Routes of migrating soaring birds

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Soaring migrants travelling through Israel use three principal routes which are used in the opposite directions during the spring and autumn: (1) the Western Route lies mainly along the western edge of the central mountain range, (2) the Eastern Route lies mainly along the Jordan Valley, crossing the mountain range during part of the day, continuing southward along the Dead Sea towards the Sinai, and joining the Western Route in autumn and (3) the Southern–Elat Mountains Route. The geomorphological structure of Israel, with a central mountain range dividing the country roughly into three landscape units, plays a central role in route selection. In the autumn, the Western Route migration axis is deflected at the beginning of the day from east to west for 10–25 km, depending on weather conditions and the flock's roosting locations. Between 10.00 h and 11.00 h, the daily breeze blowing from the Mediterranean Sea influences the migration axis, which is slowly deflected back to the east. A parallel deflection of the migration axis occurs in the Eastern Route in the autumn. The route moves southwest over the eastern slopes of the central mountain range during the morning hours and over the slope, which absorbs direct radiation from the sun, creating good soaring conditions. Towards late afternoon, when the breeze from the sea starts, the axis is deflected to the east, to the Jordan Valley. In the Elat Mountains, the wind flow plays a similar role, but because the topography of the southern Arava Valley causes a change in wind direction, the axis moves during the day in a north–south direction. In addition to the axis movement on a daily scale, a seasonal deflection of the migration axis from east to west also exists. During autumn migration, early migrants (e.g. White Storks *Ciconia ciconia*) tend to travel on an eastern route, while late migrants (e.g. White Pelican *Pelecanus onocrotalus*) travel along the Mediterranean coast. This fluctuation was probably because of sub-optimal soaring conditions along the coastal plain during August. In September, temperature differences between the sea and land decrease and the influence of the marine inversion gradually declines, until its influence disappears completely in October. A comparison of the numbers of soaring birds seen over Israel in the autumn and spring shows significant seasonal differences in the use of the various routes. For example, only one species, the Steppe Eagle *Aquila nipalensis*, flies over the Elat Mountains in the autumn, compared to more than 30 species in the spring. In the autumn, White Storks pass over only along the Jordan Valley axis, whereas in the spring, about half the migrating storks also pass over the western edge of the central mountain range. Honey Buzzards *Pernis apivorus* fly along the Western Route in large numbers in the autumn, while concentrating almost totally over the Elat Mountains in the spring. These differences are related to the global migration routes between the breeding and the wintering grounds in relation to the Red Sea, which birds avoid crossing, thus causing them to follow different routes in autumn and spring.

Medium and large birds, whose wing loadings are relatively high, tend to migrate by soaring, using horizontal or vertical (thermals) winds rather than active flight (Alerstam 1990). Geomorphology and climate have a major role in determining the location and direction of such winds (Kerlinger 1989). Mountain ridges, such as the Kittatinny Ridge in eastern North America (Broun 1945), the Rocky Mountains in western North America (Hoffman 1985) and the Rift Valley in East Africa (Brown 1970), create "highways" for soaring birds. Large atmospheric pressure cells (such as the Bermuda high pressure cell) and prevailing winds have considerable influence in determining directional strategies of migrants in North America (Gauthreaux 1978, Kerlinger & Gauthreaux 1985). However, little field work has been carried out on the actual relationship between geomorphology and climate and the determination of the migratory routes of soaring birds. The location of the Mediterranean, Black and Caspian Seas between the breeding and wintering grounds of western Palaearctic migrants forces these birds to encircle these large water bodies, and, in places along their migration routes, they fly in relatively narrow corridors rather than on wide fronts (Yom-Tov 1984). Hence, the migration routes of most western Palaearctic soaring birds pass over Israel, where they are funnelled between the Mediterranean Sea and the Rift Valley, a distance of about 100 km at its widest point. This situation creates a unique opportunity to observe large numbers of soaring birds, comparable only with Panama, and to determine how climate and geomorphology affect the routes of soaring migrants.

Observations on the routes of soaring migrants passing through Israel revealed that the routes of some individual species change diurnally and seasonally (Safriel 1968, Shirihai 1987, Shirihai & Christie 1992, Liechti *et al.* 1997, Spaar 1997, Spaar & Bruderer 1997a,b). Even locally, the two main factors which affect these changes are geomorphology and climate. Geomorphologically, Israel has three north–south structures (Fig. 1). (1) There is a coastal plain along the Mediterranean shore, whose width varies from a few hundred metres near Mount Carmel in the north to about 40 km in the south. (2) There is a central mountain ridge, composed of the Galilee, Gilboa, Samarian, Judean and Negev Ridges, intersected by several west–east valleys (the largest being Yizre'el and Bet She'an in the north and Beer Sheva in the south). These ridges extend several hundred metres above sea level, and their highest peaks are between 1000 m and 1208 m. The western slopes of these ridges rise gradually, but their eastern slopes are much steeper, and in the Judean desert, near the Dead Sea, these ridges create a line of high cliffs (up to 400 m). (3) The Rift Valley, which stretches from southern Africa to Syria and in Israel is composed of the Jordan and the Arava valleys, is also an important geomorphological structure. The Jordan River and Dead Sea lie at the bottom of the Rift Valley and are up to 400 m below sea level.

The geomorphological structure of Israel has an important effect on its climate, particularly on the wind patterns. In the east, the Rift Valley is ideal for the creation of thermals because its low position causes adiabatic heating of air, and this heating is enhanced by the sparcity of the vegetational cover. In the west, there is a daily wind pattern. The land heats faster than the sea, causing air masses to rise above the land. These rising air masses create thermals while cool sea air streams eastward, creating a sea breeze which starts several hours after sunrise. This sea breeze climbs along the western slope of the mountains, reaching the tops at about noon. Similar phenomena are known along other coastlines (Lyons 1972, Pielke 1984).

This paper reports the results of migration surveys of soaring birds carried out in Israel during the 1980s and

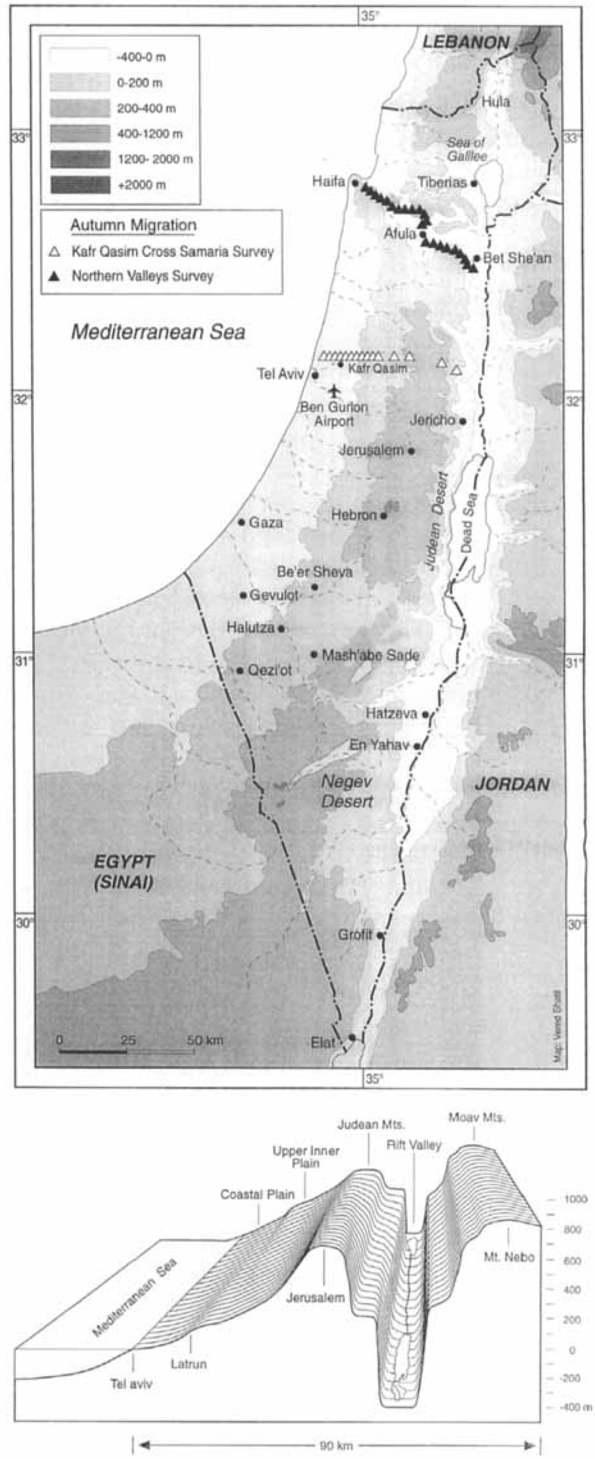

Figure 1. (a) Topographical map of Israel; (b) A cross-section from the Mediterranean Sea to the east. The Northern Valleys and cross-Samaria–Kafr Qasim surveys are marked.

discusses the effects of geomorphology and climate on the routes of migrants.

MATERIALS AND METHODS

The study was carried out for four successive autumn (August–November) and four spring (March–May) migration seasons during 1986–1989. The methods used were described in detail in Leshem and Yom-Tov (1996a,b). Briefly, we used four methods: spreading ground observers along a broad front between the Mediterranean Sea and the Jordan Valley, using a two-seat motorized glider which joined the flocks during flight, using a light aircraft which followed specific flocks and using data concerning flocks seen by the Ben Gurion Airport radar.

For spring migration, we also present data from 6 years of raptor migration tracking in the Elat Mountains area: during 1977 (Christensen *et al.* 1981), during 1983 and 1985–1988 (Shirihai & Christie 1992) and, after we had learned where the western migration axis passed, during stork migration in 1987–1990. Incomplete data for other years were ignored. Pelican spring migration was not followed systematically because most migrating pelicans in the spring flew parallel to the coastline, over the Gaza Strip, and we were unable to spread observers regularly in this area.

To study the long-term regularity of arrival times for different species, the average first sighting day for all survey years in Israel was calculated for each species. The calculation of the appearance date was weighted so that the date took into account the number of birds counted on each survey day. Each day of the calendar year was numbered from 1 to 365 (or 366). For each species, we then calculated the average weighted appearance day for each year, the average arrival day for all years and their 99% confidence intervals (CI). In addition, for each species, we also calculated the peak migration day and the proportion (percentage) of birds passing during the peak migration day.

All means are shown with ±1 s.d.

RESULTS

Migration routes in the autumn

Data from the cross-Samaria–Kfar Qasim autumn migration survey (ground observer network) showed that, on average, 87% (±5.1%) of all individuals of 35 raptor species (total annual average was 508,676 birds) passed over a 20.3-km-wide front, between observation posts located 10.7–31.0 km east of the Mediterranean coast. A second concentration of 7% (±3.0%) of the birds passed over a 22.5-km-wide front, 37.5–60 km east of the coast. The largest concentration, which included an average of 17% (±4.2%) of the raptors, passed over the station located at the Kfar Qasim fields 16 km east of the coast. While most raptors migrated west of the mountain ridge, the majority (88%) of migrating White Storks *Ciconia ciconia* passed over a narrow front 52–70 km east of the Mediterranean coast (Jordan Valley route) and only 12% of the storks passed over west of this area.

The results of the ground observer network were confirmed by radar observations at the Ben Gurion International Airport. These data showed that a large concentration of migrating birds occupied a front whose width was 31.0 ± 14.4 km (n = 1400) on average, lying 11.2–42.0 km west of the Mediterranean coast. Flocks progress on an azimuth of 195.5 ± 13.1°). A similar front of 25.6 ± 9.4 km (n = 700) was observed in the spring 12.5–38.1 km from the coast. Flocks in spring progressed on an azimuth of 18.4 ± 14.2°. Hence, the radar data revealed that migration routes in the spring and autumn overlap almost completely. Similar results were obtained from analysis of motorized glider data and showed that, during 85% of the flights, the flocks flew along a well-defined route 10–30 km east of the Mediterranean coastline.

Unlike raptors, which migrate along the western route 10–30 km east of the coastline, White Pelicans *Pelecanus onocrotalus* used a route a few kilometres to the west. Most raptors flew northeast of Mount Carmel and immediately continued to the Samarian slopes. Pelicans, after roosting in the Hula area or in fish ponds in the northern valleys (Yizre'el Valley or farther west in the Zevulun Valley), tended to cross Mount Carmel, flying 8–20 km east of the coastline. When they reached the coastal plain, they kept continuous visual contact with the Mediterranean coast, changing direction to the south about 30 km south of Tel Aviv, then approaching the coast even more, and in most cases, crossing into Egypt south of Gaza, 40–50 km northwest of the raptor and stork crossing point (Fig. 2). However, the cross-Samaria–Kfar Qasim survey ended each year between 15 and 20 October. Thus, the data on White Pelican migration, which continued to the end of November, were incomplete.

During 1988–1989, the survey was moved 60 km north of the cross-Samaria–Kafr Qasim axis to the Yizre'el–Bet She'an Valleys. The data from this survey presented a different picture, with raptor migration spread over a broader and less well defined front. Most (79.7 ± 3.0%) Honey Buzzards *Pernis apivorus* passed over 30–50 km east of the coast, most (76.0 ± 6.1%) Levant Sparrowhawks *Accipiter brevipes* between 24 and 44 km and most (69.7 ± 4.0%) Lesser Spotted Eagles *Aquila pomarina* between 14 and 28 km. Cessna and motorized-glider flights confirmed these observations. The main reason for the difference between the results obtained by the two surveys during the autumn seems to be related to the topographical structure of Israel. Raptors migrating along the Northern Valleys Route pass over on a broader front, which narrows as the raptors converge on their way south to the western slopes of the Samaria Mountains or on their way east to the Jordan Valley.

The above results indicated that soaring birds migrated over northern and central Israel along two routes, both in a general north–south direction. A western route which followed the western slopes of the central mountain ridge (Samaria and Judea) and an eastern route which followed the Rift (Jordan) Valley parallel to the eastern slopes of the cen-

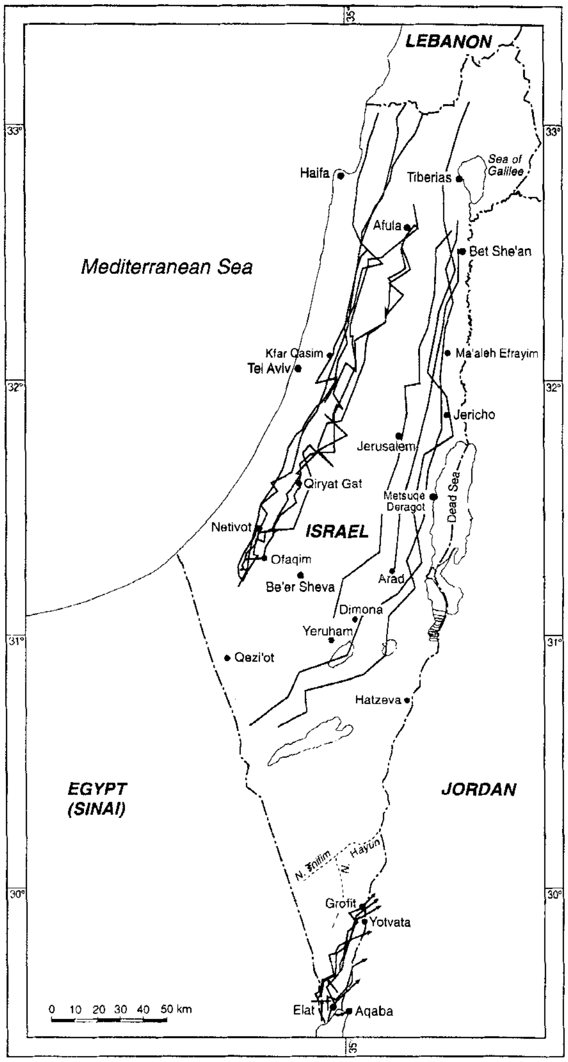

Figure 2. Migration routes of soaring birds in Israel, as determined by following flocks with a motorized glider and light aircraft during the spring. Flocks using the western route were White Storks, the eastern route were White Storks and Lesser Spotted Eagles (the easternmost line) and the Elat region were Honey Buzzards.

tral mountain ridge. Figure 2 depicts a number of characteristic White Stork and Honey Buzzard flights, mapped along the eastern migration route. The eastern route was a continuation of the raptor and stork route which ran from the Baq'a Valley in Lebanon, as observed by Hasson (1984) and M. Adar and E. Haddad (pers. comm.). This route continued south along the Hula Valley and Sea of Galilee (Fig. 2).

As the winds extended farther inland in the afternoon, the eastern migration route drifted east, and storks and raptors were seen along the Jordan Valley and the Judean Desert Plateau. As evening neared, flocks landed on the fault escarpment or above it on the Judean Desert Plateau. Flocks arriving in the evening in the southern part of the Jordan Valley between the Jericho area and the southern coast of the Dead Sea took off in the morning, continued parallel and southeast to the route described above, flew southwest above the central Negev and entered the Sinai at about midway between the Mediterranean and the Red Seas (Fig. 2). The width of both parts of the eastern migration route was 15–20 km. The magnitude of the passage varied with weather conditions and the daily wind regime.

A third route of migration was located in the Elat Mountains, where soaring birds avoided crossing the Red Sea by flying north of it (Fig. 2). For reasons explained later, this route was hardly used by soaring birds in the autumn.

Migration routes in the spring

Migration routes in the spring were almost identical to the autumn routes, with birds flying in the opposite direction. Although some pelicans and raptors took the western route, White Stork migration was the most conspicuous. At least half of the migrating White Storks moved along the western slopes of Israel's mountains (239,100 ± 61,400 birds). Despite the fact that this route lies partly over heavily populated areas, this route was not known previously, and both Paz (1987) and Schuz *et al.* (1963) considered the Jordan Valley Route to be the main migration route of the White Storks. Tens of thousands of raptors passed over with the storks, but their numbers were smaller than in the autumn by at least an order of magnitude. The spring stork route generally overlapped the western raptor route of the autumn, except that the spring stork route frequently continued directly north after crossing the Yizre'el Valley, whereas the raptor route continued in a northeasterly direction. Occasional glider flights with flocks of White Pelicans in the spring and many random observations led us to believe that pelicans also followed overlapping routes in the spring and autumn.

In the Negev Desert, the major mass of White Stork migration passed in the north, across a 27.5-km front. This route was confirmed with radar and motorized glider. Manpower problems prevented us from following the southeasterly axis every survey year.

Near Elat, the main mass of migrating raptors converged over the Elat Mountains from Sinai and crossed into Jordan (Southern Route; Fig. 2). It included raptors, mainly Honey Buzzards, as well as a small number of White Storks which passed over the Elat Mountains in a north–northeast direction and then turned northeast into Jordan at the Grofit junction area, about 50 km north of Elat. During light aircraft scans over the Arava Valley, from the Grofit junction to Hatzeva, almost no migration was seen. Only on days when initially northerly winds became southerly were some of the flocks deflected to the north, crossing into northern Jordan.

Daily variation in the migration path

Sequential photos taken on the Ben Gurion Airport radar showed that the direction of migration was remarkably sta-

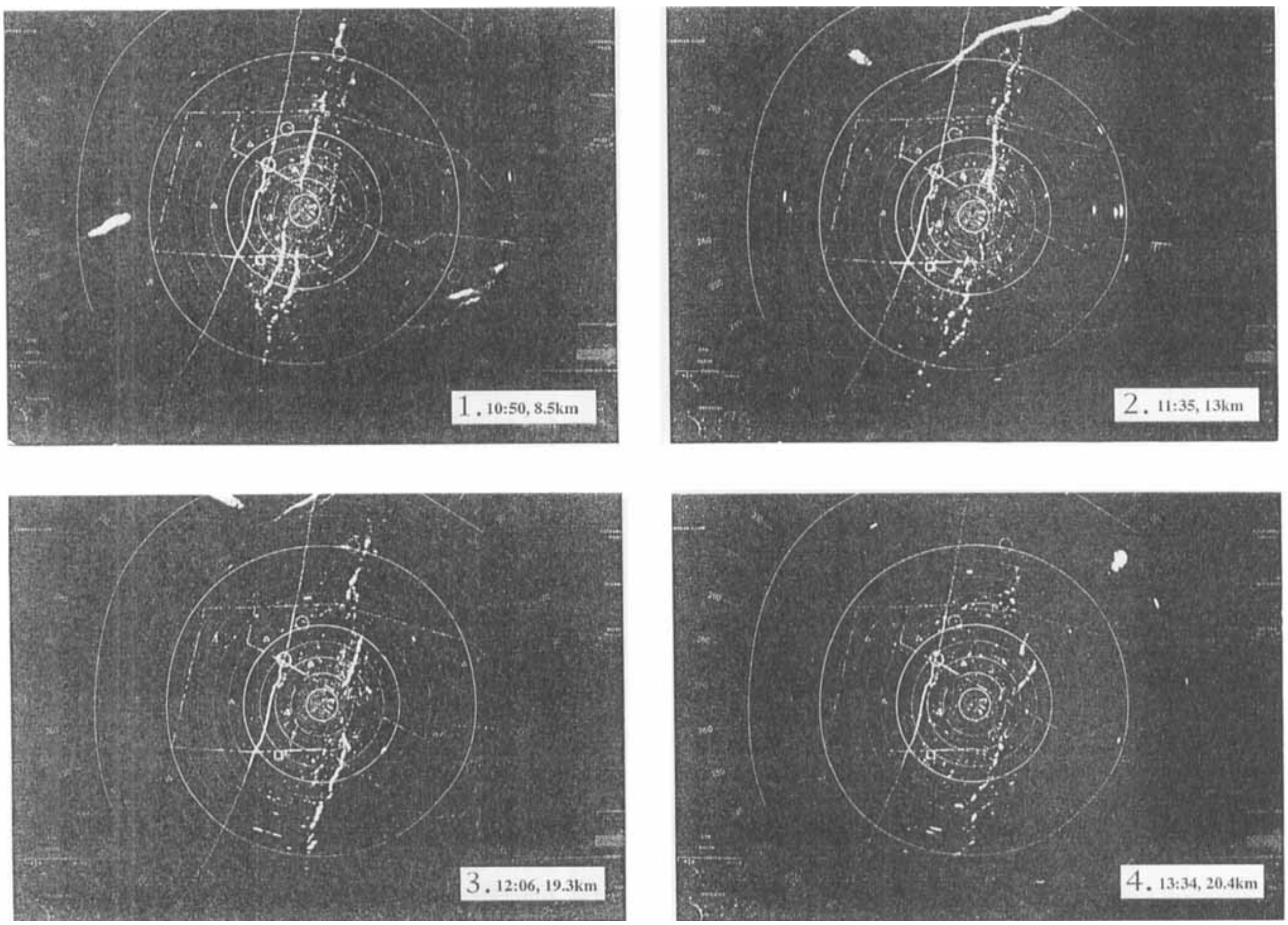

Figure 3. Four photographs taken from a continuous sequence of flocks of Lesser Spotted Eagles taken on the Ben Gurion Airport radar, 27 September 1988 between 09.13 h and 14.13 h (5 h). The centre of the circles is Ben Gurion Airport and the circles are intervals of two nautical miles. The thin line crossing the figure approximately from north to south is the Mediterranean coastline. The thicker lines east of the coastline are flocks of migrating birds, some of which are 90 km long. Data on time and distance from the coastline are in the bottom right of each photograph (1–4). The birds were deflected by the sea breeze from a mean distance of 8.5 km to 23.3 km from the sea.

ble. The mean directions of 700 flocks of Lesser Spotted Eagles and Honey Buzzards in the autumn were 198° ± 10.1° and 201° ± 16.1°, respectively, and that of 700 flocks of White Storks in the spring was 18.1° ± 14.2° (i.e. almost exactly in the opposite direction). These directions drifted during the day by not more than 5°, first from east to west and later from west to east. These fluctuations occurred within the migration routes described above, and only in some unusual cases, as a result of weather conditions, was the axis deflected outside those boundaries. Figure 3 showed an easterly deflection in time, along the Judean and Samarian Mountain slopes. Between 10.50 h and 13.34 h, the route of White Storks drifted 19.6 km east. However, in the spring, unlike autumn, no westerly drift was detected. The pattern from the Northern Valleys survey was similar, although slightly deflected. Honey Buzzard migration, in this case, drifted more to the west between 07.00 h and 11.00 h and only then did the easterly drift commence. This difference resulted from the fact that in the Northern Valleys the migration route of all flocking raptor species was more easterly than the Kfar Qasim route. In both survey areas, Lesser Spotted Eagles tended to travel about 14–16.5 km farther to the west than Honey Buzzards, and when comparing the two surveys, the differences in the former species were less noticeable than in the latter (Table 1). The deflection of the Honey Buzzard migration axis is demonstrated in Figure 4. At 07.00 h, it converged mainly in the east (40–50 km from the coast); until 11.00 h the axis moved west, up to 10–15 km from the coast, and then moved east with the sea breeze later on. A similar situation was found for Lesser Spotted Eagles but over a narrower front.

Daily migration route fluctuations

To study diurnal fluctuations in the distribution of migratory flocks, we selected the two principal species migrating in the autumn, Honey Buzzard and Lesser Spotted Eagle, for comparative study (Fig. 5). Honey Buzzards started to mi-

Table 1. *Distance from the Mediterranean Sea and passage times of 90% of the migrating Honey Buzzards and Lesser Spotted Eagles in the Northern Valleys and cross-Samaria surveys. The mean interspecific difference of the distance from the sea is 14.0 km in the Northern Valleys and 16.5 km in the cross-Samaria surveys*

	Honey Buzzard		Lesser Spotted Eagle	
	Northern Valleys	Cross-Samaria	Northern Valleys	Cross-Samaria
Passage times				
Start and finish	08.00–16.00 h	07.00–14.30 h	10.00–17.00 h	09.30–15.00 h
Duration (h)	8	7.5	7	5.5
Distance from the sea (km)				
Range	20–50	18–40	12–30	10–15
Mean	35	29	21	12.5

grate earlier and finished later than Lesser Spotted Eagles. Ninety percent of the Honey Buzzards passed over the observers in *c.* 8 h in comparison with *c.* 6 h for Lesser Spotted Eagles in both the Northern Valleys and the cross-Samaria surveys. The difference was probably caused by the greater dependence of the eagles on thermals. Honey Buzzards started their morning migration by active flight, while the eagles waited for the thermals to develop before leaving the ground. Lesser Spotted Eagles arrived 22 days later in Israel than Honey Buzzards (i.e. when days were shorter by 20 min) and this fact was reflected in their shorter daily activity.

The peak migration of Honey Buzzards occurred well before noon in the Northern Valleys and at noon in the cross-Samaria survey, while the opposite was true for the Lesser Spotted Eagles. These results were probably a result of differences in the roosting behaviour of the two species. Honey Buzzards tended to roost in large concentrations in olive groves in northern Samaria, while Lesser Spotted Eagles were spread out all over their route.

A daily deflection in the migration axis was also noted over the Elat area. Here the migration axis changed direction according to the wind regime. In motorized-glider flights with Honey Buzzards, flocks could be seen entering Jordan at the Grofit junction area, about 50 km north of the Gulf of Elat, in the morning. Toward afternoon they crossed into Jordan farther to the south and as far as the northern part of the gulf (Fig. 2).

Seasonal variation in the migration route

Among flocking migrants, there was seasonal variation in the horizontal migration axis, with early species travelling more to the east than late ones. Figure 6 illustrates this phenomenon as observed in the Northern Valleys survey. Most White Storks travelled more than 60 km east of the Mediterranean coast, Honey Buzzards 22–60 km, Levant Sparrowhawks 5–40 km, Lesser Spotted Eagles 5–22 km and White Pelicans 5–10 km from the coast (Fig. 6). These ground observations were confirmed by data collected by following migrants with the motorized glider. A similar phenomenon was observed using the weather radar at Qez'iot, 200 km south of the Northern Valleys survey area (Fig. 7), where two clear parallel migration axes of Honey Buzzards in the west and a combination of Honey Buzzards and pos-

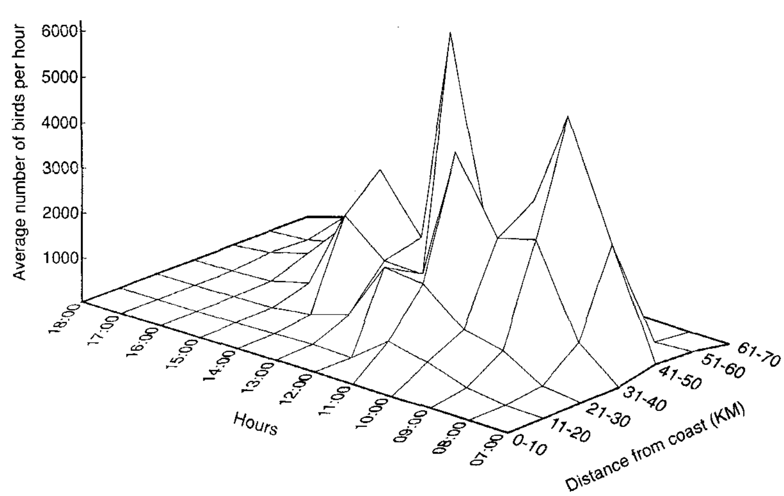

Figure 4. Mean movement of flocks of Honey Buzzards (n = 29 days) in the Northern Valleys survey area during the autumn on days of heavy migration during 3 years (1988–1990). The distance from the centre of the flocks to the Mediterranean Sea is given for each hour.

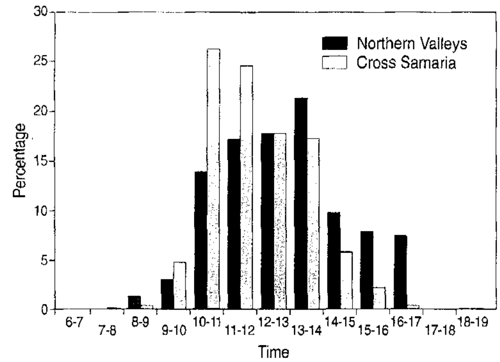

Figure 5. Proportions of Lesser Spotted Eagles observed during the day in the autumn in the Northern Valleys and cross-Samaria surveys.

sibly storks in the east were observed during 12–13 September 1987. On 29 September, 17 days later, only one westerly axis of Lesser Spotted Eagles was observed.

Spring and autumn variation in migrant numbers in relation to migratory routes

Table 2 shows that for most soaring migrants, large differences occurred between the spring and autumn in the numbers of migrating birds. These differences arose from differences in the migration routes between the two seasons. Table 2 shows eight major results.

(1) Of the soaring migrants, only the Steppe Eagle *Aquila nipalensis* migrated over the Elat Mountains in autumn. Other Palaearctic migrants which did not migrate over the western slopes of the central mountain ridge and the Jordan Valley passed over east of Israel, and only the fringes of the migration passed over Israel.

(2) The White Storks migrated in autumn only along the eastern Jordan Valley–Negev route. The migrants during this season formed about 46% of the number which migrated through Israel in spring. The remaining storks almost certainly migrated over Jordan in the autumn.

(3) Only the Honey Buzzards travelled in the autumn along the eastern (about 20%) or the western axis (about 80%). The remaining four flocking species (Lesser Spotted Eagle, Levant Sparrowhawk, White Pelican and Red-footed Falcon *Falco vespertinus*) migrated entirely along the western axis.

(4) Among non-flocking species, a significant portion of the Short-toed Eagles *Circaetus gallicus*, which originate from central and eastern Europe, migrated along the western axis in Israel. In spring, only 20% of the number passing in the

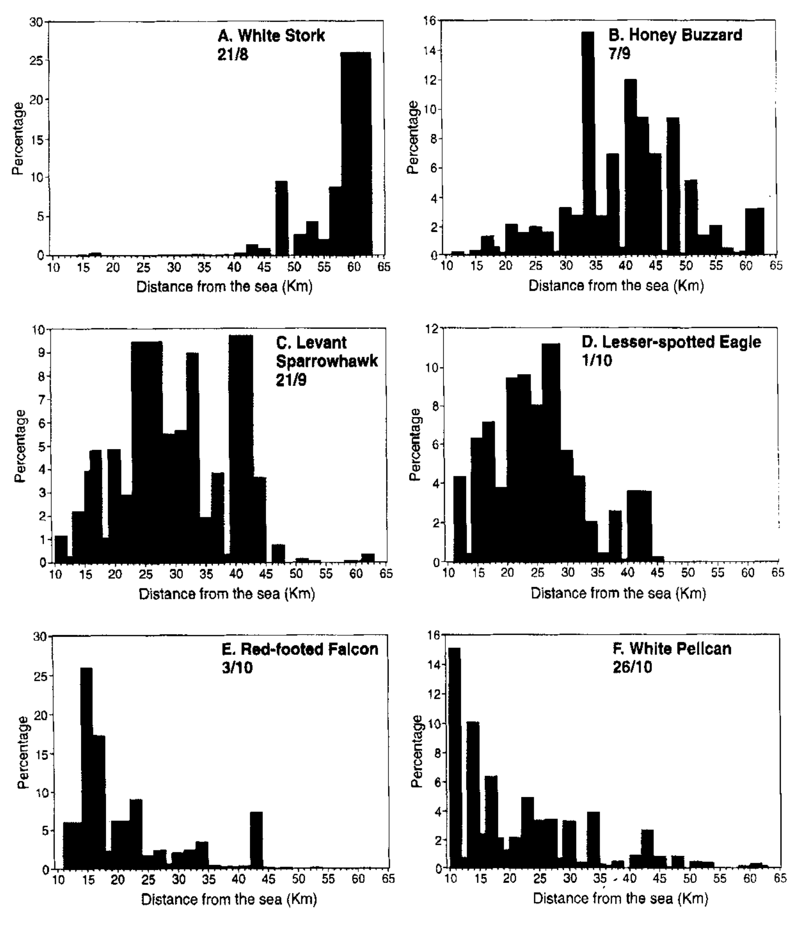

Figure 6. Distance from the Mediterranean Sea and mean peak day (in the upper part of each figure) of White Storks, Honey Buzzards, Levant Sparrowhawks, Lesser Spotted Eagles, Red-footed Falcons and White Pelicans in the autumn. Note the inverse relationship between time of appearance of a species and its distance from the coastline: early migrating species travel a more easterly route than late ones.

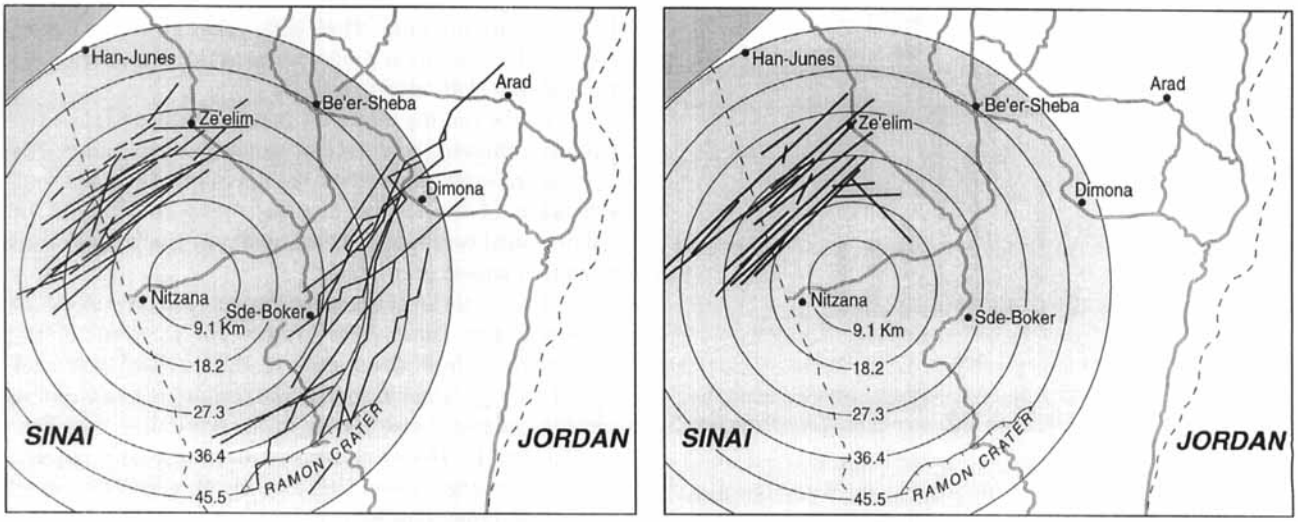

Figure 7. (Right) Migration routes of flocks of Lesser Spotted Eagles taken on a peak day (28 September 1987) as seen by the weather radar at Qezi'ot; (left) Several representative flocks of Honey Buzzards on the northwest route and flocks of Honey Buzzards with flocks of White Storks in the southeast route as seen on 2 days of autumn migration (12–13 September 1987) by the same radar. The two routes are clearly seen.

autumn were seen over Israel, and there were no records from the Negev and Jordan Valley axis.

(5) The Marsh Harrier *Circus aeruginosus*, Booted Eagle *Hieraetus pennatus* and Egyptian Vulture *Neophron percnopterus* are non-flocking species, migrating along a broad front. The first two species (and possibly also the Egyptian Vulture) are cross-sea migrants. This is probably the reason why only small numbers of these species were seen in the autumn and even smaller numbers were seen in the spring. We assume that these species also fly, at least partially, along the Negev and Jordan Valley axis, a route which has not been studied in detail.

(6) In the autumn, most of the Lesser Spotted Eagles flew along the western axis and none were seen in the Elat

Table 2. *Magnitude of migration of soaring birds in the autumn and spring and percentages seen passing along each of the three routes in Israel. Most species migrating through Elat during the spring continue their migration in a north to east direction, while the Levant Sparrowhawk is the only species which continues its migration due north along the Eastern Route thus appearing in both the Eastern and Elat routes as 100%. Counts given for White Storks are from a single year and only from the Western Route. However, this species also migrates along the Eastern Route and the proportions here are estimates. The number of Lesser Spotted Eagles in the spring is not accurate, as no systematic study was conducted on this species. For the Short-toed Eagle, Marsh Harrier and Booted Eagle in spring, data are available only from Elat, hence no percentages are given for this season*

	Autumn				Spring			
	Annual mean	Percentage in route			Annual mean	Percentage in route		
Species	numbers	Western	Eastern	Elat	numbers	Western	Eastern	Elat
Steppe Buzzard	767	25	75	—	321,021	5	16	79
Honey Buzzard	345,456	80	20	—	361,279	—	5	95
Steppe Eagle	24,246	1	1	98	28,134	—	14	86
Levant Sparrowhawk	34,592	100	—	—	16,278	—	100	100
Lesser Spotted Eagle	93,166	100	—	—	About 20,000	5	95	—
Red-footed Falcon	2847	100	—	—	—	—	—	—
Black Kite	887	100	—	—	28,418	5	12	83
Egyptian Vulture	277	100	—	—	425	—	70	30
Short-toed Eagle	5988	100	—	—	170	—	—	—
Marsh Harrier	948	100	—	—	178	—	—	—
Booted Eagle	1180	100	—	—	137	—	—	—
White Stork	190,908	—	100	—	239,213	60	40	—
White Pelican	71,421	100	—	—	—	—	—	—
Total	772,683				995,253 (without the Lesser Spotted Eagle)			

Mountains. However in spring 1991, D. Yisra'eli (pers. comm.) counted 19,311 Lesser Spotted Eagles during 4 days (25 March–1 April) in the Hula Valley, and flocks comprising tens to hundreds of individuals have been seen over the Negev and the Jordan Valley (Y. Leshem, pers. obs.). These data led us to suspect that during the spring, all migrating Lesser Spotted Eagles passed over the Negev and Jordan Valley, but this has to be confirmed by further surveys.

(7) The Red-footed Falcon is the only species which was seen only in the autumn and was completely absent in spring. It is known to be a cross-sea migrant (Cramp & Simmons 1980), crossing the Mediterranean south of Turkey with the eastern fraction passing over western Israel. On its way back to the breeding grounds from southwest Africa, the Red-footed Falcon crosses the Mediterranean along a broader front, between Algeria and Morocco (Lindhal 1981), and is not seen over Israel in the spring.

(8) Five flocking species travelled over the Elat Mountains in spring: Steppe Buzzard *Buteo vulpinus*, Black Kite *Milus migrans*, Steppe Eagle, Honey Buzzard and Levant Sparrowhawk. Three of these five species (Honey Buzzard, Steppe Eagle and Black Kite) turn east–northeast from the Elat Mountains towards their breeding grounds. About 20% of the buzzards migrate parallel to the Elat Mountains in the spring, along the Negev and Jordan Valley axis and along the western axis over the Coastal Plain. About an eighth (13.5%) of the Steppe Eagles and 12% of the Black Kites fly along the Negev–Jordan Valley axis. The Levant Sparrowhawk was the only raptor which migrated south–north in the spring and continued north along the Arava–Jordan Valley–Hula Valley from the Elat Mountains. Many thousands of Levant Sparrowhawks have been seen along the Rift Valley between En Yahav and the Sea of Galilee.

DISCUSSION

The combined effects of geomorphology and climate on migratory routes

In the autumn, soaring migrants used three principal routes while crossing Israel (Fig. 2): (1) the Western Route, (2) the Eastern Route and (3) the southern–Elat Mountains Route. Migration in the spring more or less followed the same routes as those used in the autumn, but the migration was in the opposite direction. However, the Eastern Route crossed the central mountain ridge either farther south or north of the eastern Hebron slopes in the spring than in autumn.

One of the principal reasons for the character of migration over Israel is the geomorphological structure of the country. The two parallel routes in northern and central Israel occurred where favourable soaring conditions exist along the Rift Valley and along the western slopes of the central mountain ridge. Each of these routes is 20–30 km wide.

In the autumn, the birds kept almost the same azimuth direction throughout the whole day (flying south) on both the Eastern and Western Routes. However within these routes, in the morning the migrants drifted to the west and after midday towards the east. At sunrise, most solar radiation is absorbed by the eastern, sun-facing slopes of the mountains, and the first thermals are formed there, attracting the migrating soaring birds (Fig. 5). The same was seen in the early afternoon when the sea breeze arrived and progressed rapidly over the eastern slopes towards the Jordan Valley at an average velocity of 30–40 km per h (Bitan 1982). The combination of the change in radiation and wind direction deflected the migration axis towards the Jordan Valley. Thus in the afternoon, most flocks flew along the Jordan Valley axis and in the evening, landed to roost along the Rift Valley and the mountain slopes bordering it. In the morning, the flocks progressed in a southwesterly direction (Fig. 2).

For the Western Route, the main deflection of the migrating flocks was caused by the sea breeze, which pushed the birds eastward. As temperature differences between the sea and land became more pronounced during the day, a sea breeze was created, reaching the highest intensity at about 15.30–16.00 h and then slowly fading (Katzenelson 1966, Bitan 1982, Mahrer 1985). The breeze penetrates up to 60 km inland and has a velocity of 10–18 km per h (Bitan 1982). The progress of the sea breeze to the east affected the migrating flocks, pushing them in a west–east direction between 10.00 h and 17.00 h (Fig. 5).

The wind regimes in the southern Arava and Elat Mountains are a case apart. Here, on 86% of the days the winds were northerly and northeasterly (Katzenelson 1966) with the winds funnelled by two tall "walls", the Negev Mountains in the west and the Edom Mountains (Jordan) in the east. Other factors combine with these to determine the precise wind direction: towards noon, a southerly tendency predominates and towards evening a west–northwesterly tendency predominates. In accordance with the wind direction, there was a regular fluctuation in the route of migrants to Jordan: from the Grofit junction in the morning, towards the Gulf of Elat in the afternoon and evening.

Seasonal variation in the migration axis

Among flocking migrants, there was a clear seasonal variation in the migration axis, with early species travelling more to the east than late migrants. Climate is a major factor in determining seasonal variation. In summer, the climate of the Middle East and the North African coastal area is dominated by two factors: a subtropical high which lies above these areas and the southern part of the "Persian trough". Hot, dry air comes from the Persian Gulf, cooling off and absorbing moisture as it nears the Mediterranean. This cool air creates an inversion in the temperature gradient of the air column, termed a marine inversion. The inversion creates a stable layer, in which temperature increases with altitude instead of decreasing (1°C/150 m). As a result, favourable conditions for the formation of thermals do not develop on the western slopes of the mountain range

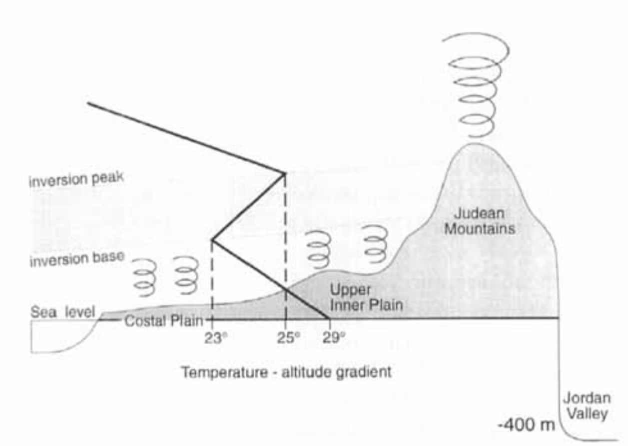

Figure 8. Schematic description of the conditions responsible for the creation of the summer inversion over the Mediterranean coastal plain and western slopes of the mountain ridge of Israel. The schematic is shown as a west–east cross-section and is not to scale.

where the inversion is present (Fig. 8). However, the marine inversion weakens towards the east, allowing thermals to develop there. Hence, migrants travelling in the summer prefer the eastern part of Israel. In September, the Persian trough gradually retreats, replaced by the Red Sea trough from the south. Temperature differences between land and sea decrease, and the inversion effect gradually decreases and then completely disappears in October. The disappearance of the inversion allows thermals to develop on the western slopes of the mountain range. For this reason, migrants through Israel move their routes from east to west with the transition from summer to autumn. Favourable soaring conditions in the spring, before the summer regime is created, enable about half of the storks returning north in the spring (March–April) to migrate on the western axis, along the western slopes of the mountain range.

The relationship between the location of breeding grounds and migratory routes in the Middle East

Differences in routes between the spring and autumn are termed "loop migration" (Mead 1973, Lindhal 1981, Alerstam 1990) and are related to weather (Kerlinger 1989) and available food sources (Alerstam 1990). Yom-Tov (1984, 1988; see Fig. 9) has suggested that the difference in migratory routes in the autumn and spring is related to the inability of soaring migrants to fly over large water bodies, such as the Red Sea. Welch and Welch (1989), who followed the autumn migration in this area, corroborate this assumption. In the spring, raptors which did not cross the Red Sea at Bab el Mandeb flew north along the western coast of the Red Sea to avoid crossing it. When the raptors reached the Elat Mountains, at the northern edge of the Gulf of Elat, they turned northeast and flew to their breeding grounds (Fig. 9).

Israel and the Gulf of Elat lie on the 35°E parallel, and

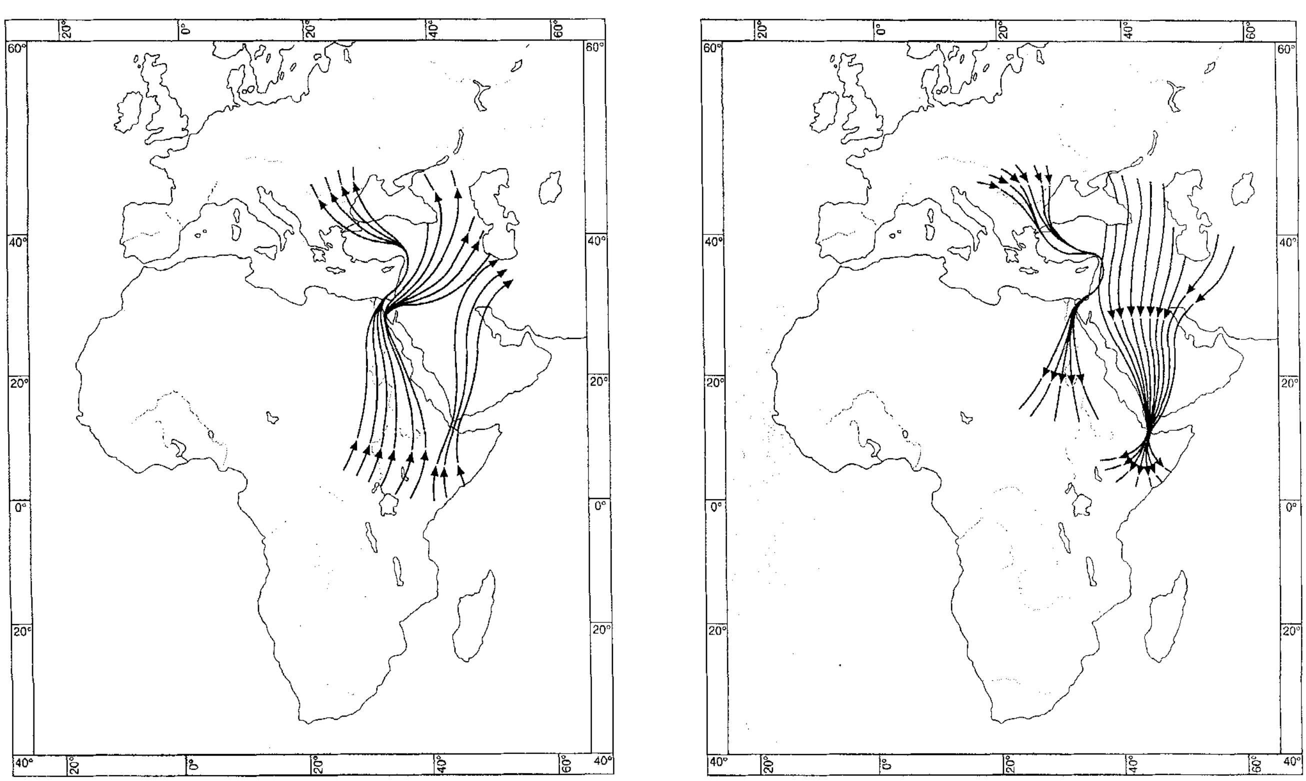

Figure 9. Schematic view of the migration routes of soaring birds in the Middle East. (A) Spring; (B) Autumn. Schematic from Yom-Tov (1988).

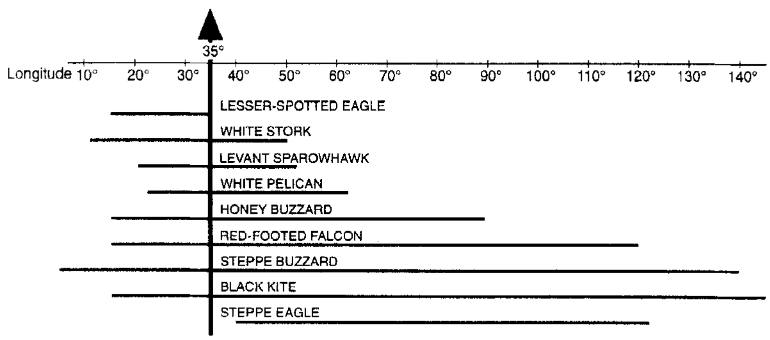

Figure 10. The whole longitudinal spread of the breeding range of flocking migrants in relation to the mean longitude of Israel (35°E). Some western birds cross the Mediterranean at Gibraltar and some eastern populations winter in southern Asia.

Figure 10 depicts the breeding range of each species' breeding site relative to this parallel. Migratory flocking birds can be divided into two groups: those that breed at longitudes west of Israel (Lesser Spotted Eagle) or spread roughly equally on both sides of the 35°E parallel (Levant Sparrowhawk, White Stork and White Pelican), and those which breed mainly east of 35°E (Honey Buzzard, Red-footed Falcon, Steppe Buzzard, Black Kite and Steppe Eagle). The world population of the Lesser Spotted Eagle migrates over Israel and only along the Western Route. In the spring, all members of this species may return along the Negev–Jordan Valley route. Similarly, in the autumn, the entire Palaearctic populations of the Levant Sparrowhawk and White Pelican pass over Israel along the Western Route, returning in the spring along the Arava Valley between Israel and Jordan. The migratory White Storks are probably divided almost equally between Israel and Jordan in both seasons.

In contrast, only part of the Palaearctic populations of the second group (species breeding mainly east of 35°E) pass through Israel. Only part of the global population of the Honey Buzzard migrates over Israel in the autumn, using both the eastern and western slopes of its mountain range. In the spring, most of these birds converge into the Elat Mountains, turning northeast from there towards its principal range. The Red-footed Falcon passes through Israel along the Mediterranean coast only in the autumn. Only small proportions of the numbers of the Steppe Buzzard and Black Kite which pass over Israel in the spring do so in the autumn (Table 2). Much larger proportions of both species migrate over the Elat Mountains in the spring, turning northeast from there towards breeding grounds in Russia. A small proportion of these two species fly along the Negev–Jordan Valley eastern axis, and another 5% of both species migrate along the western axis. Finally, the Steppe Eagle, all of which breed east of Israel, showed a completely different migration pattern to the other species, migrating along an east–west route from Asia to Africa. It is the only species to pass north of Elat in the autumn, continuing in a westerly direction towards the Suez Canal. Because of its large size, Steppe Eagle movements are strongly dependent on weather conditions. It seems that in some years, most of the migrants of this species converge via Elat–Suez into Africa and others converge via Bab el Mandeb (Welch & Welch 1989). The data from Suez and Bab el Mandeb show that, on average, a third of the Steppe Eagle population which migrates through the Middle East passes via Elat in both the autumn and spring. Thus, these observations support Yom-Tov's (1984) hypothesis concerning the determination of the routes of soaring birds in the Middle East.

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