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Take-off mechanics in hummingbirds (Trochilidae)

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Summary

Initiating flight is challenging, and considerable effort has focused on understanding the energetics and aerodynamics of take-off for both machines and animals. For animal flight, the available evidence suggests that birds maximize their initial flight velocity using leg thrust rather than wing flapping. The smallest birds, hummingbirds (Order Apodiformes), are unique in their ability to perform sustained hovering but have proportionally small hindlimbs that could hinder generation of high leg thrust. Understanding the take-off flight of hummingbirds can provide novel insight into the take-off mechanics that will be required for micro-air vehicles. During take-off by hummingbirds, we measured hindlimb forces on a perch mounted with strain gauges and filmed wingbeat kinematics with high-speed video. Whereas other birds obtain 80–90% of their initial flight velocity using leg thrust, the leg contribution in hummingbirds was 59% during autonomous take-off. Unlike other species, hummingbirds beat their wings several times as they thrust using their hindlimbs. In a phylogenetic context, our results show that reduced body and hindlimb size in hummingbirds limits their peak acceleration during leg thrust and, ultimately, their take-off velocity. Previously, the influence of motivational state on take-off flight performance has not been investigated for any one organism. We studied the full range of motivational states by testing performance as the birds took off: (1) to initiate flight autonomously, (2) to escape a startling stimulus or (3) to aggressively chase a conspecific away from a feeder. Motivation affected performance. Escape and aggressive take-off featured decreased hindlimb contribution (46% and 47%, respectively) and increased flight velocity. When escaping, hummingbirds foreshortened their body movement prior to onset of leg thrust and began beating their wings earlier and at higher frequency. Thus, hummingbirds are capable of modulating their leg and wingbeat kinetics to increase take-off velocity.

Key words: rufous hummingbird, *Selasphorus rufus*, force, perch, velocity, kinematics, flight.

Introduction

Take-off velocity is potentially of great importance to flying animals needing to escape predators (Kullberg et al., 1998; Veasey et al., 2001). Also, as slow, powered flight is energetically costly (Nudds and Bryant, 2000; Askew et al., 2001; Tobalske et al., 2003), a fast initial velocity should help reduce aerodynamic power requirements.

The velocity (v) of the center of mass as an animal takes to the air is determined by mass-specific impulse:

$$v = Ft/M_b \,, \tag{1}$$

where F is the average force applied to the environment using the hindlimbs and wings, t is the duration of force application, and M_b is body mass (Schutt et al., 1997). Among geometrically and dynamically similar animals, F should scale proportional to $M_b^{2/3}$, and t should scale proportional to $M_b^{1/3}$ (Hill, 1950; Pennycuick, 1992; Marsh, 1994). Thus, take-off velocity should be independent of body mass ($v \propto M_b^0$).

Among the bird species studied to date, take-off appears to be 'hindlimb-driven' in that acceleration to an initial flight velocity is produced largely by leg thrust during jumping rather than lift from the wings (Heppner and Anderson, 1985; Bonser and Rayner, 1996; Earls, 2000).

We hypothesized that hummingbirds would depart from this pattern of dominant hindlimb contribution and use slower initial flight velocities than other birds because of their hindlimb morphology. Using what appears to represent an active upstroke during hovering, hummingbirds move their wings in a different manner compared with all other flying birds (Greenewalt, 1960; Weis-Fogh, 1972; Stolpe and Zimmer, 1939; Chai and Dudley, 1996). Lift production during upstroke may enhance take-off impulse relative to other birds. However, as members of the Apodiformes, hummingbirds have proportionally tiny hindlimbs compared with other birds (Cohn, 1968), and their tarsometatarsi make up a smaller proportion of total leg length (19%) compared with those of passerines (31%; Gatesy and Middleton, 1997). During

jumping, their morphology should provide decreased relative hindlimb contribution to F and t (Bennett-Clark, 1977; Johnston, 1991). Some insects enhance jump performance using morphological specializations that permit elastic energy storage in their limbs (Alexander, 1995; Burrows and Wolf, 2002), but hummingbirds do not appear to share this design feature (Zusi and Bentz, 1984).

We test the effects of motivational state upon take-off mechanics because these effects are largely unknown. Most studies of animal locomotion assume an animal is exhibiting either 'typical' or 'maximal' performance without testing this assumption or describing the observed behavior within the range of motivational states available to the animal. In previous investigations of leg thrust during take-off in birds (Fisher, 1956; Heppner and Anderson, 1985; Bonser and Rayner, 1996; Bonser et al., 1999; Earls, 2000), birds initiated flight of their own volition or in response to hand signals that were intended to stimulate or startle the birds. Earls (2000) reports that patterns of force development in the European starling, *Sturnus vulgaris*, do not vary according to flight-initiating stimulus but did not explicitly test for an effect. Seemingly in contrast, Kullberg et al. (1998) and Lind et al. (2002, 2003) report that a mock predator's attack angle, approach speed and the distance at which the predator is detected all affect take-off trajectory in tits (*Parus* spp.).

The high metabolic rate of hummingbirds (Berger, 1985) and their competitive aggression when food resources are potentially limited (Carpenter et al., 1993) allowed us to vary hummingbird motivation for initiating flight. We report on leg forces and kinematics measured during take-off in rufous hummingbirds (*Selasphorus rufus* Gmelin) as the birds initiated flight in three motivational states: autonomously to feed, startled to escape a hand movement, and aggressively to chase a conspecific from a feeder.

Materials and methods

Animals

Five female and one male rufous hummingbird (mean body mass 3.2 g; Table 1) were captured from the wild under permits from the US Fish and Wildlife Service and Oregon Department of Fish and Wildlife. All housing and experiment protocols were approved by the University of Portland Institutional Animal Care and Use Committee (IACUC).

We measured morphology of the hummingbirds using standard techniques (Pennycuick, 1989; Tobalske et al., 1999); differences between genders were not significant, so all birds were pooled in our sample (Table 1). For a given bird, body mass (g) was an average of all measurements obtained during experiments as the bird sat motionless on our force perch. Wing measurements were made with the wings spread as during mid-downstroke. Linear measurements (mm) were obtained using digital calipers, and areas (mm^2) were measured using digitized photographs with a known scale for pixel-to-metric conversion.

During experiments, we marked the birds using removable strips of 1-mm-wide tape applied at the shoulder and base of tail to assist us in identifying these anatomical landmarks during later kinematic analysis.

Table 1. *Morphological data for rufous hummingbirds (*Selasphorus rufus*)*

Variable	Mean value
Body mass (g)	3.2±0.1
Single wing length (mm)	46.1±2.6
Wing span (mm)	104.9±4.9
Average wing chord (mm)	13.0±0.3
Aspect ratio	7.1±0.3
Single wing area (mm^2)	599.2±46.4
Area of both wings and root box area of body (mm^2)	1364.4±93.7
Wing loading ($N\ m^{-2}$)	36.7±3.0
Disc loading ($N\ m^{-2}$)	3.7±0.4
Tibiotarsus length (mm)	12.0±0.7
Tarsometatarsus length (mm)	5.0±0.3

Values are means ± S.D. (N=6).

Experimental protocol

The experiments took place within a flight cage, 1 m wide × 2 m long × 2 m high, constructed of 2.5 cm plastic pipes and covered with 1.36-cm nylon mesh. Four halogen lights were distributed around the cage to continuously illuminate the field for video recording. Perches and feeders were 1 m above the floor and centered within the flight cage except for the subdominant perch present only during aggressive take-off. This perch was placed laterally and 25 cm away from the feeder. Feeders were filled with Nektar-Plus (NEKTON®; Günter Enderle, Pforzheim, Baden-Württemberg, Germany) and suspended from the ceiling of the cage. In aggressive experiments, we exercised the option of blocking the hummingbirds' access to the food by lowering the feeder(s) into a container on a platform under the feeder.

Birds took to flight in one of three motivational states: to feed on their own volition (hereafter referred to as 'autonomous'), to respond to a startling human motion (hereafter 'escape') or to chase a conspecific away from a feeder (hereafter 'aggressive'). We obtained two take-offs per bird for each motivational state sampled, although only four out of six birds were sufficiently dominant to provide aggressive take-off.

Autonomous and escape take-off occurred with one bird, two freely available feeders at either end of the flight chamber, 1 m above the ground, and a force perch 1 m high and located in the center of the flight chamber. During autonomous take-off, the bird voluntarily initiated flight from the perch to a feeder, flew directly to a feeder and immediately began feeding. During escape take-off, the bird on the perch was startled by a single hand elevation performed by one of the experimenters seated a distance of 6 m from the cage. The bird initiated flight from the perch and flew around the cage without feeding.

Aggressive take-off involved a dominant bird as the test subject chasing a subdominant bird away from a single feeder in the cage. The pair of birds remained in the cage together, with free access to food, for 3–24 h before the recording of aggressive take-off. During the experiment, we would periodically block access to the feeder. Because the dominant bird always preferred the perch in the center of the flight chamber, the subordinate bird was relegated to a non-instrumented perch located laterally and 25 cm away from the feeder. When the feeder was raised to permit access, the subdominant immediately took off and flew to the feeder to begin feeding. The dominant bird would then take off and chase the sub-dominant bird away from the feeder before returning to feed itself.

Data acquisition

We used a custom-made perch instrumented with strain gauges (120 Ω, type EA-06-125ad-120; Micro-Measurement, Vishay Measurements Group, Rayleigh, NC, USA) to measure leg thrust. Our single-beam design was adapted from Biewener and Full (1992). It had an 11-cm steel rod 1.5 mm in diameter in the center. On both ends of this rod, two twin-bladed force transducers were constructed as half-bridge circuits to yield horizontal and vertical forces; signals were amplified 2000× using separate channels of a strain gauge amplifier (2120B; Vishay Measurements Group). We used known masses (g) to calibrate the strain-gauge amplifier output from volts into Newtons. Resonant frequency of the perch was 75 Hz. Ideally, all bending in this perch would occur at the force transducers but, due to the small diameter of the central rod, necessary to accommodate tiny hummingbird feet, the central rod flexed slightly during experiments. This flexure caused the transducers to be most sensitive to force when a bird was centered on the rod. Thus, we calibrated horizontal and vertical forces along the central rod and, for each take-off, used a location-specific calibration appropriate for the bird's position on the perch as verified using high-speed video (250 Hz; Motionscope 250; Redlake, San Diego, CA, USA). Analog output from the strain-gauge amplifiers was sampled at 5000 Hz using a 16-bit data acquisition system (Digidata 1320A; Axon Instruments, Union City, CA, USA) and subsequently stored for analysis on a computer. Force recordings were synchronized with our Motionscope camera and an additional high-speed video camera (1000 Hz; PCI-2000; Redlake) using a Transistor-Transistor Logic (TTL) pulse that triggered our video cameras.

Flight kinematics were obtained from digital video. The Redlake PCI-2000 provided a lateral view (1000 Hz; stored using PCI-R v2.18 software) to digitize wing and body motion. The Redlake Motionscope 250 (250 Hz) provided a cranial or caudal view for perch calibration and correction of lateral-view parallax. Analog output from the Motionscope was imported to computer and stored using Quicktime v. 3.5 software (Apple, Cupertino, CA, USA). For both cameras, we used a shutter speed of 1/4000 s.

Data analysis

To facilitate comparison with other species, we adapted methods in Earls (2000) in our definition of take-off and its components. In brief, take-off started (relative timing=0%) when horizontal force production, as recorded using the force perch, reached 5% of body weight (henceforth called 'begin leg thrust'). The end of take-off (relative timing=100%) was the first upstroke–downstroke transition after the feet broke contact with the force perch. The end of foot contact, when horizontal and vertical forces reached 5% of body weight, represented 'end leg thrust'. Wing movements were classified as upstroke or downstroke based on movement of the wrist relative to the midline of the body. Body angle was the acute angle between the midline of the body and horizontal, with the midline described as a line connecting the shoulder and middle base of the tail. We assumed that the center of mass of the body was halfway between the shoulder and the base of the tail. Counter-movement was identified using vertical movement of the center of mass; because this movement was sometimes minimal, we used vertical head movement to help verify its timing.

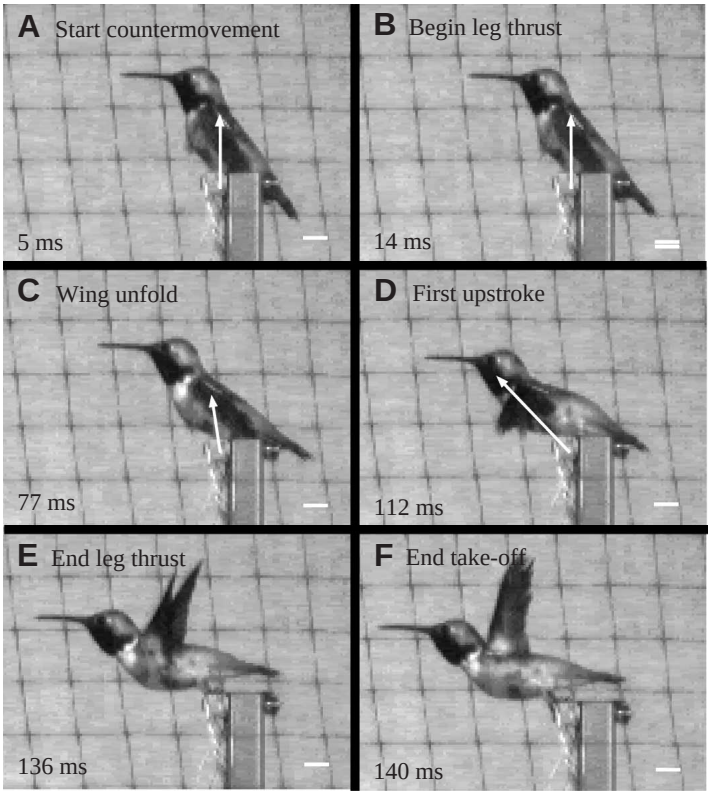
We sampled take-off from 10 ms (10 frames at 1000 Hz) before the start of any change in body angle or position of the center of mass to 10 ms after end of take-off. For each frame of video in the sample, we digitized the wing tip, base of the shoulder and base of the tail using Didge software (v. 2.1; Alistair Cullum, Creighton University, Omaha, NE, USA). During experiments, we marked the birds using removable strips of 1-mm-wide tape applied at the shoulder and base of tail to assist us in identifying these anatomical landmarks during later kinematic analysis. Digitized points were converted to metric coordinates using a known scale, and subsequent analysis was performed using Igor Pro software (v. 3.5; Wavemetrics, Inc., Lake Oswego, OR, USA).

We plotted position of the center of mass as a function of time and fitted the data with a polynomial curve. The degree of the polynomial curve was selected using the constraint that residuals must be <0.5 mm. We calculated body velocity and acceleration using differentiation of this fitted curve. Total velocity represents the time history of total accelerations derived from the combined forces produced by the legs and the wings.

To evaluate accuracy of our digitizing and kinematic analysis, we conducted a ball-drop acceleration test. The second derivative of position of the ball as a function of time yielded a value for $\boldsymbol{g}$ of 9.79 m s^{-2}, a 0.14% error.

Measurements from our force perch were used to calculate the relative contribution of the legs to velocity of the center of mass (Earls, 2000). Body weight was subtracted from vertical force. Horizontal and vertical velocities were then integrated from acceleration after the measured force was divided by the bird's body mass. We used our video measurements of horizontal and vertical velocity at the start of leg thrust to define our horizontal and vertical integration constants for the force data.

After analyzing 33 take-offs, we tested for statistically significant differences among treatment means using repeated-measures analysis of variance (ANOVA; StatView v. 5.0.1;



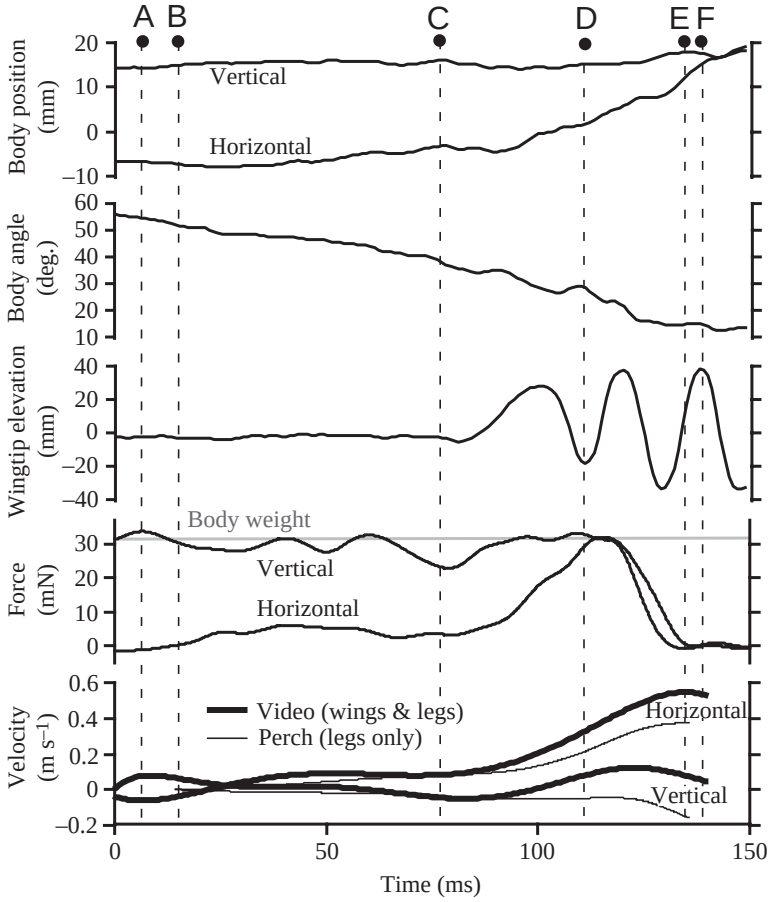


Fig. 1. Kinematic events during an autonomous take-off in a male rufous hummingbird (*Selasphorus rufus*; body weight=30.7 mN). (A–F) Selected frames from 1000 Hz video illustrating body and wing posture; letters and timing (ms) for each frame correspond directly to those on the graph below. Vectors represent reaction forces produced by the hindlimbs on the perch; white scale bars, 10 mN. This sequence lasts 150 ms, and two wingbeats were completed prior to the end of take-off, defined as the start of the first downstroke after end of leg thrust.

SAS Institute, Cary, NC, USA). We report means±S.D. for N=6 birds for autonomous and escape take-off and N=4 birds for aggressive take-off, so d.f.=3,2 for all repeated-measures ANOVA.

Comparative analysis

We compared hummingbird take-off performance with that of other species using previously published accounts (Bonser and Rayner, 1996; Earls, 2000; Tobalske et al., 2000). Additionally, we obtained unpublished data collected in association with Tobalske (1996), Tobalske and Dial (2000), Tobalske et al. (2000), Zimmerman and Tobalske (2000) and a new empirical study in the field (B. Brandsma, unpublished data). In cases where body mass was not measured, we used average mass for the species, specific to gender if known (Dunning, 1993). Kinematic and force data for one zebra finch (*Taeniopygia guttata*; 15.2 g) engaged in autonomous take-off in our flight chamber at a flight distance of 10 m were recorded in the same manner as for hummingbirds. We also incorporated data on velocity at end of take-off in 15 other species up to the mean body mass of wild turkey (6.5 kg).

We tested for an effect of body mass on velocity at end of take-off using reduced-major axis (RMA) regression of independent contrasts [Phenotypic Diversity Analysis Program (PDAP) v. 5.0; J. A. Jones, P. E. Midford and T. Garland, Jr, University of Wisconsin, Madison, WI, USA]. Independent contrasts account for the non-independence of species due to phylogenetic relationships (Garland et al., 1992). Our hypothesized phylogeny was based on DNA–DNA hybridization data and average linkage (UPGMA) data in Sibley and Ahlquist (1990); we assumed uniform branch lengths. With 16 contrasts and all nodes resolved, d.f.=15 for the RMA regression. Velocity and body mass were log-transformed prior to this analysis. As take-off data from birds in the field probably included birds with varying motivation, for the hummingbird velocity we used a mean velocity among all three motivational states.

Results

General patterns of take-off

Relative to other bird species (Earls, 2000),

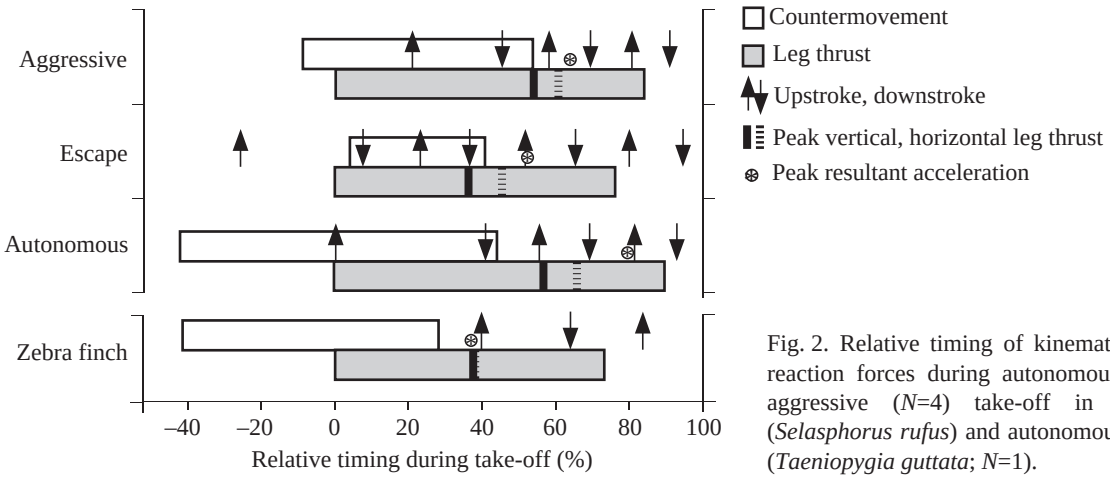
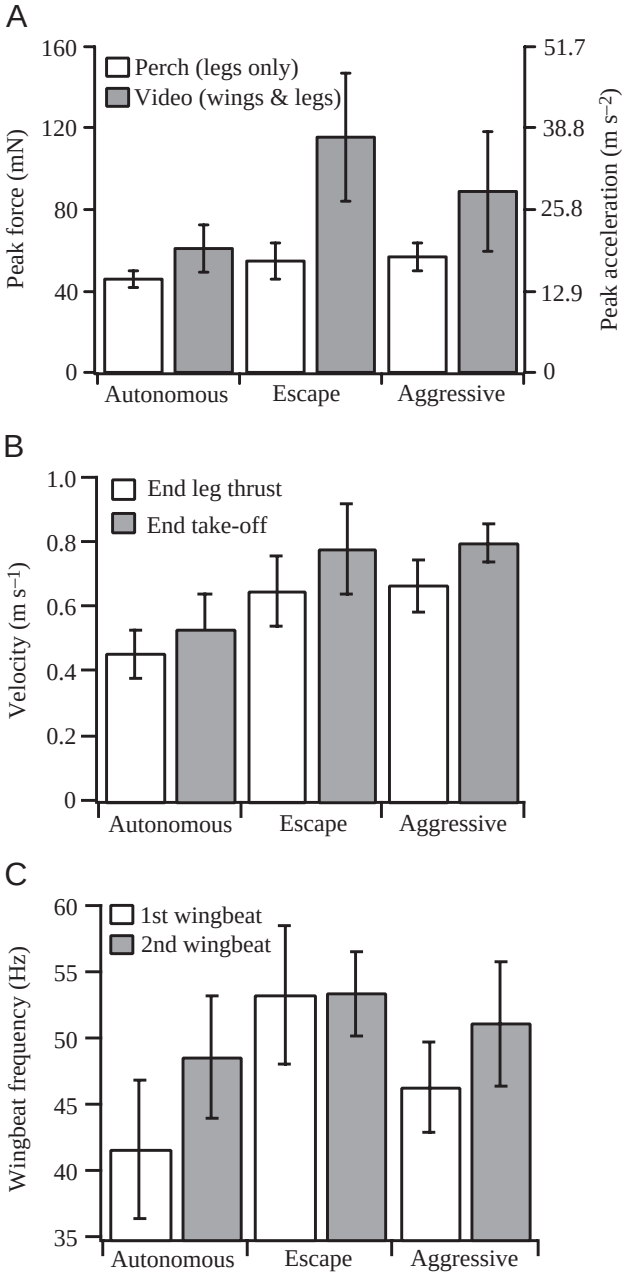


Fig. 2. Relative timing of kinematic events and peak ground-reaction forces during autonomous (N=6), escape (N=6) and aggressive (N=4) take-off in the rufous hummingbird (*Selasphorus rufus*) and autonomous take-off in the zebra finch (*Taeniopygia guttata*; N=1).



hummingbirds exhibited only minor counter-movement of the center of mass prior to take-off (Fig. 1). After being motionless, the bird began to drop its head and shoulders and elevate the base of its tail, which effected a decrease in body angle relative to horizontal but little change in center of mass. The start of downward rotation preceded the start of leg thrust during autonomous take-off and in most (66.6%) of the escape and aggressive take-offs (Figs 1, 2).

Mean duration from start of body movement to the end of take-off was 120.8±26.0 ms during autonomous take-off (Figs 1, 2). Within this time interval, mean take-off duration, from the start of leg thrust to the start of the first downstroke after the end of leg thrust, was 81.3±8.7 ms. Hummingbirds used their legs to apply thrust to the perch for 71.0±10.8 ms. After the start of leg thrust, vertical force on the perch varied about a mean value representing weight support, while horizontal force increased until reaching a peak of 25.4±5.2 mN (0.8× body weight) after the first downstroke. Peak vertical ground-reaction force averaged 47.3±5.5 mN (1.6× body weight) and occurred 6.9±5.7 ms after peak horizontal force (Fig. 2). Peak horizontal acceleration due to leg thrust averaged 8.3±1.8 m s^{-2}, and peak vertical acceleration (including $\boldsymbol{g}$) was 14.8±2.0 m s^{-2}. Peak acceleration due to the hindlimbs was 50–75% of peak acceleration due to the legs and wings combined (Fig. 3A); the peak acceleration due to legs and wings averaged 27.0±7.6 m s^{-2}.

Velocity increased between the end of leg thrust (0.56±0.08 m s^{-1}) and the end of take-off (0.06±0.08 m s^{-1}; Figs 1, 3B). The percent contribution of leg forces to total

Fig. 3. Selected kinematic and mechanical variables in the rufous hummingbird, *Selasphorus rufus*, as a function of take-off treatment. (A) Peak vertical and horizontal ground-reaction forces (N) and peak accelerations (m s^{-2}). Vertical forces are net after subtracting $\boldsymbol{g}$. (B) Velocity (m s^{-1}) at the end of leg thrust and take-off. (C) Wingbeat frequency (Hz; inverse of wingbeat duration) during the first and second wingbeat in the take-off. N=6 hummingbirds for autonomous and escape and N=4 for aggressive; error bars represent ± S.D.

velocity at the end of leg thrust was 62.5±18.6%; by the end of take-off, this percent contribution declined to 50.5±11.4%.

Hummingbirds completed 2.4±0.4 wingbeats (range 2–5) before ending leg thrust. This is different from other bird species (Earls, 2000), including the zebra finch (Fig. 2), which are only partially through one downstroke before ending leg thrust. Also, in comparison with other bird species, hummingbirds took off more slowly (Bonser and Rayner, 1996; Earls, 2000; Tobalske et al., 2000; Zimmerman and Tobalske, 2000; Fig. 4). Our regression of species data and independent contrasts illustrated that velocity at the end of take-off increased as body mass increased (P<0.01; Fig. 4B). Velocity varied from 0.7 m s^{-1} to 4.1 m s^{-1} over a size range from the 3.5 g hummingbird to the 6.5 kg wild turkey (Fig. 4A). Although the slope of the independent contrasts regression, proportional to $M_b^{0.26}$, was significantly different from zero, only 42.3% of the variation in take-off velocity was explained by variation in mass. This suggests that other unmeasured variables, including morphology and motivation, will help account for variation in performance.

Effects of motivational state

Hummingbirds altered certain aspects of their take-off performance according to their motivational state. Mean duration from start of body movement to the end of take-off was shorter for escape and aggressive take-off compared with autonomous take-off (P=0.02; Fig. 2). Percent leg contribution to total velocity was less during escape (46.2±18.5%) and aggressive (47.0±9.9%) compared with autonomous take-off (59.1±12.2%), but the differences were not statistically significant (P>0.3). Peak acceleration, due to combined hindlimb and wing forces, varied significantly with motivational state (P=0.008; Fig. 3A); a maximum of 37.4±10.1 m s^{-2} was exhibited during chase take-off. There was a significant effect of motivation on the magnitude of peak vertical force from the legs (P=0.02), which was lower during autonomous take-off than during escape and aggressive take-off. Although peak horizontal force from the legs was greater during escape take-off than during autonomous or aggressive take-off, differences were marginally non-significant (P=0.09). Likewise, peak resultant hindlimb force and direction varied according to motivational state, but the differences were marginally non-significant (P=0.11 and P=0.14, respectively). Peak resultant force, measured using the force perch, varied from 46.7±4.4 mN (1.5× body weight) during autonomous take-off to approximately 55 mN (1.8× body weight) during chase and aggressive take-off (Fig. 3A). The angle of this resultant, relative to horizontal, was greater during startle (77.9±12.0°) than during autonomous (65.8±9.4°) and aggressive (65.1±6.5°) take-off.

Velocities were lower during autonomous take-off compared with escape and aggressive take-off. Among motivational states, there was a significant difference in velocity at the end of leg thrust (P=0.04), but the observed differences were marginally non-significant for velocity at the end of take-off (P=0.08).

Compared with autonomous and aggressive take-off, escape take-offs featured earlier start of wing movement and more wingbeats before the end of leg thrust. There was a significant effect of motivational state upon wingbeat frequency (inverse of wingbeat duration) in the first wingbeat (P<0.05) but not the second wingbeat (Fig. 3C). There was also a significant difference among motivational states in the relative timing of

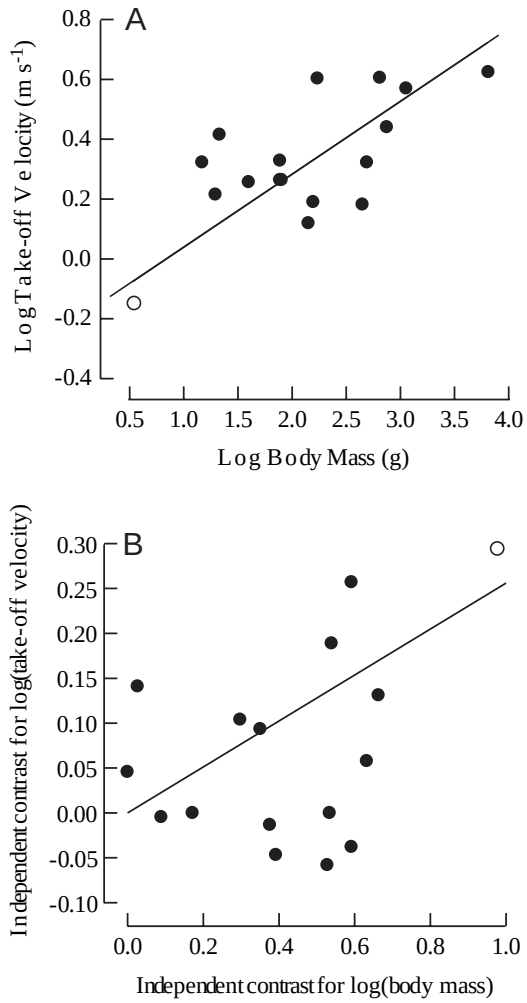


Fig. 4. Scaling of velocity at end of take-off in 17 bird species including, in order of increasing body mass: rufous hummingbird (*Selasphorus rufus*); zebra finch (*Taeniopygia guttata*); dark-eyed junco (*Junco hyemalis*); house finch (*Carpodacus mexicanus*); diamond dove (*Geopelia cuneata*); American robin (*Turdus migratorius*); European starling (*Sturnus vulgaris*); western scrub jay (*Aphelocoma californica*); northern flicker (*Colaptes auratus*); ringed turtle-dove (*Streptopelia risoria*); European migratory quail (*Coturnix coturnix*); American crow (*Corvus brachyrhynchos*); rock dove (*Columba livia*); black oystercatcher (*Haematopus bachmani*); ring-necked pheasant (*Phasianus colchicus*); herring gull (*Larus argentatus*); wild turkey (*Meleagris gallopavo*). Regression lines from reduced-major axis regression of log-transformed data. (A) Species data, with open circle representing rufous hummingbird; y=0.25x–0.21, r=0.68. (B) Independent contrasts. Open circle represents contrast that includes rufous as daughter taxon; y=0.26x, r=0.65.

wing kinematics, including start of wing unfolding (P=0.04), start of first downstroke (P=0.02), start of first upstroke (P=0.01) and start of second downstroke (P<0.01).

Discussion

Consistent with our hypothesis, hummingbirds, with small body size and proportionally small hind limbs, took to flight differently compared with other birds. One important consequence of their unique method of take-off is that their initial flight velocity is comparatively slow (Figs 3, 4). Due to their insect-like wingbeat style, thought to produce lift during upstroke and downstroke, hummingbirds appear particularly well suited for hovering flight (Altshuler and Dudley, 2002). Their flight style results in a higher energetic cost of submaximal fast flight compared with hovering and slow flight. This may be unique among birds (Berger, 1985; Ellington, 1991) and may ultimately account for their use of slow take-off velocity during autonomous take-off. Increased motivation to take off quickly, for escape or aggression, increased velocity relative to autonomous take-off. However, take-off velocity in motivated hummingbirds was still less than mean take-off velocity in other species.

As take-off velocity is proportional to impulse (equation 1), our results indicate that hummingbirds exhibited proportionally lower F or t relative to other birds. Given that the upstroke is presumed to be active in hummingbirds, and lift from the wings should contribute to F, it is significant that their unique wingbeat style did not result in a comparatively faster take-off velocity (Fig. 4).

Positive scaling of take-off velocity with body mass among species ($M_b^{0.26}$; Fig. 4) suggests that species in our sample were not geometrically or dynamically similar (Hill, 1950; Pennycuick, 1992; Marsh, 1994). Inferring from data available on functional morphology and jump mechanics in anuran amphibians (Marsh, 1994), we anticipate that relatively small hindlimb muscles in hummingbirds limit F, whereas relatively short limb length, proportionally small tarsometatarsi and high intrinsic rates of muscle shortening limit t. However, regardless of hindlimb proportions, take-off velocity was relatively slower in smaller birds. As the hummingbirds were the smallest species in our sample, small body mass and unique hindlimb morphology are confounded. Further comparative study is, therefore, warranted before it may be accepted that hindlimb morphology limits take-off velocity in the hummingbird.

Evidence of a de-emphasis of leg contribution to take-off in hummingbirds includes early onset of wing beating (Figs 1, 2), hindlimb forces contributing only half of the total velocity at the end of take-off, and small accelerations due to hindlimb forces (Fig. 3A). In comparison, other species are only halfway through their first downstroke, when their feet end contact with the ground (Earls, 2000; Fig. 2), and hindlimb contribution to take-off velocity is greater than 80% in other species (Earls, 2000; Tobalske et al., 2000; Zimmerman and Tobalske, 2000). Peak accelerations due to hindlimb force are also greater in other species, ranging from a reported low of 15.6 m s^{-2} in pigeons (Heppner and Anderson, 1985) to 25–40 m s^{-2} in starlings (Bonser and Rayner, 1996; Earls, 2000) and to 76.5 m s^{-2} in quail (*Coturnix coturnix*; Earls, 2000).

Motivation had an effect upon wingbeat kinematics and mechanics including peak resultant acceleration due to leg and wing forces, peak vertical force from the hindlimbs, and velocity at the end of leg thrust (Fig. 3). Using velocity as a measure of performance, escape and aggressive take-off were similar and, therefore, may both potentially represent maximal effort in hummingbirds. However, these types of take-off were not equivalent. Compared with aggressive take-off, during escape hummingbirds started wing motion relatively earlier and used wingbeats of higher frequency. Also, during escape take-off, hindlimb forces tended to be greater, resultant peak force from the hindlimb was oriented more vertically, total peak acceleration was greater, and the duration of leg thrust was shorter (Fig. 3A,C).

Our results provide new insight into the role of motivational state upon locomotor performance, particularly with regard to wing kinematics and leg thrust (Fig. 2). Ecologically relevant motivational states should be incorporated into experimental design in much the same way that morphological or physiological characteristics often have been (e.g. Witter et al., 1994; Swaddle et al., 1999; Veasey et al., 2001; Burns and Ydenberg, 2002). The importance of animal motivation may be broadly underestimated in lab and field studies of locomotion. Among the range of possible behavioral motivations for taking into the air, perceived risk of predation is the only factor that has received extensive study (Kullberg et al., 1998; Lind et al., 2002, 2003). Kullberg et al. (1998) show that attack avoidance has an effect on take-off performance, whereas daily variation in body mass does not. When escaping models of predators, small birds tend to vary flight trajectory rather than velocity (Kullberg et al., 1998; Lind et al., 2002, 2003); this may hint that velocity at the end of leg thrust is always maximal when a bird perceives a threat.

As many investigations into animal take-off focus on the flight path of a bird after it has left the ground, data are often lacking regarding what are likely to be significant leg contributions to take-off performance (Earls, 2000; Fig. 1). Comparative experiments that couple behavioral manipulations with mechanical measurements should, therefore, improve our understanding of the ecological and evolutionary implications of take-off flight.

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