Die Vogelwarte 32, 1984: 206—218

Aus der Schweizerischen Vogelwarte

Nearest neighbour distances in day and night migrating birds
A study using stereophotography

by Bob Zuur

Introduction

Although much has been written about the flock structure of large birds (eg. GOULD & HEPPNER 1974), relatively little information about passerine flocks is available. Tracking radar has generated useful data on the dispersion of birds migrating at night (see BRUDERER 1971), but the nearest neighbour distances of most day migrants has been below the resolution of the radar units available. Only when the total energy reflected by a tracked flock is measured and related to it's range and species composition, is it possible to estimate the number of birds within the radar „pulse volume“ (BRUDERER & JOSS 1969). However, it proved necessary to develop an optical system to determine the actual structure of passerine flocks.

The present study serves to:

I develop a simple optical measurement system in which the nearest neighbour distances of day migrating birds can be determined with a high degree of precision.

Fig. 1: A photo of the study area in the south-west of Switzerland. Col de Bretolet (1920 m) is ndicated by the arrow.

II apply this stereophotography system to the description of the flock structure of passerines migrating over an alpine pass.

III determine what distance separates birds migrating at night.

Methods

Stereophotography

Stereo pairs of photographs were taken of birds migrating above Col de Bretolet (VS), a 1920 m pass in the south-west of Switzerland, during September, 1981. The pass is almost ideal for the study as large numbers of migrating birds (predominantly passerines) fly low overhead due to the funnelling effect of the valley and the steepness of the pass itself (Fig. 1).

The stereophotography system consisted of a 5 m aluminium box-section beam, mounted on two tripods (Fig. 2). Distortion of the beam due to it's own weight and

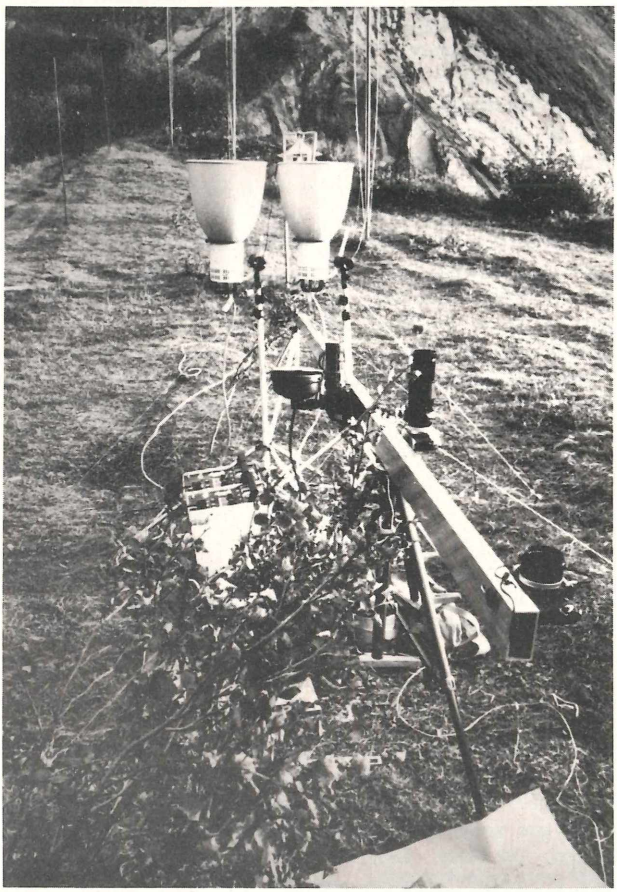

Fig. 2: The stereophotography system described in the text. From the right (foreground) to the left (background) the following elements of the system are visible: One of the two stereo cameras, an additional camera with a tele-lens, the infrared viewing equipment, the two Broncolor 404 flashes, and the power pack on the ground. The second stereo camera, mounted at the other end of the aluminium beam, is hidden by leaves.

that of the cameras was considered to be negligible (Mr. R. Isler, mechanical engineer, pers. comm.). Two camera motor drives were semi-permanently mounted on the beam so that the attached cameras (35 mm Canon AE-1) had their centres of focus 4,86 m apart. The cameras were adjusted so that the image of a distant object (the moon) at the focal plane of the cameras differed by no more than 0,5 mm. The exact position of the moon's image was measured on a sheet of translucent graph paper placed in the focal plane. Any residual inaccuracy with this technique was corrected in subsequent calculations (see below). The beam was left untouched between photography sessions, the cameras being removed from the motor drives which remained (protected from the weather) attached to the beam.

It was necessary to expose the photos simultaneously because rapidly moving objects were to be photographed. As the cameras were electronically controlled, the shutters would not function until they were supplied with power. A battery substitute with leads to the camera's battery contacts was placed in each camera, and these were connected to a common switched power source (6v DC). With the shutters advanced and the shutter buttons locked with a cable release, the cameras exposed simultaneously on the second of two pulses of electricity. The degree of synchronisation could be checked by connecting a small electronic flash in series with the X-contacts of both cameras. The flash could fire only if both shutters were open at the same time. Both cameras synchronised satisfactorily at the shutter speed used (1/500 sec.).

The cameras were fitted with 50 mm lenses, as these provided the optimum compromise between image size and field of view. Agfapan 100 black-and-white film yielded high resolution with adequate film speed.

Initially the cameras were aimed upwards (Fig. 2) and the photographs made when birds were seen in the viewfinder of one of the cameras. This proved to be satisfactory when photographing swallows and martins at heights in excess of 40 m, but finches often flew lower than this and were more easily photographed with the cameras aimed 10° above the horizon. Flock species composition was determined by identification through binoculars and from the bird calls emitted.

Night photography proved to be somewhat more complicated. Previous tests in the Swiss midlands demonstrated that sparrow-sized birds could be photographed from underneath to a distance of 75 m, using the 50 mm lenses at f 2.8, ASA 100 film and two Broncolor 404 electronic studio flash units fitted with narrow angle reflectors (each with 1500 watt-seconds power). ASA 400 film was found to be unsatisfactory because the grain size approached that of the birds' images. The flash units were connected in series with the cameras' X-contacts, and were directed along the cameras' optical axes. Exposures were made when a bird entered the field of view of an infra-red night viewer aimed along the optical axes of the cameras (Fig. 2). A third camera fitted with a 300 mm lens assisted with the identification of any bird it photographed. Indirect evidence for identification could be obtained from birds captured at the same time in mist-nets near by.

Photogrammetry

The bicoordinate positions of the birds' images on the film were measured with an accuracy of ± 0,025 mm, by projecting the image on the underside of a sheet of translucent graph paper. Test photos of a calibration pattern showed that radial distortion of the camera lenses and the projection apparatus along the film edge was less than 0,2 %, and was therefore ignored. Any inaccuracy in the photographic system due to non-parallel cameras was corrected by measuring the on-film deviations between the cameras of the images of jets (vertically) and mountain peaks (horizontally) at distances of at least 5 km. This correction (usually about 0,3 mm) was made to all x-coordinates. The y-coordinate was the same in both cameras. The identification of corresponding birds in paired photos was further assured as the birds were in the same wing-beat phase.

A schematic diagram of the stereo-photographic system is shown in Fig. 3, and of the measurements made on the film in Fig. 4. The range (D) of the object photographed (in metres) was calculated from the formula:

$$D = \frac{B \qquad f}{(x_R - x_L)}$$

where: f is the focal length of the lens used (50,5 mm).
B is the separation of the cameras (4,86 m).
and x_L and x_R are the on-film measurements of the image in the left and right cameras respectively (measured in mm). The height of the object above the plane of the cameras' optical axes (Y) was calculated through the formula:

$$Y = \frac{y \cdot D}{f}$$

where y is the on-film y-coordinate of the image measured in mm (this value is the same for the same object in both photos in a stereo pair).

The distance to the left or right of the mid-line between the cameras (X) was calculated through the formula:

$$X = \frac{1/2\, B\, (x_R + x_L)}{(x_R - x_L)}$$

After these coordinates were calculated for all members of a flock, the distances between each (A) were calculated using the formula:

$$A = \sqrt{(X_2 - X_1)^2 + (Y_2 - Y_1)^2 + (D_2 - D_1)^2}$$

where the subscripts 1 and 2 refer to the reference bird and it's neighbour respectively. The distances to nearest neighbour were calculated for each bird photographed, but the values for birds which *may* have had nearest neighbours outside the combined field of view of the cameras were ignored.

Estimates of the errors involved in the system were obtained by photographing test targets with known separations in three dimensions at distances of 40 m, 60 m and 80 m.

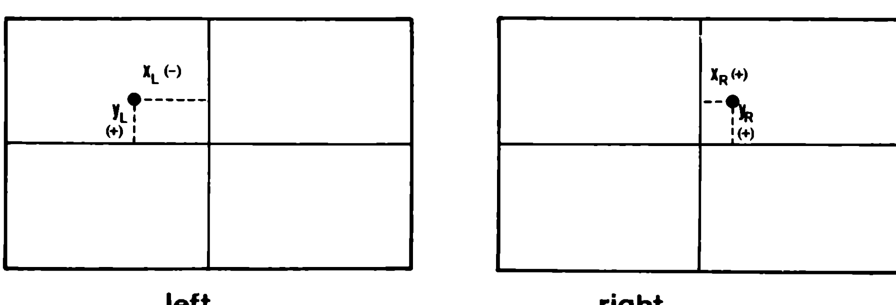

Fig. 3: A schematic diagram of the stereophotography system, illustrating the symbols used in the text. A = separation of the objects, B = separation of the cameras, D = distance from the cameras to the object, f = focal length of the camera lens, X = distance of the object from the centre line between the cameras.

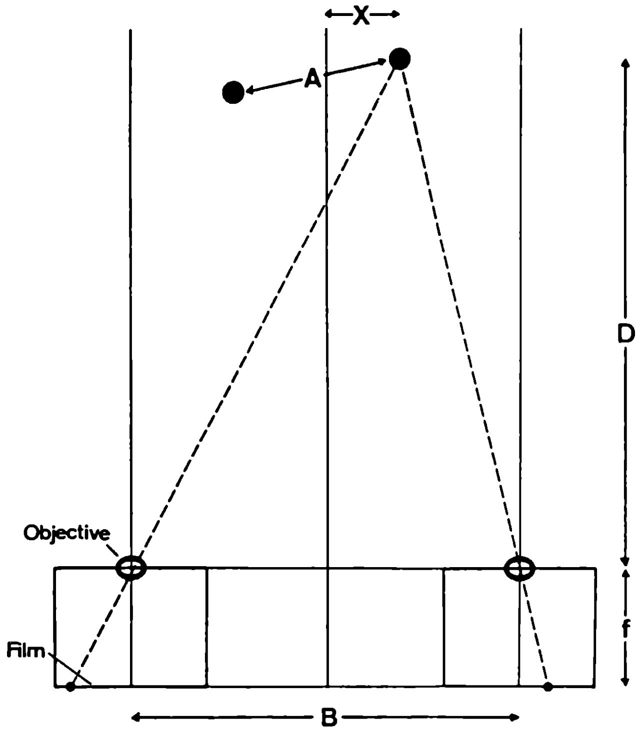

Fig. 4: A diagram of the measurements made on the film, left and right refer to the orientation of the cameras.

Intraflock dispersion

The method for the analysis of dispersion in two dimensions proposed by CLARK & EVANS (1954) has an advantage over many similar techniques in it's freedom from the effect of quadrat size. This technique has recently been extended to three dimensions (CLARK & EVANS 1979).

In a flock of birds with a density of φ the expected distance to nearest neighbour is:

$$\bar{r}_E = \frac{0.5540}{\varphi^3}$$

A value of the ratio: $\frac{\bar{r}_A}{\bar{r}_E}$

where $\bar{r}_A$ is the observed mean nearest neighbour distance, less than unity implies aggregation and a value over unity uniformity. The significance of any departure from randomnes can be tested by calculating the normal variate

$$c = \frac{\bar{r}_E - \bar{r}_A}{\sigma_{\bar{r}_E}}$$

where $\sigma_{\bar{r}_E}$ ist the standard error of $\bar{r}_E = \frac{0.2014}{\varphi^3}$

The density of the flock was determined by dividing the volume of the largest cuboid enclosed by the flock, by the number of birds the cuboid enclosed.

Simberloff (1979) noted that CLARK & EVANS' model assumes that the reference object and it's neighbours are all infinitely small points, and that this model may lead to the wrong conclusions if, in the real situation, the diameter of the circle is greater than half the expected mean nearest neighbour distance for points. This criticism does not apply to the application of this model here, as the largest circle enclosing a swallow (sphere with a diameter of the wingspan, 33 cm — Géroudet, 1973) proved to be about one tenth of the expected mean nearest neighbour distance.

Acknowledgements

Dr. BRUNO BRUDERER (Schweiz. Vogelwarte) provided invaluable assistance in all aspects of this study. ROLF ISLER (Dipl. Ing.) gave helpful advice in the development of the stereophotographic system, and LUKAS JENNI and THOMAS STEURI assisted at Col de Bretolet. I thank Bron Elektronic AG for providing the flash units and Canon AG for a camera lens.

Results

Few operational problems were experienced with the stereophotography system, but it's use was hampered somewhat by the weather. Persistent tailwinds caused the birds to fly high over the pass and therefore out of range, and an early snowstorm finished the study prematurely. Nevertheless, several dozen flocks of daytime migrants were photographed.

An example of the descriptive properties of this technique is shown in Fig. 5, in which the positions of all the photographed members of a flock of swallows are shown in three dimensions. It can be seen that the flock is skewed upwards from left to right on the XZ plot — this is attributed to the slope of the crest of the ridge underneath. The size of the dots in the figures corresponds to the wingspan of the birds.

The total errors of measurement of the system are shown in Table 1. Errors in range estimation increased from 0,4 % at 40 m, through 1 % at 60 m to 2,5 % at 80 m. The greatest errors in determining the separation of objects were made along the Z-axis (ie. towards and away from the cameras), and the smallest errors were made along the X-axis. It should be noted that the error involved in the determination of the total separation of two objects is not the sum of the errors in three dimensions, as the measurements made were to a certain extent selfcompensatory. If a given error was made in the calculation of the position of one object, it was probable that an error was made in the same direction with the second object, and hence the separation between the two could be measured more accurately than their positions.

Table 1: Estimation of errors: The mean (± standard error) or the errors in measurement in metres of targets whose separation and distance was known. Range is the distance to the object, Z, X and Y are the distances the targets were separated along the optical axis of the cameras, and parallel and perpendicular to the beam the cameras were mounted on, respectively. The targets were separated in the three dimensions by about 3 m. The numbers in parentheses refer to the number of measurements made.

Dist.	Separation			
Range (9)	*Z* (6)	*X* (6)	*Y* (3)	*Total* (9)
40 m 0.094 ± 0.018	0.157 ± 0.042	0.057 ± 0.003	0.078 ± 0.006	0.110 ± 0.022
60 m 0.609 ± 0.082	0.199 ± 0.092	0.063 ± 0.008	0.063 ± 0.010	0.203 ± 0.064
80 m 1.985 ± 0.120	0.310 ± 0.122	0.109 ± 0.017	0.274 ± 0.002	0.189 ± 0.061

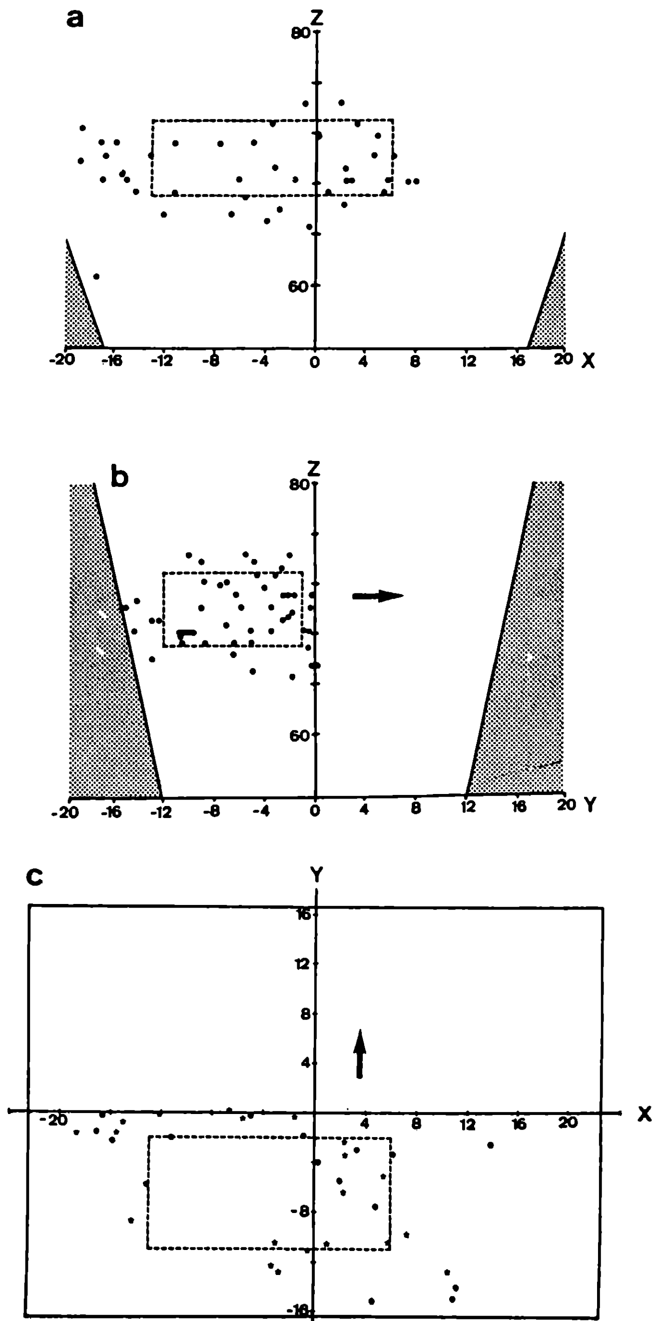

Fig. 5: The dispersion of a swallow flock flying above Col de Bretolet illustrated in three dimensions (X/Z, Y/Z, X/Y). The stippled area is outside the field of view of both cameras and the arrow indicates the direction of flight. In the XY plot, the stars refer to birds with an altitude less than 70 m above the cameras. The dashed line refers to the cuboid used to calculate the density of the flock. All scales are in metres.

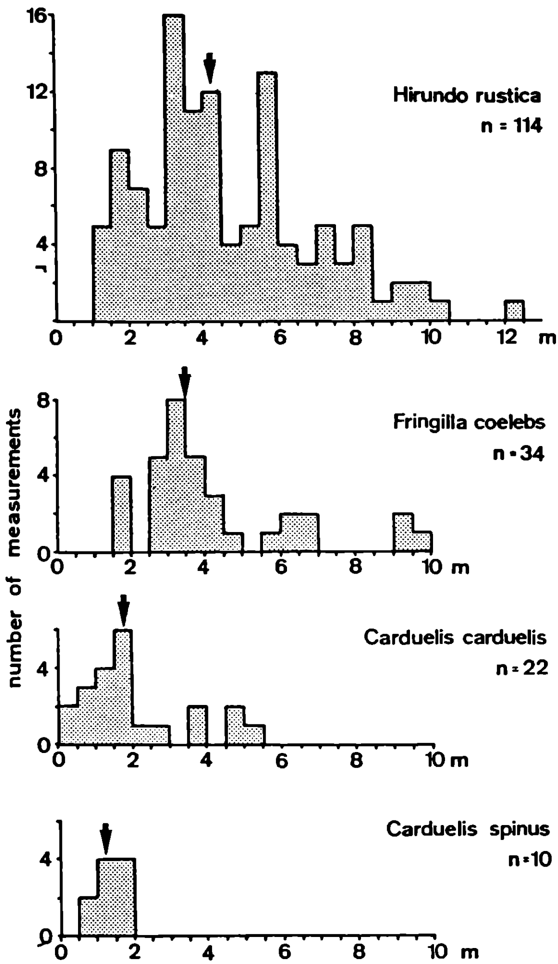

Fig. 6: The distribution of the nearest neighbour distances of four passerines migrating above Col de Bretolet: Barn Swallow, Chaffinch, Goldfinch, and Siskin. The arrow indicates the median value.

The distributions of the measured nearest neighbour distances of four species migrating during the day above Col de Bretolet are shown in Fig. 6. The curves are obviously skewed with the modes of all but the last lying below the mean. The median values obtained supported subjective observations, i.e. that cardueline finches, especially siskins, fly in tighter flocks than do chaffinches and swallows. It appears from Fig. 7 that the nearest neighbour distances within swallow flocks were largely independent of flight altitude, time of day, and the strength of the headwind. However, these birds tended to fly at very much higher altitutes with a tailwind, and flock structure may have been affected under these conditions.

Flocks of finches in our sample contained too few birds for a satisfactory analysis of intraflock dispersion. Two swallow flocks, one with a relatively high bird density (Fig. 5), the other with a relatively low density, were analysed (Table 2). Both flocks tended towards a more regular dispersion than random

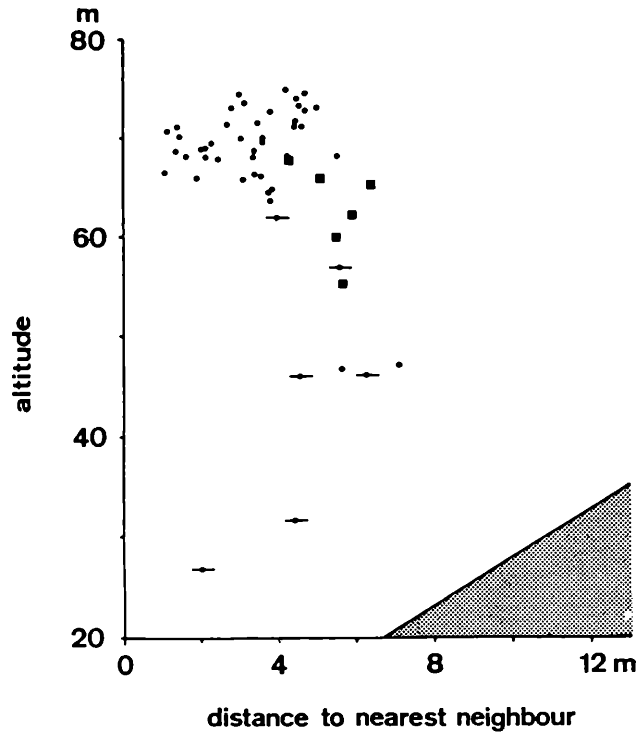

Fig. 7: Variations in measured nearest neighbour distances with altitude, time of day and strength of headwind. The stippled area is beyond the field of view of both cameras. Circles (●) are measurements before 9 a.m., squares (■) after 9 a.m.; measurements taken under windspeeds of less than F 2 are indicated by a horizontal line (—●—).

(R > l) i.e. underdispersion according to Elliott (1971), but the dispersion of the latter flock was not significantly different from randomness. Underdispersion was supported further by the fact that the variance to mean ratios of the nearest neighbour distances in a flock were usually below unity.

The distribution of the X-, Y- and Z-components of the nearest neighbour distances of the birds in the larger swallow flock are shown in Fig. 8 The modal value of the Y-component is distinctly below that of the X- and Z-components, implying that these birds tended to fly above or below, rather than in front, behind or to the side of, their nearest neighbours.

Large numbers of moths (Sphingidae and Noctuidae) complicated the interpretation of photos taker ɂ night. These moths made up most of the objects recorded within 20 m, but very fe˙ oi those above this range. Nevertheless, it appeared that most of the birds migrating at night were flying singly or at nearest neighbour distances considerably greater than those of birds migrating during the day. Of the twelve birds photographed at ranges greater than 20 m, ten were alone on the photos while the other two were 24,6 m apart. This was supported by our observations through the infra-red viewer — the birds seen were virtually always flying alone. It was probable that the birds observed and photographed at night were members of the Turdidae (Robin *Erithacus rubecula,* Redstart *Phoenicurus phoenicurus,* Song Thrush *Turdus philomelos* and Wheatear *Oenanthe oenanthe)* as these were the species most commonly caught in mist nets on the pass at the time (L. Jenni, pers. comm.).

Table 2: Nearest neighbour distances: Mean distances (in metres) between nearest neighbours in flocks of various bird species. Only some of van Tet's (1966) figures have been included — his density values have been converted into nearest neighbour values using Clark and Evan's (1979) model: (1) assumes random intraflock dispersion, (2) assumes a more regular distribution (ie. $\bar{r}_A = 1.2$). The numbers in parentheses refer to the number of measurements made.

Species	van Tets 1 (1966)	van Tets 2 (1966)	Major & Dill (1978)	This paper
Swift *Apus apus*	0.59 (2)	0.71 (2)		
Cliff Swallow *Petrochelidon pyrrhonata*	0.25 (2)	0.30 (2)		
Barn Swallow *Hirundo rustica*				4.65 (114)
Starling *Sturnus vulgaris*	0.25 (22)	0.30 (22)	1.33 (71)	
Knot *Calidris canuta*	0.20 (6)	0.24 (6)		
Dunlin *Calidris alpina*			0.63 (771)	
Chaffinch *Fringilla coelebs*				4.03 (34)
Goldfinch *Carduelis carduelis*				2.01 (22)
Siskin *Carduelis spinus*				1.46 (10)
Redpoll *Carduelis flammea*				3.17 (5)

Discussion

The errors calculated for the stereophotography system described above were somewhat greater than those calculated by Major & Dill (1978: 113) for their system; but the distances involved in the present study were considerably greater. It is probable that any errors at similar distances would be comparable — the accuracy in the mounting and calibration of Major and Dill's system was compensated by the use of shorter focal length lenses in their system. Nearest neighbour distances of under one metre were only rarely measured at Col de Bretolet, even for the small *Carduelis* species, which appear to fly in dense flocks. This is in contrast to the findings of van Tets (1966) who recorded birds as large as Grey Teal (*Anas gibberifrons*) and domestic pigeons (*Columba livia*) flying at densities greater than two birds per cubic metre. It is possible that specific differences may explain this, but the nearest neighbour distances calculated for the barn swallow in this paper are more than an order of magnitude greater than those calculated for the cliff swallow (*Petrochelidon pyrrhonata*) by van Tets (Table 3). Similar differences exist for the values obtained by him and Major and Dill (1978) for the starling and two *Calidris* species.

Van Tets made his measurements from two-dimensional photos, under the assumption that the birds occupied a spherical airspace with the same diameter as the smallest circle enclosing them in the photo. This assumption is not always justified and will often lead to large overestimations in flock density. The measurements were made perpendicular to the camera axis and did not take the third dimension, depth, into account. The

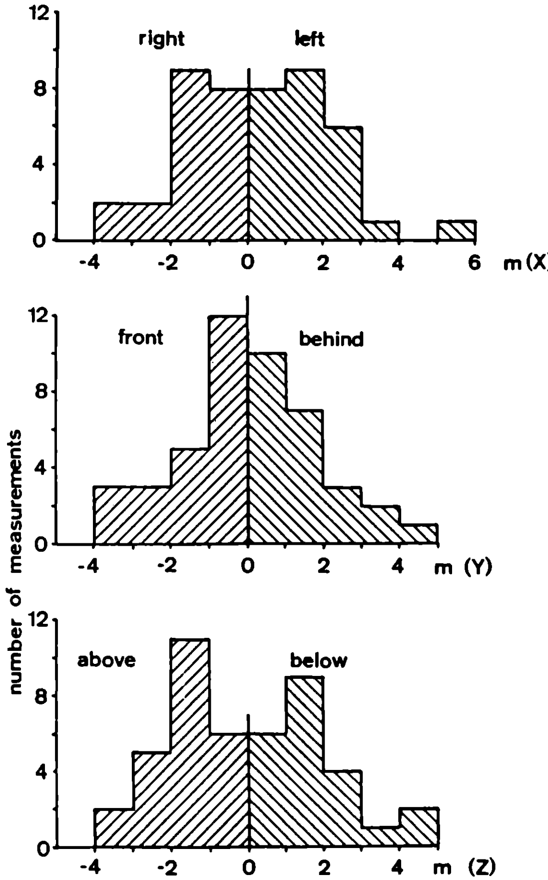

Fig. 8: Distribution of the X-, Y- and Z-components of the nearest neighbour distances of the flock of swallows illustrated in Fig. 5.

Table 3: Intraflock Dispersion: Statistics and measurement of two swallow flocks analysed for dispersion characteristics. Flock A is illustrated in Fig. 6.

	Flock A	Flock B
Number of Birds	53	23
Volume of cuboid	798 m^3	2088 m^3
Enclosed birds	13	5
Density P	0.0163	0.00239 birds/m^3
Expected distance to nearest neighbour $\bar{r}_E$	2.185 m	4.141 m
Observed distance to nearest neighbour $\bar{r}_A$	3.018 (n=46)	4.926 m (n=8)
$R = \frac{\bar{r}_A}{\bar{r}_E}$	1.381	1.190
$\sigma\ \bar{r}_E$ (Std. dev. of exp. dists)	0.7943	1.505
$c = \frac{\bar{r}_E - \bar{r}_A}{SE_{\bar{r}_E}}$	− 3.781	− 1.166

problem lies with the perspective foreshortening typical of photos taken through telephoto lenses. Although van Tets only considered birds "whose measurable parameters showed little difference", a bird whose beak- or body-length was only 10 % smaller than that of it's "neighbour" would have been 10 % of the range behind the other bird — and for photos taken with a telephoto lens at a range of 50 m, the separation unaccounted for would be 5 m. The densities listed by van Tets (1966: 107—109) should therefore be considered at best as maxima.

MAJOR & DILL (1978) used a similar technique to that used in the present study, and the results are therefore comparable. The nearest neighbour distances they measured were somewhat lower than those recorded at Col de Bretolet. These differences are probably real and due to differences in specific flocking behaviour in the first instance, and to lower flight altitudes than those in the present study.

The two swallow flocks analysed were underdispersed, implying that the birds were maintaining a minimum distance from each other, possibly to avoid collisions. The positioning of a nearest neighbour above or below, rather than in front or beside the reference bird would minimise any interference with vision. MAJOR & DILL (1978) also found that the flocks they analysed (Dunlins *Calidris alpina*) possessed a weak structure, in which the bird's nearest neighbour was most likely to be above and slightly in front, or below and slightly behind it.

BRUDERER & STEIDINGER (1972) monitored the flight of night migrants using an anti-aircraft fire control radar, and determined that the majority of the echo signals received were from single birds. After calculating the size of the radar "pulse volume" they concluded that these birds were flying at least 50 m apart, and therefore considerably further apart than day migrants. This was disputed by JELLMANN (1979) who refered to a photo of birds circling around a lighthouse at Helgoland. However, it is not possible to relate the flock densities of birds flying in an intense beam of artificial light to that of birds flying in natural, nighttime conditions. The attracting effect of constant light sources on birds has been noted previously (Verheijen 1980).

Photographic evidence and direct observation through the infra-red viewer in the present study lend support to BRUDERER and STEIDINGER's assertion that the nearest neighbour distances of nighttime migrants is an order of magnitude greater than those in the daytime. It should be noted that no light was visible to birds flying towards the pass. The infra-red light used in the viewer is invisible to the chicken eye (KARE & ROGERS 1976), and the brief flash exposures (one flash every five or ten minutes) were aimed upwards or behind the birds.

Summary

A relatively simple stereophotographic system is described, with which the tricoordinate positions of moving objects at distances to 80 m may be calculated. The system is accurate, but does not require complex photogrammetric equipment or techniques. The nearest neighbour distances of birds flying over a Swiss alpine pass were considerably larger than those determined with other non-stereo photographic techniques. Swallows were more regularly dispersed than random within their flocks, possibly minimising the risk of collisions. Birds migrating at night flew with nearest neighbour distances much larger than those of birds migrating during the day.

Zusammenfassung

Individualdistanzen tag- und nachtziehender Vögel. Eine Untersuchung mittels Stereophotographie.

Es wird ein relativ einfaches Stereophoto-System beschrieben, mit dessen Hilfe die drei Raumkoordinaten beweglicher Objekte bis zu Distanzen von 80 m bestimmt werden können. Das System ermöglicht genaue Positionsberechnungen ohne daß dazu komplexe photogrammetrische Ausrüstungen oder Techniken notwendig wären. Die Individualdistanzen (nearest neighbour distances) von Zugvögeln über einem schweizerischen Alpenpaß (Col de Bretolet) waren deutlich größer als die bisher mit anderen, nicht-stereoskopischen Methoden ermittelten. Schwalben waren innerhalb ihrer Schwärme eher regelmäßig verteilt als zufällig, wobei die Art der Verteilung (eher unter oder über vom nächsten Nachbarn, statt in dessen Flugachse) als Verminderung des Kollisionsrisikos gedeutet werden könnte. Die Individualdistanzen nachts ziehender Vögel sind wesentlich größer als diejenigen von Tagziehern (in der Regel nur ein Individuum im Sichtwinkel der Kameras).

Literature cited

Bruderer, B. (1971): Radarbeobachtungen über den Frühlingszug im Schweizerischen Mittelland. Orn. Beob. 68: 89—158. ● Bruderer, B., & J. Joss (1969): Methoden und Probleme der Bestimmung von Radarquerschnitten frei fliegender Vögel. Rev. Suisse Zool. 76: 1106—1118. ● Bruderer, B. & P. Steidinger (1972): Methods of quantitative and qualitative analysis of bird migration with a tracking radar. NASA SP-262: 151—167. ● Clark, P.J., & F.C. Evans (1954): Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology 35: 445—453. ● Clark, P.J., & F.C. Evans (1979): Generalisation of a nearest neighbour measure of dispersion for use in K dimensions. Ecology 60: 316—317. ● Elliott, J.M. (1971): Some methods for the statistical analysis of samples of benthic invertebrates. Freshw. Biol. Assoc. Sci. Publ. 25. ● Géroudet, P. (1973): La vie des oiseaux. Les passereaux. Delachaux & Niéstlé, Neuchâtel. ● Gould, L. L., & F. Heppener (1974): The vee formation of Canada Geese. Auk 91: 494—506. ● Jellmann, J. (1979): Flughöhen ziehender Vögel in Nordwestdeutschland nach Radarmessungen. Vogelwarte 30: 118—136. ● Kare, M., & J. G. Rogers (1976): Sense organs. In: Sturkie, P. D. (Ed.): Avian Physiology, third edition, p 30—52, Springer Verlag. ● Major, P. F., & L. M. Dill (1978): The three-dimensional structure of airbourne bird flocks. Behav. Ecol. Sociobiol. 4: 111—122. ● Simberloff, D. (1979): Nearest neighbour assessments of spatial configurations of circles rather than points. Ecology 60: 679—685. ● Van Tets, G. F. (1966): A photographic method of estimating densities of bird flocks in flight. CSIRO Wildl. Res. 11: 103—110. ● Verheijen, F. J. (1980): The Moon: a Neglected Factor in Studies on Cillisions of Nocturnal Migrant Birds with Tall Lighted Structures and with Aircraft. Vogelwarte 30: 305—320.

Present address: Waikato Valley Authority, P. O. Box 4010, Hamilton East, New Zealand