AUTUMN MIGRATION OF TRANS-SAHARAN MIGRATING PASSERINES IN THE STRAITS OF GIBRALTAR

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ABSTRACT.—Radar observations of passerine trans-Saharan migrants during autumn migration (August and September 1981, 1983, 1984, and 1985) in the Straits of Gibraltar revealed intense movements to the south and southwest. On average birds flew to the southwest (211°). Thus, after crossing the coast of southwestern Europe, migrants did not change their direction to the southeast towards the interior of Africa. If the birds maintained their southwesterly direction, they would continue along the west coast of Africa. Along this route the birds might find better conditions than on any route through the interior of the continent.

The reported average direction of birds at Gibraltar represents a sample of the general behavior pattern in the southern Iberian Peninsula. The variance of nightly directions could be explained by the fact that birds fly on a fixed heading in strong crosswinds that alternate between east and west, but are only of local importance on a southbound migration route.
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MOREAU (1961, 1972) believed that passerine migrants crossed the Mediterranean and the Sahara anywhere, but banding results (Zink 1973–1985, 1977) demonstrated that most European and many Asian migrants fly around the Mediterranean in autumn. Consequently, a larger number of migrants would be expected to start their migration through Africa from southwestern and southeastern Europe. Many migrants have to change their direction during migration. On the westerly route, the change from southwest to southeast was thought to occur in the area of the southern Iberian Peninsula and North Africa (Zink 1977, Gwinner and Wiltschko 1978). Recent radar observations (Hilgerloh 1985a, 1988) demonstrated that in the southwestern Iberian Peninsula migrants still maintained southwesterly directions. To determine if migrants maintained a southwesterly direction leaving the coast of Europe or if the coast acted as a releasing factor for a change of direction, I conducted a radar study at Gibraltar, where Europe is closest to Africa.

The tunnel effect of the Straits of Gibraltar produces strong easterly and westerly winds. This provides a rare opportunity to evaluate the behavior of birds under conditions of strong crosswinds. Behavior in relation to winds has been reported in several locations to depend on meteorological conditions and on whether a sea-crossing or an overland flight follows (Drury and Keith 1962; Drury and Nisbet 1964; Gauthreaux and Able 1970; Richardson 1972, 1976; Alerstam 1976; Williams et al. 1977; Williams and Williams 1978). Unusual migratory behavior might be used to compensate for the unique conditions in the Straits of Gibraltar.

MATERIAL AND METHODS

I observed migration using the military S-band surveillance radar on top of the Rock of Gibraltar (Houghton 1970). Gibraltar is about 25 km northeast of the narrowest point between Africa and the Iberian Peninsula. The distance from Africa is ca. 24 km. The radar has a wavelength of 10 cm and each rotation of the aerial lasts 4 s. To suppress echoes from fixed objects or waves, the radar was used with a Moving Target Indicator (Eastwood 1967, Hilgerloh 1980). More technical data cannot be given because of military secrecy. The radar gives a survey of the typical small and diffuse echoes of nocturnal passerine migration within a radius of 16 km. Migrants flying over the African mainland cannot be observed. Shorebirds were visible as clear dots, and passed alone or in small groups between the Mediterranean and the Atlantic. Gulls that sleep on the Rock of Gibraltar or, farther to the northeast, waterfowl that feed in the evening at the mouth of the river Guadarranque, and herons complete their main activity before night migration starts. In the Bay of Algeciras next to Gibraltar disturbed gulls fly around during the night, but do not contribute to the regular pattern of passerine migration. I believe that the type of echoes, the regular pattern of migration, and the time of the year suggest that a significant proportion of the birds detected were passerines. Because of the topography, I measured migration over water only; it was not possible to detect migrants overland to the north of the radar. Eval-

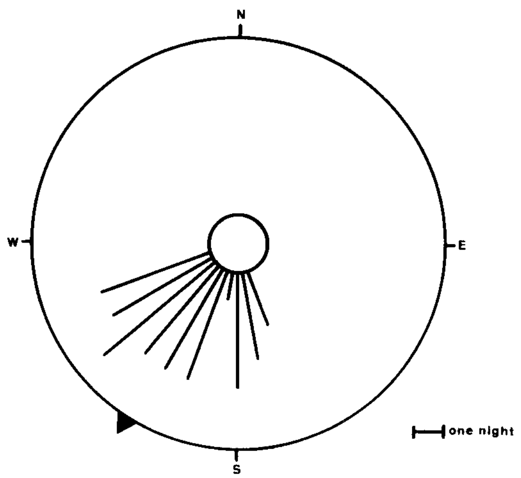

Fig. 1. Mean flight directions (rounded to 10°) for 35 nights during autumn migration in Gibraltar. The triangle at the outer circle shows the mean direction.

uation of modal migration direction was accomplished by examining photographs of the Plan Position Indicator (PPI). Five nights were evaluated directly from the PPI. I took two photographs of the PPI every 30 min. I chose this time period to insure that the measurements were independent. For the first photograph, I left the shutter open during one rotation of the radar beam; for the second, I left it open during 19 rotations. Often only parts of the nights were documented.

I calculated mean direction for each observation night from individual 30-min values by vector addition (Batschelet 1981). Seasonal mean direction was determined from the nightly mean directions. All further evaluations were based on nightly mean directions in order to give each night the same weight.

I assumed that the nightly calculated mean direction approximated the real mean of the entire night. Normality of distribution was tested on only two nights with sufficient measurements (Kolmogorov-Smirnov test, $P < 0.01$). Statistical evidence for directedness was tested by the Rayleigh test (Batschelet 1981). The nonparametric Mardia Watson Wheeler test, the standardized Mardia Watson Wheeler test, and the Mann-Whitney U-test were used for between-group comparisons.

Speeds of nightly migrating passerines cannot be accurately determined with a surveillance radar because migrants generally fly with large distances between individual birds (Bruderer 1971). The same individuals will not always contribute to one track on a long exposure photo. Density of migration and fluctuations of the radar set can alter the perceived speed of migrants. Tracking radar studies showed that, although migrants compensate partly for wind speed of tail and head winds (Bloch and Bruderer 1982), the wind vector in flight direction and the speed of a bird are correlated (Bruderer 1971). To calculate the birds' heading (defined as the vector difference of track and wind vector), I used the value predicted from the known regression between the wind vector in flight direction and the speed of migrants 500–1,000 m high (Bruderer 1971).

My study was restricted to night-migrating passerines, which winter mainly to the south of the Sahara. All observations were from the months of August and September (Hilgerloh 1985b) in 1981, 1983, 1984, and 1985.

Every 6 h the Gibraltar Royal Air Force recorded wind measurements for altitude lines of ca. 305 m. To study the relation of the wind to the direction of migration, I used the wind value at 610 m. I made a supplementary analysis with winds at 1,525 m, because at this height easterly wind direction often changes in a clockwise direction in Gibraltar and winds often become weak. The birds might take advantage of these conditions. Birds flying much higher could not be detected clearly on an Air Traffic Surveillance radar (Hilgerloh 1980). I defined calm nights as those in which the strength of the wind did not exceed 3 m/s (11 km/h) between ground level and a height of 610 m. To study the relationship between wind vector and flight direction, I determined the east and west components of wind, using the formula $y = \sin$ (wind direction) $\times$ wind strength (Hilgerloh 1981).

RESULTS

In 35 nights of research the nightly mean direction of migration varied between 160° and 250°. On average the birds migrated towards 211° ($n = 35$, $r = 0.889$, $P < 0.001$) (Fig. 1). The birds had no chance of migrating with favorable tail winds (Fig. 2), as crosswinds prevailed (with an average strength of 31.5 km/h in westerly winds and 27.8 km/h in easterly winds during observation nights) (Fig. 3). I found a strong correlation between the nightly direction of migration and the wind vector at 610 m (Fig. 4): $y = 154.40 + 1.71x$ (x = wind vector, y = track direction, $r^2 = 0.86$); but I found a weaker correlation with the wind vector at 1,525 m ($r^2 = 0.66$). Similar to conditions in England (Eastwood and Rider 1965), Switzerland (Bruderer 1971), and Louisiana (Able 1970), migrants seem to fly at a median height of ca. 610 m. Over Florida (Williams et al. 1977) and the Caribbean Islands (Hilditch et al. 1973, Richardson 1976), they fly much higher. Migrants may be more likely to fly high in areas with constant wind patterns than in areas, such as

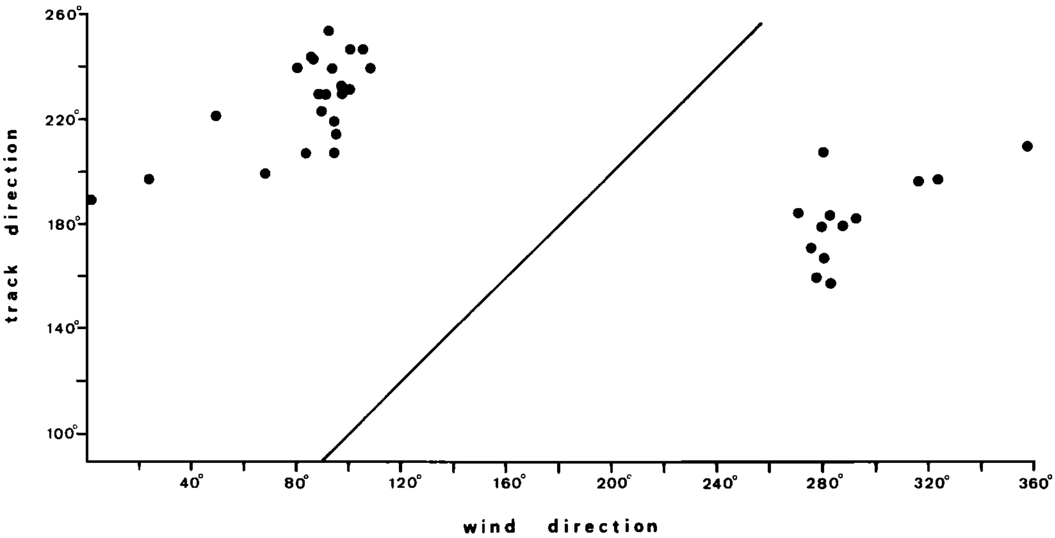

Fig. 2. Flight directions (track) in relation to tailwind direction (line) on 35 autumn nights.

Gibraltar, with strong and unpredictable crosswinds.

The mean directions for easterly winds of 232° ($n = 18$, $r = 0.971$, $P < 0.001$) and for westerly winds of 180° ($n = 11$, $r = 0.965$, $P < 0.001$) (Fig. 5) were significantly different (Mardia Watson Wheeler test, $P < 0.001$; standardized Mardia test, $P > 0.05$; Mann-Whitney U-test, $P < 0.001$).

I tested whether the migrants fly with a fixed heading and whether or not they compensate for wind. If they compensate for wind, headings in easterly and westerly winds should differ from each other. The mean heading in easterly winds of 210° ($n = 18$, $r = 0.974$, $P < 0.001$) and in westerly winds of 212° ($n = 11$, $r = 0.989$, $P < 0.001$) (Fig. 6) did not differ significantly (Mann-Whitney U-test, $P > 0.05$). Thus, migrants flew with a fixed heading and did not compensate for drift.

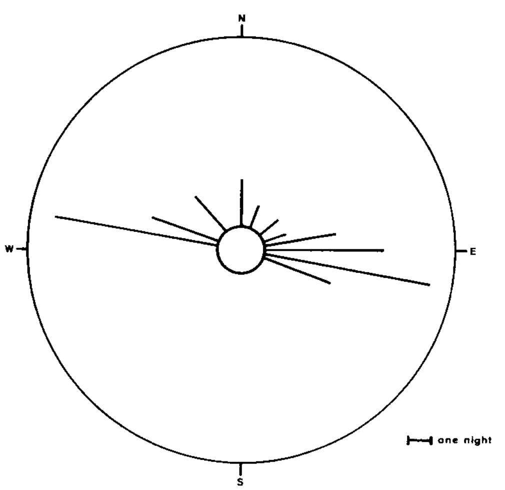

Fig. 3. Wind directions (rounded to 10°), measured at ca. 305 m above ground level ($n = 35$, $\alpha = 55°$, $r = 0.309$).

The mean direction of migration of the entire sample was influenced by the frequency distribution of the winds on the research nights. There were more nights with easterly than with westerly winds (Fig. 3), so the mean of the sample was more to the west than in a sample with evenly distributed winds. On calm nights the mean direction was 202°, and the theoretical value of expectation for nights without easterly and westerly wind vectors was 205° (derived from the regression line in Fig. 4).

Discussion

Over the Straits of Gibraltar trans-Saharan migrants on average fly to the southwest. After leaving the coast of Europe they do not change direction to fly the shortest path to Africa nor do they change direction to the southeast to reach central and south African wintering quarters more directly.

Migration directions observed in the middle of the Straits were similar to those of Beja in southern Portugal (Hilgerloh 1985a, 1987) and

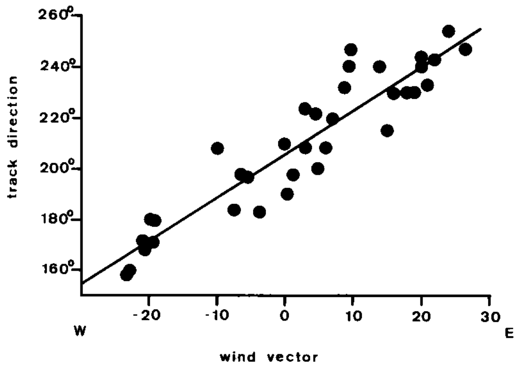

Fig. 4. Correlation between the migration direction (abscissa) and the wind vector (ordinate). Each point represents the mean direction of one observation night.

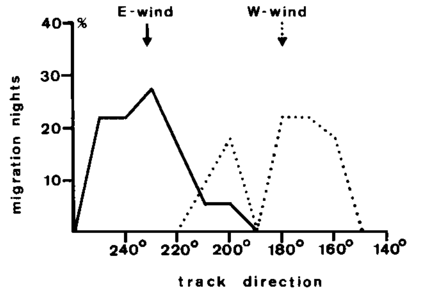

Fig. 5. Directions (rounded to 10°) of migration with easterly winds and with westerly winds (broken line). The mean directions in easterly winds (n = 18, α = 232°, r = 0.971) and in westerly winds (n = 11, α = 180°, r = 0.965) are shown by arrows.

the southwestern coast of Portugal (Wallraff and Kiepenheuer 1963). Southwesterly migratory movements were observed even southeast of the Iberian Peninsula on a ship voyage through the Mediterranean (Casement 1966).

In many places migrants take advantage of winds (see Gauthreaux and Able 1970; Alerstam 1976; Richardson 1976, 1982; Hilgerloh 1977; Williams et al. 1977; Williams and Williams 1978; Kerlinger and Gauthreaux 1985). This is not possible in the Straits of Gibraltar (Fig. 2), because strong crosswinds prevail (Fig. 3). In Gibraltar migrants have the advantage of a short sea crossing and the disadvantage of wind drift. The birds drift but do not compensate (Figs. 4, 5). The wind conditions are local and drift may be minimal after some time of migration. During nights with good visibility, migrants can see the African coast and presumably can measure precisely the amount of drift. They may compensate for drift once they are over land. This seems to be a valid strategy in strong crosswinds of local importance, as the migrants do not spend energy to compensate for these winds (Alerstam 1981). Birds migrating in strong easterly winds will even cross European land after passing over the peninsula of Gibraltar (Fig. 7). They can interrupt migration in Europe to avoid further drift on a particular night.

The drift might be interpreted as pseudodrift (Evans 1966, Nisbet and Drury 1967), if on nights with easterly winds only birds with westerly destinations migrate. Birds that migrate in westerly winds should reach their wintering quarters more successfully on an easterly route. The mean direction in easterly winds (Fig. 5) would drive the birds over the Atlantic and the mean direction in westerly winds would push them to the most inhospitable regions of the Sahara (Bairlein 1985a). Thus pseudodrift cannot account for these directional deviations. The birds drift locally and probably compensate for their drift later (Rabol 1974). The strategy of flying with a fixed heading evolved in this area probably because of the unfavorable wind directions alternating between west and east, and because they are only of local importance on a southbound migration route.

Birds may follow two directions after passing through the Straits of Gibraltar. First, the migrants could continue in the same direction as in Gibraltar, and fly just along the African west coast (Fig. 7), and then change direction to the east after passing the Sahara at its western bor-

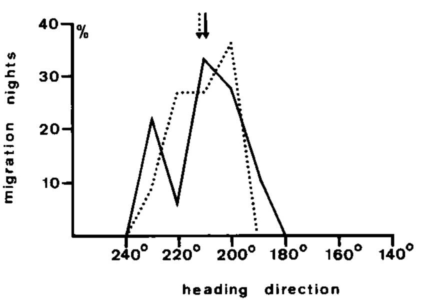

Fig. 6. Directions of heading (rounded to 10°) with easterly winds and westerly winds (broken line). The mean directions of heading in nights with easterly (n = 18, α = 210°, r = 0.974, $P < 0.001$) and with westerly winds (broken arrow; n = 11, α = 212°, r = 0.989, $P < 0.001$) are shown by arrows.

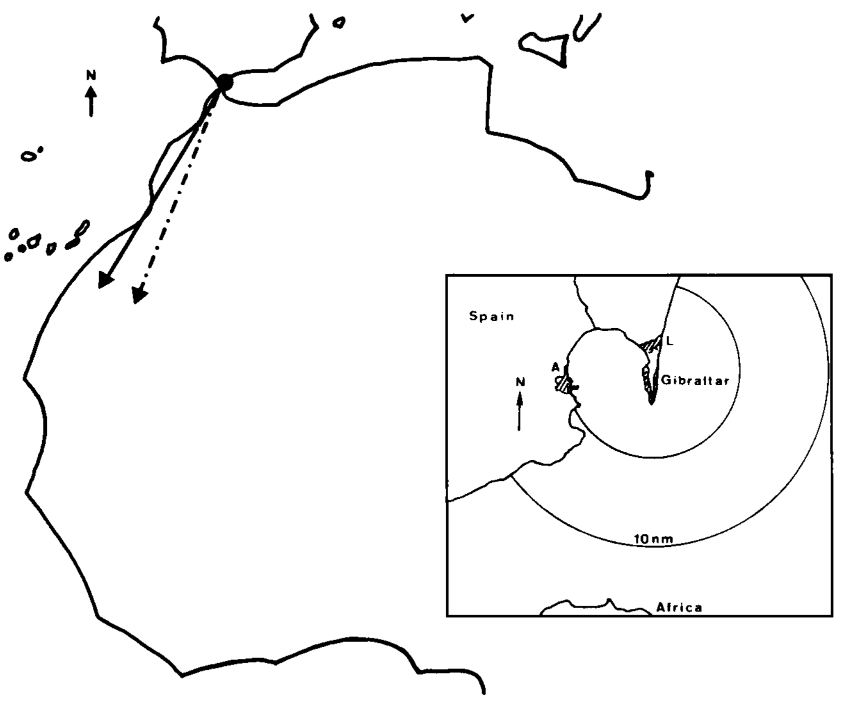

Fig. 7. Projected landfall of migrants in the directions flown in Gibraltar. The line shows the mean direction of the whole sample; the broken line, the mean direction in calm nights. Inset: map of the area of observation (A = Algeciras; L = La Linea).

der. Alternatively, the migrants could change their direction soon after their arrival in Africa and migrate towards the interior of Morocco and the Sahara. Migration along the African coast would be the most ecologically advantageous route as birds would more easily find shelter and food (Valverde 1957, Moreau 1961) than in the Sahara interior. Thus, a nonstop flight through the desert (Moreau 1972) would not be necessary for these migrants and they would fly with favorable winds (Hilgerloh in press). I believe that migrants that leave Europe west of Gibraltar migrate with similar directions to those that leave at Gibraltar (Hilgerloh 1988). Migrants that winter in central and southern Africa would have to change direction to the east after passing the Sahara. Migration directions parallel to the coast in Liberia (Gatter 1987, 1988) argue for this route.

A route through the interior of Africa would have the advantage of being shorter for migrants that winter in central and southern Africa but has the disadvantage of being much more inhospitable. Passerine migrants occur in the interior of Morocco (Thevenot 1974, Vaughan 1960) and in the desert (Bairlein 1985b), but the main route seems to be along the African coast. Further investigations may document the extent to which passerines migrate on different routes and whether routes are determined by the location of breeding and wintering grounds of the migrating populations.

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The second and final **Circular of the Congress** will be available after 1 October 1989 and will include the registration papers and forms for submitted papers. New Zealand will also host the **20th World Conference of the International Council for Bird Preservation** in Hamilton on **21–27 November 1990** and a **Pacific Festival of Nature Films**, in Dunedin on **27 November to 1 December 1990**.

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