Attack strategies in birds of prey

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Thesis submission for the
Degree of Doctor of Philosophy

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Abstract

Pursuit behaviours are vital in predator-prey interactions and in courtship for many flying animals. Existing research on target-directed flight behaviours in insects[1-9], birds[10-12] and bats[13] has aimed at identifying simple geometric rules describing the pursuit-flight trajectories. However, these geometric rules are only part of the picture as they only consider the outcome of the commanded changes in flight kinematics, and not the underlying guidance laws (dynamics) which generate these commands. To intercept a target, a pursuer implements a guidance law using sensory feedback to determine the required change in flight velocity, and the resulting kinematics determines the flight geometry.

Most of the research until recently has examined insect flight systems, as the ethics of working with birds of prey are more complex and measuring their wide-ranging flight trajectories is difficult. Studies of predator-prey pursuit in birds have only described the geometrical rules for target interception, therefore overlooking the guidance laws which implement them. Therefore the aim of this thesis is to complete the picture by identifying the guidance laws used by birds of prey as they pursue and intercept targets both in the air and on the ground.

I used onboard cameras and GPS to study attack flights in peregrine falcons (*Falco peregrinus*), and high-speed ground photogrammetry for attacks in Harris' hawks

(*Parabuteo unicinctus*), to show that two different raptor species effectively implement the same guidance law of pure proportional navigation for intercepting manouevring and non-manouevring prey-targets.

Proportional navigation is a feedback law whereby the bird's line-of-sight rate is fed back, in order to command a turn-rate in proportion to the change in line-of-sight rate, with a constant of proportionality N. Harris' hawks were found to use this guidance law in its simplest case with an N of approximately 1. This amounts to a pure pursuit course, meaning the bird maintains a heading angle of zero at all times (its velocity vector points at the target). Peregrine falcons were found to use a variety of values of N resulting in a quicker path to interception.

A remarkable feature of most bird of prey eyes is that they possess two regions of high visual acuity - the shallow and deep foveae. The deep fovea is optimised for long-range vision, and is directed at approximately 45° to the side of the head. It has been proposed that the head is held in line with the body for streamlining, while the body is turned in flight to fixate the image of the prey on the deep fovea, resulting in a curved trajectory. My results contradict this theory, as falcons were seen to use saccadic head movements to maintain the image of the prey in their field of view whilst flying along curved trajectories - suggesting a different visual strategy.

I provide the first quantitative analysis of how birds are able to guide their flight for successful prey capture. Not only does this provide new insights into animal behaviour and evolution, but this research has many applications in engineering, where there is a wide and growing interest in vision-based approaches to guidance and control in both civil and military spheres.

Chapter 1

Literature Review and Introduction to Thesis

Introduction

I begin by discussing the morphology and ecology of two distinct raptor species to gain insight into the suite of possible hunting behaviours we may replicate in our experiments. Chosen test species are from the families Falconidae and Accipitridae, representing a contrast in wing shapes, hunting behaviours and habitat type, having diverged more than 60 million years ago[14]. The role of vision and associated effects on hunting behaviour are then considered, in relation to the physiology of the avian eye and predicted flight trajectories. There is a vast amount of literature on the structure and function of the avian eye and on visual perception in the animal kingdom, therefore only a summary of information relevant to this study will be described. I then review the current information on pursuit strategies drawing from the engineering literature, non-human animal study, and human study. This literature review aims to evaluate the current understanding of pursuit in the animal kingdom, and how ecology and physiology may influence the chosen strategy.

At the end of chapter 1 I explain the thesis rationale, with an overview of my experiments and methodologies, followed by the aims and hypotheses of this thesis. The key to the design of the experiments is that they record free-flying birds of prey pursuing targets in their natural environment.

Hunting ecology of falcons and hawks

Peregrine falcons

From the family Falconidae, the general habitat of peregrine falcons (*Falco peregrinus*) comprises open countryside. Peregrines have narrow wings with a large surface area for high manoeuvrability and endurance[15] and are known in falconry circles as the “longwings”. They remain airborne for very long periods, gliding on air currents to save energy. Falcons have high power-to-mass ratios, and consequently, greater flight capabilities and accelerative performance[16, 17].

Prey species

Peregrine falcons are generalist predators, feeding on a wide variety of bird species (mainly passerines, shorebirds and water fowl), with local and individual specialisations for hunting mammals (namely rabbits, hares, voles, lemmings, ground squirrels and bats), reptiles (lizards) and large insects (dragonflies and wasps), and occasionally fish and carrion[18-23]. Prey abundance is a strong determinant of prey selection in peregrines[24], thus in one population where small microtines were very abundant, 29% of prey taken by peregrines was found to be mammalian, which is much higher than in other populations[19]. This highlights a certain level of plasticity in terms of diet in peregrine falcons[19, 25]. In addition, peregrines will attack both single birds and flocks[23, 26].

Hunting mode

Peregrine falcons have developed unique hunting strategies as a consequence of adaptive morphology. Peregrines have two distinctly different flight styles during attack behaviour; the first is the swoop, and the second - synonymous with hunting peregrines - is the stoop[27]. The swoop involves beating of the wings and an increase in velocity accompanied with a sudden change in flight direction, and can be aimed either upwards or downwards at prey[27]. A stoop is defined as a fixed wing glide down a steep flight path[28]. When initiating a dive, a peregrine beats its wings to accelerate, then rapidly folds them to reduce wingspan and drag, and steepens its dive path. A stooping peregrine may reach speeds of up to 157ms^{-1}, based on mathematical models of ideal falcons[29], although measurements of real birds were found in the range of 52 – 58ms^{-1}[30]. Contrary to popular belief, the infamous vertical stoop is not often executed and in fact there are innumerable variations. Stoops of between 30° and 45° are most frequent, and sometimes even flatter angles or horizontal approaches are used[21, 23, 24, 31-33]. Moreover, the stooping technique, whether vertical, oblique or flat, is only used in about a third of attacks (36.3%[26]), and peregrines actually possess a repertoire of distinct hunting techniques. These have been subdivided below according to the peregrine's starting position and that of its prey[22, 23, 27, 31, 32, 34]:

Stoop from a soaring position at ground-level targets: A stoop may be curved or straight, convex or concave, vertical or oblique, with distance travelled varying between less than 10m and more than 1km, and most stoops are levelled out far in advance of reaching the prey.

Stoop from soaring position at aerial targets: A stoop may be curved or straight, convex or concave, vertical or oblique, terminating in a single hit or a series of swoops.

Long distance flapping flight and descent to ground-level targets: A moderate altitude attack approximately 50 – 150m above ground level.

Low surprise attack at ground-level targets: Flying with great speed 1m above the surface, aiming to flush prey - immature falcons begin foraging with this method. This is stated as being the most frequent method by Dekker, and in particular, in marine peregrines hunting seabirds over water, as they use the waves to conceal their approach[27, 35].

Short-range attack at aerial targets: These are opportunistic hunts on prey that appears unexpectedly, thus involving a sudden change of direction and burst of speed to meet prey, (sometimes head-on).

Take-off from a perch to pursue aerial targets: Also known as 'still-hunting', peregrines will keep watch from a suitable perch and launch a surprise attack on passing prey. This method has also been described as the most successful and widely used, and in particular, in coastal peregrines[34, 36], or those living alongside wetland habitats[37].

Active searching for crouched targets: After a failed long-range attack (or miss) where the prey was grounded, or when perches are scarce, the peregrine will conduct a deliberate search by flying slowly with their head bent down.

Tenacious pursuit with over 10 swoops: These are very long chases, mostly seen in immature peregrines, involving repeated swoops (20% of hunts by autumn juveniles[27]).

Tandem pursuits: Two peregrines, usually mixed sex, sometimes coordinate their attacks and alternate their swoops onto prey.

Ground pursuit: Occasionally peregrine falcons will pursue birds or small mammals when on the ground themselves, using their feet to explore the vegetation.

There is some disagreement in the literature as to the most common or preferred hunting mode adopted by peregrines, reflecting the differences in demographics, topography or meteorology within and between studies. For example, atmospheric conditions may affect the hunting mode, as during sunny and windy weather they are more often seen soaring, in contrast to very cloudy, wet or cold days, when they more often use flapping flight at lower altitudes[27]. However, most studies concur that surprise is an important factor[27].

Attack from the air at flying prey is stated as being the most common technique in some studies - which includes flights from a soaring or short-range position, using stooping or flapping flight - while attacks on ground prey are much less common[20, 24, 26, 34]. However, Dekker claims he found little support that peregrines most frequently pursue flying targets from high in the sky[27]. He believes these findings come from falconry circles, where dogs are used to flush game for trained falcons “waiting on” overhead. Cresswell supports the view that the majority of hunts were at ground or perched (i.e. stationary) prey[26]. Even though other studies reported this method is used to a lesser extent, they still provide evidence for prey being taken directly from the ground (e.g. ducks, waders and grouse chicks[27, 37-40]).

Overall, a range of hunting modes are used to differing degrees by peregrines, but whichever method they may favour, ultimately the evidence shows that individual birds perform the whole suite of hunting behaviours, which includes attacks on both aerial and ground prey targets, that may be moving or stationary.

Hunting success

Much of the work on hunting behaviour in raptors comes from anecdotal data, and relatively little has involved quantitative study[18, 23, 31, 32]. Many factors determine the hunting success of peregrines, including age, season, time of day, level of hunger, weather, abundance of prey, prey species and level of surprise[27, 37]. Therefore, a large range in success rates are quoted in behavioural studies - between 7.5% and 60% - depending on these factors (7.7%[27]; 47%[23]; 12.7%[26]; 52%[20]; 7.5%[31, 32]; 60%[34]; 22%[35]). However, the level of motivation of the peregrine during a hunt seems to be of critical importance[27]. Firstly, adult peregrines have been found to have significantly higher success rates during the breeding season when the food needs for feeding young are much greater, than at other times – 34.9% and 12.7% respectively[23, 24, 34]. Also peregrines are not always intent on capturing the prey when they initiate a hunt, and perform mock or play hunts when not hungry[41]. Hunting efforts have been categorised as either low-intensity or high-intensity chasing - dependent on hunger levels[34]. Of the 45 flights diagnosed as high-intensity hunts by Treleaven, 60% ended in a kill, which is a more accurate estimate of hunting success since we can be confident of the bird’s goal in each case. Therefore, seasonal differences in hunting effort may explain the discrepancy in success rates reported for adult raptors when hunting either within or outside the breeding season[26, 34].

Other factors influencing hunting success include the age-group and status of birds. Some studies reporting the lowest success rates include peregrines on migration or juvenile first year birds, and thus these groups may be expected to have lower hunting success due to unfamiliarity with the hunting site or having lower skill levels than adults, respectively[23, 27, 31, 32]. Furthermore, the time since the last hunting attempt in any particular area may be of importance. Significantly higher success rates were found if no other peregrine had flown over the hunting ground in the preceding hour, compared to when a peregrine had flown over within the hour, providing the peregrine made an attack within the first minute of arriving on the hunting ground[26]. Therefore a true estimation of hunting success in peregrines must take account of all these factors, and it is likely it may vary throughout the year as well as on a daily basis. Furthermore, success rates also depend on the chosen mode of hunting, with differences between peregrine populations according to locality, or even individual specialisations[26, 39].

Harris' hawks

From the family Accipitridae, the preferred habitat of Harris' hawks (*Parabuteo unicinctus*) comprises of woodland edge, thriving best in areas with a patchwork of woods and fields[28, 42]. They possess broad wings with a large surface area[15] and represent the "shortwings" in falconry circles. Larger hawks soar on thermals while scanning for prey, while smaller species use a more manoeuvring flight in pursuit of prey.

Prey species

Harris' hawks take a variety of prey species – as many as 68 have been described in one study, comprising of lagomorphs, rodents, birds, lizards and insects[43-47]. In both number and biomass the most common prey are mammals (78% in number and 90% of biomass[45]), namely rabbits and hares, with avian prey the second most important[43, 45]. Reptiles only constitute around 2% of dietary mass[45]. Harris' hawks are therefore most reliant upon ground-dwelling mammalian prey.

Hunting mode

Harris' hawks are unusual among raptors in that they commonly live in family groups and perform cooperative hunting - however no research has yet fully uncovered the evolutionary benefits of such behaviour. The most popular theory is that hunting in a group provides a performance advantage in terms of improved capture success and allowing larger prey to be taken. Consequently, each member of the group benefits from an increased average energy intake, and observations have shown that all hawks flying away from kills had bulging crops - meaning the prey had indeed been shared[48]. Successful capture of large prey (lagomorphs) was found to be correlated with group size – up to 5 or 6 individuals, corresponding with the most common group size observed (means of 4.8[48] and 5.9 hawks[49]). These patterns therefore indicate that sociality in Harris' hawks may be due to the evolutionary advantages of cooperative hunting. Other advantages of cooperative hunting may emanate from an improved ability to distract and harass prey, thus heightening its vulnerability[48, 50]. This may be crucial in capturing jackrabbits, which are significantly larger than the hawks. In addition, team hunting may allow kills to be better defended against kleptoparasitism by other predators[48, 50]. Leaving their overnight roosting positions, Harris' hawks will perch conspicuously and assemble together at one site. They may then divide into smaller groups of one to three hawks and perform alternating 'leap-frogging' flights through their home range in search of prey[50].

Solo hunting is also used by Harris' hawks - not only at nests attended by only one pair, where males usually hunt alone while the female guards the nest - but also in breeding groups[51]. Solo hunting was observed in 18% of hunts by Harris' hawks which had the option of cooperative hunting (i.e. where only observations from groups comprising of more than 3 were included)[51].

Harris' hawks generally perform perched hunting in cluttered habitats and rely on high manoeuvrability and early acceleration to perform surprise attacks on ground-dwelling prey[42, 52]. These perched attacks may be divided as follows, however they are often intermixed in a spectrum of collaborative hunting behaviours[42, 46, 49, 50]:

Short surprise stoop: This is the most frequently used strategy, for prey that is in the open and away from cover. It often involves multiple dives by different hawks converging from different directions before the prey is dispatched.

Flush and ambush attack: If the prey animal temporarily finds cover then the hawks will intently watch the area where it was last seen while one or two group members land on the ground and attempt to penetrate its cover on foot. Once they have accomplished a flush, one of the perched birds will 'pounce' and make the kill.

Relay attack: This method is not commonly used, and involves a longer, constant chase where the lead bird is alternated among group members. The switch occurs after the initial lead bird stoops and misses the prey and then the chase is continued by another group member, sometimes involving more than 20 switches.

Solo hunting: Involves an individual scanning for prey from a perch and launching a short surprise stoop attack. Lone hunting is commonly used by breeding pairs as one of the pair must attend the nest.

Hunting success

Success of capturing prey is directly dependent on group size - a success rate of 20% was found in singly hunting birds, while this increased with group size up to 50% for groups of five[49]. This may be due to higher detection rates as group size increases, or simply that during group hunting any miss by an individual may be reconciled by another group member and still result in a kill[45]. The observations by Mader do not support these findings, as he found that cooperative hunting did not demonstrate an increase in prey captures[53]. However his findings were based on only three groups comprising of three birds, which is lower than the optimum group sizes described in other studies[48, 51], thus any increase in hunting success when compared to singly hunting birds is likely to be less obvious.

Adaptive hunting in raptors

Raptors perform a range of hunting behaviours which are influenced by wing shape, habitat structure and food availability[54-61]. Harris' hawks typically perform short attacks onto ground prey in more cluttered habitats, whereas peregrine falcons typically perform longer attacks onto both aerial and ground prey in open habitat. These hunting techniques have therefore evolved under different selective pressures, which place different demands on the morphology and physiology of the raptors. Due to these differences it is likely that peregrine falcons and Harris' hawks may have evolved different guidance strategies for intercepting prey. Fitzpatrick provides evidence for an evolutionary basis of aerial pursuit strategies in bird species, showing that bill and wing shape were strongly associated with aerial attack method and habitat[62].

A further factor, discussed later, is the visual system of raptors and how this may also contribute to the behavioural strategies observed in different species. This is especially relevant for raptors, as they hunt active prey and so require greater visual capacity for bringing down moving targets[63].

Bird vision

Eye size and sensitivity

Falcons, hawks, eagles and other predatory species, rely greatly on being able to interpret and react to their visual environment. Consequently they have evolved rather large eyes in relation to skull size (approximately 50% of skull volume compared to 5% in humans[64]) that are globose in shape and directed frontally. Consequently birds have a large visual field which in turn enables a larger image to be focussed on to the retina for much increased visual acuity [65]. It is thought that birds have big eyes relative to body mass as an adaptation to fast-speed flight - a principle known as Leuckart’s law [66]. Support for this theory is provided by several studies which found that in many animal groups body mass correlates positively with eye size and speed of locomotion, and thus faster moving animals have proportionately larger eyes[67, 68]. In addition, flightless birds - which experience comparatively lower speeds of locomotion – usually have smaller eyes relative to body mass. It follows that larger birds may be able to resolve object’s at a greater distance than smaller birds due to their proportionately larger eyes.

The avian eye must therefore also be able to change optical power as an object’s distance changes, to focus and maintain a clear image. This mechanism is called accommodation, and is essential for attaining high visual resolution[65]. Birds have high photoreceptor densities and are thus able to resolve rapid movements of greater than 100Hz[64, 69]. This is clearly evident in species such as Goshawks, which are able to perform high-speed pursuits of agile prey within densely wooded environments. They can detect every movement of their quarry and adjust their own flight accordingly while also avoiding any vegetation and obstacles in their path. Such a chase to the human eye would appear as a blur[64].

Past research has shown that birds also excel in both colour vision and colour perception[70-72]. Rich colour detection enhances visual acuity by improving contrast and the ability to distinguish objects in the environment, enhancing prey capture and survival[73]. Until recently, studies have focussed on the absorption of photopigments in passerines and waterfowl[70-72], but one study has now examined spectral sensitivity in raptors[74]. This work described ultraviolet sensitivity in sparrowhawks (*Accipiter nisus*), kestrels (*Falco tinnunculus*), common buzzards (*Buteo buteo*) and red kites (*Milvus milvus*), and found that UV cues were not important during foraging. However, without supporting behavioural experiments the role of colour vision in raptors remains unclear.

Visual fields

Visual field orientation plays a critical role in determining eye and head movements for scanning the environment and may directly influence pursuit behaviours. The visual field refers to the area of space around the head available for gathering information at any instance in time[75]. Visual fields vary greatly in birds due to both foraging and predation pressures[76]. The relative sizes of the three visual field components - the binocular area, lateral area and blind area - can determine sensory-related adaptations to the environment[77]. Orbit orientation within the skull influences the size of the binocular visual field; thus species with orbits converging more towards the frontal region of the skull are likely to have larger binocular fields. Likewise, species with larger lateral visual fields are expected to have more laterally pointing orbits[78, 79]. Large blind areas are thought to reduce the sun's glare, and are thus more common in species that perch in open areas and experience higher levels of glare[80].

In general, retinal resolution is improved by having a larger image projection, therefore it is probable that large eyes have evolved to give increased visual acuity[81].

It is argued however, that the features of bird visual fields are governed by the perceptual challenges of foraging rather than those posed by locomotion, or more specifically, the accurate positioning of the feet or bill during capture of food[81]. It follows that species which do not rely on bill positioning have very small binocular field widths, and conversely, New Caledonian crows (*Corvus moneduloides*) which expertly use tools when foraging, possess the largest recorded binocular overlap. Constraints imposed by the perceptual demands of predator or prey detection are thus traded-off, with large-eyed species being subject to the added constraint of needing to avoid the glare of the sun on the retina (such species possess brow ridges).

The lateral field of view is used for detecting prey and moving towards distant objects, and at some unknown distance to target, visual control of interception is passed from the lateral to the frontal field of view, within which the bill projects[81]. Species which take prey with their feet are found to bring them into a central position in the binocular field prior to striking. Binocularity is therefore proposed to be a consequence of having a section of the frontal visual field looking in the direction of travel, rather than an adaptation for increased depth perception through stereopsis (possibly excepting owls)[81].

The visual fields of predatory raptors have received little attention in comparison to prey species[66, 78, 80, 82]. The limited research has generalised their visual system as having relatively large eyes, with wide binocular areas, narrow blind areas and little degree of eye movement[73]. In a study by O’Rourke *et al* into visual field configuration and eye movements in three diurnal raptor species, a great deal of inter-species variability was in fact found[77]. Red-tailed Hawks (*Buteo jamaicensis*) are large perched hunters operating in open habitats to capture ground-dwelling prey, and were found to have the narrowest binocular area at 33° and widest blind area at 82°, but their degree of eye movement was intermediate at 5°. This suggests the lateral visual fields are the key to gathering visual information, as they search for distant prey over large open areas. Cooper’s Hawks (*Accipiter cooperii*) are medium-sized ambush predators of vegetated habitats that chase down tree-dwelling prey[83] and were reported as having the widest binocular field arrangement at 36°, a narrow blind area of 60°, and a much higher degree of eye movement at 8°. This configuration may serve to increase overall visual coverage and with more binocular overlap may improve prey capture when performing surprise attacks in visually complex and closed habitats[84, 85]. American Kestrels (*Falco sparverius*) are small falcons hunting in open areas by stooping onto prey from a perch or hovering overhead[86] and were found to have intermediate-sized lateral and binocular areas. This may enhance depth perception when locating targets at close distances, consistent with having only 1° of eye movement for improving image stabilisation when hovering over prey[87].

Broadly speaking, we can conclude that there is a large degree of variation in eye movements and visual field configuration within raptors (Fig.1). These differences appear to be related to their different hunting modes and prey scanning strategies, which in turn are influenced by the visual obstruction in the environment[77, 88]. In addition, this study suggests that raptors use eye movements to reduce retinal blur when tracking a moving target, rather than moving their head.

The fovea

Birds of prey possess further vision-associated adaptations essential for successful and swift prey capture. Specialised regions of the retina with higher densities of photoreceptors and ganglion cells, produce heightened acuity[89]. In the centre of this area is a section with even greater photoreceptor density, called the fovea, offering the best possible visual acuity. The fovea represents a cone-rich, rod-free depression acting to improve colour hues, resolution and depth perception of daylight vision[90]. Typically, foveae exist in species that rely on supreme visual acuity for survival, and are thus present in most avian species - including raptors - testament to the significance of vision in birds. Interestingly primates represent the only foveate mammals[89].

The most significant characteristic of raptor eyes is that many species are in fact bifoveate - they have two foveae, one located centrally within the retina known as the deep fovea[89, 90] and one in the temporal region known as the shallow fovea (Fig.1). The remarkable result of this bifoveality is that raptors have two functionally separate visual fields[11] granting them with sight along two visual axes for enhanced distance and speed perception of prey (excluding Owls and 'New World Vultures') [89, 90]. The deep foveae subserve monocular viewing of more distant targets, permitting independent motion of each eye, while the shallow foveae subserve binocular viewing, requiring coordinated eye movements[91]. Raptors are able to see an object most acutely when its line of sight falls on the deep fovea. The anatomy of the deep fovea tells us it has the greater acuity as it has a higher density of cone photoreceptors and the capacity for resolving images is directly dependent on this[92]. It has also been proposed that binocular vision in hunting birds may be important when prey is at the point of seizure, for capturing and handling it[93], and that a bird may switch from monocular to binocular vision in the final pursuit stages.

Raptors have limited ability to rotate their eyes in their sockets, due to their large size, and therefore to benefit from having these two fields of vision, have evolved to repeatedly orient the head into different positions when looking at an object[94]. Tucker showed how several species of raptors, including wild peregrine falcons, orient between three positions when looking at an object - described as straight, with the head axis pointing forwards at the object, or sideways left or sideways right, with the head axis pointing at 40° to the object[11]. These movements suggest the bird is focussing the image onto both the shallow and deep foveae individually, and the amount of time assigned to either deep or shallow fovea vision is determined by the distance of the object. It was found that for objects less than 8 metres away most time was spent looking straight on at an object; however, with a distance of 21 metres, they spent significantly more time looking sideways on. As the distance was increased to over 40 metres, the raptors were reported to be using sideways vision more than 80% of the time to look at an object. Furthermore, some birds favour a particular visual field depending on the velocity of the object being observed. When a slow moving object was presented to pigeons and chickens, they kept the image in front of their head, whereas for a fast object they kept it in their lateral visual field[95]. These studies provide evidence that raptors use their higher acuity deep fovea vision when looking at distant or fast moving objects, and their less acute shallow fovea binocular vision for close or slow moving objects.

While many drawings and photographs of bird fovea's can be found in the literature [89, 96-100], which focus on eye topology, relatively little quantitative study exists for non-mammalian animals. This is very surprising given the belief that foveal vision is one of the most highly developed features of vision, especially among raptors.

One detailed study of the American kestrel found that the line of sight of the shallow foveae points forwards at approximately 12° degrees to the left and right of the head axis, and at 48° to the left and right in the deep foveae [101] (Fig.1). Therefore, in the absence of such information for peregrine falcons and Harris' hawks, we must assume that the foveal angles of other Falconiformes and Accipitriformes are similar. There does not seem to be any other direct measurements of foveal angles in birds of prey, as studies have focussed on foveal anatomy – i.e. depth and cell density[73, 89, 92, 97], perhaps due to the uncertainty involved in working with eye specimens (where the fovea may be more diverged in death than they would have been in life)[96, 97].

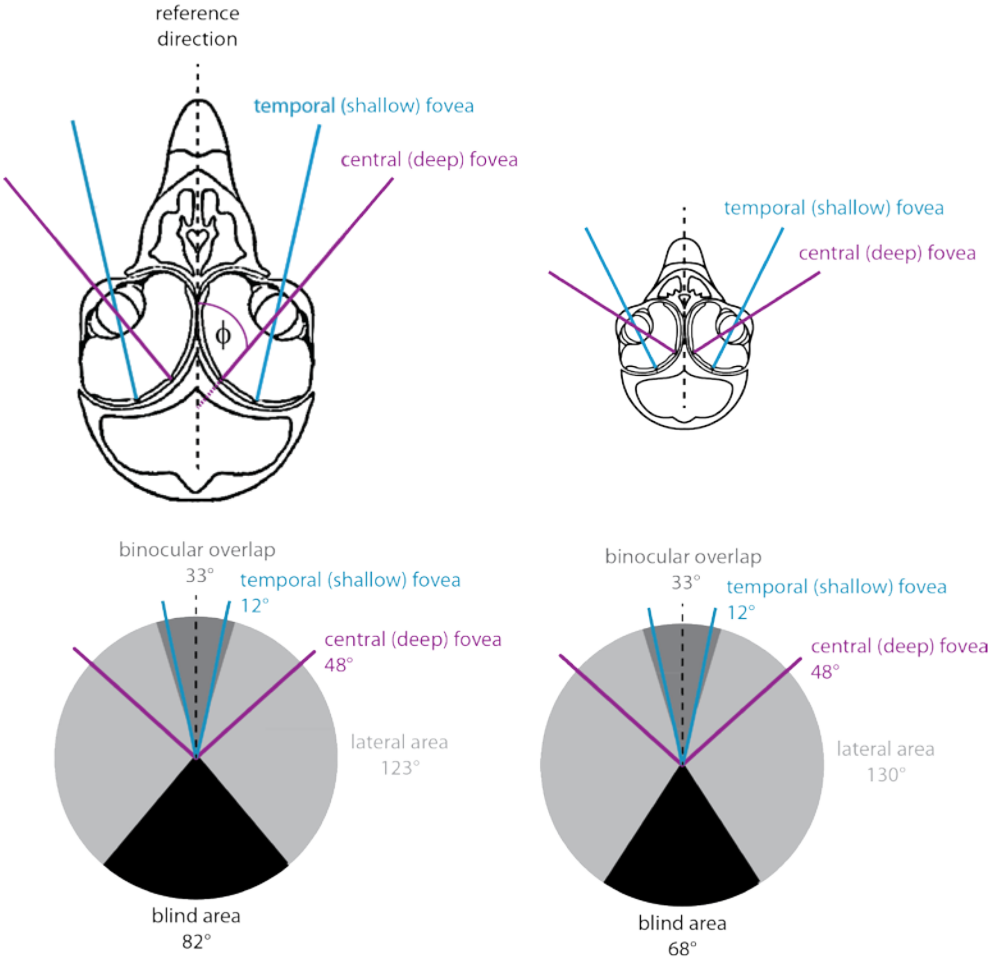


Figure 1: Comparison of a broad-winged hawk (*Buteo platypterus*) skull (top left) and American kestrel (*Falco sparverius*) skull (top right), showing the eye anatomy and locations of the two foveae on the retina and their respective gaze directions. The foveal angle ϕ denotes the angle between the gaze direction of the lateral fovea and the sagittal plane. Note that the eyes of the specimens may be more diverged in death than they would have been in life. Modified from [96]. The visual field orientations are shown for a similar hawk species, the red-tailed hawk (*Buteo jamaicensis*; bottom left) and the American kestrel (bottom right). The dashed line denotes the sagittal plane. Data from [77, 96, 97, 101].

Visual perception during self-motion

Optic flow

When an animal moves relative to a stationary environment, a change in the position or orientation of the eye causes light from a given point in the environment to fall on a different point on the retina - this is known as optical flow. Gibson first described these optical flow patterns and their potential importance for controlling visually guided behaviour, especially locomotion[102]. If two surfaces at different distances are textured similarly, the light projected to the animal's eyes will present different densities of optical texture[102]. A change in position or head movement produces motion parallax – "differential velocity of elements in the array" – and this increases with distance[103].

The optic flow field comprises of i) the global optic flow of the background, ii) the local optic flow from the target, and iii) the egocentric direction of the target[102]. Global optic flow is the motion pattern of a moving observation point and its projection on the retina against a stationary background. By aligning the optical expansion with the target (i.e. moving towards an object) and specifying the heading point, this can be used to steer towards an object[102, 104]. Local optic flow is the relative motion pattern between the pursuer and the target itself, with heading determined by the optical flow of the contours of the moving target - assuming that rotation of the target does not provide additional flow. The egocentric direction is defined as the target's visual direction relative to the locomotor axis, equivalent to the target-heading angle. Honeybees flying through gaps were shown to equalize the optic flow from each eye and thus balance the boundary distance on each side, and by maintaining the flow at a certain value they automatically slowed down when narrow gaps were encountered[105]. Therefore bees are directly estimating the relative distances of obstacles in relation to their apparent motion in the visual field.

For a pure pursuit strategy, a pursuer aligns its locomotor axis with the target, and thus the target's image is centred on the pursuer's visual field at all times. For a deviated pursuit strategy, a pursuer manoeuvres to keep a constant positive angle between the target and locomotor axis. Under parallel navigation, a pursuer manoeuvres to reduce the motion-parallax cues in the target's visual field and maintain a fixed visual bearing of the prey relative to a point in the environment. These strategies all rely on the perceived target distance decreasing, perhaps using optical expansion or binocular distance information - although binocular information may only be effective over a few metres' distance. The motion disparity of the target between the left and right eyes may instead be used to specify the passing distance[106]. In birds it has been suggested that the distance to an object is less important than determining its direction and time-to-contact, and information on travel direction to a target is most efficiently derived when heading straight towards it, i.e. using the binocular projection[81]. This results in optical flow information from each eye which is symmetrically expanding about the bill, called contralateral vision. However, the eyes need to be stable relative to the focus of interest in order to maintain visual acuity[107], and animals have thus evolved specific adaptations to counteract the effects of optic flow, described below.

Image stabilisation

Any movement of the head or neck when fixating on an object impedes ocular stability and could result in a "retinal slip" (described as blurred and corrupted acuity caused by movement of the retina). Birds are able to avoid this and stabilise their vision by combining vestibular and visual head and eye reflexes[108], described as a "compensatory eye movement response"[73]. Any head movement causes velocity information to be sent straight to the oculomotor system, thus controlling eye, head and neck motion[108]. Presumably a moving image on the retina is very difficult for the visual system to interpret due to its being blurred. This strategy of visual stabilisation has been well described in insects, where head rotations are made relative to the visual environment by active steering in flight to minimise retinal drift of the prey image, resulting in less blur and improved conditions for vision[7, 109]. In addition, neurones in the optic lobe that detect small target movement have been found in flies[110], with exactly the required properties for controlling tracking behaviour. This group of neurones are directionally sensitive to head movement and provide input to the wings[111].

While movement of the prey's image produces a rotation of the head and flight steering in the predator, it has also been observed that the rotation of the head is faster than the response of the wing. Co-ordination between both the head and the wings is necessary for orientation control. The results therefore suggest that the control of flight interception in insects must involve a neural pathway that transmits information about head position to the wings. However, for the visual system to correctly interpret its visual surroundings, the brain requires "self-directed" changes of gaze as well as stable views of the surroundings. The next section thus examines how visual information is used for controlling specific motor patterns of the visual system (for a more in-depth narrative, readers are directed to Zeigler and Bischof[112]).

Pursuit eye movements: target fixation versus background fixation

During pursuit in a structured environment, any movement towards the target unavoidably leads to the entire retinal image being displaced in the opposite direction. The images of the extensive background and the small target moving relative to it cannot be simultaneously stabilised on the retina[113]. Therefore two broad control systems exist for guidance of movement, which rely on adopting appropriate eye, head or body movements[114]. Studies of visual tracking in insects and primates describe these two groups of behaviour as gaze-changing (target fixation) and gaze-holding (background fixation)[115]. Gaze-changing includes smooth tracking and saccadic tracking. Smooth tracking attempts to match the target's velocity by allowing the target's position to be maintained in the foveal region. Saccadic tracking ignores target velocity and tries to match the target's position by inducing rapid movements (saccades) of the eye, interrupted by periods of no rotation[113]. Gaze-holding acts to maintain a stationary image of the surroundings on the retina, despite any head or body movements of the pursuer[115]. Gaze-changing behaviours (target fixation) have been shown in free-flying houseflies[116], blowflies[114], fish[117, 118], humans[119, 120] and robots[121], and Gaze-holding behaviours (background fixation) during target pursuit have been described in insects, cats and primates [113, 122-127], but either method may depend on distance and target behaviour.

At present no conclusive work has determined whether raptors use gaze-holding or gaze-changing pursuit eye movements when chasing prey, although certain studies have tried to answer this [11, 12]. Research has discovered an oculomotor behaviour that is unique to birds, called saccadic oscillation. This is where the eye does not follow the target directly in a straight line during a saccade, but produces a series of spiralling oscillations (owls: [128]; chickens: [129]). These oscillations are caused by birds having separate “saccade-related” and “position-velocity” motorneurons that are activated in turn, showing complementary responses[115]. This may be an adaptation for increasing saccadic eye-speed during pursuit or evasion of an object. However, head stabilisation is particularly important in birds for associated visual behaviours[115] - especially in raptors whose degree of eye movement is minimal. Rotational perturbations which alter the angle of the head in relation to the surroundings, and translational perturbations which alter distances, must be accompanied by compensatory movements of the head for stable vision[115].

Visual pursuit in birds of prey

Previous research has proposed falcons maintain head nystagmus (stable head and gaze) even during rapid turns[130, 131] since the airflow surrounding the head generates significant aerodynamic forces, the strength of which depends on the position of the head. Therefore maintaining a straight head during flight allows a bird to increase airspeed and limit the amount of aerodynamic drag. Tucker *et al* (2000) stated that when a bird initiates a hunt after sighting its prey from a distance, it will fly with its head straight and one eye looking sideways at the prey along a logarithmic spiral path, instead of directly towards the target[10]. This curved flight path suggests the bird is placing its deep fovea, suited for distance vision, in the line of sight whilst maintaining a straight head relative to its body. As the distance to the prey is subsequently closed, the bird will divert from this curved path onto a straight and direct path making use of its stereoscopic binocular vision for precise aiming. Tucker argues that the speed advantage incurred from the straight-head strategy counteracts the increase in distance of the non-direct curved path.

Although research has been conducted on the interaction between flight and vision, supporting the use of optical flow cues (budgies *Melopsittacus undulatus* navigating through an artificial environment[132]; obstacle avoidance in zebra finches *Taeniopygia guttata*[133]; and Pigeons *Columba livia* and Harris' hawks *Parabuteo unicinctus* landing on a perch[130, 134]), previous work has not explored how the pursuit strategy of an avian predator may be influenced by the prey's motion within its visual field. The study by Kane and Zamani investigated the visual motion-based pursuit behaviours in three falcon species hunting real prey, while fitted with head or back mounted miniature cameras, and found they maintained the target position at a constant visual angle using parallel navigation strategy[12]. However, the findings from the body-mounted camera data in this study were pinned on the assumption that falcons fly with their head aligned to their body axis, whereas in Tucker *et al* the falcon is assumed to be flying with its head aligned with its velocity vector[10]. Furthermore, the optimal visual angle was consistent with use of their shallow - rather than deep - fovea, suggesting the falcons are not using their more acute vision for viewing distant prey during pursuits[12].

Raptor eyes have a relatively limited range of motion (between 2° and 24° depending on species)[73] and so they may need to move their heads during a pursuit in order to scan or realign their field of view. In Kane and Zamani two of the videos support this view, as saccadic head motions were exhibited during these pursuit flights[12]. Several other studies also support the view that birds turn their heads in flight when viewing prey, rather than their eyes[94, 135].

From their head-mounted data, Kane and Zamani reported that the falcons had a strong preference for using the left visual field, though no such bias was observed in the back-mounted data, and so it is difficult to ascertain whether this was a real observation[12]. Tucker *et al* reported a similar bias in the falcon's flight paths; however it was to the right, i.e. the right visual field[10]. Certain (non-raptor) avian species have been found to favour their left or right eye, depending on the task, possibly due to the lateralization of avian brains as each hemisphere is specialized for different functions (for detailed review see[135]). However, brain studies have focused on prey species (mostly pigeons and chickens) which have more sideways pointing eyes with less binocular overlap than raptors, and so lateralization may be more prominent in these species.

To date, no research has investigated how the flight trajectories during prey pursuit may be affected in raptors with differing degrees of reliance on deep and shallow fovea vision. Although a study of prey-scanning strategies (head movement rates and duration) in perched raptors did indeed show inter-species variation in relation to visual field arrangement and the visual complexity of the habitat[88]. The slower head movements of Red-tailed Hawks increases their ability to detect cues (or prey movement) in the lateral visual fields, and may reduce the chance of detection by prey. This is beneficial to a species with larger lateral visual fields that generally scans from exposed perches in open habitats. Higher rates of regular head movements in Cooper's Hawks (*Accipiter cooperii*) may improve visual tracking in the cluttered environments they occupy, by shifting the image of the prey between the right and left central foveae more quickly. Hence they have the widest binocular areas to increase the amount of space they can scan without head movement[88]. American Kestrels had the highest translational head movements and since these movements are considered to generate motion parallax for depth information[136], a high frequency may compensate for their low degree of eye movement when scanning for distant prey in open habitats. However, head movements were recorded in perching birds, and movements while perching seem to be more flexible than when flying, due to a lack of aerodynamic drag[137].

Overall, the visual system of raptors must have a significant influence on the evolution of hunting strategies, or vice versa. The head movement strategies for scanning the environment are strongly associated with visual field configuration and habitat type. Therefore investigation on flying birds searching and pursuing targets is essential.

Pursuit strategies

Introduction

Pursuit problems have attracted much interest from biologists, engineers and mathematicians - predatory animals acquire food by pursuing prey, humans pursue moving objects when playing sport, and military guidance systems intercept moving vehicles. Therefore pursuing and intercepting moving targets are significant processes in nature and engineering.

Pursuit dynamics have been extensively studied in engineering circles, focusing on missile and aircraft guidance laws for steering along an interception path to a target[138-141]. Nahin provides a popular review of the topic in his book[142]. In biology, despite pursuit phenomena having a vital role in species survival, their dynamics have only been analysed from this perspective in a small number of papers, though the context of the pursuits are not predator-prey interactions in these cases[1, 2, 5, 143]. The majority of biological research has sought to explain the guidance problem by identifying simple geometric rules characterising the observed flight trajectories (dragonflies:[6-9, 144]; birds of prey:[10-12, 145]; bats:[13]), each dependent on the constancy of one of two angles; 1) the line-of-sight angle (θ), defined as the bearing of the line-of-sight between the pursuer and its target, and 2) the deviation angle (α), defined as the angle between the bearing of the pursuer's velocity vector (γ) and its line-of-sight to target (θ).

Missile guidance systems use several different navigational laws for steering along an interception path to a target. The method used depends upon the target flight path and the mechanical and aerodynamic limitations of the missile. Nature may not face the same limitations, since a bird or insect wing presents a much more dynamic flight control surface. However, animals are subject to additional neurophysiological constraints. The processing time for nervous signals to be transmitted, for muscles to contract, and for the inertia associated with the movement to be overcome, is not insignificant. For a flying insect the delay between presentation of a visual stimulus and response movement is about 10ms, whereas for the human eyeball this is around

100ms, however when whole body movements are involved it can be considerably longer[4]. Olberg provides an up to date review of the neurophysiology of prey pursuit, in relation to visual pathway signalling of target motion[6].

Engineering

There are many text books describing the mathematics of pursuit, and specifically how the kinematics (geometry) relate to the dynamics (guidance laws). Readers are directed to Siouris[146] and Shneydor[147] for a full account, however the essentials are summarised here. The terminology we use is standard in the missile literature, but a variety of other terms have been used in the biological literature and are summarised in Table 1.

History

The mathematician Pierre Bouguer - described as the father of the pure pursuit problem - started an analytical approach back in the 18th century. He used a pirate ship pursuing a fleeing merchant vessel in his explanation. As the pursuit begins the merchant ship travels at constant speed along a straight line, while the pirate ship moves along a curved path that is always moving towards the merchant. The slope of the tangent line to the pursuit curve solves the equation for the line of pursuit, and capture will always occur by this strategy when the curves intercept, assuming the pirate ship is travelling faster than the merchant vessel. The closer the speeds of the two vessels the further along the vertical line they will intercept, and if the merchant ship is faster capture will not occur. Bouguer also noted that the pirate ship could catch its quarry much more quickly if it headed it off and sailed in a straight line towards the merchant vessel, thereby following a deviated pursuit instead of a pure pursuit course. However, if the merchant ship then diverged from its straight course to execute an evasion plan then the pirate ship would have to recalculate its intercept course continually. Bouguer therefore described a pure pursuit as a method of specifying repetitive new course calculations, and this represents the basis of pursuit research.

Guidance laws and geometry

More recently, in the aerospace community, the most common approach to the pursuit problem is to adopt a guidance law[147]. Classical missile guidance laws are all variations upon a control law called pure proportional navigation, in which the line-of-sight rate $(d\theta/dt)$ - i.e. the rate of change in the bearing of the line-of-sight vector - is fed back to command a turn rate $(d\gamma/dt)$ proportional to the line-of-sight rate[146] (Fig.2):

$$\frac{d\gamma}{dt} = N\frac{d\theta}{dt} \tag{1}$$

Where γ is the bearing of the missile's velocity vector, θ is the line-of-sight between the pursuer and target and N is the gain of this proportional feedback called the navigation constant[147]. If there is zero rotation of the line-of-sight angle, no steering commands are generated, while any rotation of the line-of-sight angle generates steering commands to reduce its rotation rate. Therefore, if the target steers away from the pursuer (line-of-sight angle θ increases) the pursuer's velocity vector angle γ likewise increases, resulting in the pursuer turning towards the target.

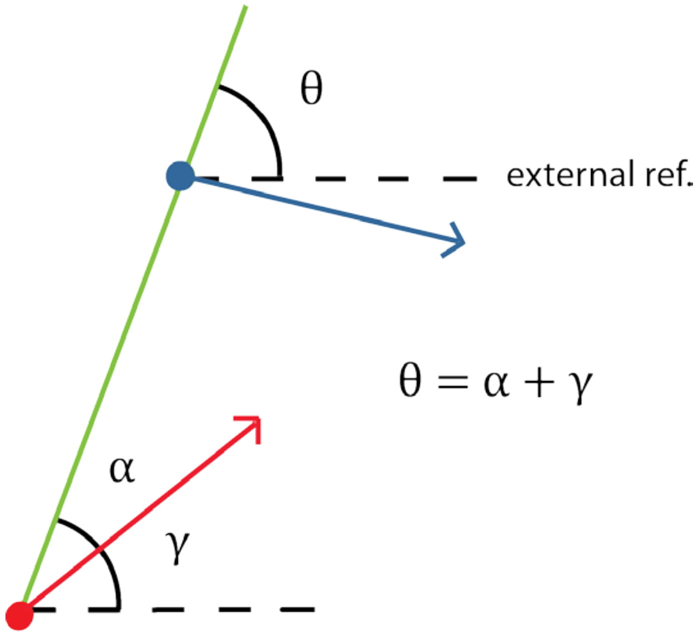


Figure 2: Definition of angles of a pursuer (red) following a target (blue) using proportional navigation. The pursuer's turn rate (change in bearing of its velocity vector γ) is kept proportional to the line-of-sight rate to target (change in bearing of line of sight angle θ) in relation to an external reference (e.g. true north), α is the deviation angle.

The proportional navigation trajectory is influenced by the effective navigation ratio, N, which determines the heading error (deviation angle α) and pursuer time constant (time lag between any target manoeuvres and associated pursuer responses). In the simplest case where $N = 1$, proportional navigation implements either the pure pursuit geometrical rule:

$$\alpha(t) = \alpha(0) = 0 \tag{2}$$

Or the deviated pursuit geometrical rule according to the initial conditions defined by $\alpha(0)$, where $t = 0$ defines the start of the pursuit.:

$$\alpha(t) = \alpha(0) \neq 0 \tag{3}$$

A missile undergoing a pure pursuit strategy travels directly towards the target at all times, so its heading remains the same as the line of sight, and thus the deviation angle is zero (assuming perfect guidance) (Fig.3). This may result in a ‘tail chase’ scenario if the speeds of the target and missile are similar. The forces applied to a missile’s airflow control surfaces (e.g. wing and tail fins) increase with acceleration and so there are two disadvantages to the pure pursuit strategy. Firstly, the missile must make tighter and more difficult turns as its speed increases and it nears its target in the terminal phase[142]. Therefore if the target employs evasive action, the aerodynamic capabilities of the missile may be insufficient to meet the requirements of this last-second angular acceleration, resulting in a large miss distance. Secondly, the speed of the missile must be significantly greater than that of the target. As a result, there must be a maximum speed limit beyond which a missile’s control system is unable to generate the required forces to move the wing and tail fin surfaces. Therefore very fast missiles cannot implement a pure pursuit strategy from start to finish, and so this strategy is applied for slow moving craft, or when the missiles are launched directly behind or in front of the target[146].

Pure pursuit guides the pursuer to the target itself, whereas deviated pursuit guides the pursuer to the expected intercept point by maintaining a fixed angle pointing in front of the target[146] (Fig.3). Deviated pursuit courses are not implemented in missile applications, however sometimes random errors and bias lines result in a deviated pursuit flight[146]. When a target's motion is restricted within a plane, the course of the pursuer will follow a curved path with the radius of curvature determined by the distance, relative speed, and angular velocity between the two. When an object is on a curved path, the force exerted on it varies inversely to the radius of curvature, thus there is a limit to the sharpness of any turn[148]. Therefore a pursuer may not always be able to turn sharply enough to follow the pure pursuit course, in which case, a deviated pursuit path with suitable navigational correction is theoretically advantageous. Yuan presents a mathematical analysis of optimum pure pursuit and optimum deviated pursuit paths of automatic target-seeking devices[148]. This study described the existence of an optimum navigational ratio between too slow an approach to a target, resulting in a failure to intercept it, and too fast an approach, leading to instability. Using this optimum navigational ratio results in a path that should achieve a successful target interception in the least possible amount of time.

As the navigation ratio N approaches infinity, the line-of-sight bearing θ approaches zero, and so proportional navigation effectively implements the parallel navigation rule:

$$\theta(t) = \theta(0) \tag{4}$$

when N is very large. Under parallel navigation the bearing of the line-of-sight vector θ is therefore held constant (Fig.3C) and leads coincidentally to a form of motion camouflage, because from the target's perspective the pursuer appears stationary relative to distant landmarks[149]. By following a parallel navigation course and minimising changes in the line-of-sight bearing to target, the instantaneous optimum bearing of the pursuit is maintained. This is commonly used in missile applications[146, 147], and is referred to as parallel navigation for the reason that the bearing lines from target to pursuer (line-of-sight) appear parallel when viewed externally – thus this strategy can be inferred informally from plots of pursuit trajectories.

Pure proportional navigation, defined by the guidance law in equation 1, is therefore capable of implementing any of the three geometric rules that have been identified here. Moreover, the same guidance law is capable of producing a continuum of intermediate trajectories, depending upon the numerical value of the navigation constant. As N increases, the heading error decreases and the required acceleration during the terminal phase of pursuit is reduced[146]. Too high a navigation constant leads to overshoot, whereas too low a navigation constant requires excessively high accelerations if the target manoeuvres in the terminal phase of the pursuit. Consequently, values of $3 \leq N \leq 5$ are used in order to minimise the acceleration requirement of the missile and provide an acceptable miss distance at interception[146]. More modern missile guidance laws are based upon optimal control techniques (for optimising the value of N), and involve solving minimization problems numerically[150].

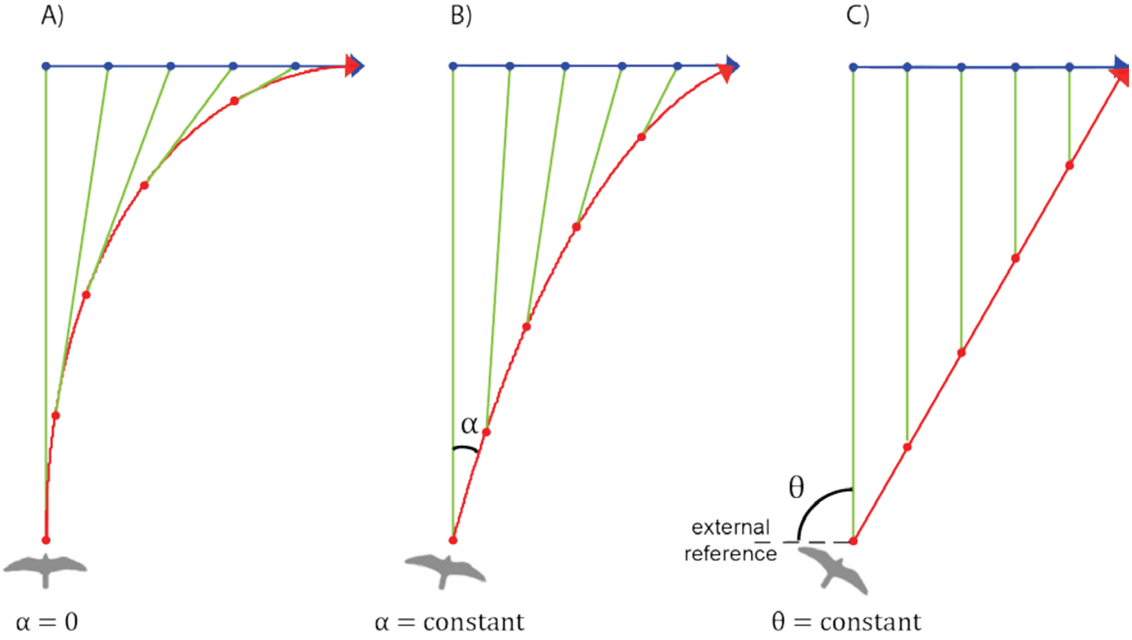


Figure 3 (A-C): Theoretical pursuit trajectories for a pursuer (red) capturing a non-manoeuvring target (blue) showing the line of sight (green) between corresponding pursuer and target positions for the three geometric rules discussed in the text: A) pure pursuit course with zero deviation angle α between the pursuer's velocity vector and the line of sight to target, i.e. $\alpha = \alpha(0) = 0$ such that the line of sight is always tangent to the pursuer's trajectory; B) deviated pursuit course with a constant non-zero deviation angle α, i.e. $\alpha = \alpha(0) \neq 0$; C) parallel navigation course with a constant line-of-sight angle θ measuring the geographic direction of the line of sight relative to an external reference, i.e. $\theta = \theta(0)$.

Biology

The majority of pursuit research in biology leaves unanswered the question of how the geometrical rules are implemented in nature, despite the fact that missile engineers have been designing guidance laws that implement these geometrical rules using feedback control for over half a century [142, 146, 147]. Until recently, most pursuit research in biology has described animals adopting either a ‘tracking’ or ‘intercept’ strategy. During tracking a pursuer follows the instantaneous position of the target at all times thereby maintaining zero deviation angle α between its line-of-sight vector to the target and its velocity vector – describing a pure pursuit course. This strategy has been observed in chasing flies[5, 151, 152] and hawks flying at stationary targets[145] – where the pursuer turns so as to drive its deviation angle α to zero. Equivalent behaviours have been observed in bees landing on a moving target[153], fish swimming after sinking food[154], and tiger beetles running after dummy prey[143, 155]. During interception, a pursuer aims ahead of the target to an anticipatory collision point by maintaining a constant deviation angle α that differs from zero – describing a deviated pursuit course. This strategy for target capture was first proposed for falcons[10, 11] but empirical support for this behaviour is lacking[12]. Both pure and deviated pursuit strategies only work well assuming the target moves at a constant speed and in a straight line[146]. More recently, research on dragonflies[6-9, 156], bats[13, 157] and birds[12, 145] - chasing unpredictably moving targets - has suggested they use a parallel navigation strategy whereby the constant absolute target angle is kept constant.

FLIES

Land and Collett first investigated chasing behaviours in lesser houseflies (*Fannia canicularis)* by filming and analysing the flight trajectories of male flies pursuing other flies[5]. They described two types of control system for chasing an object, forming the basis for subsequent insect pursuit experiments. First is a continuous tracking system, where the input variables (position or angular velocity of the target on the pursuer’s retina) continuously control the output (rotational and translational velocities) of the pursuer’s course, i.e. any change in the prey’s flight speed or direction elicits a change in the pursuer’s flight course. Secondly a discontinuous interception system, where the input is sampled periodically and the output is a series of open-loop responses (not modified by feedback), i.e. each manoeuvre of the leading fly is mimicked by a stereotyped reply-manoeuvre. In both dolichopodid flies (*Poecilobothrus nobilitatus;* [1]) and houseflies[5] a strong and linear relationship was found between the angular velocity of the chasing fly's course and the relative angular velocity of the leading fly. This is therefore a continuous control system whereby each time the target changed its position the pursuing fly turned towards the target fly with an angular velocity proportional to the divergence, and therefore continuously adjusted its flight path relative to the target's position, represented by:

$$\omega_f \propto k\theta_e \tag{2}$$

Where ω_f is the angular velocity, θ_e is the error angle and k is the gain. Although they propose this as a guidance law, it is not strictly a test for proportional navigation, as they define the line-of-sight angle, and therefore the angular velocity, in reference to the body axis (error angle; Fig.4) and not to external coordinates[2], thus Land and Collett are describing some other kind of control.

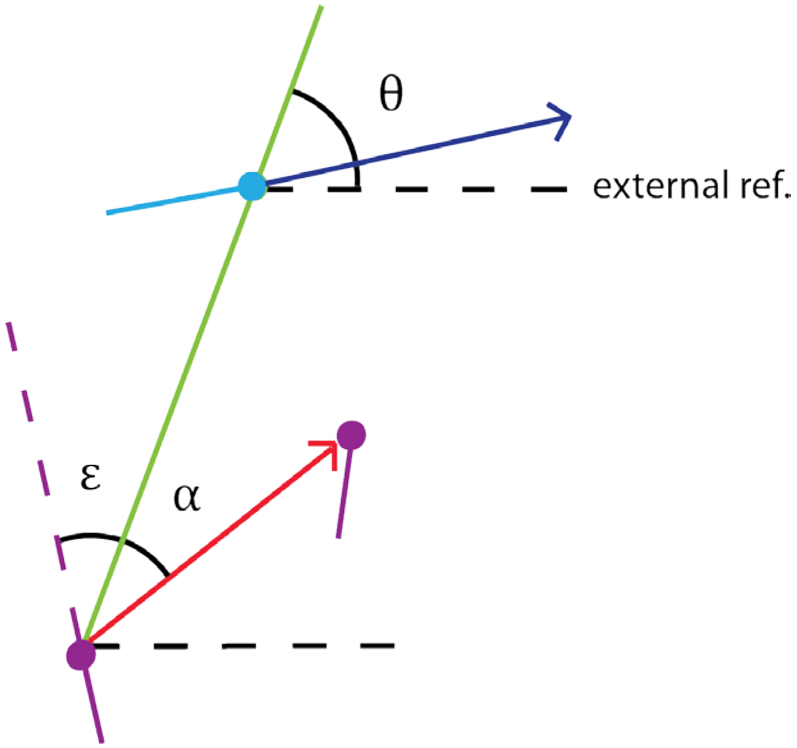


Figure 4: Intercept trajectory highlighting the error angle (ε) as measured in the earlier biological pursuit literature. The error angle is the angle between the line-of-sight to target (green) and the body axis of the pursuer (purple) and is thus not measured relative to external coordinates (equivalent to the deviation angle). The line-of-sight angle (θ) is the bearing of the line-of-sight, and heading angle (α) is the angle between the line-of-sight and the angular velocity.

Other pursuit research conducted on free-flying common houseflies (*Musca domestica*[116, 151]), fruit flies (*Drosophila melanogaster*[158]) and marchflies (*Bibionidae*[159]) also describe a continuous tracking control system. The angular velocity of the pursuer's course, or body orientation, was directly driven by the target's relative position. None of these papers discuss the guidance laws underlying their data, however the results are consistent with a pure pursuit course.

In hoverflies (*Eristalis* sp. or *Volucella pellucens*), a saccadic (discontinuous) open-loop interception control system was described. Analysis of flight paths showed that whether pursuing a female or a pea shot from a peashooter, male hoverflies did not simply turn and fly towards the projectile, as if following a pure pursuit, but selected an interception path after seeing the target[2, 3]. Open-loop control implies the hoverflies are not pursuing the target at all, just simply flying in an appropriate direction. However, these open-loop behaviours were infrequent (only occurring during larger turns where the target was outside of foveal vision) with continuous tracking (pure pursuit) the default method[2]. Like their fly papers, Collett and Land measured the error angle (in relation to the pursuer's body axis) and not the deviation angle (using the direction of the pursuer's velocity vector), when body orientation and flight path may differ (Fig.4). Also, findings were pinned on the assumption that there is a 20ms delay between the target's movement and the pursuer's corresponding movement, without direct testing. Moreover, the authors' interpretation of 'interception' is flawed, as here it simply means 'aiming ahead of the target', which is not the same as a deviated pursuit. They justify this conclusion on the basis that flies did not modify their trajectory in response to sudden changes in target trajectory. Therefore, it is wrong to assume hoverflies are adopting an interception course without considering all other possible pursuit courses. Other studies on the visually guided flight behaviour of hoverflies (*Syritta pipiens*[2]; *Eristalis* sp. and *Volucella pellucens*[3]) when tracking moving targets, have reported an interception strategy equivalent to a deviated pursuit.

Srinivasan & Davey[160] were the first to propose that hoverflies use a strategy amounting to parallel navigation, where the pursuer acts to minimise the motion parallax cues perceived by the pursued. The male will shadow a female in flight, keeping a constant distance and emulating a stationary object behind by yawing and moving vertically or laterally as necessary, and when the female lands on a flower to feed, the male darts in rapidly to mate with her[160]. However they do not provide information on the absolute angle measurement, and so we cannot conclude this is a parallel navigation strategy.

The early experiments on insect pursuit examined male-male interactions, male-female chases and shadowing, and so the function of these pursuit behaviours is not known. Therefore, since flights do not represent true interception where the goal is to capture a target, the findings are only of limited relevance to this thesis. Overall, much of the work on fly pursuit is inconclusive since the angular velocities of the chasing flies were calculated in relation to their body axes, not their heading, and flies do not necessarily align their long body axis with the direction of flight[1, 116, 158, 159]. Therefore body orientation may differ significantly from flight path orientation[159].

BEES

One study focused on the neural processes underlying target pursuit behaviour in honeybees (*Apis* sp.) trained to collect a reward from a moving target. It was found that during pursuit they also controlled their angular orientation and velocity on approach[153]. This work also measures the angular bearing to the target with reference to the bee’s midline, and so is not a test of proportional navigation.

BEETLES

Similarly, the angular velocity of tiger beetles (*Cicindela repanda*) chasing artificial prey items was found to be driven by target position[143, 155]. The earlier paper simply concluded that beetles use closed-loop control (consistent with a pure pursuit) with a discontinuous tracking method of several iterations of stop-and-go running, due to the prey’s image being degraded while running[155]. The recent study by the same author went further, and tested for a control algorithm proper[143]. From their correlation analyses of beetles pursuing prey dummies, they found the beetle’s angular velocity, relative to the prey, was driven by a proportional control law with a delay of 28ms. They also examined whether the beetle’s orientation could be predicted from its angular velocity, using a simulation which forward integrated the differential equation of the control law:

$$\omega_b(t) = k\theta_e(t - r) \tag{3}$$

Where ω_b is the angular velocity, θ_e is the error angle, k is the gain and r is the time delay. They compared the predicted orientation of the body to the actual measured data and found a close match. Beetles were also shown to adopt a nearly-optimal gain value, to minimise the error angle in approximately the shortest amount of time. However, the angular velocity of the beetle was again measured in relation to the orientation of its body axis. Therefore this control law is not describing proportional navigation, which requires calculation of the bearing of the angular velocity relative to the target.

ANTS

In another study on a terrestrial species, ants (*Lasius fuliginosus*) were shown to walk sinusoidal paths as they followed a straight, artificially laid, pheromone trail[127], and maintained a proportional relationship between their goal angle and speed of a turn. Goal angle here is defined as the angle between the goal and the ant's direction – which is the same as the error angle in the above studies. Therefore this research also provides evidence for a proportional control law but not for proportional navigation.

LEECHES

A pursuit study using leeches (*Hirudo verbana*) was based on the assumption that they rely on continual sensory input for tracking a target, and thus will localize a constant stimulus much better than an intermittent stimulus[161]. Conversely, an animal that pursues a target using interception will perform equally well with either a constant or intermittent target-stimulus. When leeches were presented with a constant target they were much more successful at locating its source than with an intermittent target, thus suggesting they indeed require constant sensory information for tracking prey[161]. Furthermore, when the location of the stimulus was changed, leeches were seen to retarget their search towards the new position, without reference to the original position, as required under a tracking approach. However, the researchers did not look at the geometrical relationship between the relative positions of the leech and the target, but instead tested the probability of locating the target under constant and intermittent conditions, and is therefore not a true test of pursuit.

FISH

Lanchester and Mark were interested in the approach and capture strategies of hunting leather-jackets (*Acanthaluteres spilomelanurus*) in terms of the path, eye and body movements[154]. Experiments involved moving food at right angles to the movement of the fish, in a constant-velocity path. When food was moved through the water vertically at constant velocity, the fish would follow trajectories that aimed constantly at the food by following its instantaneous position. They measured the deviation angle (between the tangent of the fish's trajectory and the target) and distance to target, and found an approximately constant near-zero angle - consistent with a pure pursuit strategy. Interception pathways with a constant non-zero deviation angle were occasionally observed when food fell from above. However, this may have been a result of the forward movement of the fish creating a stable image on the retina when pursing food under such conditions, and therefore may not represent a true interception strategy. This work on fish was the first to report the use of fovea vision during target pursuit in a vertebrate, as target position must be fixated on the pursuer's retina for capture.

Another study examined prey-capture behaviour in weakly electric black ghost knifefish (*Apteronotus albifrons*) and brown ghost knifefish (*Apteronotus leptorhynchus*), by observing their electrosensory movement in response to prey[118]. Analysis of fish orientation showed they can also adapt their strike trajectory to account for prey movement. The authors proposed a closed-loop tracking strategy, rather than an open-loop intercept strategy, to capture prey. However, most of the prey movement seemed to be caused by turbulence from the fish itself, and so results are inconclusive since the effects of prey position on the predator would be hard to predict.

A study on Mottled Sculpin fish (*Cottus bairdii*) showed they respond to a dipole source (inert vibrating sphere) by initially orienting towards it, followed by a step-like progression towards the source and then a final strike[162]. Fish were recorded heading either directly towards the source, or indirectly, with the source to one side, resulting in an arching path, or alternating between sides, resulting in a zigzag path. Results suggest the fish were also using a closed-loop tracking strategy, as they moved in the direction of increasing pressure and not to an anticipatory point. However this is not strictly a pursuit study, as although it involved trajectory analysis, the motivations of the fish were unknown (i.e. they were not capturing prey).

BATS

Bat species which pursue flying prey must be extremely fast and precise in their foraging strategy - moths typically emerge from cover for a very brief time, fly erratically, and return to the vegetation. Therefore bats have a very short time window in which they must detect, pursue and intercept their quarry, and consequently can make a successful capture in less than one second from the point of detection. This suggests bats have adopted the most time-optimal strategy due to evolutionary pressures. Ghose *et al* examined the three-dimensional flight paths of the big brown bat (*Eptesicus fuscus*) during pursuit of free-flying and tethered insect prey in a dark laboratory room[13]. They used high-speed stereo infrared videography, combined with the following simple delay differential equation to quantify the bat's flight trajectories during prey pursuit:

$$\frac{d\phi_e(t)}{dt} = k\phi_e(t-\tau) \tag{4}$$

Where ϕ_e represents the error angle, k is the gain parameter and τ is the delay. This is different from the control laws in equations 2 and 3, as the rate of change of error angle is not the same as the turn rate (or change in angular velocity) – the bat does not have full control over the error (or deviation) angle and so this is not a guidance law.

However, they show that the path of an erratically moving target may be divided into shorter and shorter linear sections each of constant velocity. If the bat follows an optimum-bearing capture path for each linear section, by constantly manoeuvring to minimise shifts in the absolute direction to the pursued, then the time to interception is at a minimum. This represents the optimal strategy for pursuing erratically moving targets. Ghose *et al* therefore proposed that bats use a parallel pursuit - termed constant absolute target direction in the biology literature - for maintaining the optimum bearing when capturing highly erratic prey[13, 157]. The bats in their study were found to reduce the rate of change of their absolute target direction to zero, consistent with a parallel pursuit, rather than reducing their change in deviation angle as necessary for a pure or deviated pursuit strategy. Bats also maintain the absolute direction of their head in space independently from their body orientation. However, the parallel pursuit strategy was only observed for sections of the pursuit trajectories, and furthermore when a tethered insect target was used, discriminating between strategies was said to be more difficult.

DRAGONFLIES

Olberg *et al* hypothesised two strategies in their work on dragonfly pursuit; one is equivalent to parallel navigation (maintaining a constant absolute bearing), whereas the alternative maintains a constant error angle (in relation to body angle)[8]. While the absolute angle is measured relative to space, their second hypothesis does not specify a condition for maintaining body angle in relation to the velocity vector (and therefore in relation to space). Though body angle may be correlated with direction, it is free to vary independently, so their second hypothesis is not an interception strategy since ultimately it will not lead to a collision. Olberg’s prey-capture trajectories of dragonflies show that they steer to follow an interception course and that this is under continuous visual control. They did this by maintaining a more constant absolute angle (compass direction) rather than error angle. Therefore Olberg *et al* proposed dragonflies may be using a parallel navigation strategy by steering to maintain a constant line-of-sight bearing (or deviation angle) to the target (bearing here refers to the angle between the forward direction and line-of-sight to target)[6]. This amounts to a proportional relationship between the line-of-sight angle to the target and target angular velocity, and hence describes proportional navigation. Although dragonflies appear to adopt a constant bearing strategy for capturing prey, it has not yet been determined whether their turning responses do indeed reflect a proportional navigation mechanism[6]. If they are using a proportional navigation technique, the dragonfly only needs information on the angular velocity of the prey image in order to perform compensatory proportional turning. This seems likely in view of the highly variable flight speed and size of their prey, making distance estimation difficult. Furthermore, target-selective descending neurons (TSDN's) in the nerve chord of the dragonfly are strong candidates for perceiving changes in angular velocity[6].

This work also provides evidence of fovea vision in guidance, where the image of the prey is maintained on their dorsal fovea. There are two ways visual guidance works; either the head is stabilized on the visual environment and the pursuer responds to drift of the prey across the retina, or the head is stabilized on the target followed by compensatory flight corrections - thus dragonflies are using the latter.

Recent work on dragonflies also found evidence for the use of parallel navigation, but only over very short stretches of flight[144]. Mischiati *et al* examined prey interception in terms of forward internal models – defined as the ability to predict the "sensory consequences of self-movement" rather than using simple reactive control[156]. By tracking the time-varying head and body positions of dragonflies, they found that head rotations cancelled out any drift of the prey-image caused by both self-motion and prey motion, with a near-zero delay. They claim that such a short lag suggests predictive internal control rather than reactive control. This research concludes that most steering behaviours are under model-driven control, however, they offer no explanation as to how this may be implemented.

A guidance strategy described only in biology, called motion camouflage, has also been proposed in dragonflies[9] - contrary to other research with this species[7, 8], in a re-analysis of work by Collett and Land[2, 3, 160]. Motion camouflage centres on the fact that as an animal moves the image of any objects in the environment, whether stationary or not, moves on the retina. So when a predator is moving itself, it must be able to pursue another animal without giving away its presence by its own motion. Therefore predators may have evolved to also use concealment to aid their attack[149]. A leopard or lion stalking its prey uses a simple technique - it moves slowly. Stealth however, is only feasible for stationary objects and thus is not possible when the prey animal is moving away from the predator[160]. There are two different motion camouflage techniques, one where the predator is said to camouflage itself against a stationary point on the immediate background as it closes in (Fig.5A) and a second where the pursuer maintains a constant absolute angle with the target against a distant point, consistent with a parallel navigation strategy (Fig.5B) [149]. Both techniques involve maintaining the same image on the target's retina so no optic flow is picked up (relative motion between predator and prey and hence the essential cue for detection).

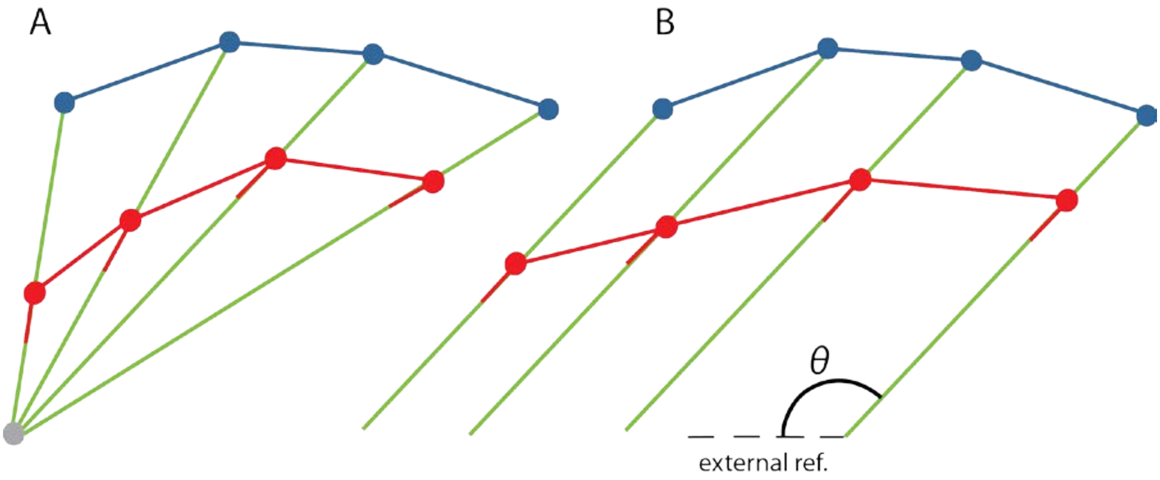


Figure 5: Intercept trajectory of a pursuer (red) following a target (blue) using motion camouflage: A) The pursuer maintains its position against a stationary point behind it; B) The pursuer maintains its position against a point at infinity (distance background) and keeps the line-of-sight bearing (θ) constant as for a parallel navigation strategy.

Executing a motion camouflage pursuit would require extremely precise flight control from the pursuer which is difficult to envisage in the animal kingdom, though little is still known of such positional sensing[160]. However, considering compound eyes are highly sensitive to optic flow (i.e. movement), motion camouflage would seem to be a plausible strategy for certain insectivorous species[160].

It is important to note that in Mizutani *et al*'s study only 6 out of 15 flight trajectories showed evidence of motion camouflage[9]. Furthermore, the lines of intersection between the pursued and the pursuer did not perfectly meet at a single point in the background, as would be expected for accurate motion camouflage, with a sphere of uncertainty of 11.3mm radius reported (zero would be required for perfect motion camouflage - though probably unattainable in natural systems). Other research on dragonflies where a deviated pursuit was observed were restricted to very short flights (between 5cm and 15cm[8]), when dragonflies may actually chase prey at more than 50cm away. Therefore, this highlights an interesting question about whether a different pursuit strategy may be adopted depending upon the distance from the target, or even whether animals may actively switch between strategies as they near their target.

Overall, though the results are interpreted as motion camouflage interception courses in several papers, it is unclear whether motion camouflage is a true navigational strategy. Srinivasan and Davey acknowledge it may be an “illusory by-product” of a strategy intended for tracking pursuit[160]. They also state motion camouflage isn’t fool proof since it is based on “simplifying assumptions” and so may only apply under certain conditions. Practically speaking, as a guidance strategy it is rather weak, since any two vehicles moving parallel to each other will inadvertently result in the motion camouflage geometry (bearing lines meeting at a fixed point on the background)[149]. Furthermore, it is not always possible to distinguish a navigational path from an interception path based on the flight trajectory alone. Therefore, findings may represent a misconception of pursuit geometries in the field of biology, as there is no concrete evidence of the use of motion camouflage in nature or engineering, and the authors do not provide a biologically plausible feedback law for implementing it.

BIRDS OF PREY

In separate experiments, Tucker used binocular observations and tracking devices on wild peregrines, and computer-modelling of ‘ideal falcons’, to propose that hunting falcons fly with their head held in-line with the body for streamlining, while their body is turned in flight to fixate the image of the prey on their deep fovea field of view[10, 11]. An ‘ideal falcon’ would thus maintain a constant angle between its body axis and the line-of-sight to target, by default resulting in a deviated pursuit strategy in which the deviation angle is kept constant at approximately 45˚. The flights of the wild falcons were executed from distances of up to 1500m, and so it is more than likely that a bird would use its highest acuity vision at such long ranges. Furthermore, they observed a strict bias in the flight trajectories (always curving to the right) suggesting there may be other explanations for the behaviour. For example, since all flights were observed in the same location, this may reflect features of the geography, or that the bird was hiding from its prey by approaching it out of the sun, or simply making its intentions misleading by not following a straight flight path. From his work on 'ideal falcons' Tucker also proposed a strategy switch, where a bird will divert from its spiral path and fly straight at prey, when close enough to see it using its less acute binocular vision. This is plausible in light of the potential aerodynamic constraints imposed on missiles and animals during the final stages of target interception, and needs testing.

In a laboratory study, five barn owls were each exposed to a live vole, and the owls' head movements were recorded in relation to the voles' position[163]. The results showed that the patterns of head movement are consistent with an intercept rather than a tracking strategy, as the owls orient towards the predicted clash point and then back to the target, consistent with a deviated pursuit strategy. However, this study only involved head movements and not the pursuit path towards the target, but the findings are supported by a study of escape behaviour in voles[164], suggesting they alternate between fleeing and freezing to evade owl attacks. This model proposed that when the vole stopped suddenly, the owl continued to its anticipated collision point, thereby losing sight of the vole which was no longer generating auditory or visual cues.

Two recent studies in birds of prey provide support for the use of parallel navigation in nature. Kane and Zamani[12] and Kane *et al*[145] reported that falcons and goshawks pursue prey by manoeuvring to maintain the prey's image at a constant visual angle (between the line-of-sight to target and bird's head axis) in the horizontal and vertical directions, via parallel navigation. These papers also provide evidence for a possible strategy switch in hunting raptors, as in both falcons and goshawks, erratic motion of the prey image was observed during the final stages of attack, meaning birds had diverted from a parallel navigation strategy when closing in. In addition, they found that the pursuit strategy was dependent on prey behaviour, since when flying at stationary prey or perches, goshawks apparently used a pure pursuit strategy, while parallel navigation was only used for manoeuvring prey. However, the experimental protocols in the above papers are somewhat dubious, as they used on-board footage from head and back-mounted cameras, and did not address issues concerning camera unsteadiness. It is implausible that a camera positioned on top of a hood worn by a bird in flight will not shift with respect to the head during turns, though their results are pinned on the assumption that the cameras were completely static in relation to the bird’s head. In Kane and Zamani[12] one quarter of their head-mounted data were obtained from an internet download site (YouTube) without any knowledge of the post-processing (image stabilisation) applied to the movies, and in at least some cases motion of the sun and of lens flares clearly demonstrates that image stabilisation had been applied in post processing. Furthermore, only 54% of their back-mounted data showed evidence for parallel navigation, and their overall conclusions were based on inferred positions of the prey on the falcon’s retina, which they used to identify the pursuit strategy. It follows that these positional coordinates are only reliable if the camera is fixed in a known way relative to the bird’s retina. Furthermore, the authors assume that eye movements relative to the birds head are minimal, even though certain raptor species have been shown to have eye movements as large as 24° [77].

These two studies did not directly measure the flight trajectories of the predator or prey, and thus are not definitive tests for a pursuit strategy, since no reliable information on line-of-sight orientation is available. They did state that when constant bearing angles were not observed, falcons sustained the prey image at a constant angular rate of change - possibly indicative of a higher guidance law - but provide no further analysis.

HUMANS

The pursuit of moving targets in human beings has been relatively well studied in experimental psychology, and focuses on the visual information required for intercepting balls or avoiding obstacles, and the resultant run-paths[119, 165-169]. The cues to help guidance and depth perception, such as stereo, image size change and accommodation, are inoperable until the final stages of a pursuit, thus the moving position of the ball in relation to its background, or its optical trajectory, is the only usable information[167]. Therefore more recent studies have addressed visual target pursuit in humans in terms of the optical acceleration cancellation (OAC) of the ball, and the linear optical trajectory (LOT) of the ball relative to the background. OAC is defined as keeping the optical ball speed constant - though humans seem to have low visual sensitivity to acceleration and lack the ability to judge accurately[170], therefore the LOT theory was proposed to explain the problem in spatial rather than temporal terms. LOT requires a balance between the lateral and vertical optical angular changes to ‘control’ the shape of the ball’s trajectory, and does not require any discrimination of ball distance. The LOT strategy maintains a constant target angle in the optical projection plane relative to the background. The result is a relatively constant running path bearing, consistent with a deviated pursuit strategy, with a curved path of differing speeds to minimise total running speed[119]. OAC theory predicts a straight running path of constant speed, as expected under a pure pursuit strategy, producing a curved optical ball trajectory. However, they are not mutually exclusive and different actions may require one type of information or the other in certain phases of execution[170], thus the extent to which we rely on both is unclear[170, 171]. Shaffer and McBeath found that fielders engaged in the LOT strategy for longer and more often than the OAC alignment strategy when tracking balls [167, 172]. However, exactly how to interpret these studies in the context of pursuit geometry is unclear.

Further studies of collision avoidance in pedestrians[173] and people riding tricycles to intercept moving targets provide evidence for a deviated pursuit strategy. Participants adjusted their speed to keep a constant target-heading angle greater than zero[166]. Similarly, humans walking on a treadmill to intercept a moving virtual ball also produced the same result[170, 174]. Participants in these cases were limited to a straight path intercept, with variable speed, so it is unclear whether the deviated pursuit strategy would still be adopted when direction can be fully commanded. Rushton *et al* used an open field setting and found that people walked to the current visual direction of a moving target, and not its anticipated future position, in accordance with a pure pursuit strategy[165]. Although this study used slow targets and so may not represent behaviour when pursuing faster targets.

DOGS

The same principles from the pursuit research on humans have also been applied to dogs. Micro-cameras were attached to the heads of two dogs to examine their optical behaviour during interception of a Frisbee[175]. It was found that dogs use the same vision-based strategy as used by baseball fielders catching balls – they maintained the target along a linear optical trajectory, LOT, with optical speed constancy, achieving optical acceleration cancelation, OAC (OAC was thus a complement to LOT). In other words, the dog’s running speed and direction maintained a proportional rate of change between the lateral and vertical optical ball movement, i.e. a constant angle of the target in the optical projection plane relative to the background. They also tested for unpredictable changes in target trajectory, and found that the dogs simply established a new LOT.

Summary of literature review

The majority of animals spend a significant amount of time either pursuing or escaping other animals. Since survival is often dependent on the outcome, it is a behaviour that requires accurate processing[173] and should have great influence on the design and function of nervous systems. However, certain study species were seen to use a simple control system linking eye and body motion to fixate retinal images[7, 11, 154], therefore complicated nervous systems are not a prerequisite for accurate guidance control[4, 176]. The advantage of large and mobile eyes may enable a predator to successfully capture moving prey without increasing the complexity of the central nervous system. Species studied showed aptitude for navigating to a target using visual cues only (fish[154]; houseflies[5]; humans[119, 167]; dogs[175]), thus remarkably, animals with very different eyes show similar behaviour in this respect.

The pursuit strategies undertaken by hunting raptors have evolved under constraints from their flight aerodynamics (morphological and physiological factors), their visual system, features of the environment, and prey behaviour. Each presents a different demand on a bird, requiring specific behavioural strategies for survival. Differences in visual field configuration and degree of eye movement have been shown to be closely associated with behavioural variation in prey scanning and foraging strategies and with the level of visual impediment in the environment. Therefore the sensory capabilities of a raptor together with habitat structure are likely to influence steering behaviour during pursuit of prey[177].

The majority of research in biology on collision trajectories across animal taxa (including insects, fish and mammals [8, 170, 175, 176]), have focussed on identifying the simple geometric rules of pursuit and overlooked the true guidance laws underpinning these behaviours. Hence, most pursuit work has described animals adopting either a ‘tracking’ or ‘intercept’ strategy. Tracking pursuers follow the instantaneous position of the target by maintaining zero deviation angle, thereby following a pure pursuit course. Intercept pursuers aim ahead of the target to an anticipatory collision point by maintaining a constant non-zero deviation angle, resulting in a deviated pursuit course. Pure and deviated pursuit strategies only work well if the target moves at a constant speed and in a straight line. In nature, many prey species take evasive action against a predator, and thus perform highly unpredictable manoeuvres. Therefore subsequent investigation involving erratic prey targets has revealed another pursuit strategy used by predators. Recent research into the pursuit behaviours of mating hoverflies[160], territorial dragonflies[9], hunting falcons[12] and echolocating bats capturing aerial prey[13] has suggested they use a parallel navigation strategy. Instead of maintaining a constant deviation angle, they maintain the compass bearing of their line-of-sight angle and direct their position towards the target against a point on the background. Parallel navigation is an interception strategy which may have arisen in nature for solving the problem of intercepting highly unpredictable and manoeuvrable prey as quickly as possible[13].

Guidance commands must be generated by an underlying guidance law, according to which sensory feedback is used to specify the desired acceleration[32]. In engineering circles, classical missile guidance laws are all variations upon a control law called pure proportional navigation, in which the line-of-sight rate (i.e. the rate of change in the bearing of the line-of-sight vector) is fed back to command a turn rate proportional to the line-of-sight rate[146, 147]. The insights from this field have not been lost in the research analysing chasing behaviours in flies[2], bats[13] and beetles[143], which sought to identify the guidance laws used to control their flight trajectories. Despite this, research in biology has yet to demonstrate the existence of a proportional navigation strategy in nature. Insect pursuit studies have only provided information on angular movements (direction of body axis) and not velocity. The research on pursuit in falcons also fails to empirically test for a proportional navigation guidance strategy[10, 12]. The authors did not make use of the curvature of the measured trajectories, or know the position of the target, thus these studies were not set up for testing guidance laws even though geometrical rules were proposed.

Proportional navigation implements all of the pursuit geometries discussed above, and reduces the complexity of the interception problem since information on the size, velocity, or distance of the target is not necessary[6]. These remarkable properties make proportional navigation an obvious candidate for explaining how natural systems intercept moving targets. Above all, the proportional navigation guidance law commands the pursuer to respond to changes in line-of-sight angle θ and therefore an attack depends on the relative, rather than absolute, motion of the pursuer in relation to its target. Proportional navigation may thus correct for the effects of wind drift and accumulated steering errors[147] and may be equally useful against ground targets that could take off at any moment, as well as aerial targets.

More modern missile guidance laws are based upon optimal control techniques, and involve solving minimization problems numerically. It is unlikely that animals perform such computations, and so the geometrical rules observed in nature may indeed be implemented by guidance laws involving proportional navigation. The variation in navigation constant could explain some of the observed variation in pursuit trajectories in nature. Since the majority of biological research has failed to look at guidance dynamics, a re-analysis of previous vision-based guidance data is therefore required.

Besides being of obvious interest in behaviour, physiology, and biomechanics, pursuit research has many applications in engineering, where there is a wide and growing interest in vision-based approaches to guidance and control in both the civilian and military spheres.

symbol	description	Collett and Land, 1978	Land, 1993	Land and Collett, 1974	Collett and Land, 1975	Olberg et al, 2000	Tucker, 2000	Ghose et al, 2006	Justh and Krishna., 2006	Srinivasan and Davey, 1995	Wagner, 1986	Buelthoff et al, 1980	Wehrhahn et al, 1980	Zeil, 1983	Zhang et al, 1990	Gilbert, 1997
ω_v / $\frac{d\gamma}{dt}$	Angular velocity of V (turn rate) in reference to external			ω_f					u		$\dot{\alpha}_v$		$\dot{\alpha}$	γ_{ext}		
ω_b	Angular velocity of body axis (yaw rate)	$\emptyset$	$\emptyset_p$		$\emptyset_p$					θ	$\dot{\alpha}_t$	α		γ_{fly}	T_b	$\emptyset$
δ	Delay		d	d												
α	Deviation angle (between LOS and direction of V)			θ_e		θ_a		$\emptyset$					φ_f			
ε	Error angle (between LOS and body axis)	θ_e	θ_e		θ_e	θ_e					φ, θ	φ		φ	T_h	θ_e
θ	Line of sight angle (bearing/absolute angle)	γ			γ		α, θ	α	r						T_a	
$\frac{d\theta}{dt}$	Line of sight rate								$\dot{\lambda}$							
$\frac{d\alpha}{dt}$	Rate of change of deviation angle			ω_e												

Pure pursuit: $\frac{d\alpha}{dt} = 0$

Deviated pursuit: $\frac{d\alpha}{dt} = constant$

Parallel navigation: $\frac{d\theta}{dt} = constant$

Proportional navigation: $\frac{d\gamma}{dt} = N\frac{d\theta}{dt}$

Table 1. Summary of notation and terminology used in the biological pursuit literature.

Thesis rationale

Our experiments consider pursuit flights from the perspective of guidance laws[147], in free-flying birds of prey in their natural environment. We aim to test whether birds of prey use a) pure proportional navigation, or some variant thereof, or b) a simpler form of pursuit, whilst being open to the possibility that neither hypothesis is correct. We also aim to investigate the broader framework of how birds of prey may adapt their guidance strategy to different situations and how this may be implemented in relation to their vision. We begin by analysing the pursuit trajectories in two-dimensions (latitude and longitude only) on the grounds that the GPS altitude measurements are highly unreliable. Although we relax this assumption later by using the projection of the 2D position of the first two principal components of the bird's 3D trajectory within the plane of best fit.

Birds of prey use a variety of behavioural methods for capturing prey, although whichever mode is adopted it must be initiated either from a perch, or during forward or soaring flight, and some raptor species have a strong preference for one or the other[26, 42, 178]. We therefore use two species with differing hunting modes, and use different experimental protocols for each species to best measure the kinematics of attack flights to a target, and then infer the dynamics. Most attacks by hawks are initiated from perches[42, 178], whereas falcons mostly attack prey from the sky[26, 31], thus we have examined perched hunting in Harris hawks and aerial hunting in Peregrine falcons.

Peregrine falcons

In the wild, peregrine hunts are usually initiated from the air and at great distance to the prey[26], so using on-board instrumentation is most practicable for this species. To preserve a rule of 5% of body mass or less for all on-board equipment, study was limited to birds with a mass greater than 1.4kg. Therefore, a single GPS device along with a mini camera were the most suitable on-board instruments for recording the free and far-ranging pursuit flights of smaller birds such as Peregrine falcons. The low weight and central position of the instruments (mounted on the birds back) kept any adverse effects on flight performance to a minimum. The GPS logged position and speed to provide detailed flight trajectory information, while the on-board camera recorded head movements during flight. Both instruments were used in unison in order to verify timings of interceptions. The main concern with the use of GPS is the accuracy of the measurements, and we therefore provide a detailed error analysis in chapter 4. Inertial measurement units combine information from multiple sensors, such as accelerometers, gyros and magnetometers - as well as GPS - to calibrate the orientation and velocity of the sensor relative to the earth[179]. Unfortunately, we were unable to use additional sensors due to the weight restrictions – the combined weight of our onboard instruments had to be less than 5% of the bird's body weight, as required by our ethically-approved protocol.

To start, we reduced the equations of motion for proportional navigation to their simplest case by using a stationary target, before increasing their complexity to more dynamic situations. We therefore designed two experimental tests for identifying the guidance laws used by falcons as they pursue targets from the air:

Experiment 1: Air-to-ground attack against stationary targets

Captive-bred peregrine falcons (*Falco peregrinus*) were flown against an essentially stationary target which was thrown to the ground by the falconer, simulating a low-level swoop against a perched or otherwise stationary ground prey item. This represents an ecologically important foraging behaviour in this species, since the majority of peregrine strikes involve low-level strikes at perched, sitting or floating prey[26, 35, 37-39], while keeping the equations of motion to a closed-form solution.

Experiment 2: Air-to-air attack against manoeuvring targets

Captive-bred peregrine falcons were flown against a manoeuvring aerial target which was towed through the air by a remotely controlled airplane, simulating a high-level strike against flying prey. This also represents an important foraging strategy in this species[20, 24, 27, 31, 34], and introduces complex target dynamics.

Harris hawks

Work with the Harris hawks used an external measurement system as an alternative to on-board instrumentation. In the wild, Harris Hawks typically hunt from perches over much shorter distances and durations than peregrine falcons[26], and so using external measurements is suitable for this species. Due to the recent development of ruggedized high-speed digital video cameras[180], photogrammetric measurements with sufficient resolution can be collected under field conditions. Associated problems with using high-speed cameras are that the duration of recording time is limited, and the fixedness of the system constrains the flight test volume. In addition, the velocities, accelerations and forces cannot be directly measured - the bird's kinematics must be estimated from its measured position, using a Kalman filter, which acts to minimise the sampling error. Overall, the photogrammetric data that the external measurement system provides show detailed kinematics of free-flying birds that cannot be derived from on-board instrumentation alone.

We therefore designed an experiment to identify the guidance laws used by hawks as they pursue targets from a perch, within a set volume:

Experiment 3: Air-to-ground attack against manoeuvring targets

Captive-bred Harris' hawks (*Parabuteo unicinctus*) were flown against a manoeuvring target which was towed along the ground in an unpredictable zigzag trajectory, simulating a surprise attack against a fleeing terrestrial prey item. This represents the typical foraging strategy of this species[46, 49, 50], whilst also adding target motion, within the same plane, into our analysis.

Thesis aims and hypotheses

The main aim of this thesis is to establish what pursuit strategies hunting birds of prey adopt, in relation to the pursuit laws described in the literature, and how target behaviour may affect this. A secondary aim is to understand the influence of vision and head movements when pursuing prey. We may also be able to extend the findings to a species comparison between aerial attack in falcons and perched attack in hawks. The following bullet points list the main hypotheses:

Pursuit strategy

- Under a pure pursuit the bird will fly directly at the instantaneous position of the target with a deviation angle of zero.
- Under a deviated pursuit the bird will fly at the predicted future position of the target, with a constant deviation angle (expected to be approximately 45° as proposed by Tucker *et al[10]*).
- Under a parallel navigation strategy, the bird will fly on a constant bearing to target in relation to either an inertial reference or some suitably distant fixed point on the background.
- Following a proportional navigation guidance strategy, the bird will fly to maintain a turn-rate that is proportional to the line-of-sight rate.

Target behaviour

- Raptors may switch strategy, and the amount of time spent using any strategy, depending on the speed, manoeuvrability and distance of the target.
- Birds performing aerial attacks against ground or airborne prey may use a different strategy, or combination of strategies, than birds performing perched attacks, on account of their differing hunting modes.

Head movements

- Birds will fly with a straight head and turn their body in flight to fixate the image of the prey onto the deep fovea [11].
- Birds will switch from their 45° deep fovea visual field for distant prey, to their 15° shallow fovea visual field when close to prey.
- Birds will fixate on the background and measure the drift of the target across their retina, by performing head saccades to keep the target within the centre of their field of view.

Ethical review

The experimental protocols were approved by the United States Air Force, Surgeon General's Human and Animal Research Panel, and by the Local Ethical Review Committee of the University of Oxford’s Department of Zoology, and were considered not to pose any significant risk of causing pain, suffering, damage or lasting harm to the animals involved. We are pleased to confirm that no pain, suffering, damage or lasting harm was caused to any of the animals used during the course of this research. One of the birds died of natural causes before the end of the project, for reasons unrelated to the experimental work and husbandry. A Home Office licence was not required since we used captive bred birds and none were subject to any invasive procedures.

Chapter 2:

Methods - GPS error analysis

Introduction

GPS position is estimated from the common intersection point of multiple spheres, whose centres are defined by the location of each reference satellite, with radii equal to their corresponding ranges[181]. Many factors affect the estimation of the assumed position, and together, are an amalgamation of random noise and slowly varying biases that are statistically independent of one another and may impact upon the precision and accuracy of our GPS flight data[156].

According to the GPS Standard Positioning Service Performance Standard[182], civilian GPS units typically provide an *absolute* horizontal positioning accuracy of ≤ 7.8m (95% of data falls within this range of the actual position, as a global average). However, this figure is not representative of the much greater accuracy with which even consumer GPS units can measure changes in horizontal position over short periods of time. This is because the absolute error of a GPS fix varies slowly if the number of visible satellites does not change, enabling a *relative* positioning accuracy of only a few centimetres when measuring changes in position over periods of a few seconds. To prove this point, we quantified the relative positioning accuracy of our Qstarz BT-Q1300 GPS units over a sampling period relevant to the measured attack passes.

GPS measurement error

We first provide an overview of the main sources of error affecting GPS receivers – namely the satellites, atmospheric conditions, multipath effects, GPS smoothing and orientation of the antenna.

The accuracy of GPS position measurements is influenced by the geometry of the satellites from which the pseudorange measurements are taken (range estimates between the receiver and satellite with synchronisation errors). The geometric configuration affects the dilution of precision (DOP), which is the positioning error ascribed to satellite positioning in the constellation. Closely positioned satellites result in a higher DOP in the GPS position estimate, whereas a group of visible satellites which are far apart will lower the DOP value (Fig.6).

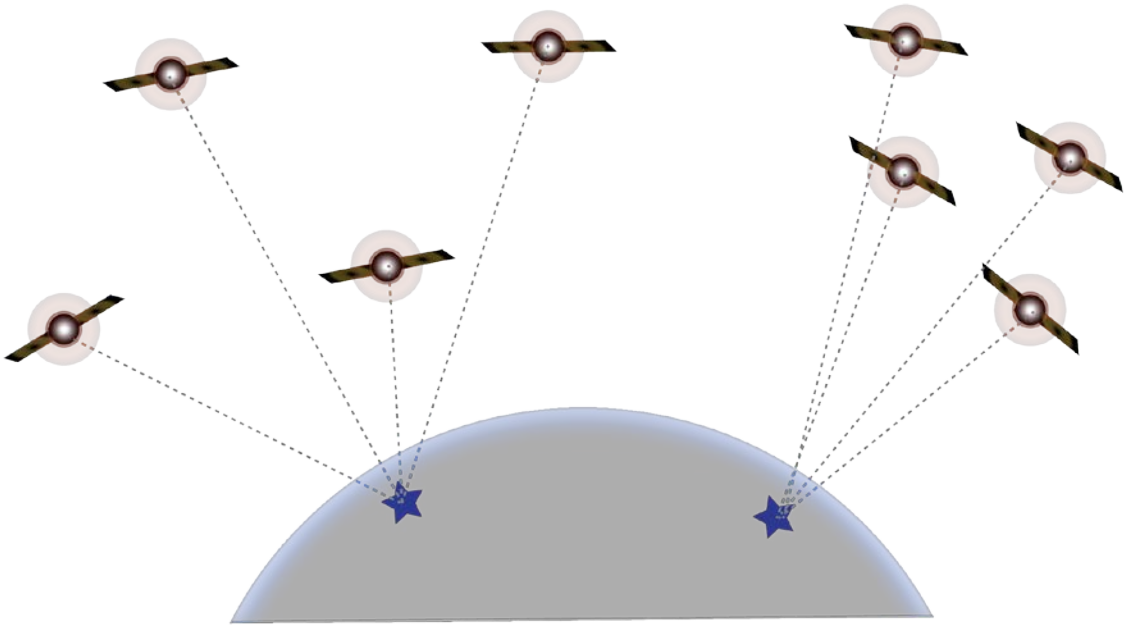


Figure 6: Showing good geometry (left) and bad geometry (right) of satellite positions (redrawn from[181]).

Electromagnetic radio signals from the satellites travel at the speed of light, so although this is a very short time, variation in the actual speed of travel owing to the composition of the atmosphere, compared to the assumed speed of travel, is a source of error. Only 10ns of clock error on the receiver amounts to a positional error of around 3m. In addition, the satellite clock is only updated every 12 hours, and drifts about 10ns during this time, causing a positioning error of 1 - 2m.

A further source of receiver error due to satellite configuration comes from the calculation of the mathematical description of the satellite's orbit (ephemeris data) - required for determining position. Uncertainty in the satellites' transmitted location leads to a build-up of errors in the pseudorange calculations, introducing errors of between 1 - 5m.

The presence of free electrons in the uppermost layer of the earth's atmosphere (ionosphere) cause delays in GPS signal transmissions, resulting in errors on the order of 2 - 5m. Variations in the weather, including temperature, humidity and pressure, in the lowest layer of the earth’s atmosphere (troposphere) can also affect the pseudorange estimates, though errors are slightly lower - typically around 1m.

Multipath signalling occurs when a GPS unit receives reflected signals due to features in the environment, such as large buildings, which mask the true signal. However, in most circumstances the errors are below 1m.

The inherent limits of the GPS to resolve the timing of the satellite signal - namely signal tracking and processing - represents another source of error. However, most modern receivers keep any ranging errors due to the limitations of the GPS to less than 0.5m.

Receiver measurements are subject to Kalman filtering. A Kalman filter is an algorithm which estimates the dynamic state of the sensor, using a series of measurements observed over time (including noise), and finds the optimum averaging factor for each state[181]. The state of the sensor is defined as the variables describing the conditions of the sensor, e.g. position, velocity, acceleration, heading, etc. The algorithm involves a two-step process, firstly predicting the current state variables, as well as their uncertainties, and secondly assigning more or less weight to the state estimates depending on their certainty. The key reason for having a Kalman filter is to estimate the receiver time, which is included as an additional state in the system (this is why GPS receivers drift towards the right location when they are first turned on, as the receiver time estimate improves). Using a Kalman filter is said to reduce the overall noise in the GPS measurements, however the biases due to satellite geometry, atmospheric factors and multipath are not removed[156].

In dynamic situations, GPS receivers are inevitably subject to additional error. The orientation of the antenna affects the accuracy of position measurements, due to the sight of the antenna dropping and picking up different satellites as orientation changes. One study found only marginal differences between the quality of measurements when the antennas faced directly upwards compared to downwards. However, the quality was significantly worse for the bottom antennas in more challenging environments[183]. This study only used stationary GPS’s however, where the sources of error will be much less. Therefore formal testing of GPS orientation in a dynamic situation is needed.

GPS error analysis

The *absolute* horizontal positioning accuracy of typical civilian GPS units is stated as being ≤ 7.8m (95% of data falls within this range of the actual position, as a global average)[184]. However, we hypothesize that over short periods of time (a few seconds), consumer GPS units can measure changes in horizontal position with much greater accuracy, because the absolute error of a GPS fix will vary slowly if the visibility of the satellites does not change[181], resulting in a *relative* positioning accuracy on the order of a few centimetres. We therefore quantified the relative positioning accuracy of our Qstarz BT-Q1300 GPS units to show that they can measure changes in horizontal position to much greater accuracies over sampling periods relevant to our measured attack passes.

We conducted three separate experiments to test the GPS devices under different conditions. These were; 1) static testing, to investigate basic signal drift; 2) dynamic testing to examine accuracy when moving; 3) dynamic orientation testing to investigate the possible effects of changing which satellites the receiver was looking at. These experiments will therefore determine the reliability of the GPS devices, and identify any potential implications for our flight research.

<u>1) Static testing</u>

We first tested the relative positioning accuracy of our GPS devices by leaving a pair of units logging in a stationary position, and sampling time periods comparable to the maximum duration of the attack passes we measured (≈10s). Two GPS units were left to settle for 300s before sampling the next 200s in 10s blocks of position data. Then, for each 10s block of data, we calculated the horizontal distance of each of the position fixes within a block from the mean of all of the position fixes for that block. Since there was no appreciable difference in the noise level in the two units, we pooled the data (Fig.7). Median distance deviation was found to be 0.011m, with 95% of the 20,000 position fixes falling within 0.050m of the mean position fix for their corresponding 10s block. The relative positioning accuracy of our GPS devices, under stationary conditions, was ≤0.05m over the maximum timescale of our attack flights. However, this figure could well underestimate the relative positioning error during unsteady motion because consumer GPS units typically use a Kalman filter to improve their estimates of position, tuned to the dynamics of conventional use cases such as walking, running, and driving.

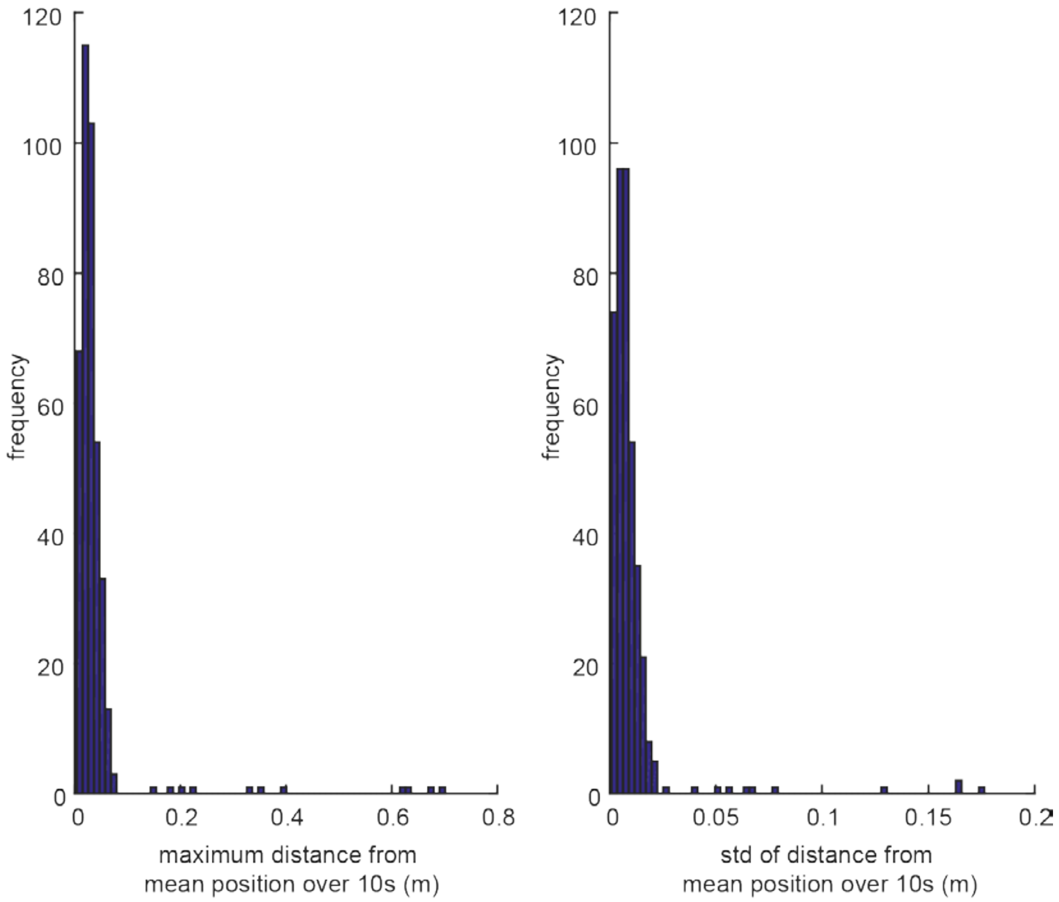


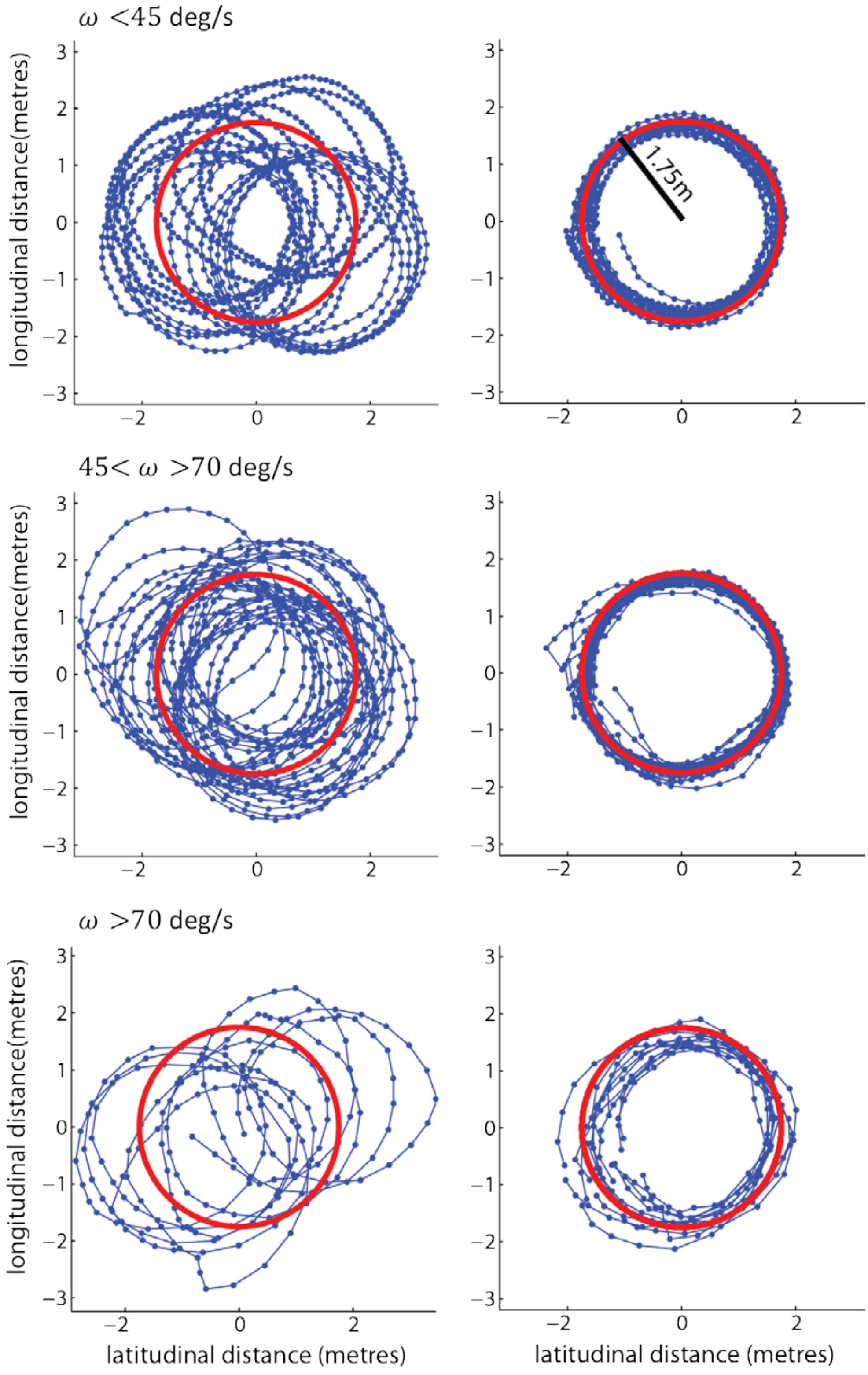
Figure 7: Histogram of relative positional accuracy of two stationary GPS devices, sampled in blocks of 10 seconds. Left-hand graph shows the maximum drift in metres from the mean position. Right-hand graph shows the standard deviation of this drift from the mean.

2) Dynamic testing

We then set out to quantify the relative positioning accuracy during unsteady motion, by rotating a unit on a circle of known radius at different speeds. A GPS unit was left to settle for 300s before being securely attached to a playground roundabout (on a radius of 1.75m). The roundabout was rotated approximately 20 times at 3 different speeds, keeping the acceleration as constant as possible (smooth pushes with no sudden pulses of speed, as this best imitates a bird accelerating in flight). Figure 8 compares the raw GPS positional data with those corrected for any drift in the GPS. We applied the correction by subtracting the mean position for each circuit and plotting relative to the origin. We binned the data according to the following angular velocities ω: ω<45, 45<ω>70 and ω>70 deg/s. Each circuit was identified from its latitudinal velocity (where it crossed zero). We show that for angular velocities below 70deg/s, a circle of 1.75m is tracked very closely indeed, however, above 70deg/s, the error in the tracked radius of the circle is far greater (Fig.8). The standard deviation of the estimated radius for each binned angular velocity was 0.11, 0.11 and 0.24 respectively, with mean radii of 1.69, 1.72 and 1.62. The range of our angular velocity measurements were: 22.4-41.8 deg/s, 48.0-68.2 deg/s and 73.8-88.6 deg/s respectively.

To further test the limits of the GPS units, we then rotated one on an even smaller circle. A GPS unit was left to settle for 300s before being securely attached to a bike wheel (0.35m from the centre) positioned horizontally on the ground. The wheel was slowly rotated about the axel approximately 20 times, gradually increasing the speed. The mean radius of the bike wheel was found to be 0.22m with a standard deviation of 0.04m. The minimum and maximum angular velocities were 112 and 182 deg/s. Figure 9 compares the raw GPS positional data with those corrected for any drift in the GPS, by subtracting the mean position for each circuit and plotting relative to the origin. Its circumference becomes readily visible when the position fixes are plotted relative to the apparent centre of rotation for each revolution.

In order to directly compare against our static tests, we split the data into consecutive 10s blocks. We used a nonlinear least squares solver to estimate the apparent centre of rotation for each 10s block and calculated the horizontal distance of each of the position fixes within a block from the apparent centre of rotation for that block, and expressed this as an unsigned distance deviation from the mean. This is not quite equivalent to the horizontal distance deviation measured in the stationary case, because it is calculated relative to the assumed centre of rotation rather than relative to the assumed true position of the device. Nevertheless, the median radial distance deviation of 0.065m over all 10s blocks should be broadly representative of the scale of the relative positioning error during unsteady motion. Figure 10 plots the median distance deviation for each 10s block of data under both test cases, from which it can be seen that the relative positional error is typically smaller at lower angular velocities. In fact, 99% of GPS fixes in the stationary tests and 84% of fixes in the unsteady tests had a distance deviation ≤ 0.20m. Figure 10 also shows that the relative error could be higher than this in some tests, perhaps related to the visibility of GPS satellites, but even in the worst case, the median unsigned distance deviation was still ≤ 0.33m, which may be taken as a conservative upper limit on the expected relative positioning error of our GPS units for sampling periods on the order of 10s.



ω <45 deg/s

45< ω >70 deg/s

ω >70 deg/s

Figure 8: Position of a GPS unit (blue) whilst being rotated on a circle of radius 1.75m (red – from mean for all circuits), for angular velocities ω of ω<45, 45<ω>70 and ω>70 going from top to bottom. Left; raw GPS position for each binned velocity. Right; corresponding plots corrected for drift - each circuit is centred on its origin by subtracting the mean radius for that circuit. For lower angular velocities the circle is tracked more accurately.

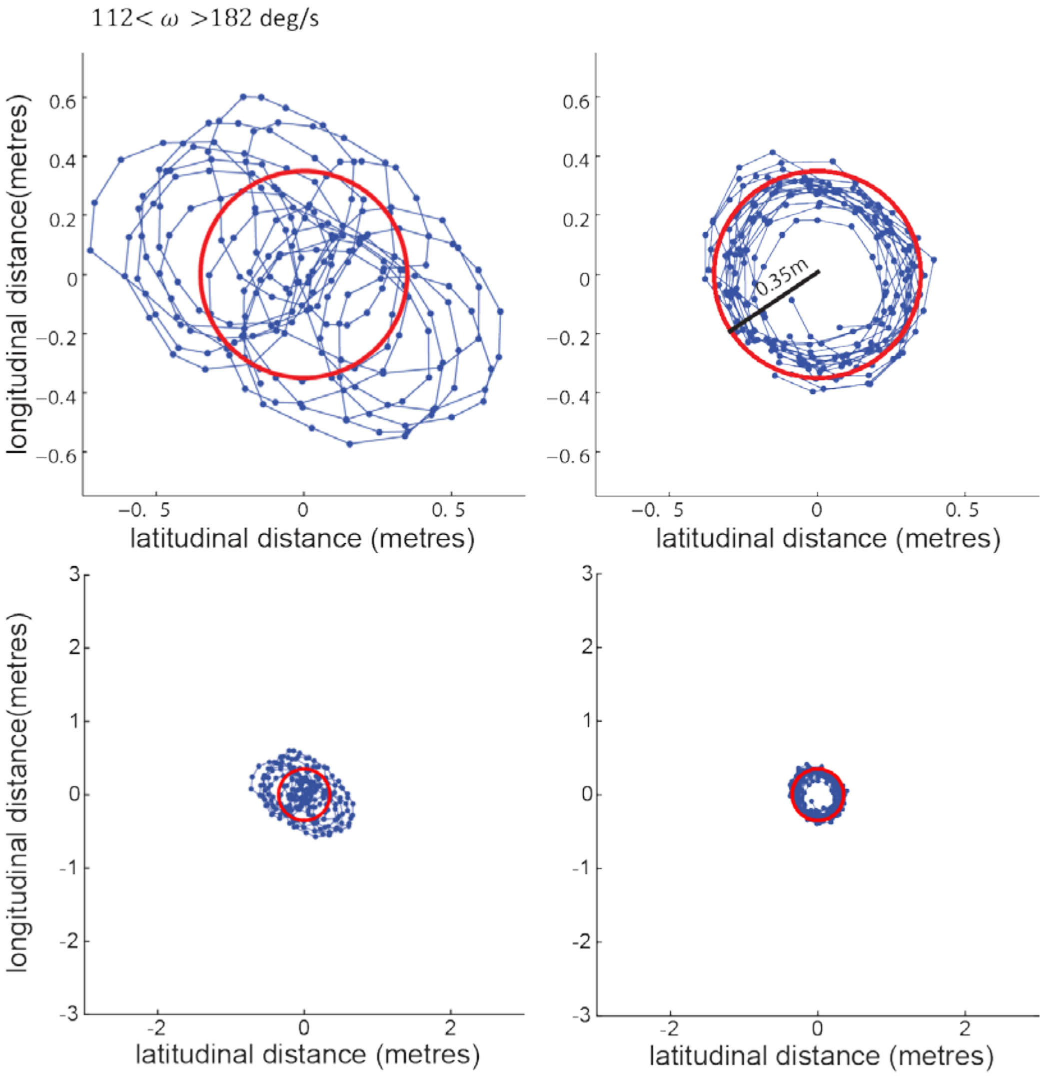


Figure 9: Position of GPS unit (blue) whilst being rotated on a circle of radius 0.35m (red – from mean for all circuits), for angular velocities ω of 112<ω>182. Upper left; raw GPS position for velocity range. Upper right; corresponding plot corrected for drift - each circuit is centred on its origin by subtracting the mean radius for that circuit. The lower panels plot the data on the same scale as the previous roundabout tests in Fig.8, for direct comparison.

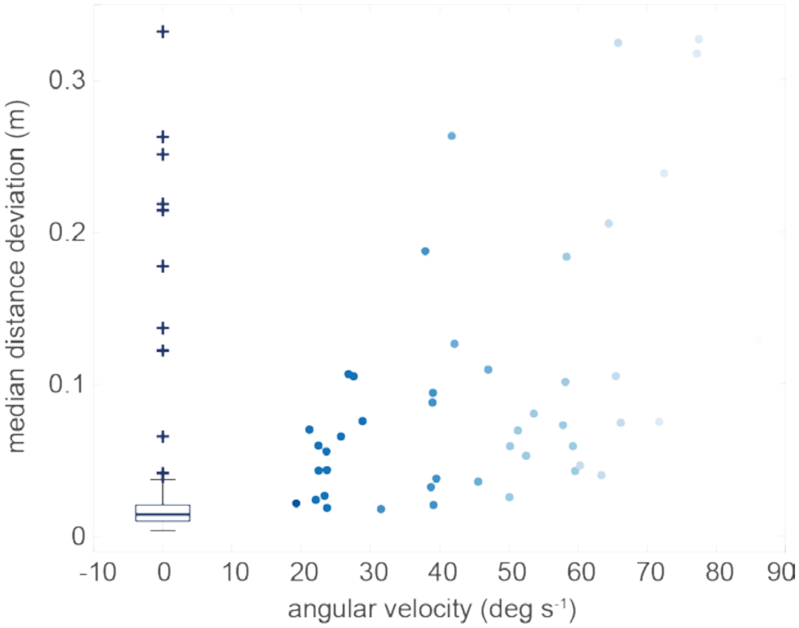


Figure 10: Graph shows the median distance deviation for each 10s block of data under both test cases – static (crosses) and dynamic (circles), showing that the relative positional error is smaller at lower angular velocities (see text). Blue colour scale represents increasing angular velocities – darkest blue being zero angular velocity (for the stationary case).

3) Dynamic orientation testing

Next we set out to investigate how GPS orientation affects the relative positioning accuracy, under dynamic conditions, to simulate the effect of birds banking in flight. We simultaneously rotated 3 units at three different angles, on a circle of known radius. GPS units were left to settle for 300s before being securely attached to a playground roundabout (on a radius of 1.50m), each at 0° to the sky and then tilted at 45° and 90°. The roundabout was smoothly rotated 10 times for each orientation. Figure 11 plots the raw trajectories from the 3 GPS units on an aerial image to show how the tracks relate in reality, showing that with a 90° orientation the GPS signal experiences much more wandering. Figure 12 (top panels) shows the detailed raw trajectory plots for 20 seconds of rotation under each orientation. It clearly demonstrates that when the GPS's are in a horizontal orientation (0°) they track the circle very accurately indeed, however the accuracy gets progressively worse as devices are inclined at 45° and 90°.

As a next step to compare the accuracy of measurements between orientations, we looked for differences between the GPS-derived speed, and the velocity calculated from differencing the position estimates. GPS receivers determine speed by measuring the frequency shift (Doppler shift) in the pseudo range signal from the satellites. Doppler-derived speeds are much more accurate than those obtained by differencing position estimates. The velocity of GPS receivers using Doppler measurements can be calculated to accuracies with standard deviations of 0.01 to 0.05m/s of the true value[156]. Therefore we tested positional accuracy by measuring the discrepancy between GPS Doppler speed and speed calculated from the differenced position, for each GPS orientation (Fig.12; lower panels). From the plots we can see that the speeds match exactly when the GPS's are horizontal, and become more diverged when they are inclined at 45° and 90°. The mean 95th percentiles pooling all 3 GPS's were ±0.0012m/s, ±1.98m/s and ±3.37m/s for 0°, 45° and 90° respectively.

Therefore it is evident that the accuracy of GPS position measurements deteriorates when the antenna is angled between 45° and 90°, although they were still able to track an approximate circle - albeit shifted in space. We also show that comparing the velocity derived from the differenced position to the GPS Doppler speed, is a very reliable and effective way for identifying problematic sections of data.

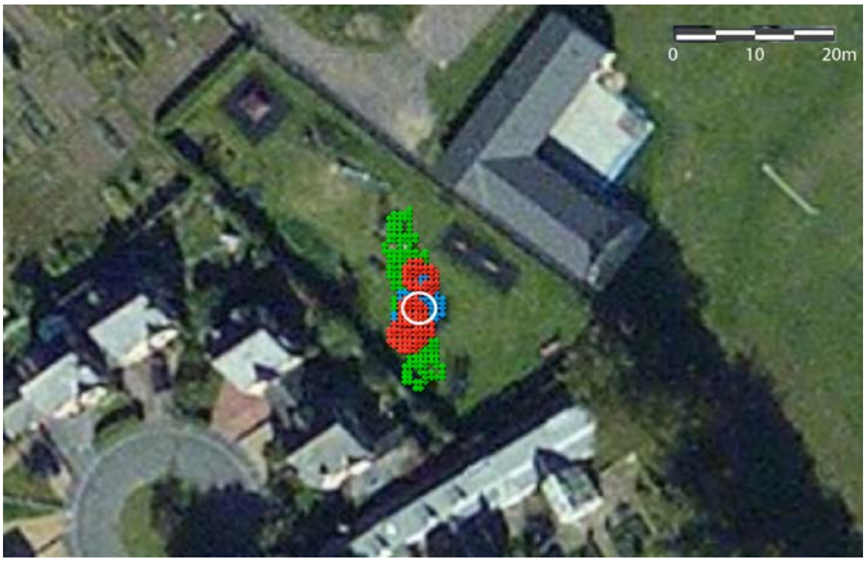


Figure 11: Raw positions of 3 GPS units in three different orientations, rotated on a roundabout. Colours correspond to angle of the units; red = 0°, blue - 45° and green = 90°. The white circle shows the approximate circumference of the roundabout (1.5m radius). It is evident that when the GPS is oriented at 90°, the signal is less accurate.

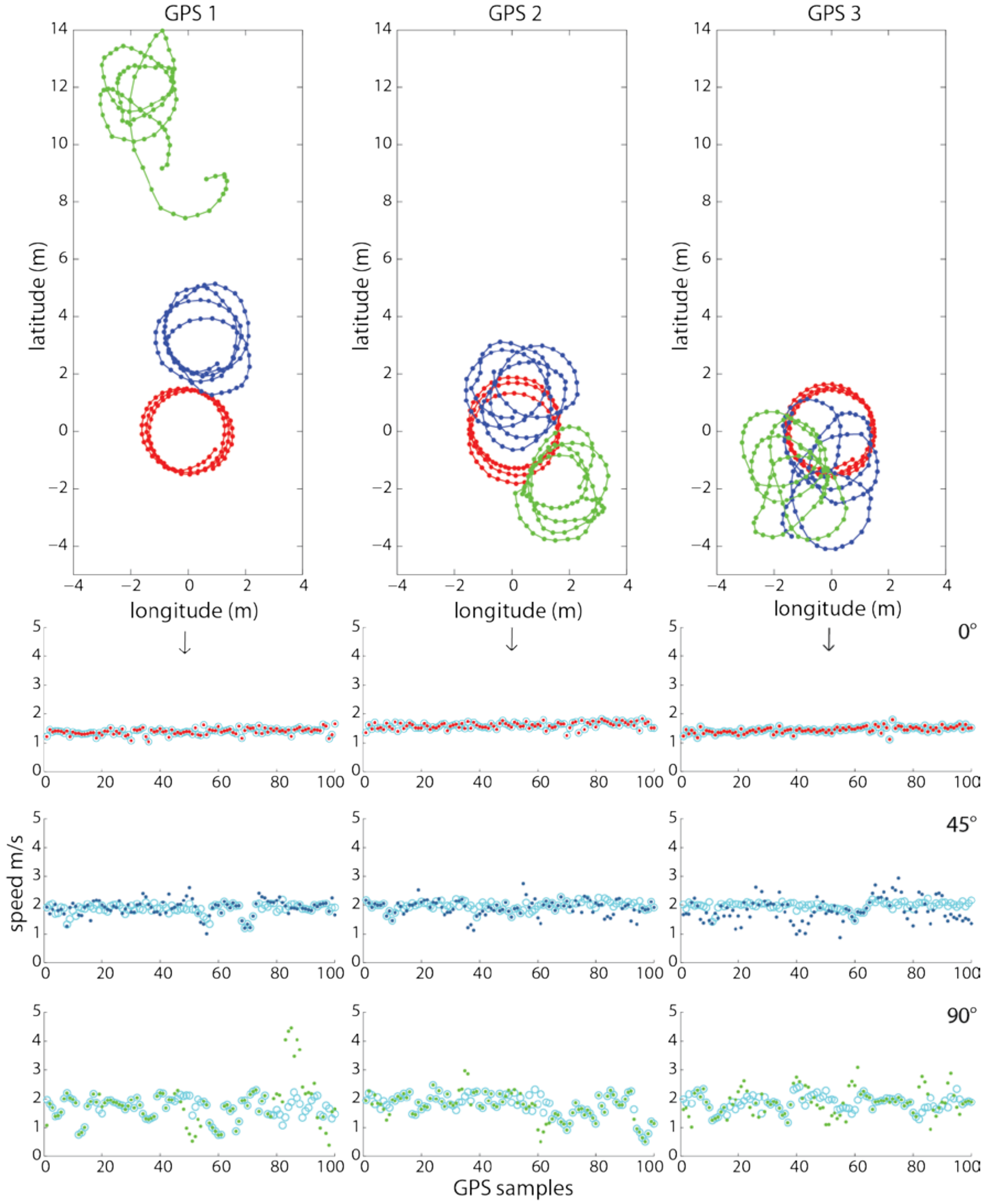


Figure 12: Top panels show positions of 3 GPS units when angled at 0° (red), 45° (blue) and 90° (green) and rotated on a roundabout – each plotting 20s duration. Lower graphs plot the corresponding speeds comparing the differenced position (coloured as above) and the GPS Doppler speed (light blue circles), showing that with a 0° orientation the speeds match exactly, and diverge when the GPS is angled at 45° and 90°. NB at 90° the Doppler measurements also have more noise.

Implications for our flight data

The GPS devices were shown to be both accurate and precise under certain test conditions – i.e. in one location and positioned with the antenna in a sky-ward facing orientation. However, these conditions are not necessarily met by our flight experiments, which were conducted in different locations in Wales and involved GPS units moving through many orientations. Location and antenna orientation are therefore the principal factors in determining GPS measurement accuracy, producing varying degrees of signal degradation. The environment in which our experiments were carried out comprised of hillsides and valleys, and so the dominant sources of error were expected to be due to multipath and signal obstruction by the surrounding hills. Birds also regularly performed fast banked turns, resulting in sudden changes in orientation and potentially causing jumps in positional measurements due to dropping and re-sighting of satellites.

Therefore it is necessary to screen our data and filter out any problematic flights for which we cannot be confident of the precision. As we have shown in figure 12, comparing the GPS Doppler speed with the speed derived from differencing the position data is a good quality control test. We can also use our on-board camera data as a secondary check.

GPS discrepancy tests

We tested the position measurements of our flight data by calculating the discrepancy between GPS Doppler speed and speed from differencing the position, for our peregrine flights against both stationary and aerial targets (Fig.13). The 95th percentiles are ±1.98m/s and ±4.35m/s for stationary and aerial target flights respectively. Therefore the stationary target flights are more reliable on the whole than the aerial flights, although the median values are both very small indeed at -0.001m/s and -0.002m/s respectively.

The stationary-target experiments used only a single GPS unit on the bird, but in the aerial-target flights we had multiple GPS's – including one on the bird and one on the lure. This allowed us to test the relative positional discrepancy *between* GPS units - since we know at the moment of intercept that both GPS's should be in the same location in space (see Chapter 5 for how the intercept was identified). We found that in some flights, surprisingly large adjustments were needed in order to bring together both GPS's at the point of intercept (table 2). This made us cautious about the reliability of the GPS positional data, and led us to apply very stringent quality control parameters, discussed below.

Flight	Discrepancy at intercept (m)
1	20
2	13
3	24
4	31
5	64
6	31
7	109
8	60
9	5
10	280
11	84
12	79
13	9
14	50

Table 2: Measured discrepancy between bird and lure GPS's at interception for 14 peregrine aerial attack flights, revealing that some flights had very large discrepancies.

Quality control

In our flight experiments using GPS, we calculated the speed discrepancies between the GPS Doppler and the differenced position over our entire datasets (all flying time). The 95th percentiles of the data were <1.98m/s for stationary target flights and <4.35m/s for aerial target flights (Fig.13). In order to choose an appropriate proportion threshold for rejecting flights, we summed the number of points which fell outside the 95th percentiles for each flight, and used a binomial cumulative distribution function (which calculated the probability of observing that many errors by chance, over the duration of a flight). We subsequently chose an arbitrary proportion threshold of <0.05 (Fig.14). Therefore, for each final intercept flight we required 95% of GPS points to have a speed discrepancy below an error threshold. The error threshold was arbitrarily chosen to be the value of the 95th percentile calculated for the whole dataset.

Figure 15 is an example of one good and one bad final intercept trajectory against a stationary target, highlighting any GPS points outside the error threshold of 1.98m/s (red circles). Plotted beneath are the corresponding speed discrepancies between the GPS Doppler and differenced speeds - the good flight example shows no discrepancy.

For all flights which passed these selection criteria, we then performed a second quality control using the video data as a qualitative check on the validity of the positional data. We plotted the trajectories onto geographical images in ArcGIS in order to directly compare the alignment of the bird's field of view in the camera to the GPS trajectory, for approximately the last 30 seconds of each flight before interception. Using features in the environment, such as field boundaries, trees and buildings, we could quite confidently determine whether the GPS track matched the video footage for that flight (Figs.16, 17). We include any flights where the track looked precise (correct trajectory shape) but was not accurate (in the wrong place - e.g. wrong side of a hedge). Overall, we scored each flight as either passing or failing each selection criterion below:

1. GPS speed discrepancy thresholds (between Doppler and differenced position)
2. Precision (correct trajectory shape) judged from video
3. Accuracy (correct trajectory position) judged from video

We therefore discarded any trajectory that failed on either (1) or (2), and marked any trajectories as potentially problematic that pass on both (1) and (2) but which fail on (3). For flights which passed on all three scores, we can therefore be very confident about the validity of the data, and there was only a single flight which passed on both (1) and (2) but failed criterion (3).

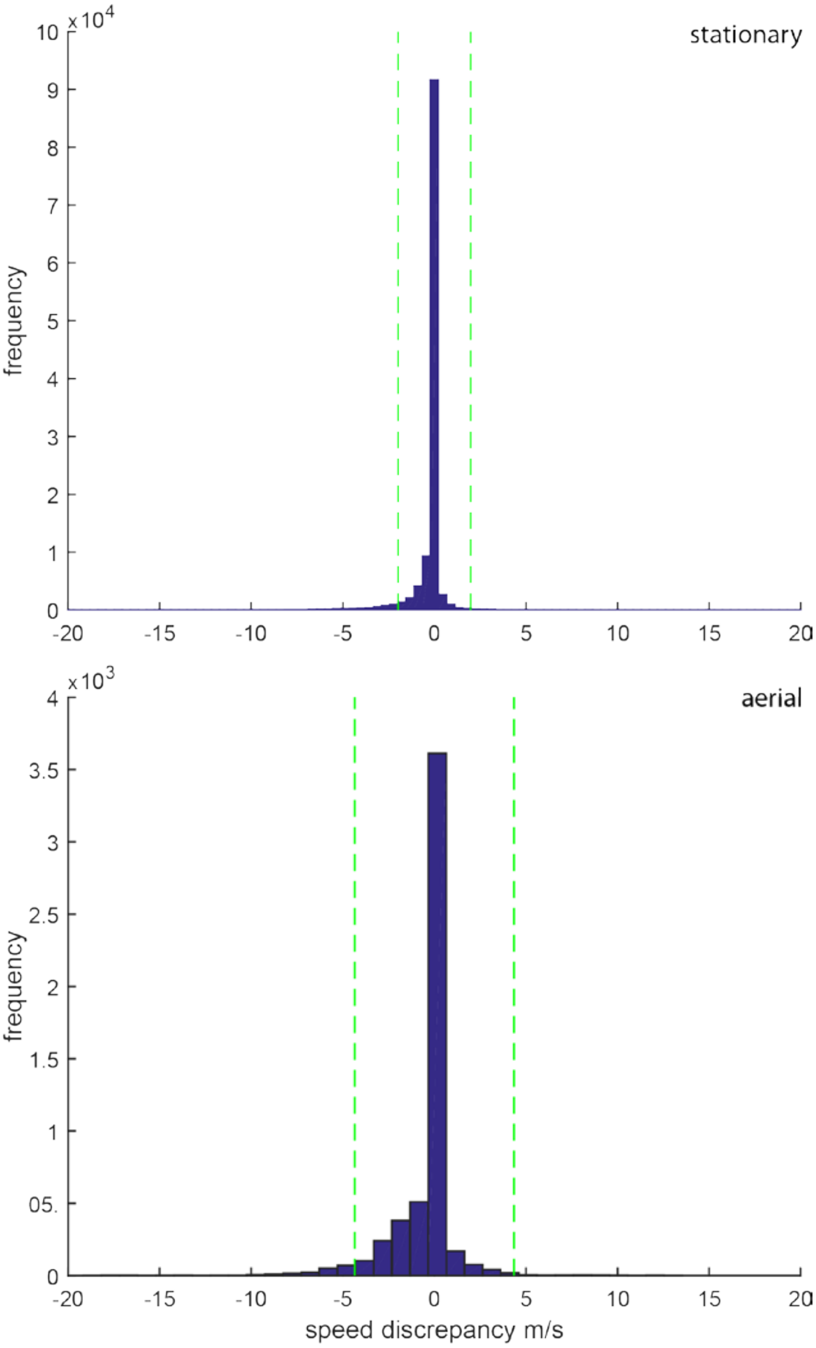


Figure 13: Histogram of discrepancy between GPS Doppler speed and speed from differenced GPS position, for all flying time against both stationary and aerial targets in peregrines. Green lines show the 95th percentiles; ±1.98m/s for stationary targets and ±4.35m/s for aerial targets.

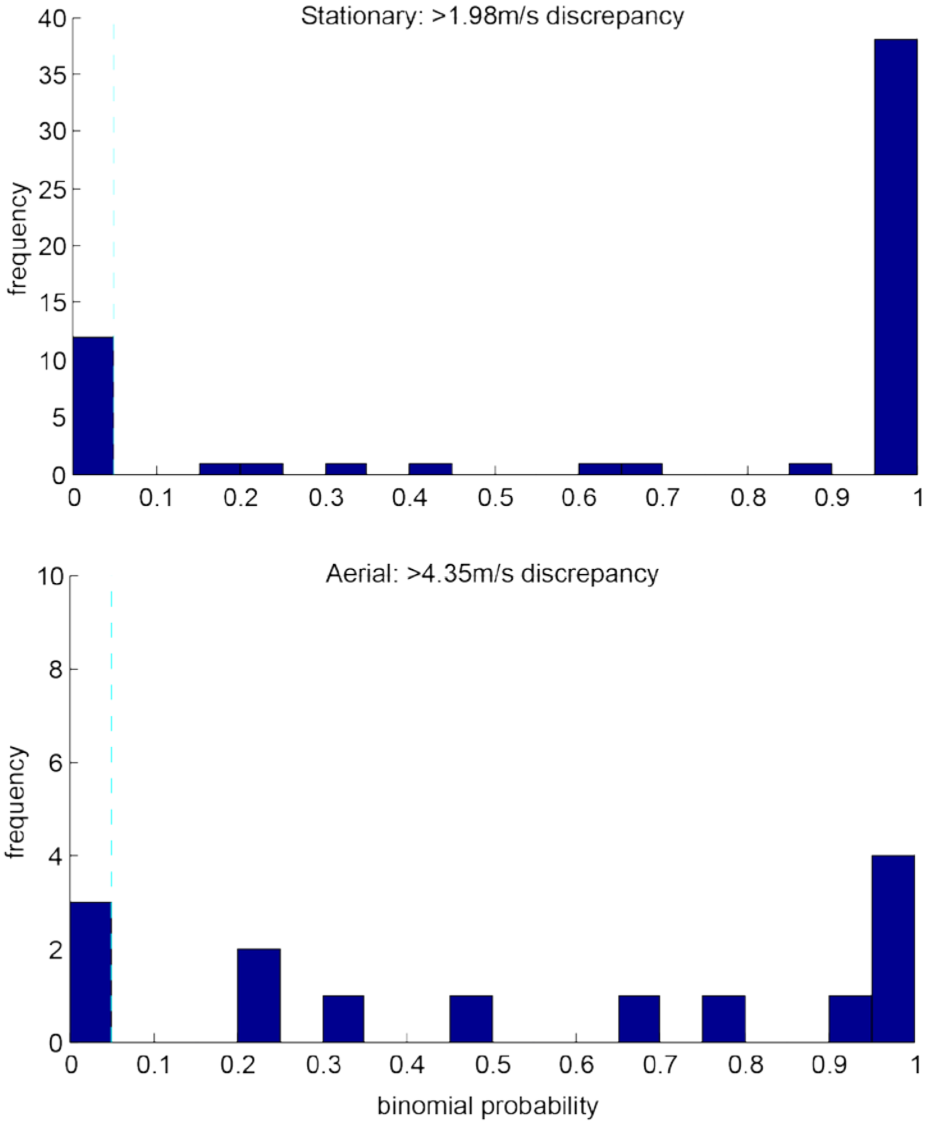


Figure 14: Histograms showing the binominal probability of the proportion of points above the speed-discrepancy threshold for each flight occurring by chance. Speed discrepancy thresholds were determined from the 95th percentiles of total discrepancy between GPS Doppler speed and speed from differenced GPS position, for all flying time, for both stationary and aerial target flights.

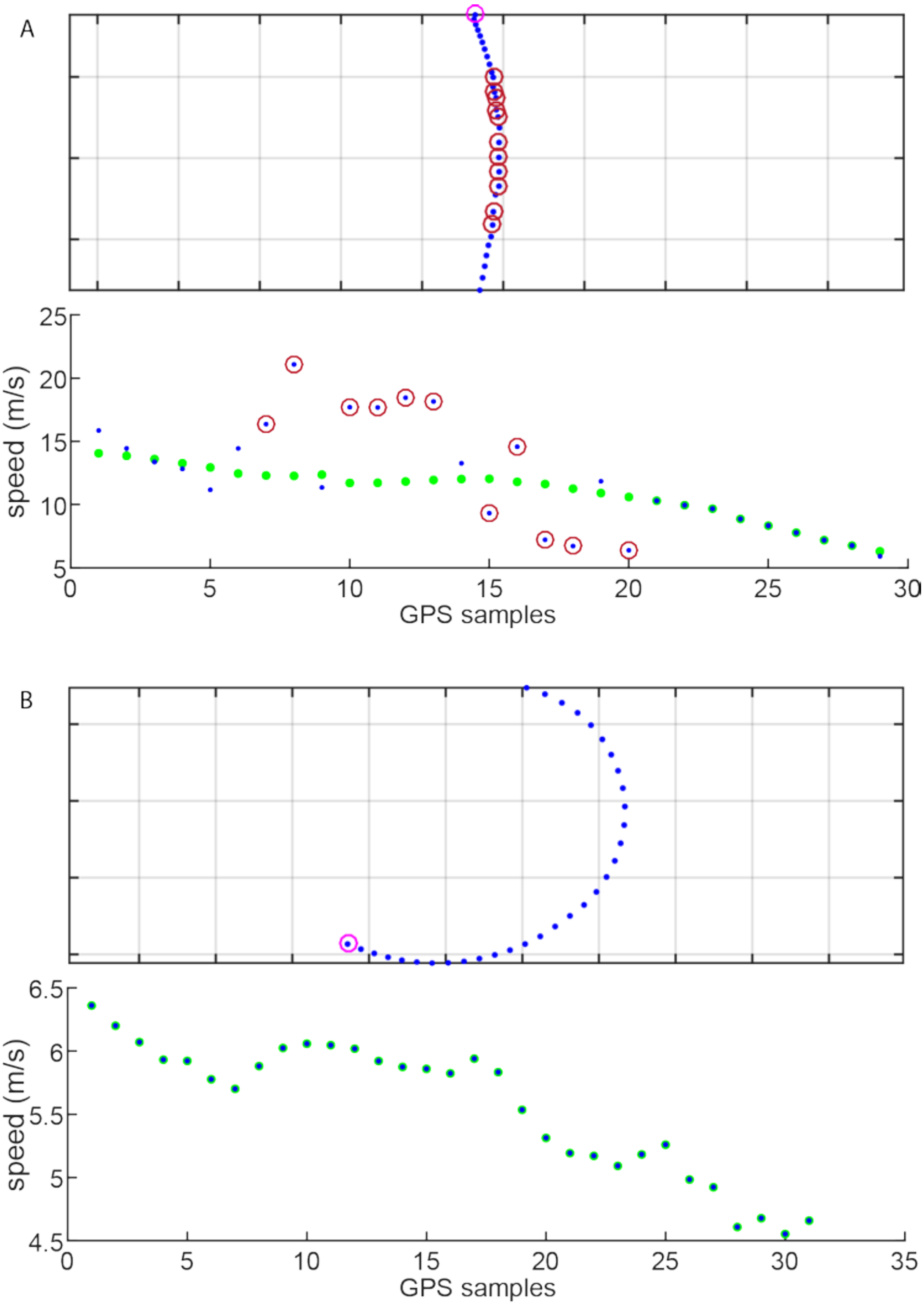


Figure 15: Examples of a bad trajectory (A) and a good trajectory (B) against a stationary target, showing GPS points which exceed the speed discrepancy error threshold of >1.98m/s (red circles). Trajectory A represents a flight which fails to pass our proportion threshold of 0.05 and so is excluded. Grey lines represent 10m intervals. Subplots show the GPS Doppler speed (green) and speed from differenced position (blue) – flight B shows very little discrepancy as the points match exactly.

Figure 16: Above; an example of a GPS trajectory of an attack flight to a stationary target (red) which closely matches the video data below (still from video) - showing the peregrine fly to the right hand side of the same tree pictured in both data sources. Blue circle highlights the approximate position of the bird at this instance in time.

Figure 17: Above; an example of a GPS trajectory of an attack flight to a stationary target (red) which closely matches the video data below (still from video) - showing the peregrine fly over a hedge, to the left of the same tree pictured in both data sources, and aiming at the target ahead, at the edge of the tree line. Blue circle highlights the approximate position of the bird at this instance in time.

Discussion

Our GPS error experiments have tested both the accuracy (displacement from the actual position of the roundabout) and the precision (distortion of circular orbit), and have shown the precision to be very good. It may have been useful to check these errors in the locations where the flight experiments were conducted; but since many different locations were used this was unfeasible. It follows that as long as we can be confident of the shape (or precision) of the flight trajectory, any displacement in space (loss of accuracy) does not affect our subsequent analyses since it is the trajectory shape only that we are concerned with.

Nonetheless, we found that all but one flight which passed on our GPS speed discrepancy thresholds also passed on both precision and accuracy from the video. The accuracy of two such flights is shown in figures 16 and 17, demonstrating how closely the video data matched the GPS data. For all these flights we can be very confident that the trajectories are an accurate representation of the bird's actual flight path.

Most problems occur in the bird GPS data against aerial targets, perhaps due to the extreme manoeuvres performed in these experiments. We can be confident that atmospheric conditions are not to blame, since the GPS tracks were not uniformly bad, which we would otherwise have expected. Furthermore, the data from on-board the plane and lure were in agreement with one another (the lure was approximately behind the plane until interception and then diverged). This suggests that changes in GPS orientation - which causes changes in the sighting of satellite constellations - may be the issue, as depending on which way the antenna is pointing the precision will be different. However, as our subsequent testing revealed the aerial-target data to be so much worse than the stationary-target data, this suggests there may have been a hardware fault. The same GPS receiver was used on the birds in most of our aerial intercept flights which leads us to assume the problem may have been receiver error, combined with the fact that the data was not completely wrong (it just showed reduced GPS performance). Location may also play a part, though errors caused by multipath are very small.

These unwanted error components are all additive in nature, and so when coupled with banking errors during extreme manoeuvring, this might have led to a large accumulation of error. Thereby at some unknown point the signal would become unintelligible, and once it is detected again it will cause a large shift in position while the GPS drifts into its current location. This may explain the large position discrepancies we observed between our bird and lure GPS data in the aerial-targets work. It is also possible that time accuracy errors due to variation in the speed of travel of the electromagnetic radio signals (owing to the composition of the atmosphere) compared to the assumed speed of travel, may lead to discrepancies in position. But such time errors result in positional inaccuracies on the order of only 1-2m[181], and so does not explain the large discrepancies we found in our GPS data.

Overall, we have identified serious issues of working with GPS devices, with implications for all published research using on-board GPS data. The redeeming feature however, is that any problematic data are easily identified by our quality control criteria and so we can be confident that all the remaining flights are reliable.

Chapter 3:

Air-to-ground attacks in Peregrine falcons

Abstract

Here we show Peregrine falcon (*Falco peregrinus*) target-interception trajectories against non-manoeuvring ground targets, recorded by on-board instruments, accurately match the trajectories predicted for the guidance law of proportional navigation, with an adaptive variable navigation constant. This commands that the bird turns at a proportional rate to the change in the line-of-sight angle from pursuer to its target. Proportional navigation reduces the terminal accelerations required for interception and serves to correct for wind drift or steering errors, and is therefore commonly used by modern missiles to intercept unpredictably moving targets.

Introduction

Peregrine falcons have developed a unique hunting strategy as a consequence of adaptive morphology – the infamous stoop (explained in chapter 1)[24, 25]. However, the stooping technique is only used in about a third of attacks[26] and there is disagreement in the literature as to the most common hunting mode in peregrines[27, 31, 34]. What is clear is that peregrines possess a repertoire of distinct hunting techniques. They usually initiate their attacks from the sky and, contrary to popular belief, regularly take prey that is on the ground as well as taking aerial prey[20, 24, 34]. As a first step, we therefore set out to replicate attack flights against prey-targets that were stationary on the ground, with the aim of identifying the guidance laws underpinning air-to-ground attacks in peregrines. The methods and procedures are detailed below, followed by an explanation and discussion of the results.

Materials and methods

Animals

Three captive-bred, trained, peregrine falcons (B: ♀, 0.96kg; N: ♀, 0.90kg; W: ♂, 0.65kg) were flown at targets (a dead pheasant *Phasianus colchicus*) or an artificial falconer's lure) thrown to the ground by the falconer. A total of 26 flight tests were carried out, and individual birds often made multiple passes at the target, resulting in $n = 57$ attack passes at the target. The peregrines twice flew at live prey (mallard, *Anas platyrhynchos*; red-legged partridge, *Alectoris rufa*) encountered incidentally during a flight. Neither was harmed, but both were forced to the ground. The mallard remained stationary by a fence, and we were therefore able to include the 4 passes made at it in the analysis of stationary ground targets. (Fig.18). The attacks on the partridge and mallard in flight are analysed in Chapter 3.

Experimental protocol

Each bird was fitted with a GPS receiver logging position and groundspeed, at 5Hz (Qstarz BT-Q1300; Qstarz International Co. Ltd, Taipei, Taiwan), and a high-definition video camera looking forward over the head (HD720P Mini DV, frame rate: 30Hz, resolution: 1280 x 720 pixels) (Fig.18). The equipment weighed 0.031kg in total, representing less than 5% of the bird's body weight, as required by our ethically-approved protocol. It was carried dorsally on a commercially available harness (Marshall Radio Telemetry, Trackpack) comprising a plastic mounting plate held in place between the shoulders by a pair of flat Teflon ribbons wrapped once around the bird's body in a figure-of-eight pattern. Each bird also carried a tail-mounted radio transmitter for tracking purposes (Marshall Radio Telemetry Micro Transmitter).

All flight tests were carried out in various countryside locations in Monmouthshire (Wales, UK), chosen according to local wind conditions. The GPS unit was allowed to settle for at least 5 minutes before beginning the experiment, after which time the peregrine was released by its falconer and allowed to gain height. The falconer then shouted a command that the birds associated with food, and threw the target a short distance up in the air. The birds sometimes caught the target as it fell vertically, but more commonly reached the target after it had hit the ground, however, since the targets were never thrown more than a few metres from the falconer we therefore treat them as being essentially stationary. This assumption satisfies the majority of the attack passes exactly, and approximately in the remaining passes.

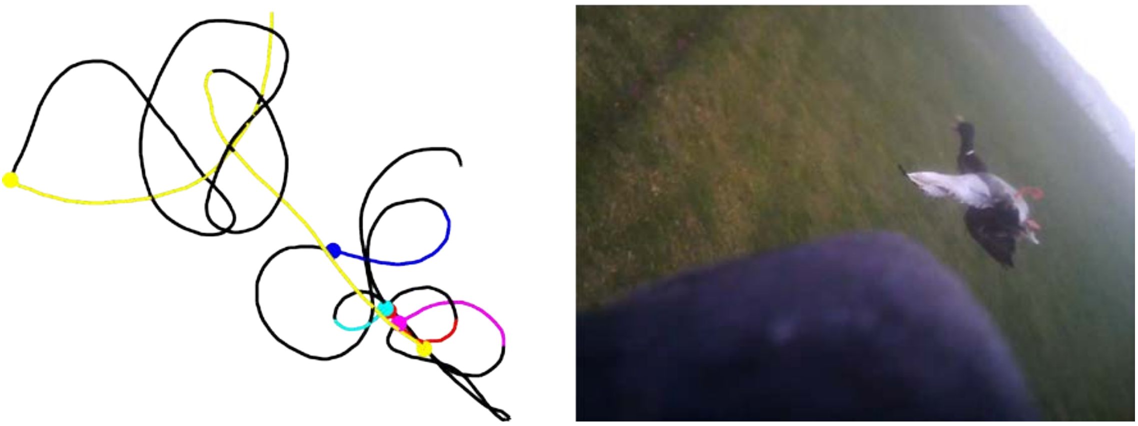


Figure 18: GPS trajectory (left) and on-board camera image (right) where the peregrine chased a duck. The different colours represent the separate terminal phase target passes (last turn to target) with target position at the corresponding coloured circle (yellow corresponds to pursuits which were not included in the analysis as the duck was flying, thus its position, until the point of interaction, could not be determined). The image shows the duck with its body inverted as it attempts (successfully) to evade the peregrine, and the tilt of the horizon indicates the bank angle of the peregrine during the terminal phase of this attempted interception.

<u>Data synchronisation</u>

The raw data from the GPS consisted of latitude (degrees), longitude (degrees), groundspeed (ms^{-1}) and elevation (m). Groundspeed was plotted against time for each data log in order to extract the flying portions for each flight and eliminate all other sources of movement (e.g. carrying of the bird by the falconer). We synchronized the GPS data and on-board video data by identifying the start and end time of each flight in both of the data streams. We then used the on-board video data to identify the precise time(s) at which the peregrine contacted or otherwise passed immediately over its target, and used this time to identify the GPS position of the target on each pass. The latitude and longitude measurements were then transformed to a Cartesian grid for the purposes of trajectory analysis, using a mapping specific to the local latitude and longitude.

Quality control procedure

Although the GPS units are accurate to within <0.05m when measuring changes in position over short time scales (see chapter 4), their absolute positional accuracy is only expected to be on the order of 7.8m (95% of measurements fall within this distance of the true position)[182]. We then applied our quality control criteria, which firstly involved measuring the discrepancy between the GPS Doppler speed and the speed derived from the differenced position, and excluded any flights which exceed our thresholds (see chapter 4). As a second quality control we also validated the precision of our GPS position data by plotting the trajectories onto aerial photographs of the Earth, in ArcGIS, and checking against the on-board video data. Subsequently, we concluded that in 33 out of 57 flights we can be confident that the shape of the GPS trajectory matches what happens in the video sequence, and that the speed calculated from the differenced GPS position matches the Doppler speed for the last 10 seconds of flight before interception (see Fig.15B for an example of a close match). For the remaining flights, we cannot be certain that the shapes of the trajectories are correct. So to preserve a standard of reliability in the data we have excluded these flights from subsequent analysis.

Results

Data processing

As in previous studies (Tucker, 2000), the peregrines usually followed a curved trajectory in the final stages of an attack. This was true of attacks on both stationary and moving targets, as illustrated by the sequence of passes made at a mallard in the air and on the ground shown in Fig.18. In order to select sections of the flights for detailed analysis in a consistent and objective way, we defined a nominal start time (t_0) for each pass. It must be noted that we attribute no biological meaning to t_0: for example, it is not to be interpreted as the point at which the bird locks on to the target. In the first instance we took the arbitrary time of 10 seconds (or 50 GPS samples) before interception as our starting point t_0.

The peregrines followed a shallow, and usually planar, flight path in the final stages of their attack. At 10 seconds before interception, the median altitude to target was 0.66m (interquartile range: 11.7m), and the median horizontal distance to target was 97.7m (interquartile range: 36.7m). The ratio of these distances defines the mean slope of a pass, with median 0.004m (interquartile range: 0.11). We therefore assume the trajectories are planar, and provide two distinct methods for defining the planes in each pass:

1) Projecting the 2D position of the first two principal components of the bird's 3D trajectory within the plane of best fit.

- This approach has the advantage of capturing as much of the positional variation as possible within a single analysis, but has the disadvantage of mixing accurate latitudinal and longitudinal data with less accurate altitudinal data.

2) Analysing only the latitudinal and longitudinal GPS positions, on the grounds that these contain most of the information on changes in position in the majority of cases.

- This approach captures most of the positional variation because all of the attack trajectories were shallow, and avoids the disadvantages of considering the first two principal components of the trajectory.

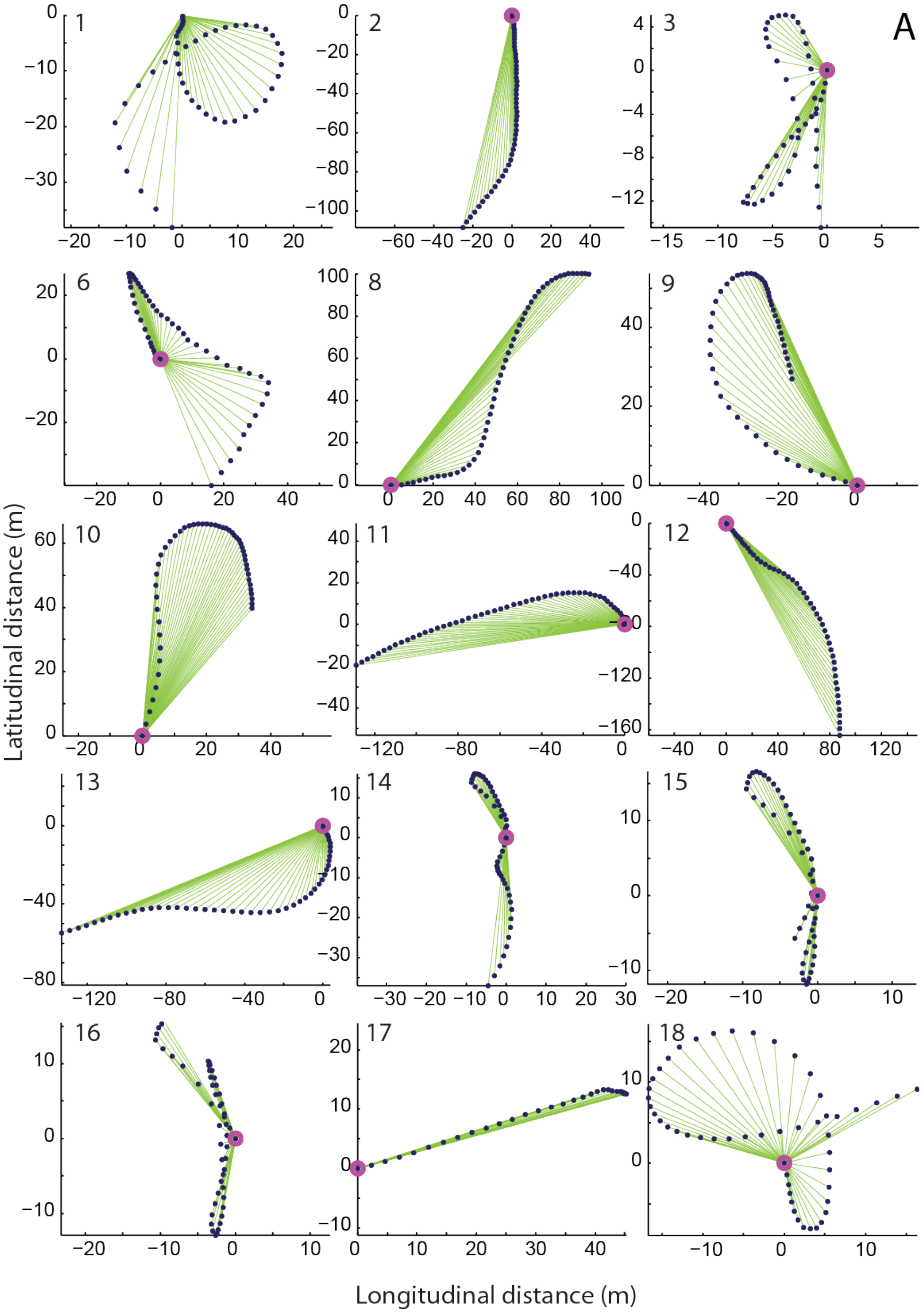
We therefore begin our analysis by adopting the simpler approach of using only the horizontal components of the attacks and assuming planar trajectories, although we relax this assumption later.

Testing for geometric rules

We then computed various derived quantities from the GPS position data, in a polar coordinate system. Using a forwards-differencing procedure we estimated the bird's horizontal ground velocity and track azimuth γ (compass bearing of its velocity vector), followed by the target azimuth θ (compass bearing of the line-of-sight angle between pursuer and target), and deviation angle α (angle between track azimuth and target azimuth).

If the peregrine had been manoeuvring to follow a pure pursuit, the deviation angle α (difference between track azimuth γ and target azimuth θ) would have been approximately constant through a pursuit and equal to zero. During a deviated pursuit, the result would be a constant deviation angle not equal to zero. Measurements of deviation angle showed no evidence for either strategy, as deviation angle is highly variable within a pass and hence $d\alpha/dt \neq 0$. This is illustrated in figure 19A-C, which plots the instantaneous lines-of-sight between the bird and the target, and shows they are not held at a constant angle. Figure 20 plots the deviation angles of the last 10 seconds of each flight, and shows much variation within and between flights. Attack flight is therefore more complex than proposed by Tucker (2000), who hypothesised a strategy amounting to a deviated pursuit with a constant deviation angle of approximately 45˚.

If the peregrine had been manoeuvring to maintain a constant absolute target direction, the bearing to target (target azimuth θ) would be a constant value with zero variation about the median, as proposed for bats[13] and falcons[12]. Measurements of target azimuth showed little evidence for being constant within a pass, and hence $d\theta/dt \neq 0$. Figure 20 plots the target azimuths of the last 10 seconds of each flight, and shows considerable variation within and between flights.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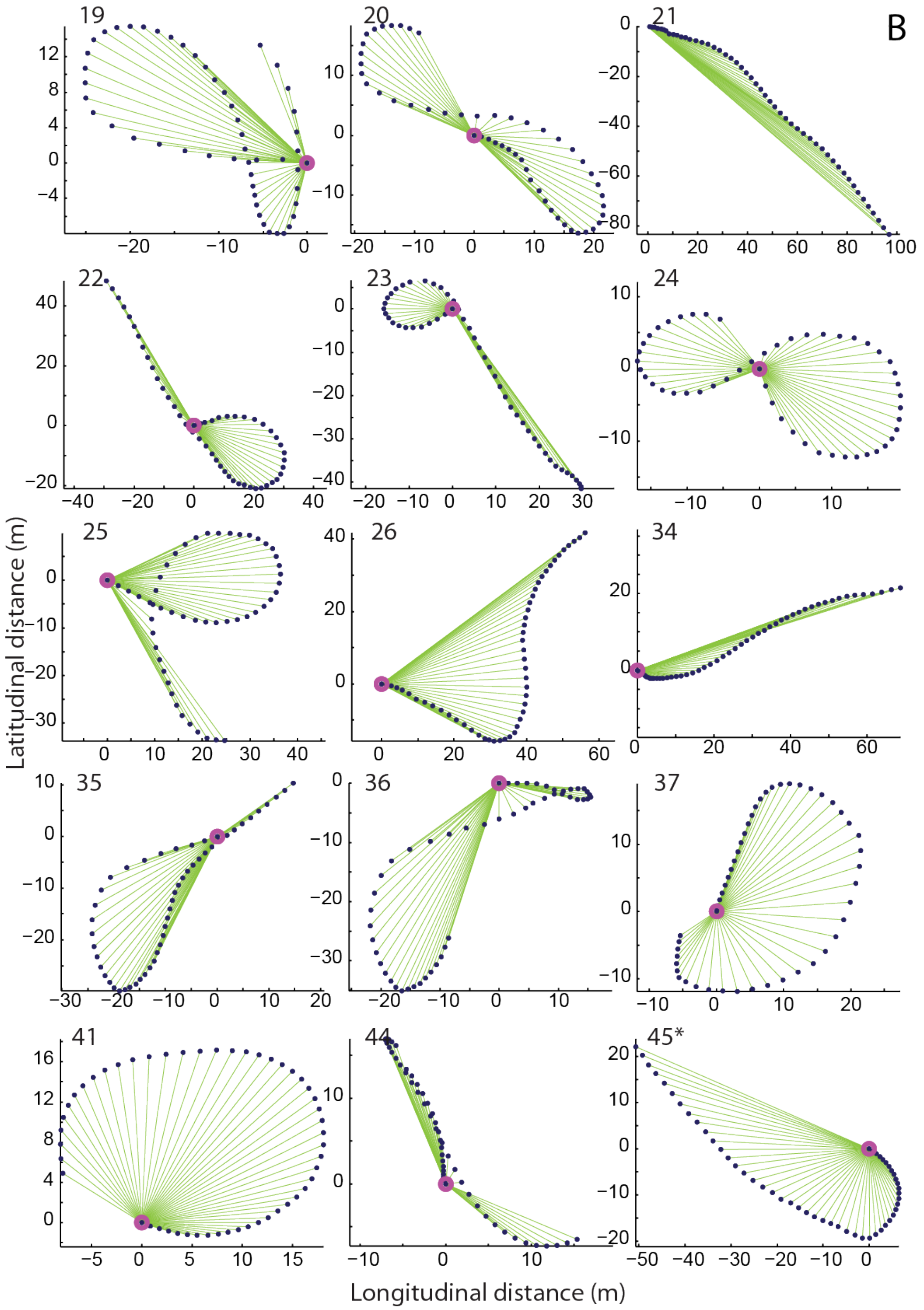
Longitudinal distance (m)


B
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Longitudinal distance (m)
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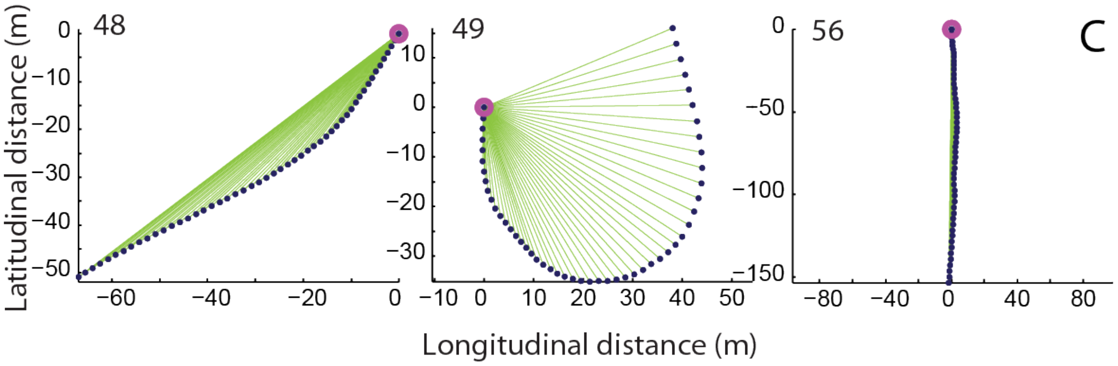


Figure 19 A-C: Measured raw GPS positions (purple points) for 33 attack trajectories of peregrines intercepting stationary targets (Bird B = 1 – 25; Bird N = 26 – 34; Bird W = 35 – 57) which passed the quality controls described in Chapter 4. Green lines show the instantaneous line of sight to target (magenta circle), for the last 10 seconds before interception. Note that the deviation angle between the velocity vector and line-of-sight to target is not constant, demonstrating that the birds did not use pure or deviated pursuit. A '*' marks the one potentially problematic flight identified in our quality control procedure.

For straight flights, where the bird is flying directly towards the target, we would expect the variation in target azimuth to be small. It should be noted that any of the predicted pursuit strategies will generate a straight flight to target if the target is stationary and the initial velocity vector of the pursuer points directly at the target, as both the deviation angle and the line-of-sight bearing are necessarily constant. But such flights are uninformative about the guidance law being used, because the dynamics are not excited in these cases.

We also represented the data on a polar plot (Fig.21), plotting the line-of-sight angle versus distance to target (distance from centre) for each final-stage flight from figure 19, to show the relative distances. Datapoints following the radial lines indicate periods where the birds are decreasing their distance (flying towards the target) while maintaining a constant line-of-sight angle, thereby performing parallel navigation. Non-radial sections (the majority of flights) indicate periods where the birds are employing a different method as they decrease their range and intercept the target.

Overall, figure 19 shows a huge diversity in trajectory shape, reflecting the fact that the birds were not always locked on to the target at 10 seconds before interception. Since we cannot know when target-directed flight behaviour is initiated, we must therefore find a quantitative criterion for choosing the start point in our proportional navigation simulations.

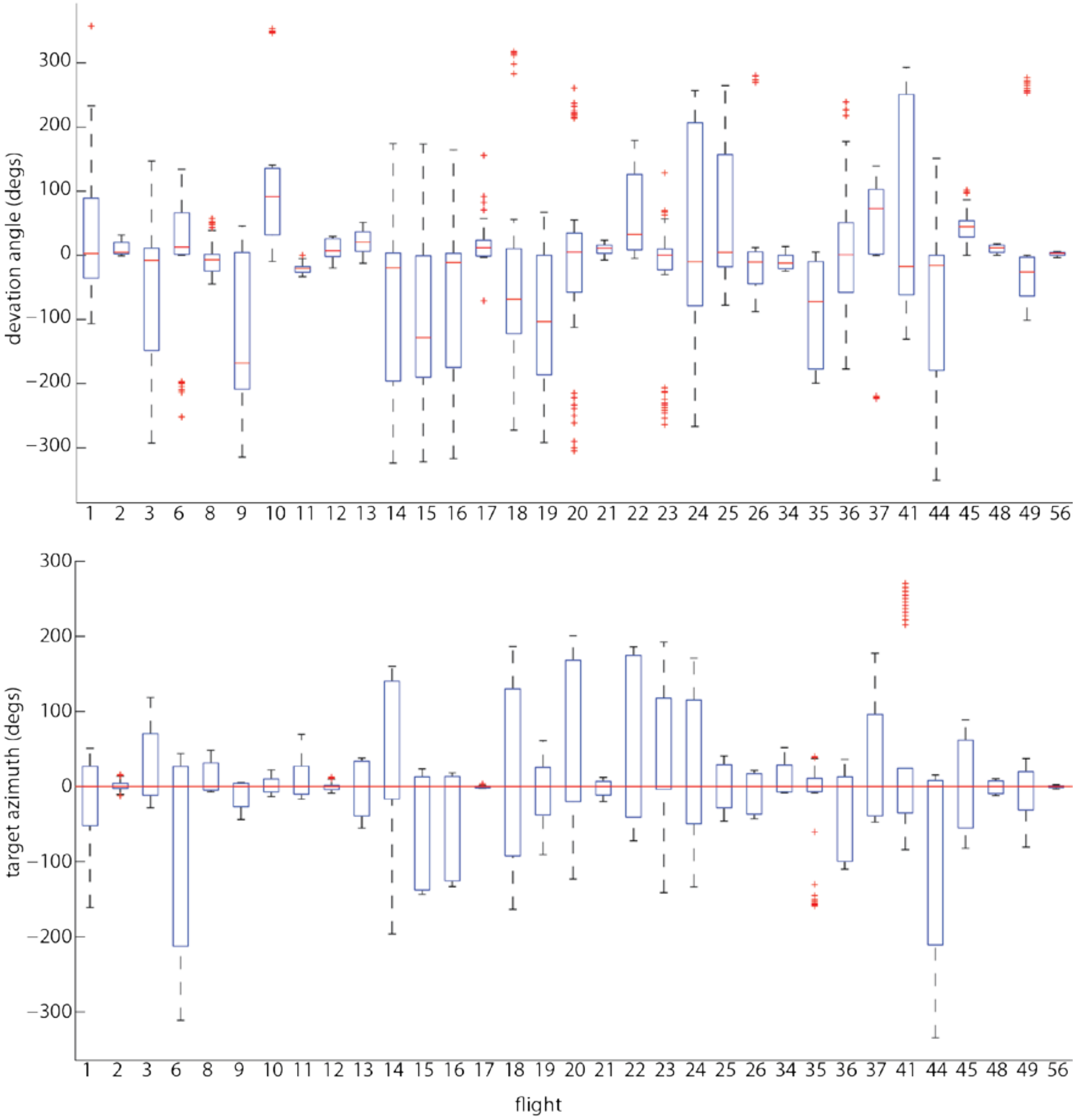


Figure 20: Box plot of A) deviation angles and B) target azimuths, for the last 10 seconds of 33 peregrine attack flights to a stationary target from figure 19. Red lines are the median values, edges of boxes are the 25th and 75th percentiles and red crosses are the outliers.

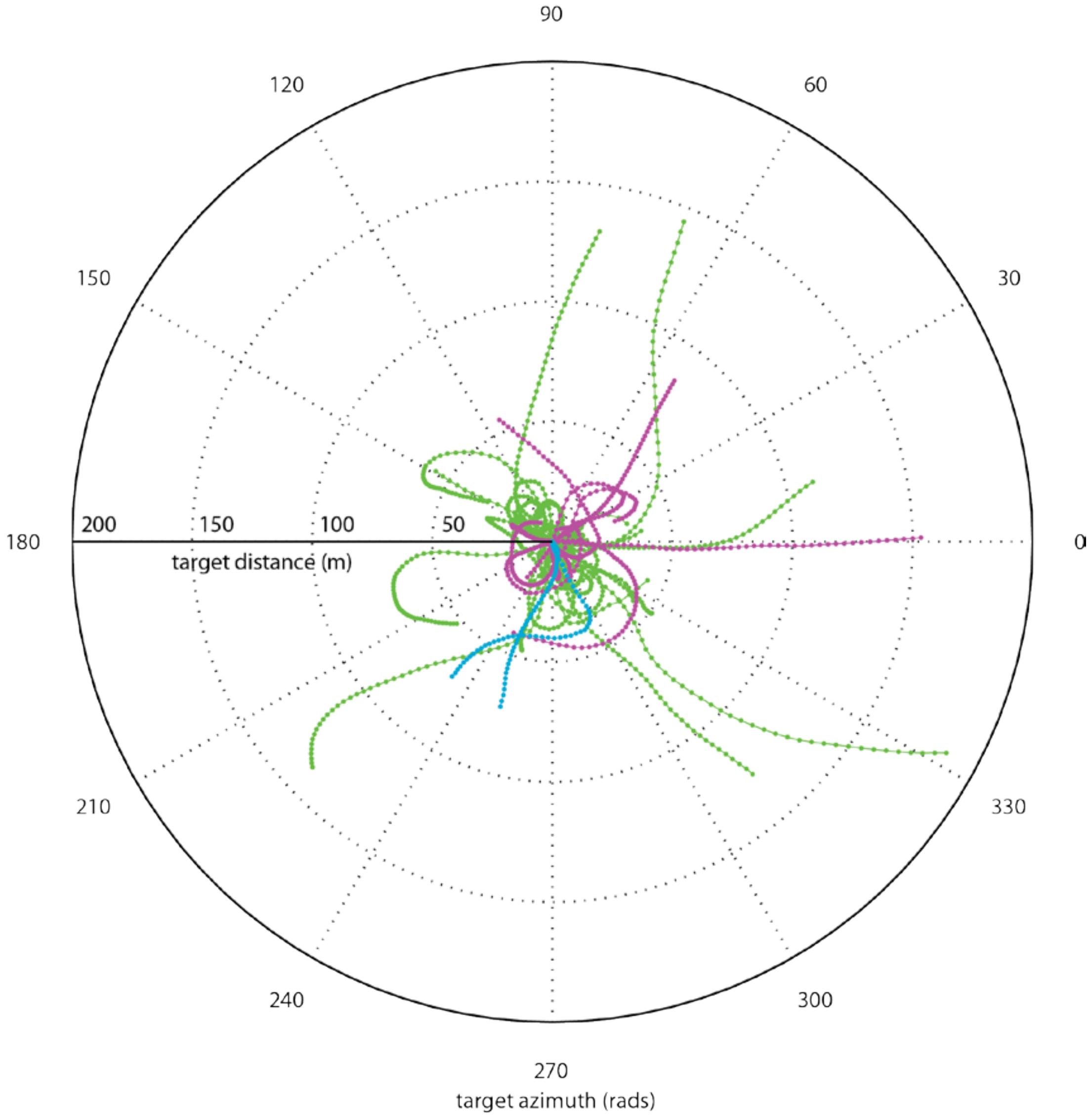


Figure 21: Polar plot of line-of-sight angle from target to bird with distance from target to bird, for the last 10 seconds of 33 intercept flights to stationary targets for three peregrines (Bird B = green; Bird N = cyan; Bird W = pink). Datapoints following the radial lines indicate sections where the birds are maintaining a constant line-of-sight angle and thereby performing parallel navigation.

Testing for a guidance law

The horizontal GPS position data clearly shows there is no simple geometric rule which can describe our measured trajectories. Next, we set out to determine if the flight behaviour could be described by the guidance law of proportional navigation. Basic proportional navigation requires the pursuer to control its turn rate in proportion to the line-of-sight rate to target and move in a direction defined by which variant of proportional navigation is employed. For pure proportional navigation (PPN), the pursuer accelerates perpendicularly to its velocity vector, whereas for true proportional navigation (TPN), the pursuer accelerates perpendicularly to the line-of-sight. However, PPN is considered the more 'natural' guidance law in practice, as TPN has several limitations with regards its implementation and trajectory behaviour (requires forward velocity variation, restrictions on initial engagement conditions to ensure intercept, and can lead to unbounded acceleration), and so here we use pure proportional navigation in the analysis. Our data were thus modelled on the differential equation for pure proportional navigation[146], by calculating the turn rate ($d\gamma/dt$, or rate of change of track azimuth) and the line-of-sight rate ($d\theta/dt$, or rate of change of target azimuth) using central differencing. Turn rate was found to be positively correlated with line-of-sight rate across passes (Fig.22), as required under the hypothesis of proportional navigation guidance, in that line-of-sight rate commands a proportional turn rate. However, because of the numerical difficulties associated with computing line-of-sight rate and turn rate from noisy position data, and problems with pseudoreplication, we sought to test this hypothesis formally from the detailed shapes of the measured trajectories.

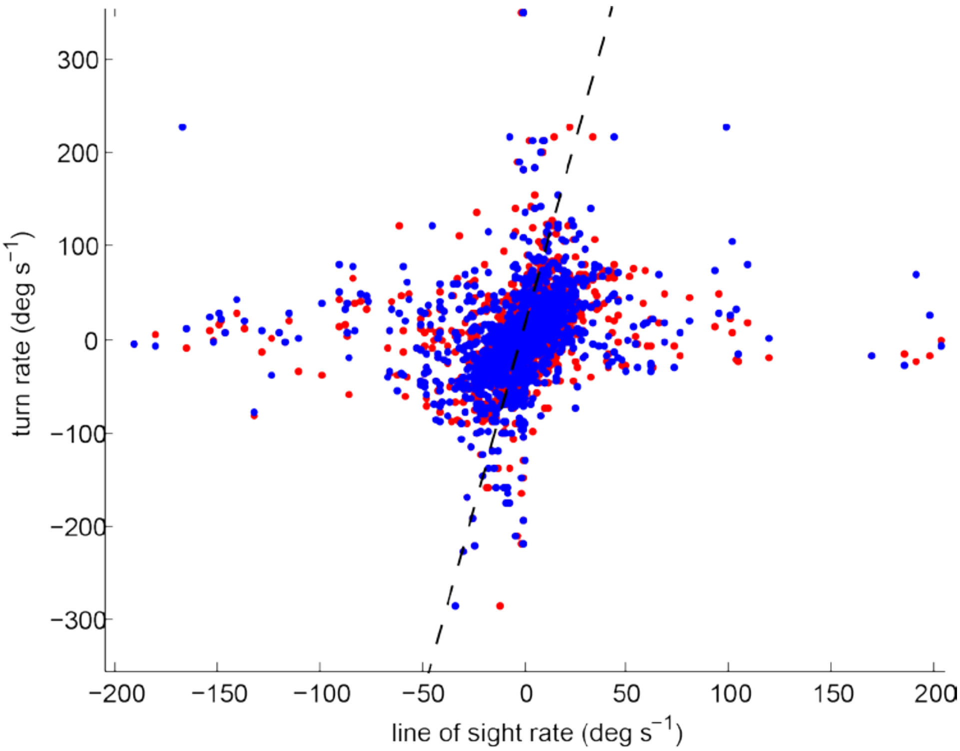


Figure 22: Estimated turn rate versus estimated line-of-sight rate for all measured instants during 33 peregrine air-to-ground attack passes for the last 10 seconds before intercept. Points in red are outliers, defined as points falling within the upper and lower 2.5% percentiles for turn rate and line-of-sight rate, and are likely to reflect measurement error rather than real data. The black line denotes the linear regression of turn rate on line-of-sight rate. The turn rate is positively correlated with line-of-sight rate, as required under the hypothesis that the birds use proportional navigation, however the data are noisy and are subject to problems of pseudoreplication.

Simulating proportional navigation trajectories

It is straightforward to simulate the trajectory that an attacker would follow to a stationary target under pure proportional navigation, given knowledge of its initial position and flight direction relative to the target, and assuming a fixed navigation constant (N). Using the GPS data to supply position and flight direction at t_0, we used our simulations to compute the change in line-of-sight rate for each successive time point, from the initial start position to target interception, and identified the best-fitting value of N for each flight. We did this using a quintic spline interpolation of the bird GPS data to lessen the effects of sudden jumps in position. We used an integration step-size of 300 per sample period therefore increasing our sampling frequency from 5Hz to 1500Hz. We then used analytical differentiation and evaluation of the splines to estimate the bird and lure velocities and interpolate the positions of the bird and lure. Next we determined the initial direction of the bird's velocity vector, between the first raw position and the first interpolated position. The speeds of the bird during an interception flight were very variable, so we also estimated the instantaneous groundspeed from the interpolated data in order to update the velocity of our simulation to match the speed of the bird. The simulation then used the initial interpolated bird velocity at the starting position t_0, the change in velocity between t_0 and t_1, and bird speed, to estimate the angular change in velocity vector direction for each subsequent sample point until interception. This was achieved by firstly calculating the rate of change of the line-of-sight between the bird and lure, from the cross product of the range of the line-of-sight vector r (position vector of the lure relative to the bird) and the relative velocity vector v_r (velocity of the lure relative to the bird), divided by the magnitude of r squared:

$$\frac{d\lambda}{dt} = \frac{r \times v_r}{\|r\|^2}$$

Next, the acceleration of the bird at time $t - 1$ was calculated from the rate of change of line-of-sight, multiplied by the velocity V of the bird, and then optimising the numerical value of N based on minimising the L1-norm of the distance between the interpolated position and simulated bird trajectory at each point according to the following equation:

$$a = N\left(\frac{d\lambda}{dt} \times V\right)$$

The velocity of the simulated bird trajectory was then updated according to the estimated acceleration a and then adjusted to match the ground speed of the bird, and finally, used to update the position of the bird at the next time step.

There is no way of knowing from first principles when a bird first switches to target-directed flight behaviour. We therefore used an arbitrary but objective empirical criterion to define two start times - t_0 and t_{01} - at which to begin our simulations. We attribute no particular biological meaning to this definition of t_0, which is merely intended to provide a consistent and objective criterion for selecting sections of flight for analysis. Thus, there is no reason to think, for example, that t_0 must coincide with the time at which the bird initiated target-directed flight behaviour.

Firstly, we ran the simulation starting from every single point along the bird's trajectory - from 10 GPS samples before interception (to include enough datapoints), up to 75 (which amounts to 15 seconds of flight). We therefore obtained the mean L1-norm error values and flight distances for each possible starting position. We identified t_0 as the last point (working backwards from 2 seconds before interception) for which the mean prediction error in position was <0.5% of the distance flown (minimum R^2 value from the least-squares regression, divided by flight distance). As a comparison we also identified an additional start point - t_{01} - for a mean prediction error of <1% of the distance flown, which allowed the simulations to extend further back in time from interception.

Figures 23 and 24 therefore show the actual bird and lure positions with simulated proportional navigation trajectories overlain, from t_0 and t_{01} to interception, against stationary targets, for all flights which were deemed reliable. Figure 23 shows the 15 flights quantitatively chosen as those with the most amount of turning (most variation between the first and second principal components, respectively, from t_{01} to interception) - and we provide all the remaining flights in figure 24 A-B. To ensure our simulations were physically valid, they were stopped at the point where the calculated acceleration exceeded 2.5g. This removed any highly erroneous simulations (e.g. where the simulation fitted a straight line by tending towards an unrealistically high value of the navigation constant), and also avoided fitting the trajectory when very close to the lure (<0.2s) where the demanded acceleration tends towards infinity. In addition, we also excluded any fitted trajectories which were insignificant at the $p<0.05$ level and thus for which N values could not be reliably predicted (though we show these in our plots as dashed lines). Overall, our simulated trajectories matched the measured data very precisely for long flight sections. In order to quantify the closeness of fit, we calculated the correlation coefficients between the measured and simulated bird positions, for both error thresholds, by performing a principal component analysis on bird latitude and longitude. We compared the second principal component of the measured position (i.e. the lateral component of the flight) with the component of the simulated position in the same direction (neglecting the first and last points of the simulation since the first point is constrained to be the same and the last point is prone to numerical error; table 3). The first principal component offers no useful information as it is aligned with the average velocity vector of the bird, so we would expect a high correlation even for a straight flight. Therefore the correlation between the measured and simulated first principal component is a necessary but insufficient condition for assessing the goodness of fit of the simulation. However, the second principal component will be zero for a straight flight, and we would only expect a high correlation if the flight had a significant lateral component (i.e. lots of turning) and was also well predicted by the simulation. Therefore a high correlation between the measured and simulated positions for the second principal component (i.e. high COEFF; Table 3) is a sufficient condition for assessing goodness of fit.

We use graphical representation in figure 25A–E to qualitatively assess the stability of our estimated N values, by plotting all computed values from 10 to 75 GPS samples before interception (2 – 15 seconds). The first subplot for each flight shows the variation in relative error values of our predicted proportional navigation trajectories when the simulations were started at each point of the bird's trajectory. The second subplot shows the actual L1-norm values for each simulation above. The third subplot shows the corresponding N values for each start point, and shows that the starting positions under a 2% error threshold (green circles) are much more unstable and so we chose to model the 0.5% and 1% thresholds only. Therefore, for the majority of flights it can be seen that the value of N at our defined starting points (orange and red circles) are approximately similar to the median for that flight, and thus are reliable predictors of trajectory shape.

We also asked whether our estimation of target position may have affected the computed values of N. Therefore, to obtain a quantitative estimate of target measurement error on the prediction of N, we re-ran the proportional navigation simulations for each flight, for target positions one before and one after the current best estimate (0.5% error threshold) and calculated the resultant range of estimates (min and max) against the best estimate (table 3). The majority of flights show a small range in N across target positions (mean range of ±0.2) suggesting target position had minimal influence on our best estimation of N.

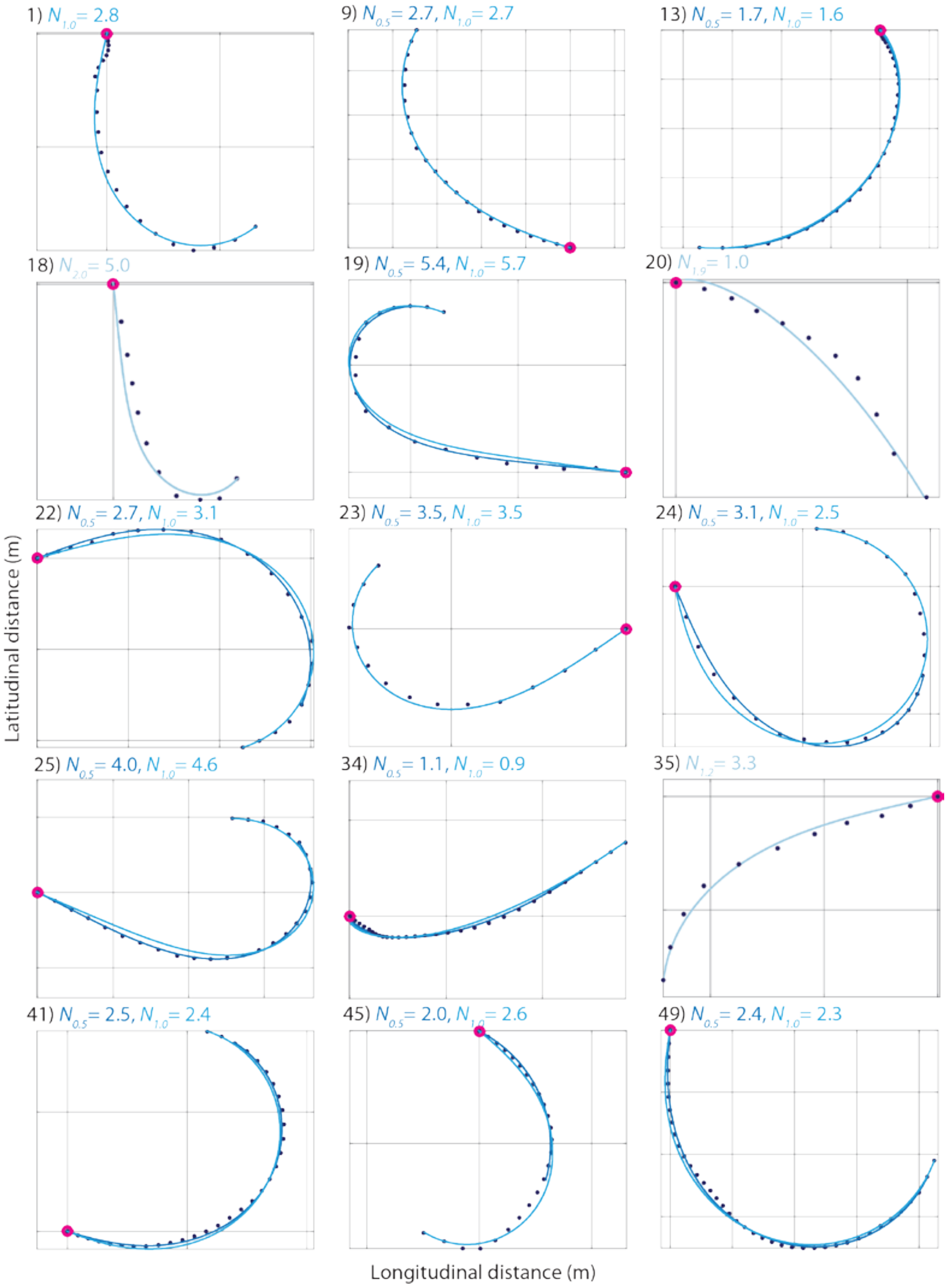
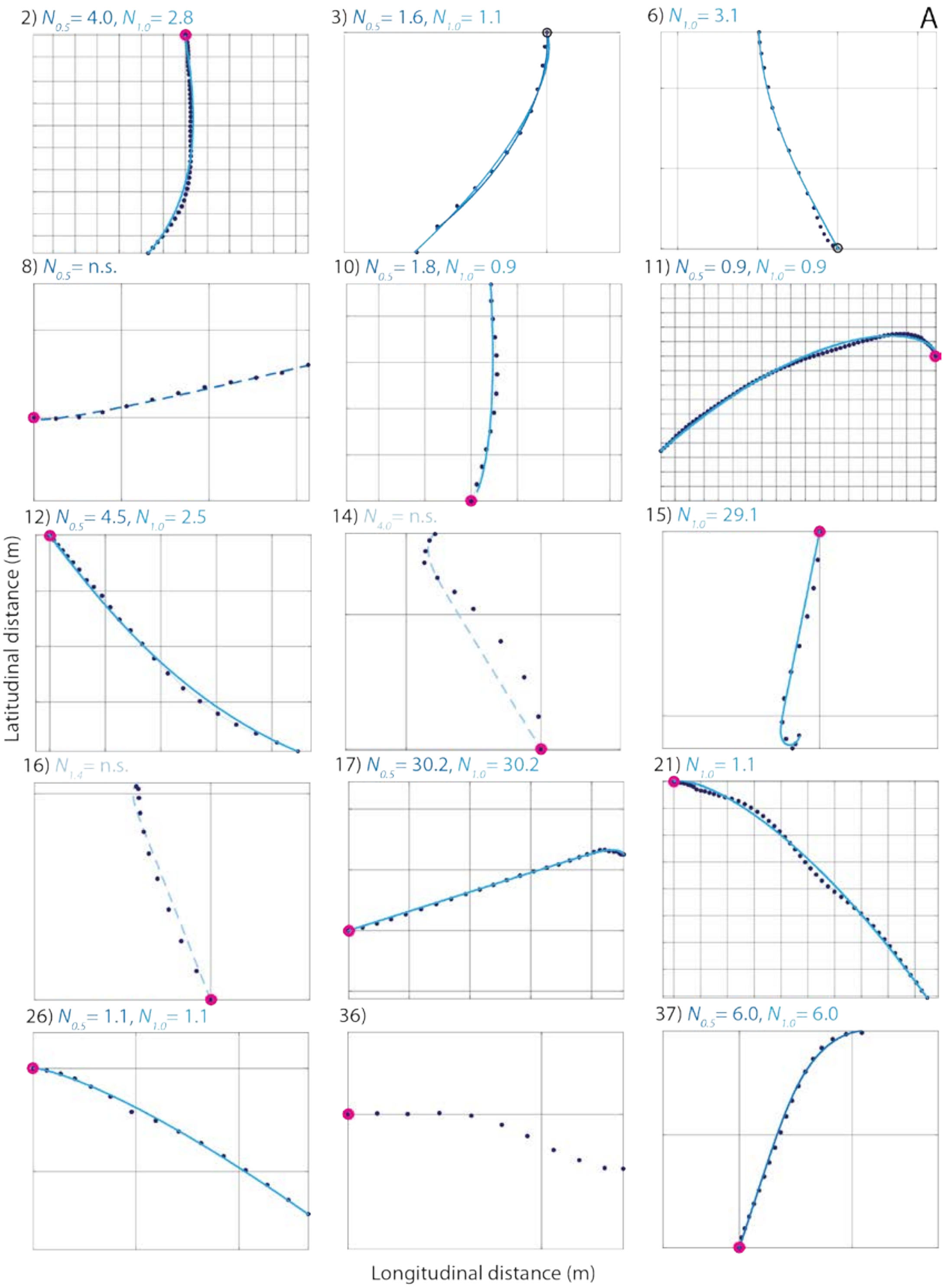


Figure 23: Proportional navigation simulations (blue lines) of the raw GPS trajectories of the 15 lowest aspect ratio air-to-ground attacks by three peregrines (blue points) against a stationary lure (magenta circle). Aspect ratio was determined from the latent values (i.e. amount of variation) of the first and second principal components, respectively, from t_{01} to interception (see Fig.24 A-B for all remaining attack trajectories). Grid lines denote 10m intervals. Two simulations are shown for different starting positions, defined as mean relative L1-norm error thresholds of 0.5% (dark-blue) and 1% (mid-blue) - light-blue simulations did not meet our 1% error threshold criterion. Note the very close match between the measured and simulated trajectories, confirming the use of proportional navigation. Missing simulations exceeded our acceleration criteria of 2.5g and thus were excluded for being physically unrealistic. Dashed trajectories indicate simulations which were non-significant and so *N* values could not be reliably predicted. Flight 45 is a potentially problematic flight identified in our quality control procedure.


A
2) $N_{0.5}$ = 4.0, $N_{1.0}$ = 2.8
3) $N_{0.5}$ = 1.6, $N_{1.0}$ = 1.1
6) $N_{1.0}$ = 3.1
8) $N_{0.5}$ = n.s.
10) $N_{0.5}$ = 1.8, $N_{1.0}$ = 0.9
11) $N_{0.5}$ = 0.9, $N_{1.0}$ = 0.9
12) $N_{0.5}$ = 4.5, $N_{1.0}$ = 2.5
14) $N_{4.0}$ = n.s.
15) $N_{1.0}$ = 29.1
16) $N_{1.4}$ = n.s.
17) $N_{0.5}$ = 30.2, $N_{1.0}$ = 30.2
21) $N_{1.0}$ = 1.1
26) $N_{0.5}$ = 1.1, $N_{1.0}$ = 1.1
36)
37) $N_{0.5}$ = 6.0, $N_{1.0}$ = 6.0
Latitudinal distance (m)
Longitudinal distance (m)

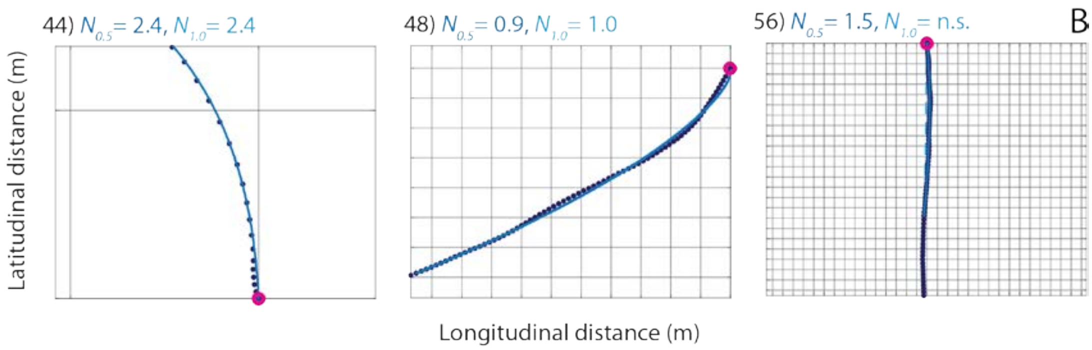
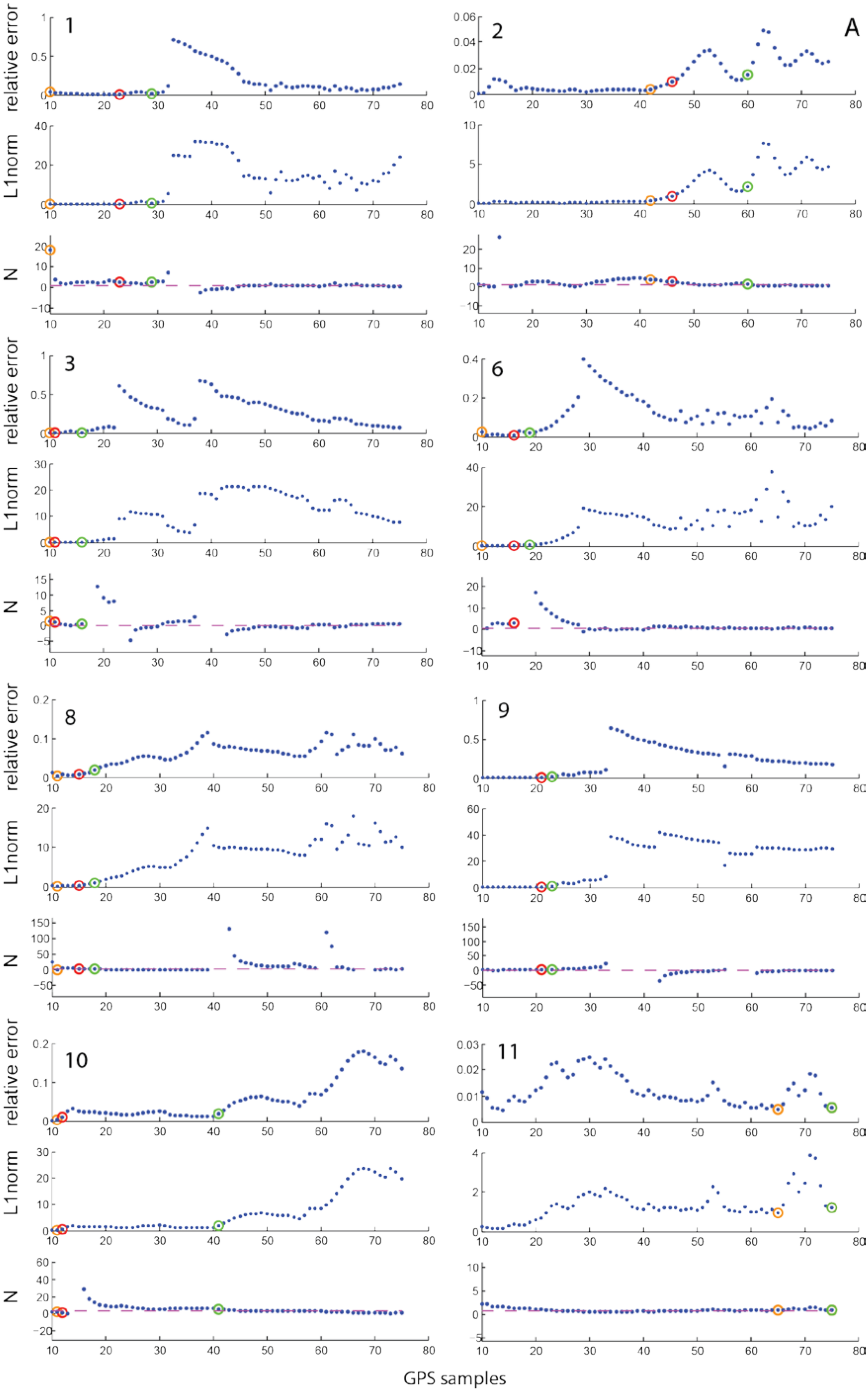


Figure 24 A-B: Measured GPS positions (blue points) overlain with trajectories simulated under the hypothesis of proportional navigation (blue lines), for all remaining flight trajectories of peregrines intercepting stationary targets (magenta circle). Grid lines denote 10m intervals. Three simulations are shown for two different starting positions, defined as mean relative L1-norm error thresholds of 0.5% (dark-blue) and 1% (mid-blue) - light light-blue simulations did not meet our 1% error threshold criterion. Note the very close match between the measured and simulated trajectories, confirming the use of proportional navigation. Missing simulations exceeded our acceleration criteria of 2.5g and thus were excluded for being physically unrealistic. Dashed trajectories indicate simulations which were non-significant and so N values could not be reliably predicted.

Flight	Bird	Best N 0.5% error	COEFF 0.5% error	N 1.0% error	COEFF 1.0% error	min N	max N	±range	PCA N
1	B	x	x	2.8	0.9979	x	x	x	2.7
2	B	4.0	0.9871	2.8	0.9664	3.9	4.0	0.1	3.9
3	B	1.6	0.9932	1.1	0.9786	1.5	1.6	0.1	1.4
6	B	x	x	3.1	0.8636	x	x	x	x
8	B	x	x	x	x	x	x	x	x
9	B	2.7	0.9983	2.7	0.9983	2.7	2.8	0.1	2.6
10	B	1.8	0.9829	0.9	0.8706	1.7	1.9	0.1	2.0
11	B	0.9	0.9899	0.9	0.9914	0.8	0.9	0.0	0.9
12	B	4.5	0.9784	2.5	0.9147	4.4	4.6	0.1	4.2
13	B	1.7	0.9997	1.6	0.9992	1.7	1.7	0.0	1.7
14	B	x	x	x	x	x	x	x	x
15	B	29.8	0.8291	29.1	0.9292	29.8	29.8	0.0	30.0
16	B	x	x	x	x	x	x	x	x
17	B	30.2	0.9838	30.2	0.9838	27.8	33.1	2.6	135
18	B	5.0	0.9866	5.0	0.9866	4.2	5.9	0.9	5.6
19	B	5.4	0.9988	5.7	0.9985	4.9	6.1	0.6	4.9
20	B	1.0	0.8406	1.0	0.8406	1.0	1.0	0.0	1.2
21	B	x	x	1.1	0.9523	x	x	x	x
22	B	2.6	0.9995	3.1	0.9986	2.6	2.7	0.1	2.6
23	B	3.5	0.9994	3.5	0.9994	3.0	3.9	0.4	3.4
24	B	3.1	0.9985	2.5	0.9996	2.9	3.3	0.2	3.0
25	B	4.0	0.9995	4.6	0.997	3.7	4.2	0.2	4.0
26	N	1.1	0.8286	1.1	0.8286	1.1	1.3	0.1	1.2
34	N	1.1	0.9945	0.9	0.9893	1.1	1.1	0.0	1.1
35	W	3.3	0.9565	3.3	0.9565	3.0	3.7	0.4	3.0
36	W	x	x	x	x	x	x	x	x
37	W	6.0	0.9784	6.0	0.9784	5.9	6.0	0.0	5.7
41	W	2.5	0.9994	2.4	0.9993	2.5	2.6	0.0	2.5
44	W	2.4	0.996	2.4	0.996	2.2	2.6	0.2	2.2
45	W	2.0	0.9911	2.6	0.9958	2.0	2.1	0.0	2.0
48	W	0.9	0.9571	1.0	0.9503	0.9	0.9	0.0	1.0
49	W	2.4	0.9991	2.3	0.9986	2.4	2.5	0.1	2.3
56	W	1.5	0.9682	x	x	1.5	1.6	0.0	1.7

Table 3: N values and correlation coefficients computed from the proportional navigation simulations against stationary targets for each flight for each of our relative error thresholds (0.5% and 1.0%). We also test the reliability of our best N values for target positions one before and one after the current best estimate, to obtain a quantitative estimate of target measurement error on the prediction of N – quoting the resultant range of estimates (min and max) against the best estimate. Also shown are the N values of the PCA analysis, using the 0.5% error starting position (NB flight 1 PCA uses 1% error as 0.5% did not meet simulation criteria). Any missing N values represent simulated flights which either exceeded our acceleration criteria of 2.5g and were excluded for being physically unrealistic, or were non-significant and so N values could not be reliably predicted. Similarly, any missing $COEFF$ values represent simulated flights which exceeded our acceleration criteria of 2.5g. (See text for how $COEFF$ was calculated). The majority of flights show a very small range in N across target positions, providing evidence for a variable N between passes.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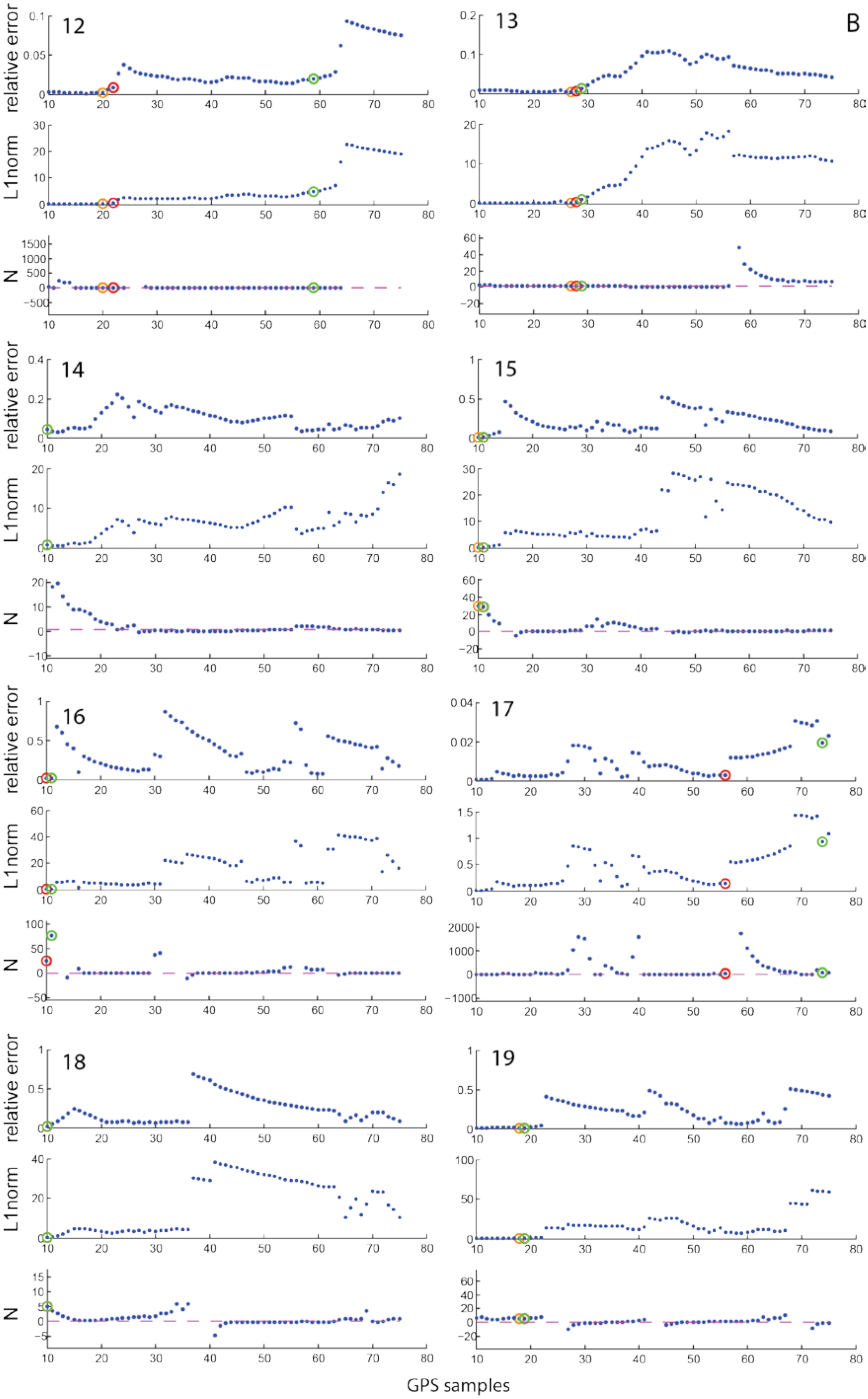
GPS samples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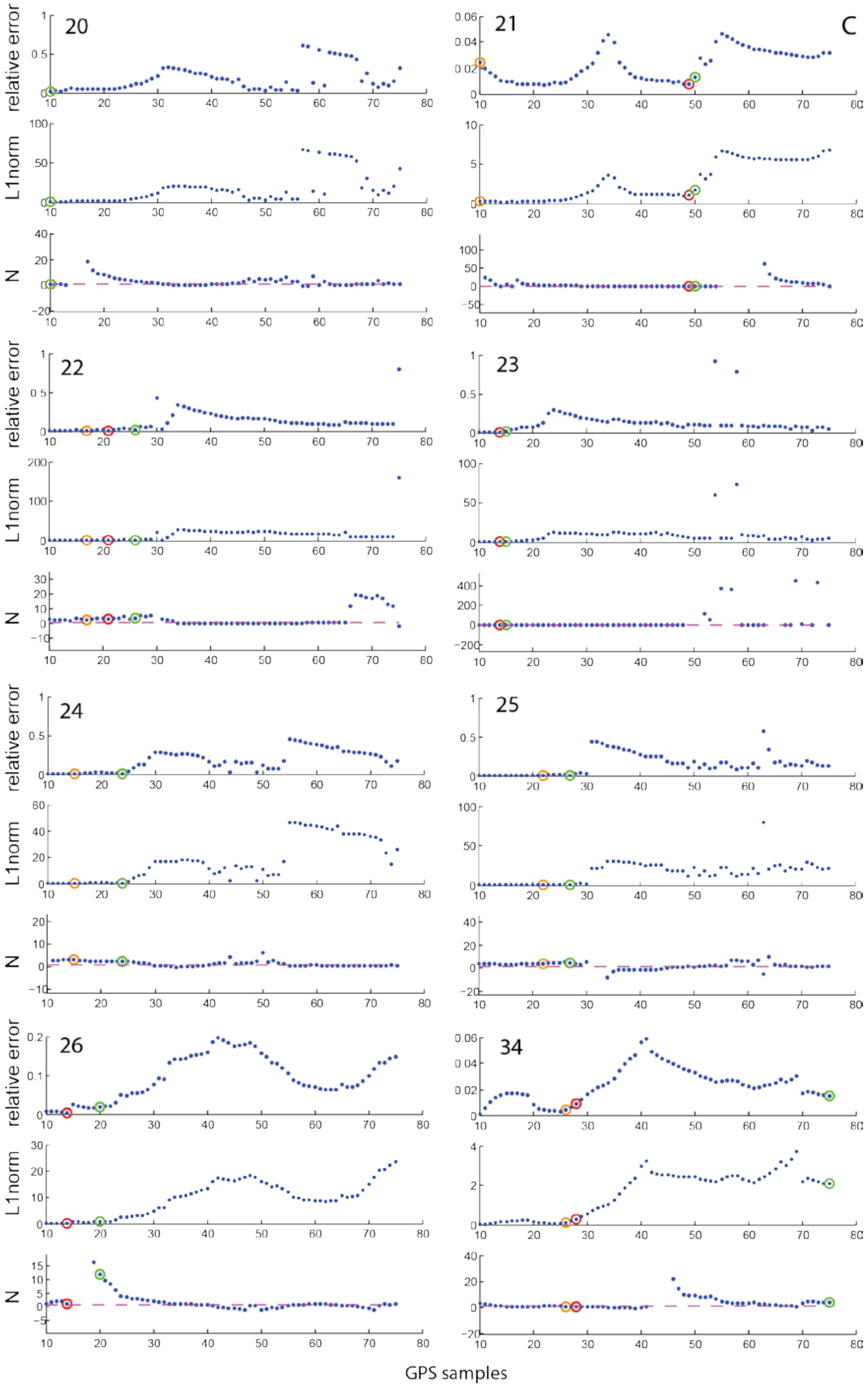
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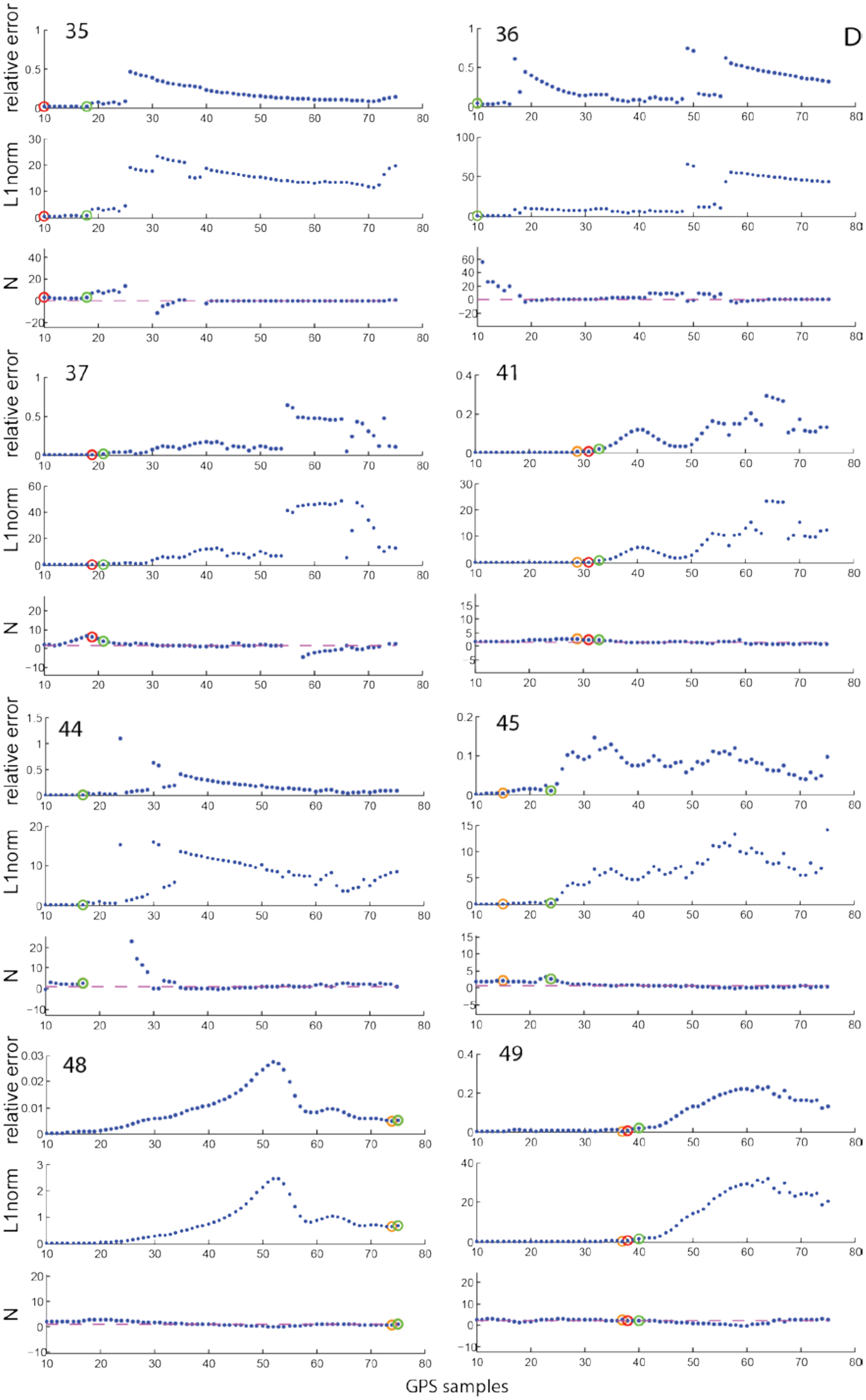
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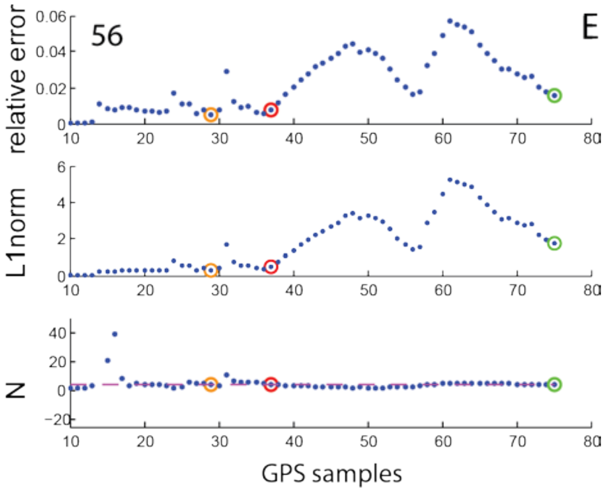


Figure 25 A - E: Comparison of relative error, L1-norm and N values from the PN simulations for peregrine attack flights against a stationary target, starting from every point along the bird's trajectory from 2 to 15 seconds before interception. The N values are plotted about their 75th percentiles for ease of viewing. The orange, red and green circles highlight the start points for three error thresholds (0.5, 1.0 and 2.0% respectively). N values are extremely unstable in places, and so we can determine from the plots whether our chosen value is within a stable region, and therefore is a true representation for that flight. Note that we did not simulate PN trajectories for the 2% error threshold for this reason. Purple dashed line represents the median N value.

Variable navigation constant

The simulations show a wide variety of navigation which holds across the different error thresholds (range for 0.5% and 1% = 0.9–6.0, *n*=22; Fig.26). The range of these intervals covers ±5.1, so we can be confident that at least some of the variation in the fitted values of N reflects genuine variability in its true value. Note that straight flights, where the bird is flying directly towards the target (flights 15 and 17) are uninformative about the guidance law being used, because the dynamics are not excited in these cases, and so were left out of the analysis.

We then conducted a graphical sensitivity test to see whether this variation in the best-fitting value of the navigation constant was genuine, by plotting the trajectories of ±0.5, ±1.0 and ±1.5 of our estimated value of N for the flights at stationary targets from figure 23 (Fig.27) using the N values from our best-fitting simulations (0.5% error threshold). For the more highly curved trajectories, the ±0.5, ±1.0, ±1.5 N lines have a markedly different curvature to the measured trajectory (Fig.27). For the less highly curved of the trajectories in figure 27, the curvature of the ±0.5, ±1.0, ±1.5 N lines is not as clearly distinguishable from the curvature of the measured trajectory. In these cases, the measured trajectories may still be explained by the hypothesis of proportional navigation, but we are unable to estimate the value of the navigation constant with high accuracy, because the shape of the measured trajectory is consistent with a wide range of values of the navigation constant. We would naturally expect a reduction in the accuracy of estimation of the navigation constant with decreasing curvature of the trajectory, as can be seen by considering the limiting case of a perfectly straight flight at target. Such a trajectory could of course be explained by proportional navigation, but because the dynamics of the guidance law would not be excited, the navigation constant would be unidentifiable.

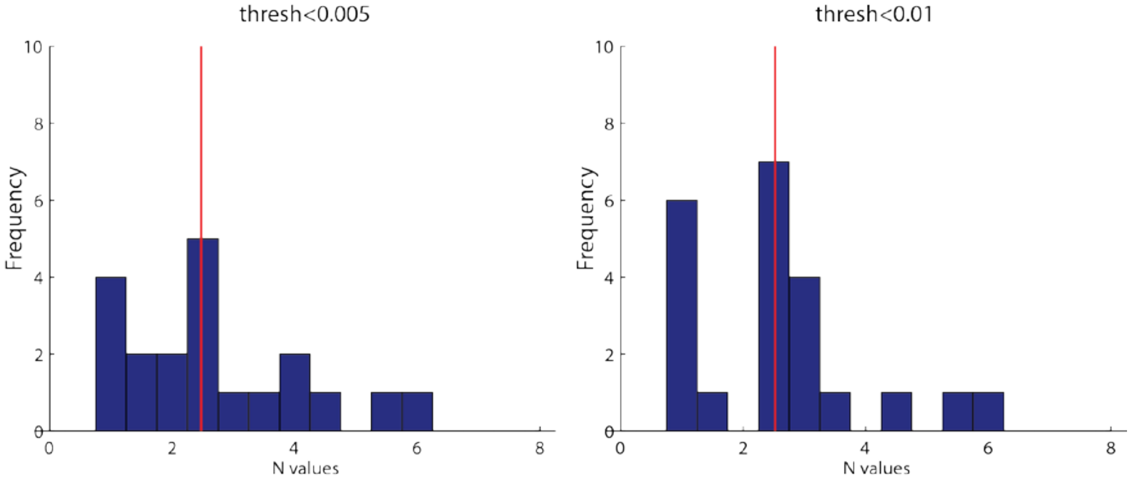


Figure 26: Histogram of N values from our proportional navigation simulations of peregrine flights against stationary targets, for our 0.5% and 1% error thresholds. Red line shows the median N values for the 0.5% and 1% error thresholds (2.52 and 2.49 respectively). Excludes all simulations which exceeded our acceleration criteria of 2.5g, those which were non-significant at $p<0.05$, and flights 15 and 17 where the simulation fitted straight lines.

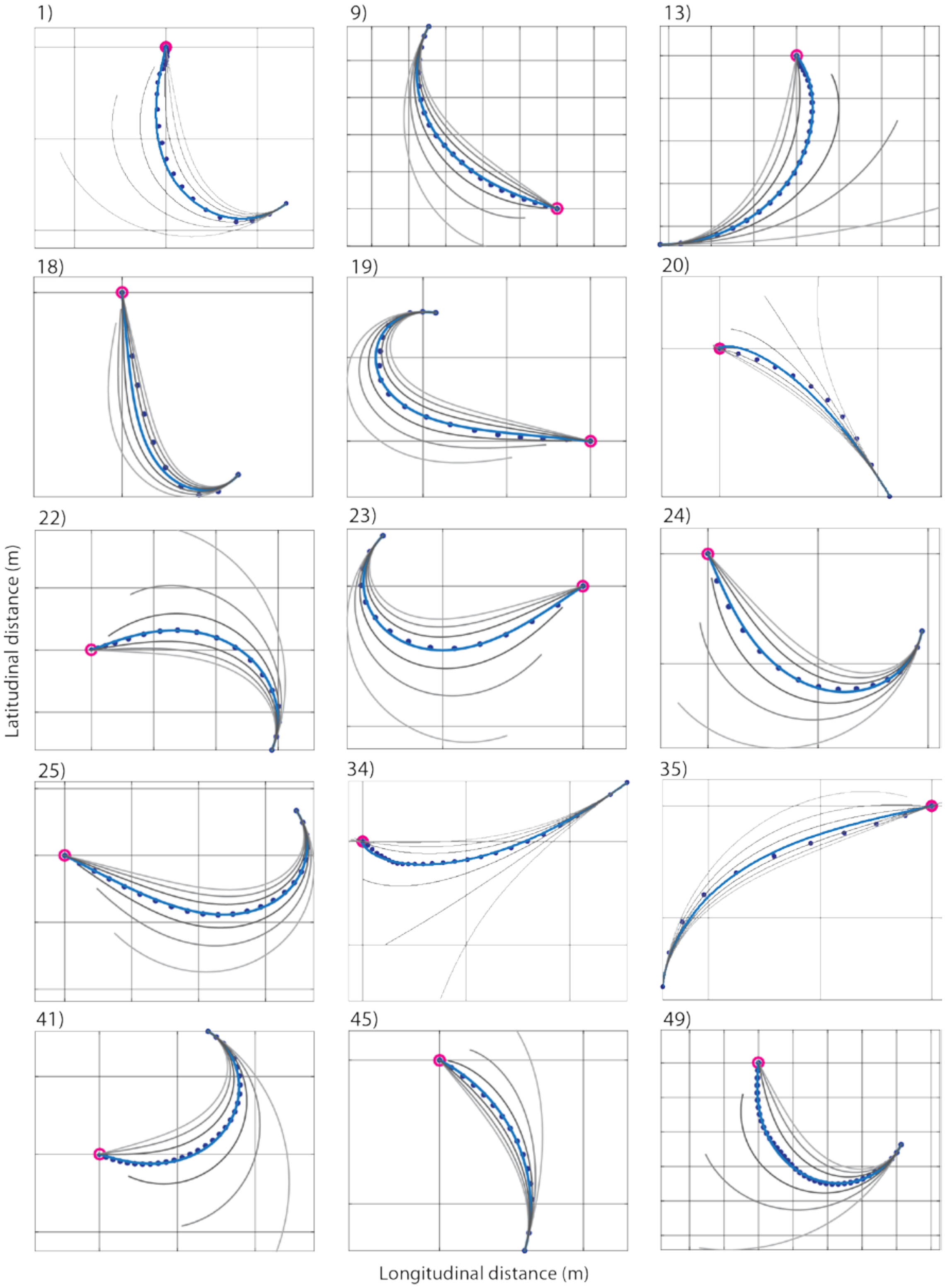


Figure 27: Peregrine intercept flights (blue points) against stationary targets (magenta circle) from Fig.23, with proportional navigation simulations for our best estimate of N (0.5% error threshold - blue line; NB flight 1 = 1% error threshold), showing predicted trajectories for values of ±0.5, ±1.0 and ±1.5 N (grey lines). Note that the grey lines are clearly distinguishable from the best estimate. Grid lines denote 10m intervals.

To investigate the reasons for having a variable navigation constant between pursuit flights, we tested whether the variation in navigation constant (for our best estimates of *N*) could be predicted by any other properties of the flight in question (table 4). There was no evidence that the navigation constant varied with the altitudinal gradient (slope) of the flight ($F_{(1,23)}=3.28$, $p=0.08$, $R^2=0.13$). This was true also of the average speed of the trajectories ($F_{(1,23)}=0.14$, $p=0.71$, $R^2=0.01$) and flight distance ($F_{(1,23)}=2.61$, $p=0.12$, $R^2=0.11$). Furthermore, there was no effect of flight day on the navigation constant ($F_{14,23}=1.01$, $p=0.51$, $R^2=0.61$). We tested for an effect of flight duration on the navigation constant and again found a non-significant relationship ($F_{1,23}=2.94$, $p=0.10$, $R^2=0.12$). Note that the statistical results for altitude and flight duration are close to significant, so there remains a possibility that these may be false negatives (type II errors), since measurements of altitude are not very accurate and the sample sizes are small.

Lastly, we tested for an effect on the navigation constant of whether the bird bound with the target or just hit it (non-binding), and found a significant relationship ($F_{1,22}=4.23$, $p=0.05$, $R^2=0.16$). The mean values of N were 2.1 and 3.3 for binding and non-binding intercepts respectively, suggesting that the birds fly slightly straighter trajectories when aiming to grab or land directly on the prey, and more curving trajectories when hitting and dropping the prey. Perhaps this is associated with injury risk, since during a more highly curved turn the birds experience greater torque - therefore by dropping prey the likelihood for injury may be reduced. However, as we saw from our qualitative analysis of the attack flights from the video data in chapter 3, the comparison of N values in this instance is biased as the birds would perform multiple curving swoops at the prey if they failed to bind with it on the initial encounter. Therefore we are unable at present to explain why the birds are varying their navigation constant between flights. Perhaps they are preventing prey from learning the particular shape of attack trajectory they may follow, by constantly changing their navigation constant.

flight	flight day	binds to prey	target	mean speed (km/h)	flight distance (m)	slope (alt change / dist)	flight duration (s)
1	1	yes	s	22.9	29.3	-0.02	4.6
2	2	no	s	40.5	103.5	-0.02	9.2
5	4	no	s	54.4	39.2	0.52	2.6
6	4	no	s	28.0	32.85	-0.36	3.2
8	5	no	s	55.3	46.0	-0.12	3
9	5	no	s	59.9	69.8	0.08	4.2
10	5	yes	s	71.6	47.7	-0.04	2.4
11	6	yes	s	52.5	218.6	-0.12	15
12	7	yes	s	49.3	60.3	0.43	4.4
13	8	no	s	45.7	71.0	-0.03	5.6
14	8	no	s	34.7	19.2	0.05	2
15	8	no	s	21.0	12.8	0.02	2.2
16	8	no	s	20.2	11.2	-0.02	2
17	9	no	s	15.3	47.5	0.08	11.2
18	9	no	s	19.5	10.8	0.33	2
19	9	no	s	39.4	41.6	0.09	3.8
20	9	yes	s	26.8	14.9	-0.06	2
21	10	yes	s	47.0	128.0	-0.05	9.8
22	11	no	s	44.1	51.4	0.14	4.2
23	11	no	s	29.8	23.1	-0.08	2.8
24	11	no	s	33.6	44.7	-0.06	4.8
25	11	no	s	39.2	58.8	-0.04	5.4
26	12	yes	s	39.1	30.4	0.01	2.8
34	17	yes	s	20.4	31.8	0.22	5.6
35	18	no	s	56.4	31.3	0.00	2
36	18	no	s	26.8	14.9	0.26	2
37	18	yes	s	21.9	23.1	0.09	3.8
41	19	no	s	20.1	34.6	-0.22	6.2
44	19	yes	s	15.3	14.4	0.20	3.4
45	20	no	s	22.2	29.6	-0.02	4.8
48	21	yes	s	31.2	130.2	0.04	15
49	22	no	s	34.6	73.1	0.03	7.6
56	25	yes	s	59.0	245.9	0.03	15

Table 4: Various parameters of attack flights by peregrines against stationary targets. We identified the start of the flight as the last point (working backwards from 2 seconds before interception) for which the mean prediction error in position was <1% of the distance flown (see text for more details).

Principal component trajectory analysis

Lastly, although the measured trajectories were very nearly planar, they were not usually horizontal, so in a final step we projected the three-dimensional GPS coordinates of the peregrines onto the inclined plane defined by their first two principal components (Fig.29). The resulting trajectories were closely similar in shape to the trajectories projected onto the horizontal, and when we re-ran the simulations to compute the best-fitting value of the navigation constants (using the same start point that we had identified earlier) we found little change in our estimates of N (mean of 3.72, compared to 3.75 for the lat/long analysis, excluding flight 17 where the PCA simulation fitted a straight line; Fig. 29, table 4). This validates the earlier analysis that used only the horizontal components of each trajectory.

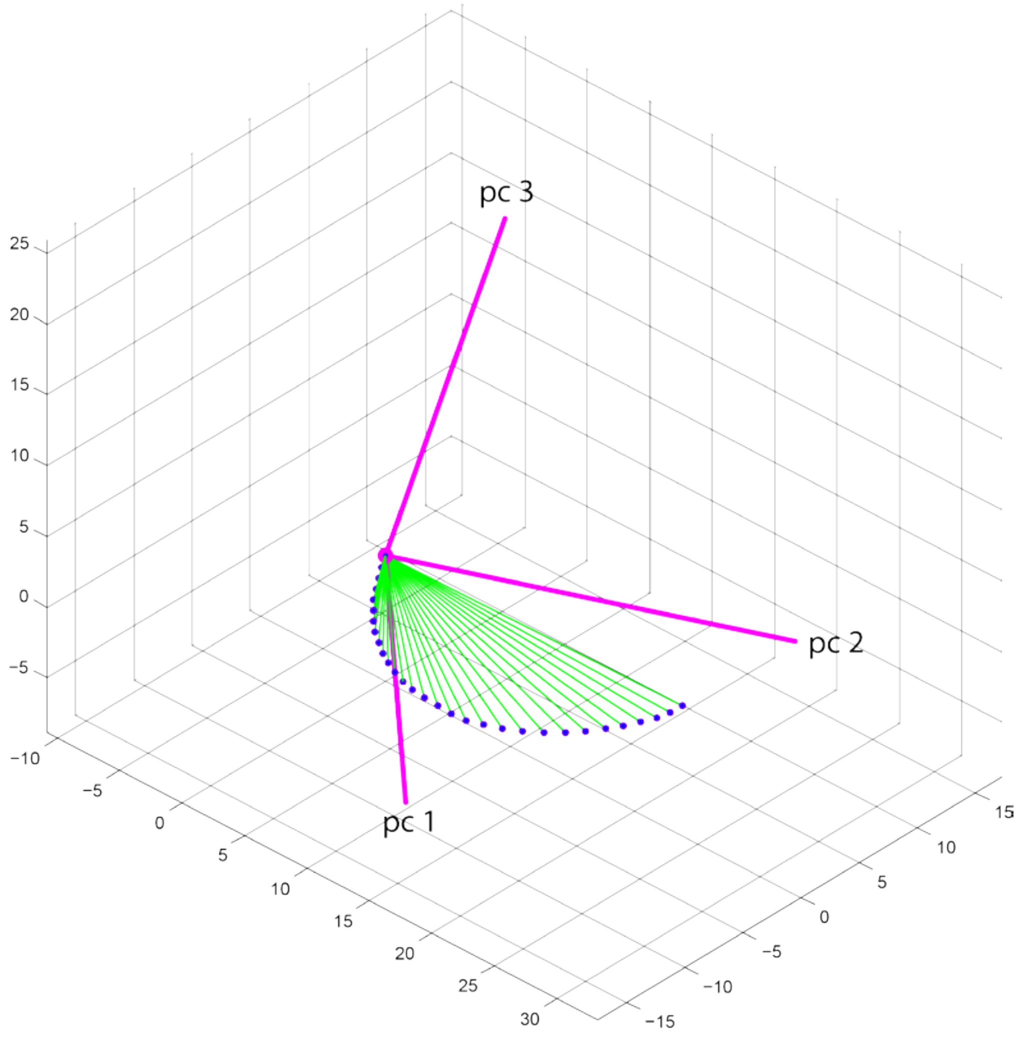


Figure 28: Example three-dimensional plot of GPS points from one typical planar flight to target by a peregrine (purple), showing the line-of-sight (green) to target and the principle component axes (magenta).

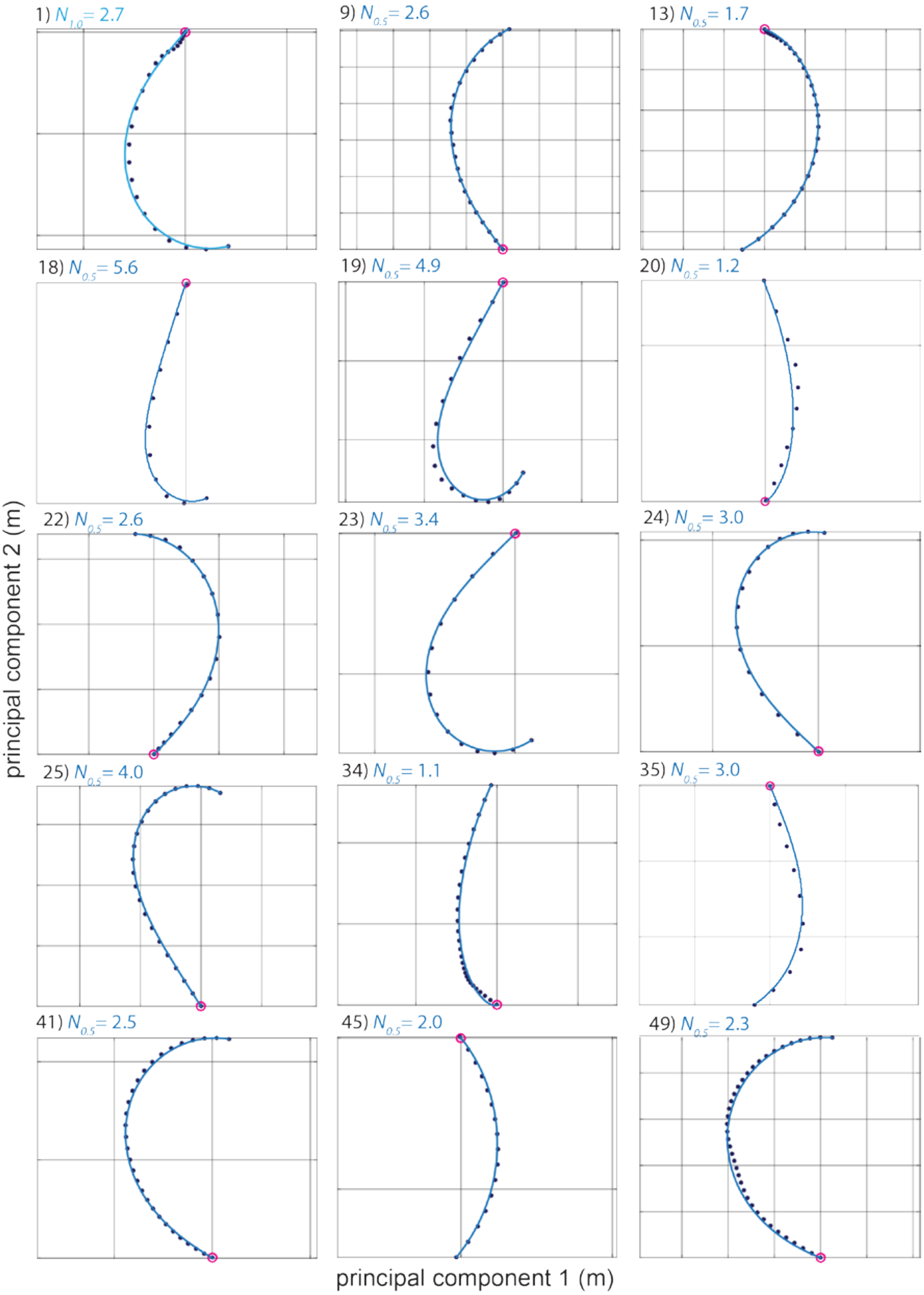


Figure 29: Graphs comparing principal component 1 and principal component 2 from the measured trajectories (blue points) with the trajectory predicted under the best-fitting proportional navigation strategy for a prediction error of 0.5% (blue lines; NB flight 1 = 1% error as 0.5% did not meet simulation criteria) for the fifteen flights to target from figure 23. Grid lines denote 10m intervals. Similarity of PCA N values for all flights can be compared to our horizontal trajectory analysis in table 3.

Discussion

Overall, we show that peregrines behave as if implementing proportional navigation when intercepting stationary ground targets. Hypothetical proportional navigation pursuit curves were generated simply from the initial velocity vector of the bird. This method greatly reduces the noise in fitting the navigation constant, as it is performed on position data rather than quantities obtained by numerical differencing. The closeness of fit to the actual trajectories (Figs. 23,24) indicates that the measured trajectories match precisely the family of curves that would be expected under a proportional navigation strategy, and also show some potentially interesting variation in the best-fitting value of N across flights, suggesting the peregrines may be adapting their navigation constant. Many advanced missile guidance systems use a form of augmented proportional navigation, in which the value of N is effectively updated in light of information about the target to give the best performance against some criterion such as time to intercept[146, 147, 150]. We hypothesise that variation in N may be similarly adaptive in peregrines, but a formal test of this hypothesis must await equivalent data from manoeuvring targets.

From our GPS data we found the maximum flight speed during an attack flight to the lure to be 71km/h – significantly lower than proposed by other research[11]. However, this only corresponds to the final phase before interception, when our birds had lowered their speed or levelled out their flight path before impact, to reduce the likelihood for injury. At extreme speeds, birds would have to begin at a greater distance and be able to end a stoop with sufficient clearance from the ground, and thus wild peregrines do indeed level out their flight in the final stages in order to reduce speed on impact[24, 27, 31]. We chose to model only the final phase of each attack pass, since we cannot know when the peregrines initiate target-directed flight behaviour. If we fitted our simulations over longer periods, when the birds were not locked on to the target, this would likely result in a poor fit of our proportional navigation trajectories. We therefore chose to prioritise the closeness of fit between our flight data and our simulated trajectories by using time periods working backwards from interception, where the mean distance error was below a threshold and where we could be relatively confident the birds were exhibiting targeting behaviours.

The level of motivation of peregrines during a hunt is said to be of critical importance[27, 34], therefore since our birds were always flown when hungry and chased the lures under the expectation of food, we can assume they were sufficiently motivated. In addition, the distance of our attack flights were very variable, but this is consistent with the literature which quotes anything up to 800m, with 40% of hunts initiated at less than 100m[26]. We did not observe any head-on intercepts of our aerial targets. Wild peregrines are also likely to avoid this behaviour, due to higher risks of injury, and accordingly we find no reports of head-on prey strikes in the literature.

Previous biological research has focused upon identifying simple geometric rules describing pursuit trajectories or gaze directions. Our trajectory data rule out the use of a single geometric rule in peregrines, but are consistent with the use of a single guidance law that is capable of implementing any of the geometric rules that have been considered by biologists to date. Simple geometric rules, such as pure pursuit, deviated pursuit and parallel navigation, are best understood as emergent properties of an underlying guidance law. Proportional navigation implements all of these geometrical rules and therefore has the potential to provide a unifying mechanism for all the predatory pursuit behaviours described to date. Peregrines appear to use proportional navigation as their guidance law, and future research should aim to identify how widely this is used in other animals.

Chapter 4:

Air-to-air attacks in peregrine falcons

Abstract

Here we show Peregrine falcon (*Falco peregrinus*) target-interception trajectories against manoeuvring aerial targets, recorded by on-board instruments, match the trajectories predicted for the guidance law of proportional navigation, with an adaptive variable navigation constant. This is the same result as was found with our stationary ground targets, suggesting a blanket attack strategy in peregrine falcons across different target types. However, due to GPS error, after applying our strict quality control on the data our sample size was very small, thus more flight experiments are required before we can consolidate our findings.

We also analysed our on-board video data from the birds - for attacks against stationary targets on the ground (from chapter 3) and moving targets in the air (this chapter) to show that the behaviours we recorded were ecologically relevant. In a final step, we used the on-board video data to examine the 14 incidental flights made at real prey. This is important because we lack GPS position data for these live targets, thus the on-board video data provide us with a unique opportunity to explore the guidance of attacks on live targets and also allows us to validate our conclusions from the GPS analyses.

Introduction

Peregrine falcons regularly take prey that is flying in the air[27, 37], and so as a follow on from the previous work involving stationary targets on the ground, we aimed to replicate attack flights against manoeuvring aerial targets. Our goal was to confirm our findings from the work with stationary targets - that peregrines use the guidance law of proportional navigation for pursuing prey - but in a dynamic context. We therefore used the same model from Chapter 3 - adapted for a moving target - to simulate proportional navigation trajectories on the flight data.

We then conducted a qualitative analysis of hunting behaviour from our on-board video data, in order to compare the behaviours we recorded against those described in the literature for wild peregrines. Although peregrines are popularly renowned for their high-speed, near-vertical stoops, this is by no means their dominant hunting behaviour in all environments. For example, when foraging over open habitats such as flooded fields [37-39], estuaries [26] or the open sea [35], a large proportion – or even a majority – of peregrine attacks involve low-level chases at perched, sitting, or swimming prey [22, 23, 26, 35, 37-39]. In general, peregrines adopt a suite of different hunting behaviours depending on many factors[27, 31, 34], and our video data reveal a similarly flexible range of hunting behaviour (Table 2).

Two recent studies used on-board video to test whether falcons [12] and hawks [145] use any of the three geometric rules described in Chapter 1 when attacking stationary and manoeuvring targets[12, 145]. The methodology of these studies is questionable, but they conclude that the birds make use of parallel navigation (called CATD in these papers). Therefore in a last step, we used our peregrine flights made at live prey to test whether the line-of-sight to target was kept on a constant compass bearing. The method of analysis that we used relied upon a comparison of the position of the target with the position of distant background features, and did not therefore suffer from the problems associated with the video analysis in Kane and Zamani (2014)[12]; see Chapter 1. Since parallel navigation can be implemented by proportional navigation, finding evidence for a constant line-of-sight bearing provides further support for our previous findings in Chapter 3 - that peregrines pursue their prey using proportional navigation.

All the methods and procedures are detailed below, followed by an explanation and discussion of the results.

Materials and methods

Animals

Two trained, captive-bred peregrine falcons (“Lizzie”: ♀; “Isabel”: ♀) were flown at a target towed behind a remotely piloted aircraft, giving 14 test flights in total.

Experimental protocol

All flight tests were carried out in various countryside locations in Monmouthshire (Wales, UK), chosen according to local wind conditions. Each of the peregrines carried a GPS receiver logging position and groundspeed at 5Hz (Qstarz BT-Q1300) and a high-definition video camera looking forward over the head (HD720P Mini DV, 30fps, resolution: 1280 x 720 pixels). The equipment weighed 0.031kg in total, and was carried dorsally on a commercially available harness (Marshall Radio Telemetry, Trackpack) comprising a curved plastic mounting plate held in place between the shoulders by a pair of flat tubular Teflon ribbons drawn once around the bird's body in a figure-of-eight pattern. The equipment weighed 0.031kg, representing less than 5% of the bird's body weight, as required by our ethically-approved protocol. Each bird also carried a tail-mounted radio transmitter for tracking purposes (Marshall Radio Telemetry Micro Transmitter). The bird was filmed from the ground by two JVC GC-PX100 HD video cameras mounted on tripods spaced approximately 20m apart. The cameras were zoomed out so as to cover as much of the test volume as possible, and were set in a convergent configuration so that their fields of view overlapped. The positions of the two cameras were recorded by leaving a GPS unit stationary on the camera, and all of the cameras were synchronised using a digital stopwatch display.

The target – a leather falconer's lure with food reward attached – was towed by a small remotely piloted aircraft on *c.* 5m of kite line attached to the aircraft's tail boom (Fig.30). A Qstarz BT-Q1300 GPS logger was attached to the airplane close to the centre of mass, and an HD720P Mini DV camera was fixed beneath the aircraft so that it faced backwards towards the towed lure. A third Qstarz BT-Q1300 GPS logger was attached directly to the lure. The bird was released by the falconer at the start of each flight test, and was allowed to gain height. The aircraft was then launched and operated by a pilot on the ground. On windy days, the plane and lure were launched while the bird remained hooded, to encourage an attack upon first sight of the target and to reduce the risk of the bird flying off. The birds chased the target as it swung behind the aircraft, which was flown through a series of manoeuvres by the pilot. As a safety precaution, the lure was released from the aircraft as soon as the bird had made contact with it.

Data synchronization

We plotted the groundspeed of the bird GPS data and used this to establish the start and endpoints of the bird's flight trajectory. We checked the duration of the flight against the ground-based video recordings. We then identified the time the bird intercepted the lure from the on-board plane camera footage (the moment of intercept was easier to see from this view than from the bird mounted camera view), and also the take-off time of the plane. The duration between these two points allowed us to locate the point of interception from the plane GPS, after multiplying by 5 to convert the time in seconds to GPS samples (logging at 5Hz). Therefore using the plane GPS timestamp data we could then match this to the timestamps from our bird and lure GPS data to identify their corresponding positions at intercept. Occasionally the GPS data streams would drop points, affecting the alignment of our data streams, thus we also checked for missing data points and where applicable, interpolated these points to ensure that the bird and lure trajectories were exactly matched in time.

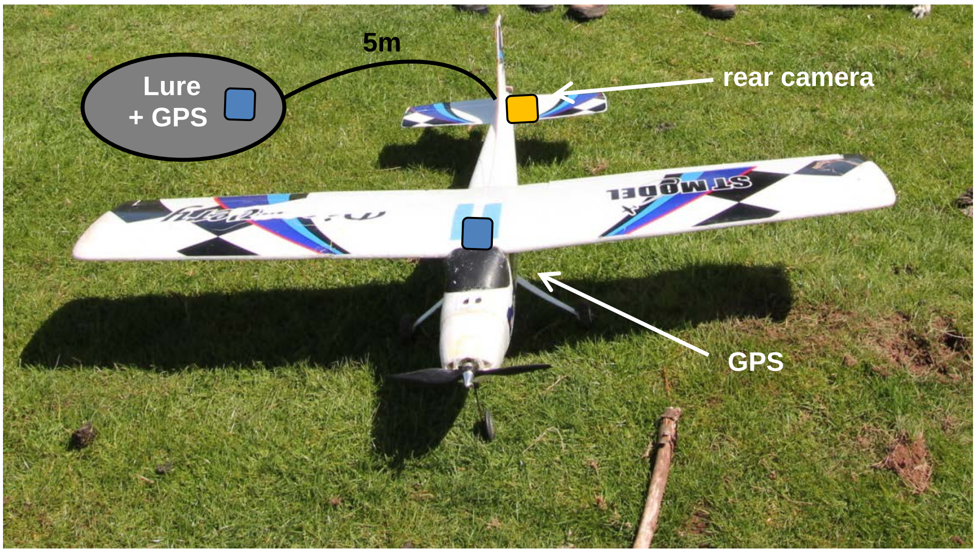


Figure 30: The remote controlled airplane used in the experiments, showing positions of the GPS units and cameras, and attachment point of the lure line.

Video analysis of attack behaviours

Although we did not set out to test this specifically, we expected the hunting mode to differ between target types, since our stationary lures represented predictable targets, and our aerial lures were highly unpredictable - in agreement with the literature which states that target behaviour does indeed influence hunting behaviours[27, 31, 34]. We therefore identified a number of distinct hunting modes in flights against stationary targets and in flights against aerial targets.

Flights to stationary targets

We used the on-board camera footage, together with the GPS data from chapter 2, and identified 6 different attack methods (Figs.31-33):

- *SHALLOW STOOP*: Initiated from a soaring position, beginning with a sudden increase in speed, then a slight steepening of the dive path (with an angle less than 45° approximately), followed by a curved or straight plunge to the target.
- *STEEP STOOP*: The same as a shallow stoop only with a steeper dive path with an angle greater than 45° approximately (Fig.31).
- *LEVEL FLAPPING FLIGHT*: A long, straight, flapping flight just above ground level, where the distance travelled is greater than 100m (low overall gradient; Fig.32).
- *TURNING SWOOP*: A fast arced or hairpin turn with both flapping and gliding flight. Generally low to the ground and close to the target. Usually follows an initial contact and can be aimed either upwards or downwards at prey (Fig.33).
- *STILL HUNTING*: Consisted of taking off from a stationary or perched position and flying directly to the target on a straight and horizontal flight path.
- *GROUND PURSUIT*: Searching and flushing prey from the ground, on foot.

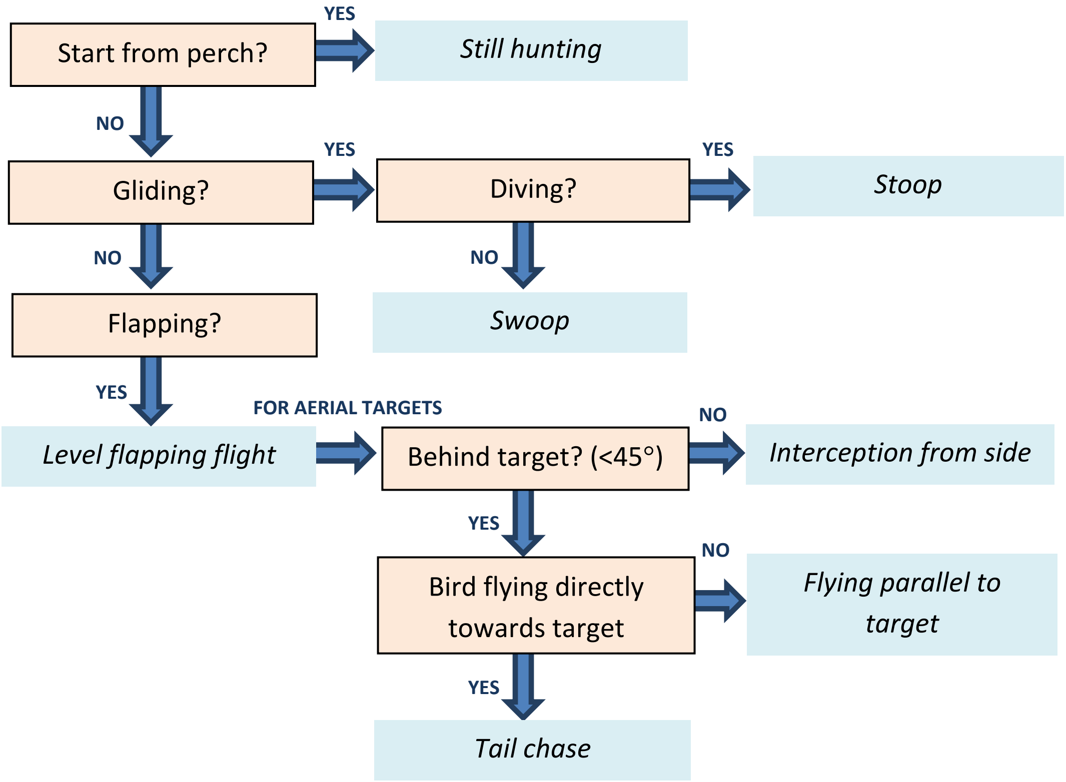
Flights to aerial targets

We used the footage from on-board the bird, supplemented by the on-board footage from the remote controlled airplane, and identified 4 attack methods associated to those from the stationary target flights (Figs.31-36):

- *STOOP:* Sudden increase in speed, then a steepening of the dive path, followed by a plunge to the target (Fig.31).
- *LEVEL FLAPPING FLIGHT* - Three sub-categories:
    - *Tail chase:* Long chase from behind the target aiming directly at it (Fig.34).
    - *Interception from side*: Flapping flight aiming from the side to head off the target, the flight path is usually approximately perpendicular (90°) to the target (Fig.35).
    - *Flying parallel to target*: Not flying directly at the lure but approximately parallel to its flight path, while decreasing the distance (Fig.36).

Dichotomous tree

Below is our dichotomous decision tree used for categorising the flights. We also provide a series of visual aids - in the form of stills from the videos - showing examples of each type of interception, in figures 31 to 36.



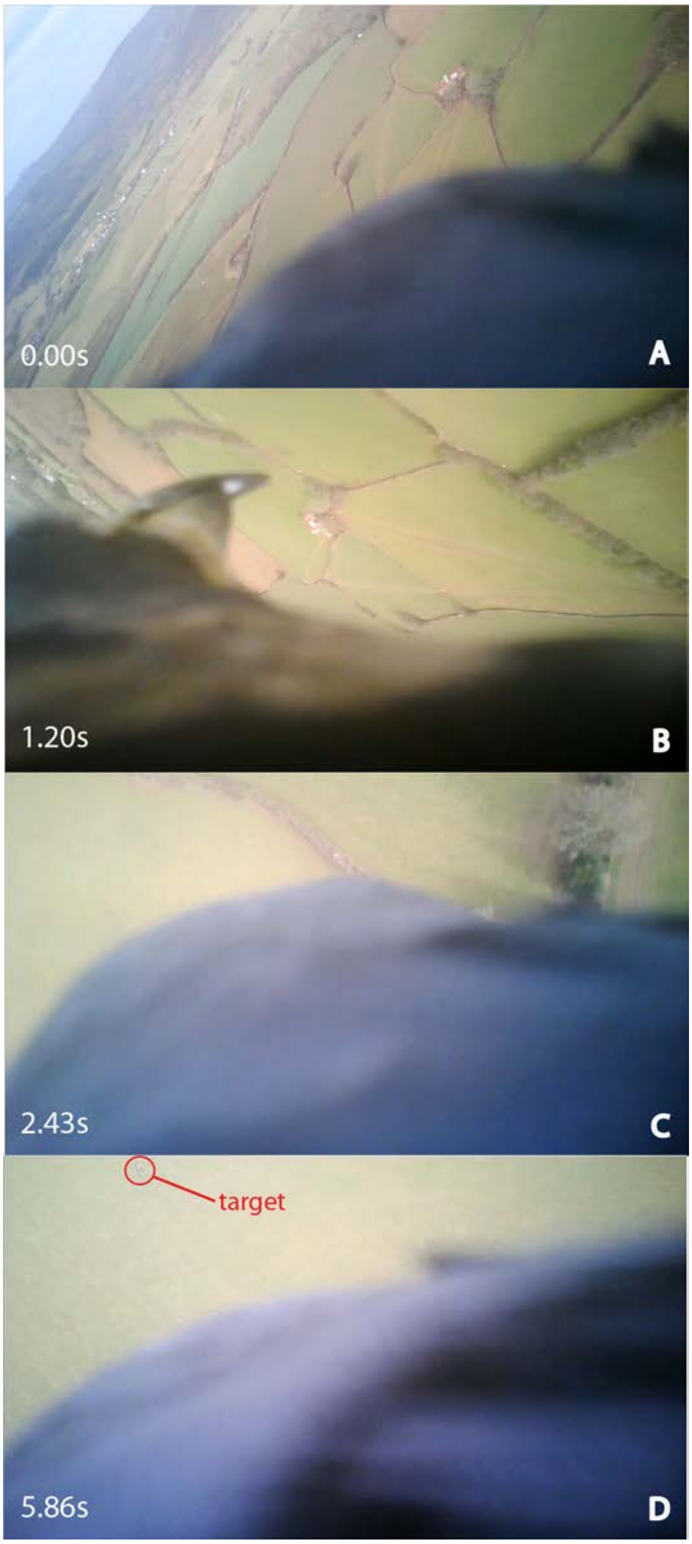


Figure 31: Example ‘stoop’: Video stills from the camera on-board the peregrine showing A) moment before the stoop is initiated; B) mid-turn as the bird tilts its body downwards; C) start of the dive – the bird is facing the ground; D) mid-dive - the bird begins to level out the stoop when approaching the falconer (red circle). Note the extreme banking (A) and resulting inversion (B) of the peregrine as it initiates the stoop.

Figure 32: Example ‘level flapping flight’: Video stills from the camera on-board the peregrine showing A-B) low and straight approach to target (red circle) from a long distance; C) closing in. The target is always approximately straight ahead of the bird (allowing for errors caused by movement of the camera), and the overall gradient of the flight is very low.

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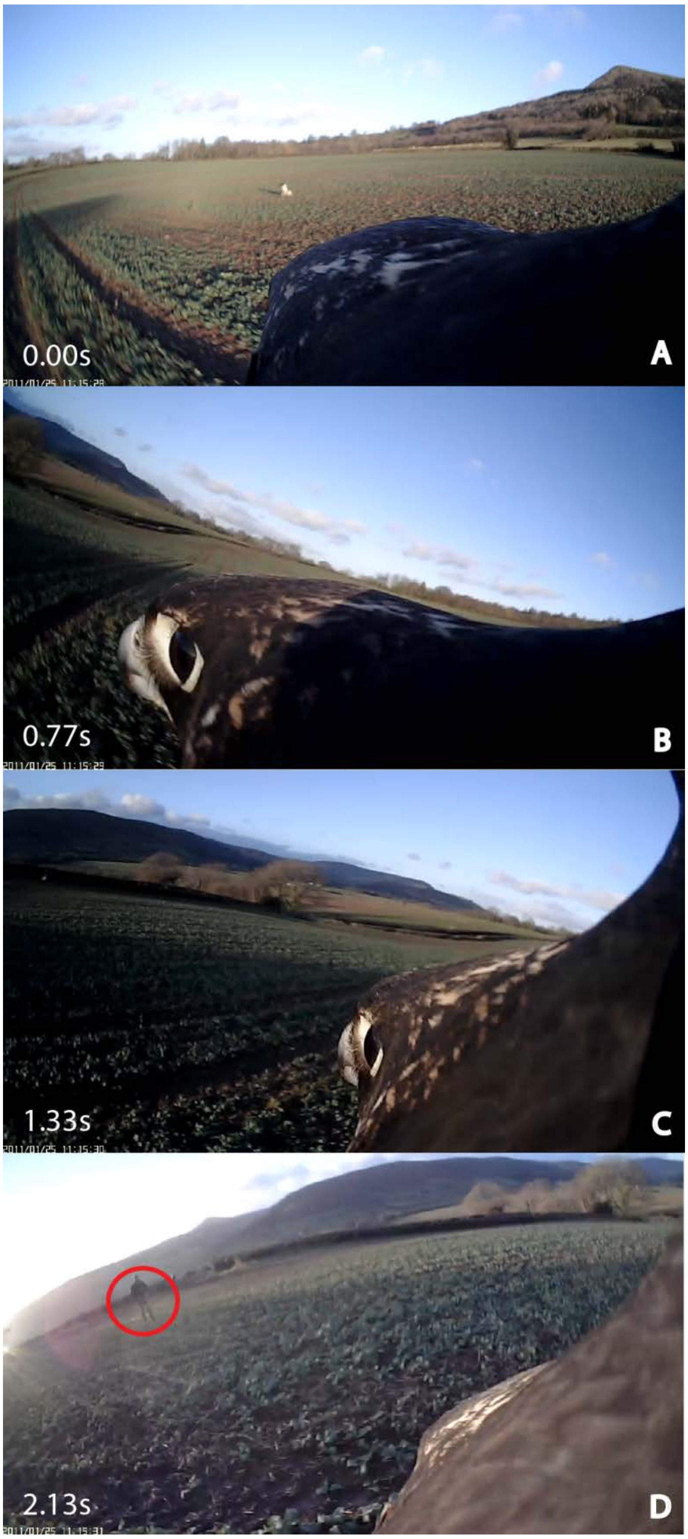


Figure 33: Example 'turning swoop': Video stills from the camera on-board the peregrine showing A) just before initiation of turn; B-C) turning to the left in a large arc; D) straightening up before interception – the target is being held by the falconer (red circle). Note that although the peregrine's wings and body are banked strongly to the left during the swoop (B-D), the peregrine's head is stabilized about the roll axis so that it is kept approximately level with the horizon at all times. Note also that the head is yawed into the turn at the initiation of the swoop (B), but yaws back towards the centreline of the bird's body during the swoop, as the direction of gaze is held approximately constant against the background (B-D).

Figure 34: Example ‘tail chase’: Video stills from the camera on-board the plane showing A-C) the bird (blue circle) following behind the lure (red circle); D) interception. The bird is always heading in approximately the same direction as the lure, shown by the arrows.

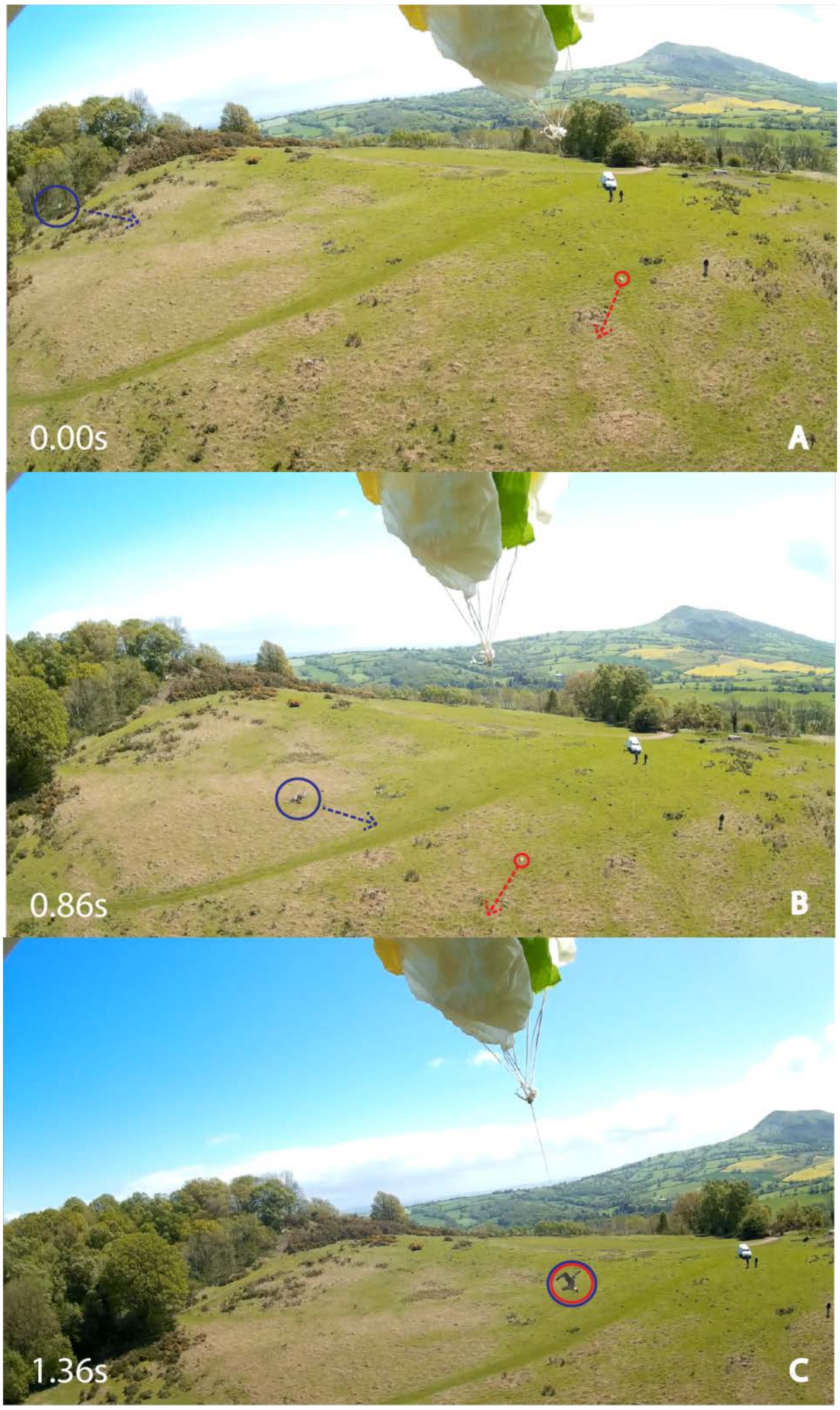


Figure 35: Example ‘interception from side’: Video stills from the camera on-board the plane showing A-B) the bird (blue circle) closing in on the lure (red circle) from the side; C) interception. The bird is always heading in a different direction to the lure and its approach is approximately perpendicular, shown by the arrows.

Figure 36: Example ‘flying parallel to target’: Video stills from the camera on-board the peregrine for a flight against a mallard duck showing A-B) the bird flying approximately parallel to the flight path of the target (the bird is heading in approximately the same direction as the lure but offset to the side, shown by the arrows); C-D) the bird closing in on the target whilst still flying alongside it. Flight directions are estimated from the video sequence.

Flights against real prey

During our experiments, the peregrines made several passes at real prey (mallard, *Anas platyrhynchos*; red-legged partridge, *Alectoris rufa;* common buzzard, *Buteo buteo* – likely to be a territorial rather than predatory interaction*;* carrion crow, *Corvus corone;* jackdaw*, Corvus monedula*; wood pigeon, *Columba palumbus*) encountered incidentally during a flight (though none were harmed). We used the onboard video data from these flights to test for the geometric rule of parallel navigation, by determining whether the line-of-sight angle λ was constant. This was straightforward to do using onboard video data with a suitably distant background, because the camera's displacement between frames will have a negligible effect on the absolute bearing of points on the distant background. Hence, if the target appears stationary with respect to the distant background, then its line-of-sight angle λ must also be constant, and in this case the bird must be achieving parallel navigation. Since the relevant frame of reference here is the distant background, rather than the camera, the same litmus test can be applied even if the camera is rotating. We applied this test for the final seconds of each attack sequence, from where the target came into view.

We could not perform the analysis in this way on our artificial-target data, since against a stationary target, a parallel navigation is equivalent to a pure pursuit (the bird would be flying a straight course directly to the target) and in our aerial-target experiments the background was not deemed suitable.

Results

Plotting the flight trajectories

A total of 14 successful intercepts were achieved between the two birds (8 flights from "Isabel"; 6 flights from "Lizzy"). Figure 37 plots the latitude and longitude measurements from the GPS units carried by the bird, aircraft, and the lure for all 14 flights, using a mapping specific to the local area, for the last 10 seconds before intercept. Due to differences in absolute positional accuracy between GPS devices (see chapter 4), it is necessary to adjust the relative position of the GPS tracks separately so that the trajectories of the bird and lure meet at the established point of intercept. There are obvious long sections of flight where the birds maintain a constant line-of-sight angle, shown by the parallel lines-of-sight between the bird and target, and very clear switches in the angle-bearing where the bird passes the lure (e.g. Fig.37, flights 2, 6). Many of the flights also show non-parallel sections.

Quality control procedure

We then calculated the distance error, at intercept, between the raw bird and lure trajectories and to our surprise found that many flights had a large discrepancy in absolute position (table 2). We plotted the raw GPS trajectories of the bird, lure and plane in ArcGIS, to demonstrate that it seems to be the GPS carried by the bird causing the problems, as the plane and lure tracks look sensible (within reasonable distance of each other; see images below). However, although the accuracy of the bird flights may be suspect - in terms of position in space - they may still be precise in terms of shape, at least for the short sections of flight we are interested in (as shown by our roundabout GPS tests in chapter 4). In order to exclude all flights for which we cannot be certain of the precision, we then applied our quality control criteria by measuring the discrepancy between the GPS Doppler speed and the speed derived from the differenced position. Our exclusion thresholds were rather strict (see chapter 4), and so out of the 14 flights a total of 8 passed our speed discrepancy thresholds (marked by a ‘*’ in Fig.37). We then validated these 8 flights against the video data, by checking the compass direction and orientation of attack sequences from the video footage, against the GPS data plotted on aerial photographs of the Earth in ArcGIS. Subsequently, we concluded that in only 2 flights can we be sufficiently confident that the shape of the GPS trajectory matches what happens in the video sequence (marked with a ‘**’ in Fig.37). For the remaining flights, we cannot be certain that the shapes of the trajectories are correct, since it is possible that when the bird banks the patch antenna may drop satellites thereby causing sudden shifts and shape changes in the position data. Therefore we err on the side of caution and conduct no further analysis on these flights.

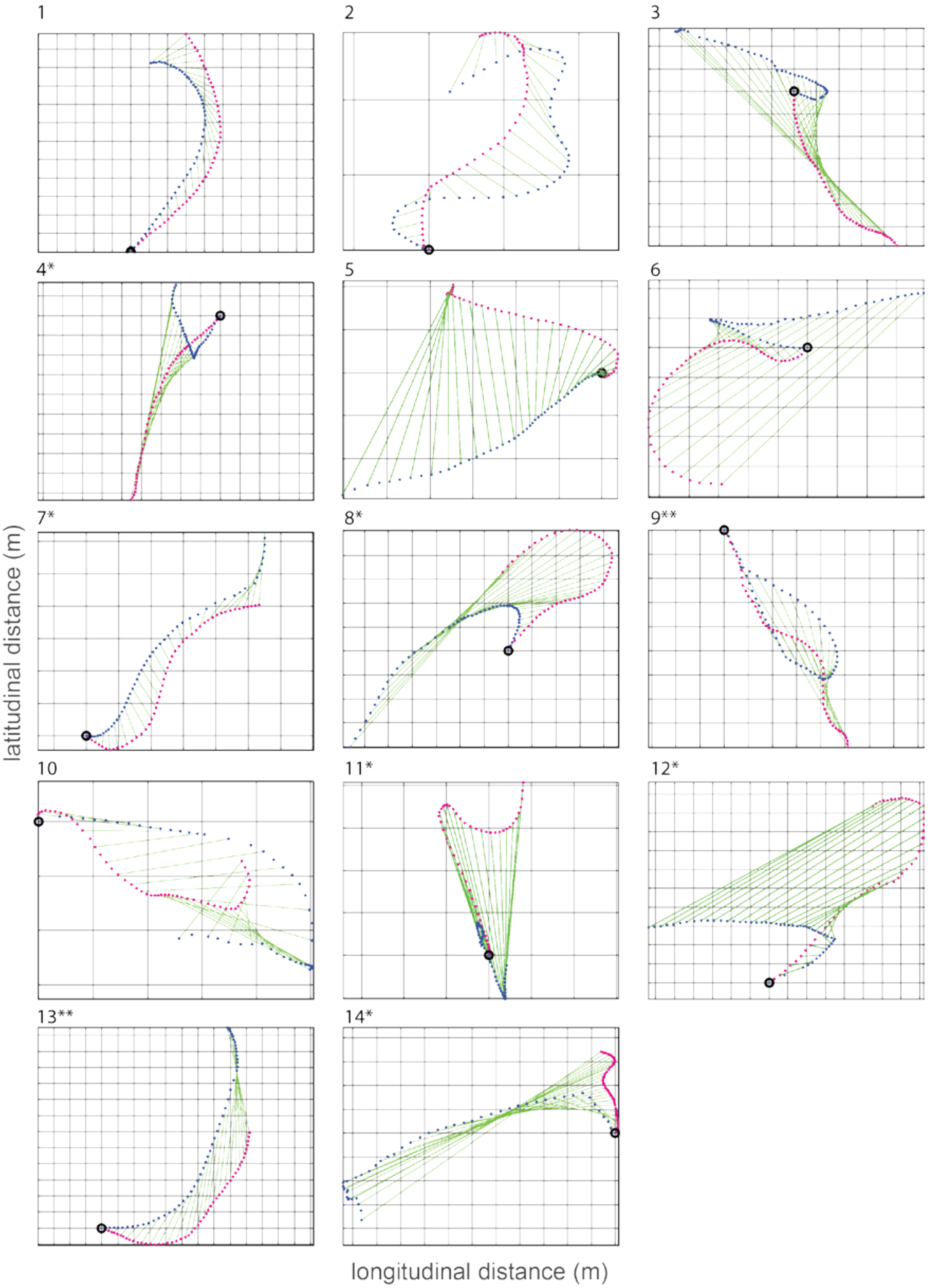
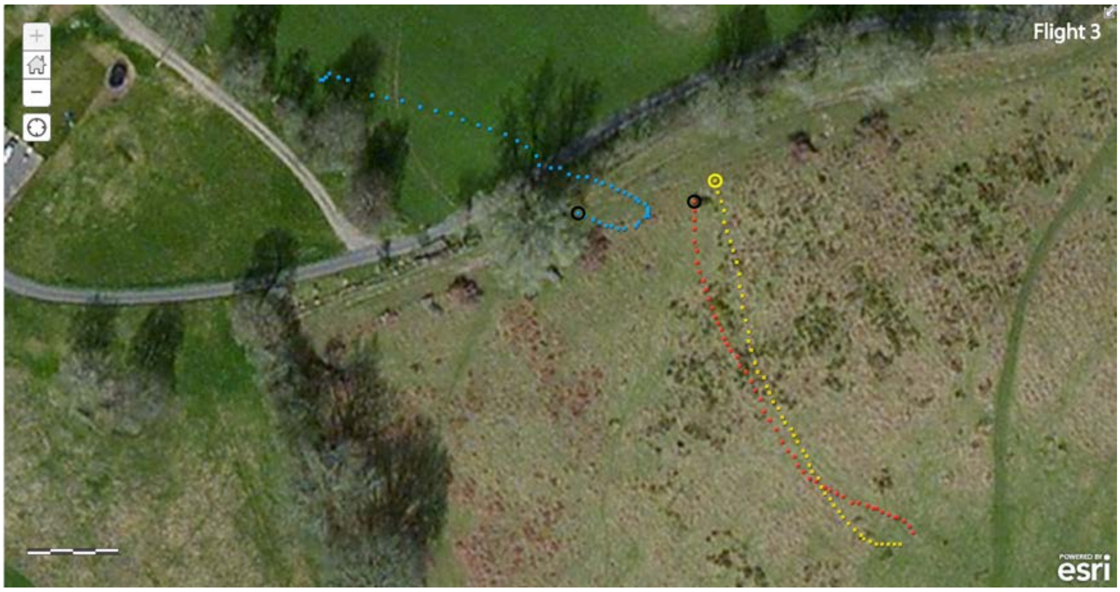


Figure 37: Raw GPS trajectory plots of final stage air-to-air attacks by two peregrines (blue points: Bird I = 1 – 8; Bird L = 9 -14) against a lure (magenta) towed behind a remotely piloted air vehicle (not shown), for the last section 10 seconds of flight before intercept. A '*' denotes flights which passed on our GPS speed quality control criteria (described in the text) and failed on accuracy judged from the video, but may still be precise, and a '**' denotes flights which passed on both counts. The instantaneous lines-of-sight between bird and lure are shown in green. Grid lines denote 10m intervals. Absolute positional error in the GPS has been corrected by aligning the trajectories with regards to the interception point (black circle).

The following 14 images show the bird (blue), lure (red) and plane (yellow) raw GPS data for the last 10s before interception for all peregrine flights against aerial targets, highlighting the position discrepancy between GPS devices. The black circle identifies the point of interception where the bird and lure are together (in reality), and the yellow circle shows the corresponding position of the plane at this time (should have been approximately 5m away from the towed lure). Flights 9 and 13 passed all our quality controls, and have very low position discrepancies at intercept.


Flight 3
esri


Flight 4
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Flight 5
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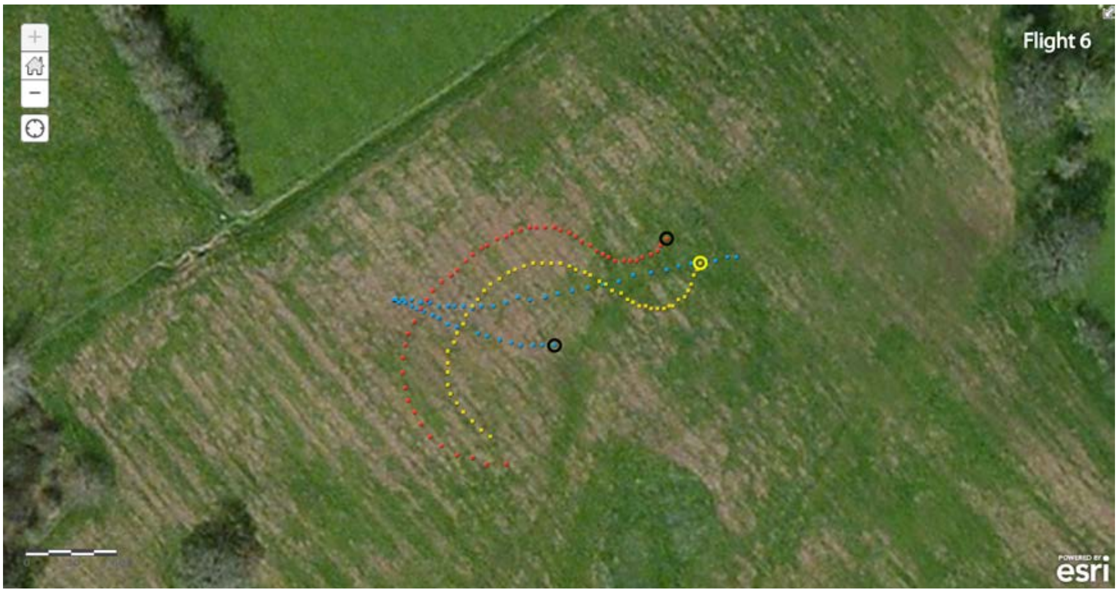
Flight 6
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Flight 7
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Flight 9
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Flight 10
0 100 200ft
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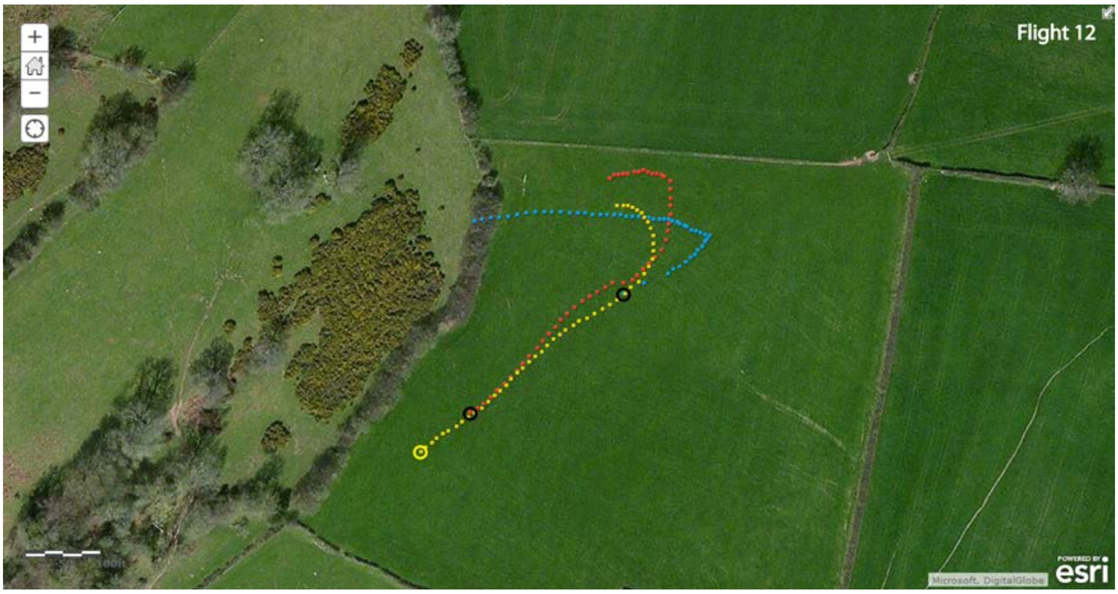
Flight 11


Flight 12
Microsoft, DigitalGlobe


Flight 13
esri


Flight 14
esri

Simulating proportional navigation trajectories

We modelled pure proportional navigation trajectories on our remaining data in two dimensions (latitude and longitude only), since GPS altitude measurements are highly unreliable, and it is possible the birds are implementing proportional navigation in the horizontal plane only. We use the same procedure as described in our work on stationary targets in chapter 3.

Figure 38 shows the actual bird and lure positions with simulated proportional navigation trajectories overlain from t_0 to interception, for 3 different starting positions defined as the mean relative L1-norm error thresholds of 0.5%, 1% and 2% (see chapter 5 for a full explanation of the simulations). To ensure our simulations were physically valid, they were stopped at the point where the calculated acceleration exceeded 2.5g. This removed any highly erroneous simulations (e.g. where the simulation failed and plotted a straight line), and also avoided fitting the trajectory when very close to the lure (<0.2s) where the demanded acceleration tends towards infinity. In addition, we also excluded any fitted trajectories which were insignificant at the p<0.05 level and thus for which N values could not be reliably predicted (though we show these in our plots as dashed lines).

Overall, our simulated trajectories matched the measured data quite precisely for long flight sections. In order to quantify the closeness of fit, we calculated the correlation coefficients between the measured and simulated bird positions (table 5), for all error thresholds in the same way as for stationary targets (see Chapter 3), and found a high correlation between trajectories.

By extending the simulations further back along the bird’s trajectory we show that portions of the simulations fit well for different N values, suggesting that the birds may be changing the value of their navigation constant during their intercept flight. Peregrines may therefore have the ability to optimise their proportional navigation flight trajectory - and thus the value of the navigation constant - during the course of their pursuit, depending on prey behaviour, but a formal test of this hypothesis awaits more data.

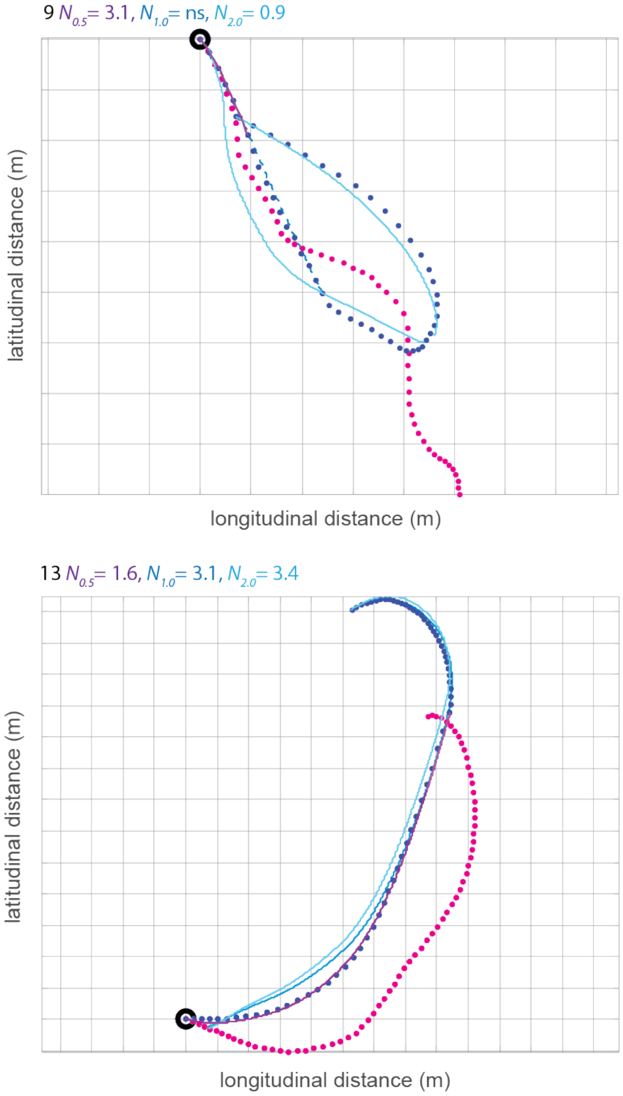


Figure 38: Proportional navigation simulations for our raw GPS trajectory plots of air-to-air attacks by a peregrine (blue points) against a lure (magenta) towed behind a remotely piloted air vehicle (not shown). We fitted 3 simulations for different starting positions, defined as mean relative L1-norm error thresholds of 0.5% (purple), 1.0% (mid-blue) and 2.0% (aqua-blue). Note the close match between the measured and simulated trajectories. Dashed trajectories indicate simulations which were non-significant and so N values could not be reliably predicted. Grid lines denote 10m intervals.

Bird	Flight	N 0.5% error	COEFF 0.5% error	N 1.0% error	COEFF 1.0% error	N 2.0% error	COEFF 2.0% error	Absolute discrepancy (m)
L	9	3.1	0.90	x	0.91	1.0	0.79	5
L	13	1.6	0.77	3.1	0.93	3.4	0.94	9

Table 5: N values and correlation coefficients computed from the proportional navigation simulations against aerial targets for each flight for each of our relative error thresholds (0.5%, 1.0% and 2.0%). An 'x' represents a simulation which was non-significant and so N values could not be reliably predicted (see chapter 5 for how $COEFF$ was calculated). We also show the absolute position error between the bird and lure at intercept.

Validating our observed behaviours

In total we analysed 93 attacks made at stationary targets and 35 attacks made at aerial targets. In our experiments against stationary targets, the peregrines usually intercepted the target while it was on the ground, or sometimes as it was thrown in the air by the falconer, often followed by multiple swoops when it was on the ground, before finally landing on it. In our experiments against aerial targets, the birds either bound to the target in the air and dragged it towards the ground, or hit the target and let go, subsequently following it to the ground. Our video data reveal a flexible range of hunting behaviours. The totals of each attack type for our two experiments are shown in table 6.

Type of attack	Stationary target (predictable)	Percentage	
Shallow stoop	12	13	19
Steep stoop	6	7	
Level flapping flight	11	12	
Turning swoop	53	57	
Still hunting	10	11	
Ground pursuit	1	1	
	Aerial target (unpredictable)	Percentage	
Stoop	1	3	
Tail chase	15	43	
Interception from side	13	37	
Flying parallel to target	6	17	

Table 6: Classification of peregrine attack flights, against stationary ground targets and moving aerial targets, from our on-board camera data. Birds used in the stationary target experiments were 1 adult and 2 first year birds, and in the aerial target case were 2 adults.

Stationary targets

A typical attack flight to stationary targets consisted of a longer approach phase - using either stooping or level flapping flight - and a shorter flap-glide swooping flight after an initial hit of the target. Turning swoops were by far the most common flight strategy, but this simply reflects the fact that birds were performing multiple passes at the target on any test day. If we calculate the proportion of stoops and horizontal flights in relation to the number of *first* target intercepts on each test day (total of 42), they occur in 42.9% and 23.8% of flights respectively - a more accurate representation.

The stooping technique, whether vertical, oblique or flat, is said to only be used in a third of attacks in wild peregrines[26], which is slightly lower than our findings. Out of the 42 initial intercepts, near-vertical stoops were only performed in 2 flights (4.8%) but steeper angles of more than 45° were observed in 14.3% of flights. The most frequent stoop angle was much shallower at less than 45°, in 28.6% of flights. This is consistent with the literature, stating that the most common flight angle of peregrines is in the range of 30-45° or less, with vertical stoops being the exception rather than the rule[21, 23, 31, 33].

A high proportion of flights in wild peregrines involve multiple swoops onto prey that is on the ground or water surface[20, 26, 27, 34, 36, 37], analogous to the multiple pass behaviours we observed after initial interception of stationary targets. We also observed that when performing a swooping turn, birds would straighten their flight path before making contact with the target. This is in agreement with research by Tucker *et al* which stated that as the distance to the prey is closed, peregrines will divert from a curved path onto a straight and direct path[10].

Against stationary targets, we also observed many intercept flights initiated from a perch*,* known as still-hunting. This is reported to be widely used by wild peregrines, where they keep watch from a suitable perch and launch a surprise attack on passing prey [34]. In addition, one of our on-board videos provided evidence for the use of ground pursuit in peregrines, showing the peregrine on the ground actively searching and attempting (unsuccessfully) to flush a prey animal from a tree hollow.

Aerial targets

A typical attack flight to aerial targets involved following from a distance, before closing in to the target either from behind or from the side, often with a rapid pitch up at the point of interception. Level flapping flight was the most commonly observed strategy, and when separated into its different categories, the peregrines most often approached the target from behind in a tail chase (43%). We also observed the birds coming in at an angle either side of the target in many flights (37%). This is in agreement with Tucker *et al* who stated that when a peregrine initiates a hunt it will fly a curved path in order to intercept prey at an angle, instead of aiming directly towards it[10]. In the remaining flapping flights the birds appeared to fly parallel to the target's flight path - rather than aiming directly at it - before closing in it (17%).

Unlike flights against stationary targets, only 1 stoop out of 35 flights was observed in our flights against aerial targets, and this occurred in a chase against a wood pigeon *Columba palumbus* which was flying low and straight over the ground. No stoops were observed against our artificial aerial target, but we biased this result by putting the plane up *before* the bird in windy weather. Swooping behaviours were only observed once the target had reached the ground, subsequent to the peregrine dropping it.

Visual pursuit

We used our video data of peregrine flights made at live prey to test whether the line-of-sight to target was kept on a constant compass bearing, and therefore provide further support that peregrines pursue their prey using proportional navigation. It is important to note that constancy of target position relative to the distant background does not imply that the pursuer is making use of background features to position itself relative to its target, although this is one mechanism by which parallel navigation could be achieved.

The peregrines used a comparable range of attack behaviours when flying at real prey as when flying at our artificial targets - comprising stoops, swoops and flapping flight. Of the 14 hunting bouts we observed against real prey, we were only able to qualitatively assess the LOS angle against suitably distant features in the background in 5 hunts (Figure 39-43). Our analysis of the onboard video data indicates that the line of sight drifted by ≤ 3˚ over the last 1s of each of the 5 attacks, and typically drifted by less than half this amount (Figs. 39-43). This statistic is consistent with something close to parallel navigation occurring during the terminal phase of an attack, but it illustrates the fundamental problem inherent in the traditional approach of looking for geometric invariants in the attack behaviours of animals: *viz*. that their geometry is never truly invariant, so that we are always left with an arbitrary choice as to whether we regard it as being approximately so. Moreover, in the 3 cases for which we could track the target further back in time (Figs. 39, 41, 43), it is clear that the line-of-sight angle was not always held constant during the earlier phases of the chase. This therefore highlights a major problem in the previous work by Kane and Zamani (2014) and Kane *et al* (2015)[12, 145] who use a subjective approach when proclaiming the use of parallel navigation.

Our video data also reveals that peregrines use a different visual strategy than that proposed by Tucker [10, 11]. This earlier work stated that a peregrine would keep its head in line with its body at all times for streamlining, and would turn so as to fixate its target in the left or right lateral field of view for the duration of a hunt, only switching to the frontal fovea when within a few metres of the prey. We found evidence that the birds were only using their forward facing fovea during pursuit flights, as found in other previous studies of hunting hawks and falcons[12, 145]. The peregrines were always facing the target during all phases of their approach, thereby fixating the target's image upon their forward facing temporal fovea. Our video data suggests that the birds stabilise their gaze against the visual scene and use fast saccadic head movements to keep the image of the target within their frontal field of view.

Figure 39: Video stills from the camera on-board the peregrine during a hunt against a natural target (common buzzard; circled in yellow). The constancy of the peregrines line-of-sight bearing to the buzzard can be judged by looking at how well the buzzard's position is maintained within reference window (transparent circles) over time. The centre of the reference window is positioned on the same point in the distant background in all frames, with the smaller circle having a radius equivalent to 3° and the larger equivalent to 5°.

Figure 40: Video stills from the camera on-board the peregrine during a hunt against a natural target (carrion crow; circled in yellow). The constancy of the peregrines line-of-sight bearing to the buzzard can be judged by looking at how well the buzzard's position is maintained within reference window (transparent circles) over time. The centre of the reference window is positioned on the same point in the distant background in all frames, with the smaller circle having a radius equivalent to 3° and the larger equivalent to 5°.

Figure 41: Video stills from the camera on-board the peregrine during a hunt against a natural target (carrion crow; circled in yellow). The constancy of the peregrines line-of-sight bearing to the buzzard can be judged by looking at how well the buzzard's position is maintained within reference window (transparent circles) over time. The centre of the reference window is positioned on the same point in the distant background in all frames, with the smaller circle having a radius equivalent to 3° and the larger equivalent to 5°.

Figure 42: Video stills from the camera on-board the peregrine during a hunt against a natural target (mallard duck; circled in yellow). The constancy of the peregrines line-of-sight bearing to the buzzard can be judged by looking at how well the buzzard's position is maintained within reference window (transparent circles) over time. The centre of the reference window is positioned on the same point in the distant background in all frames, with the smaller circle having a radius equivalent to 3° and the larger equivalent to 5°. As the duck was flying well below the horizon, in order for the reference window to be in a suitable position we identified two points on the background and drew overlapping arcs from each point (shown on figure; preserving the same radii across frames) – the point of overlap therefore represents the same point in each frame.

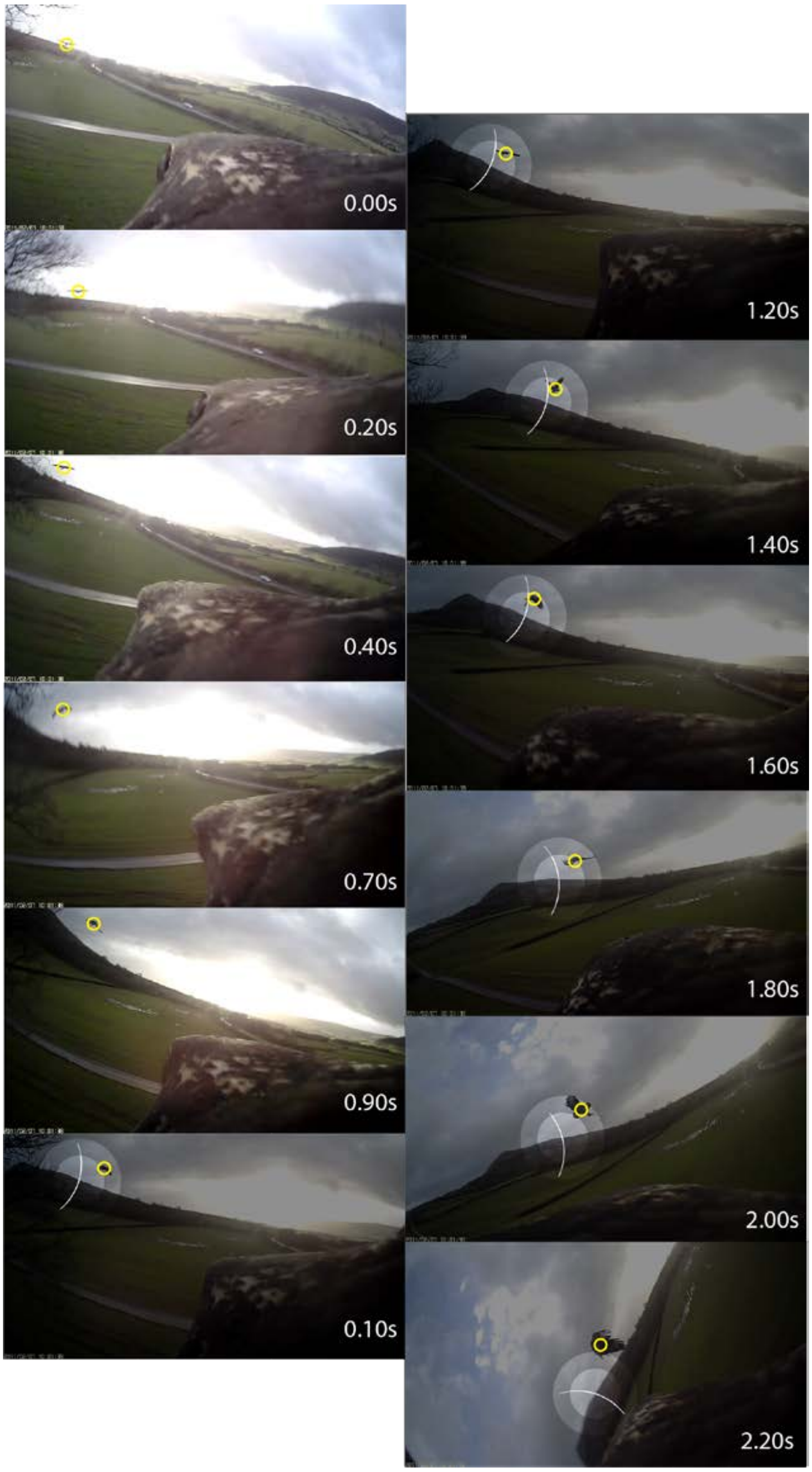


Figure 43: Video stills from the camera on-board the peregrine during a hunt against a natural target (common buzzard; circled in yellow). The constancy of the peregrines line-of-sight bearing to the buzzard can be judged by looking at how well the buzzard's position is maintained within reference window (transparent circles) over time. The centre of the reference window is positioned on the same point in the distant background in all frames, with the smaller circle having a radius equivalent to 3° and the larger equivalent to 5°. The most suitable reference point here was the top of the hill, and so in order for the reference window to be in a suitable position we drew an arc from this point (shown on figure; preserving the same radii across frames) – the point where the arc crosses the horizon line therefore represents the same point in each frame.

Discussion

GPS trajectory analysis

There were 6 additional flights which passed our speed discrepancy thresholds but failed on our accuracy analysis judged from the video, suggesting the GPS position data may have been valid for these flights but was simply not in the right place (i.e. the trajectory was the right shape but shifted in space). This shows how stringent we have been with our flight selection criteria, and that our remaining GPS data - though only consisting of 2 flights - provide reliable evidence for the use of proportional navigation in peregrines. They also show a further intriguing finding; that the birds may be changing the value of the navigation constant during their attack flight. We hypothesize that the peregrines may be optimizing their intercept trajectory against highly manoeuvring targets, in order to decrease the time to interception. Therefore, when faced with more erratically moving prey we expect the bird's to perform more switches of N value in accordance, resulting in a more unpredictable flight trajectory from the prey's perspective.

Concurrently, our line-of-sight plots demonstrate the use of parallel navigation - a geometric rule which can be implemented using proportional navigation[146]. However, we were unable to confirm this from the on-board video data due to excessive camera 'wobble' (very jerky images as a result of the flapping flight of the birds meant that the background was distorted or not suitable).

Nonetheless, this work did highlight several deficiencies in our model. For instance, the aerial target data was much noisier than the stationary target data, since in the latter, much of the noise associated with measuring the line-of-sight angle was eliminated. Furthermore, the bird was trying to keep up with the aerial target and so spent more time flapping rather than gliding. During gliding, the wing is fixed and so there is no active thrust production, thus flapping flight introduces many complications by the addition of a thrust component[16]. At present our model does not include any control laws from the wings and tail, and consequently the direction of the thrust vector during flapping is unknown. This may influence the shape of the bird's intercept trajectory and thus explain some of the observed differences between the actual data and our proportional navigation simulations. As a final test, we integrated a time delay into our simulations against aerial targets. We shifted the bird's position compared to that of the lure, in our aerial target data, by intervals of 0.07s up to 1 second, but found no convincing evidence for a delay in the system.

Further factors to consider are that the bird's visual system may have some kind of filtering mechanism whereby it does not respond to high frequency changes in the line-of-sight rate, however there is no evidence for this in our line-of-sight plots (Fig.37). Also, the altitude change may play a part, though modelling the trajectories in three-dimensions did not result in a better fit of the proportional navigation simulations. However, our model does not include a gravitational component, as it was designed for simulating horizontal movement where the effect of gravity and the potential energy of the bird do not change. Or perhaps the birds are using separate guidance strategies in the vertical and horizontal planes.

Lastly, our simulations modelled pure proportional navigation, which incorporates a pursuer velocity referenced system (acceleration of the bird is perpendicular to its velocity vector), but it is possible they may be using true proportional navigation, a line-of-sight referenced system (acceleration is perpendicular to the line-of-sight), or even some other variant[147, 185].

Ecological relevance of behaviours

Overall, peregrines make flexible use of a range of hunting modes, and change their hunting mode based on target behaviour. Against stationary ground targets our birds most frequently executed a stooping dive for the initial strike, followed by multiple swooping for prey retrieval. Against manoeuvring aerial targets birds most often performed direct level flapping flights from behind the target, followed by multiple swoops after the target had landed on the ground.

In wild peregrines, during aerial attacks on flying prey, they either bind to it in a hit-and-hold flight, or strike it and let it fall downwards in a hit-and-drop flight[20]. In the former, peregrines will often seize prey from underneath by performing a rapid pitch-up at the end[22, 36]. In the latter, the prey is recovered either in mid-air, on the ground[20, 24, 34]. We observed all these behaviours in our videos, suggesting our captive birds were not dissimilar to wild peregrines in their behaviour at the point of intercept. The frequency and necessity of recovering dropped aerial prey means interception of stationary targets is an important evolutionary behaviour, and may explain the high prevalence of the swooping turns that we observed in our birds. In addition, one study claims that the majority of prey is killed on or just above the ground, and not in mid-air[22]. Therefore wild peregrine falcons do regularly hunt prey that is stationary on the ground[20, 24, 34], and therefore our experimental design replicated ecologically relevant behaviours.

Further evidence for proportional navigation

Two studies have reported that falcons and hawks pursue prey by manoeuvring to maintain the prey's image at a constant visual angle (between the line-of-sight to target and bird's head axis), via parallel navigation[12, 145]. This is a geometric rule which may be implemented by proportional navigation[146].

We therefore used our video data of chases made at real prey to similarly test for the use of parallel navigation in our peregrines (our artificial-target data was unsuitable for this analysis). The method we used involved comparing the position of the target with the position of distant background features, and thus did not suffer from problems of camera unsteadiness. Surprisingly, this test was not applied systematically in the previous studies using onboard video, although the authors comment that their data "did not indicate that falcons kept the prey's image fixed with respect to distant objects" [12], in direct contradiction of the overall conclusion of their study.

Our video analysis provided support for the use of parallel navigation in peregrines - by means of an approximately constant LOS bearing. However, the period of time over which it was maintained was very brief (a few seconds at most) so it is unclear whether this was a deliberate hunting strategy, or an inadvertent result of closing in on another moving object. It should be noted that under the criteria defined by Kane *et al*[12, 145] our birds would be said to be using parallel navigation - which demonstrates the problems with their approach.

Overall, we show that a qualitative approach to examining pursuit behaviour - as in two recent papers[12, 145] – is very subjective and does not explain the overarching question of how peregrines implement their intercept flights. Nonetheless, the result of our video analysis does comply with the use of proportional navigation for describing our flight behaviours, and rules out the use of a single geometric rule. Definitive evidence for the use of proportional navigation in peregrines against aerial targets must therefore await further repeat flight experiments using GPS.

Chapter 5:

Air-to-ground attacks in Harris' hawks

Abstract

Here we show Harris’ hawk (*Parabuteo unicinctus*) target-interception trajectories against manoeuvring ground targets, recorded by high-speed ground photography, are consistent with a pure pursuit strategy. This is the easiest strategy to implement, as birds are simply required to respond to the instantaneous direction of the target, albeit with a slight reaction-time delay (measured as 0.19s), likely due to the time needed for visual processing, muscle activation, or dealing with unsteady aerodynamics. We found that birds consistently maintained a proportional relationship between their turn-rate and their line-of-sight-rate to target. This is equivalent to using the guidance law of proportional navigation with a navigation constant of $N = 1$ but does not necessarily mean that birds were implementing their pursuit using proportional navigation. The simpler strategy of a pure pursuit may be the best method for the short-range, surprise attacks performed by Harris’ hawks in the wild.

Introduction

Harris’ hawks most frequently take ground prey from a stationary vantage point[42, 52], whereas peregrines generally take ground or aerial prey when on the wing[20, 24, 34]. Though Accipitriformes (in which Harris’ hawks are found) and Falconiformes (which includes peregrines) share many characteristics, the orders diverged as early as the Telluraves (landbirds) clade, more than 60 million years ago[14]. Therefore, Harris’ hawks are completely separated from falcons in phylogeny and thus have evolved their pursuit behaviours independently. By means of convergent evolution, we hypothesise that Harris’ hawks will use the same pursuit strategy as peregrine falcons, and so we model the same guidance law on these data. The methods and procedures are detailed below, followed by an explanation and discussion of the results.

Materials and methods

Animals

We used five captive bred Harris Hawks (“Ruby”: ♀, 0.93kg; “Findo”: ♂, 0.70kg; “Aggy”: ♀, 0.92kg; “Jake”: ♂, 0.62kg; “Spitfire”: ♂, 0.66kg), all trained to capture an artificial lure pulled along the ground to simulate a manoeuvring terrestrial prey item. We achieved a total of 20 good flights for each bird, defined as a flight in which the bird actively chased and intercepted the lure within view of all four of the high-speed cameras that we used to film the chase. We captured data from many more flights in which the bird failed to intercept the lure, recording well in excess of 100 chases in total. The experimental protocol was reviewed by the Animal Research Panel (US Air Force) and by the Local Ethical Review Committee (Department of Zoology, Oxford University) and approved on the basis that it did not pose any significant risk of causing lasting damage, pain or suffering to the research animal.

Equipment

Each bird was fitted with a Trackpack harness (Marshall Radio Telemetry) before each flight (see chapter 5 for a detailed description). The birds were then fitted with two 4cm diameter polystyrene balls coloured with fluorescent paint for ease of visualization: a pink ball attached to the crossover point of the harness on the breast, and a green ball attached to the mounting plate of the harness on the back, each using Teflon ribbon (Fig.43). A measurement of wind speed and direction was taken at the end of each flight day, using a Kestrel 4500 Pocket Weather Tracker anemometer and Kestrel Wind Vane (Nielsen-Kellerman, Boothwyn, PA, USA).

An artificial lure was attached via 100m of kite line to a 12V DC motorised winch (‘Expert Winch’, Gliders Distribution, Newark, Notts, UK.) powered by a car battery. The lure was made from a fluorescent yellow mitt, to facilitate visualization and to provide a good gripping surface for the birds. On days when the grass was very wet, this was substituted for a waterproof version to prevent the lure being saturated and thus too heavy for the winch to pull at speed. A food reward was attached to the lure to motivate the birds. The lure was run around a series of pulleys to generate abrupt changes in direction simulating those of an evasively moving prey item (Fig.44). We used ten pulleys in total, six of which were built into tunnels for the purpose of guiding the lure around the pulley, and to provide the birds with additional motivation to chase the target. (In pilot trials without the tunnels, the birds appeared less motivated to chase the target, but adding the tunnels seemed to provoke them to attempt to capture the lure before it disappeared.)

The birds were filmed using four synchronised S-PRI high-speed cameras (Lake Image Systems Ltd, Tring, Herts, UK) giving 8 seconds of record time (resolution: 1280 x 1024 pixels; frame rate: 250 Hz; exposure time: 0.002s). The cameras were fitted with Nikon AF Nikkor 28mm f/2.8D wide-angle lenses (Nikon UK Ltd, Kingston upon Thames, Surrey, UK) giving a field of view adequate to cover the volume in which the lure moved. The cameras were arranged in a rectangle measuring approximately 12m by 25m, with the long axis of the rectangle aligned with the slope (gradient approximately 1:10), and were pointed uphill with overlapping fields of view (Fig.44).

Figure 43: Photo of one of our Harris' hawks, showing how the coloured marker balls were positioned on the bird.

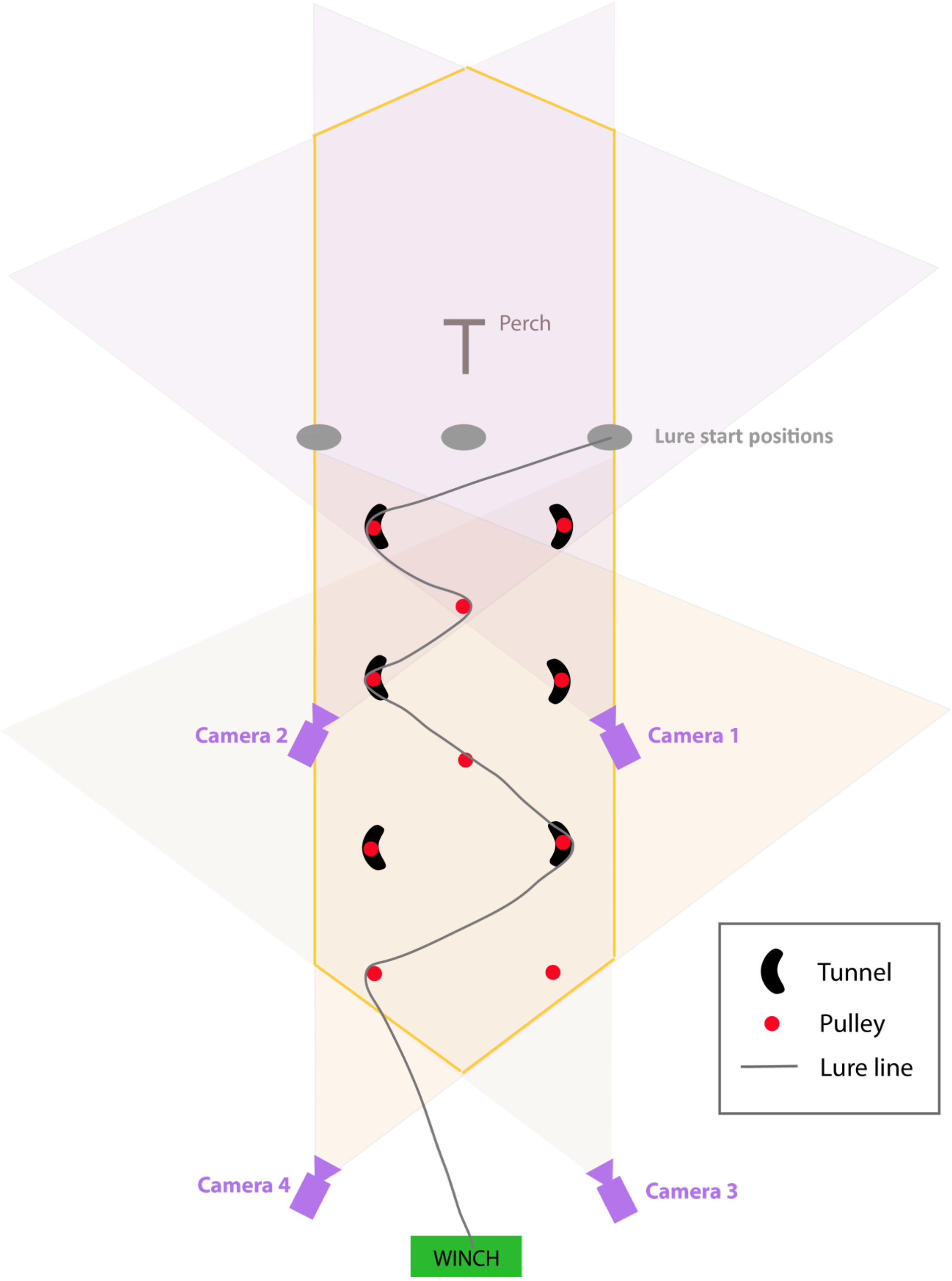


Figure 44: Diagrammatic representation of the pulley set-up showing camera positions and pose (purple), camera field of views (opaque triangular areas), winch (green), pulleys (red), tunnels (black), perch (brown), lure starting positions (grey ovals), and one example lure-course (grey line).

Experimental protocol

The tests with two of the birds (Ruby and Findo) were conducted on an open grassy field at Great Llywgy Farm (Lower Cymyoy, Abergavenny, UK) between October and December 2012. The tests with the other three birds (Aggy, Jake and Spit) were conducted on an open grassy field near Ffawydden Cottage (Llandewi Rhydderch, Abergavenny, UK) between July and September 2013. The birds were flown individually, either from the falconer's fist, or from a perch positioned at head-height at the top of the test area, or from a nearby tree. The winch was activated at the start of each flight, which prompted the bird to take off and chase the target down the hill. The speed of the winch was controlled manually according to the bird's proximity to the lure, so as to maintain the bird's motivation (pilot trials indicated that the birds were not motivated to continue chasing the lure if it was allowed to run too far ahead of them). Interception occurred within the measurement volume, and the winch was stopped immediately upon capture to avoid harming the bird. The cameras were set to post-trigger, and were triggered manually after the bird had caught the lure. The video data from each camera pair was immediately saved onto a laptop in the field (Toshiba Tecra R850-140, Dell Latitude E5510). Together, the cameras captured the whole of the attack sequence, typically involving an initial wing beat acceleration, followed by fast twists, turns and wingover manoeuvres, terminating with a rapid leg extension at the point of capture.

We found that it was possible to undertake 2 to 4 flights on a single day with each bird. If the bird proved not to be highly motivated on a given flight (e.g. because it spent a long time gliding after the lure, rather than in active flight), then it would be made to experience a 'miss' by stopping the lure out of reach to prevent interception (either in a tunnel or by winding the lure in fully and covering it). This approach was found to improve the bird's motivation on subsequent trials, and was intended to create more realistic hunting conditions. In any case, the bird always received a full crop of food after its last flight to keep it motivated for subsequent test days.

<u>Experimental design</u>

With the pulley setup that we used, it was possible to pull the lure along 16 different courses beginning at one of 3 different starting points (Fig.45). We randomly selected which course to use on each flight, and laid decoy lure lines to control for the possibility that the birds might simply follow the line, as well as decoy covers over the starting positions to prevent the bird anticipating from where the lure would appear and in what initial direction of travel. The lure switched its direction of travel 4, 5, or 6 times on each complete run, depending upon the course that was set (Fig.45). The lure always switched its direction 4 times at the periphery of the course, which resulted in the lure being pulled towards the middle of the course, so it was possible in principle for the bird to anticipate the direction of these switches if it had learned this aspect of the task. On the other hand, it should not have been possible for the bird to anticipate whether the lure would change direction as it passed around the two pulleys in the middle of the course (excepting the possibility that the bird could discriminate which of the lines was under tension on a given run). By the same reasoning, it would have been possible in principle for the bird to anticipate the lure's initial direction of travel on any of the 8 courses in which the lure started at the periphery of the course. On the other hand, it should not have been possible in principle for the bird to anticipate the lure's initial direction of travel on any of the 8 courses in which the lure started in the middle of the course.

We could not use a truly random set-up as it was not possible on a practical level – the effectiveness of the winch in pulling the lure through the course was extremely sensitive to the positioning of the pulleys. Therefore the best approach was to fix their positions and randomly assign which pulleys the lure line was set around in each trial.

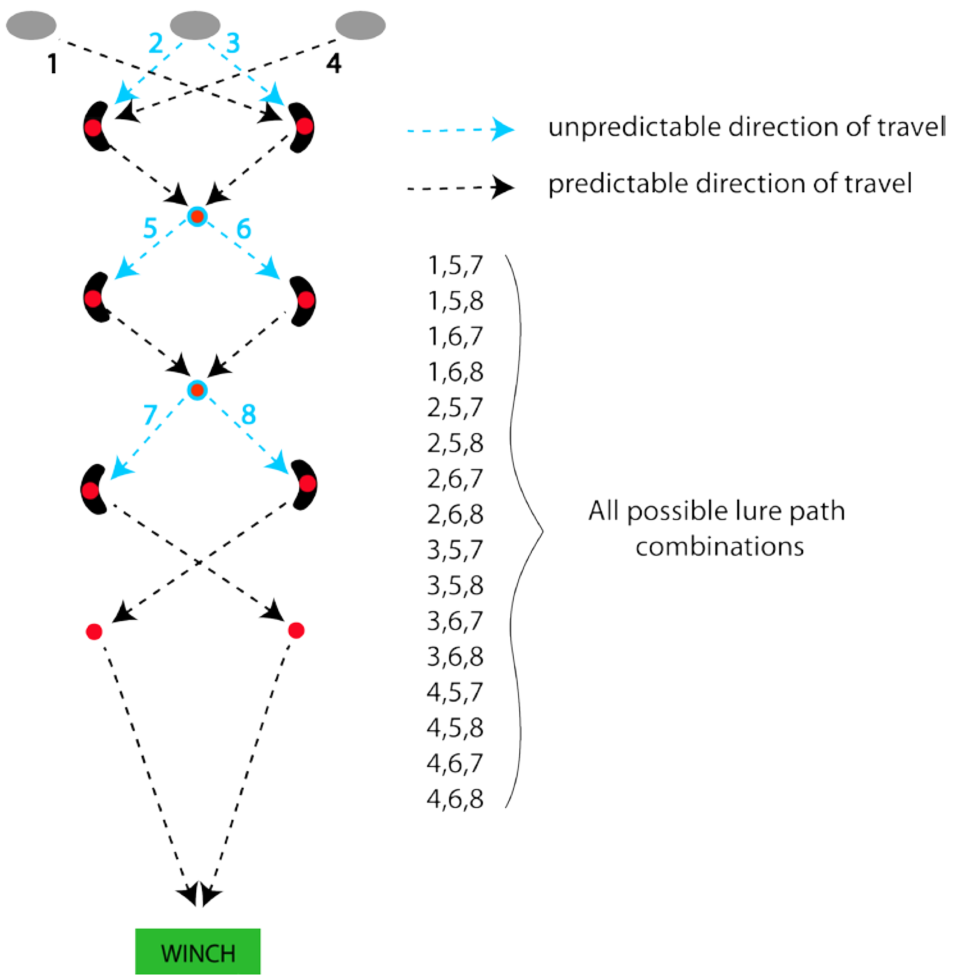


Figure 45: Diagram showing the 16 possible lure courses in the pulley set-up that we used, highlighting where an unpredictable change in lure direction occurs (blue). Red circles are the pulleys, black shows the tunnels, and grey are the starting positions of the lure.

3D Reconstruction

Marker tracking software

The pixel coordinates of the lure and of the marker balls on the bird were identified for each camera view using in-house software in Matlab v.7.4 (courtesy of Shane Windsor, Fig.46). In brief, the user first creates a colour template by outlining the pixels corresponding to the object to be tracked in a series of specified video frames. A local search area around the marker is also defined, and the software then uses the colour template to identify matching pixels in each frame of the video sequence, updating the search area by centring it on the last successfully tracked point (Fig.46). The colour of each pixel within the search area is then compared to the distribution of the colour template by computing its Mahalanobis distance (distance between a point and mean of a distribution). Any pixels having a Mahalanobis distance less than a set threshold are assumed to be candidate marker pixels, and the centroid of the single largest contiguous group of candidate marker pixels is assumed to correspond to the centroid of the marker itself. The software uses a Kalman filter to estimate the position of the marker if no marker was found, or in the event that the estimated position of the marker jumps by more than a given amount between frames. The markers were obscured when the lure entered a tunnel or if the bird flew outside of the field of view, and in these cases the data were treated as missing. All estimated marker positions were checked manually and corrected if necessary using in-house software in Matlab v.7.4 (courtesy of Simon Walker).

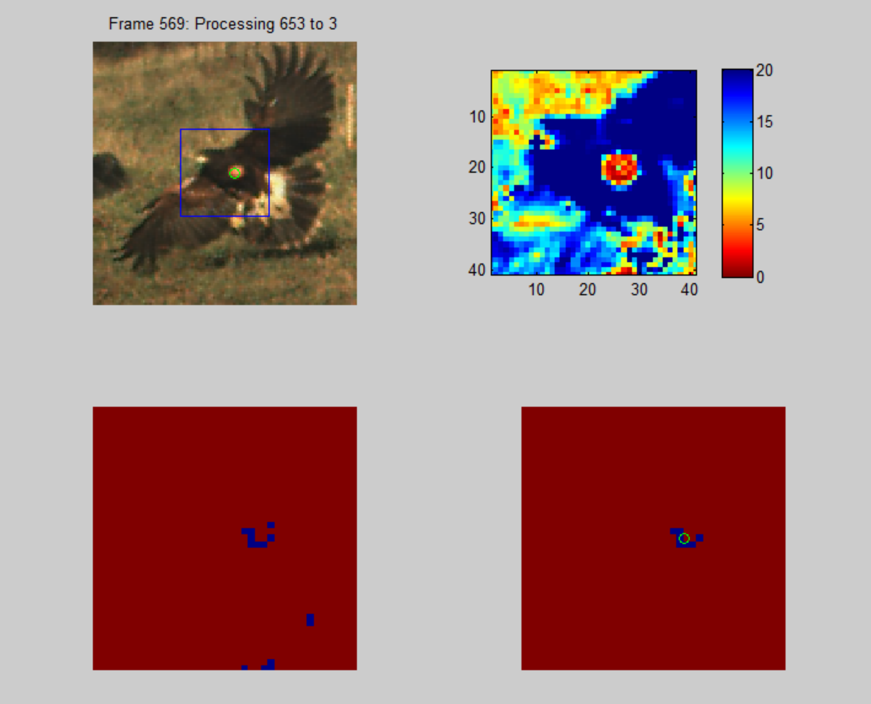


Figure 46: Screenshot of colour tracking software graphical user interface. The top left panel shows the search area defined by the user (blue square) and the estimated centroid of the marker (green circle). The top right panel shows the Mahalanobis distance of the pixels within the search area, measured with respect to the colour distribution of the user-defined colour template. The bottom left panel shows all of the candidate marker pixels, identified as those pixels whose Mahalanobis distance falls below a set threshold. The bottom right panel shows the largest contiguous group of candidate marker pixels, the centroid of which is taken as an estimate of the marker position.

Photogrammetry

The cameras were set up and taken down at the beginning and end of each test day, so had to be calibrated separately each day. This was done by filming a dumbbell-shaped calibration object of 1.05m in length, comprised of a long clear acrylic tube with a ball secured at each end, while it was moved through the test volume in a range of different orientations. The pixel coordinates of the two marker balls were tracked automatically offline using the colour-tracking software described above. The camera collinearity equations were then solved using nonlinear least squares in a bundle adjustment that identified jointly optimal estimates of the position and pose of the calibration object and the cameras (Fig.47).

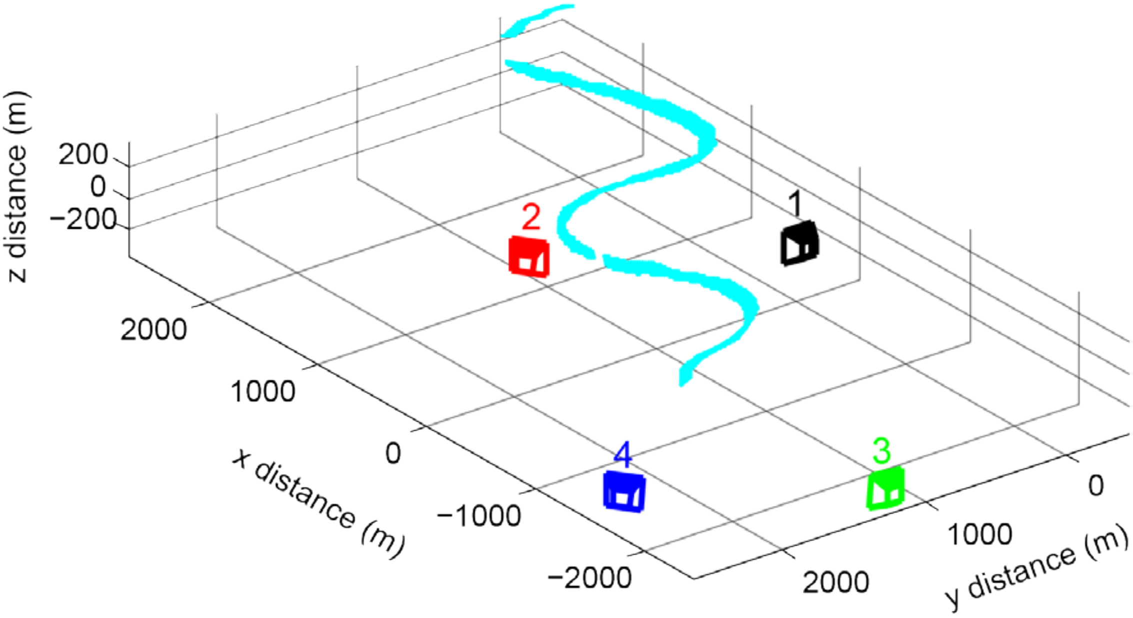


Figure 47: Example 3D reconstruction of the camera calibration for one test day, showing the estimated position and pose of the calibration object (cyan line) and estimated position and pose of the four cameras. The snaking path of the calibration object shows how it was moved through the test volume – the pose is not visible because of the dense sampling.

Lens distortions were found to be minimal and we therefore assumed a central perspective projection, assuming no lens distortion and no offset of the principal point with respect to the centre of the camera sensor. Field measurements of camera position and pose were used to provide initial values for these parameters in the optimization, in order to guarantee convergence. Having first optimized the focal length separately for each flight, we ultimately fixed the principal distance of the cameras at 28.42mm for all flights, calculated as the mean for all cameras over flights. This was done on the grounds that the data gave no reason to think that the small variations in the estimated principal distances between flights or between cameras were real, so that the grand mean represents the best estimate of the true value of this parameter.

The resulting camera calibration parameters were used to solve, in a least squares sense, for the position of the lure mitt and of the two marker balls on the bird at each time step.

Choosing the colours for the tracking software

Before experiments were conducted with birds, preliminary tests were carried out in order to optimize the four-camera set-up, based on image resolution calculations, the capabilities of the colour tracking software, and the size and position of the marker on the bird. The aims were to:

1) Maximise the distance between the camera pairs (to enable a longer pursuit flight) without losing too much image resolution.

2) Find the most appropriate marker colour for the automated tracking software.

3) Determine the best size and position of the marker on the bird for tracking without compromising flight manoeuvrability.

For the colour tracking software to be able to detect the coloured marker on the bird, it needed to be at least 2 pixels in size at the maximum distance, and so an area approximating 15m by 25m was chosen according to resolution calculations. For the marker, two hollow plastic balls of 40mm diameter, attached to the bird’s breast and back, were found to be optimal. One was painted fluorescent green and the second fluorescent pink (Fig.43), as the best colours for tracking (out of the eight colours tested). This reflects the properties of the Bayer filter used in the high-speed cameras to assign pixel colour. The following graphs show the difference in output of the tracking software between a good marker (fluorescent green, Fig.48a) where it tracks well, and a bad marker (pale orange, Fig.48b) where it struggles to distinguish it.

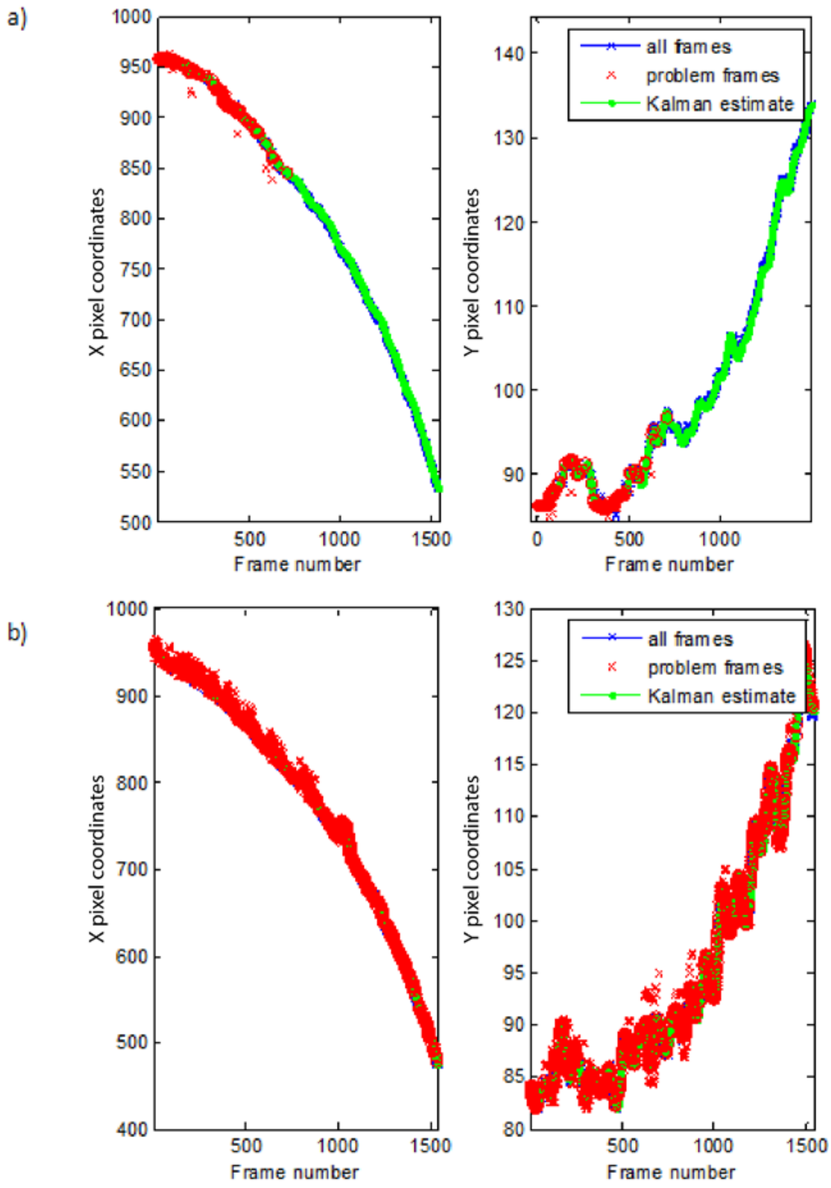


Figure 48: The tracked x and y pixel coordinates from one camera view of a) a successfully tracked 'fluorescent green' marker and b) an unsuccessfully tracked 'pale orange' coloured marker, using colour-tracking software. Green points show where the marker has been successfully tracked, while red highlights frames where the marker position was neither found directly nor estimated by Kalman filtering.

Error analysis

We established the measurement error of our photogrammetric technique by calculating the standard deviation of the estimated distance between the two calibration markers over the 14 camera calibrations that we ultimately used (see below). In the camera calibration software (see above), the distance between the calibration markers is treated as a known (i.e. fixed) parameter, so having run the calibration software already we then estimated the positions of these markers separately using the same software that we used to estimate the position of the lure mitt and of the two marker balls on the bird. Because the calibration object itself is a rigid body that had been moved through the test volume in a range of different positions and orientations, the standard deviation of our estimate of its length (i.e. the distance between the calibration markers) provides an isotropic estimate of the measurement error.

A fixed-effects ANOVA testing for differences in mean estimated calibration object length with respect to calibration date revealed the presence of small but statistically significant differences between days (one-way ANOVA: $F_{13,21174} = 48.4$, $p<0.0005$). These differences could have been due to random error in the calibrations, or due to real variation in the length of the calibration object between days, but the effect size was very small, and we therefore considered it reasonable to pool our estimates of calibration object length for all days (Fig.49). The grand mean and standard deviation of the estimated calibration object length were 1.054m and 0.023m, respectively, and 95% of the measurements fell within the interval [0.032m, 0.036m] of the mean. It follows that the isotropic positioning error of our photogrammetric measurements is typically <0.04m.

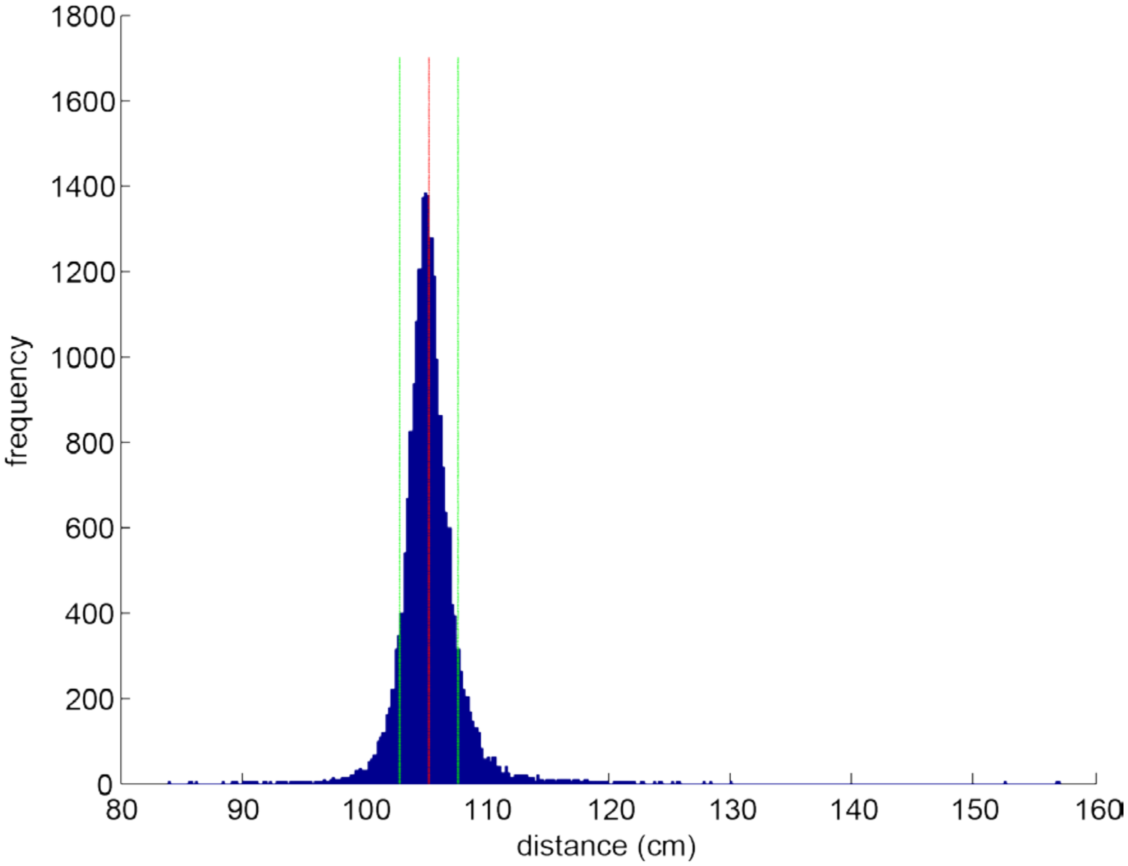


Figure 49: Distribution of estimated calibration object length for all of the 14 calibrations that we used, showing the mean estimated length (1.054m; red line) and standard deviation (±0.023m; green lines). The measured distance assumed in the calibrations was 1.05m, and the true length of the calibration object should not have varied by more than a few millimetres between calibrations. The dispersion of this distribution therefore provides an estimate of the isotropic measurement error.

Results

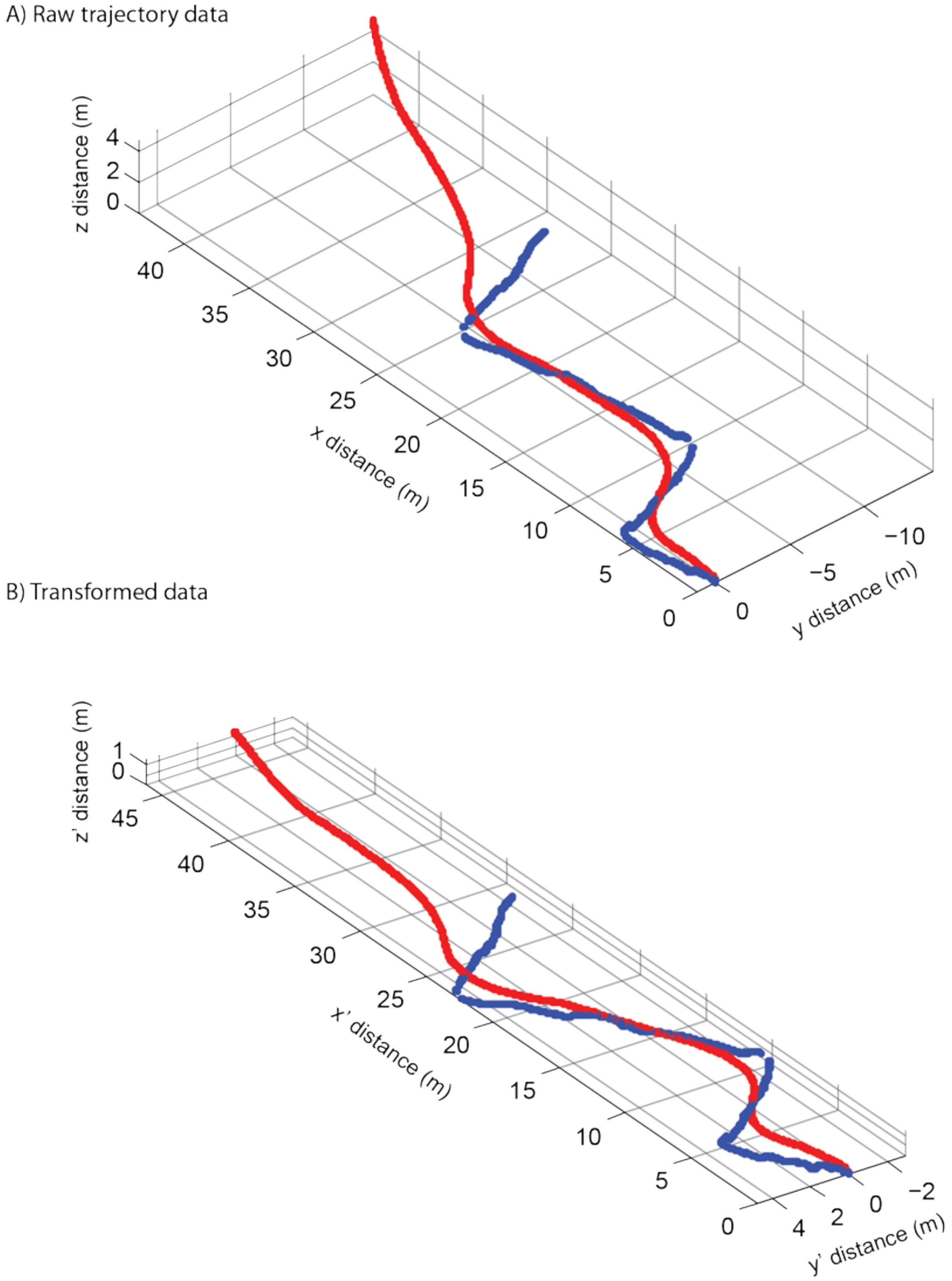
Data selection

In order to deal practically with the volume of data that we had collected, whilst preserving the deliberate balance of the experimental design, we determined to analyse only the last 10 flights from each of the 5 birds. Given that we recorded at least 20 good flights from each bird in total, it follows that each of the birds had already experienced a training period comprising at least 10 good flights before the block of 10 good flights that we actually analysed. Future work will test whether there is evidence of learning during the training phase, but at present the data remain unanalysed owing to the challenges in automating the image analysis.

Data processing

We took the estimated position of the marker carried on the breast of the bird as our estimate of the bird's instantaneous position. This marker was not fully visible in a small number of cases, and in those cases we instead used the estimated position of the marker carried on the back of the bird. Because we had selected flatly sloping fields for the flight tests, the chase trajectories that we recorded were all close to planar, but the planes of the trajectories did not in general coincide with the axes of the Cartesian coordinate system generated by the camera calibration software (Fig.50A). The first two principal components of the bird's three-dimensional flight trajectory measure its two-dimensional position within the plane of best fit. We therefore computed the principal components of the bird's three-dimensional flight trajectory, and used these to rotate the Cartesian coordinate system generated by the camera calibration software so that the $x'y'$-coordinates of the rotated coordinate system corresponded to the plane of best fit (Fig.50B). All of the subsequent analysis is performed on the $x'y'$-components of the position data in this rotated coordinate system.

Determining the bird's flight velocity involves differencing its position, but because we had used high-speed video data at 250Hz, the bird only travelled a short distance between consecutive video frames. We were therefore obliged to calculate the bird's flight velocity by differencing over a longer time interval than the separation between the video frames. Since the relative positioning error of our photogrammetric method was comparable to the relative positioning error of the GPS units used in our work with peregrines (<0.05m in both cases; see above) we chose to calculate the bird's flight velocity by central differencing the position estimated on every 50th frame (Fig.51A,B), which resulted in the same 0.2s temporal separation between the position fixes used to estimate flight velocity as was already present in the 5Hz GPS data that we had collected with the peregrines. We then calculated the track angle of the bird as the azimuth of the resulting velocity data and determined the line-of-sight angle to target at the corresponding point in time (Fig.51A,B). Finally, we computed the turn rate of the bird and the rate of change in its line-of-sight angle by central differencing the track angle and the line-of-sight angle, respectively, using the same 0.2s temporal separation as before (Fig.51C). Hence, because the relative positional error (<0.05m) and temporal separation (0.2s) used in differencing the position data are similar in both the GPS (when working properly) and photogrammetric analyses, it follows that the measurement error in all of the measured quantities should be similar in all of the various analyses presented in this thesis.



A) Raw trajectory data

B) Transformed data

Figure 50: Example trajectory of a Harris’ hawk (red) chasing the towed lure (blue) from one flight test, with interception occurring where the two trajectories meet at the origin. A) Data plotted in the Cartesian coordinate system generated by the camera calibration software (see also Fig.47); B) Data plotted in the rotated Cartesian coordinate system in which x’ and y’ denote the first and second principal components of the bird’s flight trajectory. The x’y’ plane is the plane which best fits the measured trajectory (i.e. the plane which captures most of the measured variation in position).

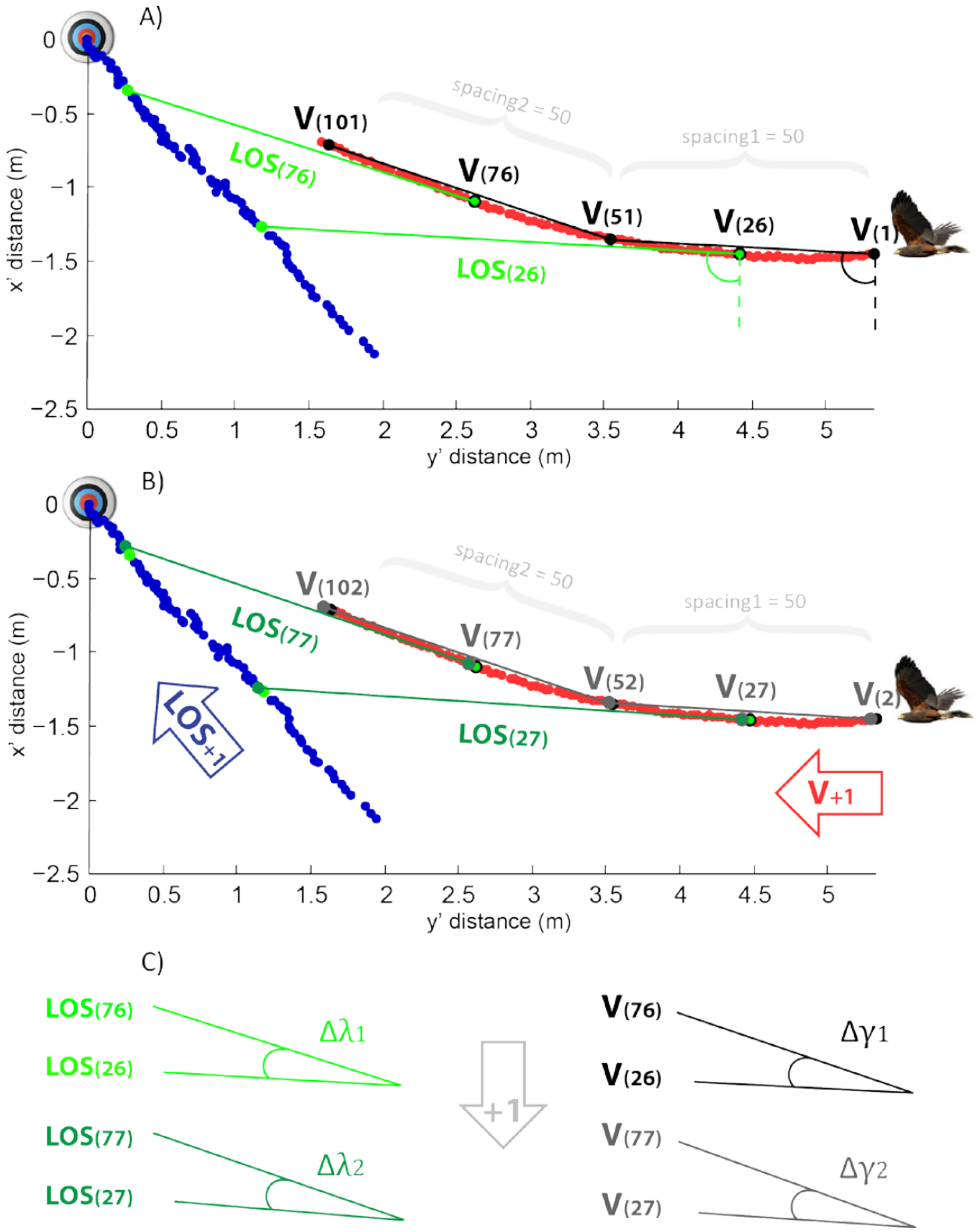


Figure 51: Calculation of line-of-sight angle, track angle, line-of-sight rate and turn rate from our photogrammetric measurements of bird position (red points) and lure position (blue points). LOS: line of sight; V: velocity vector; numerical subscripts denote camera frame numbers. A) Track angle at Frame 26 is calculated as the bearing of the velocity vector V_{26}, calculated from the difference in position between Frames 1 and 51. Line-of-sight angle at Frame 26 is calculated as the bearing of the line of sight LOS_{26} drawn from bird to target at Frame 26. The track angle and line-of-sight angle at Frame 76 are calculated similarly as shown. B) Calculation of the same quantities at Frames 27 and 77, to show how the calculation preserves the 250Hz sampling rate of the data, despite using a temporal separation of 0.2s for the calculations. C) Turn rate and line-of-sight rate at Frames 51 and 52 are calculated from the difference in track angle $\Delta\gamma$ and line-of-sight angle $\Delta\theta$ at Frames 26 and 76, and 27 and 77, respectively.

Analysis of guidance law

The track angle of the bird closely follows the line-of-sight angle to the target in all of the 50 flight trajectories that we analysed, albeit with a small time delay (Fig.52). This indicates that the Harris' hawks were following a pursuit course in which the deviation angle was held approximately constant – in most cases, the deviation angle was close to zero (Fig.52), implying that the birds were normally using a pure pursuit strategy (see chapter 1). To provide a quantitative estimate of the delay in the pursuit dynamics, we calculated the correlation coefficient between the track angle and the line-of-sight angle for lags within the interval ±0.5s (Fig.53). The correlation coefficient was low on a handful of the flights, which may indicate that the bird was not always locked-on to the lure in these cases. In most cases, however, the correlation coefficient had a maximum >0.8 and was maximal having lagged the track angle by approximately 0.19s (median of the lags corresponding to peak correlation coefficient for each flight; Fig.53). This is confirmed by Fig.54, which plots track angle and line-of-sight angle against time for all 50 flight trajectories, with a lag of 0.19s applied to the track angle data.

As discussed in the Introduction, it is possible in principle to implement pure or deviated pursuit by using pure proportional navigation with a navigation constant of $N = 1$. Conversely, it is easily seen that if a bird is engaged in a pure or deviated pursuit, then its turn rate must necessarily equal its line-of-sight rate (albeit with a possible lag in the dynamics). It follows that any predator engaging in pure pursuit will look as if it is engaging in pure proportional navigation with $N = 1$. This is shown directly in Fig.55, which plots turn rate and line-of-sight rate against time. Although the plots are noisier than they are for the track angle (Fig.52) and line-of-sight angle (Fig.54), on account of the numerical differencing, it is obvious that the turn rate indeed follows the line-of-sight rate. Fig.56 plots the same data again, but with the turn rate lagged by 0.19s.

Even though the Harris' hawks were normally using a pure pursuit strategy, there were some sections of flight during which the track angle differed from the line-of-sight angle by some near-constant amount. Thus, there are some sections of flight during which the lagged track angle is substantially different to the line-of-sight angle, but during which the lagged turn rate and line-of-sight rate are approximately equal. These sections of flight correspond to a deviated pursuit, and although this observation is not in itself sufficient to demonstrate that the birds were using proportional navigation with $N = 1$ to implement their pursuits, it does at least show that the hypothesis that the birds use proportional navigation with $N = 1$ has the potential to explain most of the data. In summary, the Harris' hawks were using pure pursuit for most of the time, but occasionally made use of a deviated pursuit. In each case, the dynamics of the pursuit involve a time delay of approximately 0.19s.

Visual inspection of the raw trajectory data confirms that the bird's trajectory does indeed only begin to turn approximately 0.19s after the lure's trajectory turns. This presumably reflects not only the latency of the bird's physiological response to the lure, but also the finite time that is required physically to develop the unsteady aerodynamic force needed to initiate a turn.

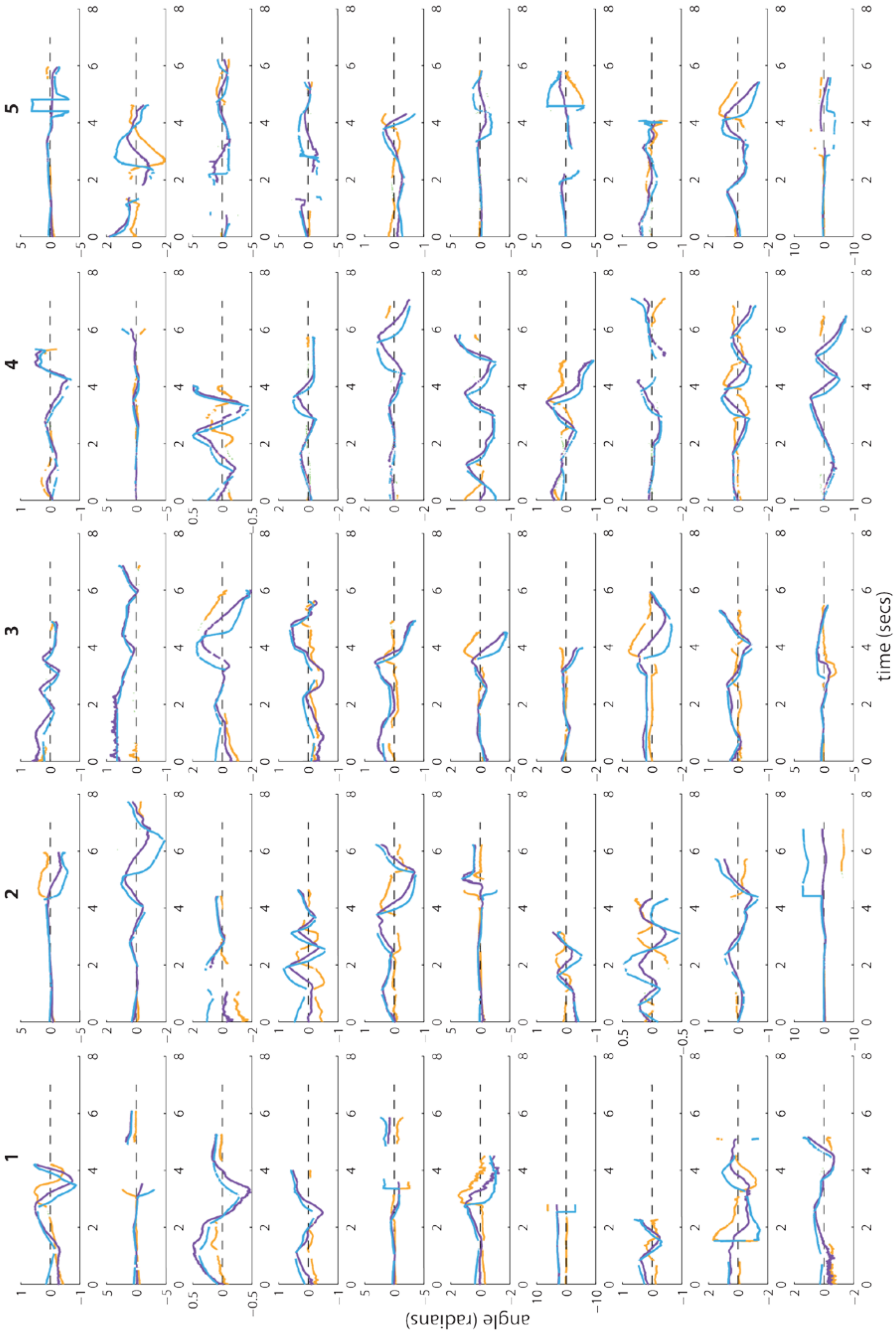


Figure 52. Track angle γ (blue), line-of-sight angle θ (purple), and deviation angle $\alpha = \theta - \gamma$ (orange) plotted against time for all of the air-to-ground attack passes by Harris' hawks that we analysed. Each column (1-5) corresponds to a different bird. Note the close match between γ and θ, but with θ lagging behind γ.

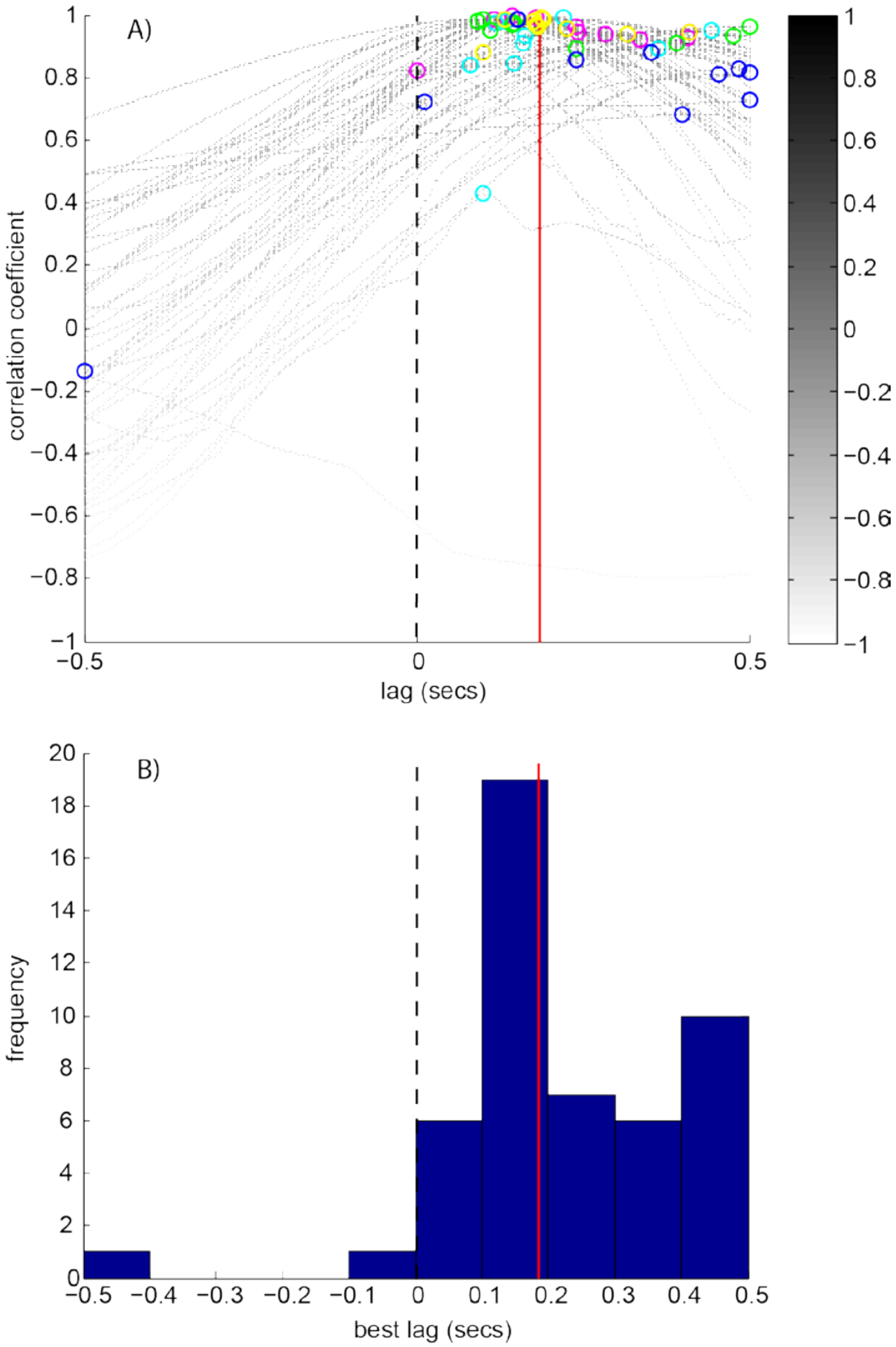


Figure 53: A) Correlation coefficients of track angle γ against line-of-sight angle θ for assumed lags in the interval ±0.5s for all analysed air-to-ground attacks in Harris' hawks. The lines plotting how the correlation coefficient for each flight varies with time lag are coloured grey according to their value, to draw attention to the regions of highest correlation coefficient. The point of maximum correlation coefficient for each line is identified by a coloured circle (colour identifies individual birds), and the median of the lags corresponding to the peak correlation coefficient for each flight (0.19s) is shown as a vertical red line. B) Histogram of best lags, defined as the time lag corresponding to the point of maximum correlation coefficient for each of the flights in (A). The red line denotes the median of the lags corresponding to the peak correlation coefficient for each flight (0.19s). Note that all peak correlation coefficients were significant at $p<0.05$ level.

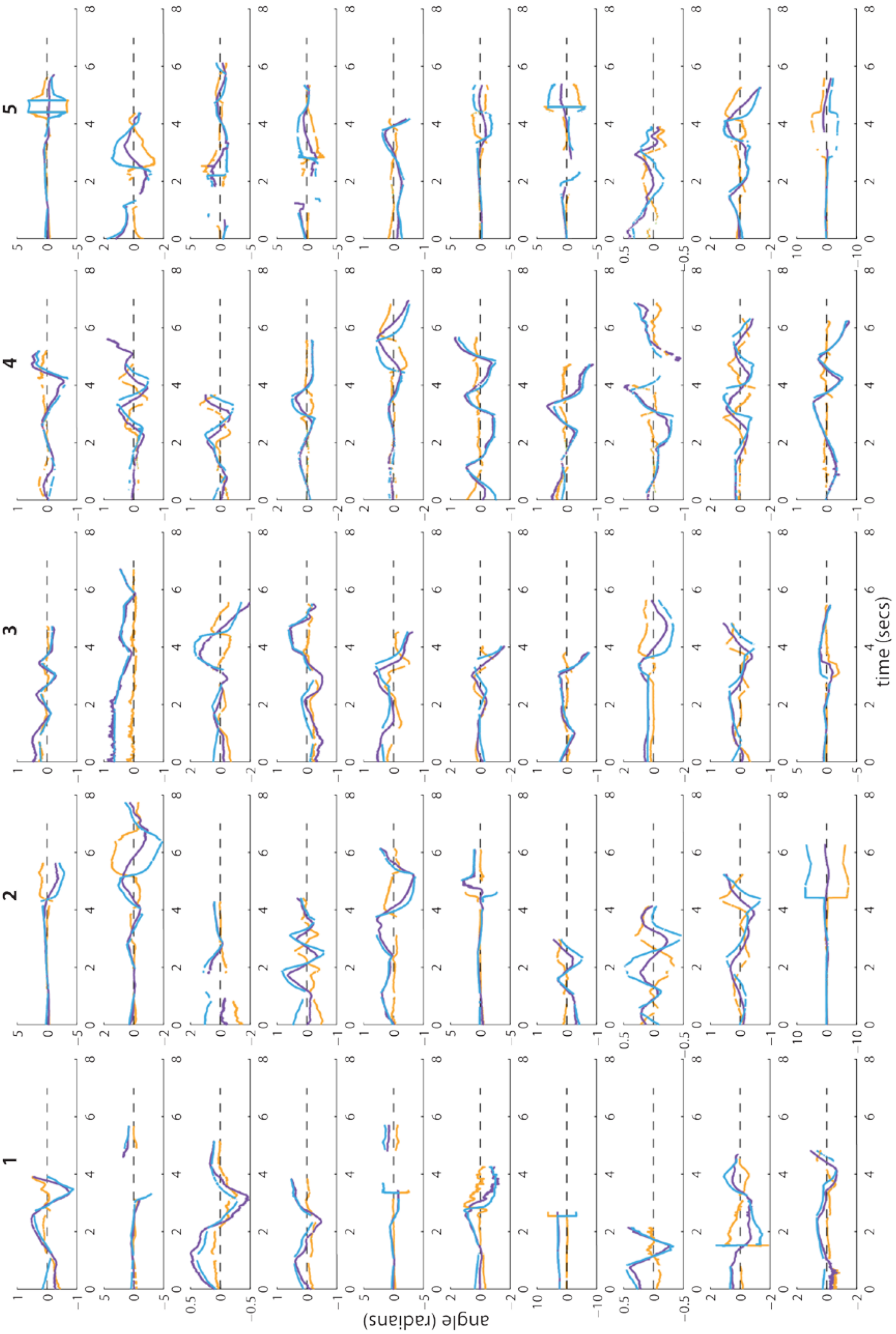


Figure 54. Lagged track angle $\gamma(t+0.19)$ (blue), line-of-sight angle $\theta(t)$ (purple), and lagged deviation angle $\alpha(t+0.19)=\theta(t)-\gamma(t+0.19)$ (orange) plotted against time for all of the air-to-ground attack passes by Harris' hawks that we analysed. Each column (1-5) corresponds to a different bird. The time lag of 0.19s is our best estimate of the average lag from the correlation coefficient analysis in Fig.53. Note the close match between γ and θ, with θ not lagging behind γ after the addition of the delay.

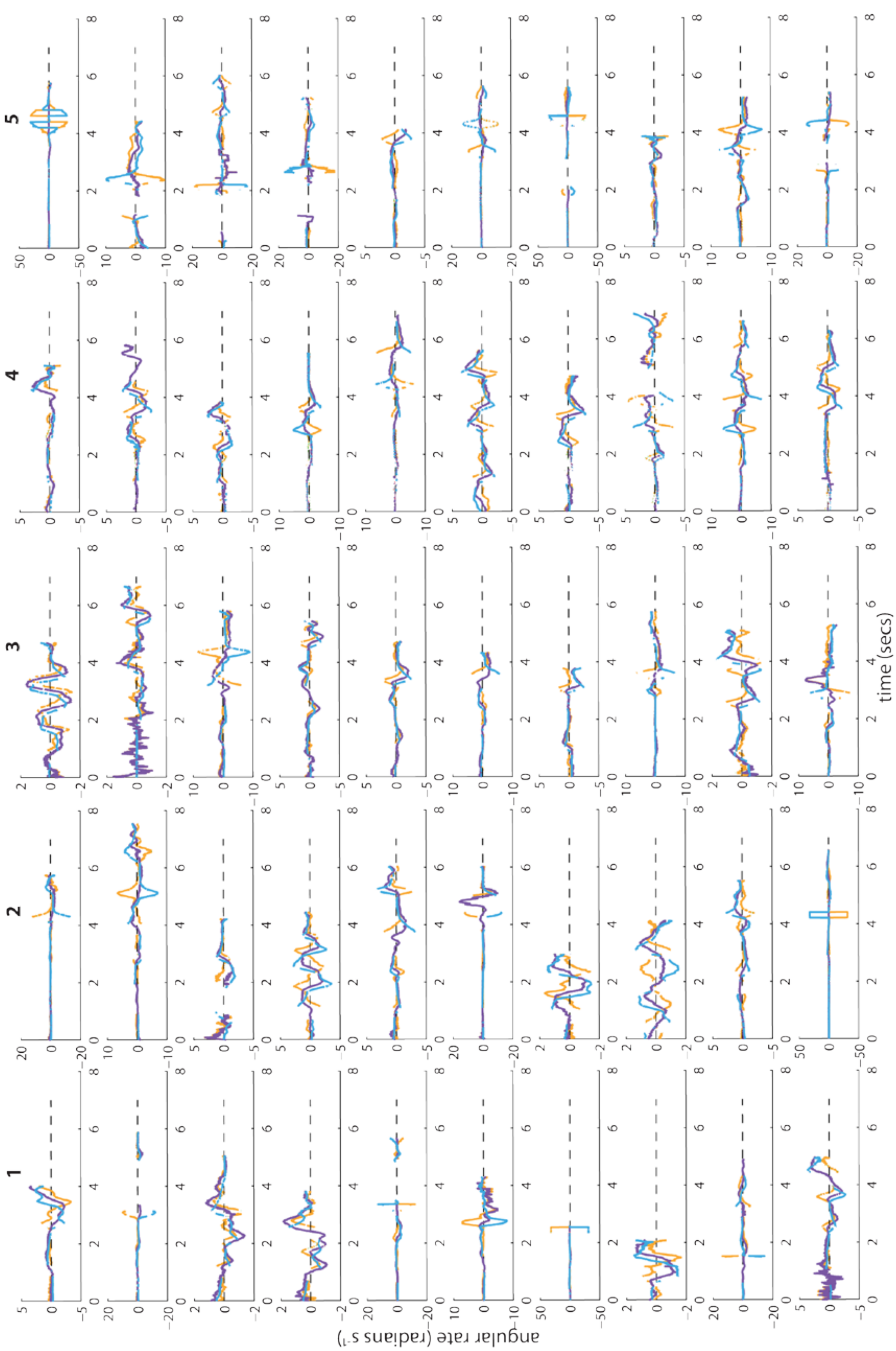


Figure 55. Turn rate $\dot{\gamma}$ (blue), line-of-sight rate $\dot{\theta}$ (purple), and deviation rate $\dot{\alpha} = \dot{\theta} - \dot{\gamma}$ (orange) plotted against time for all of the air-to-ground attack passes by Harris' hawks that we analysed. Where the deviation rate is flat, the bird is following either a pure or a deviated pursuit. Each column (1-5) corresponds to a different bird. Note the close match between $\dot{\gamma}$ and $\dot{\theta}$, but with $\dot{\theta}$ lagging behind $\dot{\gamma}$ (though noisier than Fig.52).

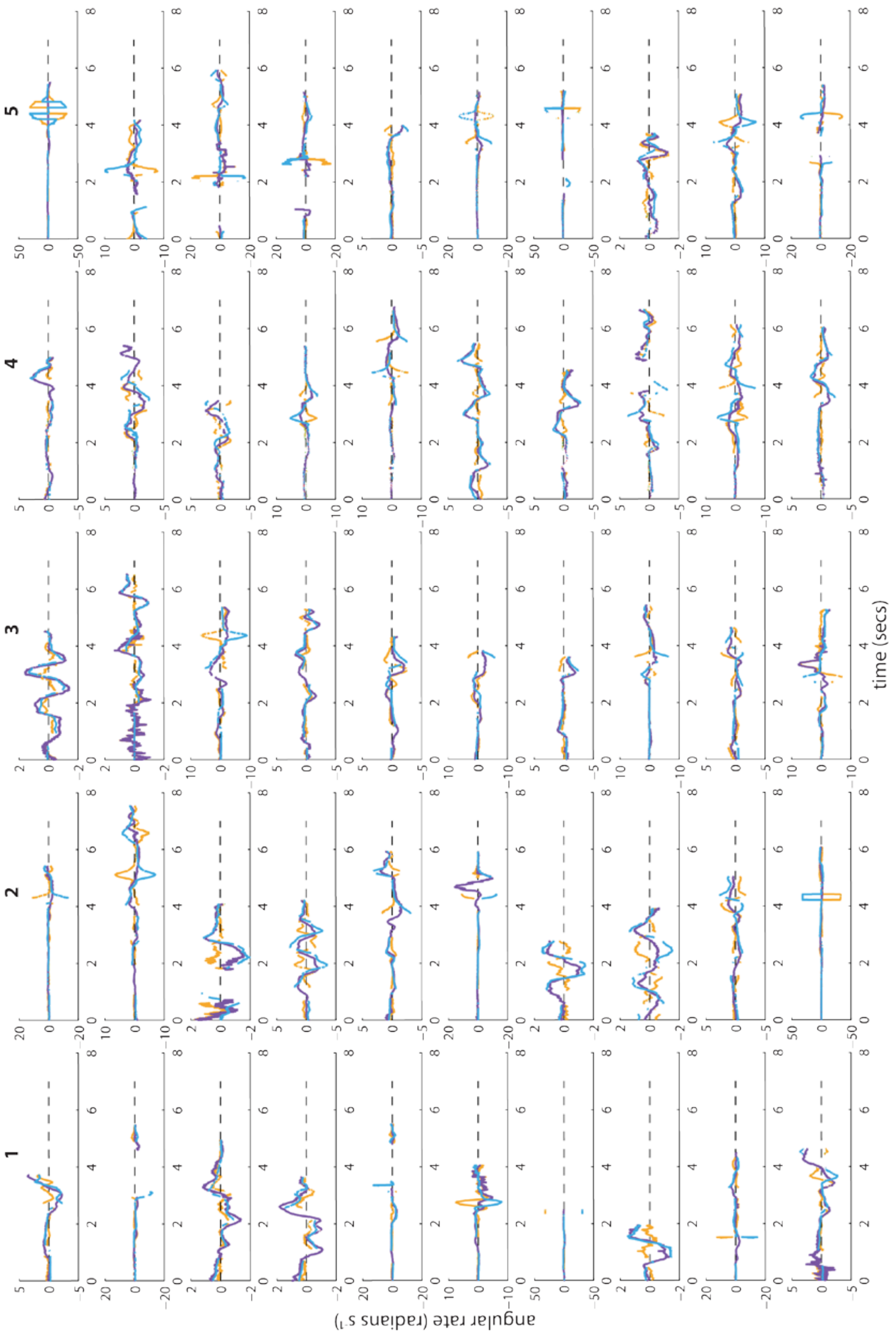


Figure 56. Lagged turn rate $\dot{\gamma}(t+0.19)$ (blue), line-of-sight rate $\dot{\theta}(t)$ (puple), and lagged deviation rate $\dot{\alpha}(t+0.19)=\dot{\theta}(t)-\dot{\gamma}(t+0.19)$ (orange) plotted against time for all of the air-to-ground attack passes by Harris' hawks that we analysed. Where the deviation rate is flat, the bird is following either a pure or a deviated pursuit. Each column (1-5) corresponds to a different bird. The time lag of 0.19s is our best estimate of the average lag from the correlation coefficient analysis in Fig.53. Note the close match between $\dot{\gamma}$ and $\dot{\theta}$, with $\dot{\theta}$ not lagging behind $\dot{\gamma}$ after the addition of the delay (though noisier than Fig.54).

Proportional navigation simulation

We modelled pure proportional navigation trajectories on our transformed data (’X’ and ‘Y’). Firstly, we conducted a quintic spline interpolation of the bird and lure data to improve the signal to noise ratio, using a tolerance calculated from a Butterworth filter with a 3Hz cut-off (calculates the overall closeness between the smoothed and raw data and fits a spline with the same closeness). All position data was then subtracted from the interception point of the lure for plotting purposes (so that interception occurred at the origin). We then ran the proportional navigation simulation used in our peregrine analyses in chapter 5.

To eliminate subjectivity in the identification of the start point t_0 in our simulations, we ran the simulation starting from every single point along the bird’s trajectory - from the start of the flight to 100 samples before interception (0.2s). We therefore obtained the mean L1-norm error values, N values, and flight distances, for each possible starting position. We identified t_0 as the last point (working backwards from 0.2 seconds before interception) for which the mean prediction error in position was <2.0% of the distance flown. Figures 57-61 show the smoothed bird and lure positions with simulated proportional navigation trajectories overlain, from t_0 to interception, with the time-delay of 0.19s identified in the previous section. Overall, our simulated trajectories matched the measured data in most flights - a large proportion of which were fitted over the whole flight duration. However, simulations fitted over less than 2 seconds of flight data (17 in total) are too short to obtain any meaningful information on the dynamics of the pursuit.

Discussion

We show that the pursuit trajectories of Harris' hawks intercepting targets moving along the ground can be explained by a simple geometric rule. Birds were usually following a pure pursuit strategy by responding to the instantaneous position of the target. Over some sections of flight, the bird's track angle was found to differ from its line-of-sight angle but they were still changing at same rate (turn rate and line-of-sight rate were equal). These represent stages where the birds were using a deviated pursuit (deviation angle was constant but not zero - as required for a pure pursuit)[147]. Deviated pursuits are generally used for faster targets, so perhaps the birds are switching from a pure to a deviated pursuit when the target's speed goes above some level [146], and needs testing. Where the deviation angle did not follow the line-of-sight angle, the bird was either not locked on to the target, or was not following a pure or deviated pursuit and thus implementing some other guidance strategy.

We also found that the trajectories were well fitted by proportional navigation with a mean estimated N value of 1.02, which results in a pure pursuit[146, 147]. However, we cannot determine whether they implement a pure pursuit using proportional navigation or not. In contrast, in our peregrine data there was no simple geometric rule which described all the data - the proportional navigation simulations only achieved a good fit if N was allowed to vary. Therefore it is reasonable to assume that because the Harris' hawk data *is* explained by a simple geometric rule, they may not be implementing this via proportional navigation. Under a pure pursuit, birds are not required to estimate the line-of-sight rate as they would be under proportional navigation[142, 186], thus with the value of N fixed at 1 it may be needless to implement a more circuitous guidance law. Future work should investigate different target behaviours to see whether they do indeed vary N in different attack scenarios via proportional navigation. In the context of their ecology, wild Harris' hawks most often perform attacks against highly-manoeuvrable ground prey in cluttered habitat[15, 44], so following a pure pursuit means birds will automatically avoid all obstacles in the environment (so long as the prey they are chasing has) and so may represent the safest strategy.

Interestingly, we also found a mean time delay of 0.19s between the measurements of line-of-sight rate and turn rate in the hawks. This delay would barely have been detectable in our peregrine data using 5Hz GPS data. There are various reasons why we would expect such a delay, for example, the time needed for visual processing, muscle activation, or dealing with unsteady aerodynamics. Since we tracked the centre of mass only, the time taken to perform positional changes was likely to have been greatly overestimated. It was evident from our high-speed videos that the response time for the control components, i.e. wings, head and tail, of the flight were much quicker. Future analysis of the high-speed video data will aim to measure the latency with which control inputs are first visible in the wings and tail.

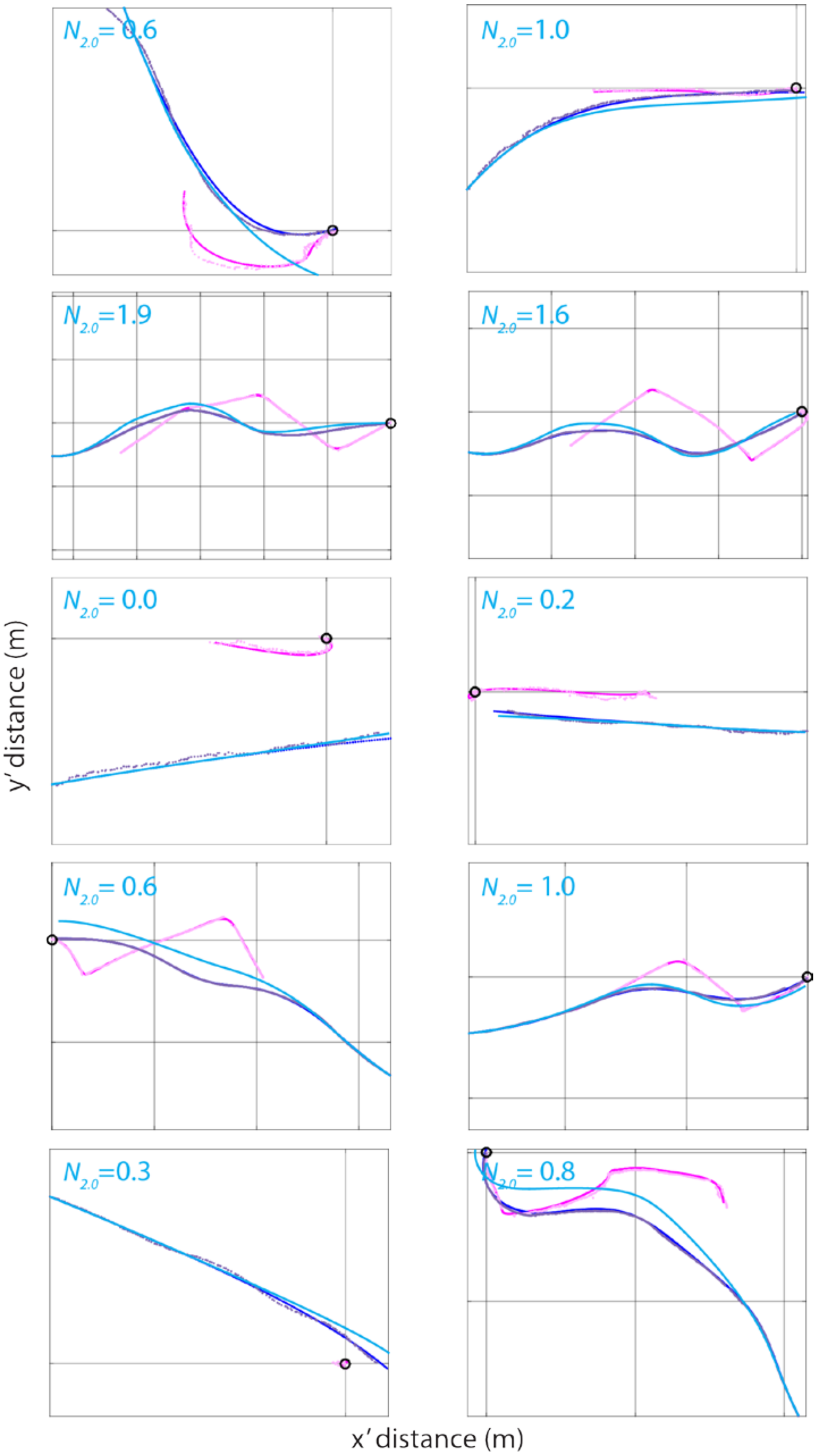


Figure 57: Proportional navigation simulations (light blue) of the spline-fitted measured data for Harris hawk 1 (dark blue) pursuing a target (magenta) moving along the ground, with a time-delay of 0.19s (see Fig.53), with corresponding values of the navigation constant. Also shown is the unsmoothed bird PCA data (light purple), and unsmoothed lure PCA data (light pink). Grid lines represent 10m intervals. Black circles indicate point of interception. Note the close match between the measured data and the simulations in many of the flights.

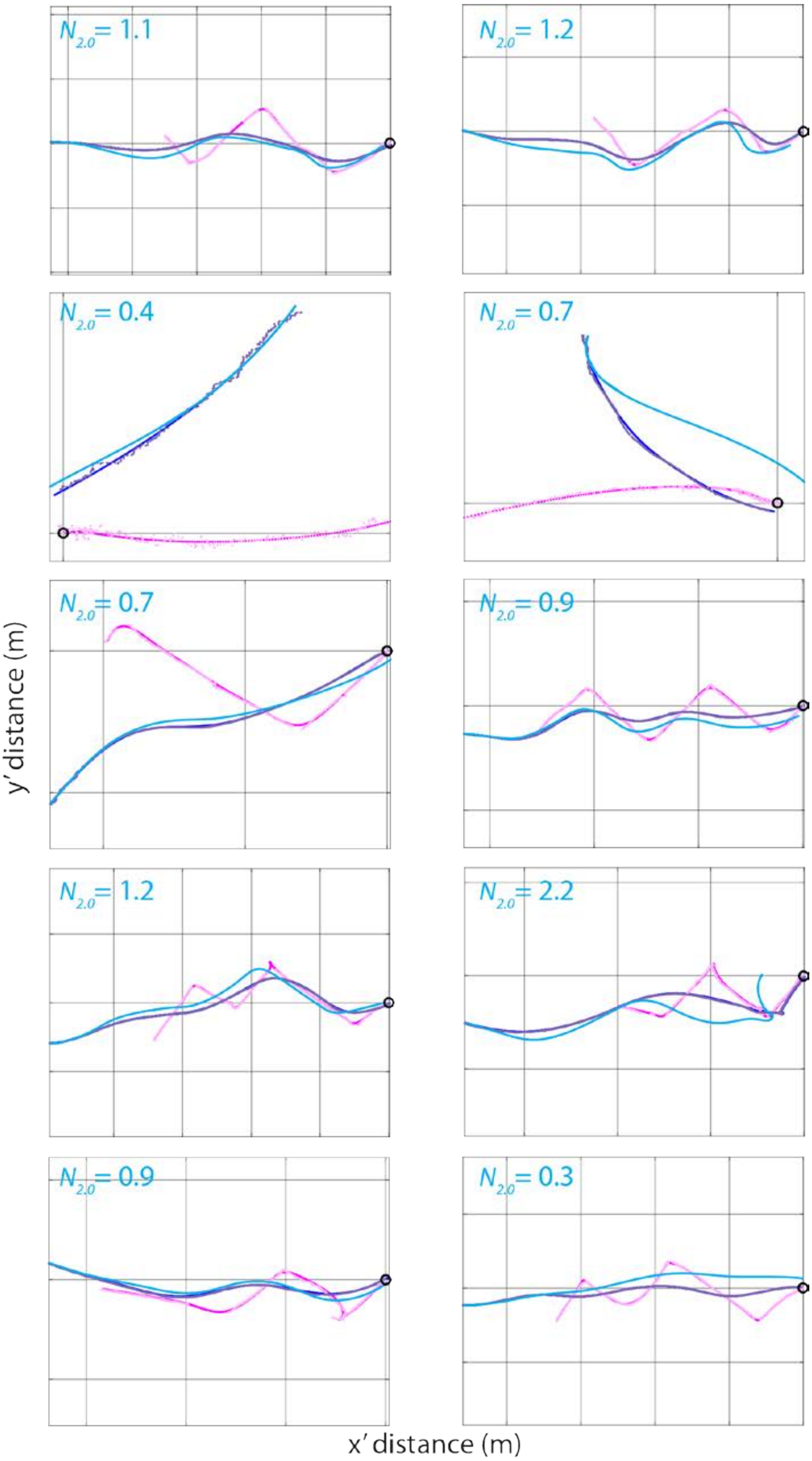


Figure 58: Proportional navigation simulations (light blue) of the spline-fitted measured data for Harris hawk 2 (dark blue) pursuing a target (magenta) moving along the ground, with a time-delay of 0.19s (see Fig.53), with corresponding values of the navigation constant. Also shown is the unsmoothed bird PCA data (light purple), and unsmoothed lure PCA data (light pink). Grid lines represent 10m intervals. Black circles indicate point of interception. Note the close match between the measured data and the simulations in many of the flights.

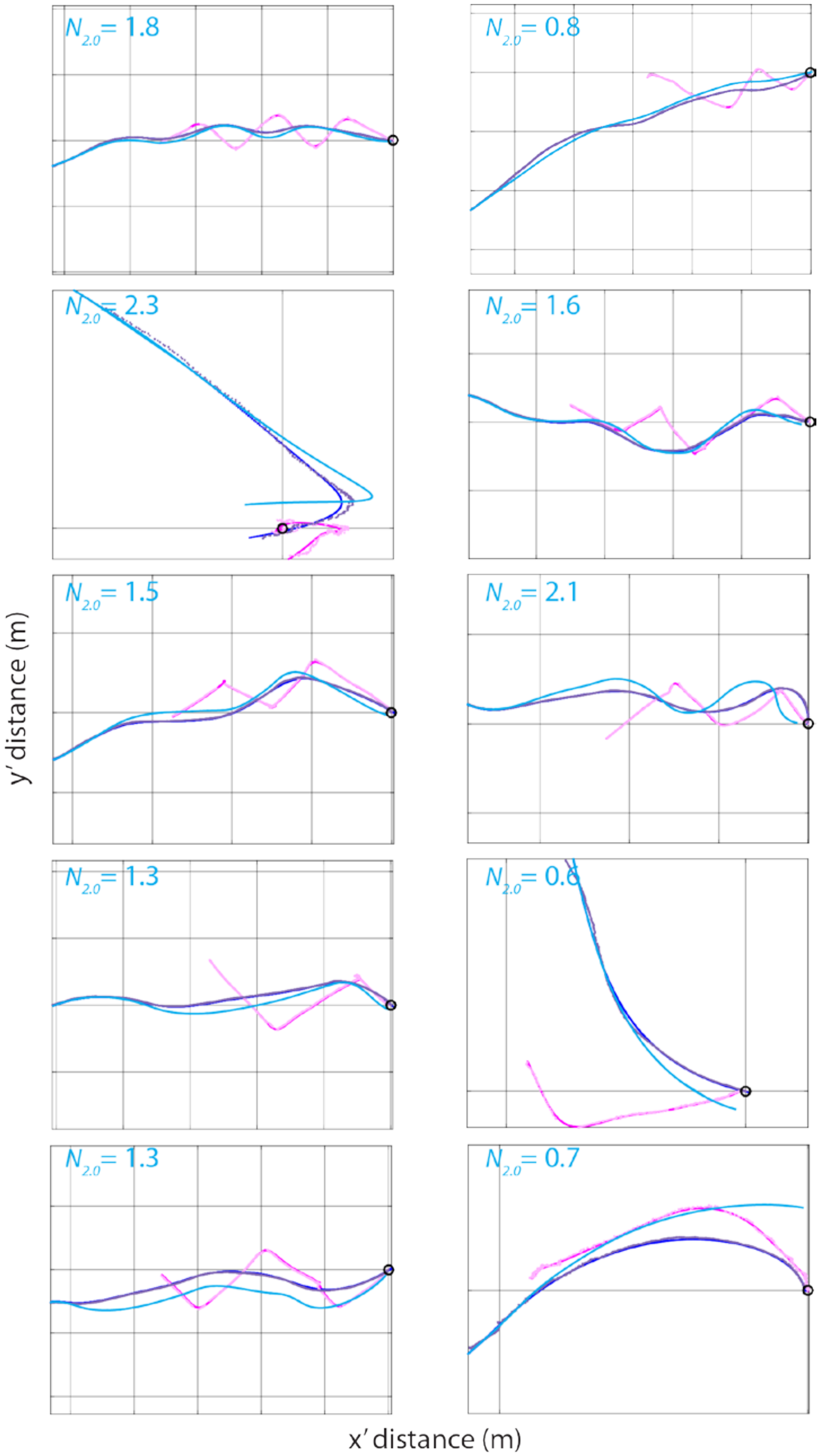


Figure 59: Proportional navigation simulations (light blue) of the spline-fitted measured data for Harris hawk 3 (dark blue) pursuing a target (magenta) moving along the ground, with a time-delay of 0.19s (see Fig.53), with corresponding values of the navigation constant. Also shown is the unsmoothed bird PCA data (light purple), and unsmoothed lure PCA data (light pink). Grid lines represent 10m intervals. Black circles indicate point of interception. Note the close match between the measured data and the simulations in many of the flights.

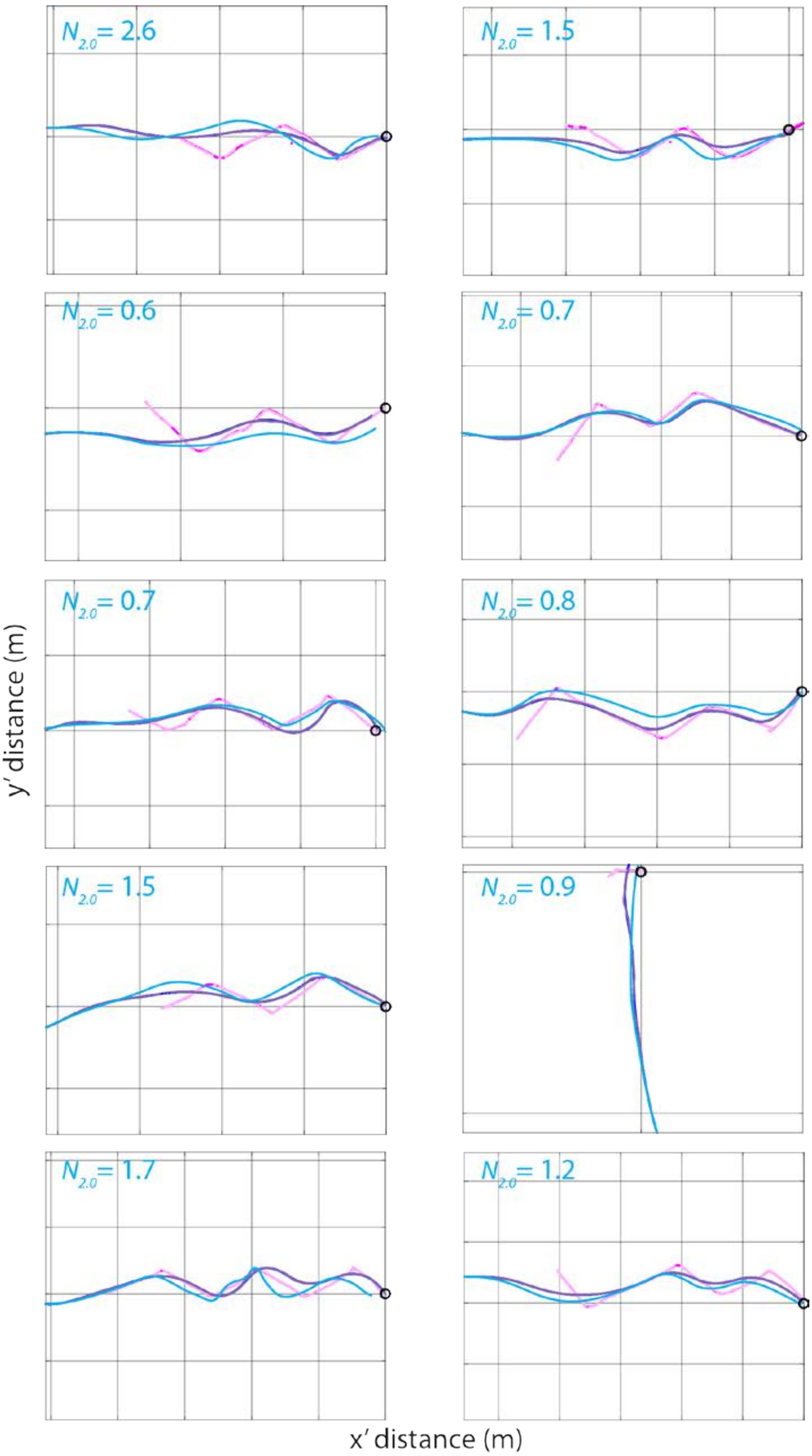


Figure 60: Proportional navigation simulations (light blue) of the spline-fitted measured data for Harris hawk 4 (dark blue) pursuing a target (magenta) moving along the ground, with a time-delay of 0.19s (see Fig.53), with corresponding values of the navigation constant. Also shown is the unsmoothed bird PCA data (light purple), and unsmoothed lure PCA data (light pink). Grid lines represent 10m intervals. Black circles indicate point of interception. Note the close match between the measured data and the simulations in many of the flights.

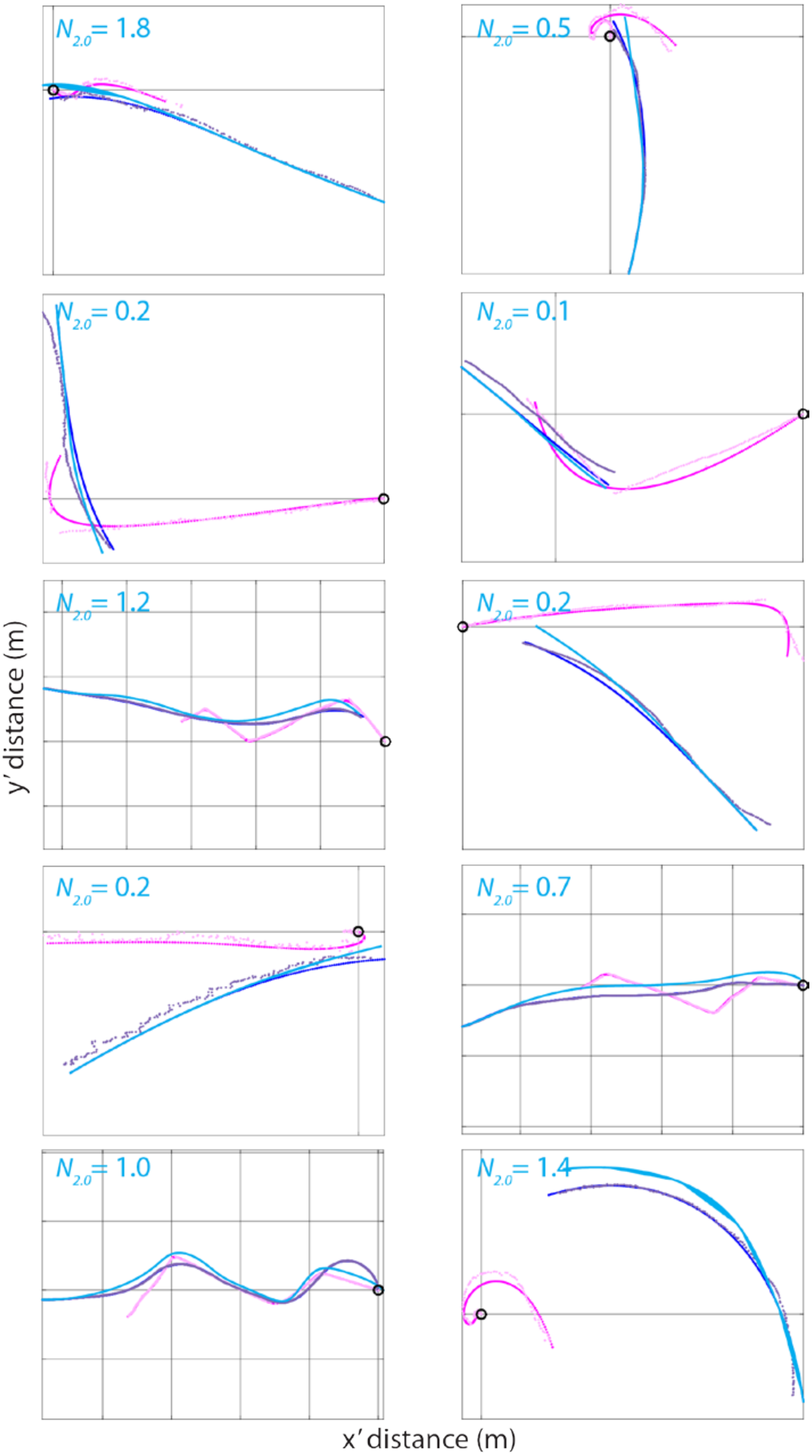


Figure 61: Proportional navigation simulations (light blue) of the spline-fitted measured data for Harris hawk 5 ((dark blue) pursuing a target (magenta) moving along the ground, with a time-delay of 0.19s (see Fig.53), with corresponding values of the navigation constant. Also shown is the unsmoothed bird PCA data (light purple), and unsmoothed lure PCA data (light pink). Grid lines represent 10m intervals. Black circles indicate point of interception. Note the close match between the measured data and the simulations in many of the flights.

Chapter 6:

General discussion

This thesis has identified the guidance law used by free-flying birds of prey in their natural environment as they intercepted artificial prey items, and represents an important advance in the field of animal pursuit. We chose to use two species with different hunting modes and evolutionary histories - Peregrine falcons and Harris' hawks. Peregrines perform a variety of hunting modes but typically hunt from the sky at prey that is on the ground as well as in the air[10, 27]. Harris' hawks typically hunt from a perch and chase prey which runs on the ground. We therefore carried out three separate experiments - air-to-ground attacks against stationary targets in peregrines, air-to-air attack against manoeuvring targets in peregrines, and air-to-ground attacks in Harris' hawks against manoeuvring ground targets. All experiments involved multiple birds, making species-specific assumptions possible. Care was taken to ensure the birds were sampled adequately, by undertaking many days of free-flight testing, giving confidence that consistent pursuit strategies are representative of that species.

Our results were consistent with the use of a proportional navigation strategy in both raptor species. That is to say, the observed trajectories were well modelled by simulations in which we assumed that the bird always flew at the same instantaneous speed as we had measured, but turned at a rate proportional to the rate of change in the simulated line-of-sight to target. Our proportional navigation simulations were computed from the initial position and flight direction of the bird only (with no positional updating), and so the very close fit we found between the measured and simulated trajectories is extremely convincing. Proportional navigation implements all of the geometrical rules described in biological pursuit research to date (dragonflies:[6-9, 144]; birds of prey:[10-12, 145]; bats:[13]), but has never been formally identified in animals. We therefore provide a unifying mechanism for predatory pursuit behaviours across species.

In Harris' hawks, the turn rate was found to be approximately equal to the line-of-sight rate with a mean time delay of 0.19s, consistent with a proportional navigation with a navigation constant N of 1. However, this is also consistent with a pure or deviated pursuit, under which the deviation angle α (between the bird's velocity vector and its line-of-sight to target) is kept constant. In this case, guidance may be implemented by responding directly to the deviation angle itself, rather than the line-of-sight rate. We also postulate that the observed time delay is due to the time taken to perform physiological responses such as visual processing, muscle activation, and dealing with unsteady aerodynamics.

The evolutionary advantage of a pure pursuit is that it is simpler to implement than proportional navigation. Pure pursuit is typically used in missile technology when faced with slower, constant-speed targets, the downside being that the pursuer's speed must be significantly greater than the target's speed[147]. This may explain why the hawks would sometimes switch to a deviated pursuit, perhaps when the target's speed reached some critical value, and needs testing. Deviated pursuit is used for faster, constant speed targets – so the advantage to switching to a deviated pursuit is that the pursuer's speed does not need to be significantly greater than the target's speed[146],

In peregrines, the navigation constant was found to vary between attack flights, with a range of $N = 0.9 - 6.0$ (n=22) for stationary targets, and N was either 0.9 or 3.4 (n=2) for aerial targets. The evidence for proportional navigation was much stronger in the flights against stationary targets, since we had many more flights which passed our strict quality control criteria. The problems with the aerial data were likely due to equipment issues – a faulty GPS causing receiver errors, associated with higher levels of manoeuvring undertaken by the birds during these experiments. Although we were very strict with our quality control criteria, it meant that we only included data of which we could be confident of its precision. In order to remove any issues concerning GPS orientation, we need to repeat the experiments with the GPS antenna mounted on the head (as the head is stabilised in flight). Although the results are based on two-dimensional trajectory analysis, we found that modelling the trajectories in three-dimensions did not result in a better fit of the proportional navigation simulations. We therefore hypothesize that the peregrines may be using separate guidance strategies in the vertical and horizontal planes.

The onboard video analysis succeeded in validating the general behaviours we recorded against those in the literature for wild peregrines[22, 23, 26, 27, 37]. The results from the 5 flights against live aerial prey identified some major problems with the previous work on visual pursuit in hawks and falcons[12, 145]. However, it showed evidence for the use of parallel navigation - which is consistent with (but insufficient to conclude) the use of proportional navigation against moving targets[146, 147].

There are considerable evolutionary advantages to flying a proportional navigation trajectory. Firstly, it corrects for wind drift, in the same way as it corrects for changes in relative position due to target movement (if the pursuer drifts relative to the target). This explains why we did not incorporate wind measurements into our trajectory simulations. Note that if the target and the pursuer drift together, the line-of-sight angle is not affected. Under proportional navigation the time to intercept is reduced for unpredictable prey[13], and the accelerations required during the terminal phase of interception are also reduced[147]. In addition, proportional navigation is simple to implement as only information on line-of-sight rate is required and not the speed or direction of the target, thus it relies on relative rather than absolute information.

In one of the most recent studies of animal pursuit, by Mischiati *et al* (2015) on prey interception by dragonflies[187], they conclude that most steering behaviours are under model-driven control. If we apply the definitions from this work then closed-loop (i.e. reactive) control sufficiently explains the attack trajectories of our hawks and falcons[144]. This holds across target behaviours, as reactive control explained our observations against both non-manoeuvring and evasively manoeuvring targets. The authors state that a closed-loop guidance law is less computationally demanding than open-loop control and allows for error caused by wind drift or other source (as does proportional navigation) though they offer no explanation as to how this may be implemented, and so their approach is too simplistic.

Though proportional navigation is sufficient to explain our observed attack trajectories, whether the birds are directly implementing this guidance law within their control system is difficult to determine using the black box modelling we perform here. In the case of the variable navigation constant in peregrines, it is difficult to see how this could be achieved by any models other than directly implementing proportional navigation within their guidance system. Therefore a reasonable explanation of our data is that peregrine falcons do actively implement a pure proportional navigation strategy.

In the case of a fixed navigation constant in Harris' hawks, an alternative model also explains the data, under which the birds are not required to respond to the line-of-sight rate as they would be under proportional navigation. Instead, the hawks may be implementing a pure pursuit, by responding to the instantaneous position of the target and measuring the line-of-sight angle directly.

Until recently, hawks and falcons were grouped closely on the evolutionary tree due to shared morphological traits such as sharp beaks, talons and large eyes[188]. We now know that although these species share many characteristics, these have transpired through convergent evolution[14]. Peregrine falcons and Harris' hawks are now believed to be from two very different lineages which diverged more than 60 million years ago[14]. This means that they have evolved their pursuit behaviours completely independently, and we therefore postulate two scenarios; i) both hawks and falcons have converged on the same guidance law of proportional navigation but use different values of the navigation constant, or ii) hawks have evolved different underlying guidance principles to falcons by implementing a pure pursuit strategy.

We can attempt to shed some light on the possible adaptive explanations for this by considering the pursuit trajectories in the context of their foraging habits. Harris' hawks generally perform surprise ground attacks in cluttered habitat at a close distance to prey. We speculate that proportional navigation may not work well in cluttered habitats, since the feedback loop does not incorporate obstacle avoidance (Fig.62). Implementing a pure pursuit therefore seems most appropriate in a cluttered habitat, since a consequence of following the prey's instantaneous position means the predator automatically avoids all obstacles, as long as the prey has (though for this to be guaranteed, the predator needs to be following closely behind the prey, and have a minimal time delay; Fig.62). In contrast, peregrine falcons generally perform aerial attacks in the open often at a great distance to the prey. Implementing proportional navigation with a variable navigation constant seems most appropriate in open habitat, since it provides a flexible flight trajectory and reduces the time to intercept.

Furthermore, the differences in pursuit strategy between species may well be a result of differing wing morphology and resultant flight performance. Harris' hawks have lower aspect ratio wings (shorter and broader), which means they are able to roll more quickly and perform tight manoeuvres in confined spaces (i.e. dense vegetation)[15, 17]. Whereas peregrines have higher aspect ratio wings (long and pointed) to accommodate high speed flight when closing in on distant prey[16, 17].

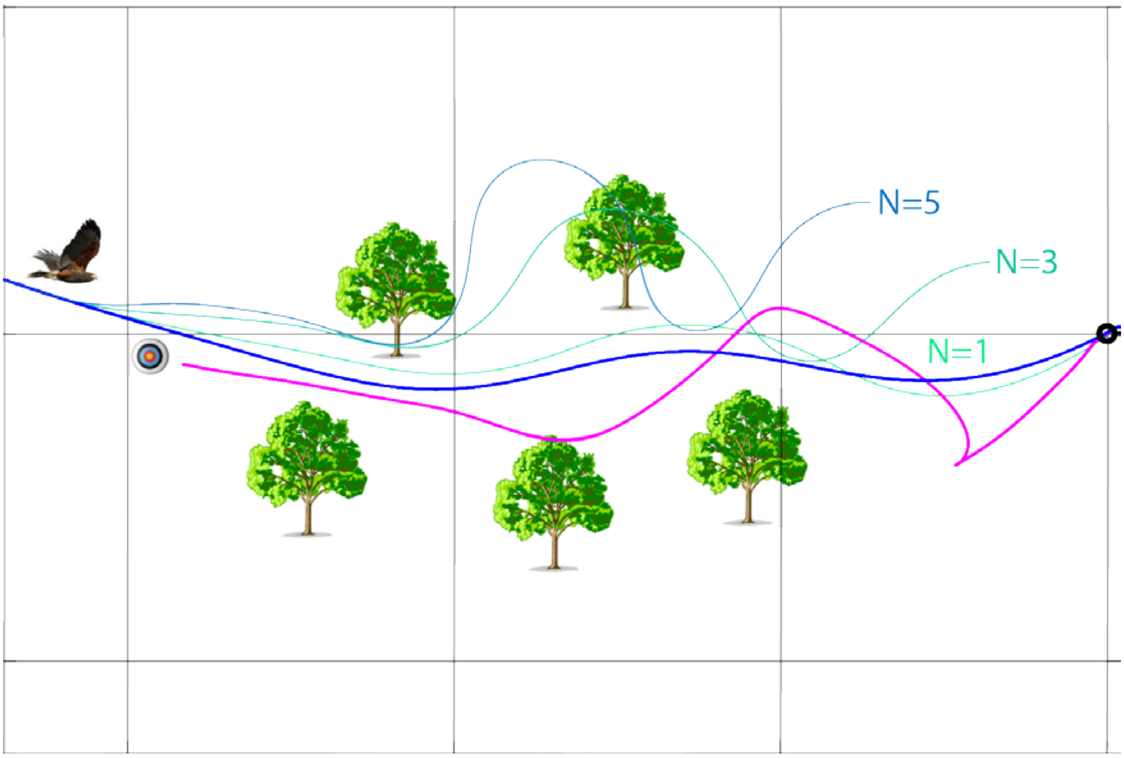


Figure 62. Spline-fitted measured data from one Harris hawk flight (dark blue) against a lure towed along the ground (magenta), showing three proportional navigation simulations where $N = 1$, $N = 3$ and $N = 5$, in a fictitious cluttered habitat. Only when the hawk follows a pure pursuit ($N = 1$) does it avoid all the trees. Black circle represents the point of interception. Grid lines denote 10m intervals.

Our work allows us to reject Tucker's hypothesis which proposed that falcons use a deviated pursuit[10, 11]. This earlier work stated that a peregrine would keep its head in line with its body at all times for streamlining, and would turn so as to keep its target on the left or right deep fovea. Since the deep fovea is directed approximately 45˚ to the side, the result of this strategy would be a deviated pursuit with a constant deviation angle of 45˚. In contrast, our on-board video data suggests peregrines stabilise their gaze against the visual scene and use fast saccadic head movements to keep the image of the target within their frontal field of view. Whereas our ground photography data suggests Harris’ hawks stabilise their gaze on the target rather than the background, thereby establishing a head-fixed reference frame to keep it in their frontal field of view.

The frontal field of view is said to be used only for close or slow moving prey, and that the deep fovea or lateral field of view is used for fast prey or when it is more than 40m away[11, 77, 88, 95]. Therefore, it is possible that by only analysing the terminal sections of the flights, the prey was not sufficiently distant or may not have been fast enough to necessitate the use of the lateral field of view. However, it has been suggested for birds that knowing the distance to prey is less important than determining its direction and time to contact, and travel direction is most efficiently determined when heading straight towards the prey – i.e. using binocular vision[93, 95]. This provides evidence for an evolutionary basis for the use of the frontal field of view during hunting in raptors.

A necessary condition for implementing proportional navigation is that a non-rotating reference direction must be established, against which the line-of-sight rate can be measured. We hypothesise that this inertial reference is established visually in peregrines, by stabilizing the head with respect to distant features of the visual landscape (Fig.63). In this case, the line-of-sight rate needed to command the turn rate would simply equal the angular rate at which the target drifted across the retina. In Harris' hawks, the drift of the target across the retina cannot be directly measured without knowing how the angle of the head relates to the body (assuming the body is aligned with its velocity vector). We hypothesise that Harris' hawks will stabilise their head in relation to the target by performing head rotations relative to the target along with active steering in flight to minimise retinal drift of the prey image (Fig.63). Therefore, any deviation from 0° in the angle between the head and body can be directly nullified based on sensory feedback from the target-image drift, thereby implementing a pure pursuit without information on the line-of-sight rate.

The cost of not implementing proportional navigation is a need to discriminate drift of the target-image which arises through motion of the target alone, from the optic flow of the whole visual scene that arises from self-motion, and so head movements may serve to nullify this and reduce steering errors. In dragonflies, compensatory head movements have been found to drive prey-image drift cancellation[144]. In addition, by moving the head independently, the initial reaction time of the sensory system may be reduced, since whole-body movements require a longer time to execute – possibly important for Harris' hawks which pursue highly agile prey such as Jackrabbits.

The different visual strategies between hawks and falcons may be associated with differences in visual field arrangement between species, and in turn, due to the visual complexity of the habitats in which they hunt. In the absence of detailed eye anatomy information for peregrine falcons and Harris' hawks, we can only make assumptions based on similar Falconiformes and Accipitriformes. Cooper's hawks have a wider binocular field and higher degree of eye movement (8° compared to 1° in American kestrels[77]), which increases binocular overlap to improve capture in visually complex environments and possibly overcome the field of view limitations associated with the head-fixed approach. American kestrels have wider lateral areas[77] which may enhance detection and depth perception of distance prey. In support, a study of prey-scanning strategies (head movement rates and duration) in perched raptors showed inter-species variation in relation to visual field arrangement and the visual complexity of the habitat[88].

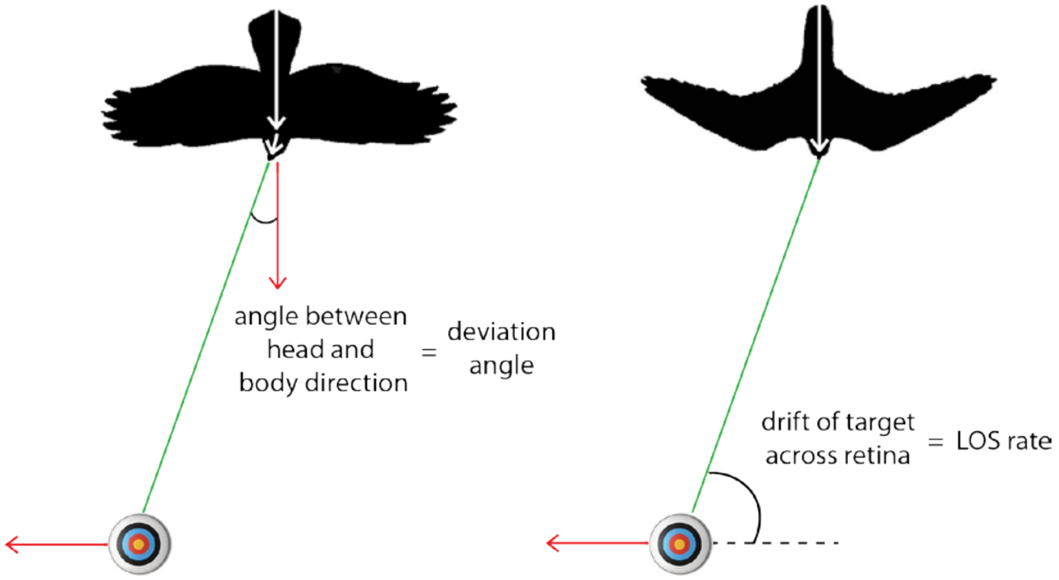


Figure 63. Proposed visually guided pursuit behaviours of Harris' hawks and peregrine falcons. Left; hawks stabilise their head in relation to the target by performing compensatory head rotations and require knowledge of their head angle relative to the body (assuming the body is aligned with the velocity vector). Right; falcons stabilise their head and body relative to the environment and measure the change in line-of-sight (LOS) angle to the target as it moves across their field of view.

Guided missiles commonly use gimballed seekers to continuously track the target and measure its line-of-sight rate in relation to an inertial reference derived from on-board gyro sensors. Harris' hawks are therefore using their head rather like a seeker, in contrast to peregrine falcons - thus peregrines and Harris' hawks implement their guidance strategies through very different mechanisms. Future work will aim to determine the role of head and eye movements during pursuit.

Our analysis of GPS positional error has major implications for other studies which employ GPS devices for positional tracking, and we have demonstrated a very good quality control test. We therefore recommend that all studies using GPS devices should measure the discrepancy between Doppler speed and speed derived from differencing the latitudinal and longitudinal data, as a means of filtering out problematic data, using some defined threshold.

The birds in this study are the first organisms shown to use proportional navigation when intercepting targets. In biology, though pursuit dynamics have been analysed from the perspective of guidance laws in a small number of papers, the context of these pursuits are not predator-prey interactions[1, 2, 5, 143]. The majority of biological research has only sought to explain the guidance problem by identifying the simple geometric rules characterising the observed flight trajectories (dragonflies:[6-9, 144]; birds of prey:[10-12, 145]; bats:[13]). We therefore expect the guidance law of proportional navigation to be widely used across living organisms, and note that proportional navigation is in principle capable of producing trajectories following all of the geometric rules that have been identified in nature to date (as well as many intermediate trajectories), according to the value of the navigation constant.

It is of particular interest that peregrine falcons vary their navigation constant, because many modern missile guidance systems use a variant of pure proportional navigation in which the navigation constant is updated in light of information about the target[146, 147, 150]. Typically these systems introduce a bias term, which acts as a predictor of target acceleration, to select the value of the navigation constant giving the best performance against some specified criterion such as time to intercept[146, 147, 150]. We hypothesise that variation in the navigation constant of peregrines may be similarly adaptive - i.e. that birds may be optimising their pursuit trajectory depending on target behaviour, but a formal test of this hypothesis must await further studies against manoeuvring targets. The study by Kane et al (2015)[145] provides support that hunting strategies are dependent on prey behaviour, as they found that birds of prey used a different strategy when flying at stationary prey than when flying at manoeuvring prey.

Other reasons why peregrines may vary the value of their navigation constant may be due to the constraints imposed by the flight dynamics. Figure 64 illustrates how the shape of the proportional navigation trajectory is distinctly varied for different values of N (for ±0.5, ±1.0 and ±1.5 of the estimated N). Each flight path therefore requires different flight dynamics (accelerations, turn rates, speed, etc.) and thus it may be physical constraints which determine the value of the navigation constant.

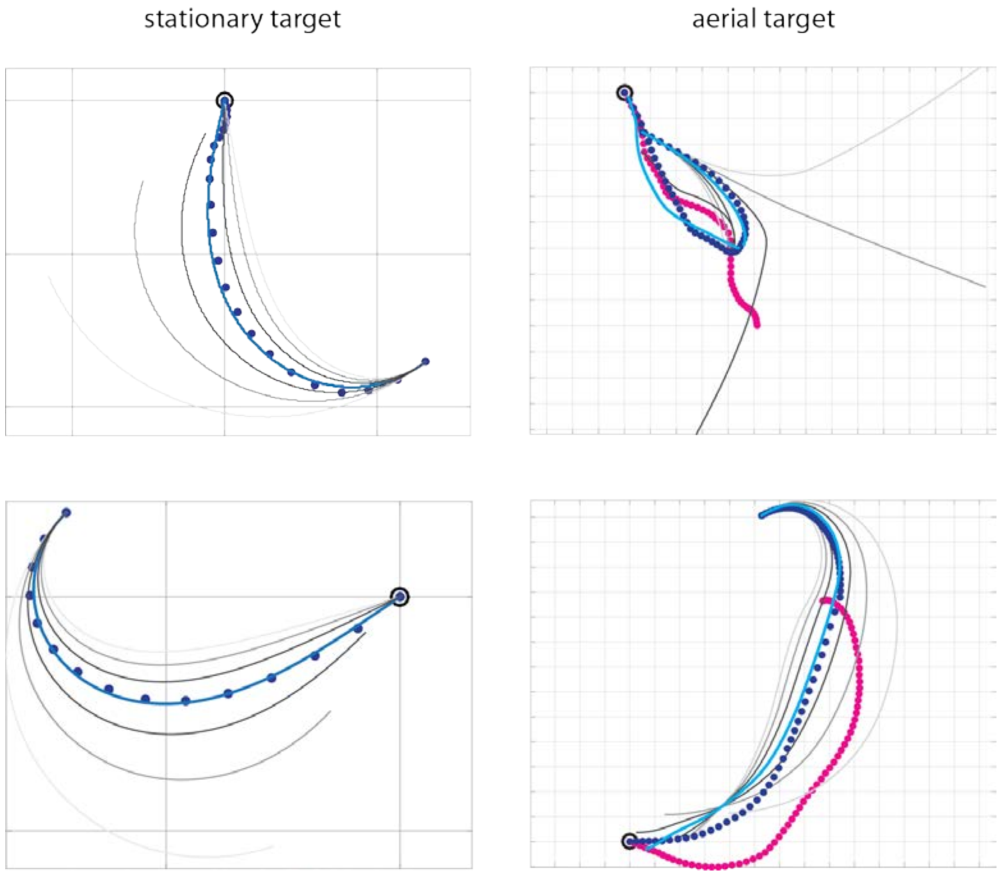


Figure 64: Peregrine intercept flights (blue points) against stationary targets and moving aerial targets (magenta points), with corresponding proportional navigation simulations (cyan) for our estimates of N (using the 1% error threshold for the stationary target flights and the 2% error threshold for the aerial target flights). Grey lines show the predicted trajectories for values of ±0.5, ±1.0 and ±1.5 N - note that they are clearly distinguishable trajectories. Grid lines denote 10m intervals.

Alternatively, perhaps the variation in navigation constant – leading to different curved paths - is an adaptation to restrict prey from learning the family of possible pursuit curves, and help disguise the predator's approach. It follows that we would expect species with different wing morphologies and ecological niches to have evolved to use different values of N – consistent with our findings.

We hypothesize that all Falconidae species which hunt prey in the open (such as hobbys pursuing dragonflies), will implement proportional navigation during prey pursuit, and will vary the value of their navigation constant between flights. The need for adopting the most time-optimal approach against manoeuvring prey may present a significant evolutionary pressure. In addition, this may extend to other non-raptor species which perform aerial prey pursuits in the open (namely aerial insectivores; such as swallows, swifts, nightjars, and non-avian species including dragonflies and certain bat species). In contrast, we expect that *Accipiter* species which perform ambush attacks in cluttered habitats (such as goshawks and sparrowhawks pursuing small birds) will adopt a pure pursuit. In these cases, the need for a simple strategy which incorporates obstacle avoidance may be very strong selective pressures (since the consequence of unsuccessful obstacle avoidance may result in death). This may also extend to many Strigiform species which pursue small mammals in cluttered habitats.

Following this line of reasoning, we may then expect terrestrial species which adopt a stealth approach to hunting, in cluttered habitats, (such as leopards and tigers) to also adopt a pure pursuit. Whereas terrestrial predators which generally hunt prey in more open ground over longer distances (such as cheetahs and lions) may instead use proportional navigation. The study by Wilson, (2013)[189] shows that cheetahs do indeed run curving trajectories during prey pursuit (qualitatively consistent with a proportional navigation), however without any information on prey position we are unable to draw any firm conclusions about their underlying guidance strategy.

Furthermore, species may be phylogenetically constrained - for example, birds with high aspect ratio wings may not be able to turn quickly enough in the terminal phase of interception to adopt a pure pursuit (hence, this problem is eliminated using proportional navigation). Therefore we predict that predatory animals have evolved their guidance strategies as a result of the behaviour and habitat of their prey, and are in turn influenced by physiological constraints (e.g. wing shape). Diving seabirds are an interesting group - their high aspect ratio wings have evolved for prey location (gliding over the ocean in search of fish shoals), and their shape does not play a significant part in their predatory attack behaviour (they are swept back during plunges at submerged fish)[144]. But due to the short-range stealth-type nature of their attack dives, we thus expect evolution to favour a simple and direct strategy - i.e. a pure pursuit. We assume that pursuit behaviours are inherent, and not learned behaviours, since our juvenile peregrines (which had never previously hunted) and our adult peregrines were shown to use the same strategy.

Overall, the literature on hunting modes in wild peregrines shows that individual birds perform a whole suite of hunting behaviours, including attacks on both stationary ground prey and moving aerial prey[27, 31, 34]. The literature on wild Harris' hawks shows that they most often perform perched attacks against highly-manoeuvrable ground prey[15, 44]. Therefore we can be confident that our experiments conducted in this thesis were ecologically relevant. In addition, we have shown that a qualitative approach to examining pursuit behaviour by means of the flight geometry - as in the paper by Kane *et al* (2014) - does not explain the overarching question of how birds implement their intercept flight.

In summary, proportional navigation may be a good strategy for peregrine falcons which perform a repertoire of different hunting modes generally initiated at greater distance from prey in open habitat. Selection may thus favour a strategy which is most time-optimal for long distance chases, thereby limiting the energetic costs, and also enabling a flexible trajectory if the prey decides to take evasive action. Whereas a simple pure pursuit may be most suitable for Harris' hawks which have less variety in their hunting modes and initiate their pursuits much closer to prey and in cluttered habitat. In this case, selection may favour the strategy which is simplest to implement and that incorporates obstacle avoidance (under certain conditions). Hawks and falcons also appear to use different *visual* strategies for pursuing prey, therefore future work needs to investigate their eye and head movements during pursuit. A further avenue is to study what counter strategies the prey may have, and to model the pursuer trajectories over different phases of the attack - e.g. immediately after a miss. We conclude that birds of prey and missile engineers have solved the problem of target interception through the use of proportional navigation, but have implemented this same guidance law through fundamentally different mechanisms.

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References

1. Land, M.F., *Chasing and Pursuit in the Dolichopodid Fly Poecilobothrus-Nobilitatus.* Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 1993. 173(5): p. 605-613.
2. Collett, T.S. and M.F. Land, *Visual Control of Flight Behavior in Hoverfly, Syritta-Pipiens L.* Journal of Comparative Physiology, 1975. 99(1): p. 1-66.
3. Collett, T.S. and M.F. Land, *How Hoverflies Compute Interception Courses.* Journal of Comparative Physiology, 1978. 125(3): p. 191-204.
4. Land, M.F., *Visual Tracking and Pursuit - Humans and Arthropods Compared.* Journal of Insect Physiology, 1992. 38(12): p. 939-951.
5. Land, M.F. and T.S. Collett, *Chasing Behavior of Houseflies (Fannia-Canicularis) - Description and Analysis.* Journal of Comparative Physiology, 1974. 89(4): p. 331-357.
6. Olberg, R.M., *Visual control of prey-capture flight in dragonflies.* Current Opinion in Neurobiology, 2012. 22(2): p. 267-271.
7. Olberg, R.M., et al., *Eye movements and target fixation during dragonfly prey-interception flights.* Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology, 2007. 193(7): p. 685-693.
8. Olberg, R.M., A.H. Worthington, and K.R. Venator, *Prey pursuit and interception in dragonflies.* Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 2000. 186(2): p. 155-162.
9. Mizutani, A., J.S. Chahl, and M.V. Srinivasan, *Motion camouflage in dragonflies.* Nature, 2003. 423(6940): p. 604-604.
10. Tucker, V.A., et al., *Curved flight paths and sideways vision in peregrine falcons (Falco peregrinus).* Journal of Experimental Biology, 2000. 203(24): p. 3755-3763.
11. Tucker, V.A., *The deep fovea, sideways vision and spiral flight paths in raptors.* Journal of Experimental Biology, 2000. 203(24): p. 3745-3754.
12. Kane, S.A. and M. Zamani, *Falcons pursue prey using visual motion cues: new perspectives from animal-borne cameras.* Journal of Experimental Biology, 2014. 217(2): p. 225-234.
13. Ghose, K., et al., *Echolocating bats use a nearly time-optimal strategy to intercept prey.* Plos Biology, 2006. 4(5): p. 865-873.
14. Jarvis, E.D., et al., *Whole-genome analyses resolve early branches in the tree of life of modern birds.* Science, 2014. 346(6215): p. 1320-1331.
15. Jaksic, F.M. and J.H. Carothers, *Ecological, Morphological, and Bioenergetic Correlates of Hunting Mode in Hawks and Owls.* Ornis Scandinavica, 1985. 16(3): p. 165-172.
16. Tobalske, B.W., *Morphology, velocity, and intermittent flight in birds.* American Zoologist, 2001. 41(2): p. 177-187.
17. Norberg, U.M., *How a Long Tail and Changes in Mass and Wing Shape Affect the Cost for Flight in Animals.* Functional Ecology, 1995. 9(1): p. 48-54.
18. Stager, K.E., *A group of bat-eating duck hawks.* Condor, 1941. 43: p. 137-139.
19. Bradley, D.M.a.L.W.O., *The diet of Peregrine Falcons at Rankin Inlet, Northwest Territories: an unusually high proportion of mammalian prey. .* Condor, 1991. 93: p. 193–197.
20. Stevens, L.E., B.T. Brown, and K. Rowell, *Foraging Ecology of Peregrine Falcons (Falco Peregrinus) Along the Colorado River, Grand Canyon, Arizona.* Southwestern Naturalist, 2009. 54(3): p. 284-299.
21. Ferguson-Lees, J., Christie, D.A., *Raptors of the world.* Princeton University Press, Princeton, NJ U.S.A., 2001.

22. White, C.M., and Nelson, R. W., *Hunting range and strategies of tundrabreeding Peregrine and Gyrfalcons observed from a helicopter.* Journal of Raptor Research 1991. 25: p. 49-62.
23. Buchanan, J.B., S. G. Herman, and T. M. Johnson., *Success rates of the Peregrine Falcon hunting Dunlin during winter.* Raptor Research, 1986. 20: p. 130–131.
24. Ratclife, D., *The Peregrine Falcon.* Smithsonian, 1981. 11(12): p. 156-158.
25. Court, G.S., C.C. Gates, and D.A. Boag, *Natural-History of the Peregrine Falcon in the Keewatin District of the Northwest-Territories.* Arctic, 1988. 41(1): p. 17-30.
26. Cresswell, W., *Surprise as a winter hunting strategy in Sparrowhawks Accipiter nisus, Peregrines Falco peregrinus and merlins F-columbarius.* Ibis, 1996. 138(4): p. 684-692.
27. Dekker, D., *Hunting Success Rates, Foraging Habits, and Prey Selection of Peregrine Falcons Migrating through Central Alberta.* Canadian Field-Naturalist, 1980. 94(4): p. 371-382.
28. Brown, L., *British Birds of Prey.* Collins, London, 1976.
29. Tucker, V.A., *Gliding flight: Speed and acceleration of ideal falcons during diving and pull out.* Journal of Experimental Biology, 1998. 201(3): p. 403-414.
30. Tucker, V.A., T.J. Cade, and A.E. Tucker, *Diving speeds and angles of a gyrfalcon (Falco rusticolus).* Journal of Experimental Biology, 1998. 201(13): p. 2061-2070.
31. Rudebeck, G., *The Choice of Prey and Modes of Hunting of Predatory Birds with Special Reference to Their Selective Effect.* Oikos, 1951. 3(2): p. 200-231.
32. Rudebeck, G., *The Choice of Prey and Modes of Hunting of Predatory Birds with Special Reference to Their Selective Effect.* Oikos, 1950. 2(1): p. 65-88.
33. Palleroni, A., et al., *Predation - Prey plumage adaptation against falcon attack.* Nature, 2005. 434(7036): p. 973-974.
34. Treleaven, R.B., *High and Low Intensity Hunting in Raptors.* Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology, 1980. 54(4): p. 339-345.
35. Dekker, D. and L. Bogaert, *Over-ocean hunting by Peregrine Falcons in British Columbia.* Journal of Raptor Research, 1997. 31(4): p. 381-383.
36. Herbert, R.A.a.H., K. G. S., *Behavior of Peregrine Falcons in the New York City region.* Auk, 1965. 82: p. 62-94.
37. Dekker, D., *Prey Capture by Peregrine Falcons Wintering on Southern Vancouver-Island, British-Columbia.* Journal of Raptor Research, 1995. 29(1): p. 26-29.
38. Dekker, D., *Peregrine Falcon Predation on Ducks in Alberta and British-Columbia.* Journal of Wildlife Management, 1987. 51(1): p. 156-159.
39. Dekker, D., *Peregrine Falcon and Merlin Predation on Small Shorebirds and Passerines in Alberta.* Canadian Journal of Zoology-Revue Canadienne De Zoologie, 1988. 66(4): p. 925-928.
40. Weir, D.N., *Wild peregrines and grouse.* Falconer, 1978. 7: p. 98-102.
41. Jenkins, A.R., *Hunting mode and success of African Peregrine Falcons: Does nesting habitat quality affect foraging efficiency?* Ibis, 2000. 142: p. 235–246.
42. Kenward, R.E., *Goshawk Hunting Behavior, and Range Size as a Function of Food and Habitat Availability.* Journal of Animal Ecology, 1982. 51(1): p. 69-80.
43. Figueroa, R.A. and D. Gonzalez-Acuna, *Prey of the Harris's Hawk (Parabuteo unicinctus) in a suburban area of southern Chile.* Journal of Raptor Research, 2006. 40(2): p. 164-168.
44. Jimenez, J.E. and F.M. Jaksic, *Observations on the Comparative Behavioral Ecology of Harris Hawk in Central Chile.* Journal of Raptor Research, 1993. 27(3): p. 143-148.
45. Mader, W.J., *Breeding-Behavior of a Polyandrous Trio of Harris Hawks in Southern Arizona.* Auk, 1979. 96(4): p. 776-788.

46. Coulson, J.O. and T.D. Coulson, *Reexamining Cooperative Hunting in Harris's Hawk (Parabuteo Unicinctus): Large Prey or Challenging Habitats?* Auk, 2013. 130(3): p. 548-552.
47. Santander, F.J., et al., *Prey of Harris' Hawks (Parabuteo Unicinctus) during Autumn and Winter in a Coastal Area of Central Chile.* Southwestern Naturalist, 2011. 56(3): p. 417-422.
48. Bednarz, J.C. and J.D. Ligon, *A Study of the Ecological Bases of Cooperative Breeding in the Harris Hawk.* Ecology, 1988. 69(4): p. 1176-1187.
49. Dawson, J.W., *The cooperative breeding system of the Harris' hawk in Arizona.* Master's thesis, University of Arizona, Tuscon, 1988.
50. Bednarz, J.C., *Cooperative Hunting in Harris Hawks (Parabuteo-Unicinctus).* Science, 1988. 239(4847): p. 1525-1527.
51. Dawson, J.W. and R.W. Mannan, *Dominance Hierarchies and Helper Contributions in Harris Hawks.* Auk, 1991. 108(3): p. 649-660.
52. Beebe, F.L., *Field studies of the falconiformes of British Columbia.* British Columbia Provincial Museum Occas. Pap. , 1974. 17: p. 163
53. Mader, W.J., *Extra Adults at Harris Hawk Nests.* Condor, 1975. 77(4): p. 482-485.
54. Robinson, S.K. and R.T. Holmes, *Foraging Behavior of Forest Birds - the Relationships among Search Tactics, Diet, and Habitat Structure.* Ecology, 1982. 63(6): p. 1918-1931.
55. Martin, T.E., Karr, J. R., *Behavioural plasticity of foraging maneuvres of migratory warblers: multiple selection periods for niches?* Studies in Avian Biology 1990. 13: p. 353-359.
56. Neuweiler, G., *Auditory Adaptations for Prey Capture in Echolocating Bats.* Physiological Reviews, 1990. 70(3): p. 615-641.
57. Remsen, J.V.a.R., S. K., *A classification scheme for foraging behaviour of birds in terrestrial habitats.* Studies in Avian Biology, 1990. 13: p. 144-160.
58. Wakeley, J.S., *Activity periods, hunting methods, and efficiency of the ferruginous hawk.* Raptor Research, 1974. 8: p. 67-72.
59. Wakeley, J.S., *Use of hunting methods by ferruginous hawks in relation to vegetation density.* Raptor Research 1979. 13: p. 116-119
60. Shrubb, M., *Farming Influences on the Food and Hunting of Kestrels.* Bird Study, 1980. 27(2): p. 109-115.
61. Village, A., *The ecology of the kestrel (Falco tinnunculus) in relation to vole abundance at Eskdalemuir, south Scotland* Unpublished Ph.D. thesis, Edinburgh University, 1980.
62. Fitzpatrick, J.W., *Form, Foraging Behavior, and Adaptive Radiation in the Tyrannidae.* Neotropical Ornithology 1985. 36: p. 447-470
63. Garamszegi, L.Z., A.P. Moller, and J. Erritzoe, *Coevolving avian eye size and brain size in relation to prey capture and nocturnality.* Proceedings of the Royal Society B-Biological Sciences, 2002. 269(1494): p. 961-967.
64. Waldvogel, J.A., *The Birds-Eye-View.* American Scientist, 1990. 78(4): p. 342-353.
65. Güntürkün, O., *Sensory physiology: vision.* Sturkie's Avian Physiology, 2000. 5: p. 1-19.
66. Martin, G.R., *Total Panoramic Vision in the Mallard Duck, Anas-Platyrhynchos.* Vision Research, 1986. 26(8): p. 1303-1305.
67. Brooke, M.D., S. Hanley, and S.B. Laughlin, *The scaling of eye size with body mass in birds.* Proceedings of the Royal Society B-Biological Sciences, 1999. 266(1417): p. 405-412.
68. Hughes, A., *The topography of vision in mammals of contrasting lifestyles: comparative optics and retinal organisation.* In The Visual System in Vertebrates 1977. VII/5: p. 613-756.

69. Maddocks, S.A., A.R. Goldsmith, and I.C. Cuthill, *The influence of flicker rate on plasma corticosterone levels of European starlings, Sturnus vulgaris.* General and Comparative Endocrinology, 2001. 124(3): p. 315-320.
70. Chen, D.M., J.S. Collins, and T.H. Goldsmith, *The Ultraviolet Receptor of Bird Retinas.* Science, 1984. 225(4659): p. 337-340.
71. Emmerton, J. and J.D. Delius, *Wavelength Discrimination in the Visible and Ultraviolet-Spectrum by Pigeons.* Journal of Comparative Physiology, 1980. 141(1): p. 47-52.
72. Jane, S.D. and J.K. Bowmaker, *Tetrachromatic Color-Vision in the Duck (Anas-Platyrhynchos L) - Microspectrophotometry of Visual Pigments and Oil Droplets.* Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 1988. 162(2): p. 225-235.
73. Jones, M.P., K.E. Pierce, and D. Ward, *Avian vision: A review of form and function with special consideration to birds of prey.* Journal of Exotic Pet Medicine, 2007. 16(2): p. 69-87.
74. Lind, O., et al., *Ultraviolet sensitivity and colour vision in raptor foraging.* Journal of Experimental Biology, 2013. 216(10): p. 1819-1826.
75. Martin, G.R. and G. Katzir, *Visual fields in short-toed eagles, Circaetus gallicus (Accipitridae), and the function of binocularity in birds.* Brain Behavior and Evolution, 1999. 53(2): p. 55-66.
76. Martin, G.R., *Visual fields and their functions in birds.* Journal of Ornithology, 2007. 148: p. S547-S562.
77. O'Rourke, C.T., et al., *Hawk Eyes I: Diurnal Raptors Differ in Visual Fields and Degree of Eye Movement.* Plos One, 2010. 5(9).
78. Fernandez-Juricic, E., et al., *The visual fields of two ground-foraging birds, House Finches and House Sparrows, allow for simultaneous foraging and anti-predator vigilance.* Ibis, 2008. 150(4): p. 779-787.
79. Iwaniuk, A.N., et al., *Relative Wulst volume is correlated with orbit orientation and binocular visual field in birds.* Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology, 2008. 194(3): p. 267-282.
80. Martin, G.R. and G. Katzir, *Sun shades and eye size in birds.* Brain Behavior and Evolution, 2000. 56(6): p. 340-344.
81. Martin, G.R., *The subtlety of simple eyes: the tuning of visual fields to perceptual challenges in birds.* Philosophical Transactions of the Royal Society B-Biological Sciences, 2014. 369(1636).
82. Martin, G.R. and T. Piersma, *Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper.* Proceedings of the Royal Society B-Biological Sciences, 2009. 276(1656): p. 437-445.
83. Curtis, O.E., Rosenfield, R N, Bielefeldt, J, *Cooper’s Hawk (Accipiter cooperii).* The Birds of North America Online (A. Poole, ed.), 2006. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/075.
84. Changizi, M.A. and S. Shimojo, *"X-ray vision" and the evolution of forward-facing eyes.* Journal of Theoretical Biology, 2008. 254(4): p. 756-767.
85. Heesy, C.P., *Seeing in Stereo: The Ecology and Evolution of Primate Binocular Vision and Stereopsis.* Evolutionary Anthropology, 2009. 18(1): p. 21-35.
86. Smallwood, J.A., and Bird D.M., *American Kestrel (Falcosparverius).* The Birds of North America Online (A. Poole, ed.), 2002. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/602.
87. Fox, R., S.W. Lehmkuhle, and R.C. Bush, *Stereopsis in Falcon.* Science, 1977. 197(4298): p. 79-81.

88. O'Rourke, C.T., et al., *Hawk Eyes II: Diurnal Raptors Differ in Head Movement Strategies When Scanning from Perches.* Plos One, 2010. 5(9).
89. Fite, K.V. and S. Rosenfieldwessels, *Comparative Study of Deep Avian Foveas.* Brain Behavior and Evolution, 1975. 12(1-2): p. 97-115.
90. Inzunza, O., et al., *Topography and Morphology of Retinal Ganglion-Cells in Falconiforms - a Study on Predatory and Carrion-Eating Birds.* Anatomical Record, 1991. 229(2): p. 271-277.
91. Pettigrew, J., *Comparison of the Retinotopic Organization of the Visual Wulst in Nocturnal and Diurnal Raptors, with a Note on the volution of Frontal Vision.* Frontiers in Visual Science, 1978.
92. Pumphrey, R.J., *The Theory of the Fovea.* Journal of Experimental Biology, 1948. 25(3): p. 299-312.
93. Martin, G.R., *What is binocular vision for? A birds' eye view.* Journal of Vision, 2009. 9(11).
94. Land, M.F., *The roles of head movements in the search and capture strategy of a tern (Aves, Laridae).* Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 1999. 184(3): p. 265-272.
95. Maldonado, P.E., H. Maturana, and F.J. Varela, *Frontal and Lateral Visual-System in Birds - Frontal and Lateral Gaze.* Brain Behavior and Evolution, 1988. 32(1): p. 57-62.
96. Slonaker, J.R., *A Compararive Study of the Area of Acute Vision in Vetebrates* 1897, Boston: The Athenaeum Press.
97. Wood, C.A., *The Fundus Oculi Of Birds Especially As Viewed By The Ophthalmoscope* 1917, Chicago The Lakeside Press.
98. Walls, G., *The Vertebrate Eye and its adaptive Radiation*1942, Michigan: Cranbrook Institute of Science.
99. Tansley, K., *Vision in Vertebrates*1965, London: Chapman and Hall.
100. Ruggeri, M., et al., *Retinal Structure of Birds of Prey Revealed by Ultra-High Resolution Spectral-Domain Optical Coherence Tomography.* Investigative Ophthalmology & Visual Science, 2010. 51(11): p. 5789-5795.
101. Frost, B.J., et al., *Retinotopic Representation of the Bifoveate Eye of the Kestrel (Falco-Sparverius) on the Optic Tectum.* Visual Neuroscience, 1990. 5(3): p. 231-239.
102. Gibson, J.J., *The perception of the visual world.* Oxford, England: Houghton Mifflin, 1950. 12: p. 242.
103. Walk, R.D. and E.J. Gibson, *A Comparative and Analytical Study of Visual Depth-Perception.* Psychological Monographs, 1961. 75(15): p. 1-44.
104. Gibson, J.J., *Visually controlled locomotion and visual orientation in animals (Reprinted from British Journal of Psychology, vol 49, pg 182-194, 1958).* Ecological Psychology, 1998. 10(3-4): p. 161-176.
105. Srinivasan, M.V., et al., *Range Perception through Apparent Image Speed in Freely Flying Honeybees.* Visual Neuroscience, 1991. 6(5): p. 519-535.
106. Regan, D., *Binocular Correlates of the Direction of Motion in-Depth.* Vision Research, 1993. 33(16): p. 2359-2360.
107. Martinez-Conde, S., S.L. Macknik, and D.H. Hubel, *The role of fixational eye movements in visual perception.* Nature Reviews Neuroscience, 2004. 5(3): p. 229-240.
108. Maurice, M., H. Gioanni, and A. Abourachid, *Influence of the behavioural context on the optocollic reflex (OCR) in pigeons (Columba livia).* Journal of Experimental Biology, 2006. 209(2): p. 292-301.
109. Van Hateren, J.H. and C. Schilstra, *Blowfly flight and optic flow II. Head movements during flight.* Journal of Experimental Biology, 1999. 202(11): p. 1491-1500.

110. Gilbert, C. and N.J. Strausfeld, *The Functional-Organization of Male-Specific Visual Neurons in Flies.* Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 1991. 169(4): p. 395-411.

111. Olberg, R.M., *Object-Movement and Self-Movement Detectors in the Ventral Nerve Cord of the Dragonfly.* Journal of Comparative Physiology, 1981. 141(3): p. 327-334.

112. Zeigler, H.P., and Bischof, H.J., *Vision, Brain and Behavior in Birds*1993: MIT Press, Cambridge.

113. Kirschfeld, K., *Tracking of Small Objects in Front of a Textured Background by Insects and Vertebrates - Phenomena and Neuronal Basis.* Biological Cybernetics, 1994. 70(5): p. 407-415.

114. Trischler, C., R. Kern, and M. Egelhaaf, *Chasing behavior and optomotor following in free-flying male blowflies: flight performance and interactions of the underlying control systems.* Frontiers in Behavioral Neuroscience, 2010. 4.

115. Wallman, J., and Letelier, J.C. , *Eye movements, head movements and gaze stabilization in birds.* Vision, Brain and Behavior in Birds, 1993. Ed. Zeigler H.P., Bischof H.J., MIT: : p. 245-254.

116. Wagner, H., *Flight Performance and Visual Control of Flight of the Free-Flying Housefly (Musca-Domestica L) .2. Pursuit of Targets.* Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 1986. 312(1158): p. 553-&.

117. Ben-Simon, A., et al., *Predictive saccade in the absence of smooth pursuit: interception of moving targets in the archer fish.* Journal of Experimental Biology, 2012. 215(24): p. 4248-4254.

118. MacIver, M.A., N.M. Sharabash, and M.E. Nelson, *Prey-capture behavior in gymnotid electric fish: Motion analysis and effects of water conductivity.* Journal of Experimental Biology, 2001. 204(3): p. 543-557.

119. Oudejans, R.R.D., et al., *Shedding some light on catching in the dark: Perceptual mechanisms for catching fly balls.* Journal of Experimental Psychology-Human Perception and Performance, 1999. 25(2): p. 531-542.

120. Mcleod, P. and Z. Dienes, *Running to Catch the Ball.* Nature, 1993. 362(6415): p. 23-23.

121. Priebe, N.J., M.M. Churchland, and S.G. Lisberger, *Reconstruction of target speed for the guidance of pursuit eye movements.* Journal of Neuroscience, 2001. 21(9): p. 3196-3206.

122. Rossel, S., *Foveal Fixation and Tracking in the Praying Mantis.* Journal of Comparative Physiology, 1980. 139(4): p. 307-331.

123. Shibata, T., et al., *A model of smooth pursuit in primates based on learning the target dynamics.* Neural Networks, 2005. 18(3): p. 213-224.

124. Miall, R.C., D.J. Weir, and J.F. Stein, *Manual Tracking of Visual Targets by Trained Monkeys.* Behavioural Brain Research, 1986. 20(2): p. 185-201.

125. de Brouwer, S., M. Missal, and P. Lefevre, *Role of retinal slip in the prediction of target motion during smooth and saccadic pursuit.* Journal of Neurophysiology, 2001. 86(2): p. 550-558.

126. Ilg, U.J., et al., *Neuronal Coding of Retinal Slip during Smooth Pursuit Eye-Movements.* European Journal of Neuroscience, 1992: p. 253-253.

127. Collett, T.S., D.D. Lent, and P. Graham, *Scene perception and the visual control of travel direction in navigating wood ants.* Philosophical Transactions of the Royal Society B-Biological Sciences, 2014. 369(1636).

128. Steinbach, M.J., and Money, K.E., *Eye movements of the owl.* Visual Research, 1973. 13: p. 889–91.

129. Turkel, J., and Wallman, J., *Oscillating eye movements with possible visual function in birds.* Neurosciences Abstracts, 1977. 3: p. 158.

130. Davies, M.N.a.G., P.R., *Optic flow-field variables trigger landing in hawk but not in pigeons.* Naturwissenschaften, 1990. 77: p. 142-144.
131. Warrick, D.R., M.W. Bundle, and K.P. Dial, *Bird maneuvering flight: Blurred bodies, clear heads.* Integrative and Comparative Biology, 2002. 42(1): p. 141-148.
132. Bhagavatula, P.S., et al., *Optic Flow Cues Guide Flight in Birds.* Current Biology, 2011. 21(21): p. 1794-1799.
133. Eckmeier, D., et al., *Gaze Strategy in the Free Flying Zebra Finch (Taeniopygia guttata).* Plos One, 2008. 3(12).
134. Lee, D.N., et al., *Visual Control of Velocity of Approach by Pigeons When Landing.* Journal of Experimental Biology, 1993. 180: p. 85-104.
135. Rogers, L.J., *The two hemispheres of the avian brain: their differing roles in perceptual processing and the expression of behavior.* Journal of Ornithology, 2012. 153: p. S61-S74.
136. Kral, K., *Perspectives on the role of head movements in depth perception.* Behavioural Processes, 2003. 64(1): p. 21-22.
137. Tucker, V.A., *Gliding flight: Drag and torque of a hawk and a falcon with straight and turned heads, and a lower value for the parasite drag coefficient.* Journal of Experimental Biology, 2000. 203(24): p. 3733-3744.
138. Pontani, M. and B.A. Conway, *Optimal interception of evasive missile warheads: Numerical solution of the differential game.* Journal of Guidance Control and Dynamics, 2008. 31(4): p. 1111-1122.
139. Karelahti, J., K. Virtanen, and T. Raivio, *Near-optimal missile avoidance trajectories via receding horizon control.* Journal of Guidance Control and Dynamics, 2007. 30(5): p. 1287-1298.
140. Raivio, T., Ehtamo, H., *Visual aircraft identifcation as a pursuit-evasion game.* Journal of Guidance, Control and Dynamics, 2000. 23(4): p. 701-708.
141. Neuman, F., *On the Approximate Solution of Complex Combat Games.* Journal of Guidance Control and Dynamics, 1990. 13(1): p. 128-136.
142. Nahin, P., *Chases and Escapes: The Mathematics of Pursuit and Evasion.* Princeton University Press, Princeton, NJ U.S.A., 2007.
143. Haselsteiner, A.F., C. Gilbert, and Z.J. Wang, *Tiger beetles pursue prey using a proportional control law with a delay of one half-stride.* Journal of the Royal Society Interface, 2014. 11(95).
144. Furness, R.W. and P. Monaghan, *Seabird ecology*. Tertiary level biology1987, New York: Blackie; Published in the USA by Chapman and Hall. ix, 164 p.
145. Kane, S.A., A.H. Fulton, and L.J. Rosenthal, *When hawks attack: animal-borne video studies of goshawk pursuit and prey-evasion strategies.* Journal of Experimental Biology, 2015. 218(2): p. 212-222.
146. Siouris, G.M., *Missile guidance and control systems*2004: Springer-Verlag.
147. Shneydor, N.A., *Missile guidance and pursuit: kinematics, dynamics and control*1998: Woodhead Publishing Limited.
148. Yuan, L.C.L., *Homing and Navigational Courses of Automatic Target-Seeking Devices.* Journal of Applied Physics, 1948. 19(12): p. 1122-1128.
149. Justh, E.W. and P.S. Krishnaprasad, *Steering laws for motion camouflage.* Proceedings of the Royal Society a-Mathematical Physical and Engineering Sciences, 2006. 462(2076): p. 3629-3643.
150. Shukla, U.S. and P.R. Mahapatra, *Optimization of Biased Proportional Navigation.* Ieee Transactions on Aerospace and Electronic Systems, 1989. 25(1): p. 73-80.
151. Wehrhahn, C., T. Poggio, and H. Bulthoff, *Tracking and Chasing in Houseflies (Musca) - an Analysis of 3-D Flight Trajectories.* Biological Cybernetics, 1982. 45(2): p. 123-130.

152. Boeddeker, N. and M. Egelhaaf, *A single control system for smooth and saccade-like pursuit in blowflies.* Journal of Experimental Biology, 2005. 208(8): p. 1563-1572.
153. Zhang, S.W., et al., *Visual Tracking of Moving Targets by Freely Flying Honeybees.* Visual Neuroscience, 1990. 4(4): p. 379-386.
154. Lanchester, B.S. and R.F. Mark, *Pursuit and Prediction in Tracking of Moving Food by a Teleost Fish (Acanthaluteres-Spilomelanurus).* Journal of Experimental Biology, 1975. 63(3): p. 627-645.
155. Gilbert, C., *Visual control of cursorial prey pursuit by tiger beetles (Cicindelidae).* Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 1997. 181(3): p. 217-230.
156. Beard, R.W., T.W. McLain, and ebrary Inc., *Small unmanned aircraft theory and practice*, 2012, Princeton University Press: Princeton, N.J. p. xv, 300 p.
157. Ghose, K., et al., *Behavioral responses of big brown bats to dives by praying mantises.* Journal of Experimental Biology, 2009. 212(5): p. 693-703.
158. Buelthoff, H., T. Poggio, and C. Wehrhahn, *3-D Analysis of the Flight Trajectories of Flies (Drosophila-Melanogaster).* Zeitschrift Fur Naturforschung C-a Journal of Biosciences, 1980. 35(9-10): p. 811-815.
159. Zeil, J., *Sexual Dimorphism in the Visual-System of Flies - the Free Flight Behavior of Male Bibionidae (Diptera).* Journal of Comparative Physiology, 1983. 150(3): p. 395-412.
160. Srinivasan, M.V. and M. Davey, *Strategies for Active Camouflage of Motion.* Proceedings of the Royal Society B-Biological Sciences, 1995. 259(1354): p. 19-25.
161. Harley, C.M., et al., *Discontinuous locomotion and prey sensing in the leech.* Journal of Experimental Biology, 2013. 216(10): p. 1890-1897.
162. Coombs, S. and R.A. Conley, *Dipole source localization by mottled sculpin .1. Approach strategies.* Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology, 1997. 180(4): p. 387-399.
163. Fux, M. and D. Eilam, *How barn owls (Tyto alba) visually follow moving voles (Microtus socialis) before attacking them.* Physiology & Behavior, 2009. 98(3): p. 359-366.
164. Edut, S. and D. Eilam, *Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns.* Behavioural Brain Research, 2004. 155(2): p. 207-216.
165. Rushton, S.K., et al., *Guidance of locomotion on foot uses perceived target location rather than optic flow.* Current Biology, 1998. 8(21): p. 1191-1194.
166. Lenoir, M., E. Musch, and N. la Grange, *Ecological relevance of stereopsis in one-handed ball-catching.* Perceptual and Motor Skills, 1999. 89(2): p. 495-508.
167. Shaffer, D.M. and M.K. McBeath, *Baseball outfielders maintain a linear optical trajectory when tracking uncatchable fly balls.* Journal of Experimental Psychology-Human Perception and Performance, 2002. 28(2): p. 335-348.
168. Fajen, B.R. and W.H. Warren, *Behavioral dynamics of steering, obstacle avoidance, and route selection.* Journal of Experimental Psychology-Human Perception and Performance, 2003. 29(2): p. 343-362.
169. Fajen, B.R. and W.H. Warren, *Visual guidance of intercepting a moving target on foot.* Perception, 2004. 33(6): p. 689-715.
170. Mcbeath, M.K., D.M. Shaffer, and M.K. Kaiser, *How Baseball Outfielders Determine Where to Run to Catch Fly Balls.* Science, 1995. 268(5210): p. 569-573.
171. Dannemiller, J.L., Babler, T.G., Babler, B.L. , *On catching flyballs.* Science, 1996. 273(5272): p. 256-257.
172. Chapman, S., *Catching a baseball.* American Journal of Physics, 1986. 36(10): p. 868.
173. Cutting, J.E., P.M. Vishton, and P.A. Braren, *How We Avoid Collisions with Stationary and Moving Obstacles.* Psychological Review, 1995. 102(4): p. 627-651.

174. Chardenon, A., et al., *The visual control of ball interception during human locomotion.* Neuroscience Letters, 2002. 334(1): p. 13-16.
175. Shaffer, D.M., et al., *How dogs navigate to catch frisbees.* Psychological Science, 2004. 15(7): p. 437-441.
176. Lee, D.N., *Guiding movement by coupling taus.* Ecological Psychology, 1998. 10(3-4): p. 221-250.
177. Wei, E., E.W. Justh, and P.S. Krishnaprasad, *Pursuit and an evolutionary game.* Proceedings of the Royal Society a-Mathematical Physical and Engineering Sciences, 2009. 465(2105): p. 1539-1559.
178. Rutz, C., *Home range size, habitat use, activity patterns and hunting behaviour of urban-breeding Northern Goshawks Accipiter gentilis.* Ardea, 2006. 94(2): p. 185-202.
179. Gillies, J.A., A.L.R. Thomas, and G.K. Taylor, *Soaring and manoeuvring flight of a steppe eagle Aquila nipalensis.* Journal of Avian Biology, 2011. 42(5): p. 377-386.
180. Taylor, G.K., et al., *New experimental approaches to the biology of flight control systems.* Journal of Experimental Biology, 2008. 211(2): p. 258-266.
181. Acharya, R., *Understanding satellite navigation*, 2014, Elsevier : Academic Press: London ; Waltham, MA. p. xv, 389 p.
182. Department of Defense Positioning, N., and Timing Executive Committe. *Global Positioning System Standard Positioning Service Performance Standard*. Washington: Department of Defense 2008 [cited 4th edition.
183. O'Driscoll, C., Izadpanah, A., Lachapelle, G. *Investigation of the effect of Antenna Orientation on Indoor GPS Signal Reception*. in *Proceedings of NAV07 Conference*. 2007. Royal Institute of Navigation, London.
184. Department of Defense Positioning, N., and Timing Executive Committee, *Global Positioning System Standard Positioning Service Performance Standard*. 2008: Washington: Department of Defense.
185. Murtaugh, S.A. and H.E. Criel, *Fundamentals of Proportional Navigation.* Ieee Spectrum, 1966. 3(12): p. 75-&.
186. Reddy, P.V., *Steering laws for pursuit.* MS thesis, University of Maryland, 2007.
187. Mischiati, M., et al., *Internal models direct dragonfly interception steering.* Nature, 2015. 517(7534): p. 333-U410.
188. Livezey, B.C. and R.L. Zusi, *Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion.* Zoological Journal of the Linnean Society, 2007. 149: p. 1–95.
189. Wilson, A.M., et al., *Dynamics of high speed locomotion and hunting in free ranging cheetah.* Integrative and Comparative Biology, 2013. 53: p. E229-E229.