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Courtship dives of Anna's hummingbird offer insights into flight performance limits

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Behavioural displays are a common feature of animal courtship. Just as female preferences can generate exaggerated male ornaments, female preferences for dynamic behaviours may cause males to perform courtship displays near intrinsic performance limits. I provide an example of an extreme display, the courtship dive of Anna's hummingbird (*Calypte anna*). Diving male Anna's hummingbirds were filmed with a combination of high-speed and conventional video cameras. After powering the initial stage of the dive by flapping, males folded their wings by their sides, at which point they reached an average maximum velocity of 385 body lengths s^{-1} (27.3 $m s^{-1}$). This is the highest known length-specific velocity attained by any vertebrate. This velocity suggests their body drag coefficient is less than 0.3. They then spread their wings to pull up, and experienced centripetal accelerations nearly nine times greater than gravitational acceleration. This acceleration is the highest reported for any vertebrate undergoing a voluntary aerial manoeuvre, except jet fighter pilots. Stereotyped courtship behaviours offer several advantages for the study of extreme locomotor performance, and can be assessed in a natural context.

Keywords: acceleration; *Calypte anna*; courtship display; dive; hummingbird; performance

1. INTRODUCTION

Female animals use diverse male signals to select a mate, including various morphological ornaments and behavioural displays (Andersson 1994; Prum 1998; Hebets & Papaj 2005). Differential male mating success based on these signals can place them under directional selection for exaggeration (Andersson 1994), resulting in the classic examples of exaggerated male morphological characters, such as the long tails of birds. Just as male morphological traits can become exaggerated, female preferences could also place behavioural displays under directional selection, causing them to become exaggerated in some way, until physiological, neurobiological or other performance limits are reached. Performance, broadly defined, could include any aspect of locomotion that stimulates the sensory systems of a female, or is of interest to a biologist, including whole-animal power output, endurance, velocity, acceleration, manoeuvrability, coordination and potentially many others (Dial *et al.* 2008). Understanding locomotor performance limits is a goal of the fields of animal behaviour and biomechanics.

Here, I demonstrate the use of courtship displays for the study of locomotion, using the aerial display dive of the Anna's hummingbird (*Calypte anna*). Aerial dives are a component of the courtship behaviour of many birds, including nighthawks (Miller 1925), snipes (Bahr 1907) and hummingbirds. Falcons (Tucker 1998; Tucker *et al.* 1998), kingfishers and pelagic seabirds also use aerial dives to attack prey. By trading potential for kinetic energy, an organism can rapidly attain very high velocities. Aerodynamic forces scale as approximately velocity squared, so I tested the hypothesis that high-speed

courtship dives result in the production of large aerodynamic forces and concomitant accelerations. I calculated the velocities and accelerations of diving hummingbirds, and estimated the body drag coefficient and aerodynamic forces the birds experienced.

2. MATERIAL AND METHODS

Male Anna's hummingbirds were located on their courtship territories at the 'Albany Bulb' in the East Shore State Park, Alameda Co., CA, USA in 2006, 2007 and 2008. This location is at sea level, and is flat and relatively devoid of obstructing topographical features, facilitating the collection of video in which diving birds were a few dark pixels silhouetted against the sky. Recordings were not made on windy days. Dives were elicited by placing a model—a stuffed mount of a hummingbird, or a live hummingbird in a cage—near a male's perch. Dives were recorded by combinations of digital video (DV) cameras (filming 60 fields s^{-1} with a resolution of 640 × 480 pixels), high-definition (HD) DV (60 fields s^{-1} , 1900 × 1080 pixels) or high-speed video (Redlake MotionMeter, 500 frames s^{-1} , 292 × 210 pixels; Fastec Troubleshooter, 500 frames s^{-1} , 1280 × 1024 pixels; Vision Research Phantom HD, 400 frames s^{-1} , 2048 × 1080 pixels).

The trajectory of a diving male usually lies within a vertical plane (the dive-plane), and males almost always dive towards the sun, rather than in a random direction (Stiles 1982), which allows prediction of the trajectory of a diving bird. Close up, high-speed videos of diving birds were collected to record the bird's wing and tail kinematics over the course of the dive. Sounds produced by the bird's wings and tail were recorded with a microphone, as described in Clark & Feo (2008).

To obtain two-dimensional trajectories of the males' dives, I placed a single camera normal to and 22–27 m from a bird's anticipated dive-plane. Videos in which the bird's dive-plane appeared to not coincide with the camera's

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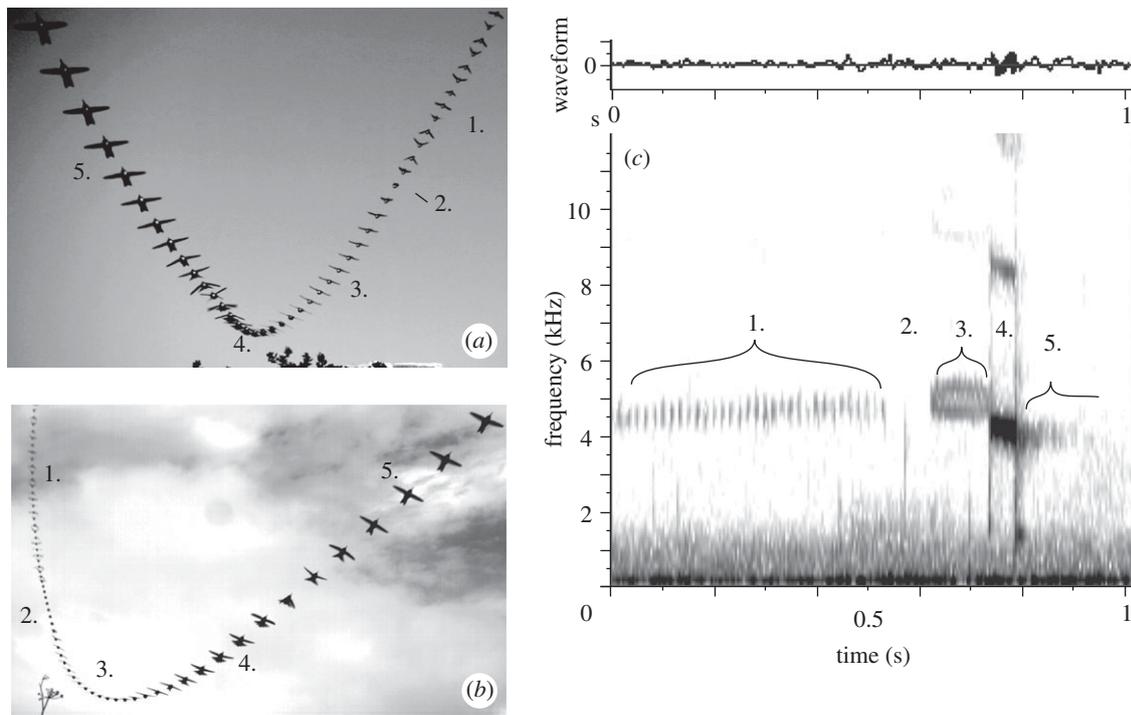


Figure 1. Kinematic stages of the display dive of the male Anna's hummingbird, as indicated by high-speed video and sound recordings. Also see videos in the electronic supplemental materials. (a,b) Composite images from high-speed videos of birds diving towards and then past the camera. Consecutive images are 0.0125 s apart (a) or 0.01 s apart (b). See table 1 for descriptions of the five (1–5) stages of the dive kinematics. (c) A sound spectrogram of the sounds produced during the course of the dive.

image plane were discarded. A meter stick oriented horizontally and vertically at the bottom of the dive was used to calibrate distance.

In addition to these two-dimensional trials, the three-dimensional kinematics were recorded from a single male holding a territory with topography uniquely suited for filming from multiple directions. Six cameras (four DV, two HD) were placed 22–27 m (depending on camera pixel resolution) from the bottom of the dive, in two sets of three cameras. The two HD cameras were placed on opposite sides of the dive-plane, arrayed so that the bird's dive was nominally coincident to the image plane of each camera. The four DV cameras were flanked one on either side of each of the two HD cameras, so that the bird dove roughly 30° towards or away from each of the DV cameras. The cameras were synchronized to within 17 ms using two camera flashes, and spatially calibrated in the program PEAK MOTUS 8 (Vicon, Centennial, CO, USA), using landmarks on a cube measuring $1.6 \times 1.1 \times 1.1$ m that was placed in the volume at the bottom of the dives. The position error of this calibration was less than 1 per cent in all three dimensions. To test the accuracy of computed accelerations, a projectile was launched vertically to estimate the acceleration from gravity. This six-camera setup allowed three-dimensional kinematic analyses of dives, to confirm the validity of the assumption of minimal motion in the third dimension.

The videos used for the two-dimensional and three-dimensional trials were digitized using PEAK MOTUS 8. Within PEAK MOTUS, a quintic spline was used to smooth the position data and calculate the time-course of the bird's velocity and acceleration (Woltring 1985; Walker 1998). The spline's error variance was selected to smooth the trajectory of the calibration projectile sufficiently (known to be accelerating under the force of gravity and some drag), and

that same error variance was used to smooth all the dives. After the spline was fit to the data, the first and last 10 samples were discarded to eliminate edge effects (Woltring 1985; Walker 1998). Estimates of the projectile's acceleration indicated acceleration errors of less than 10 per cent at <4 m of the calibration cube.

For the two-dimensional and three-dimensional trials, sets of one to eight dives were obtained from individual males, and each set of dives had a single calibration. Because calibration errors could be a significant source of variance between sets of dives, replicate dives within sets were averaged, and each set was treated as independent. Morphological measurements obtained from various males indicated an average body mass (m) of 0.0045 kg ($n = 29$), a projected frontal body area (A) of 2.6 cm² ($n = 7$) and a pectoralis muscle mass of 7.8×10^{-4} kg ($n = 8$).

3. RESULTS

The Anna's hummingbird's display dive is composed of five stages, summarized in figure 1, table 1 and the high-speed videos in the electronic supplemental material. Birds initiated the dive out of the frame of the videos (figure 1a,b). In stage 1, they descended into view, propelling themselves earthward on wings flapping at 55.5 ± 1.72 Hz ($n = 16$ high-speed videos), while producing a trill (figure 1c) with a temporal frequency of 55.4 Hz (Doppler-corrected; 59.2 ± 5.6 Hz uncorrected). In stage 2, the males ceased flapping and tucked their wings by their sides, and ceased producing the trill. Stage 2 was omitted in approximately 10 per cent of dives (missing in 2 of the 16 videos, and 12 of the 118 sound recordings). In stage 3, the birds spread their wings to glide (figure 1a,b), while producing a

Table 1. Stages of the courtship dive of the male Anna's hummingbird, as determined by high-speed videos ($n = 16$) and sound recordings ($n = 118$). Means are ± 1 s.d. See figure 1.

stage	kinematics description	high-speed video (s)	sound (s)
1	descends on flapping wings	N/A	>0.5
2	ceases flapping and tucks wings by sides	0.053 ± 0.044	0.064 ± 0.036
3	spreads wings and glides, with tail shut	0.15 ± 0.041	0.144 ± 0.027
4	continues gliding, spreads tail	0.071 ± 0.0077	0.054 ± 0.007
5	shuts tail while flapping wings once, glides, then transitions to another behaviour	N/A	N/A

pure tone (figure 1c). This transitioned into stage 4 as the birds abruptly spread their tails at the bottom of the dive, which corresponds to the tail-generated sound described in Clark & Feo (2008). They then flapped their wings once and shut their tails in stage 5, which was the final stage of the dive. The kinematic stages 1–4 correspond one-to-one with sounds produced during the dive (table 1, figure 1c).

Two-dimensional or three-dimensional dive trajectories suitable for analysis were obtained for 26 dives across nine sets. In one set, eight dives were recorded in three dimensions at 60 fields s^{-1} , and in a second set, two dives were recorded in two dimensions at 500 frames s^{-1} . The remaining 16 dives were two-dimensional, filmed at 60 fields s^{-1} , and spread across the remaining seven sets (one to three dives per set). The three-dimensional dives indicated that, although there was a slight component of motion in Z (< 1.5 m), neglecting this motion did not significantly affect calculations of X and Y velocity or acceleration. Similarly, the velocity and acceleration profiles from the two two-dimensional trials recorded at 500 frames s^{-1} were similar to the remaining dives, suggesting that the 60 Hz videos were not temporally undersampled relative to the velocity and acceleration profiles presented here (Walker 1998). Therefore, all nine sets of dives are combined for the remaining analyses presented.

Position, velocity and acceleration profiles of diving Anna's hummingbirds are presented in figure 2. The trajectory (figure 2b) of the dive resembled a tilted 'J', with the start of the dive at a height of roughly 30 m above the recipient of the display. The birds initially descended at a steep angle relative to the horizontal (stage 1), then pulled up during stages 2 and 3 so that by stage 4, they passed horizontally over the recipient. In stage 5, they ascended and transitioned to another behaviour.

Velocities of diving hummingbirds, relative to the global coordinate system, are presented in figure 2c. During stage 1, the birds' average vertical (Y_{global}) velocity was in excess of -16 m s^{-1} , but as the birds pulled up in stages 2 and 3 this velocity lessened as the horizontal (X_{global}) velocity increased. The horizontal velocity reached a maximum of 26.1 ± 2.8 m s^{-1} ($n = 9$ sets) just before stage 4. During this time, the bird's overall speed increased until the start of stage 3, at which time it reached a maximum of 27.3 ± 3.2 m s^{-1} (97 km h^{-1} ; $n = 9$). Given a body length (bl) of 7 cm, (including the tail but excluding the 1.5 cm bill), this was a top speed of 385 bl s^{-1} .

The accelerations in a quasi-bird-based coordinate system are plotted in figure 2d. Tangential acceleration (X_{bird}), which corresponded to changes in the birds'

speed (figure 2c), was initially positive during stages 1 and 2, as the birds sped up under a combination of the force of gravity and, in stage 1, thrust from flapping wings. At the start of stage 3, this acceleration switched sign and became negative, reaching a value of -23.5 ± 10.1 m s^{-2} ($n = 9$) at the middle of stage 4, at which point the birds were travelling horizontally, and thus were slowing down due to the force of drag (including drag on the spread wings and tail). Tangential acceleration reached an average peak of -32.2 m s^{-2} in stage 5, at which point the birds were ascending, and thus slowing both due to drag and transfer of kinetic energy into gravitational potential energy.

Centripetal accelerations (Y_{bird}), indicative of changes in direction caused by lift, were initially low in stages 1 and 2, but exceeded 75 m s^{-2} ($n = 9$) in stage 3, and reached a maximum of 86.6 ± 13.1 m s^{-2} ($n = 9$), as the birds spread their wings. Because the birds were moving nearly horizontally at the point of maximum centripetal acceleration, they were simultaneously supporting their body weight with an additional mg of lift. Males thus experienced centripetal forces of approximately 0.43 N, nearly 10 times higher than what they would experience solely from g , gravitational acceleration (9.8 m s^{-2}).

4. DISCUSSION

During their courtship dive, male Anna's hummingbirds reach maximum speeds and accelerations that exceed the previous performance records for vertebrates undergoing a voluntarily aerial manoeuvre. These kinematic measurements extend the known limits for flight performance-related variables. It would appear sexual selection can cause behavioural displays to elaborate until performance constraints are reached, which in this case may be set by either velocity- or acceleration-related constraints, as discussed below. This example illustrates the potential use of courtship displays for the study of general limits to animal locomotor performance, in an ecologically relevant context.

(a) Dive speeds

Diving allows an animal to attain much higher speeds than can be attained in powered forward flight. Male Anna's hummingbirds reach an average maximum speed of 215 bl s^{-1} (15 m s^{-1}) in forward flight in a wind tunnel (Clark & Dudley 2009), whereas the average maximum speeds reached during the dive were 385 bl s^{-1} . I hypothesize that maximizing speed is an important component of the courtship display of Anna's hummingbirds, because the loudness of the sound

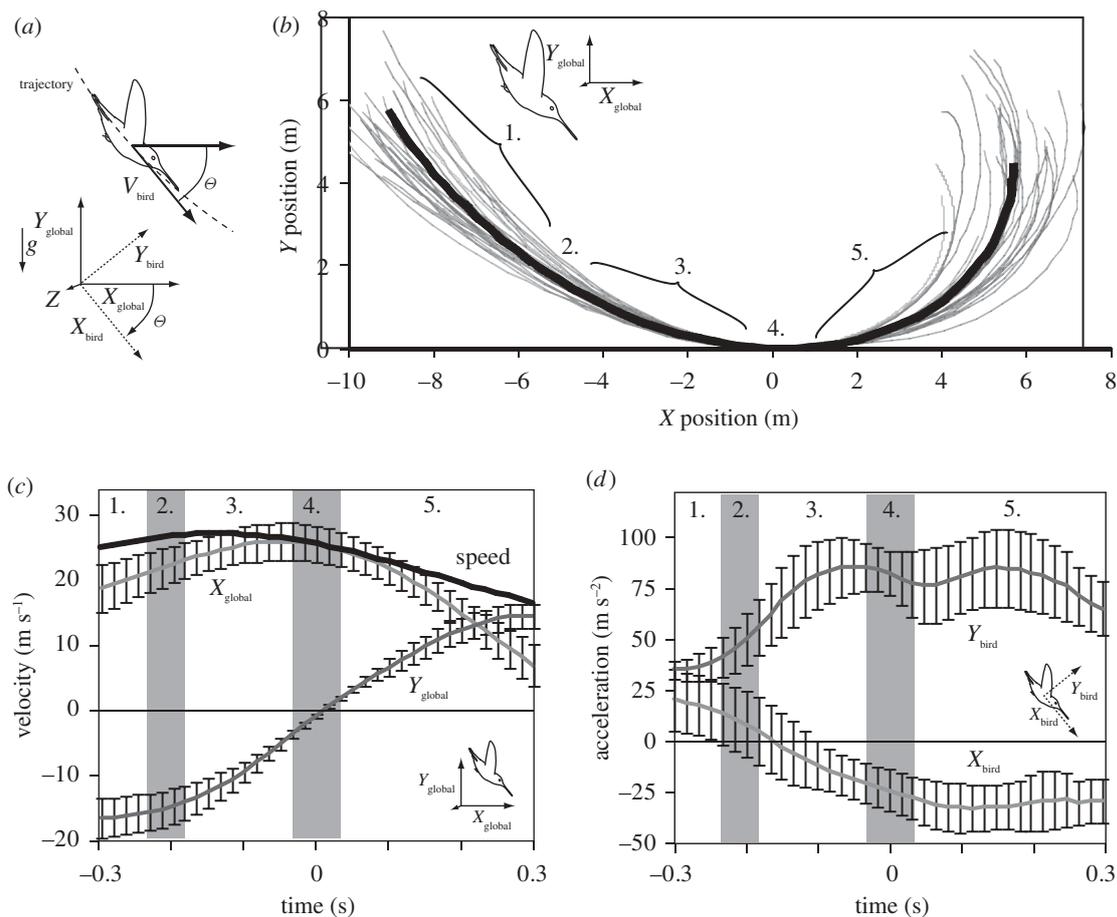


Figure 2. Position, velocity and acceleration profiles of diving Anna's hummingbirds. 1–5 indicate the kinematic stages of the dive (figure 1, table 1). (a) Two inertial coordinate systems were used in the analyses of diving male Anna's hummingbirds: a static, global coordinate system with the Y_{global} axis opposite to gravity (g), X_{global} horizontal in the direction of the dive (solid lines), and Z normal to X and Y ; quasi-bird-based coordinate system (dotted lines) in which the X_{bird} and Y_{bird} axes were rotated by θ about the Z axis, so the X_{bird} axis was parallel to the bird's instantaneous velocity (V_{bird}), and tangent to the bird's XY trajectory (dashed line). This coordinate system was inertial (the origin did not move). (b) Bird trajectories at the bottom of the dive. Solid black line: a representative trajectory. Faint lines: all 26 individual dive trajectories. (c) Average velocity of diving Anna's hummingbirds in X_{global} , Y_{global} and overall speed (black line) over the course of the dive ($n = 9$ sets). Bars are ± 1 s.d. Dives were aligned temporally at the instant Y velocity = 0. (d) Average accelerations of diving Anna's hummingbirds in X_{bird} and Y_{bird} ($n = 9$). X_{bird} acceleration is the bird's tangential acceleration and corresponds to changes in speed (black line) shown in (c). The Y_{bird} acceleration is centripetal acceleration and corresponds to changes in direction that cause the curved trajectory evident in (b).

produced by the tail feathers during stage 4 (see Clark & Feo 2008) may be correlated with air speed (C. J. Clark 2009, unpublished data).

The average maximum speed of 385 bl s^{-1} sets a new record for maximum length-specific speed attained by a vertebrate. This speed is nearly twice the maximum speed of 200 bl s^{-1} (70 m s^{-1}) that has been reported for peregrine falcons (*Falco peregrinus*) diving in pursuit of prey (Tucker *et al.* 1998). It is also slightly higher than the very highest velocity of 350 bl s^{-1} (50 m s^{-1}) reported for swallows diving from high altitude, at the culmination of migratory flights (Hedenström & Liechti 2001). Incidentally, it is also greater than the top speed of a fighter jet with its afterburners on, 150 bl s^{-1} (885 m s^{-1}), or the space shuttle during atmospheric re-entry, 207 bl s^{-1} (7700 m s^{-1}), although these aircraft operate at far higher Reynolds numbers than flying animals. Assuming the body drag coefficient (C_D) \propto (Reynolds number) $^{-1/2}$ (Vogel 1994), which may be valid for diving animals (but not the aircraft),

length-specific terminal velocity is expected to be size-independent. Thus, the length-specific speed record set here is not simply an artefact of allometry.

One factor limiting the terminal velocity of a diving bird is C_D . For bird bodies, wind tunnel and theoretical analyses have suggested a range of C_D values that typically include 0.1–0.2, but also values as high as 0.4 (see Pennycuik *et al.* 1996; Tobalske 2007 and references therein). Hedenström & Liechti (2001) used dive speeds and descent angles to estimate C_D , which they suggested to be no greater than 0.4 for small birds. The stereotyped dive kinematics of the Anna's hummingbird allow for a similar calculation of C_D . The hummingbirds tucked their wings during stage 2, at which time they were descending with a dive angle (θ) of 45° (figure 2b). By conservatively assuming that the speed of the bird during stage 2 is terminal velocity, the C_D can be estimated as:

$$C_D = 2mg \cos(\theta) / (\rho v^2 A), \quad (4.1)$$

(Tucker 1998) where A is 2.6 cm^2 , m is 0.0045 kg , the birds' maximum speed (v) is 27 m s^{-1} (figure 2c) and air density (ρ) is 1.2 kg m^{-3} . This results in an estimate of $C_D = 0.3$. Because the birds only began to decelerate as they spread their wings in stage 3 (figure 2d), it is probable that the birds' top speed in stage 2 was less than the true terminal velocity, suggesting that 0.3 is an overestimate of the true C_D .

(b) Dive accelerations

The instantaneous, centripetal accelerations that occur during stages 3, 4 and 5 of the dive reached nearly $10g$ and remained high for at least 0.3 s (figure 2d). This is greater than the previously reported accelerations for any organism undergoing aerial manoeuvres, except jet fighter pilots (Latham 1955). In level flight, directly powered by muscle contractions, cockatoos and swallows (Hirundinidae) manage accelerations ranging from 0.56 to $1.2g$ (Warrick 1998; Bowlin & Winkler 2004; Hedrick & Biewener 2007), whereas insects can achieve up to $2.6g$ during manoeuvres (Rüppel 1989; Schilstra & Hateren 1999), and hummingbirds can achieve nearly $4g$ in escape takeoffs (Tobalske *et al.* 2004). The much higher centripetal accelerations reached by diving Anna's hummingbirds appear possible because energy is stored in the form of gravitational potential energy and then released, analogous to the sudden release of stored elastic energy that produces the phenomenal accelerations attained by leaping fleas (Bennet-Clark & Lucey 1967) or the mandibles of trap-jaw ants (Patek *et al.* 2006).

Maximal accelerative performance will be subjected to physical constraints. Two potential physiological limits on dives are hydrostatic effects and wing torque. In fighter pilots, accelerations above roughly $7g$ can cause temporary blindness and blackouts resulting from circulatory fluid shifts, but these hydrostatic effects are primarily manifested in manoeuvres lasting longer than 1 s (Latham 1955), which is longer than the acceleration peak experienced by the diving Anna's hummingbird (figure 2d). Moreover, the shorter fluid columns of the hummingbird circulatory system may make them less sensitive to acceleration-generated changes in hydrostatic pressure (Larimer & Dudley 1995).

Wing torque on the shoulder was the reason Tucker *et al.* (1998) suggested their diving gyrfalcon did not attain accelerations higher than $1.6g$. The average centripetal force of 0.43 N transiently experienced by the male Anna's hummingbird at the bottom of the dive is generated by lift produced by a combination of the body, tail and both wings. Assuming each wing produces 0.2 N , with a centre of pressure halfway down the wing, the resulting torque on each shoulder is 0.006 N m . Further, assuming the pectoralis inserts 3 mm from the wing's point of rotation (Welch & Altshuler 2009), this predicts the pectoralis muscles must each produce forces of 2 N to balance this torque during stage 3 of the dive, or nearly 3000 N kg^{-1} . Owing to this muscle's complex architecture, an estimate of the physiological cross-sectional area is not yet available (K. Welch 2009, personal communication), but this could be close to the maximum isometric force the pectoralis muscle can generate. By contrast, I estimate this torque would apply maximum stresses of less than 10 MPa to the

wing bones, well below the breaking strength of bone (Wainwright *et al.* 1976). Moreover, slight increases in bone size would greatly increase flexural strength, whereas increases in isometric force production of the pectoralis would require comparatively large increases in muscle size. Therefore, I hypothesize that diving hummingbirds may be constrained by the isometric force their pectoralis muscles can produce.

(c) Courtship displays provide the opportunity to study extreme performance

Extreme performances are of interest to both ecologists and physiologists. Physiological relationships are often the easiest to study in extreme examples (the Krogh principle: Krebs 1975). Moreover, extreme locomotor performances occur in ecological contexts that have large fitness consequences riding on the result, such as fights, attacks on elusive prey, escape behaviour (Irschick & Garland 2001; Husak 2006) or courtship displays. Courtship displays would appear to offer several advantages for scientific study over these other contexts.

Variability in the kinematic parameters that describe a successful interaction makes fights, attacks or escapes difficult to study. A prey escaping a predatory strike is selected to avoid capture, rather than maximize a performance variable like velocity or acceleration *per se*. In a given encounter, there may be several kinematic options available for success, and unpredictability may be beneficial, so escapes, fights and attacks tend not to be stereotypical. Courtship displays are frequently stereotypical, evidenced here by the similarity of the dive trajectories of different males (figure 1a).

Two other features that facilitate courtship displays for biomechanical study are their predictability, and the ability to elicit them in a natural context. The courtship displays studied here were often elicited by placing a crude, unresponsive mount of a female on a male's territory (see the electronic supplemental online videos), yet some ardent males would perform dozens of dives before becoming habituated. By contrast, it may be difficult to simulate the conditions of a natural fight in the laboratory, or to anticipate precisely where a natural fight will occur in the field. Likewise, natural predatory attacks are difficult to predict, and experimentally providing prey for a predator to attack (e.g. Webb 1983; Tucker *et al.* 1998) may not mimic the context for a natural predatory attempt; for example, the prey may not behave naturally.

There may be similar systems in which additional variables of behavioural and biomechanical interest could be examined using natural courtship behaviour. Many other highly visual organisms have complex visual courtship displays, like butterflies, jumping spiders (Elias *et al.* 2005) and hoverflies; for hoverflies, it has been suggested females may have visual sensory systems attuned to male flight (Nordström & O'Carroll 2006). Females could prefer a diverse array of visual aspects of male movements in these species, suggesting that courtship displays may offer the opportunity to study a range of interesting biomechanical questions about locomotion.

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