M.-P.T.J. (1989) A package-attachment technique for penguins. *Wildlife Society Bulletin,* **17**(1):77-79.

WITTER, M.S. and CUTHILL, I.C. (1993) The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London B,* **340:**73-92.

WITTER, M.S., CUTHILL, I.C. and BONSER, R.H.C. (1994) Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Animal Behaviour,* **48:**201-222.

WOODCOCK, A.H. (1940) Observations of herring gull soaring. *The Auk,* **57**(2):219-224.

YASUDA, T. and ARAI, N. (2009) Changes in flipper beat frequency, body angle and swimming speed of female green turtles *Chelonia mydas*. *Marine Ecology Progress Series,* **386:**275-286.

YODA, K., NAITO, Y., SATO, K., TAKAHASHI, A., NISH I KAWA, J., ROPERT-COUDERT, Y., KURITA, M. and LE MAYO, Y. (2001) A new technique for monitoring the behaviour of free-ranging Adélie penguins. *Journal of Experimental Biology,* **204:**685-690.

ZEHNDER, S., ÅKESSON, S., LIECHTI, F. and BRUDERER, B. (2001) Nocturnal autumn bird migration at Falsterbo, South Sweden. *Journal of Avian Biology,* **32:**239-248.