

Flight mechanics of the Ivory-billed Woodpecker

(Campephilus principalis)

Michael D. Collins

Background Abstract: Two independent groups of ornithologists have recently reported observations of the Ivory-billed Woodpecker (*Campephilus principalis*), which was feared to be extinct despite a steady flow of reports since the last known nest sites were studied in the 1930s. From specimens and historical observations, it is known that this species has an unusual physiology and fascinating flight characteristics, including a high flap rate, a fast and direct flight, and dramatic swooping takeoffs and landings.

Methodology/Principal Findings Abstract: Known physiological parameters and historical accounts are applied in the two leading flap rate models to obtain predictions that the flap rate should be significantly greater than that of the Pileated Woodpecker (*Dryocopus pileatus*), which is the only conceivable confusion species. Video footage of birds that were identified in the field as Ivory-billed Woodpeckers is analyzed in terms of the flap rate models, historical accounts, and physiology.

Conclusions/Significance Abstract: A video obtained in Louisiana in 2006 shows a large woodpecker that is consistent with Ivory-billed Woodpecker in terms of posture while perched, large crest, large bill, and takeoffs involving deep and rapid flaps. A video obtained in the same area in 2008 shows a large bird with the flap style of a large woodpecker, a flap rate and flight speed that are much too high for Pileated Woodpecker, and large white patches on the wings that are consistent with Ivory-billed Woodpecker. A video obtained in Florida in 2007 shows a swooping takeoff and landing and a takeoff with deep and rapid flaps that are consistent with the 2006 video.

Introduction

Despite a steady stream of reports over the years, the Ivory-billed Woodpecker (*Campephilus principalis*) was feared to have been extinct since shortly after a study of the last known breeding pairs [1]. Two independent teams of ornithologists have recently reported multiple sightings and various forms of evidence from Arkansas [2] and Florida [3]. This paper reports on additional sightings and evidence from Louisiana and Florida, including video footage that provides insights into the fascinating flight mechanics of this species—according to John James Audubon [4], “the flight of this bird is graceful in the extreme.”

Videos were obtained during three encounters in which key field marks consistent with the Ivory-billed Woodpecker were observed, including footage of a cruising flight, two takeoffs into level flight, a short flight, a swooping takeoff, and a swooping landing. The flight mechanics of the birds in these videos are consistent with Ivory-billed Woodpeckers in terms of historical accounts, physiology, and empirical [5] and physics-based [6] models for flap rate. Various additional characteristics of the birds in the videos are consistent with Ivory-billed Woodpeckers, including apparent field marks, a massive bill, a large crest, and an exaggerated leaned-back posture while perched.

Methods and Results

Historical accounts, physiology, and flap rate models

The Ivory-billed Woodpecker has a wingspan that is only slightly greater than that of the superficially similar Pileated Woodpecker (*Dryocopus pileatus*) but a body mass that is much greater and a wing surface area that is much lower. The unusual physiology of this species would be expected to translate into unusual flight characteristics, and in fact historical accounts mention remarkable cruising and swooping flights. The cruising flight was described as fast and direct like that of a duck [1,4]. Short flights made with graceful swoops were described as “forming an elegantly curved line” by Audubon [4]. Tanner

reported rapid wingbeats during cruising flight, short flights involving gliding and swooping, and “particularly hard” flaps at takeoff [1]. Christy described “deep and rapid strokes” at takeoff [7]. The flap rate of an Ivory-billed Woodpecker taking off from a nest in 1935 was determined to be 8.4 Hz from an acoustic recording of the flaps [8].

The flap rate of a bird in cruising flight is restricted to a relatively narrow distribution. For example, “mass and wing morphology, together with some environmental variables such as gravity and air density, define a ‘natural’ frequency, from which the bird cannot stray too far, in the same way that a pendulum has a natural frequency and can only be driven at frequencies close to this” according to Pennycuick, who obtained flap rate data for 47 species and found the standard deviation to be less than 10% for 45 of them and less than 18% for all of them [5,9]. Similar results were obtained for woodpeckers by Tobalske, who found the standard deviation to be less than 10% for each of five species [10]. The flap rates and standard deviations listed in Table 2 of Ref. 5 and Table 3 of Ref. 9 are based on extensive sampling; at least 10 observations and 100 flaps were sampled for most species, and the data set represents species with a wide variety of physiological parameters. A multi-parameter fit was applied to these data to obtain the flap rate model [5],

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

where f is the flap rate, g is the acceleration due to gravity, ρ is the air density, m is the body mass, b is the wingspan, and S is the wing surface area. This model is based on statistics and provides an estimate for the mean flap rate in terms of mean estimates of the physiological parameters, even when only one measurement is available [9].

Two definitions for flap rate are used for woodpeckers, which often hold their wings fixed for a significant percentage of the time (intermittent flaps). The raw flap rate is defined to be the number of flaps divided by the elapsed time. The intrinsic flap rate is obtained by subtracting out intervals in which the wings are held fixed [10]. Since Pennycuick’s model was designed for birds in cruising flight, the intrinsic flap rate

should be used in Eq. (1). Since the Ivory-billed Woodpecker has a direct flight, the intrinsic and raw flap rates would be expected to be the same for this species in cruising flight.

Due to the complexity of the physics and physiology of flight, it would be difficult to interpret the details of Pennycuick's model from basic principles, but the signs of the exponents appear to be consistent with the expected effects of varying one parameter at a time. Since birds tend to flap harder when carrying heavy prey or missing primary flight feathers, for example, flap rate would be expected to increase with body mass and decrease with wing surface area as the model predicts. Similar reasoning applies to the accounts of Tanner [1] and Christy [7] on takeoffs of the Ivory-billed Woodpecker, a relatively massive bird with relatively low wing surface area that would be expected to struggle during takeoffs. Swooping takeoffs are evidently an alternative to deep and rapid flaps in which gravity is used to assist the acceleration to cruising speed.

Although no historical footage exists of an Ivory-billed Woodpecker in cruising flight, an estimate of flap rate can be obtained from Pennycuick's model. Due to the apparent lack of a published value for the wing surface area of the Ivory-billed Woodpecker, we apply Eq. (1) in a way that does not directly require this quantity. Applying Eq. (1) to both the Ivory-billed Woodpecker and the Pileated Woodpecker and taking the ratio of these equations, we obtain

$$f \cong \left(\frac{m}{m_0} \right)^{3/8} \left(\frac{b_0}{b} \right)^{23/24} \left(\frac{S_0}{S} \right)^{1/3} f_0, \quad (2)$$

where the subscripted quantities correspond to the Pileated Woodpecker.

Assuming that wingspan ratio is approximately equal to wing length ratio for these species and applying estimates for the aspect ratio of a single wing of 1.65 for Pileated Woodpecker and 2.4 for Ivory-billed Woodpecker [12], we obtain

$$\frac{S_0}{S} \cong \frac{2.4}{1.65} \left(\frac{b_0}{b} \right)^2. \quad (3)$$

Applying the mean value $f_0 = 5.2$ Hz from Tobalske [10], the mean values $m = 510$ g and $m_0 = 295$ g from Winkler *et al.* [11], and the mean values $b = 0.775$ m and $b_0 = 0.724$ m from various sources, we obtain

$$f \cong \left(\frac{510}{295} \right)^{3/8} \left(\frac{0.724}{0.775} \right)^{39/24} \left(\frac{2.4}{1.65} \right)^{1/3} 5.2 \text{ Hz} \cong 6.5 \text{ Hz}. \quad (4)$$

Although the flap rate prediction was obtained using appropriate inputs (mean estimates of the physiological parameters), it is worthwhile to explore the sensitivity of this result to the parameters of the Ivory-billed Woodpecker, which are not as well sampled as the parameters of the Pileated Woodpecker (e.g., only one aspect ratio measurement exists for the Ivory-billed Woodpecker). Varying one parameter at a time, we obtain $f \cong 6.2$ Hz for $m = 450$ g, $f \cong 6.3$ Hz for $b = 0.787$ m, and $f \cong 6.2$ Hz for an aspect ratio of 2.1. Changes in these parameters of opposite sign result in predicted flap rates greater than 6.5 Hz. Differences between individuals of a species are better represented by variations that are approximately isometric than by variations of one parameter at a time. For example, we obtain $f \cong 6.2$ Hz for $m = 450$ g, $b = 0.762$ m, and an aspect ratio of 2.2.

Flap rate can also be estimated using the physics-based model [6],

$$f = \frac{St \cdot U}{b \sin(33.5b^{-0.24})}, \quad (5)$$

where St is the Strouhal number, U is the flight speed, and b is the wingspan in meters. It was determined that $St = 0.21$ is an effective value for birds (such as the Ivory-billed Woodpecker) that have direct flights [6]. Although the flight speed of the Ivory-billed Woodpecker was never measured, it should be safe to conclude from historical accounts

of a fast and direct cruising flight that this quantity is significantly greater than the maximum flight speed of 11.6 m/s that Tobalske [10] observed for the Pileated Woodpecker (which has an intermittent flight). Substituting these values into Eq. (5), we conclude that the Ivory-billed Woodpecker would be expected to have a flap rate significantly greater than 5.4 Hz .

It would be natural to assume that Tanner was tacitly making a comparison with the Pileated Woodpecker (the only comparable species within the range of the Ivory-billed Woodpecker) in his account of rapid wingbeats during cruising flight [1], and indeed the two leading flap rate models predict that the Ivory-billed Woodpecker has a much higher flap rate than the 3.7 Hz mean of the raw flap rate of the Pileated Woodpecker [10], which is obtained by multiplying the intrinsic flap rate by the percent cycle time spent flapping (see Table 5 in Ref. 10). High flap rates have been observed in a putative Ivory-billed Woodpecker video [2] and in Pileated Woodpeckers that were intentionally flushed [13], but those birds were gaining altitude during escape flights. Flap rate in level cruising flight should be more reliable for species identification.

Fieldwork, observations, and video footage

Three putative Ivory-billed Woodpecker videos were obtained during a total of 84 weeks of fieldwork between November 2005 and October 2008. Although no clear image of an Ivory-billed Woodpecker has been obtained in recent decades, flap rate, flap style, and other aspects of the flight mechanics are unambiguously resolved in these videos. Most of the searching involved kayaking and walking through bottomland forest habitat, but some time was spent observing from exceptionally tall baldcypress (*Taxodium distichum*) trees that provide views out to long distances over the surrounding forest. Most of the fieldwork was conducted in the Pearl River basin in Louisiana, where there were clusters of sightings and long periods with no sightings, including a total of 51 weeks between November 2006 and February 2008. On February 20, 2006, a video was obtained in the Pearl River basin, approximately 8 km from the location where David Kulivan reported a pair of Ivory-billed Woodpeckers in 1999. During a visit with the authors of Ref. 3 on

January 19, 2007, a video was obtained in the Choctawhatchee River basin in Florida. On March 29, 2008, a video was obtained 840 m from the site where the 2006 video was obtained.

The 2006 video was obtained immediately after the last of five sightings in which deep and rapid flaps and field marks consistent with Ivory-billed Woodpecker were observed in a concentrated area over a five-day period. Vocalizations consistent with the characteristic “kent” calls of this species were heard on two occasions in the same area during this period. During the morning of February 16, a large dark bird flushed from near the bank at close range and provided a clear view of large white patches on the trailing edges of the dorsal surfaces of the wings as it flew into the woods with deep and rapid flaps. Late that afternoon, three kents heard at the same location were immediately followed by the territorial calls of a Pileated Woodpecker that seemed to be reacting to the kents. On February 17, a large dark bird glided low across the water and provided a clear view across the dorsal surfaces of both wings, which had large white patches on the trailing edges. On February 18, kents were heard coming from behind a fallen tree on the bank at close range. An American Robin (*Turdus migratorius*) was scolding the source of the kents from a few meters above. More than a minute into the encounter, kents began coming from a second bird on the opposite bank. After the second bird apparently noticed the author near the first bird, a few harsh scolding calls and then a series of high-pitched calls came from the direction of the second bird.

At the same location on February 20, a large woodpecker was briefly observed perched on the side of a dead tree. Large white patches were observed on the trailing edges of the dorsal surfaces of the wings as the bird flew into the woods, and high-pitched calls immediately began coming from that direction. Less than a minute into the encounter, a video camera was turned on and kept aimed at the source of the calls, which were recorded at 1, 6, 15, 45, 52, 56, 67, 82, 85, 86, 90, 92, 100, 104, 110, and 120 s into the video (Audio S1). Two American Crows (*Corvus brachyrhynchos*) that appeared to be harassing the bird can be heard in the recording. The calls seemed to have stopped by 195 s, and the kayak was backed into an observation position near the opposite bank. Four

more high-pitched calls came from deep in the woods between 337 and 363 s. The high-pitched calls sound similar to the Blue Jay (*Cyanocitta cristata*) bell call [14] but also seem to fit Tanner's description of an alarm call of the Ivory-billed Woodpecker [1]: "When the bird is disturbed, the pitch of the kent rises." During both encounters, the calls began at a moment when the bird was disturbed and came from the direction of the bird. During the second encounter, the calls made it possible to track the movements of the bird through more than 200 m of dense habitat. It is possible that a hidden Blue Jay made the calls, but the sonogram (Fig. S1) has characteristics in common with the sonograms of known and putative vocalizations of the Ivory-billed Woodpecker and does not match published sonograms of bell calls [14].

At 609 s, the motion of a large woodpecker was detected in the fork of a tree near where the last calls originated. This tree is 128 m from the observation position, 77 m deep in the woods, and 218 m from the tree on which the bird was perched at the beginning of the encounter (Movie S1). Footage of the bird was obtained by keeping the camera aimed in the direction of the motion while unsuccessfully attempting to observe the bird through binoculars. This is the first putative Ivory-billed Woodpecker footage that shows the head, the bill, the crest, the neck, a perched bird, level flight, and a bird that is unquestionably a woodpecker. While climbing upward and rotating around the left branch of the fork, the bird remained in an exaggerated leaned-back posture (Fig. S2) that would be unusual for a Pileated Woodpecker (which typically has a more upright posture) but is consistent with historical photos of Ivory-billed Woodpeckers, including the upper photos in Plates 11 and 15 of Allen and Kellogg [15]. Various additional characteristics of the bird in the video are consistent with Ivory-billed Woodpecker (Fig. S3, Fig. S4, Fig. S5) but inconsistent with Pileated Woodpecker (the only conceivable confusion species). Appearing in Fig. 1 is a series of frames that show a level takeoff into a short flight across the fork at 635 s (Movie S2); the wings were raised high above the plane of the body during a deep and rapid flap that corresponds to about 7.5 Hz. At 690 s, the bird took off into level flight with deep flaps and a flap rate of about 7.5 Hz (Movie S3, Movie S4). The deep and rapid flaps during these takeoffs are consistent with the physiology of the Ivory-billed Woodpecker and the accounts of takeoffs by Tanner [1]

and Christy [7]. Pileated Woodpeckers have relatively low body mass and high wing surface area and do not require deep and rapid flaps in level takeoffs (Movie S5, Movie S6).

The 2007 video was obtained while following up on a report of a possible sighting of a pair of Ivory-billed Woodpeckers the previous day. The encounter began when two large birds were observed swooping between perches in the distant canopy. A video camera was running when the birds were detected, but there was a brief delay in obtaining footage since the tape needed to be rewound. During one of the swoops, a large white patch on the trailing edge of the dorsal surface of the right wing was observed through binoculars. The video includes a swooping takeoff from a high perch at 122 s (Movie S7), a takeoff into level flight that shows deep and rapid flaps similar to those in the 2006 video at 337 s (Movie S8), and a swooping landing in which the underwings appear to be mostly white at 923 s (Movie S9). At about 465 s, several White-tailed Deer (*Odocoileus virginianus*) moved through the area and passed nearly directly below the birds.

The 2008 video was obtained from a vantage point approximately 23 m above the water in a baldcypress. A large bird approached along a small bayou, flew nearly directly below the observation tree, and then continued along the bayou beyond the observation tree. Based on the fast and direct flight, the bird was assumed to be a Wood Duck (*Aix sponsa*) when initially detected in the distance, but two white dorsal stripes (a key field mark of the Ivory-billed Woodpecker) were observed just before it passed nearly directly below. This is the first putative footage of an Ivory-billed Woodpecker in cruising flight. The wingspan (Fig. S6) and the large white patches on the dorsal surfaces of the wings (Fig. S7, Fig. S8, Movie S10) are consistent with Ivory-billed Woodpecker, and a putative double rap (which is characteristic of *Campephilus* woodpeckers) was recorded in the video 77 s before the bird flew into view (Movie S11).

Historical accounts of a duck-like flight caused a widespread misconception in recent years that the Ivory-billed Woodpecker has duck-like flaps in which the wings remain extended throughout the flap cycle, a flap style that is often referred to as “stiff

wingbeats.” As can be seen in clips from the 2008 video (Movie S12, Movie S13), however, the wings are folded close to the body in the middle of each upstroke, and the flap style is actually consistent with that of other large woodpeckers (Bret Tobalske, personal communication). Being among those who expected duck-like flaps, the author was faced with an apparent paradox after examining this footage; the dorsal stripes implied Ivory-billed Woodpecker, which the flap style seemed to rule out. The photos by Tanner that appear in Fig. 2 (the significance of which had apparently been overlooked for many years) helped to resolve this issue. The flap rate varied between 6.6 ± 0.05 Hz (15 flaps in 2.27 s) during the approach to 7.5 ± 0.2 Hz (4 flaps in 0.533 s) just beyond the observation tree (the uncertainties account for the fact that the periodic return of the wings to a specific point in the cycle may occur between frames). These values are consistent with the estimates obtained using the flap rate models and much greater than any flap rate that has been reported for a Pileated Woodpecker in cruising flight. If the standard deviation of the raw flap rate is comparable to the standard deviation of the intrinsic flap rate, which Tobalske found to be 7.7% for the Pileated Woodpecker [10], it would not seem to be statistically reasonable for this species to achieve a raw flap rate of 6.6 to 7.5 Hz, which is 78 to 103% greater than the 3.7 Hz mean.

Since the bird and its reflection are visible in the video, the horizontal position of the bird can in principle be determined precisely as a function of time in order to obtain the flight speed. In practice, such measurements are difficult due to variations in water level, changes in the amount of foliage, and the high vantage point. An estimate of the flight speed was obtained by climbing back up the observation tree and directing assistants to reference points below, where they placed marker stakes. The reference points that are known with the highest degree of certainty correspond to when the bird passed just to the side of a water tupelo (*Nyssa aquatica*) during the approach and when the bird passed nearly directly below the observation tree. The estimated distance of 37.5 m between these points is believed to be correct to within 1 m and was covered in 2.48 s, which corresponds to 15.1 ± 0.4 m/s. There is no need to correct for wind, which was negligible that morning (as can be seen from the smooth surface of the water). The flight speed is consistent with Eq. (5) and the 6.6 to 7.5 Hz flap rate, and it is significantly greater than

the maximum of 11.6 m/s that Tobalske observed for Pileated Woodpecker [10]. The high flap rate and fast and direct flight are consistent with historical accounts of the Ivory-billed Woodpecker.

With the exception of the higher flap rate, the wingtip elevation and wingspan curves in Fig. 3 are similar to the corresponding curves for a Pileated Woodpecker in Fig. 8 of Tobalske [10]. The wingtip elevation increases during the upstroke, decreases during the downstroke, and changes sign in the middle of these strokes. At the zero crossings of the wingtip elevation curve, the wingspan curve has much smaller values on the upstroke than on the downstroke; this behavior and the brief pauses in the middle of the upstroke are consistent with a large woodpecker (Bret Tobalske, personal communication). There does not appear to be any mention of pauses in the middle of the upstroke in historical accounts of Ivory-billed Woodpeckers, but the short duration would make them difficult to detect in the field. A possible explanation for the pauses is that some families of birds that consist mainly of intermittent fliers (such as woodpeckers) have members that are direct fliers but retain a vestige of intermittent flight.

Discussion

A great deal about the flight mechanics of the Ivory-billed Woodpecker can be deduced from historical accounts, physiology, and flap rate models. The cruising flight is fast and direct and involves rapid flaps. Due to its relatively high mass and low wing surface area, takeoffs into level flight require deep and rapid flaps. As an alternative to deep and rapid flaps, an Ivory-billed Woodpecker can take off by dropping from a high perch and using gravity to accelerate. The two leading flap rate models predict that the Ivory-billed Woodpecker has a significantly higher flap rate than the Pileated Woodpecker in cruising flight.

Video footage was obtained during three encounters in which key field marks consistent with the Ivory-billed Woodpecker were observed. The flight mechanics and other characteristics of the birds in these videos are consistent with the Ivory-billed

Woodpecker in terms of physiology, historical accounts, and flap rate models. The bird in the cruising flight footage has the flap style of a large woodpecker, a flap rate that is well above the range of the Pileated Woodpecker but consistent with flap rate models and historical accounts, a fast and direct flight that is consistent with historical accounts, and large white patches on the dorsal surfaces of the wings. A large woodpecker with a massive bill, large crest, and leaned-back posture takes off into two level flights with deep and rapid flaps that are consistent with the physiology of the Ivory-billed Woodpecker, historical accounts, and a historical acoustic recording of flaps. Two birds were observed swooping between perches in the distant canopy in a way that fits historical accounts of the Ivory-billed Woodpecker. A key field mark was observed on one of the birds, and swoops and a takeoff with deep and rapid flaps were captured in the video.

Ivory-billed Woodpeckers have large territories in inaccessible habitat and are ultra-wary according to most reports since the 1940s. Several years of major efforts to document this species at locations in Arkansas and Florida have resulted in numerous sightings and a few low-quality videos, but no high-quality imagery has been obtained at any location in decades. This is a serious problem since efforts to save the Ivory-billed Woodpecker from extinction will be dependent on determining locations where it exists. The unusual flight mechanics of this species may prove to be the most useful factor for establishing its presence. According to Pennycuik [5], for example, birds are often identified based on “small differences of wingbeat frequency to distinguish between similar and closely related species, at distances too great to see plumage details.”

Acknowledgments

The author gratefully acknowledges Bret Tobalske for analyzing the 2008 video and providing expertise in woodpecker flight mechanics; Steve Sillett, Jim C. Spickler, and Michael Taylor for helping locate suitable observation trees, providing tree climbing expertise, donating climbing gear, and rigging the tree from which the 2008 video was obtained; Meg Lowman and Bryson Voirin for identifying the cause of a belaying

problem and thus making it possible to resume climbing shortly before the 2008 video was obtained; Geoff Hill and Dan Mennill for hosting the visit to the Choctawhatchee River in 2007; Adrian Thomas for pointing out that some direct fliers retain vestiges of intermittent flight; Michael DiGiorgio for providing the artwork; Dalcio Dacol for pointing out that two of Tanner's photos provide clues to the understanding of the flap style of the bird in the 2008 video; Dave Martin for performing a preliminary analysis on images from the 2006 video; Dave Coke, Gretchen Dawson, and Susan Epps for assisting with measurements that were used to estimate wingspan and flight speed in the 2008 video; Tasha Martin, Grayson Rayborn, David Roth, Tim Salman, and Charles Williams for assisting with the tree rigging; David Jones, David Martin, and Tamara Martin for providing boat rides to remote sites in the Pearl River basin; and Jay Boe, Bob Brown, Joe Bucaro, Stan Chin-Bing, Chris Feeney, Lou Fishman, Bud Fox, Dave Golden, Roman Grochowski, Floyd Hayes, Bill Holliday, Andy Horn, Bob Kemp, Rusty Ligon, Nick Makris, Paul Martin, Richard Martin, Mark Michaels, Dave Mueller, Mike Nicholas, Bob O'Brien, Greg Orris, John Perkins, Carl Perry, Bob Russell, Bill Siegmann, Steve Stanic, Jan Swart, Rob Tymstra, Fred Virrazzi, Rob Zingarelli, and especially Kim Collins for providing encouragement, suggestions, and assistance.

References

1. Tanner JT (1942) The Ivory-billed Woodpecker. New York: National Audubon Society.
2. Fitzpatrick JW, Lammertink M, Luneau MD, Gallagher TW, Harrison BR, et al. (2005) Ivory-billed Woodpecker (*Campephilus principalis*) persists in Continental North America. *Science* 308: 1460–1462.
3. Hill GE, Mennill DJ, Rolek BW, Hicks TL, Swiston KA (2006) Evidence suggesting that Ivory-billed Woodpeckers (*Campephilus principalis*) exist in Florida. *Avian Conserv Ecol* 1(3): 2.
4. Bent AC (1964) Life Histories of North American Woodpeckers. New York: Dover.
5. Pennycuick CJ (1996) Wingbeat frequency of birds in steady cruising flight: New data and improved predictions. *J Exp Biol* 199: 1613–1618.
6. Nudds RL, Taylor GK, Thomas ALR (2004) Tuning of Strouhal number for high propulsive efficiency accurately predicts how wingbeat frequency and stroke amplitude relate and scale with size and flight speed in birds. *Proc Roy Soc Lond B* 271: 2071–2076.
7. Christy B (1943) The vanishing ivorybill. *Audubon* 46: 99–102.
8. Fitzpatrick JW, Lammertink M, Luneau MD, Gallagher, TW, Rosenberg KV (2006) Response to Comment on Ivory-billed Woodpecker (*Campephilus principalis*) persists in Continental North America. *Science* 311: 1555b.
9. Pennycuick CJ (1990) Predicting wingbeat frequency and wavelength of birds. *J Exp Biol* 150: 171–185.
10. Tobalske BW (1996) Scaling of muscle composition, wing morphology, and intermittent flight behavior in woodpeckers. *Auk* 113: 151–177.
11. Winkler H, Christie DA, Nurney D (1995) Woodpeckers: An Identification Guide to the Woodpeckers of the World. New York: Houghton-Mifflin.
12. Cornell Laboratory of Ornithology (2008) Wing shape – Ivory-billed Woodpecker. Available: <http://www.birds.cornell.edu/ivory/evidence/segments/wingshape>. Accessed 2008 Oct 22.

13. Collinson JM (2007) Video analysis of the escape flight of Pileated Woodpecker *Dryocopus pileatus*: Does the Ivory-billed Woodpecker *Campephilus principalis* persist in continental North America? *BMC Biol* 5: 8.
14. Kramer HG, Thompson NS (1979) Geographic variation in the bell calls of the Blue Jay (*Cyanocitta cristata*). *Auk* 96: 423–425.
15. Allen AA, Kellogg PP (1937) Recent observations of the Ivory-billed Woodpecker. *Auk* 54: 164–184.