FLIGHT BEHAVIOUR OF WHITE STORKS *CICONIA CICONIA* ON THEIR MIGRATION OVER SOUTHERN ISRAEL

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More than 200 flight paths of White Storks were recorded during spring and autumn 1991/92 at two sites in southern Israel by tracking radar. White Storks did not adapt flight behaviour to maximize cross-country speed as predicted by theory. Gliding airspeed was not adjusted to climb rate in thermals; cross-country speed increased simply with climb rate due to longer gliding phases. Large flocks had on average better glide ratios than single birds. Lateral wind drift was compensated only by large flocks, and the scatter of directions was reduced in flocks compared to single birds. Following the start of migration 2-3 h after sunrise, flight altitude increased until early afternoon up to 2000 m above ground. High flying birds profited from powerful thermals, while those close to the ground used all kinds of thermals. Differences in flight behaviour between spring and autumn were caused by environmental conditions. Storks adapt their flight behaviour to a lesser extent to vertical and horizontal winds than raptors, but seem to compensate this lack by profiting from migrating in flocks.

Key words: *Ciconia ciconia* - migration - Israel - flight behaviour - radar study

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INTRODUCTION

On their migration, European White Storks *Ciconia ciconia* concentrate along the western and eastern edge of the Mediterranean (Porter & Willis 1968; Bernis 1980; Sutherland & Brooks 1980; Dovrat 1991). The eastern route is used by the majority of the birds, where huge numbers can be observed crossing the Bosporus and flying over Israel. In autumn 1990 over 188 000 individuals were counted in the northern valleys of Israel (Tsovel & Allon 1991). The main passage is from the last third of March to the end of April and from the last third of August until the second third of September (Leshem 1992). White Storks are typical soaring migrants, with limited capacities for persistent flapping flight (Pennycuick 1972). Like pelicans, buzzards, vultures or eagles, they gain potential energy by exploiting upwinds, mainly benefiting from raising air in thermals. This en-

ergy is consumed in the gliding phase, when the birds progress in the direction of migration. For a White Stork, this flight strategy reduces the energy requirements for migration drastically compared to flapping flight, but the limited occurrence of thermals, which is restricted to landmasses and daylight, leads to extended migratory journeys. If the duration of migration is an important factor in the lifecycle, flight behaviour should be adapted to maximize cross-country speed.

The aim of this study was to investigate soaring and gliding behaviour and to compare it with flight theory predictions (Pennycuick 1975, 1989). Flight paths of White Storks on spring and autumn migration were used to test the following questions: What determines the height of flight? Do White Storks adjust optimal gliding speed according to the strength of the thermals as predicted by flight theory? Do they fly along fixed tracks and therefore compensate for lateral wind

drift while gliding? Do flight characteristics differ between two geomorphologically different sites in southern Israel? Does flock size influence flight behaviour?

STUDY AREAS AND METHODS

Flight paths of White Storks were recorded in southern Israel during a tracking radar study aimed at studying flight behaviour of migrating raptors (Bruderer *et al.* 1994; Spaar 1995). One study site was situated in the northern Arava Valley (30°50'N, 35°20'E), 150 m below sea level, within the arid part of Israel (mean temperature in August 33°C). Observation periods lasted from 10 September to 30 October 1991, from 1 March to 20 May, and from 10 August to 20 September 1992. Most recordings were made during spring and autumn 1992. The other site was on the Negev Highlands (30°51'N, 34°49'E), 450 m above sea level, at the southern edge of the semiarid part of Israel, 45 km west of the other radar station. Observation periods lasted from 10 September to 30 October 1991, and from 31 March to 30 April 1992. At this site all flight paths, except two, where recorded in spring. Single White Storks could be tracked by radar up to a distance of about 10 km and optical identification was possible up to 3-6 km depending on visibility.

In order to record wind directions and speeds, a balloon was released every four hours and tracked with the radar. Airspeed and heading of the birds were calculated by subtracting the wind vector at the corresponding altitude. For the analyses of wind influence on airspeed, the tail-/headwind component as well as the sidewind component was calculated with respect to the mean flight directions during gliding. Headwind-component is expressed as negative tailwind. Migratory directions (direction by which the bird flew from point A to point B irrespective of detours) and cross-country speed relative to ground were calculated for flight paths where the horizontal distance was at least two kilometres. Height of climb in thermals was calculated for complete climb phases only. A phase was considered complete when a change of flight behaviour was visible at the beginning and at the end. For more information on radar equipment, recording and evaluation of data see Bruderer *et al.* (1994, 1995). To test differences in directions the Watson-Williams, the Watson U^2 and a nonparametric test for dispersion were used (Batschelet 1981). Differences in distributions of heights, speeds, sink and climb rates were tested for significance by analysis of variance (ANOVA) for single and multiway classification (Sokal & Rohlf 1981).

Some 349 flight phases of at least 40 seconds (gliding or soaring) were analysed from 241 different tracks of storks. Out of 144 thermal flight phases 32 were complete (see above) and from 205 gliding phases 31 were complete. No difference between complete and incomplete flight phases was found according to climb rate (V_{zc}), airspeed (V_a) and sink rate (V_{zs}), thus, data were pooled for further analysis. Airspeed was calculated for 100 gliding phases, where wind data were available within 2 hours. Cross-country speed was calculated from V_{zc}, V_a and V_{zs} for 24 tracks with a gliding and soaring phase of at least 40 seconds. Tracking of large flocks was mainly done optically in order to follow the track of a single bird within the flock. Flight paths, where the radar tracking switched between different subsamples of a flock, were excluded from this analysis. Spring data ($n=$ 189) were mainly from April (74%), autumn data ($n=$ 52) mainly from the last decade of August until 20 September (85%).

RESULTS

Height distribution

Mean heights of tracks did not change significantly in relation to flocksize, data were thus pooled. The height distribution was significantly different between spring and autumn and between the two observation sites (multi-way ANOVA; $P<$ 0.01). In the Arava 50% of the spring migrants flew below 500 m above ground level (AGL) and
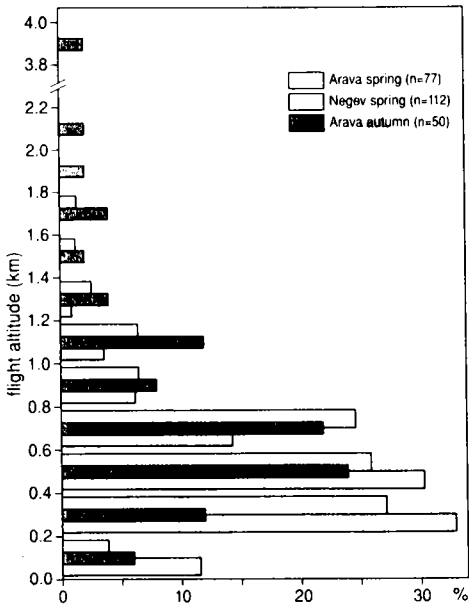
Fig. 1. Proportional distributions of mean flight altitudes above ground in spring and autumn at two sites (Arava and Negev) over southern Israel.

90% below 1060 m (fig 1.), while in autumn the same limits were at 670 m and 1640 m AGL, respectively. In the Negev the median was 420 m AGL and 90% of the birds were below 820 m in spring. Maximum altitude was 3836 m AGL, (3686m above sea level; ASL), measured in autumn above the Arava for a flock of at least 200 birds gliding southward. White Storks appeared at the radar stations 2 to 3 hours after sunrise, when thermals usually start to develop (Fig. 2). They gained altitude as the day progressed and the highest individuals were recorded in the afternoon. Mean flight altitude did not decrease until 1 to 2 hours before sunset. In autumn, above the Arava, some birds were still flying at about 900 m at sunset and even close to dusk. If data were grouped according to time intervals (see stepped line Fig. 2), significant differences between the two sites occurred only in the first morning interval (10-30%) and the last one before sunset (70-90%; ANOVA, $P < 0.05$), but not around noon and in the early afternoon (30-70%), in spite of an overall tendency to higher flight levels in the Arava.
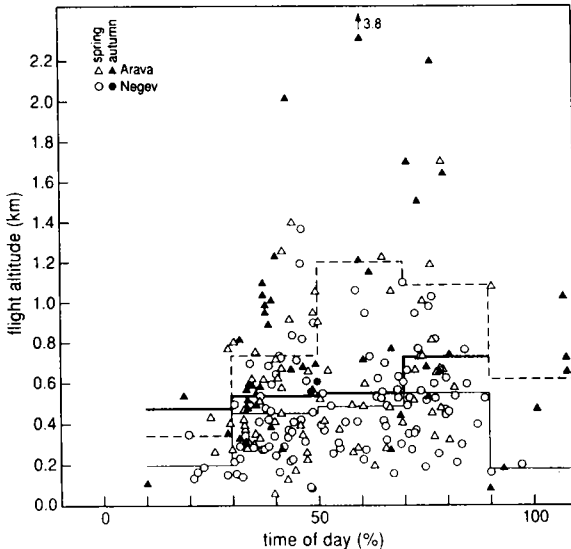

Fig. 2. Mean flight altitude for each track during the course of the day in the Arava (triangles) and on the Negev Highlands (circles) separated for spring (white) and autumn (black). Time of day is converted into percent of the whole day from sunrise (0%) to sunset (100%). Time before sunrise and after sunset is shaded. Average flight altitudes per time intervals of 20% are indicated by stepped lines. A solid thin line stands for Negev spring data (average according to white circles), a solid thick line for Arava spring (white triangles) and a dashed thick line for Arava autumn (black triangles). No average line is given for Negev autumn because only two tracks were recorded (black dots).
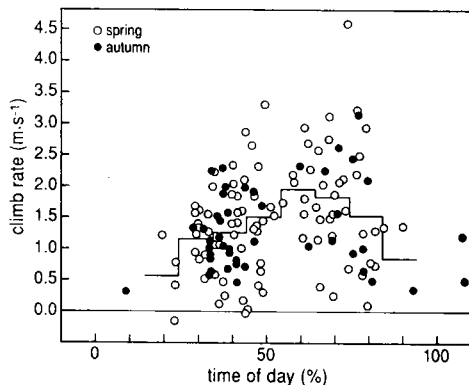
Fig. 3. Mean climb rate in thermals during the course of the day for spring (white circles) and autumn (black circles; data from both sites were pooled). The stepped line indicates the average climb rate for time intervals of 10%.
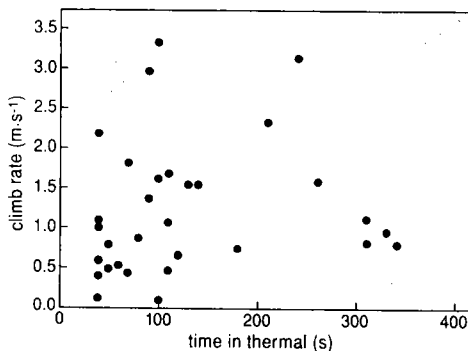

Fig. 5. Height above ground at the beginning of soaring in a thermal, in relation to climb rate within this thermal. The dashed line indicates the geometric mean regression ($r = 0.33$, $P < 0.01$; after Sokal & Rohlf 1981).

Fig. 4. Time spent soaring in relation to the climb rate in a thermal. Only flight paths of complete thermal phases are included (see method). The dashed line indicates the arbitrary split of data (see text).

Soaring phase

Mean climb rate in thermals was 1.4 ± 0.8 ms⁻¹ (mean ± SD). Climb rates did not differ significantly between sites and in relation to flock size (single and multi-way ANOVA, n.s.), but increased significantly with height and were higher in autumn than in spring (ANOVA with covariate,
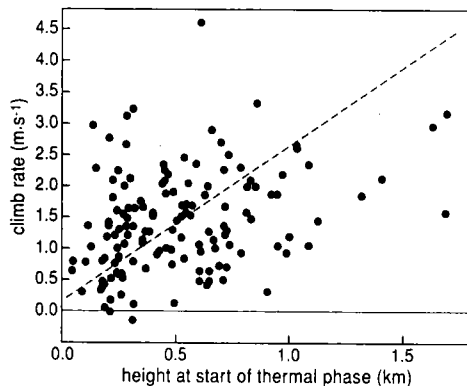
$P < 0.001$). Climb rate culminated in early afternoon; average climb rate was at or above 1.5 ms⁻¹ between 45% and 85% of the time of day (Fig. 3). The highest climb rate of 4.6 ms⁻¹ was recorded 2.5 h after noon in spring above the Negev. The median of the duration of a complete thermal phase was 100 s and the median of height gain was 125 m (max. 780 m). Soaring time of single individuals was significantly shorter than for flocks (ANOVA, $P < 0.05$). It was, however, not correlated with seasons and sites (single and multi-way ANOVA, n.s.), neither was it related to the climb rate ($n = 32$, $r = 0.13$, n.s.); except that with climb rates below 0.7 ms⁻¹ no bird spent more than 2 min soaring (Fig. 4). An arbitrary split of the data at that level of climb rate resulted in a significant difference in soaring time (not related to flocksize; multi-way ANOVA, $P < 0.05$). The height, at which birds started to soar in a thermal was positively correlated with the climb rate within this thermal (Fig. 5); i.e. birds that flew at higher altitude benefited either from powerful thermals or they flew high up because of strong convection ($r = 0.33$, $P < 0.01$).
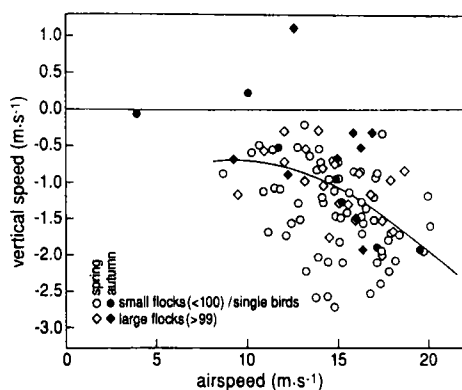
Fig. 6. Airspeed in relation to vertical speed during gliding phase. Circles represent tracks of single birds and small flocks (flocksize <100) and diamonds large flocks (>99). Spring data are white symbols, autumn data are black). Only flight paths were included, where wind information was available within 2 hours. The curve indicates the theoretical glide ratio for a White Stork (mass 3.5 kg, wing span 2 m, wing area= 0.535 m^2, from Pennycuick 1972) calculated after Pennycuick (1989, program Version 1.1).

Gliding phase

Mean ground speed while gliding was 13.0 ± 3.0 ms^{-1} ($n= 161$) in spring, which was significantly slower than the 15.0 ± 2.7 ms^{-1} ($n= 44$) in autumn (ANOVA, $P< 0.01$). No difference occurred according to site and flocksize (ANOVA, n.s.). Airspeed did not differ significantly between seasons, sites and in relation to flocksize (single and multi-way ANOVA, n.s.). Therefore, higher groundspeeds in autumn are explained only by more frequent tailwinds. Of course, airspeed was correlated with sink rate, as height loss is transformed into horizontal flight speed ($n= 97$, $r= 0.36$, $P< 0.001$; Fig. 6). Mean vertical speed was -1.2 ± 0.8 ms^{-1} with a mean horizontal airspeed of 14.8 ± 2.7 ms^{-1}. Sink rates of large flocks were significantly closer to 0 than those of small flocks and individual tracks (ANOVA, $P< 0.05$; Fig. 6), but no difference occurred in relation to site and season (n.s.). Most glide ratios were scattered around the curve of the theoretical glide ratio, the
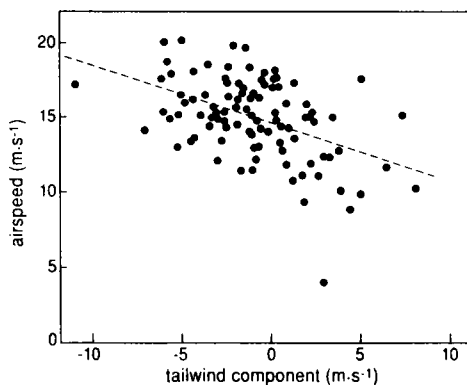

Fig. 7. Airspeed while gliding in relation to tailwind component (negative for headwinds). Wind component calculated with respect to mean flight directions while gliding. Dashed line indicates linear regression ($n= 97$, $r= -0.44$, $P< 0.001$)

superpolar calculated after Pennycuick (1989). There was a significant differences in glide ratios according to flocksize, with better glide ratios for large flocks compared to small flocks and single tracks (ANOVA, $P< 0.05$; Fig. 9). Several flight paths had vertical a speed close to zero and two were even positive, corresponding to straight line soaring observed in large raptors (Spaar & Bruderer in press). Both were at heights above 2000 m AGL. A notable change of vertical speed and airspeed in the course of the day could not be observed. Groundspeed was positively related to tailwind-component ($r= 0.61$, $P< 0.001$), while airspeed was negatively correlated to tailwind-component (Fig. 7) and positively to sidewind-component ($r= 0.48$, $P< 0.001$). No correlation existed between wind component and glide ratio. This means that birds decreased gliding airspeed in tailwinds, and increased it in headwinds and with increasing lateral winds. The influence of wind-components was independent of season, site and flocksize.

Cross-country speed

Mean cross-country speed relative to the ground (V$_{ccg}$) was 9.2 ± 3.3 ms^{-1} ($n= 35$) in
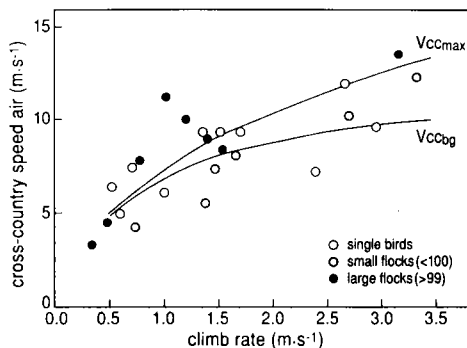
Fig. 8. Cross-country speed relative to air in relation to climb rate in thermals. Only flight paths with at least 40 seconds of thermal and gliding phases are included. Tracks are separated according to flocksize: white= single birds, shaded= small flocks (<100), black= large flocks (>99). The curves indicate the theoretical prediction for maximizing cross-country speed (Vcc_{max}) or flying with best glide ratio (Vcc_{bg}; after Pennycuick 1989).
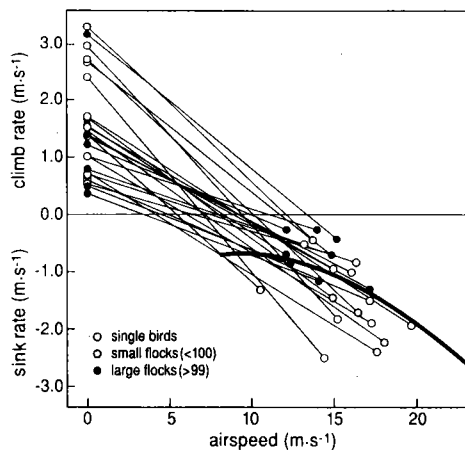

Fig. 9. Glide ratio (airspeed to sink rate) in relation to climb rate for three groups of flocksizes (white= single birds, shaded= small flocks, black= large flocks). Climb rate of each track is connected with a line to glide ratio. The curve indicates the theoretical glide ratio for a White Stork (see Fig. 6).

spring, differing from autumn (12.2 ± 3.1 ms^{-1}; $n= 44$) due to wind. Mean cross-country speed relative to air (V_{cca}) was 8.0 ± 2.5 ms^{-1} ($n= 19$) in spring and 8.5 ± 3.5 ms^{-1} ($n= 5$) in autumn. V_{ccg} was significantly lower in spring than in autumn ($P< 0.05$), while V_{cca} was not different between the seasons. V_{cca} clearly increased with climb rate (Fig. 8). However, the scatter is too large to decide, whether the storks were optimizing their V_{cca} to achieve maximum cross-country speed (V_{ccmax}, minimizing time) or if they were following the strategy to fly with best glide ratio (V_{ccbg}, maximizing range per gliding phase). Large flocks seemed to be slightly faster in relation to climb rate than small flocks and single birds. The fact that airspeed while gliding was not correlated to climb rate in thermals ($r= 0.01$), indicates that they were probably flying with a glide ratio independent of thermal strength. Figure 9 shows climb rate in thermal, airspeed and sink rate while gliding for each track. To maximize V_{cca} the glide ratio should increase with climb rate, according to the tangent drawn from the climb rate on the y-

axis to the curve of the superpolar (Pennycuick 1975, 1989). In relation to this predictions most birds with high climb rates were gliding too slow and those with low climb rates too fast. Within this small sample, no significant difference was found for climb rates according to flocksize, but again glide ratios of large flocks were significantly better (on or above the predicted curve in Fig. 9) compared to those of small flocks and single tracks (ANOVA, $P< 0.05$).

Directions

In spring, gliding did not differ significantly between sites and according to flocksize (Fig. 10; for test statistics see Study areas and Methods). Headings while gliding were mainly towards NNW, reflecting the influence of the common, but moderate westerly winds. With an average of 5.5 ms^{-1} winds on the Negev plateau were somewhat stronger than in the Arava Valley (3.5 ms^{-1}), which resulted in slightly more westerly headings on the plateau with $346° \pm 52°$ compared to $354°$
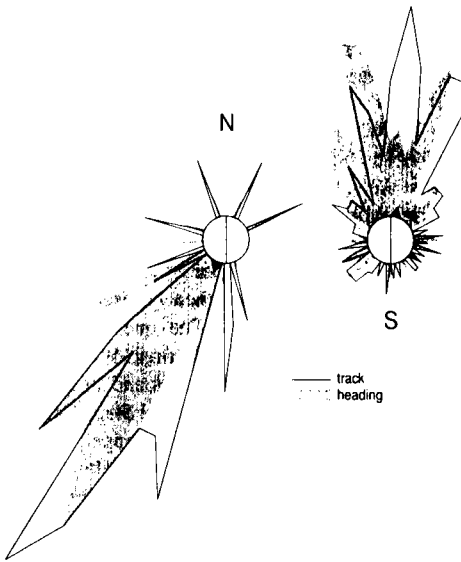
Fig. 10. Mean tracks and headings during gliding in spring (left) and autumn (right). Data from the two sites were pooled. The means of migratory directions estimated from flight paths tracked for at least 2 km are represented by the black triangle (autumn: *n*= 39, mean track= 212°, mean heading= 220°; spring: *n*= 157, mean track= 3°, mean heading= 349°).

± 42° in the valley (difference n.s.). In autumn all tracks except two were recorded in the Arava. No significant difference occurred according to flocksize. Winds were similar to spring, i.e. prevailing NNE winds at low levels and increasing proportions of westerly winds at higher levels. The only difference according to flocksize was a larger scatter of track directions among single birds compared to flocks (*P*< 0.05). Flight behaviour according to lateral wind drift was analysed by plotting the tracks and headings in relation to the angle between them (α). This universal measure for wind drift, introduced by Alerstam (1976), illustrates if birds fly on a constant track and therefore compensate for wind drift or if they are drifted from a fixed heading. No correlation was found plotting all data in one plot, but, splitting
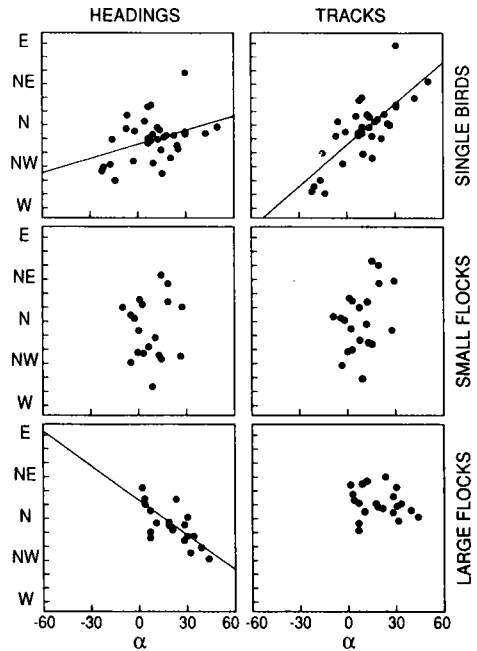

Fig. 11. Tracks and headings during gliding in spring in relation to the angle (α) between track and heading (data from both sites were pooled). Data are separated by flocksize (see Fig. 8). According to the universal measure for drift (Alerstam 1976), regression lines indicate if birds compensate for lateral wind drift or not (see text).

the data into 3 groups according to flocksize shows significant differences among them (Fig. 11). Single birds do not compensate for lateral wind drift, because tracks vary significantly with α (*n*= 33, *r*= 0.77, *P*< 0.01). On the other hand large flocks show a clear compensatory behaviour, indicated by the more or less constant tracks and the significant negative correlation of the headings with α (*n*= 21, *r*= -0.72, *P*< 0.01). Small flocks show no correlations (*n*= 21), which points out that within this sub-sample tracks and headings might vary independently of the wind influence. The slight positive correlation of headings with α for single birds (*r*= 0.38, *P*< 0.05),

implies that they tend to shift towards downwind direction, if lateral wind drift increases.

DISCUSSION

Mean heights over the Negev were somewhat lower than those reported by Leshem in Frumkin *et al.* (1995) for northern Israel (460 to 700 m AGL), and much lower than the 1000 to 2500 m AGL (2500 to 4000 m ASL) reported for East Africa by Pennycuick (1972) as normal cruising height. While, in the two studies with motorized gliders, a certain preference for high flying flocks is highly probable, the radar operators may slightly be biased towards targets close to the study site. Nevertheless, it seems unlikely that a large proportion, flying above 1000 m AGL, was missed by the radar study. They would have been well within the tracking and identification range (see Study areas and Methods). For the Honey Buzzard *Pernis apivorus*, Bruderer *et al.* (1994) found (with the same method) that the height distribution of unidentified raptors did not differ significantly from the species in question. As it is the case for other soaring migrants, the height distribution of storks varied during the day. Birds took off 2-3 hours after sunrise and reached their maximum heights in the early afternoon, when the depth of thermal convection reached its maximum. The decrease in flight height in the evening was smoother than the increase in the morning. The difference in height distribution between spring and autumn can be explained by the better climb rates according to stronger thermals, caused by higher temperature in autumn (Bruderer *et al.* 1995). The difference between the two observation sites is restricted to the morning and late afternoon hours, which indicates that thermals started earlier and lasted longer in the Arava. Probably thermals developed early on the western slopes and persisted longer on the eastern slopes of the valley than above the plateau of the Negev. This assumption is supported by the tracks of some large flocks (50-200, Fig. 3), still flying after sunset, coming from the eastern slope of the

Arava Valley, which is exposed to the setting sun. Similar inter site differences were observed in migrating Steppe Eagles *Aquila nipalensis* (Spaar & Bruderer in press).

Thermals are the limiting factor in soaring flight. The birds encounter them while gliding, or locate them, using visible clues, for instance other soaring birds, like glider pilots do. White Storks often travel in flocks and they spread on a large front while gliding, increasing their chance to encounter a lift, which can then be used by all of them (Pennycuick 1972). The question is how long to soar in a particular thermal. White Storks did not distinguish between weak and strong thermals in such a clear manner as Steppe Eagles (Spaar & Bruderer in press) and Steppe Buzzards *Buteo b. vulpinus* (Spaar 1995) did. Height gain was related to climb rate, but not to the time spent in a thermal, except that very weak thermals were left quicker than others. White Storks do not maximize their cross-country speed, i.e. they do not increase sink rate in favour of high gliding speed when strong thermals are available. Hence, their gliding range increases with climb rate; longer gliding increases the chance of locating further upwind zones. At higher altitudes birds glide for a longer time and can therefore be more selective for stronger thermals. Generally we assume that the closer a stork comes to the ground, the more it starts to soar also in weaker thermals, in order to avoid the risk of using powered flight for the continuation of the journey. On average White Storks had lower climbing rates (1.4 ms^{-1}) than raptors in the same area. Even Steppe Eagles with similar wing loading climbed with 1.9 ms^{-1} earlier in spring. Steppe Buzzards, migrating in the same period as the White Storks, had average climb rates of 2.0 ms^{-1}, the same as Honey Buzzards migrating later in spring (Spaar & Bruderer in press).

During gliding phases, glide ratios of large flocks were better than those of small flocks and single birds (Fig. 6 and Fig. 9). Probably, large flocks were formed under good thermal conditions and they might have crossed upwinds while gliding. At least one large flock (n>100) climbed

considerably while gliding forward for about 1.5 km. We suppose that all tracks with vertical speeds close to zero were profiting from gliding through rising air. This soaring in straight line was observed in several large migrating and particularly in resident raptors in the same area; it was explained by linear arrays of thermals in the Arava Valley and by updrafts along a cliff at the Negev site (Spaar & Bruderer in press). The reason, why many birds with higher airspeeds were descending much faster than predicted, is unclear. Adjusting parameters in the model (body size, aspect ratio, profile drag coefficient) within a realistic range, does not explain these fairly steep glides. Most of these flight paths were from single birds or small flocks (<20), therefore this flight behaviour might be governed by other reasons than flight mechanics, such as heading for another flock to rejoin it, or looking for a site to land (but no relation to daytime or height of flight could be observed). A more speculative explanation might be that there is a profit when gliding in a large flock, although White Storks do not fly in obvious formations, like e.g. pelicans (Pennycuick 1972).

White Storks were tracked only for few kilometres, but cross-country speeds relative to ground proved to be in the range of those reported for Israel (Frumkin *et al.* 1995_), around 10 ms^{-1}, and those for East Africa by Pennycuick (1972), around 12 ms^{-1}. Both followed birds for long distances (up to 100 km) with motorized gliders. The wind as an important factor for cross-country speed was not given for their data, therefore direct comparisons are not possible. According to theory, wind should not influence flight behaviour to achieve maximum cross-country speed, because regardless of the proportion spent soaring or gliding, the wind vector will be added to the birds' flight path all the time. Nevertheless, as observed for raptors (Spaar 1995), a reduction in airspeed while gliding occurred among storks with considerable tailwind. Although they reduced airspeed, cross-country speed against ground was still 12 ms^{-1}. Airspeed while gliding is related to sink rate (Fig. 6), therefore the time accessible for gliding is prolonged in tailwind, which increases the

chance to find randomly scattered thermals. The average time used for soaring was 43%, which is 1.5 times more than the 28% of Steppe Eagles (Spaar & Bruderer in press). This compensates for the lower average climb rate of 1.4 ms^{-1} compared to the 1.9 ms^{-1} of Steppe Eagles and other raptors. For a stork with an average climb rate of 1.4 ms^{-1}, the mean cross-country speed relative to air - 8 ms^{-1} - fits the theoretical prediction of flying at best glide ratio (to reach maximum glide range). Adopting optimal glide ratio (to reach V_{cc-max}) would increase cross-country speed up to 9 ms^{-1} (after Pennycuick 1989), which would correspond to a significant reduction in flight time of about 12%.

The flight directions in spring and autumn correspond well to the course of migration described in a review by Frumkin *et al.* (1995). The observed autumn directions as well as a few thousand birds counted at the radar station in autumn over the Arava, indicate that the Jordan mountains are frequently crossed by White Storks. Taking into account that the compensation of lateral wind drift is related to flocksize and that most White Storks migrate in large flocks, we conclude that, as a rule, they avoid to be drifted from their migratory direction.

For birds travelling by soaring and gliding, the metabolic energy spent for flying is independent of the speed at which they progress (Pennycuick 1972). Thus by migrating as fast as possible, they save time and minimize energy expenditure. In contrast to White Storks, buzzards and eagles do not migrate in dense flocks, although large concentrations occur during high peak migration. Individual flight paths of White Storks are adapted to wind and thermals to a lesser extent than those of raptors, for instance of Steppe Buzzard (Spaar 1995) and Steppe Eagle (Spaar & Bruderer in press). It is surprising that such a highly evolved soaring migrant like the White Stork, seems to be less constrained by time and energy than large raptors. It seems that for White Storks, the profit from flying in flocks is more advantageous than achieving a perfect individual flight behaviour. Displacement experiments performed in Ger-

many (Schüz 1971) demonstrated the strong social influence of adults on the migratory direction of juvenile White Storks. Juveniles from an eastern population released in the area of the western population, at the time when the local population started migration, were joining these flocks towards SW, while those released in the same area after the local populations had left, flew towards SE according to their innate direction. For inexperienced birds, to join a flock in autumn could be a necessity to find a proper flyway around the Mediterranean Sea. In addition, the present data indicate that large flocks are better in optimizing cross-country speed, in drift compensation and in minimizing directional deviations. The profit of communal orientation or location of thermals, or risk reduction by the guidance of experienced birds with respect to optimal flight paths and location of patchily distributed food resources seem to be more important for White Storks than individual optimization of flight performance.

ACKNOWLEDGEMENTS

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SAMENVATTING

Met behulp van een volgradar werden ruim 200 vluchten van Witte Ooievaars vastgelegd gedurende de vooren najaarstrek 1991/92 boven twee locaties in Israel. Uit de analyse van deze waarnemingen bleek dat vooral vogels die alleen vlogen geen optimaal gebruik maakten van de thermiek. Compensatie van verdrifting door zijwind werd alleen waargenomen bij grote groepen. De trekrichting van alleen vliegende individuen vertoonde een grotere spreiding dan de trekrichting van groepen. Vanaf het begin van de trek, twee tot drie uur na zonsopgang, steeg de vlieghoogte tot 2000 m vroeg in de middag. Hoogvliegende vogels konden profiteren van de sterkste thermiek, terwijl zij die lager vlogen alle soorten thermiek gebruikten. Verschillen in vlieggedrag tussen voor- en najaar werden veroorzaakt door verschillen in de omstandigheden. De aanpassing van het gedrag aan de verticale en horizontale luchtstromingen is bij Ooievaars minder goed dan bij roofvogels, maar de nadelen hiervan lijken gecompenseerd te worden door de voordelen die het trekken in troepen oplevert.   (A. Perdeck)