

DYNAMICS OF THE TRANSISTHMIAN MIGRATION OF RAPTORS BETWEEN CENTRAL AND SOUTH AMERICA

NEAL GRIFFITH SMITH

*Smithsonian Tropical Research Institute, Apartado 2072, Balboa,
Republic of Panama*

ABSTRACT

Observations over ten years of the passage of *Buteo platypterus*, *B. swainsoni*, *Cathartes aura*, and *Ictinia* spp. through the Isthmus of Panama suggest that for the autumnal or rainy season migration from North to South America, the enormous numbers that can be seen can be counted only by photographic analysis. The method is expensive and time-consuming, but these counts are verifiable and indicate that most 'estimates' are gross exaggerations. Yet even at the Isthmus, where the flight is most concentrated, the vagaries of meteorological conditions make meaningful year to year comparisons of numbers impossible. In addition, no comparison is possible between the numbers moving through the Isthmus into South America with those coming back. This is because, in addition to the unpredictable cloud cover, the north-east trade winds cause the flight to spread out so that even photography from several sites fails adequately to sample the birds. Thus even at the best site in the New World, counting raptors would seem to be futile, for it yields no biologically meaningful data.

During the southward passage, once the flocks have been concentrated by the Mexican plateau and the Gulf of Mexico, the flight is an almost straight line, avoiding extensive overwater passage into South America. The converse is true on the northward flight except that the raptors fly more on the Caribbean side of the Central American mountains. At the time when *Buteo swainsoni*, *Cathartes aura* and *B. platypterus* become concentrated into flocks, usually south of latitude 30 N, they apparently do not feed until they reach their non-breeding resident areas. The same would appear to be true on their northward flight until the flocks disperse, usually just north of the U.S.-Mexico border. *Ictinia plumbea*, an intratropical migrant, feeds during migration, but its close relative, *I. mississippiensis*, feeds much less and probably travels farther. That some species should feed while others do not correlates well with their chief mode of flying. *Ictinia* spp. use powered flight much more than do other raptors.

Aircraft were employed in 1981 to examine more closely the various methods of flight exhibited by these raptors. Significant midday passage by all except *Cathartes* occurred inside the base of long lenticular clouds in which lift was constant. The birds were able to cover considerable distances without sink, and were invisible to ground observers. Normal flight altitudes were between 375m and 2650m above ground. In mountain areas flocks often travelled at 4000-6000m above sea level. Under mid-afternoon storm conditions, the flocks either tried to avoid the storms, often unsuccessfully, or rose to altitudes possibly approaching 9000m.

INTRODUCTION

This paper describes the passage of several raptor species through the Isthmus of Panama to and from North and South America. The Isthmus is approximately 80km wide at its narrowest part but the actual migration path is in reality much narrower, as the raptors, with the exception of the *Ictinia* kites, seldom deviate more than 16km from the low continental divide (*Figures 1, 2, 3 and 4*). Thus it is one of the best locations in Central America for the study of raptor migration.

Smith (1980) gave an overview of the rainy season (October–November) movement of the raptors into the tropics with observations from 1970–78, describing three species and their ecology in passage and during their residence for up to six months in Central and South America. Here, the data are extended through 1981, comparing the movements in both directions and also the *Ictinia* spp. kite movements, which are somewhat peculiar. Emphasis is placed on the methodology of counting the raptors and the question of whether such attempts yield biologically meaningful information. The use of aircraft and telescopes as tools to obtain information on the energetics involved and the flight strategies employed are described. Some data are presented which permit speculation on the possible sources of mortality for soaring raptors when making such flights.

SPECIES OF MIGRANT HAWKS, VULTURES AND KITES

Broad-winged Hawk (*Buteo platypterus*)

This small buteo (350g to 500g) is resident on some West Indian islands; it also occurs from October to April in secondary habitats from Costa Rica southwards throughout northern South America as a non-breeder, and migrates to its breeding area in eastern North America where it resides from late April to early September (Brown & Amadon 1968; Heintzelman 1975). Its migration route may be viewed as the straightest line between eastern North America and the tropics without flying over the Gulf of Mexico. There is a possibility that some individuals might shorten this route by flying down the peninsula of Florida and overwater to Cuba, whence they might move down the West Indies or cross directly to Yucatan and then onward into Central and South America (Smith 1980). Whether or not this occurs has still not been resolved, but it is of interest that the first mention of a raptor migration in the New World (in approximately 1520) was by Olviedo, who remarked on a hawk flight coming from the north-west and passing over Cuba to the south-west (Baughman 1947). A sighting of some 500 migrating Broad-wings over the island of Tobago is again suggestive of a trans-West Indian Route for at least some individuals (Rowlett 1980).

Swainson's Hawk (*Buteo swainsoni*)

A medium-sized hawk with several colour phases. Most of the population migrate approximately 10,000km or more between southern South America and western North America. Between November and March it is said to be a non-breeding resident of pampa-like habitat in Uruguay, Argentina and possibly elsewhere in Brazil and Chile (Brown & Amadon 1968; Houston 1974; Smith 1980). It breeds in western North America in similar habitat from late April to September. Thus almost four months a year are spent on migration. There is an increasing number of sightings in North America during the North Temperate winter (Browning 1974) and at least one record from Argentina in May (Houston 1974). I have seen individuals in December and February in Panama.

Weight data collected show a wide range, from 508g to 1200g (W. Clarke *in litt.*; P. Bloom *in litt.*), which is to be expected in a species displaying this sort of movement pattern. None of the nine migrants that I collected in Panama weighed less than 954g. (See Energetics section for further discussion.)

Turkey Vulture (*Cathartes aura*)

This 1200g–2000g long-winged cathartid vulture breeds almost throughout the New World. Although birds withdraw from the northern limits of their range in the North Temperate Zone winter (and presumably do the same at the corresponding season in southern South America), Turkey Vultures appear to be present throughout southern North America, Central and South America all the time. Yet the numbers of migrants passing through the Isthmus of Panama are enormous, exceeding in 1978 those of *B. platypterus* or *B. swainsoni* (Table 1). Wetmore (1965) described three races for Panama, two migrant ones characterized by having all-red heads, and a third, *C. a. ruficollis*, a supposed resident form characterized by a yellow band on the back of its red head. In December 1977 45 percent of the vultures surveyed were red-headed birds (Smith 1980). In 1981 and 1982, despite a much more intensive survey, I could find only red-headed birds. No yellow-banded vultures were seen between October 1981 and March 1982. But Robert Ridgely (pers. comm.) informs me that in December 1983, in northern Colombia, he found *C. a. ruficollis* to be abundant, and did not see any of the red-headed migrants that so dominated the Panamanian skies. I do not know the head colour of the birds that breed in Panama nor when they breed, so I do not know if the 'resident' *C. a. ruficollis* breeds here or is simply a migrant from South America. Finally, I have no idea of the location of the geographic areas that generate these enormous numbers.

Table 1: Counts of migrating raptors passing through the Isthmus of Panama into S. America from late November. Data from 1972 onwards represent actual counts of individuals recorded on film. 1971 and 1974 were incomplete samples. Counts of *I. mississippiensis* began in 1978.

Date	<i>Buteo platypterus</i>	<i>Buteo swainsoni</i>	<i>Carthartes aura</i>	<i>Ictinia mississippiensis</i>	Total
1970	114,509	175,644	190,017		480,641
1971	80,641	77,014	99,612		257,267
1972	395,003	344,409	219,222		958,634
1973	341,414	299,718	230,154		871,286
1974	42,209	54,403	31,114		127,726
1976	301,011	207,115	194,646		702,772
1978	283,716	192,011	307,114	2,807	785,648
1981	235,340	267,946	152,887	27,452	773,625
1982	401,270	277,610	296,418	6,107	981,405

Plumbeous Kite (*Ictinia plumbea*) and Mississippi Kite (*Ictinia mississippiensis*)

These allopatric kites are very similar in appearance. The adults of *I. plumbea* have rufous in their primaries and three distinct tail bands. Adults of *I. mississippiensis* lack the rufous patch and have no tail bands. Mississippi Kites nest in south central United States and appear to migrate into South America; their occurrence in the non-breeding range is poorly documented (Brown & Amadon 1968). The Plumbeous Kite is essentially a tropical species, occurring from southeastern Mexico to northern Argentina. It, too, migrates; from both ends of its range. The

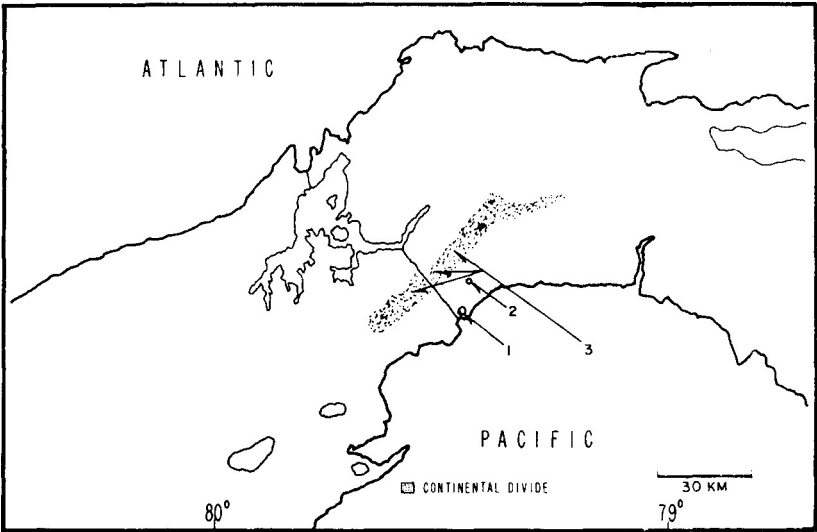


Figure 1: Sites used for observing migrating raptors at the Panama Canal Area. 1. Ancon Hill (197m); 2. Bahai Hill (236m); 3. Continental Divide (from 90m to 525m).

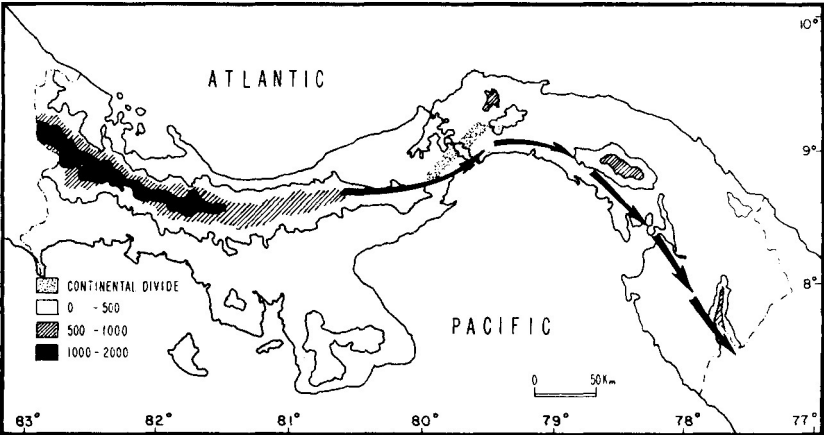


Figure 2: The usual October–November (rainy season) migration path taken by soaring raptors through the Isthmus of Panama under early (07.30–10.00hrs) localized thermal/and or weak wind conditions.

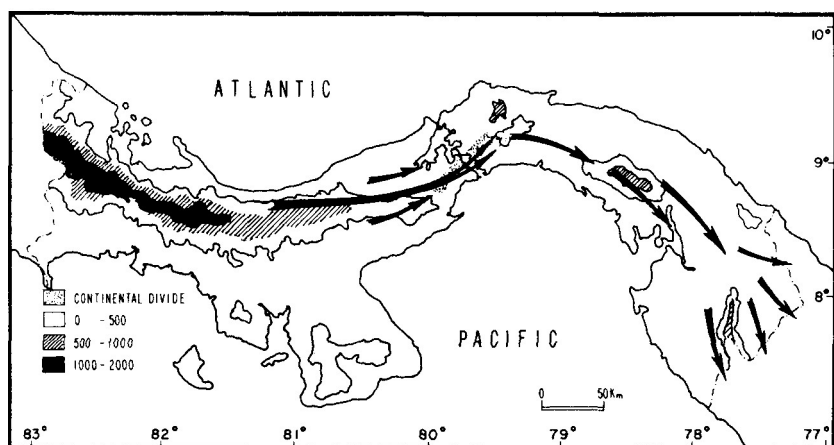


Figure 3: Paths taken by soaring raptors in the same area during mid- to late day conditions on days when no widespread storms occurred. At these times (10.30–15.00hrs) thermal lift is widespread and a mixture of thermal soaring, slope soaring and thermal street gliding is employed.

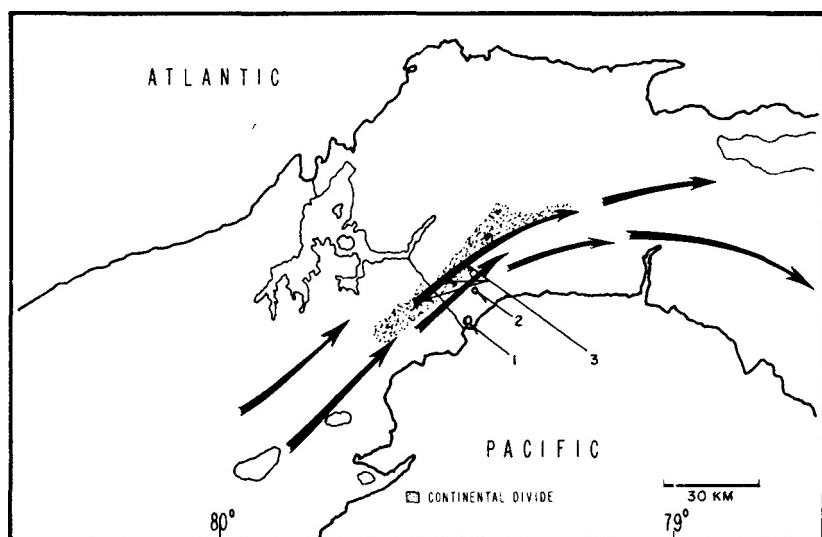


Figure 4: Normal midday flight paths shown in relation to observation sites. They reflect the usual location of the Isthmian thermal 'streets' employed by the raptors in long distance gliding.

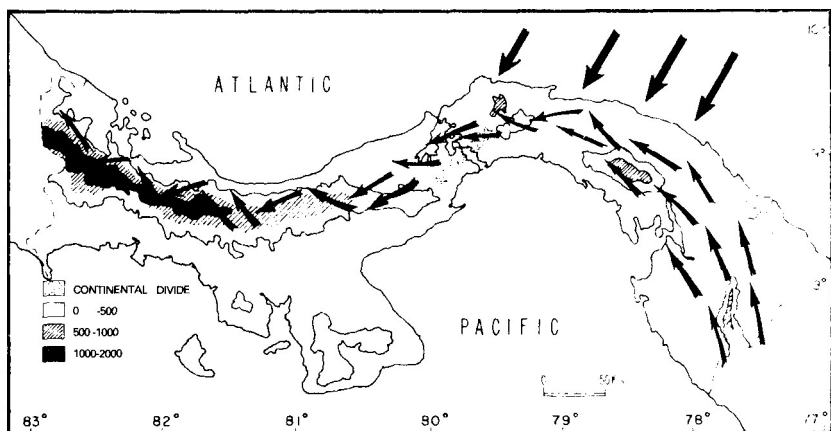


Figure 5: The Isthmus of Panama showing the March-April (dry season) flight routes taken by *Buteo platypterus*, *B. swainsoni* and, to a lesser extent, *Cathartes aura*. The broad arrows indicate the trade winds prevailing at that time.

two kites are possibly the same biological species and would appear to represent a classical leap-frog migration pattern in which the terminal populations migrate the farthest while those in the central tropics migrate hardly at all.

Up to 1978 I ignored *Ictinia* kites, possibly because they had passed through the Isthmus before I began my surveys (see Figure 5). But *B. platypterus* arrived 'early' that year and I was forced to discriminate the kites from the buteos as they occurred together in the same thermals. In the following three years I had a chance to watch kites of both types on migration in both directions through the Isthmus. The adults of the two can be separated easily using the proper optical equipment (see Counting section) but I cannot discriminate between immatures. Nevertheless, the problem of identification is largely moot since the two kites migrate at different times.

Plumbeous Kites pass through the Isthmus in early August in flocks of *c.* 70–100, usually on the Atlantic slope. This route is rather different from that used by the other raptors (Figures 1 and 2). While often seen soaring in thermals, unlike the buteos they are more usually seen flapping with powerful wing strokes. Again unlike the other raptors, they are often observed actively feeding. Their movement coincides with a large-scale flight of dragonflies, which they are adept at catching. The reverse movement occurs in February along more or less the same route. I have observed feeding also at that time, but much less frequently. There appear to be fewer insects then.

Mississippi Kites migrate roughly a month later. Although I have observed both species in the same flock, the major movement of *I. mississippiensis* occurs in the absence of *I. plumbea* in late September, and follows a route to the south of the Continental Divide. I have seen Mississippi Kites feeding only once during the movement into South America. On 3 September 1982, under windless (no thermal) conditions, five adults were observed for approximately 20 minutes, sallying out from a dead tree in a marsh to feed on dragonflies. They then flew on. Thiollay (pers. comm.) observed mixed flocks of *I. plumbea* and *mississippiensis* in Mexico in an area where grasshoppers were abundant. The Plumbeous Kites actively hunted the insects while the Mississippi Kites apparently ignored them.

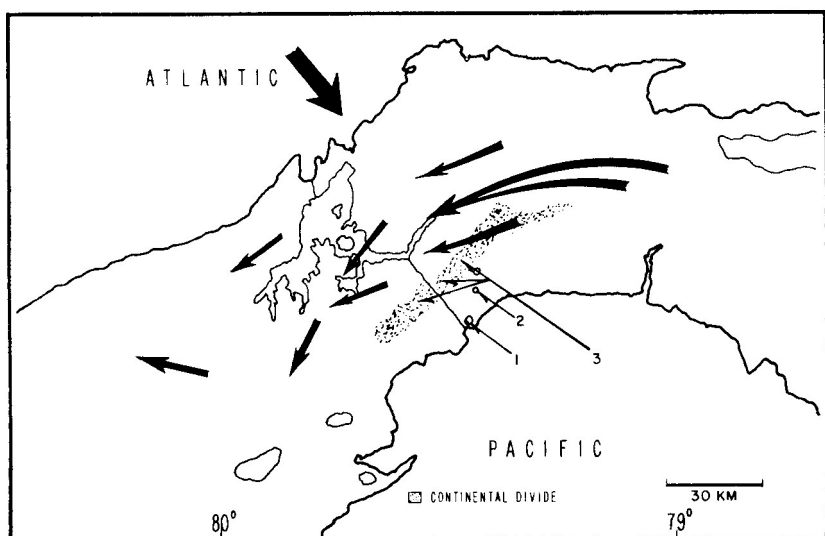


Figure 6: The February–April (dry season) passage of most of the soaring raptors, including *Ictinia* spp., is to the north of the Continental Divide at the Panamanian Isthmus lowpoint, when the birds employ slope soaring, tacking in and out of the mountain passes against the northerly trade winds. Should the winds slacken, the birds revert to thermal soaring. Locations as in Figure 1.

The latter are said to put on large amounts of fat prior to the southern flight (Bent 1937). The reverse movement in the dry season occurs in April and, as with the other raptors at that time, is on the Atlantic side of the divide. I have never seen Mississippi Kites feeding during that season. The adaptive value to these kites of feeding or not feeding on migration is difficult to evaluate because we really have no idea of how far they move into South America, or even if this is regular.

COUNTING MIGRATING RAPTORS

Rationale

My initial involvement with this raptor movement was simply to document on film its spectacular nature. It soon became apparent that it was impossible to estimate by eye, let alone count, the numbers passing through the narrow aerial corridor over Panama City. Only after examination of the photographs did I realize how overestimated were the 'counts' made by me and other observers. There are at least two reasons for attempting such counts: (1) to obtain reliable data comparable within a season between species, and between years for the individual species; and (2) to compare the numbers of each species moving into South America with their corresponding numbers in the following reverse migration.

Counting methods

From 1972 onward, I employed 35mm motorized cameras with lenses with focal lengths of 85mm, 300mm, and later 1000mm, 1600mm and 2000mm. I used Kodak Tri-X black and white negative film and also colour positive Kodachrome films of

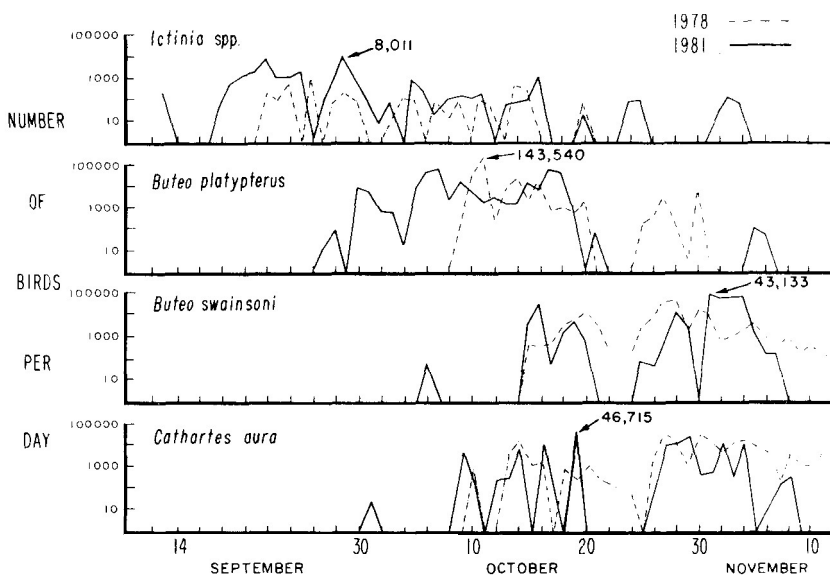


Figure 7: A comparison between two years of the numbers and passage times of the major migratory raptors passing through the Isthmus. The numbers represent mainly, but not entirely, counts made from 35mm negatives and positives. No counts were made during this period in 1980. The 1982 counts are shown in Table 1.

various speeds. When raptor numbers were obviously below 100 individuals I used a hand counter, but photographed all other groups, usually when they were in a glide in such a manner as to avoid any overlap. The counts were then underestimates of *what could be seen* (Table 1). The actual counting procedure is straightforward, but tedious beyond belief. The negatives are projected in an enlarger at high magnification on sheets of 40 × 50cm white paper. Each 'white spot' is then marked out with a black ink pen and counted with a hand counter. When no more images are visible, all the birds on the negative have been counted. In 1978, 2224 b/w negatives and 234 colour transparencies were so treated and in 1981, 2470 b/w negatives and 151 colour positives.

There was temporal overlap in the passage of the various species, and on certain days flocks with three or even four species occurred (Figure 7). A tape recorder was used in synchrony with the camera to provide supplemental species identification information for each negative. But even with this aid, not all images could be identified as to species and these were *not* counted.

Problems

During the September–November passage into South America, an observer on Ancon Hill or Bahai Hill (Figure 1) could probably see and photograph with the 85mm lens all the raptors passing in the early hours of the day when thermal activity was just beginning and the birds were not densely packed in the 'aerial river' crossing the Panama Canal (Figure 2). But after c. 1030hrs on most days, thermal activity became more widespread and the passage route split into two or three parts, spreading out northward to the continental divide (Figures 3 and 4).

There were two solutions to this problem: (1) Have two observers, one on Ancon Hill (200m) and the other at a high point in the divide (a T.V. tower at 525m); (2) Use powerful optical instruments from Ancon Hill to aid counting of the flocks passing 10km to the north. Both methods were tried with varying degrees of success. With two observers, radio contact was essential, but the need to locate the hawks, identify them, synchronize these data with the cameras and at the same time communicate with another observer was simply too much for one person under heavy flight conditions.

In the second solution, I employed 15×60 Zeiss binoculars, an 8.9cm Questar Maksutov-type telescope of 1300mm basic focal length at powers from 80 to 360, and a 'Rich-field' refractor-type telescope of my manufacture which had an objective lens of 13cm and a basic focal length of 600mm. The mirror telescope could resolve 1 sec. arc while the less powerful refractor was at least its equal in resolving power and had a much wider field of view. The photographs (e.g. *Figures 12 and 13*) produced by these instruments always showed images much inferior to those that could be seen by eye.

Thus it would appear that a solution to the problem of counting during the rainy season was available, as I tacitly inferred (Smith 1980). But during the reverse movement one has to deal with somewhat different meteorological conditions. The general passage routes then (*Figures 2 and 3*) are under the influence of the NE trade winds which dominate the dry season in lower Central America. In the early hours the flocks were often concentrated much as in the rainy season on the other side of the divide. But as thermal activity broadened and the winds increased in speed, the flocks disintegrated, making counting very difficult. This does not occur with *Cathartes aura*, which are vastly superior to the other raptors in slope soaring and maintain their long black lines despite the trade winds. The overriding problem in both seasons is cloud cover. As discussed later, the raptors fly *in* and *above* clouds. Cloud cover and storm frequency vary between years in both seasons. The local radars cannot detect birds in or above water-laden clouds.

Thus I conclude that with present technology it is impossible to obtain count data that are comparable from season to season, at least under the conditions of the Isthmus of Panama. 'Counts' made in Texas of 100,000+ Broad-winged Hawks per day might suggest that clouds may not be a problem there (Schumacher-Donohue 1978). These counts yield estimates of up to 1,000,000 Broad-winged Hawks entering Mexico in September. To reconcile this figure with observations in Panama one might assume that (1) massive mortality occurs between there and Panama; (2) significant numbers drop out before reaching Panama [but only in Costa Rica are they noted regularly (Slud 1964)]; (3) vast numbers are hidden by clouds above Panama; or (4) the estimates in Texas are too high.

DYNAMICS OF THE PASSAGES

Methods

I used observation from the ground to correlate local meteorological conditions with the flight strategies employed by the raptors. In addition I relied on reports from observers 400km west of Panama City for their meteorological and hawk flight conditions. A local pilot, G. Vaucher, provided valuable data on weather and hawks in various parts of the Republic. I flew with him in his Cessna single-engined aircraft and was able to obtain information on the altitudes at which the raptors flew and the thermal lift conditions prevailing at various times

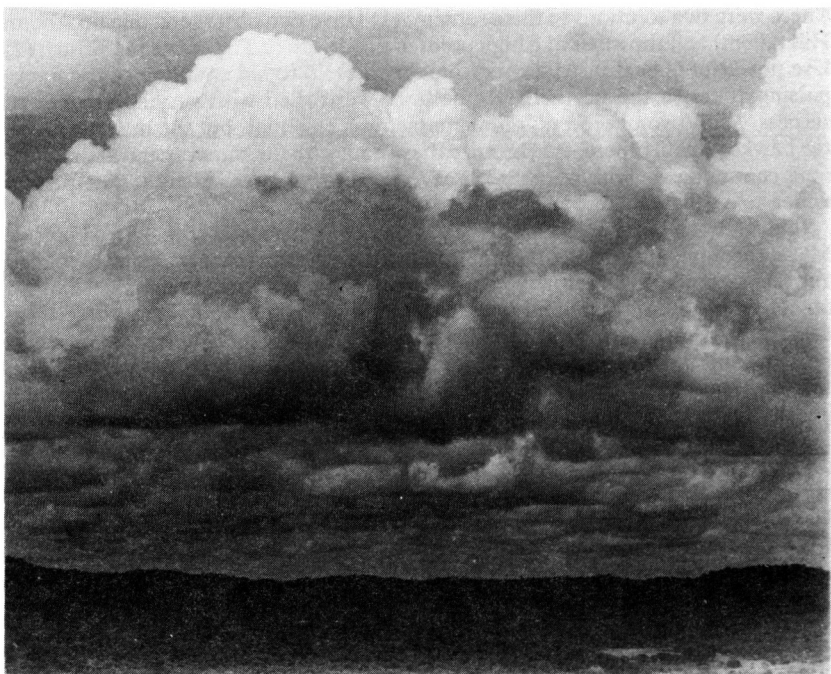


Figure 8: Cloud conditions prevailing October 19, 1981 (13.15hrs) looking NW from Ancon Hill, Panama City. The dark concave bases of these clouds (thermal or cloud streets) run SW to NE, and thousands of *Buteo platypterus* passed in a long 58km glide just inside their bases, which were at 500m to 600m altitude.

over different areas throughout the passage route. C. Crawford flew me in his Blanik L-13 sailplane over the Canal area. This provided me with some understanding of 'cloud streets' (see Pennycuik 1972, 1975), long lenticular zones of thermal lift, and how they were utilized by the raptors in a way I had not previously suspected.

None of these methods is ideal by itself. Both powered aircraft and gliders are essentially blind to hawks flying below them, and a ground observer is usually necessary to direct the pilot where to look. Radar reports were often useful in locating flocks, even though they were unable to give altitude information. Such reports were often misleading, however, as radars often identified clouds as birds, or small flocks of low-flying Black Vultures (*Coragyps atratus*) as 'thousands of hawks'. The noise of the powered aircraft clearly frightened the birds, and its inability to fly at speeds under 60kph made it difficult to follow individual flocks.

The birds showed much less fear of the glider, and in fact joined it in thermals. But the plane was limited in its range and, if the birds were gliding between thermals early in the day, their altitude seldom exceeded 700–850m. The glide ratio of this craft in still air was 1:28, while the best that we measured for any of the hawks was c. 1:14. Thus it always overtook the birds and if no thermal was located quickly the pilot had to land. It also lacked the instruments to fly 'blind' in clouds, so could not safely follow the raptors that entered them, particularly big, fast-rising cumulus types (see below).

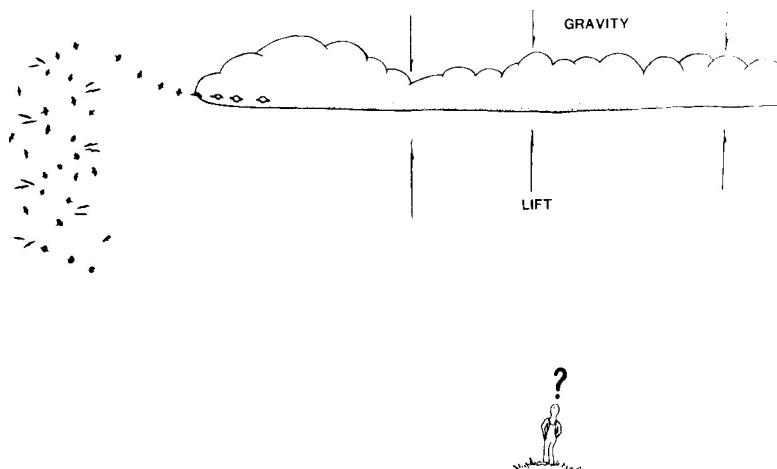


Figure 9: Raptors entering the base of such a thermal street are essentially invisible to a ground-based observer using only binoculars. The birds inside such a cloud base glide with their wings flexed backward and could often attain 40km/hr.

A two-man powered glider with proper instrumentation and reliable information from the ground might be the best craft for studying hawk flights. I marvel at Pennycuick's ability to fly his powered glider and watch birds at the same time (Pennycuick 1972) and suggest a pilot to fly the craft and a biologist to study the birds as the safest system to anyone anticipating such an endeavour.

Routes

The maps in Smith (1980) and Figures 2 to 6 summarize my knowledge of the routes migrant raptors take. It is not simply in response to the trade winds that the passage from South into Central America occurs primarily along the north slope of the divide. Because of the peculiar bend of the Isthmus, this route is the shortest straight line from South America into Central and North America. Raptors use it whether winds are blowing or not. I am still unsure of the exact entry and exit points on the Panama-Colombian border (Smith 1980), but several airplane chases to the east suggest that *Cathartes aura* and *Buteo swainsoni* enter South America on the west side of the Andes and must cross into Amazonia, perhaps near the Colombia-Ecuador border. Because *Buteo platypterus* resides in the Santa Marta area of northeastern Colombia some, perhaps most, of that species must turn north and east to the north of the Andes in the Atrato basin.

Flight altitude

From the ground I often overestimated the altitude at which raptors were flying as well as their distance from me with respect to some terrestrial feature. I discovered this when I tried guiding an aircraft to the birds that I could see with my binoculars. I estimated that the normal migration altitude at 10.00hrs was around 1200–1700m, when it was actually no more than 600–800m. To remedy the degree of error I used extension tubes to increase the focal length of the mirror telescope and calibrated the focusing knob at high magnification on objects of known distance. I was then able to read distance out to about 8000m with an error factor of perhaps ± 350 m under ideal conditions.



Figure 10: A classical columnar thermal being used by *Cathartes aura* over Panama City at 11.30hrs.

I have earlier cited reports by pilots that migrating raptors often attained 3600m to 4000m between 11.00hrs and 13.30hrs on days of 'favourable thermal activity', and suggested these as possible explanations of the so-called 'noon-day lull' (Smith 1980). In 1981 we searched these altitudes and could not locate any hawks despite assurances from ground observers that large numbers had flown upward beyond their view. In addition we could not detect any thermal lift, in its strict

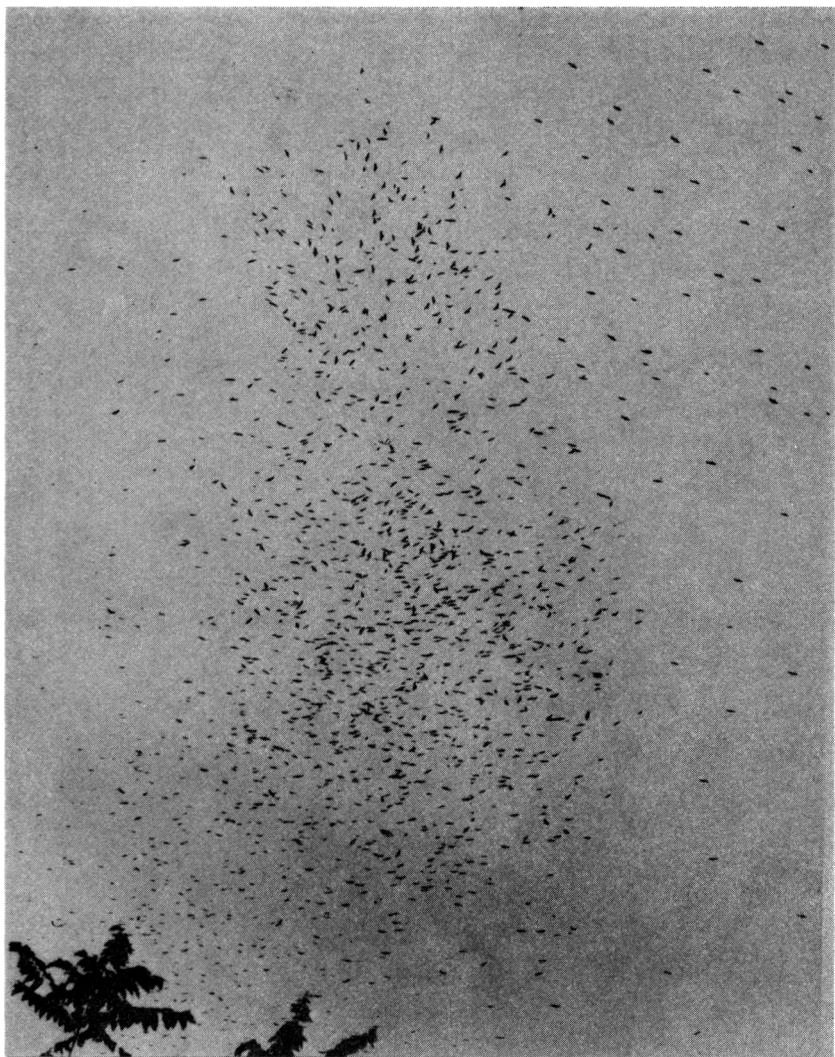


Figure 11: A classical vortex ring thermal containing *Buteo platypterus* at 09.30hrs over Ancon Hill, Panama City.

sense (Cone 1962; Pennycuick 1975), above 2400m over the Canal area. Local glider pilots confirmed the absence of thermals at these altitudes as normal. I do not doubt those reports but I doubt that the birds reached those altitudes via thermals. There is no question that the hawks and vultures easily exceed these altitudes in mountain areas, particularly in the dry season when they use the trade winds which directly strike the side of the Central American mountain chain, creating waves. The birds soar up these waves and can regularly be seen to disappear from the sight of observers standing atop Volcan Baru (3450m) in western Panama. There is circumstantial evidence that hawks, probably *Buteo*



Figure 12: A flock of 3147 *Buteo swainsoni* shown on the full frame of a 24×36 mm negative produced by a 9cm aperture telescope of 1600mm f.l. This flock was part of a larger group totalling 11,453 individuals which passed over the Continental Divide at a point estimated to be 7.5km away.

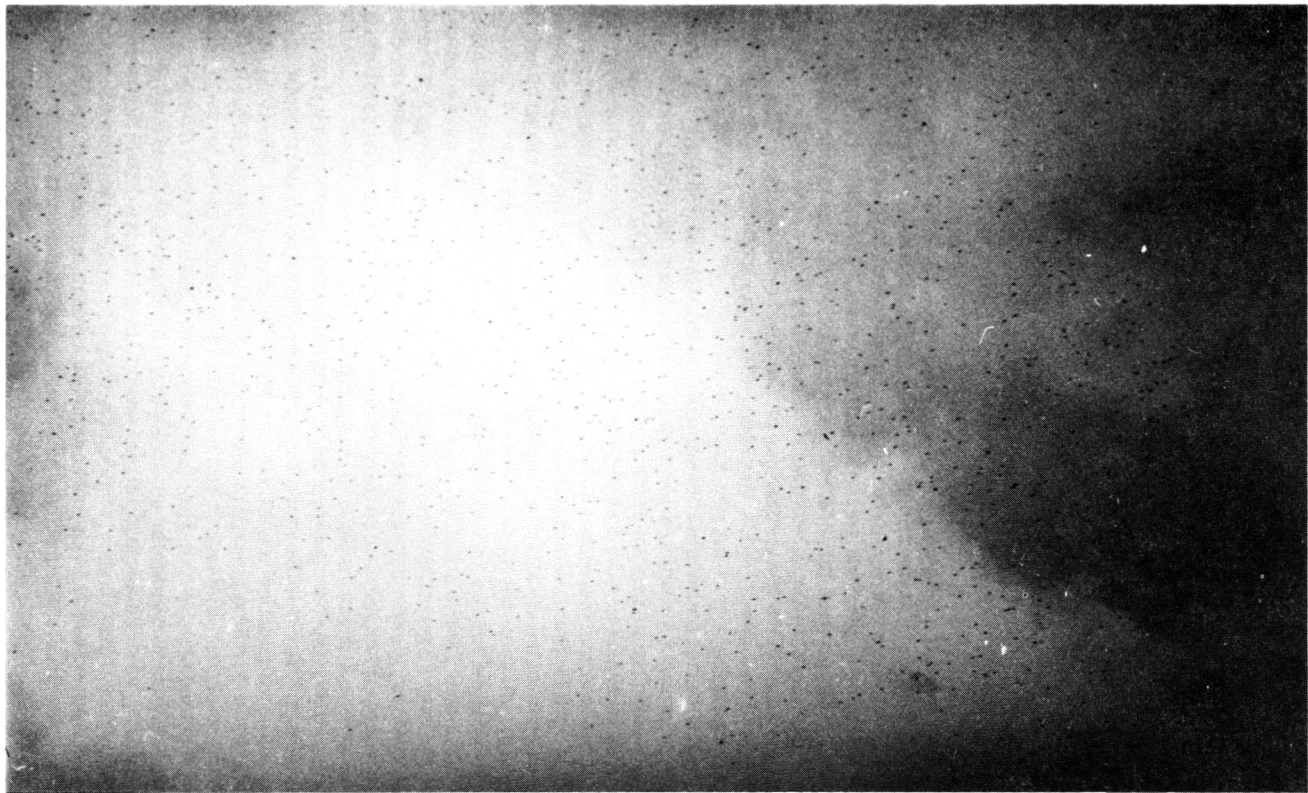


Figure 13: Compare *Figure 12* to these images taken at the Zenith with the same instrument from Ancon Hill. The birds were completely invisible through 10×40 binoculars. This photograph and others like it constitute evidence of very high altitude migration in the Isthmian area.

swainsoni, may attain altitudes of almost 9000m. The photograph in *Figure 12* was taken of a flock of Swainson's Hawks above the spot which my calibrated telescope indicated was over 7000m from my vantage point but perhaps only 1500–2000m above the ground. The photograph in *Figure 13* was taken after a huge storm system had passed by Panama City and included a group of birds that appeared suddenly out of a blue patch of sky, obviously gliding downward. The telescope (1600mm) was pointed almost at the zenith. The finding of this group was purely fortuitous for they were completely invisible even through $\times 10$ binoculars. A comparison of the image sizes suggests that these birds were very high indeed, but if they were on a glide then one must be very careful about using image size as an indicator of height, for all the raptors fold their wings back to increase their speed across the sinking air areas between thermals (see Nisbet 1962) and thus appear smaller than when soaring upward on columnar (*Figure 10*) or classical vortex ring thermals (*Figure 11*). The current world's record for altitude is the Rüppell's Griffon (*Gyps ruppellii*), reported to have struck an aircraft at 11,212m (Laybourne 1974). The temperature at 10,000m is -40°C and the air is rather free of oxygen. I will later discuss a possible adaptive reason for flying in the 6000–7000m range, but I am dubious that flight occurs at 9000m+ with any regularity. Most of my observations from the air indicate that in the absence of strong winds or storms, all the species discussed here fly between 370 and 2650m above the ground, but the ground may be 100, 1000 or 3500m above sea level.

Flight strategies

Everything that Broad-winged Hawks, Swainson's Hawks and Turkey Vultures do while on migration appears to be aimed at conserving energy. Long-distance migrants which regularly use soaring in some form seek to minimize the use of their own body fuel (fat) by drawing energy from their environment. They group together, often in enormous numbers because they are seeking energy sources which are not randomly distributed through space. Their atmosphere is a complex matrix of rising, sinking and dead air. This is in turn often further mixed by lateral movement which can be very strong.

The birds do not fly at night. I have seen thousands descending between 17.00–18.00hrs from an energy-poor sky to roost in the hilly forests around Panama City. They will not ascend if there is complete cloud cover (hence no thermal activity) in the morning. They will not attempt to fly if it rains while they are roosting. In fact they will sit for several days waiting for the rain to stop or the clouds to dissipate (Loftin 1967).

Smith (1980) inferred that once the raptors enter the tropics, thermal soaring (*sensu* Cone 1962) was the mode of migration. That was an oversimplification reflecting my inexperience with movements in the mountains. Winds do occur during the September to November passage and both the Buteos and the Turkey Vultures slope soar, and tack in and out of winds as weak as 3km/hr. I estimated that their average speed during this time was *c.* 25km/hr for a 10-hour day. Measurements made from the air of slope-soaring raptors or those engaged in a combination of slope soaring and thermal gliding suggest that in some areas 35–40km/hr is a more realistic figure. These are average speeds, however, and with wings folded on a 1 : 14 glide, I have measured terminal speeds of 65–75km/hr.

As the day progresses the flight line crossing the Canal splits (*Figure 4*). This occurs because lenticular thermal lift zones form (thermal streets, cloud streets, cf. Pennycuik 1972, 1975) which in the Isthmus run SE to NW and are spaced roughly five kilometres apart until the Atlantic is reached. A glider entering such a 'street' may sail 60km or more in a straight line without losing altitude. As the

day progresses these lift lanes become visible (*Figure 8*). What I had not realized was that as this occurred the hawks began to disappear. When the glider was used to enter the base of these lenticular clouds, Broad-winged and Swainson's Hawks were found gliding in the mist of the bottom few metres, almost invisible to a ground observer. Two such flights revealed several hundred hawks, none flapping, all with wings folded slightly back gliding forward at approximately 25km/hr for distances of 46 and 57km. There were occasional breaks in the mist which surely allowed them to see the ground. But it did not allow a ground observer the chance to count them (*Figure 9*).

This raises the question of how often raptors fly in clouds. My observations with the long focal length telescope indicate that in the Isthmian region at least, hawks (but not vultures) regularly enter the bases of the lenticular thermal clouds and glide forward for several hours or until overconvection takes place (i.e. when clouds have built up to a point where they cut down the effect of the sun so that heating no longer occurs). This may or may not happen on any given day. In addition, cloud streets may not form every day during the migration. But do birds enter the core of rapidly rising cumulus clouds and thus ascend to great heights? Griffin (1973), discussing the problem of bird orientation between and within opaque clouds, concluded that they do. I have seen raptors break out of apparently solid banks of cloud several thousand metres in altitude. But I now believe that my ground perspective caused me to misinterpret what had happened. When I flew with the flocks it became apparent that (1) the birds were attaining heights of 2000–4000m by a combination of thermal and slope soaring in the nearby (east or west) mountains; and (2) from that altitude they could clearly see their forward route for hundreds of kilometres. They were then simply gliding down through a deep but relatively narrow cumulus association. Most tropical storms seem omnipresent to a ground observer but to these high-flying raptors, and to aircraft, they are generally fairly localized and usually easily avoided. The birds may ascend in clouds, but I have no supporting observational data.

As the clouds built up and the thermal streets coalesced, the hawks and vultures employed yet another strategy. When a rain front approached, the falling rain displaced the air upward, and I have seen thousands of raptors hugging the very front of such a storm, being pushed forward and upward. But as Nisbet (1962) put it, when air goes up, air must come down. A glider pilot approaching rapidly rising cumulus cloud cannot usually tell on which side the air is sinking (as I discovered several times to my discomfort) and it is my belief that the hawks and vultures cannot do this either. They make mistakes, by which I mean that they make a directed glide to an area of sinking air where they must flap their wings in order to maintain altitude. Usually when this happens, especially in mountainous situations, they land.

On 21 October 1981 I witnessed a spectacular example of such a mistake. A group of approximately 8000 Swainson's Hawks converged on the front of a huge storm system from the NW, between Bahai Hill and the Continental Divide (*Figure 1*). The birds appeared to be maintaining an altitude of 1000–1300m. All of a sudden they came down, began heavily flapping, and landed in a wooded valley. 'Landed' is perhaps a euphemism, for they crashed through the trees, many falling to the ground where they lay apparently stunned. When I walked among them in the rain, they hopped away but did not attempt to fly. Several had damaged wings. How frequent such occurrences are I cannot guess. This phenomenon is analogous to the 'wind shear' problem encountered by aircraft in the process of taking off or landing.

Over a ten-year period I acquired 34 dead hawks and 7 others which sub-

sequently died. They came from areas where migrating flocks roosted. All were *Buteo platypterus*, and all but one were in immature plumage. Seven had broken wings but the others showed no obvious external damage. None had fat and, with four exceptions, no food was found in their stomachs. They may have starved to death.

The reverse flight in the dry season has been described in the Mexican lowlands (Thiollay 1980) where it appeared to be much like its counterpart in September. This is not the case in lower Central America. Although rain does not normally fall at this time, the trade winds are full of moisture and the north-facing slope of Central America is often completely occluded by clouds which preclude thermalling and slope soaring. Yet the turbulence at the divide is often considerable. Thus Broad-winged and Swainson's Hawks tack into the trade winds at an angle to the north and, as they reach the crest of the divide or the turbulence zone, turn and are propelled at speeds often exceeding 80km/hr (Figures 5 and 6). It is almost analogous to the dynamic soaring of albatrosses moving against the wind and sliding forward and downward behind the wave crest. Clearly such behaviour does not occur in flocks. If clouds have not formed on the north slope, the raptors cut in and out through the mountain passes—from the Pacific slope to the Atlantic and back.

The major result is that a raptor can traverse the entire country in less than a day, whereas it requires perhaps three days to make the same journey in the rainy season. I do not know the relative energetic costs. The few Broad-winged Hawks that I examined during early March were quite fat. Their numbers began to dwindle in late March, but the migration lasts until late April.

ENERGETICS

Swainson's and Broad-winged Hawks migrate thousands of kilometres (Tables 2 and 3). Given the uncertainty as to the extent of the non-breeding range of *B. swainsoni* and the very wide breeding range of the species in North America, the distances can only be approximated.

Table 2: Approximate distances between localities pertinent to migratory raptors, especially *Buteo swainsoni*, in the New World.

Missoula, Montana, USA to Las Cruces, New Mexico, USA	1,700km
Las Cruces to Veracruz, Mexico	1,900km
Veracruz to Costa Rica/Panama border	2,000km
Border to Panama City, Panama	410km
Panama City to point midway between Tucuman and Cordoba, Argentina	4,700km
Total	10,710km

Table 3: Approximate distances between localities pertinent to migration of *Buteo platypterus*.

New Brunswick, Canada to U.S.–Mexico border at Brownsville, Texas	3,600km
U.S.–Mexico border to Panama City, Panama	3,100km
Total	6,700km
Panama City, Panama to line bisecting southern Venezuela, Colombia and northern Peru	1,200km
Total	7,900km

Whether the birds feed on the migration depends on which species, when and where. And even then there are additional qualifiers. For example not all Turkey Vultures, Swainson's Hawks or even Broad-winged Hawks emigrate from North America. An observer on a mountain top in North America could scarcely guess which of the migrants will travel 100, 1000, or 10,000km. But they might be able to do so if they weighed the birds. Fat is the primary fuel for long distance migration (Weiss-Fogh 1952; Tucker 1971; Berthold 1975; Pennycuick 1975). Oxidation of one gramme of fat yields more than nine kcal while one gramme of carbohydrate or protein yields only four kcal.

Long-distance, non-stop, non-feeding migrations are common in birds. Such flights are almost invariably by powered flight, and of relatively short duration. Long-distance migrations over a month or more with feeding are also common, particularly among Procellariiform and Charadriiform birds. But long-distance flights lasting more than a month in which no feeding occurs may be relatively restricted to the soaring raptors and storks of the New and Old Worlds (Pennycuick 1975).

Hawks must put on fat between the time of fledging young and the time of massing into migrating flocks. I assume that they do this in southern North America but do not discount the possibility that many have attained sufficient fat much farther north. G. Bartholomew and I have constructed a model of sorts, the exact details of which will be published elsewhere. The Swainson's Hawk was the species considered, but the model holds for any soaring raptor. We assumed that Swainson's Hawks cease feeding at Las Cruces, New Mexico, near the U.S.-Mexican border. Under what conditions could they fly to Argentina? We calculated a fat-free body mass of 600g and a variety of energetic costs to the flight. Into this was inserted varying amounts of fat up to 50 percent body weight. Real data were fitted into the model. We know that the time to reach Argentina is a few days less than two months. We made numerous calculations of speed per day. It turned out that the average 870g-plus Swainson's Hawk will have no trouble soaring down to Argentina in two months on fat alone. If they are forced to exert themselves, the margin becomes slimmer; hence to drop out of a flock to feed on something that cannot instantly be converted into pure fat is not an adaptive strategy. Little wonder that there are no faeces or pellets at their roosts. That the majority of birds remaining in North America appear to be immatures suggests that inexperience might be a factor in failure to obtain sufficient fat reserves. I might add that the majority of the adult Broad-wings move through Central America into South America. In Costa Rica and Panama, most of the birds that drop out and become residents are immatures. Here the ratio of immatures to adults is roughly 4 to 1, whereas it is the reverse in Colombia (Ridgely, pers. comm.).

Finally, the model does not consider water loss, which some physiologists have considered important in long-distance migration (Berthold 1975). Tucker (1968) has pointed out that water loss decreases with decreasing environmental temperature. Here, then, is a possible adaptive reason for flying at a high altitude, where the temperature is lower than near the ground in the tropics.

ACKNOWLEDGEMENTS

I thank W. Clarke, P. Bloom and J. Strauch for providing weight data on Swainson's and Broad-winged Hawks. G. Vaucher and C. Crawford, in addition to being superb pilots, provided me with information that all glider pilots know

but which is seldom available to biologists. N. Tow, J. Fryxell, R. Foster and N. Currie were helpful counters in various years.

REFERENCES

- BAUGHMAN, J. L. 1947. A very early notice of hawk migrations. *Auk* **64**, 304.
- BECHARD, M. 1981. DDT and Hexachlorobenzene residues in south-eastern Washington Swainson's hawks (*Buteo swainsoni*). *Bull. Environm. Contam. Toxicol* **26**, 248-53.
- BENT, A. C. 1937. Life histories of North American birds of prey. *Bull. U.S. Nat. Mus.* **167**, 69.
- BERTHOLD, P. 1975. Migration: control and metabolic physiology. In: Farner, D. S., King, J. R. & Parkes, K. C. (eds.), *Avian Biology*. Vol. 5, 77-128. Academic Press, New York.
- BROWN, L. & AMADON, D. 1968. *Eagles, Hawks, and Falcons of the World*. (2 vols) McGraw-Hill, New York.
- BROWNING, M. R. 1974. Comments on the winter distribution of the Swainson's Hawk (*Buteo swainsoni*) in North America. *American Birds* **28**, 865-7.
- CONE, C. D. 1962. Thermal soaring of birds. *Amer. Sci.* **50**, 180-209.
- GRIFFIN, D. R. 1973. Oriented bird migration in or between opaque cloud layers. *Proc. Amer. Philo. Soc.* **117**, 117-41.
- HEINTZELMAN, D. S. 1975. *Autumn Hawk Flights*. Rutgers Univ. Press. New Jersey.
- HOFSLUND, P. B. 1973. Do hawks feed during migration? *Raptor Research* **7**, 13-14.
- HOUSTON, S. 1974. South American Recoveries of Franklin's Gulls and Swainson's Hawks banded in Saskatchewan. *Blue Jay* **32**, 156-7.
- LAYBOURNE, R. C. 1974. Collision between a vulture and an aircraft at an altitude of 37,000 feet. *Wilson Bull.* **86**, 461-2.
- LOFTIN, H. 1967. Hawks delayed by weather on spring migration through Panama. *Florida Nat.* **40**, 29.
- NISBET, I. C. T. 1962. Thermal convection and trans-saharan migration. *Ibis* **104**, 431.
- PENNYCUICK, C. J. 1972. Soaring behaviour and performance of some East African birds, observed from a motor glider. *Ibis* **114**, 178-218.
- PENNYCUICK, C. J. 1975. Mechanics of flight. In: Farner, D. S., King, J. R. & Parkes, K. C. (eds.), *Avian Biology*. Vol. V. 1-75. Academic Press, New York.
- ROWLETT, R. A. 1980. Migrant Broad-winged Hawks in Tobago. *Journal of Hawk Migr. Assn. of N. Amer.* **2**, 54.
- SCHUMACHER-DONOHUE, G. 1978. Spring and autumn records 1977. Reports for South central. *Newsletter Hawk Migr. Assn. N. Amer.* **3**, 7-8, 16-18.
- SLUD, P. 1964. The birds of Costa Rica. *Bull. Amer. Mus. Nat. Hist.* **128**, 1-430.
- SMITH, N. G. 1980. Hawk and vulture migrations in the Neotropics. In: Keast, A. & Morton, E. S. (eds.), *Migrant Birds in the Neotropics: Ecology, behavior, distribution and conservation*. Smithsonian Inst. Press, Washington, D.C.
- THIOLLAY, J. M. 1980. Spring hawk migration in eastern Mexico. *Raptor Research* **14**, 13-20.
- TUCKER, V. A. 1971. Flight energetics in birds. *Am. Zoologist* **11**, 115-24.
- WEISS-FOGH, T. 1952. Weight economy of flying insects. *Trans. Ninth Int. Congr. Ent.* **1**, 341-347.
- WETMORE, A. 1965. The Birds of the Republic of Panama. Part 1. Tinamidae (Tinamous) to Rynchopidae (Skimmers). *Smith. Miscel. Coll.* **150** #4617, 1-483