

## **The Study of Bird Migration by Radar**

### **Part 2: Major Achievements**

Bruno Bruderer

Swiss Ornithological Institute,  
CH-6204 Sempach,  
and Zoology Institute University of Basel,  
CH-4051 Basel

This is a brief review of the main insights into bird migration provided by radar. Radar is the main tool to study the flight behavior of migratory birds under the influence of environmental factors, i.e., the ecology of migratory flights, ranging from the large-scale pattern of migration in relation to the distribution of land masses, geomorphology, and weather systems down to the variation of flight behavior of single birds in response to leading lines, obstacles, particular atmospheric conditions, and flight phases.

**R**adar has revolutionized research on bird migration. It provides data on the patterns of migration in various geographical areas and is the main tool for studying the reactions of migrants to topographical features and weather, and the variation of flight behavior in time and space under the influence of environmental conditions. It will continue to play an important role, particularly for the analysis of flight and orientation strategies. This review briefly summarizes the major contributions of radar ornithology to our knowledge of bird migration. To limit the reference list I refer to review papers whenever possible. The most comprehensive synopses are [1] for migration as a whole (with an update on migratory strategies in [2]), [3] for radar ornithology, and [4, 5] for weather-dependence of migration. A methodological update is provided in [6].

### **Geographical Patterns of Migration**

#### *Diurnal Migration*

Visual observation of passerine migration is restricted to the lowest few hundred meters; birds beyond 50 m above ground are missed. Fan-beam surveillance radars are biased towards birds flying a few hundred meters above ground. Even a short-range fan beam used in connection with a pencil-beam to measure altitudes is restricted to heights above about 30 m [8]. The smaller the birds, the more the two methods diverge.

#### **Soaring Migrants**

Large soaring birds provide bright echoes on the screens of surveillance radars and, migrating nor-

mally in daytime over land, are often perceptible by visual observers. Due to limited visual range in the horizontal plane, observatories are normally located where concentrated soaring migration takes place, while radar provides information on how the birds move between the concentration points.

Most raptors fly individually, the scattered migrants becoming aggregated where the best updrafts are available. They may accumulate to very large numbers (*a*) in thermals, from where they often glide away in lines resembling a chain of pearls; (*b*) in updrafts occurring along the sunny or windward slopes of mountain ridges; (*c*) in wind-induced linear arrays of thermals; (*d*) when slightly shifting direction approaching the boundary of an unfavorable habitat [1, 7] or mountain ranges [9]. Additional concentration may be due to wind drift towards an obstacle or a leading line [10]. Surveillance radars in Israel show line echoes produced by thousands of raptors between the coast of Israel and the mountain chains of the Negev; these lines move in a diurnal cycle with the sea-breeze front between the coastal plain and the mountains [12].

Social birds such as storks, cranes, and pelicans fly in flocks, often along (traditional) corridors, and gather in large numbers at (often traditional) stopover sites. Spreading out from a flock over a wide area seems, at least in white storks (*Ciconia ciconia*) to assist in finding good thermals [1].

## Large Birds Using Powered Flight

Birds capable of powered flight enjoy more freedom in the choice of time and route for migration than pure soaring migrants. Alerstam [32] suggests that for cranes (*Grus grus*), in contrast to white storks, powered flight may be the primary mode of migration, available thermals being used as a supplementary source of energy to reduce the cost of transport. Ospreys (*Pandion haliaetus*) and falcons cross sea and mountain areas without hesitation [1, 23]; honey buzzards (*Pernis apivorus*) using powered flight may fly early in the morning [11], harriers and sparrowhawks even at night [13].

Large birds using flapping flight, such as waterbirds, migrate at day and at night. Many show specific reactions according to the time of day when flying over land and water, respectively. Marine ducks and geese on diurnal spring migration between the Baltic Sea and the White Sea fly below 200 m over water and 500–3000 m over land [14]. Pronounced adaptation to topography is reported for diurnally migrating eider ducks (*Somateria mollissima*) in southern Swe-

den, where spring migrants from the Kattegat fly southeastward over Scania or even southward and all around the coast of southern Sweden [1].

Wood pigeons (*Columba palumbus*) are ideal for tracking by surveillance radars over long distances because of their size and the fact that they gather in flocks and migrate in fair weather rather high above ground. They move on a broad front over land and concentrate along coast lines, particularly when these do not deviate at a large angle from the preferred direction; for example, they converge towards the southwestern tip of Sweden [1].

## Small Flapping Fliers

The first generation of radar observers tended to neglect the low-level migration seen by visual observers. Recent comparisons between visual and radar observations showed that in opposing winds these movements at low levels made up more than 50% of total migration even in flat country without any concentration by leading lines [8].

Medium-sized passerine migrants such as the redwing (*Turdus iliacus*) have been observed to fly across southern Sweden and the Baltic Sea during daytime in a similar pattern as wood pigeons, showing concentrated departures from peninsulas or abrupt bends of the coast [15]. In most cases, however, radar provides an incomplete picture of diurnal passerine migration. In southern Sweden most intense diurnal autumn migration of passerines has been noted by surveillance radar studies as a broad-front migration under following winds, while visible observations show most intense migration along the east and west coasts under offshore winds or at promotories over the sea with opposing winds [16]. Similar behavior is observed in Denmark and has been interpreted as a strategy of overcompensation at low levels and tolerated drift at high altitude [17].

## Nocturnal Migration

Most small long-distance migrants fly at night. Fortunately nocturnal migrants avoid flying close to potential obstacles on the ground and thus are usually above 30 m [1, 7]. Radars with narrow pencil beams may thus miss only minor proportions of nocturnal migration. Surveillance radar studies are, however, even at night prone to underestimate migration at low levels.

According to the early surveillance radar studies, nocturnal migration was ideal broad-front migration,

the effect of topographical features such as coastlines or valleys being negligible. Even when crossing large obstacles such as the Mediterranean Sea no obvious concentration at the main narrows was detected [3]. In the area of the straits of Gibraltar recent surveillance studies confirm nocturnal broad-front migration, which simply shifted in direction according to crosswinds [18], and waders on the coast of Ghana are reported to migrate inland across the African continent instead of following the sea shore [19].

On the other hand, detailed radar studies, for example, in the Alps [21, 23], Netherlands [22], and Nova Scotia [50] show that the migratory stream may be deviated locally or regionally by topographical features even at night. Knot (*Calidris canutus*) migration across southern Sweden does not follow any of the predicted paths according to known orientation mechanisms; rather, the overall migration route seems to be influenced by topography in a way to maximize association with coastal areas [24].

Radar has detected important movements of birds in winter [3]. In southern Sweden the movements of waterbirds take place in all directions, invariably under tailwind conditions, and thus generally from colder to warmer areas [25]. In Switzerland from late November to the middle of January the movements of waterbirds are strong and concentrated towards WSW in anticyclonic weather with mainly northeasterly winds; in cyclonic weather they are weak, scattered in all directions, but with a downwind tendency towards NE. From February onwards flight directions are focused NE irrespective of weather conditions [26].

### *Migration Across Large Ecological Barriers*

Long-distance flights of migrants across thousands of kilometers of ecological barriers, like oceans, glaciers and deserts are known from ringing recoveries as well as from the seasonal and day-to-day variation in the appearance of migrants. Radar observations added information about the flight strategies which enable the birds to accomplish such phantastic journeys.

### Transoceanic Migration

While most North American birds follow the land-bridge to South America, quite a few cross the Gulf of Mexico, particularly in spring; taking off, for example, from the Yucatan at dusk, they reach southern

Louisiana in plain daylight after 20 h of flight (unless delayed by opposing winds en route) [1].

Some waders and even a few passerines take an overwater route of more than 3000 km from the northeast coast of North America to the Caribbean and South America. Radar observations suggest that their route is an optimal compromise between maximal benefit from winds and minimal detour. The birds depart from northeastern North America towards SE (waders) or SSE-S (passerines), taking advantage of the strong northwesterly winds after the passage of a cold front. They climb to heights of 3000–6000 m and enter the tradewind zone south of Bermuda. With these stable northeasterly winds their track directions gradually shift towards S or even SSW, bringing them towards South America, where they descend after flights in the order of 75–100 h. In accordance with this wind regime, northward migration in spring takes a more westerly rather land-bound route [1, 27].

Wind-supported transoceanic autumn flights are reported also from the western Pacific. Radar comparisons showed that the SE movements are in the order of 100 times less dense than the SW movements following the coast [27].

### Bird Migration in the Arctic

Migration in the Arctic comprises on the one hand the N-S movements of birds, such as waders, geese, and terns which spend the Arctic winter in temperate or tropical areas. On the other hand, there are large numbers of marine and coastal species that move inland to nest on the open tundra. Due to the fact that circumpolar tundra habitats generally lie to the south of EW oriented coastlines, migration of waterbirds at high latitudes often occurs on an EW axis [28]. Along the north coast of Alaska millions of waterbirds move EW in arctic spring (mid-May to mid-June), most of them on a broad front. Some species migrate westwards with easterly winds, while others wait for westerly winds to move eastwards [29]. Selectivity for following winds is also observed for birds crossing Greenland and Iceland. Waders and geese depart from Iceland with the same (300°) direction by which they cross the icecap of Greenland, following rather a rumblineline to northern Canada than the predicted great circle route. Brent geese fly low over the water and are prone to follow coastlines, while departing waders steeply climb up to altitudes of 600–2000 m to cross the ice on a straight course [30, 31].

Important radar contributions to the understanding of this multifaceted system are available from Scandinavia [1], the British Isles [3], and Switzerland [3, 21, 23]. In spite of some pioneer studies [3] and some recent additions in the Mediterranean area [18, 20] further radar studies are necessary to decide whether uniform broad-front migration across sea and deserts or concentrated migration across the land bridges is the dominant feature, and whether nonstop flights across both barriers or intermittent flights making use of oases, islands, and coasts prevail in these critical areas [33].

Most bird migration in central Europe takes place on a broad front, with basic directions around SW (230°), for long-distance migrants slightly more S, and for short-distance migrants slightly more W. Important deviations from the basic direction are caused by the frequent westerly winds, which drift birds towards S and SE, and thus towards the Alps. In the area of the Alps both the winds and bird migration are funneled regionally by the main mountain ranges and locally by single ridges. The effect of topography on the birds increases with increasing headwind component and cloud cover and with decreasing flight altitude. High-flying birds have more southerly headings even above southern Germany. Birds above the Alps fly more rapidly than those above the Lowlands at the same height. Diurnal soaring birds tend to avoid the Alps, increasingly from early to late autumn. Among raptors the tendency to cross the Alps increases with the proportion of flapping flight. The propensity to cross mountain ranges depends on the innate directions, flight capabilities, actual physiological state, weather conditions, and angle and location at which a bird happens to approach the boundary of a mountain range [23].

## Density and Timing

### *Variation Between and Within Seasons*

Only few quantitative radar studies cover complete migratory seasons. In Israel spring migration comprises about 65% of the volume of autumn migration [20, 34]. The density of nocturnal migration peaks in the last third of April when it is ten times higher than in the first third of March. In autumn high densities (comparable to peak spring densities) occur throughout September (Fig. 1) [34]. In central Europe, long-term trapping and radar data show that massive passage of long-distance migrants starts earlier than in Israel, and due to the late passage of short-distance migrants peak densities are recorded until mid-October [35].

### *Short-Term Variation Due to Weather*

Field observers record most intense diurnal migration of finches in opposing winds. Radar observations suggest that the large numbers of finches registered by field observers under headwinds does not mean that the finches prefer headwinds for their migration, but rather that circumstances make them more visible to observers on the ground, and that finches do not stop migration under adverse conditions [32]. Radar observations of nocturnal migration is less biased by extremely low-flying birds. Recent studies using pencil-beam radar to quantify the night-to-night variation in migratory intensity emphasize the statistical pitfalls in biometeorology [35] but corroborate the main conclusions drawn by Richardson in his comprehensive reviews of the subject [4, 5]: maximum numbers of most birds are recorded with fair weather and following wind. In the northern hemisphere such conditions tend to occur when a low-pressure area is to the left and/or a high-pressure

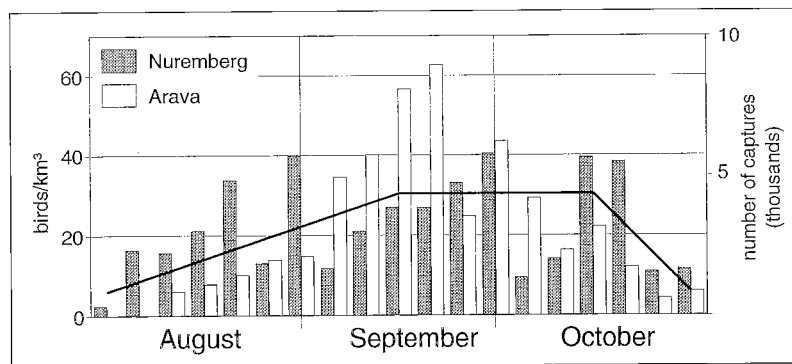


Fig. 1. Seasonal course of nocturnal migration in southern Israel (Arava Valley) compared to central Europe (Nuremberg). Each column represents the mean density of nocturnal migration per 5-day-period measured by pencil-beam radar. Solid line, the course of migration according to long-term capturing of nocturnal migrants on a pass in the Alps (Based on [34, 35])

area to the right of the main direction of migration, in autumn often after the passage of a cold front, and in spring in a warm sector. In the absence of precipitation single weather factors other than wind, such as temperature, pressure, and visibility which are correlated with these general weather conditions seem to have only minor effects on the number of birds taking off for migration at night.

### Reversed Migration

Most studies agree that wind against the normal direction of migration is the main stimulus for reversed migration. In spring these wind conditions often coincide with cold weather, suggesting hard-weather avoidance making use of favorable winds, an explanation which is, however, inapplicable to reversed migration in autumn [3, 4]. Reversed migration often occurs simultaneously with normal migration, but usually at different heights. In southern Israel the wind regime is characterized by fairly stable northeasterly tradewinds below a windshear at 1500–2000 m ASL. Above this windshear the winds are more southerly or westerly. Therefore reversed migration in autumn takes place above the windshear and in spring below it [38]. Wind-dependent reversed migration is also observed in the Alps. An important additional facet of the phenomenon is the high proportion of waders involved in these movements, which might bring these specialized birds back to more appropriate (and probably known) resting areas in the lowlands [23].

### The Diurnal Course

In inland areas of temperate regions nocturnal migration starts with a few birds, mostly waders or waterbirds, during the hour (sometimes even up to 2 h) before sunset. The main takeoff period starts between

30 min and 1 h after sunset, i.e., around dusk. In fair weather peak densities and highest altitudes are reached 1–2 h after dusk. Migration shows a slight decrease as early as around midnight and declines progressively during the second half of the night, usually ceasing before sunrise unless resting possibilities are limited or lacking. Day migration starts before nocturnal migration has completely ceased. Peak densities of diurnal migration are reached around or soon after sunrise. Migration declines in the second half of the morning. Occasionally a slight increase is observed again before sunset, but normally migration fades out during the afternoon. Woodpigeons start later in the morning than passerines, and soaring birds have their peak migration when thermal activity is highest [1, 34, 37].

In spring the nocturnal migration in the Negev (southern Israel) declines less rapidly throughout the night, suggesting that in autumn birds migrating towards deteriorating habitats tend to land earlier in the course of the night, while spring migrants continue migration towards better habitats [20].

### Height Distribution

The height zone in which most migrants fly comprises levels up to 4000 m (Figs. 2, 3). In Switzerland 50% of diurnal spring migration takes place on average below 400 m above ground while the median in nocturnal migration is at about 700 m [37]. In autumn the height distribution of nocturnal migration is similar to that in spring, but diurnal migration occurs often at considerably lower heights (Fig. 2). The distribution in single nights is influenced by the altitudinal profile of winds [36, 37].

Radar data show that low temperatures do not prevent birds from migrating at great heights. The highest migrants over Puerto Rico experience temperatures of about  $-12^{\circ}\text{C}$ , and over Switzerland migra-

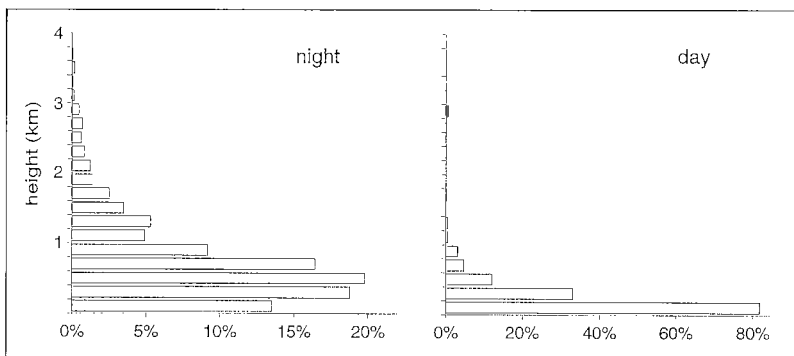


Fig. 2. Height distribution of nocturnal and diurnal autumn migration in southern Germany. The columns per height interval are based on numbers of radar echoes per unit volume. In diurnal migration – due to flocking – the number of echoes, but not necessarily the number of birds, is lower than in nocturnal migration

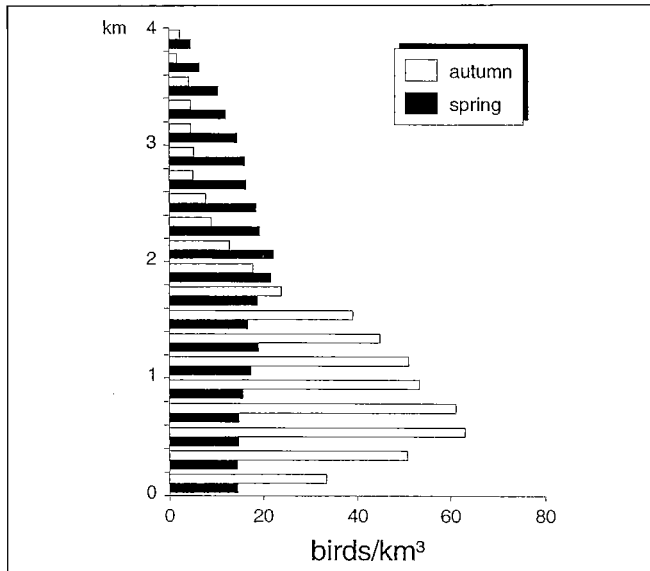


Fig. 3. Height distribution of nocturnal spring and autumn migration in southern Israel (Arava). The trade wind regime (winds from NE below and from SW above a wind shear at about 1800 m ASL) induces autumn migration to occur below the windshear. Spring migrants prefer to climb above the opposing winds at low levels for cruising flight but must cross these levels for climb and descent. (Based on [20])

tion occurs regularly at heights with temperatures around  $-10$  to  $-15^{\circ}\text{C}$ . In case of cloud layers at normal migratory heights birds often concentrate above and below the clouds [1, 37].

In southern Israel, due to the tradewind regime, the altitudinal distribution differs greatly between regions and seasons (Fig. 3). In autumn most birds fly below 1500 m; the median is 1000 m above ground in the Arava Valley (at a site 150 m below sea level) and at 450 m above ground in the Negev (450 m above sea level), thus at the same height compared to sea level. In spring the corresponding medians are at about 1800 and 1200 m [20, 34]. Maximum heights over southern Israel are reached by some large migrants (mainly flocks of waterbirds and waders) which at dawn, on their northward flight, do not descend but climb higher to profit from cooler air while aiming for better resting habitats. Thus they reach altitudes of 5000 and even 7000 m [20].

Spring migrants arrive at high altitude over Louisiana after crossing the Gulf of Mexico; about three-quarters of them fly between 1000 and 3000 m. Shorebirds departing across the Atlantic from Nova Scotia in autumn fly higher than over the mainland; they have an overall median altitude at 1700 m, and 10% fly above 3900 m, the highest flock at 6650 m. Migration across the West Atlantic proceeds at altitudes between 1000 and 5000 m, as demonstrated by

radar studies at Bermuda, Puerto Rico, and the Lesser Antilles. Especially over Puerto Rico (mainly passerine migration) and over Antigua and Barbados (mainly shore bird migration) median height may be as high as 4000–5000 m. Some migrants have been detected as high as 6800 m over Puerto Rico. In contrast, over Tobago close to the South American mainland, altitudes are mostly below 500 m, and the birds are obviously preparing to land [32].

## Directions and Orientational Behavior

If species or populations with different migratory directions migrate at different times, i.e., when winds are favorable for them, they provoke directional shifts on the radar screen which are called pseudodrift. Pronounced pseudodrift is seen in redwings, which may even reach different winter quarters in subsequent autumns when their departure takes place under different wind conditions. Taking advantage of following NE or NW winds Swedish birds may travel either to Britain and western Europe or to south-east Europe or Middle East [1].

In central Europe migration is mainly directed towards SW; the number of S and SE migrants is very small and shows no correlation with northerly or northwesterly winds; thus pseudodrift is negligible [45]. Nocturnal migrants show partial compensation for wind drift. The amount of compensation corresponds to an average speed of side-winds of 2–3 m/s. If wind speed is higher, the birds are drifted off their preferred direction of  $230^{\circ}$  (SW). High-flying birds ( $> 1000$  m AGL) maintain a heading compensating for the wind below 1000 m, i.e., increasing side wind higher up leads to increased drift. Under strong headwinds (SW  $> 10$  m/s) many birds let themselves be drifted towards SE by shifting their headings towards S [39]. When the birds reach the northern border of the Alps and fly along or between mountain ridges, the winds and the birds become canalized to a certain extent and drift effects are reduced accordingly [23]. Partial compensation at high altitudes over land is observed in many studies, while at low levels, particularly along leading lines compensation or even overcompensation occurs. Cranes and woodpigeons compensate completely over land and partially over sea according to the movements of the waves, suggesting the use of patterns on the ground for drift compensation [1]. This is confirmed by birds drifting with the wind above extended fog layers (own unpublished data).

There is evidence that increased scatter of directions occurs under fully overcast skies and is particularly

pronounced when the cloud cover is low and/or combined with rain [3], or when the sight of the sun and the stars is prevented for several days. The headings and tracks of single birds are, however, consistent and straight even when no celestial cues are available. Even birds flying in or between opaque cloud layers maintain fairly straight and level flights [40].

Radar studies from the Arctic Ocean illustrate the importance of map projections for interpreting flight paths and suggest that birds in these areas accomplish approximate great circle orientation [49]. Gradual changes of direction shown by migrating knots (*Calidris canutus*) monitored by radar in Scandinavia are in contrast to expected changes if the birds were to use star, sun, or magnetic compass over longer distance. Contrary to expected constant direction (if using star compass), or clockwise directional shifts of a few degrees (if relying on the sun or magnetic compass), the knots showed an anticlockwise directional shift [24, 49].

## Flight Behavior

Since the late 1960s flight theory predictions and exact data on actual migratory flights, provided particularly by tracking radar, have improved our understanding of flight strategies, optimization of migratory flights, and flight mechanics [1, 42]. Echo signatures provide information on flocking behavior and on the wing beat pattern of birds tracked individually [6]. They can also be used to study flight mechanics under different environmental conditions and in different flight phases.

### *Flying Singly or in Flocks*

In daytime, most migrants fly in flocks. The main exceptions are the birds of prey; large raptors usually fly singly. Smaller species such as some falcons and the Levant sparrowhawk (*Accipiter brevipes*) may migrate in flocks; however, when migrating at night, they are detected singly [13].

The start of nocturnal migration often takes place in flocks; this is true particularly for waterbirds and waders. Nocturnal passerine migrants and to a lesser extent waterbirds and waders segregate to fly singly or in very loose associations in progressing darkness. Most nearest neighbor distances over central Europe are larger than 50 m even in very dense migration [37]. Above the Swiss Lowlands, 90% of the nocturnally tracked targets are single passerines [37].

Above southern Israel 50–60% are single passerines, 20–30% of the targets show the continuous wing beats characteristic for wader- and waterfowl-type birds. The remaining 20% were unidentifiable targets (including insects, bats and flocks of birds) [20, 34].

### *Airspeed*

Tracking radar data show astonishingly similar airspeeds for different wing-beat categories but explainable differences between sites [38, 45]. Birds with slow continuous wing beats SC (comprising waders and waterfowl, but also slower flyers such as swifts) have airspeeds of roughly 14 m/s above the Swiss Lowlands (a), nearly 15 m/s above the Swiss Alps (b), and 12–13 m/s in southern Israel (c); the higher speed in (a) and (b) than in (c) is due to a higher proportion of ducks in the European samples; the difference between (a) and (b) in all wing beat classes is due to the selectivity of fat and long-winged long-distance migrants for flights across the Alps. The airspeeds of birds with fast continuous wing-beats FC (comprising among others small waders) at the corresponding sites are: (a) 11 m/s, (b) 12.5 m/s, (c) 12–14 m/s, comprising a wider spectrum of fast long-distance migrants in Israel. The values for SI (slow intermittent flapping) are: (a) 13.5, (b) 14.5, (c) 10.5 with a high proportion of fast-flying starlings and big thrushes in Europe and many chats and shrikes in Israel. For FI (fast intermittent flapping comprising mainly warblers and flycatchers) the values are: (a) 11, (b) 12.5, (c) 11–11.5.

There is a discrepancy between the relatively low speeds of SC and FC mentioned above and the high speeds of identified waders in Iceland (14.8 and 15.4 m/s in two climbing flights) and Sweden (16.4–20.3 m/s). The average airspeed of 77 bird echoes departing from Iceland was 17 m/s and even 20.3 m/s in 104 knots (*Calidris canutus*). Relatively low airspeeds are reported, for example, for Arctic tern (*Sterna paradisea*; 11.3 m/s, which is faster than the maximum range speed for this species) and for several Antarctic seabirds (mostly between 11 and 14 m/s) [24]. Low airspeeds were also recorded in waders departing from Mauretania with high fat loads. If only birds with climbing rates of less than 0.5 m/s are considered, the airspeeds are for FC: 10–14 m/s (3 *Calidris alpina*), 14 m/s (1 *Arenaria interpres*); for SC: 13 m/s (1 *Calidris canutus*), 12–14 (2 *Tringa totanus*), 15.5–19.5 (2 *Tringa nebularia*), 12–17 (5 *Pluvialis squatarola*), 7–18 (8 *Limosa lapponica*), 9–15 (20 *Numenius phaeopus*) [46]. These single species accounts demonstrate a high intra- and inter-specific variation.

## Vertical Speeds

Climbing and descending birds are found in similar proportions throughout the night. Only in the first hour after dusk is there a surplus of climbing birds, while in the hour before dawn the proportion of descending birds is slightly increased. In Israel the proportion of climbing birds during the first hour of the night is different between autumn (60% climbing) and spring (75% climbing) because in spring birds must climb above the trade winds. The average climbing rates of all birds with positive vertical speed throughout the night is 0.5 m/s in autumn and 0.9 m/s in spring (maxima up to 4 m/s) [36].

Measurements of sustained climbing rates and airspeeds of 15 species of different size reveal an inverse correlation between body size and climbing rate; the lowest mean climbing rate (0.31 m/s) was observed in the mute swan (*Cygnus olor*) and the highest in the dunlin (1.63 m/s). Radar data on waders departing from Iceland show climbing rates which agree with optimal climbing rates calculated on the basis of prevailing winds. However, shorebirds departing from Mauretania in spring climb at slower rates (and with lower horizontal speeds) than predicted [46].

## Flight Mechanics of Small Birds with Intermittent Flapping

The flight of small and medium-sized passerines is characterized by alternating flapping and pausing phases. Medium-sized species may keep their wings partially open during the pauses, while smaller species close their wings completely, maintaining high speed while losing height in undulating flight.

A recent tracking radar study emphasizes high individual variation in all the measurable parameters (wing beat frequency, length of beating and resting phases, horizontal and vertical speed) [41]. Variation is extreme in released birds; but even in free flying birds a variation of  $\pm 10\%$  or even 15% in wing beat frequency seems to be quite normal. The vertical speed is in most species controlled by the duration of flapping over a certain time, mainly by varying the length of the beating phase; some species additionally adjust their pausing phases. Slight variations in wing beat frequencies with vertical speed are inconsistent between species. First indications derived from European robins (*Erithacus rubecula*) suggest that species closing their wings completely during the pausing phases may increase horizontal speed by higher wing beat frequency and longer pausing

phases. In species keeping their wings partly open during pausing phases (e.g., thrushes, swifts), there is no consistent variation in the measured parameters, suggesting that factors that have not been measured such as the amplitude or angle of wing beats may be important. Higher flight altitudes are correlated with increased airspeeds and higher wing beat frequencies in some but not all the studied species.

According to theory, the speed of migration is not the one with minimum energy consumption per unit time but the one with minimum energy consumption per distance covered [42]. Tracking radar studies on common swifts (*Apus apus*) proved for the first time in free-flying birds that these two distinct flight speeds exist, the swifts using the speed of minimum power (around 23 km/h) for nocturnal resting flights and the speed of maximum range (around 40 km/h) for migratory flights [43].

Theory also predicts that the speed of maximum range ( $V_{mr}$ ) varies with wind, because maximum range can be attained at slightly reduced air speed in tailwinds and requires increased air speed in headwinds [42]. Radar data provide broad support for this theory. Large sets of radar data have allowed the theoretical models to be improved to include sidewinds instead of being restricted to direct head- and tailwinds.  $V_{mr}$  depends not only on the effect of wind on the actual groundspeed of the birds but also on its angle of compensation for sidewinds. As a result, optimal flight speeds are higher in sidewinds than in tail- or headwinds with the speed increment caused by wind [39].

## Flight Mechanics of Birds with Continuous Flapping

Continuous wing beats are used by a large variety of taxonomic groups and size classes [20, 38]. Birds as large as swans, geese, ducks, and herons as well as small birds such as small waders fly large distances by continuously beating their wings. Even large passerines such as crows use continuous flapping in sustained level flight. Only in fairly steep or extended descending flights or in considerable updrafts do these birds interrupt their wing beats. As continuous wing beats would not allow varying the vertical speed by variation of pausing and flapping phases, wing beat frequency was the obvious candidate to be responsible for such maneuvers. However, data are not consistent with this hypothesis. The following preliminary results of various authors are discussed in [44]. Free-flying migrants with continuous flapping flight altering their vertical speed did not show



the expected change in wing beat frequency and were thought to use other means (e.g., angle of attack or amplitude of wing beats) for their moderate climbing and descending. Waders under extreme conditions (released from a helicopter) showed the expected variation of wing beat frequency in steep climbs and descents (+2 to -3 m/s). A species with low wing-loading (*Corvus corone*) in free flight varied its vertical speed from -1 to +2 m/s by varying the wing beat frequency (average 3.6 Hz) over a range of 1.5 Hz, which accounts to more than  $\pm 20\%$ .

### *Birds of Prey and Other Soaring Birds*

Average climbing rates in thermals range from 1.5 to 2.1 m/s in Israel; the highest climbing rates, occasionally up to 5 m/s, are reached around noon. The climbing rates do not differ significantly among species but do differ according to atmospheric conditions [47]. Honey buzzards, for example, have average climbing rates of 1.67 m/s in Israel and 0.44 m/s in Switzerland, where they compensate for lack of thermals by additional wing-flapping at low flight levels [11].

During interthermal gliding the mean airspeed of various raptor species is positively and gliding angle negatively correlated with body mass, the larger species compensating power constraints due to size by better gliding performance. Large species such as eagles and buzzards show soaring-gliding flight during more than 95% of their migratory flights, while smaller species such as harriers, sparrowhawks, and falcons show increasing proportions of flapping in spite of the fact that they also prefer the energy-saving soaring-gliding strategy in good thermal conditions. The larger the raptor species the more the birds optimize their flight behavior by adjusting gliding speed to the actual climbing rates achieved under the given conditions. Harriers prove to be just in the transitional size category where the largest species is closer to the typical soaring migrants, maximizing cross-country speed when soaring and gliding, whereas the smaller species are less adapted to this optimal use of thermals but efficiently combine different flight styles [47]. White storks show less adjustment of gliding speed to climbing rate, suggesting that for these social birds it is more important to keep contact with a flock of conspecifics than to optimize flight performance [48].

Levant sparrowhawks have an extremely flexible migration strategy which includes nocturnal activity [47]: (a) when good thermals are available, the predominant flight style is soaring-gliding; (b) under

such conditions they maximize cross-country performance relative to the air according to optimal flight theory and thus minimize time per distance traveled in an overall cheap flight style; (c) they can also use flapping-gliding flight when thermal activity is low and thus are able to extend the time available for migration; (d) high numbers of Levant sparrowhawks have been tracked at night, flying by typical flapping-gliding flight at significantly higher altitudes than in diurnal flights. The use of flapping flight at the edges of the day and nocturnal flights by migrants with good soaring capabilities indicates a preference of minimizing time versus minimizing energy. The fact that nocturnal migrants are observed mainly in the Arava Valley (at the edge of the migratory corridor), nearly exclusively in autumn and increasingly towards the end of the season, suggests that night flights may be a means for late individuals to keep up with the tight endogenous schedule of the species.

An analysis of the soaring performance of Antarctic and Atlantic seabirds showed, for example, that albatrosses under calm conditions reach travel speeds of about 10 m/s, using swell-soaring, turning, and twisting extensively within a width of 300–500 m laterally from the overall direction of movement. In windy conditions they traveled at a faster rate (22.5 m/s on average) using a combination of wave soaring and dynamic soaring. Airspeeds of most of these marine species fall between the minimum power and maximum range speed estimated from aerodynamical theory [24].

### **Conclusions**

This paper does not deal with the subject of bird migration as a whole; it is confined to a specific research method which aims primarily at recording the course of the migratory movements of free-flying birds. Radar studies are compared best with visual or infrared observations and with moon watching. These are the core methods behind our knowledge of the phenology and geographical pattern of bird migration all over the world. In contrast to catching, ringing, and radiotracking studies, there is no need to trap and mark the birds except when data on identified individuals are requested. Unlike physiological studies, wind tunnel measurements on aerodynamics and cage experiments on activity patterns or orientation of birds, radar studies can usually do without manipulating the birds and are thus important complements to work in the laboratory. Long-term stud-

ies involving a large number of observations under different environmental conditions or the careful selection of observation sites in view of the questions asked replace to a certain extent an experimental approach. Thus radar offers important research capacities in determining reactions of migrants to environmental conditions. Reactions of birds to geomorphological and meteorological factors as well as to variation in the appearance of orientational cues such as the sun, stars, and magnetic field can be tested by recording variations in (a) density and altitudinal distribution of migration, (b) directions (tracks, headings, compensation for wind drift), (c) vertical and horizontal speeds over ground and relative to the air (including compensational efforts), and (d) flight mechanics (e.g. wing beat pattern in varying flight phases). The results combined will continue to improve our understanding of migratory strategies in birds.

Major supporters of Swiss Radar Ornithology are: The Swiss Army, Oerlikon-Contraves AG, and the Swiss National Science Foundation with several grants since 1969, currently grant no. 31-43242.95. Thomas Alerstam, Lukas Jenni, Verena Keller, Felix Liechti and W. John Richardson provided valuable suggestions to improve the text.

1. Alerstam, T.: Bird Migration. Cambridge, University Press 1990
2. Alerstam, T., Lindström, Å., in: Bird Migration (E. Gwinner ed.). Berlin: Springer 1990
3. Eastwood, E.: Radar Ornithology. London: Methuen 1967
4. Richardson, W.J.: *Oikos* 30, 224 (1978)
5. Richardson, W.J. in: Bird Migration (E. Gwinner ed.). Berlin: Springer 1990
6. Bruderer, B.: *Naturwissenschaften* 84, 1 (1997)
7. Kerlinger, P.: Flight Strategies of Migrating Hawks. Chicago, University of Chicago Press 1989
8. Buurma, L.S., Lensink, R., Linnartz, L.G.: *Limosa* 59, 169 (1986)
9. Schmid, H., Steuri, T., Bruderer, B.: *Orn. Beob.* 83, 111 (1986)
10. Richardson, W.J. in: Proc. N. Am. Hawk Migr. Conf. (M. Harwood ed.). Syracuse 1975
11. Bruderer, B., Blitzblau, S., Peter, D.: *Ardea* 82, 111 (1994)
12. Leshem, Y.: Proc. Bird Strike Committee Europ 21, 243; Jerusalem (1992)
13. Stark, H., Liechti, F.: *Ibid* 135, 233 (1994)
14. Bergman, G. in: Rassegna Intern. Elettronica Nucleare ed Aero-spaziale (Roma) 24, 215 (1977); Bergman, G.: *Oikos* 30, 393 (1978)
15. Alerstam, T.: *Die Vogelwarte* 28, 1 (1975)
16. Alerstam, T., Ulfstrand, S.: *Ornis Scand.* 5, 99 (1972); Alerstam, T., Ulfstrand, S., *Ornis Scand.* 6, 135 (1975)
17. Rabøl, J.: *Dansk orn. Foren. Tidsskr.* 68, 5 (1974)
18. Hilgerloh, G.: *Naturwissenschaften* 76, 541 (1989); Hilgerloh, G.: *Auk* 106, 233 (1989)
19. Grimes, L. G.: *Ibid* 116, 165 (1974)
20. Bruderer, B.: *Ostrich* 65, 204 (1994)
21. Bruderer, B., Jenni, L. in: Bird Migration (E. Gwinner ed.). Berlin: Springer 1990
22. Buurma, L.S.: *Isr. J. Zool.* 41, 221 (1995); Buurma, L.S.: *Veilig Vliegen* 33, 10 (1986)
23. Bruderer, B.: *Orn. Beob.* 93, 119 (1996)
24. Gudmundsson, G.A.: Flight and migration strategies of birds at polar latitudes. Thesis., Lund 1992
25. Alerstam, T., Ulfstrand, S.: *Ornis Scand.* 5, 13 (1974)
26. Kestenholz, M.: Movements and roosting behavior of diving ducks (*Aythya fuligula* and *A. ferina*) wintering in Switzerland. Thesis, University of Basel, Sempach 1995
27. Williams, T.C., Williams, J.M. in: Bird Migration. (E. Gwinner ed.). Berlin: Springer 1990
28. Johnson, S.R., Herter, D.R. in: Bird Migration. (E. Gwinner ed.). Berlin: Springer 1990
29. Richardson, W.J., Johnson, S.R.: *Arctic* 34, 108 (1981)
30. Alerstam, T., Gudmundsson, G.A., Jönsson, P.E., Karlsson, J., Lindström, Å.: *Arctic* 43, 201
31. Alerstam, T., Hjort, C., Högstedt, G., Jönsson, P.E., Karlsson, J., Larsson, B.: *Medd. Grönl. Biosci.* 21, 3 (1986)
32. Alerstam, T. in: Animal Migration (Aidley, D.J. ed.) Cambridge, Cambridge University Press 1981
33. Bruderer, B., Liechti, F., Steuri, T.: *Alauda* 64, 7 (1996)
34. Bruderer, B., Liechti, F.: *Isr. J. Zool.* 41, 477 (1995)
35. Baumgartner, M.: Wetterabhängigkeit des nächtlichen Vogelzuges im Herbst über Süddeutschland. Thesis, University of Basel, Sempach 1996
36. Bruderer, B., Underhill, L.G., Liechti, F.: *Ibis* 137, 44 (1995)
37. Bruderer, B.: *Orn. Beob.* 68, 89 (1971)
38. Liechti, F., Bruderer, B.: *Isr. J. Zool.* 41, 501 (1995)
39. Liechti, F.: *J. Orn.* 134, 373 (1993); Liechti, F., Hedenström, A., Alerstam, T.: *J. theor. Biol.* 170, 219 (1994)
40. Able, K.P.: *Acta Congr. Int. Orn.*, 540, Berlin (1980)
41. Stark, H.: Flugmechanik nachts ziehender Kleinvögel. Thesis, University of Basel, Sempach 1995
42. Pennycuik, C.J.: *Isr. J. Zool.* 41, 307 (1995); Pennycuik, C.J.: Bird flight performance. Oxford: Oxford, University Press 1989; Rayner, J.M.V.: *Isr. J. Zool.* 41, 321 (1995)
43. Bruderer, B., Weitnauer, E.: *Rev. suisse Zool.* 79, 1190 (1972)
44. Althaus, H.P., Bruderer, B.: *Orn. Beob.* 79, 45 (1982)
45. Liechti, F.: Flugverhalten nächtlich ziehender Vögel in Abhängigkeit von Wind und Topographie. Thesis, University of Basel, Al-lenspach 1992
46. Hedenström, A.: Ecology of avian flight. Thesis, Lund 1995
47. Spaar, R.: Flight behavior of migrating raptors in southern Israel. Thesis, University of Basel, Sempach 1996
48. Liechti, F., Ehrlich, D., Bruderer, B.: *Ardea* 84 (in press)
49. Alerstam, T.: *J. exp. Biol.* 199, 9 (1996)
50. Richardson, J.W.: *The Auk* 95, 717 (1978)