

## THE DEEP FOVEA, SIDEWAYS VISION AND SPIRAL FLIGHT PATHS IN RAPTORS

VANCE A. TUCKER\*

*Department of Biology, Duke University, Box 90338, Durham, NC 27708-0338, USA*

\*e-mail: vtucker@duke.edu

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### Summary

Raptors – falcons, hawks and eagles in this study – have two regions of the retina in each eye that are specialized for acute vision: the deep fovea and the shallow fovea. The line of sight of the deep fovea points forwards and approximately 45° to the right or left of the head axis, while that of the shallow fovea also points forwards but approximately 15° to the right or left of the head axis. The anatomy of the foveae suggests that the deep fovea has the higher acuity.

Several species of raptors in this study repeatedly moved their heads among three positions while looking at an object: straight, with the head axis pointing towards the object; or sideways to the right or left, with the head axis pointing approximately 40° to the side of the object. Since raptors do not rotate their eyes noticeably in the sockets, these movements presumably cause the image of the object to fall on the shallow and deep foveae. The movements occurred approximately every 2 s on average in hawks and falcons, and approximately every 5 s in bald eagles.

The proportion of time that the raptors spent looking straight or sideways at an object depended on how far away the object was. At a distance closer than 8 m, they spent more time looking at the object straight, but as the distance increased to 21 m, they spent more time looking at it

sideways. At distances of 40 m or more, raptors looked sideways at the object 80% or more of the time. This dependence of head position on distance suggests that raptors use their more acute sideways vision to look at distant objects and sacrifice acuity for stereoscopic binocular vision to look at close objects.

Having their most acute vision towards the side causes a conflict in raptors such as falcons, which dive at prey from great distances at high speeds: at a speed of 70 ms<sup>-1</sup>, turning their head sideways to view the prey straight ahead with high visual acuity may increase aerodynamic drag by a factor of 2 or more and slow the raptor down. Raptors could resolve this conflict by diving along a logarithmic spiral path with their head straight and one eye looking sideways at the prey, rather than following the straight path to the prey with their head turned sideways. Although the spiral path is longer than the straight path, a mathematical model for an ‘ideal falcon’ shows that the falcon could reach the prey more quickly along the spiral path because the speed advantage of a straight head more than compensates for the longer path.

Key words: flight, vision, deep fovea, raptor, flight path, drag, logarithmic spiral.

### Introduction

Birds and mammals use their heads in different ways, related to the fact that most birds fly and most mammals do not. For example, both birds and mammals direct the field of view of their eyes by moving their head, and this behavior is more extreme in birds because their large eyes are less mobile in their sockets (Land, 1999). But head position has an additional role in flight: the air flow around the head is fast enough during flight to generate significant aerodynamic forces, and these forces depend on head position (Tucker, 2000). The head position for looking in a particular direction may differ from that for low aerodynamic drag, and this conflict is the subject of this paper.

Many avian species have regions of the retina known as foveae (Meyer, 1977; Walls, 1942; Wood, 1917) that are specialized for acute vision (the ability to perceive fine details in the retinal image; Riggs, 1965), and the line of sight (LOS)

of the fovea typically points 45° or more to one side of the head axis. The conflict between vision and aerodynamics arises when the bird looks at an object straight ahead. The head has minimum aerodynamic drag when pointed straight ahead (Tucker, 2000), but the line of sight for maximum visual acuity points sideways with the head in this position. If birds cannot rotate their eyes much in the sockets, they must turn their heads sideways to see acutely straight ahead. For brevity, I shall refer to this conflict as the ‘AV conflict’.

The AV conflict is particularly interesting in raptors – falcons, hawks and eagles in this study – because many raptors attack their prey by diving at high speeds from great distances. The raptor needs to keep its head aligned with its body for high speed, but it also needs to view distant prey with its most acute vision.

Raptors have an unusual visual system that may solve this

problem. Unlike humans, they have two foveae in each eye, one (the deep fovea) with a line of sight that points approximately  $45^\circ$  to the side of the head axis, and another (the shallow fovea) with a line of sight that points forward and may provide acute vision straight ahead. However, anatomical studies (cited below) suggest that vision is more acute at the deep than at the shallow fovea, and observations of raptor behavior incidental to laboratory studies of vision indicate that raptors turn their head sideways to view objects with maximum acuity.

This study systematically investigates the behavior of several species of perched raptors to determine whether they hold their head sideways when looking at objects in natural conditions. The results show that they do and that this behavior would cause the AV conflict in flight. The paper then analyzes a solution to the AV conflict: a raptor could hold its head straight and keep the LOS of a deep fovea on the prey by flying along a spiral path towards the prey. Although the spiral path is longer than the straight path, the raptor's higher speed along the spiral path can compensate for the longer distance.

Tucker et al. (2000) show that wild peregrine falcons (*Falco peregrinus*) do follow curved paths that resemble spirals when approaching prey.

### The ideal falcon and its visual system

The visual systems of raptors have several properties that are relevant to this study, but detailed, quantitative descriptions of these properties may be complex, if available at all. To avoid these difficulties, I shall use the concept of an 'ideal falcon' which, like the ideal gas of physical chemistry, is a simplified mathematical model of its real counterpart. Previous papers (Tucker, 1998, 2000) have described some of the anatomical and aerodynamic properties of ideal falcons, and this paper endows ideal falcons with a visual system.

Although the properties of ideal falcons are simplified, and some may be assumed, they are meant to represent reality closely enough to provide an understanding of the behavior of real raptors. The following description of the visual system of ideal falcons includes, for comparative purposes, descriptions of real visual systems.

The ideal falcon in this paper has three roles: its properties have quantitative definitions that can be used with real raptors, its behavior can be used to guide observations on a real raptors and its distinctive name emphasizes that its properties and behavior come from a mathematical model and are distinct from those of real raptors.

The anatomy of the ideal falcon's eye (Fig. 1) closely resembles that of a real raptor, described by Walls (1942). A pair of lenses (the lens and the cornea), with a pupil centered between them, forms an image on an array of photoreceptors on the retina. Each receptor has a line of sight, which is the straight path taken by a ray of light that travels from a viewed object to the receptor through a nodal point at the center of the pupil.

The number of functional receptors per unit area of retina – the receptor density – varies from one region of the retina to another. Density depends both on the size of an individual

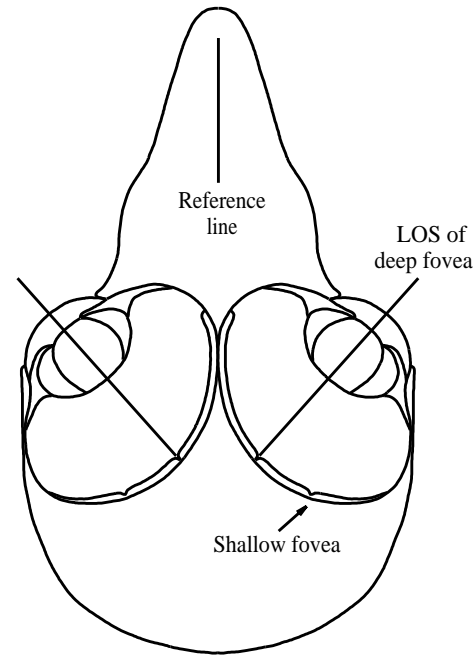


Fig. 1. A frontal section through an ideal falcon's head at the foveal plane. Both foveae and the center of the pupil in each eye are on the plane, as is the line of sight (LOS) of every point on the surfaces of the retinae cut by the plane. Drawing modified from Wood (1917).

receptor, i.e. the area that it occupies on the retinal surface, and on the number of receptors that connect to a single neuron and function as a single receptor. The density is highest in two depressions known as foveae on the retina of each eye, and the foveae are small enough that each may be considered as having a single LOS. One fovea, known as the deep fovea (also the central, nasal or anterior fovea) is deeper than the other and has a pit-like cross section. The other fovea is known as the shallow fovea (also the lateral, temporal or posterior fovea).

The eyes of the ideal falcon cannot move relative to the skull, and the four foveae fall on a foveal plane (Fig. 1) that extends indefinitely in all directions. The two centers of the pupils also fall on this plane, as do the LOS of the receptors in the retinae cut by the plane. The foveal plane intersects the midsagittal plane of the head along the 'reference line', and the structures in one eye cut by the foveal plane are symmetrical around the reference line with the analogous structures in the other.

Each LOS in the foveal plane can be identified by the angle ( $\alpha$ ) that it makes with the reference line. For example, the LOS of the deep fovea points forward and laterally at an angle ( $\alpha_d$ ) of  $45^\circ$ , while the LOS of the shallow fovea points more forward at an angle of  $15^\circ$ .

In real raptors,  $\alpha_d$  is greater than  $30^\circ$ , and it may exceed  $45^\circ$  in American kestrels (*Falco sparverius*) (Frost et al., 1990; Lord, 1956; Wood, 1917). Real raptors can also rotate their eyes in their sockets (Pettigrew, 1978; Polyak, 1941), perhaps by  $12^\circ$  in the kestrel (Frost et al., 1990). Thus,  $\alpha$  for an LOS varies as the eye rotates, but the variation is small compared with  $\alpha_d$ , and small enough to be unnoticed by a casual observer.

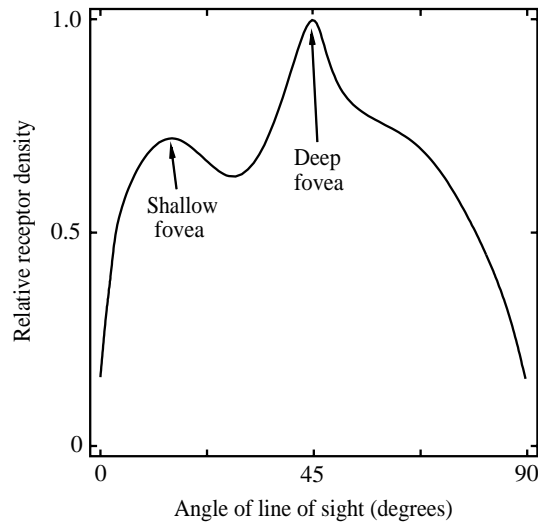


Fig. 2. The relative receptor density for different lines of sight in the foveal plane of the ideal falcon. The shape of the curve is assumed on the basis of data for a Chilean eagle (*Buteo fuscensens*; Inunza et al., 1991). A relative density of 1 represents 62 000 receptors  $\text{mm}^{-2}$ .

The receptor density is greatest at  $\alpha_d$  for the deep fovea (Fig. 2), with a second, lesser maximum at the shallow fovea. The ideal falcon's visual acuity is directly proportional to the square root of receptor density (Miller, 1979), so the falcon can see an object most acutely when the object lies on the LOS of the deep fovea.

Whether the deep fovea in real raptors has a single LOS with maximum visual acuity has not been determined, but measurements on humans suggest that it does. Humans have a single fovea in each eye, and visual acuity is a continuous function of  $\alpha$  in the vicinity of the fovea (Weymouth, 1958). A sharp cusp for maximum acuity (Fig. 3) defines the LOS of the fovea. Raptors presumably have a similar cusp, particularly since the pit-like structure of the deep fovea may narrow the field over which vision is most acute (Pumphrey, 1948; Snyder and Miller, 1978).

Real raptors also appear to have higher visual acuity along the LOS of the deep fovea than along the LOS of the shallow fovea, because the receptor density in the deep fovea is higher than that in the shallow fovea (Fite and Rosenfield-Wessels, 1975; Inunza et al., 1991; Nalbach et al., 1993; Polyak, 1941; Reymond, 1985). Other species of bird that have deep and shallow foveae also have this property (Güntürkün, 2000; Moroney and Pettigrew, 1987). In addition, Snyder and Miller (1978) suggest that the deep fovea further enhances acuity by acting as a telephoto lens. The brown falcon (*Falco berigora*) is exceptional in having equal receptor densities in the deep and shallow foveae (Reymond, 1987), and this species also has other unusual characteristics for falcons (Cade, 1982).

Behavioral studies also suggest that real raptors have their highest visual acuity along the LOS of the deep foveae. Raptors hold their head cocked to one side when viewing distant objects, presumably to point the LOS of the deep fovea at the object and examine it with their most acute vision (Frost et al.,

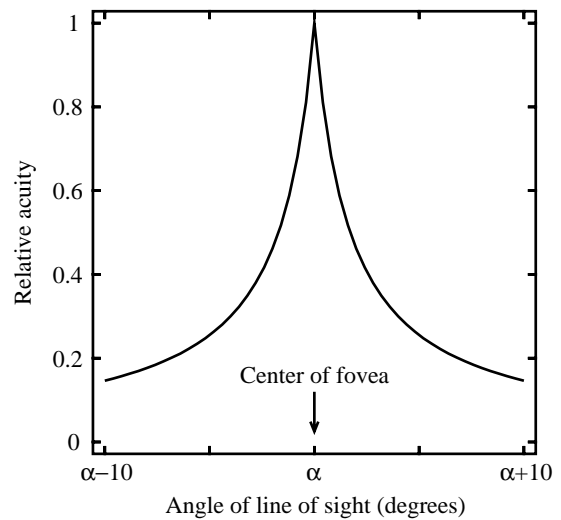


Fig. 3. The relative acuity of a human eye for the region of the retina around the fovea. Vision is most acute over an almost unmeasurably narrow field of view, represented by the cusp in the curve. The curve has been computed from the equation  $Y=0.331 |X|+0.568$ , fitted by Weymouth (1958) to Ludvig's data, where  $X$  is the angular deviation of the line of sight from the center of the fovea in degrees, from  $-10^\circ$  to  $10^\circ$ , and  $Y$  is the minimum resolvable angle (in min). Relative acuity is  $Y_0/Y$ , where  $Y_0=Y$  at  $X=0$ .

1990; Lord, 1956; Nalbach et al., 1993; Pettigrew, 1978; Polyak, 1941). In contrast, they point the reference line of the head to near objects and view them stereoscopically (Fox et al., 1977). Most experimenters report that, during visual acuity tests, raptors rotate their head, first to one side and then the other, to point the LOS of each deep fovea at the test target (Fox et al., 1976; Hirsch, 1982; Reymond, 1985, 1987).

This paper investigates head positions in raptors, and I shall define two useful measures of head position for ideal falcons. Both are angles measured from the reference line of the head, but to different lines, described below.

The only objects that an ideal falcon looks at in this study are points on the foveal plane, and the angle  $\alpha$  between the reference line and the LOS to an object is the first measure of head position – the head position relative to the object being looked at. For example, the head position is  $\alpha_d$  when the falcon looks at an object with the deep fovea, and  $\alpha_d$  cannot change since the eyes cannot rotate in their sockets. I shall refer to the head position as straight when  $\alpha=0^\circ$ , and sideways when  $\alpha=\alpha_d$ .

The second measure of head position applies only to a falcon in flight and is the angle  $\beta$  between the reference line of the head and the body axis. The body axis runs from the 'point of intersection', where the reference line intersects the posterior margin of the skull, to the tip of the tail when the body of the ideal falcon is bilaterally symmetrical and in the normal flight position. In this position, the body axis is in the foveal plane, and the head rotates right or left around an axis that is perpendicular to the foveal plane at the point of intersection.  $\beta$  measures the head position relative to the body axis, and the ideal falcon in this paper holds its head in only two positions:

either straight ( $\beta=0^\circ$ ) or turned sideways ( $\beta=\alpha_d$ ) to point the LOS of the deep fovea in the direction of flight.

### Materials, methods and results

To measure the angle  $\alpha$  in a real raptor, the investigator must define two lines in terms of observable points: the reference line of the head and the LOS to the object at which the raptor is looking. An adequate approximation for the reference line is the head axis – the line from the tip of the beak to the midline of the posterior margin of the head, viewed from above. An adequate approximation of the LOS is the line between a raptor's head and the object looked at, but the investigator might not always know what that object is. Accordingly, this paper reports the angle  $\alpha^*$  between the head axis and a reference LOS that is likely to be the actual LOS. Thus,  $\alpha^*$  and  $\alpha$  are probably equal (see Discussion).

This paper uses two methods to measure  $\alpha^*$ : 'by coordinates', measured on photographs; or 'by categories' of head position, determined from visual observations. To measure coordinates, I used photographs taken from directly above a raptor's head and enlarged to one-third life-size. A computer connected to a digitizer calculated  $\alpha^*$ , accurate to within  $2^\circ$ , from four digitized points on each photograph: the tip of the beak, the mid-point of the posterior margin of the head, and the ends of a 0.3 m ruler that appeared in each photograph and marked the reference LOS.

To categorize head positions, I used the following nomenclature. The head position is 'straight' when  $\alpha^*$  is within  $22.5^\circ$  of  $0^\circ$  (i.e. the raptor has its beak pointed straight at the object at which it supposedly is looking), 'sideways left' or 'sideways right' when  $\alpha^*$  is within  $22.5^\circ$  of  $45^\circ$  or  $315^\circ$ , or 'not looking' when  $\alpha^*$  has any other value. For completeness, the term 'looking' means that the head was straight or sideways. The value of  $22.5^\circ$  above makes the categories cover a full circle but, in fact, almost all the straight and sideways head positions were within  $15^\circ$  of the lines at  $0^\circ$ ,  $45^\circ$  and  $315^\circ$ .

#### *Measuring $\alpha^*$ from photographs*

##### *Measuring $\alpha^*$ from coordinates in raptors trained for falconry*

The purpose of these experiments was to determine  $\alpha^*$  for raptors with their head in sideways positions. The raptors – a peregrine, a gyrfalcon (*F. rusticolus*) hybridized with a peregrine, a prairie falcon (*F. mexicanus*), two northern goshawks (*Accipiter gentilis*) and a red-tailed hawk (*Buteo jamaicensis*) – were trained for falconry and sat tethered one at a time to a perch outdoors while a falconer attracted the raptor's attention with food, a falconer's lure or a falconer's glove (Beebe and Webster, 1964) that the raptor had learned to fly to for food. The falconer stood 17 m or more from the perch, and the reference LOS ran from the raptor to the falconer.

A 35 mm motor-driven camera photographed the raptors from above as they sat on the perch. The perch was centered

between the legs of a tripod that supported the camera approximately 2 m above the bird's head. The legs of the tripod were steel tubes, 3 m long and 2 cm in diameter; and a circular steel plate, 10.5 cm in diameter, formed the top of the tripod and held the legs splayed out at an angle of  $30^\circ$ . The plate also held the camera with its 50 mm lens pointed straight down.

I triggered the camera a total of 122 times, mostly when the raptors appeared to be looking fixedly at the falconer, and particularly when they bobbed their head. Raptors often bob their head while looking at objects; during head-bobbing, the body is stationary while the head moves upwards from its normal position by approximately half the interocular distance and then returns to its normal position. This motion takes 0.3–0.5 s in a raptor the size of a peregrine, and a second bob may immediately follow the first. I also took some photographs for reference purposes when the bird was not looking at the falconer, and some photographs showed the bird moving its head and not fixated on an object.

The photographs showed the raptors with their heads sideways more often than straight, and a frequency diagram (Fig. 4) for all 122 photographs showed peak frequencies for  $\alpha^*$  between  $30^\circ$  and  $50^\circ$  on either side of the reference LOS. Thus, I shall use  $\alpha^*=40^\circ$  for raptor heads in the sideways position.

#### *Measuring $\alpha^*$ from categories of published photographs*

Wheeler and Clark (1995) illustrate all North American raptor species using photographs and, judging from the section entitled 'Photographic equipment and techniques', the photographs are primarily of wild birds and were probably taken from distances within the range 30–60 m at which wild raptors are likely to fly from humans. Hence, most of the photographs should show birds that are looking at the photographer. I categorized the head positions in all 168 photographs of perched raptors (excluding duplicate photographs and those of vultures) and used the line from the bird's head to the camera as the reference LOS.

The raptors had their head sideways in 77% of the photographs, straight in 2% of the photographs and were not looking at the camera in the remainder.

#### *Time/motion studies and measuring $\alpha^*$ from categories*

In these studies, I observed a raptor and pressed one of four keys on a portable computer whenever its head position changed between categories. The keys corresponded to the categories straight, sideways left, sideways right and not looking; the reference LOS was the line between me and the raptor. A computer program recorded the time of each key press to the nearest 0.1 s.

#### *Raptors trained for falconry*

These raptors – two gyrfalcons, a gyrfalcon/peregrine hybrid, a prairie falcon, two northern goshawks and a Harris' hawk (*Parabuteo unicinctus*) – sat on a perch as a falconer attracted their attention as described for the procedure with the motor-driven camera. The falconer stood 5–21 m from the bird,

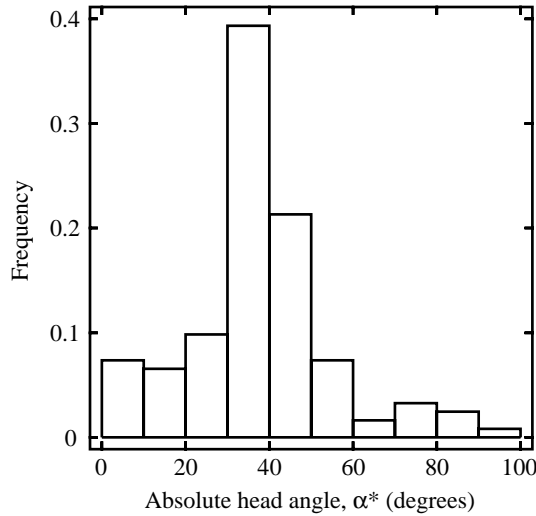


Fig. 4. The frequencies of 122 head positions in raptors while a falconer attracted their attention. The head angle on the horizontal axis is the angle ( $\alpha^*$ ) between the head axis of the raptor and the line from the raptor to the falconer.

and I stood behind the falconer. The reference LOS extended from the bird to the falconer.

The pooled data for these birds revealed that they looked straight or sideways at the falconer during 81% (27 min) of the combined observation periods and changed between straight and sideways head positions 734 times. The average time interval between these changes was 2.2 s, although the birds sometimes held a single position for up to 11 s. A Poisson distribution (Fig. 5) with mean and variance of 1.64 s approximates the frequency distribution for the times between changes of head positions, compartmentalized into 1 s intervals. The birds often bobbed, leaned forward or stretched upwards while looking at the falconer. Wheeler and Clark (1995) show examples of the latter two postures on the front and back covers of their book.

The proportion of the time that the birds held their head straight, rather than sideways, decreased as the distance between the falconer and the bird increased (Fig. 6). The values on the vertical axis are ratios of fractional times defined as follows. The 'looking time' is the total time that a raptor held its head in the straight or sideways position, and  $F_S$  is the fraction of that time that the head was straight.  $F_B$  is the fraction of that time that the head was sideways (bent), and  $F_B = 1 - F_S$ . A Wilcoxon signed-ranks test (Sokal and Rohlf, 1969) showed that the ratios  $F_S/F_B$  at 8 and 21 m were different, with a probability of the difference being due to chance of less than 2%.

*Bald eagles*

A pair of bald eagles (*Haliaeetus leucocephalus*) looked at me and a companion standing 100 m away as they perched on or near their nest, which contained at least one chick, perhaps a week old. The eagles were used to humans watching the nest from that distance, but were wary. The reference LOS was from an eagle to me.

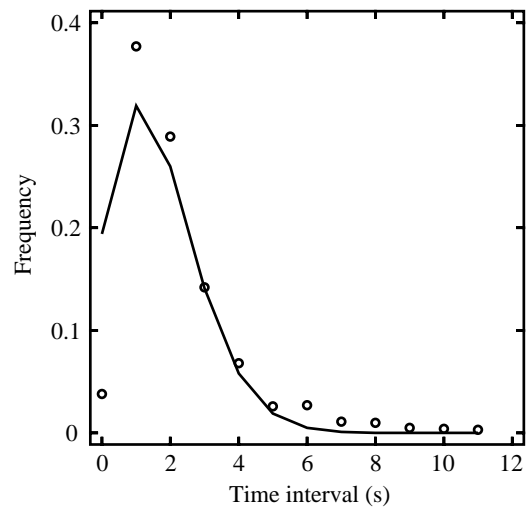


Fig. 5. The frequencies of 734 time intervals between changes in head positions while raptors trained for falconry looked at the falconer. The points are centered in compartments 1 s wide, and lines connect points on a Poisson distribution (mean and variance=1.64 s) fitted to the data.

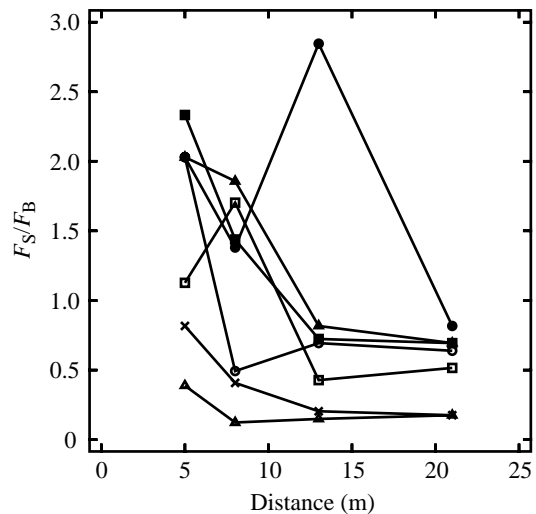


Fig. 6. The relative times (vertical axis) that seven raptors trained for falconry held their heads straight while looking at a falconer from various distances (horizontal axis). A different symbol represents data for each bird.  $F_S$  is the fraction of the looking time that a bird held its head straight, and  $F_B$  is the fraction of the looking time that a bird held its head sideways (bent), where the looking time is the total time that the bird looked at the falconer with its head straight or sideways at each distance.

The eagles looked at me 70% of the time during three observation periods totalling 5.7 min. The time intervals between head position changes during the looking period were twice as long as those for raptors trained for falconry: these intervals divided by 2 fitted the observed data and curve in Fig. 5. The eagles changed their head position 57 times while looking at me, and looked sideways 95% of this time.

*Hand-written notes and measuring  $\alpha^*$  from categories*

I observed both wild and captive raptors under conditions in which I could categorize head positions but could only record the data later by writing notes from memory. The reference LOS was from the raptor to me. The wild raptors were a red-tailed hawk perched within 3 m of its nest and several red-shouldered (*Buteo lineatus*) and Cooper's hawks (*Accipiter cooperii*) perched in trees. All were less than 60 m away from me and appeared to be watching me intently.

*Wild raptors*

A red-tailed hawk in Oregon in May began following me, shrieking, as I approached its nest in a tree 200 m away. When I was within 40 m of the nest, the hawk perched on a branch near the nest, leaned forward and continued to shriek, with its head position alternating between sideways left and right every 2 or 3 s. Its head paused in the straight position for a small fraction of a second as it moved between sideways positions, but otherwise was never straight. During the 5 min that I watched the hawk, it gave a convincing demonstration that I was the sole object of its attention.

I noted the behavior of perched red-shouldered and Cooper's hawks before they flew away as I approached within 30–60 m. These birds turned their heads between right and left sideways positions every few seconds, and used a straight position less than 20 % of the time and often not at all.

*Captive raptors*

The captive raptors were three pairs of gyrfalcons, peregrines and hybrids of these species, kept in separate rooms (3 m wide by 2.5 m high by 6 m long) for breeding purposes. I fed these falcons daily at the same time over a 9-day period and observed their behavior as they waited for me to deliver food (dead coturnix quail *Coturnix coturnix*). They could not see me, but they could hear me approach to drop food into a room through a feeding tube that penetrated an opaque wall. I could see the falcons through a small port with one-way glass as they eyed the end of the feeding tube from a distance of 5 m, anticipating the arrival of a quail. The reference LOS was from a falcon to the end of the feeding tube.

The falcons appeared to give their exclusive attention to the feeding tube as I approached. They bobbed, leaned forward, stretched upwards and moved their head every few seconds between straight and sideways positions. Their head was sideways for approximately 80 % of the time.

**Discussion**

One goal of the present study was to determine whether flying raptors encounter the AV conflict when they look at objects. In this context, 'look at' refers to visual perception rather than a straight or sideways head position, and the term 'object' refers to an object that can be seen with high acuity because its image falls on a shallow or deep fovea.

A human can only infer what a raptor looks at from its behavior, and the differences between raptor and human visual

systems make this behavior misleading. Humans look at one object at a time with binocular vision, usually straight ahead, but a raptor could look at least three objects simultaneously – one with the shallow foveae and binocular vision, and two more with each deep fovea and sideways monocular vision.

Humans are likely to recognize the object that a raptor looks at straight ahead, but may misidentify the object that the raptor looks at sideways. For example, most of the falcons with whom I worked agreed that their birds looked sideways at food in addition to straight at it, but were surprised by the sideways looking. In fact, one falconer commented that sideways looking explains why falconers commonly complain that their birds do not pay attention to them but look to one side. The birds evidently do pay attention, but the falconers misidentify the object to which they are paying attention.

Most people, such as the surprised falconers just mentioned, would agree that the raptors in this study with their head in the straight or sideways positions were looking at the object at the far end of the reference LOS. Thus, I shall assume that the reference LOS is the true LOS, and  $\alpha^* = \alpha$ .

Given the anatomy of the raptor eye, a reasonable explanation of the straight and sideways head positions of raptors in this study and during visual acuity tests in the laboratory is that raptors position their head to make the retinal image of an object fall on the shallow or the deep foveae. Raptors continuously change their head position between straight and sideways, or sideways right and left, usually every 2 or 3 s (except in bald eagles, for which the duration was twice as long), with the change in position taking approximately 0.2 s. Presumably, they are looking at the same object with each head position, but with different foveae.

An alternative explanation, that they are regularly examining up to five different objects spaced at 40° intervals, seems unlikely. Thus, I shall add a condition to the assumption that  $\alpha^* = \alpha$ : that  $\alpha$  is the angle of the LOS of a shallow or deep fovea. Now the different meanings of the phrase 'look at an object', one in the context of head position and the other in the context of visual perception, become the same, and the following list of 'looking criteria' operationally defines a single object at which a raptor looks.

*Looking criteria*

Twenty-five raptors of nine species all exhibited nearly identical, distinctive behavior that can be classified into three looking criteria. (i) Raptors look at an object from one of three head positions: straight, with the head axis pointing towards the object, and sideways left or right, with the head axis pointing approximately 40° to the side of the object. These positions cause the image of the object to fall on a fovea, and raptors usually use the deep fovea to look at objects more than 15 m away. (ii) Raptors looking at an object continuously change their head position between straight and sideways, or sideways right and left, every 2 or 3 s for a raptor in the size range of peregrines and red-tailed hawks. (iii) When looking at objects, raptors often bob their heads, lean forward or stretch upwards.

These criteria and the results presented in this study indicate that perched raptors in natural conditions look at objects more than 40 m away almost exclusively monocularly with the deep foveae for maximum acuity. They look at closer objects binocularly and stereoscopically (Fox et al., 1977), with some loss of acuity. Furthermore, they do not rotate their eyes enough to bring the LOS of the deep fovea closer than approximately  $40^\circ$  to the head axis. Land (1999) suggests that another avian species with two foveae in each eye, the gull-billed tern (*Gelochelidon nilotica*), also switches from the shallow to the deep fovea for better visual acuity.

The shift from straight to sideways looking as range increases is consistent with a shifting balance of benefits of range perception *versus* high acuity. Stereoscopic range perception becomes more accurate at short ranges (Graham, 1965), just where range perception is necessary to judge imminent contact with the prey, a predator or a landing site. However, high-speed aerial hunters such as gyrfalcons and peregrines appear to identify prey from such great distances that the prey is invisible to humans (Tucker et al., 2000). At these distances, stereoscopic range perception is ineffective and high acuity is essential.

#### *Use of the deep fovea for distant vision, and the AV conflict*

Since perched raptors look at distant objects almost exclusively with the deep fovea of one or the other eye, the AV conflict should arise during flight. The next section shows how a raptor could avoid the AV conflict by flying along a spiral path with its head straight and the LOS of the deep fovea pointing sideways to its prey.

#### *Aerodynamic effects of looking sideways*

This section develops equations for a spiral path from raptor to prey and answers a related question: the spiral path to the prey is longer than a straight path, but since a raptor's speed along the spiral path is higher, might the raptor reach the prey as quickly along either path?

For simplicity, the equations describe a specific raptor – an ideal falcon with a body mass of 1 kg (the size of a small gyrfalcon or a large peregrine), with the anatomical and aerodynamic characteristics described in detail by Tucker (1998, 2000). The falcon dives with fixed wings along a path in a plane inclined at  $45^\circ$  to the horizontal, and its body axis is always at a tangent to the path. It holds its head in one of two positions while diving: either straight ( $\beta=0^\circ$ ) or turned sideways so that the LOS of the deep fovea is parallel to the direction of flight ( $\beta=\alpha_d$ ). With its head straight, it can reach speeds in excess of  $70\text{ m s}^{-1}$  (Tucker, 1998).

#### *Derivation of the logarithmic spiral path*

Suppose that the ideal falcon is diving at its prey from a distance such that it can only see the prey with the deep fovea. To keep the prey in view, the falcon must keep the LOS of the deep fovea of one eye pointed towards the prey; one way that it can do this is by diving straight towards the prey with its head turned sideways and  $\beta=\alpha_d$ .

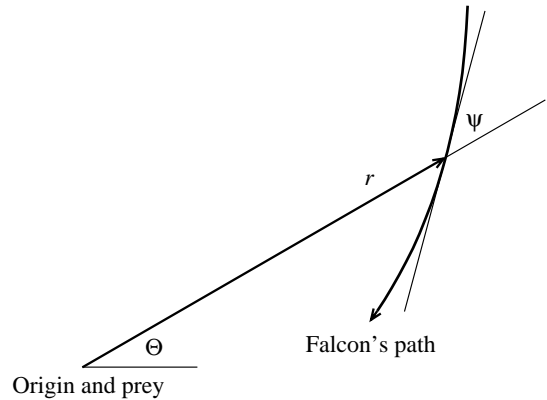


Fig. 7. The system of polar coordinates ( $r, \Theta$ ) and the position vector (straight arrow) that describe the two-dimensional flight path (curved arrow) of an ideal falcon. The position vector of length  $r$  extends at angle  $\Theta$  from the origin, where the prey is, and traces out the points on the path as  $\Theta$  and  $r$  vary. At any point on the path, the tangent to the path (thin line) makes the angle  $\Psi$  with the position vector. When the falcon follows the path with its body axis at a tangent to the path and its head straight ( $\beta=0^\circ$ , where  $\beta$  is the angle between the reference line of the head and the body axis), the angle ( $\alpha$ ) of its line of sight to the prey equals  $\Psi$ . Since  $\alpha$  is constant, the path is a logarithmic spiral.

Alternatively, the falcon could keep the prey in view with its head straight ( $\beta=0^\circ$ ) if it flew along a curved path that kept the LOS of the deep fovea on the prey. The derivation of the equation for the curve is straightforward in polar coordinates. A position vector points from the origin (where the prey is) to the falcon, and the vector has a length (or radius)  $r$  and meets a reference line at angle  $\Theta$  (Fig. 7). Both  $r$  and  $\Theta$  vary as the falcon approaches the prey, and the angle between the position vector and a tangent to the curve at any point is  $\Psi$ . Most calculus texts derive the relationship:

$$\tan\Psi = r\,d\Theta/dr. \quad (1)$$

Since the falcon's body axis is at a tangent to the curve, and  $\beta=0^\circ$ , the LOS of the deep fovea will always fall on the prey when  $\Psi$  is constant and equal to  $\alpha_d$  as  $\Theta$  varies. In the following,  $\Psi$  will be constant in this sense, and all angles will henceforth be expressed in radians rather than degrees to simplify mathematical notation.

Integration of equation 1 yields an expression for the path:

$$\Theta = \tan\Psi \ln r + \pi, \quad (2)$$

or

$$r = e^{(\Theta-\pi)\cot\Psi}, \quad (3)$$

when  $r=1$  at  $\Theta=\pi$ .

Equation 3 describes a logarithmic (or equiangular) spiral (Fig. 8), a curve that has received continued attention since it was discussed by Descartes in 1638 (Archibald, 1920). Logarithmic spirals describe many natural shapes – for example, spiral galaxies of stars (Kennicutt, 1981) and structures in several plants and animals (Thompson, 1959).

Some insects move towards a light along a logarithmic spiral (Wigglesworth, 1972), evidently because they keep a constant

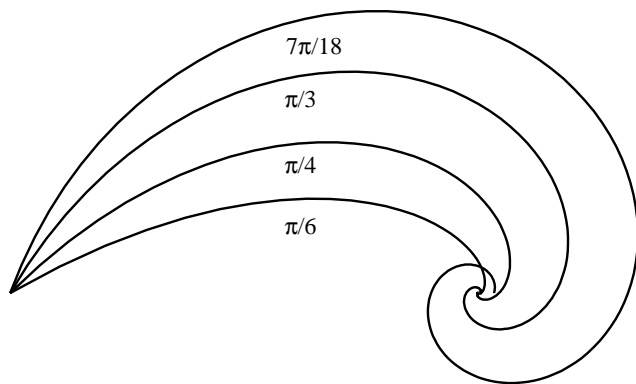


Fig. 8. Four logarithmic spirals, each with the value of  $\Psi$  shown near the middle of each curve. As the position vector that generates each curve rotates counterclockwise from  $\Theta=0$ , each curve spirals outward from a point near the origin at the right and ends at a point at the left where  $\Theta=3\pi$ .  $\Psi$  is the angle between the position vector and the tangent to the curve at the end of the position vector.

angle between the body axis and the LOS to the light. This behavior results in an essentially straight path if the light is the sun, because  $\Delta\Theta$  for a movement of, say, 1 m along the spiral path is small when the origin of the spiral is at the distance of the sun. A moth approaching a candle flame, however, follows an obviously curved path to its destruction, because a movement of 1 m along a spiral path to a nearby candle causes  $\Delta\Theta$  to be much larger, perhaps in excess of  $\pi$ .

An ideal falcon that keeps its head straight while viewing prey with maximum acuity also follows a logarithmic spiral path towards the prey, but encounters one problem: the spiral never reaches the origin. The falcon solves this problem by turning from the spiral path and flying straight towards the prey when close enough to see the prey clearly with its less-acute binocular vision.

The distance from which the ideal falcon begins its straight approach to the prey increases with the size of the prey and so does the distance at which the falcon begins its spiral approach. This behavior is a reasonable model for the behavior of real raptors, since they probably see and attack large prey from farther away than smaller prey, whether they use their more-acute monocular vision or less-acute binocular vision. The next section analyzes the time that the ideal falcon takes to reach its prey and incorporates the relationship between distance and prey size in the analysis.

#### The time to reach prey

The ideal falcon flies farther to reach its prey along a spiral path than along a straight one, but it also flies faster. It is possible that the speed difference could compensate for the longer distance so that the falcon would 'break-even' and reach the prey in the same travel time along either path. The speed difference along the two paths depends on the aerodynamic drag of the falcon with a straight or turned head, and this section develops a break-even criterion by analyzing drag, path lengths and speed differences. The ideal falcon, in fact, exceeds

this criterion, and so can reach the prey more quickly by flying along a longer path.

#### Aerodynamic drag

Ideal falcons experience aerodynamic drag in flight to an extent that depends on the lift that they produce and the shape that they maintain in flight (Tucker, 1998, 2000). Total drag ( $D$ ) is the sum of three components:

$$D = D_i + D_{pr} + D_{par}, \quad (4)$$

where the first two components (induced drag  $D_i$  and profile drag  $D_{pr}$ ) are associated with the wings, and the third component (parasite drag  $D_{par}$ ) is the drag of the body exclusive of the wings (see Tucker, 1987; Pennycuik, 1989; or aerodynamics text books for information on these components). Parasite drag makes up more than 75% of  $D$  at high speeds (Tucker, 1998) and depends on air density  $\rho$ , the cross-sectional area of the falcon's body ( $S_b$ ), the parasite drag coefficient ( $C_{D,par}$ ) and the speed through the air ( $V$ ):

$$D_{par} = 0.5\rho S_b C_{D,par} V^2. \quad (5)$$

For the purposes of this paper, total drag can be approximated by a relationship similar to equation 5:

$$D = K C_D V^2, \quad (6)$$

where  $K=0.5\rho S$  and is constant,  $S$  is an undefined but constant area of the falcon's body, and the total drag coefficient  $C_D$  has two values:  $C_{D,S}$  when the head is straight ( $\beta=0$ ) and a higher value,  $C_{D,B}$ , when the head is sideways ( $B$  for 'bent', with  $\beta=\alpha_d$ ).

The approximation in equation 6 makes possible a simple, general definition and computation of the break-even criterion and is sufficiently accurate for the purposes of this paper. Exact calculations of drag and the break-even criterion are possible, but laborious, in specific cases (Tucker, 1987, 2000) and, below, I shall compare both approximate and exact results for the ideal falcon.

#### Straight and curved paths

The falcon approaches the prey in a dive along two alternative paths, straight and curved, each in a plane inclined at an angle of  $\pi/4$  to the horizontal, and each starting from the same point at distance  $r_2$  from the prey (Fig. 9). The falcon has constant but different speeds along the two paths, because it dives along the straight path with its head turned sideways at  $\beta=\alpha_d$  and along the curved path with its head straight ( $\beta=0$ ). The curved path has two segments: a spiral segment of length  $s$  that starts at  $r_2$  from the prey when  $\Theta_2=\pi$  and a short, straight final approach of length  $r_1$  that starts when  $\Theta_1=\pi/2$ .

Logarithmic spirals have the convenient property for this study that  $r_1$  is proportional to  $r_2$  for all values of  $r_2$  when  $\Theta_2-\Theta_1$  and  $\Psi$  are constant. This property can be seen by taking the definite integral of equation 1:

$$\Delta\Theta = \tan\Psi \ln(r_2/r_1), \quad (7)$$



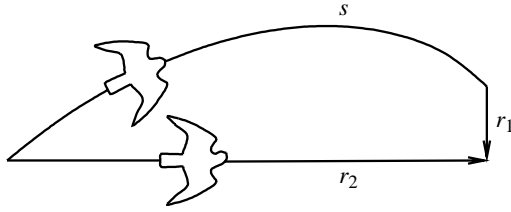


Fig. 9. The alternative straight and curved paths that an ideal falcon follows to the prey. The falcon with its head turned sideways flies along a straight path of length  $r_2$  to the prey at the end of the arrow. The falcon with its head straight flies along a curved path with two parts: the first part, of length  $s$ , is a segment of a logarithmic spiral between  $\Theta=\pi/2$  and  $\Theta=\pi$ , with  $\Psi=\pi/4.5$ , or  $40^\circ$ ; the second part, of length  $r_1$ , is the straight path from the end of the spiral to the prey. See Fig. 7 for definitions of  $\Theta$  and  $\Psi$ .

where  $\Delta\Theta=\Theta_2-\Theta_1$ , and after rearrangement:

$$r_1/r_2 = e^{-\Delta\Theta \cot\Psi}. \quad (8)$$

For example,  $r_1/r_2=0.15$  when  $\Delta\Theta=\pi/2$  and  $\Psi=\pi/4.5$ , or  $40^\circ$ , the angle  $\alpha$  of the LOS that perched raptors commonly used to look at distant objects (Fig. 4).

The distance  $s$  along the spiral path may be found from the relationship:

$$(ds)^2 = (rd\Theta)^2 + (dr)^2, \quad (9)$$

which is derived in most calculus texts. After substituting for  $d\Theta$  from equation 1 and integrating between  $r_1$  and  $r_2$ :

$$s = (\Delta r) / \cos\Psi, \quad (10)$$

where  $\Delta r = r_2 - r_1$ .

Now consider the distance that the falcon flies along the straight path with its head turned to one side. This distance is  $\Delta r$  since, at distance  $r_1$ , the falcon can straighten its head and see the prey clearly enough with its less-acute binocular vision. With its head straight, the falcon will begin to accelerate to the same speed it would have on the spiral segment of the curved path. I shall assume for simplicity that the acceleration is instantaneous, so that the falcon's speed is the same over distance  $r_1$  for both the straight path and the straight segment of the curved path. Thus, the ratio of the lengths of curved and straight paths over which the falcon has different speeds is, from equation 10:

$$s/\Delta r = 1/\cos\Psi. \quad (11)$$

Consider an ideal falcon that reaches the prey after the same travel time along either the straight or the curved path. The falcon flies at constant speed  $V_B$  with its head bent along the straight path for distance  $\Delta r$ , and at constant speed  $V_S$  with its head straight along the curved path for distance  $s$ . Thus:

$$V_S/V_B = s/\Delta r = 1/\cos\Psi. \quad (12)$$

The falcon's drag is the same along both  $s$  and  $\Delta r$ , because the falcon does not accelerate, and both paths have the same angle relative to the horizontal (the glide angle, equal to  $\pi/4$ ). Under these conditions:

$$D = mg \sin\pi/4, \quad (13)$$

where  $m$  is the falcon's body mass and  $g$  is the magnitude of gravitational acceleration. The ratio of the drag coefficients  $C_{D,S}$  and  $C_{D,B}$  therefore determines the ratio of speeds since, from equations 6 and 12:

$$C_{D,B}/C_{D,S} = (V_S/V_B)^2 = 1/\cos^2\Psi. \quad (14)$$

$C_{D,B}/C_{D,S}$  is the break-even ratio – the ratio for equal travel time along straight or spiral paths when the falcon's head is turned to  $\beta=\Psi$  along the straight path and to  $\beta=0^\circ$  along the curved path. For example,  $C_{D,B}/C_{D,S}=1.7$  when  $\Psi=\pi/4.5$ , or  $40^\circ$ .

The break-even value of 1.7 is an approximation because of equation 6. The exact break-even value for the ideal falcon, calculated from equations in Tucker (1998, 2000), is 1.8.

If the ideal falcon chooses the quicker path to the prey, does it follow the straight or the curved path? The break-even ratio answers this question: if the actual ratio of drag coefficients is less than the break-even ratio, the falcon chooses the straight path; if more, then the curved path.

The actual ratio of the drag coefficients can be estimated from measurements of the drag on model raptor bodies with straight and turned heads (Tucker, 2000). The symbol  $R_{tot}$  in that paper represented the actual ratio of total drags for a 1 kg ideal falcon with its head position at  $\beta=0$  and  $\pi/4.5$ . However,  $R_{tot}$  is also the actual ratio of the total drag coefficients, since it describes total drags at the same speed.

$R_{tot}$  may plausibly have values between 2 and 6 (Tucker, 2000), and even the low end of this range exceeds the break-even ratio of 1.8. Therefore, the ideal falcon could get to the prey quicker along the curved path than along the straight path.

One of the roles of the ideal falcon in this paper is to guide observations on real raptors. Do real raptors that dive towards their prey from great distances and at high speeds follow curved paths? Tucker et al. (2000) show that peregrines do.

### List of symbols

$C_D$	total drag coefficient
$C_{D,B}$	total drag coefficient with head sideways
$C_{D,par}$	parasite drag coefficient
$C_{D,S}$	total drag coefficient with head straight
$D$	total aerodynamic drag
$D_i$	induced drag
$D_{par}$	parasite drag
$D_{pr}$	profile drag
$e$	2.718, the base of the natural logarithms
$F_B$	fraction of looking time with head sideways
$F_S$	fraction of looking time with head straight
$g$	magnitude of gravitational acceleration
$K$	a constant
LOS	line of sight
$m$	body mass in kilograms
$R_{tot}$	$C_{DB}/C_{DS}$
$r$	length of a position vector
$r_1, r_2$	lengths of a straight path
$S$	surface area
$S_b$	cross-sectional area of the ideal falcon's body

$s$	distance along a logarithmic spiral
$V$	air speed
$V_S$	air speed with head straight
$V_B$	air speed with head bent
$X$	angular deviation
$Y$	minimum resolvable angle for acuity
$\alpha$	angle on the foveal plane between an LOS and the reference line of the head
$\alpha_d$	$\alpha$ for the LOS of the deep fovea
$\alpha^*$	angle between the reference LOS and the head axis
$\beta$	angle between the reference line of the head and the body axis
$\Delta$	symbol for change in a variable
$\Theta$	angle of a position vector
$\pi$	ratio of the circumference of a circle to the diameter
$\rho$	air density
$\Psi$	at a point on a curve, the angle between the position vector and the tangent to the curve

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