Evidence for widely dispersed birds migrating together at night

Ronald P. Larkin[1] and Robert E. Szafoni

Illinois Natural History Survey, 1816 S. Oak Street, Champaign, IL 61820, USA

Synopsis Lore and indirect evidence from previous studies suggest that nocturnally migrating vertebrates (perhaps bats but mostly birds) sometimes fly widely dispersed from each other, but in flocks. The observations include stationary and scanning radars, recordings of flight calls, and watching the moon with telescopes. Direct observations of such flocks have been lacking. This article presents data from novel tracking of nocturnal aggregations of radar targets. Statistical analysis of straight, detailed flight paths supported the hypothesis that vertebrates, almost certainly birds, flying within about 200–300 m of each other fly parallel (in the same direction at the same speed) more often than do vertebrates flying farther apart. This inference was strengthened by comparisons with a partial control for wind and for small-scale atmospheric structure: namely, small nocturnal arthropods tracked by the identical method did not fly parallel. Radar data also indicated that birds flying together may have similar wing beats, suggesting taxonomic similarity between birds flying parallel. Possible functions include not only mutual benefits on the ground during migratory stopover (habitat use, avoidance of predators, and social feeding) but also in-flight sharing of information about orientation.

Introduction

In daytime, the concept of a flock implies a compact group of flying birds. Measured spacing within daytime flocks is indeed close (Major and Dill 1978). Migrating songbirds crossing the Gulf of Mexico in daytime fly in recognizable flocks (Gauthreaux 1972). Although some species of waterfowl and shorebirds are known to fly in pairs or larger groups (Richardson 1979; Alerstam et al. 1990), spacing within flocks at night is poorly studied. Compact flocks of songbirds are uncommon during nocturnal migration, as shown by observations with stationary light beams (Balcomb 1977), radar-mounted tracking spot lamps (Larkin and Thompson 1980), wing-beat records of migrating animals (Bruderer 1971), long-range radar (Gauthreaux 1972), and watching birds crossing the face of the moon (Lowery and Newman 1955).

Nevertheless, there are numerous indications that night-migrating songbirds are not distributed evenly or randomly in the air. An equally diverse array of observational techniques has provided indirect evidence for widely dispersed groups, or at least aggregations, *sensu* (Allee 1938). Nocturnal flight calls of passing migrating songbirds are often bunched in time (Ball 1952; Farnsworth 2005), suggestive of groups of birds calling to one another. Detailed records of passage of birds through ceilometer beams (Balcomb 1977) and stationary radar beams (Larkin 1982) showed aggregations clumped nonrandomly in time. Certain species of European birds flying over lighted structures at night were observed to be in "loose flocks" (Svazas 1990) as were migrating North American owls observed with night-vision equipment (Russell et al. 1991). One species of North American warbler appears to maintain pairs during crossings of the Gulf of Mexico (Moore 1990). After a night's migration, recognizable mixed-species flocks of migrating songbirds are commonly observed on and near the ground, although it is not known whether the flocks persisted from cruising flight or formed only after birds landed (Wiedner et al. 1992; Rodewald and Brittingham 2002). Such observations are not limited to birds: groups or "waves" of bats of several species have been seen in cruising flight or entering roosts during migration (Fleming and Eby 2003).

Thirty years ago, in a brief review of dispersed flocks of birds in nocturnal migration, Wallraff (1978) suggested taking into account, "… not only the spatial distribution of migrants, but also the directions of their tracks," to ascertain if the birds kept together over a long period of time. This article follows and extends that suggestion using data from tracking radar.

The radar observations concern *parallel targets*, animals that appeared to be traveling together because they fly near each other along similar paths.

The phenomenon suggests an aggregation or a loose flock, but only certain conventional attributes of flocks were observable in the present study. The radar could record details of flight paths of individual animals for a few seconds or minutes but, among other limitations, it could not determine whether the flocks may have been of single species or of multispecies, whether they observed each other or communicated, the extent to which animals maintained a certain spacing between individuals, or whether members actually kept together or associated socially beyond the brief time they were tracked by the radar.

The work described here rests on several plausible assumptions: (1) On any night of migration, many species of birds are aloft over the eastern United States. When the air temperature is above freezing, arthropods (mainly flying insects), and sometimes bats are intermixed with birds. (2) One can discriminate vertebrates from arthropods using data from a tracking radar (Larkin 1991). (3) Arthropods do not travel together in aggregations that are widely spaced (17 m or more between nearest individuals). (4) Small arthropods with very low air speeds act as radar-trackable markers in the atmosphere and provide instantaneous rough estimates of local wind (Wilson and Baynton 1980; Riley 1999). (5) Birds are more common than bats in nocturnal migration at most times. Bats do not engage in long-distance migration during cold weather. (6) Distinguishing between North American bats and birds is not currently possible with radar (Bruderer and Popa-Lisseanu 2005). Hence, radar-tracked flying animals are "targets." (7) Although precise taxonomic identification is seldom possible with radar, vertebrates flying together are taxonomically related to some extent. (8) During any night's radar operation, distributions of directions of flying animals, particularly vertebrates, are often tightly clumped around a certain migratory direction, such that even some widely separated targets might be expected to fly parallel, by chance. (9) Flying animals tracked by the low-power-density radar used in these studies were engaged in natural migratory flight and did not react to pulses of microwave radar (Bruderer et al. 1999).

Methods

General methods

Previous publications give background information including details of study sites and equipment (Larkin and Thompson 1980; Larkin 1991). A specialized tracking radar recorded paths of single, nocturnal flying animals (hereafter, "targets") while an operator observed flight paths ("tracks") and other data on electronic displays. Tracks analyzed here were taken between civil sunset and civil sunrise during migrations of songbirds in spring and autumn and a few nights during insect migration in summer. Study sites were of flat or rolling terrain in Illinois, New York, Michigan, and Massachusetts, USA (see "locales dates" in Supplementary Material).

Data gathered in November 1974 were organized differently and analyzed separately from those gathered in 1982–1987 (hereafter, "1980s"). Data from 1974 included sessions in which the radar operator specifically sought to find and track parallel targets (see subsequently), whereas data from the 1980s were obtained during the course of collecting data for other studies. In the 1980s, rate of sampling of target positions was faster; tracking accuracy was improved; and quantitative recording of wing beats and size and identity of targets was routine.

Tracks of flying animals

The radar had a narrow, 3-degree conical, steerable, "pencil beam" and an A-scope display of target strength versus slant range from the radar along the beam (hereafter "A-scope" and "range," Fig. 14 in Larkin 2005). The A-scope did not indicate directions and, in general, did not show animals outside the 3-degree beam. After seeing a target, or sometimes a clump of two or more targets on the A-scope close together in range (see subsequently), the operator actuated a control placing the radar into autotrack mode. The radar then followed targets automatically in three dimensions by moving its antenna and measuring the range. This continued until the operator intervened or the autotrack mechanism lost the target, often when the target passed behind an intervening object on the ground.

The minimum interval to resolve two targets in range was determined largely by the length of the radar pulse, about 38 m. Two targets spaced at distances greater than approximately half the length of the radar pulse appeared as narrow peaks that were close together, but separate, on the A-scope. When the operator chose to track such a pair of close targets, tracking could proceed in any of four ways: (1) The radar autotracked one of the targets, ignoring the other nearby target(s), which may, however, have been visible to the operator using the A-scope. (2) The operator intervened with manual controls to cause the radar to lock onto each of the targets in alternation as potential parallel targets, tracking each one for a long enough time to permit
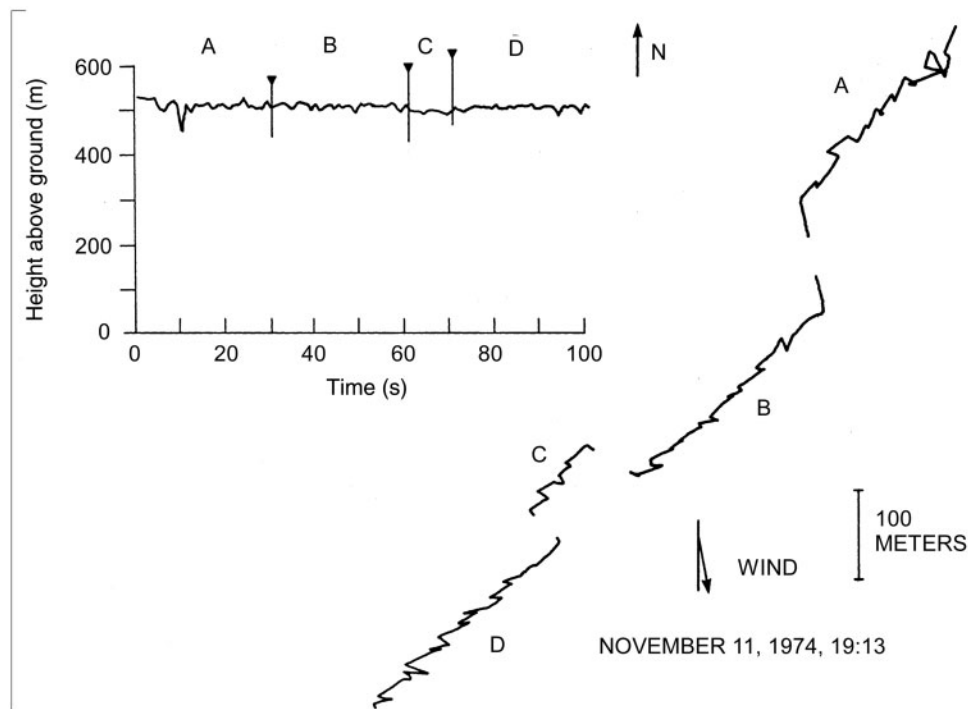
Fig. 1 Two parallel targets tracked on November 9, 1974 traveling 221° and 228°, respectively. The two targets (A + C and B + D) are separated by vertical lines on the height plot (upper left) and by gaps in the XY plot. Jitter in each of the tracks is a result of angular tracking error and measurement error at a range of about 1 km and is typical of data from 1974.

later measurement of its speed and direction of flight (Fig. 1). (3) The autotracking mechanism switched in range from one target to another and back, producing a fractured path similar in appearance to Fig. 1, but did so automatically and spontaneously instead of by operator intervention (Fig. 2). (4) With multiple targets (Larkin 1991) that were especially close together in range (see Discussion section), the radar behaved as in (3) but switched back and forth among them so rapidly that the targets could not be clearly distinguished in the data. The true total number of flying animals in an aggregation was difficult to determine. In each of the four cases, one of a pair of parallel targets could itself be a multiple target, implying at least three targets flying together; however, this was not documented from the tracking data.

The operator could immediately see that targets were close to each other in range along the axis of the radar beam, but could never determine the extent to which the targets were traveling in the same direction until they were each tracked long enough to paint lines on a separate computer display showing their paths. Therefore, opportunity for bias was negligible because the operator could not initially select parallel targets, only nearby ones. In the 1980s, all parallel targets were tracked during the course of unrelated studies with the tracking radar.

Sometimes, parallel targets were discovered only during later off-line analysis of radar tracks.

Only those flying animals in, or at, the edge of the radar beam were visible on the A-scope, not those right, left, above, or below the beam. Therefore, only a minority of potential parallel targets or members of a flock were visible and their arrangement in space was not directly observable. Flying animals at the same range appeared as one target on the A-scope.

Analysis

Paths

Real-time software recorded XYZ (eastward, northward, height above the radar) positions of putative parallel targets to 1-m precision at 0.67 or 1 position/second, except that in 1974 an assistant measured some nonparallel tracks from photographic enlargements. Tracks were edited to correct errors such as impossible positions and extraneous points and also to separate the tracks of different flying animals (see "XY edit of a track" in Supplementary Material). After editing, straight lines were fitted to segments of tracks (including whole tracks) by the method of (Larkin and Thompson 1980, see also "method of linear fit" in Supplementary Material). We used the resulting linear equations to describe the target's path in three dimensions, including ground
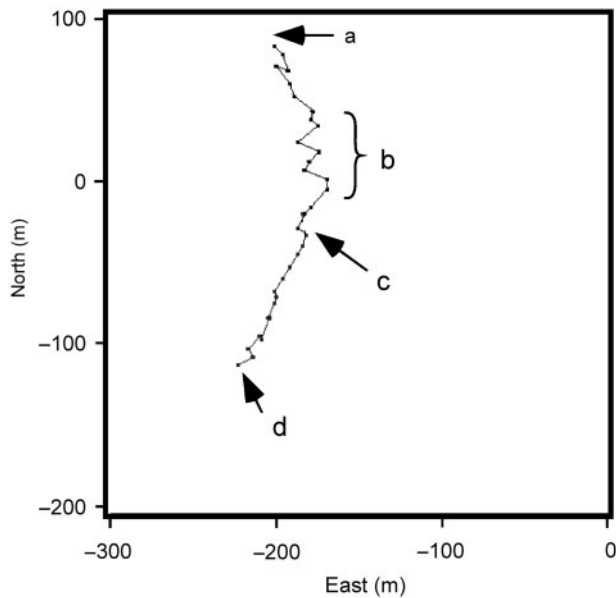
Fig. 2 Radar track of two parallel targets, both of which reacted to the sound of thunder (Larkin 1978) by turning away: (**a**) Autotracking begins. (**b**) Radar operator reports that the radar is switching back and forth between two parallel birds about 17 m apart. (**c**) Sound recording (thunder) started; birds turn away from the sound, the source of which was at (0,0) on the right. (**d**) Autotracking ends as elevation drops below radar fence. This track is an example of animals presumably flying in parallel that were separated by the minimum discriminable distance apart as determined by the pulse length of the radar. The reaction appears slightly delayed because the sound took about 0.5 s to reach the animals. At least one point is artifactual because it was taken when the autotracking mechanism was switching from one target to the other and locked onto neither. Data were recorded September 23, 1976, 22:40:29, 1 position/s.

speed, direction, rate of climb (where negative values are descending), and amount of deviation from a straight line at constant ground speed (standard error, XYSE). Although no track is perfectly straight and level, we discarded curving segments with XYSE >2.0 m/s.

Parallel targets

We defined parallel targets operationally as members of pairs (or multiples) of tracked targets that had highly similar XY ground vectors; that is, that were traveling in almost the same direction at almost the same speed. Both direction and speed were important to this definition. Nearby targets were, in fact, observed flying in indistinguishably similar directions but at quite different speeds, and not keeping together, therefore. The relative XY speed (V_r) was computed as the magnitude of the difference between the two targets' vectors over the ground. This measure of V_r was always positive. Ideally, V_r of

parallel targets might be zero; that is, the targets would maintain a constant distance apart, but, because of measurement errors and flight behavior (see Discussion section), even single tracks are never perfectly straight with perfectly constant speed and V_r seldom or never equals zero. Therefore, the analysis concentrated on parallel targets defined as pairs of segments with low but nonzero V_r.

Flock members

To determine whether low-V_r targets were members of a flock, we measured whether distance between parallel segments was also small. Using the fitted lines, we computed the position of the earlier tracked segment at the time of the beginning of the later segment. Performing the computation using the time at the beginning of the earlier (rather than the later) segment in the analysis did not change the conclusions (see "method of linear fit" in Supplementary Material). We measured the relative XYZ distance (D_r) between the two fitted segments at that time. Pairs of targets with both low V_r and low D_r were potential members of a flock.

Statistical tests

We applied single-sided tests under the assumption that parallel targets were not significantly dissimilar or divergent because they were flying together. Behaviorally, the assumptions were that they did not specifically seek to associate with taxonomically divergent animals and they were not repelled from one another. Because distributions of ratios, target cross-sections (see subsequently), and subtracted values were far from Gaussian, we tested statistical significance using the nonparametric 1-way Wilcoxon test. We applied strong inference to explore nonsocial explanations of the observations.

Wind

Radar tracks of free balloons in the 1980s provided estimates of wind at the height of, and within 2 h, of each tracked target (Larkin and Thompson 1980). A target's motion over the ground is the vector sum of its motion through the air and the wind (motion of the air relative to the ground). Differing wind represents an important potential source of variation in tracked segments that are not near to one another. Animals subjected to different wind speeds and out of contact with each other are *a priori* unlikely to fly parallel; therefore, animals in winds differing >3 m/s were not compared. For similar reasons, statistical comparisons were made among targets <10 km from each other to assure that they were under comparable wind conditions. At the median ground speed of

20 m/s, such targets are within about 500 s of one another, a tiny fraction of their night's journey.

Wing beats and target size

The data from the 1980s included digital recordings of unfiltered receiver voltage. Rapidly sampled (700/s) time series of 2 s duration provided information on quick temporal changes in size of the target such as generated by wing beats and other body motions. Wing beats were categorized from plotted time series of wing beats by an assistant without knowledge of relative speed of targets and usually without knowledge of the characteristics of the track. Records of wing beats of vertebrates were further categorized as flap-coast, intermittent flap-coast, pause, or steady flapping. We classified targets with no observable wing beats or with wing beat rates >30/s and radar cross-sections ≤1 cm to be small arthropods. Taking advantage of the property that, in general, larger animals reflect a greater amount of radar energy (Larkin 2005), size of targets was measured by comparing the output of the radar receiver produced by pulses backscattered from a tracked flying animal to those produced by a balloon-borne tracked metal sphere at a given range on the same night.

Nocturnal visual observations

During the 1980s, operators sometimes mounted visible light spot lamps on the radar antenna to illuminate and attempt to identify tracked targets during nocturnal migration. Operators switched on spot lamps only after recording sufficient data on undisturbed flight to describe a target's path flight, speed, wing beats, and radar-measured size. Only the parts of a target's track before it was disturbed by being illuminated with the spot lamp were used here. One or more observers saw and counted a subset of targets with binoculars, a telescope that was electrically coupled to the radar antenna to follow the tracked target automatically, or both. Binoculars were 7× or 8× magnification. The telescope was a Celestron with 125 mm aperture, usually used at 40–46×. The light source was usually a Xenon lamp of beamwidth 1° and rated at 10^6 cd luminous intensity. Five percent of visual observations used a 120-W VNSP ceilometer lamp as a light source.

Results

Statistics describing the targets used in the analysis appear in "descriptive material" in the Supplementary Material.

Parallel birds in November 1974

Data from November 1974 suggested that, at least on some nights, parallel birds are observed and may be more frequent than expected considering the ground vectors of all targets tracked (Table 1, Fig. 3, see also "1975 example" in Supplementary Material). However, height was a confounding factor (Table 1), the accuracy of the positional data was marginal for this work (Table 2), and discrimination of birds from arthropods was unsatisfactory. (Numerous migrating bats are unlikely in New York in November.) Furthermore, these data do not permit one to distinguish between social behavior by birds aloft and passive "bunching" of birds by small-scale atmospheric motion (Larkin 1982).

During autotracking of targets in close proximity, radar operators observing the A-scope noted that targets sometimes maintained a certain separation

Table 1 Pairs of targets in November 1974

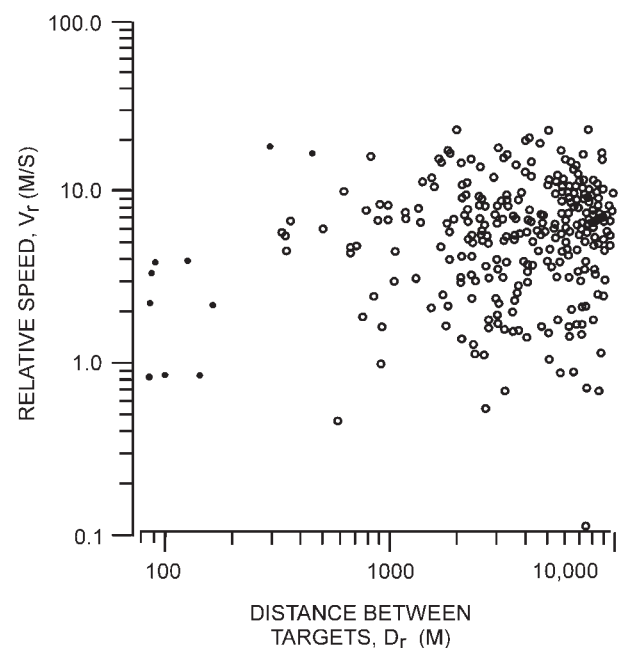| Date | Number of pairs of tracks | | P | |
	D_r 0–250 m	D_r > 250 m	V_r	Height
November 2	0	197		
November 7	7	76	0.055	0.010
November 9	1	193	0.048	0.056

Fig. 3 Relative speed of two targets, V_r, as a function of distance between the targets, D_r, for all tracks on the night of November 9, 1974, plotted on log–log axes. The darkened circles indicate pairs of targets selected by the radar operator as possible parallel targets. Pairs with low values of V_r are a small proportion of the observations except when D_r is less than about 250 m.

Table 2 Descriptive statistics of tracked targets

	November 1974		1980s		
	$D_r > 250\,m$	$D_r < 250\,m$	Vertebrates, $D_r > 250\,m$	Vertebrates, $D_r < 250\,m$	Small arthropods
Fitted segments, mean (SD)					
N	15[a]	7	348	15	24
Duration (s)	26 (21)	30 (23)	44 (40)	43 (47)	35.8 (17)
Number of points per track	25 (18)	23 (14)	34 (27)	43 (43)	34 (17)
Length (m)	515 (429)	646 (479)	609 (525)	171 (157)	576 (366)
Standard error of fit (m)	0.91 (5.46)	0.87 (0.84)	0.25 (0.24)	0.27 (0.21)	0.12 (0.09)
Pairs of targets separated by <10 km					
N	62	7	348	15	24
Median V_r (m/s)	7.53	3.14	5.87	1.33	3.18
Median air speed (m/s)			10.39	8.62	2.87

[a]These descriptive statistics were not calculated for the 47 targets measured from photographs.

in range while being tracked, further suggesting that the targets were flying together (see "double target" in Supplementary Material). Separations of 60–120 m were noted but the temporal course of changes in the distance between targets, if any, could not be recorded.

Parallel birds in the 1980s

On the basis of the data from 1974 (Fig. 3), we used 250 m as the maximum separation of parallel targets in analysis of the data from the 1980s. Segments were generally well fitted by straight lines (Table 2). V_r of pairs of targets with $D_r < 250\,m$ was significantly slower than V_r of pairs with $D_r > 250\,m$ ($P = 0.0001$, $n = 15$). The significance of the V_r–D_r relationship (Fig. 4) maintained when a D_r of 250 or 300 m was used as the criterion for parallel targets. The reverse test was also significant ($P = 0.0001$) for D_r of pairs having $V_r > 2.5\,m/s$ compared with those below that value. Correlation of D_r with absolute difference in height of members of a pair was negligible ($R^2 = 8 \times 10^{-4}$).

There was some evidence of similarity in type of wing beat among members of a pair. Eleven of the 15 parallel targets also shared the same categorical type of wing beat, a nonsignificant result ($P = 0.067$) compared with more distant pairs using Fisher's Exact Test. As seen in Fig. 5, wing beat frequencies of members of a pair of parallel targets were never dissimilar (again, not significant; $P = 0.22$, one-tailed test). Of the 30 pair-members of parallel targets, 28 showed discontinuous flapping (the categories "intermittent flap-coast," "flap-coast," or "pause") and two flapped steadily without interruption.

Pairs of small arthropods serving as controls (markers of local wind) were >390 m apart (Fig. 6). Small arthropods were not parallel; their median V_r
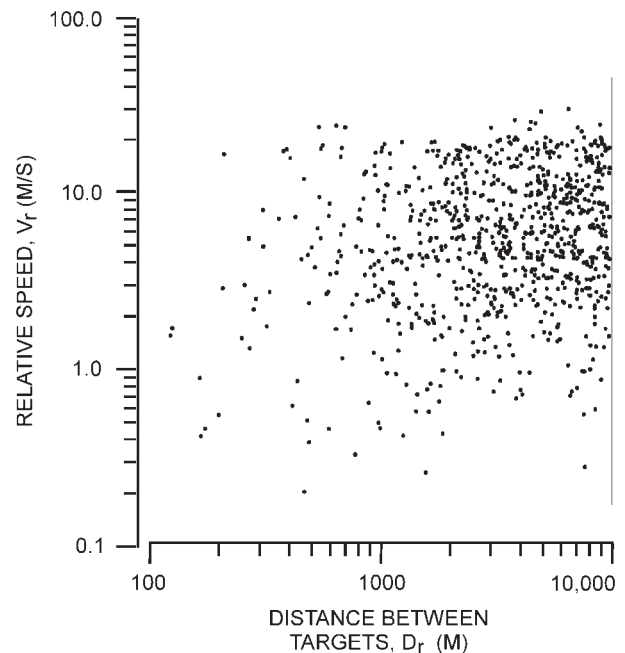

Fig. 4 All pairs of targets in the 1980s meeting the selection criteria (see Methods section), plotted as in Fig. 3 except that axes differ. As in Fig. 3, pairs separated <250 m show low values of V_r.

(Table 2) was 2.4 times the median V_r of parallel vertebrates ($P = 0.005$). When balloon-measured differences in wind for small arthropods were subtracted, their median V_r, 1.81 m/s, was still greater than V_r of parallel vertebrates. Like that of vertebrates, small arthropods' correlation of D_r with height was negligible ($R^2 = 3 \times 10^{-6}$).

Telescopic observations in 1982–1987 revealed that, of 209 vertebrate targets, 14 (6.7%) consisted of a compact flock of >1 animal. Observers with binoculars reported the same result (6.9%). Almost all the animals in such visually observed groups were
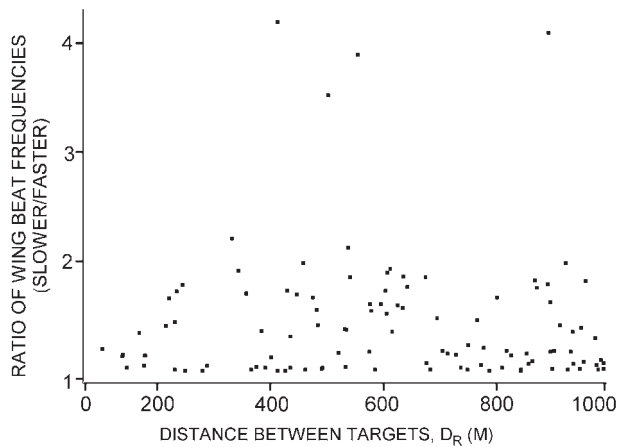
Fig. 5 Ratio of wing-beat frequencies between members of pairs of targets within 1000 m of each other. Wing-beat frequencies of pairs with D_r <200 m do not differ by >1:1.36. The distribution of ratios of wing-beat frequency beyond 1000 m was not different from that shown. Data from 1980s.
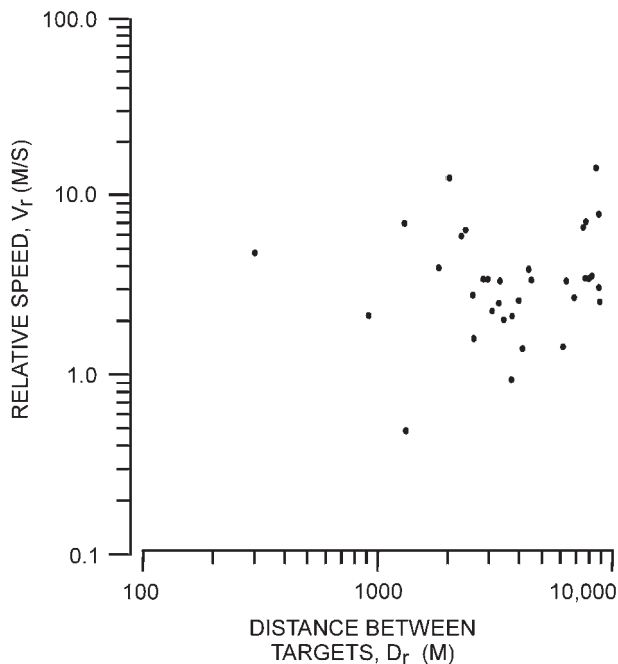

Fig. 6 Pairs of small arthropods (mostly, or entirely, insects) plotted as in Figs 3 and 4 except that the axes differ. These nearly passive, wind-borne targets do not show low values of V_r.

seen to be flying in the same direction and keeping together. None were parallel targets. They stayed within about half the 1.1 field of view of the 40× telescope, in the azimuth-elevation plane at radar-measured distances of 334–965 m, or <3–9 m apart. Six of these 14 compact flocks were observed visually during a 28-min period beginning at 1958 CDT on May 10, 1984. They appeared to be shorebirds; observers reported 5–20 birds "tightly bunched,"

"dark, pointy wings," "flying in a line," and "guessing plovers." If this cohort of shorebirds is excluded from the tally, 3.9% of the radar targets were confirmed visually to be compact flocks of >1 flying animal.

Radar cross-sections of parallel vertebrate targets were measured separately at different angles and consequently the two members of parallel-target pairs were irradiated by the radar beam from quite different aspect angles ($\bar{\times}39°$ difference in 2D angle of aspect). Their sizes were not significantly more similar to each other than were those of nonparallel pairs up to 10 km distant ($P = 0.23$).

Discussion

The 3.9% of vertebrates that were visually observed to fly in compact flocks at night in 1982–1987 (excluding one pulse of putative shorebirds) slightly exceeds the 2.4% previously reported for 1975–1978, Larkin and Thompson 1980), but is still a tiny minority. Certainly, factors responsible not only include better optics, but also possible differences among species (e.g., shorebird flocks) and geographic locations. As previously mentioned, individuals within such tightly spaced flocks could never be resolved with the radar as trackable targets.

The taxonomic identity of radar targets is seldom a simple issue. In this study, the data from November 1974 strongly suggest that radar targets were not migrating bats. Telescopic visual observations of some targets, wing beats, and estimates of size from radar provided multiply confirming evidence in most cases that migrating birds could be distinguished from migrating arthropods (mainly insects, Larkin 1991). Wing beat patterns of parallel targets in data from the 1980s were overwhelmingly those of small birds such as passerines. Moreover, although birds can communicate with one another across tens of meters (or farther) at night, it is unlikely that insects can do so. Hereafter, we use "birds."

Aggregations are observable with the A-scope on the radar equipment used in this study, but only if individual members are spaced at least 17 m apart in range so that they appear as separate peaks distributed along the narrow radar beam. Such aggregations offer some support that birds may fly together in loose flocks. Nearby avian targets on the A-scope sometimes kept in approximate relative position as one bird was tracked by the radar; however, the A-scope traces could not be quantified with the instruments used in this work.

The data from tracking agreed with the A-scope observations, revealing aggregations of parallel birds spaced <250 m between individuals. As with the A-scope observations, birds spaced closer than a minimum distance (about 17 m for tracking) could not be distinguished. Wing beats of parallel birds were suggestively more similar than expected by chance. Differences in radar aspect precluded detailed comparison of radar-estimated size of these targets. Low values of V_r for parallel birds were not an artifact of targets advected by the same wind simply because they were at the same height.

Slowly flying small arthropods (mainly insects) became dispersed from one another faster than did parallel vertebrates, even when locally measured wind was taken into account. Those results show that a population of almost-passive targets do not appear to travel together as parallel targets, implying rejection of small-scale atmospheric motion (Larkin 1982) as an explanation for "bunched" radar targets. Furthermore, there is no indication from the data (for instance unfilled circles in Fig. 2) that distance between birds separated by >250 m has any relationship to their relative speed. At scales exceeding that of parallel birds, changing winds, or bird behavior does not produce a tendency toward parallelism. On this basis, atmospheric motion at scales of >250 m is unlikely. Something special happened at a scale of <250 m.

Relative speed, V_r, has at least three components: true linear divergence (which is hypothesized to be zero over the long-term for cohesive social flocks of birds), radar and other inaccuracy in the observations and linear fits, and short-term fluctuations as a result of birds not flying perfectly straight at constant ground speed. Certainly, inaccurate tracking data inflated the values of relative speed in this study, especially in 1974. In addition, even if one overlooks the simple geometrical reality that "straight" paths are actually a Great Circle, the applicability of fitted linear functions to describe migratory flight is scale-dependent, even over a portion of a night's flight. Assuming that migrants have imperfect sensory systems that are imperfectly integrated, they need to correct their course at least occasionally (Nams 2005). Further, flight speed varies as animals use chemical energy and according to mode of flight (Rayner 1999). Therefore, one expects heading, track, air speed, and ground speed to vary for each migrant. If that expectation is correct, almost no short segment of a night's migration constitutes a really accurate estimate of a bird's long-term speed or direction of flight. In fact, for animals in cruising flight that are observed on radar to rise or fall gradually, this must be the case (Larkin and Thompson 1980). The results reported here suggest paths that are straight only when considered at a large-enough scale and are maintained by corrections of course *en route*. A certain amount of variation is expected for any single flying animal. Consequently, short-term observations of two animals flying together may be expected to show a low, but nonzero, relative speed between them. Perhaps more importantly, the means by which loose flocks of animals migrating at night communicate their relative position to one another is probably intermittent and imperfect (Hamilton 1962).

Functions of flocks are reviewed by (Alerstam 1990). At night, loose flocks may be an aid to orientation by pooling sensory information (Hamilton 1967; Tamm 1980; Thake 1981). In daytime in Europe, larger sizes of flocks under overcast conditions are posited to aid orientation (Rabol and Noer 1973). Similar flight speeds permit a group to cohere.

Another benefit is suggested by the observation that migrating birds select the height at which to fly on the basis of favorable winds (tail winds) (Bruderer et al. 1995). By attending to conspecifics at other heights and climbing or descending toward those that make faster progress, a bird could find an energetically more favorable height at which to fly.

Too few groups of parallel birds were documented on any one night to usefully compare their directions of flight with targets not observed to be in parallel flight. In addition, the radar equipment used in these studies is a very narrow window pointed into the sky. Because of the slender beam, an unknown number of birds may fly parallel to a certain tracked bird without the radar operator necessarily being aware of their existence. Any tracked bird in the study may have been part of a social group.

Pencil-beam tracking radar as used in this study reveals the existence, but not the prevalence, of loose flocks of birds at night. As contrasted with birds in compact flocks commonly seen during daytime and perhaps shorebirds and waterfowl at night, members of loose flocks are widely separated from one another. Judging by their wing beats and radar-measured sizes, these parallel targets were small birds, mainly songbirds. These radar observations substantiate previous indirect and anecdotal reports that songbirds engage in social grouping in the dark during long-distance migration though the physical structure of these groupings can be quite different from flocks observed in daytime.

Supplementary data

Supplementary data are available at ICB online.

Acknowledgments

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