

# Mechanics and Control of Perching Flight

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# Declaration

I declare that this thesis has been composed solely by myself and that it has not been submitted, in whole or in part, in any previous application for a degree. Except where states otherwise by reference or acknowledgement, the work presented is entirely my own.

*26th April 2019*

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Lydia Allegranza France



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*There is an art to flying, or rather a knack. The knack lies in learning how to throw yourself at the ground and miss.*

Douglas Adams

# Abstract

Perching is an example of high risk, high reward behaviour executed within tight physical constraints. Despite the high risks posed by collision and stall, perching is performed routinely by most birds. However, surprisingly little is understood about the energetics and control of aerodynamic braking, nor the detail of wing and tail kinematics during perching.

In this thesis, detailed wing and tail kinematics were quantified for over 1000 indoor perching flights by Harris hawks using high-speed motion capture. Similar measurements were also taken from 15 outdoor flights by a Steppe eagle, and trajectories were tracked from wild passerines landing on a fixed or oscillating feeder. Aerodynamic braking is typically achieved in raptors through a rapid pitch-up manoeuvre executed at the end of a gliding approach. This manoeuvre produces high drag as predicted by published unsteady aerodynamic models, but unexpectedly the data shows no accompanying peak in lift. The complexity of wing-tail morphing and rotation during the rapid pitch-up manoeuvre points to the careful control of aerodynamic forces during unsteady deep stall.

A high degree of variation in the perching manoeuvre was evident in the Steppe eagle flights, likely in response to local air conditions. However the hawk flights were exceedingly consistent under the controlled experimental conditions. Different perch distances were used to induce variation in the hawks' braking strategy. Braking was achieved in a flapping rather than gliding approach in the shortest flights, although the observed pattern of body pitch-up was consistent across flight distances. Systematic inter-individual variation was recorded in both wing motion and trajectory shape.

As a visually-guided flight behaviour, braking is controlled precisely with respect to the target such that the bird may land with low impact force and avoid injuries. Flights from the eagle and hawks show evidence for control of braking in line with the predictions of tau theory: during approach to the perch, both the rate of change in the optic flow variable tau and the rate of deceleration were constant. This was not the case for wild passerines using intermittent flight, although they might still use optic flow in feedback control.



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# Introduction and Literature Review

## 1.1 Perching Flight Behaviour and Ecology

The apparent effortless nature of birds in manoeuvring flight has impressed and inspired generations of engineers and biologists, yet little is known how they achieve such aerial feats. The accuracy of flight manoeuvres is critical for survival and relies on sensorimotor feedback in controlling wing and tail kinematics to produce aerodynamic forces and moments. From the acrobatics of fly-catching swifts, the missile-like stoops of a peregrine falcon, the obstacle negotiation of goshawks through cluttered branches, or the seamless transition from air to water of diving cormorants, the complexity and diversity of bird flight is an exemplar of evolutionary design.

Many flight behaviours are closely tied to feedback from external cues, where even seemingly simple behaviours rely on rapidly processing sensory information from ever-changing complex environments. Vision is pivotal to flight, and a bird has been described as a "wing guided by an eye" (Rochon-Duvigneaud, 1943). Visual information is rapidly processed to allow environment navigation, obstacle avoidance, predator detection, and trajectory targeting.

Perching, or landing on a specific target, is one such visually guided behaviour. Transitioning safely to the terrestrial environment or a substrate is critical for any animal performing a jump, glide or flight, and simple controlled landing behaviours have evolved in frogs, snakes, geckos, and flying squirrels (Roderick et al., 2017; Socha et al., 2005; Jiménez Manzanera and Smith, 2015; Bishop, 2006). The high velocity of powered flight makes safe landing even more critical for birds and their perching behaviour is more complex than a simple touchdown mechanism. To avoid dangerous impact forces, birds reduce their groundspeed prior to contact with their target (Provini et al., 2014; Berg and Biewener, 2010; Green and Cheng, 1998). Injuries from collisions are often fatal (Bonser, 1999; Klem Jr, 2009) and yet perching is integral to many foraging behaviours, for rearing young, and for resting safely away from ground-based predators. Powered flight is energetically expensive (Biewener, 2011; Martin, 2011) and making frequent landings can still be advantageous despite the high risks.

The experiments in this thesis investigate the main challenges of perching flight, which can be summarised as: i) generating sufficient braking force to reduce ground speed to a safe speed; ii) maintaining flight ability and control authority during braking; iii) controlling braking with respect to the perch.

There are additional challenges associated with perching strategy, where a bird ought to find an optimum between the energy expenditure of caution and potential injury from recklessness (Green and Cheng, 1998). As birds fly in varied and diverse environments and conditions, selecting different braking strategies might prove favourable in certain situations. Differing techniques allow birds to perform perching manoeuvres whilst missing flight feathers due to moult/injury, or whilst carrying a heavy prey item or nest component, and in spite of gusts or other punishing weather conditions.

## 1.2 Flight Kinematics as Control Inputs

In animal flight, generating an aerodynamic force is futile without stability and control. There are two external forces acting upon a bird in flight, its weight and aerodynamic force, and during equilibrium all such forces are equal and opposite (Thomas and Taylor, 2001). If the flying object is inherently stable, disturbances to equilibrium are reversed over time by structural and mass distribution properties. However, inherently stable flight is uncontrollable and cannot perform manoeuvres. An inherently unstable bird required feedback to correct perturbations using wing and/or tail motion in order to maintain control and execute manoeuvres (Taylor and Thomas, 2002; Windsor et al., 2014). An eagle using soaring flight maintains equilibrium by the inherent stability of its wing shape, mass distribution, posture, and tail position but additionally uses frequent correctional control to overcome gusts and changes in airflow (Gillies et al., 2011).

The precise control of bird flight required for rapid manoeuvres is possible due to the dexterity of their wings and tails. Production of aerodynamic forces is critical for lift generation and therefore weight support, but also for flight control. The vast majority of aerodynamic force production is from the wings, with remaining forces generated from the tail and body. To perform a manoeuvre, it is primarily the wings and tail that provide the imbalance of resultant forces required to execute a desired change in course.

There are three mechanisms for modulating aerodynamic forces: independent wing velocity about the shoulder; dynamic shape changes; and angle of attack (the angle between the wing chord and the oncoming airflow) (Hedrick et al., 2012; Lentink et al., 2007; Baier et al., 2013). These mechanisms affect the aerodynamic force generation, as predicted by the lift equation:

$$L = \frac{1}{2} \rho V^2 S C_L \quad (1.1)$$



where  $V$  is the total velocity,  $S$  is the flight surface area,  $C_L$  is the coefficient of lift, and  $\rho$  is the air density. Lift is defined as the aerodynamic force perpendicular to the oncoming airflow. Morphing wing shape alters the flight surface area and  $C_L$ , while changes to angle of attack alters the lift coefficient, and finally wing motion velocity also affects lift. In fixed-wing flight,  $S$  is constant and lift production is determined by  $C_L$  at a given velocity. However, if wing surface area is decreased, high  $C_L$  has no little impact on lift.  $SC_L$  provides a parameter of the lift effectiveness of the wing (Reynolds et al., 2014).

Wing surface area may be altered by folding during flight, but wing camber and thickness varies along the wing surface as demonstrated in armwing measurements of a Steppe eagle (Carruthers et al., 2010). Camber during flight has only been measured in the last few years due to technological advances that allow surface reconstruction from birds in flight with a multi-camera setup (Durstion, 2018; Durstion et al., 2019). In addition, feathers act as flexible flaps and slots along the wing and tail (Tucker, Vance A., 1993; Carruthers et al., 2007; Brücker and Weidner, 2014; Klein Heerenbrink et al., 2017). These passive morphing mechanisms alter airflow across the wing and therefore the force magnitude and direction.

Bird wings move independently to the body with many degrees of freedom afforded by the underlying musculoskeletal structure, unlike the rigid design of an aircraft. A bird wing is roughly separated into two parts, the arm-wing and the hand-wing. The arm-wing starts at the shoulder joint and ends at the wrist joint and host the secondary and tertiary flight feathers. The hand-wing section starts at the wrist and ends at the wingtip and contains the primary flight feathers. The two wing sections when held out at maximum span form a complete surface. By bending the wrist and elbow the hand-wing folds into the arm wing and the feathers slide over one another, reducing the wing area. The hand-wing may also flex upwards by dorsoventral rotation of the wrist (Stowers et al., 2017). A bird can also twist its wing along the length to vary the angle attack along the wing (Norberg, 2012). Measuring wing twist in flight has been limited due to experimental techniques, however it is thought to reduce flow separation at high angles of attack as well as modulate aerodynamic force production across the wing surface (Hedrick, 2004). Such wing kinematics can be implemented during gliding flight in order to control manoeuvres.

Wing folding and twisting is also key during flapping flight, with dynamic shape changes occurring during each wing flap cycle. During the upstroke most birds fold their wings to reduce counterproductive forces by flexing the elbow and drawing the wrist inwards (Robertson and Biewener, 2012; Muijres et al., 2012). The downstroke is responsible for most of the lift and thrust generation for most species of bird (Tobalske, 2007; Crandell and Tobalske, 2015), but drag production differs along the wing. Drag is defined as the aerodynamic force parallel and in the opposite direction to the oncoming airflow. Wing velocity comprises of body velocity and relative wing motion velocity. Wing

motion can be described using parameters such as stroke amplitude, stroke plane angle, mean positional angle of the wings, angular velocity, or angle of attack and alterations of these kinematics can induce body rotations or velocity changes within a wingbeat cycle (Altshuler et al., 2012; Paranjape et al., 2012).

Dynamic wing shape, twist, camber and angle of attack can affect the position of the centre of pressure – defined as the point on the wing where the resultant vector of lift and drag acts. The centre of gravity is the average point of the weight of the bird, and is also dependent on wing/tail/leg configuration.

While birds can redirect aerodynamic forces relative to their bodies through kinematic changes, it is likely more cost effective to instead rotate its body (Ros et al., 2011; Ros et al., 2017; Altshuler et al., 2012). To induce a turning manoeuvre, the bird rotates its body such that the direction of force changes in the global reference frame. Such rotations are possible through kinematic control inputs that alter the distance between the centre of pressure and the centre of mass. Roll rotations can be controlled in gliding and flapping flight from bilateral asymmetric motions of the wings, for example different angles of attack for each wing (Pennycuik, 1975). Angle of attack may be altered through rotation around the shoulder or, more finely, by wing twist at the wrist joint. Alternatively, roll rotations can be caused by increasing the span of one wing by asymmetrical folding, normally resulting in banked turns (Brown, 1963). In flapping flight, the wingbeat amplitude may also be altered asymmetrically (Hedrick et al., 2007). Twisting the tail can induce a roll but a large force is required (Thomas, 1993). Rotations about yaw are rarely independent except in hovering hummingbirds, and most course changes are achieved through banked turns (Pennycuik, 1975; Lighthill, 2013). Asymmetry in motion or anatomy does not necessarily lead to unstable flight, as a bird missing feathers from one wing can use compensatory motions to generate symmetrical forces and stabilise flight.

Pitch control is effected by adjusting the position of the centre of pressure relative to its centre of gravity, for example by changing wing sweep (Tucker, 1992; Pennycuik, 1975). Adjustments to the tail also alter pitch rotations. Relatively small kinematic changes can lead to whole body rotations, for example Hoey (1992) used a model to demonstrate pitch rotation can be controlled entirely by tail angle of attack. In slow flight, the tail is often lowered and spread in order to contribute to lift production (Thomas, 1993). In isolation, this control input would also lead to a nose-down pitch rotation, as the centre of pressure is drawn backwards from the centre of gravity. However, it has been observed that the wings are swept forwards during slow flight, or elevated relative to the body (increased dihedral angle) (Carruthers et al., 2010; Tucker, 1992). Both these kinematic adjustments push the centre of pressure forwards and therefore induce a nose-up pitching motion which counters the rotation of the tail during slow flight.

Studies in flight manoeuvres have been more numerous in recent years due to advances in photography and computing technology. Bird flight kinematics are finely-controlled and difficult to record unobtrusively. It is

also difficult study the effects of flight dynamics without quantifying wing and tail morphing to a high level of accuracy. Recent experiments have used semi-automated marker tracking (Hedrick, 2008; Hedrick et al., 2002; Ros et al., 2015; Tobalske, 2007), feature tracking (Carruthers et al., 2010; Walker et al., 2009) or visual-hull based reconstruction methods (Fontaine et al., 2009; Muijres et al., 2014; Ristroph et al., 2009) to quantify flight kinematics. New advancements in recording and image tracking have begun to reconstruct the wing surface at high resolution during bird flight (Durstun, 2018; Durstun et al., 2019).

Measuring flight performance in butterflies was achieved through using retro-reflective markers and using motion capture technology to track them (Slegers et al., 2017). Motion capture is used to capture biomechanics in many species of animal for clinical purposes but also for the entertainment arts. The ability to capture high-speed detail of motion opens up new possibilities for flight research (van der Kruk and Reijne, 2018). With more detailed kinematics measurements an more integrated model of the control mechanisms in manoeuvring flight will be one day possible.

## 1.3 Descriptions of Perching Flight Behaviours

Due to its importance in behavioural ecology, birds engage in frequent landings and yet the braking manoeuvre is complex and not well understood. Birds significantly reduce their airspeed in perching flight, and this is achieved through aerodynamic braking (Bonser and Rayner, 1996; Berg and Biewener, 2010; Provini et al., 2014; Polet and Rival, 2015). Such deceleration is very rapid – a large eagle can reduce its groundspeed from 10m/s to almost a complete stop in 0.4s. For comparison, a standard car at the same speed would take over one second to stop (Driving Standards Agency UK, 2007). Similarly, Provini et al. (2014) measured decelerations in doves and zebra finches from 15 to 7 body lengths in 0.15 seconds entirely through aerodynamic means. Unlike deceleration on the ground, the mechanism for braking does not use surface friction and instead the bird must lose kinetic energy to its wake. Remaining kinetic energy is transferred to the perch upon impact.

How such kinetic energy loss is achieved varies between species and circumstance. Birds use different forms of powered flight related to their body size and wing design. Small birds with rounded, low aspect ratio wings use flap-bounding where a flap cycle is followed by a period of ballistic flight with wings folded against the body. Larger birds such as pigeons primarily use flapping flight with short periods of gliding where the wings are held at higher span. Large birds such as eagles mostly use gliding and soaring flight and can fly for long durations without flapping. While braking is generally defined as kinetic energy loss to the wake there are multiple mechanisms for achieving this end.

Carruthers et al. (2007) described a male adult Steppe eagle (*Aquila nipalensis*) landing on a handler's glove in varying outdoor conditions. The eagle either used a gliding approach or flapping flight. Three stereotyped phases were described during the flights: a gliding approach, a rapid pitch-up manoeuvre, and a parachute phase. First the eagle approached its target from below, flying very close to the ground while its wings were outstretched with high wingspan. Next the wings folded into an M-shape while the tail elevated, both control inputs thought to facilitate the rotation of the entire bird known as the rapid-pitch up. While pitching the eagle gained height and the feet swung forwards in preparation for contact. In the final phase before contact, the eagle's posture had reached upright and the wings maximal spread. The tail was additionally at maximum span and swung down to form a complete surface with the wings. This parachute formation results in deep stall, and the authors noted the feather deflections associated with reversed airflow.

The eagle also used an alternative flapping flight approach where its trajectory was described as roughly level with its target. The stroke plane was described as having a sharp downward incline. The tail was described as beating forwards and backwards in phase with the wing motion, and coordinated with a increase and decrease in span. A final or penultimate wingbeat was noted for its distinct kinematics and described as the likely source of deceleration. Like the rapid pitch-up in the gliding perching manoeuvre, the wings were rotated to a high angle of attack during this decelerating flap. In coordination with the downstroke, the legs were outstretched for contact while the tail swung down and fanned, resembling the parachute phase.

Work by Carruthers et al. (2007) provided the first detail into how an eagle lands on a target in a range of conditions. A large number of flights were used in the research (n=37) and included variation in the form of flapping and gliding approaches. The eagle was not restricted in its approach and a combination of indoor and outdoor flights were used. The manoeuvre as described by the authors has gone on to influence tests of passive flap devices as well as perching manoeuvres for UAVs **Choi2012**; Brücker and Weidner, 2014; Johnston and Gopalarathnam, 2012; Zhang et al., 2018. However, this research did not provide quantified detail into the wing and tail kinematics nor the energetics of aerodynamic braking. Such measurements would require camera views from multiple positions in order to track and reconstruct features on the wings and tail, whereas in this study a single camera view was used. Greater detail into the perching manoeuvre in both its mechanics and wing kinematics could assist with understanding how high deceleration is achieved while maintaining weight support using wing morphing.

Other flapping perching flights performed by pigeons have been measured by Berg and Biewener (2010). A similar increase in stroke plane angle was measured on approach to a perch, where the flapping wing path tilted upwards and pushed the aerodynamic force more forwards. Provini et al. (2014) measured aerodynamic forces during descending

landing flights by zebra finches and diamond doves, both species using flapping flight. The zebra finches slowed their wingbeat duration for the final flap, particularly the duration of the downstroke, and the final two wingbeats produced significantly less aerodynamic force. There was a small increase in body pitch angle during the final wingbeats, and a small decrease in angle in the instant before touchdown. For diamond doves, the final wingbeat was quicker than the preceding wingbeats with decreased downstroke duration, in contrast to the zebra finches. However this final wingbeat also produced less aerodynamic force than the preceding wingbeats, as with the zebra finches. The body pitch of the diamond doves increased steadily during their approach. Both the zebra finches and diamond doves lost over 90% of their total energy prior to contact, with the remaining transferred through the legs to the perch. These studies use simplified wing kinematic measurements to describe how flapping is altered during deceleration to the perch.

Some small birds favour bounding flight, where wingbeats are alternated with ballistic phases where the wings are folded against the body. Polet and Rival (2015) described the bounding flight perching sequences of black-capped chickadees. After a ballistic phase, the chickadees used a deceleration flapping phase where the wings pitched up during the first downstroke. The body also pitches to a vertical posture and the tail spreads outwards at the same time. The chickadees used a further 1-4 wing flap cycles prior to contact while maintaining this vertical posture. 78% of total energy was lost through aerodynamic braking. The data recorded by Polet and Rival (2015) was again reasonably simplistic, with only data collected on the wings and not the body and tail which are also pitched during the manoeuvre.

There have been several studies which point towards variation in aerodynamic braking strategy during perching flight. Green and Cheng (1998) showed that pigeons land with greater force on familiar perches compared with novel ones, and suggesting the birds choose to reduce their aerodynamic braking and engage in riskier behaviour. High kinetic perching flights are likely less energetically expensive. Carruthers et al. (2007) describe different flight behaviour during perching by a Steppe eagle, where either a flapping approach or gliding approach was used, both with variations in trajectory shape and seem to be influenced by wind direction. Both these studies suggest that like other behaviours there may be variations and optimal strategies dependent on circumstance and potentially individual. Unfortunately the relatively low number of recorded flights, small number of individuals, and low variation in experimental conditions means the scope of perching behaviour variation has not been well explored.

## 1.4 Aerodynamic Braking Mechanisms

Despite the differences in flight behaviours between species aerodynamic braking is achieved like any other manoeuvre by altering the net resultant forces, both through changing force magnitudes and by rotation. Whole body rotations are a more efficient mechanism for redirecting aerodynamic forces, and so pitching the whole body redirects forces from vertical (and upwards) to horizontal (and backwards) and therefore slows the bird (Berg and Biewener, 2010). While some adjustments to the wings and tail can create asymmetrical forces, it is easier to rotate the whole-body instead. While in horizontal, steady flight the aerodynamic force perpendicular to the airflow known as lift supports the body weight, while the force in the direction of the velocity vector is known as thrust. By rotation these forces take on new functions. Altering the direction of net aerodynamic force by rapid whole body pitch-up can lead to airspeed reduction through rotation and does not rely on altered flapping kinematics. Control inputs from wing and tail kinematics drive such rotations. In order to pitch up a bird could elevate its tail, sweep its wings forwards, fold its wings into an M-shape, alter the stroke plane angle of its flapping cycles, or rotate its wing around the shoulder to pitch the wings upwards during a glide. Such kinematics move the centre of pressure with respect to the centre of gravity and lead to a nose-up pitch rotation.

A further aerodynamic braking mechanism has been explored by Polet and Rival (2015). By quickly changing the angle of attack of a wing, the frontal area increases/decreases and this results in rapid area change. Weymouth and Triantafyllou (2013) showed an expanding body can drastically change the added mass and boundary layer vorticity leading to a change in aerodynamic force generation. Polet and Rival (2015) used pitching airfoils undergoing deceleration to measure such forces. The pitching rate and deceleration can be parametrised by a shape change number  $\Xi$ :

$$\Xi = \frac{V^2}{aL} \quad (1.2)$$

where  $V$  is the rate of area change,  $a$  is the acceleration, and  $L$  is the body length scale. The shape change number in 2D pitching airfoils decelerating to a halt as investigated by Polet and Rival (2015) can also be described as a ratio between the speed of frontal area change ( $V$ ) and initial translational speed ( $U_0$ ):

$$\Xi = \frac{V}{U_0} \quad (1.3)$$

Researchers found that a rapidly pitching airfoil produces drag as:

$$D \propto \Xi^2 \quad (1.4)$$

Therefore a rapidly pitching wing quickly dissipates energy and produces enough weight-supporting lift force simultaneously. Polet and Rival (2015) measured the angular velocity of pitching wings in black-capped chickadees performing perching flights in order to estimate the shape change number. Other mechanisms that were not measured but can also affect rapid frontal area change include wing span increases and the tail pitching and increasing in span.

The unsteady aerodynamics of rapidly pitching airfoils include impacts to the boundary-layer vorticity. A large leading edge vortex was produced by a pitching airfoil that remained close to the surface, while a smaller trailing edge vortex formed a shear layer. Such vortices generate high levels of lift that cannot be predicted by steady-state aerodynamics (Ellington et al., 1996; Polet and Rival, 2015). In addition, added mass effects from a pitching airfoil also produce large instantaneous drag and lift. It describes how the inertia from a virtual mass is added to an accelerating system due to moving or deflecting the surrounding fluid.

A final braking mechanism which aids kinetic energy loss prior to landing on a perch may be achieved through the trajectory of flight. A gliding eagle was described as swooping up to the perch, therefore exchanging kinetic energy for gravitational potential energy. This simple redirection of velocity through ascending flight can therefore lead to flight speed reduction. The exchange of kinetic and potential energy is present in passive paper aeroplanes and in part leads to the characteristic phugoid flight path. However, as shown in other experiments, birds can successfully perch even with a level or descending approach (Berg and Biewener, 2010; Robertson and Biewener, 2012; Provini et al., 2014). Aerodynamic braking through force generation and redirection is therefore still the dominant mechanism.

In addition to aerodynamic braking mechanisms, some kinematics during perching flight function to increase lift generation, as this is critical during slowing flight. Extreme angles of attack coupled with dramatic airspeed loss leads to flight conditions dominated by unsteady aerodynamics, and few aircraft could maintain control under such conditions. For a pitching airfoil, the fluid stops flowing over the surface and instead detaches to form vortices, resulting in increased drag forces. As an aerodynamic braking mechanism the resultant loss of kinetic energy to the wake is both effective and rapid. Less favourable is the additional loss of lift force. Aircraft designs aim to avoid or delay flow separation in order to maintain effectiveness of the control surfaces and prevent loss of manoeuvrability. To maximise lift production, birds increase wing and tail span at low flight speeds, and also lower the tail (Tucker,

1992; Thomas, 1993). The increase in lift generation from the previously mentioned added mass and boundary layer effects from rapid area change may also aid weight support and flight control during the manoeuvre. Even so, the flight conditions towards the end of the perching manoeuvre are likely post-stall, where lift may be insufficient to support weight.

Regardless birds perform such rapid pitch-up manoeuvres during normal perching behaviour where precise control is critical to prevent collision or missing its target. Such a braking mechanism is paradoxical yet effective, and contrast with our own aircraft designs which principally brake on the runway, or by a production of backward thrust. In our aircraft designs manoeuvres can be highly dynamic (such as the Pugachev's cobra) or highly accurate (such as a carrier landing) but in perching flight and other manoeuvres birds achieve both accuracy and dynamism in concert.

## 1.5 Visual Control of Braking

Birds have the largest eyes relative to body size of any animal (Jones et al., 2007) and their high-speed flight is dependent on a sophisticated visual system capable of rapid processing. Performing complex flight behaviours relies on visual information for finely-tuned sensory feedback during prey pursuit (Brighton et al., 2017; Kane and Zamani, 2014), obstacle avoidance (Lin et al., 2014; Bhagavatula et al., 2011), navigation (Guilford and Biro, 2014), and flocking behaviours (Nagy et al., 2010). In perching flight visual information about the bird's target is used to guide its trajectory and to control braking. Without this visual information, birds risk colliding with the perch or braking prematurely and losing height. Flight is energetically expensive and high risk, placing high demands for accuracy and precision in visually-guided behaviours.

To control braking such that a bird stops at the perch, it must judge its movement relative to the target. One solution is to judge its relative distance continually during approach, and to apply a braking mechanism at the appropriate distance. Estimating distance without binocular vision is reasonably difficult, and even though many birds have some binocular vision, during flight it is likely monocular vision dominates (Martin, 2009).

Lee and Reddish (1981) suggests an easier mechanism for controlling visually guided behaviours which relies on estimating the time-to-contact rather than a relative distance. The researchers measured diving gannets closing their wings at a critical time before contact with the water, preventing injury and aiding a smooth transition from air into water. The authors argue that for rapid coordination of motor systems and visual systems, information might be processed as an optic flow field. As the approaching water surface grows in the bird's visual field, under a constant



velocity approach the bird could accurately estimate its time to contact. The parameter of the "expansion rate" in the visual field is known as  $\tau(t)$ , and is defined as the ratio between the relative distance to the target  $x(t)$  and the speed of approach  $\dot{x}(t)$ :

$$\tau(t) = \frac{x(t)}{\dot{x}(t)} \quad (1.5)$$

Under constant velocity, the birds can judge the time to close their wings as a critical value of  $\tau(t)$ , and Lee and Reddish (1981) found evidence for gannets using this parameter during dives. They argued that judging this optic field parameter is a far simpler solution to judging relative distance, velocity, and acceleration.

The use of  $\tau(t)$  in landing flights was studied by (Davies and Green, 1990) using pigeons and hawks. They measured how the birds timed their foot extension prior to contact with the perch, and found that there was some evidence for using  $\tau(t)$  in hawks, but not for pigeons. In further experiments, covering one eye led to pigeons leg extension was best explained by a  $\tau(t)$  strategy, and the authors argued that the head bobbing on approach to the perch was used to judge relative distance rather than  $\tau(t)$  in birds with both eyes uncovered (Green et al., 1992).

However, the majority of kinematics that occur during perching flight are not discrete actions that are deployed at a critical time before contact. The aerodynamic braking mechanisms must be controlled with respect to the perch such that braking is neither excessive nor deficient and braking occurs continually during approach. In perching flight a bird decelerates prior to landing, and so by definition, flight speed is not constant. As a result,  $\tau(t)$  is not an accurate representation of the time to contact.

Lee et al. (1993) suggested different hypotheses about how braking could be controlled such that a bird comes to a stop at the perch. If the bird could judge its relative distance to the perch and its initial velocity, then it could set an appropriate constant deceleration magnitude accordingly. However, Lee et al. (1993) argued that the rate of change of  $\tau(t)$  ( $\dot{\tau}(t)$ ) might be used instead to control braking.  $\dot{\tau}(t)$  does not rely on constant velocity and provides information about applying braking over a duration rather than as a discrete action. To stop at the perch, a bird could apply constant braking and keep  $\dot{\tau}(t)$  fixed at 0.5. Other braking strategies may also be controlled using this dimensionless parameter, as discussed in more detail in Chapter 4. Lee et al. (1993) measured  $\dot{\tau}(t)$  during pigeon perching flights and found they used a controlled collision strategy, where  $\dot{\tau}(t)$  is held constant around 0.7 while braking is increased on approach.

Using  $\tau(t)$  and  $\dot{\tau}(t)$  allows the timing of visually-guided manoeuvres without directly measuring relative distance and speed, and so has been implicated in many other behaviours (Baird et al., 2013; Srinivasan et al., 2000; Lee

et al., 1991). However, evidence for its use in humans has been criticised (Brouwer et al., 2003; Tresilian, 1999). One limitation to  $\tau$  theories is that the presence of a constant  $\dot{\tau}(t)$  value does not necessarily mean it is used for controlling braking. A car without a driver decelerating to collide into a wall could have a constant  $\dot{\tau}(t)$  value. To truly provide evidence that  $\dot{\tau}(t)$  as a feedback parameter, experiments that involve a moving target in perching are necessary.

There have been numerous criticisms of tau theory, particularly for evidence of its use in humans (e.g. Harrison et al., 2016; Wann, 1996; Tresilian, 1999). In a review by Wann (1996), the author argues that the measured dives by gannets were less than 0.5m above the water surface and closing their wings occurred within 0.14s of the start of the dive, raising questions about whether this example of controlled behaviour is long enough for input information by optic flow. In addition the author argues relative distance can be directly measured with binocular or monocular cues which could explain the results from gannets as well as tau theory. Tresilian (1999) provided a critique that holding constant  $\dot{\tau}$  ignores the physical limitations of deceleration, which is clearly an important consideration for control. For example, deceleration cannot be applied instantaneously and its magnitude cannot be infinite. For many species of bird, constant braking is also infeasible due to its flight behaviour. For birds using gliding flight, for example raptors, it is possible to produce constant braking. During flapping approaches, as performed by pigeons and other smaller birds, this ability is more limited. In flap-bounding flight, control is sporadic and so holding  $\tau(t)$  or braking constant is more or less impossible.

Bardy and Warren (1997) have criticised the methodology for measuring  $\dot{\tau}(t)$ . In general, if  $\tau(t)$  is curved it can be approximated as a linear function by just taking a very small section at the end, thus falsely providing evidence for constant  $\dot{\tau}(t)$ . The use of an  $r^2$  value has also been criticised as too vague to point to a truly linear value. In addition, Bardy and Warren (1997) have argued evidence for use of  $\dot{\tau}(t)$  as a control parameter does not necessarily require constant  $\dot{\tau}(t)$  recordings, and that even the recorded values Lee et al. (1993) made from pigeons show oscillation in  $\tau$  around a constant  $\dot{\tau}(t)$  value. This could instead provide evidence for a control feedback mechanism using  $\dot{\tau}(t)$  with a delay.

Yilmaz and Warren (1995) argued that using measurements of hummingbirds and pigeons,  $\dot{\tau}$  oscillates around a constant value, rather than being held constant. This instead suggests  $\dot{\tau}$  is kept close to a marginal value, analogous to a regulated variable in a closed control loop. As part of control theory, the critical  $\dot{\tau}$  value which determine collision outcome takes the form of a *desired state*. Physical constraints may mean constant braking and/or  $\dot{\tau}$  is impossible, but keeping  $\dot{\tau}$  approximately constant is possible and would lead to the same outcome. Therefore oscillation or variation around a constant  $\dot{\tau}$  is still evidence for its use in braking control.

Collision strategy has been shown to change dependent on the situation, where Green and Cheng (1998) showed pigeons use a high impact for perches they are familiar with, rather than novel ones. In addition, the measurements from Chapter 2 show a range impact forces during perching, influenced by external circumstances and varying approaching velocities. In the natural environment, birds land on a range of objects with different pliancy properties which may require softer landings. It is therefore a requirement of any braking control method to allow for different collision outcomes, and measuring  $\dot{r}$  provides such flexibility, as the value of the critical  $\dot{r}$  used could be altered as necessary. Vision has critical function in flight behaviours, and yet there is still little understanding in how birds acquire and use visual cues to guide flight controls.

## 1.6 Data Chapter Summaries

In Chapter 2, I set out analysis of fifteen perching flights by a male Steppe eagle (Cossack). Previous research into perching flights by a large eagle has not quantified the energetics of perching flight nor the magnitude of aerodynamic braking. I compare the mechanisms of kinetic energy loss during these flights to determine the contributions of height gain versus aerodynamic braking. In the fifteen flights recorded by Dr. Anna Carruthers and Dr. Tonya Müller in 2010 and 2011, the eagle flew preferentially into the wind. I therefore examine how this strategy influences the differences in energy loss between the air reference frame and inertial reference frame. Kinetic energy loss in the inertial reference frame is crucial to prevent high-speed collision, but kinetic energy loss in the air reference frame leads to loss of flight control. Previous work by Carruthers et al. (2007) also noted the eagle's preferred trajectory with initial height loss before swooping up the perch. In this chapter I quantify the contribution kinetic and potential energy exchange to deceleration along with the contribution of aerodynamic braking and impact force with the perch. The videos had eighteen points manually tracked by Dr. Anna Carruthers across the eagle's wings, body, and tail, which I reconstructed into three-dimensions. These detailed measurements of wing and tail kinematics during the perching flight manoeuvre are quantified for the first time in this chapter and compared with descriptions of the wing M-folding, rapid pitch-up, parachute phase made by Carruthers et al. (2007). I then discuss the evidence for coordination between the wings and tail during the manoeuvre. Although the data set in this chapter is small and uses a single bird, the data provide a examples of outdoor perching behaviour under windy conditions and to two different perch types. No two flights are alike, and demonstrate the variation of the manoeuvre in a natural environment, where trajectory and approach speed are not restricted by an indoor environment. Therefore this analysis provides insight into the scope of this behaviour in more natural conditions.

In Chapter 3 I describe experiments where multiple retro-reflective markers are attached to the wings, body and tail of four Harris hawks and recorded with a high speed motion capture system as the hawks perform perching flight. Motion capture improves upon the methods described in Chapter 2 as they provide three-dimensional reconstruction of points in detail without the use of manual tracking and associated human error. I also describe an automatic marker labelling system for feather markers based on boundary definitions around the body unique to each hawk. Automatic tracking and labelling meant 1365 perching flights could be recorded and analysed, two orders of magnitude higher than the eagle data set and using four individuals rather than one. Like the previous chapter, the energetics and the wing, tail and body kinematics are quantified in detail. Four perch distances were used to experimentally explore varying braking strategies, and in particular the hawks' ability to lose kinetic energy through height gain was reduced with the 5m flights. Previously, Carruthers et al. (2007) had described a flapping approach as well as a gliding approach in different conditions, which is recreated here. A comparison of these two braking strategies is explored, and due to the higher accuracy of motion capture, the aerodynamic forces were also measured. Following work by Polet et al. (2015), pitching rate measurements were characterized by the shape change number during the perching manoeuvre. The shape change number provides a metric comparing the rate of frontal area increase to acceleration, providing a means to dissipate energy quickly while maintaining lift and drag despite the slow flight speed. Finally the individual variation during the flights are also explored. The large data set analysed in this chapter is with direct contrast to Chapter 2, with higher number of flights but a heavily reduced level of variation. The controlled conditions of the experimental setup led to stereotyped behaviour. This chapter focusses on the rapid pitch-up manoeuvre but further insight into take-off, flapping, and gliding flight are discussed. These data are hugely detailed and there is huge potential for further analyses.

In Chapter 4 I investigate the control of braking using different bird species: Steppe eagle, Harris hawks, and wild Great tits and Blue tits. I test multiple hypotheses about how an optic flow variable "taudot" or  $\dot{\tau}(t)$  may provide feedback for deceleration relative to an upcoming target, as first described by (Lee, 1976). Previous work has proposed that birds make use of  $\dot{\tau}(t)$  during perching flight, and in this chapter I compare the different species and further test this hypothesis. The variable  $\dot{\tau}(t)$  can be used in different ways, for example provide feedback for an approach with increasing or decreasing braking magnitude, or to control an approach with constant braking. The hawks and an eagle use a gliding approach to the perch from below, but the wild passerines use an entirely different flight strategy known as intermittent or bounding flight. The inability to hold neither  $\dot{\tau}(t)$  nor braking constant upon approach presents an interesting challenge for visually guided braking control. In this chapter I also describe 91 flights to a swinging perch in an attempt to manipulate the observed  $\dot{\tau}(t)$  value and influence braking output. A compensatory response to the perch would be expected if the perch were moving much faster than the bird's approach speed. These

experiments aimed to address the criticism put upon  $\dot{\tau}(t)$  theory, particularly as its use cannot be inferred without experimental manipulation.



# Mechanics and Energetics of Perching Flight in a Steppe eagle (*Aquila nipalensis*)

## 2.1 Abstract

A captive male Steppe eagle *Aquila nipalensis* was recorded performing 15 perching flights under different atmospheric conditions and with two different perch types. From photogrammetry methods, 14 points across the wings, body, and tail were reconstructed into 3D. Detailed quantification of wing and tail morphing provide insight into the control of the perching manoeuvre.

The eagle lost most of its inertial kinetic energy before contact with the perch through a combination of aerodynamic braking and gaining gravitational potential energy. Remaining inertial kinetic energy was transferred to the perch at impact. Magnitude of braking was affected by wind conditions and trajectory shape, resulting in a range of impact forces with the perch.

In the final 0.5 seconds before contact, the eagle rapidly pitched up to an upright posture. Adjustments of the wings and tail were coordinated to move the centre of pressure ahead of the centre of mass, inducing a whole body nose-up rotation. Stall occurs at high angles of attack, and aerodynamic braking is achieved through losing energy to the wake. However, the eagle simultaneously maintained aerodynamic kinetic energy by flying into the wind, ensuring weight support even post-stall.

## 2.2 Introduction

Birds are capable of transitioning from high-speed flight to high-precision perching in a fraction of a second. Perching is a challenging behaviour which requires reaching the correct speed at the correct place. Although some energy is transferred to the perch at the point of contact, birds slow before contact in order to avoid dangerous collision (Martin, 2011; Bonser and Rayner, 1996; Berg and Biewener, 2010; Provini et al., 2014). The accurate control achieved during perching behaviour is of particular interest for aerospace engineering (Moore et al., 2014; Anderson, 2009; Wickenheiser and Garcia, 2006; Glassman et al., 2012; Cory, Rick E., 2010). However, little has been quantified in studying the mechanisms for aerodynamic braking in birds, particularly during gliding flight.

Carruthers et al. (2007) described the perching flight manoeuvre of a captive male Steppe eagle (*Aquila nipalensis*) flying to land on a falconer's glove. During a gliding approach, the eagle flew close to the ground. The eagle then performed a rapid pitch-up where its posture rotated from horizontal to almost upright in the final second before contact. While pitching, Carruthers et al. (2007) highlighted an M-shape wing folding event where the handwing was folded and wingspan briefly reduced. Finally in the last instant before touchdown, the eagle spread its tail and wings to maximum span in a "parachute" configuration. Feathers deflected up on the leading edge act as a Kruger flap and are thought to enhance lift production during high angles of attack by preventing flow-separation. Another area on the leading edge known as the alula is actively protracted during perching, thought to promote leading-edge vortex production during stall. The mechanics and aeroelastic devices described by this study have led researchers and engineers to investigate the aerodynamics of pitching airfoils, produce perching UAVs, and test how morphing affects performance in new wing designs (Moore et al., 2014; AliKhan et al., 2013; Granlund et al., 2010; Brücker and Weidner, 2014). As a qualitative study, however, the detail of the perching manoeuvre and the associated rapid pitch-up has remained unquantified. Here the same eagle is recorded performing perching flights with a gliding approach under different flight conditions with multiple cameras in order to quantify measurements of the wing and tail kinematics.

For a successful perching flight manoeuvre, a bird must brake sufficiently before landing to avoid injury (Klem Jr, 2009; Martin, 2011). In particular, its inertial kinetic energy defines the force of impact and should be minimised. In the inertial frame of reference, the velocity of a bird is known as its groundspeed and is measured in reference to the Earth. However, the bird's airspeed (velocity in reference to the air mass) is critical for lift production. Insufficient airflow over the wing leads to stall where flight control is compromised along with weight support. During perching flight, it is therefore critical to reduce groundspeed but maintain airspeed, which can be facilitated by using a



headwind. The Steppe eagle was described by Carruthers et al. (2007) as preferentially flying into the headwind during perching, and used gliding flight on its approach. Flapping flight is energetically expensive for large birds, as required muscular power increases steeply with body mass, and so this preference is not surprising (Ellington, 1991). However, the eagle used flapping flight in the absence of a headwind, and wing motion provided airflow over the wings to sustain lift production. In this study gliding flight approaches were recorded in order to study the mechanism of aerodynamic braking in the absence of wingbeat cycles.

The underlying mechanism for the eagle's rapid reduction in groundspeed is not well understood. Carruthers et al. (2007) suggested two main mechanisms: aerodynamic braking and gain in height. The eagle was observed gliding up to the perch, which leads to an exchange in kinetic energy for gravitational potential energy. The authors estimated gain in height accounts for 10-30% of energy loss prior to landing. However, reduction in flight speed has been recorded in birds using level or descending flight to a perch (Green and Cheng, 1998; Berg and Biewener, 2008; Provini et al., 2014; Carruthers et al., 2010) and so this mechanism is not critical for perching flight. The primary mechanism for slowing groundspeed appears to be through aerodynamic braking, where kinetic energy is lost to the wake. To study the underlying aerodynamic braking mechanism, detailed kinematics measurements are required from the wings, which was not possible from the single-camera measurements made by Carruthers et al. (2007). Here we use multiple cameras and to track the body, wings, and tail from multiple views, and reconstruct the points into three-dimensions. We aim to quantifying the kinematics underlying the aerodynamic braking mechanism during the eagle's flights.

In order to change flight speed or direction, a bird must alter its net resultant force direction or magnitude (Gillies et al., 2011; Taylor and Thomas, 2002). A change in the magnitude of aerodynamic force may be achieved through altering flapping speed, dynamic shape change, or through changing their angle of attack (Altshuler et al., 2015). Aerodynamic braking has been previously studied in pigeons and other small birds, where alterations to wingbeat kinematics lead to deceleration (Berg and Biewener, 2010; Provini et al., 2014; Polet and Rival, 2015). During gliding, morphing wings provide many degrees of freedom and a bird can alter span, flex, folding, twist, rotation, and sweep. Greater drag and thus deceleration may result from increased surface area, and the eagle was described spreading its wings and tail fully during a "parachute phase". At low airspeed, lift can also be increased with various wing and tail kinematics, for example spreading and lowering the tail (Tobalske et al., 1996; Tucker, 1992); varying twist along the wing (Altshuler et al., 2015); and feathers act as aeroelastic devices to prevent airflow separating from the wing surface (Carruthers et al., 2007).

Wing and tail morphing can also change the direction of the net resultant force by affecting the balance of lift and drag production (Norberg, 2012). Carruthers et al. (2007) described the Steppe eagle's wings reaching extreme angles of attack, and severe compromises in lift are predicted from steady aerodynamic theory along with increased drag (Anderson, 2005; Cook, 1997). As the angle of attack increases, deceleration will occur due the force direction being altered from normal to the flow to normal to the wing. A third distinct mechanism is also possible through whole body rotation, where the line of action of the force is altered (Ros et al., 2011; Berg and Biewener, 2010). If net resulting force points upwards from the bird while it is horizontal, pitching the whole body nose-up will redirect the resultant force backwards. Pitching rotations can be controlled using wing kinematics such as an M-shape wing folding, tail movement, lifting the wings (dihedral angle), or sweeping the wings forwards, all of which move the aerodynamic centre of pressure forwards relative to the centre of mass (Carruthers et al., 2007; Thomas and Taylor, 2001; Pennycuik, 1975; Gillies et al., 2011; Tucker, 1992). Evidence for wing morphing controls that cause aerodynamic braking by increasing drag magnitude, redirect forces backwards, and induce pitching will be examined from the quantified wing and tail kinematics data.

Recent research has provided insight into how large lift and drag forces can be produced from a rapidly pitching airfoil despite predictions from steady aerodynamics theory (Polet et al., 2015; Anderson, 2005). Additional force generation is achieved through added-mass energy transfer. As the airflow pitches, frontal area meeting the oncoming airflow rapidly increases in size. A volume of air in front of the decelerating airfoil must be moved leading to an addition of inertia to the system. This leads to force generation an order of magnitude larger than those at steady-state peak values. Greater lift than drag is produced, and in order to produce sufficient drag the pitch manoeuvre may produce excessive lift which could mean the low height approach acts as an altitude correction (Polet et al., 2015). The angle of attack measurements from the eagle during the rapid pitch-up will be compared with the airfoil experiments and whether added mass effects could play a role in aerodynamic braking along.

Studying the effects of wing and tail kinematics and morphing on flight performance was limited before the advent of digital high-speed photography, and quantitative studies are still limited with reliance still on qualitative data and observations (Tucker, 1992; Hedrick et al., 2007). The complexity of wing morphing and its effect on flight remains challenging to quantify. Understanding morphing wings can provide insight into the precise flight control mechanisms at play during complex flight manoeuvres. There have been multiple studies into quantifying wing flapping kinematics during decelerating and landing flight (Provini et al., 2014; Berg and Biewener, 2010; Polet and Rival, 2015), but less attention aerodynamic braking mechanisms in gliding flight.

## Aims

Here we recorded a captive male Steppe eagle (Cossack) in two experimental periods. In 2010 the eagle was recorded flying to a 1.5m wooden perch, and in 2011 the eagle was recorded at a cliff site flying to a falconer's arm. The 15 flight sequences were recorded with multiple high-speed cameras and photogrammetry was used to reconstruct 14 points across the wings, body, and tail in 3D. The aims of this study were to quantify aerodynamic braking during gliding approaches to the perch by a large eagle. The energetics of kinetic energy loss through both a gain in height, braking, and impact with the perch will be explored and compared. Fifteen flights were recorded in different outdoor conditions in two locations, and this study aims to compare measurements in both the inertial and aerodynamic reference frames to better understand this behaviour in natural conditions. This work follows descriptions of the manoeuvre from previous authors and aims to quantify the M-shaped wing folding, rapid pitch-up, and parachute phases by using detailed 3D measurements of wing and tail motion. Evidence for wing and tail coordination during perching will also be discussed.

## 2.3 Methodology

### 2.3.1 Experimental Procedure

A captive, male Steppe Eagle (*Aquila nipalensis*) was used for all experiments following prior work with the same animal by Carruthers et al. (2007). The eagle's wingspan was 1.8m, mean chord length of 0.35m, and average mass of 2.5kg. The experimental protocol was approved by the Local Ethical Review Committee, Department of Zoology, Oxford University and by the Surgeon General's Human and Animal Research Panel, United States Air Force. Experiments were considered not to pose any significant risk of causing pain, suffering, damage or lasting harm to the animal involved. Experimental data was collected by Dr. Tonya Mueller, Dr. Anna Carruthers, and Prof. Graham Taylor in 2010 and 2011.

Perching sequences were recorded over 6 days in two sites. The first site was an open field near Abergavenny, Wales, where total wind speed ranged between  $2.4 - 4.5\text{ m s}^{-1}$ , and the eagle was trained to fly to a 1.5m high wooden perch for a food reward. The second site was located near a cliff edge at Vale of Glamorgan, Wales, where wind speed ranged between  $3.3 - 6.5\text{ m s}^{-1}$ . Of the 21 recorded perching sequences, 15 met quality control criteria. Sequences shorter than 0.5s were removed as well as those with accidental camera position changes. The eagle was trained to fly to a wooden perch in the nine sequences from the first site. In the remaining six sequences from the second site, the eagle flew to a falconers arm for a food reward.

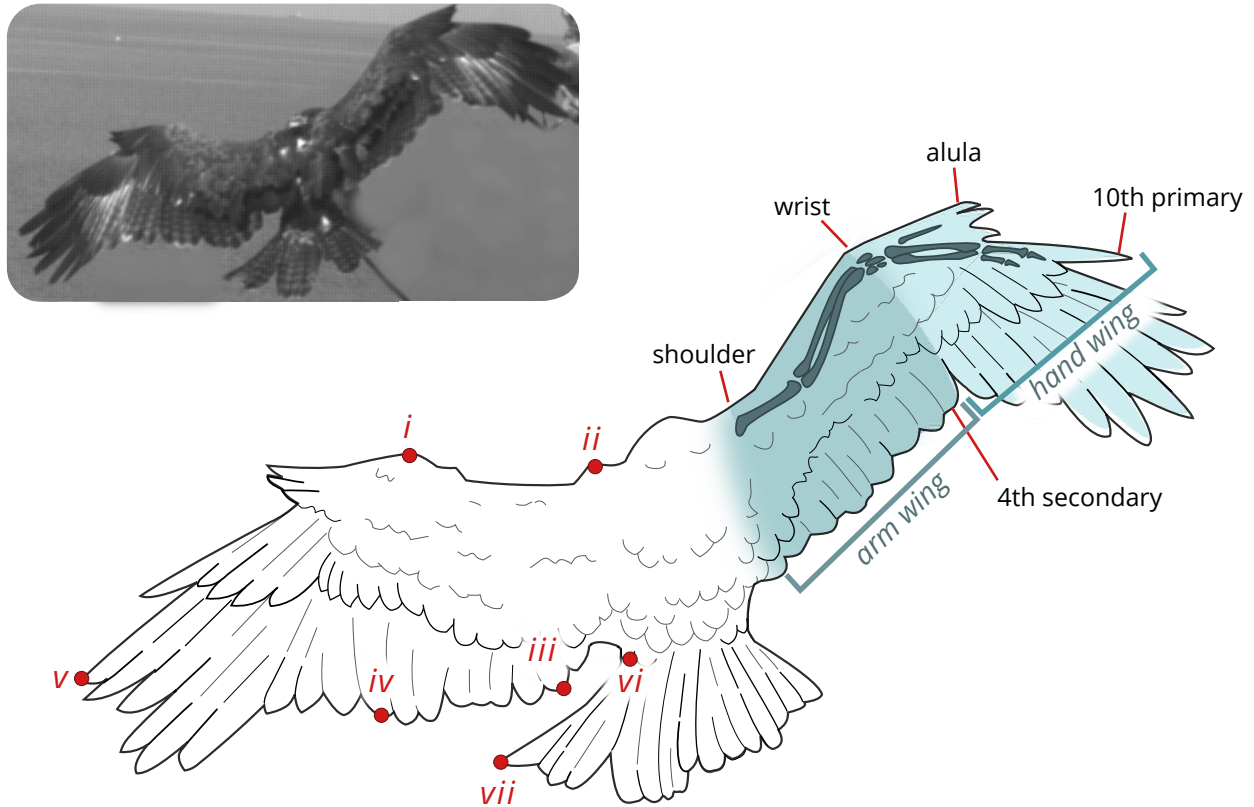
Two high-speed cameras (*S-PRI models, AOS Technologies AG, Switzerland*) were used for recordings at 500fps with a resolution of 1280x1024 pixels. In addition, a colour and a monochrome high-speed camera (*MotionScope M3 models, Redlake Imaging Inc, AZ, USA*) were used at 500 fps, 0.02s shutter length with a resolution of 1280x1024 pixels. Maximum recording length was 4s. The cameras were synchronised together and manually post-triggered. Two laptops controlled each camera pair using *Redlake MotionScope M3.0.0* software and *AOS Imaging Studio V3.5.3* software respectively. For calibration and experimental recordings, overall image levels of brightness and contrast were adjusted but no further image processing was applied. Each of the flight sequences were cropped to start during the fixed wing glide (immediately prior to the beginning of wing flexion) and end at the point of perching. The duration of the sequences range from 0.5 to 1.07s with a sample rate of 500Hz.

A three axis ultrasonic anemometer (*WindMaster Pro, 32Hz, Gill Instruments Ltd, Lymington, England*) was used to measure the wind velocity and set up to point magnetic North. A GPS recording device (*Innovative Automation Technologies, LLC, Florida*) was used to record the position of each camera and the perch to provide an absolute geographic reference for relating the orientation of the camera setup to the measured wind vector. A plumb line was used as reference for the vertical axis, and provided a scaling object. The axis system of the anemometer was combined with the axis system of the cameras by applying a correction for true North.

### 2.3.2 Photogrammetric Reconstruction

In order to quantify the eagle's motion and kinematics, the test volume where the bird flies must first be calibrated. At the start of each experimental day, synchronised calibration images were recorded from each camera. A calibration object was moved and rotated around the test volume in view of the cameras, using either a flat rectilinear grid of black circular dots or a 1m plastic tube with black spheres distributed equidistant down the length. The image coordinates of grid points/spheres in the calibration images were digitized using custom software in *MATLAB v7.4*. Following methods described by Walker et al. (2009), optimal estimates of the camera position, camera rotation, and the object coordinates are produced using a bundle adjustment procedure (Atkinson, 1996; Hartley and Zisserman, 2003). The known length of the plumbline was used to scale the calibration solution. Using the estimated camera positions and rotations, points tracked in the test volume from the camera images were reconstructed into 3D using custom software in *MATLAB v7.4*.

In the experimental recordings, anatomical landmarks on the eagle's body, wings, and tail were identified and tracked manually at each instance of the perching manoeuvre (shown in Figure 2.1). Fourteen points were chosen to best quantify wing and tail morphing and reflect the underlying anatomy.



**Figure 2.1:** Recorded anatomical landmarks on the Steppe Eagle, as shown from a dorsal view. 15 high speed videos were recorded with two pairs of synchronised cameras. 14 landmarks were tracked across the eagle to reflect the underlying anatomy and to quantify part of the wing and tail morphing during the perching manoeuvre. The wings can be divided into two sections: the arm wing and hand wing. The arm wing begins at the shoulder and ends at the wrist on the leading edge, with the secondary and tertiary feathers on the trailing edge. The primary feathers lie on the handwing, which starts at the wrist and ends at the outermost wing tip. The points recorded using photogrammetry were: i) feather on wrist; ii) feather on shoulder; iii) 11th secondary feather tip; iv) 4th secondary feather tip; v) tip of the 9th primary feather; vi) tail root; vii) tip of the outermost feather on the tail. These points were also recorded on the right side of the eagle (not shown).

Each sequence was cropped to start with the fixed wing glide immediately prior to the beginning of wing flexion, and ended at the approximate point of contact with the perch.

### 2.3.3 Velocities and Energetics

To measure the position and velocity of the eagle during the manoeuvre with respect to the perch, a single point was used at the midpoint of the shoulders called the central point. The ground velocity vector ( $\mathbf{V}$ ) was calculated by differentiating a quintic spline fitted to the central point trajectory. The relative air velocity vector ( $\mathbf{U}$ ) was calculated by combining the ground velocity vector with the wind vector ( $\mathbf{W}$ ):

$$\mathbf{U} = \mathbf{V} - \mathbf{W} \quad (2.1)$$

#### Energetics

The energetics of the eagle were calculated from the central point.  $\mathbf{V}$  was used to calculate the kinetic energy in the inertial frame of reference ( $E_{K,I}$ ):

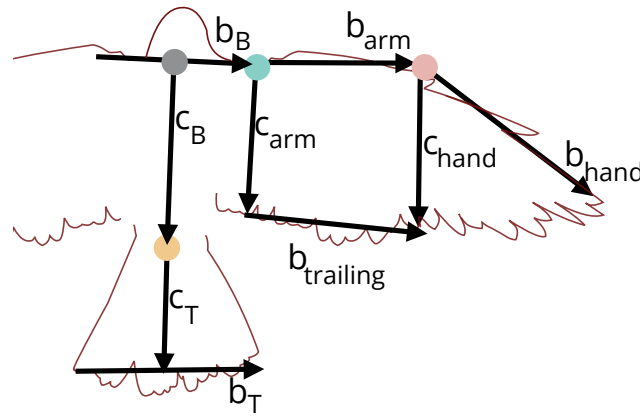
$$E_{K,I} = \frac{1}{2} m |\mathbf{V}|^2 \quad (2.2)$$

In the same way, the aerodynamic kinetic energy ( $E_{K,A}$ ) was calculated using  $\mathbf{U}$ :

$$E_{K,A} = \frac{1}{2} m |\mathbf{U}|^2 \quad (2.3)$$

The gravitational potential energy ( $E_P$ ) was calculated using the mass of the bird ( $m$ ), the gravity vector ( $\mathbf{g}$ ), and the height of the eagle ( $h$ ) from the ground.

$$E_P = mgh \quad (2.4)$$



**Figure 2.2:** The recorded points across the wings and tail (see Figure 2.1) were used to define multiple vectors across the eagle. The body, tail, arm wings, and handwings were each described with a chord vector ( $\vec{c}$ ) and spanwise vectors ( $\vec{b}$ ). The left and right armwings were described as a flat-plate panel. Vector normals pointing dorsoventrally are not shown here for clarity, but originate at the coloured circles on the diagram. The body chord vector ( $\vec{c}_{body}$ ) was used for the body axes for the body reference frame.

The total energy was calculated for both the inertial and aerodynamic reference frames ( $E_{T,I}, E_{T,A}$ ) from the sum of the kinetic and potential energy:

$$E_{T,I} = E_{K,I} + E_P \quad (2.5)$$

$$E_{T,A} = E_{K,A} + E_P \quad (2.6)$$

The impact energy at the perch was not measured directly but was be inferred from the  $E_{K,I}$  value at the point of contact with the perch.

### 2.3.4 Quantifying Body, Wing, and Tail Kinematics

To summarise the complexities of dynamic movements and wing morphing across the eagle during the perching manoeuvre, multiple points were tracked across the eagle. These are quantified as a series of vectors across the bird, simplifying into 4 panels: the body, left arm wing, right arm wing, and tail. A further two lengths are used to describe the left and right hand wing (Figure 2.2). The vectors were span-wise ( $\vec{b}$ ), chord lengths ( $\vec{c}$ ), and normal vectors ( $\vec{n}$ ).

The vectors measured across the body are given symbols  $\vec{b}$ ,  $\vec{c}$ , and  $\vec{n}$  that denote whether their direction is lengthwise, spanwise, or approximately normal to the wing's surface.

The body span-wise vector was defined pointing from the left shoulder point to the right ( $\vec{b}_{body}$ ). The lateral line of the body ( $\vec{c}_{body}$ ) describes the length from the midpoint of  $\vec{b}_{body}$  to the midpoint of the left and right points either side of the tail base. A normal  $\vec{n}_{body}$  was defined pointing dorsoventral to the body plane.

The right arm wing panel is defined with four vectors: two span-wise vectors ( $\vec{b}_{arm}$ ,  $\vec{b}_{trailing}$ ), two chords ( $\vec{c}_{arm}$ ,  $\vec{c}_{hand}$ ).

The vector  $\vec{b}_{arm}$  lies along the leading edge from the shoulder to the wrist joint, while  $\vec{b}_{trailing}$  lies on the trailing edge from the 11th to the 4th secondary feather tips.  $\vec{c}_{arm}$  is the vector from the shoulder joint to the 11th secondary feather tip close to where the wing meets the body. A normal  $\vec{n}_{arm}$  was defined pointing upwards along a dorsoventral axis and perpendicular to  $\vec{c}_{arm}$  and  $\vec{b}_{arm}$ . A lateral vector  $\vec{c}_{hand}$  was defined between the wrist joint and the 4th secondary feather tip. Finally, a surface normal  $\vec{n}_{mid}$  was defined pointing dorsoventrally and upwards to the arm wing panel surface ( $\vec{b}_{arm}$ ,  $\vec{b}_{trailing}$ ,  $\vec{c}_{arm}$ ,  $\vec{c}_{mid}$ ). The left arm wing panel was mirrored to match the right.

For the handwing, along with the  $\vec{c}_{hand}$  vector from wrist joint to 4th secondary feather, the  $\vec{b}_{hand}$  is the spanwise vector along the leading edge from the right wrist joint to the 9th primary feather tip. The left hand wing vector is mirrored to match the right.

Two vectors were used to describe the tail surface. First a spanwise vector  $\vec{b}_{tail}$  between the outermost tailtips on the left and right. The midline chord vector  $\vec{c}_{tail}$  lies between the mid-point of the tailbase and the mid-point of the tail tips. A normal  $\vec{n}_{tail}$  was defined pointing dorsoventral and upwards to the surface of the tail.

The total wing span  $b_{wing}$  was calculated as the length between the left and right 9th primary feather tips. The tail span was defined as the length of  $b_{tail}$ .

## Axis Systems

To measure how the eagle manoeuvres during perching flight, the pitch, roll, and yaw angles were calculated between the eagle and the Earth axes. The independent motion of wings and tail relative to the body can also be described using angular measurements. These angles are defined in the Earth reference frame and body reference frame, requiring separate axes.

All tracked points were reconstructed in the Earth reference frame. The Earth reference frame is described by a right-handed axis ( $X_E$ ,  $Y_E$ ,  $Z_E$ ) centred on the perch.  $X_E$  was defined using the initial heading direction of the eagle, with a downwards pointing  $Z_E$  axis coinciding with gravity as measured by a plumbline. The  $Y_E$  axis pointed to the right of the initial heading direction.



Additional reference frames were defined using vectors from the tracked points on the eagle. For the body axes, the origin was defined at the midpoint of the shoulders.  $X_B$  was defined to point forwards and coincide with the lateral axis  $\vec{c}_{body}$ , while the surface normal  $\vec{n}_{body}$  was used to define the  $Z_B$  axis pointing dorsoventrally. The final transverse axis  $Y_B$  was defined along the same plane as  $\vec{b}_{body}$  but using an angle offset such that  $Y_B$  lies orthonormal to  $X_B$  and  $Z_B$  (as  $\vec{b}_{body}$  does not necessarily lie perpendicular to  $\vec{c}_{body}$ ).

This general method was used to define the arm wing axes ( $X_W, Y_W, Z_W$ ) using the arm wing vectors  $\vec{c}_{arm}, \vec{b}_{arm}, \vec{n}_{arm}$  and the origin at the shoulder point. As before, a transverse axis with an offset from  $\vec{b}_{arm}$  was used to define  $Y_W$ . The left wing was mirrored to match the right. Finally, the tail axes ( $X_T, Y_T, Z_T$ ) were defined with the same method using the mid-point on the tail base as the origin and the following vectors from the tail:  $\vec{c}_{tail}, \vec{b}_{tail}, \vec{n}_{tail}$ , with  $Y_T$  defined to lie orthonormal to  $X_T$  and  $Z_T$  using an angle offset.

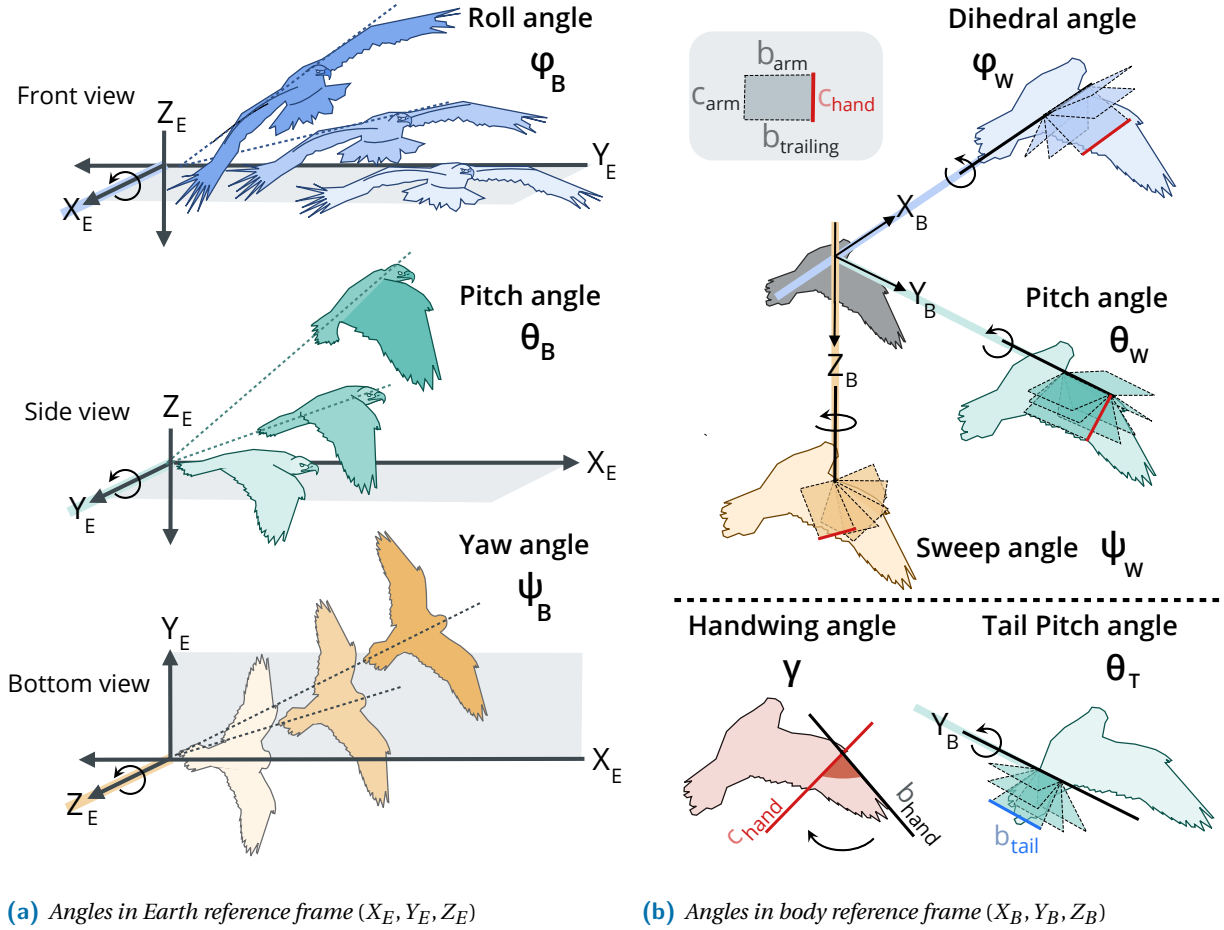
### Angles in the Earth Reference Frame

Euler angles were used to describe the rotations of the body axes with respect to the Earth reference frame (Figure 2.3). The intrinsic Euler angles were calculated in the order *pitch-roll-yaw* (i.e. 2-1-3). The sequence order was chosen to most accurately represent body pitch  $\theta_B$  with respect to the Earth reference frame. Euler angles are always non-independent, but the large amplitude of the pitch motion means the numerical values of the second and third Euler angles are contingent on the pitch angle. The large rotations in the rapid-pitch up manoeuvre leads to non-independent definitions of the Euler angles, and as a result the body yaw ( $\psi_B$ ) and body roll ( $\phi_B$ ) are not used beyond measuring the initial ( $\psi_B$ ) measurement for the Earth axis definitions. In addition, this order is robust to error in the shoulder point position that define the body transverse axis  $Y_B$ .

The wing surface angle of attack  $\alpha$  was calculated using the angle between the surface normal  $n_{hand}$  and the oncoming airspeed vector  $\mathbf{U}$  at the  $\frac{3}{4}$  point along  $c_{hand}$ . A  $90^\circ$  offset was used such that an angle of attack parallel with the oncoming airflow would equal  $0^\circ$ , while exactly perpendicular would equal  $90^\circ$ . By using the surface normal vector, the angle of attack is defined as the angle at which the airspeed hits the surface of the wing. It also minimises the effect of crosswind at very slow airspeeds.

### Angles in the Body Reference Frame

Three angles are usually used to describe independent wing position with respect to the body: pitch, dihedral, and sweep (Figure 2.3 (b)). A wing has the wingtips pointing (or canted) ventrally if the dihedral angle is positive, dorsally if it is negative, and at  $0^\circ$  the wingtips are level in height with the body. The dihedral angle therefore describes the rotation around the  $X_B$  axis. The wing pitch angle refers to the angle of wing chord length rotation about the lateral



**Figure 2.3:** Angles used to quantify the eagle's posture and wing/tail configuration in two reference systems. Three Euler angles are used to describe angles in both reference frames:  $\phi$  for rotations around the  $X$  axis;  $\theta$  for rotations around the  $Y$  axis; and  $\psi$  for rotations around the  $Z$  axis. (a) The right-handed axis Earth reference frame was used to describe the eagle's whole body posture, where  $X_E$  is defined as the initial heading direction (initial yaw), and  $Z_E$  coincides with gravity and points down, while  $Y_E$  is defined as orthonormal to the other axes and pointing right. The horizontal plane is shown in grey.  $\psi_B$  and  $\phi_B$  are not strictly independent due to the order of calculations and are not used beyond defining  $X_E$ . (b) The independent wing and tail angles measured in body reference frame.  $X_B$  coincides with the body length and points forward,  $Y_B$  points right, and  $Z_B$  follows the dorsoventral axis pointing down. For simplification, the arm wing is treated as a flat plate panel (see grey insert) and for reference the chord line  $c_{hand}$  is marked in red in the cartoons. The wing angles are averaged across the left and right wings. For the tail,  $b_{tail}$  was used to calculate the tail pitch around  $Y_B$ . The angle between the  $c_{hand}$  and  $b_{hand}$  provides a handwing angle for measuring folding.

$Y_B$  axis, at  $0^\circ$  the chord length would be parallel with the body, and a positive pitch angle would bring the trailing edge down and forwards. Finally the sweep angle describes the angle of the wing rotation around the dorsoventral  $Z_B$  axis. In positive sweep, the wing span length would point backwards, and at  $0^\circ$  the wing would be exactly perpendicular with the body length vector ( $b_{body}$ ).

To reduce the complexity of the wing configurations, each arm wing was treated as a simple panel and defined by the arm wing axis system  $X_W, Y_W, Z_W$  (Figure 2.2). During flight birds use wing twist and so independent wing rotation often differs along the length of the wing, but it was not possible to measure this level of detail in this study. Instead by treating the arm wing as a panel, the measured angles serve as estimates. To measure the angles, each  $b_{arm}$  vector was first transformed into spherical coordinates. The wing dihedral angles ( $\phi_W$ ) and sweep angles ( $\psi_W$ ) were calculated from the elevation angles and azimuth angles respectively. The left wing was mirrored to match the right.

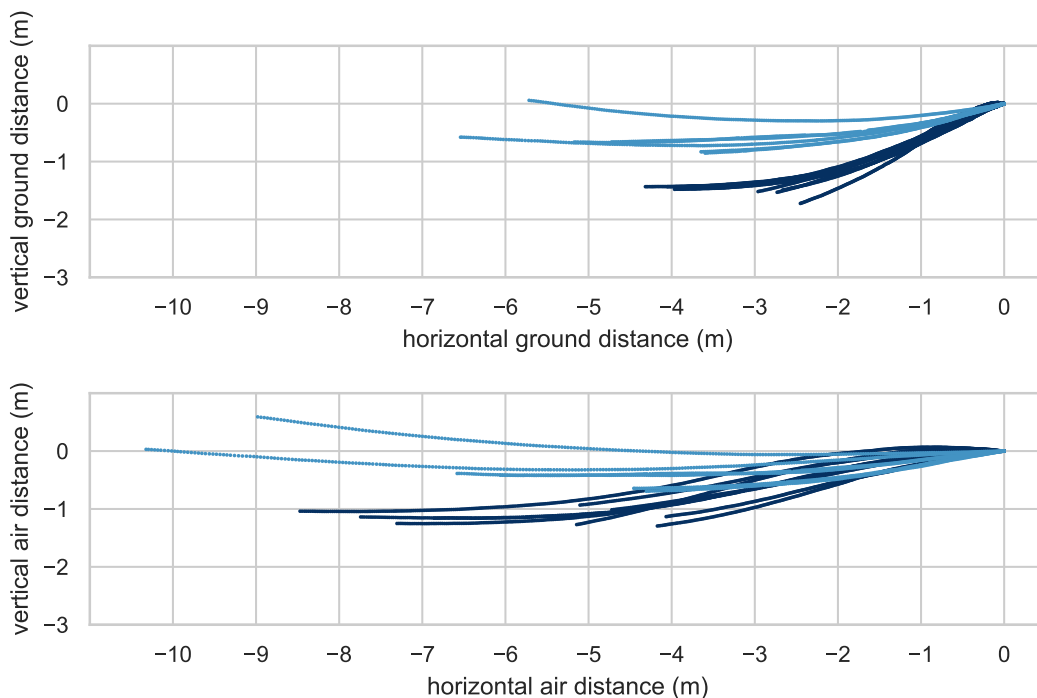
Next the arm wing axes ( $X_W, Y_W, Z_W$ ) were rotated in the body reference frame ( $X_B, Y_B, Z_B$ ) such that  $\phi_W$  and  $\psi_W$  were  $0^\circ$ . The rotations were performed sequentially, first a rotation around  $Z_B$  then a rotation around  $X_B$ . Finally the wing pitch ( $\theta_W$ ) was described as the angle measured between the rotated  $Z_W$  axis and  $Z_B$ .

The handwing angle  $\gamma$  between  $c_{hand}$  and  $b_{hand}$  describes the fanning of the handwing. The tail pitch angle ( $\theta_T$ ) was also calculated as the rotation around the  $Y_B$  axis using the elevation angle from the spherical coordinates of  $c_{tail}$  in the body reference frame.

## 2.4 Results

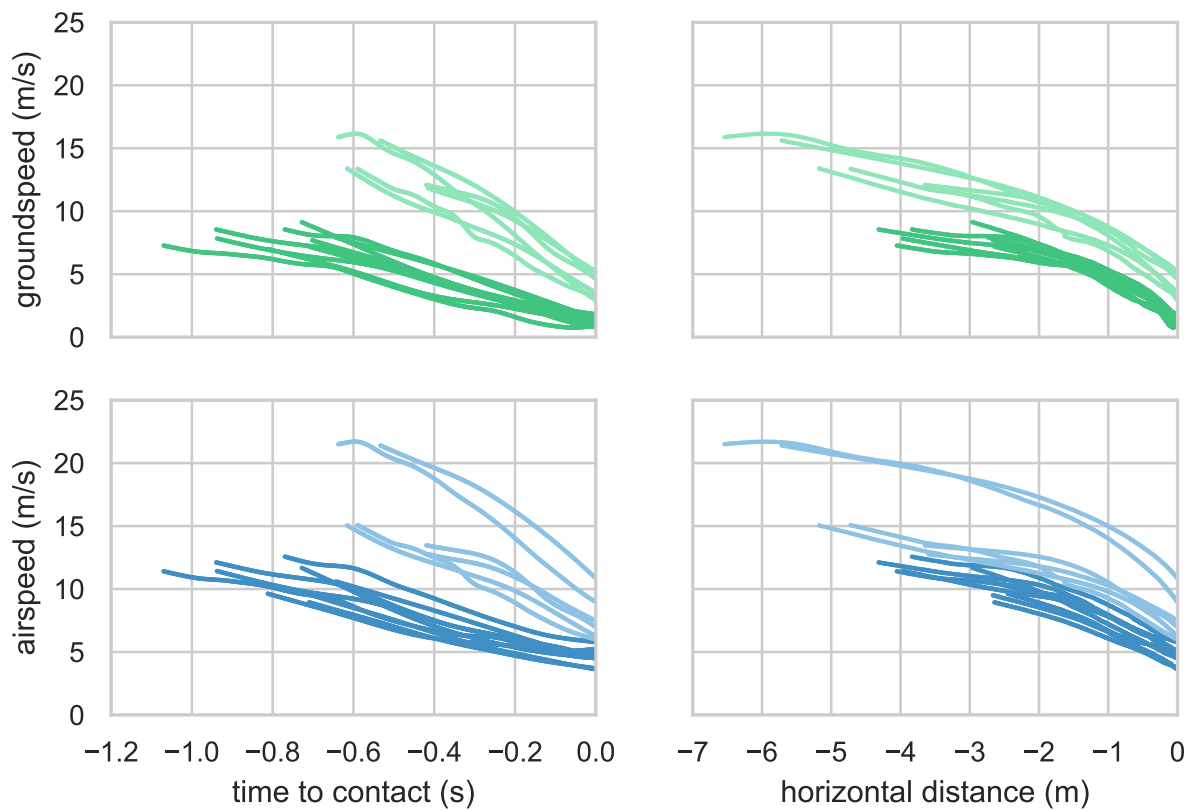
In each of the sequences ( $n = 15$ ), flight duration varied between 0.64 and 1.07s, each cropped to capture the entire period of wing morphing during the gliding approach and ended at the time of contact with the perch. The eagle was free to approach the perch from any direction, and preferentially flew into a headwind. The eagle travelled an average horizontal distance of 3.9m ( $\pm 1.2$  SD) over the ground during the sequences, and gained on average 1.2m ( $\pm 0.4$  SD) in height (Figure 2.4).

The windspeed was higher in the 2011 flights in part due to the cliff site location. Using the air reference frame the trajectories from both experimental periods shows the effect of wind compensation by the eagle (Figure 2.4). The eagle flew close to the ground in both flights, but the falconer's arm was closer to the ground compared with the wooden perch and so the trajectories in the second period are higher relative to the perch.



**Figure 2.4:** Trajectories of the 15 perching flights by a captive male Steppe eagle. Flights in 2010 shown in dark blue, while those in 2011 are shown in light blue. Displacement in the vertical and horizontal shown for both the ground frame of reference and air frame of reference.

The differences in the two experimental periods are also highlighted in the air and ground speeds (Figure 2.5). The average groundspeed at the start of the fixed wing glide for the 2010 flights was  $7.9\text{ms}^{-1}$  ( $\pm 0.7$  SD), slower than the initial ground speed average in the 2011 flights at  $13.8\text{ms}^{-1}$  ( $\pm 1.8$  SD). The air speed is higher than the ground speed due to the eagle flying into the wind on its approach to the perch. To minimise impact force with the perch, velocity



**Figure 2.5:** Total ground (green) and airspeed (blue) of the eagle compared with time to contact and horizontal distance to the perch. 2010 flights and 2011 flights shown in darker and lighter colours respectively. Decrease in velocity is close to linear over time suggesting braking is controlled with respect to time to contact rather than proximity to the perch. Airspeed is higher than groundspeed as the eagle flew into the wind.

in the Earth reference frame was minimised (groundspeed), while velocity in the air reference frame (airspeed) was sustained to enable lift production from airflow over the wings.

The eagle slows its velocity considerably prior to landing in all the flight sequences, averaging to an estimated  $19.4\text{ms}^{-2}$  for half a second. Over time, the decrease in velocity is linear for all the sequences. In contrast, there is a non-linear decrease in velocity over the horizontal distance to the perch, suggesting braking is controlled not with respect to absolute distance to the perch but instead relative to the time-to-contact (see Chapter 4).

### 2.4.1 Energetics

In order to slow before landing and prevent a forceful collision, the eagle loses kinetic energy on its approach (Figure 2.6). Due to the differences in groundspeed between the 2010 and 2011 flights, the sequences can be considered low

kinetic and high kinetic energy flights respectively. At the start of the low kinetic energy flights, the eagle has around 75J of inertial kinetic energy. For the high kinetic energy flights, this is closer to 220J.

The majority of the inertial kinetic energy is lost on the eagle's approach to the perch. This loss can be explained partially by a gain in gravitational potential energy. For the low kinetic flights, this exchange in energy accounts for on average 48% of the loss in inertial kinetic energy. For the high kinetic energy flights, just 8% of the inertial kinetic energy loss can be explained by exchange with potential energy. This confirms estimates made by Carruthers et al. (2007) that between 10 and 30% of kinetic energy loss is due to height gain prior to landing.

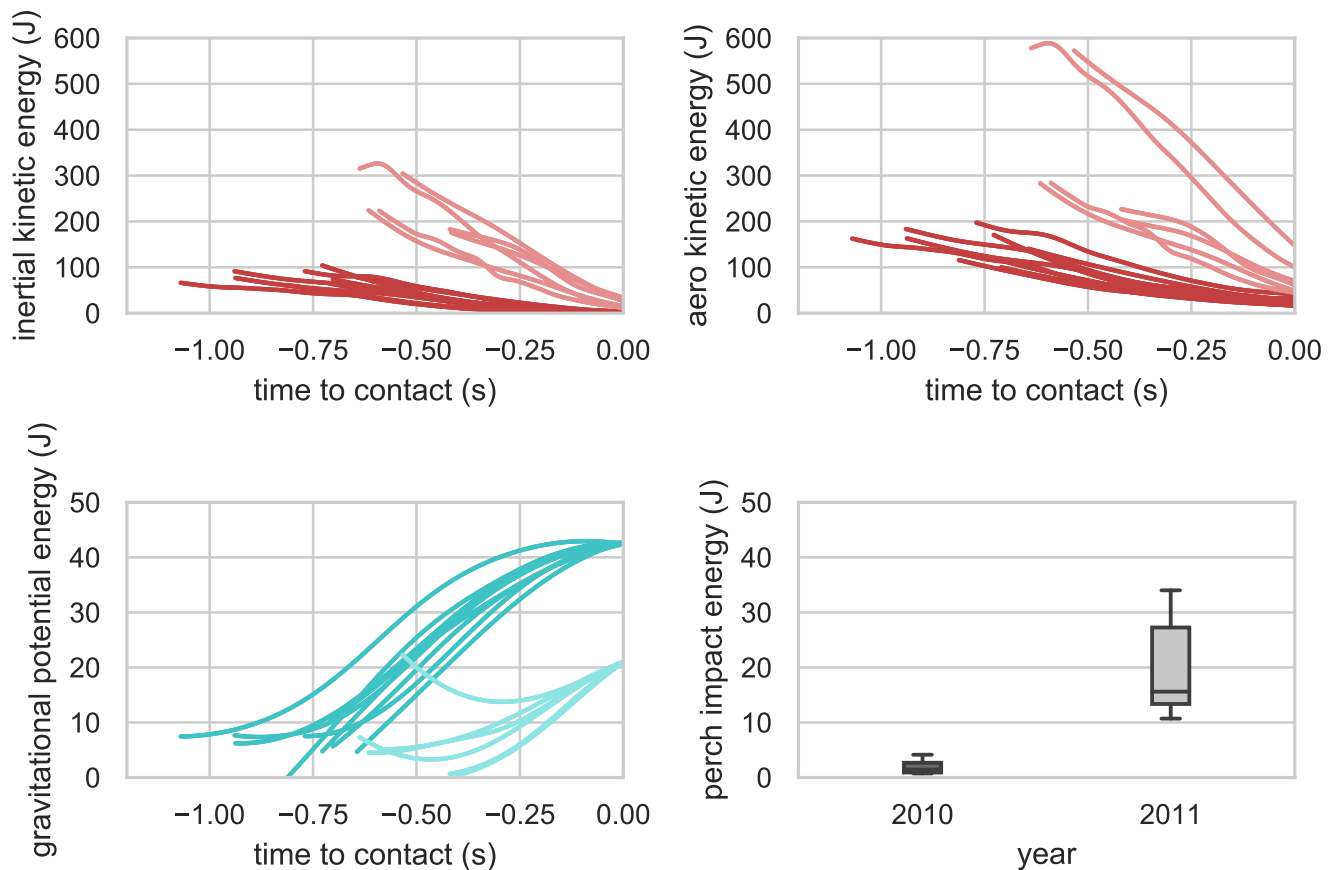
The impact with the perch is also far greater for the high kinetic energy flights. For the low kinetic energy flights, around 2% of the eagle's inertial energy is lost to the perch at the point of impact. For the high kinetic energy flights, this is on average 11%, and in one flight as high as 20%. As a result, a large percentage of the inertial kinetic energy is lost aerodynamically to the air prior to landing. For the low kinetic energy flights this is around 50% and on average 81% for the high kinetic energy flights.

Far less kinetic energy was lost in the aerodynamic reference frame than in the inertial frame during the perching manoeuvre (Figure 2.7 and 2.8). At the point of impact, the eagle maintains on average 26J and 78J of aerodynamic kinetic energy for the low and high energy flights respectively. While the inertial kinetic energy is reduced to minimise collision impact, the aerodynamic kinetic energy must be maintained to enable flight control. The aerodynamic kinetic energy is sustained despite the loss of flight speed by flying into the wind. Without wind or with a tailwind, it is likely the eagle would be forced to use flapping flight rather than the gliding, or land with a greater impact force and risk injury.

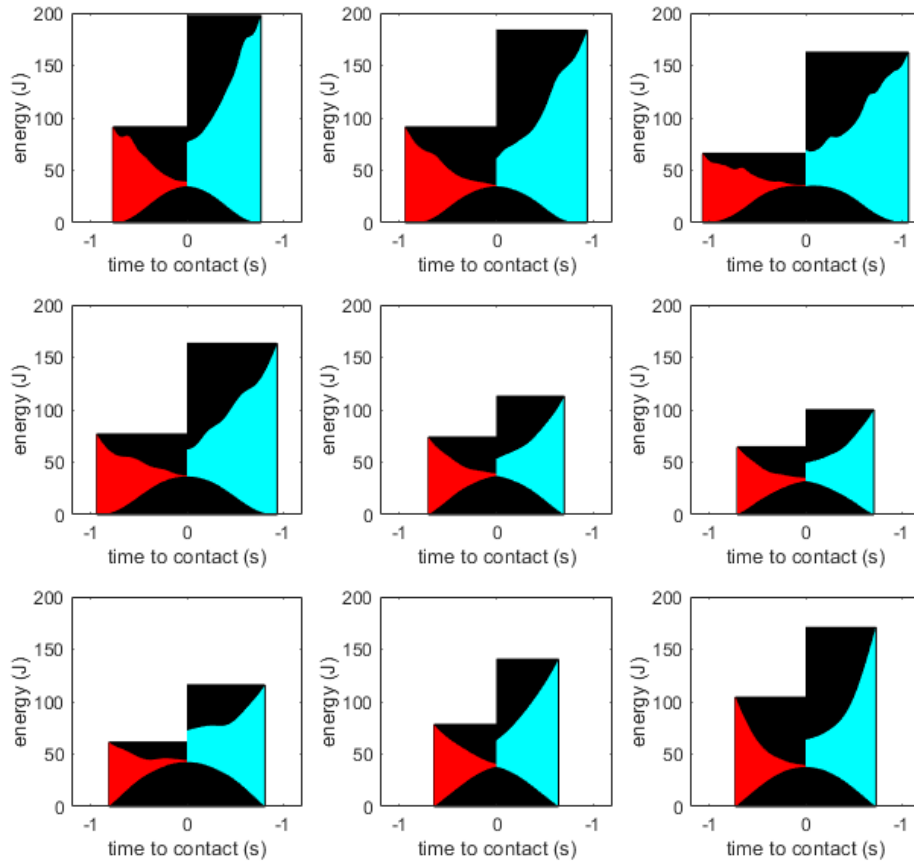
## 2.4.2 Whole Body Flight Kinematics

The flight manoeuvre is marked by the rapid-pitch up, where the eagle fixes its wings into a glide close to the ground, and pitches up while gaining height. The whole body pitch angle with respect to the Earth reference frame was quantified using Euler angles  $\theta_B$  (Figure 2.9). The initial body pitch of the eagle is on average  $20^\circ$  and rapidly rises to around  $92^\circ$  within half a second.

During the manoeuvre the eagle experiences high angles of attack ( $\alpha$ ), rising from  $16^\circ$  to  $30^\circ$  when measured across the surface of the wings. At these angles stall conditions are likely, with the airflow over the wings disrupted as the surface is pitched particularly at the low airspeed before landing. Rapidly pitching airfoils produce large forces of lift and drag even during deceleration (Polet et al., 2015). The large forces produced are used by the eagle to rapidly lose kinetic energy while maintaining weight support.

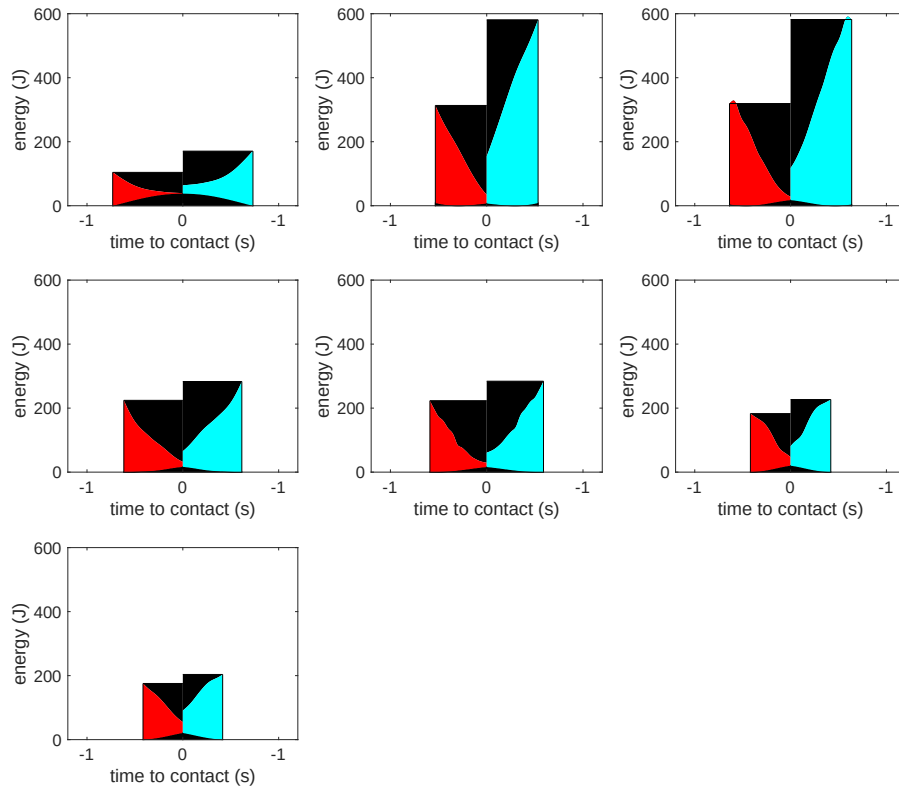


**Figure 2.6:** Comparison of energetics for the perching flights. Kinetic energy is lost over the flights to reduce the force of impact with the perch. Gravitational potential energy increases over the approach as the eagle flies up to the perch, accounting for some of the lost kinetic energy. The eagle has lower kinetic energy for flights recorded in 2010 (darker colours) and has a lower impact with the perch. Greater potential energy is also gained, particularly relative to the eagle's kinetic energy. 2011 flights (lighter colours) are higher energy flights with a higher impact. The kinetic energy is higher in the aerodynamic reference frame than the inertial due to the eagle flying into the wind. Maintaining aerodynamic kinetic energy ensures the eagle maintains flight control authority.

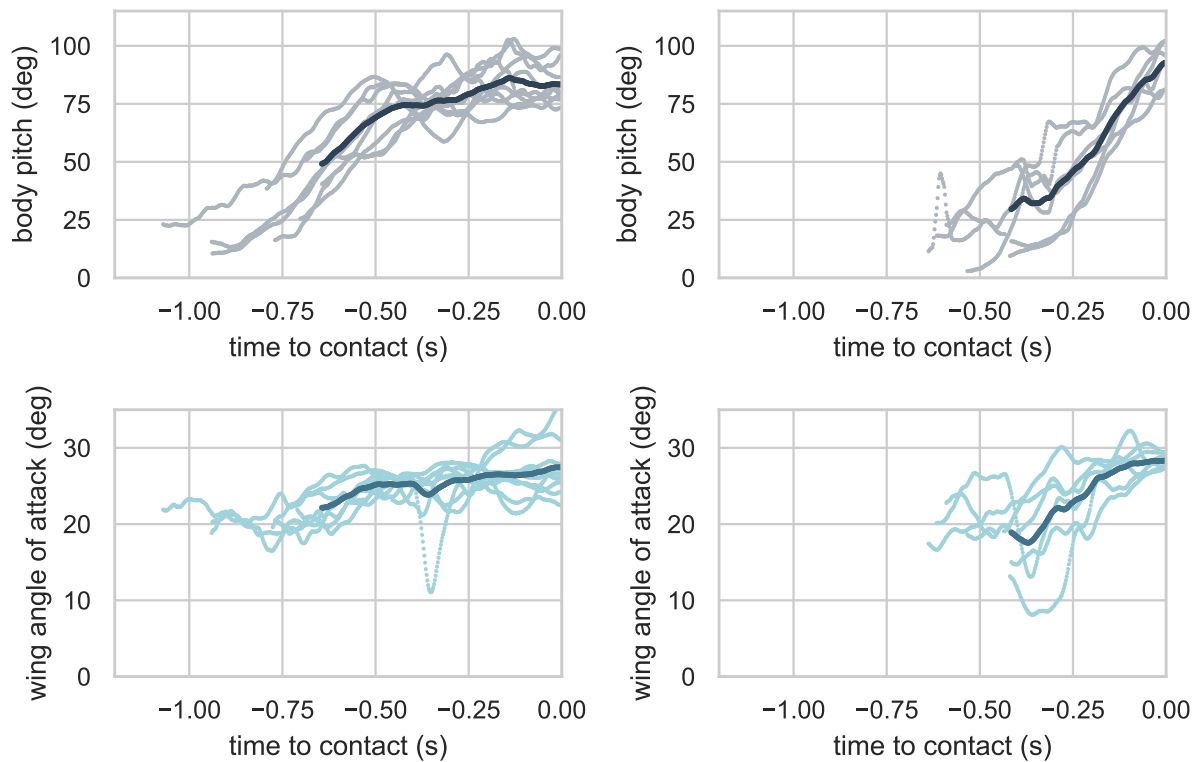


**Figure 2.7:** Comparing inertial and aerodynamic energy loss from 2010 flights. Red area shows inertial energy over time for each individual flight. Black shading shows energy loss during the flights: gain in potential energy below the kinetic energy, aerodynamic braking above. The data for the aerodynamic reference frame energy exchanges is mirrored on the right hand side, where aerodynamic kinetic energy is shaded in blue. The final inertial kinetic energy at 0s is smaller than aerodynamic kinetic energy. The eagle can reduce its inertial energy in order to reduce the force of impact, but maintain a high aerodynamic energy to maintain control by flying into the wind.





**Figure 2.8:** Comparing inertial and aerodynamic energy loss from 2011 flights. Red area shows inertial energy over time for each individual flight. Black shading shows energy loss during the flights: gain in potential energy below the kinetic energy, aerodynamic braking above. The data for the aerodynamic reference frame energy exchanges is mirrored on the right hand side, where aerodynamic kinetic energy is shaded in blue. The final inertial kinetic energy at 0s is smaller than aerodynamic kinetic energy. The eagle can reduce its inertial energy in order to reduce the force of impact, but maintain a high aerodynamic energy to maintain control by flying into the wind.



**Figure 2.9:** Quantified angles of the eagle in the Earth reference frame across the 15 flights. The body pitch angle (black) for each flight is shown, with 2010 flights on the left and 2011 on the right. The dark line shows the mean over time. The body pitch angle is measured between the body axis and the horizontal plane. The body pitch sharply increases in the final second before landing, with the eagle reaching a vertical posture at the point of landing. The wing surface angle of attack (blue) is also notably high and steadily rises over the flight. The angle is taken between the arm wing surface and the oncoming airflow and averaged across the left and right wings. These extreme flight conditions likely induce stall over the wings where the airflow is disrupted.

### 2.4.3 Wing and Tail Kinematics

While the eagle used gliding flight without wingbeat cycles, there is a significant level of dynamic morphing of the wings and tail. To quantify these complex control inputs, multiple points across the eagle were tracked and reconstructed into 3D. The following descriptions are generalised and do not fully describe the variation in wing and tail morphing in the different flights. As the perching flight manoeuvre when measured under different wind conditions and groundspeed, the wing and tail morphing was not highly stereotyped with individual adjustments occurring throughout the final second of approach.

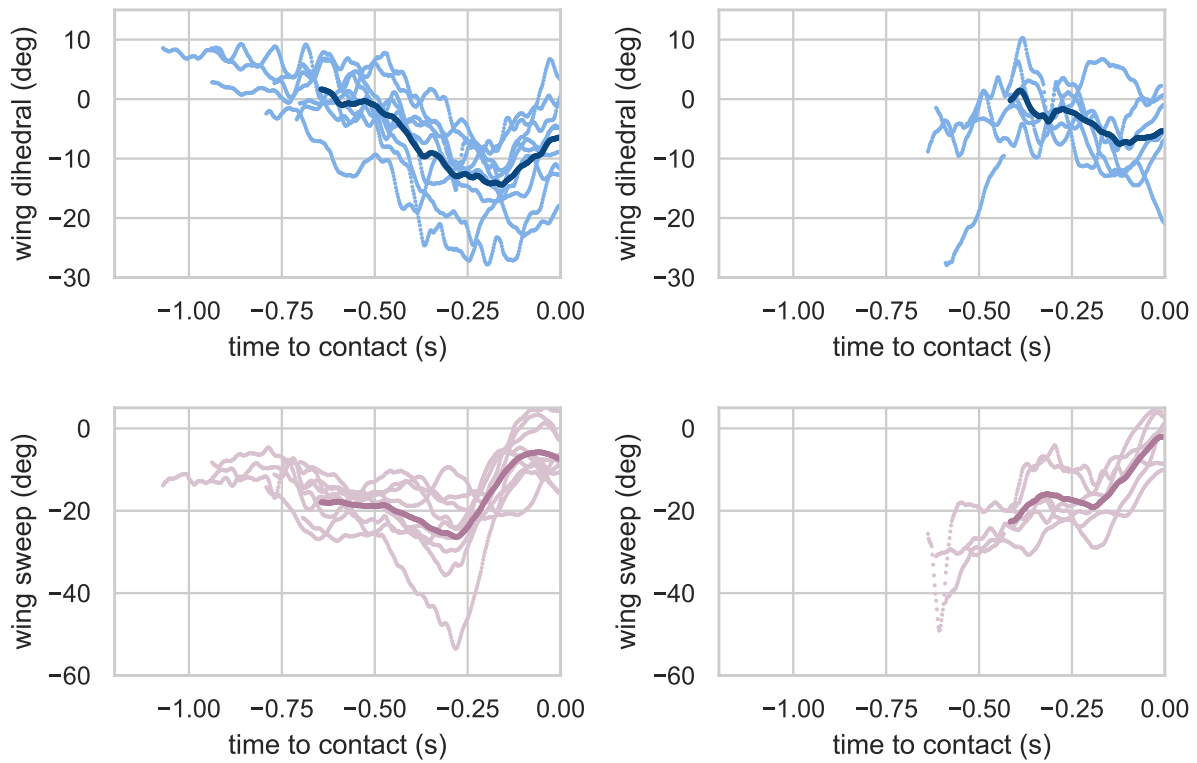
The dihedral angle of the arm wing ( $\phi_W$ ) goes from around  $10^\circ$  to  $-15^\circ$  during the approach to the perch, in other words the wingtips start lower than the body and are raised higher than the body over the approach. After a minimum at 0.25 s from the perch, the dihedral angle increased as the arm wing was lowered once again. The minimum dihedral angle in the high energy flights was later and less pronounced. The wing sweep of the armwing ( $\psi_W$ ) is negative (swept forwards) for the whole approach, reaching a minimum at less than  $-20^\circ$  around 0.3s before contact. The wings sweep back in the final 0.25s to  $-5^\circ$  or even  $> 0^\circ$  for some flights. The higher energy flights show a similar trend.

The armwing pitch ( $\theta_W$ ) is positive throughout the flight, meaning the wing chord was tilted forwards compared with the body chord. The armwing pitch remains steady at an average of  $32^\circ$  for the first part of the glide, and pitch moderately increases during the last 0.3s to around  $35^\circ$ . This corresponds to the trailing edge moving forwards while the trailing edge stays the same or moves backwards. A steady increase in pitch angle is measured in the high energy flights, from around  $33^\circ$  to around  $36^\circ$ . Some rapid fluctuations in pitch occur in many of the flights, where the wing swings backwards very briefly. This is observable in the video data, resembling "flicks" of the armwing.

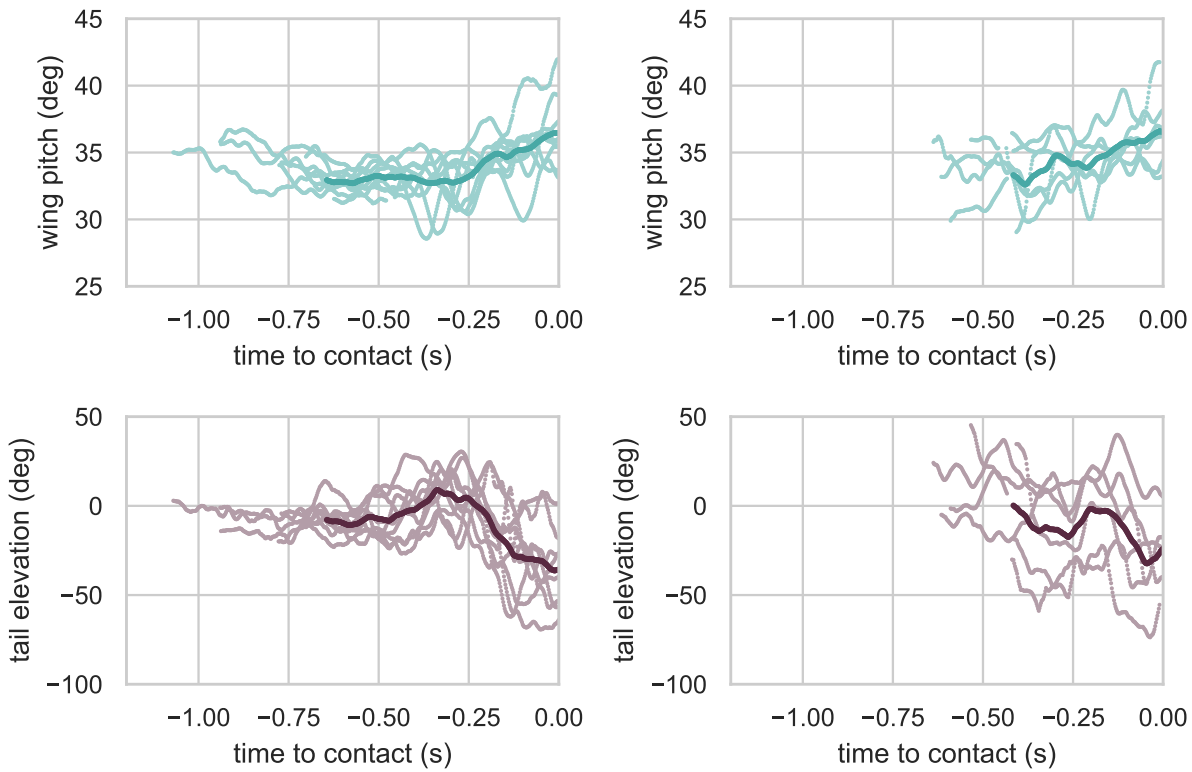
The handwing of each wing has several degrees of freedom (Stowers et al., 2017). Here we describe the folding of the handwing as a single angle, ( $\gamma$ ). The angle starts at  $> 100^\circ$ , corresponding to high spread of the wings. It decreases during the approach to around  $60^\circ$ , which has previously has been described as the M-folding of the wings, and is dramatic in some individual flights and absent in others. Finally, the angle increases again prior to impact. This has been described as the "parachute phase" by Carruthers et al. (2007), where the wing surface is maximised at the point of perching, reaching a maximum at the point of impact of at least  $120^\circ$ . The high energy flights start with a folded handwing started around  $50^\circ$  and rose to  $120^\circ$  at the time of contact.

The tail pitch angle ( $\theta_T$ ) starts generally level with the body or held slightly negative before increasing (elevated) and then sharply decreases to a negative angle (lowered). This brief elevation is visible in the video data and in some

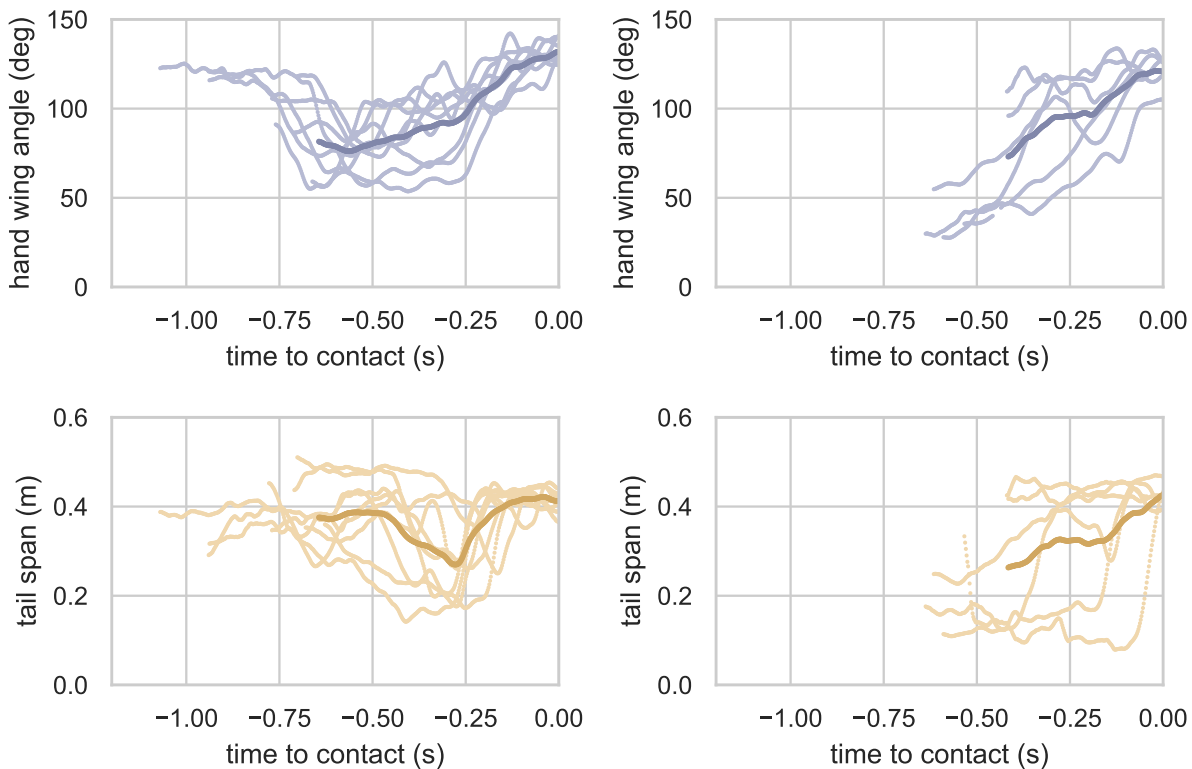
examples happens multiple times prior to landing. Tail span is generally kept high throughout the flight, as would be predicted at low flight speeds. However, in some flights the tail span is decreased briefly to almost half maximum span, coinciding with the tail elevation angle increasing. The tail spreads to maximum with the wings as part of the "parachute phase" immediately prior to contact with the perch.



**Figure 2.10:** Wing angles in the body reference frame and measured using spherical coordinates. Positive dihedral angle refers to a downward canting of the wings relative to the body. Positive sweep angle corresponds to the wings swept backwards. 2010 flights ( $n=9$ ) shown on the left side, 2011 ( $n=6$ ) on the right. Mean angle over time shown in a darker line.



(a) Independent wing and tail pitch angles.



(b) Handwing angle and tail span length.

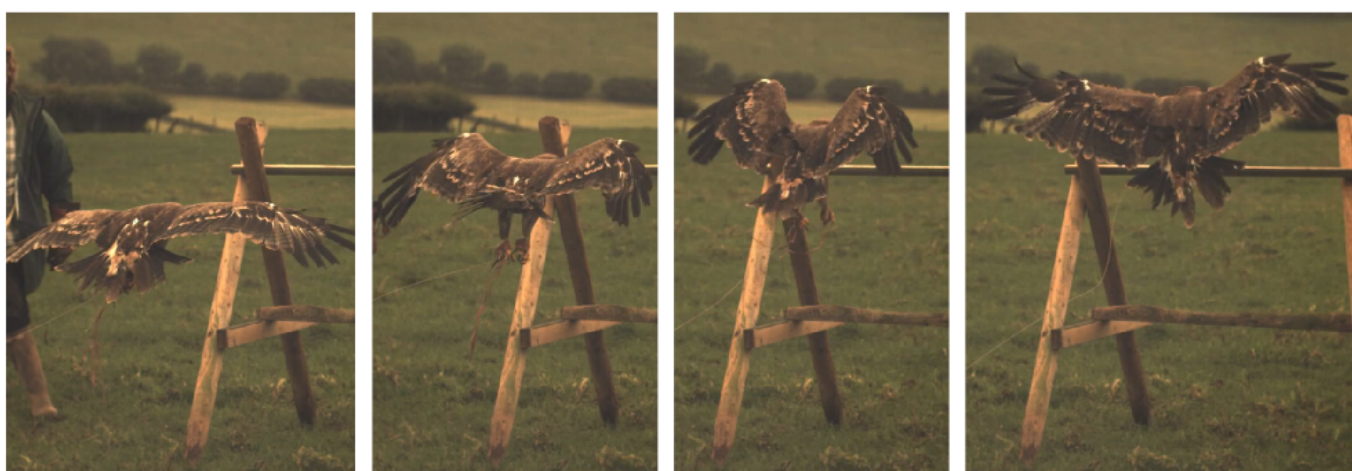
**Figure 2.11:** Further kinematic measurements of the wings and tail in the body reference frame over time, with 2010 flights on the left and 2011 on the right. Mean values over time shown as a darker line. a) Positive wing pitch corresponds to a positive tilt of the wings with respect to the body, while positive elevation of the tail refers to the tail swung up. b) A high handwing angle refers to an unfolded, spread handwing fan. Tailspan was measured between the outer tail feather tips. All angles measured using spherical coordinates of the wing and tail axes relative to the body axes.

2.4.4 Control Input Coordination

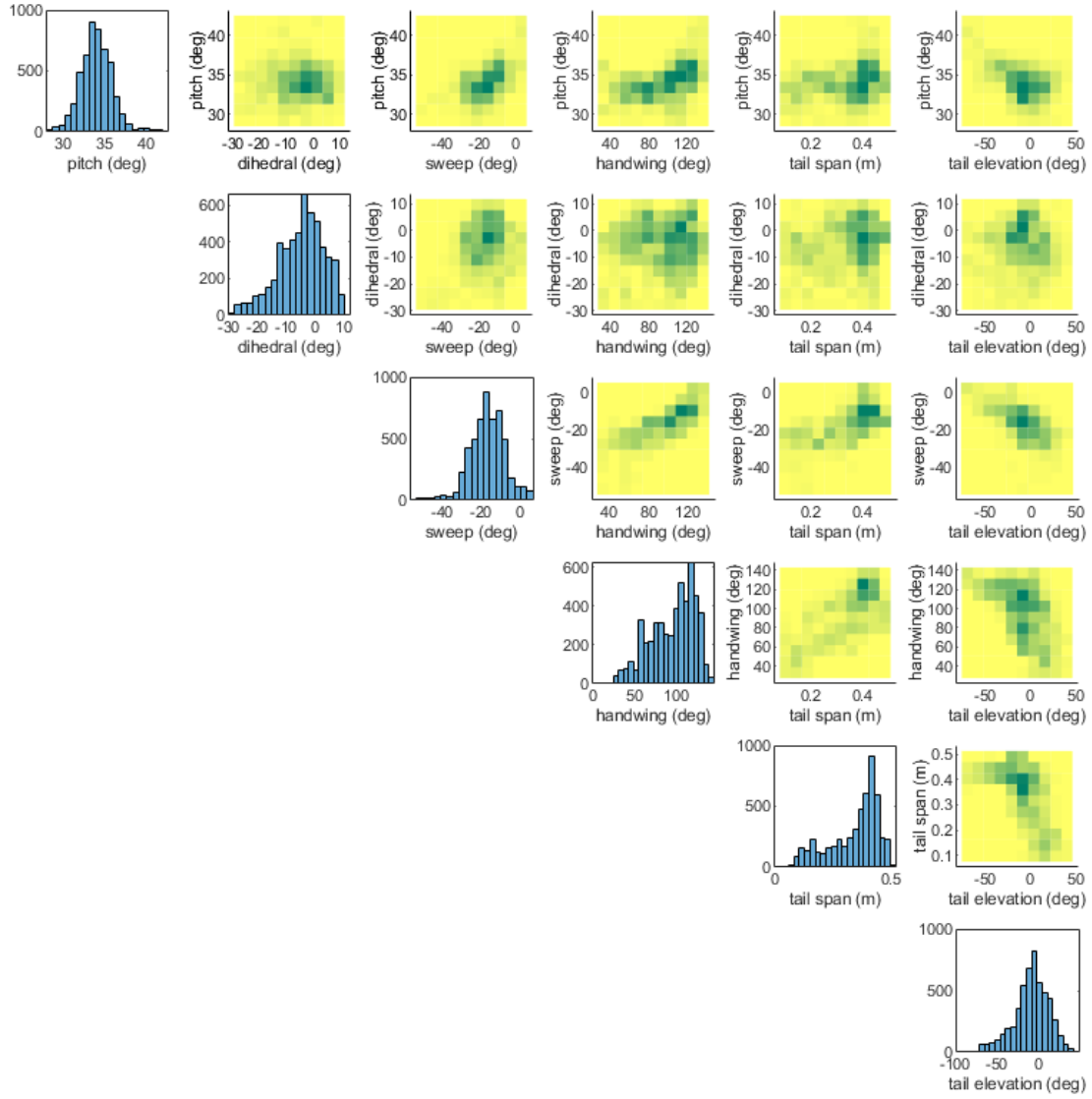
While the eagle has a high number of control inputs, some general patterns are shown across the wing and tail movements (Figure 2.13). Table 2.1 summarises the correlation coefficients and p values between the measured control inputs. The strongest correlation is seen between the handwing angle and armwing sweep, which provide the same effect of moving parts of the wing forwards. However, there is also a positive relationship between the handwing angle and tail span, which again serve a similar purpose of increasing the area of flight surfaces, likely to produce greater lift during the slow airspeed, decelerating flight. There are further moderate correlations between the wing angles and tail, for example tail elevation and wing pitch. While all of these control inputs are nominally independent, there is evidence of coordination and coupling during the perching flight manoeuvre. Strong correlations would not be expected for a non-stereotyped manoeuvre with varying time delays.

**Table 2.1:** *The correlation coefficients between control inputs across the wings and tail during perching flight and p-values. Measurements taken from 15 flights. Dihedral, sweep, and pitch angles describe the arm wing*

|            | Wing Dihedral | Wing Sweep    | Wing Pitch    | Handwing      | Tail Pitch    |
|------------|---------------|---------------|---------------|---------------|---------------|
| Wing Sweep | 0.21, p<0.00  | -             | -             | -             | -             |
| Wing Pitch | -0.01, p=0.69 | 0.52, p<0.00  | -             | -             | -             |
| Handwing   | 0.04, p<0.01  | 0.78, p<0.00  | 0.46, p<0.00  | -             | -             |
| Tail Pitch | 0.02, p=0.17  | -0.63, p<0.00 | -0.51, p<0.00 | -0.57, p<0.00 | -             |
| Tail Span  | 0.18, p<0.00  | 0.63, p<0.00  | 0.27, p<0.00  | 0.71, p<0.00  | -0.63, p<0.00 |



**Figure 2.12:** Video frames showing tail kinematics and wing folding during rapid pitch-up. On approach to the perch, the tail is lifted up while span is reduced. At the same time, the handwings fold until the wings are folded into an M-shape. The tail swings back down and forwards with the legs, simultaneously the wings are unfolded. Both tail and wings are fully spread as part of the parachute phase.



**Figure 2.13:** 2D histograms showing the relationship between the wing and tail kinematics measurements across all the perching flights ( $n=15$ ). Distribution histogram also shown for each kinematic measurement. Strong relationships could refer to control input coordination during the manoeuvre.



## 2.5 Discussion

To prevent dangerous high-speed collision, birds reduce their groundspeed prior to contact (Warrick et al., 2002; Provini et al., 2014). The trajectory shape, mechanics of wing and tail morphing, and whole body posture function together to achieve rapid deceleration. The first goal of this study was to quantify the energy exchanges during the entire gliding approach of 15 gliding flights of a Steppe eagle to a perch. The eagle used two methods to reduce its inertial kinetic energy before contact: gaining in height by gliding up to the perch and applying aerodynamic braking. Gaining height serves to exchange kinetic energy for gravitational potential energy, which was estimated by Carruthers et al. (2007) to account for 30% of the total inertial energy loss. The majority of the energy loss however is facilitated by aerodynamic braking, where kinetic energy is transferred to the wake. The energy loss is extremely rapid, with average inertial energy loss of 372 W in the high kinetic flights. For a large eagle, forceful collisions carry high risks and so substantial braking is required to prevent injury.

While the kinetic energy in the inertial reference frame determines the force of impact, in the aerodynamic frame of reference kinetic energy determines lift production. Maintaining airspeed ensures air flow over the wings as necessary for generating lift. Without aerodynamic kinetic energy, flight cannot be controlled and weight is not supported. As the eagle flew into the wind during the perching manoeuvre it maintained aerodynamic performance while reducing ground speed, and accurately executed a high-precision landing. For all the flights, the aerodynamic kinetic energy was higher than the inertial kinetic energy due to headwind. If the eagle instead flew with the wind or if the wind speed was negligible, flapping would be required to maintain aerodynamic control, as observed in previous work (Carruthers et al., 2007).

The two experimental periods provide two types of perching flight – high and low kinetic energy flights. In the high kinetic energy flights recorded in 2011 at a cliff site, the eagle's airspeed and final impact force were far higher than the 2010 flights. Windspeed was also slightly higher on average. In 2011 the eagle did not gain as much height over its approach, likely due to the lower perch height (a falconer's arm). The eagle therefore did not exchange as much energy to gravitational potential energy. However, despite these differences the final impact force was still relatively low. This is explained by an increase in energy lost aerodynamically through braking, which accounted for an average of 80% of the total energy loss. Through the perching manoeuvre the eagle is able to lose a wide range of energy as required by the specific circumstances, yet still maintain sufficient energy to control its flight.

The type of perch may also have affected the braking strategy. In the 2010 flights, the wooden perch was rigid and may warrant a safer, higher braking magnitude to ensure low momentum on touchdown. For flights to a falconer's

arm as recorded in the second 2011 data set, the target was more pliant and a higher impact force would not result in injury. While landing with force is risky, so too is using too high aerodynamic braking due to its effect on lift production. In previous work, a high and low kinetic perching strategy was noted by Green and Cheng (1998) in pigeons. The birds used a higher collision force for familiar perches and therefore limited the energy lost through braking. For novel perches, a lower risk strategy was applied, apparently favouring the greater energy expenditure for the safety of a controlled landing.

To achieve substantial aerodynamic braking, birds can alter the magnitude, and/or the direction of their net resultant force to induce a whole body pitch rotation. Birds can alter their flapping, change wing shape, and alter the angle of attack to affect aerodynamic force production (Altshuler et al., 2015). As the eagle used gliding flight in the recorded sequences, we measured wing morphing and angle of attack by reconstructing 14 points across the eagle in 3D using manual tracking and photogrammetry. From the detailed kinematics data from the wings and tail, for the first time the mechanism of aerodynamic braking was explored during gliding. Studying complex wing morphing in birds was limited before the advent of digital high-speed videography, and here we provide quantification of angles and spans from the eagle's wings and tail. The complexity and detail of wing morphing provides the greatest challenge to studying bird flight, and yet such complexity is key to the enviable accomplishments in their flight performance.

Flight surface area changes were measured in the gliding approach, where the handwing unfolded and tail lowered and spread in the final 0.2s before contact. Increase to wing and tail surface area increases drag production and therefore deceleration. In addition, the angle of attack increases on approach and force production from the wings would change from normal to the airflow to normal to the wing surface, and thus redirect the net resultant force backwards. Wing twist could also lead to higher force generation at high angle of attack at the wing chord, but measurements of twist were not possible in this study.

In the rapid pitch up manoeuvre, due to whole body rotation forces generated from the bird have a new direction of action and therefore produce a drag force and enable deceleration. Nose-up pitch rotation is caused by moving the position where the resultant force acts on the body. This can be achieved through changing the centre of mass, for example by dropping the legs. Wing shape changes can move the centre of pressure in front of the centre of mass, leading to nose-up rotation of the whole body. Kinematic measurements during the perching manoeuvre included folding the handwings such that the wings resemble an M-shape and may aid lift production by acting as a delta wing through the generation of leading edge vortices (Carruthers et al., 2007). At the same time, the eagle's wings are swept forwards using a rotation at the shoulder, and from flow visualisation, sweeping a delta wing reduces flow separation at increased angle of attack and protrusion of the alula has the same effect (Lowson et al., 1995;

Carruthers et al., 2007). By sweeping the wrist forwards  $20^\circ$ , the centre of pressure is also moved forwards and has been shown to induce large pitching moments (Greatwood et al., 2017). In addition, brief pulses in negative tail pitch at minimal tail span were measured in many of the flights. As the tail produces a proportion of the total lift, reducing surface area and its angle of attack lowers magnitude of lift generated behind the centre of mass. Rotation occurs before the tail pulses, and so it is likely not the initiation of the rapid pitch up. These control inputs can induce and modulate the whole body pitch rotation, which rises from  $25^\circ$  to over  $100^\circ$  in some flights.

The eagle also lifted its wing chord above its body into a shallow V-shape during the glide (negative dihedral angle by  $30^\circ$ ) which improves lateral stability, as shown in a perching UAV with varying dihedral angles (Paranjape et al., 2013). In addition at low airspeed increasing the dihedral angle steepens the glide path and increases the sinking speed (Sachs and Holzapfel, 2007). Therefore wing morphing maintains aerodynamic authority and sustains stability during stall. These control inputs are peak around 0.3s from contact and are quickly reversed to stop pitching from continuing and to ease off weight support. In the parachute phase (Carruthers et al., 2007) the tail is swung down and spread, which would induce a nose-up rotation. This reverse rotation force stops the eagle pitching up indefinitely and flipping over. At the same time, the wings sweep backwards and the wing dihedral angle increases (wing moves downwards) to end the manoeuvre. Both the handwing angle and tail span increase together during the parachute phase, increasing drag in the manner of a drag-parachute (Carruthers et al., 2007).

In addition to predictions of lift and drag production from steady state aerodynamics, unsteady effects are also present during the perching manoeuvre. Stall occurs at low airspeed and at high angles of attack. Flow separates from the wing surface and high levels of energy are lost to the wake. For this reason, the rapid pitch-up manoeuvre has been of interest in multiple studies (Anderson, 2009; Polet et al., 2015; Cory, 2008; Moore et al., 2014). The wing surface angle of attack was high for the duration of the flight, which has serious implications for flow separation, particularly at low airspeed. With a high angle of attack, airflow is disrupted over the wing leading to stall characterised by uncontrollable conditions. For a flat airfoil, flow separation is experienced at just  $12^\circ$ . The rough surface of the eagle's wings and the very structure of the feathers may work to reduce flow separation as demonstrated in wind tunnel studies with passive flaps (Rosti et al., 2017; Brücker and Weidner, 2014). Automatic aeroelastic devices have been previously examined during the post-stall conditions of perching flight, with the alula likely playing a role in promoting lift generation by influencing leading edge vortices (Carruthers et al., 2007). Here we also measured the presence of "wing flicks", or brief pulses of decreasing pitch relative to the body during the rapid pitch-up. These may be adjustments again for the whole body pitch, or possibly serve some function to aid the airflow over the wings. Reversed flow was visible during the wing flicks in the form of the feathers flipping up along the dorsal surface.

Other minor adjustments are seen throughout the flight for many of the wing and tail kinematics, and their exact influence cannot be fully known. While Carruthers et al. (2007) described the perching manoeuvre as "highly stereotyped" here high variation in kinematics was measured between flights. The morphing of the wings and tail is highly varied and complex with symmetric and asymmetric motions throughout the final second before landing. In addition kinematic events do not occur with consistent timings, may or may not be present at all, and do not show a clear ordered pattern across the different flights. It is apparent the perching manoeuvre is not a highly stereotyped behavioural sequence that the eagle has learnt to execute repeatedly as part of a choreographed manoeuvre. Instead, perching flight is under closed-loop control, with active adjustments of the wings and tail made by the eagle using sensory feedback throughout its approach. The latency of the visual system (50-100ms) is just about low enough for feedback control within this time-frame. Due to the local nature of the control, it is very plausible direct load sensing is involved, with forces on the wings providing critical feedback for applying constant braking. Other senses such as direct acceleration sensing from the inner ear may also play a role.

The processing demand on the eagle would appear very high for controlling multifunctional actuators responsively within a small time frame. The numerous control inputs available to the bird are in principle independent, such as independent wing pitch angle and span. From the correlations of coefficients between the wing and tail kinematics, coupling of control inputs seems to be present. In particular the handwing and tail seem to be coupled closely where wing and tail span increase occur together. Gillies et al. (2011) measured a coordination between tail span and tail pitch, which is also reflected here in these results. The wing pitch is also correlated with the handwing angle, and to a lesser degree the tail pitch and span. Much of the sweep component is non-independent to the handwing angle, as bringing the leading edge forwards unfolds the handwing. By coupling the control inputs that enhance lift production, the complexity of controlling multiple inputs across the wings and tail is reduced. In contrast, the dihedral angle shows little evidence of coupling, and so this suggests it is altered relative to feedback rather than another control input. The dihedral angle mostly influences lateral stability, while the other kinematics measured influence stability in pitch.

Further important control inputs are wing twist and shape changes along the length of each wing, but these were too challenging to record. In practice however, it seems there is some coupling of the control inputs during flight. The positive relationship between wing and tail kinematics suggests the wings and tail are somewhat coordinated. By coupling mechanisms, the control demand is reduced as well as enhancing an aerodynamic effect (where both have a similar effect) or for refining adjustments (where one effect counters the other).

Untangling the multimodal effects of individual wing and tail kinematics and the effect of coupling on aerodynamic performance is often speculative at best from recordings of flight behaviours. Wing and tail kinematics affects lift production, drag production, lateral and pitch stability, and the combinations can only be empirically tested with morphing UAV designs (Paranjape et al., 2013; Anderson, 2009; Greatwood et al., 2017; Moore et al., 2014). Direct manipulations of control inputs from a comparable replica are required to understand the combined effect of wing morphing during manoeuvres.

Unsteady aerodynamics effects undoubtedly play a role in the force production during the perching manoeuvre. Rapid increases in angle of attack increases the frontal area to the airflow, and in simulated aerofoils predict high energy transfer to the wake from flow separation and from added mass effects (Polet and Rival, 2015; Polet et al., 2015; Weymouth and Triantafyllou, 2013). As well as through pitching, frontal area change is influenced by increase in wing and tail surface area. Therefore the rapid pitch-up and parachute phase can achieve both reduction in airspeed through aerodynamic braking and also generate sufficient lift to maintain flight control during post-stall conditions.

These results provide further evidence that braking strategies can vary behaviourally based on conditions and circumstance. Far from a stereotyped manoeuvre such as jumping, perching flight is a highly controlled manoeuvre with high variety between flights. Experimental designs which drive variations in aerodynamic braking strategies would give further insight into the capacity and limits of airspeed reduction during flight. As with any other behaviour, perching flight is optimised to many factors allowing flexibility and an ability to exploit varied and changeable situations. The adjustment of braking strategy reflects the capabilities of birds to manoeuvre in a wide range of changeable and compromising conditions.

The extreme angles of attack observed during gliding flight to a perch are challenging, as flow separation could be expected to lead to a loss of controllability during a behaviour that requires a high level of control. UAVs with fixed wings simulating similar flight behaviour, forces around the wings are unpredictable and analytical methods are insufficient; forces must be measured in real-time to maintain control. Despite the risks of uncontrollable conditions, inducing stall has high benefits of force generation and can facilitate rapid deceleration. Birds balance high precision flight during highly dynamic manoeuvres, and such enviable flight performance lies in the complexity of their morphing wings and sensitivity of their sensory systems. Much still remains elusive to our understanding of the control of manoeuvring flight.

## 2.6 Conclusions

To successfully land on the perch, the eagle maintains high-precision control during post-stall conditions while inducing significant aerodynamic braking. Here we investigate the velocities, energetics, wing and tail kinematics, and coordination during perching flight. The loss of airspeed during perching flight is very rapid, and the eagle lost its kinetic energy using three methods: exchange with gravitational potential energy; aerodynamic braking; and impact with the perch. The manoeuvre is reliant on the increase in wing angle of attack, partly from the necessary increase in lift production at low airspeed, but also for the redirection of aerodynamic forces, and to rapidly lose energy to the wake through flow separation. Using detailed measurements across the wings, body, and tail, we quantify wing morphing during the perching manoeuvre to determine the mechanism of the rapid pitch-up and how such complex control inputs are coordinated. There is evidence perching flight is under closed loop control where sensory feedback guides the continual and variable kinematic adjustments during the final second before contact with the perch. Some coordination is apparent between the wing kinematics, and also between the wings and tail, which follows results from other kinematic recordings during manoeuvring flight. Braking is precisely controlled, with a constant deceleration applied during the approach.

Perching flight involves extreme flight conditions with high risks of collision and yet the eagle uses precise flight control through complex wing morphing all in less than a second. Such flight control and performance is beyond our own technological advances in UAVs and we still have much to learn before we can recreate such feats.

# Mechanics of Perching Flight in Harris Hawks

## *Parabuteo unicinctus*

### 3.1 Abstract

High-speed motion capture is used to record and reconstruct multiple markers from 1365 perch-perch flights performed by four Harris hawks in a custom-built flight arena. Rigid body marker sets were tracked automatically using pattern recognition methods, and individual markers on wing and tail feathers were labelled based on their distance from the body as wing motion was highly clustered relative to the body during both flapping and gliding. Four perch-perch distances were used to manipulate a change in braking strategy. Trajectories were U-shaped with a descending phase followed by an ascending phase, where braking is facilitated by a gain in gravitational potential energy. In the short flights, height change was minimal and braking strategy altered as a result. A flapping approach was used in the short flights rather than a glide. Regardless of flight pattern, angle of attack remained constant for most of the flights despite whole body rotation as the wings were pitched in the opposite direction to the body. In the final 2m from the perch, angle of attack rapidly increased as part of a rapid pitch-up manoeuvre. The associated peak in drag force in the longer flights is best explained by added mass effects rather than steady-state aerodynamics. High angle of attack in the shorter flights meant a net drag force was produced from wingbeats rather than thrust. As a result deceleration was possible without a long gliding ascent. Wing control inputs such as handwing folding and negative tail pulses were notably absent from the flights, in contrast to the Steppe eagle, which is likely due to the controlled indoor conditions without windspeed effects. The controlled conditions meant flights were highly stereotyped with little variation between recordings, again in contrast to the eagle. Between individuals, flight energetics varied the most as a result of differences in mass, and differences in flight technique were also measured.

### 3.2 Introduction

The complexity of wing and tail kinematics allows dynamic and precise flight ability, and yet our understanding of how such control inputs alter the energetics and aerodynamics of flight is still limited. Recording techniques and

processing has limited research, with kinematics measurements made from small numbers of flights or from one individual (see Chapter 2). Using motion capture to automatically reconstruct markers attached to Harris hawks, it is now possible to record large scale data sets of over a thousand flight trajectories and which include detail into the wing and tail kinematics.

Motion analysis requires extracting information from sequential video frames, and was first used by Eadweard Muybridge to famously capture equine gait (Muybridge, 1878). With new technological advancements, the sophistication of kinematic and biomechanics information continues to expand and improve. Measuring the complex morphing of wings requires image collection from a multi-camera system and combination of multiple two-dimensional images (2D) into a 3D reconstruction. Tracking individual points of interest on wings in flight has in the past relied on manually marking images (Gillies et al., 2011; Carruthers et al., 2010; Provini et al., 2012; Walker et al., 2009), and semi-automatic tracking (Hedrick, 2008; Tobalske, 2007; Ros et al., 2015). With recent advances in technology and methods, automated point matching is possible and variation in wing camber, twist and thickness were measured in a Barn owl (*Tyto alba*) (Wolf and Konrath, 2015). Additionally, a high spatial resolution 3D outline of two birds of prey has been reconstructed from multiple calibrated cameras images using shape-carving techniques (Durstion, 2018). However, it is often only possible to reconstruct a small number of flights, and even in the with semi- or fully-automatic tracking, manual quality checks are normally still necessary. High-resolution reconstruction of the dorsal wing surface can be automatically resolved with a new structured light technique, but this experimental technique is limited to a small recording volume and under unnatural visual conditions for the animal (Deetjen et al., 2017).

In recording human movement, the preferred methodology uses an optoelectronic method, also known as motion capture. Multiple cameras set up in an array emit infrared light to illuminate passive retro-reflective markers attached to the surface of the recording subject. Use of centroid tracking aids detection of the retro-reflective markers and in humans, an underlying skeleton model is fitted in real-time to improve accuracy. Reconstruction from 2D images into real-space coordinates from a calibrated system occurs in real time and is highly accurate; typical root mean square errors of less than 2mm for visible moving markers in a 3m volume (Colyer et al., 2018; van der Kruk and Reijne, 2018). Motion capture is used in sports biomechanics, medical professionals, and in the entertainment industry to aid animation (van der Kruk and Reijne, 2018). Many animals including dogs, cats, and horses have been recorded with motion capture for scientific research (Macpherson et al., 2007; Kim et al., 2017; Kopniak and Bocian, 2016). Retroreflective markers have also been placed on butterflies and dragonflies to measure record trajectories (Slegers et al., 2017; Mischiati et al., 2015) and wing kinematics have also been recorded from bats using multiple markers across the wing surface (Falk et al., 2015).



Similar to manually tracked 2D features from images, the motion capture system reconstructs the marker into 3D space by triangulation from the calibrated camera array. A calibrated motion-capture system can track and reconstruct markers in real-time, and reducing the processing time even for very large numbers of sequences. Labelling of tracked markers, in order to measure motion over time, relies on underlying human skeleton models. If recording a non-human subject, a manually labelled rigid skeleton template is required. In this chapter a different mechanism is used to label individual markers attached to flight feathers, making use of the closely clustered positions of wing markers relative to the body from hundreds of flights by an individual bird.

## Aims

This study aims to improve the detail of wing-tail morphing measurements during gliding and flapping approaches to a perch. High-speed motion capture was used to measure the energetics, aerodynamics and kinematics of aerodynamic braking in 1365 perching flights performed by four Harris hawks. These experiments follow from qualitative and quantitative measurements of perching by a male Steppe eagle (see Chapter 2 and work by Carruthers et al. (2007)). In addition, this study seeks to quantify the mechanism for drag during aerodynamic braking mechanism, following the unsteady aerodynamic model by Polet et al. (2015). A further aim was to explore different braking strategies and how flight distances influence the magnitude and method of braking. In order to alter braking strategy, flights were measured from four discrete perch-perch distances, where gain in height and exchange with potential energy is limited. Finally, this study aims to investigate individual variation in flight performance, energetics, kinematics, and technique between flights and between four individuals.

## 3.3 Methods

### 3.3.1 Animals and Experimental Setup

Four Harris Hawks (*Parabuteo unicinctus*) were trained to fly between two perches for a food reward. The hawks were housed in bespoke aviaries at the Wytham Field Station, Oxford and the protocol was reviewed and approved by Animal Welfare and Ethical Review Board of the University of Oxford's Department of Zoology. Three hawks were juvenile males aged between approximately 4-6 months, and one adult female hawk approximately 7 years old in addition.

Experiments were recorded within a custom-built flight arena 20m x 6.1m x 4m in size. White non-strobing LED lights provided indirect overcast daylight levels (1000lux). Camouflage netting was used around the perimeter of the room to hide structural features on the walls whilst providing uniform mottled background contrast to create optic flow stimuli during self-motion. Two trained falconers were present for each recording session and used signals and food rewards to encourage each hawk to fly between two perches. The perches were two free-standing A-frames at 1.25m in height. Experimental sessions were usually for five consecutive days of every week and one hawk was flown at a time. Between 30-50 flights were recorded per hawk during each session. Perch distance was initially 12m for the first four days and then alternated between days to either 5m, 7m, or 9m pseudo-randomly. Perch distance was conserved within each session. Sixteen sessions were recorded for each hawk, four per flight distance, over a 2.5 month experimental period.

### 3.3.2 On-Board Animal Equipment and Markers

The hawks were fitted with multiple marker sets for the motion capture to track in the room. The markers were coated with retroreflective beads designed to reflect infrared light from the motion capture system. Two sets of rigid plate markers were used on the hawks body and a modified falconry hood designed to leave vision unrestricted was worn on the head during flights (Figure 3.2). Each plate was fitted with a unique and asymmetrical configuration of markers to aid pattern recognition and also to provide orientation information about the plates in post-processing. The markers used on the plates were 9mm in diameter, with 3 markers used on one plate, 4 on another and 2 on the modified hood. Additional 5mm hemispherical markers were attached to the hood. A clip was fixed to the back of each plate to attach onto a backpack and tail mount designed for telemetry equipment. The *TrackPack Mounting System backpack* (Marshall Radio Telemetry) comprises a rigid plate worn on the back and secured in place by a pair of teflon ribbons. A *Tail Piece Mount* (Marshall Radio Telemetry) was fixed to the quill of a feather at the base of the



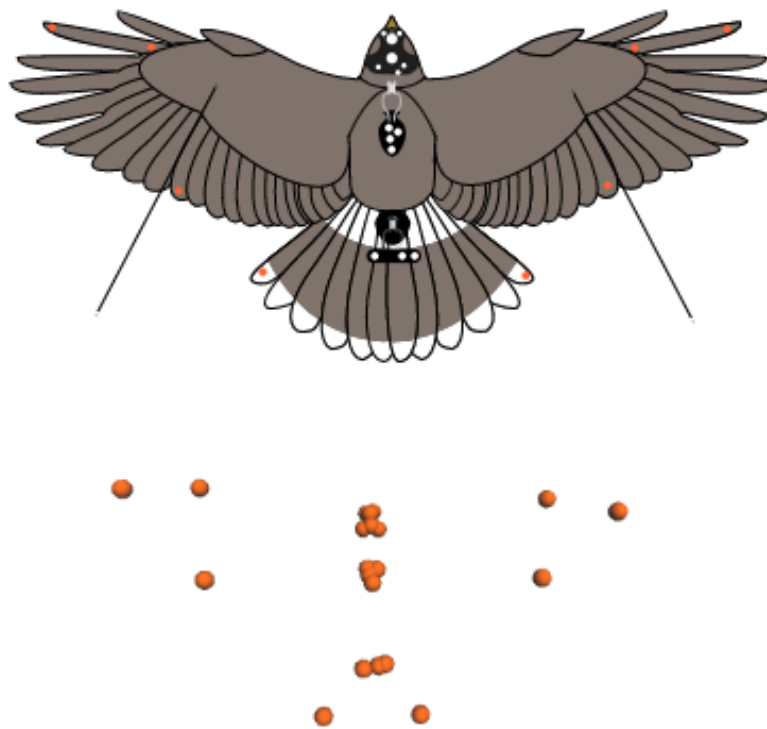
**Figure 3.1:** *Male Harris hawk on an A-frame perch. Flights were recorded between two A-frames in a custom built flight arena while recorded with motion capture.*

tail. The hawks wore the backpacks and tail mounts for the duration of the experimental season, while the marker plates and hood were attached for each session and removed afterwards. Markers were replaced periodically once the retro-reflective coating became damaged.

Prior to each experimental session, 3mm diameter self-adhesive hemispherical markers were attached to feathers on the wings and tail (Figure 3.3). On both wings markers were placed on i) the tip of the longest primary feather (wingtip markers); ii) the midpoint of longest primary feather (primary marker); and iii) the tip of the first secondary feather (secondary markers). Two additional markers were fixed to the tips of the outermost tail feathers (tailtip markers). The positions were marked with paint for consistency across the experimental period.



**Figure 3.2:** Photograph of markers and equipment. Clockwise from the top: the backpack marker plate being attached to a hooded Harris hawk prior to the experiment; the backpack and tail mount marker sets during an example flight (photograph courtesy of AngleSharp Media); the modified hood with markers; 3mm markers attached to the tail feathers.



**Figure 3.3:** Schematic of marker placement on the hawks. Reproduced and modified from an image by Dr. Marco Klein Heerenbrink with permission. Rigid marker sets were attached to the hood, backpack, and tail mount each with a unique and asymmetrical pattern. Feather markers were placed on the longest primary feather tip, the middle of the same feather, and the tip of the secondary feather. These are referred to as wingtip, primary, and secondary markers respectively. Two markers were also placed on the outermost tail feather tips (tailtip markers). The complete marker set as seen in the motion capture software shown below in orange.



### 3.3.3 High-Speed Motion Capture System

An array of twenty high-speed *Vicon Vantage 16* motion capture cameras were used to record the flights, and two reference cameras. All cameras were mounted 3m above the floor on scaffolding fixed around the perimeter of the room (Figure 3.4). Sensor resolution was 4096x4096 px and frame rate of 120fps. The strobe unit on each camera emitted infrared light at 850nm to light the capture volume, and the optical filter on the lenses blocked other light wavelengths. Shutter speed was synchronised between the cameras, along with strobing which coincided with the shutter opening. The cameras were aligned such that a marker within the recording volume would be visible to at least three cameras. Prior to each experimental session, the motion capture system and reference cameras were calibrated by moving a *Vicon Active Wand* around the recording volume. Estimated calibration error was checked using the Vicon software before experimentation, and if necessary repeated. The origin, volume axes, and floor plane were also defined at a marked position in the recording space. The motion capture system tracked the visible markers in the recording volume and reconstructed their position into 3D coordinates. Recording in Vicon Nexus software was manually triggered and ran for multiple flights. Individual flights sequences were separated and trimmed in post-processing.



**Figure 3.4:** *Flight lab experimental setup. Two A-frames were positioned 12m (shown), 9m, 7m, and 5m apart as experimental conditions. Twenty motion capture cameras positioned around the perimeter room around 3.5m high, and LED lights and white fabric on the ceiling mimic overcast daylight conditions.*

### 3.3.4 Marker Identification

Each recording contained several flights back and forth between two A-frames. To automatically crop the recordings into individual flight sequences, a mean position was calculated from all markers in each frame. A moving standard deviation of 5 frames was taken, and due to high flight velocity the start and end of flight sequences were readily identified compared with any periods of rest using a simple peak analysis function. Automatic cropping was verified and adjusted as necessary for every recording, and flights where data was cut short, unreconstructed, or otherwise improper (for example, a hawk flying to the ceiling rather than a perch) were removed.

The Vicon system was unable to label any of the hawk markers consistently. The inbuilt labelling system relies on the assumption that between two frames, markers moved a distance smaller than the distance between neighbouring markers within a frame. When tracking human motion, markers are spread out and human movement is relatively slow, and so an individual marker is easily "followed" throughout the anonymous marker pool. For the hawk markers, this assumption does not hold due to high flight speed and smaller body size. In addition, marker drop-out was not uncommon due to feathers covering the markers during wing folding, as well as some occlusion due to whole body rotation. As a result, marker labelling using the Vicon system was not reliable, and using the inbuilt manual labelling alternative was also infeasible for the large data set.

Custom written software in MATLAB (MathWorks, Inc.) was instead used to label the unlabelled marker coordinates. Pairwise distances between all the anonymous markers per frame were used to identify stationary markers on the perch and rigid plate markers. Stationary markers were identified as i) those that were less than 10mm apart; ii) those remained under this threshold for more than half the sequence length. Templates were used to search for the unique and rigid pairwise distances between marker patterns on the backpack, tailpack and the hood. Due to wear or damage, markers were occasionally replaced and so a template was necessary for each experimental day. An average marker position was used to define the backpack and tailpack trajectories, but as this was affected by the number of markers a spline was used to smooth the mean marker position over the flight. The hood was most affected by poor reconstruction as a result of centroids from multiple markers merging frequently. This was due to close marker proximity and small marker diameter. As a result, the hood data was not used for analysis. Flights were considered unsuitable when no backpack markers were identified for more than 25% of the frames, normally caused by marker occlusion by feathers or hardware problems. From the 64 sessions over a 1.5 month period a total of 1365 flights were used for analysis after checking for sufficient marker reconstruction.

Boundaries around the backpack spline were then used to create a searching area for the feather markers. The markers on the wings and tail have no fixed pairwise distance due to the morphing wing and tail surfaces, feather flexing, and underlying moving joints. However, when the anonymous feather markers were pooled from all flights and separated both by individual and flight phase, the markers clustered within tight boundaries relative to the central backpack point (CBP). In other words, for an individual hawk, its independent wing motion was closely stereotyped, but these clusters were distinct during flapping and also during gliding and had different boundary definitions. Boundaries were defined in the XY plane (sagittal plane) and in the XZ plane (transverse plane) as the different markers were more clearly separated in these two planes. Boundary definitions were estimated by hand and were individual to each hawk due to anatomical variation. Feather markers could not be identified during the first 1m and final 0.3m of the flights as there were no clearly defined clusters during take-off and final pull-up to the perch, but their configuration is again distinct to the other phases.

The markers were defined relative to the global axes of the room as determined during the calibration of the motion capture system. The Y axis was defined as the axis down the length of the room, where positive points in the direction of the starting perch to the end perch. Z pointed up normal to the floorplane, and the X axis pointed right. The markers were also described relative to the CBD and rotated with respect to the body pitch angle and the body yaw angle, with body roll assumed to be zero (see below).



**Figure 3.5:** Marker set from motion capture overlaid onto reference footage. Markers coloured by type: hood (pink), backpack (yellow), tail mount (orange), feathers (grey) during the glide and rapid pitch-up. The stationary markers on the perch are linked with an orange bar.

### 3.3.5 Trajectories, Velocity and Energetics

The central backpack point (CBP) was calculated as the mean coordinate of the backpack markers. As backpack markers were often missing or merged in individual frames as a result of the centroid tracking by the cameras or due to occlusion, a smoothing spline was applied to reduce the noise associated with finding the mean position between

a varying number of markers. The smoothing tolerance was tuned such that the spline did not fall beyond the range of the backpack markers, therefore preserving the detail of the overall backpack plate motion. The CBP spline was used to define the flight trajectory. The hawks' ground velocity calculated by differentiation over time and used to calculate the kinetic energy ( $E_K$ ):

$$E_K = \frac{1}{2}m|\mathbf{V}|^2 \quad (3.1)$$

The gravitational potential energy ( $E_P$ ) was calculated using the mass of the hawk ( $m$ ), the gravity vector ( $g$ ), and the height of the CBP from the ground ( $h$ ):

$$E_P = mgh \quad (3.2)$$

The hawks' total energy ( $E_T$ ) was calculated as the sum of the kinetic and potential energy:

$$E_T = E_K + E_P \quad (3.3)$$

The rate of change in total energy ( $\dot{E}_T$ ) was calculated by differentiating a smoothed cubic spline of  $E_T$  over time. The total energy change was weighted by the total energy ( $\dot{E}_T/E_T$ ) to compare across different flight distances.



### 3.3.6 Aerodynamic Forces

The total aerodynamic force ( $\mathbf{F}$ ) was calculated from the acceleration at the CBP calculated from the second derivative of the smoothed trajectory of the CBP, the mass of the hawk ( $m$ ), and the gravity vector ( $\mathbf{g}$ ):

$$\mathbf{F} = m(\ddot{\mathbf{x}}(t) - \mathbf{g}) \quad (3.4)$$

The lift vector component ( $\mathbf{L}$ ) was calculated as the component of the aerodynamic force perpendicular to the velocity vector measured at the CBP, while the drag vector ( $\mathbf{D}$ ) is the component normal to velocity vector.

From the standard lift equation, lift ( $L$ ) is a function of the total lift surface ( $S$ ), the lift coefficient ( $C_L$ ), the velocity vector ( $\mathbf{V}$ ), and air density ( $\rho$ ):

$$\mathbf{L} = \frac{1}{2} \rho |\mathbf{V}|^2 SC_L \quad (3.5)$$

It is not possible to directly measure the total lift surface ( $S$ ) nor directly measure the complex dependencies of shape ( $C_L, C_D$ ), and flow conditions on lift from the hawks during flight. Instead the quantity  $SC_L$  combines these into a quantity that describes the instantaneous effect of the hawk's flight surface on the lift (Reynolds et al., 2014). However, given measurements of lift, drag, and speed we computer the composite quantity  $SC_L$  by rearranging the standard lift equation:

$$SC_L = \frac{2\mathbf{L}}{\rho |\mathbf{V}|^2} \quad (3.6)$$

In the same way  $SC_D$  can be calculated from rearranging the standard drag equation:

$$SC_D = \frac{2\mathbf{D}}{\rho |\mathbf{V}|^2} \quad (3.7)$$

### 3.3.7 Body, Wing, and Tail Kinematics

Three vectors were used to describe the wing, body, and tail kinematics during the flights. To measure an estimate for the body axis, a body vector was measured between the CBP and the central tailpack point (CTP). For an estimated

true wing chord, a chord vector was measured between the primary marker and the secondary marker for both wings. Finally a tail axis was estimated using a vector between the CPT and the central point between the two tail tips.

The angle of climb ( $\theta_V$ ) was calculated between the velocity vector ( $\mathbf{V}$ ) and the floor plane, and similarly the body pitch angle ( $\theta_B$ ) was calculated between the body axis and the floor plane. The wing angle of attack ( $\alpha$ ) was measured between the chord vectors and the velocity vector at the primary marker point. The independent pitch angle ( $\theta_W$ ) between the wing chord vector and body vector was additionally calculated by subtracting the pitch angle between the wing chord and horizontal plane and the ( $\theta_B$ ).

To measure the position of the wings and tail relative to the body, the feather markers were described using spherical coordinates with respect to the CBP. The elevation and azimuth angles were measured to give an estimate for the marker sweep ( $\psi$ ) and marker dihedral ( $\phi$ ) angles respectively for each feather marker. The feather markers were also rotated using  $\theta_B$  and the body yaw angle ( $\psi_B$ ) to the body frame of reference in order to visualise the change in wing position relative to the body throughout the flight. Span distances were measured between wingtip markers ( $b_W$ ) and tailtip markers ( $b_T$ ).

### 3.3.8 Shape Change Number

For an airfoil pitching from  $0^\circ$  to  $90^\circ$  while decelerating to a complete stop, the frontal area starts increases until at  $90^\circ$  the frontal area is equal to the chord length. To parametrise the rate of rotation, rotational acceleration, and translational acceleration, Polet and Rival (2015) used a value known as the shape change number ( $\Xi$ ) from the body acceleration ( $\mathbf{a}$ ), the body length scale ( $L$ ), and the velocity of area change ( $\mathbf{U}$ ) :

$$\Xi = \frac{\mathbf{U}^2}{\mathbf{a}L} \quad (3.8)$$

To calculate  $\Xi$  the body length vector from each hawk was projected onto the normal of its velocity vector, and differentiated over time. This was repeated for the left and right wing chord vector and the tail axis vector, using a velocity vector measured at the primary marker and central point between the two tail tips respectively.

### 3.3.9 Binning Data

In order to show the described variables from every flight it was necessary combine the flights performed by all the birds from all sessions. However in order to prevent the each flight from obscuring the next, a binned 2D histogram method was used. The bins were defined in one dimension using the horizontal distance to the perch and each

measured 0.2m. The second dimension of the bins were defined using 250 evenly-spaced bins, for example, from the kinetic energy measurements. Each 2D bin was then coloured by density of markers in order to summarise the full range of flights by all birds across all sessions. Each 2D histogram represented data from one perch distance. As no time of contact could be accurately measured from the reference videos, an estimated horizontal distance to perch was used.

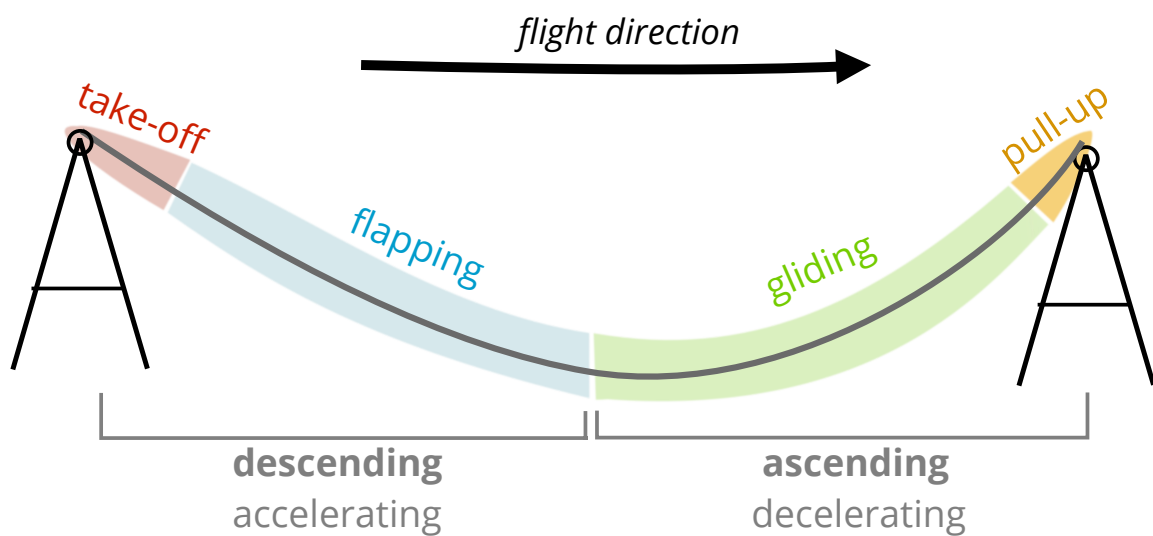
### 3.3.10 Comparing Individuals

To measure the differences between the individual hawks, the vertical height of the CBP was binned by horizontal distance from the perch (bin size = 0.2m) for each individual for each flight distance. A bootstrap method was used to calculate the 95% confidence intervals of the median value from each bin using 1000 iterations. This method was repeated for  $\dot{E}_T/E_T$ , and the vertical distance of the wingtips from the CBP. The weight, distance between the CBP and CTP, maximum wingspan, maximum tailspan were also measured from each hawk for every session for comparison purposes.

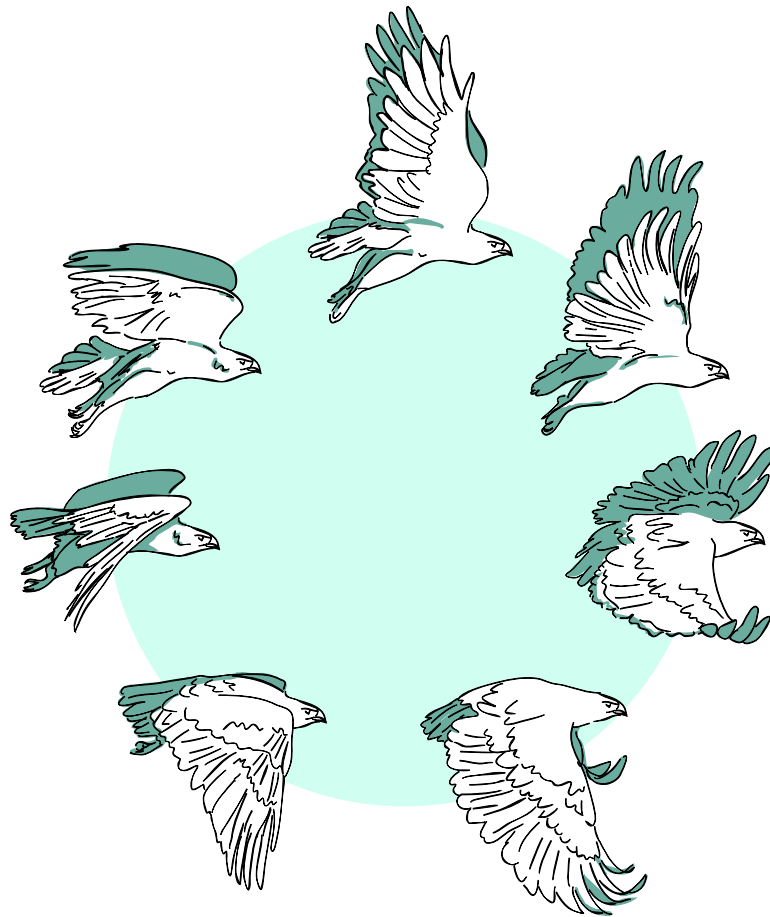
## 3.4 Results

### 3.4.1 Trajectories and Flight Phases

There are four phases during the flight based on wing kinematics: take-off, descending phase, ascending phase, and pull-up to the perch. In the take-off phase the wings and tail moves from folded resting position into flight while the hawk jumps from the perch. The hawks used flapping flight during the descending phase, and gained speed while losing height. The hawks used flapping flight during the descending phase, and gained speed while losing height.



**Figure 3.6:** Schematic of phases during Harris hawk flights between two perches (not to scale). After the take-off phase, flapping flight begins as the hawks lost height. At the trajectory minimum, gliding begins while climbing. At the point of contact around 0.3m from the perch, the hawk pulled itself up onto the perch.



**Figure 3.7:** *Cartoon of wing kinematics during flapping cycle drawn from reference video frames, with wingbeat progressing in a clockwise direction. Marker occlusion is minimal during the downstroke (right side) but during the upstroke (left side) the feathers fold over themselves and cover the feather markers on the wings.*

In the 12m perch distance flights, this descending phase lasts for around 4-5m (see Figure 3.34 on page 103). At the end of the descending phase, flapping ceased and a transition to gliding flight began. The exception was the 5m flights where flapping motion continued after the trajectory nadir. Marker reconstruction was affected during part of the upstroke during flapping as the wingtip markers were folded beneath other feathers and therefore occluded. (Figure 3.7). In addition the backpack markers and tailpack mount markers were affected by oscillations which led to measurement noise.

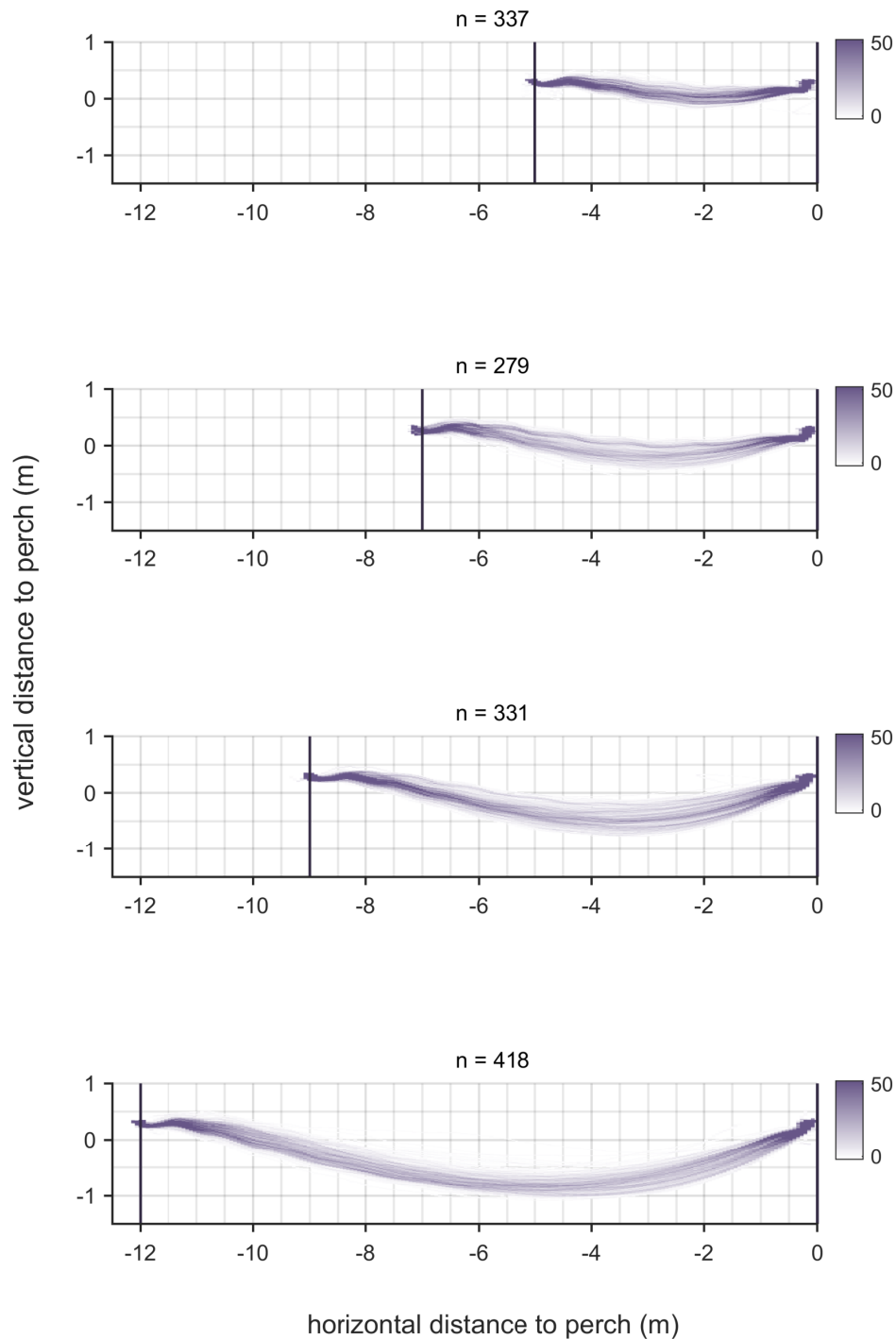
The ascending phase begins at the vertical minimum, and in all but the 5m flights the hawks kept their wings outstretched while gaining height. During their ascent the hawks rotate to an upright posture, which is known as the rapid pitch-up manoeuvre (Carruthers et al., 2007). Within the final 1m of the perch the hawk uses a "parachute" configuration where tail and wings are at maximum span and at  $>90^\circ$  to the horizontal plane. At the same time the

legs are swung forwards (Figure 3.8). Finally the pull-up phase begins at the point of contact with the feet around 0.3m in front of the perch. The hawks grasped the perch and pulled themselves up to a standing posture.

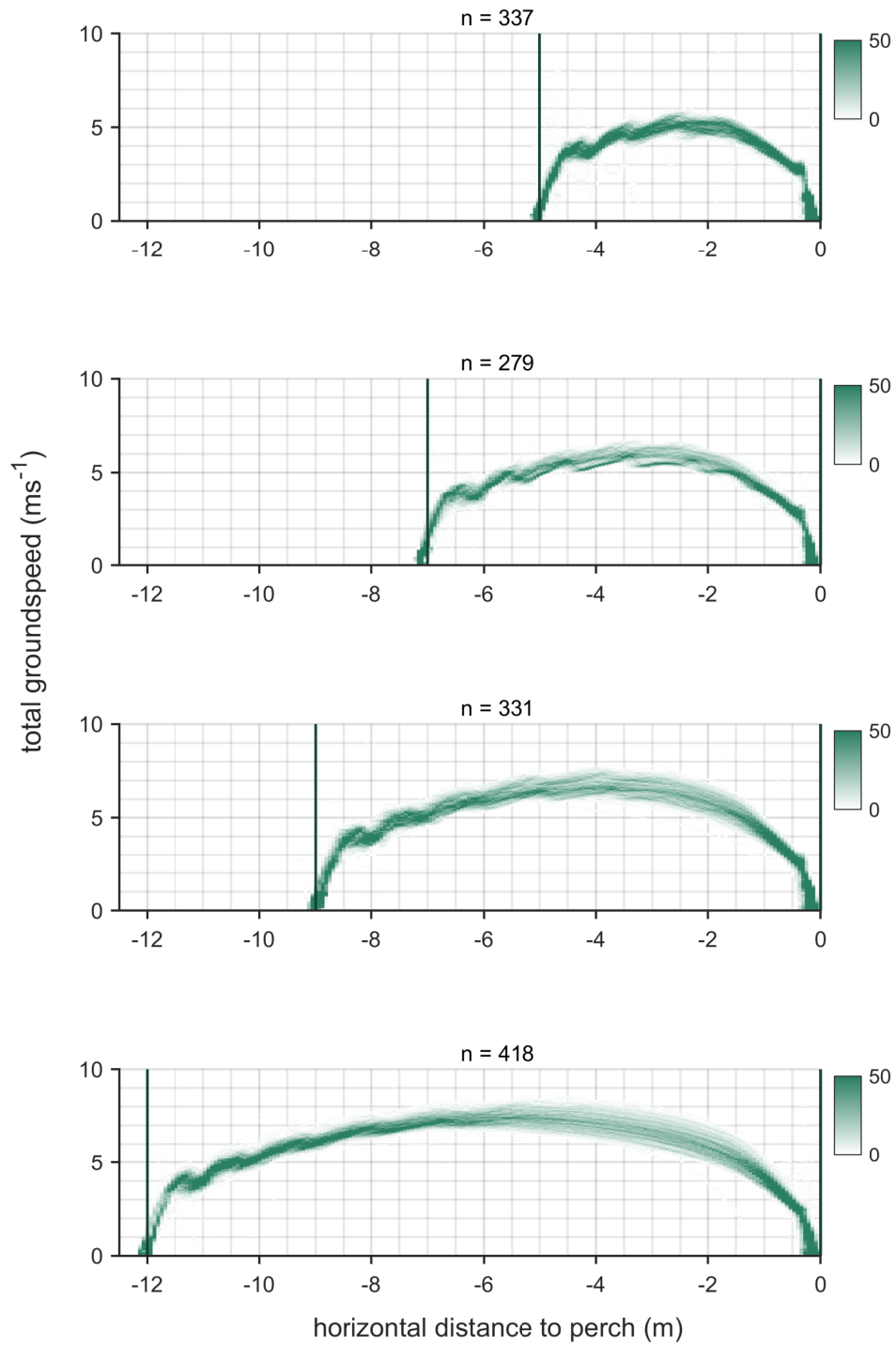


**Figure 3.8:** *Sketch of wing kinematics during rapid pitch-up and "parachute" configuration drawn from reference video frames. As the hawk pitches to an upright position the wings and tail are at held at maximum span. The legs are swung forwards to grasp the perch.*

A smoothed trajectory for each flight was reconstructed from the central point of markers on a backpack mount. Each flight from every bird was pooled by perch distance, binned and shown as a 2D histogram for clarity (Figure 3.9). In the longest flights, the U-shape of the trajectory is clear, where the hawks flew almost touching the floor surface before ascending to the perch. The height of the trajectory was affected by flight distance, with almost level trajectories in the 5m flights. Some oscillations are visible during the descending phase likely due to the backpack mount bouncing with the wingbeat cycle. The gliding distance reduced with perch distance and in the 5m flights the hawks used flapping for almost the entire flight (see Figure 3.34 on page 103, and 3.35 on page 104).



**Figure 3.9:** 2D histograms for 1365 flight trajectories between two perches by four Harris hawks recorded with motion capture. Each bin is coloured by marker density from 0 to 50. Perch-to-perch distances were 5, 7, 9, 12m respectively and perch positions shown with black bars. Perch height was 1.25m. Trajectories recorded from the central point on a mounted backpack.



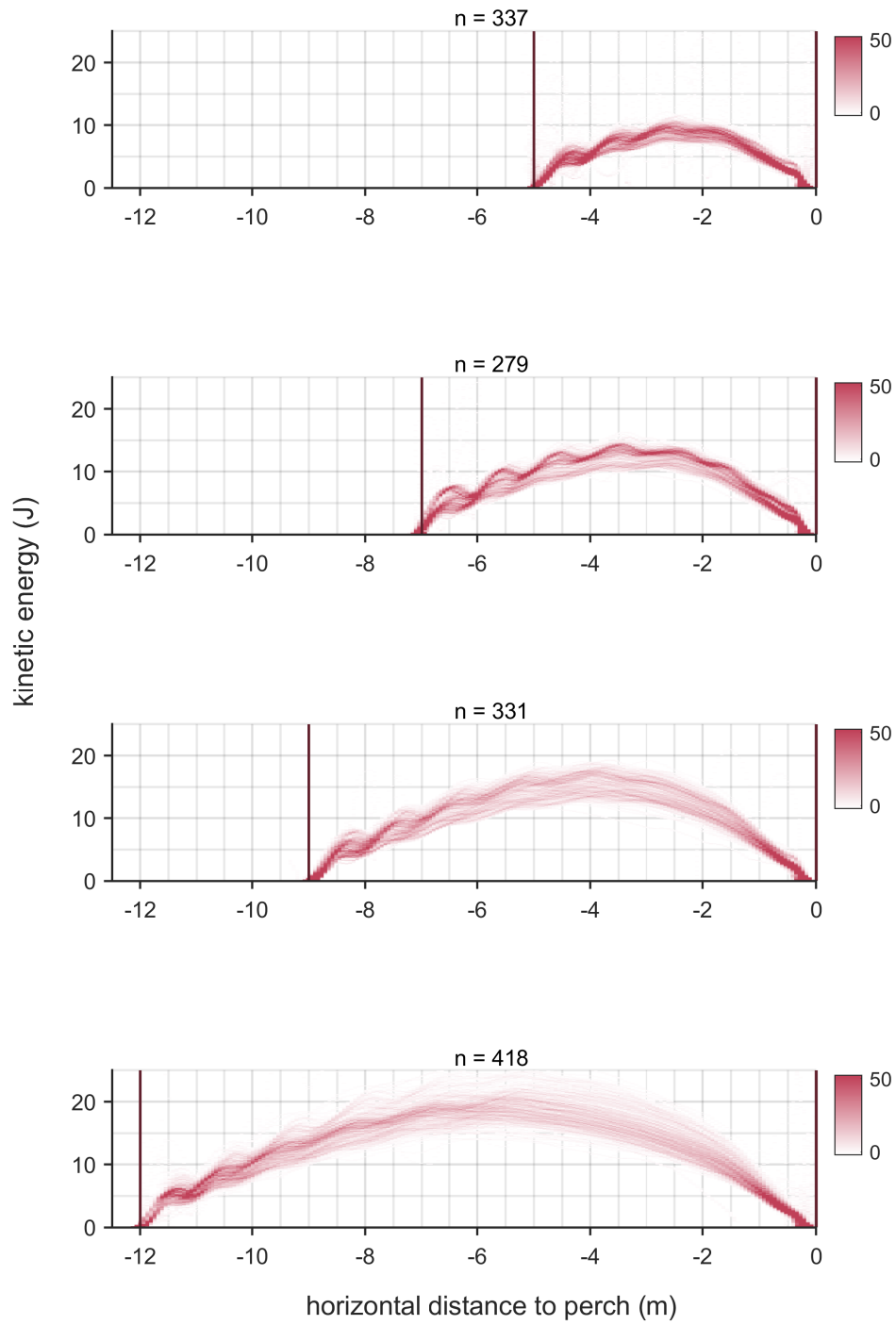
**Figure 3.10:** 2D histograms for total groundspeed during flight between two perches by four Harris hawks recorded with motion capture. Each bin is coloured by marker density from 0 to 50. Perch-to-perch distances were 5, 7, 9, 12m respectively and perch positions shown with black bars. Perch height was 1.25m. Trajectories recorded from the central point on a mounted backpack.



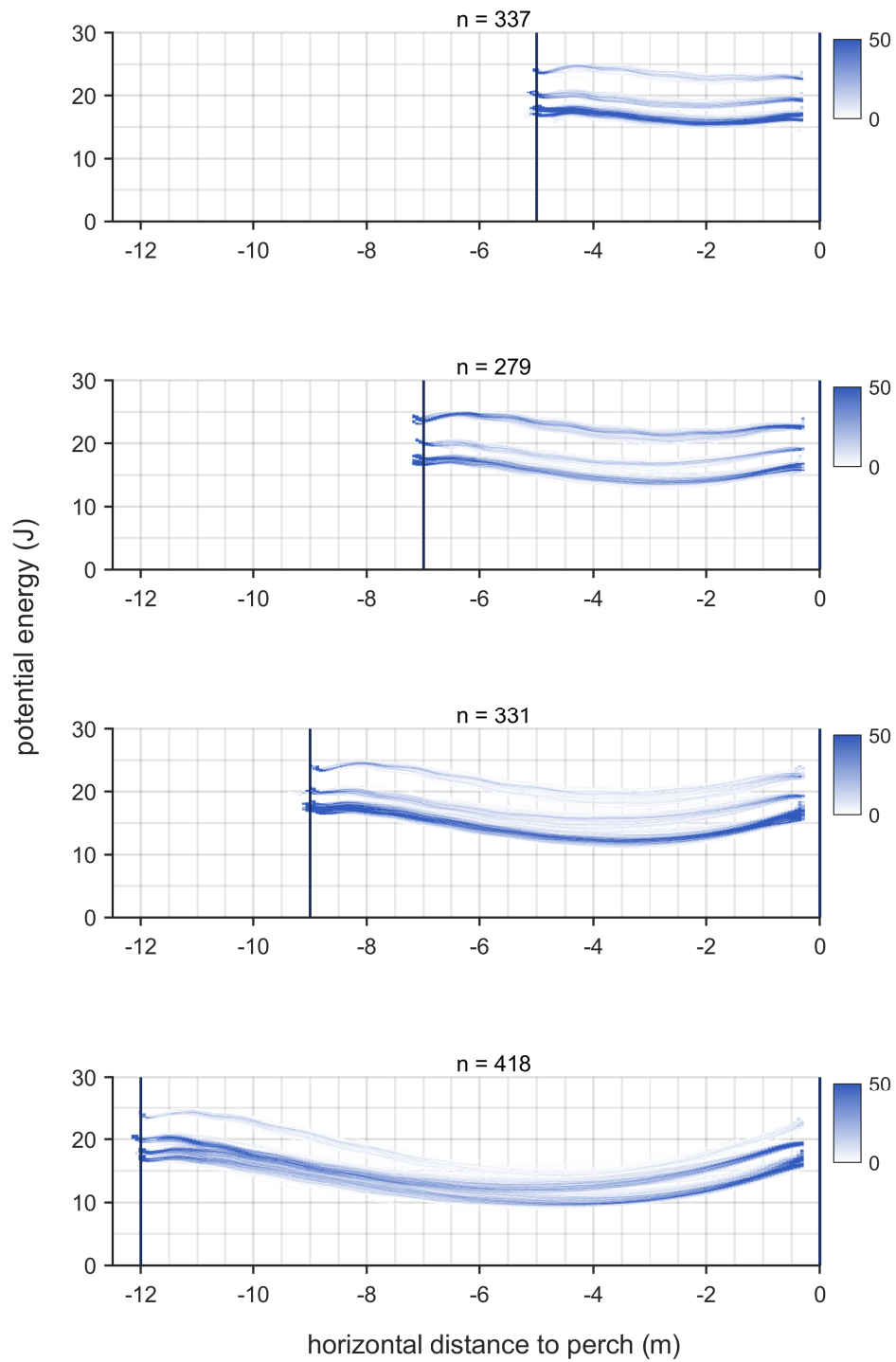
### 3.4.2 Energetics

The hawks first gain kinetic energy ( $E_K$ ) by using a jump to take-off, and regardless of flight distance gain around 5J (Figure 3.11). From the take-off jump alone the hawks reach a velocity of around  $4\text{ms}^{-1}$  prior to the first wing flap cycle.  $E_K$  continues to rise as the hawks use flapping flight while descending. Maximum  $E_K$  is highest for the 12m flights where the maximum velocity reached was  $8\text{ms}^{-1}$ , contrasted with less than  $6\text{ms}^{-1}$  for the 5m flights. The hawks lose  $E_K$  during the ascending phase in the second half of the flight and during the final pull-up phase. Most  $E_K$  loss occurs during the ascending phase. As the hawks gain height during the second half of the flights,  $E_K$  is exchanged for  $E_P$  (Figure 3.12). For the 5m flights, height gain is less than 0.5m but for the 12m flights over 1m is gained. The rest of the  $E_K$  is lost to the wake through aerodynamic braking prior to contact. The hawks did not reach  $E_K = 0\text{J}$  at the point of contact (0.3m from the perch) and remaining  $E_K$  is absorbed by the legs on impact. Potential energy varied between individuals due to mass, where the female has the highest  $E_P$  and the three males coincided closely. Some variation in  $E_P$  shape is also influenced by variation in trajectory shape (see later results). As a result,  $E_T$  is also influenced by both variation in flight speed and mass. The female hawk has far higher  $E_T$  than the males.

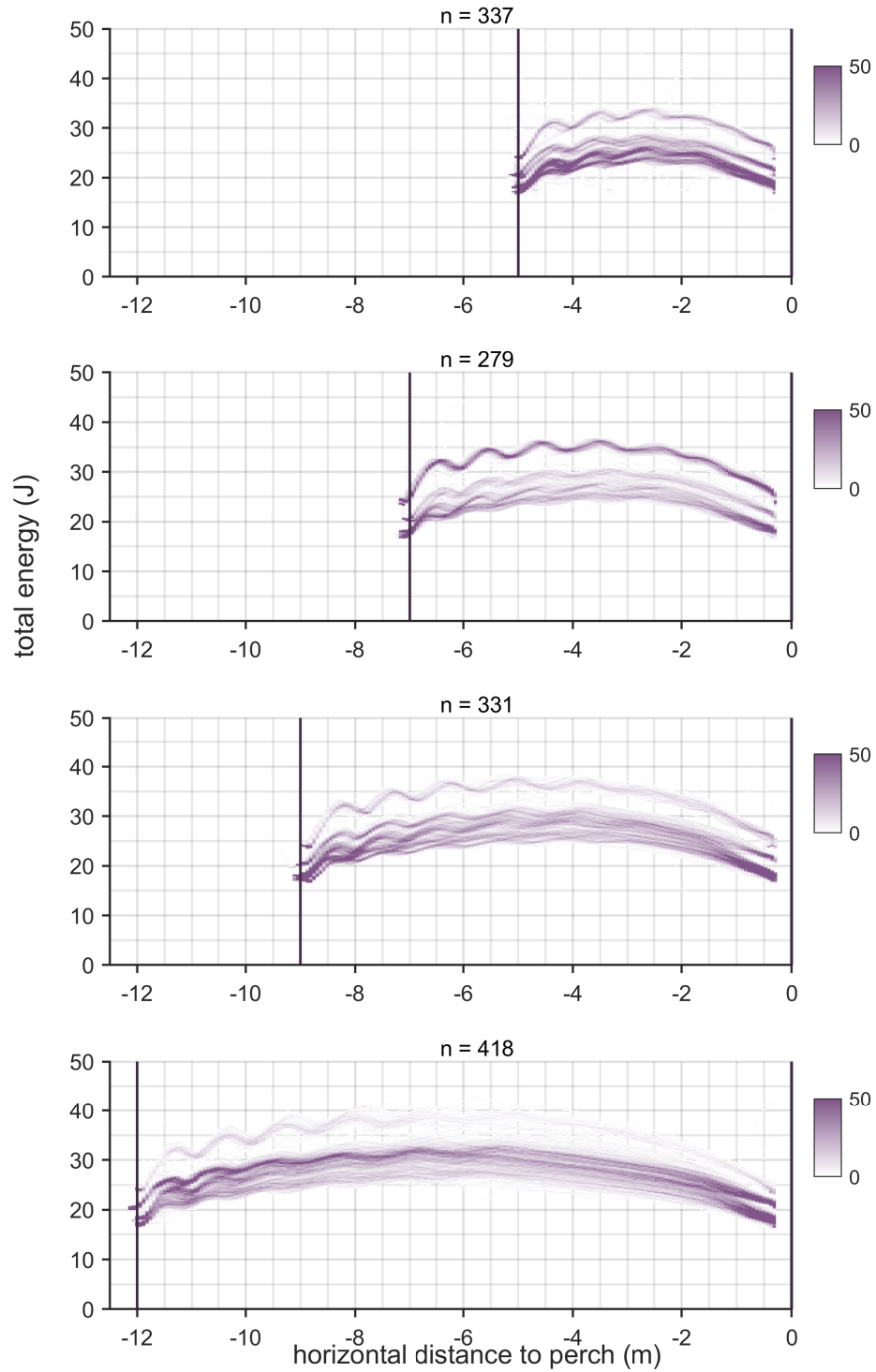
In order to compare the change in total energy by the hawks when the maximum energy varies between flight distances and mass varies between individuals, the total energy change value was normalised by total energy ( $\dot{E}_T/E_T$ ). During the descending phase the first few wing cycles lead to a net increase in  $E_T$ , while later flap cycles and the ascending phases provide a net decrease. The highest energy reduction in the approaching flight occurs around 1m away from the perch during the ascending phase.



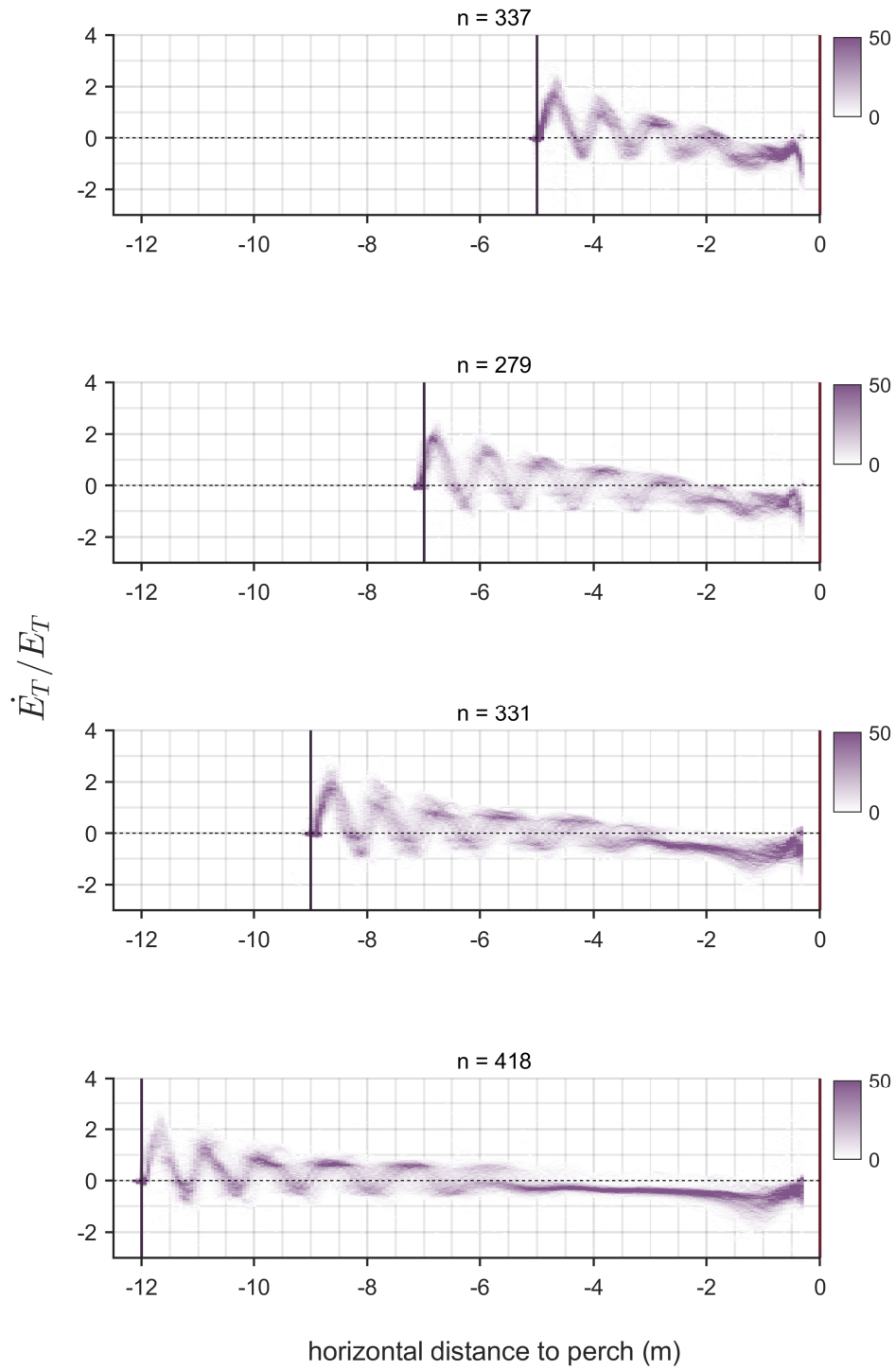
**Figure 3.11:** 2D histograms of the kinetic energy during 1365 flights by four Harris hawks between two perches. Kinetic energy calculated using the CBP tracked with motion capture and smoothed with a cubic spline. Flights separated by perch-perch distance, and locations of perches shown as black bars.



**Figure 3.12:** 2D histograms of the potential energy during 1365 flights by four Harris hawks between two perches. Potential energy calculated using the CBP tracked with motion capture and smoothed with a cubic spline. Flights separated by perch-perch distance, and locations of perches shown as black bars.



**Figure 3.13:** 2D histograms of the total energy during 1365 flights by four Harris hawks between two perches. Total energy calculated using the CBP tracked with motion capture and smoothed with a cubic spline. Flights separated by perch-perch distance, and locations of perches shown as black bars.



**Figure 3.14:** 2D histograms of the change in total energy change weighted by total energy ( $\dot{E}_T / E_T$ ). Total energy change was weighted by total energy to normalise the flights with different maximum total energy. Flights separated by perch-to-perch distance, and locations of perches shown as black bars.

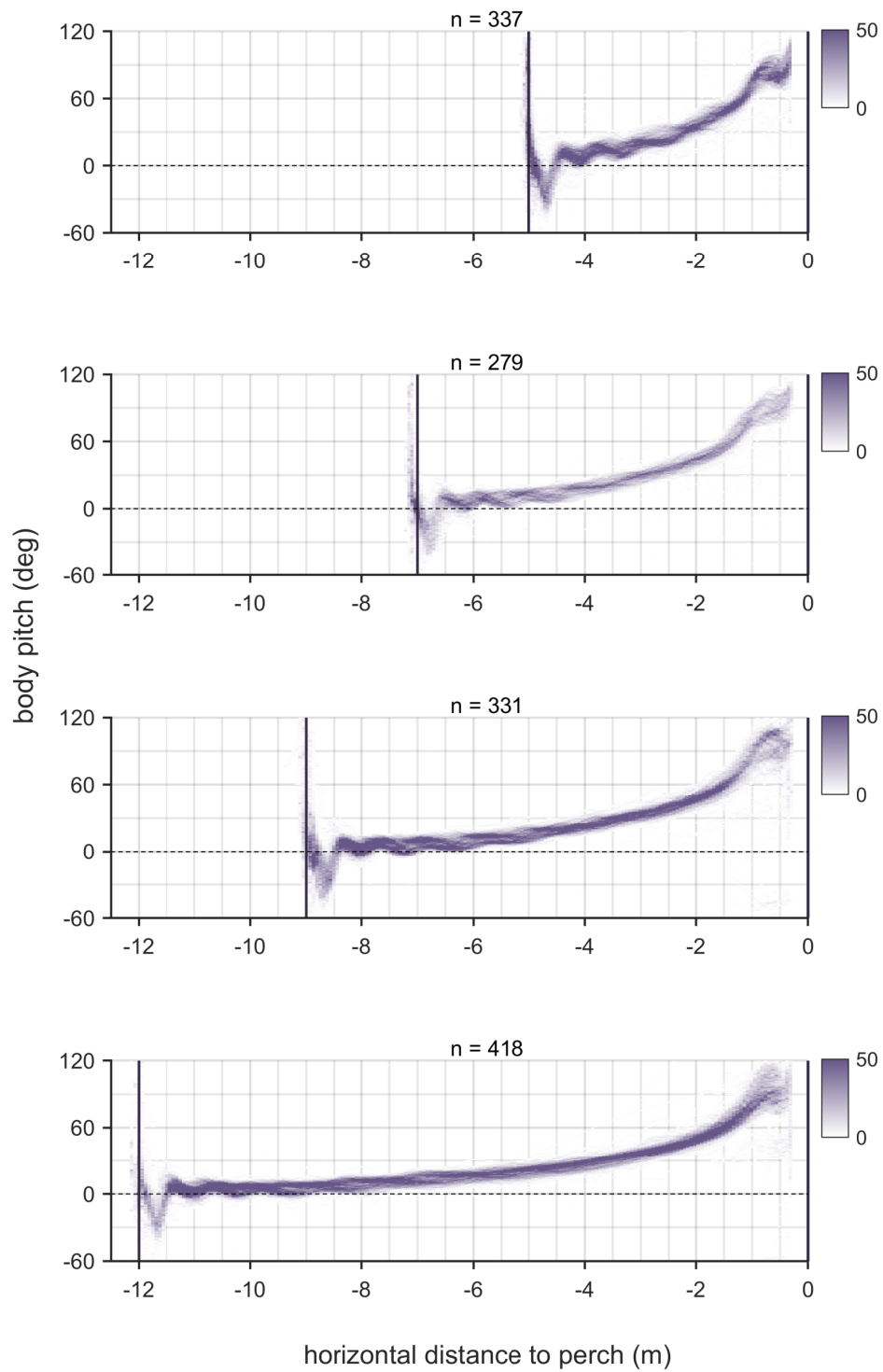
### 3.4.3 Climbing Angle and Body Pitch

In the ascending phase the hawks perform a rapid pitch-up manoeuvre where body posture is initially vertical and increases to upright immediately prior to contact with the perch. The body pitch angle ( $\theta_B$ ) of the hawks was therefore defined as the angle between the body vector and the floor plane (Figure 3.15).

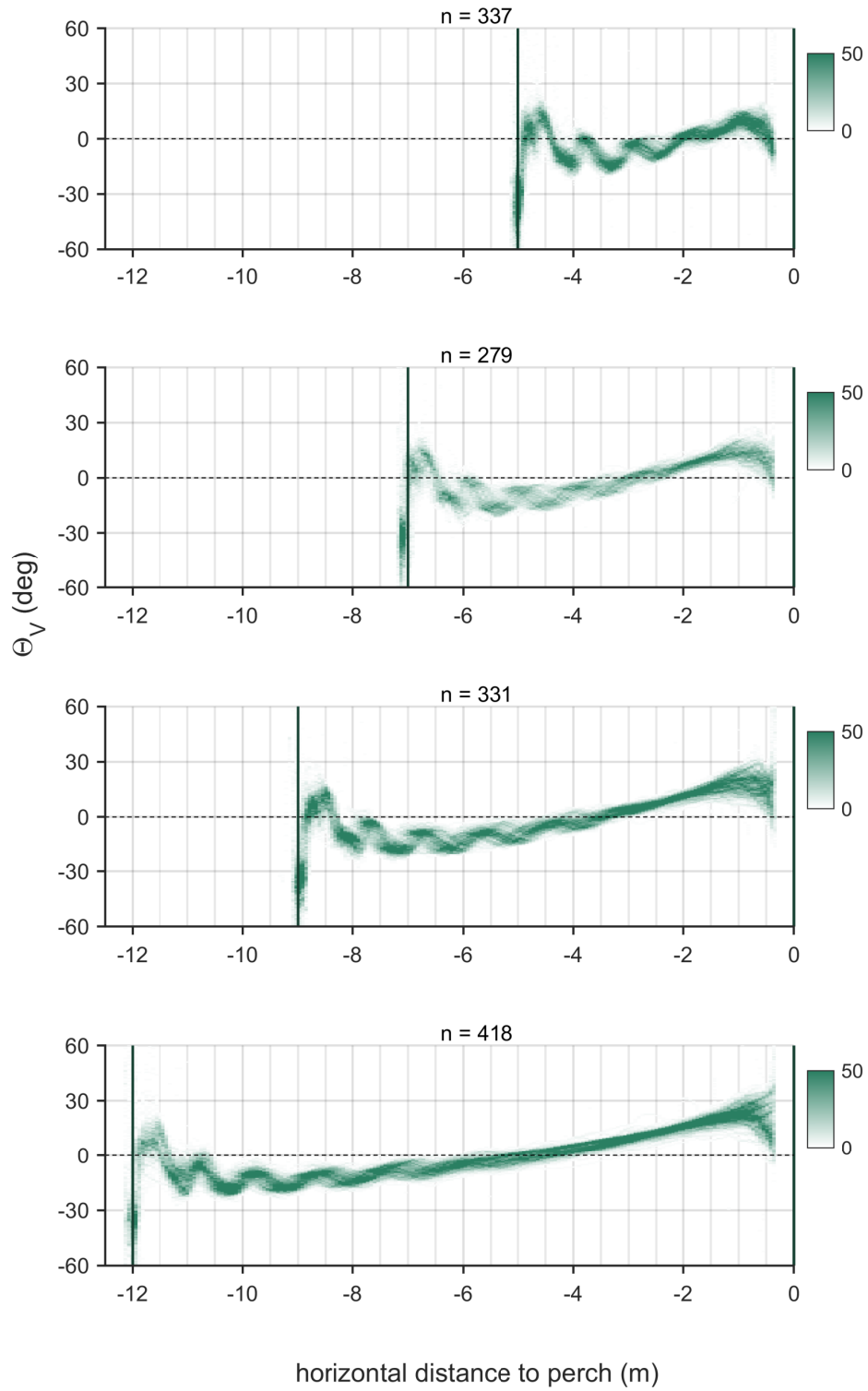
$\theta_B$  during the take-off jump was negative and nose-down, reaching a minimum of  $-30^\circ$ . A sharp increase in  $\theta_B$  occurs with the first flap. For the descending phase,  $\theta_B$  fluctuates with the wingbeats. Regardless of perch distance, the hawks reach a similar maximum  $\theta_B$  at the point of contact 0.3m from the perch. However, the shape of  $\theta_B$  change differs depending on perch distance. In the 12m flights  $\theta_B$  remains around  $10^\circ$  for 4m, while in the shortest flights  $\theta_B$  increases throughout. Increases in  $\theta_B$  begin during the later part of the descending phase to around  $30^\circ$ . The hawks continue to pitch their body nose-up during the ascending phase, and in the final metre before contact, the maximum  $\theta_B$  was often close to  $110^\circ$ . In the 5m flights the increase in  $\theta_B$  is closer to linear for the entire flight and therefore shows a more rapid change than the longer flights. A negative change in  $\theta_B$  was measured for many of the flights in the final 1m of the perch, most noticeably in the 5m flights. This event corresponds to a brief nose-down rotation before  $\theta_B$  increased to the final maximum at the point of contact. This event may correspond with a motion of the legs and/or tail affecting the measurements, or a correction to the whole body rotation.

The climbing angle ( $\theta_V$ ) was measured between the velocity vector and the floor plane (Figure 3.16), where the velocity vector was measured at the central point on the backpack. During the jump for take-off,  $\theta_V$  sharply increased to around  $15^\circ$  and quickly dropped to negative after the first flap. Minimum  $\theta_V$  is around  $-25^\circ$  just 2m from the starting perch in all the flights regardless of distance. For the rest of the descending phase,  $\theta_V$  remains negative but steadily increases. At  $\theta_V=0$  the ascending phase began by definition. For the longer flights with an extended ascending phase,  $\theta_V$  steadily increases to a maximum  $30^\circ$  around 1m from the perch before dropping once more right before contact. In the 7m flights maximum  $\theta_V$  is closer to  $15^\circ$  and occurs somewhat further back from the perch. In the 5m flights  $\theta_V$  is barely positive during the flight and only reaches a maximum of  $12^\circ$  before dropping back to negative before contact.

During perching flights the U-shape trajectory where the bird approaches the perch from below aids the loss of flight speed before making contact with the perch. The exchange of potential energy with kinetic energy leads to deceleration. With a short flight of just 5m the hawks were unable to reduce their trajectory height and therefore could not use the deceleration from high  $\theta_V$  while gliding.



**Figure 3.15:** 2D histograms of body pitch for all hawks across all flights. Pitch angle measured between the body vector (backpack central point to tailpack central point) and the floor plane and measured in degrees. Perch positions shown as black bars.

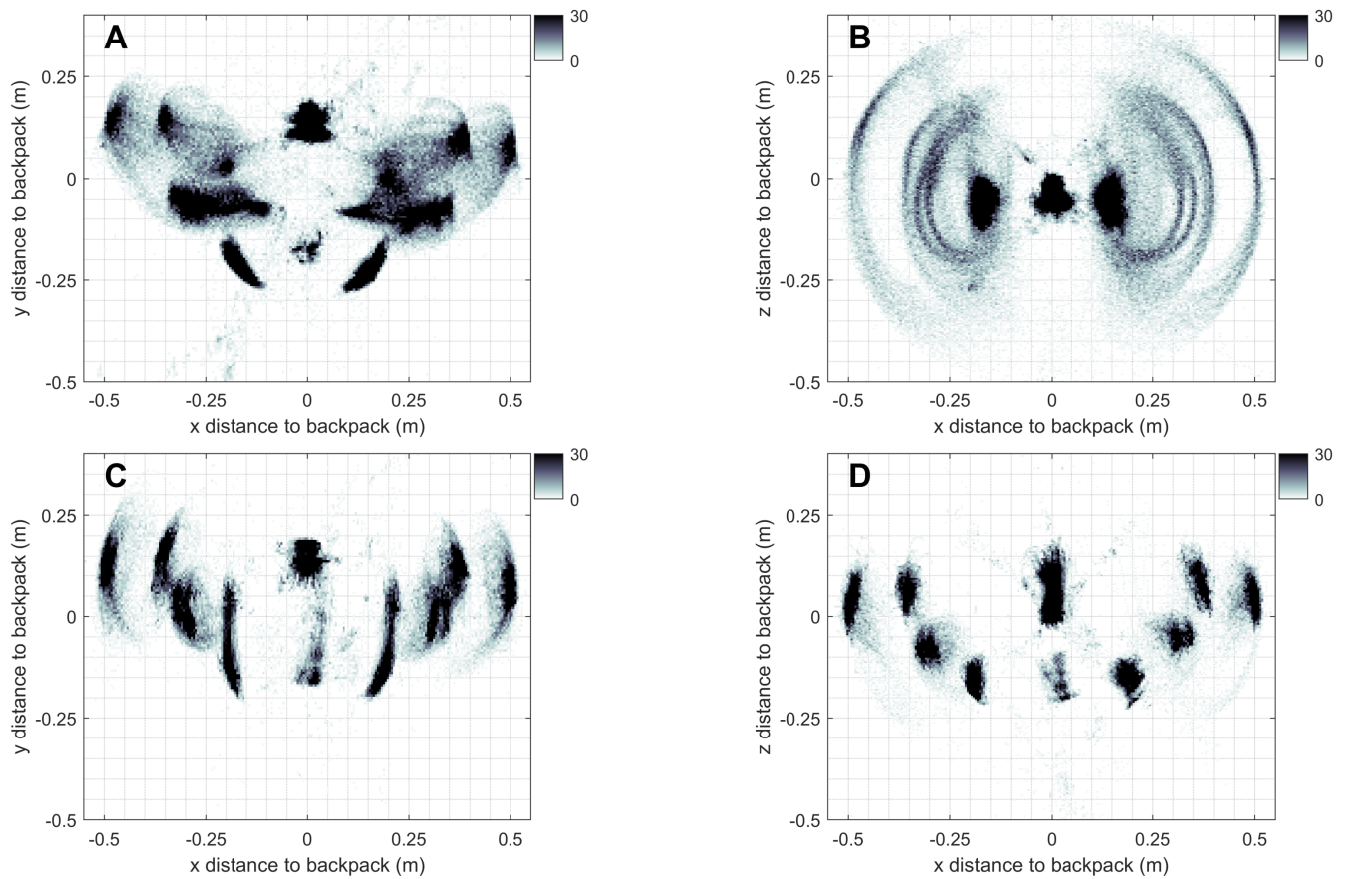


**Figure 3.16:** 2D histograms of angle of climb for all hawks across all flights. Climb angle measured between the velocity vector measured from the backpack central point and the floor plane and measured in degrees. Perch positions shown as black bars.

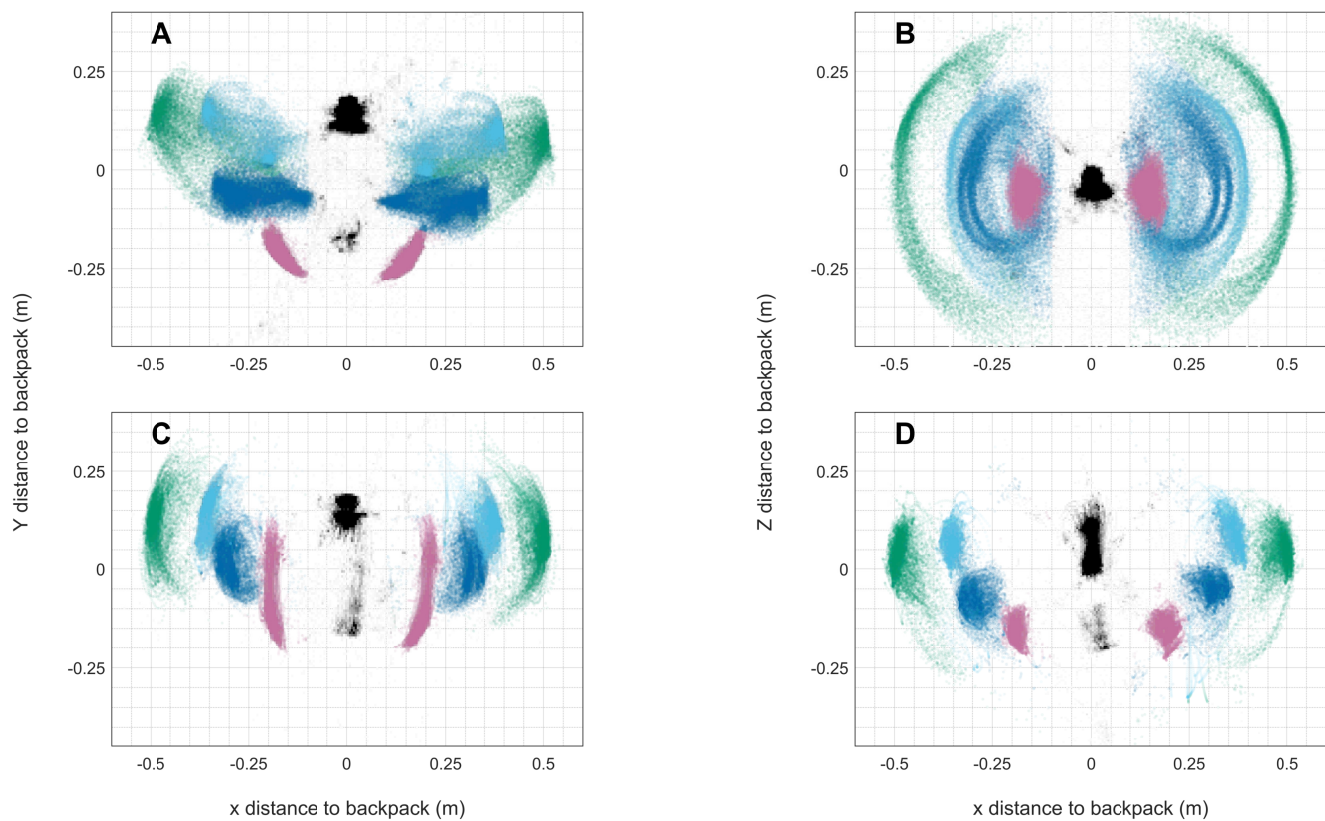


### 3.4.4 Labelling Wing Markers

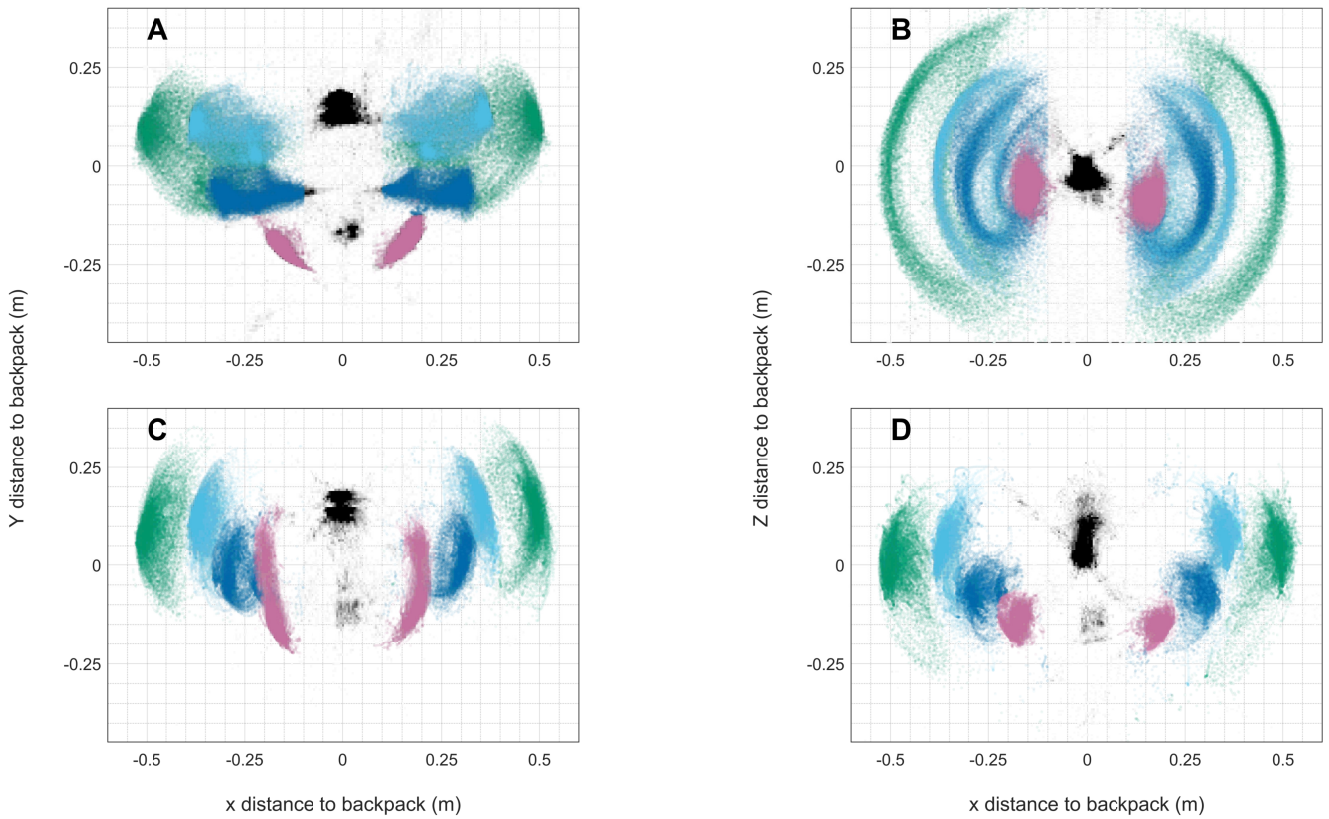
The feather marker positions are clustered relatively closely together (Figure 3.17). The wing markers were identified during the descending and ascending phases in post-processing based on their positions in the XY and XZ planes relative to the backpack, but it was not possible to accurately label during the first 1m (take-off) nor the final 0.3m (final pull-up). Each hawk had different cluster boundary definitions due to variation in morphology (Figures 3.18 to 3.21). Some inaccuracies in marker labelling occur as marker trajectories have crossovers during the flapping cycles. The two larger hawks (Ruby and Toothless) have more crossover between tail tip markers and secondary marker clusters during flapping. In addition, for all the hawks labelling the wingtip markers during the upstroke is limited by a combination of occlusion due to feathers folding and clusters overlapping. The majority of feather markers were accurately labelled.



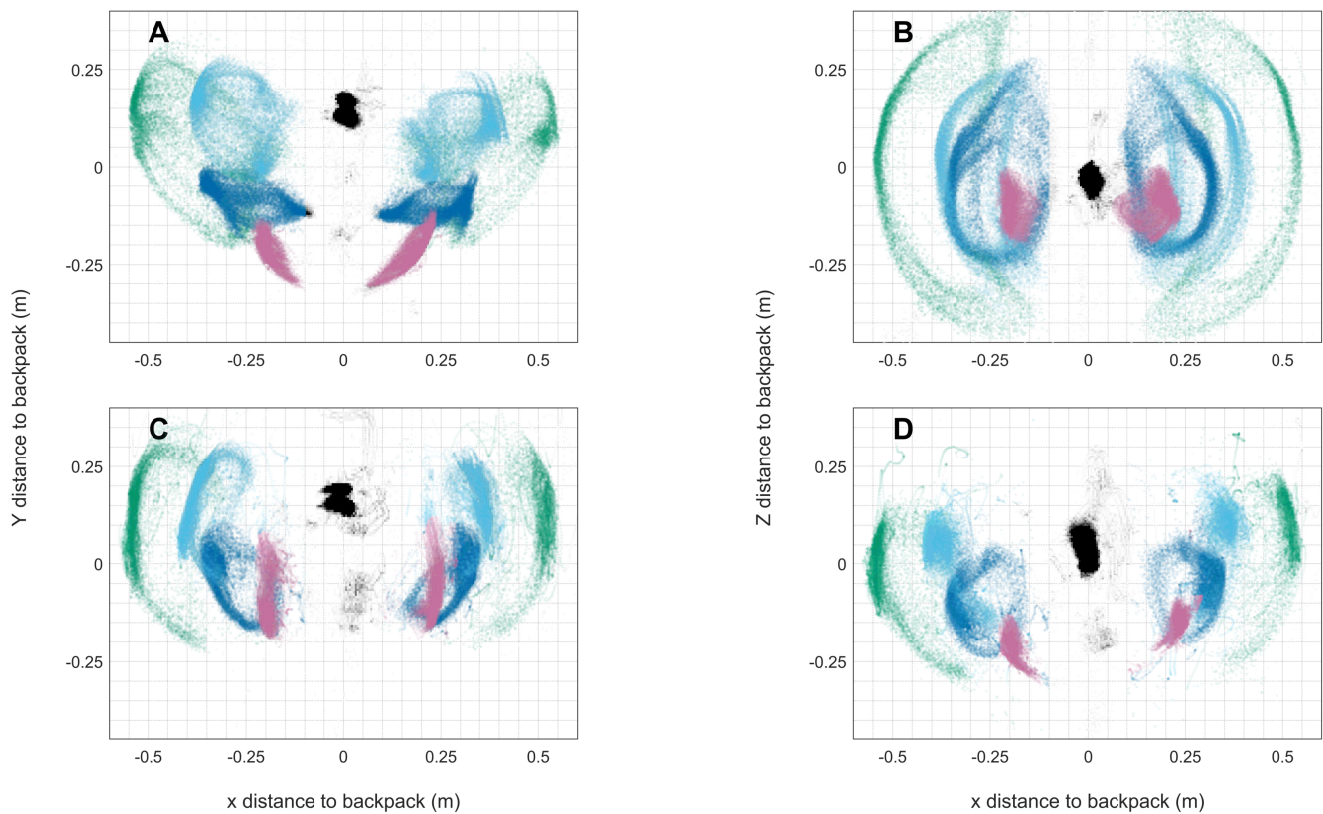
**Figure 3.17:** 2D histograms of the marker positions relative to the central backpack point (CBP). Marker sets shown are for 172 flights by one bird (Drogon) for 7m and 9m flights. Markers sets in the left column are shown from the top view (XY) and the right column shows the front view (XZ). **A** and **B** show the markers from the descending phase, and **C** and **D** are the marker sets from the ascending phase.



**Figure 3.18:** Labeled markers for one hawk (Drogon) from the feathers as captured by motion capture and identified using defined boundaries for 7m and 9m flights. Markers plotted as distances from the CBP. Markers were placed on the longest primary tip (green); the middle of a primary feather (light blue); the tip of a secondary feather (dark blue); and outermost tips of the tail feathers (pink). Remaining markers (black) are from the rigid sets on the hood and tailpack that were not identified during pattern searching method. Left column shows a top-down view (XY) while right column shows a frontal view (XZ). **A** and **B** are markers from the descending phase, and **C** and **D** from the ascending phase. It was not possible to identify markers for the take-off phase and final pull-up phase as the markers are not consistently clustered.

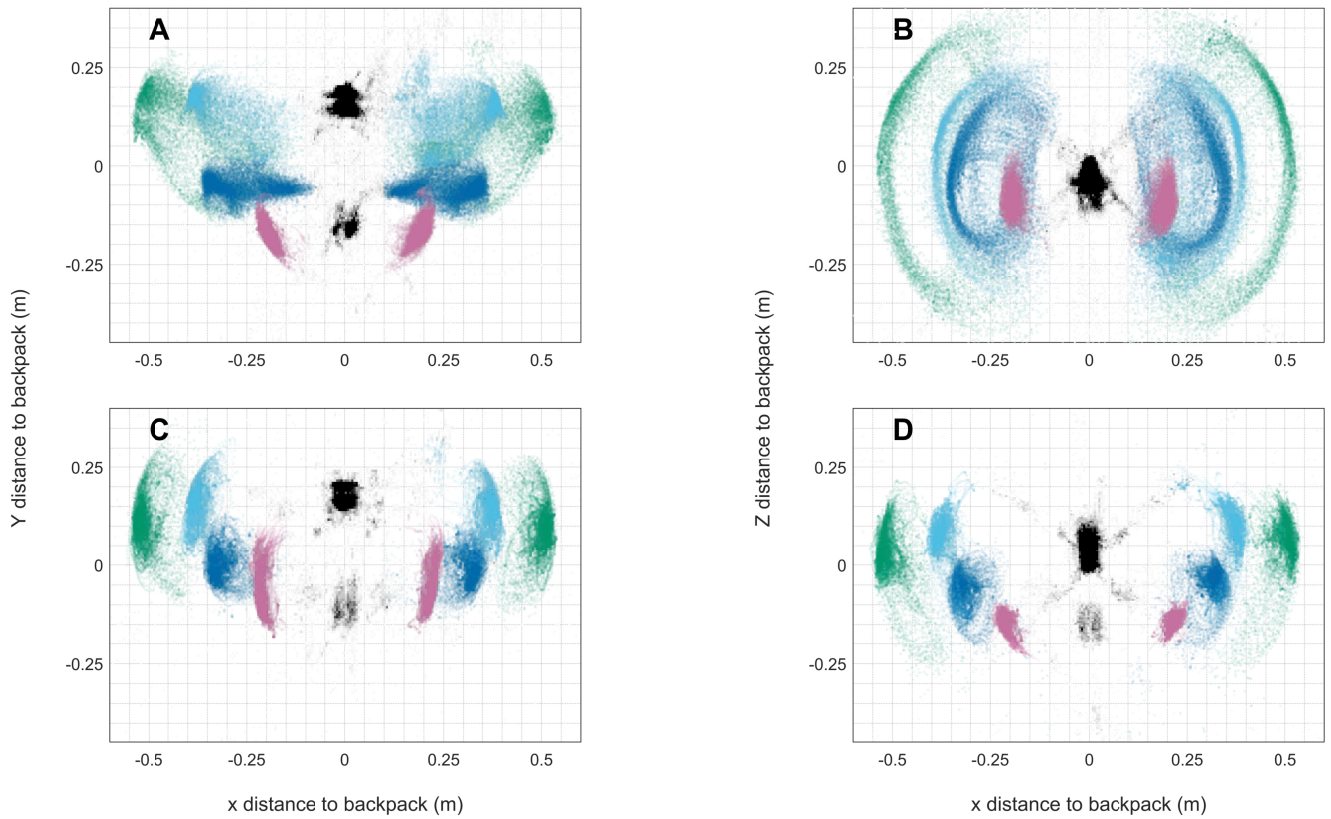


**Figure 3.19:** *Labelled markers for one hawk (Rhaegal) from the feathers as captured by motion capture and identified using defined boundaries for 7m and 9m flights. Markers plotted as distances from the CBP. Markers were placed on the longest primary tip (green); the middle of a primary feather (light blue); the tip of a secondary feather (dark blue); and outermost tips of the tail feathers (pink). Remaining markers (black) are from the rigid sets on the hood and tailpack that were not identified during pattern searching method. Left column shows a top-down view (XY) while right column shows a frontal view (XZ). A and B are markers from the descending phase, and C and D from the ascending phase. It was not possible to identify markers for the take-off phase and final pull-up phase as the markers are not consistently clustered.*



**Figure 3.20:** Labelled markers for one hawk (Ruby) from the feathers as captured by motion capture and identified using defined boundaries for 7m and 9m flights. Markers plotted as distances from the CBP. Markers were placed on the longest primary tip (green); the middle of a primary feather (light blue); the tip of a secondary feather (dark blue); and outermost tips of the tail feathers (pink). Remaining markers (black) are from the rigid sets on the hood and tailpack that were not identified during pattern searching method. Left column shows a top-down view (XY) while right column shows a frontal view (XZ). **A** and **B** are markers from the descending phase, and **C** and **D** from the ascending phase. It was not possible to identify markers for the take-off phase and final pull-up phase as the markers are not consistently clustered.



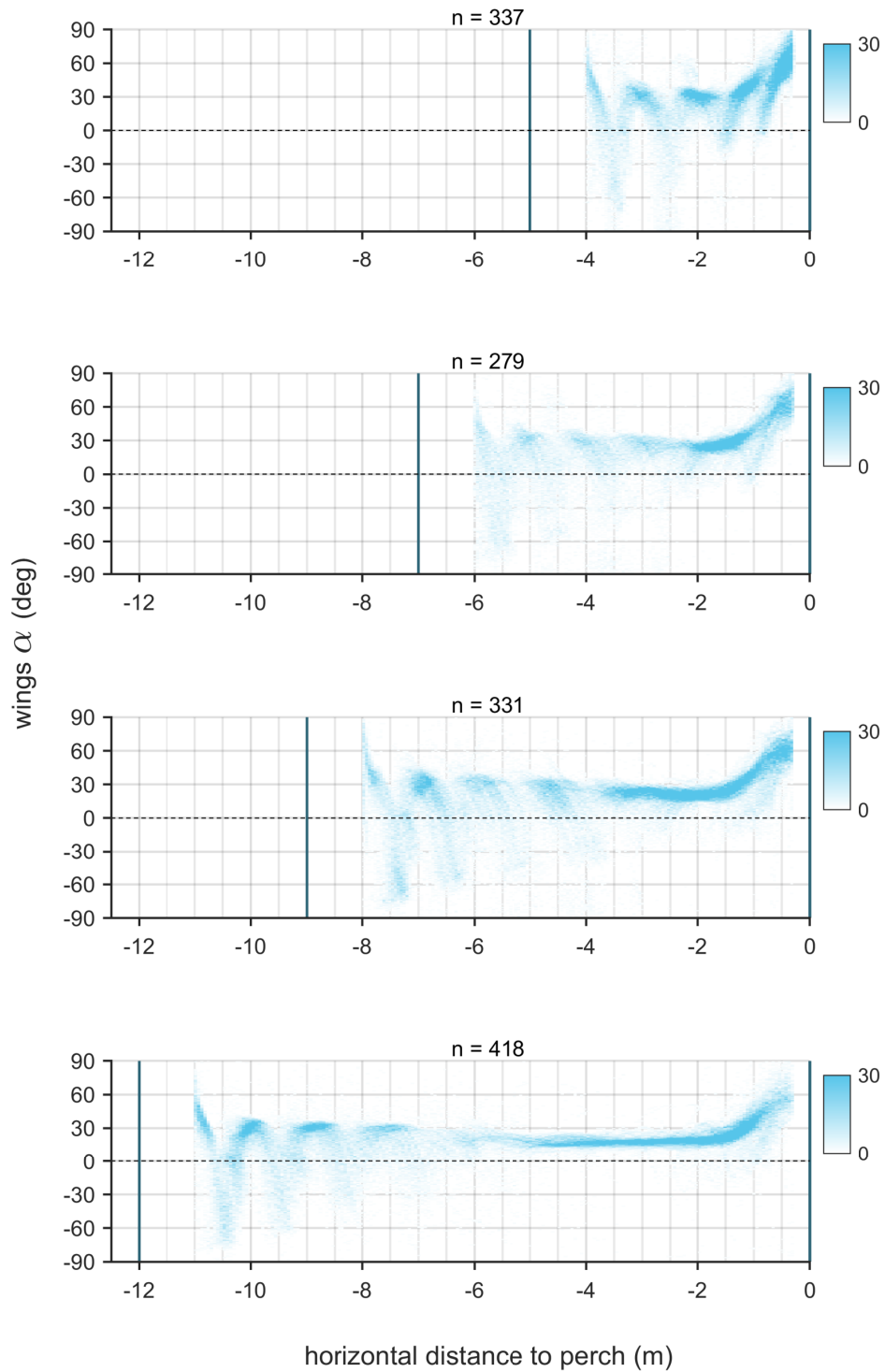


**Figure 3.21:** *Labelled markers for one hawk (Toothless) from the feathers as captured by motion capture and identified using defined boundaries for 7m and 9m flights. Markers plotted as distances from the CBP. Markers were placed on the longest primary tip (green); the middle of a primary feather (light blue); the tip of a secondary feather (dark blue); and outermost tips of the tail feathers (pink). Remaining markers (black) are from the rigid sets on the hood and tailpack that were not identified during pattern searching method. Left column shows a top-down view (XY) while right column shows a frontal view (XZ). A and B are markers from the descending phase, and C and D from the ascending phase. It was not possible to identify markers for the take-off phase and final pull-up phase as the markers are not consistently clustered.*

### 3.4.5 Wing Angle of Attack

The wing angle of attack ( $\alpha$ ) was measured for both wings between the estimated wing chord vector (from the primary marker near the leading edge to the secondary marker on the trailing edge) and the velocity vector as measured at the primary marker (Figure 3.22). During the descending phase, the minimum  $\alpha$  increased with each subsequent flap, starting from around  $-80^\circ$  and increasing to  $-20^\circ$ . However the maximum  $\alpha$  at  $30^\circ$  did not change during the descending phase.

In the ascending phase,  $\alpha$  was held at around  $20^\circ$  until the final 1.5m to the perch where  $\alpha$  sharply increased to a maximum of  $60^\circ$ . This pattern was consistent for the 7m, 9m, and 12m flights.  $\alpha$  does not follow the pattern of whole body rotation (see Figure 3.15) which is enabled by a negative pitch rotation of the wings at the shoulder in order to maintain a constant  $\alpha$ . At around 1.5m from the perch,  $\alpha$  sharply increases to a maximum of  $60^\circ$  as part of the "parachute" event (Carruthers et al., 2007). During this increase there are a few flights where negative corrections were measured.  $\alpha$  is reduced very briefly to  $0^\circ$  and then increased once again. In the 5m flights, the hawks are flapping during the ascending phase but the  $\alpha$  is still increased to  $60^\circ$  in the final 1.5m before contact. Two negative trends are apparent which correspond to flapping, but have a very different pattern to the wingbeats earlier in the flight.



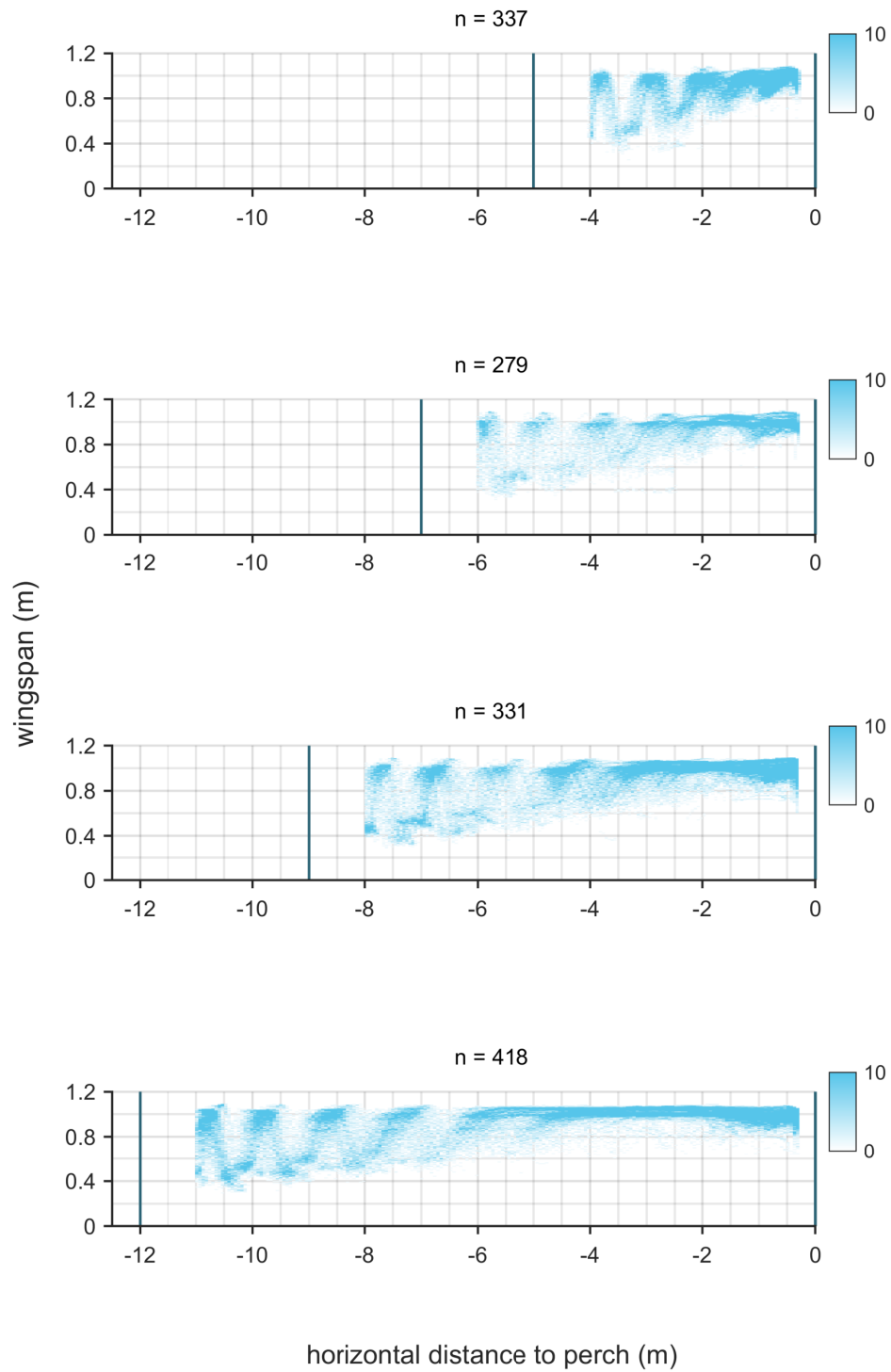
**Figure 3.22:** 2D histograms of  $\alpha$  for all hawks across all flights.  $\alpha$  measured between the wing chord vector (from primary to secondary markers) and the oncoming velocity vector as measured at the primary marker. This was repeated for both wings and all angles shown in degrees. Perch positions shown as black bars. Markers during take-off phase (initial 1m) and pull-up to the perch (final 0.5m) not shown.



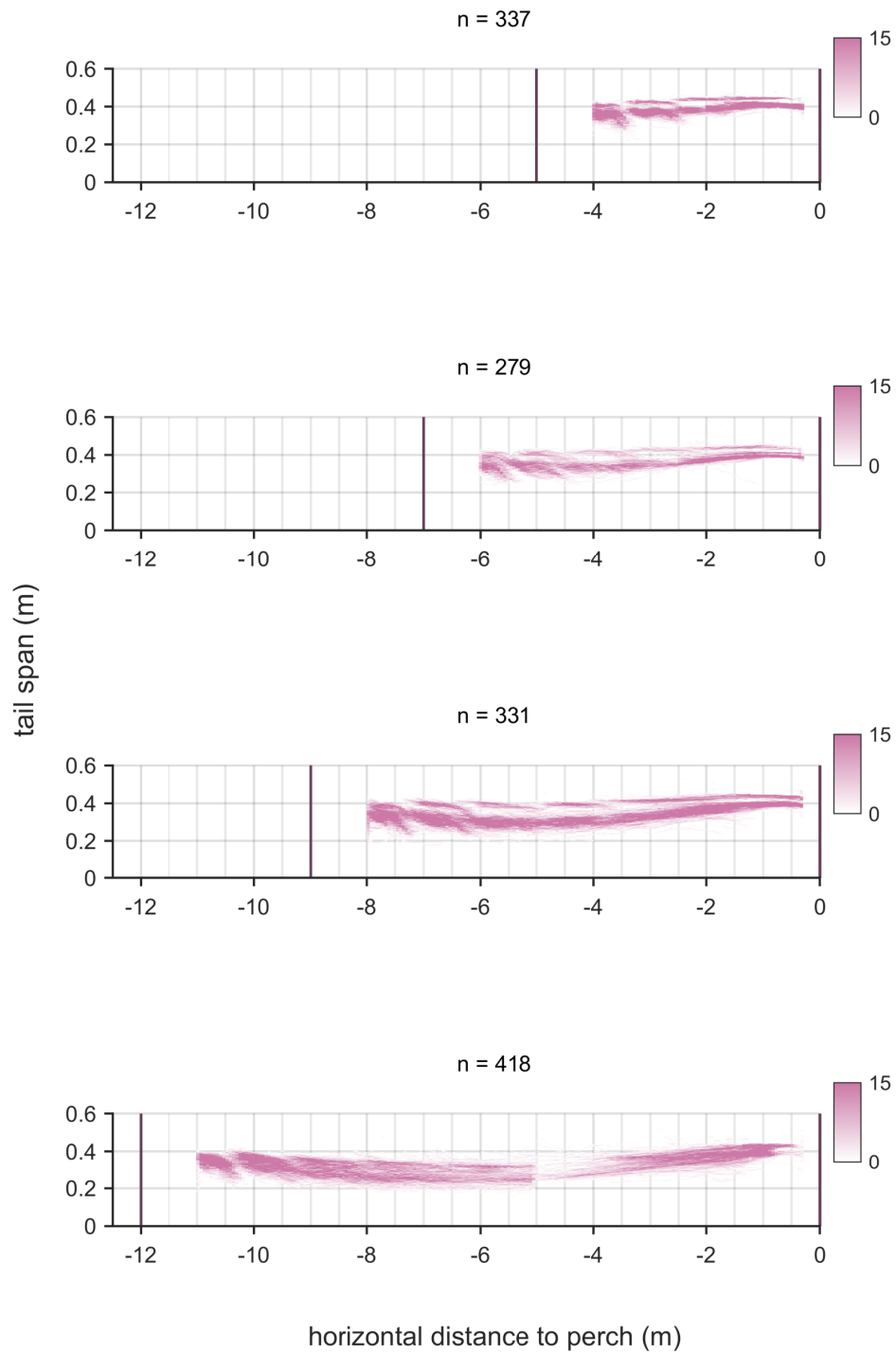
### 3.4.6 Wing and Tail Span

The total distance between the outer wingtips was measured for all the flights (Figure 3.23). The wingspan decreased from around 1m to 0.4m during flapping cycles as the hawks folded their wings. The hawks maintained maximum wingspan for the majority of the ascending phase. A reduction in wingspan was measured around 1m from the perch, but was not consistent across the flights. This may correspond to some folding of the wings, but more likely the wingspan reduced as the wings were swung forwards slightly with respect to the body (see Figure 3.41 on page 114). In the 5m flights, the flapping during the final 2m of the flights are performed with higher wingspan than previous wingbeats. A similar small wingspan reduction is also present during some 7m flights at around 1m from the perch.

The tail span (Figure 3.24) began at less than 0.4m and reduced during the descending phase while the hawks gained flight speed. The minimum tail span occurred around the minimum height of the flight and just before the onset of the ascending phase. The tail span then increased to a maximum just before contact with the perch. For the shorter flights (5m and 7m), the tailspan was higher throughout the flights which is consistent with measurements from other birds which use high tail span during slower flight. The measured tailspans were affected by errors in marker labelling with some outliers present as a result.



**Figure 3.23:** 2D histograms of wingspan during the flights, separated by perch-perch distance. Perch positions shown as black bars. Markers during take-off phase (initial 1m) and pull-up to the perch (final 0.5m) not shown.

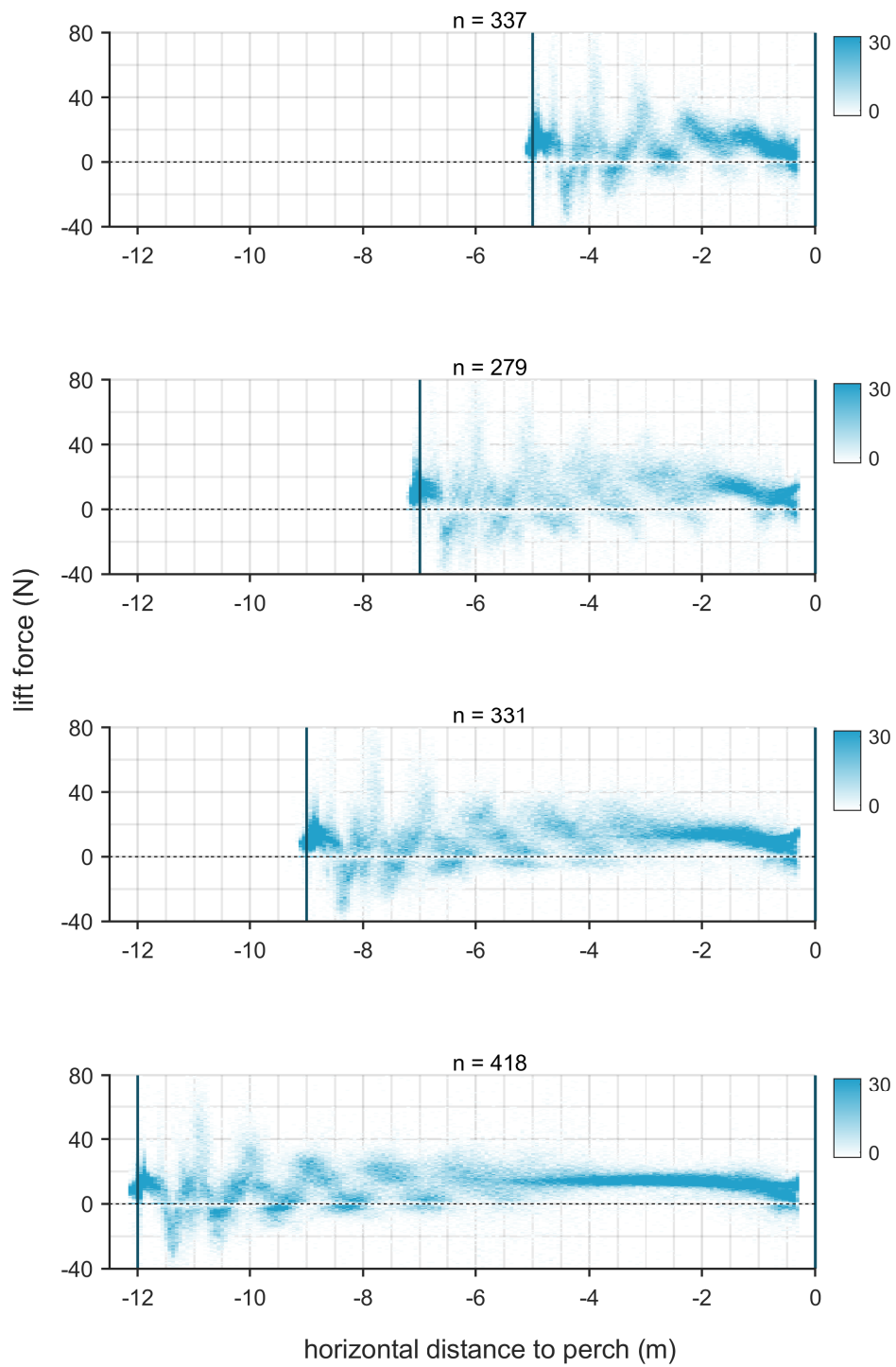


**Figure 3.24:** 2D histograms of tail span during perching flights. Some outliers are present due to errors in labelling. Perch positions shown as black bars. Markers during take-off phase (initial 1m) and pull-up to the perch (final 0.5m) not shown.

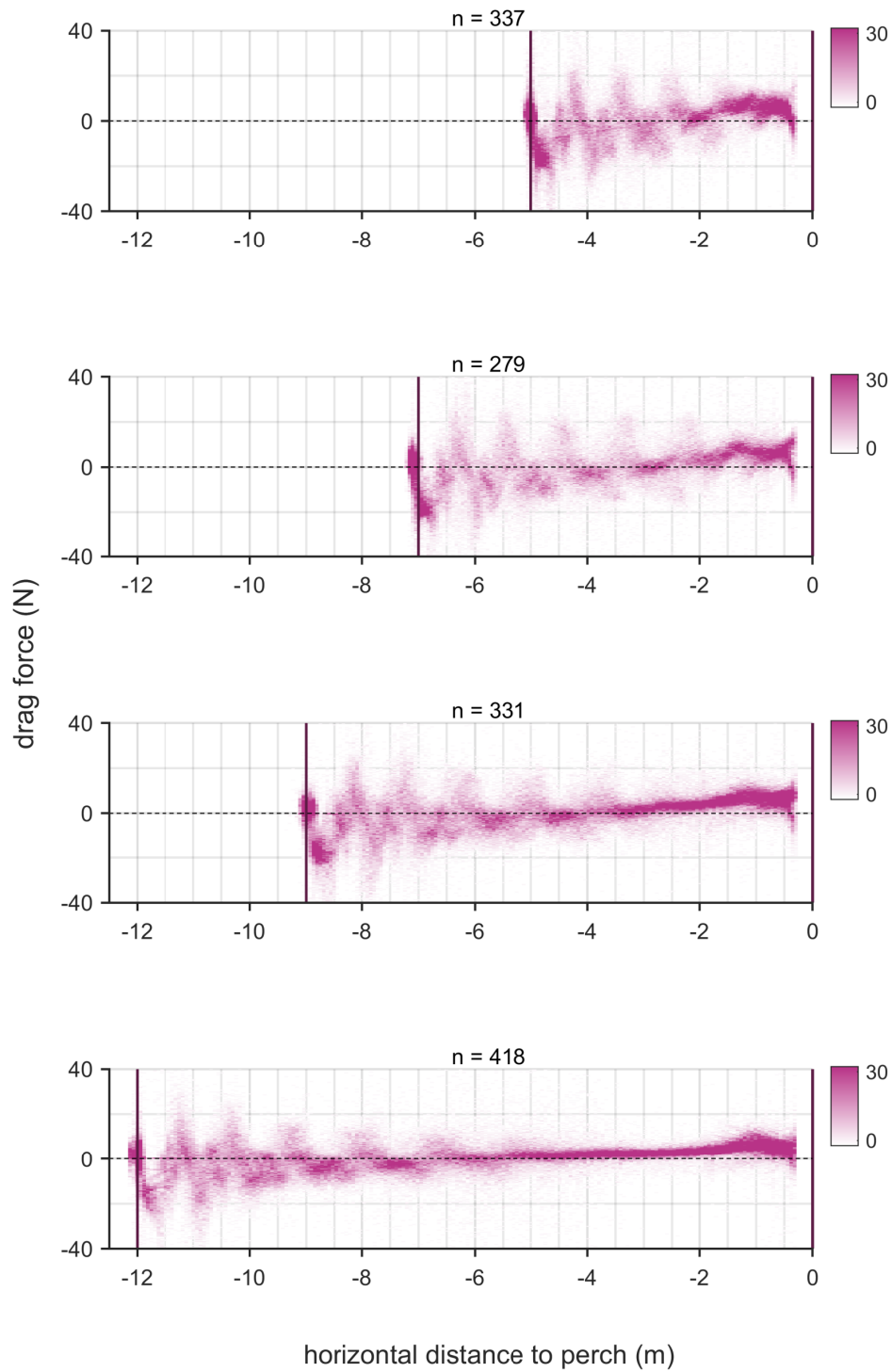
### 3.4.7 Aerodynamic Forces

The total aerodynamic force during the flights were calculated from acceleration recorded at the central point on the backpack mount. The lift force magnitude is defined as the component of the aerodynamic force in the direction of the normal to the velocity vector, where positive lift force points upwards (Figure 3.25). The drag magnitude  $D$  was calculated as the component of the aerodynamic force in the direction of the oncoming velocity vector, where positive  $D$  points backwards from flight direction (Figure 3.26). Aerodynamic forces differ between the flapping and ascending phases, where most flapping cycles have net thrust ( $-D$ ) and net lift while gliding has net  $D$  and  $L$ .

During the take-off the hawk pushes off with upward and forward force. The hawks produce highest  $L$  during the first wingbeat cycle and  $L$  diminishes with subsequent wingbeats. During the upstroke  $L$  is negative. For the first few flaps net  $-D$  is high but quickly diminishes for subsequent flaps, and final flaps produce  $+D$ . In the ascending phase there is a net  $L$  force production which decreases to close to zero but remains slightly positive until the point of contact.  $D$  increases during the ascending phase, with a modest peak around 1.25m from the perch in the 12m and 9m flights. In the 7m flights a peak occurs earlier at 1.5m from the perch.  $D$  then reduces after this peak until the point of contact. The 5m flights,  $D$  is positive in the final 1.5m before landing but no clear peak.



**Figure 3.25:** 2D histograms of the lift force magnitude, defined as the component of the aerodynamic force in the direction of the normal to the velocity vector, where positive lift points upwards. Forces measured at the central point of the backpack mount.



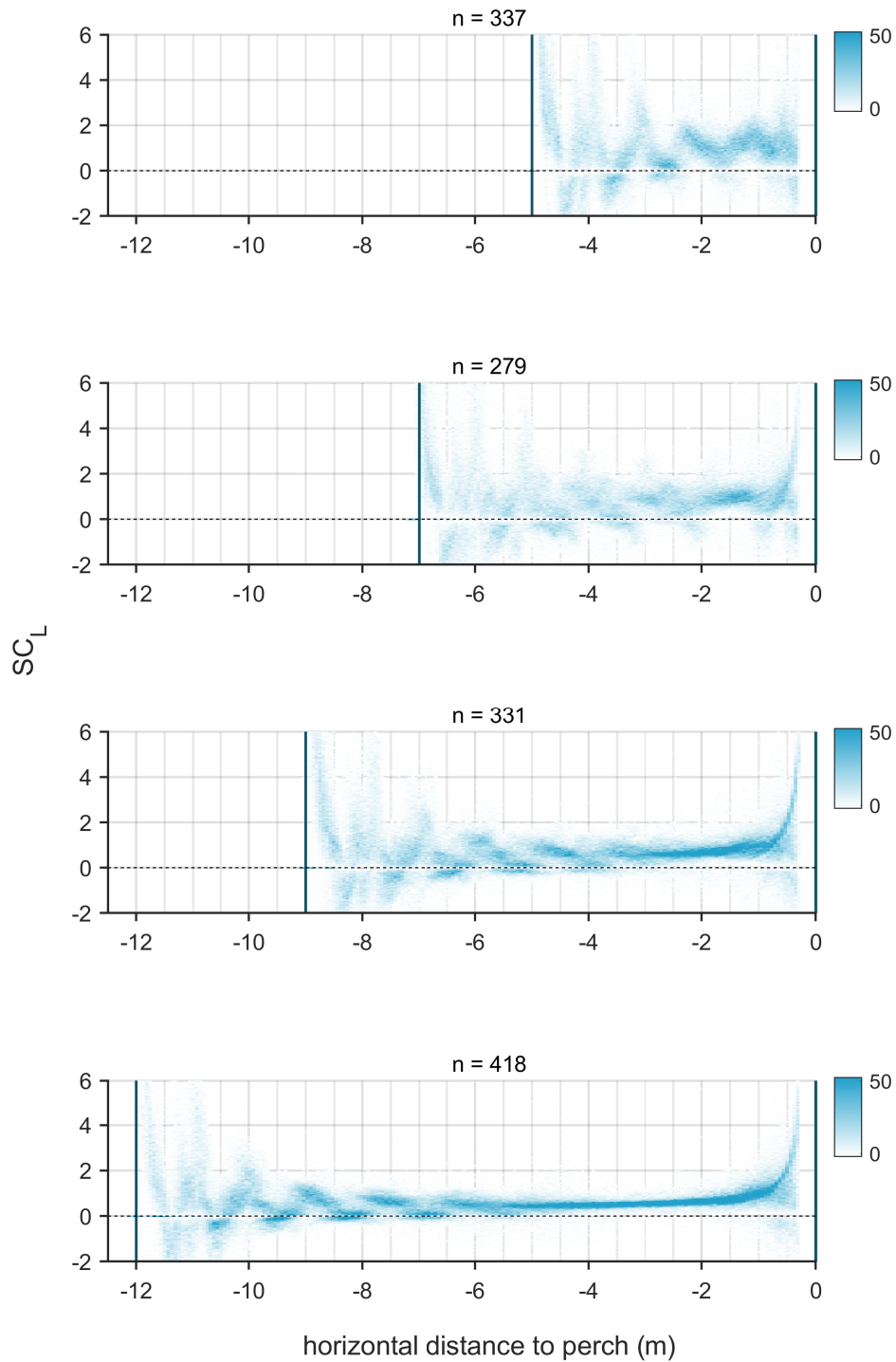
**Figure 3.26:** 2D histograms of the drag force magnitude, defined as the component of the aerodynamic force in the direction the velocity vector, where positive drag points backwards to the flight direction. Forces measured from the central point on the backpack mount.

### 3.4.8 $SC_L$ and $SC_D$

To measure the instantaneous effect of the hawks' flight configuration on the lift and drag coefficient, the  $SC_L$  and  $SC_D$  values were measured following methods described by (Reynolds et al., 2014). These values combine the lift or drag coefficient with the flight surface area, neither of which can be measured directly but can be derived from the standard lift and drag equations (Figures 3.27 and 3.28). In fixed wing flight,  $S$  remains constant and the lift coefficient  $C_L$  completely determines the produced lift at a given speed. If  $S$  is low due to wing morphing then high  $C_L$  will not improve lift. As a result,  $SC_L$  is a measure of current wing shape configuration on the effectiveness of the lift production, and  $SC_D$  for drag.

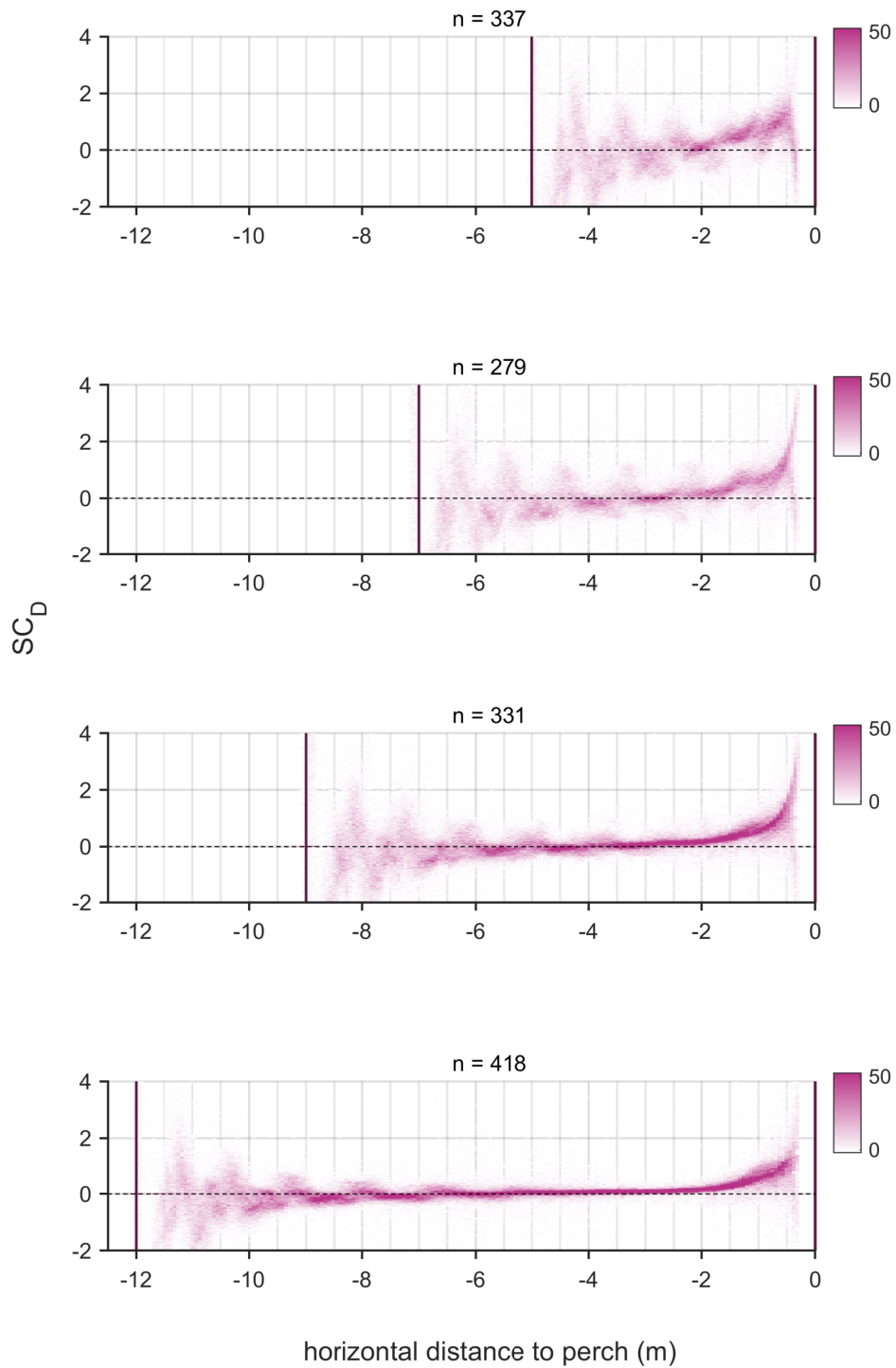
As expected, both  $SC_L$  and  $SC_D$  show high variation during flapping, and the first wingbeat contrasts with subsequent wingbeats. In gliding flight  $SC_L$  is constant while wing span is maximised and angle of attack held constant. Most notably the  $SC_L$  value increases in the 12m and 9m flights at around 1.5m from the perch and reaches high values up until the point of contact. Most notably the  $SC_L$  values increases in the 12m and 9m flights at around 1.5m from the perch and reaches high values up until the point of contact. During the 5m flights and to some extent the 7m flights,  $SC_L$  varies due to the presence of wingbeats in the final metres before landing.

$SC_D$  shows less variation during flapping, but in the 5m flights  $SC_D$  begins negative during accelerating wingbeats and increases to positive during the braking wingbeats. Increase in  $SC_D$  from around 0 to positive occurs at -2m from the perch in all the perch-perch distances, suggesting influence from a distance-dependent control input.  $SC_D$  increases to a high peak at the point of contact, but rise is more gradual than in  $SC_L$ . The extreme values just before contact are not measured in the 5m flights however.



**Figure 3.27:** 2D histograms of the  $SC_L$  values for Harris hawk perching flights.  $SC_L$  provides a value for the instantaneous net effect of the hawks' flight configuration on lift and is derived from the standard lift equation, combining the lift coefficient with the total flight surface. Flights separated by perch distance.

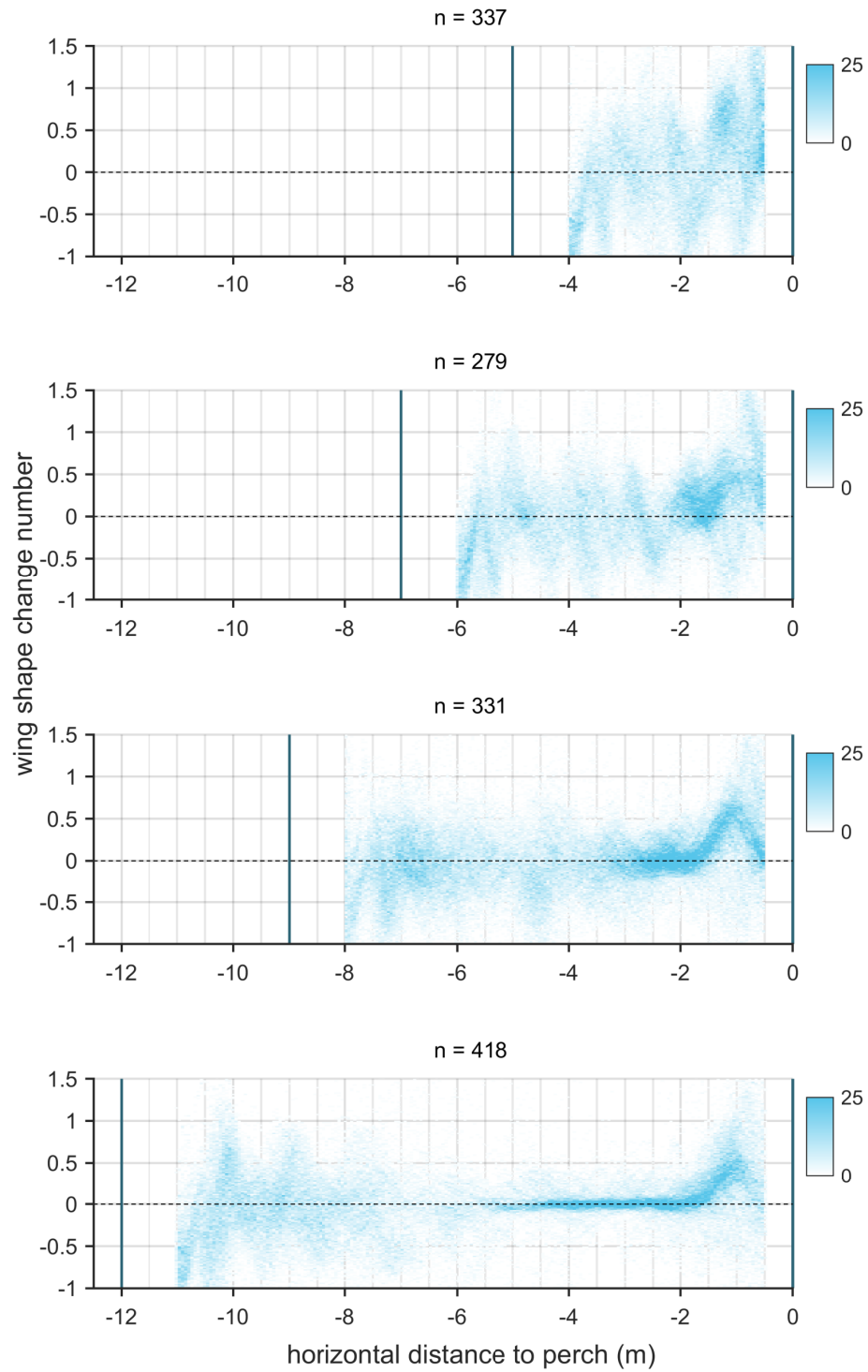




**Figure 3.28:** 2D histograms of the  $SC_L$  values for Harris hawk perching flights.  $SC_D$  provides a value for the instantaneous net effect of the hawks' flight configuration on drag and is derived from the standard drag equation, combining the drag coefficient with the total flight surface. Flights separated by perch distance.

### 3.4.9 Shape Change Number

$\Xi$  was measured for the hawks flights using the chord vectors (Figure 3.29). The rate of change in the magnitude of chord length component perpendicular to the local velocity vector and relative with total velocity this gives an estimate to frontal area change.  $\Xi$  is a calculated without knowing the exact shape number, which would require an accurate measurement of the entire flight surface. For the 9m and 12m flights which has extended gliding flight,  $\Xi$  is close to zero until a peak at 1m from the perch.



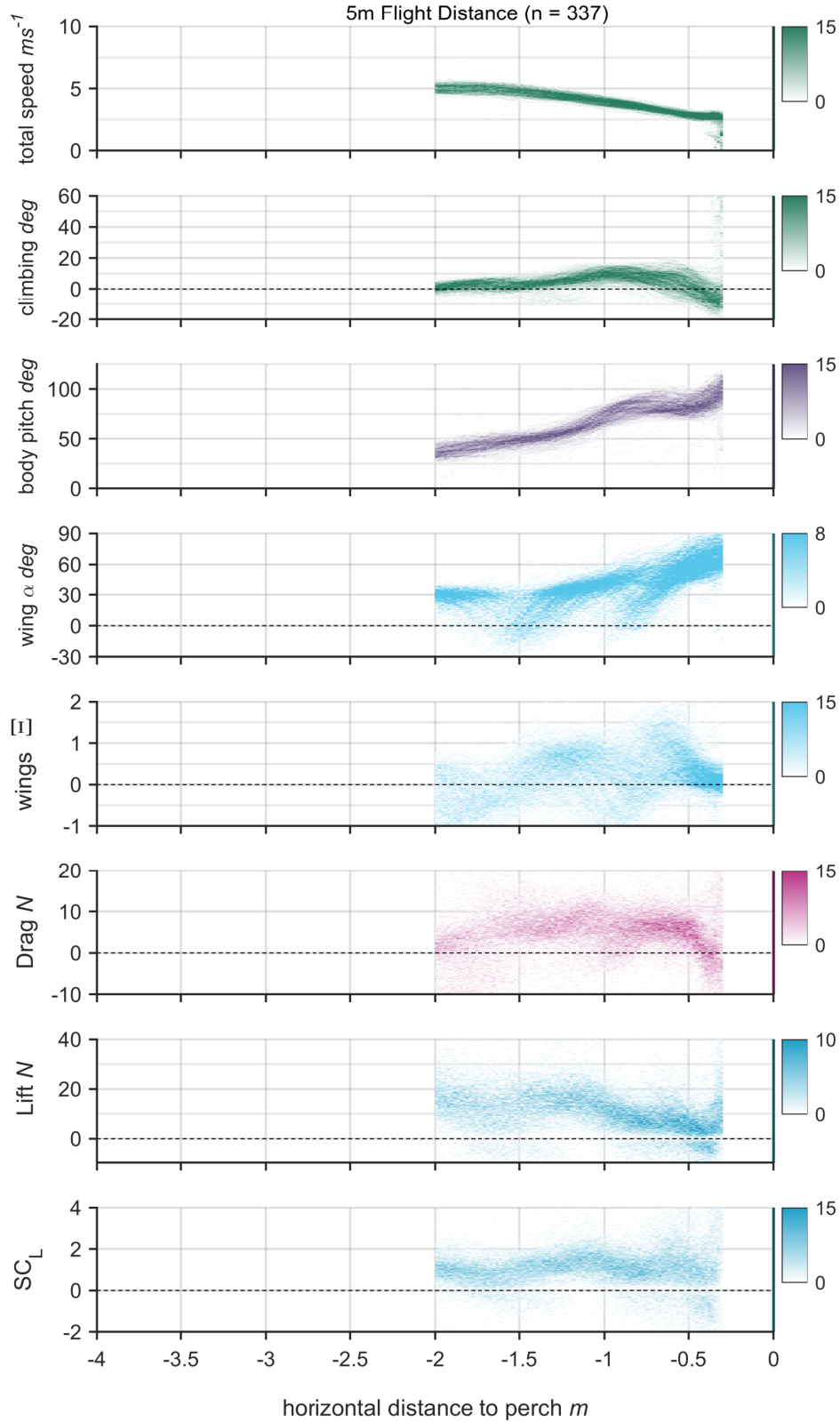
**Figure 3.29:** 2D histograms of the wings shape change number, separated by total flight distance (from top to bottom: 5m, 7m, 9m, 12m).

### 3.4.10 Combined Aerodynamic Summaries

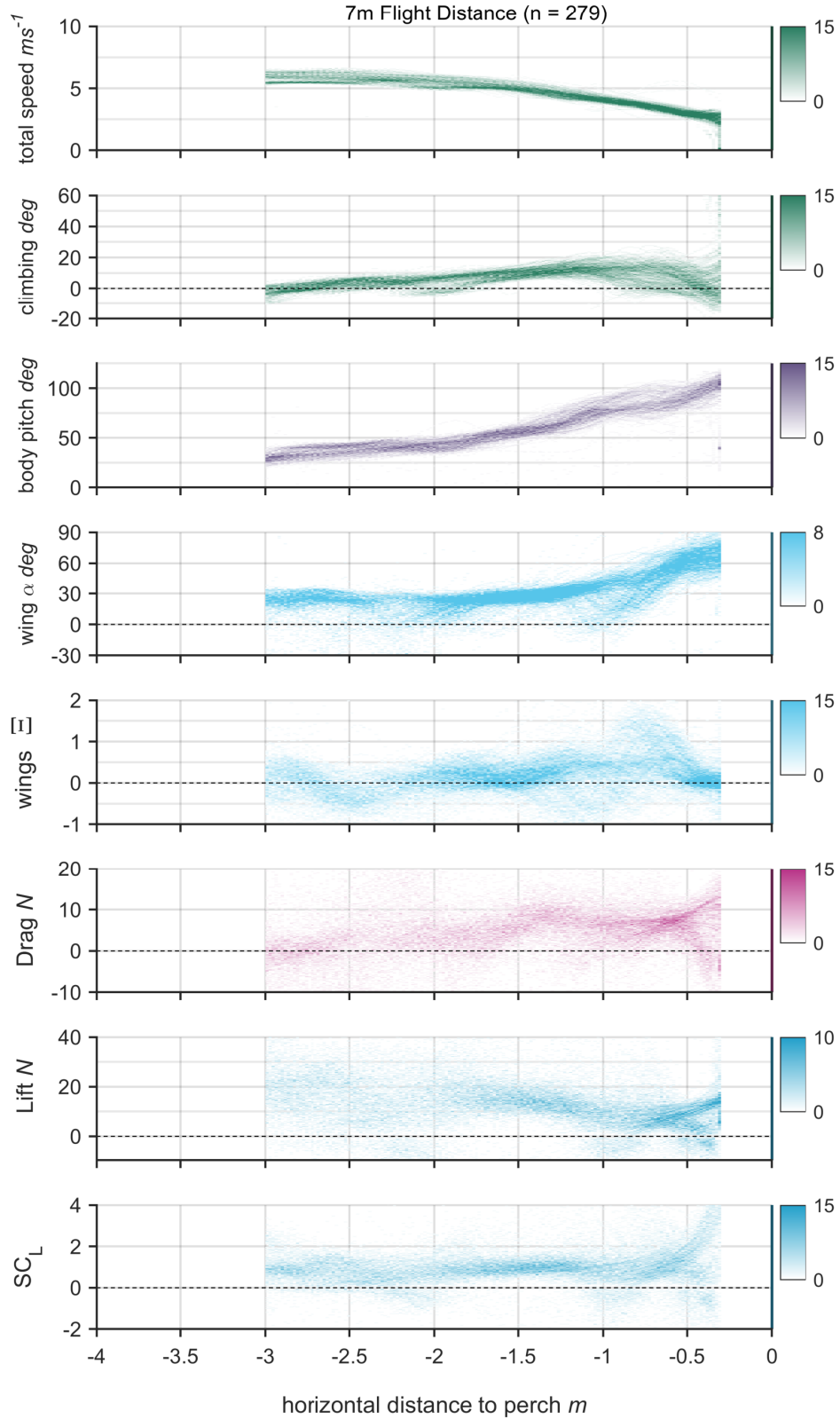
The total speed,  $\theta_V$ ,  $\theta_B$ ,  $\alpha$ ,  $\Xi$ ,  $D$ ,  $L$ , and  $SC_L$  values from the 12m flight are shown together for the final 4m in Figure 3.33 for comparison purposes. The same variables are shown in Figure 3.30 for the 5m flights for the final 2m of flight. Two different braking strategies are used by the hawks based on perch distance. In the longer flights a higher total speed is reached ( $8ms^{-1}$  versus  $5ms^{-1}$ ) and therefore greater deceleration is required overall. The hawks in the longest flights gained greater height and therefore exchanged a larger proportion of kinetic energy for gravitational potential energy, while height gain was very slight in the 5m flights. The hawks used gliding flight in the final approach almost exclusively during the 12m flights but in the 5m flights final approaches flapping motion was present. However, despite these differences the total speed decrease from aerodynamic braking in the 2m before the perch were virtually identical, where the hawks slowed from  $5ms^{-1}$  to  $2.5ms^{-1}$  at the point of contact.

The differences in braking strategy are also reflected in the aerodynamic measurements. For the 12m and 9m flights in Figures 3.33 and 3.32, drag remained steady during the final approach until a modest peak at -1m. The  $SC_L$  and  $SC_D$  values which estimate the effect of flight configuration on  $L$  and  $D$  respectively were consistent and changed gradually on approach, before a final extreme  $SC_L$  increase 1m before contact. The peak does not coincide with either a clear increase in wingspan nor closely follow the wing angle of attack increase. Instead, other wing and tail kinematics have an influence, particularly independent tailtip dihedral angle and wing sweep (see below).  $\Xi$  measurements from the wings show low values until a high peak during the final 1m. The aerodynamics measurements reflect smooth transitions with consistent peak events occurring at a critical distance before the perch, as would be expected from using a glide while executing a rapid pitch-up manoeuvre to generate high  $\Xi$  values and subsequently generate high aerodynamic forces to reduce total speed prior to impact.

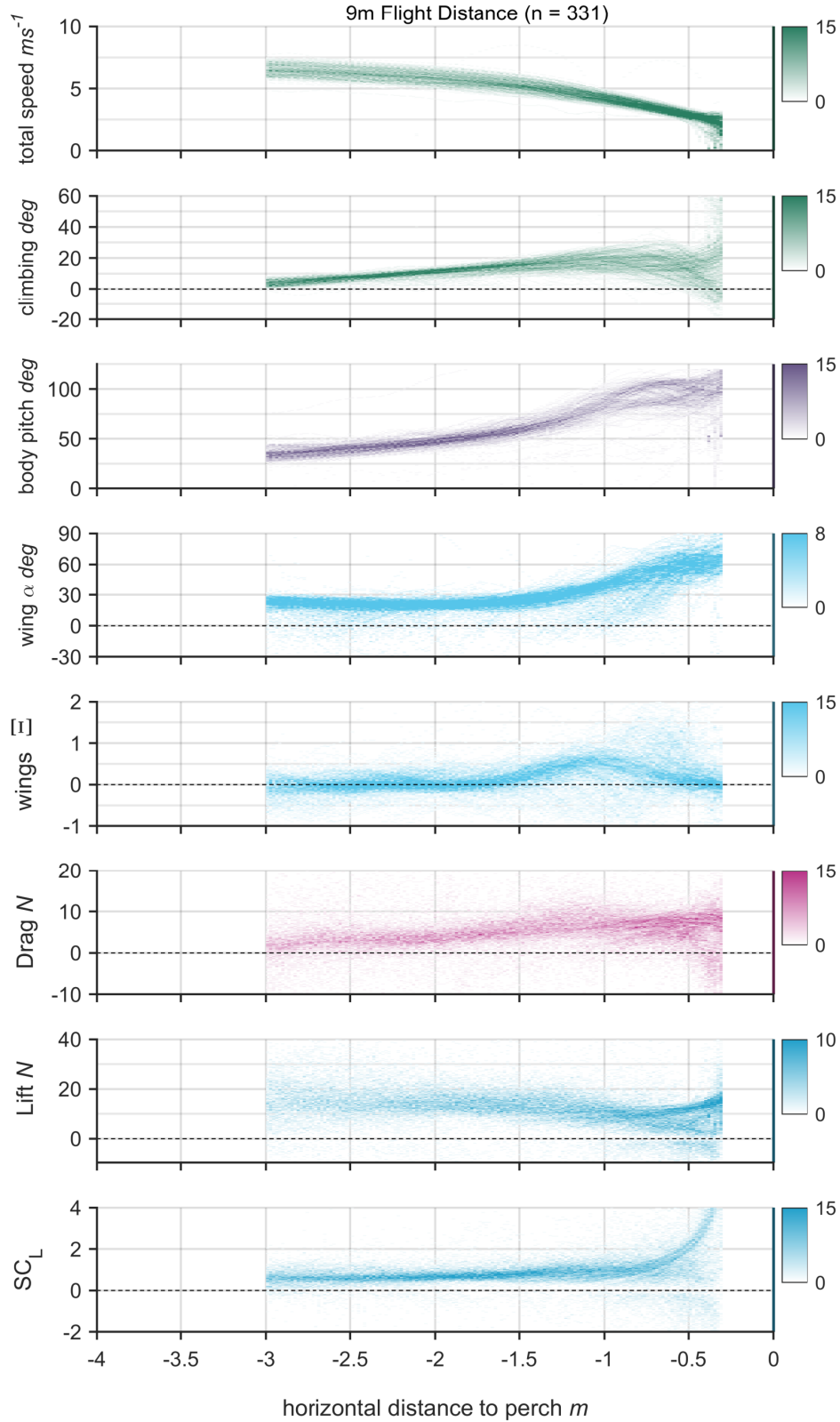
For the 5m and 7m flights in Figures 3.30 and 3.31, aerodynamic forces fluctuate with wing angle of attack and closely follow during flapping and no distinctive peak  $D$  force is present. However, the level of drag force produced is similar to the 12m flights (10N over 2m). Wing motion generates aerodynamic forces and by flapping "horizontally" with high  $\alpha$  the resultant aerodynamic forces are directed backwards with respect to the flight trajectory, which slows airspeed.



**Figure 3.30:** 2D histograms comparing different measurements from all hawks in 5m flights during the final approach to the perch. Total groundspeed, climbing angle ( $\theta_V$ ), lift, drag,  $SC_L$ ,  $SC_D$  measured from the CBP. Body pitch ( $\theta_B$ ) measured between the body length vector and horizontal plane, and wing angle of attack ( $\alpha$ ) measured between the estimated wing chord vector and the horizontal plane.

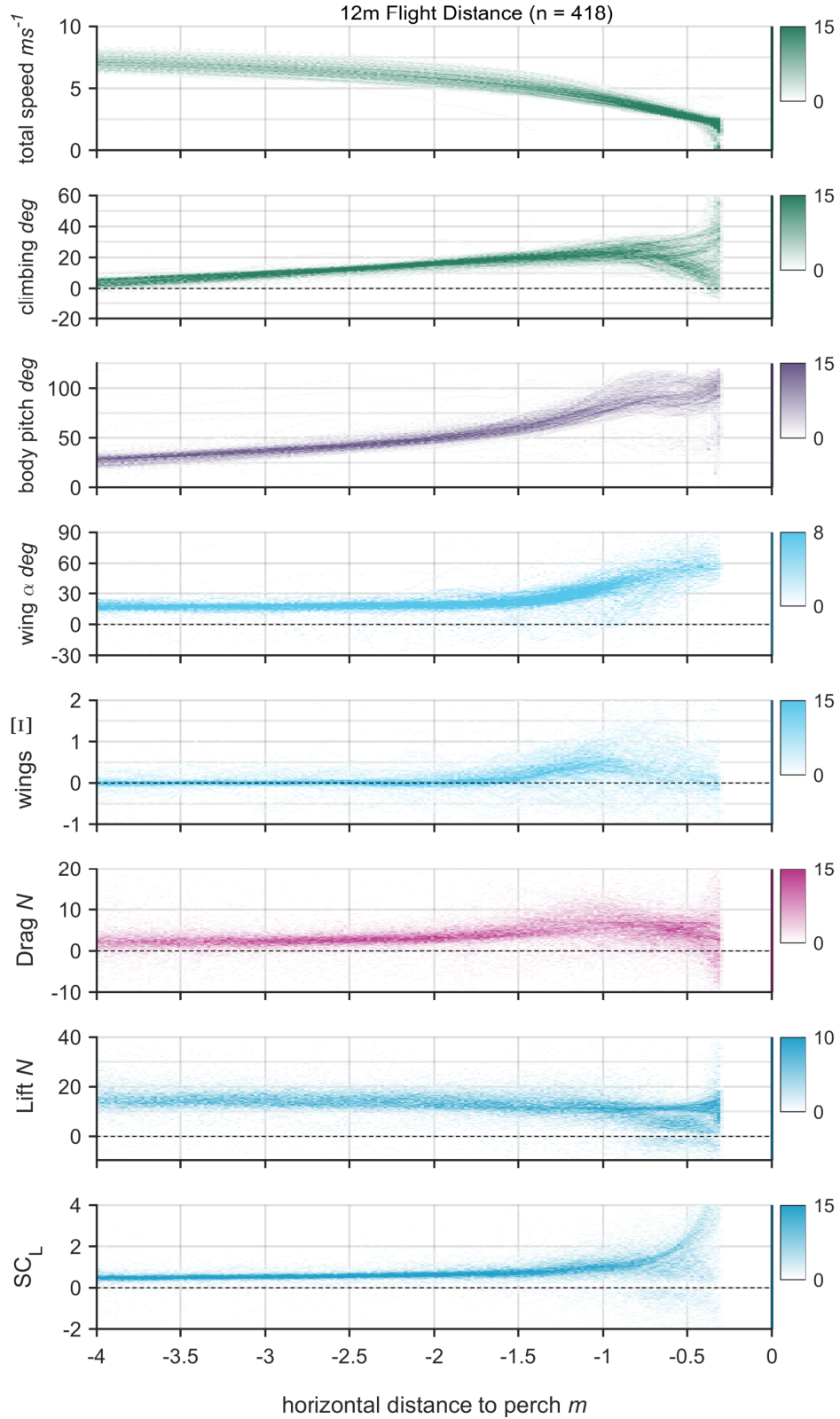


**Figure 3.31:** 2D histograms comparing different measurements from all hawks in 7m flights during the final approach to the perch. Total groundspeed, climbing angle ( $\theta_V$ ), lift, drag,  $SC_L$ ,  $SC_D$  measured from the CBP. Body pitch ( $\theta_B$ ) measured between the body length vector and horizontal plane, and wing angle of attack ( $\alpha$ ) measured between the estimated wing chord vector and the horizontal plane.



**Figure 3.32:** 2D histograms comparing different measurements from all hawks in 9m flights during the final approach to the perch. Total groundspeed, climbing angle ( $\theta_V$ ), lift, drag,  $SC_L$ ,  $SC_D$  measured from the CBP. Body pitch ( $\theta_B$ ) measured between the body length vector and horizontal plane, and wing angle of attack ( $\alpha$ ) measured between the estimated wing chord vector and the horizontal plane.





**Figure 3.33:** 2D histograms comparing different measurements from all hawks in 12m flights during the final approach to the perch. Total groundspeed, climbing angle ( $\theta_V$ ), lift, drag,  $SC_L$ ,  $SC_D$  measured from the CBP. Body pitch ( $\theta_B$ ) measured between the body length vector and horizontal plane, and wing angle of attack ( $\alpha$ ) measured between the estimated wing chord vector and the horizontal plane.



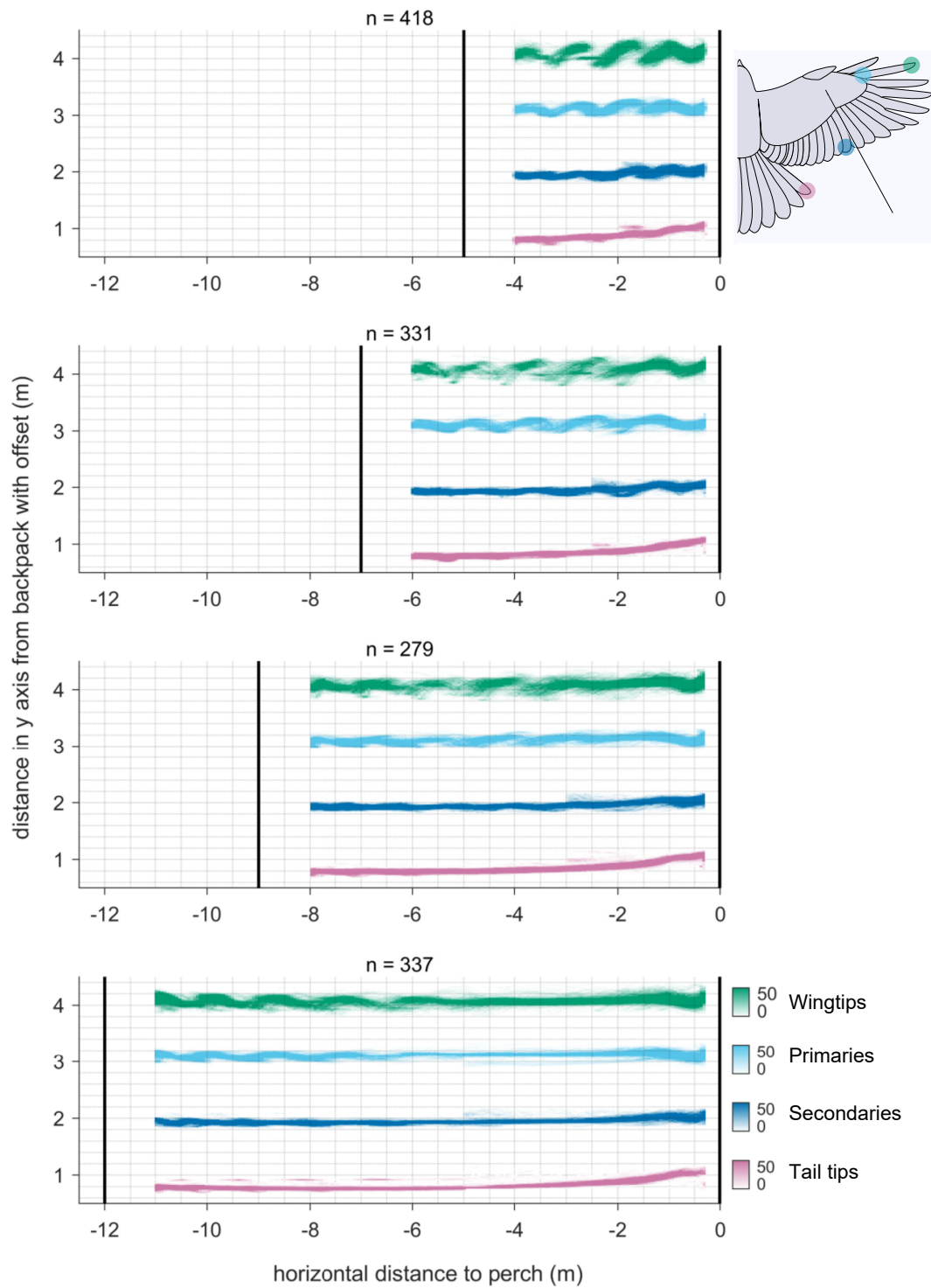
### 3.4.11 Wing and Tail Motion in Earth Reference Frame

The vertical distance of the feather markers from the CBP were measured in the Earth reference frame, where vertical aligns with gravity (Figure 3.34). The horizontal distance was also measured, where the horizontal axis aligns with the length of the room (Figure 3.35). The shape of the trajectory is therefore removed as markers are shown as relative to the backpack, but still within the room coordinate system and so no rotations have been applied. Markers are shown with an offset of 1m for comparison purposes: wingtips (top, green), primaries (light blue), secondaries (dark blue), tailtips (bottom, pink). As previously discussed, due to marker occlusion from handwing folding there were limited wingtip measurements during the upstroke.

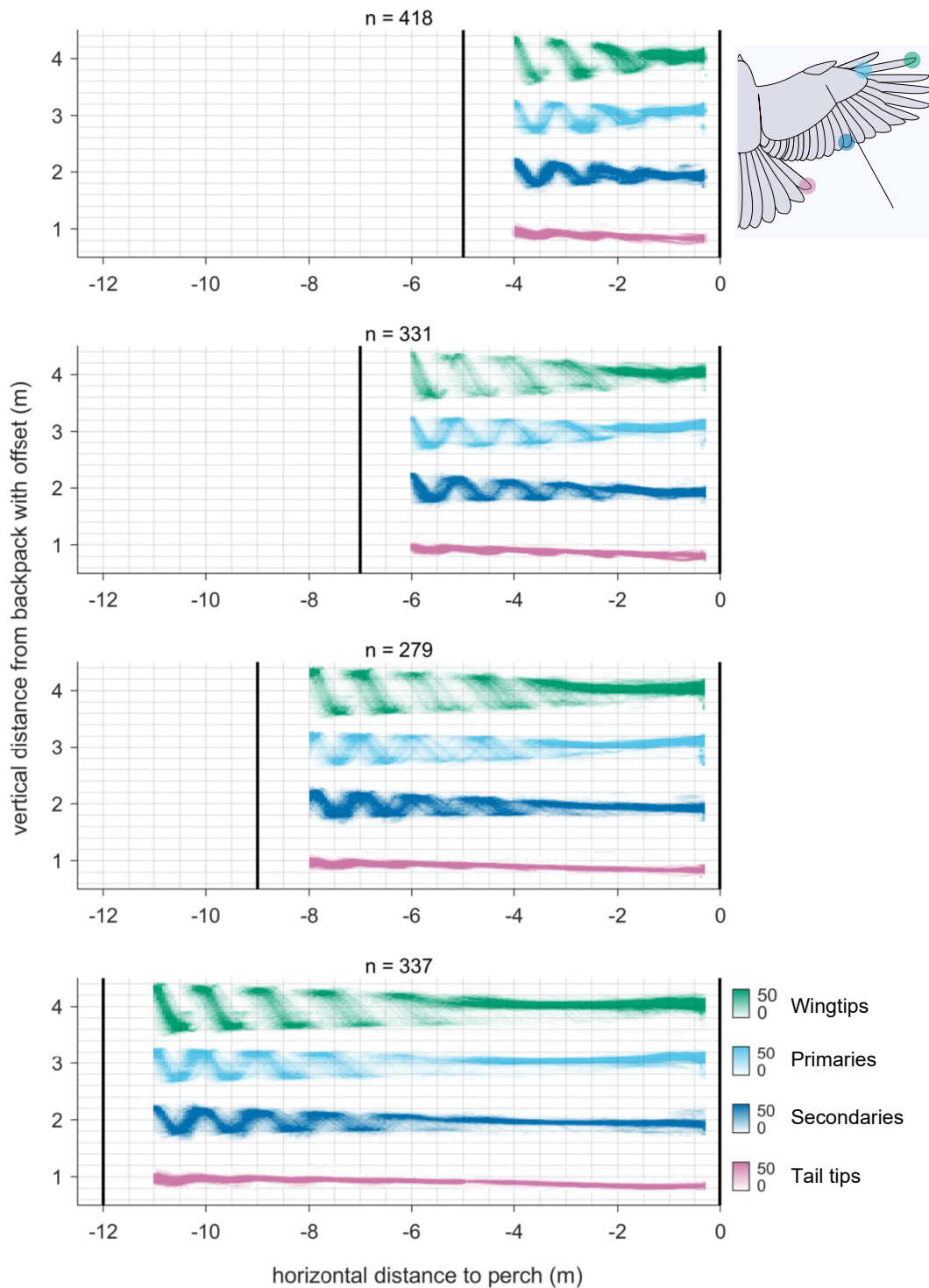
The shape of wingtip motion during the flapping alters through the descending phase. The wingtip motion vertical height reduces with each subsequent flap, most noticeably in the shorter flights. The consistency of where the flap occurs in the room also reduces. In addition, later flaps appear horizontally "stretched" as the hawks travel a longer horizontal distance for the duration of the flap cycle, corresponding to a slower flap. For the primary and secondary markers (light and dark blue) the vertical height of the motion also slightly reduces and a similar horizontal stretch is apparent. For the 5m flights, where flapping occurs throughout the flight, wingtip motion goes from vertical to horizontal, as expected from flapping while  $\theta_B$  is very high. In previous results, wing motion resembling a flap was recorded in some of the 7m flights around 1.5m from the perch. This flap is apparent in the horizontal direction for all three wing markers, but not in the vertical direction. For the longer flights, the wing markers move in a negative horizontal direction with respect to the moving CBP in the final 1m. This suggests the wings are move backwards during the parachute phase. The wingtips and primary markers steadily increase in vertical height during the ascending phase, suggesting the handwing is raised against gravity on approach.

The tail feather tip markers (pink) have some vertical sinusoidal motion during the descending phase. These likely correspond to some marker misidentification from the secondary markers, but more commonly a small amount of bouncing of the tail from the flapping motion. During the ascending phase the tail markers are lowered on approach, and there is also a steady increase in horizontal distance corresponding to the tail moving forwards.





**Figure 3.34:** 2D histograms of feather markers vertical distance to the CBP. Markers shown in Earth reference frame and vertical aligns with gravity. Offset of 1m added to space the markers. From top to bottom: wingtips (light blue), primaries (blue), secondaries (dark green), tail tips (pink). Both left and right markers depicted from all four hawks for all flights ( $n=1365$ ). Perch positions shown with black bars. Markers during take-off phase (initial 1m) and pull-up to the perch (final 0.3m) not shown.

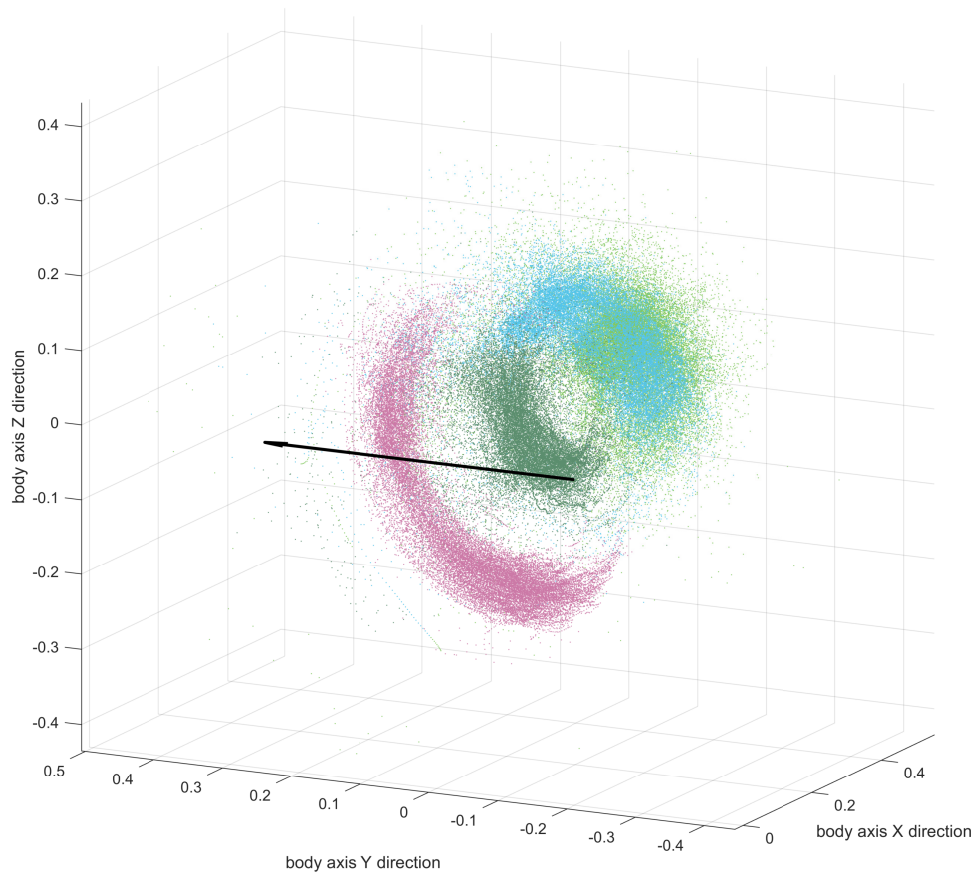


**Figure 3.35:** 2D histograms of feather markers distance to the CBP in a horizontal direction aligning with the axis in the forwards flight direction. Offset of 1m added to space the markers. From top to bottom: wingtips (light blue), primaries (blue), secondaries (dark green), tail tips (pink). Both left and right markers depicted from all four hawks for all flights ( $n=1365$ ). Perch positions shown with black bars. Markers during take-off phase (initial 1m) and pull-up to the perch (final 0.3m) not shown.

### 3.4.12 Wing and Tail Independent Angles

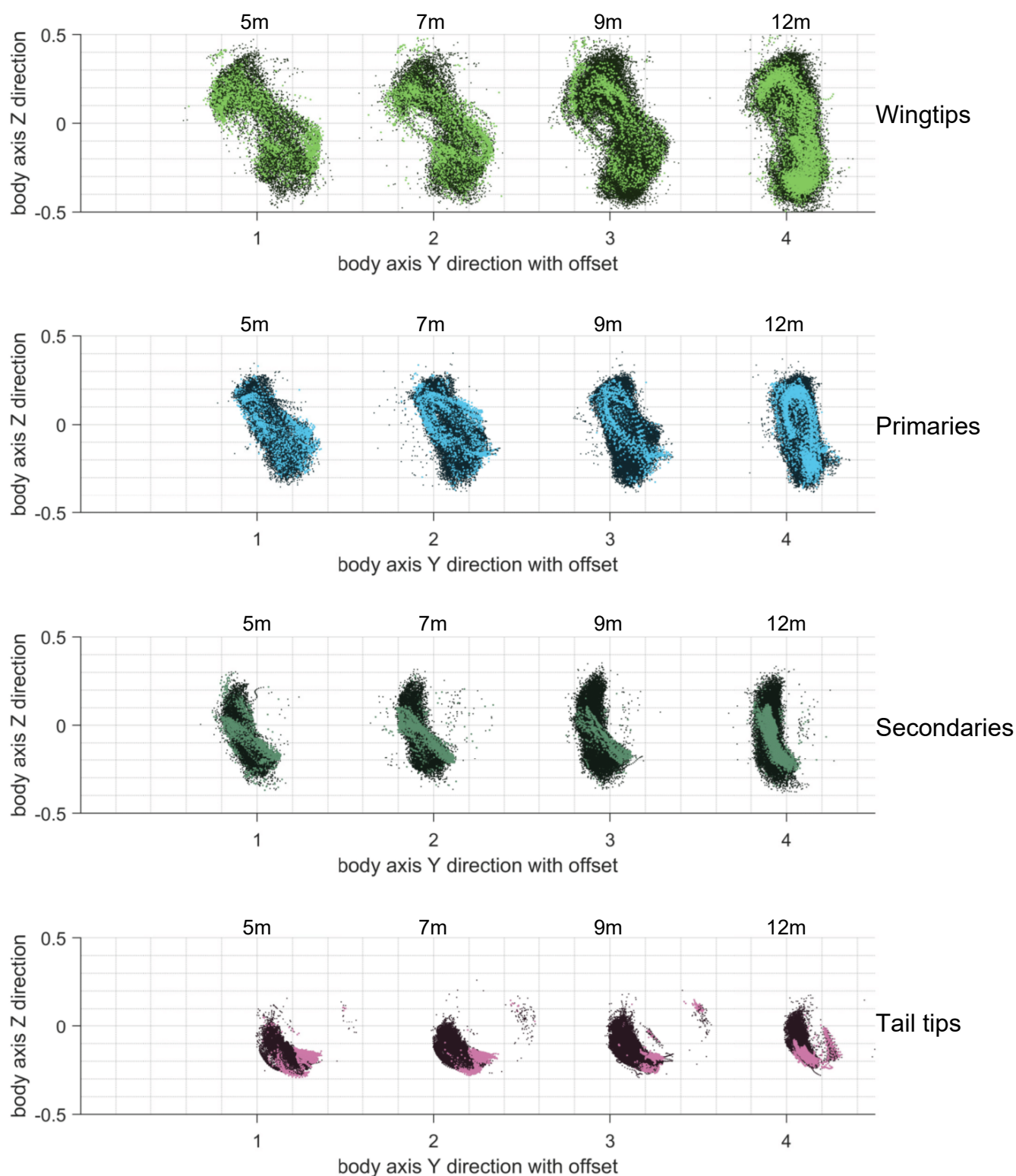
To visualise how the hawks move their wings and tail relative to their body, the wing and tail markers were rotated to the body axis using  $\theta_B$  and a body yaw ( $\psi_B$ ) measurement. Roll angles were not used as there was no accurate lateral measurement from body markers. The motion of markers from the right side were shown from a side view during the descending phase, where Z is the vertical body axis pointing up and Y is the horizontal axis in the nose to tail direction (Figure 3.37). Markers shown from top to bottom: wingtips (light green), primaries (light blue), secondaries (dark blue), tailtips (pink). Flights additionally separated by perch distance using an offset, where 5m is on the far left and 12m on the far right. The final wingbeat for each flight before the ascending phase shown in colour. The final wingbeat has a smaller path than previous wingbeats, and in the shorter flights is tilted more horizontally. Horizontal tilt is clearest in the 5m flights and very slight in the 12m flights. The tail tip markers are swung downwards during the descending phase and as the tailtips are brought together (reducing tailspan, see Figure 3.24 on page 87) tailtip markers move backwards away from the backpack. Both shifting the wingbeat to a more horizontal path and lowering the tailtips with respect to the body would shift the aerodynamic centre of pressure further backwards relative to the centre of mass. These kinematics would likely result in the body to start pitching nose-up unless countered by other control inputs.

The right side markers from all birds during the ascending phase are shown from a side view in the same way (Figure 3.38). As before, markers separated by flight distance (left to right is 5m, 7m, 9m, 12m). The final 0.5m before contact is coloured. The primary and wingtip markers are swept forwards and downwards in a circular motion, while the secondary markers remain close to the backpack position but move upwards and backwards. The wing is therefore rotating around the shoulder such that the trailing edge lifts while the leading edge falls (negative independent wing pitch). The tail moves in a reverse motion where the tailtips are swung upwards (positive independent pitch). The wings and tail rotate in opposite directions with respect to the body during the ascending phase (Figure 3.36, showing all feather markers during the ascending phase from one hawk).

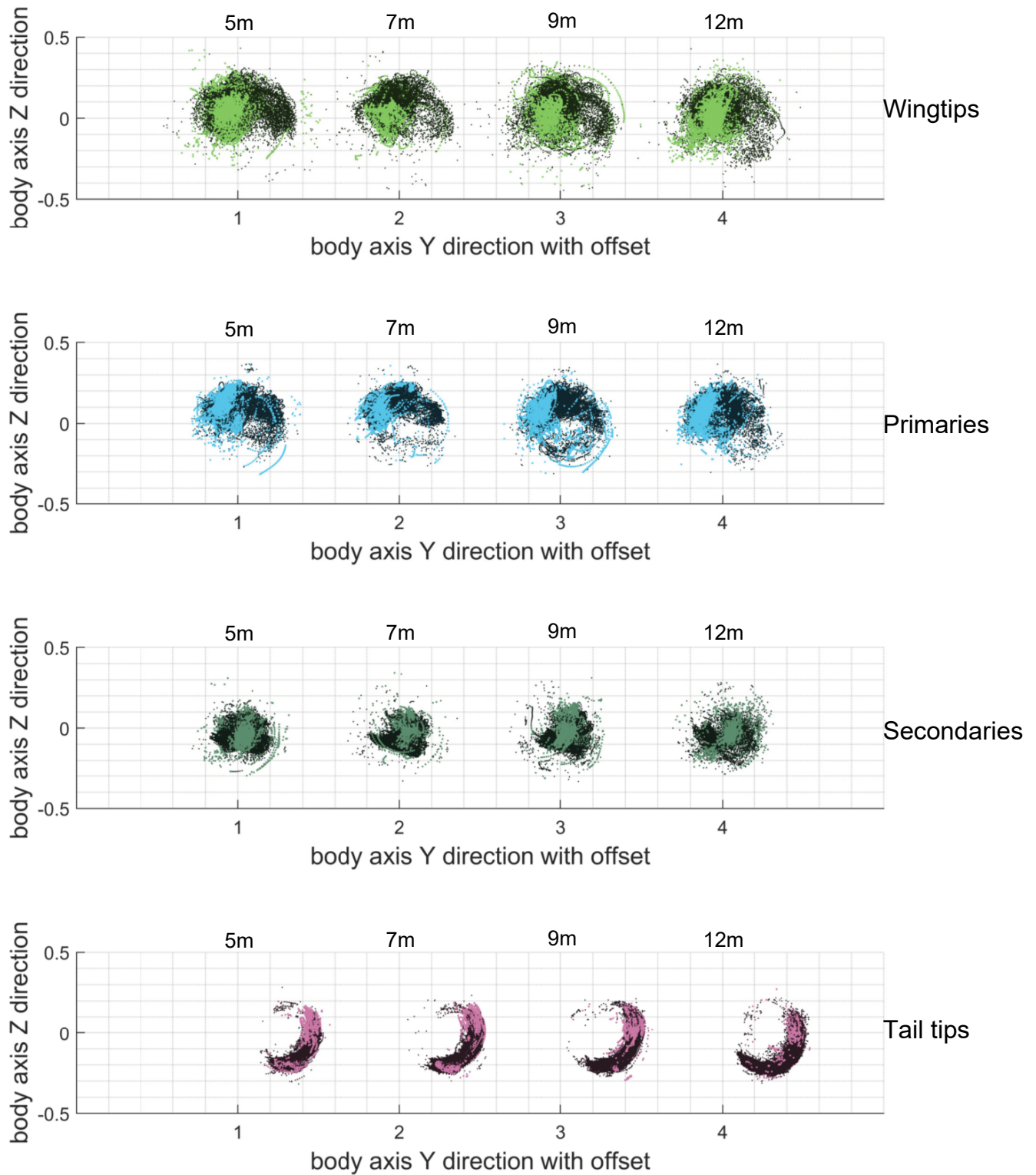


**Figure 3.36:** 3D reconstruction of feather markers during gliding in the body reference frame. Markers pooled from flights during the ascending phase from one male hawk (Drogon). Body axis direction indicated with black arrow (not to scale) pointing in the nose-tail direction along the body Y axis. Z axis points upwards. Tailtips (pink) show a large rotation during the glide in the same direction as the secondary marker on the trailing edge (dark green) while the primary (blue) and wingtip (light green) markers on the leading edge rotate in the opposite direction. The wing rotates around the shoulder affecting independent pitch angle.





**Figure 3.37:** Side view (YZ plane) of feather markers rotated to the body reference frame during flapping flight from all four hawks. Markers offset in Y by flight distance, with 5m flights on the far left and 12m flights on the far right. Body axis from nose-tail in a positive Y direction, while positive Z axis points upwards. Final wingbeat in the descending phase shown in colour for comparison purposes. From top to bottom markers are wingtips (light green), primaries (blue), secondaries (dark green), tailtips (pink).



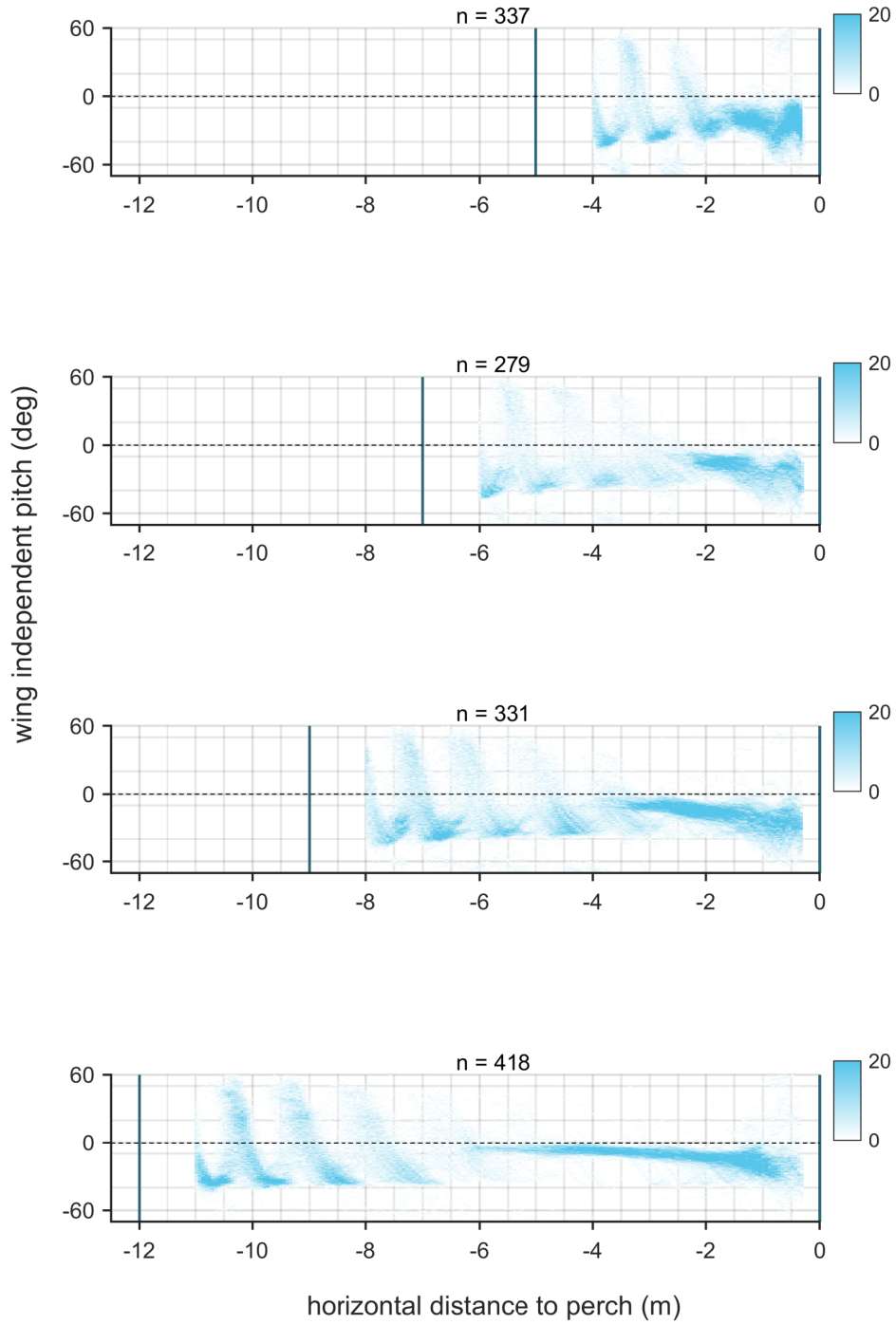
**Figure 3.38:** Side view (YZ plane) of feather markers rotated to the body reference frame during ascending phase from all four hawks. During the ascending phase the hawks used gliding flight. Body axis from nose-tail in a positive Y direction, while positive Z axis points upwards. Markers offset in Y by flight distance, with 5m flights on the far left and 12m flights on the far right. Markers from the final 0.5m before contact are shown in colour for comparison purposes. From top to bottom markers are wingtips (light green), primaries (blue), secondaries (dark green), tailtips (pink).



The independent rotation of the wings and tail occurs during the rapid pitch-up manoeuvre. To estimate the independent pitch of the wings, a wing chord vector was used between the primary marker and secondary marker for both wings, and the wing chord pitch was subtracted from the body pitch (Figure 3.39). As previously shown from the markers in the body reference frame, the  $\theta_W$  decreases during the glide as the wings rotate forwards at the shoulder. Due to the unknown offset of the backpack and tailpack markers lying higher than the shoulder joint,  $\theta_W$  includes an unknown constant. During the glide the wings rotate forwards as the body pitches up which means  $\alpha$  is kept stable (see Figure 3.22 on page 84). In the last few 1.5m of the rapid pitch up the rate  $\theta_B$  change increases at around  $60^\circ$ , reaching over  $90^\circ$  in the next 0.5m. The rate of change in  $\theta_W$  remains constant and so  $\alpha$  rapidly increases to a maximum of around  $60^\circ$ . In the 12m flights minimum  $\theta_W$  was around to  $-30^\circ$ , but closer to  $-60^\circ$  in the shorter flights. After reaching this extreme minimum in the shorter flights,  $\theta_W$  increases briefly in the final 1m before contact which was also measured as a brief negative change where  $\alpha$  reaches almost  $0^\circ$ .

Two further degrees of freedom are the sweep angle  $\psi$  (where the wings move forwards or backwards at the shoulder) and the dihedral angle  $\phi$  (where the wings move up and down at the shoulder). To measure these angles, the feather markers were described as spherical coordinates relative to the backpack and the azimuth and elevation angles were calculated. A positive azimuth angle describes the marker positioned ahead of the CBP and therefore a forward sweep of the wing ( $\psi$ ). A positive elevation angle describes the marker above the backpack and therefore an upward dihedral position.

The wingtip markers during the descending phase have continual variation in  $\psi$  as expected with the folding and rotation of the wing during the wingbeat (Figure 3.40). Noise from the descending phase results from the feathers oscillating. In general the wingtips are ahead of the CBP during the descending phase and maximum  $\psi$  is highest during the 5m flights at over  $30^\circ$ . During gliding where flapping is usually limited or entirely absent, the relative angles show less noise. For the first half of the glide in the 12m and 9m flights  $\psi$  is positive until around 1.5m before the perch where the angle reduces which corresponds to the wingtips sweeping backwards during the glide. A minimum is reached at around  $-20^\circ$  at the point of perching. For the 5m and 7m flights where gliding is minimal, there is a rise in  $\psi$  from  $-10^\circ$  to  $10^\circ$  before falling to negative  $\psi$  once again. The sweeping pattern is likely part of an upright flapping motion before contact with the perch.  $\psi$  measurements for the primary markers are similar as they are recorded from the same feather but closer to the wrist (Figure 3.42). Recorded  $\psi$  angles are higher due to the position of the marker on the wing (see Figure 3.17 on page 78) and measurements are more consistent across flights. The reduction in measurement noise is likely due to oscillation dampening as the marker lies closer to the feather root. The higher  $\psi$  values during flapping from the 5m flights is clearer, where maximum  $\psi$  reaches  $60^\circ$  while during the 12m flights maximum  $\psi$  is closer to  $30^\circ$ .



**Figure 3.39:** Independent wing pitch  $\theta_W$  measured using a wing chord vector from the primary marker close to the leading edge the secondary marker on the trailing edge. Due to the CBP location above the shoulder,  $\theta_W$  includes an unknown constant. Negative  $\theta_W$  describes a rotation where the leading edge falls while the trailing edge rises.

The secondary marker  $\psi$  angles show a different pattern (Figure 3.44). Measurements from the trailing edge on the arm wing show a negative  $\psi$  angle throughout the descending phase, but with far lower fluctuation during flapping, suggesting the handwing sweeps further forwards and backwards than the armwing.  $\psi$  increase steadily from the transition between flapping and gliding and aligns with the CBP at around 4m from the perch in the 12m flights. In the 12m flights  $\psi$  continues to rise until a maximum of around  $20^\circ$ . For the 9m flights,  $\psi$  remains constant for the final 1.5m before the perch, while in the 7m and 5m flights  $\psi$  reduces.

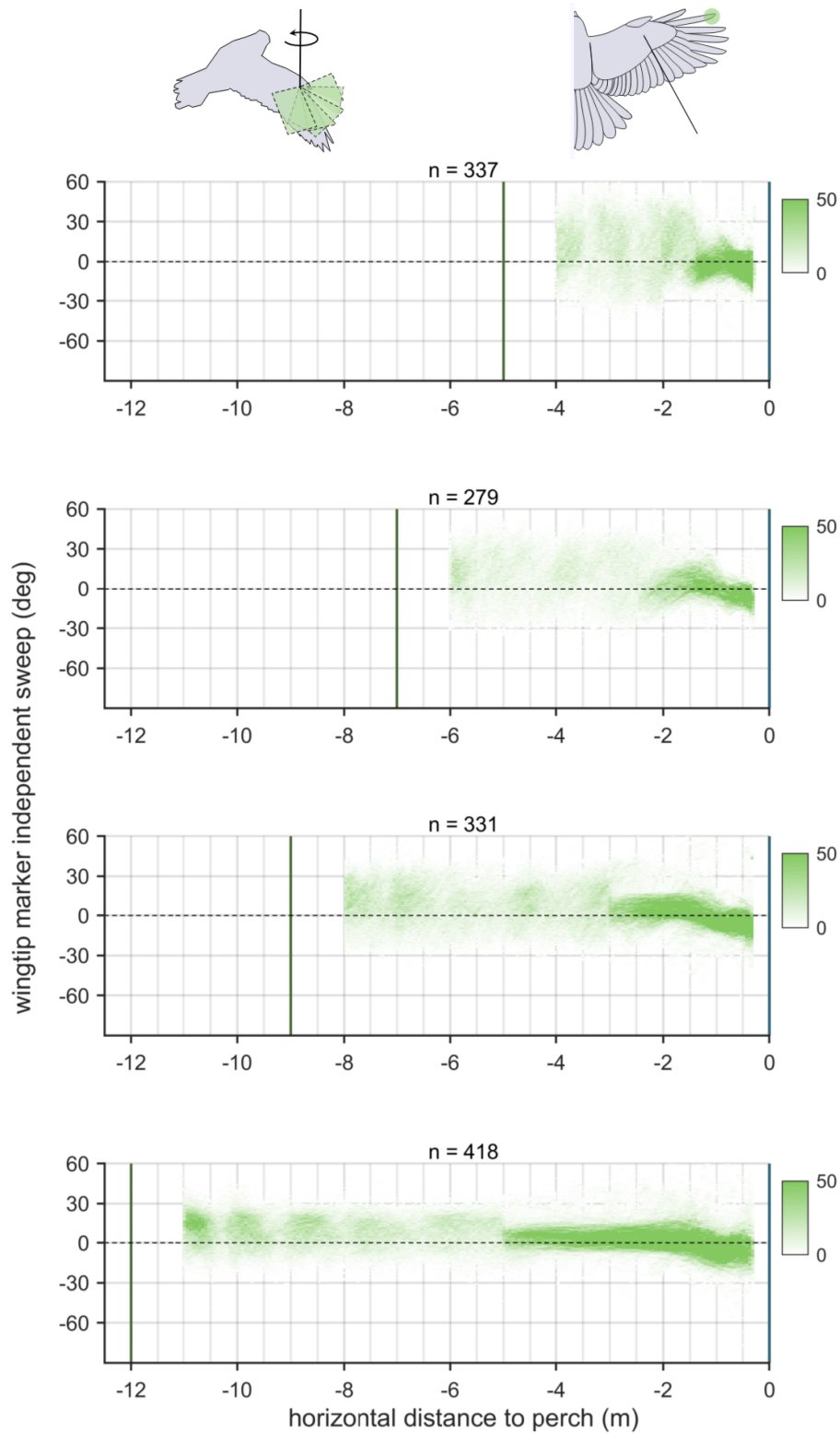
The  $\phi$  measurements for the wingtip markers (Figure 3.43) varies between  $30^\circ$  and  $-60^\circ$  during flapping, corresponding to the upstroke and downstroke motion and are similar across the flights with different perch distances. During the ascending phase  $\phi$  is positive except for just before contact where the wingtips are lowered to level with the CBP or slightly below. In the 5m and 7m flights  $\phi$  rises to a peak of  $30^\circ$  and rapidly falls which again corresponds to the upright flapping motion in the final 1m before contact. The  $\phi$  measured from the primary markers has a clear peak around 1.25m from the perch at  $30^\circ$  before falling to almost  $0^\circ$  over the next 1m of flight (Figure 3.41).

$\phi$  measurements from the secondary markers again contrast with the markers from the handwing (Figure 3.45). For the longer flights, minimum  $\phi$  remains constant at around  $-45^\circ$  during flapping, but maximum  $\phi$  falls with each wingbeat. For the ascending phase,  $\phi$  begins negative, decreases, and then rises to a maximum of almost  $30^\circ$ . For the 5m, 7m, and 9m flights  $\phi$  falls and then reaches a second peak before contact with the perch.

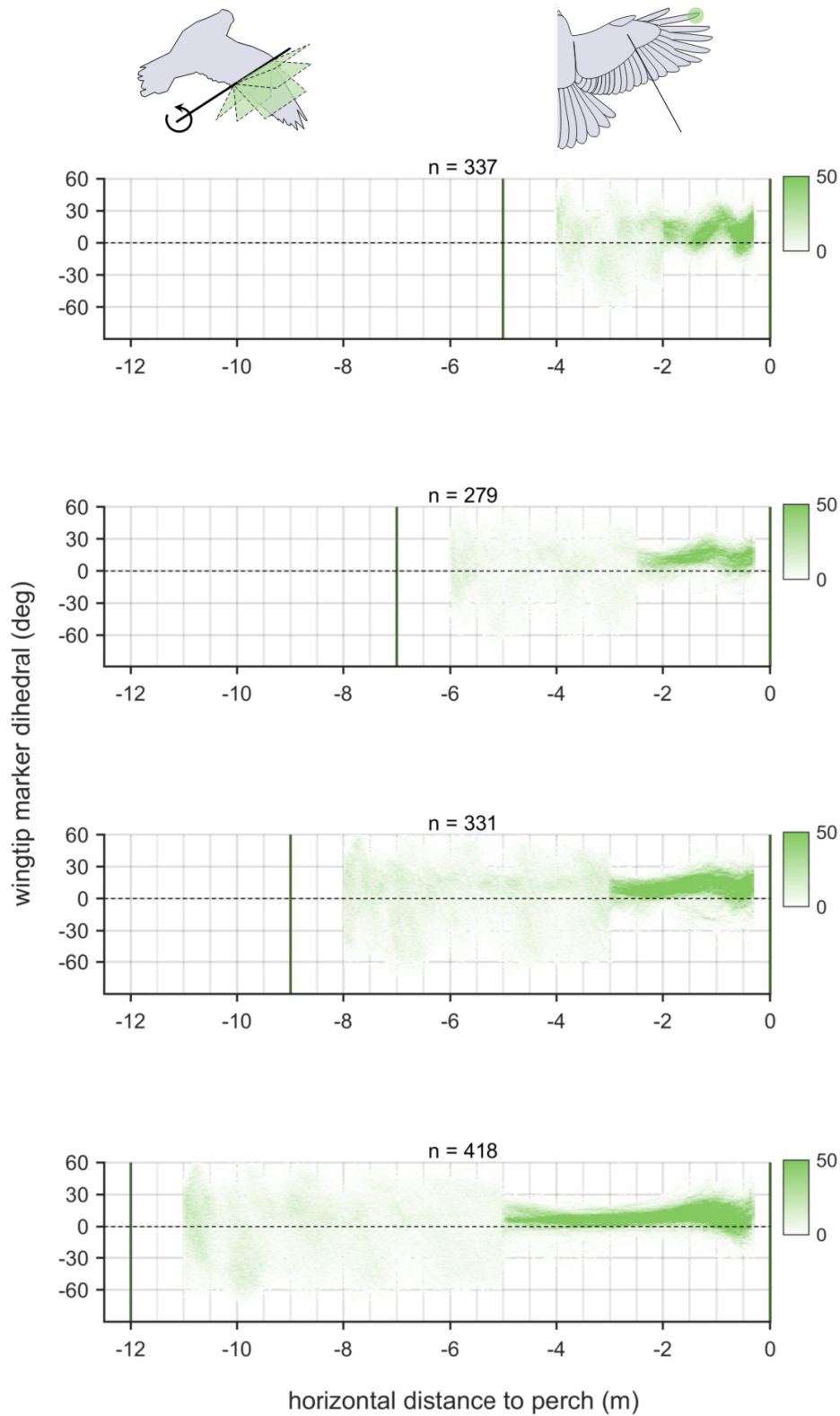
The recorded differences in  $\phi$  and  $\psi$  measurements from the trailing edge and leading edge are consistent with an extreme negative pitching rotation of the wing at the shoulder independent to the body. Further control inputs are measured during the final few metres of the perch, such as a peak  $\phi$  event at the leading edge which may correspond to independent upward flexing of the handwing. In addition, negative rotation events during the final approach resemble "flicks" of the wing that have been previously measured in the perching flights of a Steppe eagle. Such wing motions have unknown aerodynamic function, but could correspond to corrections in response to flow separation events.

The tail dihedral or elevation angle ( $\phi$ ) was measured between the tailtip markers and the CBP (Figure 3.46). Tail  $\phi$  at the start of the descending phase was close to  $0^\circ$  and therefore level with the body, and steadily fell over the descending phase until around 2m from the perch in all the flights irrespective of perch distance. Some oscillations were measured from wingbeats during the descending phase. Tail  $\phi$  increased rapidly during the ascending phase, where the tailtips were raised until a maximum of  $30^\circ$  at the point of contact. Due the high  $\theta_B$ , positive tail  $\phi$  results in the tail swinging backwards with respect to the flight direction, but in the body reference frame the tail is lifted.

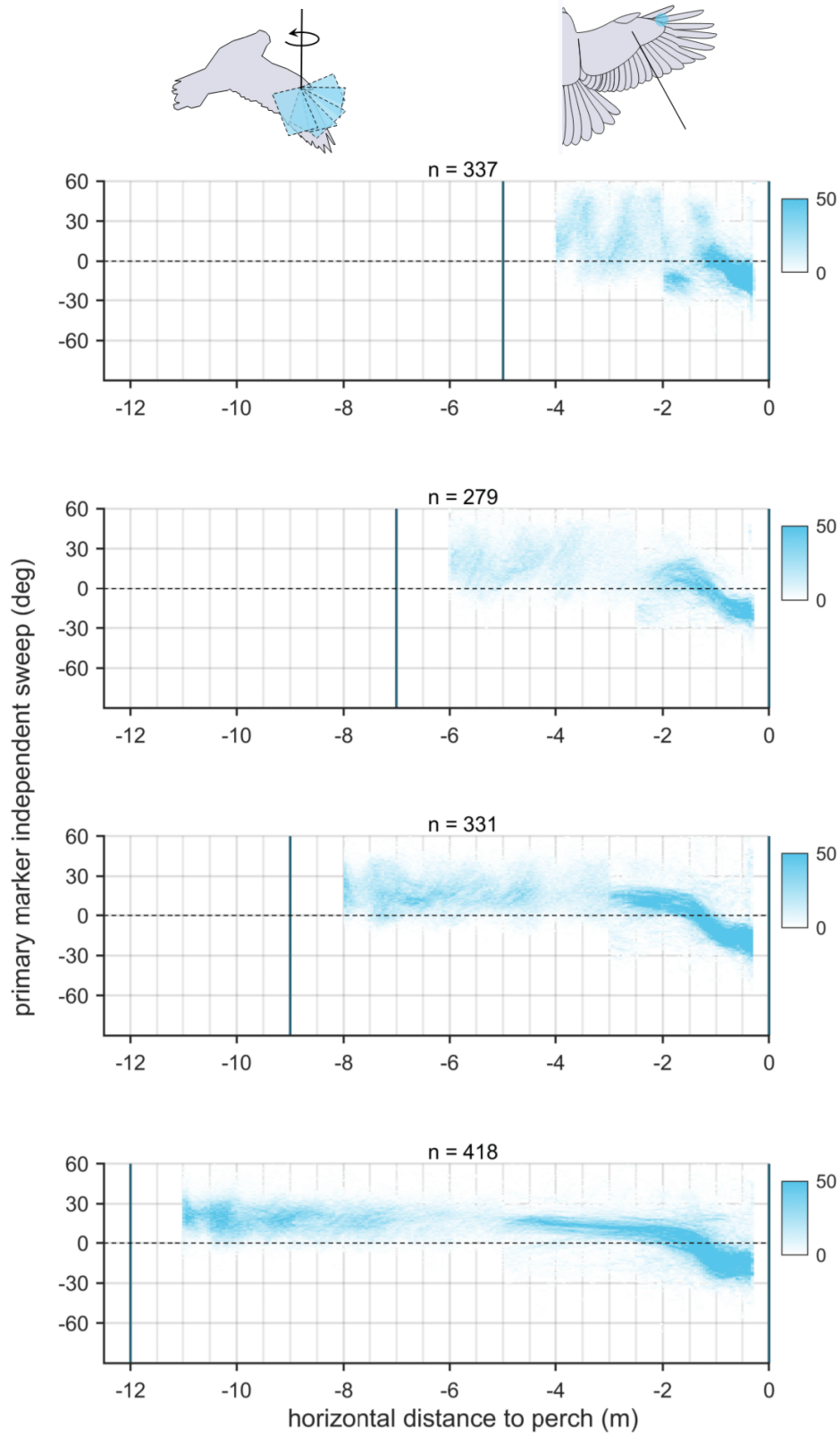
The pattern of tail  $\phi$  does not follow the pattern of tailspan directly, where the tailspan is steadily decreased and then increased with a U-shape over the whole flight.



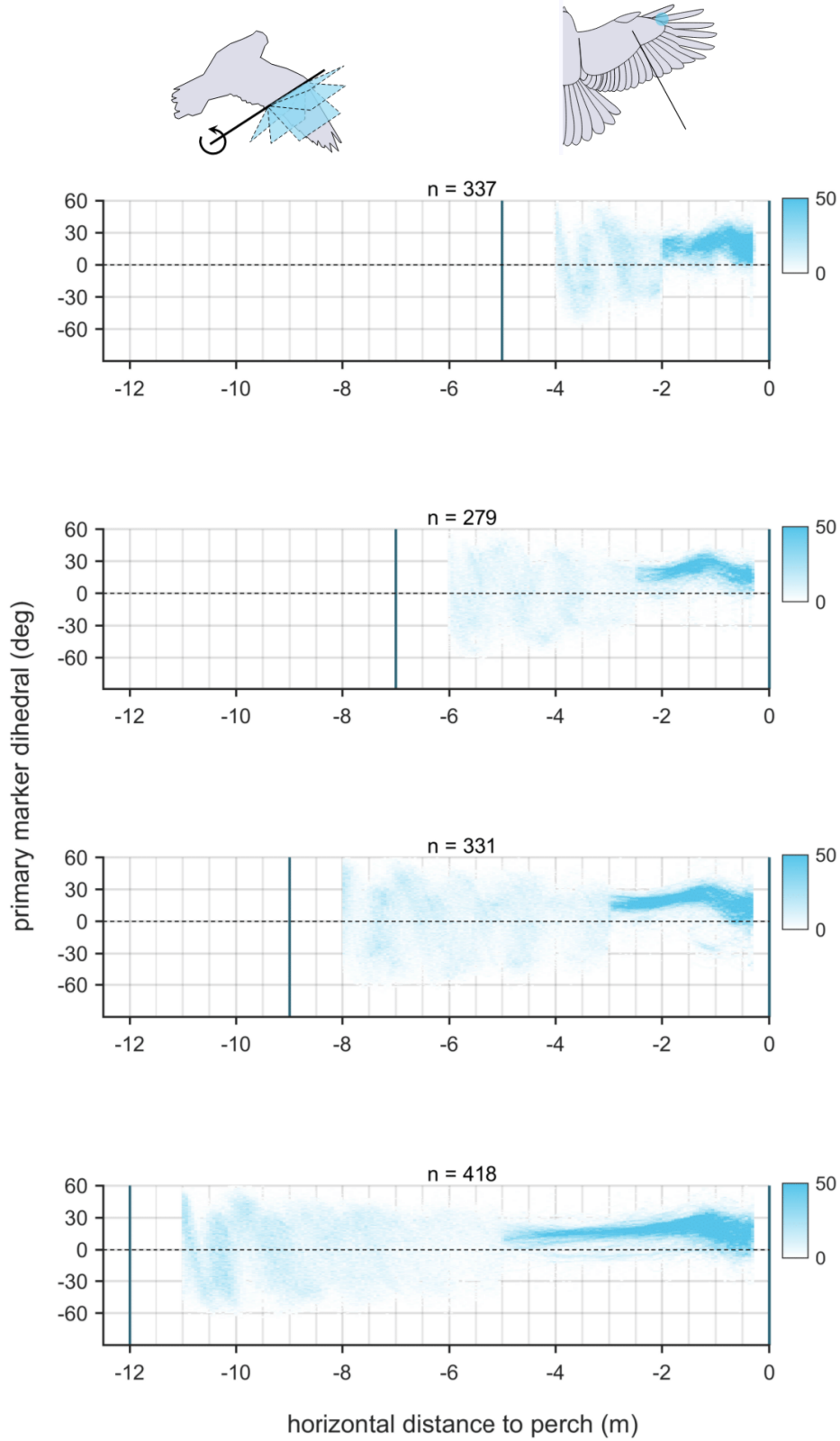
**Figure 3.40:** Independent sweep angle measured at the wingtips.  $\psi$  measured using spherical coordinates of wingtip markers relative to the CBP. Markers from all birds pooled and separated by flight distance. Positive  $\psi$  describes the marker swept ahead of the CBP.



**Figure 3.41:** 2D histograms of independent dihedral angle measured at the wingtips.  $\psi$  measured using spherical coordinates of wingtip markers relative to the CBP. Markers from all birds pooled and separated by flight distance. Positive  $\phi$  describes the marker lifted above the CBP.

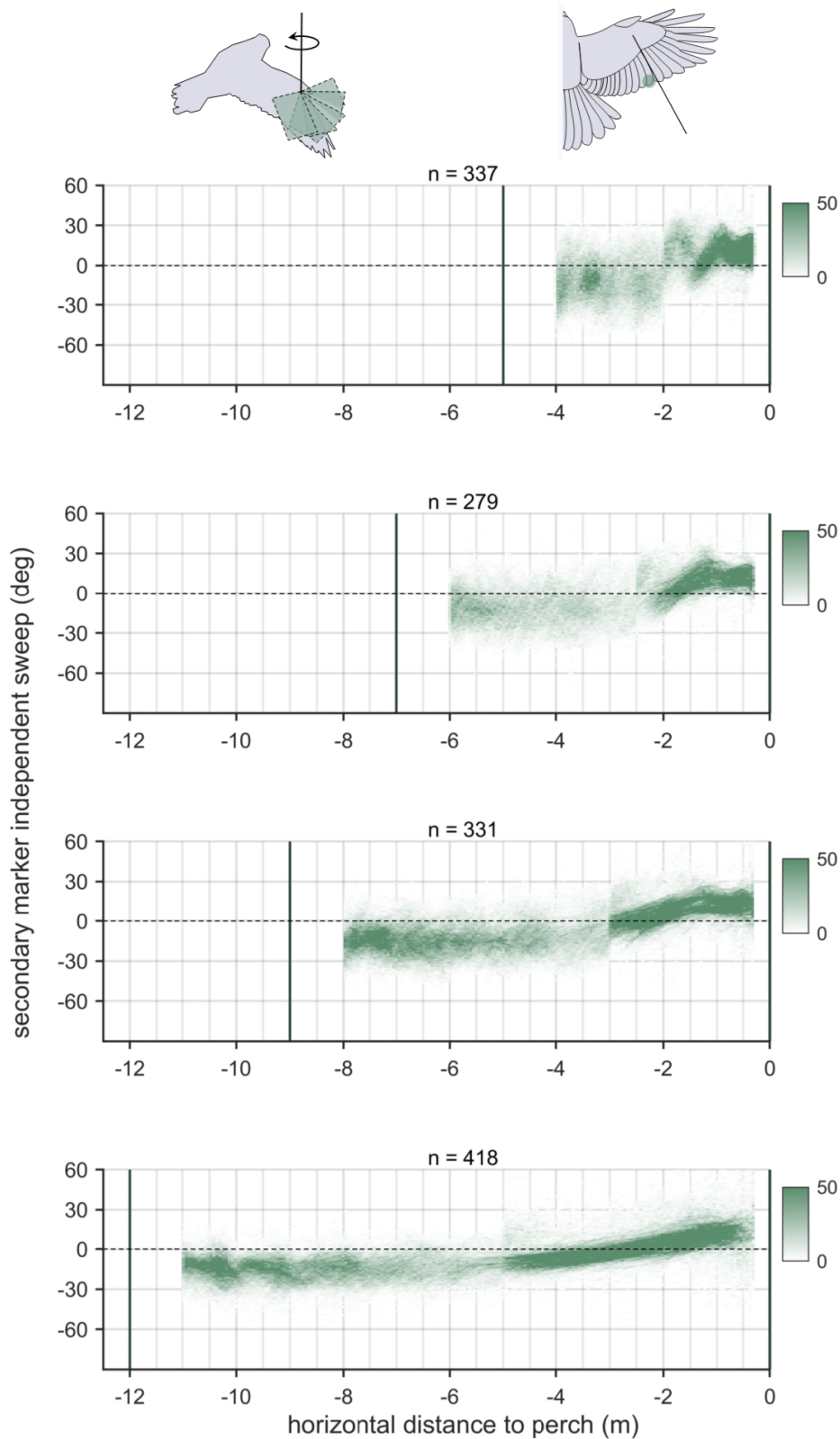


**Figure 3.42:** 2D histograms of independent sweep angle measured at the primary marker.  $\psi$  measured using spherical coordinates of primary markers relative to the CBP. Markers from all birds pooled and separated by flight distance. Positive  $\psi$  describes the marker swept ahead of the CBP.

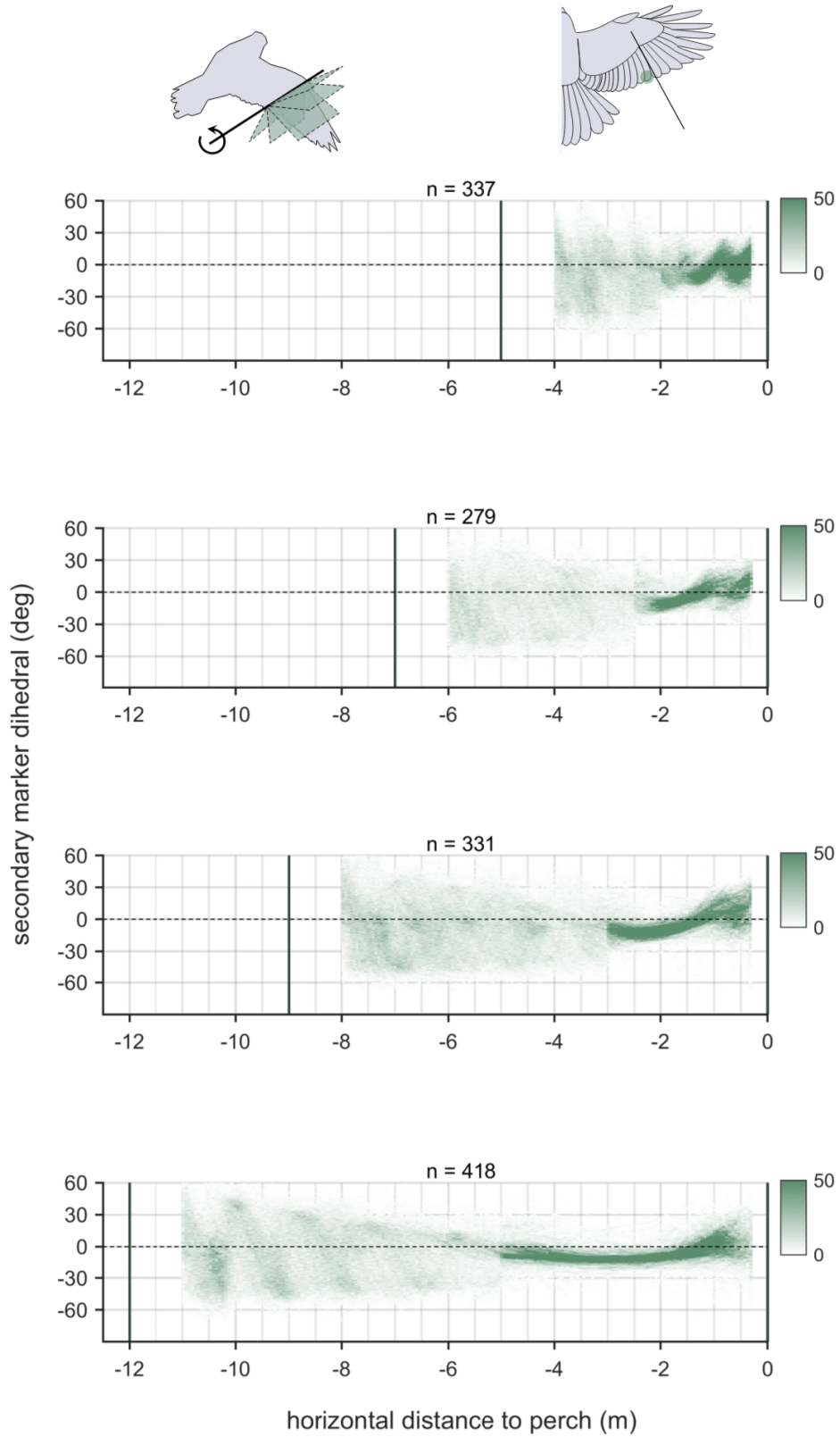


**Figure 3.43:** 2D histograms of independent dihedral angle measured at the primary markers.  $\phi$  measured using spherical coordinates of primary markers relative to the CBP. Markers from all birds pooled and separated by flight distance. Positive  $\phi$  describes the marker lifted above the CBP.

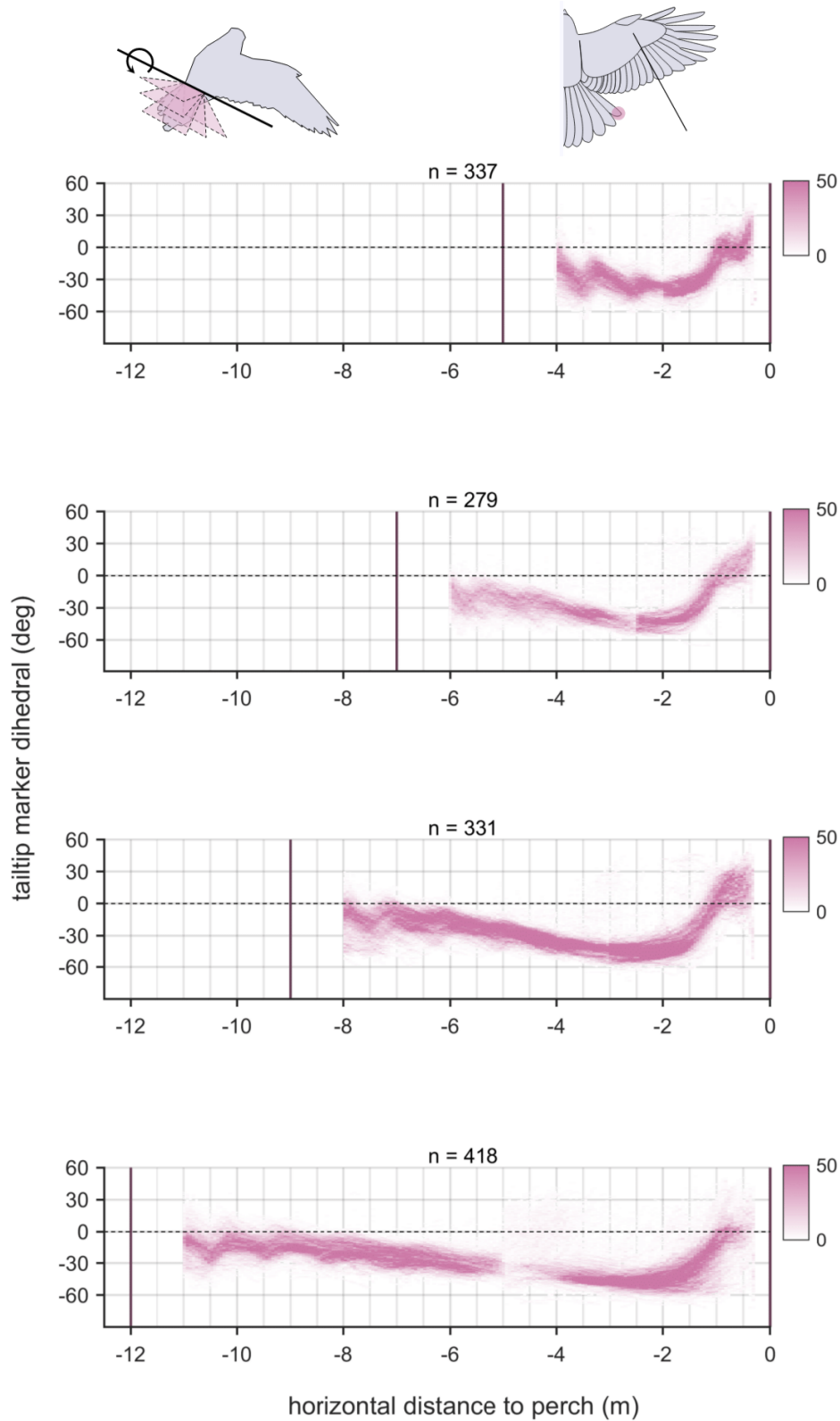




**Figure 3.44:** 2D histograms of independent sweep angle measured at the secondary markers.  $\psi$  measured using spherical coordinates of secondary markers relative to the CBP. Markers from all birds pooled and separated by flight distance. Positive  $\psi$  describes the marker swept ahead of the the CBP.



**Figure 3.45:** 2D histograms of independent dihedral angle measured at the wingtips.  $\phi$  measured using spherical coordinates of secondary markers relative to the CBP. Markers from all birds pooled and separated by flight distance. Positive  $\phi$  describes the marker lifted above the CBP.

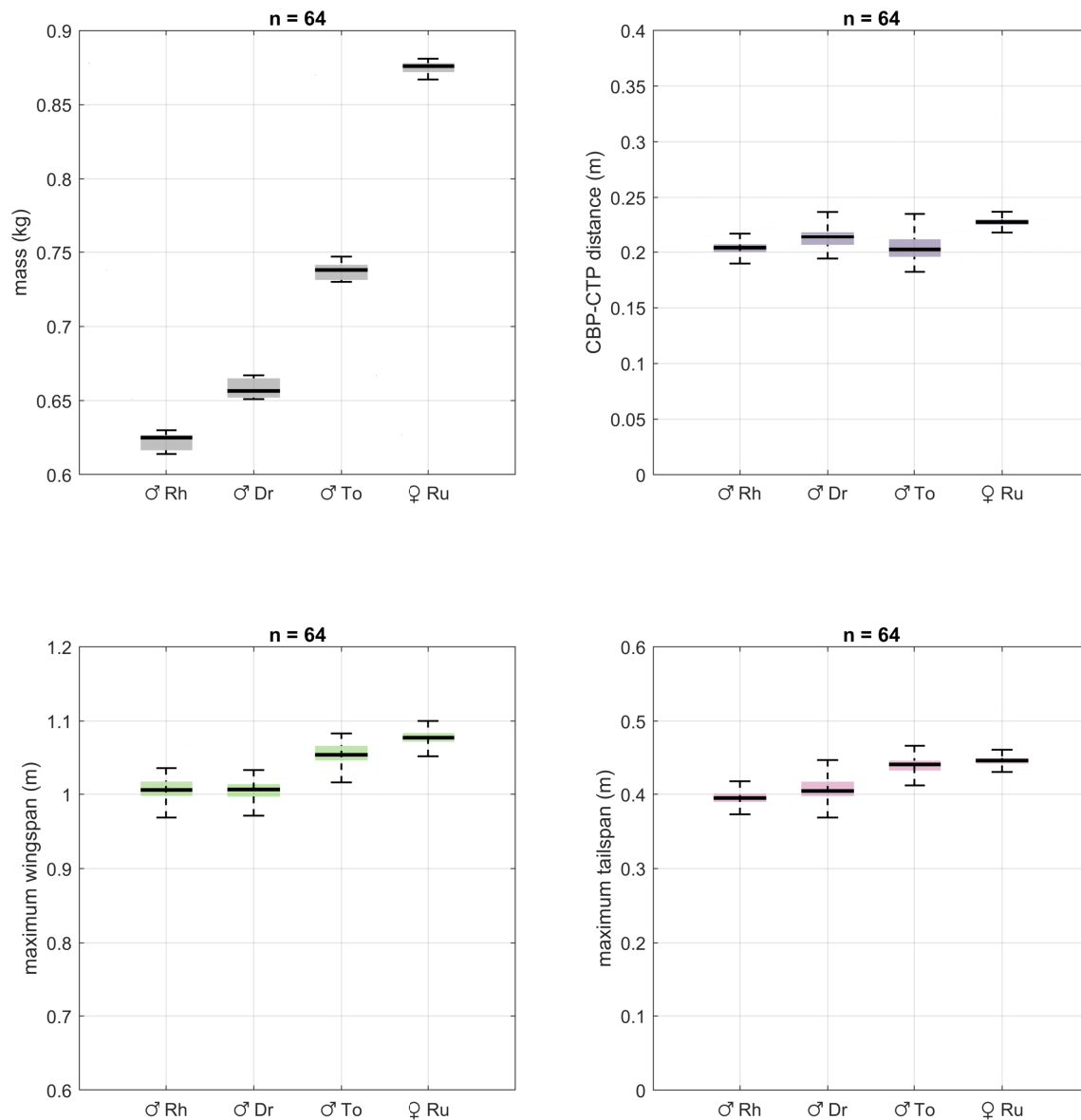


**Figure 3.46:** 2D histograms of independent dihedral angle measured at the tailtips.  $\phi$  measured using spherical coordinates of tailtip markers relative to the CBP. Markers from all birds pooled and separated by flight distance. Positive  $\phi$  describes the marker lifted above the CBP.

### 3.4.13 Individual Differences

Despite the consistency in results between the four hawks across hundreds of flights, there were individual variations in both morphology and flight behaviour. The female Harris hawk was the largest of the four birds, with average body mass of 0.87kg. Due to sexual dimorphism the males were smaller at an average of 0.74kg, 0.65kg, and 0.62kg each (Figure 3.47). To provide some estimates in size difference, the average distance between the CBP and CTP was measured from each session for each hawk; the distance only differed by <5mm. Wingspans were far more similar across the birds than body mass, differing by just 7mm between the largest female and smallest male. Maximum tailspan was also very similar, ranging between 0.4m and 0.45m.

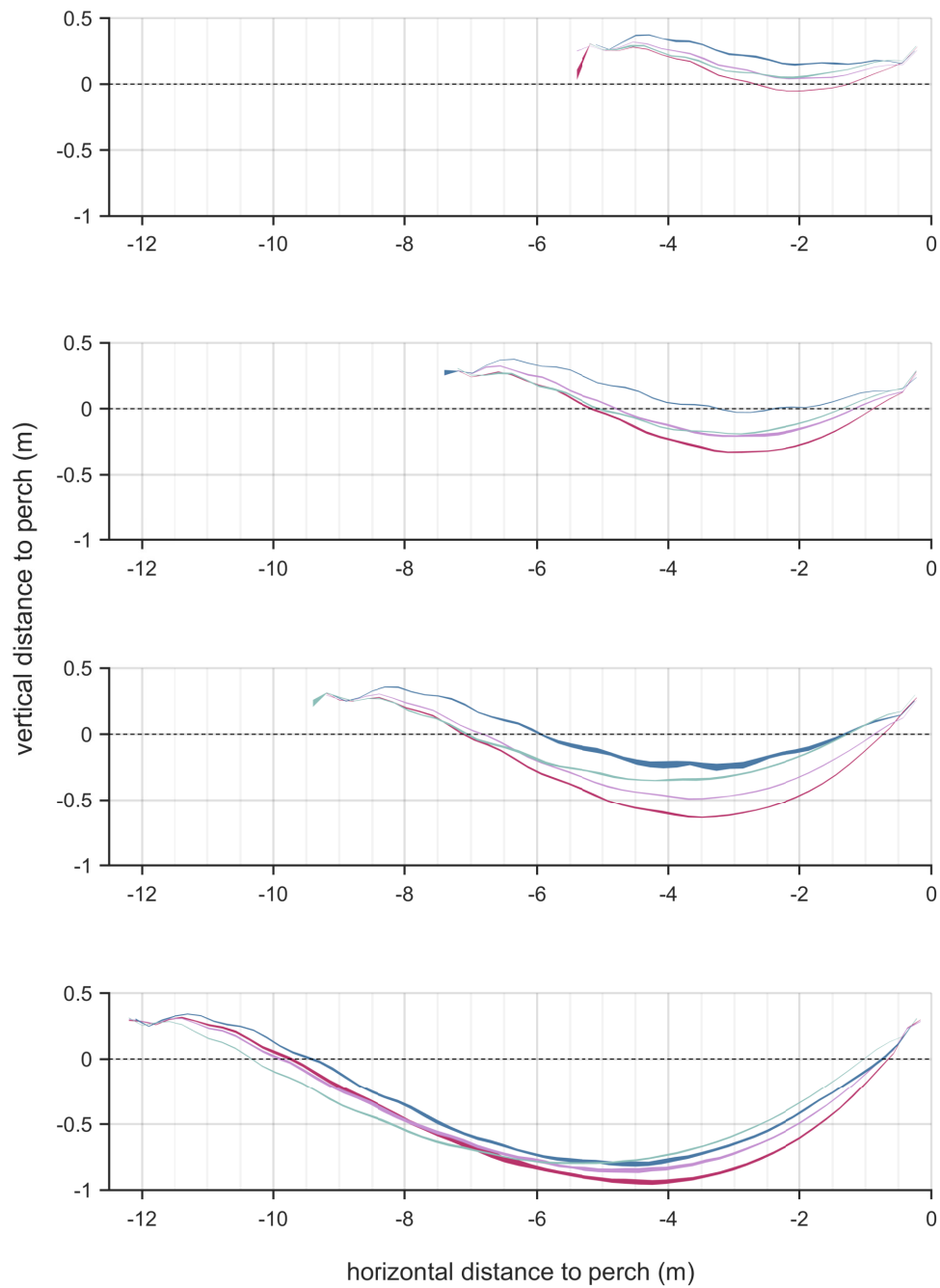
To test the individual differences in flight trajectories, the CBP vertical position for each hawk for each flight distance were binned by the CBP horizontal distance to the perch, with a bin size of 200mm. The 95% confidence intervals for the median was calculated using a bootstrap method, with 1000 iterations per bin. The upper and lower 95% confidence intervals were used plot the trajectories of each bird for each flight distance (Figure 3.48). The intervals were very tightly defined, again expressing the consistency in the hundreds of flight trajectories. In general the female hawk (shown in dark blue) flew the highest, with the exception of the ascending phase of the 12m flights, where the largest male (green) flew higher. The flight trajectories by the second smallest male (red) were the lowest during the ascending phase.



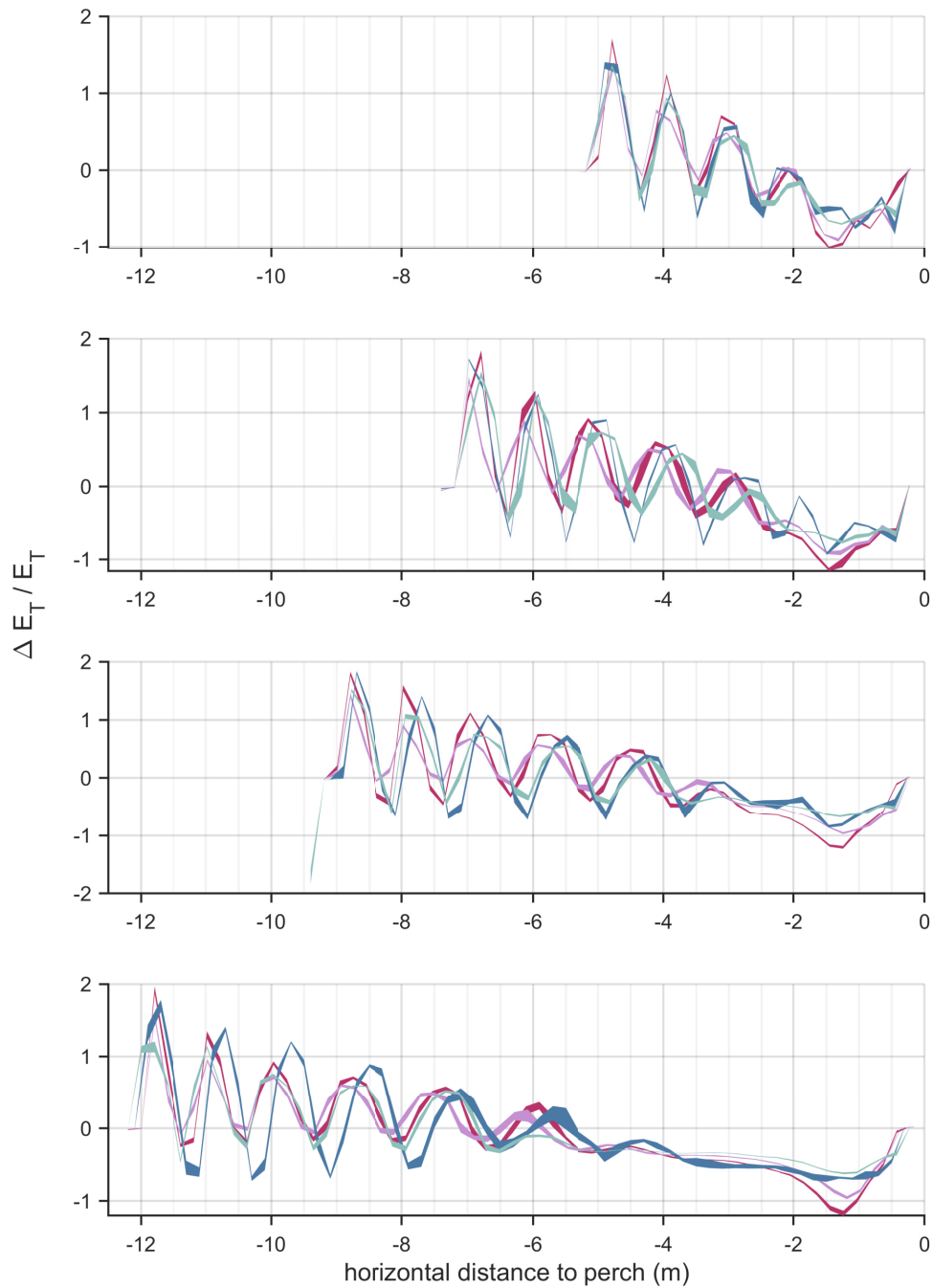
**Figure 3.47:** Morphology and mass differences between the hawks. Three hawks were juvenile males between 3-6 months, and one hawk was an adult female approximately 7 years old. Body mass was measured before each session, while spans distances between the CBP-CTP, wingtip markers, tailtip markers were averaged from each session using motion capture measurements.

To investigate individual variation in how the energetics of the hawks changed during the flights, the weighted total energy change ( $\dot{E}_T/E_T$ ) was used to normalise energy change despite different maximum total energy between the different flight distance and the hawks' different weights. Even corrected for mass, the female had greatest energy change while using flapping flight in the descending phase. The energy change of the males was far more consistent and seem to share closer wingbeat frequency. During the 12m flights the male hawks experienced a peak weighted energy loss around 1.5m from the perch which was not measured in the female hawk. The female used smoother and less extreme aerodynamic braking in the longest flights, while during the shorter flights there was a higher consistency across the four hawks.

The individual differences in wing motion is apparent in the vertical distance to the wingtip markers in the Earth reference frame, where the vertical Z axis aligns with gravity. The hawks differ in wingbeat frequencies but are highly consistent between flights. The horizontal distance travelled during a single wingbeat is longest for the female hawk, followed by the largest male, and the two smaller males were similar. In the 5m flights, however, the wingbeat pattern during flapping was highly consistent across the four individuals. In the ascending phase the female had greater overall change in wingtip vertical position.

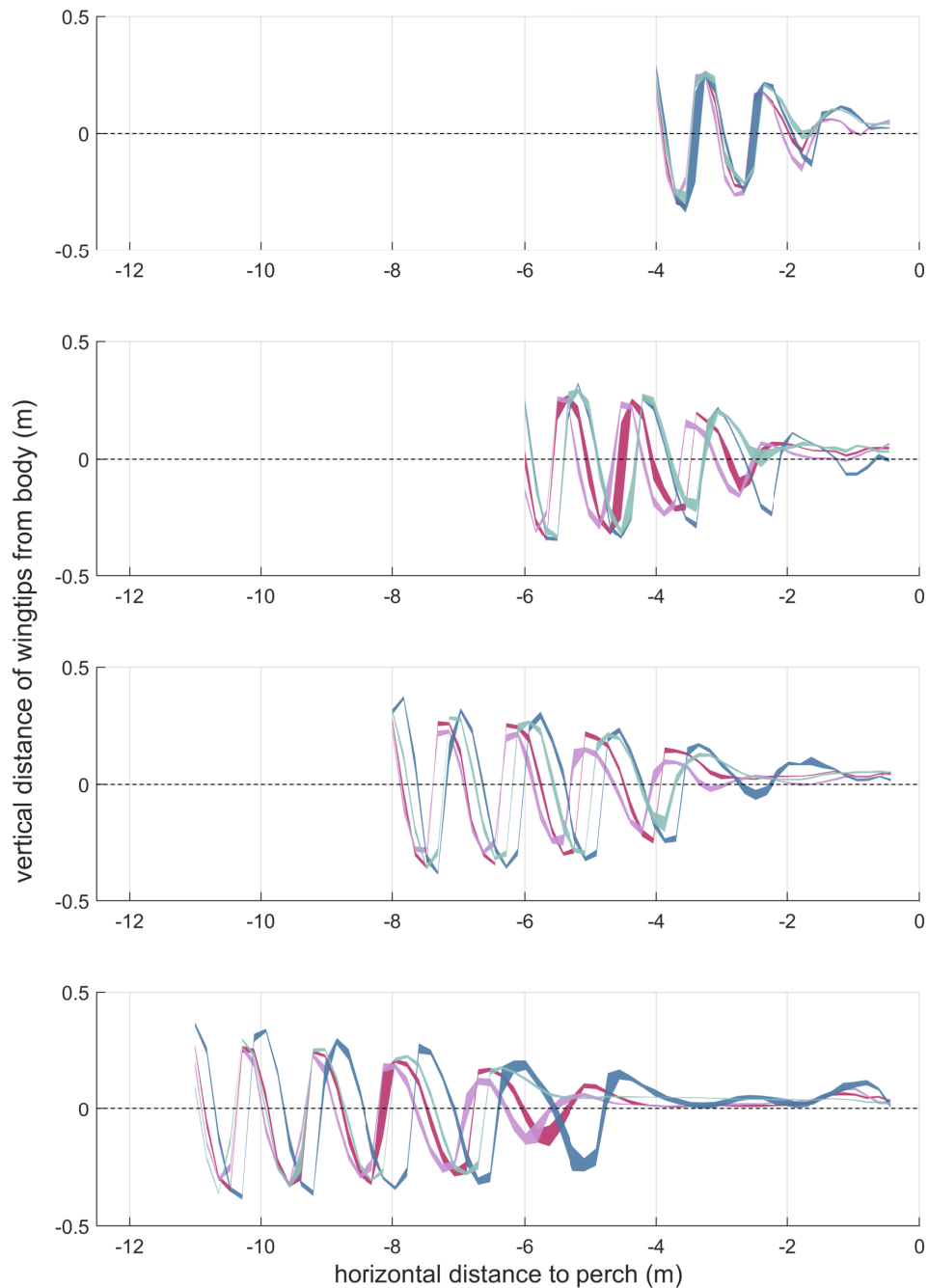


**Figure 3.48:** Individual variation in trajectory shape across the different flight distances. The vertical position of the CBP was measured from every flight separated by individual hawk and flight distance and binned by horizontal distance (bin size = 200mm). Shaded areas defined using the upper and lower confidence intervals from median values as measured using a bootstrapping method. The female (Ruby, dark blue) had highest wingspan and body mass, followed by the largest male (Toothless, green). The smaller males were similar in morphology, with the larger (Drogon, pink) and and smallest (Rhaegal, red).



**Figure 3.49:** Individual variation in weighted total energy change across the different flight distances. Total energy change was weighted by body mass to account for variation in morphology. Measurements taken from every flight separated by individual hawk and flight distance and binned by horizontal distance (bin size = 200mm). Shaded areas defined using the upper and lower confidence intervals from median values as measured using a bootstrapping method. The female (Ruby, dark blue) had highest wingspan and body mass, followed by the largest male (Toothless, green), then the smaller males were similar in morphology, with the larger (Drogon, pink) and and smallest (Rhaegal, red). Different flight distances separated from top to bottom: 5m, 7m, 9m, 12m.





**Figure 3.50:** Individual variation in vertical displacement of the wingtips from the CBP across the different flight distances. Vertical displacement of the wingtips from the CBP was measured in the Earth reference frame and markers were not rotated. Measurements taken from every flight separated by individual hawk and flight distance and binned by horizontal distance (bin size = 200mm). Shaded areas defined using the upper and lower confidence intervals from median values as measured using a bootstrapping method. The female (Ruby, dark blue) had highest wingspan and body mass, followed by the largest male (Toothless, green), then the smaller males were similar in morphology, with the larger (Drogon, pink) and smallest (Rhaegal, red). Different flight distances separated from top to bottom: 5m, 7m, 9m, 12m.

## 3.5 Discussion

Understanding the detail and complexity of wing and tail kinematics during bird flight has set a difficult challenge for scientific research. In the past, only qualitative descriptions were possible, along with some measurements between video stills. With the advent of high-speed photography quantifying kinematics became possible through photogrammetry. Measuring wing motion requires manual or semi-manual techniques to track points across the wings and body. Such tracking is often error prone due to its reliance on estimating a point consistently on a rough, feathered surface as it morphs and folds and may become obscured from view. Processing is time-consuming and as a result it has only been possible to take measurements from a handful of flights performed by a few individuals or just one animal. Motion capture technology provides real-time automatic tracking and reconstruction into 3D, allowing experimental designs with hundreds of flights testing different conditions but also recording from multiple individuals. Labelling the automatically tracked markers that are not on a rigid plate in a unique pattern still remains a challenge, but these experimental techniques provide a wealth of detail into the kinematics of manoeuvring flight at an unprecedented scale.

In previous research, there has been evidence for varying braking strategies in birds flying to land on a perch. Carruthers et al. (2007) trained an Steppe eagle landing in varying outdoor conditions, and observed the eagle preferentially choose a gliding approach to the perch while flying into the wind. However, the eagle was also observed using a flapping approach with a level or descending trajectory. In Chapter 2, photogrammetry techniques were used to quantify the kinematics during perching flights by the same Steppe eagle. The complexity and variation in kinematics were apparent despite the eagle using a similar gliding approach to the perch in the fifteen flights. Flights were recorded at two sites under different wind conditions, and the many rapid wing and tail adjustments recorded were likely corrections and compensations for wind during the final 1s before landing. Therefore there is ample evidence for different aerodynamic braking strategies under varying circumstances, not limited to flapping approach versus gliding, but also in response to different aerodynamic conditions. In addition, there is evidence the braking strategy is altered behaviourally. Green and Cheng (1998) recorded variation in aerodynamic braking in pigeon flight dependent on the novelty of a perch. The pigeons landed with greater force, thus braked less, when the perch was known to them. In this Chapter I used motion capture to investigate braking strategy by recording many hundreds of perching flights performed by Harris hawks and used automatic tracking of markers and a clustering labelling technique to measure wing and tail kinematics.

In the experimental flights, four adult Harris hawks took off from an A-frame perch and flew to land on a second A-frame perch. Measurements were taken from the entire flight and so provided detail from take-off, accelerating flight, braking, and the final pull-up to the perch. The attention in this study has been on the aerodynamic braking during the final few metres before the perch, where energy is lost and the hawks slow before impact. Experimental conditions introduced different four flight distances in order to drive a change in braking strategy.

Take-off was facilitated by the hawk jumping from the perch. There was no significant variation in take-off energetics, and the same kinetic energy and weighted energy change was measured regardless of flight distance. It would therefore appear that the hawks did not change take-off strategy dependent on flight distance. Instead the take-off is primarily used to gain necessary flight speed to facilitate flight, as aerodynamic force generation is limited at low velocity. The necessity to gain flight speed is unaffected by the eventual goal of the flight. The hawks lost height immediately and began the first wingbeat within 0.5m of take-off. The first wingbeat was the largest and the wing motion was vertical with respect to gravity and to the body, but each subsequent wingbeat was altered in multiple ways. Firstly, the duration of the wingbeat increased with each wingbeat cycle, where the hawks travelled an increasing distance with each flapping cycle. In addition, the vertical displacement of the wing markers reduced with each wingbeat, equating to a decreasing stroke path diameter. The stroke path also rotated over the flight, becoming more horizontal with respect to the body. Changes to flapping kinematics affect net aerodynamic force generation, and as the stroke path rotated, reduced in radius, and slowed, the weighted total energy change goes from net positive to net negative. This is reflected in the aerodynamic force measurements where the hawks begin producing net thrust but later wingbeats produce net drag. Acceleration is necessary to reach an optimal flight speed initially and to move towards the perch, but acceleration is quickly reduced even before the halfway point to the perch.

Changes to flapping flight kinematics also affect whole body rotation. The rapid pitch-up manoeuvre during perching flight refers to the body pitching upwards to over 90°. Body pitching is facilitated by moving the centre of pressure away from the centre of mass. The centre of mass motion could be achieved by moving anatomical parts backwards or dropping the legs, but there was no evidence for this method in the flights. Instead the centre of pressure is likely brought forwards, either through changes to the stroke path during flapping or change in angle of attack. Alternatively the wings could be swept further forwards towards the nose, or the tail elevated. Such changes to flapping kinematics and wing shape could produce the resultant torque to rotate the body, assuming no countering kinematics are applied.

A further kinematic control input was recorded during the descending phase from the tail markers. The tail dihedral angle, which measures how the tail is lifted with respect to the body axis showed the tail lowering as the hawk gained flight speed. A lowered, spread tail is normally expected during slow, manoeuvring flight due to its contribution to lift generation that can aid weight support (Thomas, 1993; Tucker, 1992). However, in this case the tail was lowered as the hawk gained flight speed and while span decreased.

As expected, maximum flight speed was affected by flight distance, where the hawks reached a maximum of  $8\text{ms}^{-1}$  in the 12m flights and just  $5\text{ms}^{-1}$  in the 5m flights. In a 12m flight, there was sufficient distance for six wingbeats followed by 5m of gliding. In contrast for the 5m flights, the hawks began braking after just 3 wingbeats. Longer flights allowed the hawks to descend until they were close to the floor before swooping up to the perch. Kinetic energy is therefore exchanged with gravitational potential energy, providing first groundspeed increase and then groundspeed reduction. In the 5m flights the trajectory was almost level, as there was not sufficient distance to fly in the U-shape trajectory and little potential energy was gained.

At the trajectory minimum approximately halfway between the two perches, the hawks ceased flapping and began a period of gliding flight while ascending to the perch. At the end of the final upstroke the wings transition to an outstretched configuration. Gliding duration was affected by perch distance, lasting as long as 5m in the 12m flights and just 2m in the 7m flights. In the 5m flights, almost no gliding occurs. While gliding has connotations with a "fixed-wing" flight configuration, the hawks rotated their wings sharply throughout the glide along with rapid kinematic alterations including changes to wing dihedral and sweep angles. Control inputs are complex during gliding despite the lack of wingbeat cycles, and affect resultant aerodynamic forces in order to precisely control flight.

Another challenge during perching flight is producing sufficient lift. The ability to support weight during flight is critical, and stall conditions where airflow is interrupted across the wing surface occur at low velocity and during extreme angles of attack. From the hawk measurements, lift remained surprisingly constant throughout the approach. As the hawk's body pitch increased during the ascending phase, the wings were rotated forwards around the shoulder such that the angle of attack was held constant. In the final 1.5m before landing, angle of attack rapidly increased as wing kinematics could not overcome the whole body rotation. However there was only a moderate fall in lift at the same time. This ability to maintain lift despite extreme flight conditions is not easily explained. Lift production from added mass effects would predict a peak of lift similar to drag. No such peak or impulse in lift force was measured. It is likely there are further unsteady aerodynamics effects at work that cannot be modelled using an airfoil.

Peak drag forces during gliding were measured around 1m before contact with the perch, and coincides with a sharp increase in wing angle of attack. Polet and Rival (2015) investigated the aerodynamics of pitching airfoils and measured large instantaneous aerodynamic forces even during deceleration to a stop. As the frontal area of the airfoil increases (parametrised as shape change number) a combination of added-mass energy transfer and vorticity generation produced high lift and drag.  $\Xi$  affects boundary layer vorticity, where a large leading edge vortex remains close to the surface while a smaller trailing edge vortex formed a shear layer. These vortices create high aerodynamic forces which are not predicted by steady-state aerodynamic theory. Additionally, added mass effects from a pitching wing also produces large instantaneous forces where the inertia from a virtual mass is added to an accelerating system due to movement or deflection of the surrounding fluid. The increase in  $\Xi$  in the hawk flights occurred during the final few metres of the gliding approach. The independent dihedral and sweep angles measured from each of the three wing markers all primarily describe a rotation of the wing chord about the shoulder throughout the glide, as the secondary marker moved upwards and forwards with respect to the CBP while the primary and wing tips markers moved down and backwards. Body pitch increased throughout the flights even before gliding began, but as the wings were rotated in the opposite direction at the shoulder,  $\alpha$  remains relatively constant. This forward rotation of the wings such that they have negative pitch with respect to the body axis continues throughout the glide, but during the last few metres the whole body rotation is much faster thus inducing a sharp increase in  $\alpha$ .

The peak in measured drag during the peak in  $\Xi$  follows the measurements and simulations by Polet and Rival (2015) well, but no peak lift force was measured in the same instant. The lift generated by the hawks was relatively smooth and constant throughout the glide, despite deceleration and high angles of attack. Lift fell in the last 1m of flight, even on occasion reaching net negative lift just before contact with the perch. As flight during perching must be highly accurate, it may be undesirable to generating an impulse of lift force within the final metre of landing. An upward force could divert the trajectory away from the target when accuracy is most critical. Polet and Rival (2015) suggest the upward force could be countered by approaching the perch from below, and in the hawk and previously measured eagle flights an ascending trajectory is favoured. However, the  $\Xi$  peak occurs when the hawk is already level with the perch. The absence of a peak lift force suggests a further mechanism is at play that has not been taken into account from the simulations and measurements with airfoils.

In the short 5m flights made by Harris hawks, the birds use a flapping final approach as an alternative braking strategy. The wing motion from kinematics measurements show rapid oscillations in both independent dihedral and sweep angles, and the displacement of the wing markers relative to the CPB also resembled the wingbeat cycle. However, these "braking wingbeats" were dissimilar to flapping during the accelerating phase. Due to the high body pitch rotation stroke path was horizontal with respect to gravity rather than vertical. The braking flaps generated net

aerodynamic forces directed backwards and away from the perch, thus slow airspeed. The contrast in aerodynamic output of the braking flaps was caused by the distinct change in wing motion. Relative to the body, the wings had net negative independent pitch throughout rather than oscillating between positive and negative independent pitch. Flapping flight is energetically more expensive than gliding flight but flapping during a rapid pitch-up manoeuvre provides aerodynamic braking over a shorter distance and does not require an ascending trajectory. The ability to brake within a minimal flight distance is valuable when flying between obstacles or encountering conspecifics, or in short flights.

The resulting drag force production and magnitude of deceleration are very similar in the final 2m before the perch for the flapping approach and the gliding approach. Despite the differences in wing motion, the rapid pitch-up characterised by extreme body pitch occurs in all flights to the perch, along with high wing angle of attack.  $\Xi$  during the braking flaps was similar to the peak in the gliding approaches, although the pattern of oscillation was quite different. In turn, the pattern of drag was distinct, resembling oscillation rather than a constant force with a pulse. Polet et al. (2015) investigated shape change number in small passerines using flap-bounding flight, and measured high  $\Xi$  that showed some correlation with braking force. The model of a pitching airfoil does not closely match that of a pitching bird using flapping flight at high  $\alpha$ , as the flapping wing motion is neglected. Therefore the predicted unsteady effects from simulations may not explain the force production well in the cases without gliding flight. While added mass effects may still occur, there are likely additional aerodynamic factors at play, particularly as vortices are influenced by local airflow over the wings. Due to whole body rotation, drag is also produced as the aerodynamic force is directed backwards during flapping.

A notable kinematic event during the flapping approach was the  $\alpha$  was briefly punctuated by rapid decreases induced by fast backwards rotation of the wing at the shoulder, occurring twice in the 5m flights and once in the 7m flights in the final 1.5m before contact. However they were absent in the 12m flights. This control input has also been measured in the Steppe eagle, and resemble wing "flicks". The function of such rapid corrections is unknown, but observations from the feathers on the high speed videos from the eagle suggest they coincide with high backwards flow across the wings, as the feathers were bent upwards at the start of the flick. High angles of attack cause flow separation across the wing, and such flow conditions are not unexpected. These flicks could be in response to such flow separation from sensory signals in the feathers and work to change the vorticity at the wing surface to continue generating lift. Further investigation with aerodynamic models and wind tunnel measurements is required to understand their purpose.

Despite the differences between strategy, in both flapping approaches and gliding approaches the  $\theta_B$  and  $\alpha$  were very similar. Both reached the same maximum value at the same position relative to the perch. In addition, in the final 2m regardless of braking strategy the deceleration magnitude, drag force production, and loss of kinetic energy were close to identical. It is therefore indeterminate whether aerodynamic braking was increased to compensate for lowered potential energy gain in the shorter flights. It is striking that despite the very different aerodynamic effects from such different control inputs the overall result is reasonably similar. In the critical final 2m of flight to land on a perch high  $\alpha$  and deceleration create challenging flight conditions just as the bird requires accurate positioning, effective braking, weight support at low airspeed, and energetic efficiency simultaneously. Success under such tight constraints leads to little variation in outcome, particularly in behaviours which are high-risk, high-reward, and high-cost. However, as selected by evolution, the means of producing the careful balance of outputs can differ greatly, as apparent in the variety of flight behaviours bird species use to approach a perch, including gliding, flapping, flap-bounding, and hovering. Even in a simple experimental setup using four individuals from one species, a range of braking strategies emerged to solve the task.

There was a remarkable consistency in flights from the different individuals. Wing marker positions coincided across hundreds of flights in the same position in the room. Experimental conditions were carefully controlled, and it appears that without influences from wind conditions flights are more or less identical across different sessions. There are variations between individuals which are seemingly driven primarily by body mass, and perhaps to a lesser extent morphology. The female hawk, who weighed almost 0.12kg more than the smallest male, showed deviation from the others in wingbeat duration and also with greater wing motion during gliding flight in the ascending phase. However, such differences in wingbeat positions faded in the 5m flights. The differences in longer flights may reflect optimisation or preference – while it is possible for the female to use wingbeats with shorter duration and smaller stroke path distance, with the lenience of a longer flights these differences between individuals manifest more clearly. In short flights, restrictions collapse the variation down to a single outcome from all the hawks. Differences in trajectory are still apparent even in the 5m flights, however, and the males still lose more energy relative to their size in the final 1.5m of flight. Flight performance and kinematics were affected by body mass but remained consistent under the same experimental conditions. In order to explore the full range of strategy during manoeuvring flight, future experiments that include wind conditions are essential. However including different individuals with morphological variation is also critical for measuring the scope of aerodynamic ability even within a single species.

In addition to the consistency of flights relative to the room, there was also surprisingly low variation in wing marker position relative to the CBP across hundreds of flights. Using a simple cluster method it was possible to label feather markers across millions of frames from over a thousand flights. While angles have been used to describe the wing



motion about the body, angles are reasonably misleading due to their non-independence. The variation along the wing surface is also not well described from angular measurements alone, and can mask the complexity of twist and camber variation. Pooling the markers with their relative position provides a different perspective of wing motion. Instead the markers exist in tightly defined configurations and move between them. Flight modes that are difficult to describe using a range of dihedral, sweep, pitch and span measurements instead clearly exist within distinct patterns or modes. Efforts into clustering insect kinematics to specific flight modes has begun as a result of large data set collections of untethered flights by flies (Dawson et al., *in press*), and in the future this may also be applied to bird flight. Future work using more markers along the wing surface could also provide for the first time accurate twist measurements, which has remained elusive in kinematics research in bird flight. It may be possible to distil the function from the complexity of wing and tail kinematics using machine learning techniques applied to thousands of flight behaviours recorded with motion capture. Flight manoeuvres and acrobatics are hugely complex and the challenge to understand even a handful is daunting. However, birds perform them with a limited range of movements and so a bottom-up approach is a reasonable one. Any behaviour can be separated into the desired goal with respect to a target or state, and the control inputs used to enact it. In this way natural selection has used simple anatomical rotations to achieve an impressive array of flight manoeuvres and acrobatics in behavioural ecology across bird species.

The motion capture system used to record the Harris hawk data set is a novel method for detailed measurements flight behaviours on an unprecedented scale. Previous studies into bird flight have been highly restricted by recording equipment, the ability to quantify flight kinematics, and the time required for analysis. As a result there have been few bird flight experiments with large data sets examining the detail and complexity of flight mechanics and control. The differences between individuals of the same species during flight has also been rarely investigated. From the data it is clear that the hawks showed similar patterns of behaviour but each had unique techniques and performance in the task. Given sufficient flight distance, the wingbeat patterns, height of glide, onset of glide, and specific wing kinematics were all subtly different between the four hawks, though variation collapsed in the shortest hawk flights, as the constraints for success were very high. Variation is the cornerstone to how life evolved, and although physical constraints reduce the window of opportunity, variation is measurable even during simple accelerating flight.

## 3.6 Conclusions

1365 flights between two perches were performed by Harris hawks and recorded and reconstructed using motion capture. A marker labelling method was used to identify different markers. As a result the data set is both large but



also accurate and has high detail. Four individuals were recorded and their individual variation was measured in both performance (energetics) and technique (trajectory and wingbeat cycles). The perch-perch distance was too short in the 5m flights to provide braking through height gain, and the birds used flapping flight from take off until landing. In the absence of gain in potential energy and without the ability to use an extended glide, hawks used flapping flight to the perch. Energetics was affected by flight distance, both from the change in potential energy gain and from maximum flight velocity. During the flapping approaches, wingbeats generated higher drag force than thrust due to horizontal tilt of the stroke path, slower wingbeat frequency and smaller stroke path amplitude. The hawks achieved similar braking ability despite using different flight patterns and despite differences in maximum groundspeeds. The aerodynamics of the rapid pitch-up was measured and how angle of attack, flight velocity influence lift and drag forces, along with providing evidence that added mass effects affect braking.

The detailed wing and tail measurements were used to explore the wing and tail morphing following analyses from the eagle flights. As the hawks were flown indoors and were not influenced by wing speed, flights were highly stereotyped even in the position of the upstroke and downstroke in the recording volume. Independent wing pitch rotation at the shoulder was clear from the measurements, and this kept angle of attack constant by turning in the opposite direction to the body. Angle of attack was then increase later in the rapid pitch-up manoeuvre and only within 2m of the perch. During body rotations large kinematic adjustments are required to sustain aerodynamic forces during flight.



# Control of Braking During Perching Flight

## 4.1 Abstract

Control of braking is critical for preventing dangerous collisions. Here the braking control method is compared between a captive Steppe eagle, Harris hawks, and wild passerines. Braking could in principle be controlled using direct measurements of relative distance, velocity, or time to contact as feedback variables, but accurate estimation of any of these is challenging at high-speed. Instead, use of a related optic flow variable known as  $\dot{\tau}$  to control braking has been tested previously in perching birds, as it provides a heuristic indication of whether to increase or decrease braking in order to stop at the perch. Evidence for constant  $\dot{\tau}$  and constant braking was found in the two bird of prey species. The eagle used a precise braking strategy while the hawks used a so-called controlled collision, in which the bird's groundspeed does not reach zero at the point of perching.  $\dot{\tau}$  was held constant in hawks even when groundspeed varies non-linearly with time at the onset of deceleration. Due to the nature of the flight, flap-bounding passerines cannot hold  $\dot{\tau}$  nor braking constant. Instead their a strategy of controlling  $\dot{\tau}$  to be near-constant is discussed. A moving perch was used in an attempt to manipulate  $\dot{\tau}$  and determine whether constant  $\dot{\tau}$  is a symptom of controlled braking or the cause. Passerine velocity was much higher than perch velocity and so  $\dot{\tau}$  was only weakly affected, suggesting passerines could functionally treat a moving perch as fixed for braking control.

## 4.2 Introduction

Performing a safe landing is fundamental to flight, and birds regularly land on objects in their environment in order to rest, forage, hide, and tend to their young. While routine, perching flight comes with high risks of collision with the target which could lead to injury or death. It is therefore necessary for a bird to slow on approach while avoiding stall. This could be achieved through hovering flight, where motion is highly controlled. A hovering bird's position and velocity are stabilised while weight is supported, and flight appears relatively motionless. However, sustained hovering flight energetically expensive and is unsustainable in most bird species for long periods. Instead, groundspeed must be reduced on approach to a perch through controlled braking. Different species of birds use a range of flight behaviours, including gliding, flapping, and flap-bounding, but regardless of mechanism, achieve aerodynamic braking prior to contact with the perch.

Precise braking control with respect to the perch is necessary to ensure touchdown occurs at low groundspeed. Braking ability in any animal or vehicle is limited and deceleration must be applied over a long enough period to be effective. In addition, flying at low airspeed can lead to stall conditions, particularly when coupled with the high angles of attack used by birds prior to contact (see Chapters 2 and 3). Thus braking too strongly or for too long could lead to uncontrollable conditions that detriment weight support. For such precise braking control, it would at first appear the bird requires information about its relative speed and distance to the target. Complex processing is required for estimating distance and speed, and due to the speed of flight the entire braking manoeuvre typically occurs in less than a second. Continuous estimation of distance, speed, or time to contact on such short timescales may be beyond the processing capability of birds, particularly as visual information for flight is mostly mostly monocular (Martin and Osorio, 2008).

Rather than judging relative distance and speed to the perch, braking can be controlled using an estimate of the time to contact. There is evidence that time to contact can be estimated from optic flow information for controlling time-sensitive behaviours in humans and other animals including birds. Input to the motion vision system can be described as an optic flow field, where objects and scenery move across the retina. Lee (1976) first investigated the braking problem and identified the optical variable  $\tau(t)$ , defined as the ratio between an oncoming object's optical size and its rate of expansion in the visual field over time. If speed is constant throughout the approach,  $\tau$  becomes an estimate for time to contact. Subsequently, Lee and Reddish (1981) argued that  $\tau$  is used to trigger time-critical events prior to a collision by measuring the timing of wing closure in diving gannets. Similar findings were reported in human subjects for interceptive motion (Lee et al., 1983).

Wagner (1982) first tested the use of  $\tau(t)$  for the landing flight of flies, and found evidence that deceleration is triggered at a critical value of  $\tau(t)$ . The same method was used by Davies and Green (1990) to test whether  $\tau(t)$  was used to time foot extension in perching pigeons and Harris hawks. Foot extension is a rapid action in both these species, and is apparently triggered at a specific time to contact. The authors found evidence that  $\tau(t)$  had little variation on approach in the hawk flights, and therefore concluded foot extension was controlled with respect to this parameter. In contrast,  $\tau(t)$  showed high variation on approach in pigeons due to head bobbing motion during the approach. Head bobbing has unclear visual function, but seems unique to landing behaviour in pigeons (Green et al., 1994).

However, aerodynamic braking is not a discrete action executed at a critical time before contact. Any use of  $\tau(t)$  to control braking is further confounded by decelerating on approach –  $\tau(t)$  is only an accurate estimate of time to contact if velocity is constant. For continuous control, Lee (1976) demonstrated that the rate of change of tau ( $\dot{\tau}$ ) can provide information on whether the current rate of braking is sufficient or excessive, to ensure a smooth touchdown at the perch.

Following Lee et al. (1993),  $\tau(t)$  is defined as

$$\tau(t) = \frac{x(t)}{\dot{x}}(t) \quad (4.1)$$

where  $x(t)$  is the one-dimensional position of the bird with respect to the perch as a function of time  $t$ . The perch is located at  $x = 0$  and a bird approaches from a negative position  $x(t) < 0$ , such that  $\dot{x}(t) > 0$ . The variable  $\tau(t)$  has units of time. In the case of approach with constant velocity,  $\tau(t)$  is equal to the time to contact with the perch.

Differentiating with respect to time ( $t$ ), Equation 4.2 gives the dimensionless quantity:

$$\dot{\tau}(t) = 1 - \frac{x(t)\ddot{x}(t)}{\dot{x}(t)^2} \quad (4.2)$$

As a dimensionless variable,  $\dot{\tau}$  is independent of units for time or length and does not require an internal model for detection and application in braking.

## 4.2.1 Hypotheses from Taudot Theory of Braking Control

Lee et al. (1993) consider three alternative strategies employed during braking control; either (i) acceleration  $\ddot{x}(t)$  is held constant such that  $\ddot{x}(t) = k$ , or (ii)  $\dot{\tau}(t)$  is held constant such that  $\dot{\tau}(t) = c$ , or in a special case (iii) where both conditions are held simultaneously such that  $\dot{\tau} = -0.5$ .

### (i) Constant deceleration scenario

In the constant deceleration ( $\ddot{x}$ ) case, the equations of motion are given by:

$$\begin{aligned}\ddot{x}(t) &= c \\ \dot{x}(t) &= \dot{x}_0 + ct \\ x(t) &= x_0 + \dot{x}_0 t + \frac{1}{2}ct^2\end{aligned}\tag{4.3}$$

where  $c < 0$  is constant.

### (ii) Constant $\dot{\tau}$ scenario

In the constant  $\dot{\tau}$  case, it follows by definition:

$$\begin{aligned}\dot{\tau} &= k \\ \tau &= \tau_0 + kt\end{aligned}\tag{4.4}$$

where  $k < 0$  is a constant. Substituting the second of Equations 4.4 into Equation 4.1 yields the first-order ordinary differential equation:

$$\dot{x}(t) = \frac{x(t)}{\tau(t) + kt}\tag{4.5}$$

with the general solution:

$$x(t) = a(\tau_0 + kt)^{\frac{1}{k}}\tag{4.6}$$

where  $a$  is a constant. With  $x(0) = x_0$ , such that  $a = x_0 \tau_0^{-1/k}$ , differentiating twice leads to the equations of motion:

$$\begin{aligned}x(t) &= x_0 \tau_0^{-\frac{1}{k}} (\tau_0 + kt)^{\frac{1}{k}} \\ \dot{x}(t) &= x_0 \tau_0^{-\frac{1}{k}} (\tau_0 + kt)^{-1+\frac{1}{k}} \\ \ddot{x}(t) &= x_0 \tau_0^{-\frac{1}{k}} (1-k)(\tau_0 + kt)^{-2+\frac{1}{k}}\end{aligned}\tag{4.7}$$

which hold for any value of  $\dot{\tau} = k$  where  $k$  is constant. The position of the bird relative to the perch at the time of contact  $t_c$  is by definition  $x(t_c) = 0$ . Using this substitution in the first of Equations 4.7, contact occurs at  $t_c = -\tau_0/k$ . Using the second of Equations 4.7, it is seen by inspection that  $\dot{x}(t_c) = 0$ , and therefore the bird comes to a complete stop on arrival at the perch.

Holding constant  $-1 < \dot{\tau} < -0.5$  predicts that at the current braking magnitude, a collision will occur with the perch. As a result, to stop at the perch while maintaining  $-1 < \dot{\tau} < -0.5$  requires a progressive increase in braking on approach. Conversely, holding constant  $-1 < \dot{\tau} < -0.5$  predicts that the current braking magnitude the bird will stop short, and so progressive decrease in braking is required. Holding  $\dot{\tau}$  at exactly -0.5 predicts that at the current braking magnitude, the bird will stop exactly at the target and so braking ought to be held constant. In this way, the value of  $\dot{\tau}$  when held constant provides information on the severity of an incoming collision given the current braking.

### (iii) Constant deceleration and constant $\dot{\tau}$ scenario

Under the scenario where both  $\ddot{x}$  and  $\dot{\tau}$  are held constant at  $\ddot{x} = c$  and  $\dot{\tau} = k$  respectively, Equations 4.3 and 4.7 are simultaneously valid. Equating the right hand sides of the respective acceleration equations we have:

$$c = x_0 \tau_0^{-\frac{1}{k}} (1 - k)(\tau_0 + kt)^{-2 + \frac{1}{k}} \quad (4.8)$$

The right hand side of which is independent of time as required if and only if  $k = -0.5$ , such that:

$$c = \frac{x_0}{2\tau_0^2} \quad (4.9)$$

Hence, it is possible for both  $\ddot{x}$  and  $\dot{\tau}(t)$  to be held constant, but only if these are held at the unique values of  $\dot{\tau}(t) = 0.5$  while Equation 4.9 is true. Substituting the identity  $k = -0.5$  into Equation 4.7 and then 4.9, the equations for motion in this scenario may be written as:

$$\begin{aligned} x(t) &= x_0(2\tau_0 + t)^2 / (4\tau_0^2) \\ \dot{x}(t) &= x_0(2\tau_0 + t) / (2\tau_0^2) \\ \ddot{x}(t) &= x_0 / (2\tau_0^2) \end{aligned} \quad (4.10)$$

Lee et al. (1993) tested constant taudot theory in landing pigeons and found their "controlled collision" strategy was to hold  $\dot{\tau}(t)$  constant at a value of around -0.7, while increasing braking on approach, and the pigeons retained some velocity upon impact with the perch. The authors also evaluated conclusions made by Davies and Green (1990), suggesting instead that head bobbing aids view of its feet with respect to the perch. This both guides foot extension at a critical value of  $\tau(t)$ , and controls braking during perching. Lee et al. (1991) provided further evidence that hummingbirds use  $\dot{\tau}$  when docking with a feeder, for perching bats which use an audio information to judge  $\dot{\tau}(t)$  (Lee et al., 1992a), and for somersaulting humans (Lee et al., 1992b). More recently, evidence for use of  $\dot{\tau}(t)$  has also been found in bumblebee landing behaviours, with moving patterns used to manipulate the retinal image flow field (Baird et al., 2013).

For its simplicity as a visual cue,  $\dot{\tau}(t)$  is merely descriptive of a collision event. A car rolling passively to collide with a wall, decelerating from friction, would have a  $\tau(t)$  value increasing  $-1$  to  $0$  despite being uncontrolled. A constant  $\dot{\tau}(t)$  measurement could also be achieved in a landing that was controlled using direct measurement of relative position and velocity with the target. Therefore precaution should be taken when interpreting  $\tau(t)$  measurements.

Applying linear regressions to non-constant  $\dot{\tau}(t)$  measurements will also merely provide an average value for  $\dot{\tau}(t)$ , which will be around  $-0.5$  in any decelerating approach to a target, both uncontrolled and controlled. There should be caution, therefore, in interpretation of results - constant  $\dot{\tau}$  is not evidence for its use.

As  $\tau(t)$  is related to the relative position and velocity between the bird and the perch, in a fixed target scenario  $\tau(t)$  is therefore only determined by bird motion. In order to hold  $\dot{\tau}(t)$  constant, the bird must vary its velocity in response to the perch motion. Thus to truly determine whether  $\dot{\tau}(t)$  is used during landing in birds, the experiment must manipulate the motion of the perch.

## 4.2.2 Hypotheses from Taudot Theory for Braking Control to a Moving Perch

Equations 4.1 to 4.10 have described the kinematics of the bird's motion with respect to the fixed target, in this case a perch. It follows that for any other coordinate system the following identities can be defined:

$$\begin{aligned} z(t) &= x(t) + p(t) \\ \dot{z}(t) &= \dot{x}(t) + \dot{p}(t) \\ \ddot{z}(t) &= \ddot{x}(t) + \ddot{p}(t) \end{aligned} \tag{4.11}$$



where  $z(t)$  is the position of the bird with respect to the perch, with position  $p(t)$ . In experiments, the bird is presented with a sinusoidally swinging perch.

### Sinusoidal Perch Motion

The horizontal movement of the perch is described by the equation of motion:

$$p(t) = \bar{p} + r \sin[A \sin(\omega t + \varphi_0)] \quad (4.12)$$

where  $\bar{p}$  is the time-averaged position of the perch,  $r$  is the radius on which the perch oscillates,  $A$  and  $\omega$  are the angular amplitude and circular frequency of the oscillation, and  $\varphi_0$  denotes the phase of the oscillation at time  $t_0$ . Differentiating:

$$\dot{p}(t) = r\omega A \cos(\omega t + \varphi_0) \cos[A \sin(\omega t + \varphi_0)] \quad (4.13)$$

$$\ddot{p}(t) = -r\omega^2 A \left( \sin(\omega t + \varphi_0) \cos[A \sin(\omega t + \varphi_0)] + A \cos(\omega t + \varphi_0)^2 \sin[A \sin(\omega t + \varphi_0)] \right) \quad (4.14)$$

#### (i) Linear Target Hypothesis

The first hypothesis for braking control towards a moving target assumes the bird uses a virtual target defined as a fixed position in space. This virtual target could be a predicted collision position or some other stationary position with an offset, for example the perch pivot. In the general case, we therefore have  $\dot{p}(t) = \ddot{p}(t) = 0$  and  $p(t) = q$ , where  $q$  is some constant. It follows that  $\dot{z}(t) = \dot{x}(t)$  and  $\ddot{z}(t) = \ddot{x}(t)$ , such that the only position of the bird is altered by this transformation, and the perch motion does not alter braking response. Such a control method would have the bird treat the perch as a fixed target (see Equation 4.1) with an offset, and the previous hypotheses for  $\dot{t}(t)$  can be tested: constant braking, constant  $\dot{t}(t)$ , or both constant  $\ddot{x}(t)$  and  $\dot{t}(t)$ .

#### (ii) Continuous Target Hypothesis

An alternative hypothesis for braking control assumes the bird responds to the movement of the perch on approach. The general case can therefore be defined:

$$\tau_z(t) = \frac{z(t)}{\dot{z}(t)} \quad (4.15)$$

where  $\tau_z(t)$  describes both the motion of the bird and the motion of the perch. The previous hypotheses can be tested using  $\dot{\tau}_z(t)$ .

However, if  $\dot{x}(t) \gg \dot{p}(t)$  then  $\dot{\tau}(t) \approx \dot{\tau}_z(t)$ , because the velocity of the bird overwhelms the velocity of the perch and any compensatory response would be difficult to measure. It would therefore be hard to distinguish control using a continuous target from control to a linear target.

## Aims

In this study the aim was to compare and contrast braking control in multiple species of bird performing perching flight. The species recorded were one male captive Steppe eagle; four Harris hawks (three males, one female); and multiple wild passerines (Blue tits and Great tits), each using varying braking strategies resulting from differences in body size, flight pattern, outdoor and indoor conditions, and perch type. The aim was to discuss the evidence for use of tau theory to control braking. tau theory can be used to control braking using a variety of methods, and evidence for these are tested. While previous Chapters discuss gliding approaches, this study also uses perching flights by wild passerines using bounding flight in order to investigate the challenges involved with intermittent control with respect to tau theory. Finally an oscillating perch was used with the wild passerines with the aim to understand braking control with a moving perch. Using a moving perch in experiments should better test the use of  $\dot{\tau}(t)$  as a control variable during perching.

## 4.3 Methods

### 4.3.1 Experimental Procedures

Three separate experiments were used to record flight trajectories to a fixed perch. In the first, a male captive Steppe eagle was trained to land on a wooden frame in an outdoor field, and in subsequent recordings, to fly and then land on a falconer's arm at a cliff-site with higher wind speed. The trajectory analysis is described in detail in Chapter 2, and this analysis uses the same data set. Points on the right and left shoulder were manually tracked from four camera views and the mean central point was reconstructed into a point in 3D space using photogrammetry. Time of contact was defined as the foot touchdown on the perch. Flight duration ranged between 0.50 – 1.07s, with reconstruction beginning at the start of the gliding ascent to the perch where the eagle is decelerating. The eagle flew an average horizontal distance of 3.9m (around 5 body lengths). Each reconstructed trajectory was smoothed with a cubic spline and the origin defined as the perch position. The Steppe eagle had an average wingspan of 1.8m, and average mass of 2.5kg.

In the second experiment, four Harris hawks were recorded using high-speed motion capture during perching flight. The hawks flew between two perches set 12m apart in sessions of 20-30 flights over 15 experimental days. Flights were recorded indoors and had no influence of wind speed. A total of 273 flights were used for analysis, as selected for the quality of marker reconstruction. For full details of the methodology for recording and tracking of trajectories, see Chapter 3. Three hawks were males between aged around 4-6 months, and a 7 year old female adult. The males weighed between 0.67 – 0.75kg, while the female weighed 0.87kg. The four hawks had similar wingspans between 1.0 – 1.1m (see Figure 3.47 on page 121). Flights were cut to just the ascending phase of the flights where the birds are decelerating, and covered around 4m in distance (around 8 body lengths) to coincide with the trajectory minimum. Flights lasted on average around 1s. There was no reference footage that could accurately show the moment of foot touching the perch, and so an estimate was used; contact with the perch was defined as the first frame where the horizontal distance to the perch is less than 0.3m, in order to account for the foot length. Measurements from energetics correspond well to this estimate. Trajectories were described using the perch as the origin and were smoothed using a cubic spline.

In the third experiment, wild passerines were recorded over a 3 day period in February 2017 at a Field Station near Wytham Woods, Oxford, UK. A 0.5m bird feeder was fixed to a wall and filled with sunflower seeds to attract wild Blue tits and Great tits. A pair of hidden high-speed cameras were used to record perching flights with a shutter speed of 0.02s and frame rate of 500Hz. Both cameras were synchronised and manually post-triggered. The distinctively pale

face-masks of Great tits and Blue tits were semi-automatically tracked using a custom digitising software by Hedrick (2008). During the flapping cycles, the face is covered with the wings and so manual adjustments to the tracking were required. The cameras were calibrated using a method identical to those described in Chapter 2 in order to reconstruct 3D trajectories. The perch was fixed to a wall and this was used to fix the vertical axis of the coordinate system, where the  $y$  axis was defined parallel with the wall. The  $z$  axis was defined pointing up with respect to gravity, as measured with a plumbline. Finally the  $x$  axis was defined orthonormal to the  $y$  and  $z$  axes, where positive pointed from the camera towards the perch. Trajectories were defined relative to the perch and smoothed with a cubic spline. Flights were cut to 0.5s before contact with the perch to analyse the decelerating part of the flights, and on average the birds covered a distance of 1.3m (equivalent to 10 body lengths). Time to contact was defined as the foot touching down on the perch. Flights were recorded during dates with moderate wind speed ( $< 5\text{ms}^{-1}$ ). Of the 20 recorded flights, the majority were of Blue tits ( $n = 17$ ), and individuals of this species on average weigh 11g with a wingspan around 0.18m. Great tits on average weigh 18g and have a wingspan of 0.24m.

An additional experiment again recorded wild Great tits and Blue tits using an identical recording method, but the perch was set to have an oscillating motion. A 0.5m bird feeder filled with sunflower seeds was fixed to a motor at a central pivot. The perch motion was controlled using sinusoidal oscillations with varying frequencies – 0.1, 0.2, 0.4, 0.6, 0.8, and 1 Hz. The perch swung 30° back and forth along the plane of a wall. The wild birds would not normally approach the perch for frequencies beyond 1 Hz, and aborted without landing. The same recording methods with a pair of high speed cameras were used as described in the fixed perch experiments. A successful landing was defined when the bird made contact with the perch and folded its wings to rest. After a successful landing was recorded, the perch frequency was randomly set to a different speed setting. In addition to the semi-automatic tracking of the bird, the perch was also tracked using custom digitising software by Hedrick (2008). The tracked perch motion fitted to a sinusoidal motion model in order to clean tracking jitter and also to track the perch while it is occluded by a bird. In total 91 flights were used for analysis. All perch speeds were pooled into the same data set for analysis.

### 4.3.2 Trajectory Analysis and Statistics

For every flight trajectory from the fixed target experiments, the horizontal distance  $x(t)$  from a point on the bird to the perch at every time-step was first quantified. In the case of the eagle and hawks, the tracked point was on the back of the bird, while in the passerines the point was on the face mask close to the eye. The horizontal velocity  $\dot{x}(t)$  was calculated as the derivative of a cubic spline fitted to  $x(t)$ .  $\tau(t)$  was calculated using Equation 4.1.

In the moving perch experiments,  $x(t)$  was defined as the distance between the bird and a virtual perch position where the bird made contact. This provides a virtual target, i.e. a stationary target with an unknown offset from the perch position, that the bird could hypothetically use as a target for controlling braking and ignore the motion of the perch. Similarly,  $\dot{x}(t)$  and thus  $\tau(t)$  was calculated with reference to this final perch position. Following an alternative hypothesis where the bird controls its flight continuously with respect to the perch,  $z(t)$  was defined as the closing distance to the perch at every time-step.  $\dot{z}(t)$  was therefore defined as the closing velocity, and these are used to define  $\tau_z(t)$ .

In order to test **Hypothesis 1** and examine whether braking is constant, linear regression was applied to  $\dot{x}(t)$ . The calculated  $R^2$  value is a measure of the extent to which the variation in  $\dot{x}(t)$  is explained by a linear function of time. The regression coefficient provides an estimate for the value of  $\ddot{x}(t)$  in the linear  $\dot{x}(t)$  model. The same rationale is used to test a linear function for  $\tau(t)$  and the subsequent estimate for  $\dot{\tau}(t)$  as outlined in **Hypothesis 2**. In the case that a linear model is a good fit for both  $\dot{x}(t)$  and  $\dot{\tau}(t)$ , this provides evidence for **Hypothesis 3**. As an additional test for **Hypothesis 3**, only the number of flights that had a  $\tau(t)$  slope estimate within  $-0.5 \pm 0.05$  were counted.

In the control of braking to a moving perch, a bird could use a linear control method by aiming towards a stationary point, or it could control braking continuously to correspond to the motion of the perch. It is only possible to distinguish these methods if  $x(t)$  significantly diverges from  $z(t)$ , which can only occur if perch velocity is comparable to the bird's velocity.  $\dot{x}(t)$ ,  $\dot{z}(t)$ ,  $\tau(t)$ , and  $\tau_z(t)$  were also used to test **Hypotheses 1-3**.

The data are time series data, and so the error between consecutive data points is non-independent. The regression slope estimator however is unbiased and is not expected to produce a higher or lower estimate of the true value of slope. Therefore a confidence interval test can be used to analyse the median regression slope. Here we use a bootstrap method with 1000 iterations to calculate the 95% confidence interval values for the linear regression slope estimates from  $\dot{x}(t)$ ,  $\dot{z}(t)$ ,  $\tau(t)$ , and  $\tau_z(t)$ . The interquartile range was also calculated for the regression slopes.

## 4.4 Results

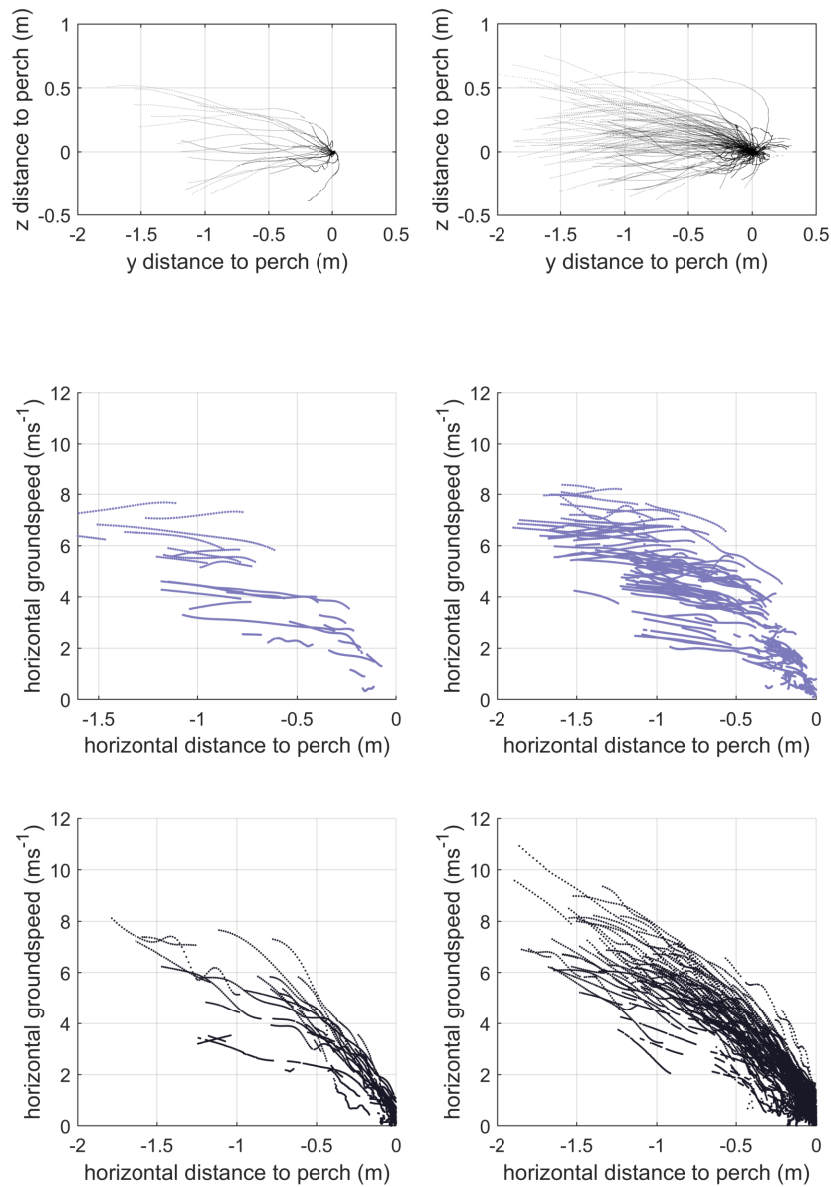
### 4.4.1 Approach to the Perch

The Steppe eagle and Harris hawks used gliding flight in the final approach to the perch, where the wings are outstretched at, or close to, maximum span. No flapping wingbeat cycles were measured in any of the approaches made by the raptors, although adjustments to the wing configuration were present (see Chapters 2 and 3 for wing measurements). Both the eagle and hawks rapidly lost groundspeed during the 4m ascent to the perch (Figure 4.3). The eagle flew in different wind conditions and initial groundspeed varied between  $7\text{ms}^{-1}$  and  $15\text{ms}^{-1}$ . The eagle flew into the wind preferentially, and swooped up to the perch gaining 1.5m of height. In contrast, experiments with Harris hawks were recorded indoors and without the effect of the wind. The hawk flights were highly stereotyped due to the controlled experimental conditions even across many days and between different individuals. The hawks reduced their velocity from  $8\text{ms}^{-1}$  during the perching manoeuvre, and flew around 1m up to the perch. The trajectories of the Harris hawks were highly stereotyped due to the controlled experimental conditions (see Figure 3.9 on page 67), and while the Steppe eagle showed greater variation in behaviour, the recorded flights show similar trajectories (see Figure 2.4 on page 32).



**Figure 4.1:** Example flight of a wild Great tit to a moving perch at 1Hz. Bounding flight is characterised by periods of flapping punctuated by ballistic periods where the wings are folded against the body.

The wild passerines flights were very dissimilar to the raptors, the wild birds approaching the perch from a range of directions and were constrained only by the position of the wall that supported the perch (Figure 4.2). As the perch was fixed to a wall, most of the flights occurred along a plane with low variation in the  $x$  direction, and there was bias towards an approach in a positive  $y$  direction due to environmental clutter. Small passerines use flap-bounding and



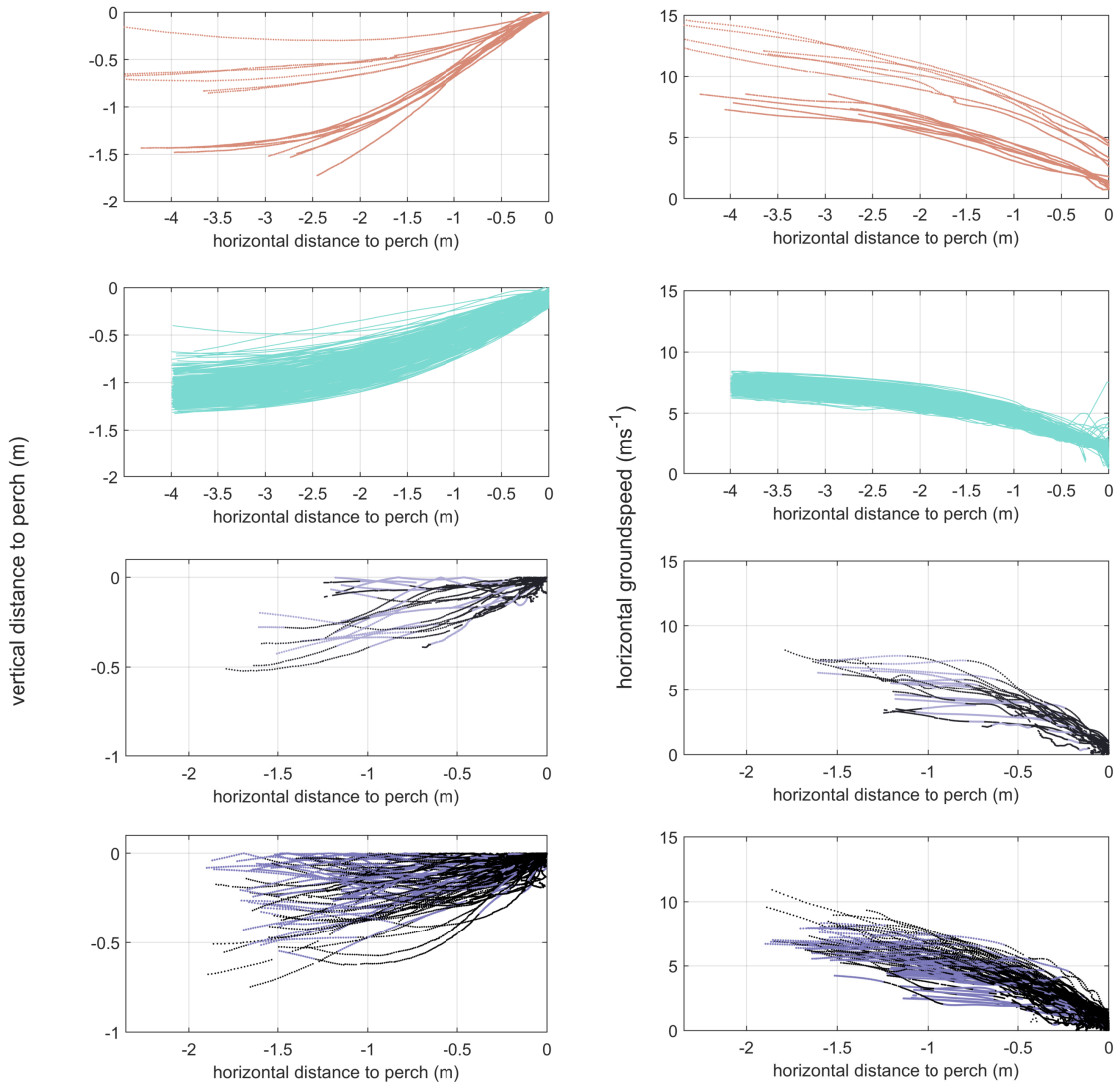
**Figure 4.2:** Measurements from flights to a fixed perch (left column,  $n=20$ ) and moving perch (right column,  $n=91$ ). Top row shows trajectories to the perch in a global axis system, with +y direction bias caused by environmental clutter. Horizontal groundspeed during bounding periods (middle row, purple) and periods with wing control (bottom row, black).

glide-bounding flight (Tobalske, 2001), where periods of flapping or gliding are punctuated with ballistic phases (Figure 4.1). During bounding, the wings are folded against the body and flight control is limited. In the perching flight recordings, the wild Blue tits and Great tits travelled an average horizontal distance of 1.5m and a vertical distance of 0.7m. The passerines seemed to prefer an approach from above rather than below. Maximum flight speed varied between  $4 - 9\text{ms}^{-1}$ . Observations from the high speed videos recorded show the Great tits and Blue tits use highly variable approaches with a range of flight behaviours. The passerines in general first approached the perch using extended ballistic phases punctuated by a flapping wingbeat (flap-bounding), as expected for long-distance flight. The flight kinematics of horizontal groundspeed over time during the ballistic phase was characteristically constant over time as expected in ballistic trajectories (Figure 4.2). In comparison, the periods of flight using wing control showed decrease in horizontal groundspeed over time.

Longer periods of flapping are also common where multiple wingbeats occur while the bird uses an upright posture. Such flight configuration would lead to aerodynamic braking from high angle of attack wingbeats (Polet and Rival, 2015), but seem to facilitate weight support at low airspeed and perhaps aid visual information collection about the perch. The birds were observed using head movements and head turns to inspect the perch or other nearby conspecifics during this flight configuration. The small perch (50mm) attached to the feeder is likely difficult to observe from further afield, so this behaviour may assist in accurate positioning for landing. Dramatic changes in course also occur after such upright flapping periods, either to direct the trajectory towards the perch or away. These extended flapping periods are similar to hovering flight, but the birds rarely maintained near-zero groundspeed and are always travelling towards the perch. In addition the passerines are not usually observed using extended upright flapping within the close vicinity of the perch (i.e. within grabbing distance). Instead close-range wing control is more commonly in the form of a single wingbeat and alternated with brief periods of bounding (flap-bounding). Often such upright extended flapping periods are not observed, and birds seemingly fly straight to their target using flap-bounding. Flap-gliding is also seen but less commonly than other flight behaviours. The birds normally used an upright posture during gliding, and could be functionally similar to the rapid pitch-up glides measured in raptors.

Perhaps unexpectedly, there was no obvious difference in flights behaviour to the oscillating perch versus the stationary perch (Figure 4.2). The frequency of landings reduced particularly at higher perch speeds, pointing to a reluctance of the wild birds to approach the feeder. Additionally a greater number of "failed perching" events were observed, where a bird approached the perch but then after an extended upright flapping period, changed course and accelerated away, seemingly making a decision to abort.





**Figure 4.3:** Comparison of flight trajectories and groundspeed between a Steppe eagle (orange,  $n = 15$ ), four Harris hawks (green,  $n = 273$ ), and wild Great tits and Blue tits (purple) performing perching flight. Wild birds recorded flying to a stationary perch (3rd row down,  $n = 20$ ) and to a moving perch oscillating with a sine function at different frequencies (4th row,  $n = 91$ ). It should be noted that a larger scale for the x-axis is used for the wild passerine data. The hawks and eagle used gliding flight on approach to the perch, while the wild passerines used a mixture of flight behaviours including flapping, bounding, and gliding. Ballistic phases marked in a lighter colour.

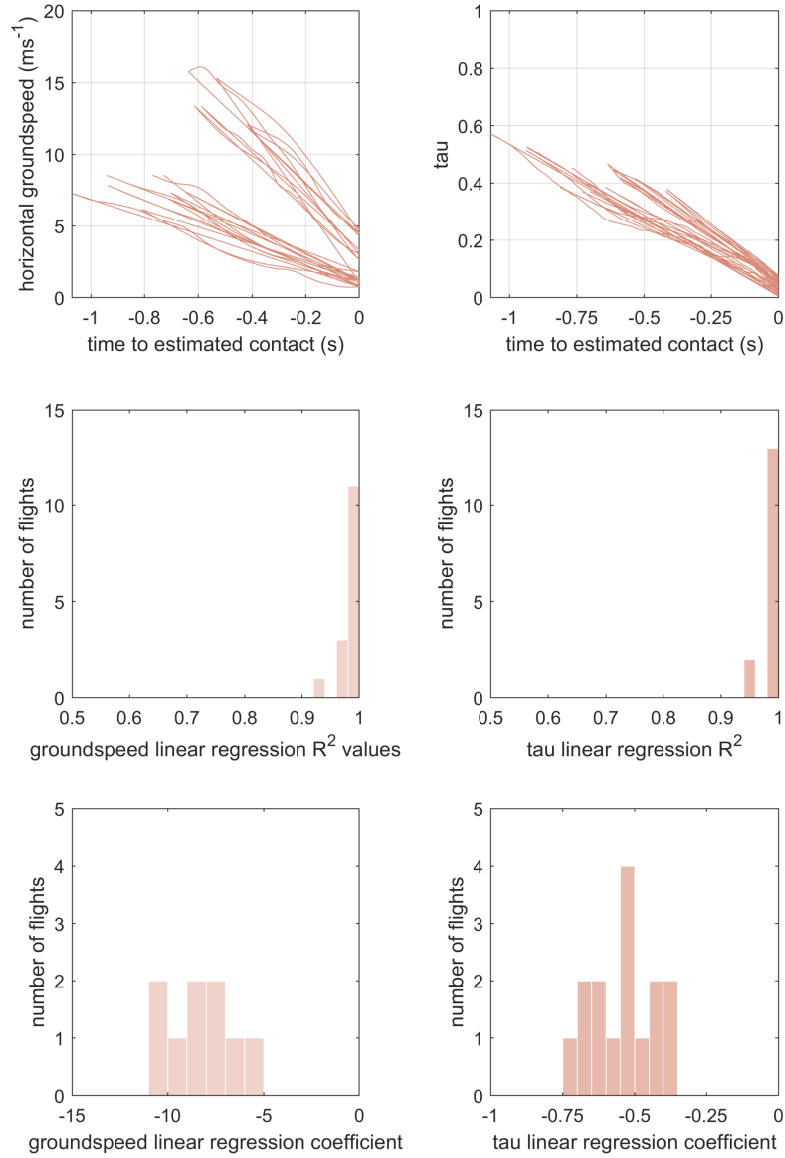


## 4.4.2 Control of Braking in Steppe Eagle Flights

The horizontal groundspeed ( $\dot{x}(t)$ ) was measured during perching flights by a Steppe eagle at the tracked midpoint of the shoulders (Figure 4.4). From a linear regression model, the  $R^2$  values had a 95% CI of 0.98 to 0.99 from the median, and so a linear model explains the vast majority of variation in  $\dot{x}(t)$  within each flight. The median regression slope had a 95% CI of  $-17.6$  to  $-7.7\text{ms}^{-2}$  and an interquartile range of  $10.4\text{ms}^{-2}$ , and this variation in braking magnitude arises from the range of maximum groundspeed values across the different flights. There is therefore good evidence for constant braking in the Steppe eagle flights (**Hypothesis 1**).

For  $\tau(t)$ , the 95% CI for the median  $R^2$  ranged between 0.990 and 0.996, again suggesting the linear model explains most of the variation in  $\tau(t)$  within each flight, providing evidence for **Hypothesis 1**. With evidence for both constant braking and constant  $\dot{\tau}(t)$ , **Hypothesis 3** was tested by calculating the slope regression estimates for  $\dot{\tau}(t)$ . The 95% CI for the median regression slope were  $-0.60$  and  $-0.45$ , and with an interquartile range of  $0.18$ . Out of 15 flights, 8 had regression slopes within a close range of  $-0.5 (\pm 0.1)$ , in line with **Hypothesis 3**.

All statistics are summarised in Tables 4.1 on page 160 and 4.2 on page 161.

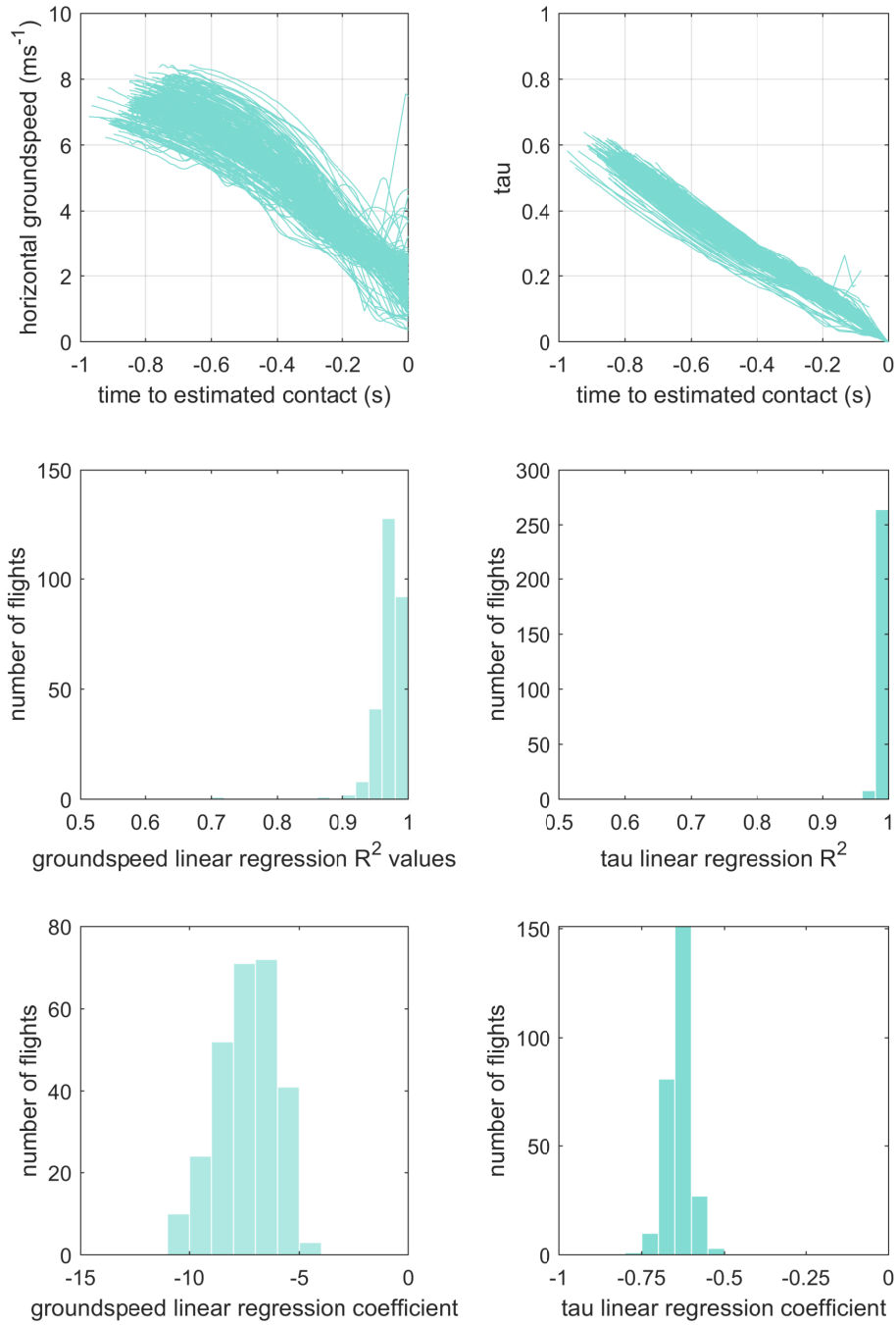


**Figure 4.4:** Measurements of horizontal groundspeed and tau in a Steppe eagle performing perching flight ( $n = 15$ ). Linear regressions were used to analyse the extent of variation in horizontal groundspeed explained by a linear function of time, or constant braking.  $R^2$  values and regression coefficients were calculated, where the linear coefficient provides an estimate for the braking constant of a linear model fitted to the horizontal groundspeed data. This was repeated for tau ( $\tau(t)$ ), in order to test for constant  $\tau(t)$  and its estimated slope.

### 4.4.3 Control of Braking in Harris Hawk Flights

The  $\dot{x}(t)$  measurements from Harris hawks did not appear strictly linear with respect to time (Figure 4.5). Braking is increased over the first 0.25s of the ascending flight to the perch, before remaining constant for the final 0.5s. The median  $R^2$  values from the linear regressions of  $\dot{x}(t)$  had a 95% CI range of -0.97 to 0.98, which suggests the majority of variation is explained by a linear model, but to a lesser degree than the eagle measurements. There is therefore some supporting evidence for **Hypothesis 1**, but increasing braking is apparent in the data. The gradual increase in braking at the start of the glide is likely inevitable due to physical constraints where braking power cannot be applied instantaneously, and it is likely the eagle has a similar  $\dot{x}(t)$  shape if the data went back further. From the linear model, the 95% CI for the regression slope median ranged between  $-7.42$  to  $-7.07\text{ms}^{-2}$  and interquartile range of  $1.82\text{ms}^{-2}$ , which again confirms the low variation in the recorded flights due to highly controlled flight conditions.

In contrast to  $\dot{x}(t)$ ,  $\tau(t)$  measurements seem highly linear over the same interval, and the  $R^2$  95% CI ranged between 0.995 and 0.996. There is strong evidence for constant  $\dot{\tau}(t)$  in the hawks' flights and thus **Hypothesis 2** as a result. Testing the regression slope estimate for constant  $\dot{\tau}(t)$ , the median value had a 95% CI range between -0.64 and -0.63 and low interquartile range of 0.04. These values follow taudot theory for applying increasing braking and keeping  $\dot{\tau}(t)$  constant at a value lower than -0.5, which results in a "controlled collision" with the perch. The groundspeed values at the point of contact verify that the hawks reach the perch with remaining inertial energy and thus an impact force. Of the 273 flights, just 3 had a  $\dot{\tau}(t)$  regression slope close to -0.5 ( $\pm 0.1$ ). There is no strong evidence therefore that the braking strategy in **Hypothesis 3** is used by Harris hawks during perching flights.

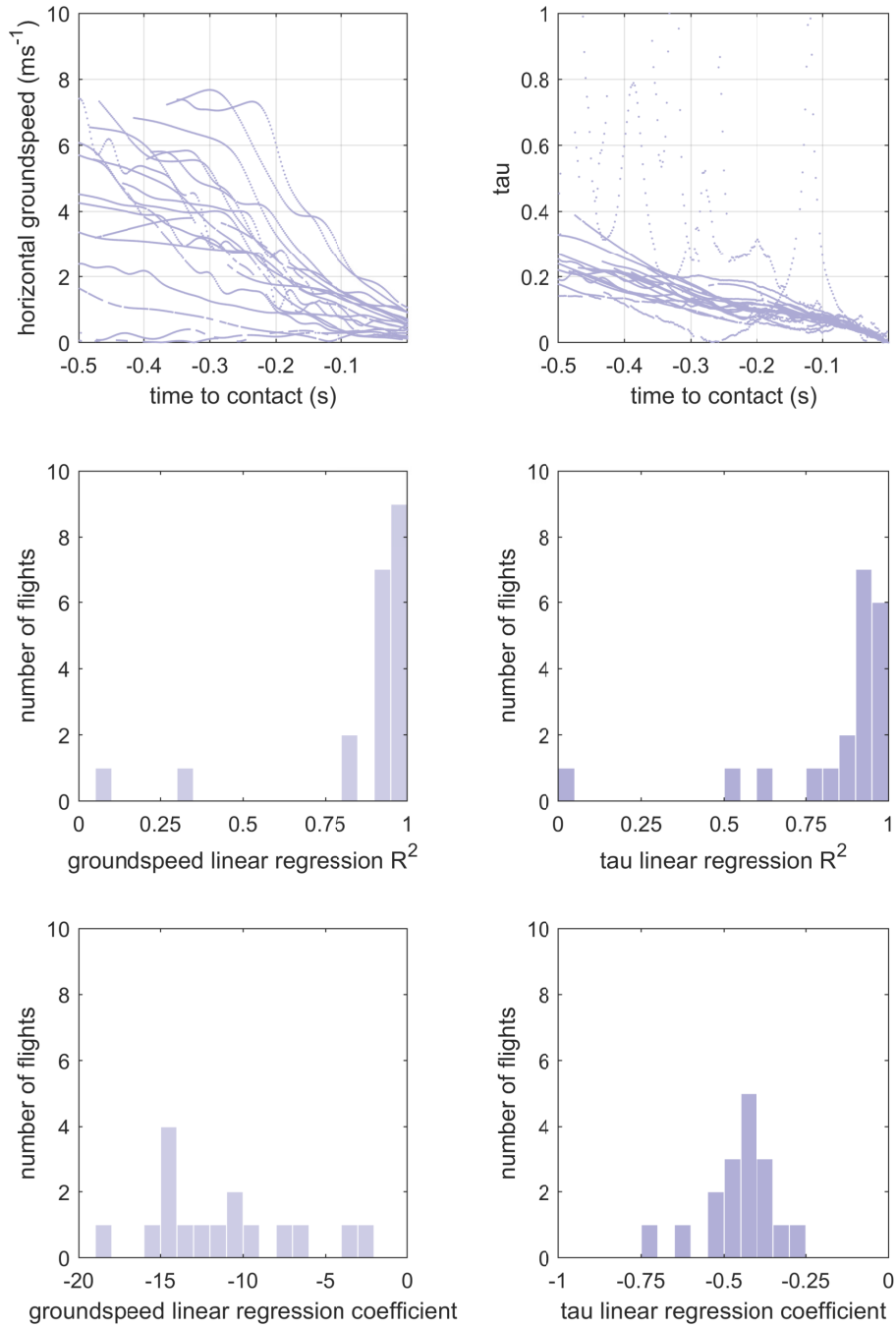


**Figure 4.5:** Measurements of horizontal groundspeed and  $\tau$  in four Harris hawks performing perching flight ( $n = 273$ ). Linear regressions were used to analyse the extent of variation in horizontal groundspeed explained by a linear function of time, or constant braking.  $R^2$  values and regression coefficients were calculated, where the linear coefficient provides an estimate for the braking constant of a linear model fitted to the horizontal groundspeed data. This was repeated for  $\tau$  ( $\tau(t)$ ), in order to test for constant  $\tau(t)$  and its estimated slope.

#### 4.4.4 Control of Braking in Wild Passerines to a Fixed Perch

As expected from the highly variable flight behaviours, the wild Blue tits and Great tits did not show constant braking during perching to a fixed perch (Figure 4.6). Within the 20 recorded flights, maximum  $\dot{x}(t)$  varied from close to  $0ms^{-1}$  (in approaches from directly above the perch) to almost  $8ms^{-1}$ . Variation in the velocity is clear, particularly in transitions from ballistic to flapping flight. The 95% CI range for the  $R^2$  values from the linear regression analysis ranged between 0.90 and 0.96. The estimate for the regression slope from the data was highly variable, with a 95% CI range for the median slope of  $-14.2$  to  $-7.06ms^{-2}$  and high interquartile range of  $7.65ms^{-2}$ . While a linear model does explain a proportion of the variation in  $\dot{x}(t)$ , it is clear non-linear elements are present and so **Hypothesis 1** for constant braking is not measured in Blue tits and Great tits flights to a fixed perch.

**Hypothesis 2** can still hold even in the absence of constant braking, however  $\tau(t)$  measurements are far noisier than measured from the raptors with non-linear trends clearly present. From the linear regression, the  $R^2$  95% CI ranged between 0.86 to 0.95. The 95% CI for the regression slope median were  $-0.50$  to  $-0.39ms^{-2}$ , with an interquartile range of  $0.15ms^{-2}$ . It would appear  $\tau(t)$  measurements cluster around a linear trend, and fall into a narrower range than  $\dot{x}(t)$  measurements. The estimate for  $\dot{\tau}(t)$  from the linear model of  $\tau(t)$  is relatively close to  $-0.5$ , but in contrast to the raptors, predicts the birds would fall short of the perch as the values are higher than  $-0.5$ .

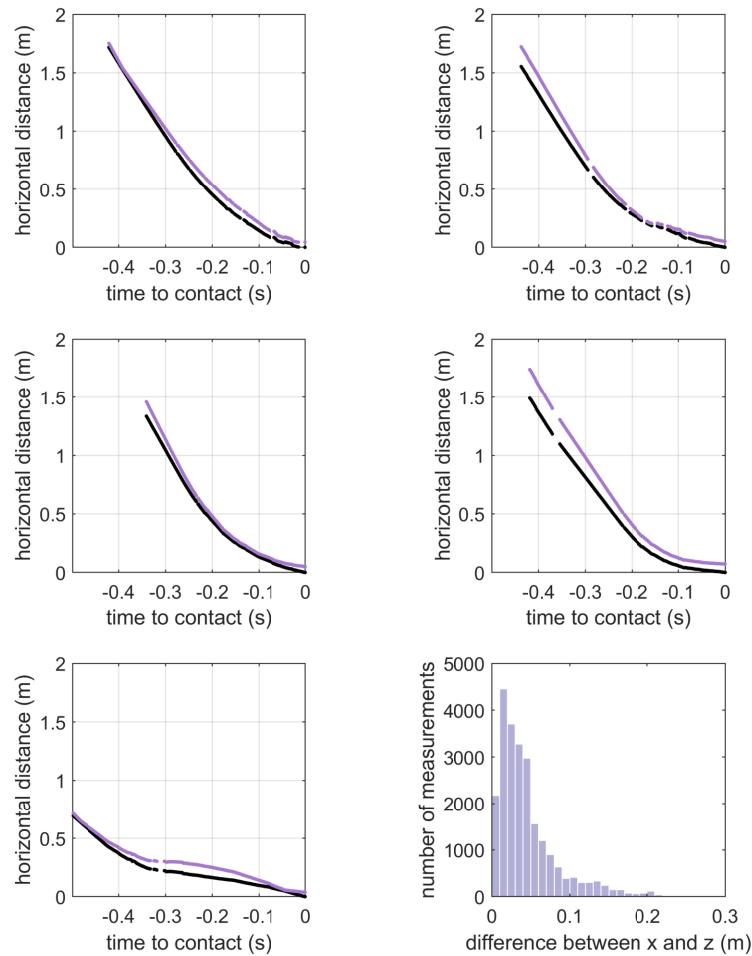


**Figure 4.6:** Measurements of horizontal groundspeed  $\dot{x}(t)$  and tau  $\tau(t)$  from wild passerines (Blue tits and Great tits) performing perching flight ( $n = 273$ ). Linear regressions were used to analyse the extent of variation in  $\dot{x}(t)$  explained by a linear function of time, or constant braking.  $R^2$  values and regression coefficients were calculated, where the linear coefficient provides an estimate for the braking constant of a linear model fitted to  $\dot{x}(t)$ . This was repeated for  $\tau(t)$ , in order to test for constant  $\dot{\tau}(t)$  and its estimated slope.



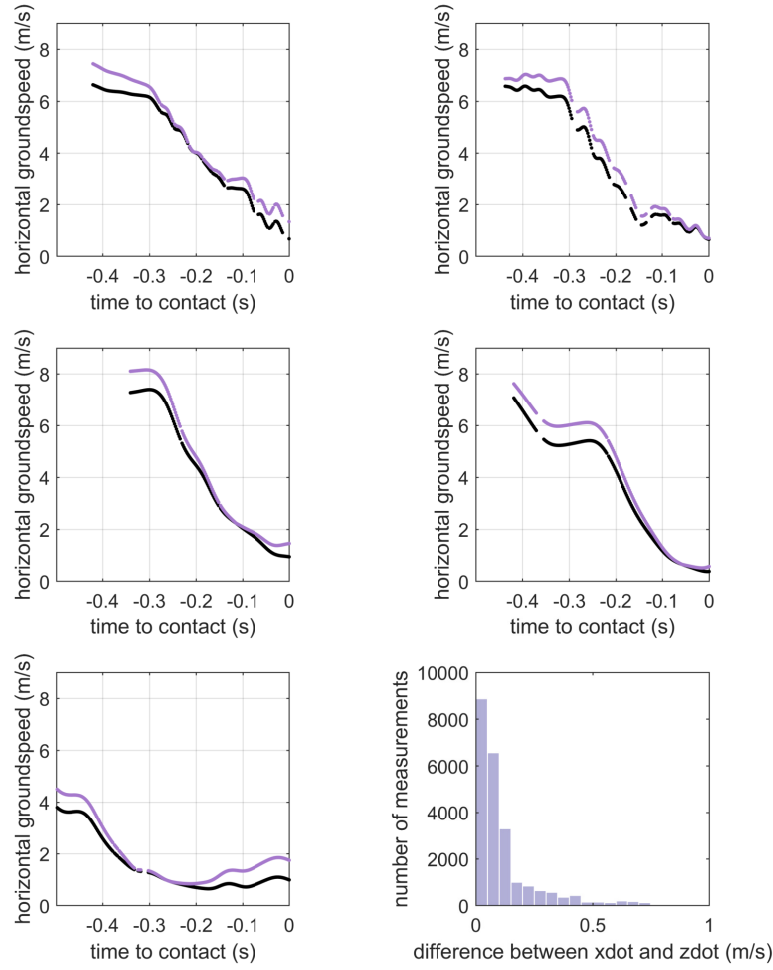
#### 4.4.5 Control of Braking in Wild Passerines to a Moving Perch

In flight to a moving perch, either  $x(t)$  or  $z(t)$  can be used to define  $\tau(t)$  or  $\tau_z(t)$ . The measured difference between values of  $x(t)$  and  $z(t)$  were extremely low and differences were mostly smaller than the body length of the bird (Figure 4.7). There were also close similarities for  $\dot{x}(t)$  and  $\dot{z}(t)$  (Figure 4.8). Therefore  $\tau(t) \approx \tau_z(t)$  making distinguishing between linear and continuous braking control with respect to a moving perch highly difficult.



**Figure 4.7:** The difference between  $x(t)$  and  $z(t)$  during wild passerine flights to a moving perch shown as a histogram across all flights and all perch oscillation frequencies. Five flight trajectories are shown to the perch oscillating at the maximum 1Hz, comparing  $x(t)$  (black) and  $z(t)$  (purple). Differences should be greatest with higher perch velocity. Lower right histogram summarises the difference between  $x(t)$  and  $z(t)$  from all wild passerine flights with a moving perch.

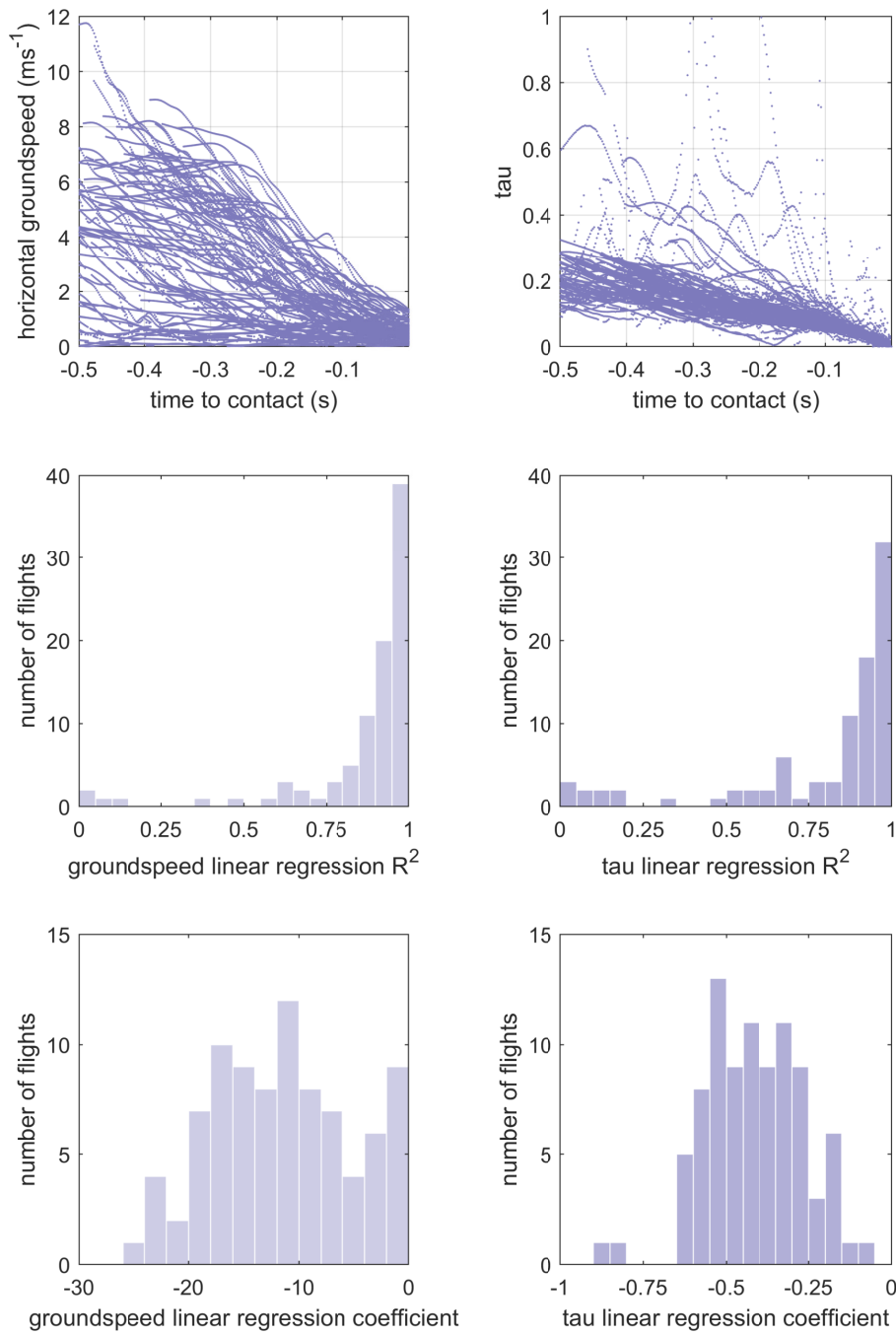
From  $\dot{x}(t)$  measurements, wild passerines did not show constant braking throughout their approach to a moving perch (Figure 4.9). The maximum  $\dot{x}(t)$  showed similar range to the fixed perch flights, with a few flights showing higher velocity. The 95% CI range for the  $R^2$  values from the linear regression of  $\dot{x}(t)$  ranged between 0.92 and 0.96.



**Figure 4.8:** The difference between  $\dot{x}(t)$  and  $\dot{z}(t)$  during wild passerine flights to a moving perch shown as a histogram across all flights and all perch oscillation frequencies. Five flight trajectories are shown to the perch oscillating at the maximum 1Hz, comparing  $\dot{x}(t)$  (black) and  $\dot{z}(t)$  (purple). Differences should be greatest with higher perch velocity. Lower right histogram summarises the difference between  $\dot{x}(t)$  and  $\dot{z}(t)$  from all wild passerine flights with a moving perch.

The median slope estimate 95% CI range was between  $-13.2$  to  $-9.61\text{ms}^{-2}$  and high interquartile range of  $10.29\text{ms}^{-2}$ . While the  $R^2$  values do suggest a linear model does account for a large proportion of the variation in  $\dot{x}(t)$ , but again there is little evidence for **Hypothesis 1** in the moving perch flights. As expected the linear regression models of  $\dot{z}(t)$  were virtually identical to those for  $\dot{x}(t)$ .

Measurements of  $\tau(t)$  were again far noisier than the raptors, with non-linear variation present across the flights. From the linear regression, the  $R^2$  95% CI ranged between 0.86 to 0.95. While this does not strongly support constant  $\dot{\tau}(t)$  and **Hypothesis 2**, the majority of  $\tau(t)$  measurements do fall within a close range and show a linear trend, and the median regression slope estimate had a 95% CI range of  $-0.47$  to  $-0.37$  and interquartile range of 0.22. These  $\dot{\tau}(t)$



**Figure 4.9:** Measurements of horizontal groundspeed ( $\dot{x}(t)$ ) and tau ( $\tau(t)$ ) from wild passerines (Blue tits and Great tits) performing perching flight ( $n = 91$ ). Linear regressions were used to analyse the extent of variation in  $\dot{x}(t)$  explained by a linear function of time, or constant braking.  $R^2$  values and regression coefficients were calculated, where the linear coefficient provides an estimate for the braking constant of a linear model fitted to  $\dot{x}(t)$ . This was repeated for  $\tau(t)$ , in order to test for constant  $\dot{\tau}(t)$  and its estimated slope.

estimates would again predict braking would not be sufficient and the bird would fall short of the perch. Of the 91 flights, 44 fell within close range of  $-0.5 (\pm 0.1)$ .

The  $R^2$  values for the linear regression of  $\tau_z(t)$  are lower than for  $\tau(t)$ , with a median  $R^2$  95% CI range between 0.72 and 0.87. The regression slope median 95% CI was  $-0.40$  to  $-0.27$ , with a slightly larger interquartile range of 0.25.

**Table 4.1:** Comparison of linear regression results for  $\dot{x}(t)$ .

| Stationary Perch    |                       | Median   | 95% CI |       | IQR   |
|---------------------|-----------------------|----------|--------|-------|-------|
|                     |                       |          | Lower  | Upper |       |
|                     | <i>Steppe Eagle</i>   | $n = 15$ |        |       |       |
|                     | $R^2$                 | 0.98     | 0.98   | 0.99  | 0.01  |
|                     | <i>Slope estimate</i> | -10.24   | -18.68 | -8.57 | 10.48 |
| <i>Harris Hawks</i> | $n = 273$             |          |        |       |       |
|                     | $R^2$                 | 0.98     | 0.97   | 0.98  | 0.02  |
|                     | <i>Slope estimate</i> | -7.25    | -7.42  | -7.06 | 1.82  |
| <i>Passerines</i>   | $n = 20$              |          |        |       |       |
|                     | $R^2$                 | 0.94     | 0.90   | 0.96  | 0.06  |
|                     | <i>Slope estimate</i> | -11.97   | 14.17  | -7.06 | 7.65  |
| Moving Perch        |                       |          |        |       |       |
| <i>Passerines</i>   | $n = 93$              |          |        |       |       |
|                     | $R^2$                 | 0.94     | 0.91   | 0.96  | 0.09  |
|                     | <i>Slope estimate</i> | -10.85   | -13.19 | -9.51 | 10.40 |

**Table 4.2:** Comparison of linear regression results for  $\tau(t)$ .

|                  |                       | 95% CI |       |       |      |
|------------------|-----------------------|--------|-------|-------|------|
| Stationary Perch |                       | Median | Lower | Upper | IQR  |
| Steppe Eagle     | <i>n</i> =15          |        |       |       |      |
|                  | <i>R</i> <sup>2</sup> | 0.99   | 0.98  | 1.00  | 0.01 |
|                  | Slope estimate        | -0.52  | -0.64 | -0.48 | 0.18 |
| Harris Hawks     | <i>n</i> =273         |        |       |       |      |
|                  | <i>R</i> <sup>2</sup> | 1.00   | 1.00  | 1.00  | 0.01 |
|                  | Slope estimate        | -0.64  | -0.64 | -0.64 | 0.04 |
| Passerines       | <i>n</i> =20          |        |       |       |      |
|                  | <i>R</i> <sup>2</sup> | 0.93   | 0.87  | 0.95  | 0.10 |
|                  | Slope estimate        | -0.43  | -0.50 | -0.39 | 0.22 |
| Moving Perch     |                       |        |       |       |      |
| Passerines       | <i>n</i> =93          |        |       |       |      |
|                  | <i>R</i> <sup>2</sup> | 0.92   | 0.89  | 0.94  | 0.27 |
|                  | Slope estimate        | -0.42  | -0.48 | -0.38 | 0.26 |

## 4.5 Discussion

We aimed to determine how aerodynamic braking might be controlled using visual cues in a Steppe eagle, four Harris hawks, and wild Great tits and Blue tits. In perching, sufficient braking is futile without accurate timing. Braking too early or too late, no matter how effective, will still result in failure and possible injury. The first hypothesis questions whether braking was held constant during approach to the perch. Using constant braking could provide a method for reaching the target with zero speed, following from the equation of constant acceleration:

$$\dot{x}(t_c)^2 = \dot{x}(t) + 2ax(t) \quad (4.16)$$

where  $\dot{x}(t_c)$  is the velocity at contact, and  $a$  is a negative acceleration constant. Where  $\dot{x}(t_c) = 0$ :

$$0 = \dot{x}(t)^2 + 2ax(t) \quad (4.17)$$

Thus if a bird could measure its relative distance to its target and its relative velocity, then it could choose a critical distance to initiate a constant braking magnitude and require no further feedback. From the flights recorded with a Steppe eagle, there is strong evidence for constant braking perching flight. The recordings from Harris hawks began at the start of deceleration, and so an increase in braking is measured for the first 0.2s, but a linear model fitted the data well as braking was constant for the majority of the flight. The eagle almost certainly had the same groundspeed shape as the hawks before the measurements began, as instantaneous braking is not possible. In contrast, the wild passerines showed almost exclusively non-linear groundspeed as a result of their ever-changing flight patterns between bounding, gliding, and flapping during their approach.

As constant braking was used by the raptors, a "distance to contact" method for controlling braking is possible for both. There would be greater evidence for use of distance to perch if a certain value of constant braking was invariably used, as the distance from the perch would be identified dependent on oncoming velocity. From the data recorded it is clear there is no consistent braking constant magnitude, except perhaps for the Harris hawks, where controlled conditions reduced the variation in the flight. These data are not reflective of the range in Harris hawk perching behaviour, and some braking strategy with different deceleration is described in Chapter 3. As constant

braking magnitude is dependent on oncoming velocity and has different magnitudes in different circumstances, then distance to perch where braking began would have to be altered. It would be surprising if braking was controlled by this principle due to the challenges of accurately determining relative speed and distance, and even anticipate the necessary braking magnitude, all with very little processing time and high penalty for inaccuracy.

An alternative to "distance to contact" control would be "time to contact" control, as shown in Equation 4.3. Lee (1976) proposed that an optic flow variable could provide an estimate for time to contact while moving towards a target. No direct measurements would be required for relative distance to the target, and the optic flow variable  $\tau(t)$  is a direct estimate from the rate of expansion of the object in the retina. Davies and Green (1990) used measurements from Harris hawks and pigeons to determine if the feet are extended at a critical value of  $\tau(t)$  during perching flight, following the work of Lee and Reddish (1981) into the control of wing folding in diving gannets. However,  $\tau(t)$  is only an estimate for time to contact during constant velocity. The deceleration during perching would lead to consistently underestimate the time to contact from  $\tau(t)$ , unless relative speed could also be measured. Using "distance to contact" or "time to contact" to initiate braking is also problematic when considering that the mechanisms of aerodynamic braking executed throughout the approach, and the control of braking is continuous and not from a single initiation event.

Lee et al. (1993) proposed that the continuous control of braking in pigeons could rely on a constant value of  $\dot{\tau}(t)$  (Equation 4.7). In its simplest form, any negative  $\dot{\tau}(t)$  is measured in a bird approaching a target, as the time to contact estimate decreases over time. In contrast, a positive  $\dot{\tau}(t)$  value would occur if the bird is moving away from the target. Holding any constant value of  $-1 > \dot{\tau}(t) > 0$  constant by altering deceleration could theoretically result in the bird stopping exactly at the perch. Evidence for constant  $\dot{\tau}(t)$  formed the basis for Hypothesis 2, and strong evidence was measured for both the Harris hawks and Steppe eagle. In the Harris hawk flights, the beginning of deceleration was recorded and braking increased during the transition from accelerating flight. However,  $\dot{\tau}(t)$  was held constant even during this increase in braking. While the wild passerines could not maintain  $\dot{\tau}(t)$  strictly constant at any value due to their flap-bounding flight pattern,  $\tau(t)$  was held within a smaller window that had a linear trend. Simultaneously, their deceleration showed high variation throughout their approach, again, as determined by their flight pattern.

The value of constant  $\dot{\tau}(t)$  predicts different outcomes upon contact with perch. A constant  $\dot{\tau}(t) > -0.5$  would require a gradual decrease in deceleration on approach in order to stop at the perch. A constant  $\dot{\tau}(t) < -0.5$  requires braking to increase, but infinite braking is required and so physical constraints dictate that the bird would maintain velocity upon impact ("controlled collision") (Lee et al., 1991). The median linear regression slope estimate measured

$\dot{\tau}(t) = -0.64$  from the Harris hawk data, and so the hawks made contact with the perch with minor force. Green and Cheng (1998) showed pigeons use a high impact for perches they are familiar with, rather than novel ones, and the hawks had performed over a thousand flight each to the perches. In addition, producing aerodynamic braking such that the bird stops exactly at the perch may be too costly, as braking uses stall and detracts lift. Minor levels of inertial kinetic energy can be absorbed using the legs which is an effective and easy method of slowing.

The wild passerines do not show any clear evidence for holding braking nor  $\dot{\tau}(t)$  constant. As the birds use a mixture of bounding, flapping, and short glides, it is a reasonable expectation that holding either constant is impossible. There is instead evidence perhaps the birds use a constant  $\dot{\tau}(t)$  value as a setpoint for their non-linear braking. The  $\tau(t)$  data do converge across the different flights, so perhaps this explanation is a reasonable one. It may be a simpler explanation that optic flow can provide a useful estimate for accurate deceleration, and the birds use this estimate but are unable to strictly hold that value constant. This has been proposed by Wann (1996) upon observations that  $\dot{\tau}(t)$  fluctuated around a constant value from the study by Lee et al., 1991 and Lee et al., 1993. In control theory, holding a control variable constant is often unrealistic due to sensorimotor delays as well as physical constraints. Oscillations around a constant  $\dot{\tau}(t)$  value have been noted from hummingbirds docking and pigeons landing, and both these species use flapping, non-gliding flight which would also produce varying accelerations.

The  $\dot{\tau}(t)$  value at  $-0.43$  predicts falling short of the perch from both the stationary and moving perch flights, which could be an overestimate from fitting a linear regression to non-linear data, but a stopping-short strategy corresponded with their observed approach behaviour. The ballistic periods shortened on approach to the perch, and flight using wing control became more frequent within a close range of the perch, where the birds often used slow flapping flight to land. This was not universal, with many perching flights were performed without slow flapping periods. It may be that a falling short strategy is important to ensure an accurate trajectory, and allowing for gathering further visual information and then decreasing braking for the last part of their flight. Many head movements were observed during the slow flapping periods within 0.5m of the perch, along with many dramatic changes in trajectory. Their target was very small in comparison to the feeder size, and it is likely not clearly visible to these birds from many metres away. With the presence of many conspecifics competing for food all trying to land on the same perch, a cautious approach may be prudent to prevent collisions. For flights to the moving perch, strategy was seemingly identical, and stopping short could allow for adjustments to account for the perch's change in position. Small birds commonly make use of moving perches in their environment, as their targets include hanging feeders and thin tree branches. Rather than processing which perch is fixed and which has motion and altering its approach accordingly, it may be more efficient to treat every perch target with caution. From observations, flights to the feeder had a reasonably high failure rate, where around 1 in 10 approaches to a fixed perch were aborted before contact, and as



low as a 40% success rate for the highest perch swinging frequency. Committing to perching with aggressive braking leaves little room for recovery of weight support and acceleration in the case of failure or requirement to divert away.

Where  $\dot{\tau}(t) = -0.5$ , the bird would come to a stop exactly at the perch if its braking remained constant. This special case was outlined in Hypothesis 3, and the Steppe eagle came within a small margin of this value for over half its flights. The eagle therefore controlled its landing with high precision to reduce its impact force as much as possible (see Figure 2.6). This result contrasts with the Harris hawks, and perhaps is explained by the body mass of the eagle. The higher momentum and higher flight speed creates higher risk for the eagle upon impact. In addition, the outdoor conditions used for the eagle recordings provide a particular challenge and more precise control of aerodynamic braking may have been necessary to overcome gusts and wind speed.

The different estimated  $\dot{\tau}$  values perhaps point to varying collision strategies between species. Collision strategy has also been shown vary between individuals dependent on the situation, where Green and Cheng (1998) showed pigeons use a high impact for perches they are familiar with rather than novel ones. In addition, the measurements from Chapter 2 show a range impact forces during perching, influenced by external circumstances and varying approaching velocities. In the natural environment, birds land on a range of objects with different pliancy properties which may require softer landings. It is therefore a requirement of any braking control method to allow for different collision outcomes, and taudot theory provides such flexibility through holding  $\dot{\tau}$  constant at another value as required.

There have been many critics of tau theory and constant taudot theory to explain the control of actions, particularly for studies into its use in humans (Tresilian, 1999; Wann, 1996). It has also been argued that the required visual properties of a target are too stringent and in humans there is ample evidence it is likely only used in concert with other visual cues (see review by Tresilian (1999)). As already mentioned, the theory does not allow for physical constraints of braking nor the time delays of a sensorimotor system (Brouwer et al., 2003; Warren et al., 1986). Braking cannot be infinite, nor can it be instantaneous, and any control system that has evolved alongside physical constraints ought to be governed by them. From studies into constant taudot theory by birds in perching (Lee et al., 1991) and docking flight (Lee et al., 1993), it has been noted that measurements of  $\tau(t)$  described as linear due to high  $R^2$  values are under closer inspection, non-linear and show oscillations around a linear average (Yilmaz and Warren, 1995; Bardy and Warren, 1997). When applied to non-linear data, a linear regression slope provides an estimate for  $\dot{\tau}(t)$  during the measurement interval.

Perhaps most crucially, the presence of constant  $\dot{\tau}(t)$  during a collision does not necessarily mean it is used in controlling it. Any object losing velocity to linear friction will experience constant deceleration, and as discussed previously braking could be controlled with direct measurement of the target. Constant  $\dot{\tau}(t)$  could occur during both these scenarios, although it is unlikely both constant deceleration and constant  $\dot{\tau}(t)$  would coincide. By using a moving target,  $\tau(t)$  is defined in part by the motion of the bird and in part by the perch. Holding constant  $\dot{\tau}(t)$  would rely on compensatory motion of the bird in response to the perch motion. However, in practise, even at the highest frequency, perch motion was too slow compared with the bird and discerning any compensatory movements from the trajectory data is impractical. The moving perch experiment could not manipulate  $\tau(t)$  to a high enough degree to test its use in birds. Regrettably, any future experimental setup that used suitable higher perch speed would also not result in any landings.

However, interesting conclusions can still be made about how birds control their flight to moving targets. As long as the bird is flying much faster than its moving target, it can treat the perch as stationary. A non-moving part of the perch could be used as the virtual target e.g. the pivot of a swinging perch, or a stationary nearby visual cue, or even the average of the perch position as an even easier target. A stationary target point would have a non-zero offset to the perch's eventual position at the point of impact. Once close, compensation to trajectory is necessary in order to reach the perch. Such changes in course were frequently observed even in flights to the stationary perch, in all likelihood because they often could not see the position of the perch on the feeder except within close proximity. This unexpectedly reveals that flying to a moving perch is no more challenging than a stationary one, and the same strategy can be used either way.

## 4.6 Conclusions

In this chapter the braking control of multiple species was explored in perching flights performed under different conditions. A Steppe eagle was found to use a constant braking strategy in 15 flights. Despite variations in braking magnitude and initial horizontal groundspeed due to different outdoor conditions, both braking and an optic flow variable  $\dot{\tau}(t)$  were held constant during the approach.  $\dot{\tau}(t)$  provides how current braking will affect the impact with the perch, and in the eagle the median  $\dot{\tau}(t) = -0.52$  predicts the bird will stop exactly at the perch.

Four Harris hawks performing 293 perching flights were recorded with high-speed motion capture. The hawks transitioned from acceleration to deceleration with increasing braking before applying constant braking. However,  $\dot{\tau}(t)$  was held constant throughout the approach at an estimated value of -0.64. This predicts a harder collision with the perch than the eagle. Due to body size, the Harris hawks can afford a higher velocity impact than an eagle, and remaining kinetic energy can be absorbed with their legs on impact.

Twenty perching flights from wild Great tits and Blue tits were recorded to a fixed perch. There was no evidence for constant braking. Due to the transitions between ballistic periods and flapping periods, closing velocity was non-linear and as a result it would be impossible to hold  $\dot{\tau}(t)$  nor braking constant. However,  $\dot{\tau}(t)$  values varied around a constant of  $\dot{\tau}(t) = -0.43$ , predicting the birds would need to decrease in braking on their approach to avoid falling short. A cautious strategy aided their perching behaviour as change in trajectory was often required within a metre of landing, as well as avoiding competing conspecifics for the target and its food source.

A constant  $\dot{\tau}(t)$  value could be caused by a controlled braking flight and does not prove its use as a control variable. Flights to a moving perch were recorded (n=93) such that  $\dot{\tau}(t)$  is dependent both on bird motion and perch motion. Holding  $\dot{\tau}(t)$  constant would result in countering the perch motion. Unexpectedly, there was no difference between flights to a moving and fixed perch. When bird flight speed is far higher than the perch speed, and as a result a moving perch can be treated as a fixed target. The birds would not approach the perch moving at a faster perch speed, and so future work with experimentally manipulating the expansion rate through optical projections could experimentally manipulate  $\dot{\tau}(t)$ . Until then, evidence for its use in birds to control braking is still ambiguous.



## General Discussion

The ability to cease flying is as fundamental in birds as the ability to fly. Powered animal flight is energetically expensive and, for the majority of birds, cannot be maintained indefinitely. Although velocity itself is not inherently dangerous, it comes with high risk. As is often noted: "*it is not the fall that kills you, it is the sudden stop at the end*". The inertial kinetic energy of a flying bird is dependent on its groundspeed, and defines the force impulse at the point of impact with a perch. Without applying braking prior to impact, the resultant forceful collision could be deadly, as sadly demonstrated by the number of birds killed in collisions with windows each year.

The first and greatest challenge of perching flight is therefore to prevent deadly impact forces by slowing groundspeed. Braking requires a change in the direction and magnitude of aerodynamic forces, as with any manoeuvring flight (Thomas and Taylor, 2001; Taylor and Thomas, 2002). Stable flight resists perturbations and is necessary for straight flight or steady turns, but unstable states are necessary to perform sharp turns, acceleration, and braking. Birds have evolved manoeuvrability alongside stability in order to perform complex behaviours on the wing.

The physical constraints of braking adds a further challenge to perching flight. Transitioning between cruising flight and contact during normal perching behaviour occurs between 0.5-1.5s and so reduction in groundspeed must be rapid (Carruthers et al., 2007; Provini et al., 2014; Lee et al., 1993). Instantaneous deceleration is impossible – time is required for the implementation of braking force, and by extension, results in a braking distance. For a Harris hawk at  $8\text{ms}^{-1}$ , in 1s the travel distance is 16 body lengths (Tucker, 1992). Thus rapid as well as sufficient braking is required prior to landing.

In this thesis the mechanism of braking during perching flight was explored. From the detailed data from flights performed by Harris hawks, it is clear the production of rapid and significant deceleration is achieved primarily through producing drag prior to contact with the perch. There is strong evidence that drag is generated through unsteady aerodynamics, in particular added mass. The rapid pitch-up, which results in a bird's body and wings in an upright posture relative to the airflow, was quantified for a Steppe eagle as well as the Harris hawks. A pitching, decelerating wing generates large, instantaneous aerodynamic forces not predicted by steady aerodynamics. By pitching, the frontal area to the airflow increases in size (shape change number) which leads to an increase in inertia and thus aerodynamic force. The added inertial comes from a virtual mass being added to the accelerating system

due to the surrounding fluid being moved. The vorticity of the airflow around the pitching surface also produce large aerodynamic forces. The drag force production measured in the Harris hawks during perching closely match the wing shape change number, providing evidence for this aerodynamics mechanism in addition to previous work by Polet et al., 2015 and Polet and Rival, 2015. A similar system is assumed in the Steppe eagle, which also used a rapid pitch-up manoeuvre with comparable flight kinematics.

The rapid pitch-up is a form of whole body rotation, which is controlled by the bird by altering the forces generated by the wings relative to its body. By moving the centre of pressure ahead of the centre of mass, the bird can induce a nose-up pitching rotation. The centre of pressure is altered through changes to wing configuration, in this thesis detailed wing and tail kinematics measurements were described from a novel motion capture method. As expected the wing and tail kinematics are hugely complex, with the eagle and hawks producing extreme independent wing rotations at the shoulder. The importance of the tail in producing the pitch-up seems key, as well as alterations to the flapping at the onset of pitch. One additional kinematic measurement in the eagle and hawks may also influence flow separation and thus lift production during stall, in the form of "wing flicks" where the independent pitch angle briefly reverses to zero before recovering. Observations of the eagle footage indicate flow is reversed across the wings as the feathers fly upwards around the time the wing flicks are measured. Other impacts on unsteady aerodynamics should also be explored in the future.

Of particular importance in perching flight is the accurate control of braking. As an example of visually guided flight, perching requires sensory feedback to ensure braking is applied accurately such that the bird stops at the target. Sufficient braking applied within a limited time frame while maintaining weight support will still lead to failure unless the bird is positioned at the perch at the end of the manoeuvre. Applying braking power such that a collision is avoided and reaching the perch is an impressive ability that has been scrutinised previously. Rather than requiring direct measurement of relative speed and distance, an optic flow variable could inform a bird about whether its current braking is appropriate. Measurements provided strong evidence for both constant braking and constant  $\dot{t}(t)$  during flights by Harris hawks and the Steppe eagle. A softer collision event was predicted in the Steppe eagle flights from the  $\dot{t}(t)$  and braking measurements compared with the hawks, which is likely explained by the larger size of the eagle and its flight speed, both resulting in higher momentum at the point of impact. The hawks could endure a higher collision force, and it is likely more energetically efficient to minimise braking and rely on absorbing a force through the legs. Too high a collision would result in injury, but too cautious a landing is also costly. The hawks performed thousands of flights to the same perches, and pigeons have been shown to preferentially land with higher forces on familiar targets (Green and Cheng, 1998).

The control of braking during flap-bounding flight is particularly interesting as flight control is intermittent. The transitions between flight modes renders strictly constant braking impossible, and because of variations in velocity it is also not possible to hold  $\dot{\tau}(t)$  constant on approach either. Experiments using a bird feeder were used to explore how Great tits and Blue tits control their flight to a perch. The trajectory data is hugely variable and in stark contrast to the highly stereotyped flights by the Harris hawks. Despite the wide ranges of flight direction, speed and behaviour, the horizontal groundspeed measurements over horizontal distance converged reasonably well and were not vastly dissimilar to the raptor flights. The ratio between these two parameters ( $\tau(t)$ ) was as expected non-linear, but measurements converged around a linear trend. While holding braking or  $\dot{\tau}(t)$  constant may be infeasible, controlling it with respect to a set value (the desired state) leads to a similar outcome while still respecting the physical constraints.

Many birds are able to land on a moving target, such as a swinging rope, a tree branch bouncing in the wind, or a feeder hanging on a string. In an experiment with a swinging perch, this exceptional ability to control braking to a moving target was also examined. Taudot theory has been under criticism for a range of reasons, and to truly test if the bird keeps the ratio of its relative horizontal groundspeed and relative horizontal distance linear then the target must be independently moved. It would be expected, therefore, that a bird using this optic flow variable would make compensatory movements in response to the perch on approach. Alternatively, if a predicted impact position could be predicted by the bird, and it controlled its braking relative to that stationary position then an approach that does not make compensatory motion would be expected. Any stationary nearby position would also suffice, as it would have a non-zero offset with the final impact position which could be overcome within a far closer range. These strategies could ultimately not be distinguished as the speed of the perch was very low relative to the bird velocity. In experiments birds would not land on a perch moving higher than 1Hz, which means this hypothesis may not be properly tested even in future experiments. However, these results are informative about the underlying control mechanism at work. As long as the perch motion is relatively small, braking can be controlled if it is treated as a fixed target. If the perch motion is too high, then the task is not attempted. High velocity perching targets are not part of an ecology for wild passerines and so there would be little selection pressure for high-speed perching behaviour to arise. However, there is scope for optical manipulation experiments in the future in order to properly test the use of  $\dot{\tau}(t)$  during braking, for example by altering the perceived expansion rate of the perch.

Regardless, the criticisms of taudot theory remain. The presence of constant  $\dot{\tau}(t)$  during a collision event where the bird stopped at the perch does not mean it was used as a control input. If a bird used another control method, say direct measurements of relative distance and velocity, then  $\dot{\tau}(t)$  would appear identical. Ultimately  $\dot{\tau}(t)$  is just a description of a collision. Its simplicity provides a compelling argument for its use, and similar optic flow

patterns has been shown to trigger specific neuronal impulses in insects. Control of braking during high speed flight to a small target is a difficult control problem, and in UAVs use of tau has led to successful landing. Until there is definitive evidence that birds do use direct measurements about its relative position and speed, or an entirely different mechanism is found, then it remains the best hypothesis for providing braking feedback in perching birds.

Perching flight by a Steppe eagle was described by Carruthers et al. (2007) as highly stereotyped, but under closer quantification the variation in wing kinematics are apparent. While trends are clear, no two flights by the eagle were closely alike. In direct contrast, the 1365 flights by Harris hawks were unmistakeably stereotyped, with the wing markers from different flights occupying the same 3D space at the same time to within a few millimetres. The greatest difference between experiments with the Steppe eagle was the outdoor conditions and presence of wind speed. The finely controlled wing and tail kinematics are likely in response to the unpredictable and unique pattern of airflow during the approach. There was also a greater range of oncoming initial groundspeed values, as the eagle approached the perch from untethered, free flight. The Harris hawk flights were tightly controlled, but differences in braking strategy were quickly apparent when changing the flight distance.

The main limitation of the Steppe eagle experiments was that only one individual was used and that just 15 flights were suitable for analysis. Photogrammetry and experimental techniques at the time made expanding the scope of the study too difficult, but in light of newer technology and equipment it is feasible for future studies. The variation provided by the windspeed meant the recorded flights were close to the natural behaviour as possible, but endless variation is difficult to unpick. The opposite limitation is clear from the Harris hawks, where flights were so stereotyped from extremely controlled conditions repeating flights providing no new information. While the perch distances did provide novel insight into the variation of braking strategies, in the absence of real flight conditions the manoeuvre is only recorded for a small range of its potential. In light of these issues, natural flight behaviours should be studied alongside controlled ones (preferably performed by the same individuals) for better investigation into underlying principles. While it is difficult to make informed comparisons across species, including a range of bird species is crucial for investigations into bird flight. As shown from this data, individuals within the same species also vary in many surprising ways, and to neglect measuring the range of variation leaves our understanding of bird flight incomplete.

With the experiments recording the wild Great tits and Blue tits, the data set recorded uses just a single point and so restricts any analysis into the mechanics of decelerating flap-bounding and how intermittent control might be implemented. The complexity of these birds' behaviour is immediately clear from the trajectory data alone, but additional variation in flight patterns on approach had to be simplified to a binary "bounding" and "not bounding".



In sum this data set is a very brief glimpse into the flight mechanics and control of manoeuvres in passerines. Future work into flap-bounding from a control perspective has exciting potential for UAVs. Small UAVs may not have the processing power for continuous control nor the energy stores to use expensive powered flight at all times, and as a result share many of the constraints with these small species.

The main limitation from the braking control experiments was that the underlying braking control mechanism was not properly manipulated through experimental conditions and the question remains whether taudot is used. Evidence for the optic flow variable being held constant is reasonably high, but other problems remain that have not yet been addressed. In light of these results further experiments are required in order to manipulate the optic flow variable artificially such that conflicting information is provided between the taudot variable and the bird's relative distance and speed. Regardless, as more information comes to light about behavioural control in birds, there should be efforts to replace taudot theory with a mechanism that accounts for physical constraints. Despite being unable to manipulate  $\dot{r}(t)$  by using a moving perch, as discussed, this does reveal braking relative to a moving perch is not a different control problem to braking to a fixed one.

Perching is an example of high-risk, high-cost, high-reward behaviour. Success relies on balancing a series of demanding physical constraints, and yet birds can perform this manoeuvre readily in a range of environments and conditions. Manoeuvres under such high selection pressure are finely-tuned and rely on complex kinematics that still remain difficult to measure, let alone fully understand. However, even the most complex of manoeuvres are achieved with a finite morphology made from simple joints and muscle power. Within the constraints of physics both aerodynamic and anatomical there is seemingly endless variation in bird flight ability, indicative of the essence of evolutionary processes as a whole.



## Conclusions

The wing and tail kinematics in perching flight were quantified to explore wing morphing control during gliding approaches. For the first time the rapid pitch-up manoeuvre during gliding flight was quantified, where the raptors rotated nose-up to over  $100^\circ$  in less than a second with respect to the horizontal plane. Wing folding, wing pitch rotation, sweep and dihedral changes were quantified during the gliding ascent to the perch in raptors. Greater measurement detail was possible through motion capture of over 1300 flights by Harris hawks, where the reverse rotation of the wings was measured to maintain stable angle of attack for most of the rapid pitch-up. There is evidence kinematics are functionally coupled between the wings and tail, and that the tail is key in effecting whole body rotations as well as generating drag forces for slowing.

Aerodynamic braking was quantified during gliding and flapping approaches to the perch. Deceleration in the eagle and hawks was achieved in part by gaining height and in doing so exchanging kinetic energy with gravitational potential energy. The majority of deceleration is achieved with aerodynamic braking. The rapid pitch-up leads to loss of energy into the wake through high angles of attack and by added mass effects. Increases in span and sweep also aid deceleration and weight support during the final instant before contact. Deceleration ensures large birds of prey can perch with very low impact forces and avoid injuries. By flying into a headwind, the eagle sustained flight authority while losing groundspeed. Deceleration varied in eagle flights due to initial groundspeed and varying outdoor conditions, attesting to the flexibility of braking control in natural environments.

A large data set of perching flight was obtained from Harris hawks wearing multiple markers and recorded with motion capture. With over 1300 flights analysed, this data set and results provides novel detail and scope in manoeuvring flight. While tracking and reconstruction of points into 3D was achieved automatically and in real-time by the software, identifying markers was not possible with the Vicon system. Instead an automatic clustering method was designed to identify markers relative to the backpack point using boundaries in two planes unique to each hawk. Wing motion relative to the body was highly conserved dependent on flight phase (gliding and flapping) despite different recording days and flight distances. This technique visualises the anatomy of wing motion in contrast with angular measurements, and perhaps pointing to future heuristic methods in partitioning bird wing and tail kinematics based on its aerodynamic effect.

From the motion capture data it was possible to examine the dynamics of the rapid pitch-up manoeuvre. The lift and drag forces were measured throughout the accelerating and decelerating flight phases, and alterations in wing kinematics were identified such that wingbeats create drag forces as opposed to thrust. Wing morphing was shown to affect lift production, as wing angle of attack and groundspeed were not sufficient to fully explain the  $SC_D$  and  $SC_L$  measurements alone. Influences from wing morphing include wing sweep and dihedral angles, and also tail pitch.

Individual variation between the hawks were found in the energetics measurements due to mass, but normalising the rate of change in total energy collapsed these variations. Individual hawks also varied in flight technique, such as wingbeat placement, and trajectory shape. In shorter flights, variation fell likely due to the physical constraints of acceleration and deceleration. Such variation could be due to preferences, or correlate specifically with mass and further tests where weights are added to birds could shed further light. Changes in braking strategy were measured in response to different wind conditions, as the perching flights in outdoor conditions showed high variation while indoor flights were highly stereotyped. Flight experience may also have an effect, where the largest hawk showed the most experience was also the eldest by many years. These results demonstrate individual variation impacts flight mechanics and performance, and automatic labelling techniques enable the analysis of higher numbers of flight and facilitate further investigation into scope in flight behaviour and the effect of experience.

Sufficient braking magnitude is not the sole precursor to a successful perching manoeuvre. Without control of braking with respect to the target, a bird would not reach its destination at all. An optic flow variable known as taudot could be used to control braking as it provides instantaneous information in the type of collision event given a current deceleration magnitude. Holding taudot constant by altering deceleration enables a bird to stop exactly at the perch, even without direct measurement of its target's relative position nor its own relative speed. In the case of a Steppe eagle, taudot is held constant while braking is held constant, which predicts the eagle will stop directly at the perch. The Harris hawks initially used increasing braking before holding it constant, while taudot held constant throughout the gliding approach. The constant was lower than in the eagle, which predicts the hawks land with a controlled collision and maintain groundspeed at the point of impact. Previous work into pigeons show birds familiar with a perch will brake less on approach and land with higher impact force than with novel perches, suggesting a preference for higher degree of force absorption by the legs in order to ease the level of necessary aerodynamic braking.

The results in this thesis were limited by several factors. Firstly, there were just 15 outdoor flights each varied in perch height, pliancy, windspeed, and initial velocity. Future experiments should make use of air conditions in order to test the flexibility of flight manoeuvres, and control other variables. The impact of windspeed and perch height

could be controlled experimentally, and provide insight into the function of wing morphing modes. However, the opposite limitation is seen in the hawk data, where variation is so low further flights do not provide new information. Determining the aerodynamic function of wing and tail kinematics based on correlation makes the assumption that a given kinematics event that coincides with a force causes it, but the motion may be for stabilisation and the reverse is true.

There is a growing demand for smaller air vehicles that can fly in cluttered, urban environments. Such designs often struggle to maintain flight control under windy conditions, and are not yet adept at obstacle avoidance. Birds flight mechanisms are of great interest to engineers looking to exploit their low-energy, highly accurate, dynamic abilities. Some recent designs have attempted to copy bird flight through flexible morphing wings or an ability to grab a surface for landing (Greatwood et al., 2017; Zhang et al., 2014; Zhang et al., 2018). Making use of post-stall conditions as birds do during perching flight is one such manoeuvre that likely will prove invaluable in future bio-inspired UAV designs. The ability to land accurately is a useful one for machine and bird alike, for saving energy, obtaining a fuel source, and for surveillance.



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