The use of a Low Cost High Speed Camera to Monitor Wingbeat Frequency in Hummingbirds (Trochilidae)

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Short Communications

THE USE OF A LOW COST HIGH SPEED CAMERA TO MONITOR WINGBEAT FREQUENCY IN HUMMINGBIRDS (TROCHILIDAE)

USO DE UNA CÁMARA BARATA DE ALTA VELOCIDAD PARA MONITOREAR LA FRECUENCIA DE ALETEO EN COLIBRÍES (TROCHILIDAE)

Ronny STEEN[1] *

SUMMARY.—Wingbeat frequency is an important parameter when studying flight performance in hummingbirds and could be put into an ecological and evolutionary context to investigate the decisions that a hummingbird takes regarding foraging efficiency. Previous studies of wingbeat frequencies in hummingbirds have been undertaken with captive birds, most probably due to limitations of experimental design and/or less mobile equipment. In the present paper I describe how I used a budget camera, which captured 220 frames per sec (fps), to film hummingbirds in order to quantify wingbeat frequency under natural conditions in Costa Rica. With this equipment I was able to obtain detailed information about stationary hovering flight in three different species; the charming hummingbird *Amazilia decora*, purple-throated mountain-gem *Lampornis calolaema* and violet sabrewing *Campylopterus hemileucurus*. Wingbeat frequency was higher for the purple-throated mountain-gem and the charming hummingbird compared to the larger violet sabrewing. It did not differ between the purple-throated mountain-gem and the charming hummingbird, which are more similar in size. In the purple-throated mountain-gem I found a higher wingbeat frequency and increased body inclination while hover-feeding compared to hovering in front of the feeder; hence it may be more costly to hover while feeding. It is hoped that the video techniques used here will encourage researchers to record wingbeat frequencies across a range of animal taxa.

RESUMEN.—La frecuencia de aleteo es un parámetro importante a la hora de estudiar el vuelo de los colibríes, y el vuelo puede interpretarse en un contexto ecológico y evolutivo para investigar las decisiones que un colibrí debe tomar en relación con su eficiencia alimenticia. Los estudios previos sobre la frecuencia de vuelo en colibríes se hicieron en cautividad, y muy posiblemente se vieron limitados por su diseño experimental y/o por limitaciones técnicas. En este artículo presento el uso de una cámara económica, que captura 220 tomas por segundo, para grabar colibríes y cuantificar la frecuencia de batido de alas en condiciones naturales en Costa Rica. Con este equipo fui capaz de conseguir información detallada sobre vuelo estacionario cernido en tres especies diferentes: el colibrí encanta-

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dor *Amazilia decora*, el colibrí montañes gorgimorado *Lampornis calolaema* y el colibrí ala de sable violáceo *Campylopterus hemileucurus*. La frecuencia de aleteo fue mayor en el colibrí montañés gorgimorado y el colibrí encantador, que son de tamaño similar, que en el colibrí ala de sable violáceo, de mayor tamaño. Además, el colibrí montañés gorgimorado presentó una mayor frecuencia de aleteo y mayor inclinación corporal durante la alimentación en vuelo estacionario, comparada a la alimentación frente al alimentador, por lo tanto es probable que sea más costosa la alimentación en vuelo estacionario. Espero que las técnicas de vídeo utilizadas en el presente estudio inspiren a investigadores que trabajan en campos ajenos a la biomecánica para registrar frecuencias de batido de vuelo en especies de diferentes taxones.

Introduction

Wingbeat frequency is an important parameter when studying flight performance in hummingbirds (e.g., Greenewalt, 1960, 1975; Altshuler and Dudley, 2002; Hedenström, 2002; Warrick *et al*., 2005; Tobalske *et al*., 2007; Altshuler *et al*., 2010). Flight performance may have implications for the energetic demands of foraging and could potentially influence foraging efficiency (Wolf *et al*., 1975) and hence could be used in an ecological and evolutionary context to investigate the decisions that a hummingbird needs to take regarding flight (Pennycuick, 1998).

Previous studies of flight performance in hummingbirds have been undertaken with captive birds, employing expensive equipment (e.g. Weis-Fogh, 1972; Feinsinger and Chaplin, 1975; Wells, 1993; Warrick *et al*., 2005; Tobalske *et al*., 2007; Altshuler *et al*., 2010), Dong *et al*. (2010) being an exception. Until the last two decades, high speed movie has been mostly film-based and, as a consequence, camera systems have been relatively large (Vollmer and Möllmann, 2011a). This, in combination with experimental procedure, may have restricted those studies to hummingbirds in captivity.

High speed cameras reveal behaviour that is otherwise invisible to the human eye (e.g., Baker, 1979; Betts and Wootton, 1988; Bostwick and Prum, 2003; Warrick *et al*., 2005; Bundle *et al*., 2007; Hedrick *et al*., 2009; Aguayo *et al*., 2011; Sakamoto *et al*., 2012). However, these cameras are costly and not aimed at the average consumer, whereas budget compact cameras with a high speed movie function have become more available in recent years (Vollmer and Möllmann, 2011b; Sakamoto *et al*., 2012). For comparison, compact cameras with high speed movie function cost about $200-1,000 USD, whilst medium to high-end ones cost from $25,000 to more than $100,000 USD (Vollmer and Möllmann, 2011a).

For the present study I used a budget camera, which records at 220 fps, to film hummingbirds to quantify wingbeat frequency while hovering. To my knowledge this is the first study of hummingbirds using a small low-cost high speed camera under natural conditions, although a similar high speed camera has been used for studying flower-visiting insects (Sakamoto *et al*., 2012). I recorded wingbeat frequencies for three different species: charming hummingbird *Amazilia decora*, purple-throated mountain-gem *Lampornis calolaema* and violet sabrewing *Campylopterus hemileucurus* under natural conditions. Previous studies have found that wingbeat frequency decreases with body size (e.g., Altshuler *et al*., 2003, 2010), and therefore I hypothesised that it would be lower in the violet sabrewing since it is about twice the size of both the charming hummingbird and purple-throated mountain-gem (Schuchmann, 1999).

Optimal flight during nectar feeding will influence foraging efficiency (Wolf *et al*., 1975), and so hummingbirds may prefer flowers orientated in a given position and direction (Fenster *et al.*, 2009; Sapir and Dudley, 2013). In the present study, the nectar hole was in the base of the feeder, only slightly angled towards the approaching hummingbird, so that it would have to tilt its body to some extent during nectar feeding. I therefore hypothesised that the angle of the body axis would differ between hover-feeding and hovering in front of the feeder, and that wingbeat frequencies will be higher during hover-feeding than in regular hovering.

MATERIAL AND METHODS

Study site

This study was conducted during February 2012 in two different areas in Costa Rica. I video-recorded the purple-throated mountain-gem (males) and the violet sabrewing (not sexed) one morning at the Selvatura Hummingbird Garden near the entrance of the Selvatura Park in Monteverde (10° 20' 31.51" N, 84° 47' 54.42" W). The Selvatura Hummingbird Garden is a patio with a dozen hummingbird feeders, surrounded by forest. The video recordings of the charming hummingbird (male) were done in a garden at Drake Bay on the Pacific coast (8° 41' 36.41" N, 83° 41' 16.88" W) as the hummingbird foraged on *Stachytarpheta frantzii* (Verbenaceae) during one morning and one evening. The garden was remote and surrounded by rainforest.

Video recording

I used a Panasonic Lumix DMC FZ-150 camera (124 × 82 × 95 mm, 528 g) with high speed movie function (220 fps, resolution 320 × 240 (QVGA)). The motion pictures were recorded in Motion JPEG format (see Supplementary Electronic Material for video examples).

Since the occurrences of hummingbirds at Selvatura Hummingbird Garden in front of the feeder were highly predictable I mounted the camera on a tripod. In Drake Bay, on the other hand, the camera was handheld since the hummingbirds occurred randomly on the flowers of the plant. Motion caused by hand movement was negligible, due to the high frame rate (see Supplementary Electronic Material for video examples).

The hovering sequence differed between the two study areas. At the feeder station the hovering sequence often consisted of a repeated quick shift between hovering in front of the feeder and hovering while sucking nectar (i.e. hover-feeding). At the *S. frantzii*, a hovering sequence mostly consisted of hover-feeding, interrupted by moving to the next flower of the inflorescence or to the next inflorescence.

Video analyses

The video recordings were evaluated frame by frame using Windows Live Movie Maker (WLMM). Since the video recordings do not have a time stamp, the real duration was indirectly obtained from the time lapse counter of the WLMM player. The high speed recordings are as default played back at 30 fps, which means that the hovering flight takes place 7.333 times slower than real time during playback (viz. 220 fps divided on 30 fps equals 7.333). Hence, the time measured from the time lapse counter of the WLMM player was divided by 7.333, which equals the real time of the hovering flight. To control for possible inaccuracy with the WLMM player, I recorded a high speed movie for exactly 60 seconds, then played it back with the WLMM player. From the time lapse counter of the WLMM player it was measured to last for 440 s (440 divided by 60 equals 7.333).

The wingbeat frequency was calculated by counting the number *(N)* of wingbeat cycles and measuring the time *(t)* taken. The wingbeat frequency *(f)* was then defined as $f = N/t$ (Pennycuick, 1990). A wingbeat cycle is defined as beginning when the wing is positioned at its uppermost, subsequently moving downward, and then back up to the uppermost position (fig. 1a). The wingbeat frequency was measured separately for hovering in front of the flower/feeder and hovering-feeding. The number of wingbeats was only measured when the hummingbirds held a steady hovering position and a minimum of five wingbeats was used to calculate wingbeat frequency (see Pennycuick, 1990).

I compared my results for wingbeat frequencies with previous findings from the literature. For the charming hummingbird I used data from Altshuler *et al.* (2010). For the purple-throated mountain-gem I used data from Dong *et al.* (2010) (conducted in the same study area as mine), which was indirectly obtained by extracting values from fig. 1 and appendix. For the violet sabrewing I used data from Greenewalt (1962), Altshuler *et al.* (2010) and Dong *et al.* (2010). Both the data from Altshuler *et al.* (2010) and Greenewalt (1962) were recorded with a high speed camera, whereas Dong *et al.* (2010) used sound recording equipment.

I obtained body mass data from the literature for each species (Schuchmann, 1999). For the charming hummingbird an average weight for males is 4.1 g; for the purple-throated mountain-gem it is 5.95 g for males

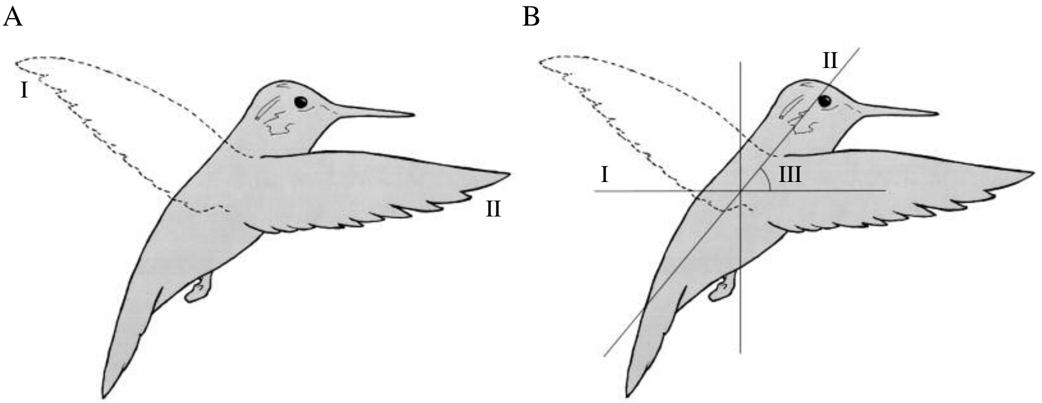

FIG. 1.—Typical body position of a hummingbird while hovering in front of a flower/feeder. (A) A wingbeat cycle consists of a downstroke phase and an upstroke phase (Greenewalt, 1960; Rósen *et al.*, 2004; Warrick *et al.*, 2005). The downstroke is the minimum interval during which the wingtip moves from its highest elevation to its lowest; the upstroke is the opposite sequence. (B) The inclination of the body axis was measured with a protractor using the coordinate axes as a reference point (I). From the body axis (II) the angle (III) was measured in relation to the horizontal plane of the reference point (I). *[Posición típica de un colibrí mientras se alimenta en flor/comedero. (A) Un ciclo de aleteo consiste en una fase de descenso y una de ascenso de las alas (Greenewalt, 1960; Rósen* et al.*, 2004; Warrick,* et al.*, 2005). El descenso es el tiempo transcurrido desde que la punta del ala está en el punto más alto (I) hasta que alcanza la extensión vertical mínina (II), mientras que la de ascenso es lo contrario. (B) La inclinación del eje corporal se midió mediante un transportador con los ejes de coordenadas en relación al punto (I). Desde el eje corporal (II) se midió el ángulo (III) en relación al plano horizontal del punto de referencia (I).]*

(the average between two given weights; 5.7 and 6.2 g); and for the violet sabrewing (not sexed) it is 10.65g (the average between two given weights; 11.8 g for males and 9.5 g for females). The body masses were used in the figure presentation.

In addition, for the purple-throated mountain-gem and violet sabrewing I measured inclination to the body axis with respect to a reference point (Sapir and Dudley, 2013), both while hover-feeding and hovering in front of the feeder (fig. 1b). These measurements were conducted with the use of the free video analysis programme Tracker 4.80 (http://www.cabrillo.edu/~dbrown/tracker/; Brown and Cox (2009)). I enabled coordinate axes as a reference point and used a protractor tool to measure angular arcs. The protractor tool has a vertex, two arms and an angle readout that displays degrees, with the lowermost arm fixed to the x-axis of the reference point.

Statistical analyses

Statistical tests were performed with R, version 2.14.2 (R Development Core Team, 2012). I used a linear mixed-effect model from the package 'nlme' (Pinheiro *et al.*, 2013) with 'treatment contrasts' function in R (Pinheiro and Bates, 2000) to test for differences in wingbeat frequencies between each hummingbird species. I included 'hovering sequence' as random effect in the statistical test to control for non-independence between measurements of hovering flight from the same hovering sequence (Pinheiro and Bates, 2000). A hovering sequence was defined as one individual being present within the camera view, enabling me to keep track of that particular individual. A new approaching hummingbird was treated as new hovering sequence. In addition to control for non-independence between measurements by including 'hover sequence' as random effect, I also controlled for other variables associated with a given hover sequence (e.g. possible variations in weather conditions) and, most importantly, controlled for repeated measurements of the same individual. However I was unable to keep track of individuals outside the camera view, so repeated measurements of the same individuals may have occurred more often than recorded. In total I recorded 5 hover sequences for the charming hummingbird from which I obtained 20 unique measurements of stationary hovering flight; 12 hover sequences for the purple-throated mountain-gem from which I obtained 31 unique measurements of stationary hovering flight; and 3 hover sequences for the violet sabrewing from which I obtained 8 unique measurements of stationary hovering flight. In total this gives 59 measurements of hovering flight within 20 hovering sequences.

Since I needed a clear lateral view of the hummingbird to associate it with the reference point I was only able to measure the inclination to the body axis for 14 out of 31 hovering flights (data from all of the 5 hover sequences) of the purple-throated mountain-gem and 7 out of 8 (data from 2 out of the 3 hover sequences) for the violet sabrewing. I was not able to achieve a precise reference point to measure the inclination to the body axis for the charming hummingbird, since the camera was handheld and the hummingbirds occurred randomly on the flowers of *S. frantzii*.

I tested for differences in wingbeat frequencies between the three species. I also tested for differences in wingbeat frequencies between hover-feeding and hovering in front of the feeder for the purple-throated mountain-gem (but not for the other two species due to low sample sizes). Finally, I tested for differences in the angle of the body axis between hover-feeding and hover in front of the feeder for the purple-throated mountain gem. In all tests wingbeat frequency was $\log_{10}$ transformed to obtain approximate normal distributions.

RESULTS

The quality of the high speed movie enabled fine scale analysis of the hummingbirds' wingbeat cycles (see Electronic Supplementary Material and fig 1). I obtained wingbeat frequencies for three different species (table 1, fig. 2). The wingbeat frequency varied significantly among the three species (linear mixed-effect model, $F_{2, 17} = 12.16$, $p < 0.001$). Wingbeat frequency was significantly higher for the purple-throated mountain-gem and the charming hummingbird compared to the violet sabrewing (linear mixed-effect model, $F_{1, 17} = 23.86$, $p < 0.001$ and $F_{1, 17} = 10.19$, $p = 0.005$, respectively). Purple-throated mountain-gem and the charming hummingbird did not differ significantly (linear mixed-effect model, $F_{1, 17} = 3.93$, $p = 0.06$).

The wingbeat frequency was significantly higher when hover-feeding compared to when hovering in front of the feeder for the purple-throated mountain-gem (linear mixed-effect model, $F_{1, 8} = 78.64$, $p < 0.001$). Due to the low sample size for either of the two categories, no statistical tests were performed for the charming hummingbird and violet sabrewing (table 1). The purple-throated mountain-gem tilted its body significantly more forward (i.e. towards the horizontal plane) when hover-feeding compared to when hovering in front of the feeder (42.3 ± 3.9° (n = 8) vs. 56.3 ± 3.0° (n = 6), linear mixed-effect model, $F_{1, 8} = 89.53$, $p < 0.001$)). Due to the low sample size no test was performed for the violet sabrewing (hover-feeding; 50.7 ± 2.0° (n = 3) vs. hovering in front of the feeder; 57.9 ± 3.2° (n = 4).

TABLE 1

Mean duration ± SD (range) of stationary hovering, number of wingbeats and wingbeat frequency (wingbeat^{-sec}) when a) hovering in front of the flower/feeder and b) hover-feeding. In total there were 59 observations of hovering flight (n) divided between 20 hovering sequences (random effect).
[Duración media ± SD (rango) del cernido estacionario, número de aleteos y frecuencia de aleteo (aleteos^{-sec}) cuando (a) el cernido es frente a flor/comedero y (b) el cernido es mientras se alimenta. Hubo en total 59 observaciones de vuelo cernido (n) en 20 secuencias de cernido (efecto aleatorio).]

	Duration (sec)	**No. of wingbeats**	**Wingbeat^{-sec}**	**No. of obs.**
Charming hummingbird				
(a)	0.642 ± 0.406 (0.355-0.929)	18.5 ± 12.0 (10.0-27.0)	28.7 ± 0.6 (28.2-29.1)	2
(b)	0.670 ± 0.495 (0.282-2.042)	20.3 ± 14.3 (9.0-60.0)	31.0 ± 2.0 (28.2-35.4)	18
Purple-throated mountain-gem				
(a)	0.376 ± 0.189 (0.213-0.839)	11.2 ± 5.8 (6.0-26.0)	29.7 ± 2.4 (25.0-32.8)	14
(b)	0.974 ± 0.563 (0.224-1.902)	34.5 ± 19.9 (8.0-68.0)	35.5 ± 0.8 (33.8-37.4)	17
Violet sabrewing				
(a)	0.529 ± 0.186 (0.296-0.801)	13.8 ± 5.0 (8-21)	26.1 ± 1.5 (23.4-27.0)	5
(b)	2.386 ± 0.931 (1.804-3.460)	63.7 ± 23.7 (49-91)	26.8 ± 0.5 (26.3-27.2)	3

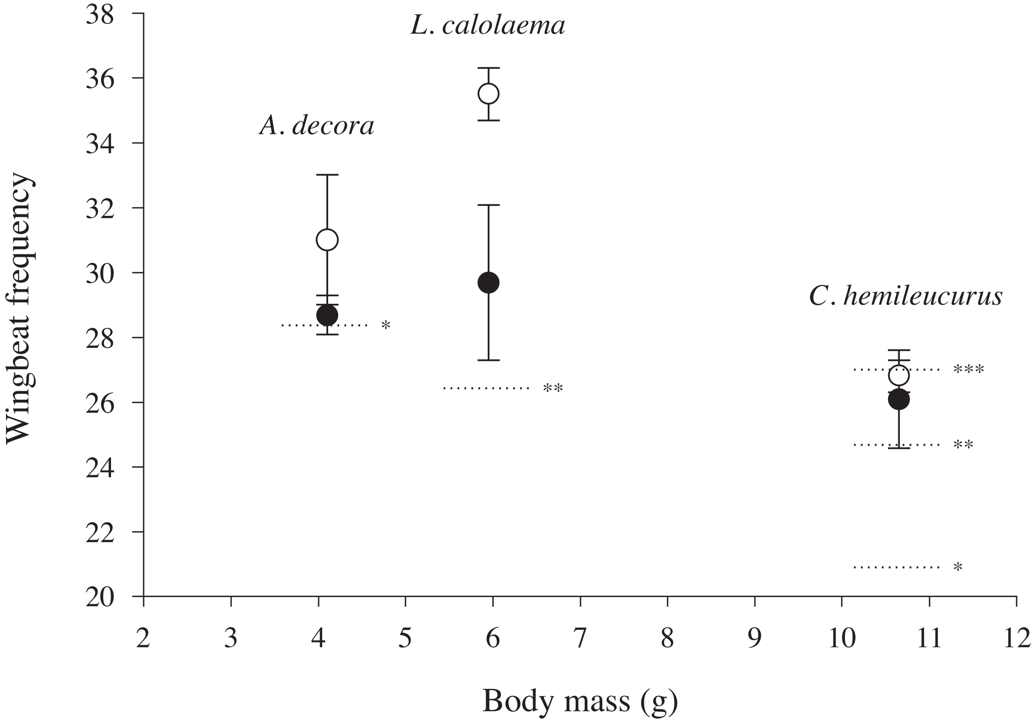

FIG. 2.—Mean (±SD) wingbeat frequency for the three hummingbird species (*Amazilia decora*, *Lampornis calolaema* and *Campylopterus hemileucurus*). Filled circles denote hovering in front of the flower/feeder and open circles denotes hovering while hover-feeding. The dotted line shows data obtained from the literature: * Altshuler *et al*. (2010), ** Dong *et al*. (2010) and *** Greenewalt (1962).
*[Frecuencia media (±SD) de aleteo para tres especies de colibríes (*Amazilia decora, Lampornis calolaema *y* Campylopterus hemileucurus*). Los círculos negros indican cernido frente a flor/comedero y los blancos cernido mientras se alimentan. Las líneas de trazos indican datos obtenidos de la literatura: * Altshuler* et al.*, (2010), ** Dong* et al.*, (2010) y *** Greenewalt (1962).]*

DISCUSSION

The budget high speed camera used in this study revealed detailed information about wingbeat frequency for three different hummingbird species. This study has shown how budget high speed cameras may be used to reveal more information about flight dynamics of hummingbirds under natural conditions, without the constraints arising from costly equipment. Since the camera shot at 220 · fps it filmed multiple frames per wingbeat cycle for all of the three hummingbird species studied (see fig. 3). Multiple frames per wingbeat cycle are necessary to directly count the number of wingbeats per sec (Altshuler and Dudley, 2003).

The wingbeat frequency of the charming hummingbird while hovering in front of the flower was very similar to that found for this species by Altshuler *et al*. (2010). The wingbeat frequency of the purple-throated mountain-gem was slightly higher than found by Dong *et al*. (2010). In addition, the

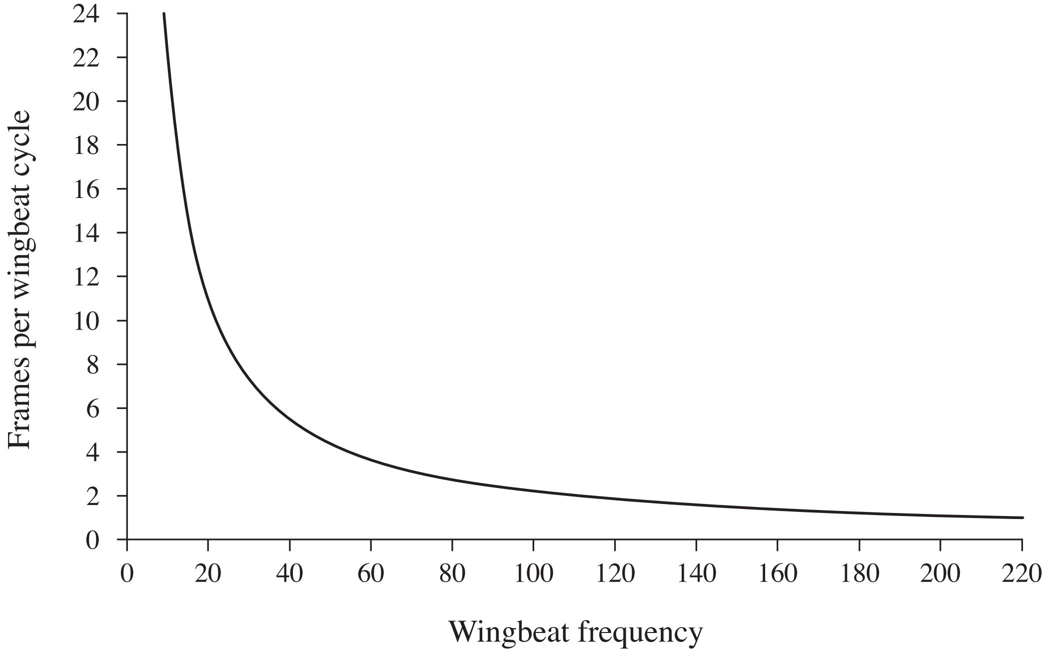

FIG. 3.—Frames recorded per wingbeat cycle ($f(x)$) as a function of the wingbeat frequency (x) with the use of a high speed camera that records 220 fps ($f(x)$ = 220 fps x^{-1}).
[Fotogramas registrados por ciclo de aleteo ($f(x)$*) en función de la frecuencia de aleteo mediante el uso de una cámara de alta velocidad que registra 220 fotogramas por segundo (*$f(x)$ = 220 fps x^{-1}*).]*

wingbeat frequency of the violet sabrewing when hovering in front of the feeder was higher in my study than found by Altshuler *et al*. (2010), although quite similar to those recorded by Greenewalt (1962) and Dong *et al*. (2010). The wingbeat frequency was found to be lower for the violet sabrewing compared to the charming hummingbird and the purple-throated mountain-gem. The violet sabrewing is about twice the size of the two other species. Hence, I found wingbeat frequency to be lower in larger than in smaller hummingbirds, as previously reported (e.g., Altshuler *et al*., 2003, 2010).

The wingbeat frequencies were rather constant for the two different hovering categories. The higher wingbeat frequency while hover-feeding compared to hovering in front of the feeder for the purple-throated mountain-gem suggests that it is more costly to hover while feeding. This may be because the purple-throated mountain-gem tilted its body significantly towards the feeder while hover-feeding. Although not tested statistically due to low sample size, the data for the violet sabrewing suggests that it maintained about the same angle of the body both while hover-feeding and hovering in front of the feeder, most probably because its larger size and long curved bill maintained about the same body angle while hovering when sucking as while hovering in front of the feeder. Since hovering flight is energy demanding (Weis-Fogh, 1972; Chai *et al*., 1998; Fernández *et al*., 2011), from the hummingbirds point of view it would be more efficient with the nectar hole of the feeder situated closer to the edge and at an angle enabling an optimal body position while hovering (see fig. 1). Provision of a perch would be even better.

In summary, the low cost high speed camera used in this study is comparable with the high speed camera used to record flower-visiting insects (Sakamoto *et al.*, 2012). With the high speed movie function the Panasonic Lumix camera captures 220 fps with a resolution at 320×240, whereas fps and resolution is not adjustable. In comparison, the Casio Exilim EX-F1camera used by Sakamoto *et al.* (2012) has adjustable high-speed movie function (1200 fps; 336×96, 600 fps; 432×192, 300 fps; 512×384). Neither Panasonic nor Casio are exceptional with respect to their high-speed movie function; currently, many camera manufactures offer compact cameras with this function (e.g., Canon IXUS HS-series, GoPro Hero 3, Fujifilm FinePix HS-series, Kodak Playfull Dual, Nikon J1 and V1, Samsung TL350 (WB2000 in Europe), Sanyo Xacti-series, Sony HDR-CX110). All are compact and inexpensive, ranging from c. $200 to $1000 USD. The video techniques used in the present study may encourage researchers in other fields to record wingbeat frequencies across a range of animal taxa. Future studies on wingbeat frequencies under natural conditions could be put into an ecological and evolutionary context to investigate the decisions that a hummingbird needs to take regarding flight (Pennycuick, 1998).

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BIBLIOGRAPHY

AGUAYO, D. D., SANTOYO, F. M., DE LA TORRE, M. H., SALAS-ARAIZA, M. D. and CALOCA-MÉNDEZ, C. 2011. Comparison on different insects' wing displacements using high speed digital holographic interferometry. *Journal of Biomedical Optics*, 16: 1-8.

ALTSHULER, D. L. and DUDLEY, R. 2002. The ecological and evolutionary interface of hummingbird flight physiology. *Journal of Experimental Biology*, 205: 2325-2336.

ALTSHULER, D. L. and DUDLEY, R. 2003. Kinematics of hovering hummingbird flight along simulated and natural elevational gradients. *Journal of Experimental Biology*, 206: 3139-3147.

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.

BAKER, P. S. 1979. The wing movements of flying locusts during steering behaviour. *Journal of Comparative Physiology A*, 131: 49-58.

BETTS, C. R. and WOOTTON, R. J. 1988. Wing shape and flight behavior in butterflies (Lepidoptera, Papilionoidea and Hesperioidea) - a preliminary analysis. *Journal of Experimental Biology*, 138: 271-288.

BOSTWICK, K. S. and PRUM, R. O. 2003. High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *Journal of Experimental Biology*, 206: 3693-3706.

BROWN, D. and COX, A. J. 2009. Innovative uses of video analysis. *The Physics Teacher*, 47: 145-150.

BUNDLE, M. W., HANSEN, K. S. and DIAL, K. P. 2007. Does the metabolic rate-flight speed relationship vary among geometrically similar birds of different mass? *Journal of Experimental Biology*, 210: 1075-1083.

CHAI, P., CHANG, A. C. and DUDLEY, R. 1998. Flight thermogenesis and energy conservation in hovering hummingbirds. *Journal of Experimental Biology*, 201: 963-968.

DONG, J. P., GOVERNALI, F. C., LARSON, E. I., SNOW, S. A. and UNGER, E. V. A. 2010. Wingbeat frequency is related to foraging strategies of hummingbirds at Monteverde, Costa Rica. *Dartmouth Studies in Tropical Biology*, 19: 26-29.

FENSTER, C. B., ARMBRUSTER, W. S. and DUDASH, M. R. 2009. Specialization of flowers: is floral orientation an overlooked first step? *New Phytologist*, 183: 502-506.

FEINSINGER, P. and CHAPLIN, S. B. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. *American Naturalist*, 109: 217-224.

FERNÁNDEZ, M. J., DUDLEY, R. and BOZINOVIC, F. 2011. Comparative energetics of the giant hummingbird (*Patagona gigas*). *Physiological and Biochemical Zoology*, 84: 333-340.

GREENEWALT, C. H. 1960. *Hummingbirds*. Doubleday. New York.

GREENEWALT, C. H. 1962. Dimensional relationships for flying animals. *Smithsonian Miscellaneous Collections*, 144: 1-46.

GREENEWALT, C. H. 1975. The flight of birds. *American Philosophical Society*, 65: 1-67.

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

HEDRICK, T. L., CHENG, B. and DENG, X. 2009. Wingbeat time and the scaling of passive rotational damping in flapping flight. *Science*, 324: 252-255.

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

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

PINHEIRO, J. C. and BATES, D. M. 2000. *Mixed-effects models in S and S-PLUS*. Springer. New York.

PINHEIRO, J. C., BATES, D., DEBROY, S., SARKAR, D. and the R DEVELOPMENT CORE TEAM. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-110.

R DEVELOPMENT CORE TEAM. 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna.

RÓSEN, M., SPEDDING, G. R. and HEDENSTRÖM, A. 2004. The relationship between wingbeat kinematics and vortex wake of a thrush nightingale. *Journal of Experimental Biology*, 207: 4255-4268.

SAKAMOTO, R. L., MORINAGA, S. I., ITO, M. and KAWAKUBO, N. 2012. Fine-scale flower-visiting behavior revealed by using a high-speed camera. *Behavioral Ecology and Sociobiology*, 66: 669-674.

SAPIR, N. and DUDLEY, R. 2013. Implications of floral orientation for flight kinematics and metabolic expenditure of hover-feeding hummingbirds. *Functional Ecology*, 27: 227-235.

SCHUCHMANN, K. L. 1999. Family Trochilidae (Hummingbirds). In, J. del Hoyo, A. Elliot and J. Sargatal (Eds.): *Handbook of the Birds of the World*, Vol. 5, pp. 468-680. Lynx Edicions. Barcelona.

TOBALSKE, B. W., WARRICK, D. R., CLARK, C. J., POWERS, D. R., HEDRICK, T. L., HYDER, G. A., and BIEWENER, A. A. 2007. Three-dimensional kinematics of hummingbird flight. *Journal of Experimental Biology*, 210: 2368-2382.

VOLLMER, M. and MÖLLMANN, K.-P. 2011a. High speed – slow motion. Technik digitaler Hochgeschwindigkeitskameras. *Physik in unserer Zeit*, 42: 144-148.

VOLLMER, M. and MÖLLMANN, K. P. 2011b. High speed and slow motion: the technology of modern high speed cameras. *Physics Education*, 46: 191.

WARRICK, D. R., TOBALSKE, B. W. and Powers, D. R. 2005. Aerodynamics of the hovering hummingbird. *Nature*, 435: 1094-1097.

WEIS-FOGH, T. 1972. Energetics of hovering flight in hummingbirds and *Drosophila*. *Journal of Experimental Biology*, 56: 79-104.

WELLS, D. J. 1993. Muscle performance in hovering hummingbirds. *Journal of Experimental Biology*, 178: 39-57.

WOLF, L. L., HAINSWORTH, F. R. and GILL, F. B. 1975. Foraging efficiencies and time budgets in nectar-feeding birds. *Ecology*, 56: 117-128.

SUPPLEMENTARY ELECTRONIC MATERIAL

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Video: Examples of wingbeat frequencies in three hummingbird species.

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