A REVIEW OF SOME PROBLEMS IN THE STUDY OF BIRD MIGRATION

JEFF SWINEBROAD
Department of Biological Sciences, Rutgers University, New Brunswick, N. J.

GENERAL CONSIDERATIONS

Field observations of migration are difficult to interpret as well as difficult to make. For example, the correct interpretation of the numbers of birds seen in migration may be in doubt. The number of birds observed is often assumed to be directly proportional to the magnitude of migration, but even this basic assumption may be questioned. Crissey (1955) estimates that not over 25,000 Black Ducks are in New York at a given time, yet over one-half million birds probably move throughout that state. Snow (1953) observed Chaffinches appearing out of a clear sky and commented, ". . . with this species therefore, perhaps more than any other, it is not at all certain how far the observed migration represents any considerable portion of the total migration that is going on." Lack and Lack (1933) noted differences in the numbers of birds moving through varying topographical situations of the same general area. Newman (1952) points out the confusing situation when a number of birds interrupting migration and flitting about in an area appear to the observer as many individuals moving through the area. Moreau (1953) calculates the large number of birds an observer could see in the Mediterranean area as opposed to those actually seen and concludes, "Such a realization helps one's sense of proportion and a realization of how great a percentage of migrants must pass undetected." The foregoing citations indicate that a large part of migration may be unobserved. Compared to the total population, fluctuations in numbers of observed birds by chance may be relatively insignificant.

A further difficulty lies in obtaining accurate counts of those birds potentially within the observers view. Lowery and Newman (1955) sum this up by stating, "A considerable portion of diurnal migratory activity doubtless takes place through the screening foliage of the trees, where the presence of non-migrating birds of migratory species adds to the observer's confusion. Under these conditions, accurate space-defined sampling of the rate and frequency of passage is next to impossible." Lowery and Newman's various publications on nocturnal bird migration (Lowery, 1951; Newman, 1952; Lowery and Newman, 1955) describe an attempt to solve the problem of sampling bird migration, for as they conclude, "The analysis of Lunar flight co-ordinates derives its research status from the fact that it permits more precise numerical measurements of migration as a mass movement than does any other method applicable either by night or by day." The lunar method is not without its own problems, and has one special difficulty in that species cannot be identified (Farner, 1952).

If observed numbers of birds were always more-or-less directly proportional to the magnitude of migration, then the effects of weather on migration could be easily ascertained. The preceding discussion suggests that the relations between observed birds and the true extent of migration is not entirely clear, and therefore the significance of weather variables on the total flight may not be as obvious as thought. In addition to this problem, a critical approach to studies of migration should consider the following:

1. The proportion of a migratory flight affected by weather may vary with different weather conditions. Many correlations between influxes of birds and weather have been noted and the numerous papers dealing with this need not be cited. Obviously, there is a relation between weather and migration, but there

are apparently no data on the porportion of the birds in flight that are influenced by given weather conditions.

2. Physiology of the migratory population may change from one observation period to the next. Studies on fat deposition (reviewed by Farner, 1955) indicate remarkable physiological activity in migrants, and suggest increased metabolism and rapid food utilization. All of these are situations of importance in establishing various levels of behavorial motivation which may change rapidly with, for example, the extent of food supply, the duration and time of previous feeding, fatigue, and the like.

Seldom are weather conditions repeated in an interval of time that permit exclusion of consideration of physiological changes in the birds. For example, after the passage of one cold front, and a subsequent influx of birds, a sufficient period of stable weather may ensue to permit such physiological changes in the migratory population that the arrival of a second cold front impinges on a physiologically changed bird. Consequently differing proportions of the population may respond to the two cold fronts. The frustration of the observer is apparent when confronted with the possibility that physiological changes in individual birds may motivate different responses to weather variables at different times and thus changing segments of the migratory population may be affected in different ways at different times!

3. When birds are seen, does this represent a migratory *movement* or a *cessation* of migration? Lowery (1945) and Williams (1945) give some examples of cessation of migration during inclement weather. Some or many of the birds seen might, therefore, be those temporarily non-migratory. Extending this line of rationalization, might there not be times when the "success" of migration is inverse to the numbers of birds observed?

4. Does an influx of birds represent a mass movement, and if so, are the accompanying weather variables the significant stimuli? One problem in analyzing weather data has been mentioned by Farner (1950). "Actually, however, such observations do not necessarily indicate whether migration would or would not have occurred in the absence of the external stimulus." Unfortunately, weather conditions do not always duplicate themselves in a time sequence condusive to good experimental design or statistical treatment. Despite the wishes of an observer, cold fronts may not occur frequently, nor may successive fronts duplicate themselves with respect to wind velocity, temperature, cloud cover, and so forth. Even slight changes in the structure of a front may significantly influence the proportion of the flight observed. Until sufficient data are available on the limits of environmental influence on migrants, this point must be kept in mind.

THE USE OF INFLUX AND DEPARTURE DATA

Some of the foregoing difficulties may be overcome by the judicious use of both influx and departure data. Regardless of what proportion of the population is involved, departure data give clues as to the influence of known environment of those birds under observation. In influx data the consequences of behavior are noted, i.e., appearance of birds, but the initiating environment may lie at a distance. When studying departures the daily behavior and numbers of the birds can be noted and their surrounding environment measured directly. In influx data it is necessary to hypothesize not only what variables were operating, but also the probable locale of activity. With departure data the locale of the start of a flight is known and need not be hypothesized.

If influx data represent cessation of migration, then the hypothesis regarding weather stimuli can be made with considerable justification, for presumably the effective environment is that present at the time of the precipitation of the birds. Many of the papers using influx data, however, are concerned with the *initiation* of flight. Of course, quite reasonable work using influx data can be done by combining mass observation data with knowledge of probable ranges of birds, what is known in general of the birds behavior, together with previous records, and weather map data.

As an example of the use of influx data, consider the study of fall warbler migration in Lincoln Park, Chicago, Illinois done by Bennett (1952). His data indicated a correlation between high numbers of warblers and cold front passage through the area, and he concluded, "Early cold fronts in late August and early September were always followed by important warbler waves." Bennett (op. cit.) also indicated that birds moving on a NW wind might become concentrated in the Lincoln Park area due to the barrier effect of Lake Michigan. The numbers noted by Bennett thus, could reflect either influx (wave) or a pile up of birds due to the lake barrier. In either case it is difficult to analyze the factors that may have initiated the movement. Was it wind, temperature, cloud cover, and how soon after the front passed did these stimuli become effective? Did all of the birds start from the same place and under the same weather conditions? When did the flight start? In a less obvious fashion all of the warblers in the waves did eventually leave the park area, "Many of the arriving birds must have remained for a considerable period of time departing gradually" (Bennett, op. cit., p. 208). "Under static conditions the birds evidently moved leisurely southward, making many short flights instead of mass movements stimulated by cold fronts" (Bennett, op. cit., p. 216). Study of the circumstances surrounding the departure of these birds should yield considerable information on the influence of weather on migration. Whether a mass flight occurred or not, many birds were stimulated to migrate *out* of Lincoln Park as well as *into* it. An observer using departure data would know the general locale of flight initiation, and could by daily sampling reduce the time error in estimating start of flights, and also could measure weather variables directly.

The use of influx data may lead to unwarranted assumptions regarding the length and magnitude of the flight. Why is the assumption frequently made that the incoming birds have made a long intense flight while the departing birds will make a short leisurely flight? Perhaps lacking the excitement attending a big warbler day, the observer feels the departing birds must be moving leisurely and in short hops. Any wave, nevertheless could be compounded from birds making short hops as well as those making distant flights. Actually, the length of flights is not usually known from either departure or arrival data, and this is a weakness of both methods of study.

Departure data may include observations of birds actually taking flight and the observer here is presented with a rare opportunity to collect the information on initiation of flight. Raynor (1956), Miskimen (1955), Ball (1952), and Lack and Lack (1953) have mentioned such observations. More often, departure data include instances of decreases in bird numbers together with daily records of weather. Dennis (1954) uses departure data in the foregoing manner and notes departure of migrants in April during periods of warm, clear weather, and southwest winds.

ADDITIONAL PROBLEMS

The examination of departure data may result in confirmation of hypotheses now erected from influx data. Usually, however, the use of departure data reveals many problems not readily apparent in influx data. As an example of specific problems encountered, and the use of both arrival and departure data in field research, some limited information may be taken from a study of bird migration at The Ohio State University from 1952 to 1956. Shorebird habitat at O'Shaughnessy Reservoir, Delaware County, Ohio, is limited to newly exposed mudflats, small in area, and separated by expanses of rocky sterile shore. The river above and below the reservoir offered little favorable shorebird habitat, and the nearest comparable water area was over 10 miles to the northwest. The small number of shorebirds regularly observed in the area, together with the limited habitat available at O'Shaughnessy made possible accurate counts of shorebirds. Individual shorebirds with peculiar water stains could be recognized for a time at least. The presence or absence of a few birds could, therefore, be detected fairly easily because of the limited habitat, small flocks, and, at times, the presence of marked individuals. The weather phenomena most commonly considered in migration studies, i.e., air temperature, light intensity, cloud cover, surface wind velocity, and frontal activity were noted daily at the reservoir. This information plus that available on U. S. weather maps enabled some consideration of the force and extent of weather changes in the area.

In using such data, a decision must be made as to what numerical changes of birds will be considered valid. The numerical loss or gain may not reflect the actual change of birds. Complete population turnover could occur and not be noticed at all if the number of birds remained nearly the same from day to day. Statistical treatment cannot be used to determine significant levels of numerical shifts because of the possibility of this hidden change. The most direct solution is to examine those changes of sufficient quantity as to most reduce the chance of sampling error. Such changes are *known* decreases (or increases), though undoubtedly this treatment *excludes* some changes that did occur. But, if information on causes of known changes can be obtained then the data may be reexamined for less obvious changes. Because of the nature of the small populations and restricted habitat at O'Shaughnessy Reservoir, a deviation of 10 or more sandpipers was selected as a reflection of true population change, and not due to sampling error.

TABLE 1

Cold front passage and increases in daily counts of Pectoral Sandpipers at O'Shaughnessy Reservoir, Fall 1952

Date of frontal passage	Date of increases of 10 or more birds
August 4–5	August 4–5
August 11–12	August 12–13
August 21–22	August 22–23
September 1–2	no data
September 6–7	no increase
September 19	September 18–19
September 26	no increase
October 1	no increase
October 5	October 5–6
October 10*	October 9–10
no front	October 11–12
October 13	no increase
October 16	October 17–18

*North of area.

Table 1 summarizes increases in Pectoral Sandpiper population and cold front passage at O'Shaughnessy Reservoir in the fall of 1952. Increases in these birds seem to be associated with the passage of a cold front. This was not the case following the weak frontal passage of September 6–7, or after the active frontal passage of September 15–16. An increase occurred on October 11–12, before, not following cold front passage in the area. In general it appears that something in the fronts may act as a stimulus for Pectoral flight. Acceptance of this hypothesis must depend on knowledge of the weather at the locale of the start of the flight, and the length of the flight, both of which are unknown quantities in this instance. Did the birds start flight from an unknown locale *after* frontal passage or is the increase observed at O'Shaughnessy just a few birds dropping out of a larger movement *with* the front? Though the arrival of birds may be associated with cold fronts, the increase data do not indicate what kind of association occurred. For example, does flight initiate with or following the front, and if flight initiates after frontal passage, how long after, and do all the birds respond alike? Apparently the increases occurred during or very shortly after frontal passage. The birds may have been moving with the front, or before it and been precipitated by the weather conditions, or they may have dropped in to the reservoir because of fatigue or hunger. Another possibility is that the birds were moving behind the front, over-extended their flight, and consequently were precipitated by weather at the front.

Examinations of the departure data should yield some information on whether or not birds will leave the area before or after cold fronts. Granted that not all departures will be detected by examination of decreases in counts, do those departures that do show up correlate with any weather pattern? When the data

TABLE 2

Decreases in daily counts of Pectoral Sandpipers and weather data, O'Shaughnessy Reservoir, Fall 1952*

Date of decrease	Percent change in cloud cover	Change in air temperature	Change in wind direction	Date of last cold front
August 5–6	25 to 75	67 to 69	SE to NW	August 4–5
August 13–14	100 to 00	64 to 66	NW to SE	August 11–12
August 23–24	00 to 00	75 to 80	N-no change	August 21–22
August 27–28	00 to 50	85 to 75	NE to E	August 21–22
September 19–20	75 to 25	63 to 70	NW to W	September 19
October 7–8	00 to 100	43 to 60	NW to N	October 5
October 18–19	100 to 00	42 to 52	NE to NW	October 16
October 20–21	25 to 00	40 to 38	NW to NW	October 19–20
October 22–23	00 to 00	40 to 52	SW to N	October 19–20

*Data reported are those recorded in the study area at the start of consecutive daily censuses.

on decreases are examined (table 2), there is some correlation apparent between numbers and weather. Comparison of the first and last columns of table 2 suggests that Pectorals left the study area in the clearing weather of a day or two after frontal passage. No decreases were noted preceding frontal passage. Combining arrival and departure data, it seems that birds may be stimulated to migrate after frontal passage, and that some birds may extend their flight into or to the front and then cease flight.

There were increases and decreases in counts that do not correlate with cold front passage (see tables 1 and 2) and there were cold front passages without apparent changes in numbers of birds. In addition, some individual variations in departure were exhibited by three Pectoral Sandpipers recognizable because of peculiar water stains. No other birds with similar staining were seen at the study area, and no dilution was noted in the intensity of the stain during the time that the birds were seen. One such marked bird was observed from October 6 to October 18, during which time one cold front passed, October 13–14. A second bird was noted on October 12 and 13, and not seen after the cold front of October 13–14. A third recognizable bird was noted from October 8 through October 22, during which time three cold fronts passed through the area. These birds appeared normal, and maintained as much activity as unmarked birds associated with them and presumably were healthy birds, in other words, the length of stop-over did not seem to be influenced by disability. The variable length of stop-over of these birds, and those changes in numbers not associated with cold fronts suggest that not all individuals of a species leave an area at the same time (following frontal passage) and that the length of stop-over varies from individual to individual. Wolfson (1954) noted a variation in length of stop-over with extensive data on White-Throated Sparrows.

O'Shaughnessy Reservoir also served as a stop-over area and wintering grounds for migratory waterfowl. All flocks of ducks on the reservoir could be observed and individuals counted. Black Ducks and Mallards made early morning and evening flights from the reservoir to nearby grain fields, but rested on the water or shores of the reservoir during the middle of the day, and counts of the individuals present could be made at that time. Concurrent studies (Swinebroad, 1956)

TABLE 3

Increases in daily counts of Black Ducks and cold front passage at O'Shaughnessy Reservoir in the Fall of 1952, 1953, 1954

Date of frontal passage	Date of increase
1952	
December 5	December 3–4
no front	December 6–8
December 10	no change
December 18	December 16–18
1953	
December 4	December 4–5
December 12	December 12–13
1954	
December 4	December 3–4
	December 4–5
cold weather	December 6–7
prevails through	December 7–8
December, increase	December 8–9
may reflect freezing	December 8–9
to north	December 9–11

indicated that counts varying 10 percent or less could have been due to sampling error, and consequently only changes of 15 percent or more were selected for analysis. Table 3 presents the increases in Black Ducks and dates of cold front passage.

Several increases in Black Ducks were associated with frontal passage. The increases were noted just before or just after frontal passage. These data suggest that flight may be initiated by factors following a cold front as in the case of Pectoral Sandpipers, and some birds may catch up with or penetrate the front. However, the decrease data on Black Ducks (table 4) show decreases not associated with frontal passage, and furthermore, decreases occurred under a variety of weather conditions, i.e., clearing, clouding, overcast, partly cloudy, and clear days, each with various wind velocities, and temperature changes. Winner (1957) also found no correlation existed between departures and any combination of weather conditions studied. A similar variation in weather during departure period is true for Pectoral Sandpiper data (table 2), though to a lesser degree.

If the study at O'Shaughnessy Reservoir had been concerned only with the influxes of birds, a hypothesis might be erected that variables associated with cold fronts stimulate migration of those species observed. When departure data (decreases) are examined, it is apparant, however, that departures of some birds from the area did take place under a variety of weather conditions and that there were individual differences in reactions to changing weather conditions. The examination of departure data, even of one year and small flocks of birds, necessitates consideration of additional hypotheses to explain the variations observed:

(1) Not all of the individuals of a species reacted the same way at the same time to weather. Whether this is due to physiological state, or to motivational level, or to both, is the subject of proposed research.

TABLE 4

Decreases in daily counts of Black Ducks and weather data, O'Shaughnessy Reservoir, Fall 1952, 1953, 1954*

Date of decrease	Percent change in cloud cover	Change in air temperature	Change in wind direction	Date of last cold front
1952				
October 24–25	00 to 00	50 to 66	W to NE	October 19–20
October 28–29	75 to 75	41 to 32	NW no change	October 27–28
November 3–4	100 to 100	49 to 32	NW to SW	November 2–3
November 14–15	00 to 90	40 to 33	S no change	November 9–10
November 19–20	100 to 25	50 to 49	NW no change	November 19–20
November 29–30	100 to 90	29 to 28	SW to NW	November 26
December 2–3	100 to 100	30 to 28	SE to N	November 26
1953				
November 1–2	00 to 00	65 to 56	SW no change	October 23–24
November 8–9	25 to 100	37 to 40	SW no change	November 3–4
November 14–15	100 to 00	42 to 22	SW no change	November 3–4
December 13–15	90 to 00	43 to 22	SE to SW	December 12–13
December 16–17	50 to 00	22 to 8**	SW to NW	December 16–17
1954				
November 14–15	0 to 0	42 to 36	SE to NE	November 14–15
November 19–21	100 to 100	57 to 41	SW to NW	November 19–21
November 28–29	0 to 100	32 to 42	SW to NW	November 29–30
December 17–20	100 to 100	31 to 37	SE to SW	November 29–30

*Data reported are those recorded at the start of consecutive daily censuses.
**Area freezing over.

(2) Weather stimuli other than that associated with fronts brought about migration.

At any rate, the use of departure data has made possible an examination of the circumstances under which migration was initiated (tables 2 and 4). Even though the exact departure was not noted, daily weather records make possible a fairly reasonable testable hypothesis about the conditions during which the departure must have taken place.

With both the sandpipers and ducks in the foregoing sample, the data presented here are not sufficient to offer any but a point for discussion. Many of the problems arising from the use of arrival and departure data, as discussed previously, remain unsolved. Some indication *is* given by the departure data that appearance of these birds correlated with cold fronts may be due to stimuli inherent in the air mass following the front, rather than in the immediate influence of the front, and the data serve as examples of the approach possible.

Perhaps most important, the examination of departure data has raised questions regarding specific migratory stimuli, the nature of influxes or waves, the distance of flight in relation to influxes, the dynamics of physiology and motivation in migration, and will initiate continuing study on avian biology along channels that may not have been foreseen via the study of influx data alone. If additional information shows a lack of correlation between those weather phenomena commonly measured and departures from a study area, attention will be turned to other environmental stimuli, including, for example, social facilitation, upper air masses, hunger cycles, etc. If additional data do show a better correlation between certain weather phenomena and departures, the data already accumulated may be examined for sampling errors, and experimentation may be directed into the exact nature of these stimuli and their reception by the bird.

The apparent correlations noted between arrivals and frontal passage in the fall and, similarly, that between arrivals and southerly winds in the spring may lead to a feeling of satisfaction in the investigator which is not warranted, and may gloss over actually complex and dynamic processes in bird migration rather than stimulate increasingly critical approaches to the problem. An intense study of both arrival and departures should provide more precise information on significant environmental variables involved in migration and may direct laboratory investigation regarding the development of migratory behavior in the individual and in the group.

SUMMARY

Problems are discussed concerning the interpretation of field data on bird migration. Particular problems noted are (1) the number of birds observed may not reflect the true migration pattern; (2) physiological changes in birds may result in their differing in response to succeeding migratory stimuli; (3) the appearance of birds may reflect a cessation of migration, and (4) statistical treatment of such field data is difficult.

The limitations due to use of only influx data are considered. The additional use of departure data may give more direct evidence as to factors, initiating migration, as weather variables and behavorial changes in the birds may be measured directly and compared with noted decreases in bird populations.

Examples of additional problems met when examining both influx and departure data are given from studies of shorebird and water-fowl migration in Central Ohio.

Consideration of departure data may cast doubt on the conclusions based solely on influx or arrival data, and may lead to new lines of study, and an increasingly critical attitude of the observer toward problems of the study of bird migration.

Note

Recent papers by Lack (see Lack, David. 1959. British Birds 52: 258–267, Ibis 101: 209–234) received too late to be discussed in this paper support some of the general inferences of this manuscript. Radar observation by Lack ". . . confirms that the migration visible by day may be not merely incomplete but also unrepresentative of what is passing overhead." The use of radar, while it entails certain difficulties and has limitations, does provide a method of obtaining masses of arrival and departure data which lend themselves to precise analysis.

LITERATURE CITED

Ball, S. C. 1952. Fall bird migration on the Gaspe peninsula. Peabody Museum Nat. Hist., Yale University, Bulletin 7. vii+211 pp.

Bennett, H. R. 1952. Fall migration of birds at Chicago. Wilson Bull. 64: 197–220.

Crissey, W. B. 1955. The use of banding data in determining waterfowl migration and distribution. J. Wildlife Management 19: 75–84.

Dennis, J. V. 1954. Meterological analysis of occurrence of grounded migrants at Smith Point, Texas, April 17–May 17, 1951. Wilson Bull. 66: 102–111.
Devlin, J. M. 1954. Effects of weather on nocturnal migration as seen from one observation point at Philadelphia. Wilson Bull. 66: 93–101.
Farner, D. S. 1950. The annual stimulus for migration. Condor 52: 104–122.
———. 1952. A review of Lowery, G. H. Jr. 1951. A quantitative study of the nocturnal migration of birds, 1951. University of Kansas publications of the Museum of Natural History 3: 361–472. Bird Banding 23: 43–44.
———. 1955. The annual stimulus for migration: experimental and physiologic aspects. Recent studies in Avian biology. University of Illinois Press, Urbana, ix+479 pp.
Lack, D. and E. Lack. 1953. Visible migration through the Pyrenees: an autumn reconnaissance. Ibis 95: 271–309.
Lowery, G. H. 1945. Trans-Gulf spring migration of birds and the cortal heatus. Wilson Bull. 57: 92–121. Wilson Bull. 57: 92–121.
———. 1951. A quantitative study of the nocturnal migration of birds, 1951. University of Kansas publications of the Museum of Nat. Hist. 3: 361–472.
——— and **R. J. Newman.** 1955. Direct studies of nocturnal bird migration. Recent studies in Avian biology. University of Illinois Press, Urbana, ix+479 pp.
Miskimen, Mildred. 1955. Meterological and social factors in autumnal migration of ducks. Condor 57: 179–184.
Moreau, R. E. 1953. Migration in the Mediterranean area. Ibis 95: 329–364.
Newman, R. J. 1952. Studying nocturnal bird migration by means of the moon. Museum of Zoology, Louisiana State University. 49 pp.
Raynor, G. S. 1956. Meterological variables and the northward movement of nocturnal land bird migrants. Auk 73: 153–175.
Snow, D. W. 1953. Visible migration in the British Isles: a review. Ibis 95: 242–270.
Swinebroad, J. 1956. Some aspects of the role of weather in bird migration. Unpublished dissertation, The Ohio State University. 333 pp.
Williams, G. G. 1945. Do birds cross the Gulf of Mexico in spring? Auk 62: 98–111.
Winner, R. W. 1957. A study of local and migratory movements of black and mallard duck populations in central Ohio. Unpublished dissertation, The Ohio State University. 139 pp.
Wolfson, A. 1954. Weight and fat deposition in relation to spring migration in transient white-throated sparrows. Auk 71: 413–434.