THE INFLUENCE OF WEATHER ON PASSERINE MIGRATION. A REVIEW*

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INTRODUCTION

THE present review was undertaken as background for my studies (1959a, 1960, and in progress) of migration by radar. I have sought to include all important field observations, published before the end of 1958, on the influence of weather on migration; but as reports of such observations not infrequently occur in papers dealing primarily with other topics, some have doubtless been overlooked. Many trivial and passing references, together with unsubstantiated opinions, have been deliberately omitted. I have, however, included the laboratory studies on migratory restlessness, and, since weather influences cannot be understood apart from the bird's internal state, the latter is also discussed, though not in such detail, owing to the comprehensive review by Farner (1955). I am extremely grateful to A. M. Bagg, W. R. P. Bourne, R. E. Moreau, and A. C. Perdeck for reading and criticizing the whole manuscript and to R. J. Andrew, J. M. Cullen, R. A. Hinde, and N. Tinbergen for detailed discussion of the terminological and other problems connected with the internal state of the bird.

Cooke (1888) was the first to correlate migration, in this case spring arrivals in the United States, with temperature and pressure, and, as pointed out by Bagg *et al.* (1950), his conclusion was essentially correct. The next sustained study appears to have been that of Eagle Clarke (1912), who between 1898 and 1912 visited many islands and lighthouses around Britain to watch migration. He did not publish his data in quantitative form, and evidently did not analyze them statistically; but his conclusions were based on so much intensive field work that most of them are still accepted. He concluded that migration is favored by fine, anticyclonic weather, also by warmth in spring and cold in autumn, while strong winds and rain are unfavorable. What are called "rushes" in England and "waves" in America occur primarily when favorable weather follows an unfavorable spell. Clarke further argued that southeasterly winds favor migration between Britain and the Continent in both spring and autumn, but as suggested by Coward (1912) and established by Williamson (1952, 1955), much of the migra-

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* This review of one small aspect of ornithology is dedicated to Prof. Erwin Stresemann, the last man to review all branches of ornithology, on the occasion of his 70th birthday.

tion to Britain with easterly winds is really due to drift. The views of Thomson (1926) were essentially those of Clarke, except that the influence of wind direction was considered doubtful.

In both field and laboratory, nearly all observations on weather and migration have been made on passerine species. Hence the present review is concerned primarily with this order of birds, and, unless specified, general remarks refer only to passerines. Furthermore, all the work reviewed here was carried out in north temperate latitudes, and none in the tropics, for which further information is badly needed.

TECHNIQUES

With the exception of Clarke, the earliest students of the subject, notably Hegyfoky (1908) and Schenk (1924, 1925) in Hungary, Defant (1913) in Austria, Cooke (1913) in North America, and a few others discussed by Thomson (1926), chiefly analyzed dates of first arrival. They considered a great deal of data, and while dates of first arrival are not a very satisfactory way of measuring the volume of migration, many of these early conclusions with respect to the weather are still acceptable.

After this early work, there was a lack of research until, particularly after World War II, two techniques pioneered by Clarke were used extensively. Quantitative observations on diurnal migration in progress were initiated on the Dutch coast by Verwey, followed by Van Dobben, Tinbergen, Deelder, and others (see review by Van Dobben, 1953). Observations were later undertaken at Öland, Falsterbo, and elsewhere in Sweden (see review by Svärdson, 1953) and on a much smaller scale in England (see review by Snow, 1953). In all three countries, detailed studies have been restricted to the autumn, since much less migration is visible in spring. On the basis of this work, Dutch investigators in particular have reached important conclusions on the behavior of migrants, notably with regard to coasting. But in assessing the influence of the weather on migration, this technique has an exceedingly serious drawback, since birds often migrate by day above visual range, and the proportion doing so varies with weather and other factors. To cite an extreme example from my radar work in Norfolk in April 1958: On those mornings on which radar detected a large seaward emigration, many migrants were visible from the ground with opposing winds, whereas none, or hardly any, were visible with following winds (Lack, 1960).

The second technique is the regular counting of night migrants on the ground by day after their passage. This has been undertaken, especially in the United States, chiefly in spring but also in autumn (Bagg *et al.,* 1950, and others cited later), and at British coastal and insular bird observatories, chiefly in autumn but also in spring (Williamson, 1955, and various writers in "British Birds," *seriatim*). This method has yielded valuable conclusions on diverse topics, but for analyzing weather influences, it likewise suffers from serious drawbacks. First, since it is the weather at the point of departure that is critical, an important step in the argument, namely the place of departure of the observed migrants, has to rest on inference. Probably the inference has often been correct, though some doubt must always remain, while occasionally it would seem to have been incorrect. Second, if the migrants are liable to drift off course, they may have started from different areas on different occasions, a difficulty that applies particularly to insular and coastal observatories. Here, for instance, the presence of migrants from a particular area on one day and their absence on another might be due, not to differences in the weather at the place of origin, but merely to the direction of the wind on their journey. This, as already mentioned, misled Clarke (1912); and Svärdson (1953) could still claim that, because of this effect, British observers exaggerate the importance of easterly winds for migration. Drift may be as prevalent over the land as over the sea, but is probably a less-serious source of bias. Its importance in continental United States was shown by Trowbridge (1895); see also Peterson (1948: 161–163) and Bennett (1952).

Third, and most serious, the number of night migrants alighting need not be proportionate to the number that passed overhead. Lowery (1951) cogently argued that concentrations of night migrants occur on the ground only at a meteorological barrier or in an "oasis" of suitable habitat (including islands). Hence "rushes" or "waves" of night migrants may provide a misleading idea of normal migration. On a continent, such "rushes" are chiefly precipitated by the rain and mist at a cold front (*e.g.,* Imhof, 1953; Bagg, 1956, 1957), while on islands, they also occur when birds have previously been drifted a long way off course over the sea. The belief that the number of migrants alighting may represent a highly variable proportion of those passing overhead was supported by my radar observations in autumn in Norfolk: Four times in September 1958, radar revealed fairly large, southwestward arrivals of night migrants, after which, respectively, many, some, very few, and none were seen in the bushes at Blakeney Point. Clearly, it is dangerous to base conclusion as to the volume of migration passing overhead on the number of night migrants seen on the ground next day. Nevertheless, especially when its limitations are recognized, this method has yielded valuable results, as shown, for instance, by Bagg *et al.*

(1950) in the United States, while British observatory investigators have analyzed the weather conditions favoring drift (Williamson, 1955).

Recently, two new techniques, which do not suffer from the above defects, have been employed to measure the volume of migration. Lowery (1951; Lowery and Newman, 1955) counted night migrants crossing the face of the moon, and from this count calculated the true numbers passing. This method permitted direct quantitative observations on night migration for the first time, but it is usable only on clear, moonlit nights, so has limited application to the problem reviewed here. Still more recently, Sutter (1957a,b) established the value of radar, and while the density of echoes cannot be related to the true number of birds flying, radar provides a relative measure of abundance that can be used all day and all night, only those migrants flying very low being undetected (Lack, 1959a). Species cannot be identified by radar, though identification can sometimes be inferred. But while this limitation must be kept in mind, it may not greatly matter in the present context if, as seems possible, most passerine species have rather similar responses to weather. The last point needs checking. For the present, the best method is probably radar combined with visual observations.

After a reliable quantitative record of migration has been obtained, it is important to analyze it in terms of all the likely weather factors by a multiple regression equation, and, for statistically significant results, a large series of observations may be required. What has sometimes been done is to examine the possible influence of one weather factor in isolation; but since the various weather factors are usually linked, this can be very misleading. When all the factors favoring migration tend to occur simultaneously, as for birds crossing from Holland to Britain in October, it may be particularly hard to tell which are critical and which coincidental. There is the final difficulty that the effects of the weather are probably not constant, but may well vary with the internal state of the bird.

In the laboratory, one further technique has proved valuable, namely the observation of migratory restlessness *(Zugunruhe)*. The review by Farner (1955) leaves no serious doubt that migratory restlessness can be regarded as the laboratory equivalent of migration itself. In captive passerines, it is not shown by nonmigratory but is highly characteristic of migratory forms. Further, in untreated birds, it normally starts in spring and ends in autumn at the same times as the normal migrations of the species. It is true that, as found by various investigators, the latest being Weise (1956), restlessness may continue throughout the summer, long after the normal cessation of spring migration, and stop only with the molt. But it may reasonably be inferred that this is because the captive birds have been unnaturally prevented from breeding. This view is supported by observations (Kay, 1944) on a pair of captive Snow Buntings *(Plectrophenax nivalis)* in a big outdoor aviary, which showed migratory restlessness only until the male, and 15 days later the female, switched to breeding behavior; the female paid no attention to the male's courtship until she too had, so to speak, "arrived," and then the pair bred successfully. Also, Wagner (1957b) showed recently that gonadal hormones may inhibit migratory restlessness in summer.

Migratory restlessness therefore provides an important means for testing the influence of both external and internal factors on migration. Further, it can be recorded automatically, and though in some early studies it may not always have been clearly separated from other forms of restlessness, this difficulty has been overcome (cf. Wagner, 1957a). Moreover, the directional element investigated by Kramer (1957) and Sauer (1957) now provides an additional criterion for its recognition.

CLIMATE AS AN ULTIMATE FACTOR

In general, the spring migration of each species appears to be so timed that the birds arrive on their breeding grounds at almost the earliest moment that they have a reasonable chance of surviving there. In many species, especially in the far north, this is only a few days before breeding starts, but in many others, especially in temperate latitudes, the birds may arrive well before breeding, in order to establish territories and form pairs. The Robin *(Erithacus rubecula)* in England is a good example of the latter group, those females that are migrants arriving to form pairs with the resident males some two-three months before nesting (Lack, 1943). Again, the autumn migration of most species appears to be so timed that the birds leave their breeding grounds ahead of the period when their continued survival there would be precarious. Some species leave well before this time, others only shortly before, depending on the molt, and on feeding conditions along the migratory route and in the wintering grounds. There are also a few species that depart only when survival becomes precarious, as discussed later under hard-weather movements.

Both the date in spring when it becomes possible to settle on the breeding grounds and the date in autumn or winter when survival there becomes precarious depend especially on the availability of food, which in turn depends greatly on day length and climate. In this sense, climate has an important influence, through natural selection, on the seasons of migration that have been evolved by each species; but as stressed by several recent authors, this does not necessarily mean that the migrants in question respond directly to those weather factors that are critical for their survival. In particular, as just mentioned, they usually leave in autumn before the time when survival would become precarious.

In this ultimate and long-term sense, the influence of the environment on migration will not be considered further here, except for one set of observations, the significance of which, though appreciated by their author, has sometimes been misunderstood by others. Using the method pioneered by Cooke (1913) in North America, Southern (1938–1941) plotted on maps of Europe the mean dates on which various summer visitors first arrived, and showed that these "isochronic" lines move northward in spring more or less in parallel with the mean isotherms. All that this implies is that temperature gives a good indication of the season at which each area normally becomes suitable for the species in question to settle on it for the summer. It does not necessarily mean that the species migrates in direct response to temperature, and it certainly does not mean that individual migrants travel northward at the slow speed of the "isochronic" lines. The last point was demonstrated for the Yellow Warbler *(Dendroica petechia)* by Phillips (1951) in Arizona, where the earliest race to arrive, in mid-March, is the summer resident *sonorana,* while more northern races do not reach Arizona until late April, and the northernmost *rubiginosa* not until late May or even June; *i.e.,* the northern forms pass through Arizona later than the southern forms. Bourne *(in litt.)* found a similar situation for Yellow Wagtails of the *Motacilla flava* complex in Cyprus. The first to arrive there in spring is the resident *feldegg,* later come members of *flava* itself and its close allies, which breed farther north, while the last to come is the arctic-breeding *thunbergi.* These forms leave the wintering grounds in tropical Africa in the same order (Curry-Lindahl, 1958).

The influence of climate on the evolution of migratory seasons is indirect, through its effect on the times when the breeding grounds become suitable for occupation in spring or unsuitable for survival in autumn. But the possibility has been raised by Williamson (1953) that climate may sometimes have had a more direct influence, migratory seasons having been evolved to coincide with those times that, on the average, are favorable for travel, and to avoid those times that, on the average, are unfavorable for travel. He advanced this view particularly because small passerine migrants leave northern Europe rather early in the autumn, when the Azores high tends to prevail in the Atlantic and the subtropical high in the Mediterranean, and before the period of disturbed weather that typically follows. Geese, in contrast, tend to leave later, perhaps partly in correlation with their breeding season and molt, and because, being stronger fliers, they are less affected by disturbed weather. This interesting idea remains speculative. I think it more likely that the passerine populations concerned have evolved their migratory seasons primarily through ecological considerations, especially those affecting their food supply on their breeding or wintering grounds or between the two. But this view is equally speculative.

Obviously, however, birds cannot migrate under very hazardous weather conditions, and natural selection may, perhaps, in some species have affected the average season of migration to at least this minimal extent.

Landsberg (1948) suggested that the times and routes of migration of diverse species have been evolved to take advantage of following winds for their journey. He was primarily concerned with nonpasserine, long-distance migrants, but the same correlation was also suggested by Williamson (1953) for passerine migrants travelling from Greenland and Iceland to western Europe in autumn. That Wilson's Petrel *(Oceanites oceanicus)* and the Greater Shearwater *(Puffinus gravis)* tend to migrate with the wind was earlier pointed out by Bourlière (1946), and later for various other species of petrels by Kuroda (1957). These species travel great distances so that, though they are capable fliers, the evolution of their routes might conceivably have been influenced by wind direction. Even so, however, I would suppose that ecological considerations, especially of food supply, are more likely to have been the overriding factor. For passerine species, nearly all of which travel much shorter distances than these petrels, I would think that ecological conditions would always be paramount. Bagg and Drury *(in litt.)* have suggested to me, however, that the seasons of migration in passerine species may have been selected in relation to travelling conditions in areas where seasonal changes in climate are relatively uniform and predictable, as in much of continental North America. My thinking on this point has perhaps been unduly swayed by the highly variable weather prevailing on the Atlantic seaboard of western Europe. Further study of this point is needed.

WEATHER MAKING MIGRATION CONSPICUOUS

It is important to distinguish the influence of weather in initiating migration from its influence in making migration conspicuous. As already mentioned, night migrants are precipitated by cold fronts and their attendant rain. In spring in northern Alabama, for instance, the average number of transient night migrants seen on the ground each day was nearly twice the average for the season with a cold front, about average with adverse winds, somewhat below average with southerly (following) winds or with rain unassociated with a cold front, and far below average on the few clear and warm days in the series observed (Imhof, 1953). Yet the last type of weather is generally accepted as being that most favorable for migration. Again, of six big groundings of night migrants in Texas, five occurred with cold fronts and northerly winds and one with a westerly wind (Dennis, 1954). Other good examples were given by Bagg (1956, 1957). With a cold front, night migrants continuing their flight evidently travel lower than usual, and they may be attracted to the lights on buildings, with the results that many may then be killed at airport ceilometers or television towers. There seem to be no records of this in Europe, a point deserving further study, but many in the United States (*e.g.,* Brewer and Ellis, 1958); the record ceilometer kill was 50,000 individuals of 53 species on the night of 8 October 1954 (Johnson and Haines, 1957). Night migrants are also attracted to lighthouses in rain or fog (Clarke, 1912) and may descend in large numbers on British islands or headlands in any type of weather after a long, overseas drift (Williamson, 1955; see also Lack, 1959b).

With regard to day migrants, adverse weather factors over the land usually inhibit migration altogether. But with strong head winds or rain, the birds sometimes fly lower without stopping, and thus come within visual range of an observer on the ground (Sutter, 1955; personal observations in England and southern France). The old belief that migration normally proceeds against the wind (cf. Gurney, 1923) is partly attributable to migrants flying lower against the wind, and so being more conspicuous. The fact that diurnal migrants may fly extremely high with a following wind was first demonstrated by Kramer (1931) and later proved for the Chaffinch *(Fringilla coelebs)* by the Dutch (review by Van Dobben, 1953).

The subject of the present section will not be considered further as it was included only as a warning, and the weather factors initiating or determining migration will now be reviewed.

GENERAL WEATHER SITUATION

In the United States in spring, nocturnal migration occurs chiefly in warm weather with southerly winds, commonly with a tropical airstream in the western part of an area of high pressure, and in the interval between a warm and a cold front, *i.e.,* the warm sector of a low-pressure system (Bagg *et al.,* 1950; Lowery, 1951; and others cited later). Likewise in Austria (Defant, 1910, 1913) and Hungary (Hegyfoky, 1908; Schenk, 1924, 1925), most migrants arrive in spring with warm, southerly or southeasterly winds, with high pressure over the Balkans and low pressure to west or northwest. In Scandinavia also, most migrants arrive with warm, southerly winds (Svärdson, 1953). In autumn, on the other hand, most migration in the United States occurs with cold, northerly winds, especially with the passage of a cold front (Bennett, 1952; and others). In Scandinavia in autumn, most nocturnal migrants depart in fine, anticyclonic weather with clear skies, light, easterly winds, and a fall in temperature, and the same holds for movements from Germany or Holland to Britain in autumn (Clarke, 1912; Jenkins, 1953; Griffin *et al.*, 1955; Nisbet, 1957a). But "rushes" or "waves" by day in Scandinavia are usually associated, not with anticyclones, but with the northwesterly winds and the drop in temperature characteristic of the hindside of a depression clearing toward the east or northeast (Svärdson, 1953; Nisbet, 1957a).

The usual view today is that migrants do not react to the general weather situation as such, but to one or more particular factors linked with it. The only recent authority to dissent from this view was Nisbet (1957a), who found that in autumn in Scandinavia "the general characteristics of the weather on the days of complete inhibition [of migration] varied considerably. . . ." This "suggests that the important factor may be cyclonic weather as such: that the birds do not react to the individual factors, either singly or in combination, but to a complex system of changes." Nisbet treated the situation solely from the viewpoint of bad weather acting as a deterrent, without refuting the alternative viewpoint that favorable weather factors might provide a positive stimulus to migration. Also, while he doubtless had more evidence than he published, he did not, in my view, convincingly distinguish his postulated response to the general weather situation from a response to separate weather factors, any one of which might deter migration. Nor did he meet the point made by Svärdson (1953) that in Scandinavia the actual weather associated with anticyclones and cyclones, respectively, varies so greatly in character with the time of year that it seems extremely unlikely that migrants are responding to the general weather situation as such (and Svärdson suggested that temperature was the critical factor).

Finally, my own findings (1960) based on radar show that the general weather situation as such had no important influence on the eastward emigration in spring from Norfolk in 1956–1959. In particular, the mean volume of emigration was the same for all anticyclonic periods on the one hand and for all periods of disturbed weather on the other. This was because, in March and April, anticyclones bring some factors (*e.g.*, clear skies and light winds), which, as will be shown later, are favorable to migration, and others (*e.g.*, cold), which are unfavorable to migration in spring. Similarly, disturbed weather brings some adverse factors, such as rain, cloud, and strong winds, but one favorable factor, warmth. Analysis made it clear that the volume of emigration was determined by these particular weather factors and not by the general weather situation as such.

In the reverse passage from Holland to Norfolk in autumn, all the particular factors favoring migration normally occur with anticyclonic weather and all those unfavorable to migration with cyclonic weather, so it has not yet been possible for me to separate their influence from that of the general weather situation. For the same reason, it was not justifiable for Williamson (1952, 1955) to conclude that the primary factor stimulating autumn migration in northwestern Europe is neither anticyclonic weather as such, nor cold, but the absence of wind, and also clear skies, since all these factors normally occur together in autumn, and he did not separate their effects, at least in his published papers. In most other areas in both autumn and spring, published data suggest that the factors favoring migration usually occur together, as do those unfavorable to migration, thus making analysis very difficult. This also raises the possibility that if all the factors favorable for migration normally occur with one type of weather situation, the birds might evolve a response to one "key" factor indicative of this situation. In particular, this may be why various migrants have an immediate response to temperature, as discussed later.

In summary, it can be stated that while most of the available evidence is inconclusive, that of Svärdson (1953) in autumn from Scandinavia suggests, and my own in spring from Norfolk establishes, that the general weather situation does not, in itself, have an important influence on the volume of migration.

BAROMETRIC PRESSURE

No recent investigator has claimed that barometric pressure as such has an important influence on migration, and those who specifically investigated it, such as Mascher (1955) in spring in Sweden and Raynor (1956) in spring in the United States, declared that it had no influence. Further, if the general weather situation has no influence, as concluded in the last section, it follows that atmospheric pressure has none. Finally, apart from some early claims not since substantiated, students of migratory restlessness have found that air pressure had no influence (Merkel, 1938; Wagner, 1957a; and others).

Hence the tendency for migration to occur chiefly in anticyclonic weather can safely be attributed to factors other than high pressure, and in particular to the concurrent light winds, clear skies, and, in autumn, cold. It should be added, however, that while in some areas at some seasons most migration occurs when pressure is high, notably in northwestern Europe in autumn, this correlation is by no means so general as some writers have implied. In particular, the emigration of winter visitors from England in spring is as frequent in rather disturbed, southwesterly weather as in anticyclonic weather (Lack, 1960). Likewise, most northward migration in eastern North America in spring occurs not in anticyclonic weather but in the warm sector of a depression (Bagg *et al.*, 1950; Gunn, 1958).

STABLE AIR

One investigator, Raynor (1956), claimed that the essential prerequisite for nocturnal migration in spring in the United States is stable air conditions, *i.e.*, with a temperature inversion. Such conditions obtained on 67 per cent of the many nights analyzed, whereas 76 per cent of the migratory movements and 86 per cent of the big waves of migration occurred with stable air. He postulated that stable air itself provided the stimulus, rather than some other weather factor linked with it, and that this was of value because, in stable air, the migrant does not have to expend so much energy combating air turbulence and keeping direction. He further postulated that the migrant is sensitive to a smooth air flow, and perhaps, as it rises up in the evening, to the changes in temperature that it experiences with height.

Although Raynor examined other weather factors, he did not make clear the extent to which they were correlated with each other, and he differed from other American observers in finding temperature unimportant. I therefore suggest that his figures might be re-analyzed, to see whether they are explicable in terms of wind strength, temperature, rain, and cloud, and that until this has been done, his conclusions should not be accepted. It may be added that, while on general grounds one might expect birds to avoid migrating in turbulent air, temperature inversions, at least around the North Sea, are often associated with mist or fog, which is unfavorable to migration.

MIST, CLOUD, AND RAIN

All authorities have agreed that migration is favored by clear weather, while fog, mist, and rain are unfavorable, and though statistical evidence is in most cases lacking, this conclusion can be accepted. The paucity or absence of migration in mist or rain has been reported in the following instances: the spring migration of ducks in Finland (Bergman, 1941), the spring return to Sweden of the Wood Warbler *(Phylloscopus sibilatrix)* (Svärdson, 1947) and various other passerine species (Mascher, 1955), the autumn passage of the Red-breasted Nuthatch *(Sitta canadensis)* in the Gaspé Peninsula (Ball, 1947), the diurnal movements of passerine migrants in spring in Suffolk (Ticehurst, 1932), and the diurnal movements of passerine species in autumn at Land's End (Lack and Lack, 1952) and in southwest Scotland (Goodbody, 1956). Further, rain and cloud inhibited the migratory restlessness of captive Snow Buntings *(Plectrophenax nivalis)* in an outdoor aviary (Kay, 1944), while Sutter (1957a,b, 1958), using radar, showed that autumnal migration did not normally occur in Switzerland in cloud or high fog, though it continued above fog up to 400 meters.

Finally, in my own studies (1960) of the spring emigration from Norfolk, a multiple regression analysis showed that, making full allowance for other factors, both rain and cloud had a significant effect in reducing the volume of seaward emigration. Further, when the emigration concerned was localized, this was normally correlated with rain in those areas from which no emigration took place.

A point requiring further study is the extent to which species differ in their response to rain. Thus, in both England and southern France in October, I have seen Chaffinches *(Fringilla coelebs)* migrating in large numbers during heavy rain when Skylarks and Starlings had ceased to travel.

With regard to behavior in fog, it is well known that migrants may then become disoriented, while they are attracted to lights. On foggy mornings at Land's End in October, I saw Skylarks *(Alauda arvensis)* repeatedly rising off the fields in the early morning as if to start on migration but then returning and alighting, evidently because of the fog, since when the fog lifted some of them departed. Also at Land's End I saw a huge flock of Starlings *(Sturnus vulgaris)* put out to sea in the direction of Ireland; but a short time afterwards some of them returned, presumably because they had encountered a patch of drizzle visible from the shore (Lack, 1952). Ticehurst (1932) saw various diurnal migrants setting out to sea from Suffolk in spring and returning because they had met fog or rain, and I (1960) have seen the same in Norfolk in spring. Since Kramer (1957) and Sauer (1957) showed that sight of the sun and stars is needed for orientation, one would expect migrants not to set out in total overcast, and to return to land on meeting total overcast at sea.

Nevertheless, the volume of high, seaward emigration tracked by radar from Norfolk in spring was not lower than usual with coastal fog, presumably because the migrants in question started inland in clear weather and flew above the fog out to sea. As already mentioned, Sutter likewise observed migration above low fog in Switzerland, while on one spring morning in Norfolk I tracked migrants arriving northwestward, presumably from the sea, which continued their flight over the land keeping above a belt of fog at a height of 1,200–1,600 meters. More remarkably, both Ash and Schifferli (cited in Lack, 1959b) have trapped migrants on passage that were released by day in fog and promptly flew vertically upward, presumably to continue their migration above the fog.

Complete cloud cover does not necessarily bring migration to a stop. If passerine migrants meet clouds at sea, they must continue, and they may also do so over the land. Thus, a statement by Tinbergen (1956) on orientation implies that there is a considerable diurnal passage of Chaffinches over Holland in autumn in fully overcast conditions. Again, Bagg *(in litt.)* informed me that in Massachusetts in spring in warm sector conditions involving complete overcast, he has often observed significant diurnal passage in raptors, American Robins *(Turdus migratorius)* and American blackbirds *(Icteridae)*. This subject needs further study.

WIND STRENGTH

It is generally agreed that light winds are favorable and strong winds unfavorable for migration. This was reported in the spring for the White Stork *(Ciconia ciconia)* in Hungary (Hegyfoky, 1908), for ducks in Finland (Bergman, 1941), for Chaffinches in Finland (Bergman, 1949), for many other small passerine species in Finland (Bergman, 1951), and for many passerine night migrants in Sweden (Mascher, 1955). Likewise in autumn, it was found for visible passerine migration in Britain (Lack and Lack, 1952; Goodbody, 1956), for many small passerine species in Finland (Bergman, 1951), and for night migrants in southwestern Europe (Jenkins, 1953), while, as already mentioned, Williamson (1952, 1955) attached particular importance to the absence of wind in initiating migration, though he did not publish critical evidence. Finally, my own (1960) radar studies of the spring emigration in Norfolk established statistically that more emigration occurred with light than strong winds; contrary to a preliminary statement (Lack, 1958b), the effect of the wind now proves to have been similar by night and day.

As in the case of rain, further work is needed on possible specific differences in the response to wind. Goodbody (1956) observed in southwest Scotland in autumn that, when the wind reached a certain strength, Skylarks continued to put out to sea, but Meadow Pipits *(Anthus pratensis)* ceased to do so. My own observations in southern England in October showed that migrating Chaffinches usually ceased travelling at a wind strength that did not deter Starlings and Skylarks.

WARMTH IN SPRING

In both Europe and the United States, nearly all investigators have agreed that spring migration is favored by warm, southerly winds. While this observation does not enable one to say whether it is the temperature or the wind direction that is critical, it strongly implies that at least one of them is important.

In Europe, arrivals with warm, southerly winds were recorded for the Swallow *(Hirundo rustica)* in Hungary by Hegyfoky (1908) and for a variety of passerine night migrants in Sweden and Finland by Rudebeck and Svärdson (1946), Svärdson (1947, 1953), Ulfstrand (1952), and Mascher (1955). In the spring of 1950, correlated with a marked difference in temperature to the southeast and southwest of

Sweden, respectively, migrants coming from the southeast were unusually early and migrants coming from the southwest were unusually late (Ulfstrand, 1952, who recorded the biggest arrival with a warm front). Rudebeck and Svärdson (1946) also stressed that the critical temperature is not that in Sweden itself but that in the area from which the migrants have come. Mascher (1955) noted that arrivals were most numerous just after a rise in temperature but decreased after a few days even when the temperature remained high, supposedly because the supply of birds in the south had become temporarily exhausted. Contrary to the findings of these observers, who stated or implied that arrivals occurred on the first day of warm weather, Bergman (1941) discovered that in Finland ducks migrated earlier in a warm than a cold spring, but that day-to-day changes in numbers were not correlated with changes in temperature. Later, working with many species, chiefly passerines, Bergman (1951) found that a rise in temperature in spring was usually followed by an arrival of migrants.

In Britain, Clarke (1912) stated that spring emigration was favored by warm, southwesterly weather, though it also occurred with anticyclones, which are normally cold. Hinde (1951) found that arrivals of terns and limicoline species in England in spring were associated with warm weather in the Bay of Biscay on the day of their arrival or on the previous day. The only factor seriously delaying the return of Swifts *(Apus apus)* to England in spring was found to be cold, anticyclonic weather with northerly winds. Other evidence strongly indicated that this species was not deterred by anticyclones or head winds as such; thus cold, which in this species directly affects the availability of food, was presumably the critical factor (Lack, 1958a). Finally, my observations by radar (1960) on the emigration from Norfolk in the spring of 1956–1959 showed that, when allowance had been made for other weather factors, warmth was favorable and cold unfavorable to emigration, the effect being statistically significant. The figures further suggest that the lower limit of temperature at which emigration occurred on an appreciable scale was some 10 degrees lower in March than February, and still lower in April. Hence, as found previously by Nice (1937), temperature had an obvious influence in the early but not the late spring.

In the United States, Cooke (1913), analyzing dates of first arrival over 10 years, found a tendency for northward movements to occur with rising temperatures. But a detailed analysis of three years showed that in 1885 two migratory waves coincided with warm spells but one with a cold snap, and though in 1889, movements generally coincided with warm weather, in the late spring of 1892, migrants arrived later than usual at below-average temperatures. In general, birds arrived in a wide variety of temperatures. This does not, however, mean that temperature is unimportant. In particular, in 1892 the birds were unduly delayed by the cold weather, and they eventually travelled despite it, not because of it, as I (1960) likewise found in the cold late spring of 1958 in Norfolk. Unusually late arrivals were likewise characteristic of the spring of 1958 in the eastern United States and Canada, when anticyclonic weather with cool, northerly winds prevailed, and the usual warm, southerly winds were absent (Gunn, 1958).

In the Song Sparrow *(Melospiza melodia)* and other species in Ohio, Nice (1937) found that a high temperature was the chief factor influencing arrivals in the earlier but not the later part of the spring. In other parts of the eastern United States, Gunn and Crocker (1947) correlated an exceptionally early spring arrival with warm, southerly winds, Williams (1950) associated big rushes in spring with high temperatures, Bagg *et al.* (1950) found that most arrivals occurred with southerly winds, especially with tropical air (see also Bagg 1956, 1957), Dennis (1954) found that most northward departures from Texas took place in warm weather with southerly winds, and Devlin (1954) similarly associated the spring migration through Philadelphia with southerly winds, which are warm. Moreover, Bagg *(in litt.)* has found that under such conditions typical nocturnal migrants may continue travelling by day, which does not normally happen under other weather conditions in spring. As already mentioned, Raynor (1956) differed from other American investigations in finding no relation between northward night migration and rising temperatures in spring; but, particularly in regard to his finding that southerly winds had an influence, I suggest that his data should be re-analyzed.

COLD IN AUTUMN

In eastern Canada, Ball (1947) found that temperature had no influence on the movements of the Red-breasted Nuthatch *(Sitta canadensis)*, but this was in July and August, and cold seems chiefly to influence migration in the latter half of the autumn. In the United States, nocturnal movements in September normally occur with cold, northerly winds, especially with cold fronts (Bennett, 1952; Lowery and Newman, 1955), but the difficulty, as in spring, is to separate the possible influence of temperature from that of wind direction.

Bagg *(in litt.)* has added three points. First, following a sharp drop in temperature in fall, typical nocturnal migrants sometimes continue migrating at tree-top level by day, as they also do with a warm front in spring. Second, the diurnal migration of the Broad-winged Hawk *(Buteo platypterus)*, expected through the northeastern United States between 10 and 25 September, comes early if there is a sharp drop in temperature early in this period, while later it is set off by a smaller drop in temperature, and later still, may occur if there has been no drop in temperature. Third, while nearly all cold fronts in fall are associated with a wind from between northwest and northeast, the front rarely moves eastward faster than the associated low center, and then the wind blows from the southwest; but the migrants set off nevertheless, thus demonstrating that the low temperature and not the following wind of the cold front is the critical factor.

In Finland, the last of five big night movements of thrushes (*Turdus* spp.) in autumn coincided with a marked drop in temperature (the others with falling pressure) (Siivonen, 1936). Haartman and Bergman (1943), studying a variety of species, found that only a small proportion of autumn departures were associated with cold, but later, Bergman (1951) found that a fall in temperature preceded the departure of many species, chiefly passerines. On the other hand, the departures of Waxwings *(Bombycilla garrulus)* from Scandinavia in autumn did not occur with a drop in temperature but at temperatures normal for the time of year (Ritchie, 1940). Jenkins (1953), however, showed a strong connection between the departures of night migrants and a drop in temperature in Scandinavia in the autumn of 1951. So, much earlier, did Clarke (1912) and Ticehurst (1932) for both day and night migrants from the eastern side of the North Sea in autumn. I have been finding the same in studies by radar for the westward movements by day and night from Holland into Norfolk in autumn. But in all these cases, the drop in temperature has also been associated with anticyclonic weather, clear skies, and light, easterly winds, so that it has not yet been possible to separate the effect of temperature from that of other factors. As regards diurnal movements in Sweden, Svärdson (1953) showed that all the big avalanches through Öland occurred with a drop in temperature in the presumed area of origin of the migrants, especially with polar air in the cold sector. Indeed, he stated that a drop in temperature was the one factor common to all observed movements. Finally, Barnes (1956) associated the unusually delayed departures of many summer residents from Britain in the autumn of 1954 with the unusually mild weather that prevailed. Hence, while a clearer analysis is desirable, it seems probable that cold is often, though not always, important in initiating autumn migration.

HARD-WEATHER AND REVERSED MIGRATIONS

In northwestern Europe, the main autumn migration ceases in about mid-November, but movements in the same directions are resumed if there is a sharp cold spell. Such "hard-weather movements," like true autumn migration, usually occur in anticyclonic weather with light, easterly winds, and no clear line can be drawn between the two. The chief difference is that true migration occurs every autumn, whereas hard-weather movements take place only if there are cold spells. Indeed, such movements occur even after the start of the return migration in spring if cold weather supervenes, though they are then usually called reversed migration *(Rückzug)*. Since they may occur with hard weather at any time during the winter and early spring, it seems likely that the birds concerned do not build up peritoneal fat stores beforehand; and if they do not do so, this constitutes another difference from true migration.

In some of the populations concerned, such as those of the Starling and Lapwing *(Vanellus vanellus)*, it would seem that some individuals regularly migrate, while others move only if there is later hard weather. In some species, too, there are movements throughout the winter and early spring, southwest with each cold spell and northeast with each warm spell, as shown for the Skylark *(Alauda arvensis)* by Drost (1929), the Lapwing by Klomp (1947) and especially Vleugel (1948), and the European Golden Plover *(Charadrius apricarius)* by Vleugel (1948). Hard-weather movements are also found in various European ducks (Schüz, 1952), while the Chaffinch *(Fringilla coelebs)* is especially liable to reversed movements after its return to Fenno-Scandia in spring (Swanberg, 1948; Bergman, 1949; Westernhagen, 1953). As pointed out by Svärdson (1953), temperature appears to have a directional effect on migration in spring, since warmth sends the birds northeast and cold southwest; in autumn, on the other hand, unusual warmth does not stimulate northward movements, though it may delay southward departures. While the southwestward movements in winter occur with hard weather, further analysis is needed to determine whether the critical factor is low temperature as such, or whether snow, frost, or actual shortage of food plays a part.

TEMPERATURE AND MIGRATORY RESTLESSNESS

The strong presumptive evidence that warmth stimulates migration in spring and cold in autumn is reinforced by the laboratory observations on migratory restlessness.

A sudden and substantial rise in temperature in early spring induced migratory restlessness in a caged Robin *(Erithacus rubecula)* (Palmgren, 1937; and doubtfully Schildmacher, 1938). Again, Weise (1956) found an increase in migratory restlessness in warm weather, including warm fronts, and a decrease in cold weather, including cold fronts, in the White-throated Sparrow *(Zonotrichia albicollis)*, Slate-colored Junco *(Junco hyemalis)*, and American Tree Sparrow *(Spizella arborea)*, kept in outdoor aviaries in spring. Likewise, in the White-crowned Sparrow *(Zonotrichia leucophrys)*, earlier experiments suggested that a rise in temperature produced both nocturnal restlessness (Farner and Mewaldt, 1953; and doubtfully Eyster, 1954) and the deposition of fat (Farner, 1955, citing Farner, Mewaldt, and McGreal); however, Farner *(in litt.)* informs me that these findings referred to a difference in temperature of 20°C., and that later work with smaller and more normal changes in temperature showed no demonstrable effect.

Migratory restlessness in autumn was associated with cold in captive Song Thrushes *(Turdus ericetorum)* (Siivonen and Palmgren, 1936; Wagner, 1937), Robin *(Erithacus rubecula)* (Putzig, 1938a), and European Whitethroat *(Sylvia communis)* (Merkel, 1938), and though Weise (1956) concluded that temperature had no particular influence in the autumn, his graphs suggest that in both *Zonotrichia albicollis* and *Spizella arborea* most migratory restlessness occurred in cold spells.

VARIATIONS IN THE EFFECT OF TEMPERATURE

While various authorities have thought temperature important, others have not. For the latter negative view, there are several different reasons. First, other weather factors are certainly important, and in some studies these may have had an overriding influence. Second, a change in temperature may usually coincide with a change in some more-conspicuous weather factor, notably wind direction, to which the observer wrongly attributed the noted difference in migration. Third, in some studies temperature probably did not reach its critical value, as, for instance, for the Red-breasted Nuthatch *(Sitta canadensis)* in the early part of the autumn (Ball, 1947), and for spring emigrants from Norfolk in May (Lack, 1960). Further, the temperature that is critical may vary with the time of year, as probably for the spring return of the Song Sparrow *(Melospiza melodia)* (Nice, 1937) and the spring emigration from Norfolk (Lack, 1960). Such seasonal differences are presumably linked with seasonal differences in the internal state of the bird, and other apparent differences in the effect of temperature may also have been due to variations in the internal state.

Authors have also differed as to whether the response to temperature is immediate or gradual. In all hard-weather and reversed movements, the response is evidently immediate. In true autumn migration, likewise, a big passage may occur on the first day of cold, as often recorded, for instance, in northwestern Europe. But here, as already mentioned, the response may not be due simply to temperature, since the change to cold is normally accompanied by a favorable change in other weather factors, and, in addition, there has usually been a previous hold up during disturbed weather. Hence, detailed analysis of this case is at present difficult. In Norfolk in spring, on the other hand, emigration did not normally start on the first day of a change from cold to warm, even when the change was large, and the marked influence of temperature on the volume of emigration from here was an average one, associated with sustained spells of warm or cold weather (Lack, 1960). A similar conclusion was reached by Bergman (1941) for Finnish ducks, though various other workers in several countries have recorded extensive movements on the first day of a warm spell in spring.

Temperature likewise had an immediate influence on the migratory restlessness of a captive European Robin in both spring (Palmgren, 1937) and autumn (Putzig, 1938a), but though various reviewers have implied that the effect was also immediate in the Song Thrush *(Turdus ericetorum philomelos)* studied in autumn by Siivonen and Palmgren (1936), their published graph does not suggest to me a day-to-day correlation with temperature. In the European Whitethroat *(Sylvia communis)* (Merkel, 1938), in the White-crowned Sparrow *(Zonotrichia leucophrys)* (Farner, 1955), and in the three other American buntings studied by Weise (1956), the influence of temperature was, or appeared to be, cumulative and gradual. In a general discussion, Hinde (1951) postulated that temperature might influence migration in two ways, either directly initiating movement or gradually changing the bird's internal state, and the evidence in this section suggests that both effects may occur.

WIND DIRECTION

As already mentioned, in both Europe and North America migrants tend to arrive in spring with warm, following winds and to leave in autumn with cold, following winds. But since the laboratory experiments on migratory restlessness show that both warmth in spring and cold in autumn are favorable to migration, the field evidence is quite inadequate to show that wind direction in itself has any influence. The observations in question need not be discussed further except for those of two American authors who definitely attributed the results in question to wind direction.

Devlin (1954) found a nocturnal migration in spring through Philadelphia on only two out of 32 nights with a northerly wind, but on 25 out of 30 nights with a southerly wind. Moreover, of the five nights of no migration with a southerly wind, four had heavy rain. This strongly suggests that following winds favor migration; but Devlin classified as "southerly" any wind blowing from between east-southeast and west-southwest, and these outside limits could hardly be classified as "following." Furthermore, he added that "southerly winds and mild weather go hand in hand." Hence, the observed effects could well have been due to temperature alone. Classifying wind directions in a similar way, Raynor (1956) found big spring arrivals of night migrants on 113 occasions with favorable winds as compared with 40 occasions with unfavorable winds; but of the latter, 19 occurred with a favorable wind higher up, seven with a favorable wind farther south, and two in a doubtful situation, leaving only 13 arrivals against the wind, in all of which the wind was light, usually 5–10 knots. As already discussed, Raynor's findings also might perhaps be explicable in terms of temperature.

Two other investigators discussing the spring migration in North America thought that wind direction was important: "whenever possible, migrating birds ride the wind" (McMillan, 1938); "most night-migrants travel by a system of pressure-pattern flying" (*i.e.*, downwind) (Lowery, 1951). But Macmillan provided no critical evidence, and I suggest that Lowery's maps for the directions of night migrants might be interpreted according to a different hypothesis, namely that the spring migration is stimulated by warmth and that, by coincidence, the northerly heading of the migrants in question is near to that of the wind direction during warm spells. Lowery's averaged tracks did not appear to be quite downwind, and might, I suggest, have been the resultant between the birds' normal headings and lateral displacement by the wind.

As regards the fall in eastern North America, Bagg *(in litt.)* has already been cited that a cold front may initiate migration even when the wind is from the southwest, demonstrating that it is not the wind direction but temperature that is important.

As regards Europe, the big diurnal movements in Sweden in autumn, all of which are associated with a drop in temperature, occur with winds varying between north and west (Svärdson, 1953), while big movements on the east side of the North Sea in autumn occur with a drop in temperature and winds varying between northeast and southeast (Clarke, 1912). Since in both areas the wind in question is anywhere between a directly following one and one at right angles to the heading of the birds, it is most reasonable to assume that the movements in question are stimulated by the drop in temperature and not by the direction of the wind. In this connection, a revealing incident was recorded by Putzig (1938a): a big October passage of crows *(Corvus spp.)* through the Kurische Nehrung in East Prussia was attributed by the local bird catchers to the southeasterly wind, but on the same day migratory restlessness started in a caged Robin, which was screened from the wind but exposed to the drop in temperature. Again, Ritchie (1940) found that southerly departures of Waxwings from Norway took place with winds varying between northeast (only once), east (6), southeast (2), and south-southeast (4), *i.e.*, the wind was usually at right angles and sometimes almost opposed. Further, Ritchie's data do not exclude the possibility of Waxwings also having taken off with westerly winds, since if they did so, they would have been drifted to the Continent and so would have escaped record in Britain. Hinde (1951) likewise considered that wind direction did not influence the return of limicoline species and terns to England in spring.

Williamson (1953, 1958) claimed that Wheatears *(Oenanthe oenanthe leucorhoa)* from Greenland and the migratory passerine species from Iceland reach Britain in autumn primarily with westerly or northwesterly following winds. "The cases examined do suggest, very pointedly, that the migration out of the northwest is simply a down-wind drift" (1953: 92). "There is thus abundant evidence in the meteorological correlation of Wheatear records at sea . . . and through Fair Isle, of extended cyclonic journeys" (1958: 219). But there is, in my view, no critical evidence as yet to support this view. In particular, the occurrence of these species on Fair Isle in autumn with westerly but not easterly winds may be merely because it is only with westerly winds that they are drifted so far off course to the east. I (1959b) have discussed this case further elsewhere, with a possible misunderstanding of it. Although I regard it as quite unproved, it needs further study, if only because the passage of the Greenland Wheatear to western Europe is, so far as yet known, the longest sea crossing regularly made by a passerine migrant.

My own observations by radar in Norfolk are as yet inconclusive for the autumn, for though most westward movements from Holland take place with easterly winds, such winds usually coincide with all the other weather factors favoring migration at this season, as already discussed. The westward movements of Lapwings from Holland to England in June and July also occur primarily with following easterly winds (Lack, 1959a), but the figures are as yet too few to test whether or not other weather factors might be involved. For the eastward emigration from Norfolk in spring, however, I (1960) have sufficient data to show conclusively that wind direction as such had no significant influence on the volume of emigration. The mean volume of spring emigration was not the same for all wind directions, being greatest for winds ranging between westerly (following) through southerly (at right angles) to southeasterly (partly opposed), and least for winds ranging through easterly (opposed) through northerly (at right angles) to northwesterly (partly following). But this was presumably because northerly winds were usually cold and southerly winds warm; following winds as such were not favored.

One important series of observations appears to be in contrast to these other findings, since the Dutch investigators reviewed by Van Dobben (1953) showed that in autumn Chaffinches migrate across Holland higher with following easterly winds than with opposed southwesterly winds, and that they tend to put out to sea with easterly winds but to turn along the coast with southwesterly winds. Less-detailed observations suggest that the same holds for the Starling. These findings have been widely quoted as showing that wind direction as such has an important influence on the volume of seaward emigration. However, Deelder (1949: 79) and Vleugel (1951) pointed out that following easterly winds are associated with other weather factors favoring migration, while opposed southwesterly winds are associated with other factors unfavorable to migration. Van Dobben (1953) stated that these other factors have some influence; further, Vleugel (1951) reported that seaward departures may occur with westerly winds. The problem is therefore essentially the same as that for other autumn movements in northwestern Europe, including nocturnal movements, which, as already mentioned, are favored by cold, anticyclonic weather with easterly winds and not by warm, disturbed weather with westerly winds. Further analysis is therefore needed as to the particular weather factors inducing Chaffinches to fly higher with easterly than southwesterly winds, and until this has been done, judgment on this case should be suspended.

In summary, with the possible exception of the autumn migration of Chaffinches in Holland, the available evidence suggests that wind direction as such does not influence the volume of migration, and that, while migration is more common with following than opposed winds, this is normally due to other associated weather factors. This conclusion was unexpected, for one might have supposed that it would be advantageous for migrants engaged on a sea crossing to wait, if possible, for a following wind; this they apparently do not do. They tend, however, to migrate with light winds, and under these conditions the direction of the wind may not be of appreciable importance.

As already mentioned, many earlier observers claimed that more diurnal migration occurs with opposed than following winds, the latest instance being Vleugel (1954), who reported that, with winds of moderate strength, migration was seven times as dense with head winds as with tail winds. The usual reason, of course, is merely that migrants fly lower with head winds, so that more of the migration is visible. A second reason, applicable locally, is that coasting migrants normally turn into the wind, which means that wind direction influences the direction but not necessarily the volume of migration (though wind direction may influence the volume passing within visual range of a particular place). Coasting birds normally turn into the wind both prior to seaward departure and after arrival from the sea (references and discussion in Lack, 1959b).

INFLUENCE OF TIME OF DAY

The volume of migration varies markedly with the time of day. The peak of nocturnal migration normally comes soon after dark and before midnight, as shown by Palmgren (1949) for migratory restlessness, Lowery (1951) by moon watching, and Sutter (1957a,b) by radar; the actual hour probably depends chiefly on the hour of sunset, and is much earlier at seasons when the day is shorter (Lack, 1959a). Diurnal movements of small, passerine species are usually heaviest about an hour after sunrise, with a steep decline later in the morning and hardly any movement in the afternoon (Sutter, 1957a,b; Lack, 1959a, 1960). However, most large, diurnal migrants, such as raptors and storks, that use thermals, tend to travel in the middle hours of the day, when thermals are strongest. The same possibly holds for hirundines and swifts, though the point does not seem to have been investigated in detail for the latter birds.

Times of day vary somewhat with the weather. In favorable weather in Norfolk in spring, for instance, emigration occasionally continued throughout the 24 hours, while typical night migrants not infrequently set off an hour before dark and occasionally in midafternoon. On the other hand, when rain fell at the usual time of the nocturnal peak, but cleared later, a big, seaward emigration occasionally started after midnight, though this might have started from farther inland (Lack, 1960).

THE INTERNAL STATE

As pointed out long ago by Cooke (1915), the internal state of the bird is primary, and the weather secondary, in initiating migration. "It must," wrote Cooke, "be a force from within, a physiological change . . . that impels them to spread their wings for their long flight." In this connection, he specifically cited the spring departure of northern migrants wintering in the tropics. The same point, often illustrated by the same example, has been emphasized by various later writers.

The subsidiary influence of the weather in initiating migration may be briefly illustrated by five instances. First, as just mentioned, species wintering in equatorial regions leave at the appropriate season in spring without any obvious change in the local weather, as recently shown by Curry-Lindahl (1958) for Yellow Wagtails wintering in Africa. Second, in England, types of weather that, in spring, would be associated with heavy migration may occur in midsummer without any migration. Third, in Scandinavia in autumn, after a hold up due to unsettled weather, the onset of weather suitable for migration may result in an "avalanche," the number of migrating birds being much greater than in good weather at other times (Svärdson, 1953). Fourth, after a long hold up due to cold weather in Norfolk in the spring of 1958, many birds eventually emigrated in cold weather during which, in ordinary years, little or no migration takes place (Lack, 1960). Finally, in addition to such broad effects, continuous watch for migration, at least by radar, shows that it is not normally a question of either a big movement or none; there are many days with a moderate or small movement on which, evidently, some individuals migrate while others do not, though the weather is the same for all.

Hence the influence of the weather cannot be properly assessed without considering the internal state of the birds. In the latter connection, the term "migratory urge" is unsatisfactory, as it is vague, carries subjective associations, and has been used in different senses by different workers. Like "drive," it has sometimes been employed to distinguish the internal from the environmental factors influencing behavior, but it has also been used for the actual motivation of behavior as a result of external and internal factors combined (Hinde, 1959: 585). Since it is valuable to have a term for the internal, physiological condition of a migrant prior to migration, I propose "migratory state," which is intended as equivalent to the German "Zugdisposition." I rejected "migratory disposition," as "disposition" carries subjective associations and, in English at least, seems too similar to "migratory mood," which is a translation of the German "Zugstimmung," a concept usually treated as distinct from "Zugdisposition."

The migratory state is recognizable, apart from actual migratory behavior, by the presence of large deposits of peritoneal and subcutaneous fat. It is also characterized by a different hormone complex from the nonmigratory condition, though details are not known. Nor is it known whether the hormone complex differs in spring and autumn, as might well be the case. Hormonal changes evidently precede the deposition of migratory fat, which once started proceeds rapidly, as it also does in a transient with depleted fat stores.

INTERNAL FACTORS INFLUENCING THE MIGRATORY CONDITION

Laboratory experiments on the hormones and other internal factors influencing migratory restlessness were initiated in Finland and Germany before the war, and have been carried out after the war, especially in Germany and the United States. This work has been reviewed so comprehensively by Farner (1955) that it need be mentioned only briefly here. The original theory behind the pioneer work of Rowan (1926) was that, in spring, hormones produced by the developing sex organs stimulate migration. But this view has now been extended to the wider one that both the migratory state and the maturation of the gonads are under the control of the anterior pituitary. Indeed, Wagner (1957) and Wagner and Thomas (1957) recently claimed that some of the gonadal hormones actually inhibit migratory restlessness in spring. If confirmed, this would explain the point mentioned earlier: that migratory restlessness continues throughout the summer in captive birds prevented from breeding, but ceases in those that breed.

In order to deposit migratory fat, a bird must have a favorable energy balance, which in spring might well be helped by the warmer and longer days. But such a favorable energy balance is merely a prerequisite, and does not mean, as tentatively suggested by Kendeigh (1949) and cited by Farner (1955), that "spring migration . . . may conceivably be induced by the change in the energy balance." As Kendeigh pointed out, resident species also have a favorable energy balance in spring yet do not migrate, and the critical question is what factors direct the migrant's, but not the resident's, energies into a special type of fat deposition and eventual migration at this season. It is now becoming accepted that fat reserves are an important special adaptation for long-distance migration. George and Jyoti (1955a,b) showed that the energy for long flights comes primarily from this source. Wolfson (cited by Bagg, 1955) and Odum (1958a,b) concluded that fat deposits may set the limit to the length of the migratory flight, while Williamson (1952, 1955) showed that passerine migrants drifted far off course to Fair Isle have commonly lost all their fat, which they normally replace before again setting out (see also discussion and references in Lack, 1959b). The physiological aspects of fat deposition have been reviewed by Farner (1955), Wolfson (1942, 1945, 1954a,b), and Odum (1949, 1958a,b) (see also Odum and Connell, 1956; Odum and Perkins, 1951; and Norris *et al.*, 1957), and need not be treated further here, except for a point stressed by Farner *(in litt.)* that it is not merely the possession of fat stores, but their rapid replenishment after depletion, that characterizes the migratory state.

Whereas in spring many birds assume the migratory state as the days lengthen and grow warmer, similar fat deposition takes place prior to the autumn migration at a time when the days are growing shorter and colder. In autumn, moreover, the anterior pituitary is in its refractory condition, at least so far as the gonadotrophins are concerned, so it cannot be playing the same role as in spring. It therefore seems better to think of the migratory state as initiated and maintained at both seasons by a combination of external and hormonal factors that are in essence timing regulators; the factors used for this timing could well be different at the two seasons. Recent work in both Germany and the United States (Farner, 1955; Wagner, 1956, 1957a,b; Merkel, 1956, 1958) has thrown valuable light on the hormones involved in spring, but little is yet known about the autumn.

INFLUENCE OF BREEDING CYCLE ON AUTUMN MIGRATION

A further factor that might perhaps influence the timing of the autumn migration is the completion of breeding. However, in nearly all migrant passerine species in north-temperature regions, there is an interval of several weeks, and in some species of a few months, between the raising of the young and the start of migration. This interval is shorter in small, insectivorous forms, such as warblers, flycatchers, and chats, which depart chiefly in September, and longer in larger species and seed eaters, such as many finches, thrushes, Starlings, and crows, which migrate chiefly in October. The interval is partly filled by the molt, but at least in those species that leave in October, there seems ample further time, and one gets the strong impression that in these species the end of breeding and the end of the molt are not critical in the timing of the autumn departure. However, since little is yet known about molting requirements, this point should be studied further. Hirundines, which differ in molting in their winter quarters, also seem to stay in their summer haunts for several weeks after breeding, though a few late-breeding House Martins *(Delichon urbica)* continue breeding until almost the day of departure.

In marked contrast to these passerine migrants are Swifts *(Apus apus),* in which each pair leaves within a few days of raising its brood (Lack, 1958a). In this species, the date of departure is clearly determined primarily by the completion of breeding, though in unfavorable climates like that of England, the parents usually stay for a few days after their young, presumably to put on migratory fat. Since the chief factor influencing the date of departure is the end of breeding, and the chief factor influencing the latter is the date when breeding starts, which itself is greatly influenced by temperature, the mean date of departure of Swifts in autumn depends on the weather in the previous May. The weather during the summer has a subsidiary influence, since in bad weather when food is scarce nestling periods are prolonged, while bad weather around the time that the young leave delays the departure of the parents by a few days, presumably because it then takes them longer than usual to put on migratory fat. In 1959, which was the finest summer experienced in England for many years, I found that Swifts also left markedly earlier than in any previous year of my 13-year study, most having gone by the beginning of August. This was because in 1959 they started breeding earlier than usual, had short nestling periods, and a short interval between the departure of young and adults. Yet in 1959, feeding conditions remained unusually favorable for Swifts throughout August. Swifts presumably leave immediately after breeding because, at this time of the year, conditions affecting their survival are more favorable for them farther south than in their breeding haunts.

A similar principle to that found in Swifts holds for arctic waders, which evidently leave just after breeding, so that the time of the autumn passage depends on the time of the preceding spring migration, and hence on the spring weather (Nisbet, 1957b). Presumably, other species of the far north leave immediately after breeding, but the subject requires further study.

In conclusion, the evidence in this section suggests that the termination of breeding or of the molt has an important influence on the date of departure in some species but not in many others.

EXTERNAL FACTORS INFLUENCING THE MIGRATORY STATE

While the weather has an immediate influence on the amount of migration in birds already in their migratory state, it may also influence the migratory state itself. In particular, the instances cited earlier in which temperature was found to have a gradual, rather than an immediate, influence on the volume of migration suggest that temperature may influence the migratory state. Hence, warmth may act as a positive timing factor in spring, and cold as a positive timing factor in autumn.

Another factor influencing migratory restlessness in captive birds is food (Wagner, 1937, 1956, 1957a), but this might mean no more than that a bird must be well nourished in order to deposit migratory fat. As already mentioned, underweight migrants drifted to Fair Isle do not normally leave again until they have replenished their fat.

Of greater interest is the fact that, in winter and early spring, an experimentally increased day length resulted in premature migration in the Slate-colored Junco *(Junco hyemalis)* (Rowan, 1926, 1929), Oregon Junco *(J. oreganus)* (Wolfson, 1942), and American Crow *(Corvus brachyrhynchos)* (Rowan, 1930, 1932), also in premature migratory restlessness in the European Robin (Putzig, 1937, 1958b; Schildmacher, 1937, 1938b), and in premature deposition of migratory fat in Oregon and Slate-colored Juncos (Wolfson, 1942, 1952), Golden-crowned Sparrow *(Z. coronata)* (Miller, 1948), White-crowned Sparrow *(Z. leucophrys)* (King and Farner, 1956), White-throated Sparrow *(Z. albicollis)* (Odum and Major, 1956), Chaffinch (de Bont, 1947; Koch and de Bont, 1952), and Brambling *(F. montifringilla)* (Schildmacher and Steubing, 1952). Although a longer day gives more time for feeding, the important factor is evidently the longer day itself, which presumably acts as a timing regulator for various physiological responses, including hormone secretions.

Different species wintering in the same area, and hence subject to the same light ration, may nevertheless start their return migration at very different dates, which may be weeks and sometimes months apart. Indeed such differences are even found in different breeding populations of the same species wintering in the same area, as shown for White-crowned Sparrows in California (Blanchard, 1941), Starlings in England (Bullough, 1942), and Yellow Wagtails in tropical Africa (Curry-Lindahl, 1958). Such differences are ultimately related to differences in the time at which breeding becomes possible in the breeding areas of the populations concerned, and they have presumably resulted through the populations concerned evolving differences in their threshold of response to day length and other external factors.

While increasing day length seems to be used as a timing regulator by many northern passerine species in spring, it cannot be used universally. In particular, the many species wintering in almost uniform conditions of day length in the tropics presumably depend for the initiation of their spring migration on different external factors, or on internal, rhythmical factors, the latter perhaps linked with external stimuli at some time when the birds are on their breeding grounds (Curry-Lindahl, 1958; Marshall and Williams, 1959). Further, almost all migrants in autumn, also transequatorial migrants in the northern spring, set out when day length is decreasing. The possibility that decreasing day length might be used as a timing regulator in autumn has not been investigated.

The reason that both day length and temperature may be valuable timing factors for the spring migration of northern birds was made clear by Hinde (1951), citing the close parallel with the work on northern breeding seasons. Such birds need some factor to bring them into their migratory state at about the same date every year, and hence a factor that is effectively constant from year to year. An internal regulator might do this, but as stressed in a review by Thomson (1950), it is probably more reliable to have an external factor where this is available. In north-temperate regions, day length provides changes that are both large and constant from year to year. However, since in northern latitudes the weather varies from year to year, between cold, late springs and warm, early springs, it is clearly advantageous for a bird to be able to modify its response to the constant influence of day length by a response to the variable influence of temperature, if it is to arrive on its breeding grounds at what is ecologically the appropriate time.

RESPONSIVENESS TO WEATHER FACTORS

A bird in its migratory state normally sets out in favorable but not in unfavorable weather. To "explain" this (though it is at best a description, not an explanation), some workers have stated that fine weather, or a particular weather factor, "stimulates" migration. Other workers have stated that bad weather, or a particular weather factor, "inhibits" or "deters" migration. Yet others have made statements of either type loosely or interchangeably. Nisbet (1957a) made a distinction between the two concepts, and after stressing that the chief factor determining migration is the bird's internal drive, concluded (p. 232) that "the external factors are therefore significant as inhibiting rather than stimulating migration." In this connection, he had particularly in mind the effects of wind and rain, and later (on p. 232) he wrote of "falling temperature providing a direct stimulus" (in autumn).

At first sight, Nisbet's distinction seems reasonable, for rain makes flying difficult, strong winds may produce drift, and fully overcast conditions impede navigation, so natural selection has presumably operated against travel in such conditions. Cold, on the other hand, carries no such obvious disadvantage, and when it is followed almost immediately by a large, autumnal departure, it certainly appears to be acting as a positive stimulus. I suggest, nevertheless, that the distinction between "stimulus" and "deterrent" in this context may be unreal. All that is observed is that the volume of migration increases as the amount of wind, cloud, and rain decreases, and as temperature rises in spring and falls in autumn. In such a quantitative relationship, it seems irrelevant to dispute whether the scale should be read in one direction (positive stimulus) or the other (negative deterrent).

Moreover, the "explanatory" value of such terms as "stimulus" and "deterrent" may be questioned, and seems largely illusory, at least without a profound analysis of the causal links in migratory behavior. Further, the terms carry inappropriate associations with subjective human states of mind, and also with energy or power. It is said, for instance, that "sudden cold is a *powerful* stimulus to autumn migration," but where the implied power might reside seems speculative. I therefore suggest that, in the present state of knowledge of migratory behavior, these terms should be omitted, and that this can be done without any loss in precision or comprehension, and with a gain in clarity. I suggest that the relationship of each weather factor to the volume of migration should be expressed quantitatively, in terms of less and more, or with actual figures where these are available, while if a vaguer statement is needed, it can be said that certain types of weather are "associated with" or "favorable to" migration, while their opposites are "unfavorable" to migration.

Certain types of weather are "favorable," of course, only when birds are in their migratory state. This is probably not an all-or-none response. It need not be supposed that migration occurs simply when the migratory state has been fully assumed and each weather factor has reached a particular threshold value. The relationship is almost certainly more complicated, since "if the internal changes are well advanced, then migration may occur even under apparently unfavorable conditions: but if the . . . drive is low, spring migration will occur only with particularly favorable weather" (Hinde, 1951: 336). Both of Hinde's postulates are presumptively illustrated by the spring emigration from Norfolk, since as already mentioned, in April 1958, after a long hold up ("internal changes well advanced"), big movements occurred in unusually cold weather, while at the start of the season in February ("drive low"), migration occurred only in very warm weather (Lack, 1960). Hinde also emphasized a further complication: that the influence of each weather factor probably varies with the state of the others. "The effects of the various external weather factors are probably additive, as in other instinctive activities (Law of Heterogeneous Summation)." While the latter principle was originally postulated for social sign-stimuli, it doubtless holds for the external factors influencing migration. For instance, one might expect migration to occur on a clear night with a moderately strong wind, or on a windless night with moderate cloud, but not, perhaps, on a moderately windy and moderately cloudy night.

The foregoing discussion applies to true migration. Hard-weather movements, as already mentioned, come in a partly, if not completely, different category, since they apparently occur as an immediate response at any time during the winter, or even after the birds have started, or completed, their spring migration. Perhaps, therefore, they occur irrespective of the internal condition of the bird, but the latter should be investigated. It may be repeated that many of the species concerned also have true autumnal migrations, which may be in the same direction as hard-weather movements, and may be preceded by the same general type of weather situation, so that the two types of movement perhaps intergrade.

MIGRATORY READINESS

Groebbels (1928) introduced from his earlier analysis of bird song the two terms "Zugdisposition" and "Zugstimmung," the first being essentially physiological and correlated with the internal secretions, and "Zugstimmung" (literally "migratory mood") being essentially psychological and correlated with the sense organs. The two terms have been used vaguely and with rather different meanings by some later investigators, and Verwey (1949) argued that two were unnecessary. However, if "Zugdisposition," like "migratory state," is restricted to the internal physiological changes preceding migration, then "Zugstimmung" might be useful for referring to the state of a migrant when the combined influence of internal and external factors has brought it into a condition of immediate readiness for migration. This is, or is close to, Groebbels' original usage, and brings it into line with one of the meanings attached to "Stimmung" in later work on animal behavior in general, where it has been particularly used in considering short-term changes in the readiness to respond to external factors.

As already mentioned, this second meaning has also been given to, or implied in, the term "migratory urge." But apart from the latter having also been used for the concept of "Zugdisposition," it has several disadvantages. First, it seems hard to measure it except by the occurrence of migration (or migratory restlessness). Hence, it might be a tautology to say, for instance, that "there is more migration (or migratory restlessness) when the migratory urge is stronger." Further, the term "urge" is vague, carries subjective human associations, and provokes the question "who is urging what?" Substitution of the term "migratory drive" might seem more objective, but the analogy that it implies is open to the same objection, since both "driver" and "driven" are the bird itself. Howard (1935) warned that such terms open the way to dualistic interpretation and mythical entities (cf. Lack, 1943), but this warning seems to have been unheeded or glossed over by nearly all later writers on animal behavior, an important exception being Hinde (1959b).

For these reasons, I at first supposed that the concept of "Zugstimmung" was unnecessary. However, I once in France observed Blue Tits *(Parus caeruleus)* migrating along the coast until they came to a bay; flocks then set off over the water, but single migrants normally hesitated and alighted in the bushes, rising into the air again when a further migrating party came in sight, joining them, and then crossing successfully (Lack and Lack, 1953). One might therefore say that the "Zugstimmung" of the single birds was counteracted by the appearance of (or fear of) open water, and supplemented by the presence of a flock (or, perhaps less probably, that the strength or level of the "Zugstimmung" was lowered by the sight of water and raised by the sight of a migrating flock). Again, limicoline species interrupting their migration for a few hours or days at the Cambridge Sewage Farm showed characteristic behavior when setting off again, running rapidly and calling, raising the wings, taking short flights, rising fairly high and again descending, until finally setting out, after which a few individuals sometimes detached themselves from the flock, returned, and did not leave that day (Lack, 1930). One might perhaps say that the "Zugstimmung" of these latter individuals was not strong enough to sustain their migration, though it is also possible that the movements of their fellows preparatory to flight caused them to fly up with them, and that they ceased to fly when the migratory, or lengthy, character of the flight became obvious. Again, in an incident already quoted, when a huge flock of migrant Starlings *(Sturnus vulgaris)* left the Cornish coast in the direction of Ireland, some turned back after meeting drizzle, perhaps those whose "Zugstimmung" was weaker, though it is also possible that these individuals had met denser drizzle than the rest. Finally, the peak of passerine night migration usually comes about an hour after dark, and the peak of passerine diurnal migration an hour after sunrise, and this diurnal periodicity is presumably due to variations not in the migratory state ("Zugdisposition"), but in the "Zugstimmung" (or in factors that counteract or supplement the "Zugstimmung").

Hence, the concept of "Zugstimmung" might be useful for analyzing certain types of difference in migratory behavior, and in the above examples, it can be given a meaning distinct from both "Zugdisposition" and the act of migration itself. The best translation for "Zugstimmung" may not be "migratory mood," with its subjective associations, but either "migratory readiness," which indicates a psychological state of the bird, or "migratory tendency," which is less satisfactory as indicating a psychological state, but more satisfactory if one has to talk of increasing or decreasing it. As this paper is not primarily concerned with motivation, I leave the choice to others. I would plead, however, that terms of this type should be used only of necessity, that they are not usually necessary at the comparatively simple level attained by most, if not all, field studies of migration, and that their omission usually means a gain in clarity.

THE SELECTIVE VALUE OF ENVIRONMENTAL INFLUENCES

While the nature of the migrant's responsiveness to weather factors is still obscure, the reason that particular responses have been evolved is in most cases clear. Summarizing what was said earlier, it is disadvantageous to migrate in rain, which impedes flight, in strong wind, which causes drift, and in fully overcast conditions, which impede navigation. Correspondingly, it is advantageous to migrate in fine, calm, and clear weather. Further, it is advantageous that a migrant's response to weather factors of this type should be immediate. On the other hand, the response of many northern migrants to day length is long term, since changes in day length act as an internal timing regulator, bringing the birds into their migratory state at that date in spring, which is, on average, that best adapted to the ecological conditions. But since in northern regions the time of appearance of suitable ecological conditions varies somewhat from year to year, primarily due to variations in temperature, it is advantageous for the birds concerned to have evolved a response to temperature, modifying the effect of day length in such a way that, in spring, cold retards and warmth accelerates the assumption of the migratory state.

It also seems probable, though the evidence is not certain, that some northern species of migrants have evolved an immediate response to temperature. An immediate response to warmth in spring might be advantageous either if, in the species concerned, warmth farther south is an indication that the breeding grounds have become suitable for occupation, or if warmth at this season is associated with conditions generally favorable for travel (which it might be on continents, though not around the North Sea). Similarly, an immediate response to cold in autumn might be advantageous either if the onset of cold immediately precedes the time when the breeding grounds become unsuitable for survival, or because cold is normally associated in autumn with the onset of anticyclonic weather favorable for travel. With respect to the autumn, the association of cold with favorable conditions for travel would seem the more likely alternative, were it not that the immediate response of various species to hard weather in winter is clearly advantageous on account, not of travel conditions, but of impending food shortage. The species concerned in hard-weather movements in northern Europe are primarily those that feed on fields, marshes, or fresh waters, habitats that quickly become frozen or covered by snow in hard weather. In either case, the migrants have presumably evolved their response to cold because of its association with some other factor, and cold acts in autumn as an immediate signal, either of conditions favorable for travel or of impending food shortage, and perhaps of both.

SUMMARY

1. This review is primarily concerned with passerine migrants in north-temperate regions.
2. The numbers of diurnal migrants seen moving by day, and the numbers of night migrants on the ground, constitute a variable proportion of the migration passing overhead. The most useful techniques for analyzing the influence of weather on migration have been migratory restlessness in the laboratory and radar in the field.
3. The rôle of climate in the evolution of migratory seasons seems primarily connected with ecological, not travelling, conditions.
4. Migration is unaffected by the general weather situation as such or by barometric pressure, while the available evidence suggests that it is also unaffected by stable air conditions, or by wind direction as such.
5. There is more migration in fine weather than in rain, more with clear than cloudy skies, and more with light than strong winds, these factors, which influence travelling conditions, having an immediate effect.
6. There is more migration in spring with warmth and in autumn with cold. Probably, the response to temperature is sometimes immediate. But at other times, at least in spring, it is certainly gradual or long term, temperature influencing the migratory state *(Zugdisposition)*.
7. The migratory state, including fat deposition, is also influenced by day length and by internal factors. Both day length and temperature may be regarded as timing regulators.

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