ALTITUDE OF BIRD MIGRATION

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One of the most commonly asked questions among birders is, "How high do birds fly during migration?" A simple answer cannot be given, for the altitude of bird migration is as variable as the types of birds that migrate. The best answer is one that relates altitude of migration to the type of bird, the time of day, the geographic and topographic situation, and the weather. This type of conditional answer may not be pleasing, but it acknowledges the complexity of migration. In this paper I will attempt to show how atmospheric phenomena and geographic-topographic setting can influence the altitude of migration for various types of birds. I will also present a brief (and selective) review of the literature on the altitude of bird migration.

Effects of Atmospheric Phenomena on Migration.

Birds, like aircraft, are subject to the whims of the atmosphere. The atmosphere is rarely, if ever, still. There is almost always horizontal wind as well as vertical turbulence. Anyone who has flown extensively in airplanes knows how uncomfortable the atmosphere can become. Even jumbo-jets can be tossed about by strong turbulence. The structure and timing of atmospheric turbulence, horizontal wind, temperature, and oxygen concentration all influence the altitude of bird migration.

Temperature and oxygen concentration represent two potential physiological constraints that might limit the altitude of bird migration. Both temperature and oxygen partial pressure become lower with increasing altitude. [Partial pressure is a standard measure for expressing the concentration of any component of a gaseous mixture.] At altitudes greater than 2000 meters, humans usually show signs of oxygen stress when engaged in strenuous exercise. Birds, however, do not show signs of oxygen stress during flight at altitudes up to at least 3000 meters. House Sparrows flown in wind tunnels at Duke University with conditions simulating 3000 meter altitudes were not stressed at all (Tucker, 1968). Other studies at the Duke University Laboratories have confirmed that birds are not oxygen-stressed at high altitudes.

What little is known about the temperatures that birds can tolerate during flight suggests that high temperatures may be more inhibiting than the lower temperatures that are experienced by birds flying at 3000 to 4000 meters. Starlings flown in wind tunnels at various temperatures showed marked respiratory water loss at temperatures greater than 28° C. (Torre-Bueno, 1976, 1978). Evaporative water loss presumably lowers body temperatures below stressful levels. Larger birds that use powered (flapping) flight and have low surface area to volume ratios may experience heat stress. I have seen loons migrating at low altitudes along the New Jersey coast fly with their mouths open when the air temperature exceeded 30° C. These same migrants frequently fly at altitudes above 1000 to 2000 meters during extended overland flights (Kerlinger, 1982). The lower temperatures at these altitudes may reduce heat stress and subsequent evaporative water loss. Thus, low temperatures and low oxygen partial pressures at altitudes up to 3000 or 4000 meters probably do not limit the altitude of bird migration.

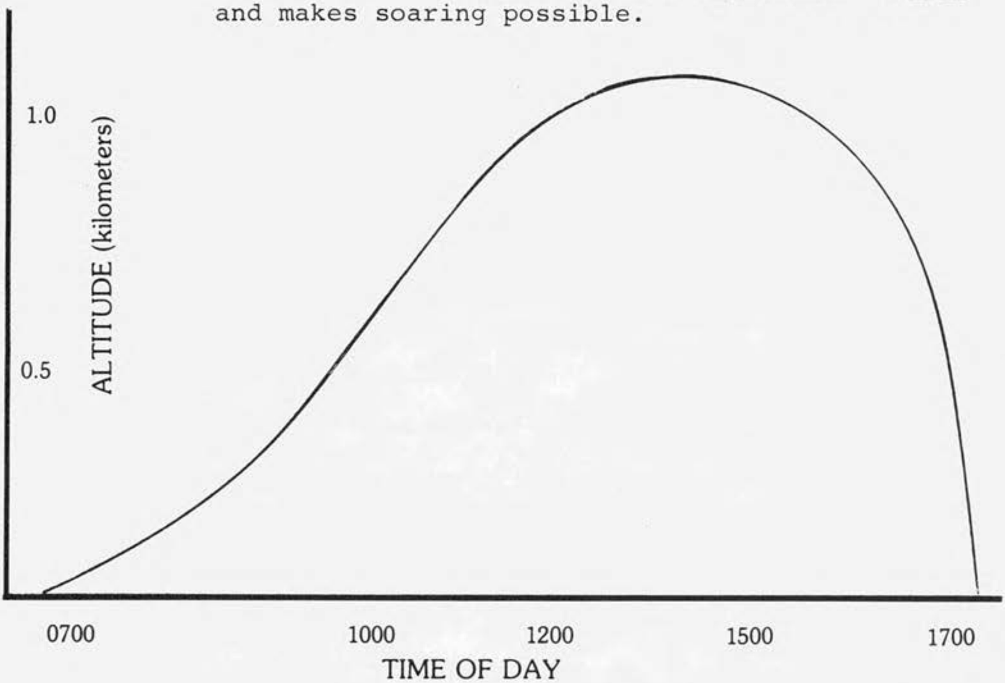
Horizontal wind and vertical turbulence are undoubtedly the most important factors affecting the altitude of bird migration. Vertical turbulence, also known as atmospheric convection or thermal convection, follows a regular circadian cycle, with greatest turbulence (instability) occurring at or near midday and the least turbulence (stability) at night or in the early morning. The difference between surface and upper air temperatures determines how much, how strong, and how quickly convective turbulence develops. When the surface is heated to higher temperatures than the air above the surface, the warmer, more buoyant surface air rises and creates an unstable layer.

Thermal convection usually makes riding in airplanes uncomfortable and may adversely influence birds using powered flight. Conversely, without thermal convection, soaring birds cannot soar for extended periods. Usable thermal convection in the northeastern United States is normally limited to the first 1300 meters above ground level, while on the Great Plains and over the Rocky Mountains, thermals rise to over 2000 to 4000 meters. Early in the day or near the surface any time during the day, convection is often unstructured and not usable by soaring migrants. Later in the day, convective elements rise to higher altitudes and become more structured. An example of the development of convective depth and the altitude to which thermals can rise is shown in Figure 1. Convective development is most rapid between 0800 and 1100 hours, but thermals do not cease forming until after 1700 hours or when weather conditions change, e.g., to total cloud cover. The base of cumulus clouds is a rough indicator of the convective depth, but more precise methods have been devised to determine convective depth and thus to predict the altitude of migration of soaring birds (Cipriano and Kerlinger, 1984). Heavy cloud cover (cumulus-stratus), generally indicative of instability, can also be a factor in determining the altitude of migration.

On most days some usable convection occurs, but sometimes the air is stable and devoid of thermals. Stable conditions occur when air above the surface is warmer than surface air. This phenomenon, known as inversion, is poor for soaring birds but makes for very smooth airplane flights.

Before leaving the topic of vertical turbulence, I should make it clear that thermal convection is not the only form of vertical air currents used by migrant birds - just the most common one. There are several other forms of updrafts that are not created by typical heating of the earth's surface, but by

Figure 1. Relation between time of day and convective depth. For a given time of day, altitudes below the curve are those where thermal convection occurs and makes soaring possible.



wind, by combinations of solar heating and wind, and by differential temperatures between bodies of water and adjacent land. Wind updrafts, probably the second most common source of vertical air currents used by migrants, are the result of wind deflected vertically off ridges, hills, tree rows, bridges, etc. The altitude of migrants using such updrafts is often below 100 to 300 meters. Wind deflected by ridges or hills can be augmented by thermal currents to create very powerful updrafts. When this occurs at locations like the Kittatiny Ridge in New Jersey or Pennsylvania, a long, linear and continuous thermal can form and allow soaring migrants to glide continuously without circling for many kilometers. The last type of vertical turbulence mentioned here is the sea breeze updraft. Created by a difference in temperature between the shore and the cooler water, these updrafts are restricted to coastlines and are presumably only useful when the coastline is aligned with the preferred direction of flight.

Horizontal winds also vary with altitude above the surface. At higher altitudes winds usually become stronger and change direction. This variation with altitude gives a migrant a choice of wind speeds to fly in. The gradient of wind speed with respect to altitude is usually greatest within the first fifty meters above the surface but continues upward for thousands of meters. Thus, a bird flying into headwinds should fly lower than one flying with tailwinds. Changes of wind direction with altitude, called wind shears, can also influence the altitude at which birds fly. Directional changes of up to 180 degrees can sometimes be found within the first 1000 to 2000 meters above the surface. For instance, in spring on the Gulf coast of Texas, surface winds are usually from the southeast, while winds at altitudes greater than 2000 meters are from the southwest or west. A bird flying to the northwest would maximize its ground speed by flying at altitudes where winds are following, i.e., well below 2000 meters.

To summarize, both horizontal and vertical components of wind can strongly influence the altitude of bird migration. The vertical wind component in the form of thermal convection and other updrafts is the most important determinant of the altitude of migration of soaring birds. The role of vertical turbulence in determining the altitude of migration of powered migrants is not clear, but it is likely that strong turbulence makes level flight difficult. The effect of horizontal winds on powered migrants is clearer: e.g., increased energy expenditure when migrating in opposing winds. Soaring migrants probably do not experience this effect, but they do realize slower ground speeds or difficulty in maintaining their course. Because wind direction and speed vary with altitude, a bird should carefully select the altitude at which it migrates in order to maximize ground speed, which in turn minimizes time and amount of energy necessary for migration. A bird that is able to maximize ground speed may have a selective advantage over birds that do not use such a strategy.

Altitudes of Major Categories of Migrants.

So far we have seen that atmospheric phenomena affect migrating birds in predictable ways and that there are good reasons for birds to fly in particular altitudinal bands or to fly only at times when atmospheric phenomena reduce the energy necessary for migration. In this section I shall present a brief comparative review of what is known about altitudes used by birds during migration including whether or not the migrants involved have demonstrated a tendency to select altitudes in accordance with variable conditions. This review is divided into subsections corresponding to three major migrant categories based upon time of day and principal mode of flight, namely, nocturnal migrants, soaring diurnal migrants, and diurnal migrants using powered flight. Some groups of birds migrate during both day and night. For these groups, the differences between the nocturnal and diurnal altitudes will be noted. Altitudinal ranges used by different groups are summarized in Table 1. Where altitudinal ranges are given, data were gathered with radar (of varying types) unless otherwise specified.

Table 1. Summary of the altitudes of migrating birds. See text for references.

TYPE OF BIRD	TIME	LOCATION	ALTITUDE (METERS)
Passerine	Night	Southeastern U.S. & elsewhere	<700
Passerine	Day	Gulf of Mexico	>800
Passerine	Day	North Atlantic Ocean	>700 - >3000
Passerine	Day	South & Northeastern U.S.	<100 - 300 ?
Loons	Day	Eastern New York (over land)	>1000
Hawks	Day	Eastern U.S. (ridge)	<100 - 300
Hawks	Day[a]	Texas, New York, New Jersey	<300 - 400
Hawks	Day[b]	Texas, New York, New Jersey	<500 - >1000
Cranes	Day	Sweden	<1500
Swallows & Swifts	Day	Texas, New Jersey, New York	<600 ?
Unidentified birds	Day	Eastern New York	>2000 - >3000

a = before 1100 hours; b = after 1100 hours.

Nocturnal Migrants.

Birds that migrate at night can conveniently be categorized by the echo they leave on a radar screen. Shorebirds and ducks make large, fast-moving echos on radar and generally migrate at higher altitudes than do passerines, which leave small, slow-moving echos. The altitude of more than 90% of nocturnal migration studied in the southeastern United States was below about 700 meters (Able, 1970). Radar studies in other locales have yielded similar altitude ranges for passerines migrating at night (Gauthreaux, 1972; Bellrose, 1966, 1971). A few studies have reported slightly higher migration of passerines at night (Lack, 1960). Interestingly, the birds studied by Able (1970) were flying downwind (Gauthreaux and Able, 1970), so selection of altitude may not have been critical for these birds. A study conducted in the Alps in Switzerland (Bruderer and Steidinger, 1971) showed that the altitudes selected by passerine migrants corresponded to the altitudinal band with winds most advantageous for migration. Not many studies have shown this type of altitudinal selection. An alternate strategy for dealing with winds is to migrate only when winds favor a swift and energetically efficient flight. The strategy of migrating on nights when winds are best for migration has been demonstrated for numerous groups of birds (see Lack, 1960 and Richardson, 1978 for reviews).

The question of why passerines migrate at night has been asked frequently. Of the many hypotheses proposed, avoidance of predation and use of daylight hours for foraging have been favored. A third hypothesis considers atmospheric turbulence as a factor. Because passerines fly at such slow air speeds, they cannot maneuver easily in strong winds. Reduced turbulence at night may allow easier maneuvering or less energy consumption during flight. None of the proposed hypotheses has been adequately tested.

Soaring Diurnal Migrants.

Hawks and other soaring migrants (pelicans, swallows, some gulls, cranes, etc.) depend largely upon thermal convection to gain altitude between periods of gliding flight. Thus, they are rarely in level flight but are mostly either climbing or descending. For such birds, determining and interpreting mean altitude of flight and some measure of variance is difficult. These measures must not be considered comparable to similar measures for migrants that use level (non-soaring) flight. Migrating hawks using wind-generated or thermal updrafts along ridges often maintain level flight, usually less than 100 meters above the level of the ridge (Broun, 1949). During flight over water or over land where no updrafts are available, soaring birds must often resort to level, powered flight. Most Peregrine Falcons, Ospreys, and other hawks making short-distance water crossings against strong headwinds fly within one to five meters of the water (Kerlinger, unpublished data).

Because soaring birds rarely use powered flight, the maximum altitude of flight must be a function of convective depth (Cipriano and Kerlinger, 1984). Convective depth can vary with time of day (as shown in Figure 1), geographic or topographic location, and atmospheric conditions. Convective activity over water is uncommon and undependable. Thermals formed over water are also less powerful than those over land (Woodcock, 1975). In the northeastern United States convection over land seldom exceeded 1300 meters (Cipriano and Kerlinger, 1984 and Kerlinger et al., MS). Hawks migrating in New York, New Jersey, and south Texas mostly flew below 1300 meters and did most of their soaring between 300 and 900 meters (Kerlinger and Gauthreaux, MS, Kerlinger and Gauthreaux, MS, Kerlinger et al., MS). Mean altitudes were below 950 meters for all species in both spring and autumn. Vultures soaring over the Serengeti Plains of Africa seldom exceeded 2000 meters above ground level (Pennycuick, 1982). Although these birds were not migrating, they too were constrained by convective activity. Cranes migrating in Sweden did not exceed 2000 meters (Pennycuick et al., 1979). So, it seems that soaring birds consistently migrate within 2000 meters of the earth's surface.

The highest altitudes reported for migrating soaring birds come from Panama where migrating hawks have been reported to use "thermal streets" and convection in thunder clouds to attain altitudes of 3000 to 6000 meters (Smith, 1979, 1984). Birds flying in thermal streets (linear arrays of thermals) were observed from a sailplane, but unfortunately the altitudes of 3000 to 6000 meters were derived from direct visual observations and from occasional reports from pilots. Intensive radar-aided studies of the altitudes of soaring birds in the tropics, as well as on the Great Plains, would not only confirm or refute these reports but would also add greatly to our knowledge of the overall picture of bird migration and atmospheric phenomena.

Altitudes of a few other soaring migrants are given in Table 1, but data are scarce. Few species of soaring migrants other than hawks and cranes have been studied, but the data that are available for birds like gulls, swifts, swallows and martins are within the range given for hawks.

Diurnal Migrants Using Powered Flight.

Practically all migrant species of birds, including many of the nocturnal migrants, do some powered-flight diurnal migration. In view of the large number of diurnally migrating birds, surprisingly few studies of altitude have been undertaken, and few empirical data are available.

Passerine migrants that migrate at night frequently fly in the daytime just after sunrise (called morning flight) or, of necessity, during long-distance water crossings. The predictable variation in altitudes used by these migrants as a function of the time of day and geography is extremely interesting. During morning flight (Gauthreaux, 1978; Bingman, 1980), large numbers of passerines can be seen flying at altitudes from only a few meters above the trees up to a few hundred meters, much lower than migrants flying in darkness hours earlier. This type of flight has been suggested to be either a means of compensating for wind drift from the previous night's flight (Gauthreaux, 1978) or a continuation of the migration (Bingman, 1980).

Many passerines and shorebirds make long-distance water crossings that necessitate flight during daylight hours. Fall migrants over the Atlantic Ocean (probably Blackpoll Warblers and shorebirds) have been tracked on radar at altitudes over 2000 to 4000 meters (Williams and Williams, 1978) during their two-to-four-day flights from northeastern North America to South America. Flight at higher altitudes presumably enables these birds to utilize stronger tailwinds and to lose less body water to evaporation because of lower temperatures. Slightly lower altitudes have been reported for passerines migrating over the Gulf of Mexico in the spring. Gauthreaux (1972) has observed passerine migrants over the Gulf with various radars in southern Louisiana. Daytime altitudes were higher than those at night and ranged from about 900 to 2000 meters. The changes in altitude when the sun rose were dramatic. Cloud cover also influenced the altitude of migrants over the Gulf. Birds flying on days with complete overcast tended to fly above the clouds (Gauthreaux, 1972).

Among the other birds that migrate during the day, some species, e.g., loons, migrate at high altitudes over land - above 1000 to 2000 meters (Kerlinger, 1982), while over water, they fly from a few meters to 100 or more meters above the surface (Cherry, personal communication). The highest fliers may be shorebirds or waterfowl, but other groups may be a part of the high-altitude flights observed. High-altitude echoes from birds are common during radar studies. During fall and spring near Albany, New York, I have tracked objects not visible with a 20X scope flying at altitudes between 2000 and 4000 meters. The objects were unquestionably birds because they flew at slower airspeeds than airplanes and left wing-beat "signatures" on the radar screen. In fall, it should be noted that many flew downwind above a continuous cloud cover in the direction of the Atlantic Coast.

Although few data are available, it seems that smaller diurnal migrants such as some finches, Blue Jays, flickers, etc., migrate in the first hundred to few hundred meters above the surface. For this group, quantitative studies would prove most fruitful. Overall, the trend seems to be for larger, fast-flying birds to migrate high and for smaller, slow-flying birds to migrate low during the day.

Conclusions. It should be clear to the reader by now that the altitude of bird migration varies considerably. I have tried to show how the altitudinal band used by migrating birds varies with atmospheric conditions, geography, topography, and type of migrant. From what we know, most migration occurs at altitudes below 1000 meters, but higher migrations are performed by some birds including soaring birds, passerines flying in daytime over water, and some shore and water birds. The relation between atmospheric structure and altitude of bird migration has been studied most for soaring migrants. Even for these birds, but especially for powered migrants, this relation is still poorly understood. Unfortunately for prospects of obtaining a better understanding, fewer migration studies are being conducted now, and even fewer are concerned with altitude of migration.

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