

SEASONAL TIMING, GEOGRAPHIC DISTRIBUTION, AND FLIGHT BEHAVIOR OF BROAD-WINGED HAWKS DURING SPRING MIGRATION IN SOUTH TEXAS: A RADAR AND VISUAL STUDY

PAUL KERLINGER AND SIDNEY A. GAUTHREUX, JR.¹

Department of Biological Sciences, Clemson University, Clemson, South Carolina 29634 USA

ABSTRACT.—Spring migration of Broad-winged Hawks (*Buteo platypterus*) through south Texas was studied using vertical, fixed-beam, and surveillance radars with simultaneous visual observations. Five years of records from Santa Ana National Wildlife Refuge and 33 years of reports from *American Birds* also were employed. The peak of migration occurred during the last week in March through the second week in April, with the migration of adults commencing two weeks earlier than immatures. Almost all migrants (>99%) passed east of 99°10'W. Winds during the migration season in south Texas were from the southeast at the surface, and from south-southeast to south at the altitude of migration, minimizing the potential for lateral drift. Only 4% of the 85,000 migrants counted in 1982 flew on days with opposing winds. Net tracks of hawks soaring in thermals were nearly downwind toward 312°. Tracks of glides were toward 6° and did not vary with wind direction, probably because of the extreme predictability of wind direction. Daily flight time averaged 8.7 h and was greater on days with good thermal lift (low percent cloud cover) and favorable winds. Altitude of migration increased from early morning to midday, averaging 652 m at midday, and varied inversely with the amount of cloud cover. Hawks often flew too high to be seen without binoculars, so direct visual counts were strongly dependent on radar detection. Ninety-two percent of the hawks flew in flocks of >100 birds after 1100, and approximately 90% landed in flocks of >40 individuals. Flocking was hypothesized to facilitate the random encounter of thermals during interthermal glides, saving time and energy. *Received 30 October 1984, accepted 10 April 1985.*

MANY species of soaring birds regularly undertake long-distance migrations (Brown and Amadon 1968, Pennycuick 1972, Smith 1980). During these flights they depend on atmospheric lift, usually in the form of thermal convection or orographically deflected wind, and infrequently resort to more costly flapping flight. These migrants also must fly through wind fields that vary with altitude and geographic location. Therefore, soaring migrants should adopt flight behaviors appropriate for the lift and wind conditions encountered at different times and locations. Little is known, however, about the flight behavior of soaring migrants in different lift and wind conditions (Kerlinger and Gauthreaux 1984, Kerlinger et al. 1985). In this paper we examine several aspects of spring migration of the Broad-winged Hawk (*Buteo platypterus*), a long-distance, soaring migrant. Specifically, we report daily and

seasonal timing of migration in south Texas, geographic distribution, flocking, altitude, and direction of flight in relation to wind.

STUDY AREA AND METHODS

Study area.—Santa Ana National Wildlife Refuge (26°07'N, 98°18'W), Alamo, Hidalgo Co., Texas (Fig. 1) was selected as our study site after consulting past spring migration issues of *American Birds*. Observations were conducted from the parking lot in front of refuge headquarters, where there is a nearly unobstructed view of the horizon. The refuge (elevation 20 m) encompasses slightly more than 2,000 ha of woodland on the north bank of the Rio Grande River and is one of the few remaining roosting sites for migrant Broad-winged Hawks in the Rio Grande Valley. Surrounding the refuge is a vast expanse of flat farmland that is almost devoid of wooded tracts.

Observations at the refuge were conducted from 28 March to 16 April 1982, from the Avian Migration Mobile Research Laboratory, a 7-m motor home equipped with two radars and other electro-optical equipment. Observations of migrants landing in the refuge were conducted on foot from an elevated (3–

¹ To whom reprint requests should be addressed.

5 m) dirt dike that extends approximately 1.9 km along the north boundary of the refuge.

We determined the distribution of migrant Broad-winged Hawks in the southern United States from southeastern Texas at the Gulf of Mexico westward to the Pacific Ocean by summarizing observations published in spring migration issues of *American Birds* (1949–1981). Seasonal timing of migration was determined using 5 years of unpublished daily counts made by the refuge personnel (1963, 1964, 1965, 1980, 1981). Standardized methods were not employed, although several refuge personnel counted hawks daily during their normal work.

To explain day-to-day variance in numbers of hawks counted in 1982, we examined the influence of surface wind upon the numbers of migrants counted. Wind direction and speed at 1200 were used to compare following winds (south-southeast >2 m/s) with opposing winds (northwest-northeast >2 m/s). Two days when winds were variable or <2 m/s were excluded from the analysis. Wind was the only weather variable employed because it has been shown to be the most important variable determining the numbers of hawks aloft (Lack 1960, Mueller and Berger 1961, Haugh 1972, Titus and Mosher 1982) and is highly correlated with other weather variables (Richardson 1978).

Daily protocol.—Observations commenced at 0700 (CST). Using 7 \times and 10 \times binoculars, we scanned for hawks taking off from the refuge or coming from farther south. The marine surveillance radar (Decca 150, 3-cm wavelength, 10 kW peak power, 20° vertical beam width, 2° horizontal beam width) was used beginning at 0745–0900 to scan for flocks of migrating hawks at the 11.1, 5.6, 2.8, and 1.4-km range settings. Radar operations began when takeoff was noted or when hawks were seen migrating from Mexico. On days when no hawk movements were evident visually, surveillance radar operations began at 0900. When a radar echo was detected on the radar screen (Plan Position Indicator), an observer attempted to make visual contact using 7 \times , 10 \times , or 20 \times binoculars (the last mounted on a tripod).

The number of birds, flock size, flight direction, age composition, and elevation angle were recorded for each flock. Age (immature = <1 yr old, adult = >1 yr old) of low-flying migrants also was noted. Net tracks of birds soaring in thermals and gliding tracks between thermals were taken from the radar screen or by hand-held compass. Altitude could not be measured with the surveillance radar because of the wide vertical beam. We employed an inclinometer to measure the elevation of the target above the horizon and then calculated altitude from the elevation angle and range of the target. The surveillance radar was most useful early in the day when migration was below approximately 300 m.

As the altitude of hawk migration increased, usually after 1000–1100, the vertical, fixed-beam radar (a

modified Marconi LN66 marine radar, 3-cm wavelength, 10 kW peak power, 4° conical beam, range $\pm 2\%$) was used. Altitudes of migrants passing through the radar's narrow beam were read directly from the radar screen (a modified Plan Position Indicator), while simultaneous visual observations were made. The vertical radar was always used on the 4.8-km range setting. For each radar echo, we noted flock size and flight behavior (soaring or gliding). Flight direction was recorded for gliding tracks either as a disappearing azimuth or until a bird began climbing in a thermal. Soaring flight direction (net track) also was recorded as a disappearing azimuth or until birds began to glide.

Radar operations ceased at about 1600 (1500 on two days) or when hawks were noticed descending. At that time, one observer (PK) walked along the dike and observed descent and landing of hawks in the refuge. Operations were halted at 1800 on all but two days (1830), although casual observations were continued until sunset.

In this study takeoff time was operationally defined as the time when the first two hawks were seen aloft simultaneously. Because departures of Broad-winged Hawks lasted for at least 1 h, the number of birds taking off in that hour was the datum used in all analyses involving takeoff. Only mornings when >25 hawks were seen were included in the analyses. When flocks of migrating hawks began descending toward the forest in the afternoon, landing times were recorded to the nearest minute for each flock containing more than 40 birds. The average daily landing time was the midpoint time for the flocks observed landing.

Weather data.—The following weather data were recorded at approximately 2-h intervals beginning at 0700 (and when marked changes occurred) throughout the day: surface wind speed and direction (taken with hand-held compass and anemometer) at about 5 m above the surface, percent cloud cover, and precipitation. Radiosonde measurements of winds aloft at Brownsville, Texas (about 50 km east of the study site) were obtained from the National Climatic Center at Asheville, North Carolina for the months of February, March, and April (1972–1982). From these data we determined direction of prevailing winds and changes in wind direction from the surface to the 900-mb level (about 1,000 m). Directional data were analyzed using circular statistics (Zar 1974).

RESULTS

Geographic distribution and seasonal timing of spring migration.—Thirty-three years of spring records from *American Birds* indicate that $\geq 99\%$ of the 884,817 Broad-winged Hawks reported moving into the United States crossed the Mexican border east of 99°10'W (Fig. 1). No flock of

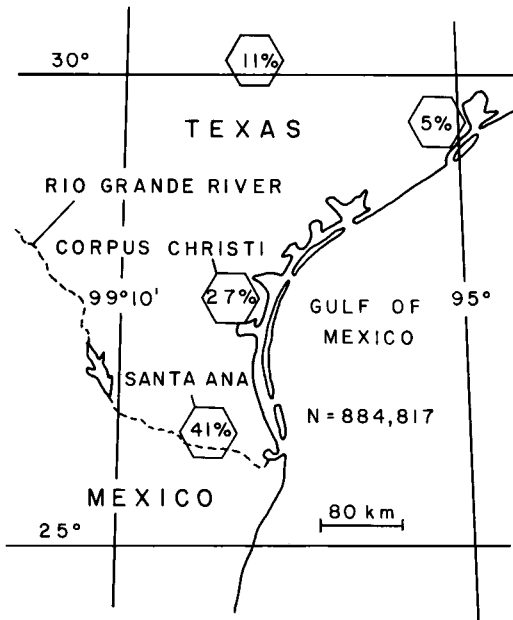


Fig. 1. Distribution of Broad-winged Hawks during spring migration in south Texas as determined by reports published in *American Birds*. The 16% not indicated in the hexagons were scattered through east Texas.

>10 individuals was reported west of this longitude. Large proportions of the birds were noted at or near Santa Ana National Wildlife Refuge (41%) and Corpus Christi (27%). Along the Mexican border, birds were spread from the Gulf of Mexico inland for approximately 140 km. The migration path widened to >350 km in north Texas as the gulf coast extends to the northeast, and fewer birds were counted than farther south.

Broad-winged Hawks began migrating through south Texas in mid-March and continued into May (Fig. 2). The first flights of >10 birds/day occurred 17–24 March. Flights of several hundred birds per day followed within one week (20–26 March), as did one-day flights of >1,000 hawks/day (24–25 March in 4 of 5 years, 3 April in the fifth year). Thus, the peak of migration began in the last week of March and lasted through the second week of April. This 3-week period (24 March to 14 April) accounted for 84.9% of all hawks seen during these five migration seasons. After the second week of April the numbers of Broad-winged hawks decreased, and by the first week in May daily flights of >50 birds were rare.

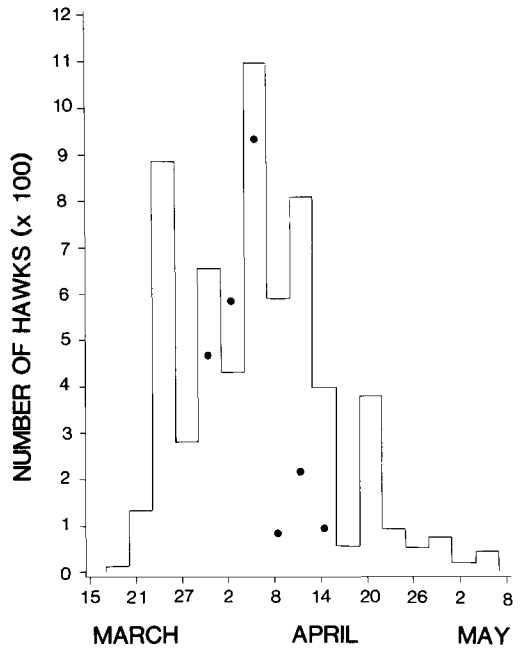


Fig. 2. Seasonal timing of Broad-winged Hawk migration in south Texas. Open histogram = Santa Ana refuge counts for 1963–1965 and 1980–1981; solid circles = our radar-assisted Santa Ana counts, 28 March to 16 April 1982. Scale for the circles is $\times 1,000$ hawks per day.

Age was determined for 989 migrants during the 1982 study period. Adults preceded immatures by several weeks, accounting for >96% of those individuals for which age could be determined before 5 April. Immature birds began migrating in greater numbers 5–12 April and accounted for up to 10% of those birds aged. A dramatic increase in the percentage of immatures was noted during the last 4 days of observations (13–16 April), when 22, 24, 25, and 36% of the birds aged were immatures.

Records of the Santa Ana National Wildlife Refuge revealed that, during the five years for which extensive observations (17 March to 6 May) were available, 89,782 hawks were recorded ($\bar{x} = 17,956 \pm 6,171$ SD per year). During our 20 days of observations (plus 1 day by refuge personnel), nearly 85,000 Broad-winged Hawks were tallied (Table 1). The large variability in daily counts noted during our study was attributable to seasonality (see above) and variable weather. On the 11 days in 1982 with favorable winds, 67% of all Broad-winged Hawks passed ($\bar{x} = 4,351 \pm 3,589$ hawks/day),

TABLE 1. Summary of spring Broad-winged Hawk migration in south Texas, 1982.

Date	Number counted	Radar estimate	Total (count + radar)	Number seen landing	Number seen taking off
25 March	12,700*	—	12,700	—	—
28	0	0	0	0	0
29	8,603	100	8,703	378	4,000
30	3,862	500	4,362	632	1,582
31	822	0	822	1,010	531
1 April	6,721	4,300	11,021	5	1,446
2	4,393	400	4,793	765	2
3	1,695	0	1,695	539	1,559
4	4,436	3,100	7,536	209	700
5	11,744	8,300	20,044	39	150
6	399	0	399	1,018	15
7	2,085	100	2,185	6	1,500
8	146	0	146	0	28
9	5	0	5	0	0
10	3	0	3	0	0
11	719	200	919	2,250	47
12	5,507	0	5,507	489	5,000
13	363	0	363	110	289
14	2,189	0	2,189	54	36
15	169	0	169	1,063	43
16	1,034	0	1,034	—	306
Total	67,595	17,000	84,595	8,567	17,234

* Count taken by refuge personnel.

while on 7 days with unfavorable winds only 4.4% ($\bar{x} = 452 \pm 741$) of the migrants were seen (Mann-Whitney U -test, $U = 70$, $P < 0.01$). The remaining 29% were seen on two other days when winds were light and variable.

Daily timing of migration and flocking behavior.—The following sequence of daily migratory behaviors was noted: (1) takeoff, (2) early climbing and flock formation, (3) onward migratory flight, (4) descent prior to landing, and (5) landing. When migrants were present in the refuge, takeoff was relatively easy to observe and occurred 93–271 min after sunrise ($\bar{x} = 139 \pm 45$ min, $n = 15$). On days when surface winds could be divided into favorable and unfavorable winds for migration, takeoff occurred significantly earlier ($\bar{x} = 116 \pm 16$ min, $n = 10$) than on days when winds were unfavorable ($\bar{x} = 203 \pm 61$ min, $n = 3$; Mann-Whitney U -test, $U = 30$, $P = 0.01$). On two days with winds < 2 m/s, mean takeoff time was 156 \pm 30 min. A low scudlike, cumulus cloud cover normally was present at sunrise and inhibited formation of thermals. Migration commenced when this cloud cover dissipated. Takeoff time was positively correlated with percent cloud cover, although not significantly ($r = 0.354$, NS, $n = 15$). Precipitation delayed takeoff on 2 of

the 15 mornings when takeoff was observed. Birds began to take off following rain showers as blue sky became visible.

Takeoff lasted about 1 h or longer. It was at times difficult to determine whether birds seen low over the forest had taken off from the refuge or from farther south. Invariably, birds emerged from the forest canopy alone and employed powered flight interspersed with short glides. Migrants began to soar after climbing 10–20 m above the canopy, although some flapping still occurred. Small flocks formed almost immediately following takeoff and frequently coalesced into larger flocks. When large numbers of birds were present in the refuge, takeoffs were dramatic. Maximum flock size in the first 60 min following takeoff was strongly correlated with the numbers of birds taking off in that period ($r = 0.906$, $P < 0.01$, $n = 15$). Flocks of several hundred birds often were seen within 20 min of takeoff. The earliest that a flock of 500 was seen was 25 min after the beginning of takeoff. Flock formation continued as individual migrants or flocks moved toward the north-northwest.

The numbers of hawks seen during the first 60 min following takeoff were positively correlated with the numbers seen landing on the

previous evening ($r = 0.899$, $P < 0.01$, $n = 18$, log-log transformation). The numbers of hawks seen taking off, however, exceeded the number seen landing on the previous evening by nearly 8,000 (Table 1). Four thousand of these birds landed in the refuge before our study began, so a discrepancy of 4,000 birds exists between the numbers taking off and landing. Casual observations in the refuge indicated that few birds remained in the refuge on days when weather for migration was favorable.

By 1100, a regular rhythm of migratory flight had developed, with birds climbing in thermals and then gliding on with little or no flapping. Flocks were distinct by 1100 and maintained integrity thereafter. Major flock breakup was witnessed on two occasions, both of which occurred after 1600. On these occasions about 50 and 100 hawks were seen leaving larger groups to land in the refuge. Flock size ranged from two to several thousand (highest actual count >2,800), and <1% of the hawks were alone after 1100 ($n = 32,313$ hawks). Greater than 92% of all hawks observed between 1100 and 1600 were in flocks of >100 birds.

During interthermal glides, flocks were much longer than wide, like the extended cluster-type formation described by Heppner (1974). Flocks of 1,000-3,000 birds were 1-2.2 km long. Inter-individual distance was approximately 5 m, and flocks covered fronts ranging from about 35 m for flocks of less than about 500 to >100 m for flocks of >1,000 birds.

Descent prior to landing began after 1600 on 8 of 11 days, and mean landing time was 82 ± 64 min ($n = 11$, range = 16-195 min) before sunset. Birds landed earlier on days with unfavorable winds ($\bar{x} = 171 \pm 28$ min, $n = 3$) than on days with favorable winds ($\bar{x} = 48 \pm 33$ min, $n = 7$; Mann-Whitney U -test, $U = 21$, $P < 0.05$). One day with winds <2 m/s was omitted. Landing time (minutes before sunset) was also positively correlated with percent cloud cover on that afternoon ($r = 0.872$, $P < 0.01$, $n = 11$).

Descents began at relatively high altitudes (see next section), and most birds (>91% of 8,767 seen landing) were in flocks of >40 birds. Descents were almost always into the wind. Flocks began to break up at about 100 m above the trees. Flight directions appeared to be random when migrants were below 10 m. After less than 2 min of flapping and gliding flight at 10-40 m above the trees, individual birds dove into

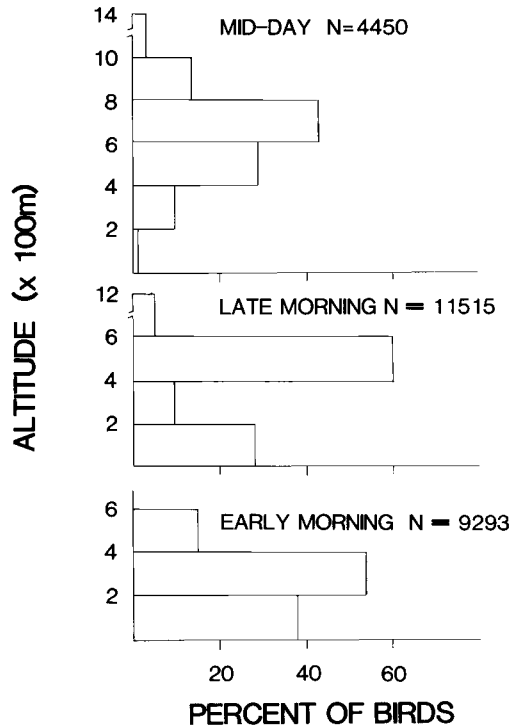


Fig. 3. Altitude of Broad-winged Hawk migration in south Texas.

the forest and usually did not reascend. Calculated flight time was 8.7 ± 1.9 h/day ($n = 10$).

Altitude and visibility of migration.—A regular pattern of altitude change was obvious within each day. On most days the altitude of migration increased until about 1000-1100 and remained fairly constant until after 1600-1700. Altitudinal data from all days were divided into three periods: early morning (EAM = 0700-0959), late morning (LAM = 1000-1059), and midday (MDA = 1100 to descent prior to landing). From EAM ($\bar{x} = 166 \pm 107$ m, $n = 87$) to LAM ($\bar{x} = 405 \pm 271$ m, $n = 48$) the mean altitude of migration increased significantly (t -test, $t = 4.14$, $P < 0.01$), as it did from LAM to MDA ($\bar{x} = 652 \pm 258$ m, $n = 79$; t -test, $t = 4.99$, $P < 0.01$, $n = 127$). In the EAM 67% of all hawks flew below 300 m, while the proportion dropped to 31% in the LAM and to only 3% in MDA (Fig. 3).

Altitude of migration varied within the MDA period, a result of climbing in thermals and then gliding downward. During MDA the height band (maximum altitude minus mini-

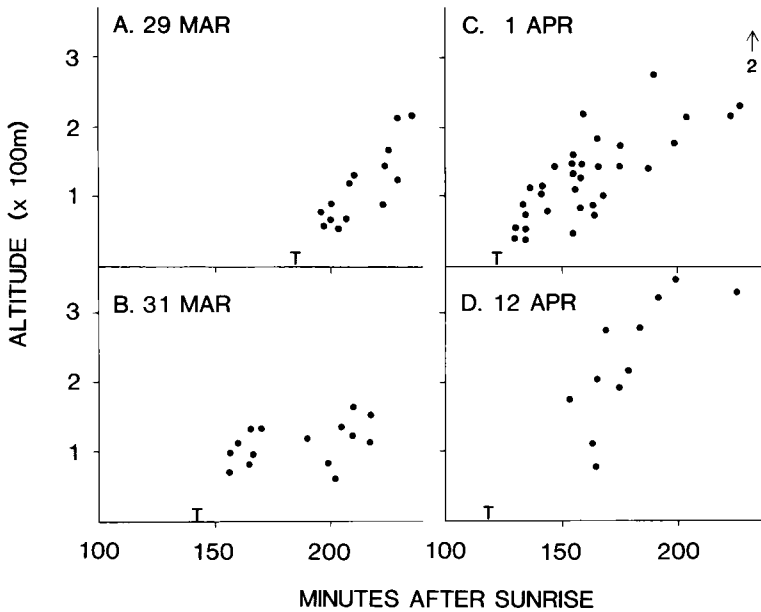


Fig. 4. Altitude of hawk migration following takeoff (T). Regression equations: (A) $y = 3.60x - 631$, $r^2 = 0.76$, $P < 0.01$; (B) $y = 0.89x - 63$, $r^2 = 0.34$, $P < 0.05$; (C) $y = 2.68x - 301$, $r^2 = 0.73$, $P < 0.01$; (D) $y = 3.53x - 405$, $r^2 = 0.72$, $P < 0.01$.

mum altitude) of migration averaged 488 ± 177 m (range = 258–724 m, $n = 11$ days). Variability in the altitudes realized by hawks on different days also was evident. Both the rate of increase of altitude and the mean altitude varied during EAM on all days. Significant differences among the regression coefficients ($F = 5.74$, $df = 3, 71$, $P < 0.01$) demonstrated that the rate of convective development varied from day to day (Fig. 4). Mean altitude for a given period from each day (e.g. EAM) was negatively correlated with percent cloud cover (arcsine transformed): EAM: $r = 0.343$, NS, $n = 5$ days; LAM: $r = 0.803$, $P < 0.01$, $n = 6$ days; MDA: $r = 0.714$, $P < 0.01$, $n = 11$ days. In summary, hawks flew higher and climbed faster on days with less cloud cover (i.e. greater thermal convection).

As a consequence of high-altitude flight after 1000–1100, the visibility of migration decreased. When directly overhead, single hawks and small flocks were readily visible to the unaided eye at altitudes below 550 m (range = 253–563 m, $n = 10$). Hawks flying between 563 and 869 m ($n = 9$) were somewhat difficult to see without $7\times$ binoculars. Higher-flying migrants (range = 879–1,368 m, $n = 10$) were not visible against blue sky without $7\times$ binoculars. At $>1,100$ m, two single Broad-winged Hawks

were difficult to detect even with binoculars. Fourteen radar echoes ($\bar{x} = 758 \pm 242$ m, range = 483–1,304 m) that could not be identified were not included in the altitude data set (Fig. 3).

Prevailing wind and flight direction.—During March and April surface and 900-mb (1,000-m) winds at Brownsville, Texas and the study site were predictable and favorable for migration. Winds in February were not as predictable, and opposing surface winds occurred 50% of the time. Winds at the 900-mb level were more favorable than at the surface, shifting 29° from southeast at the surface to south-southeast aloft in March and 24° in April. This shift resulted in a stronger following wind component for migrants aloft, with little change in lateral wind component. During the 1982 season a similar trend was evident (Table 2).

Net tracks of Broad-winged Hawks soaring in thermals were highly correlated with surface wind direction ($r = 0.884$, $P < 0.001$, $n = 120$). Mean direction of all climbs was to the northwest, only 3° different from mean surface wind (Table 2). Gliding tracks were well oriented (Table 2) and did not vary with lateral wind. When tracks of glides were regressed on the surface wind component perpendicular to

TABLE 2. Wind and flight direction of Broad-winged Hawks in south Texas, spring 1982.

		Mean direction	Length of mean vector ^a	Angular deviation	Sample size	Percent unfavorable wind days (1982)
Wind direction						
February	Surface	358°	0.281	91°	10 yr	50
	900 mb ^b	358°	0.974*	13°	10 yr	21
March	Surface	323°	0.993*	7°	10 yr	32
	900 mb	352°	0.998*	3°	10 yr	19
April	Surface	325°	0.989*	8°	10 yr	30
	900 mb	349°	0.997*	5°	10 yr	13
Study period (1982) at Santa Ana						
	Surface	309°	0.553*	62°	20 days	30
	900 mb	333°	0.679*	50°	20 days	15
Flight direction						
	Glides	006°	0.927*	22°	195 measurements	
	Climbs	312°	0.881*	29°	120 measurements	

^a * $P < 0.01$.

^b 900 mb = 1,000 m.

360°, no relationship was evident ($r^2 = 0.02$, NS, $n = 195$). Therefore, glide headings were to the east of glide tracks.

DISCUSSION

Flight behavior of migrating raptors only rarely has been examined quantitatively (Richardson 1975; Kerlinger 1982, 1984; Kerlinger and Gauthreaux 1984; Kerlinger et al. 1985). The majority of hawk migration studies has been confined to banding (Mueller and Berger 1967a) or visual counts (Mueller and Berger 1967a, Haugh 1972, Evans and Lathbury 1973, Alerstam 1978, Titus and Mosher 1982) taken at distinct topographic locations, such as coasts and ridges that function as leading lines (Mueller and Berger 1967b). Thus, most of what we know about raptor migration is from situations that occupy only a fragment of an individual migrant's pathway.

The Broad-winged Hawks we studied were near the midpoint of their migration between northern South America and eastern North America. Hawks are confronted with diverse topographic and geographic situations as well as varying wind conditions during this 3,000–6,000-km flight. The migration at Santa Ana National Wildlife Refuge is removed from topographic leading lines, although a small proportion (<20%) of the migrants we recorded were influenced by the insular nature of the

refuge as a roosting site. Thus, the migration at Santa Ana can be considered part of a broad-front migration, distinctly different from the migration described in studies at ridges and coastlines.

Prevailing winds, geographic distribution, flight direction, and seasonality of migration.—Prevailing south-southeasterly winds during spring in south Texas promote faster ground speeds during interthermal glides, as well as transporting birds to the north-northwest while soaring in thermals. Flight at higher altitudes is more advantageous because wind is from due south. Favorable winds that prevail after 1 March may select for seasonal timing of migration and flight direction (Gauthreaux 1980).

Geographic distribution and total numbers of Broad-winged Hawks reported in the present study differed from a study done near Veracruz, Mexico (Thiollay 1980). In Thiollay's study 200,000 Broad-winged Hawks were counted in a 20-km wide band along the Gulf of Mexico. Thiollay (1980) did not use a radar, and his study commenced two weeks later than our study. The wider migration path in south Texas is a result of the absence of a coastal mountain range and a change in the orientation of the gulf coast. In addition, prevailing southeast winds may drift birds westward, away from the coastline.

Most evidence for drift is based on differences in counts of raptors taken at various lead-

ing lines (Mueller and Berger 1967b, Haugh 1972). Direct evidence for wind drift of Broad-winged Hawks has been presented by Richardson (1975) and for partial drift (partial compensation) by Kerlinger et al. (1985). In contrast, Kerlinger and Gauthreaux (1984) and Kerlinger (1984) showed that Sharp-shinned Hawks (*Accipiter striatus*) compensated almost completely for lateral winds of up to about 6 m/s.

In the present study hawks were displaced slightly to the west of north while soaring in thermals, but maintained glides to the east of north that were unrelated to wind direction. If drift were occurring during interthermal glides, a significant relationship should have emerged. The paucity of migrants flying with westerly winds resulted in little variability in the lateral wind component, the independent variable. We conclude that drift is minimal (or absent) during interthermal glides.

Displacement by wind from a migratory path while soaring in thermals has been considered to be drift (Mueller and Berger 1967b), but is not comparable to downwind drift (Williamson 1955) or lateral drift (Bingman et al. 1982). Birds climbing in thermals cannot actively orient, as they do during interthermal glides. Whether or not the mean track of glides (6°) results in complete compensation for displacement during soaring is not known, although compensation is probably near complete.

Altitude and visibility of flight.—The altitude of spring Broad-winged Hawk migration in south Texas is similar to that of soaring migrants in Sweden (Pennycuick et al. 1979), New Jersey (Kerlinger and Gauthreaux 1984), and New York (Kerlinger et al. 1985). The majority of migrants in these studies were between 400 and 1,100 m above ground level, far lower than the altitudes of Broad-winged Hawks reported by Smith (1980). Because we experienced difficulties in detecting migrants at >800 m, we feel that Smith's estimates of 3,000–4,000 m from Panama are excessive. It is possible that convective conditions in Texas and Panama are different, although Smith still would have difficulty detecting migrants at >800 m.

Because of the difficulty of detecting migrants at >800 m and the narrow beam width of the radar (4°), our midday counts are probably underestimates of the numbers of hawks passing at that time. Our results seem to support the contention of Kerlinger and Gauthreaux (1984) and Kerlinger et al. (1985), who

stated that visual counts of raptors are biased to low-flying birds.

Function of flocking in long-distance soaring migrants.—Our study is not the first to show that soaring birds migrate in flocks (Pennycuick 1972, Pennycuick et al. 1979, Kerlinger et al. 1985). The overwhelming proportion of Broad-winged Hawks observed migrating in flocks and the rapidity of flock formation following takeoff suggest that flocking has an adaptive function. Flocking by Swainson's Hawks (*B. swainsoni*), Broad-winged Hawks (Hamilton 1962), and Honey Buzzards (*Pernis apivorus*; Thake 1980) was hypothesized to function in navigation or orientation. An alternative hypothesis is that flocking facilitates efficient location of thermals (Pennycuick 1972). Although flocking may have more than one adaptive function, we propose that immediate energetic gains and faster passage rates are afforded to individuals migrating in flocks as a result of more efficient location of thermals by flocks relative to lone migrants. Birds taking off in the early morning must use powered flight that is >5 times as energetically costly as gliding flight (Baudinette and Schmidt-Nielsen 1974). The sooner a thermal is found, the less energy consumed and the less time until the bird can glide toward its migratory goal.

If, during interthermal glides in the appropriate migratory direction, flocks randomly encountered convective elements, they would not need to rely on birds outside of their immediate flock to locate thermals. The geometry of flocks during interthermal glides is consistent with a random-encounter model of thermal location. By virtue of the spacing of individuals in flocks, a wide swath of air is covered, so that the probability of randomly encountering a thermal would be greater for a flock than for a lone migrant.

ACKNOWLEDGMENTS

All financial assistance was provided by the Electrical Power Research Institute, Palo Alto, California and the Zoology Department of Clemson University. We thank director R. Rauch and the personnel of the Santa Ana National Wildlife Refuge for logistical assistance and use of their data. J. Beacham, P. Hamel, and A. Ross assisted with the data analyses. T. Alerstam, W. J. Richardson, and T. C. Williams made critical comments on an earlier draft of this paper. N. Tumosa, K. Gauthreaux, and M. R. Lein made significant logistical contributions.

LITERATURE CITED

- ALERSTAM, T. 1978. Analysis and a theory of visible migration. *Oikos* 30: 273-349.
- BAUDINETTE, R. V., & K. SCHMIDT-NIELSEN. 1974. Energy cost of gliding flight in Herring Gulls. *Nature* 248: 83-84.
- BINGMAN, V. P., K. P. ABLE, & P. KERLINGER. 1982. Wind drift, compensation, and the use of landmarks by nocturnal bird migrants. *Anim. Behav.* 30: 49-53.
- BROWN, L., & D. AMADON. 1968. Eagles, hawks and falcons of the world. New York, McGraw-Hill.
- EVANS, P. R., & G. LATHBURY. 1973. Raptor migration across the Straits of Gibraltar. *Ibis* 115: 572-585.
- GAUTHREAUX, S. A. 1980. The influence of global climatological factors on the evolution of bird migratory pathways. *Proc. 17th Intern. Ornithol. Congr.*: 517-525.
- HAMILTON, W. F., III. 1962. Evidence concerning the function of nocturnal call notes of migratory birds. *Condor* 64: 390-401.
- HAUGH, J. R. 1972. A study of hawk migration in eastern North America. *Search* 2: 1-60.
- HEPPNER, F. H. 1974. Avian flight formations. *Bird-Banding* 45: 160-169.
- KERLINGER, P. 1982. Aerodynamic performance and flight speed selection of migrating hawks. Unpublished Ph.D. dissertation, Albany, State Univ. New York.
- . 1984. Flight behaviour of Sharp-shinned Hawks during migration. II: Over water. *Anim. Behav.* 34: 1025-1029.
- , V. P. BINGMAN, & K. P. ABLE. 1985. Comparative flight behaviour of migrating hawks studied with tracking radar during autumn in central New York. *Can. J. Zool.* 63: 755-761.
- , & S. A. GAUTHREAUX. 1984. Flight behaviour of Sharp-shinned Hawks during migration. I: Over land. *Anim. Behav.* 34: 1019-1024.
- LACK, D. 1960. The influence of weather on passerine migration: a review. *Auk* 77: 171-209.
- MUELLER, H. C., & D. D. BERGER. 1961. Weather and fall migration of hawks at Cedar Grove, Wisconsin. *Wilson Bull.* 73: 171-193.
- , & ———. 1967a. Fall migration of Sharp-shinned Hawks. *Wilson Bull.* 79: 397-415.
- , & ———. 1967b. Wind drift, leading lines, and diurnal migrations. *Wilson Bull.* 79: 50-63.
- PENNYCUICK, C. J. 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. *Ibis* 114: 178-218.
- , T. ALERSTAM, & B. LARSSON. 1979. Soaring migration of the Common Crane (*Grus grus*) observed by radar and from an aircraft. *Ornis Scandinavica* 10: 241-251.
- RICHARDSON, W. J. 1975. Autumn hawk migration in Ontario studied with radar. *Proc. 1974 North Amer. Hawk Migr. Conf.*: 47-58.
- . 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30: 224-272.
- SMITH, N. G. 1980. Hawk and vulture migrations in the Neotropics. Pp. 51-65 in *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation* (A. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.
- THAKE, M. A. 1980. Gregarious behaviour among migrating Honey Buzzards (*Pernis apivorus*). *Ibis* 122: 500-505.
- THIOLLAY, J. M. 1980. Spring hawk migration in eastern Mexico. *Raptor Res.* 14: 13-20.
- TITUS, K., & J. A. MOSHER. 1982. The influence of seasonality and selected weather variables on autumn migration of three species of hawks through the central Appalachians. *Wilson Bull.* 94: 176-184.
- WILLIAMSON, K. 1955. Migrational drift. *Proc. 11th Intern. Ornithol. Congr.*: 179-186.
- ZAR, J. H. 1974. *Biostatistical analysis*. Englewood Cliffs, New Jersey, Prentice-Hall, Inc.