

A tracking radar at Wallops Island, Va. (N.A.S.A.). The large telescope behind the antenna was used to identify birds detected by the radar.

Autumnal bird migration over the western North Atlantic Ocean

A radar network observes birds on a 3000-km nonstop flight from North to South America

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Introduction

SINCE THE EARLY VOYAGES of Columbus (Morrison, 1955), ships crossing the western North Atlantic in autumn have reported sighting large numbers of passerines and shorebirds migrating from eastern North America to the Caribbean and South America. Bird banding studies, surveys of species distribution, and observations on Bermuda indicate that several species of shorebirds use this route (Hurdis, 1897; Lincoln, 1939; Dorst,

1961; Hager, 1966; Palmer, 1968; McNeil and Burton, 1973). Although it has been generally assumed that passerines move southward along the eastern North American coast, many passerine species have been seen from ships in the North Atlantic (Scholander, 1955,

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Teal and Teal, 1975) and on Bermuda (Hurdis, 1897, Wingate, 1973). Drury and Nisbet (1964) and Nisbet (1970) report that the Blackpoll Warbler (*Dendroica striata*) makes long over-water flights between North America and its wintering ground in South America, although this has been disputed by Murray (1965).

With radars it has been possible during the last two decades to quantify extensive bird migrations over several large bodies of open water. Many observers report movements crossing bodies of water near Great Britain and Europe (Lack, 1959, 1960, 1963a, 1963b; Evans, 1966; Myres, 1964; Alerstam *et al.*, 1973, see also Eastwood, 1967). In North America studies have been done in the Canadian Maritimes by Richardson (1972a), on Cape Cod by Drury and Keith (1962), Drury and Nisbet (1964), and Nisbet and Drury (1967), across the U.S. Gulf Coast by Gauthreaux (1971), and Able (1973, 1974), on the Virginia coast by Williams *et al.* (1972), and over the Bering Sea by Flock (1973). Myres and Apps (1973) report extensive migration over the China Sea.

A few observations of bird migrations have been made from radars located on ships or islands: Casement (1966) from an aircraft carrier in the Mediterranean; Adams (1962) from Cyprus; Hilditch *et al.* (1973) from Antigua (W. I.); Richardson (1975, 1976) from Puerto Rico; Williams *et al.* (1972) and Ireland and Williams (1974) from Bermuda.

ALL THESE RADAR OBSERVATIONS revealed large numbers of birds moving over water. With few exceptions birds appeared to cross coastlines with no detectable deviation in course and did not tend to depart a coast from a single point or promontory; instead "broadfront" migration moved out to sea from all points along the coast. The heaviest departures of migrants from coastal sites were seen at night when winds were favorable for the preferred direction of migration. For autumnal departures from the eastern coast of North America, the heaviest south and southeast departures usually followed the passage of a cold front with associated northwest winds (Drury and Keith, 1962; Swinebroad, 1964, Nisbet and Drury, 1968; Williams *et al.* 1972, and Richardson, 1972a).

Many studies (see review in Eastwood,

1967) have raised the question of whether most birds are drifted offshore by strong winds or whether birds actively set a seaward course. The shoreward reorientation of offshore birds at sunrise (Baird and Nisbet, 1960; Myres, 1964; Richardson, 1972a) has usually been interpreted as an attempt by birds to regain land. Murray (1965 and 1976) concludes that all North American passerines seen over the Atlantic are drifted offshore and do not regularly migrate over the ocean.

All long term radar studies report great variability in the direction, speed, altitude and average radar echo size of overwater migrants indicating a complex pattern of migration by many different species. Despite this seasonal variability, patterns of migration over the sea at any one site on any one night appear relatively homogenous, usually consisting of only one or two types of movements (see especially Drury and Nisbet, 1964).

Previous studies have concentrated on long term observations at a single site. We have made simultaneous observations at several sites on the North American coast, on Bermuda, in the Caribbean and with radars on ships cruising the North Atlantic, in order to observe the departure, *en route* flight and arrival of birds on a major overwater avian migration route.

Methods

TO ALLOW COMPARISONS between radars we have used narrow beam radars whenever possible rather than search radars designed for military surveillance or air traffic control (see Eastwood, 1967 for a discussion of types of radars). Narrow beam radars survey only a small portion of the airspace at any one time, but because their radar beam can be tilted upward as well as rotated in compass direction (azimuth), they can be used to estimate the altitude of birds.

Table 1 gives the types of radars used at each site for each year of study. A brief description of each radar and references giving a more complete description are given below. "Range" is the maximum usable range for birds of each radar. Values for beamwidth are measured at the half power points.

Table 1. Locations and types of radar used in this study

Location	Year					
	1969	1970	1971	1972	1973	1974
Halifax					ASR-5	
Cape Cod	FPS-7	FPS-7	ASR-5 WSR-57	WSR-57		
Wallops I.	SPANDAR	SPANDAR	MPS-19 FPS-16		FPS-16	
Miami					WSR-57	
Bermuda	FPS-16 FPQ-6	FPS-16 FPQ-6	FPS-16 FPQ-6	FPS-16 FPQ-6	FPQ-6	
Antigua		FPQ-6	FPQ-6 RC-32-B	RC-32-B	RC-32-B	
Barbados					RC-32-B	
Tobago					RC-32-B	
Ships			AN/MPQ-29	AN/MPQ-29	R1640	D808

Search radars: (cannot determine altitude of birds)

FPS 7—a military surveillance radar; 23 cm wavelength, 8 MW (megawatt) peak power, North Truro Air Force Base, Mass. Range 180 km.

ASR 5—air traffic control radar; 10 cm wavelength, 400 kW (kilowatt) peak power (Richardson, 1972b), located at Otis Air Force Base, Mass., and Halifax International Airport, Nova Scotia. Range 20 km.

R 1640—marine radar; 3 cm wavelength, 40 kW peak power (Raytheon marine radar dealers can supply additional information). This radar, located on the R/V *Knorr*, probably did not detect birds flying above 600 m. Range 2 km.

D 808—marine radar; 3 cm wavelength, 75 kW peak power (Decca marine radar dealers can supply additional information). This radar, located on the R/V *Atlantis II*, probably did not detect birds flying above 600 m. Range 2 km.



The N.A.S.A. station at Bermuda. Photos/T.C. Williams

Narrow beam radars:

WSR-57—a meteorological radar; 10 cm wavelength, 500 kW peak power, 2° beamwidth (Gauthreaux, 1970) Cape Cod station located at Chatham, Mass. Miami station located at Coral Gables, Fla. Range 50 km.

RC-32-B—a meteorological radar very similar to the WSR-57; 10 cm wavelength, 500 kW peak power, 1.9° beamwidth (additional information available from the Mitsubishi Electric Corp.). Located at Coolidge Airfield, Antigua; St. James, Barbados; Crown Point, Tobago. Range 50 km.

SPANDAR—a long range tracking radar; 10 cm wavelength, 3.8 MW peak power, 0.39° beamwidth (Williams and Williams, 1972). Located at Wallops Island (NASA), Va. Range 100 km.

FPS-16—an intermediate range tracking radar; 5 cm wavelength, 1 MW peak power, 1.2° beamwidth (Williams and Williams, 1972). Located at Wallops Island (NASA), Va. and Cooper's Island (NASA), Bermuda. Range 80 km.

FPQ-6—a long range tracking radar; 5 cm wavelength, 3 MW peak power, 0.4° beamwidth (Williams and Williams, 1972) located at St. George's, Bermuda and Collidge Field, Antigua. Range 110 km.

MPS-19—a short range tracking radar; 10 cm wavelength, 400 kW peak power, 3° beamwidth (Williams and Williams, 1972), located at Wallops Island (NASA), Va. Range 30 km.

AN/MPQ-29—a short range tracking radar; 3 cm wavelength, 40 kW peak power, 3° beamwidth (Griffin, 1973). On board the R/V *Atlantis II*. Range 2.5 km.

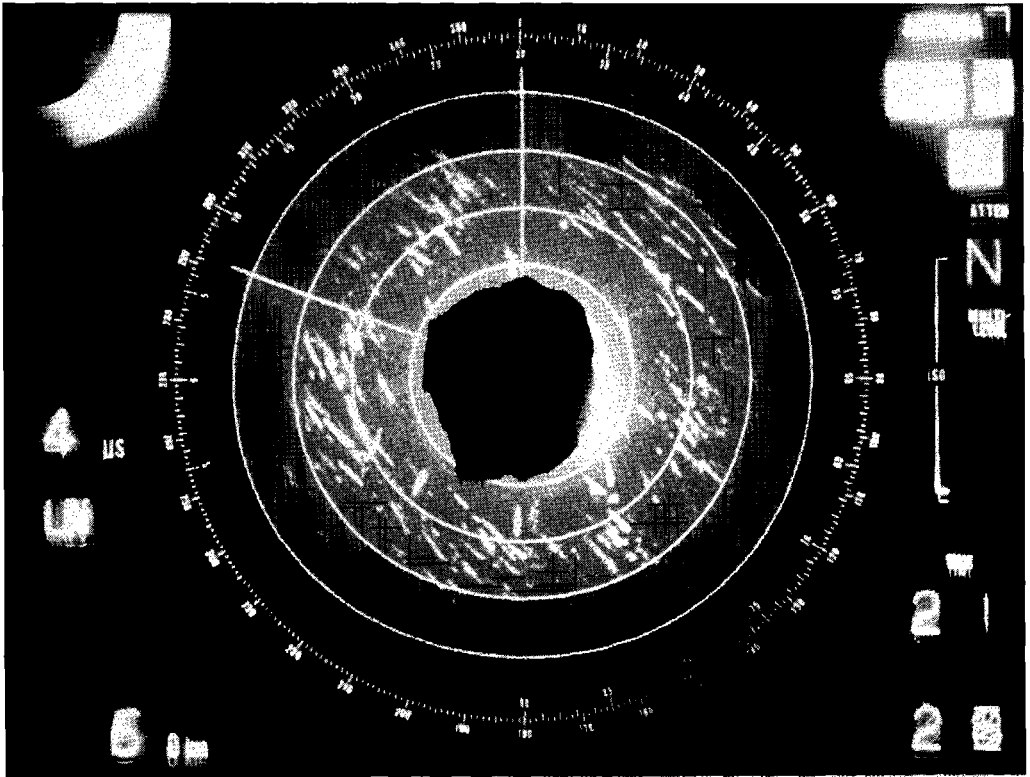


Figure 1. Time exposure of a PPI display showing heavy bird migration over Antigua 2123 GMT October 16, 1971. North is toward the top of the figure. Concentric rings are range marks at 5 km intervals. Birds produce streaks about 3 km long followed by a space and then a dot indicating the direction of movement, in this case toward the southeast. The narrow radar beam was directed upward at an angle of 7° when this photograph was made and thus the altitude of a bird on the photograph is directly related to its distance from the radar. Note that there are very few birds at less than 12 km range indicating high altitude (4 to 6 km) migration. The center of the PPI display has been blacked out with tape to prevent overexposure by the very bright echoes from land and ocean waves at less than 8 km range.

BIRDS ARE DISPLAYED by these radars as small, slowly moving dots on the Plan Position Indicator (PPI) screen of the radar. In order to record the movement of these small dots we made time exposures of the PPI screens with Polaroid film as shown in Figure 1. In most cases we used a time exposure of 3 to 10 minutes as described in Gauthreaux (1970) or Williams and Williams (1972). Slowly moving targets, such as birds, produced streaks on the film which were used to determine the direction, speed of movement, and density of migrants.

Altitudes of birds were determined with narrow beam radars by comparing photographs taken at different angles of elevation.

Altitude was computed from range, angle of elevation, and correction factors for curvature of the earth and index of refraction of the atmosphere.

Tracking radars were also used to obtain detailed information on the paths of migrants as described in Williams and Williams (1972), but for the present report these data were used only to determine the density and direction of bird movements when PPI data were not available: ships 1971 and 1972, Bermuda 1971 and 1973, and some days at Wallops Island 1971.

Over 1700 PPI photographs were scored by the first author on a relative 4 point density

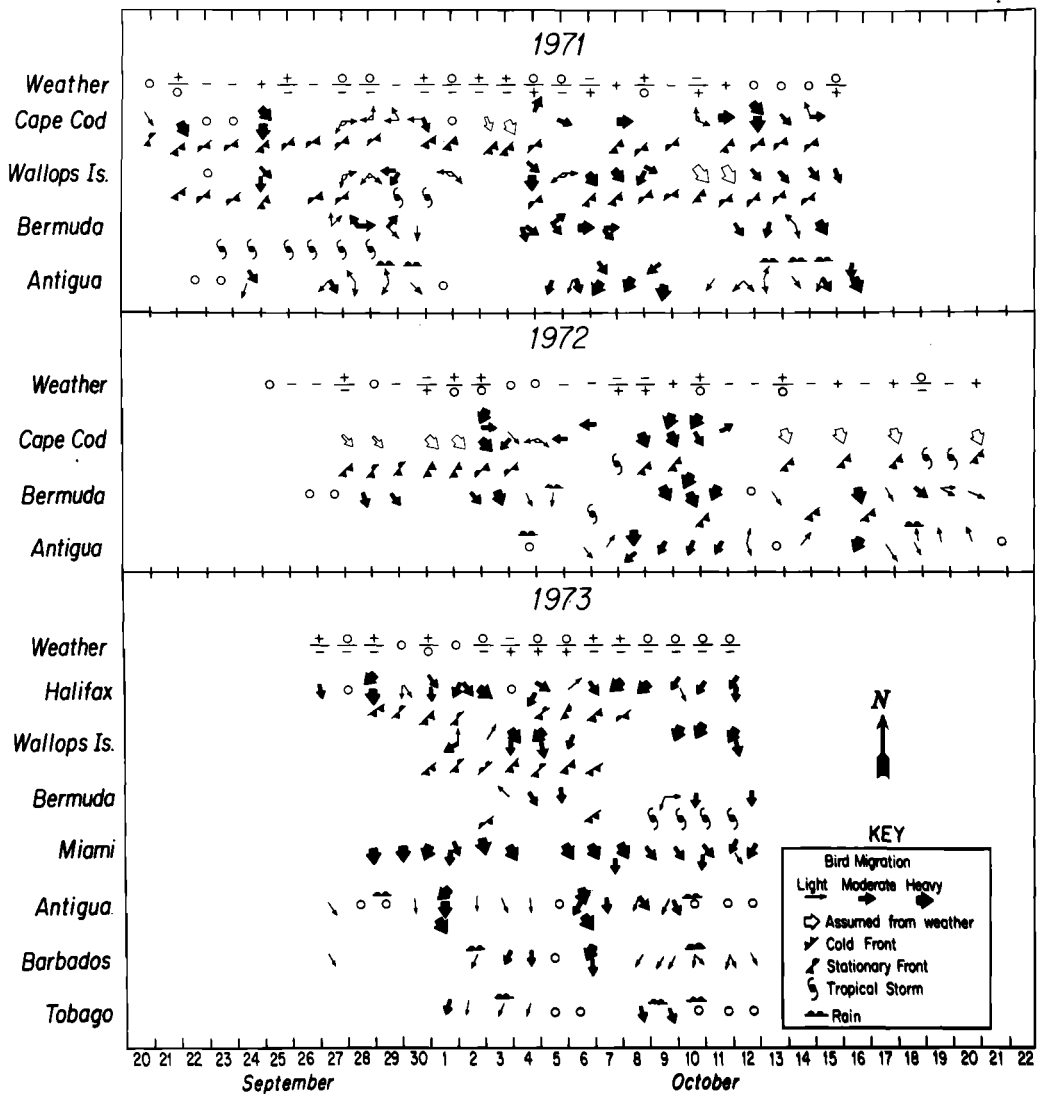


Figure 2. Average (V_g) direction and density of bird migration over the North Atlantic Ocean as detected by radar. Light, moderate, or heavy migration is indicated by the width of the arrow. An O indicates no significant migration. Direction of arrows shows the average direction of the most dense movement(s) seen during an 8 hr observation period. An arc between two light arrows indicates targets were spread between these directions. Weather symbols indicate prevailing frontal conditions between northern sites, and the presence of widespread rain (tropical depression) at Caribbean sites. Rows labeled "weather" indicate the suitability of weather conditions along the North American coast for departures of migrants: + indicates weather favorable for departure (north winds, recent passage of a cold front), - indicates unfavorable conditions (south winds, cold front approaching, rain), and O indicates no clear advantage or disadvantage (stable high pressure system, light and variable winds). The symbol \pm indicates favorable conditions on the northern part of the coast and unfavorable on the southern part.

scale (no movement, light, moderate, heavy) established for each radar. Detailed absolute comparisons between different radars are unreliable (see Eastwood, 1967; Gauthreaux, 1970; and Richardson, 1972b); thus, neither a more precise scale nor a single scale for all radars was used.

The direction of migration was estimated to $\pm 10^\circ$ by inspection of the PPI photographs for each hour of observation. Since two or more types of bird migration may occur at once, we did not average the directions for all birds but selected the direction(s) having the largest number of tracks, i.e., the modal direction(s).

U.S. Weather Service charts of the northern hemisphere were used to obtain surface weather conditions over the Atlantic. Information on the winds aloft were obtained from radiosonde weather balloons launched within 5 km of the radar sites we used (except at Tobago where the radiosonde station was located 40 km to the southwest on the island of Trinidad). In almost all cases these wind measurements were made within four hours of our radar observations.

The movement of birds as detected by radar (or an observer on the ground) is the sum of two velocities: the velocity of the bird through the air (abbreviated V_a) and the velocity of the air mass over the earth, i.e., the wind (abbreviated V_w). In order to determine the actual direction in which a bird was orienting its body and the speed with which it was moving through the air ($=V_a$), we obtained the apparent velocity from the PPI photographs (V_p) and subtracted the velocity of the wind (V_w) using the conventional techniques of vector subtraction. In the terminology of airplane pilots, V_a is airspeed and heading, V_w is windspeed and wind direction, and V_g is groundspeed and track.

At most radar sites we were able to observe for 6–8 hours per day. At Halifax, Cape Cod, Wallops Island, and Miami, observations usually began shortly before local sunset and continued until midnight (2000 to 0400 GMT). Most observations at Bermuda were made between 0800 and midnight (1200 to 0400 GMT) with less than 10% of all observations being made at other times.

Radars in the Caribbean operated only from 0800 to 1600 local time (1200 to 2000 GMT).

On three occasions radar operators were kind enough to operate at night for our benefit. At all sites observations were interrupted by equipment failures or higher priority projects. At Wallops Island, Bermuda and the Caribbean sites, observations were not usually possible on weekends or holidays. Dates of observations at all sites for 1971, 1972 and 1973 are given in Fig. 2. Observations on the ships were continuous except for equipment failures.

Daily bird counts, with the use of binoculars, were taken on Antigua in the fall of 1970, and on Antigua, Barbados and Tobago in the fall of 1973 during the period of the radar observations. Daily observations of any birds seen on or near the ship were made each fall (1971, 1972, 1973, 1974), with binoculars and in some cases the ship's spotlight.

Results

FIGURE 2 PRESENTS all the data we gathered on the direction and density of bird migration during the last three years of our study. Even when presented in this simplified form, the patterns of migration are complex and difficult to discern. Much of this paper will be devoted to the analysis of the data presented in Fig. 2. First, we will consider the patterns of direction of migration taking the western North Atlantic as a whole, and then consider other information from our radar observations such as altitude and V_a (airspeed) of the birds. This leads to the problem of identifying birds detected on radar and finally to a brief discussion of the dangers encountered by birds *en route*.

Patterns of Migration

FIGURE 3 SHOWS the locations of the radars we used in the study, the number and direction of moderate and heavy migrations observed at each site and the direction of moderate and heavy migrations observed from ships at sea.

Radar observations, like the previous visual observations of birds, suggest that there are two different routes by which birds reach the Caribbean and South America. Inspection of Figs. 2 and 3 shows three general types of movement at the three northern coastal sites

movement out to sea (SE), movement along the coast (SW), and "reverse" movements to the west, northwest, and northeast. Coastal migration was strongly influenced by local weather conditions as may be seen from the weather summary in Fig. 2. "Reverse" movements occurred with south or east winds, and departures to sea or along the coast were associated with north or northwest winds following the passage of a cold front. The importance of cold fronts in initiating departures from Cape Cod and the Canadian Maritime Provinces has been documented by Nisbet and Drury (1968) and Richardson (1972a). In our data, departures not associated with the passage of a cold front tended to be moderate movements along the coast occurring under stable high pressure conditions ("0" in Fig. 2).

Observations at Miami indicated almost continuous southeast movements (see Fig. 2) and suggest that a large percentage of the birds reaching the Caribbean move southwest along the eastern coast of North America and then southeast along Florida and the chain of Caribbean Islands (Williams *et al.*, 1977). Richardson (1976) also reports that most birds approach Puerto Rico from the west and northwest (along the greater Antilles) rather than from the Atlantic (N and NE).

COLD FRONTS WHICH TRIGGER departures from the eastern North American coast rarely penetrate the North Atlantic beyond Bermuda. Instead, these weather systems become stationary, producing a band of cloudiness with locally turbulent wind conditions stretching more or less parallel to the coast 500 to 1000 km offshore. Beyond this stationary front the winds are usually light but contrary (south or east). As shown in Fig. 2 birds penetrate the frontal zone and continue their course to reach Bermuda (October 7, 1971, September 29, October 2, 9, 10, 16, 18, 1972, and October 4, 1973; also four cases in 1969 and 1970).

As shown in Fig. 3 most birds arrive over Bermuda from the northwest, presumably from the northern U.S. coast, but significant numbers also arrive from the west and the northeast suggesting arrivals from the central U.S. coast and Canadian Maritimes.

On eight occasions the ships passed through a frontal system between the U.S. coast and

Bermuda. The majority of birds found ahead of the front were moving to the south and east, but in five cases many birds were also seen just behind the cold front. These birds showed widely scattered directions and were flying very slowly (V_a less than 22 km/hr, see McClintock *et al.*, in prep.).

Observations from the ships revealed no significant tendency for certain migration directions to be grouped in any single area of the North Atlantic. Southeast movements were found to continue at least 1000 km east and 800 km south of Bermuda, and 2000 km from the North American coast.

The primary direction of migration observed at coastal sites, on Bermuda, and from the ships is to the southeast. At Antigua the predominant V_g direction is to the southwest (see Fig. 1). From these data we conclude that the average V_g direction of Atlantic migrants must shift to the west in the area of the Sargasso Sea, as is suggested by the two most southerly observations from ships in Fig. 3. Our present data indicate that this change could be entirely owing to birds encountering the strong easterly trade winds in this area, rather than to active reorientation by the birds. If we subtract the effects of the wind from the directions observed at Antigua we see that the birds moving southwest (V_g direction between 170° and 360°) are actually flying southeast ($V_a = 163^\circ \pm 34^\circ$, 34° being the angular deviation as described by Batschelet, 1965). This direction is very close to the V_a for birds moving southeast over Bermuda ($V_a = 143^\circ \pm 28^\circ$). Thus, *birds could accomplish the crossing of the ocean by maintaining a constant southeast flight direction from the time they left the North American coast until they reached South America*. They would actually travel in a curved route first southeast to the Sargasso Sea and then southwest after they penetrated the area of the northeast trade winds.

Birds did not appear to pay any attention to Bermuda or Caribbean islands as they flew over them. They did not appear to land since there was no significant difference in the density of birds moving toward vs. away from the islands and there was no observable tendency for birds to turn toward or away from islands (see also Williams *et al.*, 1972, Hilditch *et al.*, 1973; Ireland and Williams, 1974; and Richardson, 1976).

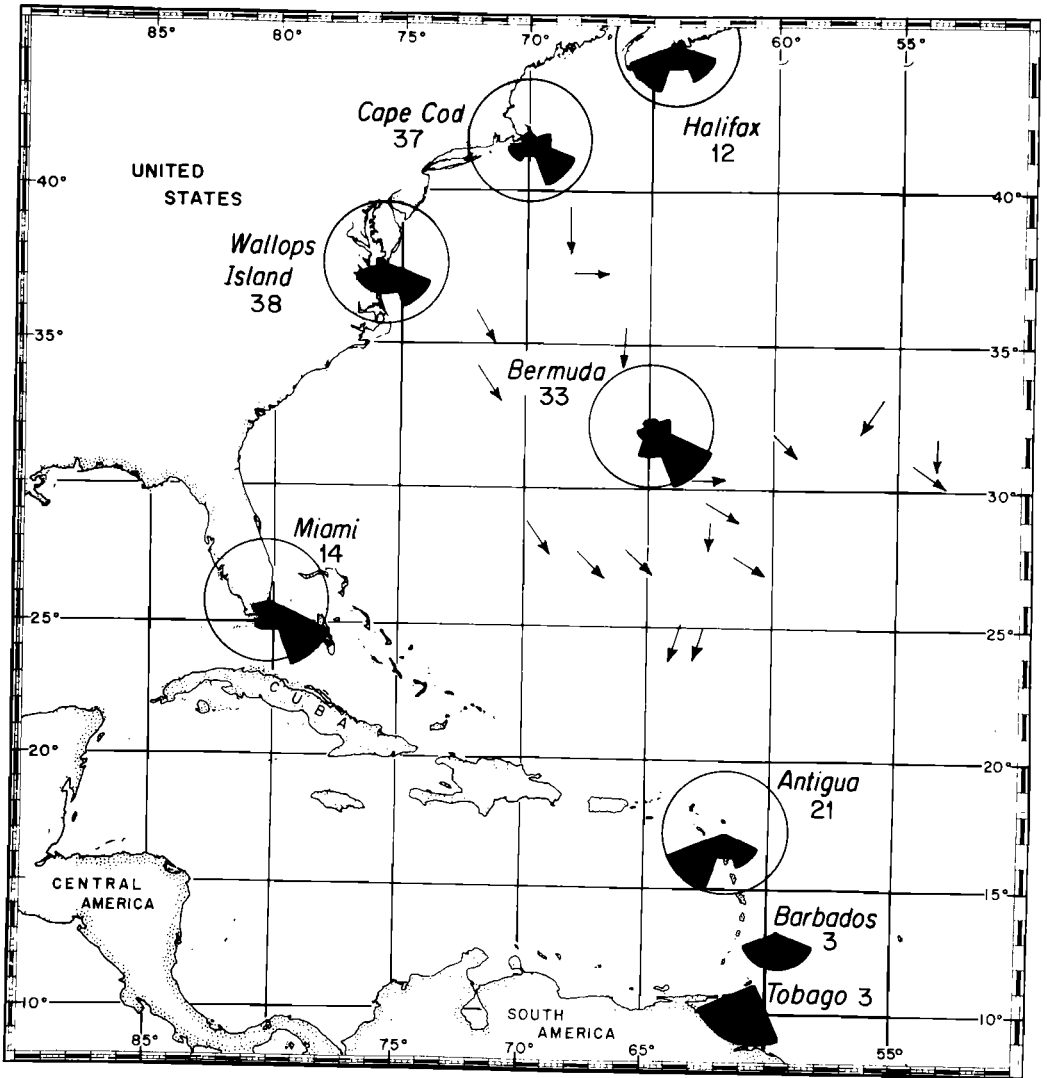


Figure 3. Map of North Atlantic Ocean showing radar sites and principal directions (V_d) of autumnal bird migration. Circular histograms at each radar site indicate per cent of moderate and heavy migrations with average directions in 8 compass sectors (ring indicates 50%; numeral indicates number of nights with moderate or heavy migration). Arrows at sea indicate daily average directions of moderate and heavy migrations observed with radars on ships.

Our observations suggest that birds moving over the Atlantic form relatively coherent patterns of migration over areas measuring several hundred kilometers in extent rather than spreading diffusely over the ocean from their point of departure.

Simultaneous observations from the three Caribbean radar sites revealed major differences in the density of migration which could not be ascribed to local weather or differ-

ences in the radars (see Fig. 2: October 4, 6, 8, and 9, 1973). The distance between Antigua and Barbados is 400 km and between Barbados and Tobago is 250 km. Simultaneous observations from the ships and from Bermuda also detected major density differences over distances of 250 km. These differences in density of migration persisted for a full day's observation and thus were not simply due to a large wave of migrants

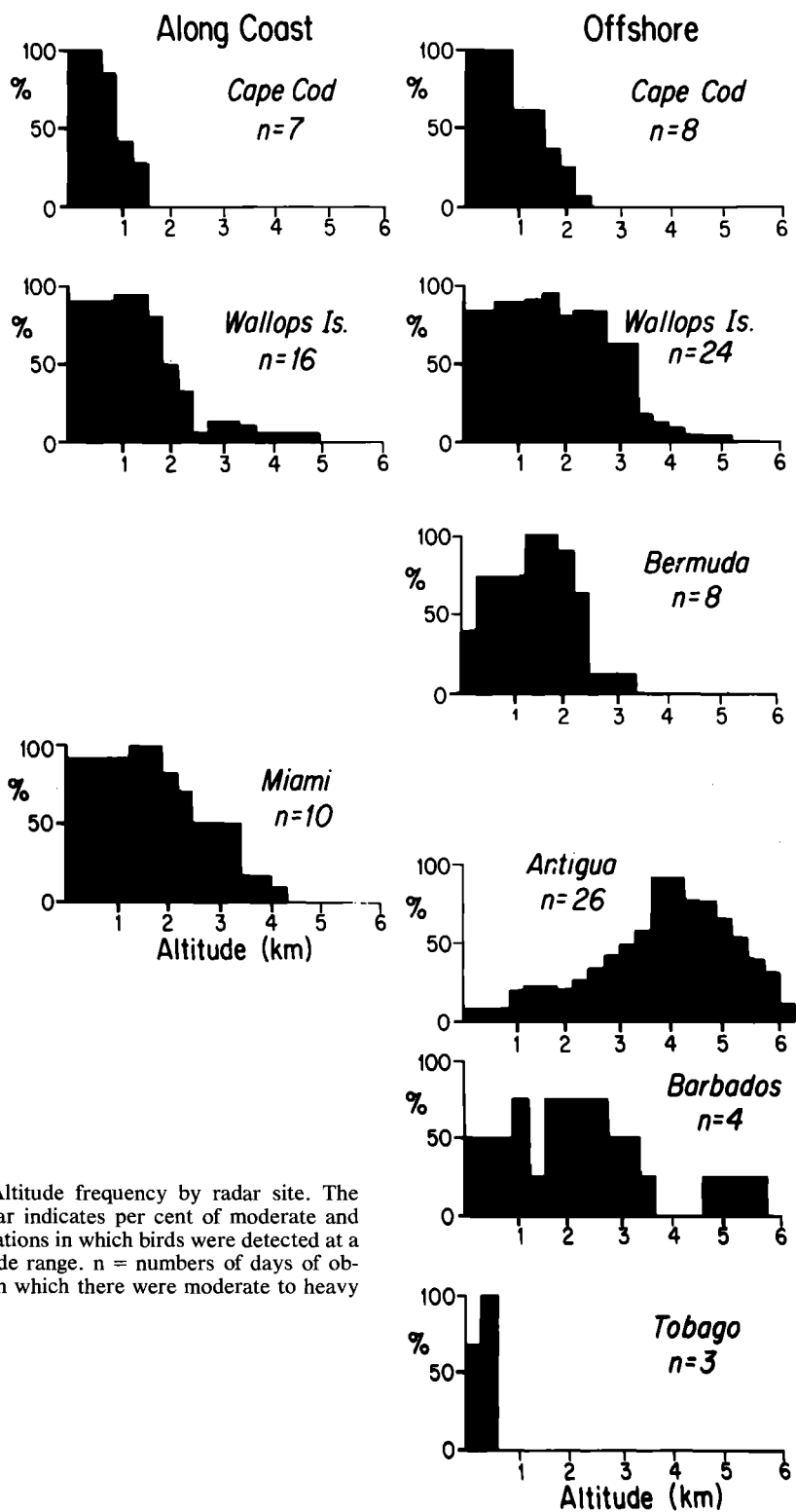


Figure 4. Altitude frequency by radar site. The height of bar indicates per cent of moderate and heavy migrations in which birds were detected at a given altitude range. n = numbers of days of observation on which there were moderate to heavy migrations.

requiring more time to reach one of the two radar sites. Rather we interpret these data as indicating relatively coherent groups of migrants passing one station but not extending to the next one. That such grouping of migrants persists after flights of 3000 km suggests that the birds in such migrations must share similar flight directions and speeds and perhaps some means of communication.

Altitude

THE ALTITUDE OF MIGRATION at all sites except Halifax (where we lacked a height-finding radar) is shown in Fig. 4. At Cape Cod, most migrants were below 2 km although Nisbet (1963a) and Richardson (1972a) report some birds at altitudes up to 6 km. At other coastal sites and Bermuda we detected targets at altitudes up to 5 km, but the bulk of migrations was still below 2 km. Antigua shows a very different pattern; most migrants there were above 4 km. Richardson

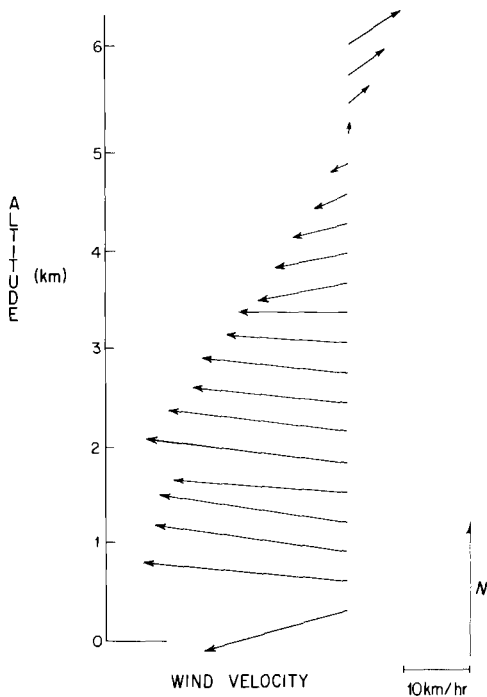


Figure 5. Wind velocity at Antigua vs. altitude. Average wind velocity at Antigua, W.I. for the 10 days with average migration altitudes above 4.5 km. Winds determined by radiosonde at Antigua at 0800 GMT. Average ground direction of bird movements on these days was 159°. North (0°) is toward the top of the figure.

(1976) reports similar altitudes at Puerto Rico for 8 day and 6 night observations (our Caribbean data, with three exceptions, were all diurnal). At Barbados we detected only one high migration, two intermediate and one low migrations. In Tobago, birds were very low, the lowest of any site; presumably birds there were preparing to land.

The advantage of high altitude flight at Antigua is clearly shown in Fig. 5 which gives the mean wind velocity at 330 m intervals for all days having moderate or heavy migrations with an average altitude above 4500 m. Most migrants detected on these days were moving SE along the Antilles (average $V_g = 159^\circ$). Birds flying above 3 km on these days experienced relatively calm wind conditions and avoided the unfavorable easterly trade winds at lower altitudes.

Airspeeds

IN FIG. 6 calculated airspeeds (V_a) of birds at each radar site are divided into two groups: those moving away from the coast and those moving down the coast. Airspeeds of birds moving away from the coast (the second column of Fig. 6) show a progressively sharpening peak between 30 and 60 km/hr, suggesting the progressive loss of both the slowest and fastest birds *en route*. The airspeeds of birds moving down the coast (first column of Fig. 6) are more difficult to interpret, since we were unable to detect small, slow-moving birds during the heavy passerine migrations at Cape Cod and Wallops Island. Movements along the coast, however, show a greater range of speeds than do movements offshore (compare Miami and the Caribbean sites in Fig. 6), suggesting a greater number of bird species on coastal routes. In summary, analysis of airspeeds indicates a great variety of birds at coastal sites. As these birds move over the ocean, certain groups of birds are either lost or turn back to the coast. Although it is possible that the reduction in the spread of airspeed distribution which we observe between the coast and Antigua could be due to a change in flight speed of individual birds, this appears unlikely in view of the severe metabolic penalties exacted by avian flight above or below the optimum flight speed for a species (Pennycuik, 1969).

AIRSPEEDS

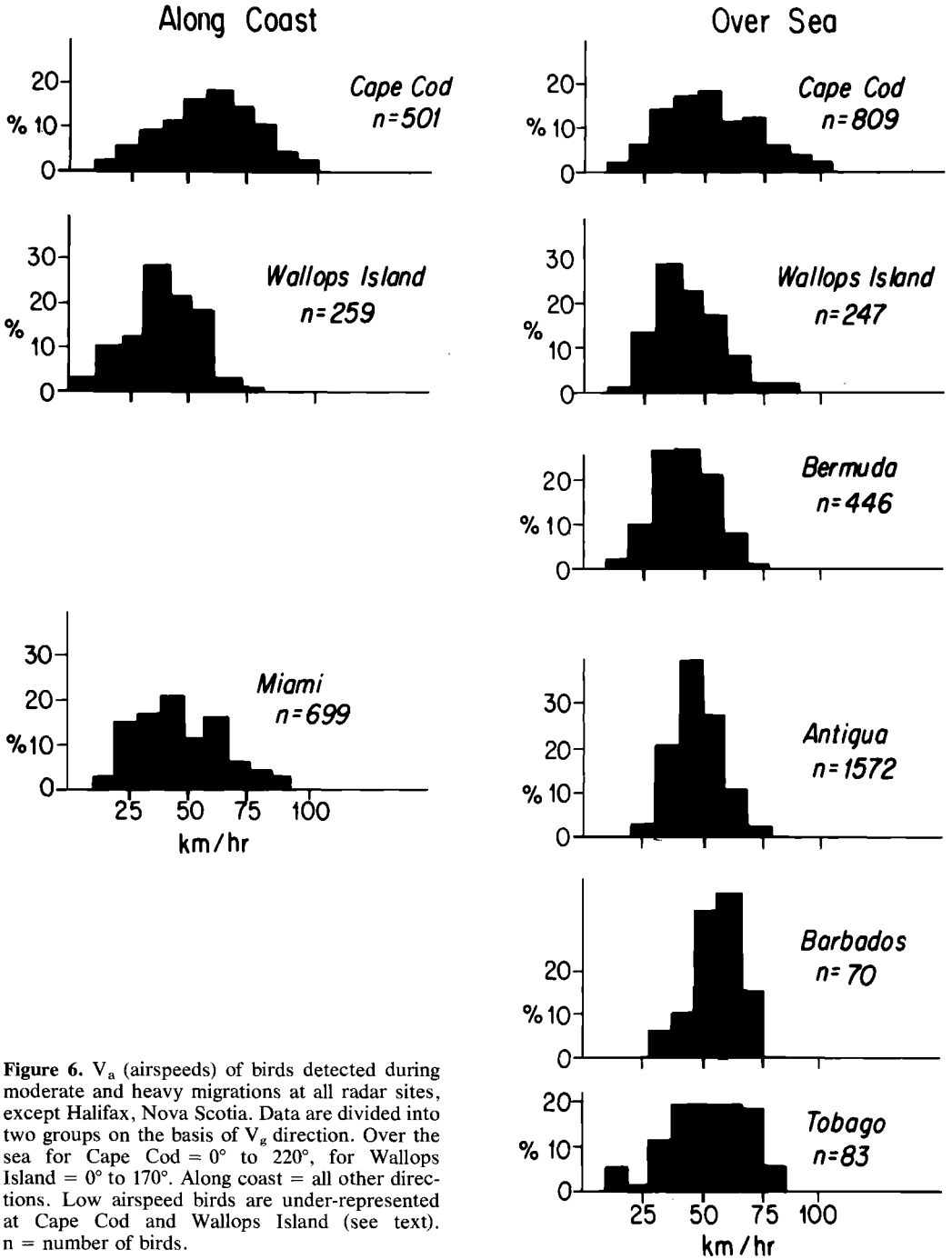


Figure 6. V_a (airspeeds) of birds detected during moderate and heavy migrations at all radar sites, except Halifax, Nova Scotia. Data are divided into two groups on the basis of V_g direction. Over the sea for Cape Cod = 0° to 220° , for Wallops Island = 0° to 170° . Along coast = all other directions. Low airspeed birds are under-represented at Cape Cod and Wallops Island (see text). n = number of birds.

Radar Identification of Migrants

WE WOULD very much like to know what species of birds we observe on radar. Both the airspeed and the appearance of the birds on the PPI display of a radar allow us to narrow the field of possible species, but neither will allow us to identify any individual bird we detect on radar. As mentioned above, the airspeeds of birds detected at coastal sites indicated a very broad spectrum of species; birds which successfully crossed the Atlantic appeared restricted to a smaller number of species. The airspeeds of these successful birds were between 30 and 60 km/hr (18 to 36 mph). These speeds seem too low for the rapidly flying migrants such as waterfowl or large shorebirds. Accurate data on the airspeeds of birds are not available, but measurements by Tucker and Schmidt-Koenig (1971) indicate that even sandpipers (*Calidris spp.*) fly at speeds of about 60 km/hr. Thus, the airspeeds indicate the presence of passerines and probably some of the smaller shorebirds.

Drury and Keith (1962), Drury and Nisbet (1964), Gauthreaux (1971), and Richardson (1972a) distinguish between two types of radar echoes. Dot echoes are persistent, bright, often fast-moving echoes which are believed to represent flocks of birds such as shorebirds and waterfowl. Passerine echoes are very fine, scintillating echoes which often appear as a fine mist on the radar screen and have been so called because they occur at times when ground observers report large passerine migrations. Almost all moderate and heavy movements we detected at North American coastal sites consisted of both passerine and dot echoes. Radars at Bermuda often detected small echoes, but they were never so dense as to produce the typical passerine "mist". With the single exception of Antigua on October 8, 1972, when a passerine "mist" moving toward 180° was detected at 4 to 6 km altitude, radars in the Caribbean detected only dot echoes which, however, were not usually bright and fast moving. Our observations in the Caribbean were made during the daylight hours when migrant passerines often form loose flocks as has been observed on radar by Gauthreaux (1970). As discussed by Williams *et al.* (1977), such flocks could well

produce the somewhat diffuse dot echoes we detected on Caribbean radars. In agreement with Richardson (1976) we believe a significant proportion of these radar echoes were due to low density passerine migrations.

Visual Observations

IN ADDITION TO the radar observations, visual bird counts were made in the Caribbean and on the ships. Caribbean site counts were made on a daily basis in 1970 and 1973 primarily in marsh and scrub areas. Our limited observations on Antigua have been greatly expanded by counts made during 1973 and 1974 by C. Holland, who has permitted us to use his data. Birds seen on or near the ships were recorded for all years (1971–1974). More detailed reports of observations made from the ships are in preparation (Larkin *et al.*, in prep.; McClintock *et al.*, in prep.). Observations of birds from Woods Hole Oceanographic Institution (W.H.O.I.) vessels prior to 1954 are reported by Scholander (1955), and subsequent to the initiation of our studies, Capt. and Mrs. E. H. Hiller of the R/V *Knorr* have kept daily records of birds, which they have kindly allowed us to use.

Over 90 species of birds have been sighted at sea from the W.H.O.I. ships, the majority being North American passerine migrants. In contrast to older reports (Hurdis, 1897), few shorebirds were seen, but significant numbers of passerines and cuckoos were seen more than 320 km from the North American coast. Larkin *et al.* (in prep.), McClintock *et al.* (in prep.) and Hiller (pers. comm.) report numerous species of passerines, predominantly warblers, 640 to 1600 km from shore. Of particular interest are three sightings of large flocks (estimated 500 to 1000 birds) which passed the ships: Hiller (pers. comm.) saw about 1000 warblers, 240 km NNW of Bermuda; Teal (Teal and Teal, 1975) saw a large flock of mixed passerines 640 km SE of Bermuda; McClintock *et al.* (in prep.) saw great numbers of warblers at night, 700 km SE of Cape Cod.

Observations through a 20-power telescope mounted on the Bermuda FPQ-6 radar antenna while tracking have identified groups of Great Blue Heron (*Ardea herodias*), Blue-winged Teal (*Anas discors*), several

species of shorebirds and unidentified passerines.

Our observations on Caribbean Islands revealed several species of shorebirds. We did not record passerines in any significant numbers. C. Holland (pers. comm. and Holland and Williams, in press) report that, at least on Antigua, this was due to our inability to survey the limited passerine habitat on the islands. Holland records the presence of at least 17 species of North American passerine migrants, predominantly warblers, arriving on Antigua from the end of September to mid-December with the peak of arrivals in October.

Estimates of en route Mortality

THE MAJOR HAZARD of an oceanic (as opposed to a coastal) autumnal migration route would appear to be the intense storms (tropical depressions, tropical storms and hurricanes) which appear in the western North Atlantic Ocean from mid-August to November. The normal track of these storms during the end of September and the beginning of October is westward along the Greater Antilles and then north and northeast parallel to the North American coast about 400 km offshore with the general eastern limit being 2000 km east of the normal track (Bowditch, 1962). Our observations indicate that frontal systems with their associated squalls and overcast do not pose a barrier to migrants, but tropical storms can cause severe disruption of normal migration patterns (see Mills, 1969; Richardson, 1972a). During our observations five tropical storms passed through the study area. They tended to follow the normal storm track described above. As they approached the North American coast they usually halted cold fronts moving over coastal areas and thus prevented any major departure of birds into their path. The winds around these storms move in a counter-clockwise direction; encountering an advancing storm from its right side will result in a bird (or a boat) being drawn into the storm's path (see Bowditch, 1962). Approaching the storm from the opposite side, one encounters strong winds blowing away from the path of the storm. On three nights birds did leave the coast when tropical storms were approaching but were more than 600 km distant. In two

cases these birds approached the left or navigable semicircle (see Bowditch, 1962) of the storm and thus were deflected away from the storm's path. (Note in Fig. 2 the movements at Wallops and Cape Cod on September 29 to October 1 and Cape Cod on October 6, 1972, as birds moved back to shore with strong east winds.) Only in one case, Bermuda on October 28 and 29, 1971, did we observe birds on the right or dangerous semicircle of a storm. Thus, storms moving up the coast usually prevent departures of birds by stopping cold fronts, and birds that do depart appear to encounter the navigable side of a storm resulting in detour rather than destruction.

The density of radar echoes can be used to estimate the numbers of migrants aloft (Nisbet, 1963b; Eastwood, 1967; Gauthreaux, 1970; Able and Gauthreaux, 1975). As discussed by Gauthreaux (1970) and Richardson (1972b) comparisons between radars must be approached with great caution, but we believe such comparisons may be useful if performed between similar radars and for major density differences. If we compare the weather radar observations on the North American coast (Chatham, WSR-57) and in the Caribbean (RC-32-B) and the SPANDAR and FPQ-6 observations at Wallops Island, Bermuda and Antigua, we conclude that the density of radar echoes departing the North American coast is much greater than the density at Bermuda or the Caribbean and that the density at Bermuda and Antigua are similar. Richardson (1976) also reports greater densities departing the North American coast than arriving in Puerto Rico.

On Gauthreaux's (1970) density scale, coastal departures frequently saturated the Chatham WSR-57 PPI screen even if we reduced the sensitivity of the radar by 12 db and exposed our film for only a single revolution of the radar (see Gauthreaux, 1970 for a description of this technique). Arrivals in the Caribbean never exceeded his lowest density level. Gauthreaux reports that such differences corresponded to a reduction of more than 100-fold in the density of birds at the radar he used (a WSR-57).

THE REDUCTION in the density of radar echoes may be due to several factors

other than mortality. Birds might disperse along the migration route due to differences in direction and airspeed (V_a). The similarity in densities recorded at Bermuda and Antigua suggest, however, that dispersion is a minor factor; almost all the reduction appears to occur between the coast and Bermuda. Migrants which left the coast flying singly might later form flocks, thus reducing the number of radar targets. Richardson (pers. comm.) believes this is a major factor. Many birds departing the coast in the early evening may later reorient their flight and return to land as indicated by our own observations (September 28 and 29, 1971 at Cape Cod and Wallops Island, October 5 and 6, 1972 at Wallops Island) and those of Swinebroad (1967), Richardson (1972a) and Murray (1976). However, our observations from ships at sea reported here and in Larkin *et al.* (in prep.) and McClintock *et al.* (in prep.) have at times revealed large numbers of birds making little progress toward land, and suggest significant mortality for at least some groups of birds.

Discussion

RADAR, DIRECT VISUAL OBSERVATION and banding studies indicate that many species of birds move between the eastern coast of North America and the Caribbean or South America by at least two different routes: southwest along the U.S. coast, and more directly across the Atlantic Ocean. Previous work (see Lincoln, 1952; Dorst, 1961) indicated that the mid-Atlantic route was primarily used by shorebirds, while passerines (with the exception of the Blackpoll Warbler, Nisbet, 1970) used the coastal route to the Caribbean. Wingate (1973) reports that 87 species of North American passerine migrants are seen regularly in significant numbers each fall on Bermuda. Of these 87 species (39 of which are warblers) seen on Bermuda, over 30 (at least 20 species of warblers) are known to regularly occur in the Caribbean (Danforth, 1934, 1935; McCandless, 1961, 1962; Voous, 1965; Voous and Koelers, 1967; Bond, 1971; ffrench, 1973; Holland and Williams, in press). These data, with the observations from ships of large numbers of passerines seen singly and in mixed flocks far to the south and east of Bermuda, suggest that the overwater route from North

America to South America may be used by many passerine species in addition to the Blackpoll Warbler. This conclusion is supported by our radar observations and those of Richardson (1976) which reveal that a major proportion of all targets approaching the Caribbean Islands from the Atlantic have airspeeds and radar echo size characteristic of passerines rather than shorebirds. We, therefore, conclude that the species most likely seen on radar were shorebirds and passerines, mostly warblers (see also Hilditch *et al.*, 1973). Visual observations on Bermuda (Wingate, 1973, and pers. comm.), in the Caribbean (Bond, 1971; ffrench, 1973; Holland and Williams, in press, and Holland, pers. comm.), in Venezuela (McNeil, 1970), and our observations at sea and in Bermuda (Teal and Teal, 1975; Larkin, *et al.*, in prep.; McClintock *et al.*, in prep.) indicate that some members of the following species also use the overwater route to the Caribbean and South America: Great Blue Heron (*Ardea herodias*), Blue-winged Teal (*Anas discors*), Osprey (*Pandion haliaetus*), Merlin (*Falco columbarius*), Sora (*Porzana carolina*), Ring-billed Gull (*Larus delawarensis*), Yellow-billed Cuckoo (*Coccyzus americanus*), Belted Kingfisher (*Megaceryle alcyon*), and perhaps others.

Neither of the two major routes between eastern North America and the Caribbean appears to be direct; both involve a change in the V_g of birds en route and flight in contrary winds. Birds following the coast move southwest from Newfoundland and Nova Scotia to Florida where they apparently turn and proceed southeast along the Antilles. Only in the northern section of this coastal migration route would birds fly with strong tailwinds. Southwest departures along the U.S. coast are triggered by the passage of a cold front with accompanying northwest winds. Below 25°N birds moving southeast encounter strong easterly winds at lower altitudes which they avoid by high altitude flight. The change in V_g from southwest to southeast would require a major change in the V_a direction.

The second route to the Caribbean involves flight over the western North Atlantic Ocean. Birds on the northeastern coast of North America wait for the passage of a cold front to depart the coast with strong tailwinds. The

birds soon penetrate a stationary front and continue to the Caribbean under variable winds until they encounter the northeast trade winds. Their flight path (V_g) is first southeast and then southwest, but this change is apparently due to drift by the trade winds with most birds arriving in the Caribbean still heading (V_a) to the southeast. Most migrants appear to maintain this course until they reach South America, with comparatively few birds stopping at Bermuda or in the Caribbean.

Our observations thus indicate that birds crossing 2500 km of open ocean between North America and the Caribbean may use a remarkably simple migration strategy. Departure is triggered by favorable wind conditions. Navigation is accomplished by maintaining a constant compass course and increasing altitude of flight as the birds encounter the strong easterly trade winds.

Although long overwater flight at first seems hazardous for migrant birds, especially passerines, the Atlantic route between North and South America offers several potential advantages over the coastal route. The ocean route from Nova Scotia to Antigua is about 2800 km shorter (47%) than a route via Florida, uses both offshore NW winds and NE trade winds as tailwinds, and is presumably with few if any predators. The marine route does not appear to exceed the known physiological limits for bird flight. McNeil and Burton (1973) conclude that several species of shorebirds store sufficient fat to have flight range capabilities from 2400 to 4600 km, and Tucker (1968b) observed no discomfort in passerines subjected to atmospheric pressures comparable to 7000 m altitude. However, most passerines should be able to fly for only 60 to 80 hrs, and so do not appear to have much margin for error (Tucker, 1968a, 1972; see also Nisbet *et al.*, 1963). The major danger would thus appear to be factors (such as storms or adverse winds) which would prolong flight time beyond the physical endurance of migrants. Our results indicate that, although some migrating groups may be caught by storms, most birds make the Atlantic crossing with a predictable series of flight conditions and there is relatively little mortality once migrants pass beyond Bermuda.

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Summary

SIMULTANEOUS OBSERVATIONS with a network of radars along the eastern coast of North America, on Bermuda, on Caribbean Islands and on ships, in conjunction with counts of grounded migrants, were used to investigate movements of birds over the western North Atlantic Ocean each fall for five years.

Birds waited on the North American east coast until the passage of a cold front provided favorable conditions for departure to the southeast. Successful migrants maintained this southeast direction, passing through the frontal weather system. Observations from ships indicated migration over a

broad area as far as 1000 km east of Bermuda. These birds arrived in the Caribbean moving to the southwest presumably having shifted direction of movement in the area of the Sargasso Sea. Analysis of the velocity of birds relative to the air indicated that this shift in direction was primarily owing to drift by the northeast trade winds, and the entire overwater flight could be accomplished by migrants maintaining a nearly constant compass heading to the southeast.

Average altitude of migration increases *en route* to a maximum of 4 to 6 km over Antigua and then decreases abruptly near the South American coast. High altitude flight over the Caribbean offers a clear advantage in terms of reduced headwinds when compared with flight at lower altitudes.

Observed reduction in the density of radar echoes occurs primarily between the North American coast and Bermuda with similar densities recorded from Bermuda and the Caribbean.

Observation of grounded migrants, air-speeds and time of year indicate that passerines, particularly warblers, as well as shorebirds constitute most of the overwater migrants observed.

A second route utilized by North American migrants moving to the Caribbean and South America follows the coast southwest, turns in the vicinity of Florida and moves southeast along the Antilles. This route appears to be used by more birds than the overwater route.

References

Able, K. P.: The role of weather variables and flight direction in determining the magnitude of nocturnal bird migration. *Ecology* 54, 1031-1041 (1973)
 ———: Environmental influences on the orientation of free-flying nocturnal bird migrants. *Anim. Behav.* 22, 224-238 (1974)
 Able, K. P. and Gauthreaux, S. A.: Quantification of nocturnal migration with a portable ceilometer. *Condor* 77, 92-96 (1975)
 Adams, D. W. H.: Radar observations of bird migration in Cyprus. *Ibis* 104, 133-146 (1962)
 Alerstam, T., Lingren, A., Nilsson, S., and Ulfstand, S.: Nocturnal passerine migration and cold front passages in autumn. A combined radar and field study. *Ornis Scandinavica* 4, 103-111 (1973)
 Baird, J., and Nisbet, I. C. T.: Northward fall migration on the Atlantic coast and its relation to offshore drift. *Auk* 77, 119-149 (1960)

Batschlet, E.: Statistical methods of analysis of problems in animal orientation and certain biological rhythms. AIBS monograph, Washington, D.C. (1965)
 Bond, J.: Birds of the West Indies. Houghton Mifflin Co., Boston. 256 pp. (1971)
 Bowditch, N.: American practical navigator. U.S. Navy Hydrographic Office publication No. 9, U.S. Govt. Printing Office, Washington, D.C. (1962)
 Casement, M. B.: Migration across the Mediterranean observed by radar. *Ibis* 108, 461-491 (1966)
 Danforth, S. T.: The birds of Antigua. *Auk* 51, 350-364 (1934)
 ———: The birds of Saint Lucia. *Monog. Univ. Puerto Rico*, No. 3, 1-29 (1935)
 Dorst, J.: The Migrations of Birds. Trans. by Constance D. Sherman. Heineman, London 476 pp. (1961)
 Drury, W. H. and Keith, J. A.: Radar studies of songbird migration in coastal New England. *Ibis* 104, 449-489 (1962)
 Drury, W. H. and Nisbet, I. C. T.: Radar studies of orientation of songbird migrants in southeastern New England. *Bird Banding* 35, 69-119 (1964)
 Eastwood, E.: Radar Ornithology. Methuen and Co., Ltd. London. 278 pp. (1967)
 Evans, P. R.: Migration and orientation of passerine night migrants in northeast England. *J. Zool.* 150, 319-369 (1966)
 French, R.: A Guide to the Birds of Trinidad and Tobago. Livingston Publ. Co., Wynnewood, Pa 470 pp. (1973)
 Flock, W. L.: Radar observations of bird movements along the arctic coast of Alaska. *Wilson Bull.* 85, 259-275 (1973)
 Gauthreaux, S. A.: Weather radar quantification of bird migration. *BioScience* 20, 17-20 (1970)
 ———: A radar and direct visual study of passerine spring migration in southern Louisiana. *Auk* 88, 345-365 (1971)
 Griffin, D. R.: Oriented bird migration in or between opaque cloud layers. *Proc. Am. Phil. Soc.* 117, 117-141 (1973)
 Hager, J. A.: Nesting of the Hudsonian Godwit at Churchill, Manitoba. *Living Bird* 5, 1-43 (1966)
 Hilditch, C., Williams, T. C. and Nisbet, I. C. T.: Autumnal bird migration over Antigua. *Bird Banding* 44, 171-179 (1973)
 Holland, C. S. and Williams, J. M.: Observations on the birds of Antigua. *Am. Birds*. In press.
 Hurdis, J. L.: Rough notes and memoranda relating to the natural history of the Bermudas by the late John L. Hurdis edited by his daughter H. J. Hurdis. R. H. Porter, London (1897)
 Ireland, L. C., and Williams, T. C.: Radar observations of bird migrations over Bermuda. *Proc. a Conf. on the Biol. Aspects of the Bird/Aircraft Collision Problem*. S. A. Gauthreaux, Ed., U.S.A.F. Office of Scientific Research, Arlington, Va. (1974)
 Lack, D.: Migration across the North Sea studied

- by radar. Part 1. Survey through the year. *Ibis* 101, 209–234 (1959)
- : Migration across the North Sea studied by radar. Part 2. The spring departure 1956–59. *Ibis* 102, 26–57 (1960)
- : Migration across the southern North Sea studied by radar. Part 4. Autumn. *Ibis* 105, 1–54 (1963a)
- : Migration across the southern North Sea studied by radar. Part 5. Movements in August, winter and spring, and conclusion. *Ibis* 105, 461–492 (1963b)
- Larkin, R. P., Torre-Bueno, J., Griffin, D. R., and Teal, J. M.: Radar observations of bird migration over the western North Atlantic Ocean. In prep.
- Lincoln, F. C.: The Migration of American Birds. Doubleday, Doran and Co., Inc., New York. 189 pp. (1939)
- : Migration of Birds. Doubleday and Co., Inc., New York. 102 pp. (1952)
- McCandless, J. B.: Bird life in southwestern Puerto Rico. I. Fall migration. *Carib. Jour. Sci.* 1, 3–12 (1961)
- : Birdlife in southwestern Puerto Rico. II. The winter season. *Carib. Jour. Sci.* 2, 27–39 (1962)
- McClintock, C., Williams, T. C., and Teal, J. M.: Radar observations of bird migration from ships in the eastern North Atlantic. In prep.
- McNeil, R.: Hivernage et estivage d'oiseaux aquatiques nord-américains dans le nord-est du Venezuela (mue, accumulation de graisse, capacité de vol et routes de migration). *L'Oiseau et R.F. O.* 40, 185–302 (1970)
- McNeil, R., and Burton, J.: Dispersal of some southbound migrating North American shorebirds away from the Magdalen Islands, Gulf of St. Lawrence, and Sable Island, Nova Scotia. *Carib. J. Sci.* 13, 257–278 (1973)
- Mills, E. L.: Hurricane Gladys and its ornithological effect on the Maritime Provinces. *Nova Scotia Bird Society Newsletter* 11, 6–16 (1969)
- : The return to the mainland of some nocturnal passerine migrants over the sea. *Bird-Banding* 47, 345–359 (1976)
- Morrison, S. E.: Christopher Columbus, Mariner. Little, Brown and Co., Boston (1955)
- Murray, B. G.: On the autumn migration of the Blackpoll Warbler. *Wilson Bull.* 77, 122–133 (1965)
- Myres, M. T.: Dawn ascent and reorientation of Scandinavian Wood Thrushes (*Turdus* spp.) migrating at night over the northeastern Atlantic Ocean in autumn. *Ibis* 106, 7–51 (1964)
- Myres, M. T., and Apps, R. F.: Migration of birds over the south coast of China recorded by radar. *Nature* 241, 552 (1973)
- Nisbet, I. C. T.: Measurements with radar of the height of nocturnal migration over Cape Cod, Mass. *Bird-Banding* 34, 57–67 (1963a)
- : Quantitative study of migration with 23-centimeter radar. *Ibis* 105, 435–460 (1963b)
- : Autumn migration of the Blackpoll Warbler: evidence for long flight provided by regional survey. *Bird-Banding* 41, 207–241 (1970)
- Nisbet, I. C. T., Drury, W. H., and Baird, J.: Weight loss during migration. Parts I and II. *Bird-Banding* 34, 107–159 (1963)
- Nisbet, I. C. T., and Drury, W. H.: Orientation of spring migrants studied by radar. *Bird-Banding* 39, 173–185 (1967)
- : Short term effects of weather on bird migration: a field study using multivariate statistics. *Anim. Behav.* 16, 496–530 (1968)
- Palmer, R. S.: Species accounts. In: *The Shorebirds of North America*. G. C. Stout [ed.], The Viking Press, New York. 270 pp. (1968)
- Richardson, W. J.: Autumn migration and weather in eastern Canada: a radar study. *Am. Birds* 26, 10–17 (1972a)
- : Temporal variations in the ability of individual radars in detecting birds. Field note #61, Associate Committee on Bird Hazards to Aircraft, National Research Council, Ottawa (1972b)
- : Spring migration over Puerto Rico and the western Atlantic, a radar study. *Ibis* 115, 172–193 (1975)
- : Autumn migration over Puerto Rico and the western Atlantic, a radar study. *Ibis* 118, 309–332.
- Scholander, S. I.: Land birds over the western North Atlantic. *Auk* 72, 225–239 (1955)
- Swinebroad, J.: The radar view of bird migration. *Living Bird* 3, 64–75 (1964)
- Teal, J. M., and Teal, M.: The Sargasso Sea. Little, Brown, Boston. 216 pp. (1975)
- Tucker, V. A.: Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* 48, 67–87 (1968a)
- : Respiratory physiology of house sparrows in relation to high-altitude flight. *J. Exp. Biol.* 48, 55–66 (1968b)
- : Metabolism during flight in the Laughing Gull (*Larus atricilla*). *Am. J. Physiol.* 222, 237–245 (1972)
- Tucker, V. A., and Schmidt-Koenig, K.: Flight speeds of birds in relation to energetics and wind directions. *Auk* 88, 97–107 (1971)
- Voous, K. H.: Check-list of the birds of Aruba, Curacao, and Bonaire. *Ardea* 53, 205–234 (1965)
- Voous, K. H., and Koelers, H. J.: Check-list of the birds of St. Martin, Saba and St. Eustatias. *Ardea* 55, 115–137 (1967)
- Williams, T. C., Williams, J. M., Teal, J. M., and Kanwisher, J. W.: Tracking radar studies of bird migration. In *Animal Orientation and Navigation a Symposium*. NASA SP262. U.S. Govt. Printing Office, Washington, D.C. pp. 115–128 (1972)
- Williams, T. C., and Williams, J. M.: Tracking radar techniques for studying migratory birds. NASA CR-62082, NASA Contractor Report, available from NASA, Wallops Station, Wallops Island, Va. 22337 (1972)
- Williams, T. C., Berkeley, P. and Harris, V.: Autumnal bird migration over Miami studied by radar: A possible test of the wind drift hypothesis. *Bird-Banding* 48, 1–10 (1977)
- Wingate, D. B.: A Checklist and Guide to the Birds of Bermuda. Island Press, Bermuda (1973)