

MIGRATION OF INSECTS AND BIRDS THROUGH A PYRENEAN PASS

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In our times the majestic phenomena of nature may still be admired, but rarely with that added zest, permitted to the ancients, of discovery. These things have been seen before, and additions to knowledge come nowadays from those who enumerate the ordinary at their backdoors. Once in a lifetime perhaps, the ecologist is translated back into a naturalist, through chancing on a spectacle which combines grandeur with novelty. Such was our fortune at the Port de Gavarnie on 13 October 1950.

The Port de Gavarnie is a narrow rocky pass, perhaps 50 yards wide, in the mountains which divide France from Spain, at about 7500 ft. above sea-level in the High Pyrenees. The main Gavarnie valley runs from the plains southwards for about 20 miles into the mountains; it has very steep sides and terminates in a huge Cirque of precipices 4000 and 5000 ft. high. The Port is 3 miles west of the Cirque, at the head of a subsidiary valley running up WSW. from the main valley through alpine meadows, with a final rather steep ascent over bare ground to the pass itself. 13 October was cloudless and sunny with a chill, fresh west wind. As we reached the divide at 11 a.m., a party of goldfinches fluttered past and dropped down on the other side into Spain. We soon realized that both birds and insects of various kinds were passing through WSW. on a considerable scale.

Small passerine birds came through in a succession of small parties, mainly of 5 to 15 individuals. Between 11.00 and 14.00 hr. (suntime), we counted 185 goldfinches (*Carduelis carduelis*), 402 chaffinches (*Fringilla coelebs*), 100 linnets (*Carduelis cannabina*), 34 serins (*Serinus canarius*), 23 meadow pipits (*Anthus pratensis*), 9 white wagtails (*Motacilla alba*) and 42 short-toed larks (*Calandrella brachydactyla*), in all 795 small passerines in 3 hr. It is unlikely that we missed many, as the pass is narrow and the birds flew low. The finches passed only just above the rocks, so that from where we sat low against a boulder, they often skimmed just over our heads. The pipits, larks and wagtails flew higher, mainly 6–20 ft. above us. It should perhaps be added that all these birds were migrating; none of them are resident at this spot, all were flying WSW. from France into Spain, and the steady flight of a migrant looks very different from normal flight.

Pigeons started passing just after midday, and at 14.00 hr. a compact flock of about 275 birds came through, some hitting the rocks with their wings as they breasted the pass, in the double fear of our unexpected presence and a pursuing peregrine falcon (*Falco peregrinus*). Including this party, 440 wood-pigeons (*Columba palumbus*) and 61 stock doves (*C. oenas*) passed in 2 hr. and we saw another hundred as we were descending later.

Butterflies were also travelling steadily through in the same direction as the birds, the numbers gradually increasing between 11.00 and 14.00 hr. Clouded yellows (*Colias croceus*)* were the commonest, particularly at first, but red admirals (*Vanessa atalanta*), which were scarcer at first, were nearly as abundant as clouded yellows at the end. We also saw a very small number of Bath whites (*Pontia daplidice*) and an extremely small number of pale-coloured clouded yellows (*Colias* sp.). (The butterflies, like the birds, were identified by sight.) All the butterflies flew steadily over the top of the pass against the wind, and then went down the other side. Most of them kept within a few inches of the ground, which made them difficult to pick up more than a few yards away. We did not count them, as we were counting the birds, but there were probably between 100 and 500 an hour, i.e. not a very big movement. A single hummingbird hawkmoth (*Macroglossum stellatarum*) was also seen near the top of the pass, but as it was not seen to cross, we are not sure whether it was migrating.

At 11.00 hr. dragonflies were passing through in numbers about double those of the butterflies, but after the first hour they became much more abundant, and at 14.00 hr. they were in very large numbers indeed, at least ten to every butterfly. Whenever we looked at right angles to the stream we could see at least six, and sometimes twenty, dragonflies in the air. They seemed to be passing at a rate of at least several thousand an hour, but they flew closer to the ground than did the butterflies and were very hard to see, so this may well have been an underestimate. All seemed to be of the same species, and the male and female which we collected were *Sympetrum striolatum striolatum*. The red males were at least ten times as abundant as the grey individuals (presumably females, but we would not have distinguished teneral males).

* The nomenclature followed for all European insects is that of Kloet & Hinks (1945).

Not until we had been at the pass for over an hour did we realize that another insect was migrating, so we do not know whether it was passing from the start. This was a hoverfly, the two collected specimens being males of *Episyrphus balteatus*. All the other individuals looked the same, and we have no reason to think that any other species was present. The syrphid flies, like the dragonflies, flew steadily forward WSW. against the wind, keeping extremely close to the ground, where the wind was, of course, weaker. Very occasionally one settled for a moment, but otherwise they travelled steadily onward. An estimate of numbers was impossible, but at a guess they were at least twenty times, and perhaps a hundred times, as numerous as the dragonflies. They were the most remarkable migrant of all.

OUR OTHER OBSERVATIONS

In 1950, we spent 10 days in various places high up in the Pyrenees. During this time, we saw enough to be able to say that small finches, swallows, pigeons and birds of prey regularly cross the high mountains on their southward migration (Lack, 1951*a*).

As regards butterflies, we saw another good passage south through the Col de Puymorens at 6000 ft. at the head of the Ariège valley in the eastern Pyrenees, between 11.00 and 15.00 hr. on 25 September 1950. There were probably about ten *Colias croceus* to every one of another species, but cabbage whites (*Pieris brassicae*) were fairly common, with small numbers of *Vanessa atalanta* and *Pontia daphidice*. They were flying south with a tailwind, keeping several feet above the ground, distinctly higher than at the Port de Gavarnie against the wind. The belt of moving butterflies was about half a mile wide, though the Col itself is several miles broad. The butterflies had very possibly been concentrated when coming up through the narrow Ariège valley a few miles back. (We have similarly seen chaffinches migrating on a narrow front through a wide valley because they had been concentrated by a geographical barrier 6 miles back.) After crossing the Col de Puymorens, the butterflies descended on the other side and we met them again 2000 ft. lower down near Spain.

On 30 September and 1 October, at the Col de la Quillane, between 5000 and 6000 ft., at the head of another southward-running valley, we saw a small number of *Colias croceus*, *Pieris brassicae* and *Vanessa atalanta* flying south, the weather being cold and misty, so presumably unfavourable. Finally on 11 October at the Port de Gavarnie, on a very chilly day with an east wind, a small but steady stream of *Colias croceus* came through WSW. with the wind, together with some *Pieris brassicae* and *Pontia daphidice*.

As regards dragonflies, we saw a few flying south on 1 October 1950, at the Col de la Quillane, and on 4 October 1947 one of us (E.L.) saw huge numbers, far more than at the Port de Gavarnie, flying south over the bracken slopes of La Rhune, about half way up this 3000 ft. mountain in the Low Pyrenees. The species was not collected. It should be added that it was only on our last day in the high mountains that we discovered the place and conditions most suitable for seeing such migrations.

OBSERVATIONS BY OTHERS IN EUROPE

Our experience at the Port de Gavarnie seems unique, but we presume that this is merely through lack of observation, and that similar movements can be seen in this and other places each year.

Surprisingly, there are scarcely any published records of passerine birds seen migrating through high mountains. There has been heated discussion as to whether birds do or do not cross the Alps, but based on indirect evidence, with the contending parties coming to opposite conclusions (Thomson, 1926). Heilfurth (1934) has, however, seen meadow pipits and swallows (*Hirundo rustica*) passing through the Graubunden Alps in spring, and Masarey & Sutter (1939) have trapped various passerine migrants at Realp in autumn. Clay & Meinertzhagen (1933) saw a passage of redstarts, flycatchers, shrikes and hirundines through the Port de Gavarnie on 21 April 1932, and many swallows and pigeons passing there in the autumn. It may reasonably be suggested that such movements would be seen regularly if ornithologists visited the Alps and Pyrenees in April and October, instead of in the tourist season.

Butterflies have been seen travelling north through the Alps and Pyrenees in spring, but southward flights in autumn have rarely been recorded from the mountains, and are only just coming to be regarded as regular anywhere in Europe (Williams, 1930; Williams, Cockbill, Gibbs & Downes, 1942; Muspratt, 1946).

For *Colias croceus*, for instance, Williams *et al.* (1942) can cite only five southward flights in Europe, a total which our records double. One record, on 10 October 1900, was at Gèdre, in the main Gavarnie valley about 8 miles north of the Port. In this and a similar movement on 14 October 1908, the butterflies moved south up the valley, passed Gavarnie and disappeared towards Spain by the Pouey-Aspé valley (which would bring them to the Port). (Rondou, 1932; Williams, 1935; Muspratt, 1950). The data of Muspratt (1950) on the appearances of *C. croceus* at St Jean de Luz, at the western end of the Pyrenees, provide strong inferential evidence for migration in this region. C. B. Williams (*in litt.*) now writes that records which he is shortly publishing demonstrate

a regular southward movement of *C. croceus* in England in autumn.

For *Vanessa atalanta*, a regular southward flight in autumn has recently been established in England, but outside Britain there are records for only one place in Switzerland and one in Austria (Williams *et al.* 1942). Williams (1930, 1939) tabulates many southward flights of *Pieris brassicae*, chiefly from Central Europe, especially Germany, in late July and August. But for Central and Southern France he lists only one southward flight and other mass appearances, these like our records being in late September. Williams (1930) gives no record of a southward flight of *Pontia daplidice*, but it is a well-known immigrant to Britain.

In summaries prepared by Williams (1929, 1930), the few records for migrating dragonflies contrast with the many for migrating butterflies. Since then, there have been some further records for dragonflies but mainly of mass appearances, not of directional flights in progress. Mass flights of *Sympetrum striolatum* have, however, been seen southward in Italy on 1 November (Fraser, 1945), northward in South Wales on 2 July (Longfield, 1950), and northward in southern Ireland in late August and early September (Longfield, 1948). In south-western France, large numbers of *S. meridionale* were seen moving west on the Gironde between mid-September and mid-October (Dannreuther, 1947), and an unidentified species passed south-west along the cliffs against the wind at Guéthary, near St Jean de Luz, on 9 November (Dannreuther, 1949). There is a record of dragonflies migrating through mountains by Fowler (1891, pp. 202-3), who saw large numbers moving west at Andermatt in Switzerland in late September 1886. The best known dragonfly migrant is *Libellula quadrimaculata*, which moves west in large numbers in northern Europe in May and June, the numbers apparently varying greatly in different years (McLachlan, 1900; Dannreuther, 1941). Dannreuther (1941) also refers to a few other species seen travelling.

We can find no previous records for migration in syrphid flies, in the sense of directed movements independent of the wind, but large swarms have occasionally been seen, as in Essex and Kent in August 1869 (Verrall, 1901, pp. 339-40), in the North Sea on 16 and 23 July 1938 (Dannreuther, 1939), in Essex on 24 July 1945 (Dannreuther, 1946), off Selsey Bill on 11-12 August 1947 (Dannreuther, 1948), and, more remarkably, in North-East Land, Spitsbergen, in early August 1924 (Elton, 1925). The record for 1945 and the first for 1938 refer to *Episyrphus balteatus*, which was also included with other species in the 1869 swarms. (Wainwright (1944) and Goffe (1945) discuss syrphid 'migrations', but only in terms of individuals of rare species crossing the sea to Britain.)

OBSERVATIONS OUTSIDE EUROPE

There appear to be no other records of birds seen migrating through high mountains, though they must do so at times, as various migrants occur, for instance, in Tibet (Kinneer & Wollaston, 1922). Butterflies have been seen migrating through the Himalayas at heights considerably greater than the Pyrenees, and there are also records from African mountains (Williams, 1930; Williams *et al.* 1942). The closest parallel with the present observations is the discovery by Beebe (1947, 1949) of bird and insect migrations at the Portachuelo Pass at 3000 ft. in Venezuela. In the case of the birds, Beebe's observations suggest more a drift through the general region than a concentrated stream through the pass itself, and only one species, the martin *Phaeoprogne tapera*, was seen actually travelling in large numbers. Butterflies, on the other hand, passed in vastly greater numbers than any we saw in the Pyrenees. Apparently the movement is unidirectional, and there is no return flight. Beebe adds that many other orders of insects migrate through the pass, and will be described in later papers.

THE VALUE OF MIGRATION

The significance of migration in birds has long been appreciated. The migrants breed in an area which at some other season is unfavourable, they move out after breeding, and return in the following year. In Europe, the migratory movements are chiefly south and west in autumn and the reverse in spring.

In addition to regular migrants, there are a few species which irrupt irregularly every few years, such as waxwing (*Bombycilla garrulus*), crossbill (*Loxia curvirostra*) and rosy pastor (*Pastor roseus*). Such invasions have usually been attributed to exodus after overpopulation, but this could scarcely be the whole story, as a habit causing the extinction of the individuals possessing it could not persist in the species. In fact, the waxwing has now been proved through ringing to return to its breeding grounds, while crossbill and pastor have been shown to shift their breeding grounds in response to food shortage, and some movement occurs each year. The wandering habit is chiefly of value in normal years, causing the birds to leave unfavourable areas, and thus increasing their chances of finding favourable ones (Lack, 1951*b*). Kalela (1949) has similarly interpreted the well-known movements of the lemming (*Lemmus lemmus*). On this view, the periodic huge, and apparently disastrous, emigrations of crossbill, lemming and others are due to the failure of suitable conditions over a wide area. The disaster is not the emigration, but the situation which gives rise to it. The animals would have perished had they stayed, and emigration (of ad-

vantage in normal years) gives them a chance of finding suitable ground even in a bad year. Crossbill and lemming have sometimes colonized new areas after big irruptions.

Both migration and emigration have been invoked to account for butterfly 'migrations', the lepidopterist using this term in a wider sense than the ornithologist, to cover any long-distance movement. As regards British butterflies, Ford (1945, p. 164) writes that 'the cause of large-scale migrations is quite unknown', and he lists overpopulation, extension of range, and climatic factors as points to be considered, while for one species, the monarch (*Danaus plexippus*) of North America, he adds that a regular, twice-yearly migration, north in spring and south in autumn, has been established. The northward movements of European butterflies in early summer are well known, but southward flights have rarely been seen. Nevertheless, Williams *et al.* (1942) now argue strongly in favour of regular two-way migrations. First, the case of *D. plexippus* shows that such a thing is possible in butterflies. Secondly, if the northward flights were merely due to overpopulation or to vain attempts to extend the range, and were followed by death, the habit would presumably be eliminated. Thirdly, the records of southward flights, though still mainly casual, are increasing. Williams suggests that the apparent rarity of southward flights may be partly due to the scarcity of observers in southern Europe, a suggestion which our observations confirm.

While the migrations of many butterflies now appear to be twice-yearly movements away from and back to the same areas, they differ from those of birds in that breeding usually takes place in both summer and winter habitats, so that it is a different generation which makes each flight. *D. plexippus* is, however, an exception, breeding only in its northern habitat. In addition to such regular migrations, it is of course possible that other butterflies have emigratory movements comparable with those of lemming and crossbill, and correlated with food shortage and overpopulation. But the apparent absence of a return flight, as reported for instance by Beebe (1949), is not by itself sufficient evidence for emigration. The return flight might occur along a different route, as happens in certain birds.

Dragonfly migrations have generally been attributed to emigration following overpopulation (Fraser, 1943, 1945; Longfield, 1948). Fraser (1943), finding the waters swarming with cannibalistic larvae, remarks 'in the fierce struggle engendered by overcrowding. . . the desire to escape from such a hell' etc., though the overcrowding in hell refers to the larvae in the pond, the migration to winged forms already in the heavens. Presumably what is meant is that adult dragonflies have a response to overcrowding similar to that of

crossbill and lemming (also locust), which takes them away from places where breeding would be unfavourable. In support of this, Fraser (1943) claims that migration occurs only in the teneral adults just after emergence, but in a later record of migration many males were fully adult (Fraser, 1945) and this also held for most and perhaps all the individuals which we saw at the Port de Gavarnie. It may therefore be suggested that some dragonflies, notably *Sympetrum*, have twice-yearly, two-way migrations like birds and butterflies. In this connexion it is interesting that the North American species *S. rubicundus* (Jay) and *Anax junius* (Drury) have been reported as flying south or southwest in September and October (Dannreuther, 1941).

In syrphid flies, as already mentioned, there is no previous evidence for directed movements. This does not necessarily mean that they are rare. Most records of butterfly migration come from inexperienced persons, usually not entomologists at all, and other kinds of insects are much less conspicuous than butterflies. If, too, the migrations normally occur on a broad front, it might well need the concentration of a geographical barrier before they became at all obvious to the untrained eye. While, therefore, it would not be permissible to argue from one flight that syrphid flies make regular migrations, this possibility should certainly be kept in mind for the future.

It has recently been shown that migratory birds normally travel on a 'standard direction', from which they can be deflected locally and temporarily by a barrier such as the sea or high ground. Concentrated flights can then be observed along the edge of the barrier. In the region of Gavarnie, for instance, the small passerine birds and pigeons fly south up the long valley from the plains, but near the head they often leave it for a less steep subsidiary valley running south-west, while many of those that continue south up to the Cirque are there deflected west by the huge precipices. Both groups are thus brought eventually to the Port de Gavarnie, where they cross at the lowest point, and so come through the pass in a concentrated stream WSW. It seems very possible that migrating insects follow the same route. Had the insects coming through the Port been travelling WSW. the whole time, there is no reason why they should have been concentrated at this place. Further, *Colias croceus* has twice been seen moving south up the main Gavarnie valley in large numbers from Gèdre, suggesting that this species, at least, may fly up southwards from the plains on a broad front, gradually becoming concentrated by the narrowing steep-sided valley, and eventually being deflected to the WSW. by the mountain barrier. Williams (1949) states that, while migrating butterflies tend to keep to their standard directions, they are sometimes deflected by a coast-line or the windings of a steep valley.

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SUMMARY

1. In the autumn of 1950, small passerine birds, pigeons, butterflies of several species, one species of dragonfly and one species of syrphid fly were seen migrating south and west through the Pyrenees. The syrphids were particularly abundant.

2. The most spectacular migration occurred (against the wind) through a pass at 7500 ft., and it is suggested that the insects, like the birds, might have been somewhat deflected from their standard flight-direction, and concentrated, by the mountain barriers.

3. Migrations and emigrations in birds are compared with the parallel phenomena in insects.

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