

DIFFERENTIAL USE OF THERMAL CONVECTION BY SOARING BIRDS OVER CENTRAL ISRAEL

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Abstract. Maximum altitudes of soaring migration for White Pelicans (*Pelecanus onocrotalus*), White Storks (*Ciconia ciconia*), Lesser Spotted Eagles (*Aquila pomarina*), and Honey Buzzards (*Pernis apivorus*) were measured in central west Israel and compared to the upper boundary of thermal convection and thermal intensity as predicted by the convection model ALPTHERM. The model predictions of upper boundary of convection explained at least 20% of the variance in maximum altitudes of migration for each species studied. Each species used thermal convection differently. White Pelicans, with the largest wing loading, used 54% of the thermal boundary layer, as calculated by dividing the maximum flight altitude by the modeled thermal depth. White Storks and Lesser Spotted Eagles used 69% and 65%, respectively; Honey Buzzards, with the lowest wing loading, used 95% of the thermal boundary layer. Mean lift rate of convection had a stronger effect on maximum altitudes of flight or the proportion of the thermal boundary layer used by Lesser Spotted Eagles and Honey Buzzards, than it did on storks and pelicans. Honey Buzzards, which combine flapping with soaring flight, were not confined to the thermal boundary layer. Changes in migration altitudes within a species and differential use of thermal convection between species were related to a combination of upper boundary of thermal convection, average lift rate, migratory behavior, wing loading, topography, and additional local meteorological conditions.

Key words: Israel, migration, soaring birds, thermal convection.

Uso Diferencial de la Convección Térmica por Aves que Realizan Vuelos Planeados Elevados Sobre Israel Central

Resumen. Se midieron las alturas máximas de planeo elevado durante la migración al oeste de Israel central para *Pelecanus onocrotalus*, *Ciconia ciconia*, *Aquila pomarina* y *Pernis apivorus*, y se compararon con el límite superior de la convección y la intensidad térmica predicho por el modelo de convección ALPTHERM. Las predicciones del límite superior de convección del modelo explicaron al menos el 20% de la varianza en alturas máximas de migración para cada especie estudiada. Cada especie utilizó la convección térmica de una forma diferente. *Pelecanus onocrotalus*, la especie con la mayor carga alar, utilizó el 54% de la capa térmica límite, lo que se calculó dividiendo la altura máxima de vuelo por la profundidad térmica modelada. *Ciconia ciconia* y *A. pomarina* usaron el 69% y 65% de la capa térmica límite, respectivamente; *P. apivorus*, la especie con menor carga alar, utilizó el 95%. La tasa promedio de fuerza ascensional de convección tuvo un efecto más marcado en las alturas máximas de vuelo o la proporción de la capa térmica utilizada en *A. pomarina* y *P. apivorus* que en *P. onocrotalus* y *C. ciconia*. *Pernis apivorus*, que combina el aleteo con el vuelo planeado, no estuvo confinada a la capa térmica límite. Los cambios en las alturas de migración dentro de una especie y el uso diferencial de la convección térmica entre especies estuvieron relacionados con una combinación del límite superior de la convección térmica, la tasa promedio de fuerza ascensional, el comportamiento migratorio, la carga alar, la topografía y condiciones meteorológicas locales adicionales.

INTRODUCTION

Many large birds such as storks, pelicans, and birds of prey use thermal convection for cross-country soaring during migration and local flights. Several studies have systematically mea-

sured soaring bird altitudes using motorized gliders or radar (Leshem and Yom-Tov 1996a, Spaar and Bruderer 1996, Pennycuik 1998). Migration altitudes of soaring birds show a typical diurnal pattern, increasing during the morning hours, peaking toward noon, then decreasing again in the afternoon, in accordance with general patterns of daily thermal convection (Kerlinger 1989, Leshem and Yom-Tov 1996a).

Manuscript received 2 May 2002; accepted 18 December 2002.

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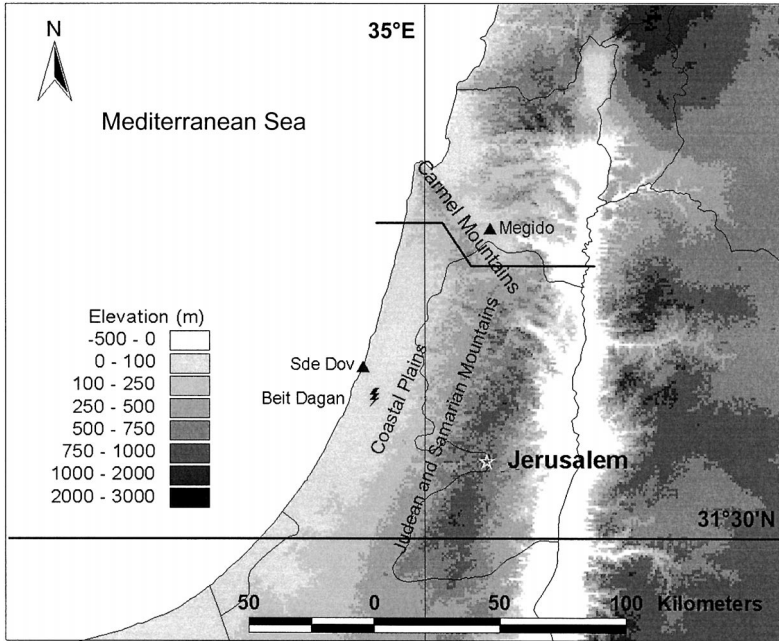


FIGURE 1. Digital elevation model of central Israel (USGS 2002). Black horizontal lines represent northern and southern borders of the study area. The eastern and western borders are the Judean and Samarian Mountains and the coastline, respectively.

However, maximum altitudes of migration change from day to day and among regions (Bruderer et al. 1994, Leshem and Yom-Tov 1996a, Spaar and Bruderer 1996).

In order to compare how different species exploit the thermal boundary layer, and to predict changes in migration altitudes, data on the thermal boundary layer is needed. The development, strength, and duration of thermal convection is affected by topography as well as changing atmospheric and environmental conditions. The amount, intensity, and duration of thermal activity also differ between mountainous and flat terrain (World Meteorological Organization 1993). For example, slopes that face the sun heat up faster than flatter surfaces below, and thermals on west-facing slopes last longer in the evening. As systematic measurements of thermal updraft intensity are generally lacking, most studies use boundary-layer forecast models to predict the development, upper boundary, and intensity of thermal convection (Spaar et al. 2000, Shannon et al. 2002), which can be compared to soaring bird flight altitudes. These parameters were estimated during this study using ALPTHERM, a

numerical model designed to simulate thermal convection (Liechti and Neining 1994).

The goal of this study was to examine how the maximum flight altitudes of four species of soaring birds, White Pelicans (*Pelecanus onocrotalus*), White Storks (*Ciconia ciconia*), Lesser Spotted Eagles (*Aquila pomarina*) and Honey Buzzards (*Pernis apivorus*), are related to the predicted thermal depth and thermal intensity.

METHODS

STUDY LOCATION

We studied the flight altitudes of White Pelicans, White Storks, Lesser Spotted Eagles and Honey Buzzards flying along the western migration route (Leshem and Yom-Tov 1998) in west-central Israel, within the coastal plain along the Mediterranean shore and the western slopes of the Judean and Samarian Mountains. The western slopes of the mountains gradually rise to a few hundred meters elevation (Fig. 1). The coastal plain is the most densely populated region in Israel and includes some agriculture, mainly orchards. The western slopes of the Judean and Samarian Mountains are covered pri-

marily by Mediterranean vegetation and olive groves. The climate in this region varies seasonally. In summer, a marine inversion creates a stable layer in the lower atmosphere and results in unfavorable conditions for thermal development on the western slopes of the mountain ranges. The inversion effect decreases in September, and disappears in October. Therefore, autumn soaring migrants arriving in August and early September use the eastern route along the Jordan Rift Valley, whereas migrants arriving later in the season can use both the eastern and western migration routes. In spring favorable soaring conditions exist along the coast and western slopes before the summer regime develops (Leshem and Yom-Tov 1998).

MIGRATION TRACKING

We tracked White Storks migrating during spring 2000 and Honey Buzzards and Lesser Spotted Eagles during autumn 2000 migration over central Israel. Additional data on migration altitudes of White Storks, White Pelicans, Honey Buzzards, and Lesser Spotted Eagles were taken from previous studies conducted between 1986 and 1988 (Leshem and Yom-Tov 1996a, 1998). Data were used for birds found in central Israel between the Mediterranean coast and the western slopes of the Judean and Samarian Mountains no farther north than the Carmel Mountains and no farther south than latitude 31.5°N (Fig. 1).

Birds were first identified by one or a combination of methods, the Airport Surveillance Radar (ASR-8) at Ben Gurion International Airport (Leshem and Yom-Tov 1996a), the MRL-5 radar at the International Center for the Study of Bird Migration at Latrun or the Israel Ornithological Center's annual autumn soaring bird migration survey in the northern valleys of Israel. Once birds were identified, a two-seater motorized glider (IS28M2, IAR S.A. Brasov, Brasov Romania) equipped with a 2000-cc, 80-hp Limbach engine took off from Megido Airstrip in northern Israel (autumn) or from Sde Dov Airfield in central Israel (spring). When the pilot or observer located a flock the glider approached the flock with the engine on but in neutral. The aircraft remained approximately 100 m from the flock, circling with it, close enough to record the altitude, time, latitude, and longitude as the soaring flock entered and left thermals (maximum flight altitude) without disturbing their flocking

behavior. Birds acclimated to the presence of the aircraft within several minutes (for details see Leshem and Yom-Tov 1996a). Flocks of 20 birds or more were tracked for several hours when possible; smaller flocks were not tracked. Flocks were not always tracked continuously for the entire duration of flight over Israel, and occasionally several flocks were followed during the same flight. During previous studies (Leshem and Yom-Tov 1996a, 1998), a single flock was generally tracked for an entire day.

A Garmin GPS (Global Positioning System; Olathe, Kansas) receiver recorded the latitude and longitude where birds entered and exited thermals. The route of the entire glider flight was recorded automatically at 2-sec intervals using the GPS. Route and thermal location data were downloaded to a PC using PCX5AVD software (Garmin International Inc. 1999). The aircraft altimeter was used to determine the altitude of flight above sea level (ASL).

Migration tracks and the locations where birds entered and exited thermals were plotted on a geographic information system (GIS) using ArcView 3.2 (ESRI 1999). These data were overlaid on a global digital elevation layer (USGS 2002) in order to determine if birds were in the coastal plain or the Judean and Samarian Mountains, the mountains defined as elevations ≥ 100 m. Table 1 summarizes the number of days, flocks, and locations analyzed for each species each season.

ALPTHERM CONVECTION MODEL

The convection model ALPTHERM was designed (Liechti and Neining 1994) to predict the onset, duration, depth (m) and intensity (mean lift rate in m sec^{-1}) of thermal convection for varying topographies. Predicted thermal depth is the vertical column (altitude) where thermals are present. Thermal depth is predicted only to cloud base. Maximum thermal depth is the upper boundary of convection, or thermal depth, up to cloud base with a minimum lift rate of 0.5 m sec^{-1} . Thermal intensity is the mean lift rate within the thermal column, ranging from 0.5 to 3 m sec^{-1} . The temporal resolution of model outputs for thermal depth and intensity is 30 min, with a spatial (vertical) resolution of 100 m. Presently, the model is in use by the German, Austrian, and Swiss weather services.

For this study ALPTHERM was configured to provide predictions for the coastal plain and

TABLE 1. Sample sizes of migrating White Pelican, White Stork, Lesser Spotted Eagle, and Honey Buzzard flocks observed over central Israel, 1986–1988 and 2000.

Species	Spring				Autumn			
	Days	Flocks	Coastal plain thermals	Mountain thermals	Days	Flocks	Coastal plain thermals	Mountain thermals
White Pelican								
1986–1988	2	2	5	10	11	13	117	18
White Stork								
2000	5	8	13	22				
1986–1988	18	18	32	191	1	1	0	9
Lesser Spotted Eagle								
2000					2	2	5	9
1986–1988					2	2	5	9
Honey Buzzard								
2000					10	19	12	62
1986–1988					1	1	0	10

mountains of central Israel. Vertical atmospheric profiles of temperature, air pressure, and dew point from nightly radiosondes (carried by weather balloons) were used to initialize the model. Data from radiosondes released at Beit Dagan in central Israel (32.00°N, 34.82°E) by the Israel Meteorological Service every night at 00:00 UTC (Coordinated Universal Time) between 1986 and 1988, and at 02:00 UTC by the Israel Air Force Meteorological Unit in 2000, were used.

In a previous study the ALPTHERM convection model outputs were compared to flight altitudes of migrating raptors measured with tracking radar in the Arava desert in southern Israel (Spaar et al. 2000) indicating that the altitudinal distribution of soaring raptors in southern Israel was significantly correlated with the predicted thermal depth.

STATISTICAL ANALYSES

The maximum flight altitude in each thermal for White Storks, White Pelicans, Lesser Spotted Eagles and Honey Buzzards, was compared to the predicted maximum thermal depth (m) and mean thermal intensity (m sec^{-1}) using linear regression. The proportion of thermal depth used by each species was calculated as maximum flight altitude divided by predicted thermal depth. The height band used by each species was calculated as the maximum flight altitude minus the altitude where birds entered the thermal or first started circling (base of thermal), divided

by the thermal depth. The height band is a description of the range of altitudes at which birds climb within the thermal boundary layer. Student's two-tailed *t*-test was used to test for differences between the proportion of thermal depth used in each region, for each species. A generalized linear model was used to analyze the relation between the maximum flight altitude in each thermal and a combination of thermal depth, thermal intensity, time of day, and topographic elevation (m). An additional analysis was performed to test the relationship between the proportion of thermal depth used and the above-mentioned predictors. In the final multiple regression models only variables with *T*-values ≥ 2.0 and *P*-values ≤ 0.05 were included. The percentage of observations above the thermal boundary layer was calculated as follows: observations ≥ 100 m above thermal depth divided by total number of observations $\times 100$. Values presented are means \pm SD. All statistical analysis were performed with S-Plus software (MathSoft Inc. 1998).

RESULTS

MODEL PREDICTIONS

The mean and maximum thermal depths in central Israel predicted by the ALPTHERM convection model during the study were 1355 ± 325 m and 2100 m, respectively. The mean and maximum predicted thermal strengths during the study were 1.42 ± 0.56 m sec^{-1} and 2.5 m sec^{-1} ,

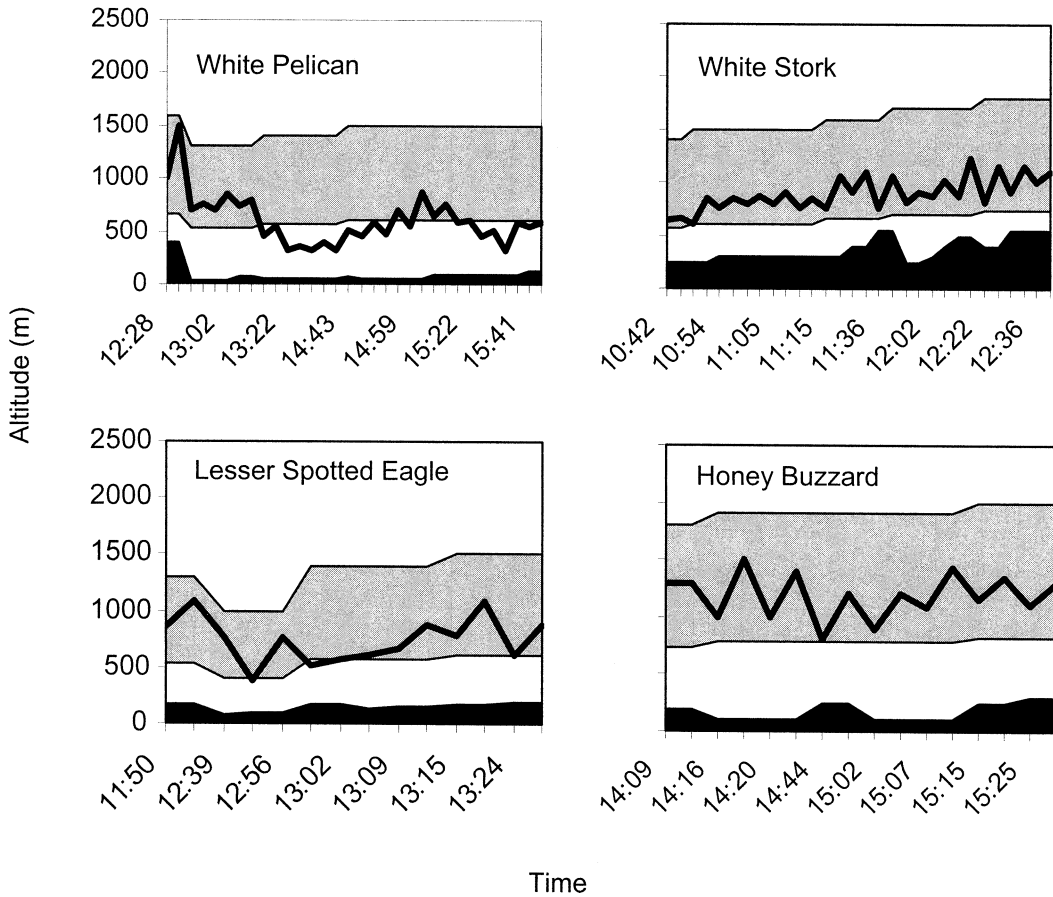


FIGURE 2. Examples of soaring paths taken by flocks of four species during migration over central Israel. Upper lines indicate the altitude at the top of thermals (maximum predicted thermal depth). Solid lines indicate the flight altitude of one flock during one day: (a) White Pelicans on 21 October 1987, (b) White Storks on 12 April 1987, (c) Lesser Spotted Eagles on 28 September 1987, (d) Honey Buzzards on 5 September 1986. All four species during this study spent the majority of soaring time at altitudes between 41% and 100% of the maximum predicted thermal depth (gray area, representing, 75%, 78%, 96%, and 74%, respectively, of all observations of each species). Filled area indicates topography.

respectively. Thermal convection generally began to develop at approximately 06:00 UTC with a peak in convection (maximum thermal depth) occurring sometime between 09:30 and 12:30 UTC. Generally, thermal convection gradually develops in the morning as ground temperatures rise. The depth and strength of thermals increase through midday and decrease slightly in the late afternoon. Soaring birds enter thermals where lift is strong enough to promote soaring; birds climb in a thermal by circling, and then glide between thermals. Maximum flight altitudes follow a pattern similar to thermal convection (Fig. 2).

WHITE PELICANS

The maximum flight altitude in each thermal varied between 200 and 1490 m (Fig. 3), with no observations above the predicted thermal depth. White Pelicans migrated mainly in the coastal plain ($n = 122$ thermals) as well as in the Samaritan Mountains ($n = 28$ thermals). There was no significant difference between the proportion of thermal depth used in the two regions, so these results were pooled. The mean proportion of thermal depth used was 0.54 ± 0.16 with 87% of the observations between 0.31 and 0.80. The maximum flight altitude of each thermal was positively and significantly related

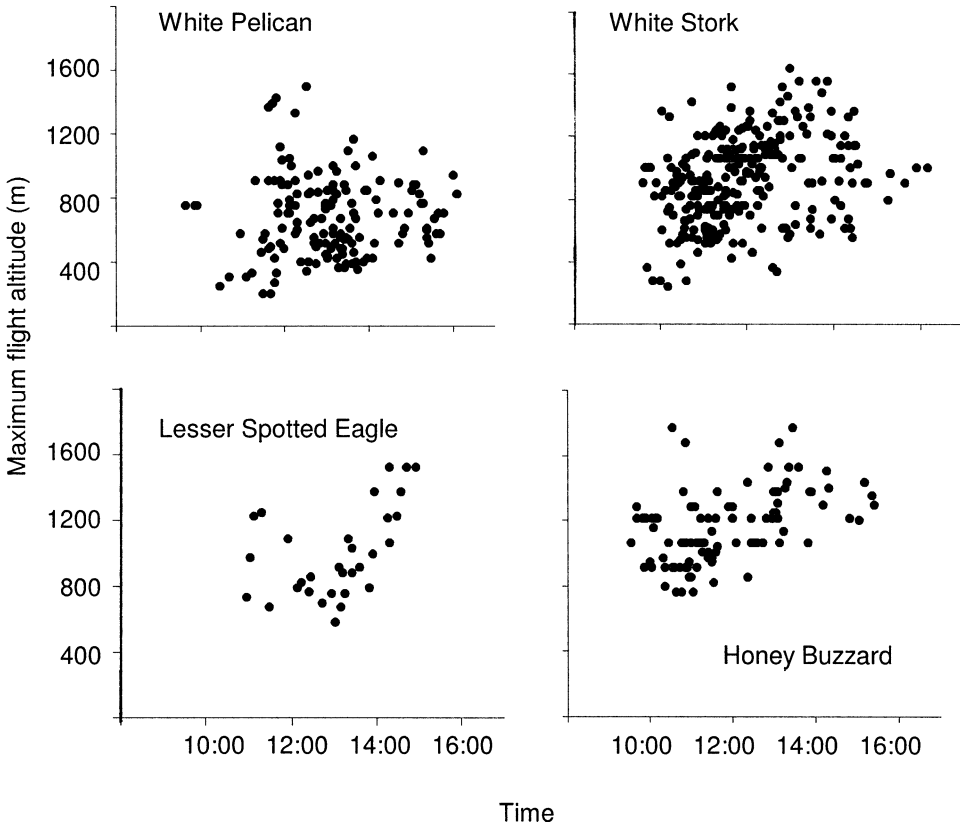


FIGURE 3. Temporal distribution of maximum flight altitudes in each thermal (m) for White Pelicans, White Storks, Lesser Spotted Eagles, and Honey Buzzards migrating through central Israel.

to thermal depth ($r^2 = 0.30$, $P < 0.001$, $y = 0.49x + 57.9$; Fig. 4). The maximum flight altitude in each thermal was also positively and significantly correlated with a combination of thermal depth ($T = 7.3$, $P < 0.001$), topographic elevation ($T = 5.5$, $P < 0.001$) and thermal intensity ($T = 3.9$, $P < 0.001$; $R^2 = 0.44$, $P < 0.001$). The proportion of thermal depth used was positively correlated with topographic elevation ($T = 4.8$, $P < 0.001$) and negatively correlated with thermal depth ($T = -3.6$, $P < 0.001$; $R^2 = 0.16$, $P < 0.001$).

WHITE STORKS

The maximum flight altitude in each thermal varied between 240 and 1640 m (Fig. 3). White Storks migrated in the coastal plain ($n = 45$ thermals) and mainly in the Samarian Mountains ($n = 221$ thermals). There was no significant difference between the proportion of thermal depth used in the coast compared to the

mountains, so results were pooled for both regions. The mean proportion of thermal depth used was 0.69 ± 0.22 , with 78% of the observations between 0.41 and 1.0 and 5% of the observations above the predicted upper boundary of thermal convection. The maximum flight altitude in each thermal was positively correlated with a combination of topographic elevation ($T = 7.2$, $P < 0.001$), thermal intensity ($T = 4.3$, $P < 0.001$), and thermal depth ($T = 3.9$, $P < 0.001$; $R^2 = 0.33$, $P < 0.001$). The proportion of thermal depth used was significantly and negatively correlated with thermal depth ($T = -10.0$, $P < 0.001$), and positively correlated with topography elevation ($T = 5.9$, $P < 0.001$), and thermal intensity ($T = 2.8$, $P < 0.01$; $R^2 = 0.31$, $P < 0.001$).

LESSER SPOTTED EAGLES

The maximum flight altitude in each thermal varied between 580 and 1524 m (Fig. 3). None

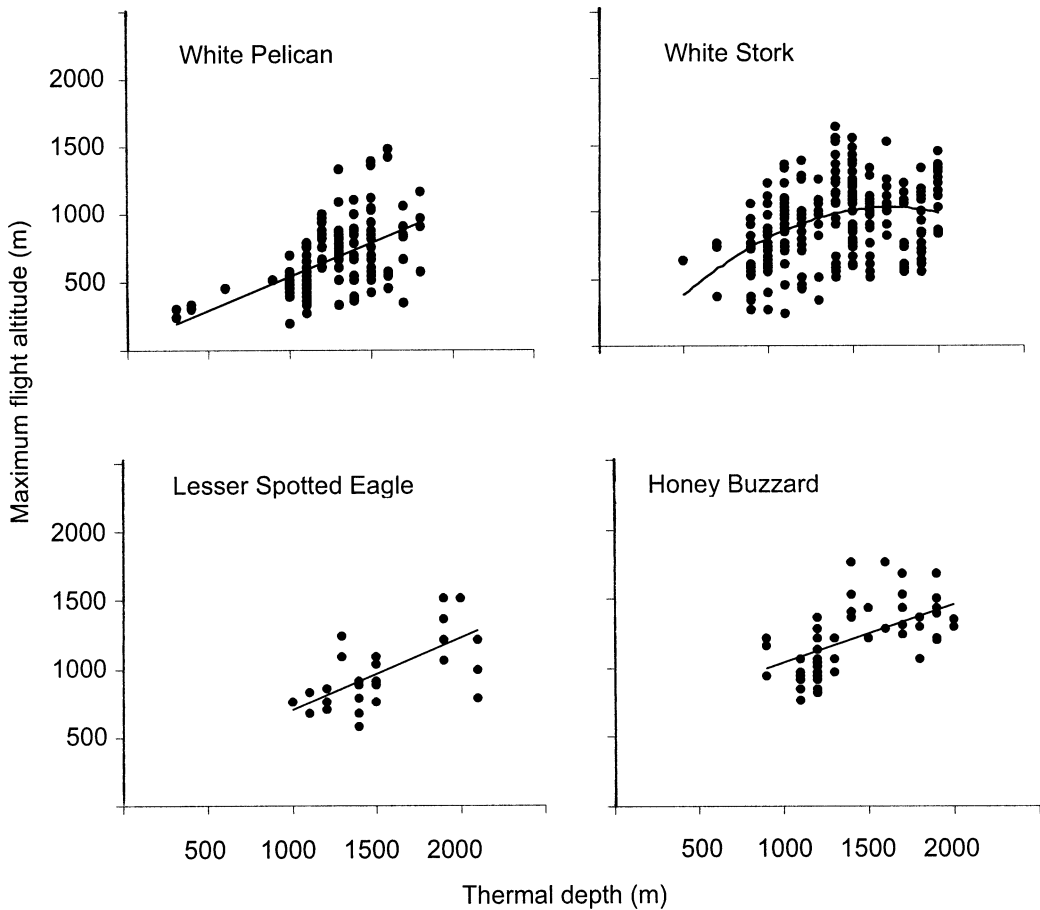


FIGURE 4. Relationship between maximum flight altitude in each thermal (m) and thermal depth (m) for White Pelicans, White Storks, Lesser Spotted Eagles, and Honey Buzzards migrating through central Israel.

of the thermal climbs exceeded the maximum thermal depth. Lesser Spotted Eagles migrated in both the coastal plain ($n = 10$ thermals) and the mountains ($n = 18$ thermals). There was no significant difference between proportion of thermal depth used in the coast compared to the mountains, so results were pooled for both regions. The average proportion of thermal depth used was 0.65 ± 0.13 with 71% of the observations between 0.51 and 0.80. The maximum flight altitude in each thermal was positively correlated with thermal depth ($r^2 = 0.42$, $P < 0.001$, $y = 0.53x + 180.5$; Fig. 4). The maximum flight altitude in each thermal was also positively correlated with thermal intensity ($r^2 = 0.29$, $P < 0.001$, $y = 307.2x + 401.4$) as well as a combination of topographic elevation ($T = 3.7$, $P = 0.001$) and thermal

intensity ($T = 3.4$, $P = 0.002$; $R^2 = 0.54$, $P < 0.001$). The proportion of thermal depth used was significantly and positively correlated to topographic elevation ($T = 3.1$, $P < 0.01$) and negatively correlated to thermal depth ($T = -2.2$, $P = 0.04$; $R^2 = 0.30$, $P = 0.01$).

HONEY BUZZARDS

The maximum flight altitude in each thermal varied between 762 and 1768 m (Fig. 3). Honey Buzzards migrated mainly in the mountains ($n = 70$ thermals) and in the coastal plain ($n = 11$ thermals). In the coastal plain the proportion of thermal depth used was slightly higher than in the Samarian Mountains (1.01 ± 0.14 vs. 0.90 ± 0.18 , $t_{80} = 2.1$, $P = 0.02$); nevertheless, regions were analyzed together because of the small sample size in the coastal plain compared

TABLE 2. A comparison of wing loading (body mass/wing area) of four soaring bird species to soaring variables observed during migration over central Israel. Soaring variables: mean \pm SD base of thermal, maximum flight altitude, and height band (each divided by thermal depth), and the mean difference between thermal depth and maximum flight altitude. The last variable is an estimate of how much of a thermal's vertical dimension remained unused.

Species	Wing loading (kg m ⁻²)	Base of thermal (m)	Max. flight altitude (m)	Height band	Thermal depth-max. flight altitude (m)
White Pelican	8.4	0.40 \pm 0.14	0.54 \pm 0.16	0.14	602
White Stork	6.3	0.52 \pm 0.19	0.69 \pm 0.22	0.17	456
Lesser Spotted Eagle	4.4	0.46 \pm 0.11	0.65 \pm 0.13	0.19	557
Honey Buzzard	3.1	0.66 \pm 0.16	0.91 \pm 0.18	0.25	142

to the mountains. Fifteen percent of the maximum flight altitudes in each thermal were above the predicted upper boundary of convection. Sixty-seven percent of the maximum flight altitudes were between 0.71 and 1.20 of the thermal depth. The maximum flight altitude in each thermal was positively and significantly related to thermal depth ($r^2 = 0.33$, $y = 0.41x + 639.8$, $P < 0.001$; Fig. 4). The maximum flight altitude in each thermal was positively correlated with thermal depth ($F_{1,69} = 41.8$, $P < 0.001$) and thermal intensity (polynomial function, $F_{2,69} = 7.7$, $P < 0.001$; $R^2 = 0.46$, $P < 0.001$). Predicted maximum flight altitude occurred at thermal intensity of 1.7 m sec⁻¹. The proportion of thermal depth used was negatively correlated with thermal depth ($F_{1,69} = 40.3$, $P < 0.001$) and positively correlated with thermal intensity (polynomial function, $F_{2,69} = 11.0$, $P < 0.001$; $R^2 = 0.49$, $P < 0.001$). Predicted maximum proportion of thermal depth used occurred at thermal intensity of 1.8 m sec⁻¹.

The mean proportion of thermal depth used by each species appeared to be negatively related to wing loading (kg m⁻²), although the small number of species investigated yielded a nonsignificant statistical test ($r^2 = 0.74$, $P = 0.14$, $n = 4$). The height band used by each species was negatively related to wing loading ($r^2 = 0.90$, $P = 0.05$; Table 2); that is, the larger the wing loading the narrower the height band (or range of altitudes from bottom to top of thermal) used by that species.

DISCUSSION

This study demonstrates the relationship between modeled thermal characteristics (depth and intensity) and flight behavior (flight altitude

and use of thermal depth) of soaring migrants in two elevation regimes in central Israel. Topographic elevation, thermal depth, and thermal intensity affected maximum flight altitudes of soaring migrants. Most species did not use the entire depth of thermal convection, but Honey Buzzards and White Storks occasionally soared above the predicted top of the thermal. We discuss possible explanations for differential use of thermal depth and intensity between species and the applicability of the ALPTHERM model for predicting maximum flight altitudes during soaring migration.

According to theoretical predictions the circling radius of a bird climbing in a thermal is proportional to its wing loading (Pennycuik 1989); birds with lower wing loading will have a smaller circling radius in thermals, and improved climbing capacity than birds with higher wing loading (Alerstam 1994). This was reflected in the results of migration altitudes and the proportion of thermal depth used. An inverse relationship was found between wing loading and proportion of thermal depth as well as the height band used by each species (Table 2). These relationships were very strong, though not significant, which may be due to the small sample size (four species). Honey Buzzards climbed highest within the thermal boundary layer and had the widest height band in contrast to White Pelicans, which had the narrowest height band and lowest proportion of thermal depth used. In addition, thermal intensity had a stronger influence on maximum flight altitudes or proportion of thermal depth used by smaller species (Honey Buzzard, Lesser Spotted Eagle) than the larger species (White Stork, White Pelican). Increasing thermal intensity was related to increasing max-

imum flight altitudes and the proportion of thermal depth used. The species with lower wing loading profited more from stronger thermal updrafts than the species with larger wing loading; species with lower wing loading may be better able to alter their behavior in response to changing thermal conditions. Our results are supported by the findings of Spaar and Bruderer (1996) that Steppe Eagles (*Aquila nipalensis*), Steppe Buzzards (*Buteo buteo vulpinus*) and Honey Buzzards in the Arava Valley, southern Israel, used different height bands, with the larger Steppe Eagles using a narrower height band than Steppe Buzzards and Honey Buzzards. In addition, Spaar (1997) found that Honey Buzzards and Lesser Spotted Eagles (as well as several other birds of prey) increased cross-country speeds by increasing their climb rate, and reacted to thermal conditions by adopting a thermal-dependent air speed. Similar to our results for the White Pelican, Shannon et al. (2002) observed that 70% of soaring flight for the American White Pelican was confined to the middle of the boundary layer between 0.2 and 0.8 of the thermal depth, using less of the thermal boundary layer than smaller species.

The applicability of the convection model predictions are limited to soaring birds using thermal updrafts and do not apply to birds using other sources of lift such as ridge lift (orographic lift) over a mountain range (Kerlinger 1989). As the Judean and Samarian Mountains are aligned with the primary axis of migration, orographic lift may be utilized by soaring migrants. The results are also affected by local conditions such as the sea breeze front, which also was not integrated into the model at this stage. Honey Buzzard migration is influenced by the sea breeze front progression (Alpert et al. 2000), which could in turn influence migration altitudes.

Bird behavior such as flapping flight or straight-line soaring may also affect the ability of convection models to predict bird flight altitudes (Shannon et al. 2002). Straight-line soaring occurs when birds glide continuously through rising air without circling, gaining little or no altitude. Pennycuick (1998) showed that straight-line-soaring birds can increase cross-country speed, and thus migration speed, above predictions based on soaring in discrete thermals. Straight-line soaring was reported in large migrating eagles, such as the Lesser Spotted Eagle and Steppe Eagle (Spaar and Bruderer 1996,

Spaar 1997). In this study despite their lower wing loading, Lesser Spotted Eagles used the same proportion of thermal convection as White Storks. By integrating straight-line soaring and discrete thermal soaring, Lesser Spotted Eagles may be using less of the thermal depth than expected based on their wing loading.

Soaring birds sample a variety of thermals across the landscape (Pennycuick 1998), which in part accounts for the variability in flight altitudes over short periods (less than 1 hr). Modeled thermal depth and intensity, however, provide average conditions across time and space (the 30-min modeling periods). This variation may explain in part why correlations between flight behavior and thermal characteristics are not always very high, in addition to the above factors. For example, in our study, Honey Buzzards (15% of observations) and occasionally White Storks (5% of observations) flew above the predicted thermal boundary layer. Shannon et al. (2002) attributed maximum altitudes of flight that were above the thermal boundary layer as errors in the forecasting model. ALP-THERM model predictions do not provide estimates of thermal intensity above cumulus cloud base; therefore, we considered cloud base the extent of thermal depth. We saw Honey Buzzards climbing into cloud base, so we know that at least some of the observations we recorded above thermal depth were accurate. In addition, the low wing loading of the Honey Buzzard and its tendency to incorporate flapping flight enable it to fly above the predicted thermal depth and take advantage of different environmental conditions that may exist there (Bruderer et al. 1994). However, White Storks are much larger birds with larger wing loading and the several observations above maximum thermal depth were unexpected. A possible explanation for some of these climbs is the use of ridge lift along the mountain ridges rather than thermal convection, or the use of the sea breeze front, observed during this study, which creates a line of extra lift along the front.

Each species we studied use a slightly different migration route through central Israel (Leshem and Yom-Tov 1998), with White Pelicans migrating closest to the coast, followed by Lesser Spotted Eagles, Honey Buzzards, and White Storks by comparison migrating along more eastern routes. In fact, during autumn migration White Storks migrate along the Jordan Rift Val-

ley, approximately 80 km to the east (Leshem and Yom-Tov 1998), which is why there are no autumn data for storks in this study. The species migrating farther west in Israel arrive later in autumn than White Storks and Honey Buzzards (Leshem and Yom-Tov 1996b). In addition to predicting migration altitudes, the ALPTHERM convection model may also be used to explain and possibly predict shifts within these routes, particularly when conditions differ significantly between regions. For example, on days when a strong marine inversion develops in the coastal plain but does not penetrate the mountains, birds would be expected to prefer routes along the mountain ridge.

Birds pose a risk to flight safety around the world (Richardson and West 2000, Robinson 2000). During the migration seasons in spring and autumn over one million soaring birds of prey, pelicans, and storks migrate through the Middle East and particularly Israel, causing, at times, severe danger, aircraft damage, and even human fatalities (Leshem 1999). During the last 25 years, the Israel Air Force has lost nine aircraft due to bird collisions most often with soaring migrants. Forecasting changes in soaring bird flight altitudes can be an important tool in reducing the risk of serious bird-aircraft collisions particularly during migration seasons. Based on the results of this study showing the relationship between predicted thermal depth and intensity, topography, and migration altitudes of soaring migrants, model predictions may be used to forecast bird flight altitudes for each species, and this may improve flight safety in the region, particularly for low, fast-flying military aircraft (see Fig. 2 as an example). For species such as the White Pelican, Lesser Spotted Eagle, and White Stork, which generally stayed within the thermal boundary layer, ALPTHERM is a useful tool to provide maximum daily altitudes above which few large soaring migrants will be found. Model predictions could be produced immediately after midnight radiosondes are processed, becoming available before daily flight training begins. ALPTHERM can be further calibrated by incorporating synoptic and local meteorological features such as horizontal wind, an important factor influencing thermal convection, ridge lift, and the sea breeze front progression (Alpert et al. 2000).

ACKNOWLEDGMENTS

We are grateful for funding from Mr. Moshe Yanai and from the Ministry of Defense Research and Development Directorate grant for new immigrants. We would like to thank the Israel Air Force, particularly the Meteorology Unit and the Radar Unit for their assistance and cooperation as well as the Israel Airport Authority and the Israel Ornithological Center, Society for the Protection of Nature in Israel. Radiosonde data were provided by the Israel Air Force Meteorology Unit (2000) as well as the NASA node in Israel, Tel Aviv University (1986–1988). We are grateful for the time and effort invested by L. Dinevitch, D. Morad, and S. Brand for locating flocks and guiding the gliders, the glider pilots, and the birdwatchers. Earlier drafts of this manuscript were improved with constructive comments from Bruno Bruderer, David Dobkin, Hugh Powell, and an anonymous reviewer.

LITERATURE CITED

- ALERSTAM, T. 1994. Bird migration. Cambridge University Press, Cambridge, UK.
- ALPERT, P., D. TANNHAUSER, Y. LESHEM, A. KRAVITZ, AND M. RABINOVITCH-HADAR. 2000. Migrating soaring birds align along sea-breeze fronts; first evidence from Israel. *Bulletin of the American Meteorological Society* 81:1599–1601.
- BRUDERER, B., S. BLITZBLAU, AND D. PETER. 1994. Migration and flight behavior of Honey Buzzards *Pernis apivorus* in southern Israel observed by radar. *Ardea* 82:111–122.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 1999. ArcView. Version 3.2. Environmental Systems Research Institute, Redlands, CA.
- GARMIN INTERNATIONAL INC. 1999. PCX5AVD user's manual. Garmin International Inc., Olathe, KS.
- KERLINGER, P. 1989. Flight strategies of migrating hawks. University of Chicago Press, Chicago.
- LESHEM, Y. 1999. Development of a real time warning system in the Middle East: from vision to reality, p. 45–69. *In* Y. Leshem, Y. Mandelik, and J. Shammoun-Baranes [EDS.], *Migrating birds know no boundaries. Proceedings of the international seminar on birds and flight safety in the Middle East*. The Society for the Protection of Nature in Israel, Tel Aviv.
- LESHEM, Y., AND Y. YOM-TOV. 1996a. The use of thermals by soaring migrants. *Ibis* 138:667–674.
- LESHEM, Y., AND Y. YOM-TOV. 1996b. The magnitude and timing of migration by soaring raptors, pelicans and storks over Israel. *Ibis* 138:188–203.
- LESHEM, Y., AND Y. YOM-TOV. 1998. Routes of migrating soaring birds. *Ibis* 140:41–52.
- LIECHTI, O., AND B. NEININGER. 1994. ALPTHERM: a PC-based model for atmospheric convection over complex topography. *Technical Soaring* 18:73–78.
- MATHSOFT INC. 1998. S-Plus for Windows. Version 4.5. MathSoft Inc., Cambridge, MA.
- PENNYCUICK, C. J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press, Oxford, UK.

- PENNYCUICK, C. J. 1998. Field observations of thermals and thermal streets, and the theory of cross-country soaring flight. *Journal of Avian Biology* 29: 33–43.
- RICHARDSON, J., AND T. WEST. 2000. Serious birdstrike accidents to military aircraft: updated list and summary, p. 67–97. *In* Proceedings of the 25th International Bird Strike Committee. International Bird Strike Committee, Amsterdam.
- ROBINSON, M. 2000. Is the possibility of a costly aircraft bird strike growing?, p. 169–178. *In* Proceedings of the 25th International Bird Strike Committee. International Bird Strike Committee, Amsterdam.
- SHANNON, H., G. YOUNG, M. YATES, M. FULLER, AND W. SEEGAR. 2002. American White Pelican soaring flight times and altitudes relative to changes in thermal depth and intensity. *Condor* 104:679–683.
- SPAAR, R. 1997. Flight strategies of migrating raptors; a comparative study of interspecific variation in flight characteristics. *Ibis* 139:523–535.
- SPAAR, R., AND B. BRUDERER. 1996. Soaring migration of Steppe Eagles *Aquila nipalensis* in southern Israel: flight behavior under various wind and thermal conditions. *Journal of Avian Biology* 27:289–301.
- SPAAR, R., O. LIECHTI, AND B. BRUDERER. 2000. Forecasting flight altitudes and soaring performance of migrating raptors by the altitudinal profile of atmospheric conditions. *Technical Soaring* 24:49–55.
- UNITED STATES GEOLOGICAL SURVEY [ONLINE]. 2002. Land process distributed active archive center. (<http://edcdaac.usgs.gov/gtopo30/gtopo30.html>) (30 December 2002).
- WORLD METEOROLOGICAL ORGANIZATION. 1993. Handbook of meteorological forecasting for soaring flight. World Meteorological Organization Technical Note No. 158, Geneva.