

ON THE TEMPORAL PATTERN OF NOCTURNAL
MIGRATION IN THRUSHES

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ONE of the singular paradoxes in investigations of nocturnal migration in America has been the apparently contradictory results between studies based on observations of migrants silhouetted against the face of the moon (Lowery, 1951) and the studies of Ball (1952) by counting flight calls of migrating thrushes. Lowery and Newman (1955: 238, 258-262) discuss this discrepancy, noting that reports of numerous moon watchers scattered over North America indicated that normally nocturnal migration shows a pattern of an increasing number of migrants in the period before midnight, with a single peak in the hour before midnight, a sharp drop thereafter, and usually little evidence of migratory movement in the predawn hours (Lowery, pp. 414-417; Lowery and Newman, pp. 258-260). Ball's work, based upon counting of flight calls by thrushes over a period of 12 years in autumn in the Gaspé, eastern Canada, indicates the opposite. Ball recorded by far the greatest number of calls in the predawn hours after midnight. Though Ball noted a minor period of activity in the early evening before 10 P.M., the second (very much greater) peak occurred during the hour or so before dawn, and with practically no activity about midnight. Ball's work convinced him that some migrating thrushes, after resting, arise an hour or two before dawn and proceed some distance before being grounded by daylight.

To explain these discrepancies, Lowery and Newman (pp. 258-262) made various suggestions, based chiefly upon the differing techniques of the two methods; but they admit that their efforts to reconcile the results seem inadequate. The most obvious explanation, that calls can only be heard when birds are rising or descending and not when they are flying high (for Ball estimated that 1,500 feet was about as far in vertical distance as the calls could be distinguished), was discounted by Ball, who tried to test this possibility by listening about midnight at higher elevations. But still he heard no flight calls.

The present paper compares with those of Ball the results of flight-call counting and other techniques used in Europe. In general they give support to the conclusions of Lowery and Newman based upon counting silhouettes of birds as they cross the face of the moon. Some suggestions are made for the reinterpretation of Ball's data, based upon the local situation in the Gaspé.

THE EUROPEAN DATA

During the autumn of 1950, I (1954) made flight-call counts of those migrant species which, in Holland, can be most easily heard at night. These nocturnal migrants included several species of thrushes (*Turdus*). In 1950, I made observations each night between 8:00 and 10:00. One or more additional one-hour observations were made at other times of the night and also after sunrise. The highest frequency of sounds generally occurred before midnight. In 23 hours of observation before midnight (the evenings with bad weather are left out), an average of 10 call notes per hour was heard. In 35 hours of observation after midnight, the average was six call notes per hour. I continued the observations in 1951, 1952, and 1953, but they have not been worked out in detail. However, no material change in the distribution pattern of thrush calls was noted. If anything, in 1951 there appeared to be a smaller proportion of thrushes migrating after midnight than in 1950.

During four exceptional nights (out of 17) in 1950 there were more call notes between 4:00 A.M. and 6:00 A.M. than between midnight and 4:00 A.M. The predawn increase in these four nights was from 4 to 20, 1 to 48, 8 to 40, and from 4 to 8 call notes per hour. Such predawn activity was found to occur when one or more of the following conditions were present: (a) before or during passage of a cold front; (b) after unfavorable weather conditions, with the weather improving during the latter part of the night; (c) after a drop in temperature (frost), with the drop in temperature greater in the predawn hours.

All European observers have found the nocturnal pattern of migration similar to that which I have observed. Siivonen (1936) in Finland made observations on call notes of migrating thrushes (*Turdus*) in autumn. He noted that the number of call notes increased until about 10:00 P.M. After that the rate declined in general, reaching zero at about 1:00 A.M. He made no observations during the remainder of the night, although he showed with a recording apparatus (*l.c.*) that there was a second peak from 4:00–6:00 early in the morning. He showed further that in captive birds there was a clear increase of *Zugunruhe* (migratory restlessness) about that time. I (1954) found, as mentioned above, the same increase in some cases. Possibly this predawn increase in *Zugunruhe* is rather general and applies to actually migrating birds. Perhaps they leave their roosts after a period of rest only when this second peak in *Zugunruhe* reaches a high value. Siivonen and I found that this increase in some cases even lasted until some hours after daybreak.

Palmgren (1949) in Finland noted the same fluctuation of *Zugunruhe* with a similar apparatus (the actograph) as Siivonen. He states (p. 571): "The activity graphs of the nocturnal restlessness of night-migrating insectivorous birds (*i.e.*, Song Thrush, *Turdus philomelos*), agree very closely in form with the rhythm of night migration as observed in nature. The activity starts, as a rule, after a short period of sleep ($\frac{1}{2}$ -2 hours), culminates before midnight and fades out gradually." Palmgren gives graphs of the nocturnal restlessness of two Song Thrushes in autumn. Both of them showed more or less restlessness until 3 A.M., but far more before midnight. At about 4 A.M., a new short period of restlessness began. Palmgren (*l.c.*) says on this second period: "In some individual birds the outburst of restlessness occurs in the last hours of the night."

P. W. P. Browne (1953) also observed and counted the call notes of migrating thrushes in autumn at night near Dublin in Ireland. He does not mention in this paper his hours of observation, but in a letter to me he wrote: "Most of the listening was carried out at times when calls were coming at a maximum rate (about 22:00-23:00 G.M.T.)." It is unfortunate that he did not observe further on in the night.

Sutter (1957), near Zürich, Switzerland, found with radar that as a rule there seemed to be more migration before midnight than after it in autumn. However, in one case (out of eight) there was more migration after midnight than before.

According to Spencer (1952), Darlington came to similar conclusions in England. He says: "Graphs show intense passage after dark reaching a peak and then rapidly declining, with little movement in the early hours of the morning. Probably renewal of activity shortly before dawn is indicated in Darlington's paper." W. G. Harper (1959) points out that recent radar studies in Britain confirm the conclusions of Lowery as to the maximum time of nocturnal migration.

POSSIBLE REINTERPRETATION OF BALL'S DATA

Summary of Ball's observations. Ball (1952) recorded thrushes by their call notes in autumn from 1940-1951, but he observed continuously only in the seasons of 1947-1950. His main observations were made on the narrow, southeasterly projecting Forillon at the tip of the Gaspé Peninsula, Canada, south of the St. Lawrence River. The thrushes he observed were the Olive-backed (Swainson's) Thrush (*Hylocichla ustulata swainsoni*), the Hermit Thrush (*H. guttata faxoni*), and Bicknell's (Gray-cheeked) Thrush (*H. m. minima*).

Except for one large evening flight (at Maria on the south coast of

Gaspé Peninsula) of 450 birds, fully 90 per cent of the calls of migrant thrushes were recorded in the hour before dawn. In fact, Ball recorded 32,700 thrush calls after midnight, but only 1,221 calls before 10 P.M.—a ratio of 27 to 1. That migrant thrushes were seldom heard by him between 11:00 P.M. and 3:30 A.M. was confirmed during more than 50 observation periods of two to three hours in 12 seasons at Gaspé. Since thrushes were noted in four cases during the night, he inferred that the great dawn flights of vocal migrants comprised not large flocks of birds that had flown all night from some distant source but rather an accumulation of small groups that had arisen, perhaps after midnight, from various areas within the river system. This conclusion was supported by the greater numbers heard in the lower parts of the valleys.

Ball also states generally that the same nocturnal pattern of thrush migration was noted by him in New England (Connecticut). As he does not give any specific observations, no analysis is possible.

An interpretation of Ball's data based on the local geography. It is curious enough that so few thrushes were heard migrating in the evening on the Gaspé Peninsula. Moreover, why were there so many flight calls in the early morning?

1. Throughout his study, Ball expressed the view that his migrating thrushes were chiefly the local breeding birds of the Gaspé Peninsula. However, he says (p. 191): "it is believed that in autumn some birds reach Gaspé from Anticosti (visible across 40 miles of water)." In his opinion the thrushes that breed north of the St. Lawrence River normally follow the north shore and as a rule do not cross it to the Gaspé. They should cross it more to the west, where the river is narrower.

This seems contrary to what has been found in Europe. Wider stretches of the North Sea, for instance, are crossed very often (*e.g.*, *Turdus pilaris*, Schaanning, 1948; *Turdus merula*, Holgersen, 1953). On two occasions I saw Blackbirds (*Turdus merula*) going off across the North Sea at The Hague at about sunset. In April 1958, many Blackbirds and also other thrushes which came from over the sea were heard on the beach there.

Ball's conclusions are supported by the following observations (p. 191): "both evening and dawn movements are mainly radial in valleys, and numbers greater at lower ends; numbers smaller in tributary valleys that lack good passes at their heads; no faint call-notes high above the ground, few above 300 feet; none above the tops, not only of the highest Shickshock mountains (4,000 feet), but even over mountains of moderate height; preliminary studies reveal no high-level migrants

crossing the moon's face; local population is much greater than required to account for the number of migrants."

However, none of these observations is really conclusive. The only observations which would reveal the truth would be observations near the coasts of the St. Lawrence itself, and these have not been made so far.

2. Ball's chief observation place was Sandy Beach. This spot is on the south shore of Gaspé Bay, which here appears to be seven miles broad. In my opinion (based upon observations on the coast of the North Sea), there are not many migrating thrushes to be expected in such a locality in the evening, for the following reasons:

(a) Thrushes that have to cross a broad stretch of water like the St. Lawrence are likely to start at about sunset. When they have arrived at the coast of Gaspé Peninsula, they will as a rule not immediately proceed much farther inland, because the mountains are a barrier to an easy passage. They are likely to rest after crossing the St. Lawrence.

(b) When the weather is good and there is no change in wind direction (Vleugel, 1954), thrushes will try to proceed farther inland. This second start is begun in general some hours before sunrise (see Siivonen, 1936; Palmgren, 1949; and Vleugel, 1954). However, on most occasions the thrushes will not start again that same night. They are more likely to continue farther south by day, as I have often seen. This has been observed in the United States, too (Dennis and Whittles, 1955; 1956). Bagg (1957: 325) reports also daytime movements of nocturnal migrants (warblers) during the spring of 1957. The thrushes that have landed north of Sandy Beach need only fly 8 to 10 miles to reach Gaspé Bay. As the urge to migrate is lowest during the "second night-migration" and the flight by day, few thrushes will make a second overwater flight to cross Gaspé Bay. Instead, they will proceed along the north shore of Gaspé Bay and will not be heard or seen at Sandy Beach. It is thus understandable that during the evening and early night there are hardly any thrushes migrating over Sandy Beach. For similar reasons in the spring I do not usually hear thrushes on the Dutch coast before about 10:30 P.M. This can be explained by assuming that they need three hours or more to cross the North Sea, which is about 200 kilometers broad here. Presumably the same reason applies at Sandy Beach: one cannot hear the call notes of the thrushes before they have arrived.

My opinion is supported by Ball's own observations. On p. 86 he notes that on 20 September 1949, he made observations at Maria on the coast of Chaleur Bay. The wind was from the east (5 m.p.h.). He

says: "Along this shore and on the fields 450 thrushes passed during the period, 7:35-9 P.M." This observation suggests that many birds must have collected there previously on or near the south coast of Gaspé Peninsula.

My conclusion is that Ball, as a rule, missed the first flight of thrushes that crossed the St. Lawrence in the premidnight hours. He generally counted only the "second flight" in the last hours before sunrise, and this he could only do when the weather was so good that the birds continued on to cross Gaspé Bay. As can be seen from his Table 3 (p. 92), there were only a few nights during which a good number of migrating thrushes were counted: in 1947, Aug. 18-Sept. 30 (44 days) only 7 nights; in 1948, Aug. 16-Sept. 30 (46 days) only 8 nights; in 1949, Aug. 19-Sept. 30 (43 days) only 15 nights; in 1950, Aug. 21-Sept. 30 (41 days) only 16 nights.

This can be explained if we assume that thrushes cross a broad stretch of water like the St. Lawrence only in good weather. Ball's weather data (p. 92) indicate that thrushes were noted only with light air or slight breeze. Out of 46 days with good or rather good flight-call counts in four years (1947-1950), there were only three days when the wind strength exceeded 5 m.p.h. We cannot wish a better indication that the thrushes Ball counted at before dawn on the Forillon probably crossed the St. Lawrence in the evening and then crossed the Gaspé mountains after a rest during the night. We know from the literature that also in Europe mountains are crossed in the early morning by night migrants (summary in Lack and Lack, 1953).

There is another possible reason, in my opinion, why the number of early morning call notes noted by Ball might be too high in comparison with those in the hours before midnight. Thrushes are early risers, and local birds habitually call and fly about at dawn. In addition, in autumn they have social roosts from which they fly in movements that may be confused with migration. In my paper (1954), I omitted thrush calls during the last hour before sunrise because I found it impossible to say which sounds were coming from actually migrating thrushes and which sounds were made by local thrushes flying around or leaving their roosts.

According to Ball's Table 1 (p. 55), 90 per cent of his call notes of thrushes during five mornings were recorded *in the last half hour before dawn*. To avoid confusion with local birds, I have found it necessary to omit call notes the first hour before sunrise and after sunset, except when the birds are unequivocally observed migrating. (Whether the period disregarded should be half an hour or a whole hour is uncertain; perhaps a period of three quarters of an hour would suffice. I have

recorded call notes of many resident thrushes for half an hour after sunset and some 10 minutes longer.) This may not be a major source of difference in Ball's data and mine, but it is a factor that should be considered.

Graber and Cochran (1959) have recently recorded automatically, with a device using a parabolic reflector, the calls of migrants in Illinois on 125 nights. They conclude (pp. 229-233) that at least some species migrate throughout the night and report that often a marked increase in the number of calls was recorded during the predawn hours. However, they believe that this does not indicate an increase in the number of migrants, but probably reflects only an increase in the frequency of calling. This was sustained by observations made during the autumn of captive *Hylocichla* thrushes (the group which provided Ball with his major data); these thrushes called most in the predawn period. As a further partial explanation of Ball's results, Graber and Cochran (p. 233) suggest, though this was discounted by Ball (1952: 57) and Lowery (1951: 419), that birds may possibly fly higher during the middle hours of the night, and thus be out of hearing.

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SUMMARY

Studies in America based on observations of migrant birds silhouetted against the face of the moon suggest that the peak of nocturnal migration usually occurs during the hours before midnight. On the other hand, a 12-year study by Ball using the technique of counting thrush flight calls in autumn on the Gaspé Peninsula, eastern Canada, indicated to him that the peak of migration was in the early morning hours.

Flight-call counting of migrant thrushes in Holland by the writer, and elsewhere in Europe by others, indicates that (except under unusual weather conditions) many more flight calls are noted in the hours before midnight than in the hours before dawn. Studies in Europe of *Zugunruhe* (migratory restlessness) in captive birds and published radar data appear to confirm the view that in Europe the peak of nocturnal migratory activity generally comes before midnight, with a lesser peak before dawn. Perhaps many migrating birds rest during

the postmidnight hours, sometimes resuming migration in the predawn period.

A possible reinterpretation of Ball's data, based mainly on the location of his observation area, is suggested: 1. Ball's main site on the Gaspé Peninsula was not only south of the wide St. Lawrence River, but on a southeastern projection south of Gaspé Bay. Birds migrating across the St. Lawrence before midnight would not be heard by him unless they also crossed Gaspé Bay, and this second crossing would occur the same night only with favorable winds, and presumably in the predawn hours after the birds had rested. Usually they probably avoid crossing Gaspé Bay by coasting along it by day. 2. In his counts Ball included calls heard in the first half hour before dawn; these probably included calls of local thrushes leaving roosts or flying around. Furthermore, it is possible that a tendency of *Hylocichla* thrushes to call more during the predawn period may have contributed to his results.

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