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The Three-Dimensional Structure of Airborne Bird Flocks

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Summary. The three-dimensional structure of flocks of dunlin, *Calidris alpina*, and starlings, *Sturnus vulgaris*, was studied while birds were in transit between feeding, loafing and roosting sites. A technique was developed that uses standard photogrammetric methods to determine the three-coordinate position of birds in flocks from stereoscopic pairs of simultaneously exposed photographs. A comparison of nearest neighbour distances indicates that dunlin have a tighter, more compact flock structure than do starlings (Fig. 2; Table 2). Analysis of interbird angles in both the vertical and horizontal planes indicates that each dunlin's nearest neighbour is most likely to be behind and below it. This spatial structure results in areas in which few nearest neighbours occur (e.g., immediately in front and below) (Fig. 3). Flight speeds during transit flights are also presented (Table 4). The spatial structure and behaviour of dunlin and starling flocks appear to be very similar to the structure and behaviour of schools of fish.

Introduction

In order to study the sensory basis of group formation in animals, or to compare such formations between species and environments, it is first necessary to have an adequate description of the structure of the social group itself. Although two-dimensional analyses of certain structural attributes of bird flocks have been attempted using both radar (e.g., Williams et al., 1976) and photographic techniques (e.g., Miller and Stephen, 1966; van Tets, 1966; Nachtigall, 1970; Gould and Heppner, 1974), measurement of the internal three-dimensional structure of airborne flocks has never been accomplished.

The purpose of this study was twofold: (1) to develop a stereoscopic camera technique to study the three-dimensional structure of flocks of small birds in the field, and more specifically (2) to characterize the structure and behaviour

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of one of a number of types of flocks of dunlin (red-backed sandpiper), *Calidris alpina*, and starlings, *Sturnus vulgaris*. In addition, flying speeds of both species, based on measurements from photographs, are presented. Although this study was limited in scope, the data obtained may allow comparison with similar data on fish schools, where structural hypotheses based on sensory physiology and hydrodynamics are being generated and tested (see Discussion).

Materials and Methods

Stereo photographs were taken of flocks of dunlin and starlings in flight near the Vancouver International Airport, British Columbia, Canada, where they are a particular hazard to turbine-powered aircraft. Filming was done during the fall of 1976, on days when wind speeds did not exceed 10 km/h. Two identical motor driven 35-mm cameras (Nikon Photomic F2) with permanently mounted 28-mm lenses were used. The cameras were attached to aluminum plates mounted on an aluminum 'I' beam such that the centres of focus for the two cameras were 5.495 m apart (Fig. 1).

The cameras were set on the 'I' beam with their lens axes parallel and with identical film planes. This was accomplished by using a neon helium laser and an auto-collimator. The 'I' beam was placed on two tripods, each with extendable legs and elevator heads. The beam and cameras were levelled to an accuracy of 20 s by adjusting the elevator heads and three-point levelling devices on each tripod. Shutter release cables from each camera were connected to a common electronic shutter release box so that cameras fired simultaneously (single-frame rate only; checked with a photocell beam through the two camera apertures mounted in tandem). The cameras were chosen so that their shutter speeds at each setting (1/250–1/1000 s) were as nearly identical as possible. Kodak Plus-X (ASA 125) film was exposed for the minimum time possible given ambient light conditions, and developed according to the manufacturer's instructions. To determine radial lens distortion characteristics, photographs were taken of a calibration field. Lens distortion corrections were subsequently applied in the analytical flock restitution process. Left and right stereo pairs of photographs were analyzed using a Zeiss-Jena Topocart Analyzer and standard photogrammetric methods.

Distances between each bird's head and the head of every other bird in the flock were determined using the coordinate positions of each pair of birds and the following distance formula:

$$\text{Distance} = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2 + (z_2 - z_1)^2}$$

Axis 'x' is the beak-to-tail axis of the birds, 'y' is perpendicular to the 'x' axis in the same plane, and 'z' is vertical and perpendicular to the '$x - y$' plane. Subscripts 1 and 2 refer to the reference and neighbour bird respectively. That bird having the shortest distance from the reference bird was considered to be the reference bird's first nearest neighbour. The second and third nearest neighbour distances were calculated in a similar fashion.

In order to determine the xz (elevation or altitude) and xy (bearing or azimuth) angles between pairs of birds, two sequential (taken less than 1.0 s apart) stereo pairs of photographs were required. From these the axes (3-D vectors) of flight of specific individual birds in a flock were calculated, and a mean value (vector) determined using methods described by Batschelet (1965). This mean value was then applied to the flock as a whole. In obtaining the vector for a given bird it was assumed that the bird had not changed direction and attitude between photographs. Indeed, if these had changed substantially, it would not have been possible to identify individuals in sequential still photographs. Only birds that were easily recognized in sequential frames were used in this analysis. In applying the mean vector to the flock, the further assumption was made that the birds were flying parallel courses. There was also assumed to be no roll component to each bird's motion (i.e., left and right wing tips were assumed to be equidistant from the ground). The calculated mean flight direction was then used as the x axis and all bird coordinates recalculated in this new framework. Thus the relative position of the birds could change with respect to one another,

Table 1. Comparison of calculated and actual distances and angles between corners of children's jungle gym (monkey bars) photographed at a distance of 25 m. Mean elevation and bearing angles are the average of complementary angles with opposite signs

Measurement:	Calculated from photographs		Actual mean
	Mean	±SD	
Distance: Horizontal	0.40 m	0.06 m	0.43 m
Vertical	0.41 m	0.01 m	0.41 m
Absolute angle:			
Elevation (xz)	90.0°	1.30°	90.0°
Bearing (xy)	0.0°, 90.0°, 180.0°	7.28°	0.0°, 90.0°, 180.0°

depending upon the magnitude of shift in the coordinate reference system. Distances and angles were then calculated as above. Note that where sequential stereo pairs were unavailable, only distances between birds could be calculated, as was the case for starlings and all but three of the dunlin flocks analyzed.

There are a variety of possible sources of error in the measurements. These include: small optical aberrations in the lenses (i.e., distortion not symmetrical around lens centres), misalignment of camera lenses and film planes, lack of perfect synchrony in firing of the two cameras, and variability in placement of the cursor on the birds' beaks during photo-analysis (pointing error). In all cases, the magnitude of the error increases as a direct function of the birds' distance from the cameras. In this study camera–bird distances ranged from 12–50 m. At much shorter distances a large flock is not simultaneously present in the fields of view of the two cameras.

To determine the accuracy and precision of the photographic/photogrammetric methods employed, stereo photographic analysis of distances and angles between the corners of bars on a children's jungle gym (monkey bars) was made. The mean distances (in both horizontal and vertical planes) did not differ significantly from those actually measured (Table 1). No xz (elevation) measurement varied by more than 3.0° from the actual mean angle (90.0°). However, the xy angles (bearing) varied by 2.0–13.0° from the actual means. This was due in part to a tilt in the entire structure.

Flock densities were calculated based on first nearest neighbour distances only. The reference bird was assumed to be in the geometric centre of a body centred cubic lattice, with potential nearest neighbours at each of the cube's eight corners. The cubic density (birds/volume) was calculated using the following formula: $3\sqrt{3}/(4\,\mathrm{NND}^3)$, where NND is the mean nearest neighbor distance for that flock.

Flight speeds were obtained from high-speed Super-8 movie (100–150 frames/s) and 35-mm still camera (3 frames/s) serial photographs of dunlin and starlings taken when the birds were judged to be flying parallel with the film plane in wind conditions <10 km/h.

Results

1. Behaviour of Birds

Stereo photographs of both dunlin and starlings were taken while the birds were flying in transit between feeding, loafing or roosting sites. During such flights the birds were relatively widely spread out and loosely organized, did

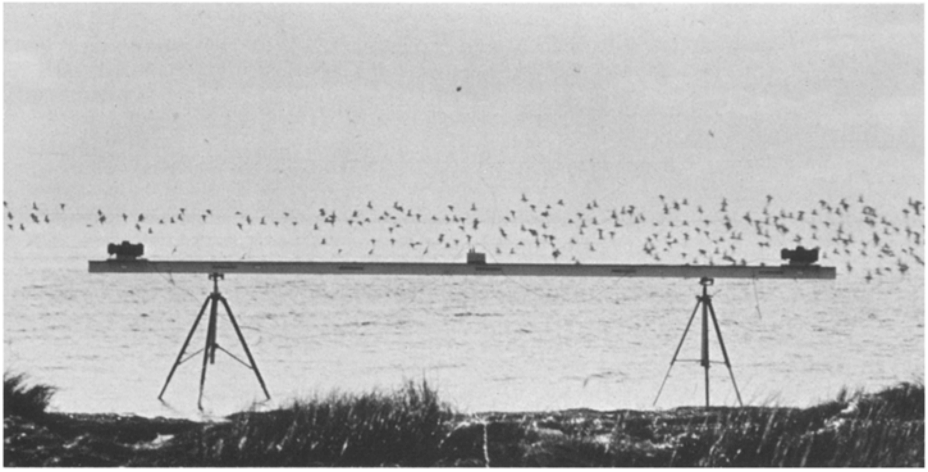

Fig. 1. Stereo camera system used during study: Cameras on ends of beam mounted on tripods. Shutter releases are connected at the box in the centre of the beam. A flock of dunlin is passing in front of the cameras

not appear to be flying at maximum speed, were generally flying parallel to (i.e., level flight) and close to the ground or water, and were flying on a relatively constant bearing. A typical dunlin flock flying in transit is shown in Figure 1. Starling flocks were similar in appearance. This type of flock was observed when predators were absent and the dunlin were flying along exposed mudflats, or the starlings between grassy areas along runways. In all photographs analyzed the birds were moving parallel with the 'I' beam and did not react to the apparatus or observers. Only when they were directly over cameras actually taking photographs (and thus producing sound) did the birds veer away.

The wind velocity was important to both species of birds. When wind velocity was greater than about 20 km/h, both species tended to fly close to the ground or water, and to spread out horizontally more so than vertically. Flock structure appeared to become looser (less dense) when this occurred. Wind velocity was not a factor contributing to the flock characteristics reported below.

Other flock shapes were also observed but not photographed. When attacked by predators such as peregrine falcons (*Falco peregrinus*), members of a dunlin or starling flock coalesced quickly into a nearly spherical 'ball,' and appeared to increase their flight speed. The tightly packed flock performed rapid, apparently protean evasive manoeuvres (Humphries and Driver, 1970), turning, circling, swirling, ascending, descending and splitting into sub-flocks, coalescing again or joining other flocks. At times the flock 'pulsated'—expanding and contracting in size, presumably as interbird distance changed. When no longer threatened, a flock once again became more loosely structured.

2. Interbird Distances

Figure 2 shows the percent frequency distributions for first, second, and third nearest neighbour distances respectively, for all flocks of both species of birds.

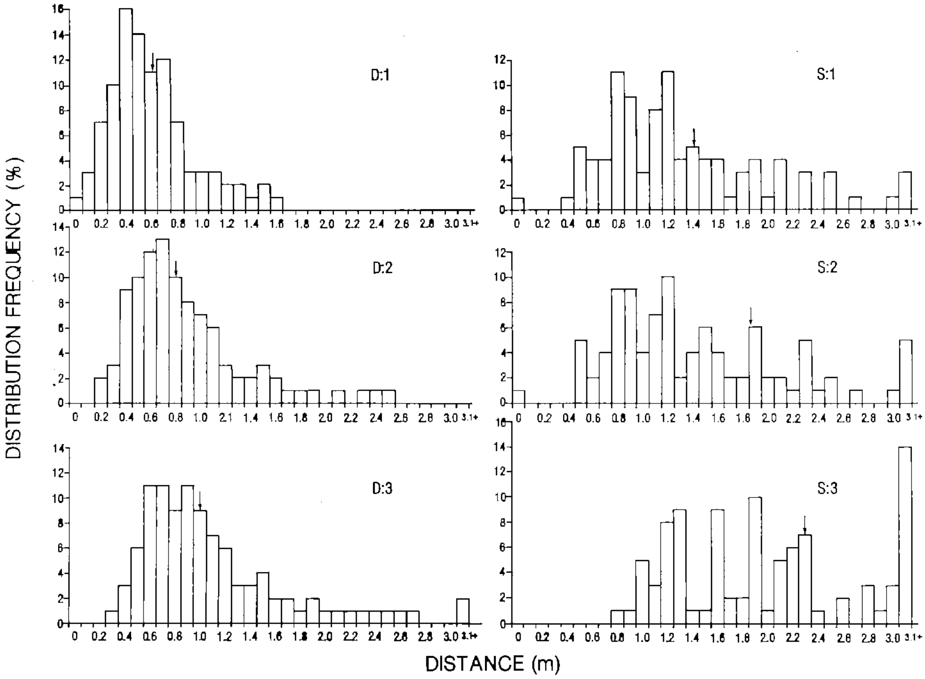

Fig. 2. Percent frequency distribution of dunlin (*D*) and starling (*S*) first (*1*), second (*2*), and third (*3*) nearest neighbour (interbird) distances. Arrows denote mean values

This method of analysis is used here to facilitate direct comparisons with similar studies of fish schools (see Discussion). When two birds are each other's nearest neighbour (forming a nearest neighbour pair), statistical bias may occur if both members are used in the analysis. Calculated mean distances, using both members of a pair as well as dropping the second member of the pair, for first nearest neighbours only, are compared in Table 2. When one member of each pair was dropped, the mean distance was consistently higher than when it was included in the analysis. Although nearest neighbour pairs comprised approximately 30% of each flock, the difference between the two calculations was not significant ($P > 0.05$). Both members of all nearest neighbour pairs (about 12% in each flock) are included in calculations of second and third nearest neighbour distances (Table 2).

Although dunlin and starlings are approximately the same size – 19.1–23.6. and 19.1–21.6 cm total length, respectively (Godfrey, 1966) – differences in flock structure between the two species are apparent. Dunlin fly in a tight, relatively closely spaced flock as compared with starlings, as evidenced by mean interbird distances about a half to a third those of the starling (Table 2; Fig. 2). The mean interbird distance for increasingly distant nearest neighbours increases, and as would be expected a distributional 'tail' occurs towards increased distances, especially for dunlin. In the starling flocks there also appears to be a certain periodicity (alternation of low and high frequency) in the distribution of the distances of first, second, or third nearest neighbours. This periodicity

Table 2. Dunlin and starling interbird distances and densities. NN = nearest neighbour

Species	Flock size	% First NN pairs in flock	Mean distance to NN (m)				Density (birds/m^3)
			First		Second (all birds)	Third (all birds)	
			Less one of each NN pair	All birds			
Dunlin	51	33	0.52	0.47	0.72	0.84	9.25
	70	30	0.60	0.58	0.81	0.98	6.02
	51	29	0.76	0.71	0.96	1.13	2.96
	56	26	0.79	0.70	1.03	1.32	2.64
	65	29	0.66	0.58	0.79	0.92	4.52
	66	34	0.93	0.88	1.30	1.67	1.62
	36	33	0.51	0.45	0.73	0.89	9.80
	52	30	0.75	0.71	1.04	1.30	3.08
	76	32	0.53	0.50	0.94	1.29	8.73
	54	31	0.50	0.43	0.64	0.86	10.40
	50	30	0.59	0.55	0.76	0.92	6.33
	49	24	1.08	1.01	1.29	1.55	1.03
	48	37	0.58	0.54	0.79	0.94	6.66
	47	31	0.75	0.69	0.89	1.03	3.08
Mean	55	29	0.69	0.63	0.86	1.05	3.96
Starling	51	29	1.55	1.42	2.08	2.62	0.35
	26	23	1.27	1.15	1.50	1.78	0.63
Mean	38	26	1.45	1.33	1.91	2.34	0.43

may be related to empty positions in the lattice in which the birds are aligned, i.e., there may be particular positions within a body-centred cubic lattice which are not occupied for aerodynamic or visual reasons.

Flock density calculations based on first nearest neighbour distances are also presented in Table 2. The values calculated for starling flocks are well below density figures given by van Tets (1966) (11–32 birds/m^3) and by Kaiser (1970) (3–11 birds/m^3). The types of flocks upon which their calculations are based may be quite different, a result of behavioural or geographical differences in the birds. Similar reasons may account for the disparity between dunlin densities calculated here and by Kaiser (1970) (1/m^3).

3. *Interbird Angles*

Stereo photographs of all members of three dunlin flocks consisting of 51, 51, and 70 birds respectively were used in the analysis of interbird angles of elevation (xz) and bearing (xy). The data presented here are pooled over all three flocks. Mean angle vectors and angular dispersion estimates were calculated using the methods of Batschelet (1965). Elevation and bearing angles for the second member of each nearest neighbour pair (based on distance) were dropped

Table 3. Comparison of first nearest neighbour mean angles (vectors) of elevation and bearing with and without both members of nearest neighbour pairs being included in the analysis

	Flock size	% Pairs in flock	Mean angle (vector) ± Angular dispersion			
			Elevation		Bearing	
			All birds	Less one bird each pair	All birds	Less one bird each pair
	70	30	40 ± 31°	41 ± 28°	49 ± 32°	49 ± 28°
	51	33	36 ± 32°	34 ± 29°	46 ± 32°	48 ± 29°
	51	29	30 ± 24°	30 ± 25°	46 ± 27°	45 ± 24°
Mean	57	30	36 ± 29°	36 ± 27°	46 ± 31°	47 ± 27°

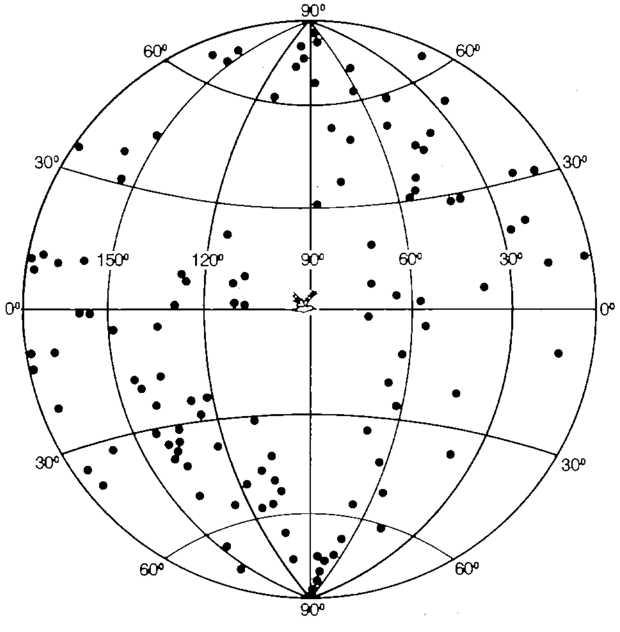

Fig. 3. Hemispherical angular distribution [elevation (xz) values plotted against bearing (xy) values] of dunlin first nearest neighbours (side view, left and right hemispheres collapsed onto right). The xz values correspond to the horizontal (latitude) lines, xy values to the vertical (longitude) lines. Each point represents a single pair of values and relates only to the reference bird's position, not to other points. $n = 117$

for the analyses of first nearest neighbours only. However, a comparison of first nearest neighbour angles with and without inclusion of both members of each pair (Table 3) showed the differences to be non-significant ($P > 0.05$). Because of this, both members of nearest neighbour pairs were included in the analysis of second and third nearest neighbour elevation and bearing angles. There were no discernable relationships between interbird distance and angles of elevation or bearing for first, second, or third nearest neighbour dunlin.

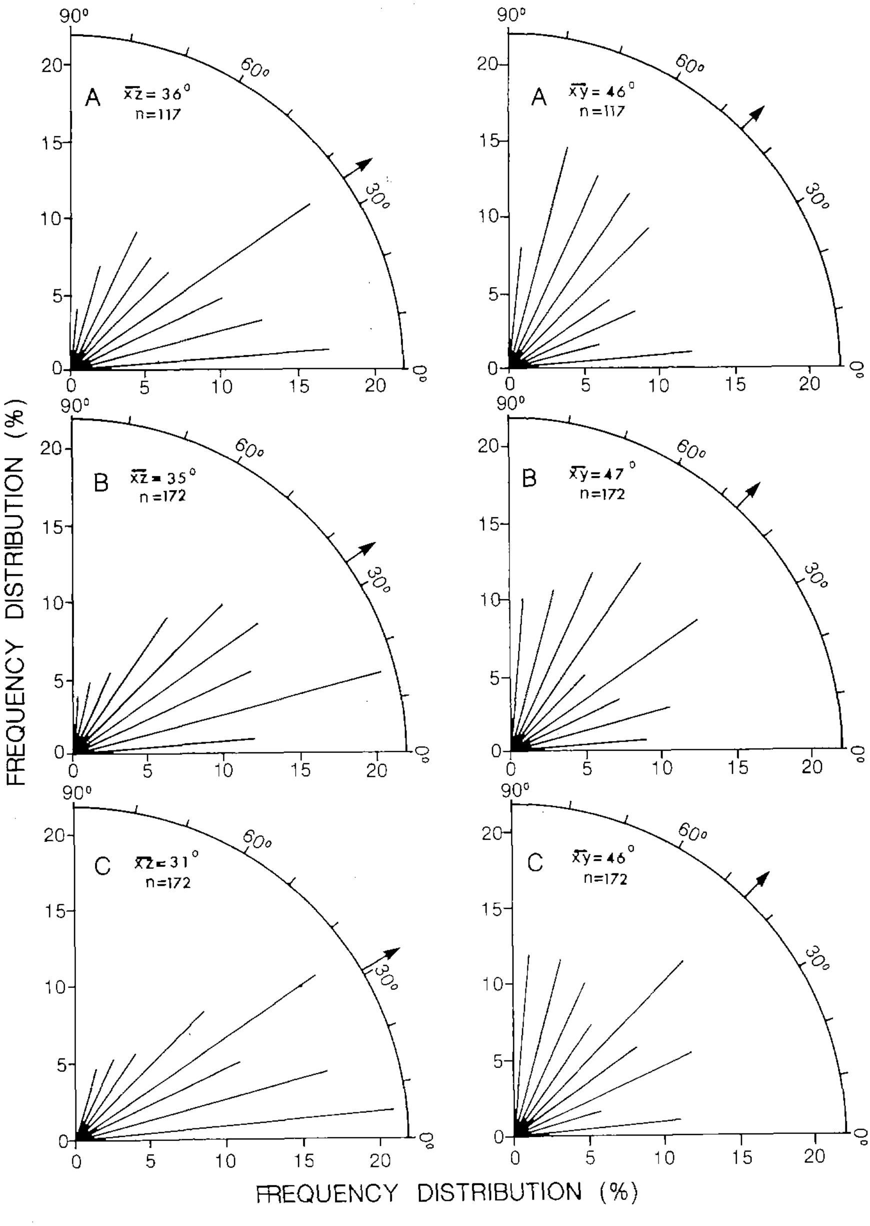

Fig. 4 A–C. Single quadrant percent frequency distribution of xz and xy interbird angles (at 10° intervals) for dunlin first (**A**), second (**B**), and third (**C**) nearest neighbours. Angular data for all 8 spherical quadrants are reflected onto one quadrant (see text). $\overline{xz}$, $\overline{xy}$ and arrows denote mean values (vectors). The origin is the bird's head, with the bird flying along the 0° axis towards the right. XZ (elevation) plots are views from the side of the bird; XY (bearing) plots are views from overhead

A plot of the elevation and bearing angles against each other is provided in Figure 3 for first nearest neighbour birds only (all three flocks combined). This figure depicts a bird flying towards the right with the distribution of neighbour birds represented on a hemisphere projecting out of the figure. One would expect to see specific distributional bands or clumps if a relationship existed between the two angles in terms of a defined structure within flocks. There are weak indications that such a structure does exist: (1) birds behind and below tend to be concentrated along the 120–135° longitude and 30–60° latitude vectors; (2) a band of birds extends along the 60° xy line (of bearing) from 'pole to pole' in front of the subject bird; and (3) relatively large areas are either devoid of nearest neighbours or have relatively few individuals as compared with corresponding regions in the other quadrants. This is most noticeable immediately in front of (0–30°) and below the reference bird. The birds appear to fly in a somewhat layered formation during transit flights, nearest neighbours being in front-above or behind-below, i.e., the front of the flock is higher than the rear. A void in front of and below each bird may be required so as to allow a continuous view of the ground or water over which the birds are passing during transit flights.

Figure 4 presents the distributional frequency of nearest neighbour birds for all eight quadrants of sphere reflected onto a single quadrant such that 180° behind becomes 0° in front and 90° below becomes 90° above (e.g., $\pm 45° = \pm 135°$). There is little difference ($P > 0.05$, based on methods discussed in Batschelet, 1965) between the mean angles (vectors) for first, second, and third nearest neighbours (xz: 31–36°; xy: 46–47°). The distribution for first, second, or third nearest neighbour angles of elevation (xz; at 10° intervals) is not uniform ($\chi^2 = 21.56$–32.36, $P < 0.025$). Bearing angle (xy; at 10° intervals) distributions are not significantly different from uniform ($\chi^2 = 5.94$–8.19, $P > 0.05$).

Table 4. Dunlin and starling flight speeds (m/s)[a] calculated from photographs

Species	Type of flight	Sample size		Flight speeds				Camera type and speed (frames/s)
		No. of flocks	No. of measurements	Mean	Standard deviation	Max.	Min.	
Dunlin	Straight (level)	4	96	19.8	±7.8	36.9	9.2	Movie (100)
Starling	Straight (level)	6	120	5.9	±2.2	12.6	2.3	35 mm (3)
	Straight (level)	3	82	9.0	±4.1	16.5	3.3	Movie (150)
	Descending[b]	1	13	7.9	±0.5	8.6	7.0	35 mm (3)
	Descending[b]	2	38	6.6	±0.7	8.4	4.4	Movie (100)
	Gliding[c]	1	39	9.0	±0.4	9.8	8.3	35 mm (3)
	Gliding[c]	2	62	9.3	±3.3	14.9	4.3	Movie (150)

[a] 1 m/s = 1.9438 kts = 2.2369 (statute) mph

[b] Descending flight was usually made at low angles with wing beats

[c] Gliding flight was usually made at steep angles without wing beats

4. Flight Speeds

Ground speeds calculated from high-speed movie and 35-mm still photographs tend to be below or similar to those reported in the literature for the same or similar species (Meinertzhagen, 1955; Eastwood et al., 1962, Hamilton et al., 1967; Pennycuick, 1969). Starling speeds averaged between 5–10 m/s and dunlin speeds about 20 m/s (Table 4).

Discussion

The work reported here more closely corresponds to recent work with fish schools than it does to other work with bird flocks. In fact, there appear to be striking similarities in both structure and behaviour of schools and flocks. Much of the work with fish involved two-dimensional analyses of school structure and behaviour (e.g., Hunter, 1966, 1969; van Olst and Hunter, 1970; Serebrov, 1976; Graves, 1977). There have also been a number of similar studies of the spatial structure and behaviour of schools or swarms of invertebrates (e.g., Clutter, 1969; Okubo and Chiang, 1974). Breder (1976) recently discussed the three-dimensional structure of schools in operational terms, and Pitcher (1975) summarized methods of measurement. Analyses of the three-dimensional structure of schools of minnows, *Phoxinus phoxinus* (Pitcher, 1973), several pilchard, *Harengula,* species (Cullen et al., 1965), and saithe, *Pollachius virens,* (B.L. Partridge and T.J. Pitcher, personal communication) indicate that the general organization and structure of schools is similar to that of the flocks of birds reported here. Pitcher (1973) found that nearest neighbours in schools of minnows tended to be behind and possibly below the reference fish – a tendency similar to the distribution of nearest neighbours in dunlin flocks. Cullen et al. (1965) present frequency distribution diagrams of nearest neighbours in horizontal and vertical planes, which appear very similar to those presented here for dunlin. However, there appears to be a relationship between interfish distance and angles in saithe (B.L. Partridge and T.J. Pitcher, personal communication), a relationship not demonstrated in dunlin flocks.

The structure of dunlin and starling flocks described here is of birds in relatively loosely organized groups during transit flights. However, this type of flock structure was only one of a number of spatial arrangements observed. The most compact (densest) observed was the nearly spherical 'ball' [globular cluster in Heppner's (1974) terminology]. The loosely organized group behaviour and the changes that occur in flock structure when predators appear are very similar to those observed in schools of three species of prey fishes when attacked by predatory fishes (Major, 1977, 1978a and b). The general characteristics used to describe bird flocks are in fact not unlike those used to describe the polarization and synchronized behaviour of fish schools (see reviews by Breder, 1959, 1967; Shaw, 1970; Radakov, 1973). Only with additional work will we be able to tell whether the apparent similarities and differences between the structure and behaviour of flocks and schools are real.

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