MIGRATION BY FLAPPING OR SOARING: FLIGHT STRATEGIES OF MARSH, MONTAGU'S AND PALLID HARRIERS IN SOUTHERN ISRAEL[1]

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Abstract. Migratory flights of Marsh Harriers (*Circus aeruginosus*), Montagu's Harriers (*Circus pygargus*) and Pallid Harriers (*Circus macrourus*) in southern Israel were used to test flight theory predictions. The body sizes of these closely related species are between those of the typical large soaring migrants, such as eagles and storks, and the typical flapping migrants, such as small falcons and sparrowhawks. In soaring-gliding flight, Marsh Harriers reacted to different thermal conditions by adjusting their gliding airspeed to the actual climbing rate in thermal circling; consequently, cross-country speed was related to climbing rate. In contrast, the smaller Montagu's and Pallid Harriers did not adopt gliding airspeeds according to thermal conditions. All harrier species regularly used flapping-gliding flight, predominately soon after sunrise and before sunset, and more often in opposing winds than in following winds. Montagu's/Pallid Harriers used flapping-gliding more frequently than Marsh Harriers. Because they alternate between different flight styles, harriers are more independent of environmental factors, such as thermal activity and wind, compared to pure soaring migrants. This allows harriers to migrate under unfavorable thermal and wind conditions. Marsh Harriers are similar to typical soaring migrants in maximizing cross-country speed in soaring-gliding flight, whereas Montagu's and Pallid Harriers are less adapted to soaring-gliding flight and thus are similar to smaller flapping migrants. Optimal soaring-gliding flight seems to be less relevant for these smaller harriers; they maximize cross-country performance by efficiently combining different flight styles.

Key words: Circus aeruginosus, Circus macrourus, Circus pygargus, flapping-gliding flight, flight strategy, harrier, soaring-gliding flight.

INTRODUCTION

Birds use two main flight styles: active powered flight (flapping) or soaring and gliding. Flapping is the common flight style in birds. Soaring and gliding is used mainly by larger birds because of energetic constraints: mass specific power required for flapping flight increases with body mass (mass specific power $\approx$ body mass$^{0.17}$; Pennycuick 1972). In contrast, soaring and gliding flight consumes about 3–4 times Basal Metabolic Rate (Ellis 1984, Adams et al. 1986), and because mass specific BMR decreases with increasing body mass (mass specific BMR $\approx$ body mass$^{-0.33 \text{ to } -0.25}$), soaring-gliding flight becomes energetically cheaper for larger birds. Theoretically, a bird heavier than 132 g should change from flapping to soaring-gliding flight in time-minimizing migration, given an energy consumption of 4 × BMR in soaring-gliding flight and a climbing rate of 1 m sec^{-1} in thermal soar-

ing; in energy-minimizing migration, the switch point is even lower (Hedenström 1993).

Thus among the Falconiformes, flapping flight is mainly used by smaller raptor species like falcons and sparrowhawks, whereas soaring and gliding flight is preferred by larger raptors such as eagles, vultures and buzzards. This difference in flight style also determines the migratory routes. Since the necessary updrafts for thermal soaring only occur over land, typical soaring migrants like *Aquila* and *Buteo* species are concentrated over land bridges between Europe and Africa at the eastern and western edge of the Mediterranean Sea (Bijlsma 1987, Shirihai and Christie 1992). In contrast, by using flapping flight, *Falco*, *Pernis* and *Circus* species cross the Mediterranean on a broad front in considerable numbers (Beaman and Galea 1974, Flint and Stewart 1983, Agostini et al. 1994). However, small concentrations of harriers do occur over land bridges (Bijlsma 1987).

Marsh Harrier *Circus aeruginosus*, Montagu's Harrier *Circus pygargus* and Pallid Harrier *Circus macrourus* show flight behavior intermedi-

ate between typical flapping and typical soaring. Harriers have evolved a typical and unique hunting behavior: they use powered flight low over the ground with 5–6 wingbeats followed by a wavering glide (Schipper 1977, Watson 1977, Porter et al. 1981). Hunting flight speeds are low. The typical V-shaped position of the wings during slow glides lowers the center of gravity, stabilizes the flight position of the body and reduces risk of a stall (Glutz von Blotzheim et al. 1971, Thies 1985). Nevertheless, they often soar high over ground for aerial display during the breeding season (Porter et al. 1981). Little is known about their flight behavior during migration. This study was designed to quantify the flight behavior of migrating harriers over land and to determine the factors influencing the selection of flapping-gliding or soaring-gliding flight. Flight behavior of harriers is analyzed with respect to daytime, season, wind, and interspecific morphological differences: Montagu's and Pallid Harrier are similar in body size and wing design, whereas Marsh Harriers are larger and heavier (Porter et al. 1981, Génsbøl 1986). Montagu's and Pallid Harrier have relatively long and narrow wings with a higher aspect ratio than Marsh Harriers. The broader wings of the Marsh Harrier resemble those of *Buteo* and *Pernis* species.

FIGURE 1.   Map of Israel: locations of the radar. M: Mediterranean Sea, D: Dead Sea, R: Red Sea (Gulf of Akaba).

MATERIALS AND METHODS

OBSERVATION SITES AND EQUIPMENT

Raptor migration was studied in southern Israel at two observation sites: in the Negev Highlands near Sede Boqer, and in the Arava Valley near Hazeva (Fig. 1). In autumn 1991, the observation period was from 10 September to 31 October at both sites, and observations were carried out mainly in the morning until 11:00 and in the late afternoon from 16:00 onwards. The break of 4–5 hours in the middle of the day was imposed for operational reasons, such as data backup and routine evaluations. In 1992 the break was shortened to 2 hours and shifted from day to day in order to cover the whole day with observations. In spring 1992, observations took place from 1 March to 20 May in the Arava Valley, and from 1 to 30 April in the Negev Highlands. In autumn 1992, observations were conducted only in the Arava Valley from 10 August to 18 September.
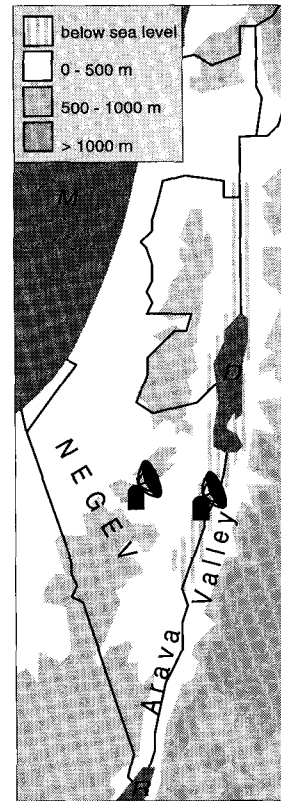
Radar of the type "Superfledermaus" were used for bird tracking (for details see Bruderer et al. 1995). Tracking a bird the size of a Marsh Harrier is possible up to distances of about 8 km. Tracking became difficult and sometimes impossible for birds flying low above ground (0–100 m; our estimation). The radar transmitted the position of the bird (distance ±10 m; azimuth and elevation ± 0.06°; Bruderer et al. 1995) each second in x, y and z coordinates to a computer, and the track was visualized on the computer screen. Simultaneously, an experienced observer identified the tracked target through a 12.4× telescope mounted parallel to the radar beam. Each bird was observed visually and phases with wingbeats were recorded. Pilot balloons, released and tracked every 4 hours, provided information about wind speed and wind direction at all flight levels up to 3,000 m above ground.

ANALYSIS OF TRACKS

Soaring migrants show two typical flight phases: by soaring (or circling) in a thermal, they climb

and gain altitude, which afterwards they transform into distance by gliding. The raptor tracks were subdivided into intervals of 10 sec and the different flight phases were marked interactively on the computer screen. A complete gliding phase lasted from the end of a soaring phase to the start of the next soaring and a complete soaring phase lasted from the end of a gliding phase to the start of the next gliding. Furthermore, the phases were classified with respect to the flapping behavior of the bird: no series of wingbeats occurred in soaring or in gliding flight, but phases with occasional single wingbeats were included. Phases containing one or more series of wingbeats were classified as flapping-and-gliding flight. Airspeed and heading while gliding were calculated by subtracting the wind vector from the track vector (Liechti 1993). Airspeed and groundspeed are the velocities of the bird relative to the air and ground, respectively. Cross-country speed relative to the ground was obtained by drawing a horizontal line corresponding to a distance of at least 2 km into a flight path and dividing this distance by the time needed to cover it. Cross-country speed relative to the air was derived by subtracting the wind vector from the vector of cross-country speed relative to the ground. In the Figures, the time of day is expressed as a percentage of the time between sunrise (0%) and sunset (100%) in order to compensate for the time shift of dawn and dusk during the observation periods. The migratory direction is the vector between the start and the endpoint of a track. Circular statistics are based on Batschelet (1981). Mean ± SD are reported in the Results section.

SPECIES AND FIELD IDENTIFICATION

In Israel, Marsh Harriers *C. aeruginosus* occur regularly in small numbers in spring and in autumn (Shirihai and Yekutiel 1991). Montagu's Harriers *C. pygargus* and Pallid Harriers *C. macrourus* are regular but scarce migrants, and are more numerous in spring than in autumn (Shirihai and Yekutiel 1991, Tsovel and Allon 1991, Shirihai and Christie 1992). Montagu's and Pallid Harrier are similar in wing, secondary feather and ulna lengths (Kemp and Crowe 1993). Montagu's Harriers are on average about 70 g lighter than Pallid Harriers (average females: 370 versus 445 g, respectively; average males: 261 versus 332 g, respectively) (Dunning 1993). However, because of sexual dimorphism in both species, there is extensive overlap in body mass. Females and juveniles of Montagu's and Pallid Harrier are very similar in plumage, and identification of the two species is possible only under optimal conditions (Christensen et al. 1981, Shirihai and Christie 1992, Lontkowski 1995). In our study, species identification often became impossible when light conditions were bad and/or distance from observer to the bird was too far. About 50% of Montagu's and Pallid Harriers could not be identified. Flight characteristics of identifiable Montagu's and Pallid Harriers did not differ statistically, therefore data for the two species were pooled for further analysis.

RESULTS

MIGRATORY DIRECTIONS

In the Negev Highlands in spring, Marsh Harriers as well as Montagu's/Pallid Harriers migrated in northerly directions (Table 1). In the Arava Valley, the mean migratory direction of Marsh Harriers and Montagu's/Pallid Harriers differed significantly: Marsh Harriers followed the course of the valley (11°), whereas Montagu's/Pallid Harriers headed northeast (47°) towards the Jordanian mountains. In autumn in the Negev Highlands, Marsh Harriers and Montagu's/Pallid Harriers traveled south-southwesterly and mainly followed the course of the Negev mountain ridges (Table 1). In the Arava Valley, the two groups had significantly different migratory directions: Marsh Harriers (191°) followed the course of the valley, whereas Montagu's/Pallid Harriers flew in south-southwesterly directions (208°), slightly heading towards the Negev mountains.

ALTITUDE OF FLIGHT AND DIURNAL COURSE OF MIGRATION

Marsh Harrier. In spring, the range of flight altitude was between 50–800 m above ground level (agl), and the 50% altitude limit slightly increased from 200 to 300 m agl during the day (Fig. 2). In autumn, the range of flight altitude was between 100–1,200 m agl, and the 50% altitude limit increased from 400 to 600 m agl (Fig. 2). Taking into account all flight paths between 20–80% of daytime in the Arava Valley, mean flight altitude was significantly higher above ground in autumn (515 ± 290 m, $n = 24$) than in spring (315 ± 170 m, $n = 24$) (Mann-Whitney U-test: $z = 2.56$, $P < 0.02$). Marsh Harriers started to migrate soon after sunrise in

TABLE 1. Migratory directions in the Arava Valley and in the Negev Highlands. Mean ± SD given, r indicates length of the mean vector. Number of birds shown in parentheses. Circular statistics are based on Batschelet (1981).

	Marsh Harrier	Montagu's/Pallid Harrier
Spring		
Negev Highlands	5° ± 26° (4)	25° ± 42° (10)
	r = 0.894	r = 0.736
Arava Valley	11° ± 37° (27)**	47° ± 40° (24)
	r = 0.796	r = 0.760
Autumn		
Negev Highlands	200° ± 9° (3)	208° ± 22° (6)
	r = 0.988	r = 0.889
Arava Valley	191° ± 31° (36)*	206° ± 22° (52)
	r = 0.857	r = 0.927

Differences between species in mean direction: Watson-Williams-test.
(**) $F_{1,49} = 9.50$, $P < 0.005$. (*) $F_{1,86} = 6.37$, $P < 0.025$.

spring and autumn. Two of the early flying birds in autumn were observed at about 700 m above ground before any thermals were available (see Discussion). Migration stopped after about 80% of daytime in spring, whereas it lasted until sunset in autumn (Fig. 2).

Montagu's/Pallid Harrier. In spring, the range of flight altitude was between 50–800 m agl (Fig. 2). Highest birds were tracked in the late morning, and the 50% altitude limit decreased during the day from 500 to 300 m agl. In autumn, the range of flight altitude ranged from 100–1,100 m agl, and the 50% altitude limit was quite constant at about 500 m agl (Fig.

2). To compare the flight altitudes between different sites and seasons, only flight paths between 20–80% of daytime were used. In the Arava Valley, mean flight altitude did not differ between autumn (540 ± 225 m, $n = 40$) and spring (505 ± 205 m, $n = 17$) (Mann-Whitney U-test: $z = 0.21$). In spring and autumn, Montagu's/Pallid Harriers had lower flight altitudes above ground in the Negev Highlands than in the Arava Valley (Mann-Whitney U-test: spring: Negev, 240 ± 130 m, $n = 6$; Arava, 505 ± 205 m, $n = 17$; $z = 2.66$, $P < 0.005$; autumn: Negev, 280 ± 80 m, $n = 6$; Arava, 540 ± 225 m, $n = 40$; $z = 2.84$, $P < 0.003$). In spring, Monta-

Marsh Harrier

Montagu's and Pallid Harrier

altitude of flight above ground (m)
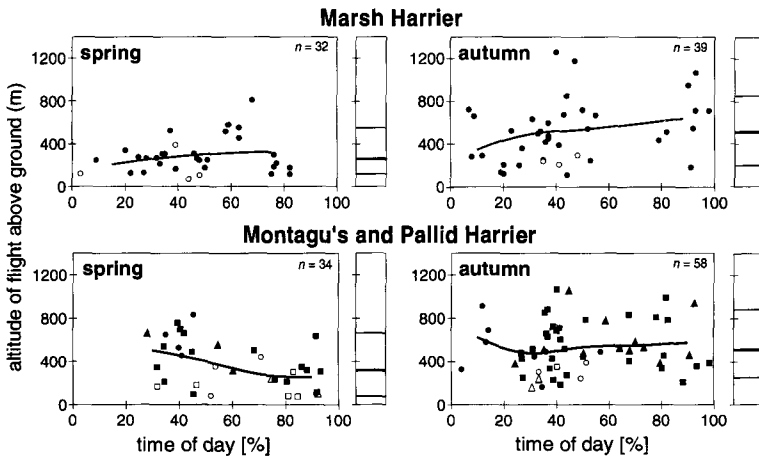
time of day [%]

FIGURE 2. Flight altitudes above ground level in spring and autumn. All tracked Harriers are included (with and without wingbeats). 0% of daytime corresponds to sunrise, 50% to noon and 100% to sunset. The lines in the scatter diagrams indicate the 50% limit of the height distribution. Symbols: solid black = Arava Valley; open = Negev Highlands. The small diagrams on the right side of the scatter diagrams show the 10, 50 and 90% limit of the height distribution.
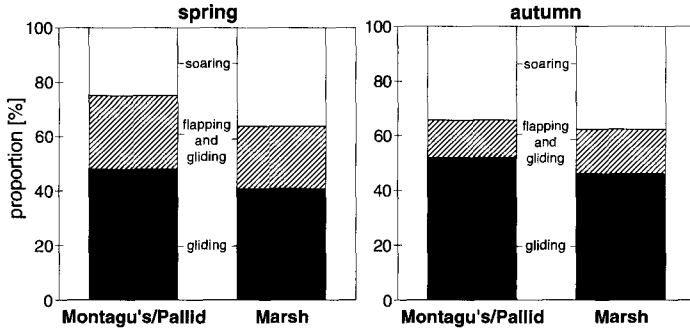
FIGURE 3.   Proportion of time spent for gliding (black), soaring (white) and flapping-and-gliding (hatched) in spring and autumn (for definitions see Methods). All tracked birds are included (Marsh Harrier: spring, $n = 31$; autumn, $n = 39$; Montagu's/Pallid Harrier: spring, $n = 34$; autumn, $n = 58$).

gu's/Pallid Harrier were not observed before 30% of daytime. In autumn, the main migration started at about the same time, but there were some birds already aloft at a time when thermal activity was too low to bring them up to such heights (see Discussion).

GLIDING, SOARING AND FLAPPING-AND-GLIDING FLIGHT

Flapping-and-gliding flight was defined as straight line flight with one or more series of wing flaps, whereas soaring and gliding flight contained no or occasional single wing flaps only. Marsh Harriers as well as Montagu's/Pallid Harriers showed a higher percentage of flapping-and-gliding flight in spring than in autumn (Fig. 3). For Montagu's/Pallid Harriers, it reached

27% of total tracking time in spring, but only 14% in autumn. For Marsh Harriers the corresponding values were 23% and 16%, respectively. Consequently, the proportion of soaring was lower in spring (25%) than in autumn (35%) for Montagu's/Pallid Harrier. For Marsh Harriers the proportion of soaring was similar in autumn (38%) and in spring (36%).

In spring, Marsh Harriers used flapping-and-gliding flight during the whole day, but more frequently after sunrise and before sunset than during the middle of the day (Fig. 4). In autumn, flapping-and-gliding flight only was used immediately after sunrise, and the proportion of soaring was constantly between 30–40% during daytime. Similarly, Montagu's/Pallid Harriers used flapping-and-gliding flight during the
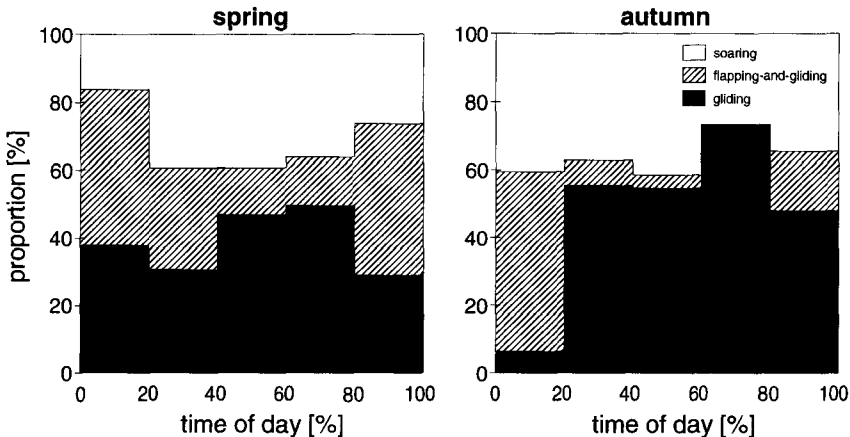
FIGURE 4.   Proportion of time Marsh Harriers spent in gliding (black), soaring (white) and flapping-and-gliding (hatched) during daytime in spring and autumn (for definitions see Methods). All tracked birds are included (spring, $n = 31$; autumn, $n = 39$).
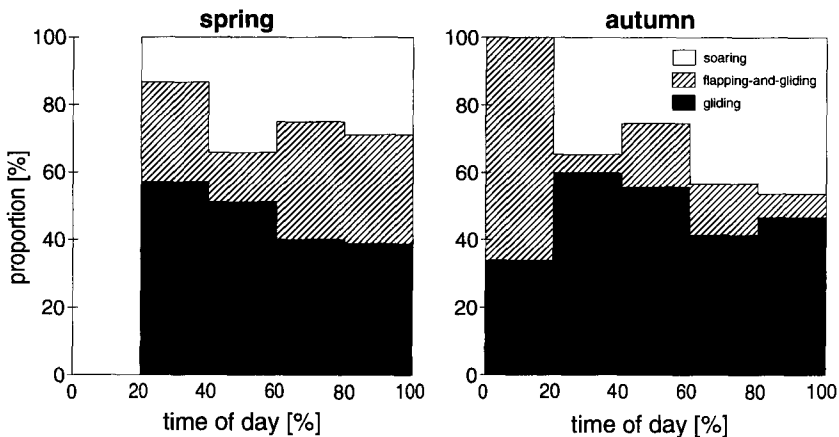
FIGURE 5. Proportion of time Montagu's/Pallid Harriers spent in gliding (black), soaring (white) and flapping-and-gliding (hatched) during daytime in spring and autumn (for definitions see Methods). All tracked birds are included (spring, $n = 34$; autumn, $n = 58$).

whole day in spring, whereas in autumn it was important only shortly after sunrise; later on during the day it was not very common (Fig. 5). For Montagu's/Pallid Harrier in autumn, the proportion of soaring increased during the day and was highest before sunset.

FLIGHT CHARACTERISTICS IN HORIZONTAL FLAPPING-GLIDING FLIGHT

Horizontal flapping-gliding flight was defined as a straight line flight including a regular change between flapping and gliding phases and a range of vertical speed between -0.5 and 0.5 m sec^{-1}. The flight characteristics of horizontal flapping-gliding showed no statistical difference between Marsh and Montagu's/Pallid Harrier (Table 2): Montagu's/Pallid Harriers (10.6 m sec^{-1}) had a slightly faster airspeed than Marsh Harriers (9.0 m sec^{-1}). However, Marsh Harriers reached a

higher mean groundspeed (13.1 m sec^{-1}) than Montagu's/Pallid Harriers (12.4 m sec^{-1}), indicating a higher tailwind support for Marsh Harriers. In both groups, the wingbeat frequency was 3.3 Hz and the proportion of flapping to pausing about 60:40. Duration of a flapping phase averaged 5.7 sec for Marsh Harrier and 5.4 sec for Montagu's/Pallid Harrier, and duration of pausing phases was 3.0 and 2.3 sec, respectively.

CLIMBING RATES AND SOARING BEHAVIOR

Marsh Harriers had a mean climbing rate of 1.72 $\pm$ 0.70 m sec^{-1} in thermal circling, and the mean circling time was 118 $\pm$ 90 sec ($n = 38$) (Fig. 6). The corresponding values for Montagu's/Pallid Harrier were 1.53 $\pm$ 0.75 m sec^{-1} and 120 $\pm$ 96 sec ($n = 48$). However, the climbing

TABLE 2. Flight characteristics in horizontal flapping-gliding flight. Mean $\pm$ SD given. Each bird was observed for 200 sec (except one Montagu's/Pallid Harrier for only 40 sec). Ten flapping and ten pausing phases were averaged per individual to obtain the mean duration of phases. Proportions of flapping and gliding were obtained by summing all flapping and pausing phases. All t-values not significant.

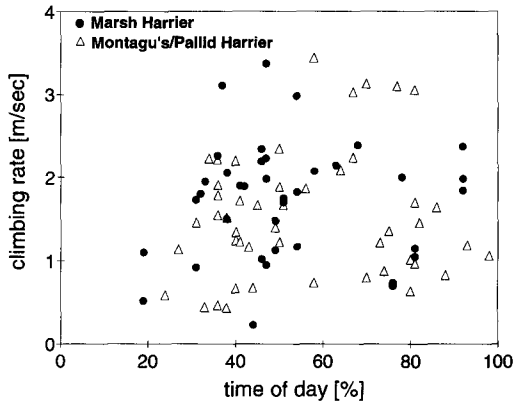|	Marsh Harrier	Montagu's/Pallid Harrier	t
Groundspeed (m sec^{-1})	13.1 $\pm$ 3.4	12.4 $\pm$ 3.0	0.73
Airspeed (m sec^{-1})	9.0 $\pm$ 1.3	10.6 $\pm$ 1.4	0.09
Vertical speed (m sec^{-1})	-0.1 ± 0.3	-0.1 ± 0.2	0.88
Flapping phase (sec)	5.7 $\pm$ 3.9	5.4 $\pm$ 2.0	0.90
Pausing phase (sec)	3.0 $\pm$ 2.8	2.3 $\pm$ 0.4	0.61
Wingbeat frequency (Hz)	3.3 $\pm$ 0.1	3.3 $\pm$ 0.1	0.81
Flapping : pausing (%)	62:38	61:39	
Range of flapping proportions (%)	48–77	32–87	
n	6	5	

FIGURE 6.   Climbing rates in complete thermal circling phases of Marsh Harriers ($n = 38$) and Montagu's/Pallid Harriers ($n = 48$) during daytime, (spring and autumn data).

rates of Marsh and Montagu's/Pallid Harrier did not differ statistically (t-test: $t_{85} = 0.24$). The mean flight altitude above ground was positively correlated with the climbing rate: higher climbing rates resulted in higher flight altitudes above ground (linear regression; Marsh Harrier: $y = 175x + 230$, $n = 38$, $r = 0.41$, $P < 0.01$; Montagu's/Pallid Harrier: $y = 131x + 367$, $n = 48$, $r = 0.41$, $P < 0.005$). The birds started soaring after about 20% of daytime, i.e., about 08:30 local time (Fig. 6). Climbing rates increased during the morning hours. Highest climbing rates of about 3 m sec^{-1} were reached in the late morning and in the first half of the afternoon. Afterwards, the climbing rates decreased. However, many individuals reached only low climbing rates during the best soaring hours of the day.

CLIMBING RATE AND GLIDING BEHAVIOR

Marsh Harrier. Airspeed and the sinking rate while gliding were correlated with the actual climbing rate in thermal circling (Fig. 7; airspeed, $y = 1.58x + 11.02$, $n = 14$, $r = 0.76$, $P < 0.002$; sinking rate, $y = -0.41x - 0.41$, $n = 14$, $r = -0.75$, $P < 0.002$). Thus, Marsh Harriers reacted to the actual climbing rate in adjusting their gliding behavior accordingly: higher climbing rates were transformed into higher airspeeds by faster sinking rates. Cross-country speed in relation to the air was correlated with climbing rate (Fig. 8; cross-country airspeed, $y = 5.07x + 20.60$, $n = 22$, $r = 0.68$, $P < 0.001$).

Montagu's/Pallid Harrier. In contrast to the Marsh Harrier, airspeed and sinking rate while gliding were not correlated with the actual climbing rate (Fig. 7; airspeed, $n = 21$, $r = 0.22$, ns; sinking rate, $n = 21$, $r = 0.12$, ns). Climbing rates had little effect on gliding behavior. A tendency of increasing cross-country speeds relative to the air with increasing climbing rates was indicated (Fig. 8; cross-country airspeed, $n = 24$, $r = 0.24$, ns).

GLIDING CHARACTERISTICS IN SPRING AND AUTUMN

Marsh Harrier. The angle between gliding (track) and wind direction was significantly higher in spring than in autumn (an angle of 0 corresponds to exact tailwind and 180 to headwind): Marsh Harrier migrated in side and opposing wind conditions in spring ($119° \pm 39$) and in following wind conditions in autumn ($51° \pm 41$) (Table 3). This was the result of the stable trade wind system in this region that provides north-northeasterly winds in the lower atmo-
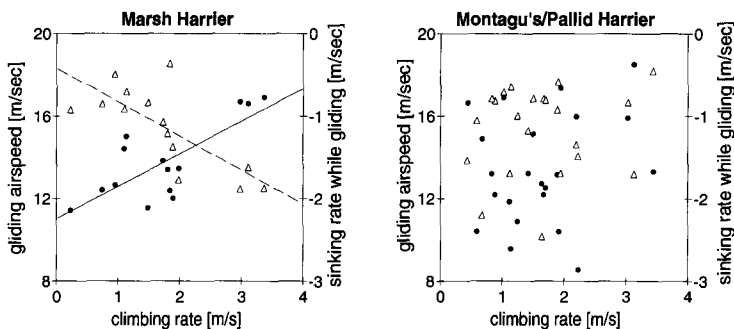

FIGURE 7.   Airspeed (solid circles) and sinking rate (open triangles) while gliding versus climbing rate in thermal circling of the same track. Only phases without wingbeats are included (spring and autumn data).
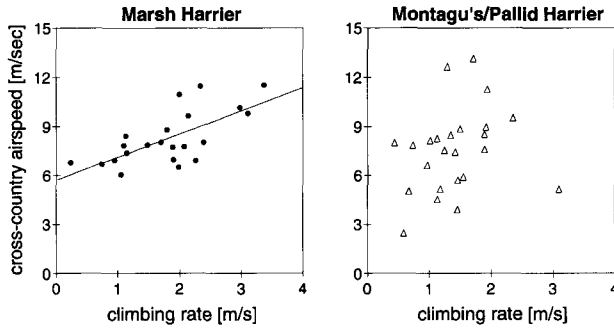
FIGURE 8.   Cross-country speed relative to the air versus climbing rate in thermal circling. Only phases without wingbeats are included (spring and autumn data).

sphere up to about 1.5 to 2 km height, particularly in autumn and most pronounced in the Arava Valley. Airspeed, sinking rate and gliding angle in interthermal gliding were similar in autumn and spring. Wind speeds were higher for the tracked individuals in spring than in autumn. The birds had similar airspeeds while gliding in spring and autumn, and therefore, groundspeeds were higher under following wind conditions in autumn. The flight altitude above ground during gliding was about twice as high in autumn (700 m) as in spring (340 m).

Montagu's/Pallid Harrier. Similar to the Marsh Harrier, Montagu's/Pallid Harrier migrated mainly under side and opposing winds in spring ($101° \pm 51$), whereas in autumn following winds predominated ($36° \pm 32$) (Table 3). Wind speeds were similar for these species in spring and autumn. The birds reached similar groundspeeds in both seasons. Under the opposing wind conditions in spring, they had higher airspeeds and higher sinking rates while gliding than in autumn. Flight altitude during these glides was similar in spring and autumn.

CROSS-COUNTRY SPEED

Marsh Harriers and Montagu's/Pallid Harriers had similar cross-country speeds (Table 4): including all flight styles, both groups reached significantly higher cross-country speeds relative to

TABLE 3.   Flight characteristics of interthermal gliding compared between spring and autumn. Mean $\pm$ SD given. Only phases longer than 60 sec and without wingbeats are included. Statistical differences between autumn and spring were analyzed by *t*-test; Watsons-U^2-test was applied to test for differences in circular distribution (Batschelet 1981).

	Autumn	Spring	Statistic	$P <$
Marsh Harrier				
Airspeed (m sec^{-1})	14.1 ± 2.0	13.3 ± 2.2	$t = 1.40$	ns
Groundspeed (m sec^{-1})	15.0 ± 2.4	11.6 ± 2.8	$t = 4.70$	0.001
Sinking rate (m sec^{-1})	-1.36 ± 0.57	-1.12 ± 0.67	$t = 1.39$	ns
Gliding angle (°)	-5.4 ± 2.0	-4.6 ± 2.3	$t = 1.32$	ns
Wind speed (m sec^{-1})	3.0 ± 1.4	4.2 ± 2.3	$t = 2.33$	0.05
Altitude of flight (m agl)	690 ± 270	340 ± 220	$t = 5.14$	0.001
Angle between track and wind (°)	50 ± 41	119 ± 39	$U^2 = 0.29$	0.01
n	25	28		
Montagu's and Pallid Harrier				
Airspeed (m sec^{-1})	12.6 ± 2.3	15.4 ± 3.2	$t = 3.96$	0.001
Groundspeed (m sec^{-1})	14.5 ± 2.2	14.2 ± 3.7	$t = 0.39$	ns
Sinking rate (m sec^{-1})	-1.27 ± 0.55	-1.70 ± 0.76	$t = 2.50$	0.05
Gliding angle (°)	-5.7 ± 2.1	-6.1 ± 1.8	$t = 0.89$	ns
Wind speed (m sec^{-1})	3.2 ± 1.1	3.8 ± 1.9	$t = 1.57$	ns
Altitude of flight (m agl)	595 ± 305	480 ± 190	$t = 1.96$	ns
Angle between track and wind (°)	36 ± 32	101 ± 51	$U^2 = 0.72$	0.001
n	43	27		

TABLE 4. Cross-country speeds relative to the ground and to the air in autumn and spring. Mean ± SD given, range in parentheses. For the calculation of cross-country speeds see Methods. Tracks with and without wingbeats are included.

	n	Cross-country speed relative to the ground (m sec⁻¹)	Cross-country speed relative to the air (m sec⁻¹)
Marsh Harrier			
Autumn	18	10.7 ± 2.6 (6.9–17.2)	7.6 ± 2.0 (4.4–11.5)
Spring	20	7.6 ± 3.2 (3.3–12.9)	8.5 ± 2.5 (4.9–15.5)
Montagu's/Pallid Harrier			
Autumn	32	9.8 ± 1.8 (5.1–13.5)	7.4 ± 2.0 (2.8–11.2)
Spring	13	7.7 ± 4.3 (2.8–16.8)	8.3 ± 3.5 (4.0–15.5)

the ground in autumn than in spring (Mann-Whitney U-test; Marsh Harrier: $z = 2.70$, $P < 0.01$; Montagu's/Pallid Harrier: $z = 2.02$, $P < 0.05$). Cross-country speed relative to the air was similar in autumn and spring in both groups (Table 4). Differences in cross-country ground-speed between autumn and spring reflected wind influence: in spring, birds migrated mainly under opposing wind conditions, whereas in autumn they had predominately following winds.

Flapping-gliding Marsh Harriers in autumn reached significantly higher cross-country speeds than soaring-gliding birds (flapping-gliding, $14.7 ± 2.1$ m sec⁻¹, $n = 3$; soaring-gliding, $10.3 ± 1.8$ m sec⁻¹, $n = 11$; Mann-Whitney U-test, $z = 2.57$, $P < 0.02$). These flapping Marsh Harriers profited from strong following winds of 5–10 m sec⁻¹, since cross-country speed relative to the air was similar in both groups (flapping-gliding, $8.0 ± 0.8$ m sec⁻¹, $n = 3$; soaring-gliding, $8.4 ± 1.8$ m sec⁻¹, $n = 11$; $z = 0.08$). For Montagu's/Pallid Harrier, cross-country speeds were similar for flapping-gliding and soaring-gliding individuals (cross-country groundspeed: flapping-gliding, $10.5 ± 1.7$ m sec⁻¹, $n = 4$; soaring-gliding, $9.4 ± 2.0$ m sec⁻¹, $n = 21$; $z = 1.04$. Cross-country airspeed: flapping-gliding, $8.0 ± 1.9$ m sec⁻¹, $n = 4$; soaring-gliding, $7.2 ± 2.0$ m sec⁻¹, $n = 21$; $z = 0.74$).

DISCUSSION

FLIGHT STRATEGIES

This study presents the quantitative results of parallel observations of three *Circus* species. Observations covered the whole day, i.e., from sunrise to sunset, regardless of favorable or unfavorable environmental conditions or abundance of migrating raptors. This method revealed species-specific behavioral reactions induced by environmental conditions such as vari-

ation in temperature and thermal activity during the course of the day, wind direction, wind speed, and topography.

The possibility of alternating their flight styles from flapping-gliding to soaring-gliding allows these harriers to migrate under various environmental conditions. If thermal convection is available, they prefer the soaring and gliding tactic, as do other large soaring migrants. Additional flapping-gliding flight is used mainly during the first hours after sunrise and before sunset when thermal updrafts are scarce or weak. By combining the two styles, the harriers are able to use the whole day for migration, some of them perhaps use even the night (see below). As in typical soaring migrants like Steppe Buzzard *Buteo buteo vulpinus* and Steppe Eagle *Aquila nipalensis,* most harriers appeared two to three hours after sunrise (Spaar 1995, Spaar and Bruderer 1996), and as in the Levant Sparrowhawk *Accipiter brevipes* (Stark and Liechti 1993) and the Honey Buzzard *Pernis apivorus* (Bruderer et al. 1994), some high altitude flights already had occurred soon after sunrise.

The theory of optimal flight behavior (Pennycuick 1989) predicts that a bird which maximizes its cross-country speed in soaring and gliding flight increases its gliding airspeed with increasing climbing rate in thermal soaring. This behavior was found in typical soaring migrants such as Steppe Buzzard (Spaar 1995, Spaar and Bruderer, in press) and Steppe Eagle (Spaar and Bruderer 1996). Despite their close relationship, Marsh and Montagu's/Pallid Harrier showed obvious differences in flight behavior. Marsh Harriers adopted their gliding airspeeds according to the actual thermal conditions. Thus, they tried to maximize cross-country speed in soaring-gliding flight. In contrast, no correlation was found be-

tween gliding airspeed and climbing rate for Montagu's/Pallid Harriers. Obviously, they did not adjust their gliding behavior to different thermal conditions. These smaller species seem to be less adapted to the soaring-gliding strategy but are more flexible, being able to migrate by flapping-gliding or by soaring-gliding flight. Because the proportion of energy consumption to weight increases with body mass during flapping flight (Pennycuick 1972), the energetic benefit of using soaring-gliding compared to flapping-gliding flight is probably low in these smaller species. However, the proportion of flapping-and-gliding flight was similar in both Marsh and Montagu's/Pallid Harrier and generally lower in autumn than in spring when unfavorable opposing wind conditions predominated. Therefore, Marsh Harriers tended to behave optimally in soaring and gliding flight like larger soaring migrants, but additionally compensated for suboptimal soaring performance by flapping-gliding flight over longer distances. They showed a higher proportion of flapping flight than Steppe Buzzards or Steppe Eagles, but predominately migrated with a soaring and gliding tactic (Spaar 1997).

TIME- OR ENERGY-MINIMIZING MIGRATION

The three harrier species used a mixed flight strategy: they minimized energy consumption per unit time by using soaring-gliding flight during daytime when thermal conditions were suitable. Additionally, they extended their daily migratory activity by using flapping-gliding flight predominately soon after sunrise and before sunset or under bad thermal conditions, probably even during the night. Thus, time minimization during migration seems to be an important consideration for these harriers. Under the same environmental conditions in Israel, larger raptors such as eagles and buzzards rarely use flapping-gliding flight and their migratory activity is restricted to the daylight hours when suitable thermal updrafts are available (Spaar and Bruderer 1996, Spaar 1997). On the other hand, small raptor species such as Levant Sparrowhawks and falcons showed the highest proportions of flapping-gliding flight (Spaar 1997).

EARLY MORNING RACE OR NOCTURNAL FLIGHT?

In autumn, a few harriers migrating by flapping-gliding flight were tracked at altitudes higher than 500 m above ground soon after sunrise and before sunset. These birds obviously started migration before sunrise or continued migration after sunset. They migrated at least during twilight and possibly during the night. Additional indication for night migrating harriers comes from the electronically recorded wing-beat pattern of nocturnal migrants (3 birds at 18:50, 21:20 and 04:20 local time) showing the same wing-beat pattern as the optically identified harriers during daytime (Table 2; unpubl. data). There are no other species with a similar wing-beat performance. Birds with similar frequencies such as herons, cranes, terns, and gulls would flap continuously without the characteristic pauses of the harriers. Nocturnal migration is suggested for the Marsh Harrier in Central Europe (Gatter 1984). In Israel, a small proportion of the Levant Sparrowhawks *A. brevipes* migrates at night (Stark and Liechti 1993). Levant Sparrowhawks can be electronically identified separately from harriers since they have a higher wing-beat frequency of about 5 Hz.

FLIGHT ALTITUDES

Compared to other species observed under the same conditions in Israel, the upper flight altitude was low for the harriers (1,200 m above ground). It was not caused by differences in seasonal timing of migration. Honey Buzzards (Bruderer et al. 1994) and Steppe Buzzards (Spaar 1995) have an upper altitude limit of about 2,000 m above ground, whereas Steppe Eagles climb to about 1,600 m (Spaar and Bruderer 1996). However, only a small proportion of these raptors fly higher than 1,000 m above ground (15% of Honey Buzzards and 10% of Steppe Buzzards and Steppe Eagles). Honey Buzzard and Steppe Buzzard seem to use the major part of the convective field and try to convert a high proportion of thermal convection into potential energy. Under strong thermal conditions, Steppe Eagles use another flight style by soaring in straight line gliding: they glide straight forward while continuously gaining height and, thus, they combine gain of potential energy and progress in the direction of migration (Spaar and Bruderer 1996). This may explain why Steppe Eagles do not soar in the upper part of the convective field. The lower altitude limit of the migrating harriers is probably caused by their ability to use flapping-gliding flight which allows them to migrate without soaring to the

highest parts of the convective field. Montagu's/Pallid Harrier do not even behave optimally in soaring and gliding flight and, thus, do not obtain maximum gain of potential energy (altitude above ground).

CLIMBING RATES

Climbing rates were lower for both Marsh Harrier (1.72 m sec^{-1}) and Montagu's/Pallid Harrier (1.53 m sec^{-1}) compared to buzzards and eagles at the same locations and under similar conditions: Honey Buzzard and Steppe Buzzard had a similar mean climbing rate of about 2.0 m sec^{-1} (Bruderer et al. 1994, Spaar 1995), as did Steppe Eagles (1.9 m sec^{-1}; Spaar and Bruderer 1996). However, climbing rates in thermal circling of these migrating raptors in Israel did not differ statistically (Spaar 1997). Flight variation during the day (Fig. 4) was very similar to those of the other soaring birds. Harriers theoretically have a lower wing loading than buzzards and eagles (mass loading: Steppe Eagle 0.73 g cm^{-2}, Steppe Buzzard 0.39 g cm^{-2}, Montagu's Harrier 0.21 g cm^{-2}) (data from Mendelsohn et al. 1989). Even if linear loadings (Jaksic and Carothers 1985) are considered, harriers still have the least loadings (linear loading: Steppe Eagle 0.22 g$^{0.33}$ cm^{-1}, Steppe Buzzard 0.21 g$^{0.33}$ cm^{-1}, Montagu's Harrier 0.17 g$^{0.33}$ cm^{-1}). Thus, harriers should reach at least the same climbing rates, given the theoretical wing loadings. There are two main reasons that could be responsible, singly or in combination, for the low climbing rates of harriers: (1) soaring harriers hold their wings in the typical V-shaped position reducing the effect of updrafts and (2) for Steppe Buzzards and Steppe Eagles, climbing rates increased with increasing flight altitude above ground, and thus, harriers probably did not take advantage of the strongest updrafts at high altitudes.

GLIDING BEHAVIOR UNDER DIFFERENT WIND SITUATIONS

Wind direction and wind speed play a major role for migrating soaring birds. Marsh and Montagu's/Pallid Harrier showed distinct differences in gliding behavior. Marsh Harriers maintained the same interthermal gliding airspeed in following and opposing winds. Therefore, Marsh Harrier had lower gliding ground speeds in opposing winds, and cross-country speeds were reduced relative to the ground. They optimized their cross-country performance in soaring-gliding

flight by adopting gliding airspeeds according to the actual climbing rates. This behavior was very similar to typical soaring migrants optimizing their flight characteristics in soaring-gliding flight. In theory, when maximizing cross-country airspeed in soaring-gliding flight, there is an optimal airspeed in interthermal gliding that depends on the actual climbing rate in thermal soaring (Pennycuick 1989). In general, interthermal gliding airspeed depends on several factors such as climbing rate in thermal circling, flight altitude above ground as well as tailwind- and sidewind-component; and different species react differently to these environmental factors (Spaar 1997).

In contrast, Montagu's/Pallid Harrier reached similar gliding groundspeeds in opposing and following winds. They accomplished it by enlarging their sinking rate in opposing winds, increasing both airspeed and gliding angle. However, a bird cannot increase its overall cross-country speed by adopting a higher airspeed than theoretical optimal airspeed, because it also increases its sinking rate and wastes part of the potential energy. This loss in cross-country speed might be compensated for by increasing the proportion of flapping flight: Montagu's/Pallid Harrier maintained a constant cross-country speed relative to the ground during migration regardless of flight style.

Assuming that the primary mode of flight for the Common Crane *Grus grus* is by flapping, Pennycuick et al. (1979) showed that thermal soaring and interthermal (powered or non-powered) glides reduce the energetic costs per unit distance, but result in a drastic decline in cross-country speeds. For the harriers, cross-country speed in relation to the air was similar in flapping-gliding and soaring-gliding flight, perhaps due to the fact that airspeeds in flapping-gliding flight were very low (8 m sec^{-1}) compared to powered flight of the Common Crane during sea crossing (18.6 m sec^{-1}; Alerstam 1975).

ACKNOWLEDGMENTS

cording and analysis of raptor tracks; he and D. Peter maintained the radar equipment during the field work. S. C. Stearns, L. Jenni, F. Liechti, and M. Kestenholz made valuable suggestions on the manuscript. We thank A. Hedenström for reviewing the manuscript.

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