Recording raptor behavior on the wing via accelerometry

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ABSTRACT. Measuring body movements using accelerometry data loggers is a relatively new technique, the full applicability of which has yet to be tested on volant birds. Our study illustrates the potential of accelerometry for research on large birds by using the technique to record the behavior of three species of raptors, mainly during flight. A tri-axial accelerometer was deployed on a trained Harris' Hawk (*Parabuteo unicinctus*), Tawny Eagle (*Aquila rapax*), and Griffon Vulture (*Gyps fulvus*). Comparison of flight-related variables calculated from video footage and that estimated from the acceleration data showed that the latter provided considerable and accurate information (usually <10% error) about the behavior of the birds, including wing-beat frequency and when they glided and flapped. Acceleration data permitted tentative comparisons of relative movement-specific rates of energy expenditure for the Griffon Vulture flying up versus flying down a small hill. The accelerometry data appeared to suggest, as expected, that the Griffon Vulture expended more energy flying uphill than flying back down. Our preliminary findings indicate that studies using accelerometers can likely provide information about the detailed time–energy budgets of large birds. Such information would aid in comparative analyses of behavior and energetics, and may also enhance efforts to conserve declining bird populations.

SINOPSIS. **Grabando la conducta de rapaces a vuelo vía acelerometría**
La medida del movimiento de cuerpos utilizando acelerometría con bitácoras electrónicas de datos (loggers), es una técnica relativamente nueva. La aplicabilidad total de esto está aún por probarse en aves a vuelo. Nuestro estudio ilustra el potencial de la acelerometría en la investigación de aves de gran tamaño, utilizando una técnica para grabar la conducta de tres especies de rapaces, mayormente durante el vuelo. Una acelerómetro triaxial, fue colocado en tres especies de rapaces entrenadas. A saber un halcón (*Parabuteo unicinctus*), un águila (*Aguila rapax*) y un buitre (*Gyps fulvus*). Comparaciones de variables relacionadas a vuelos, calculadas de pietaje de video y otra estimada de datos tomados con un acelerómetro, demostró que la última proveía información considerable y más exacta (usualmente <10% de error), sobre la conducta de las aves, incluyendo la frecuencia de batir las alas y cuando el ave planeaba o batía las alas. Los datos del acelerómetro peremitieron comparaciones tentativas de tasas específicas de movientos y gasto de energía para el buitre, cuando volaba para elleverse versus cuando volaba hacia abajo de una colina. Los datos del acelerómetro parece sugerir, como esperado, que el buitre gasta mayor cantidad de energía al subir que al bajar. Nuestros datos preliminares indican que estudios en donde se utilicen acelerómetros pueden proveer información detallada sobre el presupuesto tiempo-energía de aves de gran tamaño. Esta información puede ser de ayuda para el análisis comparativo de conducta y energética y puede también mejorar esfuerzos dirigidos a conservar poblaciones de aves que se han reducido en número.

Key words: accelerometry, data logger, flight, raptor, time–energy budgets, vulture

Among raptors, flight types range from hovering, like kestrels (Vlachos et al. 2003), through dashing pursuit flight, typical of falcons (Lorimer 2006), to ridge soaring or use of thermals by vultures (Pennycuick 1973). Information about the time spent in flight and the energetics of various types of flight is needed to understand the behavioral and energetic strategies employed by such birds. Raptors are likely to exhibit intra- and interspecific variation in flight behavior and behavioral plasticity between seasons, and such variation can affect levels of energy expenditure. Measuring these differences enables ecophysiologists and functional ecologists to further our understanding of the manner in which organisms operate in their natural

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environment. Unfortunately, studying the flight of free-ranging raptors is difficult in part because observations are limited to when the bird is in view.

A potential solution lies in the use of animal-attached data loggers that record aspects of the activities of animals in their natural environment (Cooke et al. 2004, Weimerskirch et al. 2005). For example, periods of flying and periods of wing flapping during bathing were determined for Common Eiders (*Somateria mollissima*) from simultaneous recordings of heart rate and body angle via accelerometry (Pelletier et al. 2007). A more refined approach uses recordings of body acceleration to determine specific behaviors, such as penguins walking, tobogganing and porpoising, body posture, or, along with measures of geomagnetic intensity, the movements of seals underwater (Yoda et al. 2001, Mitani et al. 2004). However, studies deploying accelerometry loggers on volant birds have thus far only provided information about when birds are flying or not flying (e.g., Red-footed Boobies, *Sula sula*; Weimerskirch et al. 2005). In addition, species studied to date tend to have fast, low, direct flight, with little variation in wing-flapping rates. For species that fly at slower speeds and use different modes of flight (e.g., wing-flapping versus gliding), interpreting the information generated by accelerometers may be more difficult. However, the precision with which acceleration can be measured (Shepard et al. 2009) suggests that tri-axial accelerometers should be useful for describing free-ranging flight more precisely, for example, different types of flight and flapping frequencies, and even for estimating associated energy expenditure (Ropert-Coudert et al. 2007).

We propose that accelerometers can help elucidate the detailed flight patterns of large raptors and, potentially, estimate flight energetics. We examined that possibility by mounting tri-axial accelerometers on a Harris' Hawk (*Parabuteo unicinctus*), a Tawny Eagle (*Aquila rapax*), and a Griffon Vulture (*Gyps fulvus*). In addition, we validated, to our knowledge for the first time, the accuracy of accelerometers by comparing data generated by accelerometers during raptor flight with data obtained from video recordings of those flights.

To estimate rate of energy expenditure using accelerometry data, the relationship between these two variables must be known and such data are not yet available for raptors. However, evidence suggests that acceleration data correlate linearly with rate of energy expenditure for a range of animal activities (Wilson et al. 2006, Halsey et al. in press). As such, it seems reasonable to assume that, for an individual bird, periods where derived values of acceleration data are significantly higher represent periods of higher rates of energy expenditure, even though quantifying such increases is not possible. Given this, we also examined differences in rates of energy expenditure during different types of flight by the Griffon Vulture.

METHODS

Data were collected during August 2007 at the Hawk Conservancy in Hampshire, UK, using a 2-yr-old female Griffon Vulture, a 24-yr-old male Tawny Eagle, and a 19-yr-old female Harris' Hawk. They weighed about 7.5 kg, 2.3 kg, and 1.0 kg, respectively, and accelerometer mass as a percentage of each bird's mass was 0.3, 1.0, and 2.4%, respectively. These birds were available for experiments between periods when they were flown in displays for the public. They had been trained to fly between handlers or posts to obtain food over distances of tens of meters. During data collection, each bird made a series of flights over several minutes. Distances flown by the Tawny Eagle and Harris' Hawk averaged about 12 m and all flights were over level ground. The Griffon Vulture traveled up and down a small hill (7 m high), covering about 120 m horizontal distance. Wind levels were low and similar during all trials.

Acceleration in *g* was measured using custom-made accelerometers (largest dimensions 42 × 36 × 13 mm, mass 24 g) and was set to record tri-axial acceleration (0–6 *g*) at 32 Hz (fast enough to record multiple measurements per wing beat cycle) with 22-bit resolution. Data were stored on a 128 Mb RA memory card. For the Griffon Vulture and Tawny Eagle, the accelerometer was attached to feathers on the upper back (as detailed by Ropert-Coudert et al. 2007) using tape (Micropore paper tape, 3M). For the Harris' Hawk, the accelerometer was attached to breast feathers because the back feathers were not large enough for secure attachment. The *y*-axis of the accelerometer measured acceleration approximately in the anterior to posterior (longitudinal) dimension, that is,

head to tail, and, hence, surge. The *x*-axis of the accelerometer measured acceleration in the plane at approximately right angles to the *y*-axis (latitudinal), that is, wing to wing, or sway. The *z*-axis measured in approximately the ventral to dorsal dimension and hence measured heave.

After birds completed a series of flights, the accelerometer was removed (without loss of feathers), and data were downloaded from the accelerometer to a PC using custom-made software. Synchronous timing on the loggers and a video recorder (Sony Handycam DCR-SR90E; 25 frames s^{-1}) used to videotape each bird's movements allowed us to extract accelerometer data for each flight.

By visualizing these data using Powerlab Chart (version 5, ADInstruments, Oxfordshire, UK), we estimated wing beat rate (beats s^{-1}) and flapping and gliding durations (s) for each flight by each bird. These variables were also calculated from the video footage, and these values were considered to be absolutely accurate. To assess the potential accuracy of acceleration data for estimating flight variables, percentage errors of these variables ([calculation from video footage − estimation from acceleration data] / calculation from video footage × 100) were calculated for each flight by each species. For each species (and also for flight types of the Griffon Vulture), the mean algebraic error of each variable was then calculated.

Overall dynamic body acceleration (ODBA; *g*) was calculated from the acceleration data for each flight by the Griffon Vulture. ODBA provides a measure of dynamic acceleration induced about the center of an animal's mass as a result of the movement of body parts (Ropert-Coudert et al. 2007, Halsey et al. 2008, Halsey et al., in press). The mean ODBA for each flight was then calculated to provide a measure of the mean amount of body movement (relative to the body) during that flight. The mean ODBA was calculated separately for uphill and downhill flights by the Griffon Vulture. All values are reported as mean ± 1 SD.

RESULTS

Accelerometry data were recorded and analyzed for six flights by the Harris' Hawk (mean flight duration = 7.2 ± 0.6 s), eight flights by the Tawny Eagle (5.8 ± 1.2 s), and nine flights by the Griffon Vulture (10.6 ± 1.0 s; Fig. 1).

For the Harris' Hawk and Tawny Eagle, the total distance was always covered by flying. In contrast, the Griffon Vulture landed and took off from the ground, used its legs to pick up speed before taking off, and took several steps (or jumps) after landing before stopping.

Mean values of wing beat rate, flapping duration, and gliding duration were calculated for each bird (Table 1). Mean algebraic errors were usually less than 10%.

Mean ODBA for the Griffon Vulture flying up and down a hill were 1.396 ± 0.114 (*N* = 4) and 0.884 ± 0.123 (*N* = 5), respectively. Calculated ODBA included short periods of travel on the ground just prior to and at the end of each flight. Mean ODBA during flight down the hill by the Griffon Vulture was lower than that during flight up the hill (Student's *t*-test; $t_7 = 9.2$, $P < 0.001$).

DISCUSSION

The custom-made tri-axial accelerometers yielded detailed information about the behaviors of the raptors studied. For example, data clearly showed when the Griffon Vulture was wing flapping and gliding, as well as taking-off and landing (Fig. 1). Furthermore, the Harris' Hawk was observed gliding more frequently and for longer periods than the Tawny Eagle, and this is indicated, for example, in traces of ODBA derived from the raw acceleration data recorded for the two birds (Fig. 2). Such information about behavioral time budgets cannot be obtained through observations once a focal bird has flown out of sight, behind a tree line, or darkness has fallen. Only accelerometers can provide such behavioral records regardless of a bird's location.

Accelerometers recording at high frequencies can also provide a higher level of detail about behavior. For example, the duration of periods spent flapping during a flight and the rate of wing beats during those periods can be estimated accurately. An example is provided in Figure 1A. After take-off, the *y*-axis trace shows 22 clear and full cycles before a short period of relatively constant values. From this, we estimated that 22 wing beats took place during this episode, close to the 21 beats that actually occurred according to video footage.

Calibrations between a measure of energy expenditure, such as rate of oxygen consumption, and a measure of body motion, such as ODBA,
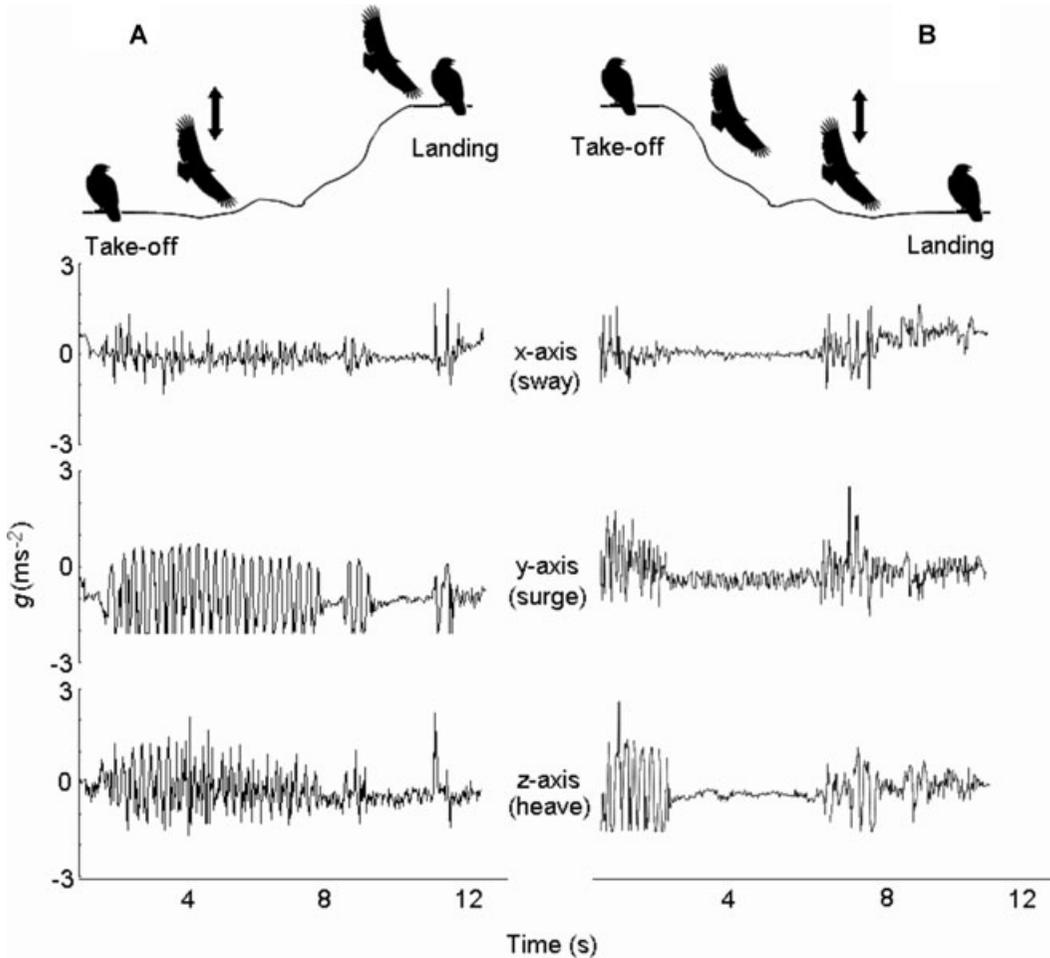
Fig. 1. Acceleration recorded by a tri-axial accelerometer deployed on a Griffon Vulture (A) flying to the top of a small hill and (B) flying back down. The Griffon Vulture flew back and forth between two handlers, each time landing on the ground in front of the handler before pausing to eat and then turning to fly back to the other handler. One handler was positioned at the top of a small hill about 7 m high and the other was about 120 m away from the bottom of the hill. The silhouettes indicate approximate periods when the Griffon Vulture was on the ground and some major periods of flapping (denoted by the presence of two-way arrows) and gliding while airborne.

are needed to estimate the absolute metabolic costs of activity from body motion data (Wilson et al. 2006, Halsey et al. 2008, Halsey et al., in press). However, without such calibrations yet assuming linearity, differences in measures of body motion can still be used to allude to differences in rate of energy expenditure in the same individual. For example, the Griffon Vulture in our study flew up and then down a hill about 7 m in height. Energy is clearly required to move the mass of the vulture from 0 m relative altitude to 7 m relative altitude at the hilltop

(the potential energy difference = mass × g × height = 515 J), whereas the vulture can use its potential energy when traveling down the hill. Therefore, the vulture should use more energy flying up the hill than down. This is suggested by the accelerometry data, with the average amount of dynamic acceleration in the center of mass (described by mean ODBA) of the vulture higher when flying up the hill. The increase in body movement, and the resulting increase in rate of energy expenditure, of the Griffon Vulture during flight up the hill is primarily

Table 1.   Calculation of flight-related variables for two raptors and a vulture using analysis of videos and estimates from raw accelerometer data.

Behavioral variable	Mean (± SD) calculation from video footage	Mean (± SD) estimation from acceleration data	Mean algebraic estimate error (%)
Wing beat frequency (beats s^{-1})			
Tawny Eagle	4.0 ± 1.1	4.2 ± 0.4	−12.2
Harris' Hawk	3.9 ± 0.6	4.0 ± 0.6	−0.6
Griffon Vulture (uphill)	3.0 ± 0.3	3.1 ± 0.2	−2.7
Griffon Vulture (downhill)	2.8 ± 1.2	3.1 ± 1.4	−9.0
Total flapping duration (s)			
Tawny Eagle	4.1 ± 0.9	4.0 ± 0.9	−0.0
Harris' Hawk	4.0 ± 0.5	4.3 ± 0.4	−5.6
Griffon Vulture (uphill)	9.1 ± 0.5	9.2 ± 0.8	−1.2
Griffon Vulture (downhill)	4.4 ± 2.6	3.9 ± 2.3	10.6
Total gliding duration (s)			
Tawny Eagle	1.8 ± 1.2	1.8 ± 1.0	1.8
Harris' Hawk	3.2 ± 0.4	3.0 ± 0.3	3.0
Griffon Vulture (uphill)	2.7 ± 0.4	2.5 ± 0.7	2.5
Griffon Vulture (downhill)	5.6 ± 2.0	6.1 ± 1.7	6.1

Mean algebraic errors of the estimates from acceleration data, against the equivalent values calculated from the video footage, are provided as percentages.

due to an increase in flapping flight (Baudinette and Schmidt-Nielsen 1974) required to increase altitude (with a concomitant decrease in gliding flight) as documented in the raw acceleration data (Fig. 1).

This simple comparison, between flight up and down a hill by a Griffon Vulture, suggests the potential for using accelerometers to assess energy expenditure of raptors and, potentially, other large birds, if calibrations are available. Obtaining such calibration data will likely involve (1) training birds to breathe into a mask while hovering (Welch et al. 2007) or flying (Bundle 2005), (2) training them to undertake terrestrial activity in a respirometer chamber and then assuming that the resultant energy expenditure–ODBA relationship holds for other behaviors (Fahlman et al. 2004), such as flight, (3) extrapolation of calibrations for more tractable bird species (Halsey et al. 2009), or (4) predicting the calibration based on known correlates with energy expenditure. Indeed, it is likely that studies employing accelerometers can provide detailed information about the flight behavior of raptors and, probably, the associated metabolic costs as well if calibrations are obtained. Importantly, however, interpretations of behavior based on accelerometry data must be made carefully until variation in the effects of logger attachment on behavior within and between species are well understood (Halsey et al. 2008).

Nonetheless, once our knowledge about applying accelerometers improves, the high-resolution time and energy data they will likely provide will be valuable for comparative studies between bird species (Prinzinger et al. 2002, Zahedi and Khan 2007). Furthermore, such data may be useful for conservation physiologists (Wikelski and Cooke 2006). Knowledge of foraging strategies and food requirements, and how these vary seasonally, can be useful for managing threatened populations (Komen 1991). Such information may permit identification of suitable habitats, development of management strategies required to create such habitats, and a better understanding of causes of fluctuations in mortality rates or reproductive success (Wikelski and Cooke 2006). For example, populations of Griffon Vultures in Pakistan have declined by up to 95% due to poisoning by the anti-inflammatory drug diclofenac that was present in many dead livestock left for scavengers (Oaks et al. 2004). Managing the recovery of these populations may be enhanced by placing feeding stations with uncontaminated food at locations where Griffon Vultures commonly fly and where energy costs of flight are low (Gilbert et al.
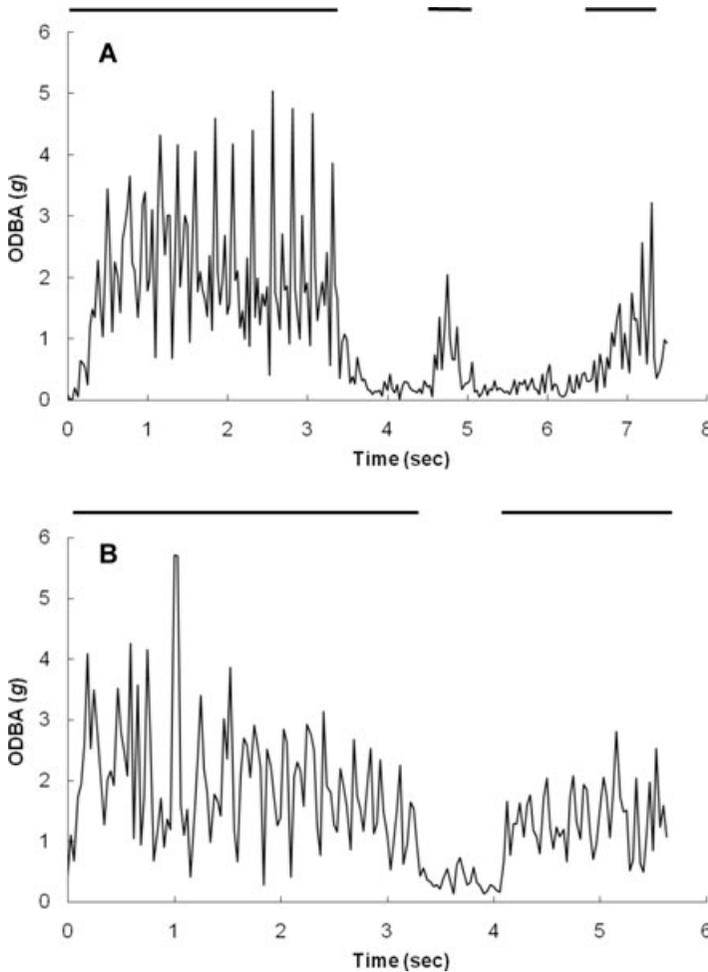
Fig. 2. Overall dynamic body acceleration (ODBA), calculated from the data recorded on a tri-axial accelerometer, during a typical short flight by (A) a trained Harris' Hawk and (B) a trained Tawny Eagle. The start and end times represent the points of take-off and landing. Periods of large gain in ODBA represent flapping flight and periods of low gain represent gliding flight (denoted by the presence and absence of a horizontal bar, respectively), verified from video records. The highest values of g may be due in part to some movement of the accelerometer relative to the bird.

2007). Concurrent efforts to remove diclofenac from the environment can be concentrated away from locations where behavioral and energetic constraints limit access by Griffon Vultures (Ruxton and Houston 2002, Gavashelishvili and McGrady 2005).

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