The Journal of Experimental Biology 203, 3755–3763 (2000)
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JEB3052

CURVED FLIGHT PATHS AND SIDEWAYS VISION IN PEREGRINE FALCONS (*FALCO PEREGRINUS*)

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Accepted 25 September; published on WWW 14 November 2000

Summary

When diving at prey straight ahead from great distances at high speeds, a peregrine has a conflict between vision and aerodynamics: it must turn its head approximately 40° to one side to see the prey with maximum visual acuity at the deep fovea of one eye, but the head in this position increases aerodynamic drag and slows the falcon down. The falcon could resolve this conflict by holding its head straight and flying along a logarithmic spiral path that keeps the line of sight of the deep fovea pointed sideways at the prey. Wild peregrines, observed with binoculars, telescopes and a tracking device, did approach prey the size of American robins (*Turdus migratorius*) and smaller birds from distances of up to 1500 m by holding their heads straight and flying along curved paths that resembled the logarithmic spiral.

Key words: flight, deep fovea, vision, logarithmic spiral, spiral flight path, peregrine falcon, *Falco peregrinus*.

Introduction

Some raptors – falcons, hawks and eagles in this study – attack their prey from great distances in high-speed dives, and this behavior creates a conflict between aerodynamics and vision: raptors must keep their heads and bodies aligned with the flight direction to minimize drag and reach maximum speed (Tucker, 2000a) but, to see straight ahead with maximum visual acuity (a measure of the ability to discriminate fine details; Riggs, 1965), they must turn their heads 40° sideways to point the line of sight (LOS) of one eye in the flight direction (Tucker, 2000b). In theory, raptors could resolve this conflict by aligning their heads and bodies with the flight direction and flying along a curved path that keeps the LOS for maximum visual acuity pointed sideways at the prey. Even though the curved path is longer than the straight one, the raptor could probably reach the prey more quickly along the curved path, because the raptor's speed with its head straight is higher than that with its head sideways (Tucker, 2000b).

In this paper, we investigate whether wild peregrine falcons (*Falco peregrinus*) do approach prey from long distances by following curved paths.

The ideal path

Tucker (2000b) describes in detail the visual system of an 'ideal falcon' (Tucker, 1998, 2000a) – a mathematical model with aerodynamic characteristics and a visual system that resemble those of real falcons – and the curved path that the ideal falcon follows towards its prey. The path has two segments: a logarithmic spiral along which the falcon keeps its head straight while looking sideways at the prey with maximum visual acuity, and a straight segment along which the falcon flies straight to the prey when it is close enough to view the prey clearly with binocular vision.

The ideal path in this paper has these same two segments and, although it is a simplified mathematical model, it is meant to represent reality closely enough to make predictions about the paths of the real peregrines that are the subject of this study. The ideal path has three roles: it provides spatial coordinates that can be computed from equations, it can be compared with real paths, and it can be used to plan observations on real paths. For example, it answers questions about how long a real path might be, what kind of observations and instrumentation might be necessary to distinguish a curved path from a straight one, and where the instrumentation should be located, relative to the path, to make the distinction.

The equations that describe the ideal path come from the properties of the visual system of the ideal falcon, and we summarize those properties here. Each eye of the falcon has a region of the retina known as the deep fovea that is specialized for maximum visual acuity, and the LOS of each deep fovea meets the head axis at an angle (Ψ) of $\pi/4$ (in rad), or 45°. During flight, the falcon holds its head and body axes in alignment, and the common axis always points in the direction of flight. If the falcon flies along a particular logarithmic spiral (henceforth, simply 'spiral'), the LOS of one deep fovea will always extend to the point in space that the falcon approaches along the spiral, e.g. the origin in Fig. 1.

A falcon that follows the ideal path begins its approach to the prey from so far away that it can see the prey only with its deep fovea. At some point along the path, the prey is close enough to be seen clearly straight ahead with the less-acute binocular vision, and the falcon leaves the spiral path and flies straight towards the prey. These maneuvers give rise to the spiral and straight segments of the ideal path.

The ideal path lies entirely in a plane – the dive plane – and the spiral segment is given by:

$$r = e^{(\Theta-\pi)\cot\Psi}\,, \qquad (1)$$

where r and Θ (in rad) are the conventional radius and angle for polar coordinates, Ψ determines the shape of the spiral, and r=1 when $\Theta=\pi$ (for the derivation of this equation, see Tucker, 2000b). The value of $\pi/4.5$ (40 °) for Ψ in this study is the angle of the LOS of the deep fovea relative to the head axis, determined from the behavior of several species of raptor (Tucker, 2000b). Note that this empirical value for Ψ is slightly less than Ψ for the ideal falcon.

The spiral segment begins at $\Theta_2=\pi$ and r_2, and ends at the point (Fig. 1) where $\Theta_1=\pi/2$ and:

$$r_1 = e^{(-\pi/2)\cot\Psi}\,. \qquad (2)$$

The straight segment runs from this point to the prey at the origin. Note that r_2 is the distance between the falcon and its prey at the start of the ideal path, and r_1 is the distance between the falcon and the prey at the start of the straight segment.

Logarithmic spirals have a convenient property for this study: r_1 is proportional to r_2 for all values of r_2 and a given value of $\Delta\Theta=\Theta_2-\Theta_1$ (Tucker, 2000b). When $\Delta\Theta=\pi/2$ and $\Psi=\pi/4.5$:

$$r_2/r_1 = e^{-\Delta\Theta\cot\Psi}=0.15\,. \qquad (3)$$

Thus, the distance (r_1) of the peregrine from the prey at the beginning of the straight segment is 0.15 times its distance (r_2) from the prey at the beginning of the ideal path, no matter how far the path begins from the prey.

This property of the ideal path is a plausible description of how a peregrine might approach prey. Other factors being constant, r_2 would be longer for a larger, more visible prey than a small one; as would r_1, because the peregrine could see the larger prey from a greater distance with its deep fovea as well as with its binocular vision.

A peregrine seems most likely to approach prey along an ideal path when the distance r_2 is so great that the peregrine must use its maximum visual acuity (i.e. the deep fovea) to see the prey. The peregrines in this study behaved as if they saw birds the size of American robins (*Turdus migratorius*, 26 cm from beak tip to tail tip) flying against a background of water or vegetation 1500 m away, and even with 7× binoculars, we could barely see robins at this distance against the same background. Therefore, we assume that the peregrines were using their maximum visual acuity when watching birds 1500 m away, and we shall use this value for r_2.

This value for r_2 suggests the characteristics of a site where one might see wild peregrines following spiral paths towards prey. (i) The site should be in open country where observers

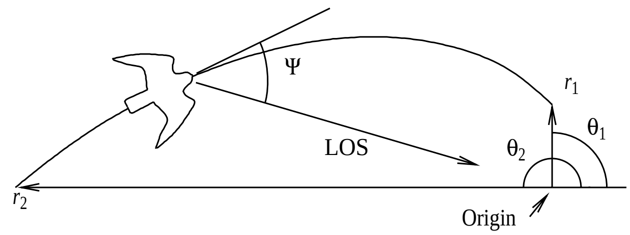

Fig. 1. A falcon flying along the ideal path from point r_2,Θ_2 to the origin while keeping its head straight and the line of sight (LOS) of the deep fovea pointed to the origin. The spiral segment of the path occurs between points r_2,Θ_2 and r_1,Θ_1; as the falcon flies along this segment, the LOS always makes the angle Θ=40 ° with the flight direction and points to the origin. The straight segment begins at point r_1,Θ_1 when the falcon turns and flies straight to the origin. During this segment, the LOS no longer points to the origin, even though the falcon's head is still straight, and Θ is still 40 °.

can see a flight 1500 m long without interference from vegetation or topography. (ii) The site should provide a known starting point for the approach to prey, such as a perch within 1000 m of the observers. This characteristic is necessary because it is nearly impossible to find a peregrine 1000 m away at a random location in the sky as it starts its approach. (iii) The peregrine should approach prey frequently from the known starting point, so that the observers can gather data in a practical amount of time.

Materials and methods

The study site and peregrine behavior

We observed peregrines at the Chalk Cliffs (Fig. 2), which rise to 3050 m above sea level in the Rocky Mountains of central Colorado, latitude 38°44′00″N and longitude 106°11′00″W. A pair of peregrines has nested in the Chalk Cliffs for many years and, during the nesting season, they frequently approach prey 1500 m away. Many of these approaches start from perches in the cliffs and end in a valley to the south and southeast.

The perches in the cliffs were approximately 425 m above and 1500 m away from an important landmark in this study, an unnamed lake locally known as Dead Horse Lake, which is 310 m long from east to west, and 270 m wide from north to south. The LOS of a falcon perched in the Chalk Cliffs and looking at Dead Horse Lake is inclined at approximately 15 ° to the horizontal, and this angle sets the orientation of the dive plane that contains the ideal path. Line r_2 in the dive plane is inclined at 15 ° to the horizontal, and line r_1 is horizontal.

We watched the peregrines for up to 3 weeks each June from 1995 to 1999, from two sites (Fig. 2): the Chalk Cliffs Site near the base of the cliffs, and the Lake Site at the east edge of Dead Horse Lake. With optical aids, we could follow the falcons over the valley from these sites for 3 km or more. In June, the peregrines had nestlings, and the male caught virtually all the prey for the female and the nestlings. We shall refer to the peregrines that approached prey during these years simply as

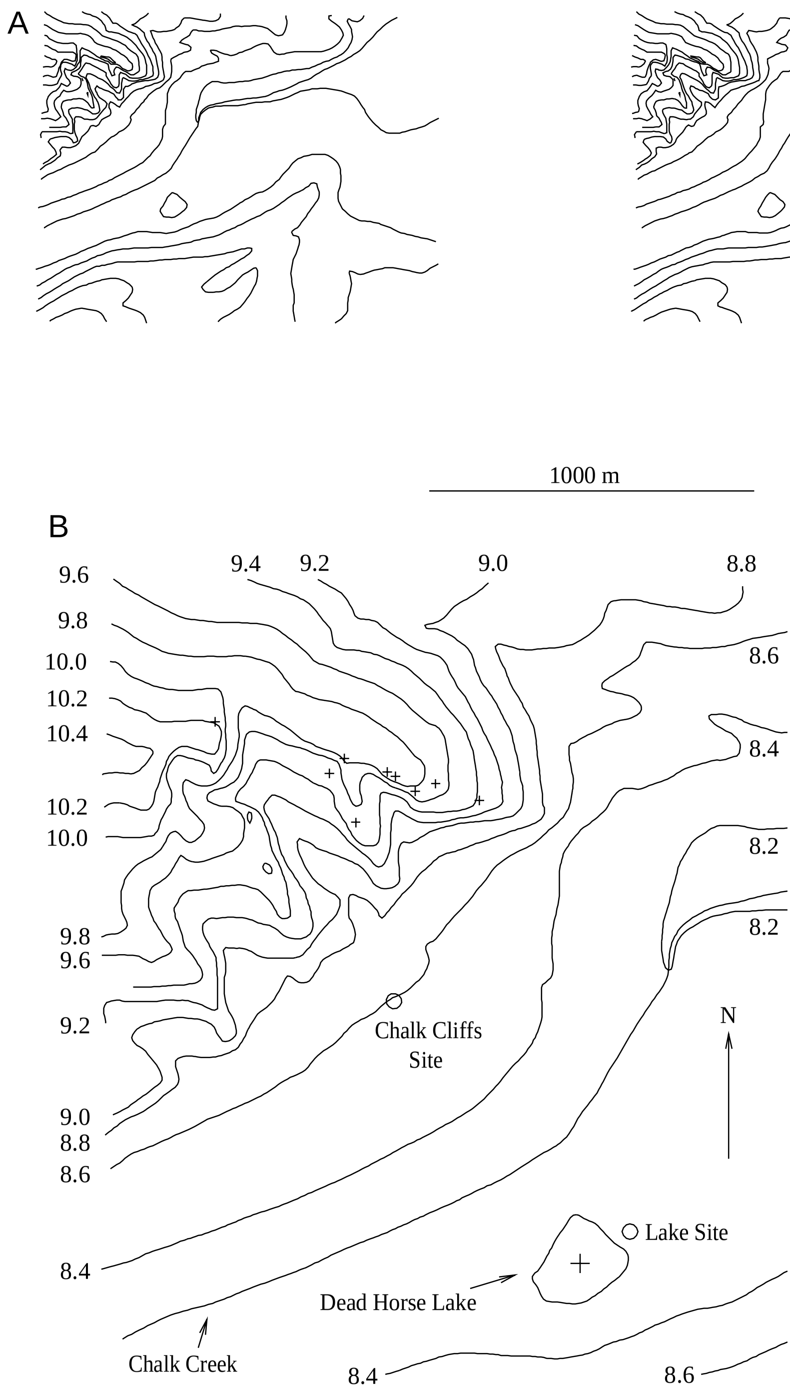

Fig. 2. A stereotriplet (A) and a topographic map (B) of the Chalk Creek Valley. Readers who fuse an adjacent pair of drawings in the stereotriplet will see a pair of three-dimensional topographic images of the valley. The topographic map shows landmarks for this study: the Chalk Cliff Site, the Lake Site, Dead Horse Lake and the Chalk Cliffs, 500 m north of the Chalk Cliffs Site. The crosses in the cliffs mark points where the falcon often perched, and the numbers at the ends of the contour lines refer to altitude above sea level in thousands of feet.

a single male falcon, although the male could have been a different individual each year.

We made observations daily between 06:00 h and 12:00 h, and occasionally at other times. Typical weather in the morning was clear with less than 25 % cloud cover and temperatures ranging from 3 °C at dawn to 20 °C by noon. The wind speeds and directions were usually less than 4 m s^{-1} at ground level, and from west through south to southeast. There was little haze or dust in the air in this region, and we could clearly see mountains more than 25 km away.

For the observations, we used our unaided eyes, 7× to 10× binoculars and 15× to 30× telescopes mounted on tripods with fluid heads. We also used a tracking device, described below, that recorded the three-dimensional path of the falcon through space as it approached prey.

The falcon preyed only on flying birds, and the prey that he brought back to the nest were as large as American robins, but more commonly the size of white-throated swifts (*Aeronautes saxatalis*; 17 cm from beak tip to tail tip). He approached prey in a variety of ways, and three examples illustrate the range of his behavior, two extreme examples and an intermediate that includes approaches to prey near Dead Horse Lake.

In the first extreme example, the falcon perched on a rock in the cliffs before dropping 100 m at an angle of 45 ° to the horizontal and seizing a white-throated swift. The falcon beat its wings four times as it left the perch, but then kept its wings folded until reaching the swift.

In the second extreme example, the falcon circled with spread wings 500 m above the valley floor before dropping at an angle of 60 ° on a robin 50 m above the ground. The falcon beat its wings five times as it started to descend, then folded them until it reached the robin.

In the intermediate example, the falcon flapped off rapidly from a perch in the cliffs along a nearly level path for 500 m, and then folded its wings and dived at an angle of 20 ° at a robin flying over Dead Horse Lake. The falcon did not circle or change direction in flight as if searching, but gave the impression that it saw the robin from the perch and flew out to catch it. Approaches of this type from a perch to prey near Dead Horse Lake were common and, since the falcon evidently saw the prey from 1500 m away, the distance r_2 for the ideal path, the approach might approximate the ideal path. We shall henceforth discuss only approaches that are of this type and towards Dead Horse Lake, and we shall identify them with the term ‘long approaches’. We shall also use the term ‘curved path’ for a long approach that resembles the ideal path.

Distinguishing a curved path from a straight one

Curved paths may be difficult to distinguish from straight paths because of an observer’s limited ability to estimate the range to the falcon accurately at long ranges. We solved this problem by using a tracking device, and we also used cues other than range to identify curved paths when observing the falcon with binoculars and telescopes.

Consider an observer on a featureless plane, watching a point move at unknown speeds along a curved path on the plane, e.g.

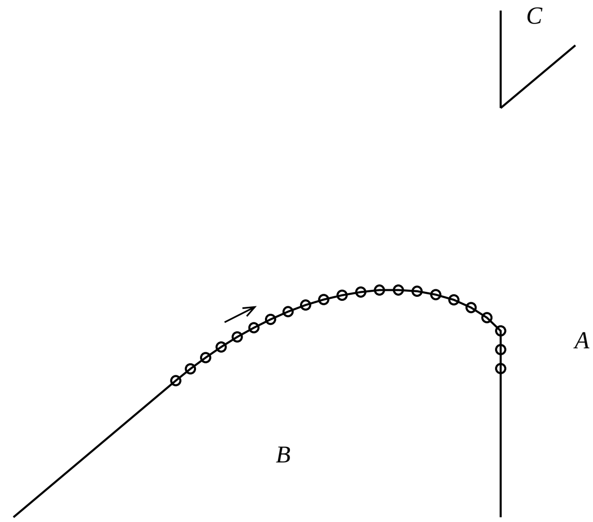

Fig. 3. The ideal path, marked by circles, and region *A* from which an observer could see a reversal in the angle (γ) of the line of sight to a falcon on the ideal path. An observer in regions *B* and *C* could not see such a reversal. The Chalk Cliffs Site is at point *B*.

an observer at point *B* (Fig. 3) watching a point move to successive positions along the ideal path. The observer’s LOS to the point sweeps through a series of angles, measured from a fixed reference line, as the point moves to each position; and the observer perceives the path as the ranges to the point at each angle. However, if the point moved along the straight line from the beginning to the end of the path, the LOS would sweep through the same angles, and the observer could distinguish the two paths only by the differences in range at each angle.

Now consider a falcon moving along the ideal path in Fig. 3. The distance between the beginning and end of the ideal path is r_2, or 1500 m, and an observer at any position on the plane will at some point be at least 750 m from a falcon. Stereoscopic vision does not provide accurate range information at this distance, and range estimated from other cues, such as relative size and speed, may not be accurate enough to distinguish the ideal path from the straight one along r_2. However, there are cues other than range that can distinguish between curved and straight paths in some circumstances.

An observer without range information could use temporal changes in two angles as cues: the angle (γ) between a fixed reference line and the LOS from the observer to the falcon, and the angle (δ) between the falcon’s body axis and the LOS from the observer. γ is constant when the falcon flies either straight towards the observer or straight away from the observer, but will change with time for other paths. The problem is how to distinguish between straight and curved paths from temporal changes in γ.

In some cases, the observer can make the distinction by noticing whether the relationship between γ and time (*t*) has a maximum or a minimum, in which case $d\gamma/dt=0$ at some point on the path. If so, the path is curved; but if not, the path may be curved or straight, depending on the observer’s position relative to the path. We shall refer to a maximum or a minimum

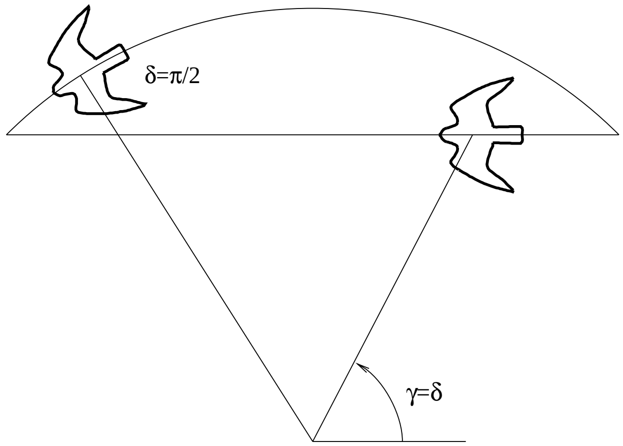

Fig. 4. A falcon following a straight and a circular path. The angle γ of the line of sight from an observer to the falcon changes as the falcon moves along both paths, but the angle δ between the line of sight and the falcon's body axis changes only along the straight path.

as a reversal in γ. For completeness, a reversal also occurs when γ changes along the path and then is constant for a time.

For example, suppose an observer at point *A* in Fig. 3 watches a falcon starting out on the ideal path. Place a straight edge between the observer and the point at the beginning of the ideal path to mark the observer's LOS to the falcon, and swing the straight edge from the observer to successive points on the ideal path as the falcon progresses. The straight edge will show a reversal in γ by first swinging clockwise and then counterclockwise, and the reversal indicates that the falcon flew along a curved path.

In contrast, an observer at point *B* (the location of the Chalk Cliffs site relative to a long approach that follows the ideal path) does not see a reversal in γ for successive points along the ideal path. Nor can the observer see a reversal from any point in the areas around points *B* and *C* bounded by the straight, unmarked lines in Fig. 3. From all other points, the observer can see a reversal.

The angle δ between the observer's LOS to the falcon and the falcon's body axis may also change as the falcon flies, and the relationship between δ and γ as they change over time is a cue to whether the flight path is straight or curved. We define δ to be 0° when the observer sees the falcon head-on and to increase as the falcon yaws from head-on and presents its left side to the observer. Now consider the falcon flying along the straight path in Fig. 4. The angles γ and δ both increase as the falcon progresses. In contrast, when the falcon flies along the curved path (the arc of a circle) in Fig. 4, γ increases but δ has a constant value of π/2, or 90°. Rather than develop a general relationship between γ, δ, time and observer location for straight and curved paths, we shall discuss specific examples below.

The tracking device

The tracking device (TD; Tucker, 1995) recorded the three-dimensional position in space of the falcon at 1 s intervals as it flew along a path. The operator of the TD watched the bird through a 14× telescope, mounted on a base that attached to a surveyor's tripod. The telescope was part of an optical rangefinder with a 1 m base length, and the operator pointed the LOS of the telescope at the falcon while adjusting a thumbwheel to keep two images of the falcon aligned in the telescope. A transducer connected to the thumbwheel digitized the range from the TD to the falcon, and two other transducers in the rangefinder base digitized the horizontal and vertical angles of the LOS. A computer read the digitized values, known as counts, from the transducers and stored them in memory as the spherical coordinates of the falcon. We set the TD up at the Chalk Creek Site on a platform supported 1.5 m above the ground by scaffolding to reduce blocking of the LOS by the surrounding vegetation.

We encountered a problem during the first year that we used the TD at the Chalk Cliffs – the operator could not follow long approaches with it, because the horizontal angle of the LOS to the falcon swept through 100° or more during a long approach. The operator had to face towards the falcon to keep the LOS on the falcon, and had to walk around the tripod to keep facing in the right direction for an angle this large; but he could not walk smoothly enough to keep the falcon in the telescope's field of view. We solved this problem the next year by adding a robotic trolley to the TD. The operator stood on the trolley, which moved smoothly on a pair of circular tracks around the TD tripod to keep the operator facing the falcon during a long approach.

The trolley had six wheels, two with rubber tyres, 12.7 cm in diameter, that rode on the inner and outer tracks and drove the trolley. The inner and outer tracks had radii of 38.1 and 68.6 cm, and separate shafts from a differential gear box turned each tyre. A 12 V d.c. variable-speed geared motor turned the input shaft to the gear box in one direction or the other through a chain drive, and a Microchip PIC16C84 microcontroller on the trolley controlled the motor through a National Semiconductor LMD18200 controller.

The microcontroller controlled the speed, acceleration and direction of the trolley to make it start and stop smoothly and follow directions from either the operator or the TD computer. The operator could drive the trolley by leaning to the left or right and pressing switches with his knees. A stand on the trolley held these switches between the operator's legs at knee height and width, and the trolley moved in the direction of lean.

The microcontroller drove the trolley when the operator did not and used information on the horizontal angle of the LOS, received from the TD computer, to position the trolley. The microcontroller automatically moved the trolley to keep the operator facing the falcon as the operator moved the rangefinder, and also kept track of the trolley's position on the tracks by monitoring the rotation of the drive shaft to the gear box. The lobes on a three-lobed cam that turned with the drive shaft operated two switches that generated a quadrature digital signal. The microcontroller decoded the signal and calculated where the trolley was with an angular resolution of 2.5°, measured from the center of the track circle.

The computer for the TD described in Tucker (1995) was a standard portable computer; but its screen, keyboard and hard

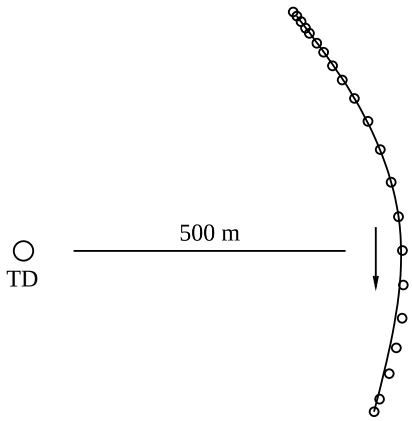

Fig. 5. A long approach path of a peregrine falcon recorded by the tracking device (TD) and projected onto the *x*,*y* plane. The circles mark 21 pairs of *x*,*y* coordinates that constitute the track, and the curved line is a cubic spline fitted to the start, end and two intermediate points of the track.

disk drive were too vulnerable to sun, dust and rain for prolonged use at the Chalk Cliffs. When we added the trolley to the TD, we also replaced the portable computer with a custom-built, dedicated computer with a Microchip PIC16C84 microcontroller for a central processing unit. Instead of a hard disk, this computer used more reliable non-volatile, solid-state memory (Microchip 24C65 EEPROM) for data storage; instead of a conventional keyboard and screen, it used two switches and a two-line liquid crystal display. It also had a speaker and a real-time clock and calendar. An input/output bus carried commands and data to and from the various peripheral devices, and two of the bus wires made up a serial I^2C bus that supported several of the peripheral devices, including the robotic trolley.

Analysis of tracks

At the end of a day of field work, we connected the I^2C bus of the TD computer to a computer in the field laboratory and transferred times, dates and transducer counts from the EEPROM to the laboratory computer. Programs on the laboratory computer converted the transducer counts for a track to spherical coordinates, and then to coordinates on a system of orthogonal *x*,*y*,*z*-axes fixed to the earth, with the *z*-axis being vertical. The paths illustrated in this paper are the projections of these tracks on the horizontal *x*,*y* plane, smoothed by fitting a cubic spline curve to four points on each path: the beginning, the end and two intermediate points approximately evenly spaced along the track. Most tracks of long approaches were quite smooth even before fitting, and the fitted curve closely approximated the lines drawn between all the *x*,*y* coordinates on a track (Fig. 5).

We used the *x*,*y*,*z* coordinates of a track to estimate the speed and dive angle of the falcon at the end of a long approach. Speed is the three-dimensional distance (relative to the ground) that the bird moved in 1 s, averaged over 3 s. The dive angle is an inverse tangent computed from Δz divided by the horizontal distance covered over the ground in 3 s. Tucker et al. (1998) describe these calculations in detail. Here, we report speeds and angles as raw data, without corrections or error analyses, to describe the falcon's behavior during long approaches. A further report will describe the aerodynamics of the falcon in detail and include our estimates of the true speeds of the falcon.

The TD artefact

We made a particular effort to avoid an artefact that the TD could introduce: recording a straight path as a curved one. This artefact could occur if the TD operator followed a falcon on a straight path but neglected to turn the thumbwheel on the rangefinder that set the range to the bird. Furthermore, the artefact would resemble the curved long approaches to Dead Horse Lake because of the location of the TD at the Chalk Cliffs Site.

To reduce this artefact, the TD operator paid particular attention to keeping the images of the falcon lined up in the rangefinder while tracking long approaches. The robotic trolley eased this chore by turning the operator always to face the falcon. The operator could keep the images aligned with an error of 25 % or less of the falcon's body length 75 % of the time at a distance of 1000 m (Tucker et al., 1998) and closer than this during the first temporal half of the approach when the falcon was closer to the TD and its speed was slower. The following error analysis shows that this error limits the size of the artefact to much smaller curvatures than occurred in the measured paths.

The range (*R*) recorded by the rangefinder is a function of the digitized values (*C*, for counts) generated by the rangefinder transducer, and a change in *C* corresponds to a change in *R*:

$$\Delta R = \Delta C R^2 / k_1 \,, \tag{4}$$

where k_1=956×10^3 m. The standard deviation (S.D.) of the range error, measured in transducer counts, is 74 at 1000 m (Tucker et al., 1998), and we assume that S.D. is proportional to range:

$$\text{S.D.} = k_2 R \,, \tag{5}$$

where k_2=0.074 m. We also assume that a 95 % confidence interval for range extends to either side of the measured range for a distance (ΔR_{95}) computed from 2 S.D. counts. Combining equations 4 and 5 with ΔC=2S.D.:

$$\Delta R_{95} = 2 k_2 R^3 / k_1 \,. \tag{6}$$

Consider a falcon flying along a straight path from the start point to the end point of the ideal path in Fig. 6. This path passes closer to the TD than the ideal path, and the TD will record the range of each point along the path with a confidence interval that depends on the range. The confidence interval has negligible width at the start of the path because the falcon is perched, and the rangefinder is more accurate for a stationary object than a moving one. Fig. 6 shows that the confidence interval along the straight path is far too narrow to contain the curved paths that we measured during long approaches to Dead Horse Lake (see Fig. 7).

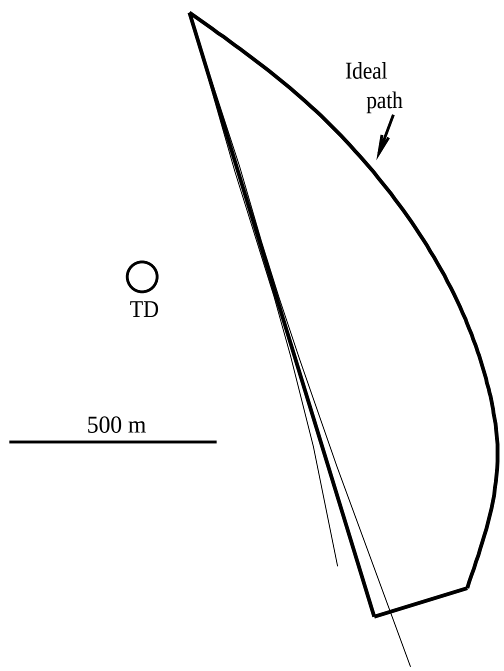

Fig. 6. 95 % confidence limits (thin lines) around a straight path (thick line) between the start and the end of an ideal path (thick lines). The circle labelled TD marks the location of the tracking device. See text for a description of how the confidence limits were calculated.

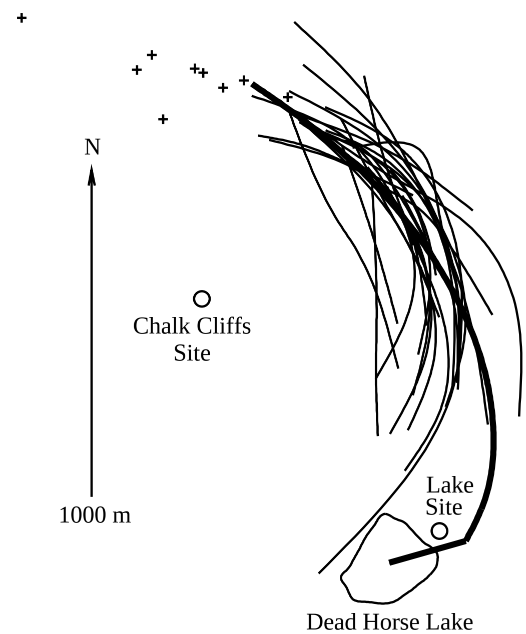

Fig. 7. 27 long approach paths of a peregrine falcon (thin lines) recorded by the tracking device at the Chalk Cliffs Site, and the ideal path (thick lines), projected on the x,y plane. The crosses mark perches in the Chalk Cliffs from which the falcon often started long approaches. The recordings ended when the falcon either went behind trees or was lost in the sun.

Visual observations

While watching long approaches with binoculars and telescopes, we particularly noted changes in the angle δ between the LOS to the falcon and the falcon's body axis; and the TD operator also noted this angle as seen in the TD rangefinder.

By the end of the 1998 season, we had many records from the TD of curved approaches; and we planned our observations in the final year to use binoculars and telescopes exclusively to confirm by another method that long approaches were curved. We established the Lake Site (Fig. 2) at Dead Horse Lake where an observer could see reversals in γ as indications of curved long approaches. Two observers at the Chalk Cliffs Site could contact the observer at the Lake Site by radio and inform him where the falcon was perched in the cliffs and when it was behaving as if it might make a long approach. The observers at the two sites also used the radios to comment on the falcon's behavior from different points of view during a long approach.

The different points of view from the two sites helped us identify curved paths unequivocally. The observers at the Chalk Cliffs Site were not situated where they could see a reversal in γ during a curved long approach, but they would see a nearly constant angle δ with a value near 270 °. In contrast, the observer watching the same curved approach from the Lake Site might see a reversal in γ and would see a marked change in δ, starting from a value near 270 ° when the falcon left its perch to a value up to 90 ° when the falcon was near Dead Horse Lake.

Results

Observations with the tracking device

We recorded over 300 tracks with the TD at the Chalk Cliffs Site in 1995–1998, and 27 % of these included dives. Of the dives, 32 %, or 27, were long approaches as defined in this study. All long approaches were recorded in 1997 and 1998, because we did not have the trolley in 1995, and the male falcon disappeared a few days after the eggs hatched in 1996.

Long approaches usually followed curved paths (Fig. 7). The paths began after the falcon had flown a few hundred meters from its perch when the TD operator switched on the TD. During long approaches, the falcon always held its head aligned with its body, never turned to one side. Curiously, all the curved paths curved to the falcon's right; so that the angle δ was approximately constant at 270 °, and the falcon approached Dead Horse Lake from the east. The falcon usually disappeared behind trees or in the sun's glare before we saw it reach its prey or pull out of the approach.

The points of disappearance for long approaches were 166 m above the ground, on average. When the falcon disappeared, its speed was typically 40–70 m s^{-1}, and it was diving at angles of 20–30 °. The falcon might have continued its approach for 356 m over the ground, on average, from the point of disappearance. This value is the distance that the falcon would travel from the point of disappearance 166 m above the ground at a dive angle of 25 ° before reaching the ground.

Observations with binoculars and telescopes

During 15 days in 1999, the observers at the Chalk Cliffs Site and the Lake Site observed 11 long approaches; and reversals in γ or changes in δ, or both, indicated that the falcon followed a curved path during all approaches. Like the paths recorded by the TD, all the approaches curved towards Dead Horse Lake from the east. The following examples describe some of these observations.

On June 6, the observers at the Chalk Cliffs Site saw the falcon take off from a perch to the northwest, fly north of them to the east, then turn south to pass under the sun, then turn west towards Dead Horse Lake. They radioed the observer at the Lake Site to look out for the falcon, and that observer soon heard a swoosh and saw a blurred shape overhead heading west. (The falcon could have been flying at a speed of $70\,m\,s^{-1}$, and would appear as a blur at this speed to an observer 50 m away.) The falcon clearly followed a curved path to Dead Horse Lake, because its take-off point, the Chalk Cliffs Site and the Lake Site were co-linear, and it would have flown directly over the Chalk Cliffs Site if it had followed a straight path to Dead Horse Lake.

On June 8, the observer at the Lake Site saw the falcon take off from a perch in the Chalk Cliffs to the northeast and head south, turning gradually towards the west until it was heading due west 300 m to the northeast of the observer. The falcon continued west until it disappeared behind trees due north.

During this approach, angle γ reversed, and angle δ changed from 315 ° at take-off to 90 ° as the falcon disappeared behind trees. When the falcon was head on (δ=0 °), the observer had a striking view of it apparently hanging motionless in the air and gradually growing larger as it approached.

On June 18, observers at both the Chalk Cliffs Site and the Lake Site watched the falcon as it took off from a perch in the Chalk Cliffs and flew in a long approach to a point 200 m east of Dead Horse Lake, where it disappeared behind trees. Observers at neither site were in a position to see a reversal in γ, but they could see different changes in δ. From the Chalk Cliffs Site, δ was near 270 ° for the whole approach; and from the Lake Site, δ changed from 270 ° at take-off to 315 ° at disappearance.

Discussion

Existence of curved paths

The results from the TD and the visual observations of changes in the angles γ and δ are conclusive evidence that the long approaches of the peregrine falcons in this study were usually curved. A plausible explanation for this behavior is the interaction between aerodynamic drag and the falcon's visual system described in the Introduction. In fact, it would be surprising if long approaches were usually straight, given the evidence (i) that a peregrine's vision is most acute along a line of sight that points 40 ° to one side of the head axis (Tucker, 2000b), (ii) that a turned head may increase the peregrine's aerodynamic drag coefficient by a factor of 2 or more (Tucker, 2000a), (iii) that a peregrine can probably approach distant prey more quickly along a curved path with its head held straight than along a straight one with its head turned sideways (Tucker, 2000b), and (iv) that we never saw a falcon hold its head turned sideways during a long approach.

It is not common knowledge that peregrines approach prey along curved paths, even though this species, because of its natural history, spectacular high-speed dives and cooperative hunting with humans in the practice of falconry (Cade, 1982) has been of special interest to humans for millennia. One reason may be that long approaches to prey may rarely be seen, either because they are rare or because a peregrine is difficult to see over the range of distance that a long approach covers.

Another reason may be that humans cannot estimate range accurately at the distances involved, and a curved path may be easily confused with a straight one. The most obvious evidence for a curved path is the relationship between γ and δ, but this relationship might be unnoticed and can be misleading. For example, an observer with binoculars may watch a peregrine following a curved path when the observer is on the concave side of the path. The observer swings the binoculars through a change in γ of 90 ° and always see the bird's image from the side. It is easy to misinterpret the nearly constant value of γ and conclude that the bird is flying in a constant direction.

Other explanations for curved paths

Hunting out of the sun

One curious characteristic of the long approaches to Dead Horse Lake was that they always curved to the falcon's right. i.e. the falcon always approached the lake from the east. We saw these approaches only in the morning, most frequently between 07:00 h and 10:00 h when the sun was also to the east of the lake. We lost the falcon in the glare of the sun on many occasions while trying to follow long approaches, so the falcon may have hidden from its prey by approaching it out of the sun. Hiding in the sun is a routine maneuver for pilots of fighter aircraft.

We tried to test the hiding hypothesis by watching for long approaches from the west in the late afternoon. Unfortunately, we never saw a long approach after midday.

It seems plausible that a peregrine might learn to approach prey out of the sun, since they can learn several different hunting techniques. For example, human falconers train peregrines and other raptors to hunt a variety of prey cooperatively with humans, and often with dogs (Beebe and Webster, 1964; O'Brien, 1997). Temple (1987) observed Mauritius kestrels (*Falco punctatus*) attacking prey from the direction of the sun and suggested that this behavior might serve for concealment. Many falconers are of the opinion that that falcons do learn to hunt out of the sun.

Misleading prey

Falcons might learn to use a curved approach because the prey is less likely to react to a falcon not heading directly towards it. For example, human bird hunters tell us that a bird on the ground may not flush until the hunter looks straight at it. Turning the tables, falconers sometimes think that their birds are not paying attention to them when the birds are looking sideways rather than straight at them (Tucker, 2000b). In fact, the bird looking sideways is probably examining the falconer with its deep fovea and most acute vision.

Curved paths of other birds

African white-backed vultures (*Gyps africanus*) flew along spiral paths with straight segments in Kenya as they approached a landing site 3 km away (Tucker, 1991). These birds are related to eagles and probably resemble them in having their most acute vision along a line of sight pointed approximately 40° to one side of the head axis. Perhaps the vultures were examining the landing site with their most acute vision as they approached.

Songbirds migrating at night sometimes mill and circle around lighted television transmission towers, and thousands may die in a single night by colliding with the tower. These birds may confuse the tower lights with stars and spiral towards the tower by flying at a constant angle to the line between themselves and a light (Kemper, 1964). The segment of the spiral that a bird follows using this method of orientation is essentially straight when the bird orients to an object as distant as a star, but the segment spirals around an object as near as an artificial light (Tucker, 2000b).

Perhaps curved approaches to prey by raptors other than peregrines will be observed now that we have shown that this behavior exists and can be explained by the interaction between aerodynamics and the visual system.

List of symbols

C	transducer counts
e	base of the natural logarithms
k_1, k_2	constants
LOS	line of sight
R	range
r	radius for polar coordinates
r_1	length of the straight segment of the ideal path
r_2	shortest distance between the start and end of the ideal path
S.D.	standard deviation of range
TD	tracking device
t	time
x, y, z	spatial coordinates
γ	angle between a reference line and the LOS from the observer to the falcon
Δ	a change in a quantity
ΔR_{95}	half of the 95 % confidence interval for range
δ	angle between the falcon's body axis and the observer's LOS to the falcon
Θ	angle for polar coordinates
π	ratio of the circumference to the diameter of a circle
Ψ	the angle between the falcon's head axis and the LOS of the deep fovea. Also, the shape factor for a logarithmic spiral

Deer Valley Ranch, Nathrop, Colorado, allowed us to use their property for the Chalk Cliffs Site and the Lake Site, and Frontier Ranch allowed us to use their property for access to the Chalk Cliffs. Grants from the National Science Foundation (DEB-9107222) and from the Duke University Research Council in 1995 and 1999 partially supported this work. David Akers spent many hours in the Chalk Cliffs watching the falcon nest and keeping us informed by radio of the falcon movements there. Tom Cade helped with some of the observations and reviewed a draft of this paper.

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