Possible Steps in the Evolutionary Development of Bird Navigation

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DESPITE SCORES OF PAPERS and hundreds of experiments and tens of thousands of field observations there still exists much mystery about bird navigation. Some findings contradict other findings. Some investigators believe that studies of the homing pigeon will point the way to further understanding of navigation in migratory birds. Other investigators believe that only studies of wild, migratory birds will yield pertinent findings about this navigation.

Differences between the navigational attributes of species are recognized, but some investigators believe that there are basic clues used by all birds while others consider most migrant species to be somewhat different in their navigational attributes. Small wonder, then, that much confusion about bird navigation still exists among experts and laymen alike.

I believe that unnecessary confusion will exist until we organize the known facts about bird navigation on the basis of its probable evolutionary development. Moreover, if we can arrange experimental and empirical findings into their proper niches in the scheme of evolutionary development, we can greatly expedite planning for future research work on bird navigation.

I have endeavored in this paper to present my conception of the possible evolutionary course of navigational development in birds. Because of the broad scope of the topic, most of the information has been obtained from the literature.

REVIEW OF AVAILABLE CUES FOR NAVIGATION

As a prelude to a discussion of lines of possible evolutionary development in bird navigation, it is essential to review briefly ostensible and potential environmental cues available for bird navigation. The cues that fall into these broad categories are: landscape features, Sun as a compass, Sun for bicoordinate navigation, stars as a compass, stars for bicoordinate navigation, wind structure, and the Earth's magnetic field.

Landscape Features

Both experimental findings and field observations indicate that landmarks are the most fundamental cue in bird navigation. The use of landmarks by homing pigeons in the vicinity of their lofts has been noticed by most investigators studying this species. The use of landmarks by wild birds in migration has been reviewed at length by Hochbaum (ref. 1); has been described for waterfowl by Bellrose and Sieh (ref. 2) and Bellrose (ref. 3), and for 38 species in the Sudan by Mathiasson (ref. 4).

In two different groups of experiments, bank swallows (ref. 5) and purple martins (ref. 6) were displaced varying distances from their nesting colonies. Observations were made on their directions of flight upon release and the times of return to their nest sites, under different sky conditions. Both investigators concluded that these diurnal migrants basically used landmarks as their cues for returning home.

Although the degree of use of the landscape is highly variable among many species, depending upon basic differences in mode of flight, range of flight, period of daily activity, and various other traits, all species appear to use landmarks for orientation purposes.

Sun Compass

I interpret a Sun compass as the ability of a bird to use the Sun for determining a fixed direction. A considerable body of evidence (summarized by Matthews, ref. 7, pp. 22–40) suggests that many migratory birds have a Sun compass. In addition to the many laboratory and field experiments that demonstrate the presence of a Sun compass in birds, certain displacement experiments provide circumstantial evidence of its presence.

Schuz (refs. 8 and 9) reported a series of experiments with white storks in which nestlings were transported from East Prussia west to the Rhineland. When East Prussian storks were released after the departure of Rhineland storks, they migrated over unfamiliar landscape, unaided by other storks, in a south-southeast direction, the standard direction taken by their parents.

Juvenile starlings displaced from Holland to Switzerland and from Holland to Spain (refs. 10 and 11) migrated in the standard direction but maintained their lateral displacement. Adult starlings behaved differently.

These displacement experiments demonstrate the ability of certain birds to maintain a direction of migration without the aid of known landscape features. Until there is contrary evidence, I believe it is only logical to assume that a Sun compass enabled these displaced birds to migrate in specific directions.

However, recent findings by Southern (refs. 12, 13) cast doubt on the presence of a Sun compass in all migratory birds. From experiments conducted with ring-billed gulls, Southern found no appreciable difference in directional response between birds tested under clear and under overcast skies. If a Sun compass is present in ring-billed gulls, it must be poorly developed.

Bicoordinate Navigation

The experimental evidence for bicoordinate navigation from the Sun is meager. It rests largely on a series of experimental releases made with Manx shearwaters under clear and under overcast skies by Matthews (refs. 14 and 15). Certain experimental releases of homing pigeons have also demonstrated bicoordinate navigation from the Sun (refs. 16 to 18); other releases of pigeons have shown only a directional type of orientation. Apparently the genetic composition of the pigeon stock, training, and loft site have influenced many of the varied results from pigeon experiments (ref. 18).

In addition to the direct experimental evidence for Sun navigation, I believe that certain displacement experiments provide circumstantial evidence that some birds have the capability of employing it. Perdeck's displacement of adult starlings (ref. 10) from the Netherlands to Switzerland resulted in these birds flying back toward their original wintering area, and, in subsequent seasons, occupying their original range. In another displacement experiment, Perdeck (ref. 11) transported 900 adult starlings from the Netherlands to Barcelona, Spain. The results agreed with those of his earlier experiment: The adults again headed for their normal winter quarters.

Kenyon and Rice (ref. 19) displaced 18 Laysan albatrosses from Sand Island, Midway, to various areas of the north Pacific extending from Japan to the state of Washington. Fourteen birds returned to their nests over minimal distances of 2116 to 6629 km. Most of them averaged over 160 km per day, and one averaged 510 km per day.

Seven Leach's petrels were displaced from Kent Island, New Brunswick, to the coast of Sussex, England, a distance of 4795 km (ref. 20). Of the four that returned, the two fastest both had minimal speeds of 349 km per day; minimal speeds of the remaining two were 301 and 195 km per day. A Manx shearwater from Skakholm Island, England, released at Boston, Massachusetts, covered at least 4910 km at a speed of 393 km per day (ref. 21).

I believe that only through using the Sun to determine their longitude and latitude displacement from that of their distant homes could these pelagic species return so quickly. There is no other source of navigational cues known at present that would justify any other interpretation.

Star Compass

There is considerable information showing that many nocturnal migrants possess a star compass. A star compass may be defined as the determination of a standard direction from the location of stars alone. Astral navigation implies that a migrant is capable of determining longitude and latitude from star positions and correcting for any displacement, such as might be caused by strong lateral winds.

Sauer and Sauer (ref. 22) were the first to report that birds could utilize stars as an aid in navigation. Unaware of their work, Bellrose (ref. 23) reported on the one-direction orientation of mallards to the starry sky. In a series of papers, culminating in a study of the golden plover Sauer (ref. 24) sought to demonstrate that several species of birds were able to use astral cues for true bicoordinate navigation.

In a careful review of Sauer's early findings, Walraff (ref. 25) concluded that true navigation from stars had not been demonstrated. Since that time, many studies made on nocturnal orientation of birds have shown only a one-direction response to astral cues (refs. 26 to 29).

Moreover, Matthews (ref. 30) has reported that clock shifting of mallards affected a compensatory change in their diurnal orientation but not in their nocturnal orientation. Therefore, it is probable that directions of flight of nocturnal migrating mallards are obtained with reference to patterns of stars, rather than to the azimuth position of individual stars. This seems to negate the possibility of determining bicoordinate navigation from planetarium experiments.

Blue-winged teal are almost exclusively nocturnal migrants. Over several years we trapped blue-winged teal in central Illinois during September, and retained the juveniles for several weeks after the adult birds had departed the region. Band recoveries from the retarded released juvenile teal showed that they migrated toward the south and southeast, directions similar to those recorded for the species (ref. 31). Certain displacement experiments also provide circumstantial evidence of a standard directional flight at night. During the fall of 1969 we air shipped 250 blue-winged teal to the Great Salt Lake marshes, Utah, 1850 km west of where they were trapped in central Illinois. Juveniles numbered 201 and were released at the Bear River National Wildlife Refuge; the 49 adults were released at the Ogden Bay State Refuge about 40 km to the south. The releases occurred on November 25 when no local blue-winged teal or cinnamon teal were in the region.

Omitting those band recoveries in the region of release, seven were reported at distant points within the following 6 weeks; all were over 640 km away in a south to south-southeast direction. Five of the seven recoveries were from juveniles and two were from adults. The blue-winged teal flew in directions appropriate to those used by teal in migrating from Illinois. There was obviously no evidence of compensation in direction of migration for their 1850-km westward displacement. I believe that these teal, represented by both adults and juveniles, used astral and possibly Sun cues to migrate in their customary direction.

The best indirect evidence for postulating true astral navigation that might occur in certain of the most sophisticated navigators is that given by Serventy (ref. 32, p. 170). He transferred 16 fledgling slender-billed shearwaters (which I calculated to be about 85 days of age from data presented by Serventy) in 1961 from nesting islands off the Tasmanian Coast to Fisher Island in Bass Strait. In the next few years, 3 of the 16 (19 percent) returned to Fisher Island, and 28 percent of the fledglings indigenous to Fisher Island returned there during the same period.

The period of sensitivity to locale imprinting apparently occurs in the slender-billed shearwater when it first emerges from its burrow at night to exercise its wings. This occurs about 14 days after the parent birds cease feeding the chicks when they are about 97 days old.

When Serventy (ref. 32, pp. 178–179) transferred 50 fledglings from other nesting islands to Fisher Island at the end of the desertion period (97 days after hatching), not one returned to Fisher Island, but 36 percent of the indigenous Fisher Island birds returned.

As I interpret Serventy's findings, there was only a 14-day difference in the ages of the young shearwaters between the two experiments. During this so-called 14-day period of desertion, prior to the young leaving the island, they are active only at night, and then only at the mouths of their nest burrows. Consequently, about the only cues available at that time would be those of the nocturnal sky.

The first returns of fledgling slender-billed shearwaters to Fisher Island (calculated in percent from data presented by Serventy, ref. 32, p. 175) for 209 birds are: 2 years, 1.4; 3 years, 23.0; 4 years, 47.4; 5 years, 16.7; 6 years, 9.6; and 7 years, 1.9.

During this long absence from the nesting island, the slender-billed shearwater migrates in a gigantic loop from west to east off the coasts of the North Pacific (ref. 33). It is truly one of the world's great migrants, and yet its navigation appears to depend primarily upon nocturnal cues obtained during a 14-day period.

Perhaps the exciting travel of one bobolink is another suggestion to true astral navigation (ref. 26). This bird escaped Hamilton on September 1, 1959, in San Francisco, California. It had been trapped at Kenmare, North Dakota, on August 9, 1959. On June 1, 1960, it was recaptured at the same banding station in Kenmare, North Dakota.

Wind Cues

The ability of birds to migrate at night when astral cues are obscured by dense cloud cover and landmarks are either invisible or indistinct has been shown by radar observations (refs. 3, 34, 35).

Radar surveillance of nocturnal migrants at night reveals little response to landscape features. In a study of bird migration at 20 U. S. Weather Bureau radar stations ranging over the entire eastern United States, the only evidence I saw of birds responding to landscape occurred between land and water along the Gulf Coast (ref. 3). Later, I observed another instance of birds responding to landscape. On the night of March 22, 1969, I watched flocks of Canada geese migrating northward on FAA radar, near Chicago, Illinois. Most of the geese were just to the west of Chicago. However, when they reached Lake Michigan, north of Chicago, many flocks turned abruptly east or northeast to head out over the lake (ref. 36, p. 281).

Birds migrating on nights when dense clouds obscure the starry sky are even less likely to view landscape than on clear nights. That poses the problem: What do they use for guidance when landscape and celestial cues are lacking?

The remaining environmental source of guidance information that is most omnipresent is the wind. Over a quarter of a century ago Griffin (ref. 37) suggested: "Birds might react to such phenomenon as prevailing winds and the characteristics of air masses. These are aspects of the environment bearing a certain relationship to geography."

Observing diurnal migrants, especially common chaffinches, in the Netherlands led Vleugel (refs. 38 and 39) to conclude that birds maintain a straight course by reference to the direction of the wind. However, at night without reference to other cues, birds could not sense direction if the wind were isotrophic. As pointed out by Nisbet (ref. 40), near the surface of the Earth the air is anisotrophic from friction with the Earth's surface features which produce wavelike currents of air correlated with the wind direction.

Most birds fly within 6100 m of the Earth's surface, which is well within the range of the turbulent wind pattern. With the addition of reference points on the Earth's surface, which are usually available, the nocturnal migrant is then provided with a minimum of two guidance cues.

Recent experiments with blue-winged teal (ref. 3, pp. 90–92 and unpublished observations) showed a similar degree of orientation under clear and under overcast skies. The direction taken by the experimental birds appeared dependent upon the temperature and wind direction.

In another series of experiments, Bellrose and Crompton (unpublished observations) placed groups of teal in two circular cages atop a 30-m tower. The teal in one wire cage were exposed to the wind; the view from the other cage was similar, but plexiglass prevented the birds from sensing the wind. After confinement in these cages for several days, the teal were released individually over unfamiliar landscape under overcast skies. Although birds from both groups tended to quarter downwind, those previously prevented from perceiving the wind flew markedly more tortuous courses and spread over a wider range than did the birds exposed to the wind.

Certain field evidence points indirectly to the use of wind as a potential cue in bird navigation. The tremendous loop migration of the slender-billed shearwater from Tasmania through the North Pacific is in accord with oceanic wind patterns (ref. 33). A similar loop migration by the greater shearwater in the Atlantic Ocean from tiny Tristan da Cunha as far north as Greenland (ref. 41) also appears attributable to prevailing wind currents. Likewise, band recoveries from giant petrels indicate that they move westward completely around Antarctica with the prevailing winds of that region (ref. 42).

The known abilities of turkey vultures, Buteo hawks, and the white stork to take advantage of thermals in their extensive migrations is well documented.

Bellrose (ref. 43) compared the response of migrating birds to a variety of wind directions and speeds. This comparison was based on radar detection of the flight direction, speed, and altitude of migrants in relation to the wind direction and speed at similar altitudes. The birds observed on radar appeared to select wind characteristics that were favorable for their migration. The migrants' awareness of wind conditions led Bellrose (ref. 43) to postulate that winds were an additional source of directional guidance.

Although there is no experimental evidence to evaluate the role of wind in bird orientation, field evidence suggests that birds can use the wind as an aid in navigation. I anticipate that the degree of use would vary greatly among birds, depending on basic migration traits.

EARTH'S MAGNETIC FIELD

The report by Keeton (ref. 44)—that carefully controlled experiments of homing pigeons showed good homing under overcast skies—was most startling. It meant that to return with demonstrated facility and speed to their home loft these pigeons did not use the following cues: landscape features, the Sun, and the wind. Their release in an unfamiliar area negated the use of landscape features; the Sun was invisible throughout their flights; and they could not have diagnosed the relationship of the wind at the release site to the location of their home loft.

If Keeton's findings are eventually confirmed, it will mean that there is still another environmental cue available to birds for navigational purposes. Of the remaining sources of navigational information potentially available to birds, the most likely one is the Earth's magnetic field.

Over the past decade Merkel and Fromme (ref. 45) and Merkel and Wiltschke (ref. 46) have presented evidence that European robins in a covered enclosure were influenced in their choice of directions by weak magnetic fields. Investigators Perdeck (ref. 47) and Meyer and Lambe (ref. 48) could not elicit a directional response to magnetic fields in similar experiments.

However, Southern (ref. 12) reported that the directional selection of ring-billed gull chicks was adversely affected when the Earth's magnetic field was disturbed by solar flares. Therefore, evidence from several sources suggests that the Earth's magnetic field may be used by certain birds for directional information.

Eugene Mueller, electrical engineer and meteorologist with the Illinois State Water Survey reported[1] that the north-south gradient of the Earth's magnetic field extends undiminished in intensity through the atmosphere. However, anomalies are usually caused by local deposits of ferromagnetic materials and where ligneous extrusions high in magnetism penetrate sedimentary rocks weak in magnetism.

Variations in the geomagnetic field are weak and usually cannot be detected with a galvanometer above 3048 m (10 000 ft). In searching for anomalies on the Earth's surface, it has been found most expedient to use an airborne magnetometer about 760 m

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[1] Personal communication from E. Mueller.

above the ground level. Therefore, if birds employ anomalies in the geomagnetic field as cues in navigation, generally the lower their flight the greater their ability to detect them. Over the oceans there are few anomalies in the geomagnetic field. Birds migrating over extensive oceanic areas would have recourse to only one reference in the geomagnetic field.

The many displacement experiments with Manx shearwaters, homing pigeons, starlings, and numerous species of waterfowl reveal their dependency upon celestial cues to depart the release areas. Because of the overwhelming evidence for the use of celestial cues, the use of geomagnetic force as a cue, if present, appears to be limited as to occasion and to number of species.

MIGRATION BEHAVIOR AS RELATED TO NAVIGATION

Among the several demonstrated and several potential cues available to birds for navigational purposes, the particular ones used by a given species are dependent upon the migration traits of the species. These traits are considered to be: (1) homing tenacity, (2) distance traveled, (3) diurnal-nocturnal periodicity of flight, (4) altitude of flight, (5) mode of flight, (6) feeding traits, and (7) social traits.

Homing Tenacity

The homing ability among most nesting sea birds studied is phenomenal. It is so well recognized that perhaps a few examples will suffice: The entire population of greater shearwaters, which roam to the far reaches of the Atlantic Ocean, nests on an island about 64 km in diameter in the Tristan da Cunha group (ref. 41). This small group of islands is isolated in the South Atlantic Ocean, some 1930 km west of Cape Hope, Africa, and a greater distance from South America.

The slender-billed shearwater returns from the northern reaches of the Pacific Ocean to nest on its specific island in Bass Strait between Australia and Tasmania. Indeed, Serventy (ref. 32, p. 180) reports that where there are several rookeries on an island ". . . no chick has settled on other than its own natal rookery." For 12 males, the average distance from natal burrow to first breeding burrow was 6.7 m; among 12 females the average distance was 7.6 m.

About 100 000 Laysan albatrosses nest on Midway Atoll and 130 000 on Laysan Island about 644 km to the east. Rice and Kenyon (ref. 49, pp. 532–533) reported that none of the thousands of albatrosses banded on Midway have been found on Laysan Island even though a diligent search was made there. Only a few of the black-footed albatrosses banded on Midway as chicks were found elsewhere; three were found nesting on Kure Atoll, 145 km to the northwest (pp. 533, 567).

Rice and Kenyon (ref. 49, p. 533) found that once they established a breeding territory, albatrosses returned to it season after season. Over half of all pairs nested within 1.3 meters of previous sites and none farther than 6.0 meters.

Austin (ref. 50) evaluated the homing of common terns to the several nest colonies on Cape Cod, Massachusetts. He concluded that young terns have a strong propensity to return to their natal colony; having once nested, most terns return year after year to sites previously used, site attachment increasing with age. Over half of the terns returning nested within 4.6 meters of their previous nest sites, the greatest distance was 19 meters.

Austin (ref. 51, p. 135) stated that most common terns migrate along the east coast of the United States as far as Cape Hatteras, North Carolina, where they continue south over the Atlantic Ocean to the Bahamas. From there they pass through the West Indies to winter from Trinidad southward along the east coast of South America as far south as Rio de Janeiro.

No study of homing in oceanic birds has shown anything other than unbelievable preciseness of return. Therefore, until contrary evidence is presented, it must be assumed that other species of oceanic birds have comparable aptitudes.

Homing records among land birds are not as plentiful as among oceanic birds because of the great number of species, the general dispersed distribution among breeding individuals, their extensive breeding ranges, the small size of most species, and the difficulty of trapping breeding birds. Nevertheless, a slow but ever-increasing amount of information is being obtained on the homing ability of land birds.

One of the early findings of homing among passerines resulted from Hann's study (ref. 52) of the ovenbird. In a three-year period he found that 11 of 21 banded adult males (52.4 percent) and 13 of 23 banded adult females (56.5 percent) returned to nest on his study area near Ann Arbor, Michigan (op. cit., p. 153). Only 1 of 68 (1.5 percent) banded young returned to nest on the area. Studies in bird mortality have demonstrated that from 40 to 60 percent of the adults in most species succumb within one year. Mortality in nestlings is much higher. Therefore, a return approaching the reciprocal of the mortality rate would indicate an almost complete return.

A few ovenbirds winter in extreme southern United States, but most winter in Central America and south to northern Colombia, northern Venezuela, and the Lesser Antilles. Therefore, they make a moderately extensive migration.

Kendeigh and Baldwin (ref. 53, p. 116) believed that their banding data showed that 92.5 percent of all living adult birds returned to the general locality where they previously nested, but only 11.5 of the banded nestlings still alive returned. From an analysis of bandings of house wrens, Kendeigh (ref. 54, pp. 16–18) concluded that the large number of returns of adults in years following banding represented practically all living banded individuals. Of the 278 returning adult males, 84 percent nested within 300 meters of previous nest sites; 70 percent of the 276 returning females nested within the same distance. However, returning yearling house wrens ranged over a broader area, for only 15 percent of 154 banded yearlings occurred within 300 meters of their birthplaces.

Several species of swallows show excellent homing. Mayhew (ref. 55, p. 29) banded 4376 adult cliff swallows at breeding colonies near Sacramento, California. He recaptured 1668 (38.1 percent) the following year at the same sites, plus 368 (8.4 percent) at nearby sites. He banded 1098 nestlings of which 104 (9.5 percent) were recaptured the following year at their natal site and 77 (7.0 percent) at nearby sites.

Low (ref. 56) reported that 31 percent of the adult tree swallows that he banded returned to their previous nest sites, but only 11 percent of the young did so. Chapman (ref. 57) found that 38 percent of the adult tree swallows returned to his colony; only 4 percent of the young returned. The bank swallow appears to have the lowest return rate among the swallows: 12 percent of the adults and 5 percent of the young were recaptured by Bergstrom (ref. 58).

The black-capped vireo breeds among the arroyos of central Oklahoma, where Graber (ref. 59) studied its life history. It winters on the Pacific slope of the Sierra Madre Mountains of Mexico. Of the 17 adult males banded, she recaptured 76.5 percent in subsequent years on the same study area. Female recaptures were somewhat lower: of 21 banded, 42.9 percent were recaptured. Mrs. Graber banded 30 young black-capped vireos, but none returned to her study area.

The Kirtland warbler has restricted breeding and winter ranges. Berger and Radabough (ref. 60, p. 184) reported on the banding of 161 adults and 296 young on its Michigan breeding grounds. The return rate in subsequent nesting seasons was: 52.9 percent of the adult males, 30.9 percent of the adult females, and only 2.7 percent of the young.

In a study made of piping plovers on Long Island, New York, Wilcox (ref. 61) banded 1173 adults and 969 young at their nest sites. I have recalculated his data (table 1 of ref. 61) to omit those years when the banding record was incomplete and to omit returns of 47 banded young that subsequently nested. Of the 893 adults initially trapped or carrying bands from previous years, 38.1 percent returned to nest the next year. This figure is minimal, because he estimated that 10 percent of the nests on the study area were not found and that he banded only 90.5 percent of the adults on the nests under observation.

Of the 47 young recaptured on nests, 34 returned to the area in which they hatched and 13 to areas 8 to 29 km away. Wilcox also trapped three young plovers banded elsewhere, which later nested on his area. One had moved 101 km east of its natal site, one 66 km east, and the third, 63 km east.

A large proportion of various species of waterfowl are known to return to their former nesting areas. Sowls (ref. 62, p. 37) found that the following adult ducks returned to the Delta Marsh area, Manitoba, to nest (by percent): mallard, 12; pintail, 39; gadwall, 37; shoveler, 42; and blue-winged teal, 14. Adjusting the return rate for mortality and for failure to trap some returning hens, Sowls concluded (ref. 62, p. 41) that most surviving adult hens returned to the marshes where they nested the previous year.

In central Illinois, Bellrose et al. (ref. 63, p. 665) captured 440 wood-duck hens on their nests, 1951–1962, of which 49.1 percent were found nesting in the same area the following year. Among 248 wood-duck hens banded as juveniles, only 6.5 percent were found nesting on their natal area the following year. Allowing for an annual mortality of 45 percent (adults) to 60 percent (juveniles) suggests that almost all surviving adult hens return to their previous nesting area as well as a moderate proportion of the surviving juvenile hens.

For many years Dexter (refs. 64 to 66) has been banding chimney swifts nesting in the same group of air shafts on campus buildings at Kent, Ohio. I interpret his reports as showing that all birds returning to these shafts had been banded by him as adults and/or nestlings in previous years.

From a banding study of mourning doves in central Missouri, Tomlinson *et al.* (ref. 67) concluded (p. 264) that ". . . most surviving adult doves return to the restricted area of the previous year's nesting." They found that only 13 of 411 doves banded as juveniles returned and concluded that homing occurs principally to first nest sites and rarely to natal sites.

In a study of homing of banded mourning doves to their nesting area near Madelia, Minnesota, Harris (ref. 68, p. 65) concluded: ". . . homing rates of approximately 100 percent for adult males and approximately 60 percent for adult females were obtained." He calculated that the return of nestlings was only about 2 percent.

Many species of adult land birds apparently exhibit an ability to home similar to that of oceanic birds. There is certainly a pronounced difference in homing between the young of sea birds and those of terrestrial birds. However, the low rate of homing among young of terrestrial species should not be construed as a lack of ability, but it should probably be interpreted in light of their last visitation point prior to their fall departure. Bandings of many species of birds show that fledglings wander at distances much greater than do their parents prior to fall migration. Experimental displacement studies suggest that young birds return to the points they visited in response to the maturation of imprinted celestial and landscape cues.

A number of years ago we shipped young wood ducks hand-reared near Havana, Illinois, until 6 to 8 weeks of age to areas 280 to 320 km away (ref. 31). They did not return to their rearing area, but to their displaced area. I concluded (*op. cit.*, p. 35) that: "Young wood-duck hens exhibited a strong homing response to the area they inhabited during late summer and early fall preceding migration."

We also displaced adult and juvenile mallards from central Illinois to Great Salt Lake Basin in Utah, midway in their fall migration (ref. 31). The following fall, most band recoveries of adults were in their native flyway whereas, most of those mallards released as juveniles were recovered farther west (*op. cit.*, p. 30).

In Germany, Löhrl (ref. 69) displaced young collared flycatchers raised by hand, releasing them 90 km to the south in an area not inhabited by the species. The following spring, 19 percent of the males returned to their area of displacement. A smaller proportion of females returned, but some were missed. In 1956 Löhrl made another displacement release of 44 collared flycatchers that were just past their postjuvenal molt. The following spring, four, perhaps five, males returned (18 percent, assuming an even sex ratio). These birds had only about 2 weeks to become acquainted with their surroundings prior to fall migration. A third group of 68 flycatchers released later during the migration season did not reappear in the area of their displacement or their area of rearing.

It is apparent from Löhrl's experiments that there was a period of only 2 weeks when the young collared flycatchers were imprinted with the cues enabling them to return in the subsequent spring. This two-week period occurred just prior to their fall departure.

On the wintering ground of the northern waterthrush in Venezuela, Schwartz (ref. 70) displaced adults and juveniles from 6–65 km. Of the 4 adult and 14 juveniles moved, only the adults returned and some of the juveniles were subsequently found in their areas of displacement. Schwartz concluded that orientation ability is learned at the time first-year birds start their spring migration. I would amend his conclusion to: First-year birds are imprinted with their wintering-area cues prior to spring migration.

What are the cues available to collared flycatchers, northern waterthrushes, and other passerines prior to their first fall and spring flights? There can be little doubt that landmarks provide the detailed cues within their temporary home ranges prior to migration. Beyond that, celestial cues apparently provide the basic means enabling birds to reach the vicinity of their home ranges.

Certainly, Emlen's experiment (ref. 71) with 10 hand-raised indigo buntings point to the imprinting of astral cues. Of the four young buntings that never saw the sky until the experiment, one showed a significant southerly orientation, one slight southerly, and the other two were random. The three buntings that saw the outdoor sky for a month during the postjuvenal molt, showed a notable improvement in selection of southerly directions. The response of Emlen's third group of buntings in his controlled laboratory experiment was remarkably similar to Löhrl's third experimental field release of collared flycatchers. Emlen held 3 buntings indoors until completion of the postjuvenal molt, when they were exposed to the sky throughout the migration season. Tests of orientation under the starry sky showed that only one bird consistently selected a southward direction; the other two birds showed no directional preference. It seems highly significant that collared flycatchers released by Löhrl after similar treatment failed to return. I believe that both groups had matured past the time of the effective imprinting of fall cues.

There is evidence that part of the low rate of return to natal areas by passerines and other terrestrial birds results from an imprinting of cues in a restricted period of maturation, prior to departure. The imprinting appears to be basically of a celestial nature, augmented by landscape. Therefore, the farther a bird migrates over featureless or obscured landscape, the more importance I attach to celestial cues in assessing navigational priorities.

Oceanic birds appear to have homing abilities superior to those of terrestrial birds. Based upon evidence at hand, I assume that the homing ability among different species of oceanic birds is similar, but that homing among different terrestrial species is on a comparable level.

Distance Traveled

The greater the distance that a bird travels in migration, the greater the feat of navigation. Further, on the basis of what we know today, navigation over the open sea out of sight of land is a greater feat than navigation over land.

Therefore, in ranking the evolutionary scale of development I have considered the distance flown over land and the distance flown over water. The distances flown in migration among species of birds were considered from the extreme northern boundaries of their wintering ranges. Banding data have indicated that individuals of a particular species that occur the farthest north in their breeding range are the individuals that winter the farthest south in their winter range.

Diurnal-Nocturnal Periodicity

Birds are basically diurnally oriented in their activity. Only a few species and proportionately fewer individuals are adapted for nocturnal feeding. Therefore, I consider that the more diurnal the migration activity, the more primitive are a species' navigational attributes. Conversely, the greater the nocturnal activity in migration (aside from the few nocturnal species) the greater are the navigational attributes of a species. Thus, I consider those species migrating predominately by day to be, as a group of species, more primitive in their navigational traits than those migrating, as a group of species, by both day and night. Similarly, I consider those species migrating almost exclusively at night, as a group of species, to be more advanced in navigational traits than those migrating about equally by day and by night.

There is, of course, a degree of overlap in the circadian activity of migration by all species. Some noted diurnal migrants, such as the purple martin, have been killed presumably at night at a TV tower (ref. 72, p. 60). All land birds crossing the Gulf of Mexico must often of necessity continue in diurnal flight until they reach land. George A. Hall has informed me[2] that several species of war-

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[2] Personal communication from G. A. Hall.

blers migrate during the early morning hours along the ridges of the Allegheny Mountains in West Virginia.

On the basis of the activity of migrants that I have observed for over 30 years, on the basis of a diligent search of the reported bird kills at TV towers and ceilometers, after searching other literature for observations on migration activity, and after numerous discussions with colleagues, especially Richard R. Graber, I have attempted to classify many species of migrants as to their periods of migration activity. The greatest difficulty in classifying the day-night period of migration has been with oceanic birds. My impression from reviewing available literature is that most long-distance migrants among oceanic birds are equally active by day and by night.

Altitude of Flight

The higher a bird flies in migration, the less contact it has with the Earth. The less contact a migrant has with the Earth, the less opportunity it generally has to use landscape features (and/or the anomalies in the Earth's magnetic field if this proves to be a source of directional information) as part of its navigational system.

As every aircraft pilot knows, the greater the groundspeed, the higher the altitude required to make best use of landmarks. Visibility is also important in determining the most advantageous altitude for recognizing landmarks. At night and in rain or mist, landmarks may be visible only at very low altitudes. The nature of the landmarks also determines the relationship between their visibility and the altitude of flight.

Diurnal migrants appear to fly lower than nocturnal ones. Starlings, crows, various species of blackbirds, along with swallows, redheaded woodpeckers, blue jays, cormorants, white pelicans, cranes, hawks, and certain waterfowl make up the bulk of the diurnal migrants in midwestern United States, the region with which I am most familiar. Most of the starlings, blackbirds, redheaded woodpeckers, blue jays, and many of the swallows migrate at heights of 15 to 45 m above the ground, well below the "umbrella" of most radar surveillance. Starlings and blackbirds make up a large proportion of the total terrestrial birdlife in the United States.

Crows, gulls, and cormorants migrate at higher altitudes, usually from 30 to 300 meters above ground level. White pelicans and hawks have been observed migrating at altitudes of 300 to 900 m. Snow geese, cranes, and whistling swans have been reported frequently by pilots up to 2400 m, rarely as high as 3600 m, and more commonly at altitudes of 600 to 1500 m.

The enumeration of small birds at night in the landing lights of a small aircraft showed that most were at altitudes between 100 and 1500 m above the ground. A comparison of small bird and waterfowl targets on the same radar scope at Havana, Illinois, indicated that ducks migrated at higher altitudes during the night than did small birds. Among waterfowl, nocturnally migrating snow geese appeared at the highest altitudes. As identified by their speed of flight and their midsummer migration, shorebirds appeared on radar at Havana at consistently higher altitudes during nocturnal hours than any other group of birds.

Unfortunately, because we do not know the species relationship to altitude of most nocturnal migrants, especially the passerines, it is possible to assign to a species only the most general rank in navigational attributes based upon altitude of flight.

Mode of Flight

The navigational attributes of certain

species of birds are regulated in part by their modes of flight. Soaring birds, such as Buteo hawks, vultures, and white storks utilize thermals extensively in their migratory flights. Because thermals occur only during the daytime, these species are restricted to diurnal migration. If they maintain their soaring mode of flight, there can be no evolution into mechanisms enabling nocturnal navigation. As a group, soaring birds do not migrate as far as do birds with other flight characteristics.

Weak-winged flyers, notably rails and ground-seeking sparrows, probably of adaptive necessity to survival, evolved into nocturnal migrants. Usually, birds migrating short distances are diurnal migrants, or, at most, diurnal-nocturnal migrants. However, even though most weak-winged flyers migrate short distances, they are, as far as known, exclusively nocturnal in their migration. Therefore, they have reached a degree of sophistication in their migrational attributes far beyond that required by the challenge of their range. They probably were day migrants for a relatively short period in the span of geological time.

Feeding Habits

Birds feeding on the wing are regulated both in altitude and in daily period of migration activity by their sources of food. All species of swallows, and most species of oceanic birds, feed as they migrate. Thus, their routes of migration are in many instances at least partially determined by the sources of their food supply.

Long-distance oceanic migrants, such as the Arctic tern, greater shearwater, and Wilson's petrel appear to migrate where the upwelling of oceanic currents creates an abundance of food. It is well known that many creatures of the ocean move toward the surface at night. Consequently, most petrels and shearwaters, as well as some other oceanic birds, have adapted their feeding activity to nocturnal hours in order to exploit the greater availability of food (see Murphy, ref. 73, for detailed accounts).

Although swallows, particularly the barn and cliff, are some of the top long-distance migrants in the world, there is no adaptive advantage to their evolving into nocturnal migrants. Therefore, they remain, as they started, diurnal migrants.

I can find no information pointing to an oceanic bird as being an almost exclusively nocturnal migrant. Most petrels and shearwaters return to their nest burrows after dark, but over the ocean they are active by both day and night. Therefore, I assume that these birds navigate by both solar and astral cues on their extensive migrations. Winds must surely play an important role in their navigational scheme when overcast skies prevent the use of celestial cues.

Writing of the trans-Atlantic flight of the Arctic tern that he witnessed, Wynne-Edwards (ref. 41, pp. 328, 329) stated that

> there is not a vestige of a landmark of any description for two thousand miles, where the wind sometimes changes direction in a few hours and the sky is often completely overcast for days at a time . . . their sense of direction must be absolute, like that of a compass. . . .

He also reported (*op. cit.*, p. 326),

> In clear weather they fly between one and five hundred feet from the surface, but when beating to windward they often keep close to the wave crests.

On overcast days, how would these terns know windward from leeward? I believe that by keeping a reference between the angle of the wind and the waves, oceanic birds are able to maintain a particular course. Depending upon the magnitude of the waves and a shifting wind, there is a considerable time lag. Hence, waves will continue in a set direction for some time before the wind gradually forces a change in the direction of their roll.

Landscape must surely play a limited role among the far-ranging pelagic birds that seldom see land except during their breeding season. Therefore, I place wind next to celestial cues in importance for navigation by these birds. Put simply, the more a bird is at sea, the less important is the role of landscape in its navigational system.

Social Traits

Birds that migrate singly rather than in flocks have evolved farther up the scale in sophistication of navigational traits. The single migrant does not have the reinforcement provided by the combined abilities of members of a flock (ref. 74), and, therefore, needs more refined abilities.

Some flocks, as in certain shorebirds, may be made up entirely of juveniles that migrate without the aid of adults. However, most birds migrate in flocks, composed of both juveniles and adults, in which case the juveniles appear to have recourse to the experience of older birds (ref. 75).

The advantage of adult leadership in navigation is especially evident in waterfowl. Because of adult guides, waterfowl not only return to the same breeding and wintering areas but also to the same migration areas (ref. 75). Among the several species of geese in North America, flocks are composed of family units that follow the same routes in migration as in previous years. Ducks do not travel as family units, but juveniles usually accompany adults from staging areas on the breeding grounds. The adults return to the same marshes that they visited the year previously, and so juveniles are indoctrinated in the sequence of water areas used by the adults they accompany.

In a system of point-to-point navigation, as shown by some species of waterfowl, landscape becomes more important than among migrants that are more flexible in locating their migration stops.

The fact that long-distance migrating Buteos (broad-wings and Swainson's) travel in large flocks while short-distance migrating Buteos (red-tailed, red-shouldered) travel singly or in dispersed malformed groups appears significant. By traveling in flocks, veteran birds are able to lead the way for young-of-the-year. As with other birds landscape is more likely to be important among species of hawks in which juveniles accompany adults.

The white stork is a soaring bird that travels in huge flocks for long distances, many from Central Europe to Central Africa. Schuz (ref. 9, p. 479) pointed out that in certain areas, storks radically change their direction of migration. I believe that landscape is the basis for the changes in direction noted one or more times in the course of their migrations.

Schuz's displacement (ref. 8) of young white storks in Germany points up the influence of old birds on the migration patterns of juveniles. I attribute the directional change in the migration of displaced East German storks to the influence of the adult storks in West Germany. When adults were available for guidance, the young East German storks became a part of the flocks of West German storks migrating southwestward. Young storks released later in the season, after the departure of the native storks, adhered to their innate southeasterly direction of migration.

Other traits being equal in the hierarchy of navigational sophistication, I place individual migrants, such as the flycatchers and yellow-billed and black-billed cuckoos, ahead of flock-supported individuals. I rate flocks containing adults and juveniles ahead of flocks containing only juveniles. Flocks of several species of shorebirds are at times composed either of young or of adult birds. Most birds migrating in flocks contain both old and young birds.

HYPOTHESIS OF DEVELOPMENT

The foundation for exploring the various lines of navigational development in bird migration has been established in previous discussion: The navigational cues now known to be available to migrating birds have been appraised; the behavioral traits that affect the use of the several navigational cues have been evaluated.

Logically, bird navigational behavior has evolved from the primitive to the sophisticated. Most ornithologists agree with the concept that birds were nonmigratory before they evolved migratory habits. Today, in almost every order of birds, there are examples of nonmigratory birds, birds that migrate short distances, and those which make extensive journeys. There is not necessarily a relationship between phylogenetic evolution and the evolution of migration behavior. The loons and grebes are near the bottom of phylogenetic classification in birds, yet I believe they display sophisticated navigational behavior far in advance of that displayed by many of their more morphologically advanced members.

In order to establish an evolutionary hierarchy in navigation, it is imperative to understand the structure of navigation among nonmigratory birds. Unfortunately, few experiments of any kind have been made exploring the orientation mechanisms of permanent-resident birds. Permanent-resident birds displaced short distances show a low rate of return to their homes (summarized by Mathews, ref. 76, p. 22). Thus, house and European tree sparrows have given only 10 percent returns, and, at that, no farther than 9 miles (ref. 77).

Apropos to the navigational abilities of permanent residents versus migratory birds is a series of displacement experiments by Sumner and Cobb (ref. 78, pp. 317–319). They simultaneously released migratory and resident birds in several displacements of from 5.95 to 54.7 km from Claremont, California. A much higher return occurred among the migratory than among the resident species; all of the resident species either failed to return or only a small proportion did so.

Permanent-resident birds appear to move about their home ranges under adverse weather conditions. Even during snow showers, woodpeckers, titmice, nuthatches, and similar species search for food, indicating familiarity with their surroundings despite poor visibility. There can be little doubt that under such conditions birds employ knowledge of the landscape to fly from point to point. The failure of permanent residents to return home when displaced even short distances outside their home ranges points to their reliance on landmarks for local orientation.

I do not know of any studies evaluating the Sun compass among resident birds. The homing pigeon derives its ancestry from the sedentary rock pigeon, but man has artificially selected this species for homing capability to the extent that it differs genetically from its sedentary ancestors. Therefore, experiments demonstrating the Sun compass in the homing pigeon do not necessarily infer its presence in the sedentary form. The Sun compass appears so strongly genetically fixed among migrant birds I anticipate that some form will be found among nonmigratory species. The diverse directional flights taken by irruptive species (such as crossbills, Bohemian waxwing, and snowy owl) over unfamiliar landscape indicate the probability of at least a rudimentary form of Sun compass among most nonmigrants.

Because soaring birds are so unique in their mode of flight and because oceanic birds are unique in the habitat they occupy, I place them in separate categories (fig. 1) from other birds.

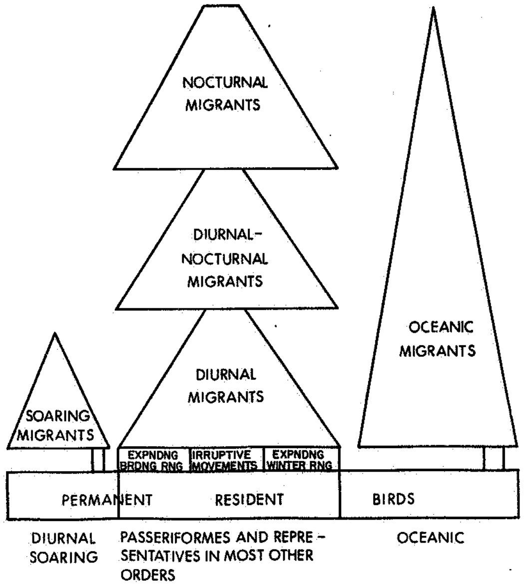

FIGURE 1. Model projecting possible evolutionary development of navigational mechanisms among soaring birds, oceanic birds, and passerines and allied species.

Migration in passerines and in the vast majority of other birds is postulated to have arisen from permanent-resident populations of birds that were in the process of expanding their breeding or their winter ranges, or were irruptive in their seasonal movements.

Partial migration probably represents the first step in the development of migratory behavior. Birds considered to be partial migrants are those in which a large proportion of the individuals are permanent residents and other individuals are migrants.

Even individuals among partial migrants may change their migratory state. Laskey (ref. 79) reported that a blue jay banded as a nestling migrated the first winter, remained the second winter, and migrated the third winter. Nunneley (ref. 80) concluded from a study of banded blue jays that some were permanent residents, some were transients, and others either summer or winter residents. She also noticed that some jays altered their migratory status between years.

Nice (ref. 81, p. 33) found that most of her marked song sparrows in central Ohio were either migratory or sedentary; a few individuals altered their migratory status in different years.

A list of the species of birds in eastern United States that best typify partial migration is given in table 1. The bulk of the partially migratory species are active in migration during the daytime. There are probably 10 times as many nocturnal species as diurnal migrants, so the proportion of partial migrants that are diurnally oriented becomes of even greater significance. The preponderance of partial migrants that move diurnally points to the first step in the development of navigational sophistication resulting from permanent residents extending their diurnal activities.

Diurnal-Nocturnal

As diurnal migrants extended their migratory ranges, certain species adapted their migration activity to both day and night to provide more time for feeding and/or to avoid losses from accipitrine predators. In regard to food supply, it appears significant that the only diurnal species with long migrations either feed on the wing (swallows) or are large birds (cranes).

An extension of diurnal migratory activity into partial nocturnal activity resulted in a further development of navigational sophistication. In order for birds to utilize nocturnal hours for migration it was essential for diurnally active species to adapt their navigational system to include nocturnal cues. And yet, by also migrating extensively during the day, diurnal-nocturnal migrants had cues (such as landscape, and the Sun) to correct for nighttime deviations from their selected courses.

Nocturnal

I believe that nocturnal migration behavior evolved from previous diurnal-nocturnal migration behavior. There is no well-defined line between diurnal-nocturnal and nocturnal migrants. Probably all nocturnal migrants continue in flight at some time during the early hours of daylight. Thus, the classification of migrants as nocturnal becomes one of degree. Perhaps a requirement for classification as a nocturnal migrant is that birds begin migration after sunset, whereas diurnal-nocturnal migrants begin migration either during the day or after sunset, depending upon the weather.

The adaptation of diurnal birds to nocturnal migration required a great evolution in navigational sophistication. Therefore, at present we are probably witnessing many stages in the development of navigational systems used by nocturnal migrants. Nocturnal migrants use cues available to diurnal migrants, in addition to the extensive use of more complex cues. It is important to recognize that, except for birds feeding on the wing, the passerine birds that migrate the farthest are all nocturnal migrants. Most intercontinental migrants in the western hemisphere are nocturnal in their migration within the United States.

TABLE 1.—*Species of Birds Considered to be Partial Migrants, Excluding Soaring and Oceanic Birds, in Eastern United States*

Diurnal migrants	Diurnal-nocturnal migrants	Nocturnal migrants
Common eider	Great blue heron	Wood duck
Willow ptarmigan	Killdeer	Red-breasted nuthatch
Redheaded woodpecker	Mourning dove	Bewick's wren
Horned lark	Flicker	Rufous-sided towhee
Blue jay	Mockingbird	Field sparrow
Gray jay	Robin	Song sparrow
Common crow	Cedar waxwing	
Black-capped chickadee	Eastern meadowlark	
Eastern bluebird		
Loggerhead shrike		
Starling		
Red-winged blackbird		
Brewer's blackbird		
Common grackle		
Brown-headed cowbird		
American goldfinch		

Soaring Migrants

Because their unusual mode of flight greatly influences their migration behavior, soaring migrants have evolved a navigational system distinctive from those of other groups. They are influenced in their routes of travel by bubbles of thermals and updrafts. The importance of continuity in the rising columns of air used by soaring birds results in their avoidance of expanses of open water. When groups of Buteos encounter the Great

Lakes in fall migration, they turn to the west (ref. 82, p. 84).[3]

After observing thousands of migrating hawks, particularly broadwings, at Duluth, Minnesota, Hofslund[4] believes that if specific points in the landscape are not used by hawks in piloting, then certainly they use the broad features of the landscape. Broad features of landscape are construed as directional axes of ridges, the breaks between woods and prairie and between woods and lakes, large river valleys, and similar features.

Mueller and Berger (ref. 83, p. 39) concluded from a band-recovery analysis and from field observations of migrating hawks that: "The system of navigation hawks use is crude and results in longitudinal and latitudinal displacements of considerable magnitude." They point out that on many days during the spring about 40 percent of the migrating hawks they observed were southbound in reverse migration.

However, their study embraced species of hawks that migrate comparatively short distances and did not include such long distance migrants as turkey vultures and broad-winged and Swainson's hawks. Extensive flights of Swainson's hawks have been recorded across the southern Great Plains. At Hutchinson, Kansas, Cruickshank (ref. 84) counted 3400 in 1½ hours, moving due south, and remarked about the generally featureless landscape. In south Texas, Fox (ref. 85) saw 25 000 cross a 0.4-km (¼-mile) line, and estimated that perhaps several hundred thousand Swainson's hawks passed directly south in a well-defined channel about 6.4 km wide on October 6, 1953. He commented on the gently rolling prairie landscape and on the flight crossing the rivers at an angle.

Large flocks of broad-winged hawks have been noted migrating through Panama in early October (ref. 86). Near Veracruz, Mexico, Bussjaeger, et al. (ref. 87) found a large northward migration of turkey vultures on March 27, 1966. One flock was 5 km long and contained several thousand members. They were restricted to the coastal lowlands.

The Nile River appears to form an important route for migrating white storks. Accounts by Mathiasson (ref. 4) and Reed and Lovejoy (ref. 88) point to the importance of the Nile landscape. Migrating storks follow the Nile Valley closely until they reach the lengthy Dongola bend, where they cut overland to reach the river again (ref. 88, p. 49).

Mueller and Berger (ref. 89, p. 55) suggested that birds utilizing updrafts in flight are especially subject to wind drift. Hofslund's (ref. 82, p. 85) observations have shown that hawks in migration quarter into the wind, shifting their position with the slightest change in wind direction. However, he did not rule out thermal drifting, and postulated that drifting of thermal bubbles on westerly winds might displace hawks eastward from their standard southwestern direction of flight, thereby concentrating them along the north shore of Lake Superior.

Mueller and Berger (ref. 90, pp. 184–185) observed reverse migration of hawks in the fall on only two occasions. Both days were overcast. Apparently a warm front with its initial southerly winds resulted in most of the hawks moving northward, a reverse direction. They observed reverse flights among hawks more frequently in the spring, often when the skies were clear (ref. 83, pp. 35–37). They believed that these birds were reorienting, possibly to their nesting areas. From Mueller and Berger's fall observations (ref. 90) it seems probable that migrating hawks in spring are carried astray by wind when days are overcast and reorient toward

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[3] Personal communication from P. B. Hofslund.

[4] Also personal communication from P. B. Hofslund.

their home areas when the Sun becomes visible.

Thus, it appears that soaring birds use the Sun, the landscape, and the wind in navigation. We postulate that as distance of migration increases, the use of the Sun and the wind for orientation increases and the use of the landscape decreases.

Oceanic Migrants

Oceanic birds appear to have the greatest homing ability among all birds. As an ecological entity, they appear to have a larger proportion of long-distance migrants than do terrestrial groups. The navigational ability of oceanic birds appears on a higher evolutionary scale than that of other birds because oceanic birds make little use of landscape features. I postulate that landscape is the most fundamental cue used in bird navigation with other sources of directional information being more advanced.

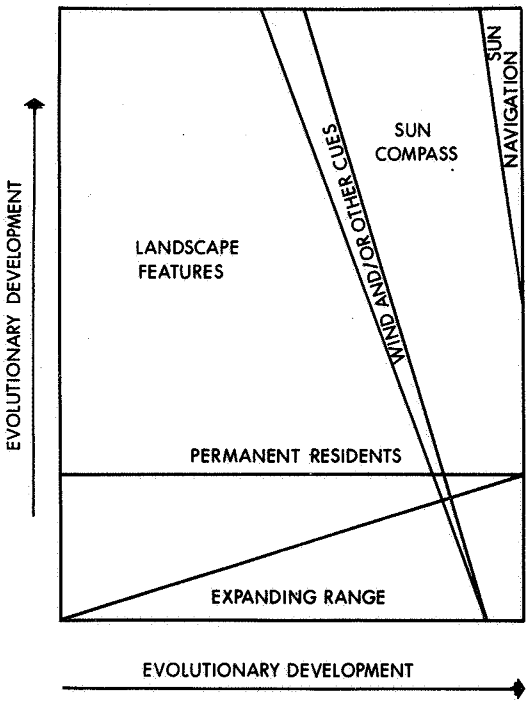

FIGURE 2. Postulated schematic diagram of gradual change in comparative use of navigational cues by diurnal migrants. As birds progressed from permanent-resident status to that of increasingly long-distance migrants, navigational sophistication became adaptive to their needs.

The problem among oceanic birds is to differentiate between diurnal, diurnal-nocturnal, and nocturnal development of navigational cues. It is apparent from the activity patterns at sea that there is an advanced state of nocturnal navigation present in certain petrels and shearwaters. Although they also may be active in the daytime, I believe that their star compass must be on a level equal to, if not greater than, that of the most advanced nocturnal migrants among terrestrial birds.

EVOLUTIONARY DEVELOPMENT OF CUES

Diurnal Migration

Figure 2 shows a model of my concept of evolutionary development among terrestrial birds with diurnal migration activity. From permanent residents, depending almost exclusively on landscape feature, the first partial migrants that evolved also utilized landscape features, perhaps with an assist from their Sun compass.

In figure 3 I have attempted to give examples of increasing sophistication in navigational ability among birds with diurnal migration traits. My criterion for greater sophistication of navigational ability among diurnal migrants is based largely upon the increasing distance flown in migration. The migrational behavior of several species are examined to illustrate the possible development in navigational sophistication.

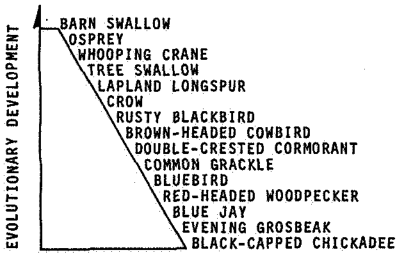

FIGURE 3. Diurnally migrating species of migrants are arranged to represent examples of increased sophistication in navigational attributes. Of those listed, the black-capped chickadee is considered the most primitive migrant and the barn swallow the most advanced migrant.

The black-capped chickadee is a permanent resident bird that probably only recently developed partial migratory behavior. An excellent review of chickadee migration is given by Bagg (ref. 91), which indicates an alternate-year intensity in the abundance of migrants. Over 30 000 black-capped chickadees have been reported in the fall, in each of 2 years, flying along the shore of Lake Ontario (op. cit., p. 12). Their response to water barriers is to fly along shorelines to where short water crossings or land bridges enable them to migrate in their preferred direction. When attempting a water crossing, they fly into the wind; observers interpret this heading into the wind as a downwind option to return if the crossing attempt fails. Thus the chickadee shows an awareness of the wind in relation to the landscape.

Figure 4 shows some band recoveries for the black-capped chickadee. The recoveries are both north and south from points of banding and at distances of 160 to 800 km. This is evidence that a bird once considered a permanent resident has developed a partial migration.

The blue jay, too, was once considered a permanent resident. However, in the last three decades numerous notes and articles have appeared about their migratory habits from Nashville, Tennessee (ref. 79), on the south, to Quebec on the north (ref. 92).

Blue jays migrate more extensively and farther than the black-capped chickadees. Band recoveries from the files of the Patuxent Banding Laboratory reveal that a number of blue jays have migrated 1600 km or more and many have migrated over 800 km.

We have traced one blue jay flight path through central Illinois for almost 160 km (fig. 5). Blue jays have been known to follow this flight path which in places is no more than 90 m wide for at least 6 years. It doglegs around the cities of Havana, Peoria, and Pekin. In this stretch of its migration, the movement is from tall-tree top to tall-tree top and from woodlot to woodlot. The migration period extends over 2 months both in fall and spring. Although several thousand jays follow this path in the spring, fewer use it in the fall. There appear to be many more routes used in the fall.

The important point as regards naviga-

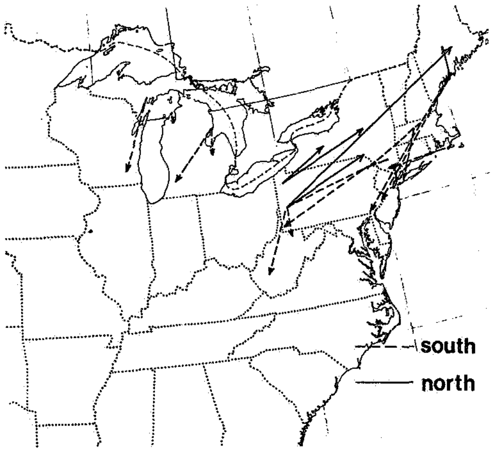

FIGURE 4. Band recoveries of black-capped chickadees in eastern United States as reported by Bagg (ref. 91).

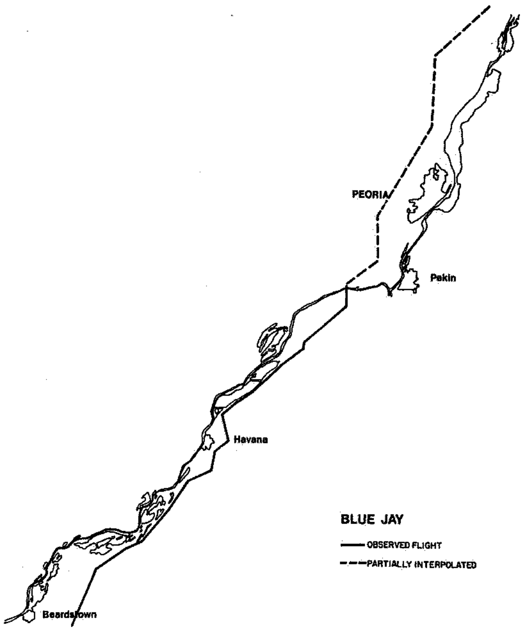

FIGURE 5. A heavily used spring migration route of the blue jay through central Illinois.

tion is that whether the day is overcast or clear makes little difference in the volume of migration. This fact was also noticed by Broun (ref. 93) at Hawk Mountain, Pennsylvania.

We have noticed, as has Schorger (ref. 94), that the velocity and direction of the wind greatly influence the magnitude of migration. Schorger noticed that migrating jays adjusted their heading in keeping with the direction of the wind in order to maintain the same track across Lake Mendota.

Our field observations on migrating blue jays appear to justify these conclusions: The blue jay is advanced in navigational development over the black-capped chickadee. The blue jay relies heavily on landmarks to follow the same narrow course year after year. The Sun compass is probably needed only to roughly determine north and south and is probably not well developed. The blue jay recognizes wind direction and velocity, and is aware of their value in crossing wide expanses of water.

I ranked redheaded woodpeckers higher in navigational development than blue jays because these woodpeckers usually migrate singly rather than in flocks. They, too, follow narrow flight paths at low heights. The same flight paths have been used year after year by adults. The young-of-the-year appear to observe the flight course taken by adults, and their Sun compass may be sufficiently developed for them to adhere to a standard direction.

All the blackbirds and the starling have similar migration behavior and often migrate together. The principal difference between these species in their rank of navigational development is their relative distance of migration. We have observed blackbirds migrating in a standard direction over 48 km under overcast skies at altitudes of 7.6 to 15 meters (25 to 50 ft), so low that landmarks would seem to have minimal value. I believe that under these circumstances a combination of landscape and wind direction was used to maintain the same flight direction.

As shown by Kramer's (ref. 95) orientation experiments with starlings, this species has a well-developed Sun compass. It is likewise apparent, from their extensive migration under overcast skies, that they do not always need it.

The common crow is placed higher in the hierarchy of navigational development than the blackbird because it migrates at higher altitudes and in smaller groups.

Whooping cranes migrate in family groups along a narrow well-defined corridor for 3620 km. They migrate at unusually high altitudes. For these reasons I have placed them near the pinnacle of diurnal navigational achievement.

Ospreys migrate singly, and some migrate

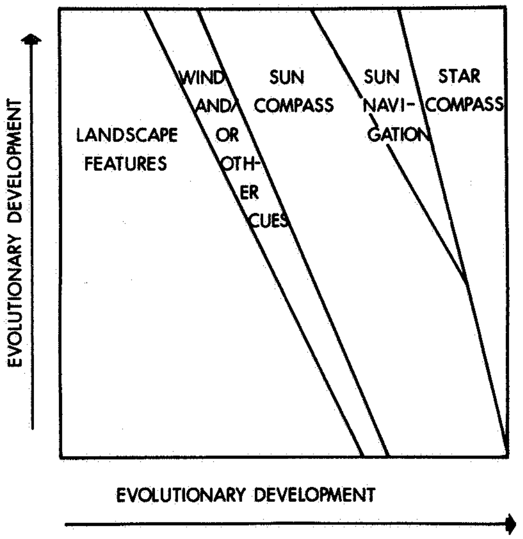

FIGURE 6. A postulated schematic diagram of gradual change in comparative use of navigational cues among diurnal-nocturnal migrants as evolutionary development progressed.

as far south as central South America. The fact that young ospreys apparently make extended migration flights without the guidance of adults suggests their probable ability to conduct true Sun navigation.

The barn swallow makes the longest diurnal flight of any terrestrial bird, from northern Alaska to southern Argentina. Many travel in flocks but some migrate singly. Experimental displacement of barn swallows in Europe (ref. 76, pp 26–27) showed reasonably good homing from long distances. Such homing over unfamiliar landscape suggests that they are able to use the Sun for bicoordinate navigation. On the basis of this cursory evidence, I have ranked the barn swallow at the peak of navigational sophistication among diurnal migrants.

Diurnal-Nocturnal Migration

As a group, diurnal-nocturnal migrants travel farther than diurnal migrants. Landscape features play an important role in the early stages of navigational evolution, but become less important in the advanced stages (fig. 6). The Sun compass is probably present in a good state of development in species that are above the migrational level of the mockingbird. The ability to use the Sun for navigational purposes probably has evolved about midway along the line of developing sophistication. Because of their ability to migrate by night, this behavioral group has a star compass that becomes of increasingly important as the distance of migration increases.

My concept that species of diurnal-nocturnal migrants represent a progressive development in sophistication of cues used in navigation is shown in figure 7. The mockingbird is only a slight partial migrant and until recently was considered a permanent resident. Banding, visual observations, and TV tower kills (ref. 72, p. 61) attest to a part of its population being migratory. Richard Graber and I have seen it migrating diurnally in Illinois, and the 26 killed at a TV tower near Tallahassee, Florida (op. cit.) point to nocturnal migrations.

As the flight distances increase, I postu-

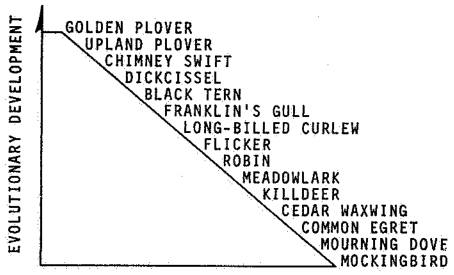

FIGURE 7. Diurnal-nocturnal migrants arranged to represent examples of increased sophistication in navigational attributes. Among those listed, the mockingbird is considered the most primitive migrant and the golden plover the most advanced migrant.

late increasing demands in navigational ability and increasing nocturnal activity. Because of a lack of knowledge, I have probably positioned some species improperly. For example, perhaps the Franklin's gull and the chimney swift are only diurnal migrants. I placed the Franklin's gull as a nocturnal-diurnal migrant on the basis of migrants observed still flying south at dark across the farm country of Nebraska. The chimney swift was classed as a partial nocturnal migrant on the basis of 19 killed at night at a TV tower in Florida.

Nocturnal Migration

Among species of birds that are almost exclusively nocturnal migrants, landscape features are of minimal value (fig. 8). Radar studies suggest that landscape plays a part in their navigational systems largely at the times of departure and arrival. During the night there are only a few records of birds altering their courses because of landscape.

A Sun compass is present but the ability to use the Sun for true bicoordinate navigation is postulated as providing the basis for any course alteration resulting from nighttime displacement. Because of their nocturnal activity, a star compass is well developed and becomes increasingly so as distance of migration increases. It is conceivable that in species with the most advanced forms of nocturnal navigation, we may find evidence of the use of stars for bicoordinate navigation.

Radar studies suggest that nocturnal migrants recognize wind patterns, which they utilize in their navigational system when other more obvious cues are unavailable. Without landscape, the characteristics of winds would be more difficult to sense at night than during the day. Accordingly, I have placed more emphasis on this source as a cue among nocturnal migrants than among diurnal migrants.

Figure 9 shows possible examples of nocturnal migrants at various stages in the development of a sophisticated navigational system. The red-breasted nuthatch appears to be the nocturnal counterpart of the diurnal

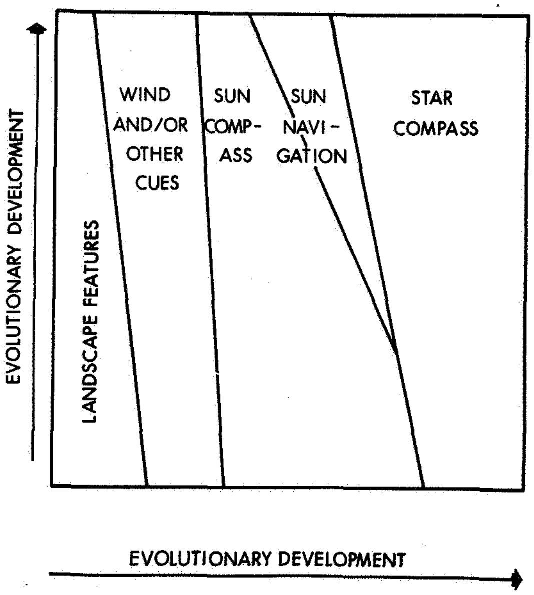

FIGURE 8. Postulated schematic diagram of gradual change in comparative use of navigational cues among nocturnal migrants as evolutionary development progressed.

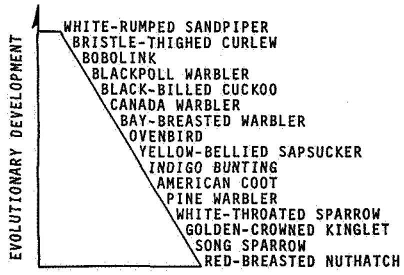

FIGURE 9. Nocturnal migrants arranged to represent examples of increased sophistication in navigational attributes. Of those listed, the redbreasted nuthatch is considered the most primitive migrant and the whiterumped sandpiper the most advanced migrant.

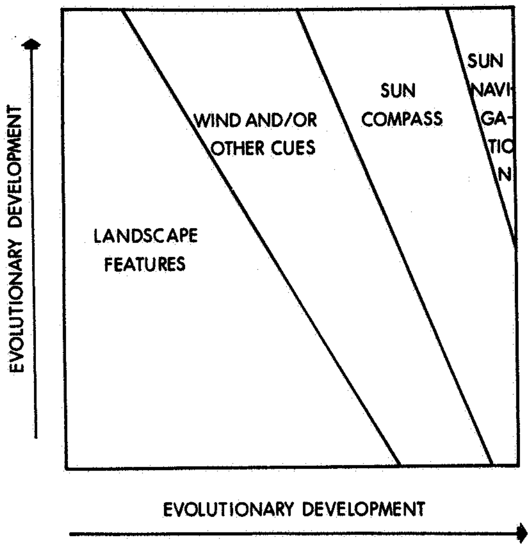

FIGURE 10. Postulated schematic diagram of gradual change in comparative use of navigational cues among migrants with soaring flight as evolutionary development progressed.

black-capped chickadee. It migrates somewhat irregularly but over longer distances than the chickadee.

Song sparrows are partially migratory in the southern part of their breeding range, but almost completely migratory in the northern part of their range, which extends to the Yukon and Alaska. From the level of the song sparrow through the level of the coot, increasingly smaller segments of their populations are partially migratory. There are increasingly greater distances between the breeding and wintering ranges from the indigo bunting to one of the champions of long-distance migrants, the white-rumped sandpiper.

The black-billed cuckoo deserves a high rank in the navigational hierarchy not only because of the long distance it migrates but also because it appears to migrate singly. Perhaps I have erred in classifying bobolinks, bristle-thighed curlews, and white-rumped sandpipers as nocturnal migrants. Bobolinks are known to migrate by day, but they apperar to be largely nocturnal migrants, judging from their nocturnal calls and the kills at TV towers. Little is known about the activity patterns of the two uncommon shorebirds (bristle-thighed curlew and white-rumped sandpiper), but based upon observations of other long-distance migrating shorebirds, I assume that they are nocturnal migrants except over a hostile environment, such as the ocean.

Soaring Migration

As previously discussed, migrants that depend upon soaring are more the captives of wind conditions and diurnal activity than are birds with other flight modes. Therefore, the wind, the landscape, and the Sun compass probably play important roles in their navigation (fig. 10).

Some species of soaring hawks are permanent residents in extreme southern United States and throughout Mexico. The black vulture and red-shouldered hawk are largely permanent residents, but part of their populations are migratory (fig. 11). The ferruginous hawk has both a sizable permanent and a migratory population.

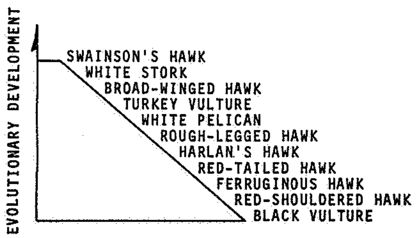

FIGURE 11. Migrants with soaring flight arranged to represent examples of increased sophistication in navigational attributes. Among those listed, the black vulture is considered the most primitive migrant and the Swainson's hawk the most advanced migrant.

Soaring birds that do not migrate far, such as the black vulture and the red-shouldered hawk, probably depend upon landscape more than any other environmental cue (fig. 11). As distance of migration increases, it is postulated that landscape became of lessening value and the Sun and wind of increasing value for navigational purposes.

The breeding grounds of the Harlan's hawk are well separated from its wintering grounds, and it appears to migrate along a rather restricted corridor. Swainson's hawks make an astonishing long-distance migration, some from as far as Alaska to southern South America.

I believe that certain long-distance migrants may be able to use the Sun for bicoordinate navigation, but this is only speculation until some experiments can be conducted to evaluate this point.

Oceanic Migration

Migration by oceanic birds may be classified as inshore, offshore, and pelagic. The closer a migrant adheres to the shore, the greater its potential use of landscape for orientation (figs. 12 and 13). The more pelagic the species and the greater the distance of migration, the less importance landscape features would assume in its navigational system.

Because of the tremendous distances flown by a number of pelagic species, almost entirely out of sight of land, their ability to use the Sun for bicoordinate navigation must be unequalled in the avian world. The great awareness of wind possessed by oceanic birds implies that it would serve as an increasingly important navigational aid as distance from shore and distance of flight increase.

Most petrels and shearwaters feed at night, indicating their ability to use the stars for at least directional guidance if not for bicoordinate navigation. I suspect that if any oceanic birds can perform astral bicoordinate navigation, they are the Wilson's petrel and the greater and slender-billed shearwaters.

Many oceanic birds are nonmigratory. In tropical regions the brown booby, blue-footed booby, and noddy terns are good examples.

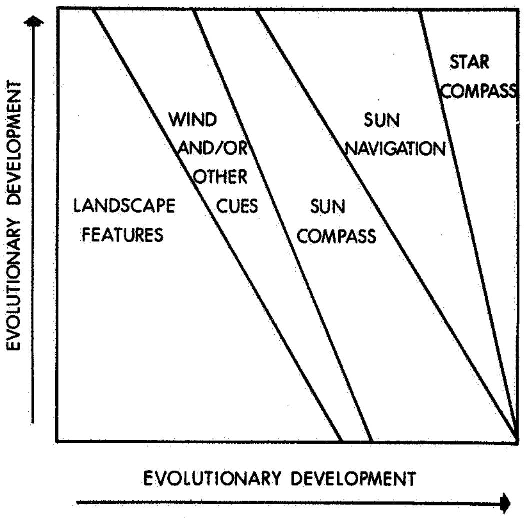

FIGURE 12. **Postulated schematic diagram of the gradual change in comparative use of navigational cues among oceanic migrants as evolutionary development progressed.**

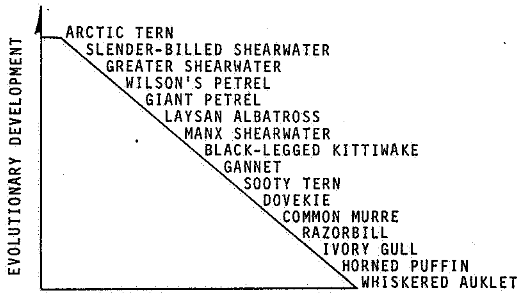

FIGURE 13. **Oceanic migrants arranged to represent examples of increased sophistication in navigational attributes. Among those listed, the whiskered auklet is considered the most primitive migrant and the Arctic tern the most advanced migrant.**

According to Orr (ref. 96, p. 141), not all shearwaters are migratory. Those breeding in tropical areas do not leave the general vicinity of their nesting islands. Unlike the Manx shearwater in the Atlantic, the Pacific coastal population spreads out only a few hundred km from breeding areas.

Many of the puffins and auklets nesting in Arctic regions migrate not at all or only short distances. From species such as these with very little demand on navigational mechanisms, oceanic birds migrate farther and farther until they have reached the opposite ends of the world. Examples of the increasing migration range among oceanic birds are given in figure 13.

As the distances of migration have increased among oceanic birds, I believe that there has been a comparable development in navigational sophistication, as shown in figure 12.

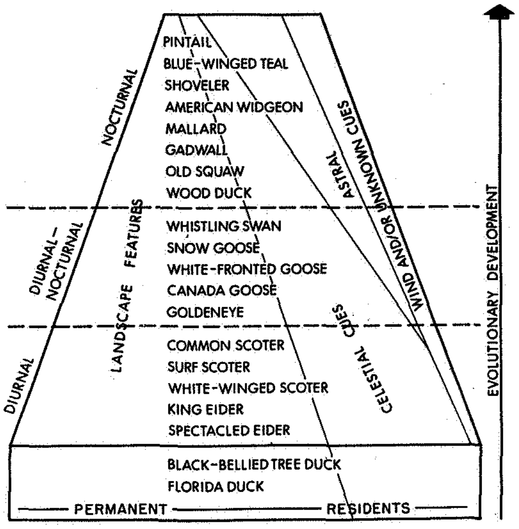

FIGURE 14. Steps in evolutionary development of navigational sophistication as postulated for one family of birds, the Anatidae.

The Evolution of Navigation in the Anatidae

I have selected one family of birds, the Anatidae, to illustrate possible steps in the evolution of navigational development, independent of morphological development. Figure 14 shows the relationships of various species of waterfowl to navigational cues.

Nonmigratory waterfowl are exemplified by the mottled duck and the Florida duck. Because they move only short distances, they probably depend largely on landscape features, assisted by a Sun compass, for basic directions. The spectacled and king eiders are diurnal migrants with short migration routes. The tremendous passage of king and common eider along the Alaskan coast near Point Barrow has been reported by Thompson and Person (ref. 97).

Common and surf scoters migrate diurnally considerably greater distances than do the eiders. In all likelihood, these sea ducks require only landscape features and a Sun compass to meet their navigational needs.

The common goldeneye illustrates the next step in navigational development, because it migrates partly by night as well as by day. Migration at night requires that the goldeneye be able to use certain star patterns for directional information. The Canada goose migrates almost equally by day or night, and generally migrates farther than the goldeneye. White-fronted and snow geese migrate farther and higher than do most Canada geese, and appear to be more nocturnal in their migration activities. Therefore, they are classified as more advanced than the Canada goose in their navigational sophistication.

Some whistling swans migrate from the Yukon–Kuskokwim Delta in Alaska to Chesapeake Bay, Maryland. On this long migration in the fall, they make few stops, migrating by both day and night. At certain points in their migration, they make significant changes in direction of flight. Most, if not all of these turns occur where there is a prominent landmark in the form of a body of water. Thus, landscape features are important as turning points in standard directions. Their migration during nocturnal hours implies the presence of an astral compass, and, when the stars are invisible because of clouds, an ability to use the wind.

Most non-sea ducks are more nocturnal in their migration habits than they are diurnal. However, at times species migrating in late fall, such as the mallard, are induced by severe weather to initiate migration during the day. They migrate under overcast skies, which suggests that the wind is a cue used to maintain a particular line of flight.

The wood duck makes especially short flights, the mallard somewhat longer, with the widgeon, shoveler, blue-winged teal, and pintails making increasingly longer migrations. Blue-winged teal frequently cross the Gulf of Mexico, and, perhaps, the Caribbean Sea to reach winter grounds in Venezuela and Colombia. Some pintails fly from Alaska to the Hawaiian Islands.

It may be significant that in conducting orientation experiments under overcast skies, we have found that the blue-winged teal, a long-distance migrant, and the mallard, a comparatively short-distance migrant, respond differently to the wind. The mallard flight is random regardless of wind direction, but the blue-winged teal quarters either upwind or downwind so that all individuals released separately in an experiment show similar flight directions. This is further evidence that the farther a bird migrates the more sophisticated its navigational system.

Orientation experiments that we made with Canada geese, mallards, blue-winged teal, and pintails (ref. 98) indicated that all four species are able to use the Sun and stars for directional purposes. None have shown bicoordinate navigation by day or by night.

DISCUSSION OF RESULTS

The behavior of migrating birds in the air space can tell us much about the cues that are used in navigation and how they may have evolved. The literature reveals that unfortunately there is a great dearth of information about the migration behavior of even common birds. In many cases it is difficult to find information relative to the most obvious behavior patterns, such as whether a bird is a diurnal or a nocturnal migrant or flies singly or in flocks. There is only scant information on such complex subjects as altitude of flight, course of migration, distance of flight, and response to sky and wind conditions.

With all of the laboratory-type experiments evaluating celestial cues used by migratory birds, it is frustrating to find not one experiment with a nonmigratory species. To understand properly the mechanics of bird navigation, the orientation capabilities of nonmigratory birds must be thoroughly analyzed. Once a base of orientational capability has been established for representative species of nonmigrants, then experimental and empirical findings on migratory species can be meaningfully classified and evaluated.

I do not believe it is necessary to be concerned about the migration behavior of all species of birds. Many species probably have similar migration traits. For example, species of warblers wintering in the tropical rain forest in Brazil and migrating to the coniferous forest of Canada probably have similar navigational systems. Although species of sandpipers usually occur in separate flocks, those species migrating from the same tundra area of Canada to the same pampas area of Argentina might reasonably be credited with similar navigational sophistication.

Although this paper is based upon some facts, much assumption, and a great deal of speculation, I believe that it presents a different view of previous findings on migration behavior and provides for an orderly approach to future investigations on this subject.

SUMMARY AND CONCLUSIONS

The hypothesis presented in this paper proposes that navigational sophistication evolved as adaptive behavior to expansion of ranges of permanent-resident birds. Other traits being equal, the farther a bird expanded its range, the greater its navigational attributes.

Because birds are basically diurnal animals, the adaptations by many species for nocturnal migration are considered progressive evolutionary development in navigational sophistication. These developments provided long-distance migrants with opportunities to feed diurnally, and provided weak-winged flyers, such as ground-hugging sparrows and rails, with protection from accipitrine hawks.

The landscape is assumed to be the single most important cue for orientation among nonmigratory birds. Therefore, landscape features are considered the most fundamental cues to migrants. The less reliance migratory birds place on landscape for orientation, the more advanced their navigational mechanisms. Therefore, long-ranging pelagic birds are considered to be among those with the most highly developed navigational attributes.

The degree that birds wander from customary migration paths between breeding and wintering grounds is largely unknown. However, a surprisingly high proportion of adult birds return to their previous nesting area. Many juvenile passerines appear to return to areas inhabited immediately prior to their fall migration, accounting at least in part for low returns to their natal areas.

Certain oceanic birds, both adults and juveniles, have an astounding ability to return to nesting islands from thousands of kilometers away. Such homing ability over the trackless sea suggests great navigational sophistication. Sun navigation surely plays an important role among the several environmental cues available to oceanic species.

The ability of many birds to remain oriented when visual cues are minimal is probably one of the more significant findings derived from radar studies. It points to wind structure and/or the Earth's magnetic field as potential sources of directional information. Certainly these are two aspects of navigation that need more investigation.

ACKNOWLEDGMENTS

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COMMON AND SCIENTIFIC NAMES OF BIRDS REFERRED TO IN THIS PAPER

Laysan albatross	*Diomedea immutabilis*
Black-footed albatross	*Diomedea nigripes*
Greater shearwater	*Puffinus gravis*

Manx shearwater	*Puffinus puffinus*
Slender-billed shearwater	*Puffinus tenuirostris*
Giant petrel	*Macronectes giganteus*
Leach's petrel	*Oceanodroma leucorhoa*
Wilson's petrel	*Oceanites oceanicus*
White pelican	*Pelecanus erythrorhynchos*
Gannet	*Morus bassanus*
Brown booby	*Sula leucogaster*
Blue-footed booby	*Sula nebouxii*
Double-crested cormorant	*Phalacrocorax auritus*
Whistling swan	*Olor columbianus*
Canada goose	*Branta canadensis*
White-fronted goose	*Anser albifrons*
Snow goose	*Chen hyperborea*
Mallard	*Anas platyrhynchos*
Florida duck	*Anas fulvigula*
Pintail	*Anas acuta*
Gadwall	*Anas strepera*
Blue-winged teal	*Anas discors*
Cinnamon teal	*Anas cyanoptera*
American widgeon	*Mareca americana*
Shoveler	*Spatula clypeata*
Wood duck	*Aix sponsa*
Black-bellied tree duck	*Dendrocygna autumnalis*
Common goldeneye	*Bucephala clangula*
Common eider	*Somateria mollissima*
King eider	*Somateria spectabilis*
Spectacled eider	*Lampronetta fischeri*
Oldsquaw	*Clangula hyemalis*
Common scoter	*Oidemia nigra*
Surf Scoter	*Melanitta perspicillata*
Turkey vulture	*Cathartes aura*
Black vulture	*Coragyps atratus*
Rough-legged hawk	*Buteo lagopus*
Ferruginous hawk	*Buteo regalis*
Red-tailed hawk	*Buteo jamaicensis*
Red-shouldered hawk	*Buteo lineatus*
Swainson's hawk	*Buteo swainsoni*
Broad-winged hawk	*Buteo platypterus*
Harlan's hawk	*Buteo harlani*
Osprey	*Pandion haliaetus*
Willow ptarmigan	*Lagopus lagopus*
White stork	*Ciconia ciconia*
Common egret	*Casmerodius albus*
Great blue heron	*Ardea herodias*
Whooping crane	*Grus americana*
American coot	*Fulica americana*

Golden plover	*Pluvialis dominica*
Piping plover	*Charadrius melodus*
Killdeer	*Charadrius vociferus*
Long-billed curlew	*Numenius americanus*
Bristle-thighed curlew	*Numenius tahitiensis*
Upland plover	*Bartramia longicauda*
White-rumped sandpiper	*Erolia fuscicollis*
Ivory gull	*Pagophila eburnea*
Ring-billed gull	*Larus delawarensis*
Black-legged kittiwake	*Rissa tridactyla*
Franklin's gull	*Larus pipixcan*
Arctic tern	*Sterna paradisaea*
Common tern	*Sterna hirundo*
Black tern	*Chlidonias niger*
Noddy tern	*Anous stolidus*
Razorbill	*Alca torda*
Common murre	*Uria aalge*
Dovekie	*Plautus alle*
Horned puffin	*Fratercula corniculata*
Whiskered auklet	*Aethia pygmaea*
Homing pigeon	*Columba livia*
Mourning dove	*Zenaidura macroura*
Yellow-billed cuckoo	*Coccyzus americanus*
Black-billed cuckoo	*Coccyzus erythropthalmus*
Snowy owl	*Nyctea scandiaca*
Chimney swift	*Chaetura pelagica*
Yellow-shafted flicker	*Colaptes auratus*
Redheaded woodpecker	*Melanerpes erythrocephalus*
Yellow-bellied sapsucker	*Sphyrapicus varius*
Collared flycatcher	*Muscicapa albicollis*
Horned lark	*Eremophila alpestris*
Barn swallow	*Hirundo rustica*
Cliff swallow	*Petrochelidon pyrrhonota*
Tree swallow	*Iridoprocne bicolor*
Bank swallow	*Riparia riparia*
Purple martin	*Progne subis*
Blue jay	*Cyanocitta cristata*
Gray jay	*Perisoreus canadensis*
Common crow	*Corvus brachyrhynchos*
Black-capped chickadee	*Parus atricapillus*
Red-breasted nuthatch	*Sitta canadensis*
House wren	*Troglodytes aedon*
Bewick's wren	*Thryomanes bewickii*
Mockingbird	*Mimus polyglottos*
Robin	*Turdus migratorius*

Eastern bluebird	*Sialia sialis*
European robin	*Erithacus rubelcula*
Golden-crowned kinglet	*Regulus satrapa*
Bohemian waxwing	*Bombycilla garrulus*
Cedar waxwing	*Bombycilla cedrorum*
Loggerhead shrike	*Lanius ludovicianus*
Starling	*Sturnus vulgaris*
Black-capped vireo	*Vireo atricapilla*
Bay-breasted warbler	*Dendroica castanea*
Blackpoll warbler	*Dendroica striata*
Pine warbler	*Dendroica pinus*
Kirtland's warbler	*Dendroica kirtlandii*
Ovenbird	*Seiurus aurocapillus*
Northern waterthrush	*Seiurus noveboracensis*
Canada warbler	*Wilsonia canadensis*
House sparrow	*Passer domesticus*
European tree sparrow	*Passer montanus*
Bobolink	*Dolichonyx oryzivorus*
Eastern meadowlark	*Sturnella magna*
Red-winged blackbird	*Agelaius phoeniceus*
Brewer's blackbird	*Euphagus cyanocephalus*
Common grackle	*Quiscalus quiscula*
Brown-headed cowbird	*Molothrus ater*
Indigo bunting	*Passerina cyanea*
Evening grosbeak	*Hesperiphona vespertina*
American goldfinch	*Spinus tristis*
Dickcissel	*Spiza americana*
Rufous-sided towhee	*Pipilo erythrophthalmus*
Chaffinch	*Fringilla coelebs*
Field sparrow	*Spizella pusilla*
White-throated sparrow	*Zonotrichia albicollis*
Song sparrow	*Melospiza melodia*
Lapland longspur	*Calcarius lapponicus*

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