DISORIENTATION AND POSSIBLE FATE OF YOUNG PASSERINE COASTAL MIGRANTS

By C. John Ralph

Each fall millions of young passerine migrants pass along the coasts of North America, accompanied by relatively few adults. Various studies (e.g. Robbins et al., 1959; Drury and Keith, 1962; Murray, 1966; Ralph, 1971; Stewart et al., 1974; Ralph, Ms) have shown that young make up approximately 85 to 95% of the birds along the coast, as compared to 65 to 75% inland.

I refer to this preponderance of young as the "coastal effect" (Ralph, 1971, Ms) and suggest that these young birds are disoriented and thus have strayed from the normal route of the species. Further, I suggest that a substantial proportion of these individuals may continue offshore to perish, their average direction being southeast.

In order to determine whether these young individuals on the coast are indeed disoriented, in this study I tested the preferred orientation of young birds taken on the coast and at inland locations. In addition, I will discuss the genetic and population consequences of disorientation.

METHODS

I captured birds in the falls of 1970 and 1971. Coastal birds were taken at the Manomet Bird Observatory, Massachusetts, just south of Plymouth. Inland birds were taken in 1970, 75 km inland at the Wachusett Meadows Wildlife Sanctuary, 15 km south of Fitchburg, Massachusetts, and in 1971, 80 km inland at Ashby Bird Observatory, 11 km NNW of Fitchburg. In 1970, all birds were tested at Manomet, and in 1971, all were tested at Ashby. These birds consisted of 37 species of long distance passerine migrants. For a list of each individual test result and species involved, see Ralph (1975). In the fall of 1974, I captured and tested three species of thrushes (*Catharus minima, C. guttata,* and *C. ustulata*) near Carlisle, Pennsylvania. In all cases, birds were captured in mist nets and kept singly in small cages (25 × 15 × 15 cm), except for the thrushes in 1974, which were kept in a large aviary. After an initial diet of orange slices for moisture and meal worms *ad libitum,* they were usually switched to ground dry dog food, as well as oranges and water. Under this regimen most birds, after an initial loss, regained weight, and some became quite fat. The thrushes in particular adapted well to cage life.

Test birds were captured over the entire fall migration, but no more than a few individuals of a species on any one day, to avoid biasing the sample with individuals present in "waves" on certain days. Since adults are very rare on the coast, only young birds were used in these experiments.

I tested the orientation of these birds in "Emlen cages" (Emlen and Emlen, 1966) under natural night skies. The walls of this cage are a cone of stiff paper; the floor is an ink pad. The caged bird, in *Zugunruhe,*

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leaves ink footprints on the paper cone whenever it hops, creating a permanent record of the direction of its activity. The cage includes a 15 cm tall shield, painted Flat Black, that limits the bird's view to that sky more than 35° above the horizon. Since the tests were run in open meadows, this shield blocked all landmarks.

Tests usually began within 1 hr of nautical twilight and continued for 75 min. At about dusk on the night of a test, birds were transferred from their cages to separate compartments in a portable holding cage and taken to the test site. There the orientation cages were arranged on large tables, 10 cages per table, with one bird in each cage. The cages were kept upside down until all birds were in place, and then rapidly turned upright to start the test. Since each paper cone has a seam, which might serve as a reference mark to the bird, the seams were aligned in different directions on different trials.

Tests were conducted only on cloudless, moonless nights. However, haziness varied between test nights, and with it, sky glow. No nights were completely without sky glow, but it was especially noticeable on hazy nights. On clear nights, the cage shield probably blocked most of the sky glow from the bird's view. At Manomet, the sky glow was from Plymouth, 10 km WNW; at Ashby, the sky glow was from Fitchburg, 11 km SSE. There was no sky glow at the Carlisle test site, which was in Green Valley over a ridge to the north of the city. Birds were tested on 30 nights between 5 August and 31 October 1970, 13 nights between 15 September and 6 November 1971, and 5 nights between 6 and 22 October 1974. Approximately 2,000 activity records resulted.

Each activity record was analyzed by assigning an "activity level" of 1–20 to each 15° sector, according to how darkened it was with footprints. This method and the scale of activity levels were the same as those of Emlen (1967). These values were summed for the whole cone to give the "activity index" of the bird. This varied from 5, typical of birds that went to sleep, to 326, for an extremely highly motivated bird. I excluded from further analysis any records with an activity index of less than 10, in order to eliminate non-motivated birds. The average index of the resulting 1,224 records was about 40.

The activity index served as n for calculating the characteristics of the circular distribution of activity (Batschelet, 1965, 1972). These are: (1) the mean direction ($\bar{x}$); (2) the length of the mean vector (r), which describes the strength of orientation; (3) the angular deviation (s), somewhat analagous to a non-circular distribution's standard deviation; and (4) the Rayleigh z statistic, which tests the significance of orientation as it departs from random. All of these values assume unimodality (a "circular normal" distribution). All but item (1) also assume independence for each data point (i.e., the value from each 15° sector's activity). Almost without exception the unimodality criterion was met, and the independence criterion was assumed (see Emlen, 1969, for discussion).

Some of the activity records met the criterion of the activity index, but activity was not significantly concentrated in any one direction, as indi-

cated by a low value of the Rayleigh z statistic. These records appeared only to add background noise to calculations of orientation. I was aware of Emlen's (1975) findings concerning apparent significance of mean of means in extensive trials of the same individual, but I found no such effect and thus eliminated records that were not oriented at the $P < 0.05$ level.

Most (89%) of the individuals used for the analyses below were tested on one or two nights; a few were tested on three (6%), four (3%), or five (1%) nights.

When individual birds were tested more than one night, their orientation usually differed markedly between nights. For example, 34 individual thrushes had more than one test that met the criteria outlined above, 10 activity units and 5% significance, for a total of 77 nights of tests. When the results of these nights are compared for each individual, in only four cases out of the 77 were the separate nights' activities not significantly different from each other ($P < 0.05$). That is, each night, in most cases, appears to be essentially an independent data point.

However, these experiments obviously do not control all the variables that affect a bird's orientation. Such is the technique. In view of this, rather than average all the records from each bird, I counted each performance as an independent datum. Although, strictly speaking, they were not completely independent, there were apparently enough uncontrollable variables between nights to justify treating each record as independent.

The sample size of usable records for any one species is limited by the number of individuals a banding station can catch, the number that can be kept healthy in captivity, the number that show sufficient activity in the test cages, and those that are significantly oriented in this activity. Furthermore, large samples are needed to make meaningful comparisons between samples when the data are as imprecise as these are. In short, obtaining adequate samples of any one species is somewhat difficult. Fortunately, the wide distribution of the "coastal effect" among species argues that for purposes of studying this phenomenon, data from all species can be and have been combined into one sample.

One small taxonomic group that I was able to analyze separately was the three species of closely related thrushes. These are all long distance, nocturnal migrants of similar diet, plumage, and migratory routes. The results of the Carlisle birds in 1974 were combined with those of thrushes captured at the inland sites in 1970–1971 and compared with the coastal thrushes from those years.

<div align="center">RESULTS</div>

Preferred Direction

I had predicted that if the birds captured along the coast reached there because they were disoriented, they would orient, on the average, southeast. By contrast, birds of inland origin would orient southwest, thus avoiding the coast and heading toward their normal wintering
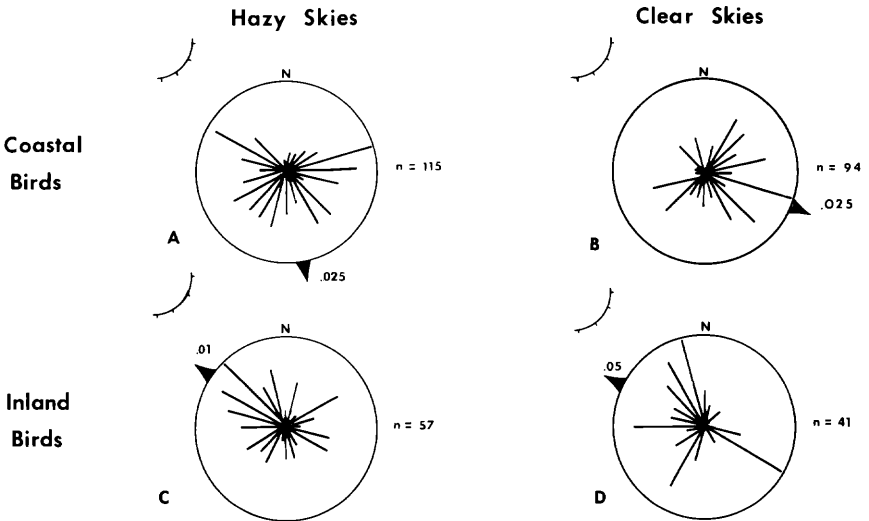
FIGURE 1.   Orientation of birds tested at the Northwest sky glow site. Location of sky
     glow is indicated by quarter circles, the average direction of orientation of all birds
     by arrows at the edge of the circle, the number of tests to the right of the circles, and
     the level of significance of orientation by the figures next to the arrows. The most
     common direction taken has a line to the edge of the circle, and the lengths of the
     other lines reflect the relative proportions of birds using the other directions.
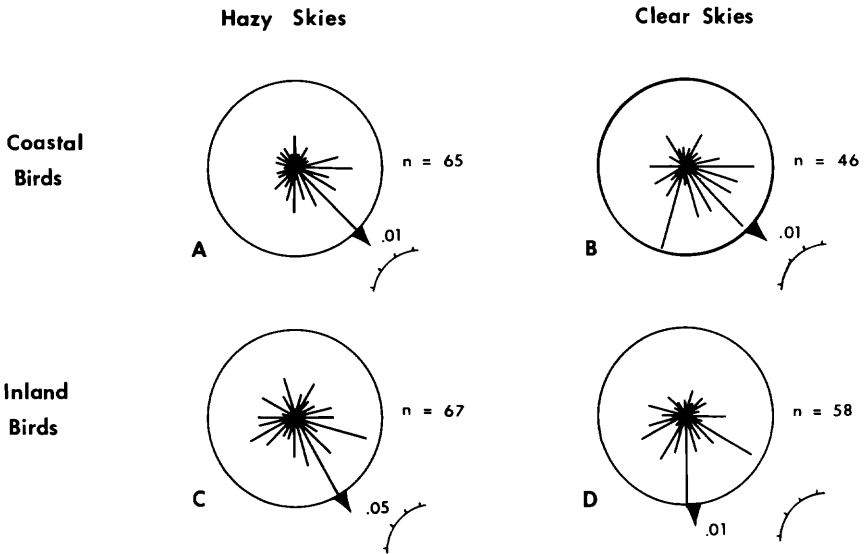

FIGURE 2.   Orientation of birds tested at the Southeast sky glow site. Symbols and nota-
     tions are as in Fig 1.

grounds. As the results below show, the test of this hypothesis was complicated by the effects of sky glow.

Coastal birds.—Coastal birds tested under clear conditions with the sky glow in the NW (Fig. 1B), had a mean direction of 113° ($P < 0.025$) to the SE. Under hazy conditions, enhancing sky glow, their average direction (Fig. 1A) was 175° ($P < 0.025$), and the scatter increased. This difference between preferred directions under hazy and clear skies is not significant ($U^2 = 0.12831, P < 0.10$).

Coastal birds tested under clear skies at the SE sky glow site (Fig. 2B) concentrated their orientation rather precisely to the SE ($\bar{x} = 135°, P < 0.01$). Under hazy conditions (Fig. 2A) orientation was in the same direction ($\bar{x} = 140°, P < 0.01$).

A comparison between coastal birds at the two sites showed no significant difference under clear skies ($U^2 = 0.08599, P < .10$) or sky glow ($U^2 = 0.01671, P < 0.10$), orienting to the SE as predicted.

Inland birds.—Birds of inland origin tested at the NW sky glow site, in contrast to the SE-orienting coastal birds, concentrated their orientation to the NW under both conditions of sky glow (Fig. 1C) ($\bar{x} = 307°$, $P < 0.01$), and clear skies (Fig. 1D) ($\bar{x} = 295°, P < 0.05$). Inland birds tested at the SE sky glow site were similar to the coastal birds tested there and headed SE. The birds' average orientation was similar under clear skies (Fig. 2D) ($\bar{x} = 177°, P < 0.01$), and with increased sky glow (Fig. 2C) ($\bar{x} = 150°, P < 0.01$).

Inland birds tested at the two sites, with different sky glow directions, were significantly different from each other. This was the case both under clear skies (Figs. 1D and 2D) ($U^2 = 0.32656, P < 0.005$), and with increased sky glow (Figs. 1C and 2C) ($U^2 = 0.27559, P < 0.01$). At each site orientation was towards the sky glow, even under clear skies, indicating the impact of sky glow on their orientation.

Coastal vs. inland birds.—Coastal birds were significantly different from inland birds at the site with NW sky glow, both under hazy skies (Figs. 1A and C) ($U^2 = 0.25239, P < 0.005$) and with clear skies (Figs. 1B and D) ($U^2 = 0.40652, P < 0.005$). At the SE sky glow site, coastal birds were not different from inland birds in their mean direction. To summarize, the results demonstrate that birds from the coast had significantly different orientation from inland birds when tested at the site with NW sky glow. When the sky glow was in the migrating direction, the directions the birds took were not different, as possibly the sky glow attracted the birds.

Experiments with Thrushes

When the thrushes used in the above analysis were combined with the experiments conducted at Carlisle, coastal birds were significantly different from inland birds ($U^2 = 0.2171; P < 0.05$). Coastal thrushes headed SE ($\bar{x} = 156°$), but were scattered ($P < 0.20$), while inland thrushes, whose mean direction was 287°, were more concentrated ($P < 0.01$).

Strength of Orientation

The second approach I used to test the disorientation hypothesis con-
cerned the possible interactions of these two potential sources of input
to the bird, celestial and geophysical cues vs. sky glow. If indeed these
two input sources were being used, there might be a lessening in the
strength of orientation when they were in conflict. To determine this,
I compared the strength of orientation from the tests in the above anal-
ysis. That is, which sky glow conditions produced the best orientation?
The *r* value, the length of the mean vector, is the measure of the
strength of orientation. All records that had activity values of at least
10 were included, resulting in a total of 1,224 tests (data in Ralph, 1975).

The best oriented birds, those with the highest average *r*, were the
coastal birds tested at the NW sky glow site. These were significantly
different (Kolmogorov-Smirnov test; Siegel, 1956) from coastal birds at
the SE sky glow site ($P < 0.001$) and inland birds at both the SE ($P <$
0.001) and NW ($P < 0.05$) sky glow site. These latter three groups were
not significantly different from each other. Thus, the strongest orien-
tation occurred where the sky glow was opposite the preferred direction.
When the sky glow was approximately the same as, or 90° from, the
preferred direction, the strength of orientation was reduced.

<div align="center">DISCUSSION</div>

Test of the Prediction

I predicted that young birds caught on the coast would have a SE
orientation, taking them offshore. When the sky glow was in the SE,
their orientation was concentrated in that direction; when sky glow was
opposite, in the NW, their mean direction was still as predicted, in the
SE, although more scattered.

I predicted that young birds caught inland would have a mean head-
ing of SW. With sky glow in the SE, approximately 90° to the E of the
predicted direction, orientation was directed towards the sky glow, and
was not different from coastal birds at that site. However, when the sky
glow was in the NW, the orientation of the birds was again apparently
drawn to the sky glow, and was NW. Under these circumstances, the
orientation of the coastal birds was significantly different from the in-
land birds. Thus, although the birds did not orient as predicted, the
divergence from the predicted orientation found a possible explanation
in positive phototaxis of the birds towards the sky glow.

Further evidence that sky glow has a confounding effect was the
result that the strength of orientation was greatest when the preferred
direction was opposite the sky glow (that is, the birds were, on the av-
erage, often facing away from the sky glow). When the birds were, on
the average, facing the sky glow, their orientation was relatively poor.

Comparison with Able's Results

Able (1977) tested 26 young coastal birds of 15 species. He divided
his results into two groups, one orienting SE and the other NW. He

suggested that the SE birds were going offshore and that the NW birds were attempting to regain land, as many birds do in the wild (Baird and Nisbet, 1960; Richardson, Ms). (An analogous situation in my experiments might be birds attempting to return to the capture site.) I found no such dichotomy in direction among coastal birds (Figs. 1, 2, A, B). Our methods differed in that I held birds for 5 to 7 days before testing, whereas Able tested birds the same day as capture. Nevertheless, the distribution of his 26 data points (his Fig. 1) fits within my much larger sample, showing many birds between the southeast and northwest "groups" Able proposed. Perhaps by the time I tested the birds, usually 5 to 7 days after capture, more of their original orientation preferences had been reestablished, so the coastal birds, in general, no longer headed inshore. If this is the case, it would argue that most coastal birds do not learn a new orientation, but eventually persist in their offshore direction, possibly to perish.

Population and Size of Disoriented Young

I (Ralph, 1975, Ms) proposed two hypothetical outcomes of coastal young having a preferred SE (offshore) orientation. The first is that the young, once having experienced an overwater flight offshore, will somehow (given sufficient energy reserves) return to land (as Able, 1977, proposed), learn, and not repeat the mistake in future flights. The second possibility is that many of the young that reach the coast persist in the offshore movements, eventually to perish.

To decide which possibility is most likely, one must first determine how the young birds reach the coast. The point of divergence of the two hypotheses occurs after this point when a bird finds itself over the water at dawn. There the choice is made, either: (1) learning will take place as the bird reorients and tries to regain land, never to take the same direction again; (2) the bird will try to regain land but will not learn to change its direction in future flights; (3) it will perish in attempting to regain land; or (4) it will not reorient and perish on continuing offshore.

First, how do they get to the coast? Some are possibly blown off their assumed normal SW course. However, there is evidence that migrants apparently have at least some ability to compensate for wind drift (see Emlen, 1975, for review). Despite this contention, when winds are from the mainland (in the study area averaging NW), all migrants, adults in particular are more common than at other times (Stewart et al., 1974; Ralph, Ms). Adults, having survived one round trip, presumably have adequate navigation abilities. Wind drift, however, does not account for the presence of most of the young. If we generously assume that *all* the adults on the coast arrive due to "unfavorable" winds, we can deduce the number of young arriving on the coast by this method. As I have shown (Ralph, 1975, Ms), adults comprise on the average 30 to 35% of migrants inland in the Northeast, but only 10% of coastal migrants. If birds of both age classes of the presumably somewhat normal inland ratio

of 30%:70% were blown to the coast, for every 10 adults (the 10% adults on the coast) reaching the coast, there would be approximately 23 young with them

$$\left(\frac{70 \text{ young}}{30 \text{ adults}} = \frac{x \text{ young}}{10 \text{ adults}} = 23.3\right).$$

Thus, 23% of the birds on the coast are young and could have reached there in the same manner as the adults, perhaps as a result of wind drift. Since the percentage of young on the coast averages 90%, two thirds (90% − 23% = 67%) of the birds on the coast are young birds that probably reached there unaccompanied by adults. The other 10% adults and 23% young having proper orientation mechanisms except perhaps the ability to compensate for wind drift, might well continue SW. They would then survive if they do not again encounter NW winds, an uncommon direction in the Northeastern U.S. The evidence from this study suggests that these young, *two thirds of the birds on the coast,* reached the coast as a result of their preferred orientation. Further, as Gauthreaux and Able (e.g., 1970) have shown in many papers, migrants tend to fly in a downwind direction. It could be suggested that birds tend to initiate migration when winds are in their preferred direction. If this is the case, perhaps more than the number I suggest reach the coast, heading ultimately offshore.

The final step still remains. Do they continue offshore, or do they learn to avoid the coast? Some may learn, but evidence of weight loss in coastal birds and reports of land birds far offshore (summarized in Ralph, 1975, Ms) argue that at least many perish in an attempt to complete their journey.

We can calculate the possible annual loss from this source on both the east and the west coasts. It has been estimated that there are about 14 billion fall migrants in North America (MacArthur *in* Moreau, 1966). The coastal effect is noticeable in the first 50 km inland from the coast. I calculate that approximately 3.6% of North America is within 50 km of the coast, thus there would be about 500 million birds on the coast during the fall, assuming, to be conservative, that migrants are equally as dense on the coast as inland. Of those birds on the coast, let us assume, as reasoned above, 33% are adults and young displaced by wind. These will survive because of their preferred orientation to the SW, an overland route. Of the remaining 67% young on the coast (ca. 335 million), again being conservative, let us say that one half will learn, not persist in offshore direction, and will survive. This would result in a minimum annual loss of approximately 170 million young, about 1% of the migrant population. The maximum loss, if we assume (as some estimates suggest) that birds are three times as dense on the coast as inland, and the entire 67% young will be lost, would result in approximately 1 billion young or about 7% of the migrant population being lost. I would suggest that the figure probably lies in the range 1 to 10%.

Genetic Maintenance of Disoriented Individuals in the Population

It might well now be asked: If young birds lacking proper navigational mechanism are eliminated each year, why have all the individuals of the species not "perfected" their migration to the point of avoiding this waste? This question might be answered by the realization that imperfection is the price a species must pay for variability. Joseph Grinnell (1922) in his paper "The Role of the 'Accidental'" discussed vagrants (birds out of their normal migratory route) as pioneers. He noted that it was occasionally advantageous to individuals to migrate in directions not taken by the majority of their species. Although the vast majority of these individuals are selected against, the survival of an occasional founder in a new habitat could, as discussed below, result in retention of misdirected individuals. North America has undergone many floristic (and resultant faunistic) changes in the past 10,000 years. The last glacial retreat made large areas available to woodland and grassland bird species, causing rapid range expansions and speciation (e.g., Mengel, 1964). The virtual elimination of the diverse and large herbivorous mammalian fauna approximately 10,000 years ago (e.g., Martin and Wright, 1967) undoubtedly resulted in drastic changes in the ranges and species composition of various plants. Finally, the advent of western man in the last 200 years has seen areas such as the Northeast change from almost pure forest to a large proportion agriculture, and back (since the Civil War) to a significant amount of forest. It has certainly been advantageous for bird species to have individuals that were somewhat flexible in their migrations so that occasional misdirected individuals are able to take advantage of new habitats, or to avoid habitats no longer suitable. Thus, in the past, and especially in the very recent past, there has been positive selection pressure favoring the genetic combinations which (perhaps as a byproduct) result in the "accidental." The accidental, as Grinnell suggested, and DeSante (1973) and I (Ralph, 1971) have shown, is usually a young bird. Despite the above argument, is this positive selection pressure alone enough to offset the negative pressure (1 to 10%) that I hypothesize to occur? Perhaps so, but there is another factor that might also result in the maintenance of this potentially lethal trait.

Dobzhansky (1955) has referred to a factor that might help offset seemingly great negative selection pressure, as the "balanced genetic load." Mayr (1963) defines this as a ". . . load (which) results from selection favoring an allelic balance of genes which by recombination and segregation produces inferior genotypes in every generation." Wallace (1968), Mayr (1963), and Haldane (1937) give many examples and discuss the persistence of maladaptive traits. For example, Mayr (1963) reports on a mosquito with a genetic load resulting in 50% mortality in each generation. It is probably not, therefore, unreasonable to postulate a genetic load of about 5% for birds during one of their most stressful and complex tasks, namely migration.

SUMMARY

The cause of large numbers of young autumn passerine migrants
along the coast was investigated. In tests in Massachusetts and Pennsyl-
vania, the orientation of these birds was found to be significantly dif-
ferent from inland migrants, and in an offshore direction. Sky glow
from nearby towns was found to have a significant effect on the direction
and strength of orientation.

It is postulated that between 1–10% of migrants in the eastern United
States are involved in these offshore movements. Although it is con-
cluded that many may perish, some individuals may benefit from the
resiliency that orientation differing from the majority imparts to the
migrants.

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