THE AUK
A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 108 JANUARY 1991 No. 1

STEREOSCOPIC VIEWS OF THREE-DIMENSIONAL, RECTANGULAR FLIGHT PATHS IN DESCENDING AFRICAN WHITE-BACKED VULTURES (*GYPS AFRICANUS*)

VANCE A. TUCKER
Department of Zoology, Duke University, Durham, North Carolina 27706 USA

ABSTRACT.—I used a tracking device to record the positions in space of 16 East African White-backed Vultures (*Gyps africanus*) as they glided to landings from altitudes that in some cases exceeded 400 m above the ground. Like many human pilots, most of the birds descended by flying along three-dimensional rectangular paths with upwind, downwind, and crosswind legs. These patterns may not be evident to observers on the ground, who at long range see a two-dimensional projection of a bird's flight path. Stereo-pairs illustrate the paths in three dimensions. The rectangular patterns may help the vultures to judge wind speed and direction, and thereby avoid flapping during the landing approach. *Received 25 April 1990, accepted 22 August 1990.*

IF A BIRD flies within approximately 100 m of us and passes in front of landmarks such as trees or boulders, we can remember with reasonable accuracy the invisible path that the bird followed through the air. However, large birds frequently can be seen at a distance of a kilometer or more flying high above the horizon. Our memories of flight paths under these circumstances can be quite inaccurate because of the lack of landmarks in the sky and the limits to our ability to judge distance.

I used a tracking device to record continuously the positions in space of East African White-backed Vultures (*Gyps africanus*) at ranges up to 3 km. These birds are large, with a typical wing span of 2.2 m and body mass of 5.4 kg. They were gliding in to a landing; and the recordings showed that, like human pilots, most of them followed a rectangular approach pattern. This maneuver was not apparent to the unaided eye, and I have not seen it mentioned in other descriptions of vulture behavior (Brown and Amadon 1968; Brown et al. 1982; Hankin 1913; Houston 1974; Kruuk 1967; Pennycuick 1971a, 1972).

STUDY AREA AND METHODS

Study area.—In late February, up to 30 vultures a day visited a temporary pond in Nairobi National Park, Kenya. White-backed Vultures were most common, but Rüppell's Griffon Vultures (*Gyps rüppellii*) and Lappet-faced Vultures (*Torgos tracheliotus*) also were present. They arrived individually from the south between 1000 and 1100 to bathe, preen, spread their wings in the sun, and rest quietly. In midafternoon, they flapped off downwind, found thermals that carried them high above the ground, and disappeared to the south. By 1500, all were gone.

The pond (1°21'18.62"S, 36°51'39.66"E) was 1,639 m above sea level on a flat, grassy part of the Embakasi Plain between two stream beds ca. 1 km apart. In February, the pond was shallow and approximately 100 m^2 in area, but in dry seasons it becomes a mud flat.

I observed the vultures through a tracking device that recorded the position in space of a vulture as it descended to land in the vicinity of the pond. The device was mounted in a vehicle parked 1.7 km SW of the pond so that the vultures would pass to one side of it as they landed.

The tracking device.—This device (called an *ornithodolite* in Pennycuick [1982] and described in detail in Tucker [1988]) was an optical range finder with a 1-m base mounted on a surveyor's transit. As I followed a bird in the range finder, a tape recorder continually recorded the range along the line of sight to the bird, and the horizontal and vertical angles of the line of sight. Later in the laboratory, analog-to-digital converters read the data from the tapes and sent them to a computer that calculated the spatial coordinates of the bird with respect to the ground at 1-s intervals.

The ornithodolite located the bird in a "volume of uncertainty" that depended on range. At 1 km, the volume of uncertainty was approximately a sphere with a 10-m diameter (Tucker 1988).

I plotted the positions of the birds in space with a computer-driven plotter after smoothing the spatial coordinates with a three-point moving average along the time coordinate. A three-dimensional computer-aided drawing program produced various projections and stereo-pairs.

Wind velocity.—I made visual observations and ornithodolite measurements on four days in February, 1972, during which the winds aloft and at ground level at the study area were steady and from the northeast. The northeast trade winds blow steadily day after day in the vicinity of Nairobi during this season. For the four days, the East African Meteorological Department reported a mean wind speed of 6.6 $m \cdot s^{-1}$ ($SD = 2.0$, $n = 11$) and a mean direction of 59° from the north ($SD = 13$, $n = 11$) at altitudes between 1,798 and 3,140 m above sea level. These data were obtained by tracking balloons as they ascended at noon from a release site 15 km WNW of the pond (East African Meteorological Department 1963). The small standard deviations indicate the steadiness of wind speed and direction with altitude. Tucker (1988) reports a comparable standard deviation (relative to mean wind speed) for surface wind speeds in the vicinity of Nairobi.

RESULTS

Visual observations.—I made visual observations with unaided eyes and through binoculars. The perceptions described in this section are considerably different from those based on three-dimensional reconstructions from ornithodolite measurements, which will be described quantitatively in the next section. The human visual system does not accurately perceive the distance to a bird—the range—at ranges longer than a few hundred meters, so the visual perceptions of flight paths in this study describe two-dimensional projections of the actual three-dimensional paths of the vultures through space.

Most of the vultures had already started their descents when I first saw them high in the sky, and they steadily lost altitude as they got closer. A typical bird had lowered its feet, which serve as spoilers and increase the rate of descent (Pennycuick 1971b). It flew along a zigzag path, swinging to the right for 10 s or more and then to the left for a similar period as it descended. It dropped nearly vertically for the last 5–20 s of the descent and flapped a few times before touching down. Figure 1, reconstructed from ornithodolite data, shows a projection of a typical descent (in this case from an altitude of 445 m above the ground) as it would be seen by an observer on the ground.

A minority of the vultures glided directly to the pond without zigzagging. Some of these came in low and skimmed the top of the grass for perhaps 100 m before landing.

The wings of a vulture during a rapid descent appeared to be stalled, because the alulae were raised, and the feathers on the upper surface of the wings lifted and fluttered in the air (Tucker 1988). The outer parts of the wings often were twisted to a high angle of attack—behavior also seen in Rüppell's Griffon Vulture (Pennycuick 1971b) and in the Andean Condor (*Vultur gryphus*) (McGahan 1973). This behavior probably increases the rate of descent by concentrating aerodynamic lift towards the tips of the wings, which increases induced drag (Pennycuick 1971b).

Ornithodolite observations.—I recorded a total of 16 paths of White-backed Vultures from the time I could first focus on the birds with the ornithodolite until they landed in the vicinity of the pond. Fourteen of these paths had portions that were >1 km from the landing site. When the birds following these paths were 1 km from the landing site, 3 were >400 m above the ground, 4 were 200–400 m above the ground, and 7 were <200 m above the ground. The remaining two paths were <1 km from the landing site, and the birds following them were <200 m above the ground.

When viewed from above, 13 of the vultures approached the landing site by flying along straight legs for 100 m or more and then turning abruptly at approximately right angles relative to the ground. The remaining 3 vultures flew along straight or continuously curved paths to the landing site. Of the 13 birds, 9 made two or more successive right angle turns in the same direction (i.e. clockwise or counterclockwise) so that their flight paths followed rectangular patterns relative to the ground. This behavior was particularly striking in the birds that were >400 m above the ground when 1 km away from the landing site. They flew around several rectangles as they descended, and their paths through space were reminiscent of vertical corkscrews with square corners. The straight legs usually were parallel to the wind direction or at right angles to it.

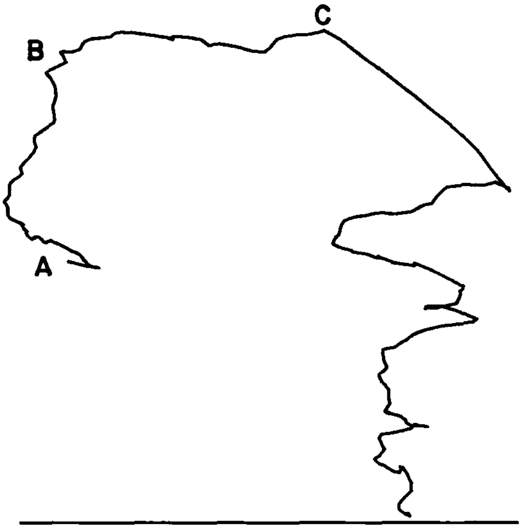


Fig. 1. A projection showing the flight path of a vulture as it would be seen by an observer on the ground plane, 1 km from the landing point. The track starts at point A. Points B and C are reference points. The horizontal line is the edge of the ground plane.

Fourteen of the vultures dropped nearly vertically relative to the ground for 30–100 m just before they landed. Ten of these birds dropped directly to the landing site. The other four dropped within a radius of 200 m from the landing site and glided at a shallow angle to a landing for the remaining distance. Relative to the air, the 14 birds dropped at angles between 15° and 55° from horizontal after accounting for a mean wind speed of 6.6 $m \cdot s^{-1}$ (computed from Tucker 1988).

Figure 2, reconstructed from the ornithodolite data for the same flight path illustrated in Figure 1, shows an example of these maneuvers. The drawing shows the path as it would be seen by an observer located above a ground plane represented by a square grid. The distortions in the grid give information on the range to the bird at various points along the path and help the viewer to perceive the path in three dimensions. Figure 3 in the Discussion illustrates the same path with a stereo-pair, which provides a true, three-dimensional image.

The vultures in this study had air speeds between 5.4 and 39.1 $m \cdot s^{-1}$, and sinking speeds between 0.2 and 8.3 $m \cdot s^{-1}$. I have discussed their air speeds and aerodynamics elsewhere (Tucker 1987, 1988).

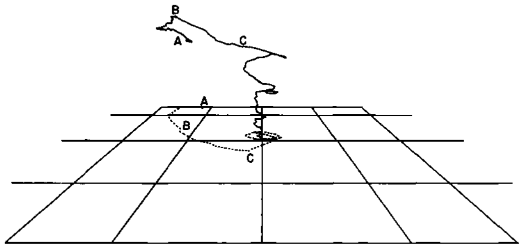


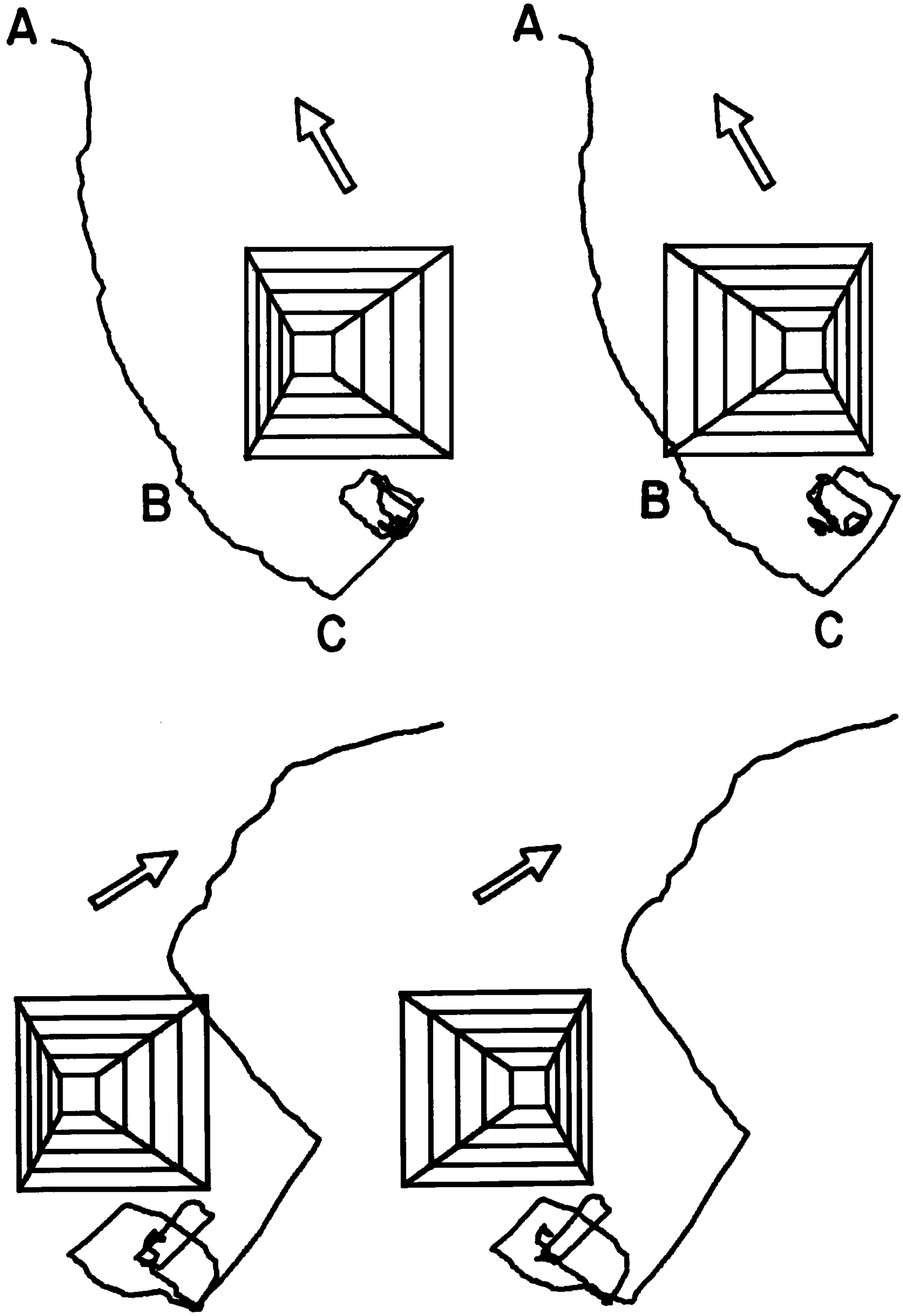
Fig. 2. A projection showing the same flight path illustrated in Figure 1 as it would be seen by an observer located above the ground. A grid of square cells, 400 m on a side, represents the ground plane. The parallel grid lines running away from the observer converge toward a vanishing point in the distance. The dotted line shows the path of the bird's shadow on the ground plane with the sun directly overhead at noon at the equator. The letters on both the flight and shadow paths indicate the same reference points shown in Figure 1.

DISCUSSION

Misleading visual observations.—I was surprised to discover from the ornithodolite data that several vultures made right-angle turns relative to the ground and flew in rectangular patterns during their descents to the landing site. From visual observations, I thought that they simply followed a zigzag path. This misconception arose because human eyes see a two-dimensional projection of the flight path, and they do not judge the distance to a bird accurately at long ranges.

The human visual system judges range from several cues (Davson 1980) that, according to geometrical optics (Ogle 1968), become less sensitive as range increases. These cues are the size of the retinal image, the focal length of the lens, the convergence of the visual axes of the eyes, and the stereoscopic depth that an object appears to have. Additional range cues (relative size, overlap, and motion parallax) arise when birds fly near other objects. These additional cues were ineffective in this study because the vultures flew above the horizon against a background of clear sky and distant clouds.

The ornithodolite data, however, allow the flight paths to be reconstructed as three-dimensional curves that can be viewed at close range and perceived in three dimensions by stereoscopic vision. The stereo-pair in the upper part of Figure 3 shows that the path illustrated in Figure 1 has a rectangular pattern in three dimensions. The lower part of the figure shows another example of a vulture descending from


A
A
B
B
C
C

a similar altitude. These stereo-pairs allow humans for the first time to perceive three-dimensional images of avian flight paths that are more than a kilometer long.

Vulture and human-pilot behavior.—Like White-backed Vultures, civilian pilots who approach a landing site under visual rather than instrumental control often use rectangular flight paths oriented with the wind. The basic rectangular approach pattern to an airport consists of an upwind leg, a crosswind leg, a downwind leg, a crosswind base leg, and an upwind final approach that culminates in landing (U.S. Department of Transportation 1980). This pattern allows a pilot to watch out for other aircraft in the vicinity and anticipate their movements. It also allows the pilot to examine the landing site and obtain information about the wind.

The pilot must evaluate the speed and direction of the wind to land the aircraft at a selected site, particularly a light aircraft whose ground speed may be changed 50% by the wind. By flying along straight legs, the pilot can avoid the distraction of a rotating horizon and concentrate on the aircraft's position relative to the ground. When the aircraft is headed parallel to the wind direction, there is no sideways drift relative to the ground. The effects of both headwinds and tailwinds on ground speed can be seen by flying on both upwind and downwind legs. The ground speed of the aircraft, together with its altitude above the ground and its characteristic glide path, determines when the pilot must turn from the downwind leg to the base leg and then to the final approach to bring the aircraft to the ground at the landing site (U.S. Department of Transportation 1980).

The reasons pilots often use a rectangular landing pattern give insights into why vultures may do so. For a vulture, anticipating movements of other flying birds would seem to be of minor importance, given the low flight speeds and high maneuverability of birds. Reconnoitering the landing site would benefit the bird, but the advantage of a rectangular pattern oriented to the wind rather than some other pattern is unclear. Perhaps the rectangular pattern helps the bird judge the wind speed and direction.

Because vultures have slower air speeds than light aircraft, vultures are more affected by the wind. The vultures in this study commonly glided at air speeds between 5 and 10 $m \cdot s^{-1}$ (Tucker 1988). At these speeds, the wind may reduce the ground speed of a bird to zero during upwind flight, or it may double around speed during downwind flight. To follow a crosswind path over the ground, the bird must use the ground as a reference and fly at an angle into the wind. For example, a bird with an air speed of 10 $m \cdot s^{-1}$ in a wind of 6.6 $m \cdot s^{-1}$ flies with a heading of 41° into the wind relative to its ground path. A vulture gliding in a rectangular pattern should perceive changes in ground speed and heading of these magnitudes.

White-backed Vultures may use knowledge of wind conditions to avoid flapping flight. The nearly vertical drops near the landing site in 88% of the flight paths in this study provide evidence for this hypothesis. A prudent gliding bird, like a prudent glider pilot, would reach the vicinity of its destination with altitude to spare. This strategy allows for vagaries of the weather en route, such as headwinds or downdrafts. It also allows the bird to examine the landing site and, if it is unsatisfactory, glide off to find a thermal that will carry the bird aloft again.

Once a vulture reaches the vicinity of its destination with excess altitude, it needs to know the wind speed and direction to select the starting point for a descent at a steep glide angle. A steep glide angle helps the bird avoid flapping, for two reasons. (1) If the bird misjudged the starting point, it could still reach the landing site without flapping by adjusting its glide angle (Tucker 1987, Pennycuick 1989, Tucker and Heine 1990). In contrast, a vulture ap-

←

Fig. 3. Stereo-pairs of paths (relative to the ground) of descending White-backed Vultures from above. The stereo-pairs give the correct three-dimensional image when viewed with crossed visual axes (see Appendix). The paths begin toward the top of the figure, and both have square-cornered, corkscrew shapes during descent. The square pyramids show the horizontal and vertical scales, and the arrows show wind direction. The bases of the pyramids are 400 m on a side, and the lines on the sides of the pyramids are separated vertically by 100 m. The upper part of the figure shows the same path and lettered reference points that Figures 1 and 2 illustrate. The lower part of the figure shows another example of a path that descends more than 400 m.

proaching a landing site at its shallowest glide angle could not reduce its glide angle further and would have to flap if it found itself falling short of the landing site. (2) A bird with a steep glide angle and a correspondingly high vertical sinking speed during the descent spends less time at low altitudes than a bird with a lower sinking speed. The bird with the steeper glide angle could abort the landing a shorter time before touch-down and still have a chance to glide off and find a thermal.

If this explanation for rectangular flight patterns is correct, then rectangular patterns may be more common in large soaring birds than in small ones. Pennycuick (1969, 1989) argues that larger birds have less power reserves for flapping flight and reported (1969) that a well-fed White-backed Vulture could not sustain flapping flight at all.

ACKNOWLEDGMENTS

This study was partly supported by National Science Foundation Grant Number GB 29389. The Department of Zoology, University of Nairobi, provided laboratory space.

LITERATURE CITED

BROWN, L., & D. AMADON. 1968. Eagles, hawks and falcons of the world, vol. 1. New York, McGraw Hill.

BROWN, L. H., E. K. URBAN, & K. NEWMAN. 1982. The birds of Africa, vol. 1. New York, Academic Press.

DAVSON, H. 1980. Physiology of the eye. New York, Academic Press.

EAST AFRICAN METEOROLOGICAL DEPARTMENT. 1963. Upper air data for Nairobi, 1957-1962. Nairobi, East African Common Services Organization.

HAMORI, E., R. D. BROAD, & C. E. REED JR. 1982. Study of unaided cross-eyed stereopsis. Perception 11: 297-304.

HANKIN, E. H. 1913. Animal flight. London, Iliffe.

HOUSTON, D. C. 1974. Food-searching in Griffon Vultures. E. African Wildl. J. 12: 63-77.

JAMES, G., & R. C. JAMES 1959. Mathematics dictionary. New York, Van Nostrand.

KRUUK, H. 1967. The competition for food between vultures (*Aegypiinae*) in East Africa. Ardea 55: 171-193

MCGAHAN, J. 1973. Gliding flight of the Andean Condor in nature. J. Exp. Biol. 58: 225-237.

OGLE, K. N. 1968. Optics, an introduction for ophthalmologists. Springfield, Charles C Thomas.

PENNYCUICK, C. J. 1969. The mechanics of bird migration. Ibis 111: 525-556.

———. 1971a. Gliding flight of the White-backed Vulture *Gyps africanus*. J. Exp. Biol. 55: 13-38.

———. 1971b. Control of gliding angle in Rüppell's Griffon Vulture *Gyps rüppellii*. J. Exp. Biol. 55: 39-46.

———. 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. Ibis 114: 178-218.

———. 1982. The ornithodolite: an instrument for collecting large samples of bird speed measurements. Phil. Trans. R. Soc. London B 300: 61-73.

———. 1989. Bird flight performance. Oxford, Oxford Univ. Press.

TUCKER, V. A. 1987. Gliding birds: the effect of variable wing span. J. Exp. Biol. 133: 33-58.

———. 1988. Gliding birds: descending flight of the White-backed Vulture, *Gyps africanus*. J. Exp. Biol. 140: 325-344.

———. 1989. Ambiguities in stereopsis. Nature 337: 605.

———, & C. HEINE. 1990. Aerodynamics of gliding flight in a Harris' Hawk, *Parabuteo unicinctus*. J. Exp. Biol. 149: 469-489.

U.S. DEPARTMENT OF TRANSPORTATION. 1980. Federal Aviation Administration. Flight training handbook. Washington, Superintendent of Documents, U.S. Government Printing Office.

WOOD, W. B., J. H. WILSON, R. B. BENBOW, & L. E. HOOD. 1981. Biochemistry. A problems approach. Menlo Park, Benjamin/Cummings.

APPENDIX. Stereo-pairs.

The brain can perceive a three-dimensional image if each eye views a different two-dimensional picture of a three-dimensional object. The members of the pair of pictures (a stereo-pair) in this study are orthogonal projections (James and James 1959) of vulture flight paths, reconstructed from the ornithodolite data. The projection plane for one member has been rotated 10° relative to that for the other to depict the projections from the points of view seen by each eye. When each eye focusses on a different member of the pair, the brain can fuse the two retinal images and perceive a three-dimensional image.

One can use a stereoscope to see three-dimensional images from stereo-pairs, but most individuals can learn to see the images with unaided eyes (Wood et al. 1981). Two methods of viewing the pair are possible. With crossed visual axes, the right eye views the left-hand member of the pair, and the left eye views the right-hand member. With uncrossed axes, the eyes view the opposite members.

The crossed axes method seems easier for most people to learn (Hamori et al. 1982). The following instructions describe the process. Focus on a finger held at the tip of your nose with the stereo-pair at reading distance in the background. Continue to focus on the finger as you move it toward the stereo-pair, but try to see two unfocused images of the pair in the background. As the finger gets about halfway to the pair, try to make the two inner members of the unfocused images overlap into one. If you can focus on the overlapped image, it will appear in three dimensions with a two-dimensional image on either side of it.

To learn the uncrossed axes method, gaze into the distance with the stereo-pair at reading distance and below your line of sight. Try to see two unfocused images of the stereo-pair in your lower peripheral vision. Make the two inner members of the unfocused images overlap, and then drop your gaze to focus on the overlapped image. It will appear in three dimensions with two-dimensional images on either side.

The depth dimension of the three-dimensional image reverses if one views the stereo-pair alternately with crossed and uncrossed visual axes (Tucker 1989). I have arranged the stereo-pairs in this paper to give the correct image with the crossed axes method. Viewers using the uncrossed axes method or a stereoscope can see the correct image by exchanging the right and left members of the pair.