Take-off and landing kinetics of a free-ranging gliding mammal, the Malayan colugo (*Galeopterus variegatus*)

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Arboreal animals negotiate a highly three-dimensional world that is discontinuous on many spatial scales. As the scale of substrate discontinuity increases, many arboreal animals rely on leaping or gliding locomotion between distant supports. In order to successfully move through their habitat, gliding animals must actively modulate both propulsive and aerodynamic forces. Here we examined the take-off and landing kinetics of a free-ranging gliding mammal, the Malayan colugo (*Galeopterus variegatus*) using a custom-designed three-dimensional accelerometry system. We found that colugos increase the propulsive impulse to affect longer glides. However, we also found that landing forces are negatively associated with glide distance. Landing forces decrease rapidly as glide distance increases from the shortest glides, then level off, suggesting that the ability to reorient the aerodynamic forces prior to landing is an important mechanism to reduce velocity and thus landing forces. This ability to substantially alter the aerodynamic forces acting on the patagial wing in order to reorient the body is a key to the transition between leaping and gliding and allows gliding mammals to travel long distances between trees with reduced risk of injury. Longer glides may increase the access to distributed resources and reduce the exposure to predators in the canopy or on the forest floor.

Keywords: gliding; kinetics; free-ranging; accelerometer; mammal

1. INTRODUCTION

Arboreal animals navigate through a highly three-dimensional world that is discontinuous on many spatial scales. This discontinuous matrix of substrates requires precise placement of appendages and modulation of locomotor forces and these feats frequently must be accomplished while animals are tens of metres above the ground. Falls from tree branches can be common (Schlesinger *et al.* 1993) and can result in significant injury (Schultz 1939; Jurmain 1997). As a result, an arboreal lifestyle requires a high level of postural and dynamic control. As the scale of substrate discontinuity increases, many arboreal animals rely on leaping or gliding locomotion between distant supports. Animals may leap or glide between trees, rather than descending to the ground, to increase locomotor efficiency (Norberg 1983; Scholey 1986; Scheibe & Robins 1998; Dial 2003; Scheibe *et al.* 2006) or to avoid predators on the forest floor (Emmons & Gentry 1983). Furthermore, an open forest structure itself might facilitate these types of locomotion (Emmons & Gentry 1983; Dudley & DeVries 1990; Dial *et al.* 2004). Regardless of the motivation for these behaviours, both successful leaps and glides require the active modulation of forces during take-off and landing.

Across six orders of magnitude, mass-specific maximum force exerted scales with mass^{-0.33} (Alexander 1985; Demes *et al.* 1999; but see Biewener 1990). Nearly all previous studies (but see Demes *et al.* 1995, 1999; Paskins *et al.* 2007) measured vertical jumping performance from a horizontal substrate, a parameter that might not directly relate to how arboreal animals leap under natural conditions. The exceptions used a compliant, instrumented force pole to measure the take-off and landing kinetics of leaping strepsirrhine primates (Demes *et al.* 1995, 1999) and flying squirrels (Paskins *et al.* 2007). Take-off forces are greater than landing forces in primates leaping between these compliant poles (Demes *et al.* 1999), whereas landing forces are generally greater for animals on rigid force plates (e.g. primates: Günther 1989, Demes *et al.* 2005; frogs: Nauwelaerts & Aerts 2006). Additionally, there is no difference between take-off and landing forces in flying squirrels using the force pole methodology (Paskins *et al.* 2007). The difference in substrate compliance and orientation between these two methods (force plate versus force pole) might have profound effects on the interpretation of these results. It is likely that animals do experience compliant substrates in nature (Crompton *et al.* 1993); however, the relative compliance (i.e. how much the substrate moves when loaded) experienced by the animal should vary with body mass. For animals with small body mass, the absolute magnitude of forces is smaller, reducing

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the relative compliance of the substrate. As a result, small animals, including gliding mammals, might encounter less-compliant substrates in their environment than larger ones. Therefore, it is important to perform measurements on substrates that animals encounter in their natural habitats.

Leaping animals must generate muscular force to propel their bodies into the air during take-off and also absorb the energy of impact with their limbs upon landing. Animals can modulate these forces to some degree by altering the period of time over which they produce muscular force. However, as take-off and landing forces increase, the probability of injury also increases. Peak forces for take-off and landing increase with the leap distance in two species of primates (Demes *et al.* 1999, 2005) and a flying squirrel species (Paskins *et al.* 2007), over distances of up to 2.5 m. Were this relationship to hold over longer distances, we would predict that long leaps and especially long glides would involve a significant risk of injury to the animal. Yet to date, these longer leaping and gliding distances have not been examined.

While the kinetics of take-off are similar for leaping and gliding animals, landing dynamics might differ due to the aerodynamic forces developed during gliding. Both leaping and gliding animals initially accelerate under the force of gravity, accumulating kinetic energy that must be dissipated at landing. However, in gliders the patagial wing begins developing aerodynamic force as the animal accelerates, reducing this acceleration until the animal reaches a steady-state glide. At this velocity, lift and drag on the wing offset the body weight and the animal undergoes no net acceleration. Therefore, once a glider reaches equilibrium, landing forces should no longer increase with distance. Just prior to landing, gliding animals pitch upward, modulating the aerodynamic forces on their body in an effort to reduce landing forces and spread the impact over all four limbs (Scholey 1986; Ando & Shiraishi 1993; Paskins *et al.* 2007). In fact, if a glide is too short to effectively reduce body momentum or allow the animal to adjust its posture for landing, short glides could result in the highest peak landing forces. It has been suggested that free-ranging flying squirrels might alter glide length or trajectory to avoid short glides, thus limiting the landing forces (Ando & Shiraishi 1993). Owing to the limitations of studying locomotor kinetics in the laboratory, this hypothesis remains untested.

Field studies allow researchers to observe leaping and gliding animals in their natural habitat, travelling over distances not confined by the laboratory setting. However, most arboreal mammals are small and can travel over long distances quickly. Furthermore, all gliding mammals are nocturnal, making it particularly difficult to study the mechanics of gliding in a natural setting using traditional or high-speed videography. Thus, in most previous work on mammals (Scholey 1986; Ando & Shiraishi 1993; Vernes 2001; Stafford *et al.* 2002; Scheibe *et al.* 2006), only average performance measures were examined (but see McGuire & Dudley 2005 and Socha *et al.* 2005 for other gliding taxa).

In response to the behavioural limitations of laboratory studies and difficulties of using traditional videography techniques in the field, we created a custom-designed accelerometry system to study the locomotor kinetics of a free-ranging gliding mammal. Accelerometry has led to breakthroughs in our understanding of the locomotor

Figure 1. (a) Tagged colugo (*G. variegatus*) showing placement of data logger aligned along the animal's craniocaudal body axis. (b) Acceleration data logger. Photo shows front and back of the logger. The logger contains two dual-axis accelerometers and a bank of flash memory to record data for up to two weeks at 100 Hz.

behaviour in animals for which access is often limited, such as marine mammals and birds (e.g. Weimerskirch *et al.* 2005; Goldbogen *et al.* 2006; Sato *et al.* 2007). While accelerometers have become an important tool for describing locomotor and feeding behaviours of many animals, the sampling rates used in previous studies have generally been too low (20 Hz or less) to provide information about the locomotor forces underlying these behaviours. Higher-frequency accelerometers have also been used in laboratory studies to measure locomotor forces in flying birds (Bilo *et al.* 1984; Hedrick *et al.* 2004), but this technique has never been used on free-ranging animals. Here we measure the dynamics of take-off and landing in free-ranging Malayan colugos (*Galeopterus variegatus*, figure 1a) and examine the relationships between glide distance, substrate orientation and locomotor forces in wild animals navigating through a natural, structurally complex setting.

2. MATERIAL AND METHODS

(a) Animal protocol

During the course of the study, 13 wild colugos (*G. variegatus*) were caught in Singapore. Animals weighing less than 700 g (i.e. logger mass greater than 4% body weight), pregnant females or those carrying young were released upon capture and not used in the study. Six animals were fitted with data loggers and of these data were retrieved from five individuals (three males and two females). Animals used in the study ranged in mass between 750 g and 1.4 kg (mean 1.1 kg) and in head-body length from 31 to 40 cm.

Animals were captured by hand just prior to their active period, measured and fitted with a data logger placed on their dorsal surface over their centre of mass. Loggers were attached by shaving a small patch of fur and affixed to the skin using cyanoacrylate glue. Once the glue had set, the animals were released at the point of capture and observed through their first glide to ensure normal behaviour. Upon release, animals climbed immediately and then rested or groomed for several minutes before gliding away.

We measured the horizontal distance of these initial glides using a laser range-finder (Nikon ProStaff Laser 440). Combining these data with the glide duration recorded from the accelerometer, we calculated the average horizontal velocity of the initial glide(s) for each animal. This average horizontal velocity reached an asymptotic value in glides longer than 2 s of duration (a distance of 20 m) for all animals. This velocity was used to estimate the distance of subsequent glides for descriptive purposes. However, because this method overestimates glide distance for the subset of glides of very short duration, all statistical analyses were conducted using glide duration, not this estimate of glide length.

Each animal was also fitted with a radio-telemetry tag (A2470, ATS, Isanti, MN, USA) incorporated into the data logger. Between sunset and sunrise, the animals were located using the radio signal each hour. The radio tag also facilitated the recovery of the data loggers after falling off the animals. Data loggers dropped off the animals as the cyanoacrylate glue naturally failed. Data loggers remained on the animals for one to four weeks.

(b) Accelerometry data loggers

The custom-designed accelerometry data loggers used in this study (figure 1b) included two dual-axis MEMS accelerometers (ADXL210, Analog Devices, Norwood, MA, USA) placed with orthogonal axes, which record three-dimensional acceleration along the three body axes of the animal (figure 2). Acceleration data were polled at 100 Hz by a microcontroller (PIC18F series, Microchip Technology, Inc., Chandler, AZ, USA) and logged to a NAND flash memory chip (ST Microelectronics, Geneva, Switzerland). The device can record three-dimensional accelerations for up to 76 hours (1 Gbit flash) or 304 hours (4 Gbit flash) at this sampling rate. Data loggers were encapsulated in epoxy for water-proofing and mechanical protection, and powered by a 3.7 V lithium-ion battery (BL-5B, Nokia, Helsinki, Finland). Data-logger dimensions including the battery were $45 \times 32 \times 11$ mm and devices weighed 29 g. Females carrying young weighing 400 g or more have been observed gliding (G. Byrnes 2006, 2007, personal observation); thus, it is unlikely that the weight of the data logger influenced the animals' natural behaviour.

(c) Data processing and analysis

Once the data loggers were recovered, data were downloaded to a computer using custom software written in MATLAB v. 7.3 (The Mathworks, Inc., Natick, MA, USA). Each accelerometer was calibrated by rotating the device through 360° about each axis and comparing the voltage output to the known magnitude and direction of gravitational acceleration. The calibration was then applied to the recorded voltage output of the accelerometers to transform the data to units of gravitational acceleration ('g'). A MATLAB script was used to identify individual glides, calculate peak forces in body weights (including mass of the data logger) and find the start and end times of each impulse. Start and end times for

Figure 2. Typical force profile of a glide. Forces along the craniocaudal (X, red), lateral (Y, purple) and dorsoventral (Z, blue) axes as well as total force (black) are shown. Corresponding axes are shown on the body at right. Shaded bars indicate duration of take-off and landing impulses, respectively. Dashed line indicates the force required to offset body weight during equilibrium. Arrows indicate time points at which the body orientation (θ) at take-off and landing was calculated. Body orientation (θ) is the average angle with respect to gravity at all time points before take-off and after landing arrows, respectively.

take-off and landing impulses were identified as the first and last points, respectively, at which the resultant force exceeded the force due to gravity (figure 2, dashed line). Using these landmarks, impulse magnitude was calculated as the integral of force between these time points (figure 2, shaded regions). Subsequently, take-off and landing velocities were calculated from the change in momentum of the body during take-off and landing impulses. We assume that the velocity prior to take-off and after landing is zero. Body orientation angle (θ) with respect to gravity was calculated immediately before and after each glide from the relative magnitude of the gravitational acceleration along the three accelerometer axes. Body orientation angle was calculated as an average of all points during the static phase before and after each glide (figure 2, arrows). In order to examine the relationships between these variables (including glide duration), we employed mixed-model regression analyses controlling for individual identity. Statistical analyses were conducted using SPSS v. 14 (SPSS, Inc., Chicago, IL, USA).

3. RESULTS

A total of 430 hours of data at 100 Hz were collected from five animals from June to August 2006 and June to August 2007 (mean = 86 hours, range = 48–154 hours per animal). The animals were active only between sunset and sunrise and glided 4–29 times per night (mean = 12.0, s.d. = 7.1). A total of 222 glides were recorded. An acceleration trace of a representative glide is shown in figure 2. Gliding behaviour comprised less than 1% of total time observed (0.05%). Glide duration varied between 0.64 and 15.14 s (mean = 3.48 s, s.d. = 2.10 s). For glides of known distance over 20 m, average asymptotic horizontal velocity ranged between 9.91 and 10.2 m s⁻¹ (mean = 10.1 m s⁻¹, s.d. = 0.17 m s⁻¹). Given this average velocity, estimated glide distances ranged between 2.5 (observed) and 150 m (mean = 31.4 m, s.d. = 16.7 m).

From the three-dimensional acceleration data, the total peak force was determined for take-offs and landings. Peak

Figure 3. Relationships between glide duration and (a) peak landing force, (b) take-off impulse and (c) landing velocity. Line through each set of data points is the mixed-model regression, controlling for individual identity. In (a), the curvilinear relationship is shown to illustrate the rapid decrease in peak force over short glides as duration increases up to 2 s.

take-off forces generated by the animals were 1.00–13.0 times body weight (b.w.; mean = 4.34 b.w., s.d. = 2.10 b.w.). Peak landing forces experienced were 2.36–17.0 times the animals' body weight (mean = 6.20 b.w., s.d. = 2.84 b.w.) and were significantly greater than those generated during take-off ($t = -8.065$, d.f. = 221, $p < 0.001$).

(a) Glide duration and locomotor dynamics

The relationships between glide duration (a proxy for glide length) and peak take-off and landing forces were also examined. Glide duration significantly predicted peak

Figure 4. Relationship between take-off orientation (θ) and peak take-off force. Fit line is the mixed-model regression, controlling for individual identity. The inset shows how this angle (θ) is calculated.

landing force duration, $b = 0.413$; $p < 0.001$; figure 3a), such that longer glides were associated with lower peak landing forces. However, peak take-off forces were not associated with glide duration ($b = -0.227$; $p = 0.661$), and peak take-off forces and peak landing forces were not related ($b = -0.080$; $p = 0.481$).

Take-off impulses ranged between 0.78 and 9.4 N s (mean = 3.85 N s, s.d. = 1.57 N s). Velocity at take-off varied between 0.61 and 8.2 m s⁻¹ (mean = 3.70 m s⁻¹, s.d. = 1.49 m s⁻¹). Despite no significant relationship between peak take-off force and glide duration, take-off impulse ($b = 0.194$; $p < 0.001$; figure 3b) and take-off velocity ($b = 0.173$; $p < 0.001$) were positively associated with glide duration.

The landing impulses and the velocity just prior to landing impact were calculated from the data. Landing impulses varied between 0.61 and 14.0 N s (mean = 4.29 N s, s.d. = 1.87 N s). Velocity just prior to landing impact ranged from 0.81 to 12.8 m s⁻¹ (mean = 4.00 m s⁻¹, s.d. = 1.45 m s⁻¹). Despite a significant relationship between peak landing force and landing impulse ($b = 0.23$; $p < 0.001$) and no relationship between glide duration and landing impulse duration ($b = 0.00$; $p = 0.912$), there was not a significant relationship between glide duration and landing impulse ($b = -0.09$; $p = 0.089$). However, there was a weakly negative but significant relationship between glide duration and velocity prior to impact ($b = -0.09$; $p = 0.047$; figure 3c).

(b) Substrate orientation and locomotor dynamics

The body orientation angle (θ) with respect to gravity was calculated immediately prior to and following each glide. Orientation angle ranged from 0° to 101° (mean = 34.8°, s.d. = 17.9°) at take-off and 0°–117° (mean = 19.7°, s.d. = 12.2°) at landing. An angle of 0° indicates that the animal is oriented head up on a vertical substrate as in figure 2. Individuals landed on near horizontal substrates in only 4 of the 222 total glides. There was a significant relationship between initial orientation angle and glide duration ($b = 0.021$; $p = 0.011$) such that longer glides were initiated from orientations with a greater deviation from the vertical. Furthermore, orientation at take-off was associated with peak take-off force ($b = -3.164$; $p < 0.001$; figure 4) with larger forces being produced against vertical

substrates. However, take-off impulse was uncorrelated with orientation at take-off ($b=0.834$; $p=0.252$). Impulse durations over which propulsive force was produced were longer when individuals leaped from less vertical substrates ($b=0.001$; $p=0.024$).

4. DISCUSSION

In this study we examined the locomotor dynamics of a free-ranging gliding mammal using three-dimensional accelerometry. This technique allowed us to examine the take-off and landing forces associated with leaps or glides covering distances ranging over two orders of magnitude (approx. 2.5–150 m). This range is consistent with the previously reported distributions of glide lengths for other large gliders in the field, including the Philippine flying lemur (*Cynocephalus volans*; Wischusen 1990) and giant flying squirrels (*Petaurista petaurista*, Scholey 1986; *Petaurista leucogenys*, Ando & Shiraishi 1993). Examining free-ranging animals offers the advantage of recording glide dynamics over the natural range of glide distances, something not feasible for laboratory studies. Another strength of the technique used in this study is that kinetic data are recorded continuously, allowing for the inclusion of all glides over a given period of time.

Previous laboratory studies on leaping and gliding animals revealed a discrepancy in the relative magnitudes of take-off and landing forces, depending on the measurement technique used. In this study, we found that peak landing forces experienced by colugos in their natural habitat are greater than take-off forces, consistent with the studies using rigid force plates (Demes *et al.* 2005; Nauwelaerts & Aerts 2006). As the average tree diameter used by colugos in the study area exceeded 45 cm, it is probable that these animals normally experience non-compliant landing substrates in their natural habitat. However, because they initiate glides from a wide range of bole and branch diameters, which generally decrease with height in the tree, it is possible that colugos may leap from compliant substrates at times, especially when they are high in the canopy.

Across a wide range of body masses, mass-specific maximum force varies with mass^{-0.33}, as predicted by geometric similarity (Alexander 1985). Our measurements of peak take-off forces in colugos fit this prediction. However, we found that the maximum forces exerted by colugos during take-off are considerably less than those in strepsirrhine primates of similar mass (Günther 1989; Demes *et al.* 1995, 1999). This might be because strepsirrhines are unable to develop significant aerodynamic forces (Demes *et al.* 1991), thus making them dependent primarily on propulsive forces. Furthermore, the current study measured the performance of colugos taking off from substrates spanning a wide range of natural variability in compliance possibly reducing average forces. We also found that peak landing forces in colugos are much lower than that in strepsirrhines (Demes *et al.* 1995, 1999), most likely because gliding colugos are able to use aerodynamic forces to reduce their pre-landing velocity and impact force.

Previous studies have found that peak take-off forces increase with distance travelled in strepsirrhine primates (Demes *et al.* 1999) and flying squirrels (Paskins *et al.* 2007), but these studies were performed only over short leap and glide distances. Our results over a wide range of

glide distances show no relationship between glide duration and peak take-off force. However, we do find a relationship between the glide duration and the total take-off impulse generated. The take-off kinetics are highly variable over all distances, suggesting that the natural variation in take-off substrates might play a large role in determining the kinetics of take-off in free-ranging animals.

In an attempt to assess this variation, we examined the orientation of the animal just prior to take-off to determine the substrate orientation. Owing to the branching morphology of trees, we would expect substrates higher in the tree to have less vertical orientations and have narrower diameters. The effect of this pattern is a vertical stratification of substrate compliance in each tree. Our results support this hypothesis. First, longer glides were initiated from less vertical substrates, demonstrating that there is probably a pattern between substrate orientation and height in a tree. Furthermore, we found that peak take-off forces decreased in leaps from less vertical substrates. One explanation is that animals high in the tree can travel long distances without generating a large take-off impulse. However, we also found that take-off impulse durations increased in leaps from less vertical substrates suggesting these substrates may be narrower and thus more compliant. This relationship should be explored further in future work.

Although landing forces have been shown to increase with distance in both primates and flying squirrels (Demes *et al.* 1999; Paskins *et al.* 2007), our study, over a wider range of distances, showed that the opposite is true in free-ranging colugos. If forces were to continue to increase linearly, the probability of injury on landing would also increase, especially over the glide lengths observed in this study. However, if a gliding mammal reaches equilibrium, velocity, and therefore kinetic energy at impact, should reach an asymptote, and we would expect to see landing forces level off at intermediate distances and remain constant for longer distances. In fact, our results show a negative relationship between glide duration and peak landing force over a naturally occurring range of glide distances. In addition, we find no relationship between glide duration and landing impulse, and a weakly negative relationship between glide duration and landing velocity. One mechanism that animals could use to reduce peak landing force is to spread the landing impulse over a longer period of time. However, in our study, this is not the case—the duration of the landing impulse is invariant with glide duration. These lines of evidence show that colugos must be reducing the landing impact by modulating aerodynamic forces while airborne, prior to landing. Our data show that colugos often glide at equilibrium for some period of time before landing and that they are capable of producing aerodynamic forces in excess of that required to offset their body weight at equilibrium (figure 2, dashed line) suggesting that colugos actually slow their descent throughout much of the glide. This result is consistent with a study of the kinematics of the gliding flight of dragonflies (Wakeling & Ellington 1997).

Another important mechanism for reducing impact velocity is changing body posture in the air prior to landing (Nachtigall 1979; Scholey 1986; Stafford *et al.* 2002). By pitching upward and reorienting the patagial wing with respect to the oncoming flow prior to landing, a gliding mammal can increase lift and/or drag on the wing, thereby

reducing the velocity and the landing impulse. In this study, we found an average landing velocity of 3.99 m s^{-1} , a reduction of approximately 60% from the average horizontal velocity of glides that reach equilibrium. This ability to modulate the forces acting on them before impact allows the gliding animals to land safely after gliding long distances.

If, however, the glide duration is too short to complete this landing manoeuvre, the energy that needs to be absorbed during landing will be greater. Furthermore, if the animal does not have sufficient time to reorient its body to land with all four limbs simultaneously, peak forces on the forelimbs could be even greater. Observational data from a giant flying squirrel suggest that these animals choose glide paths to avoid short glides (Ando & Shiraishi 1993). Our results also support the assertion that short glides may subject the animals to the highest landing peak forces. Peak forces experienced in the shortest glides were the greatest but decreased rapidly in glides up to 2 s in duration and were nearly constant for longer glides (figure 3a), indicating that changing posture for aerial braking is an important component of the glide that reduces the landing impact.

This ability to significantly modulate aerodynamic forces is probably an important trait in the transition from leaping to gliding. It enables gliders to reduce the impact forces in long glides thus reducing the risk of injury. Increasing the distance that can be safely travelled in a single glide increases access to distributed food or nesting resources. Furthermore, by travelling long distances rapidly without moving through the canopy or across the ground, colugos could avoid both arboreal and terrestrial predators.

In this study, we have validated the relationship between glide length and landing kinetics predicted by aerodynamic theory—a relationship that would be impossible to test in a laboratory setting. Furthermore, our data illustrate the dynamic nature of the glide trajectory and the importance of an animal's ability to modulate aerodynamic forces prior to impact in order to control the landing impulse. Although we focused on a single species, this study demonstrates the feasibility and benefits of studying locomotor biomechanics in free-ranging animals. Novel tools such as accelerometry allow us to gain an insight into the physical interactions between animals and their natural environment, and are key to understanding locomotion in a wide variety of animals for which laboratory-based studies are impractical.

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REFERENCES

- Alexander, R. McN. 1985 The maximum forces exerted by animals. *J. Exp. Biol.* **115**, 231–238.
- Ando, M. & Shiraishi, S. 1993 Gliding flight in the Japanese giant flying squirrel *Petaurista leucogenys*. *J. Mammal. Soc. Jpn* **18**, 19–32.
- Biewener, A. A. 1990 Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097–1103. (doi:10.1126/science.2251499)
- Bilo, D., Lauck, A. & Nachtigall, W. 1984 Measurement of linear body accelerations and calculation of the instantaneous aerodynamic lift and thrust in a pigeon flying in a wind tunnel. In *Biona-report 3* (ed. W. Nachtigall), pp. 87–108. Stuttgart, Germany: Gustav Fischer.
- Crompton, R. H., Sellers, W. I. & Günther, M. M. 1993 Energetic efficiency and ecology as selective factors in the saltatory adaptation of prosimian primates. *Proc. R. Soc. B* **254**, 41–45. (doi:10.1098/rspb.1993.0124)
- Demes, B., Forchap, E. & Herwig, H. 1991 They seem to glide. Are there aerodynamic effects in leaping prosimian primates? *Z. Morphol. Anthropol.* **78**, 373–385.
- Demes, B., Jungers, W. L., Gross, T. S. & Fleagle, J. G. 1995 Kinetics of leaping primates: influence of substrate orientation and compliance. *Am. J. Phys. Anthropol.* **96**, 419–429. (doi:10.1002/ajpa.1330960407)
- Demes, B., Fleagle, J. G. & Jungers, W. L. 1999 Take-off and landing forces of leaping strepsirrhine primates. *J. Hum. Evol.* **37**, 279–292. (doi:10.1006/jhev.1999.0311)
- Demes, B., Franz, T. M. & Carlson, K. J. 2005 External forces on the limbs of jumping lemurs and takeoff and landing. *Am. J. Phys. Anthropol.* **128**, 348–358. (doi:10.1002/ajpa.20043)
- Dial, R. 2003 Energetic savings and the body size distributions of gliding mammals. *Evol. Ecol. Res.* **5**, 1151–1162.
- Dial, R., Bloodworth, B., Lee, A., Boyne, P. & Heys, J. 2004 The distribution of free space and its relation to canopy composition at six forest sites. *For. Sci.* **50**, 312–325.
- Dudley, R. & DeVries, P. 1990 Tropical rain forest structure and the geographical distribution of gliding vertebrates. *Biotropica* **22**, 432–434. (doi:10.2307/2388564)
- Emmons, L. H. & Gentry, A. H. 1983 Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *Am. Nat.* **121**, 513–524. (doi:10.1086/284079)
- Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A. & Hildebrand, J. A. 2006 Kinematics of foraging dives and lunge-feeding in fin whales. *J. Exp. Biol.* **209**, 1231–1244. (doi:10.1242/jeb.02135)
- Günther, M. M. 1989 Funktionsmorphologische Untersuchungen zum Sprungverhalten an mehreren Halbaffenarten (*Galago moholi*, *Galago garnettii*, *Lemur catta*). PhD dissertation, Freie Universität, Berlin.
- Hedrick, T. L., Usherwood, J. R. & Biewener, A. A. 2004 Wing inertia and whole-body acceleration: an analysis of instantaneous aerodynamic force production in cockatiels (*Nymphicus hollandicus*) flying across a range of speeds. *J. Exp. Biol.* **207**, 1689–1702. (doi:10.1242/jeb.00933)
- Jurmain, R. 1997 Skeletal evidence of trauma in the African apes, with special reference to the Gombe chimpanzees. *Primates* **38**, 1–14. (doi:10.1007/BF02385918)
- McGuire, J. A. & Dudley, R. 2005 The cost of living large: comparative glide performance in flying lizards (Agamidae: *Draco*). *Am. Nat.* **166**, 93–106. (doi:10.1086/430725)
- Nachtigall, W. 1979 Gleitflug des Flugbeutlers *Petaurus breviceps papuanus* II. Filmanalysen zur Einstellung von Gleitbahn und Rumpf sowie zur Steuerung des Gleitflugs. *J. Comp. Phys. A* **133**, 89–95. (doi:10.1007/BF00663112)

- Nauwelaerts, S. & Aerts, P. 2006 Take-off and landing forces in jumping frogs. *J. Exp. Biol.* **209**, 66–77. (doi:10.1242/jeb.01969)
- Norberg, R.Å. 1983 Optimal locomotion modes of foraging birds in trees. *Ibis* **125**, 172–180.
- Paskins, K. E., Bowyer, A., Megill, W. M. & Scheibe, J. S. 2007 Take-off and landing forces and the evolution of controlled gliding in northern flying squirrels *Glaucomys sabrinus*. *J. Exp. Biol.* **210**, 1413–1423. (doi:10.1242/jeb.02747)
- Sato, K. *et al.* 2007 Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. B* **274**, 471–477. (doi:10.1098/rspb.2006.0005)
- Scheibe, J. S. & Robins, J. H. 1998 Morphological and performance attributes of gliding mammals. In *Ecology and evolutionary biology of tree squirrels* (eds M. A. Steele, J. F. Merritt & D. A. Zegers), pp. 131–144. Martinsville, VA: Virginia Museum of Natural History.
- Scheibe, J. S., Smith, W. P., Bassham, J. & Magness, D. 2006 Locomotor performance and cost of transport in the northern flying squirrel *Glaucomys sabrinus*. *Acta Theriol.* **51**, 169–178.
- Schlesinger, W. H., Knops, J. M. H. & Nash, T. H. 1993 Arboreal sprint failure: lizardfall in a California oak woodland. *Ecology* **74**, 2465–2467. (doi:10.2307/1939598)
- Scholey, K. 1986 The climbing and gliding locomotion of the giant red flying squirrel *Petaurista petaurista* (Sciuridae). In *Biona-report 5* (ed. W. Nachtigall), pp. 187–204. Stuttgart, Germany: Gustav Fischer.
- Schultz, A. H. 1939 Notes on the diseases and healed fractures of wild apes and their bearing on the antiquity of pathological conditions in man. *Bull. Hist. Med.* **7**, 571–582.
- Socha, J. J., O'Dempsey, T. & LaBarbera, M. 2005 A 3-D kinematic analysis of gliding in a flying snake, *Chrysopelea paradisi*. *J. Exp. Biol.* **208**, 1817–1833. (doi:10.1242/jeb.01579)
- Stafford, B. J., Thorington Jr, R. W. & Kawamichi, T. 2002 Gliding behavior of Japanese giant flying squirrels (*Petaurista leucogenys*). *J. Mammal.* **83**, 553–562. (doi:10.1644/1545-1542(2002)083<0553:GBOJGF>2.0.CO;2)
- Vernes, K. 2001 Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forest of eastern Canada. *J. Mammal.* **82**, 1026–1033. (doi:10.1644/1545-1542(2001)082<1026:GPOTNF>2.0.CO;2)
- Wakeling, J. M. & Ellington, C. P. 1997 Dragonfly flight I. Gliding flight and steady-state aerodynamic forces. *J. Exp. Biol.* **200**, 543–556.
- Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A. & Marsac, F. 2005 The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proc. R. Soc. B* **272**, 53–61. (doi:10.1098/rspb.2004.2918)
- Wischusen, E. W. 1990 The foraging ecology and natural history of the Philippine flying lemur (*Cynocephalus volans*). PhD dissertation, Cornell University, Ithaca, NY.