Odonatologica 2 (1): 1-20 *March 1, 1973*

MASS MIGRATION IN DRAGONFLIES, ESPECIALLY IN *LIBELLULA QUADRIMACULATA* L.: A REVIEW, A NEW ECOLOGICAL APPROACH AND A NEW HYPOTHESIS

H.J. DUMONT[1] and B.O.N. HINNEKINT[2]
[1]Institute of Zoolohy, University of Ghent, Ledeganckstraat 35, B-9300 Ghent, Belgium
[2]Stationstraat 14/7, B-9300 Aalst, Belgium

Received January 22, 1973

In June 1971, intense migratory activity was recorded in *L. quadrimaculata* L. in Belgium, France and the Netherlands. Enormous swarms gathered in the compound estuary of Zeeland. Part of them apparently moved up the river Scheldt and scattered over a large number of its tributaries in Belgium. The ultimate fate of this swarm was extinction. Compilation of literature data shows that migration in *L. quadrimaculata* is a cyclical event with a period of about 10 years. The phenomenon is thus related to population dynamics and should be density-dependent. There is a fundamental difference between conditions to migration (crowding, mass emergence, weather condition) and the ethological (optical interaction-synchronization) and ecological stimuli. The latter are believed to act as pacemaker to the former. The ecological mechanism postulated is, indeed, derived from a hypothetical parasite-host relationship, the most likely parasite being a trematode larva. This could produce an internal irritation, reinforcing the optical synchronization.

INTRODUCTION

Mass migration among dragonflies appears to be limited to some 20 species (KORMONDY, 1961). It is thus of minor quantitative importance in the order. Regular migrants are still fewer. About half of all cases known refer to the single *Libellula quadrimaculata* L. Other well documented species are *Libellula depressa* L., some *Sympetrum* species and a number of aeschnids.

Qualitatively, the fact of migration has puzzled both the public and many naturalists. This is true in particular for the European plain where, owing to the dense human population, swarms have a higher probability of being witnessed than elsewhere. In all, well over 200 notes and papers have been devoted to the question. Reviews have been given by VAN BEMMELEN (1854), HAGEN

(1861), BEUTENMULLER (1890), BARTENEF (1918), WILLIAMS (1929), FRAENKEL (1932) and CORBET (1962). In such reviews new errors may be introduced, as e.g. in TUTT (1899). Dragonfly migrations have also (to some extent), been dealt with in general textbooks on insect migration and dispersal, such as WILLIAMS (1958) and JOHNSON (1965, 1969). The latter, and also FRAENKEL (1932) include dragonflies into the general framework of insect migration. Considering the hypothesis we shall try to develop hereafter, this approach should be reconsidered.

The general impression left by the voluminous dossier on dragonfly migration is still one of confusion and dissatisfaction, in particular as far as the explanatory aspect is concerned. It therefore shall be necessary, following the description of the 1971 migrations, to review some of its elements.

At this stage, we deliberately refrain from giving a definition of migration. This is, we hope, to grow naturally out of the discussion.

DESCRIPTION OF THE 1971 MIGRATION IN *LIBELLULA QUADRIMACULATA L.*

Collecting information

The first reports came in by chance. As soon as it was realized that the phenomenon was a large-scale one, mass media were used. Articles requesting cooperation were printed in newspapers, an appeal was made over the Belgian Broadcasting Corporation and finally, two short television programs were devoted to the question. The result was a vast mass of inflowing information. Doubtful records had to be checked on the spot by questioning as many people as possible. When certain sections of the pathways followed by the swarms became reasonably clear, attempts to fill in remaining gaps were made by writing systematically to all schools in the area and contacting local public authorities.

The results of this lengthy compilatory work is shown in Figure 1 and in Table I. Doubtlessly, hiatuses remain, mainly because it is impossible to extract all available information, but also because among potential observers, only 0.1% were actual observers. Especially in the countryside, many people who saw the migration, have not realized what they were seeing. In cities, conversely, the phenomenon struck a relatively much higher number of persons.

The pathways followed

Extraordinarily great numbers of *Libellula quadrimaculata* appeared in the coastal area of Zeeland, The Netherlands around June 2, 1971. Swarming was observed here for over a week. In this area three major European rivers, the Scheldt, the Maas and the Rhine converge on the North Sea. The latter two make their way through flat, swampy valleys, that constitute ideal environments for the development of dragonflies. This same coastal area has seen the end of

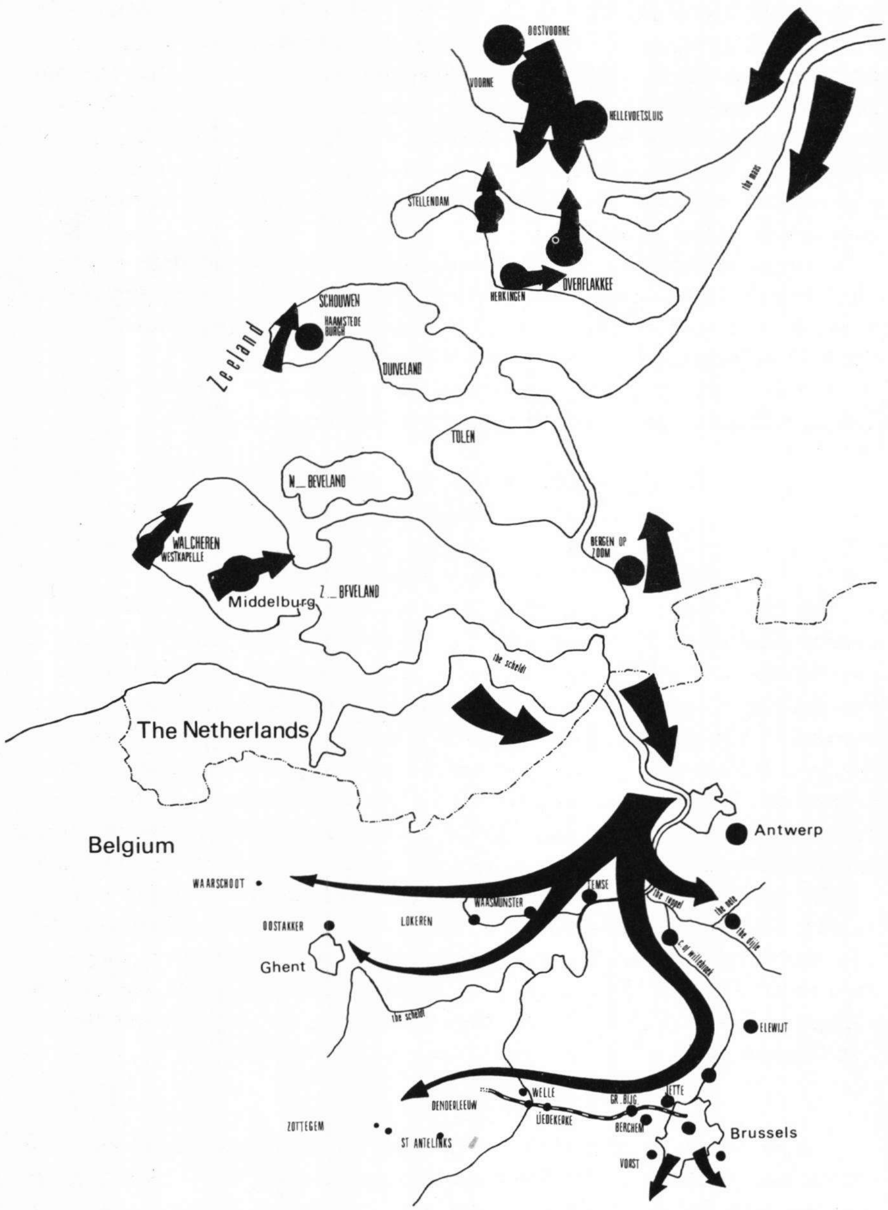

Fig. 1. Reconstruction of the pathways followed by migrating *Libellula quadrimaculata* L. in The Netherlands and in Belgium; June, 1971.

Table I

Synopsis of field observations of the 1971 migrations of *Libellula quadrimaculata* and *Sympetrum* sp. in Belgium, The Netherlands and France

Species COUNTRY Locality	Direction of flight	Dimensions of swarm	Vertical flying interval	Duration	Atmospheric conditions	Date and (or) hour	Remarks	Observer[1]
Libellula quadrimaculata								
BELGIUM								
Brussels (Molenbeek)	from Schaarbeek to Koekelberg		4-60 m	15′				1
Brussels City	over the canal of Willebroek towards Koekelberg	about 20 m wide	10-15 m			ca 17 h		2
Brussels (Molenbeek)	along Leopold III lane	about 80 m wide	0-14 m			June 4th		3
Brussels City	close to Congres Monument	"big swarm"	20-40 m	10′	hot-storm in the evening	June 4th		4
Brussels (Anderlecht)	"Veeweyde" road crossing on road Brussels-St. Pieters-leeuw	"big swarm"				June 1971		5
Denderleeuw-Welle	eastwards		0-20 m	15′	hot-storm approaching	ca 17.30	along railway 50 A	6
Liedekerke	eastwards	"big swarm"	variable	5-15′	hot-storm approaching	June 4th 1971 ca 17h 15	along railway 50 A	6
Groot-Bijgaarden	eastwards	"big swarm"				June 1971 ca 17 h.	along railway 50 A	7
Jette	eastwards, over park along railway 50 A	length 1.5 km: width ca 50 m; distance between specimens ca. 50 cm.	1-4 m		hot and cloudy thunderstorm approaching	June 4th 1971 "afternoon" 17.15 h	along railway 50 A	8
Brussels (Railwaystation North)			0-20 m		hot-strong wind thunderstorm approaching	June 4th 1971		9
Near Brussels	"from Antwerp to Brussels"						Mrs Bleys is teaching at the high-school of Tervuren (near Brussels) and collected information from her students	10
Wezembeek-Oppem	from W-O to Brussels						As the swarm entered Brussels by the Canal of Willebroek, the observer has only seen a small part of the migrants	11
Willebroek		groups of ca 20 specimens.				June 1971	idem	12
Temse	southwards	ca 500 specimens (?)	0-10 m	15′				13
Lokeren	westwards	"thousands of specimens"	0- 8 m	15′	t° 20-22°C	June 3d 1971		14
Waasmunster	to the North (compass-checked)	about 300 m wide	2-15 m mean 8 m	18 h 30-18 h 55	t° ca. 24°C windstill very cloudy air pressure high	June 3d 1971		15
Oostakker (Gent)		"several hundreds"	low				flight slow; animals uncapable of avoiding obstacles such as buildings, parked cars, etc.	16
Gent (Canal zone)		thousands of specimens	1- 8 m	15′	thunderstorm after the swarm had passed		one adult (!) male captured	17

Elewijt	to north-west	enormous numbers, "millions"	3- 4 m					18
St. Antelynck	towards Zottegem	length ca 1.5 km; width ca 200 m	not lower than 8 m			June 1971	heavy predation by swallows; next day thousands of wings found in meadow	19
Erwetegem		length ca 70 m (?); width ca 15 m				June 1971	insects hunted by swallows	20
Zottegem			low			June 1971	Mrs Coomans is teaching at the highschool of Zottegem. Information was collected from 4 students	21
Waarschoot		small group						22
Walem (Mechelen)	over the river Nete from Walem towards Duffel-Lier	compact group, 10 m long, followed by a rather long and diffuse one, then again a small compact group	low over the river				2 species (?): a smaller dark one (L.4-mac?) and a bigger green one	23
Borsbeek-Antwerpen				insects seen passing by during 2 days		June 1971		24
THE NETHERLANDS								
Bergen op Zoom	along the sea shore		2-20 m	passing by during 3 days		June 1971		25
Bergen op Zoom			2- 3 m			June 1971		26
Voorne	varying between NE and NW	enormous numbers; a counting during 15' over a width of 20 m. gave a mean number of 125 animals/minute		continuous between June 2nd and June 10th; climax on June 2nd·	warm weather especially on June 2nd after June 10th, rainy·	June 2nd till June 10th	One June 2nd: enormous swarms everywhere between Hellevoetsluis and Oostvoorne. 2 spec. captured·	27
Overflakkee								
– Middelharnis	no clear trend	continuous during several days		climax on June 3rd	thunderstorm on June 3 rd	May 31st until June 3rd	some people frightened	28
– Stellendam	North	"vast swarms"						29
– Herkingen	from SW to NE	"continuous"		"continuous"	thunderstorm on June 3rd	May 31st; June 2nd and 3rd		29
Schouwen-Duiveland	coming from the South; entering the West coast of the island.		a few meters; some higher	from 11 a.m. till late in the afternoon (rain!)	dry and sunny end May and first days of June (20-22°C) On June 3rd: 25°C	June 3rd	specimens flying higher than a few meters captured by gulls	30
Walcheren (Westkapelle and Middelburg	to the NE		low	from 2.30 p.m.; end of movement not stated	idem	June 3rd	flying low along dikes against a strong wind; also over some creeks and along the seashore	30
FRANCE								
Between Denain and Valenciennes						June 1971	enormous numbers "millions"	31
Sympetrum sp.								
BELGIUM								
Eigenbilzen	to the North, from Tongeren to Maaseik	length 2 km; width 60 m.	10-15 m			September 1971	night spent in oak trees. Left trees before 6 a.m. next day	32
Eigenbilzen			ca 10 m	10'		Summer 1971	children frightened	33
Liège						Summer 1971		13

[1]Observers: (1) F. Scheerens; – (2) L. Dardenne; – (3) R. Aerts; – (4) Cooreman; – (5) H. Vandebock; – (6) several independent observers; – (7) J. Vermeir; – (8) D. De Kuyper; – (9) Leroux; – (10) D. Bleys; – (11) H. Verhelst; – (12) R. Massart; – (13) unrecorded; – (14) R. Verstraeten; – (15) P. Dierinck; – (16) verbal communication; name of observer not recorded; – (17) J. Mertens; – (18) De Coster; – (19) L. Van Schelvergem; – (20) E. & D. Danneels; – (21) Y. Coomans; – (22) C. De Rynck; – (23) W. Poffe; – (24) Smeuninx; – (25) J. Franken; – (26) O. Wiersma; – (27) drs. R. de Jong, ass. curator Museum Leiden; – (28) P. Vroegindewey; – (29) communicated to P. Vroegindewey; – (30) cf. WEDTS DE SWART (1971); – (31) communicated to Dr. Glasson (Station biologique de Wimereux); – (32) F. Ferdy; – (33) G. Martens-Mens.

swarms many times before: during the 1850's (VAN BEMMELEN, 1854), in 1900 (LANCASTER, 1900a, 1900b), 1925, 1963; and probably many more times on which no records exist. In 1971, swarms appear to have been flying around and over the islands for a while. Part of the animals may have perished here, but others have migrated further in various directions. We have been able to find out what may have happened to part of the last category. They started migrating up the Scheldt, passing nearby the city of Antwerp for two days (as in 1900!). Some distance upstreams of Antwerp, part of the migrants went up the river Rupel and small flocks reached the river Dijle. The vast majority had chosen to follow the canal Willebroek-Brussels and actually entered into the very heart of the City of Brussels in the early afternoon of June the 4th. Inside the city, the swarm apparently broke down to several smaller groups, only one of which we succeeded in understanding the fate of. It decided to follow the railway track 50 A, between Brussels and Denderleeuw. We received reports from almost every village which this railway crosses, and their can be no doubt about the intimate link between the swarm and the track. About 17.15 h, the swarm having left the village of Denderleeuw behind, a thunderstorm began. We later learned that at least part of the swarm had been swept down into some large swamps in the village of Welle (the "Wellemeersen"). This area continued to be swarming with Libellula's also owing to a rainy type of weather which lasted for more than a week. What was then left of the original swarm still managed to migrate somewhat further West, reaching Zottegem. At this stage, the animals were completely exhausted and heavily predated on by various birds. One farmer, watching the swarm passing over his meadow, saw bunches of swallows causing a hecatomb among the insects and, the next day, collected hundreds of dragonfly wings all over the meadow.

Still, on June 4th, about half (?) of the migrants had continued following the Scheldt. A little past Temse, a fraction entered the course of the River Durme, and was spotted in two localities here; another fraction still seems to have stuck to the Scheldt and reached the city of Gent. However, at Gent at last two branches converged again and it is not possible to decide to which of them the animals just east of Gent pertained. All observations however, agree in that the animals were exhausted, crashing with parked cars, or buildings, being caught by cats, birds, etc. One specimen captured was an adult male.

From the above, it appears likely that other groups have entered other tributaries of the Scheldt, but have remained undetected. Also, in 1900, swarms were spotted along the Belgian coast. There is but little probability that this occurred again in 1971. All inquiries with light-ships were indeed negative for dragonflies, but not for other insect groups.

In May 1963 one of us (H.J.D.) had witnessed a migration of *L. quadrimaculata* at Wimereux, North of France. In order to find out whether the phenomenon had repeated itself, we contacted Dr. Glasson at the Marine Biological

Station there. It was stated that no migration had been seen in the Boulogne area in 1971, but early in June, an enormous swarm of dragonflies had been observed somewhat inland, near the city of Denain.

We finally obtained three independent reports on a dragonfly migration during the late summer, well inside the country of Belgium, in the Provinces of Liège, Limburg and perhaps Dutch Limburg as well. This may only have been *Sympetrum* spec., but no specimens were captured.

DISCUSSION

Many students of dragonfly migration have failed to realize that there is a difference between the causes of a migration (the stimuli) and the conditions necessary to make a migration possible (the prerequisites). Complex behaviour as mass migration may, however, justly be expected to arise from complex situations. In such circumstances, one should not jump to conclusions, or accept too simple cause-to-effect verdicts. Let us, therefore begin by considering some parameters which have been connected with migrations of *Libellula quadrimaculata* in Europe.

Weather conditions

FRAENKEL (1932) has brought together a large collection of data on this point. WEISSENBORN (1839) first noticed that migrations occur during hot weather, following cold and rainy spring periods. LANCASTER (1900a, 1900b), being a meteorologist himself, attached great importance to this point. Confirmations came from FEDERLEY (1908), KOHLER (1925), KOLOSOV (1916), LARSEN (1950), DUMONT (1964) and KIAUTA (1964). The same circumstances occurred again in 1971. Brief mention to similar conditions is made by GIARD (1889) and HALL (1889). It appears to be a fairly general rule that migrations take place shortly after some abrupt raise in temperature and air pressure. The relation needs, however, not to be a direct one. FRAENKEL (1932) correctly related meteorological conditions to emergence, stating that a cold spring at first delays eclosion of adults, which afterwards occurs "en masse". A cold early spring is thus equally important as hot weather during the end of May.

The so-called teneral condition of migrants

FRAENKEL's (1932) concept nicely fits CORBET's (1962) remark, based on the hypothesis of JOHNSON (1960) that true migrants are tenerals. It may well be that in *L. quadrimaculata* most if not all migrations start with the maiden flight of a number of specimens. These may, however, be no more than the pacemakers and, in *Sympetrum*, perhaps migrations begin at a later stage. There is much observational evidence in *Sympetrum* (RIVEAU, 1882;

LICHTENSTEIN & GRASSÉ, 1922; GRASSE, 1932; HUGUES, 1935; FRASER, 1945; DUPUIS, 1946; MUSPRATT, 1947; LONGFIELD, 1950; OWEN, 1958) dealing exclusively with adults, eventually flying in tandem formation. In fact, no clear-cut cases of teneral migration in this genus seem to be available. If any, they must be rare. But also in *Libellula quadrimaculata* (KIAUTA, 1964; DUMONT, 1964, this paper), occasionally adults have been seen in migration.

CORBET (1962) suggests not to regard such cases as proper migrations. However, what characterizes a migration is the movement of a large number of individuals, not the condition of these individuals. There is, so far, no theoretical argument to attach too much importance to the frequent association of both phenomena and also, if one were to accept this reasoning, some mass movements in *L. quadrimaculata* itself should be regarded as migrations and others not. In the following we shall try to show further that the sequence of emergence and migration is due to the fulfilment of one single condition necessary to migration.

The problem of the geographic origin of migration

Since HAGEN (1861) wrote down the story of his effort to track a swarm "upstreams", finally arriving at a pond "devoid of *L. quadrimaculata*" which he considered to be the origin of the migration, many later observers have continued thinking along the same line. But Hagen was evidently in error, which is easily proved from his text. The migration in Königsberg was seen from the morning hours on; the pond(s) at Dewau, visited in the course of the day were devoid of *Libellula* but the migration towards Königsberg continued until the evening.

But, even apart from this, it is materially impossible for a pond, or even a small series of ponds, to yield the several millions of individuals that were certainly involved.

The origin of large swarms should not be sought in a limited number of biotopes. Large swarms may only build up gradually, "draining" the areas over which they pass. As the movement, however, must start somewhere, it is best to select a "region", particularly suited to the development of the species involved. This was done by GIARD (1889) and LARSEN (1889), and in 1971, the Rhine and Maas valleys appear to be the best choice one can make.

The problem of orientation

The problem of orientation and pathways is not independent from the views exposed above. We shall return to this problem later.

Students or dragonfly migration have, at all times, been greatly influenced by concepts applied in other insect groups, e.g. locusts, dipterans and lepidopterans. Many migrations among these appear to be wind-governed, even in locusts (KENNEDY, 1961). In others, a sun compass-orientation has been suggested.

The possibility of a wind-governed migration has been very successful with odonatists, but in fact, there is little to be added to FRAENKEL's (1932) summary on this topic: up to 1932, out of 23 cases considered, 15 times the animals migrated against the wind, 5 times along with the wind and three times there was an angle with the wind direction. Consequently, this factor is of poor importance in orientation, except perhaps at extreme values. In spite of the weakness of this hypothesis, other possibilities remained completely unexplored.

One clue to the problem is that dragonflies are typical eye-animals. Optoreceptors are the most powerful and most effective sense-organs these insects have, and there is no reason why they should only serve at localizing preys, enemies or mating partners.

In this respect, the 1971 migration is highly instructive. The migrating pathway runs along rivers, dikes (WEDTS DE SWART, 1971) and along a railway. In earlier cases, coastlines were followed (GIARD, 1889; BORROR, 1953; KIAUTA, 1964; DUMONT, 1964). The movement downstreams ultimately leads to an accumulation of migrants in estuaries. The Gironde in France is a good example. According to RIVEAU (1882), migrations (of *Sympetrum*) should occur here yearly (?). Wedts de Swart's observations, and, in general, the majority of observations in The Netherlands, refer to the compound estuary of Zeeland.

The common feature of all these pathways is that they are linear (in some cases even rectilinear) elements in a two-dimensional environment. They are thus extremely efficient optical landmarks. In visual orientation, they are the simplest systems that can be used, and evidence is overwhelming that migrating dragonflies indeed use them. There may also be cases in which this mechanism breaks down. An extremely interesting example in 1971 was the effect of the town of Brussels, the geometry of which provides a very complex optical situation, confusing the swarm. Such effects are invisible to the local observer but become apparent upon reconstruction of the pathway.

Further relevant aspects of optical stimulation

Optical stimulation probably has more impact than merely "guiding" the swarm "en route". It might very well be the most important ethological contribution to the "causes" of migration, especially when intervening in the critical moment of take-off of the swarm, and further for securing coherence while moving.

Recently, renewed attention has been payed to ethological processes as the so-called "interaction-synchronism". Through stimulation of a sense-organ, frequently an optoreceptor, many animals species including man are subconsciously induced to synchronize their movements with those of the object seen. The accuracy of this synchronization is, at times, amazing, as LORENZ (1958) demonstrated in courting and mating ducks. In young children, interaction-synchronism was studied by means of films by BRANNIGAN & HUMPHRIES (1969). A case of non-optical synchronization has been described by THORPE (1966) in so-called duet-singing African birds. The same mechanism may exist in lower animals. Among dragonflies, examples may be found in species with highly developed mating ethology, involving specialized courtship and aggressive display, such as *Platycnemis* and *Calopteryx*.

Let us now consider a mass-emergence of dragonflies taking place under conditions permitting every individual specimen to see at least one other specimen. It is known that the maiden flight is preceded by wing vibrations of a variable duration. Let this behaviour last long enough in the first specimen, to allow many others to join in. The flying away of the first one may then stimulate the others to take off simultaneously, and a swarm is born.

One of us (H.J.D.) has witnessed such a phenomenon in *Sympetrum*. While searching Phragmites-girdles along a pond, one freshly emerged *Sympetrum striolatum* was disturbed and flew away. It was followed automatically by a small swarm of conspecifics. The animals, however, settled some twenty meters further. It thus appears that interaction-synchronism is not always stable. It is unknown whether it is more stable in *Libellula quadrimaculata*. However, some other factor might be responsible for reinforcing it (cf. below).

Let us assume that the swarm keeps on the wing. It will then quickly grow by collecting specimens "en route". In a suitable environment, this growth rate may well be exponential. The animals collected en route do not necessarily have to be tenerals or even conspecifics, which explains some facts on record. There will also be some losses as specimens get behind. But it is not certain that a specimen or group which looses contact with the body of the swarm is therefore definitively lost, since by following the landmarks reintegration may occur.

The essentials of this theory are not new, but have never been properly explored. Already GIARD (1889), opposing the view that dragonfly migration would be an anticipation to adverse conditions, suggests: "une sorte d'imitation instinctive et de groupement rythmique". FRAENKEL (1932), borrowing from the work of Uvarov and Sajo, considers at some length a number of "instincts" involved in migration, among which the "Imitations-instinkt" (more properly to be called a reflex).

Highly significant is the work by GRASSÉ (1932) on migrations in *Sympetrum*. Imitative behaviour between groups of insects is described in full detail. It is stated that when, in a settled group, one specimen starts vibrating its wings, many others join in. Smaller groups of migrants are attracted by larger groups and assimilated with them. Yet, Grassé refrained from attaching too much importance to the mechanism of interaction-synchronization, as he considered the bond between several groups to be a relatively loose one.

Other examples include KIAUTA (1964) who wrote that "animals (*L. quadrimaculata*) took off 2 or 3 at a time . ." and DUMONT (1964): "the flying up of the individual provoked the same reaction among most of the Libellula's within a radius of one or two meters around it".

It is amusing, finally, to see that even FRASER (1945), who was a protagonist of the "teneral" hypothesis, had to borrow from the interaction-mechanism in order to explain a migration in *Sympetrum* that involved many tandems.

THE IMPACT OF POPULATION DYNAMICS AND POPULATION INTERACTIONS

From the above, we may deduce that some environmental conditions are necessary for a migration to take place. The ethological mechanism in itself is, however, not a sufficient condition. Migration is mainly an ecological process, therefore, the roots of the problem are to be sought in the ecology of the species.

Concerning *L. quadrimaculata*, one of us (DUMONT, 1964) intuitively and timidly put forward: "these factors (causes), not yet understood, should probably be connected with the larval life period". The underlying reasoning is that the enormous number of adults involved in migration must come from an equally large number of larvae. These are the offspring of a previous generation and so on. This naturally leads us into the field of population dynamics and the question may be raised whether migration in *L. quadrimaculata* could be regarded as a cyclical event. We have therefore compiled all available data in Figure 2. The time scale commences around the beginning of the 19th century. Existing older records are too spaced and fragmentary to allow comments. At once, a natural grouping appears to exist, in which all data from atlantic western Europe, from Le Havre to the coasts of the baltic countries and including Great Britain stand well apart from those dealing with Scandinavia and Russia. The first group is by far the best documented one. Doubtlessly, as argued in the introduction, this is due to the much denser human population here. One cannot, however, be sure that the list is complete. Some migrations are particularly famous and appear to have been more formidable than others, but there is no guarantee that this reflects reality.

So, the 1852-55 period is extremely rich in reports, mainly due to efforts by VAN BEMMELEN (1854), DE GRAAF (1854), MULDER (1855), and HAGEN (1861). The 1860 and 1870 decades conversely are rather poorly known. The 1880 decade (with two distinct migration periods in 1880-82 and 1888-89) have again received wide attention. Our knowledge on the 1900 migration, which has been said to be "one of the most famous" (FRAENKEL, 1932) is almost entirely due to the work of a meteorologist (LANCASTER, 1900a, 1900b). Without him, small notes by KARSCH (1900), ACLOQUE (1901) and FONTAINE (1902) would have left us with an entirely different impression of it. The decade of 1910 has seen only notes by BAXTER (1911) and BEUTHAN (1914). The

1920 migrations, centred around the year 1925 have attracted much attention in The Netherlands (THIJSSE, 1925 and others), and in Germany, Austria and Poland (KEILHOLZ, 1925; GEISSLER, 1925; GALVAGNI, 1925; KÖHLER, 1927). The notes by Geisler and Galvagni refer to what may have been a compound swarm, in which *L. depressa* was said to be the dominant species.

References for the 1930's are scarce. There were, however, migrations in England (DANNREUTHER, 1935) and Denmark (LARSEN, 1950). We are much better informed of what happened in Scandinavia at that time

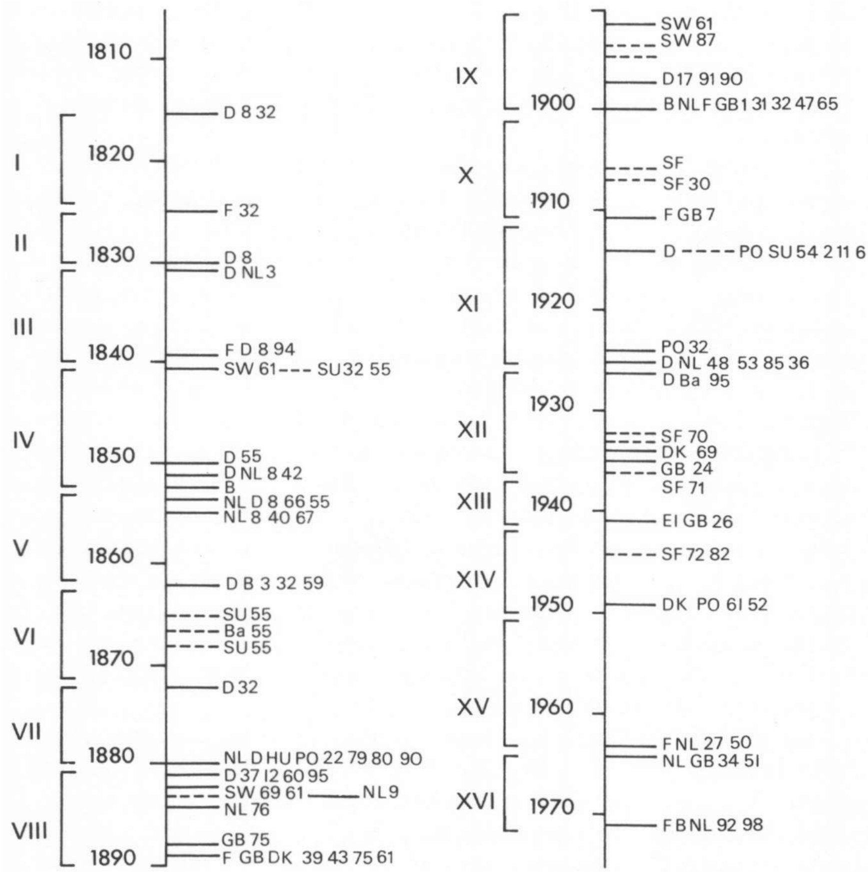

Fig. 2 The incidence of migration of *Libellula quadrimaculata* L. Full lines: Central and Western Europe; dotted lines: Norhern Eruope. Country abbreviations: B – Belgium; BA – Baltic republics of the U.S.S.R. ; D – Austria, German Democratic Republic, German Federal Republic and, for the sake of convenience, the former Prussian territory; DK – Denmark; EI – Eire; F – France; GB – Great Britain; HU – Hungary; NL – The Netherlands; PO – Poland; SF – Finland; SU – Soviet Union (without the Baltic republics); SW – Sweden.

(NORDMAN, 1935, 1937; SUOMALAINEN, 1937). The only proof of migrations during the 1940's was in Ireland and some smaller British islands (DANNREUTHER, 1941). The most interesting areas, however, at that time were the scene of the battles of World War II. Migratory activity was reported from Finland in 1945 (NORDMAN, 1945) and at the end of the decade, swarms of *L. quadrimaculata* were seen in Denmark (LARSEN, 1950) and Poland (KLIMEK, 1949).

A large-scale migratory movement marked May-June 1963 (Dumont, 1964; KIAUTA, 1964) and some minor migrations followed the year after (FRENCH, 1964; KIAUTA, 1965).

The present decade finally, is so far documented by WEDTS DE SWART (1971) and this paper only.

The mean period between migrations almost exactly equals 10 years (range 6 - 14 years). It is nearly impossible that this could be accidental. On the contrary, for a process determined by several independent parameters, this is a very satisfactory reproducibility. If thus migration in *L. quadrimaculata* pertains to the domain of population dynamics, it is here that its main causes should be looked for. ELTON (1930) suggested that migration could be a way of reducing over-crowded populations. In the literature on dragonfly migrations, various suggestions in the same sense have been made. Most of them are naive and credit dragonflies with a highly developed intelligence: the animals would be aware of forthcoming events such as food shortage, drying up of their native ponds, etc . . .

In terms of modern population biology, two possibilities are open. The first is to tackle the problem as an autecological one. Population growth in *L. quadrimaculata* can then be described by one of the various deterministic models that are in use, e.g. the logistic. Emigration should occur during the plateau phase and reduce population levels dramatically (Fig. 3). It should then take 5-6 years before plateau values are reached again, and some more before environmental conditions are again favorable to a new migration.

This simple hypothesis is tempting: evidence for it is to be found, e.g. in the 1971 events. The animals, having left their natural sheltered environments were indeed very heavily predated upon by birds and the remaining in the end were so exhausted that many simply dropped dead. Migratory years coincide with general high population levels (DUMONT, 1964; KIAUTA, 1964; observations made in Belgium in 1971). In order to explain why migrations may occur in two or three consecutive years local differences in climate conditions may be invoked. Indeed, except in The Netherlands with their extremely large drainage area, consecutive migrations during the 1850 decade were well spaced geographically within atlantic Europe.

But, for three reasons, this theory is not entirely satisfactory. The first is that it is too simple, which always inspire caution. The second is that interaction-

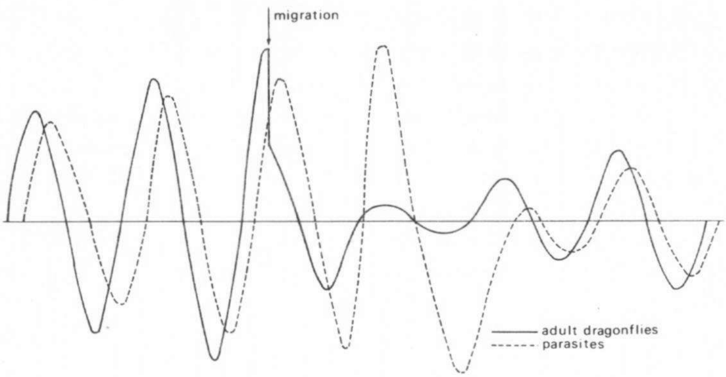

Fig. 3. The hypothetical relationship, dragonfly/parasite, expressed as an oscillating system.

synchronism in itself is probably not a sufficient stimulus for migration. The third is in a few intruiging facts on record. All three taken together convinced us that migration might be the consequence of a synecological process involving parasitism.

TARNUZZER (1921) writes that farmers along the Prussian coast have a practical experience of migratory swarms of *L. quadrimaculata*, and carefully keep their poultry away from them. Upon eating Libellula's, chickens may stop egg-laying and eventually die. The same phenomenon is known from the isle of Helgoland. This dragonfly-disease or prosthogonimosis is caused by a trematode, *Prosthogonimus ovatus*, the metacercariae of which are carried by adult dragonflies. Recent work by BODDEKE (1960a, 1960b, 1960c, 1962) has shown that the parasite is highly unselective and may be carried to a large variety of birds by many different dragonfly species. *Prosthogonimus* is thus the most important dragonfly parasite. It was the only one known to WRIGHT (1946), but TIMON-DAVID (1965), in a recent review, gives examples of at least six trematode families that may use dragonflies as intermediate hosts.

It is tempting to link up *Prosthogonimus* with the migrations of *L. quadrimaculata*. Consider the evolution of both populations as a function of time and present them as an oscillating system. The trematode should naturally lag behind the dragonfly, perhaps by one year. If now the dragonfly reaches its plateau value, the trematode will continue growing for a while, that is, as long as its populations are at levels sublethal to the host organism. At this stage, a phase of relative equilibrium is possible, which may last for several years. As soon as environmental conditions are again favourable to migration, a large quantity of hosts and parasites are carried away from the cycle. The host will be lost, but the parasites may return to the cycle along with birds. Now, experiments by KRULL (1930, etc.) on *Sympetrum* have shown that there exists a lethal treshold in the

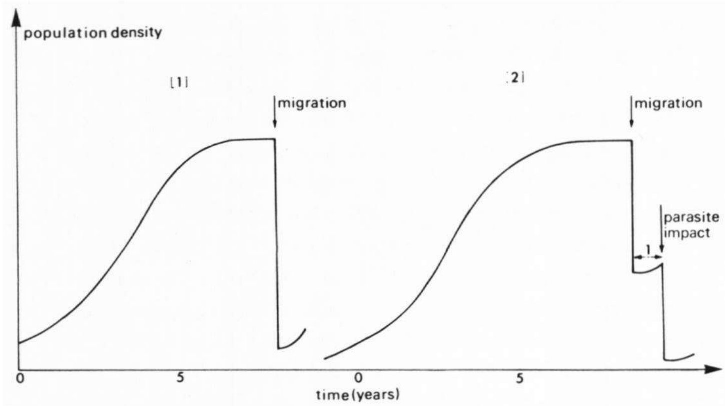

Fig. 4 Hypothetical growth cuve of *Libellula quadrimaculata* L. I. Density decrease is a consequence of migration only; – II Density decrase is a consequence of migration and subsequent parasite impact.

number of cercariae of the trematode *Haematoloechus* that individual larvae can absorb. When more than 250 are entering the larva, it dies. The same must apply to *Libellula* and *Prosthogonimus*, and this is probably what happens in environments in which a massive emigration occurred the year before. The remaining *L. quadrimaculata* are infested to a lethal level, there being more parasites for fewer dragonfly larvae. As a result, adult dragonfly populations may be reduced to extremely low levels.

As to the phenomenon of migrations continuing for several years, several possibilities are open. Either these second year swarms come from previously unaffected biotopes, or from biotopes which have been only partly affected by emigration the year before. In the latter case, a behavioural impact on migrating animals may be expected. This is perhaps exemplified in some of the migrants of the year 1964, when FRENCH (1964) found large concentrations of *L. quadrimaculata* on Lundy Island. These animals did not actually migrate, but were said to be extremely lethargic, could easily be captured by hand and made no movements unless disturbed. Simultaneous observations at Makkumerwaard, The Netherlands (KIAUTA, 1965) appear to reflect similar conditions. These seem also to have existed during some earlier migrations, but old reports lack clearness on this point.

If, at this stage, we may understand why migrations should be regularly self-repeating events, one question still remains to be answered. Does the hypothetical host-parasite relationship stimulate migration? The answer is probably yes. The impact on the larvae is known to be an increased nervousness and agitation. In adults, constant irritation caused by metacercariae could stimulate the animals to fly and keep flying.

Migration in *Sympetrum* appears to bear a fair amount of analogy to that in *Libellula*, though agreement is not complete. There are many *Sympetrum* species which have been seen migrating in Europe, and they have both a different geographical distribution and a different incidence period. Some among them spend much of their adult lifetime well away from the water. Furthermore, some of them have specific trematodes, e.g. *Haematoloechus*, with other, terrestrial terminal hosts. The mechanism here, although essentially the same, might thus present some complications. This is especially true as *Sympetrum* is also liable to be infested by *Prosthogonimus*. In 1971, at the end of the summer, a migration of *Sympetrum striolatum* or *vulgatum* occurred in Belgium. The latter spend more time near water than many others. Thus, their mass-appearance is probably not independent from that of *L. quadrimaculata* earlier during the year.

SYNOPSIS OF THE NEW THEORY

Populations of quadrimaculata in a given set of relatively close-by biotopes begin expanding, at first at a fast (exponential ?) rate. A parasite (*Prosthogonimus*) expands, approximately at the same rate, but with a time lag of at least one year. Plateau levels are reached in the dragonfly after 5-6 years. They may remain more or less stable for some years. Emergence normally takes place in a spaced way. If, during the plateau phase, weather conditions are such that emergence is impossible during early May, it may occur massively at the end of May or early in June. A situation may then arise in which interaction-synchronization between tenerals gives raise to a massive maiden-flight. A constant internal irritation, due to the presence of a high number of metacercariae may consolidate the synchronization and make the movement a continuous one. Small swarms attract other animals as they pass by and the number of animals quickly expands, becoming enormous eventually. The area through which the swarm moves is thus virtually drained of dragonflies, tenerals and adults, conspecifics and – eventually – other species. Swarms prefer to move along optically defined pathways. As areas suitable to mass-development of dragonflies are limited, and the pathways likewise, swarms regularly appear in the same geographical areas.

Swarms give up their natural shelters. Due to their dimensions, they are also easily spotted. They thus become subject to heavy predation; also many animals die from exhaustion. The ultimate fate of swarms is almost complete destruction. Due to local differences in climate conditions, prerequisites for migration may be present in some areas and not in others. Migrations may thus appear to continue for one or two years. In regions which have been only partly emptied following an emigration, remaining dragonfly populations are subject, the year thereafter, to peak values in the parasite, which may reach lethal levels and thus destroy much of what was left. As a consequence, parasite populations will not find their necessary host one year later and collapse themselves, so the cycle may start again.

EPILOGUE

The views expressed here seem partly hypothetical. But the only hypothesis (although it is still supported by some facts) is the parasite-host impact on migration. The only way to prove that it is wrong is by experimentation. To this end, first a study of the population statistics of *L. quadrimaculata* and its parasites should be undertaken. This study can be carried out with larvae, hence it may be a quantitative one.

It is necessary to stress that migrations in different species are not necessarily governed by the same mechanisms. Some longe-range dwellers as e.g. *Pantala flavescens* and *Hemianax ephippiger* certainly have other "motives". It is not even certain that we may now know the whole story of *L. quadrimaculata*. There may be several entirely different mechanisms leading to the same result.

ACKNOWLEDGEMENTS

We wish to thank all people who sent us the reports of their experiences with the 1971 swarm in Belgium. We are greatly indebted to our Dutch colleagues Dr. D.C. GEIJSKES, Dr. B. KIAUTA and Dr. M.A. LIEFTINCK for communicating us data on migrations in Holland. This paper, in a preliminary stage, was discussed at the yearly meeting of Dutch Odonatists in Utrecht and there were some new and stimulating suggestions that came out of this confrontation.

Special thanks are due to Mr. B. DAVIDSE, for space in his TV-program in order to get the cooperation of many.

REFERENCES

Numbers behind references refer to Fig. 2. Many minor notes published prior to 1932 are omitted as they can easily be found in FRAENKEL (1932).

ACLOQUE, A., 1901. Migrations de Libellules. Cosmos, Paris 44: 521-524. – [1].

ADELUNG, N., 1914. Vol en masse de Libellulides à St. Petersbourg. Russk. ent. Obozr. 14: 177. – [2].

ALTUM, 1862. Libellenzüge. Natur Offenb. 8: 382. – [3].

AZOV, Z., 1929. Migration of *Leptetrum quadrimaculatum* L. in the North Dvina district. Zashch. Rast. Vredit. 6: 533: – [4].

BARROIS, C., 1896. Une apparition de vol de Libellules. Revue scient., Paris 5: 315-316. – [5].

BARTENEF, A.N., 1918. Migration of dragonflies in 1914 and on migration in dragonflies in general. Protok. Obshch. Estest. Vrach., Tomsk 1: 49-66 (Russian). – [6].

BAXTER, T., 1911. Migratory (?) flights of *Libellula depressa*. Ent. Rec. 23: 243-244. (*Note*: this was evidently *L. quadrimaculata*, not *depressa*.). – [7].

BEMMELEN, A.A. Van, 1854. Waarnemingen over het trekken van Insekten. Hand. ned. ent. Vereen. 3: 81-103 (ed. 1857 ?). – [8].
BEMMELEN, A.A. Van, 1883. Libellentrek over Rotterdam. Tijdschr. Ent. 27: 91. – [9].
BEUTENMULLER, W., 1890. Records of migrations in dragon-flies, especially *Libellula quadrimaculata*, from 1868-1888. *In*: R.H. Lamborn, Dragonflies vs. Mosquitoes. Appleton, New York. – [10].
BEUTHAN, K., 1914. Libellenwanderung. Int. ent. Z. 8: 112. – [11].
BLASIUS, W., 1883. Uber die grossen Libellenzüge durch Norddeutschland (Sachsen, Braunschweig usw.) im Sommer 1881. Jber. Ver. Naturw. Braunschw. 3: 72-77. – [12].
BODDEKE, R., 1960 a. The life history of *Prosthogonimus ovatus* Rudolphi. I. Experiments in birds. Trop. geogr. Med. 12: 263-292. – [13].
BODDEKE, R., 1960 b. The life history of *Prosthogonimus ovatus* Rudolphi. II. The intermediate hosts. Trop. geogr. Med. 12: 363-377. – [14].
BODDEKE, R., 1960 c. The life history of *Prosthogonimus ovatus* Rudolphi. III. Taxonomy and ecological aspects. Trop. geogr. Med. 378-387. – [15].
BODDEKE, R., 1962. Some aspects of the biology of *Prosthogonimus ovatus* (Trematoda). Archs. néerl. Zool. 14: 612-634. – [16].
BOHLS, O., 1898. Wanderungen der Libellen. Jber. Ver. Naturk. Unterweser 1: 5-7. – [17].
BORROR, D.J., 1953. A migratory flight of dragonflies. Ent. News 14: 204-205. – [18].
BRANNIGAN, C. & D. HUMPHRIES, 1969. I see what you mean. New Scient. 42 (650): 406-408. – [19].
BRIGGS, C.A., 1892. Dragon-flies in 1892. Ent. Mo. Mag. 29: 8-9. – [20].
CAMPBELL, F.M., 1884. Dragon-fly migration. Ent. Mo. Mag. 21: 192. – [21].
CHYZER, K., 1884. Szitakötök vandorlasa. Rovart. Lapok 1: 125-126. – [22].
CORBET, P.S. 1962. A biology of dragonflies. Witherby, London. – [23].
DANNREUTHER, T. 1935. Migration records, 1935. Entomologist 68: 252-254. – [24].
DANNREUTHER, T., 1936. Migration records, 1936. Entomologist 69: 5. – [25].
DANNREUTHER, T., 1942. Migration records, 1941. Entomologist 75: 55-62. – [26].
DUMONT, H., 1964. Note on a migration of the dragonfly *Libellula quadrimaculata* L. in the North of France. Bull. Annls Soc. r. ent. Belg. 100: 177-181. – [27].
DUPUIS, C., 1946. Migration de *Sympetrum meridionale* Sélys. Feuille Nat. (N.S.) 1: 69. – [28].
ELTON, C., 1930. Animal ecology and evolution. Clarendon, Oxford. – [29].
FEDERLEY, H., 1908. Einige Libellenwanderungen über die zoologische Station bei Tvärminne. Acta Soc. Fauna Flora fenn., 31 (7), 38 pp. – [30].
FONTAINE, M., 1902. Migration de *Libellula quadrimaculata*. Annls Soc. ent. Belg. 46: 7-8. – [31].
FRAENKEL, G., 1932. Die Wanderungen der Insekten. Ergebn. Biol. 9: 1-238. – [32].
FRASER, F.C., 1944 (1945). Migration of Odonata. Ent. Mo. Mag. 80 (81): 73-74. – [33].
FRENCH, A.R., 1964. Migratory dragonflies on Lundy Island. Entomologist 97: 17. – [34].
FROHAWK, F.W., 1924. Dragonfly migrating. Entomologist 57: 260. – [35].
GALVAGNI, E., 1925. (Additions to a communication by R. Geissler). Bl. Naturk. Naturschutz Niederöst. 12: 116. – [36].
GAUCKLER, H., 1881. Libellenschwarm. Ent. Nachr. 7: 216. – [37].
GEISSLER, R., 1925. Libellenzüge. Bl. Naturk. Naturschutz Niederöst. 12: 115-116. – [38].
GIARD, A., 1889. Sur un convoi migrateur de *Libellula quadrimaculata* dans le nord de la France. C.-r. Séanc. Soc. Biol., 41: 423-425. – [39].
GRAAF, N.H. de, 1854. Over *Libellula quadrimaculata*. Hand. Ned. ent. Vereen. 1: 104-105. – [40].

GRASSE, P., 1932. Observations et remarques sur les migrations d'Odonates. Soc. ent. Fr. (Tome centenaire): 657-668. – [41].
HAGEN, H.A., 1861. Uber Insektenzüge. Stettin. ent. Ztg. 21: 73-83. – [42].
HALL, C.G., 1889. Migratory swarm of *Libellula quadrimaculata* at Dover. Ent. Mo. Mag. 25: 324 (with additional note by R. Mc. Lachlan). – [43].
JOHNSON, C.G., 1960. A basis for a general system of insect migration and dispersal by flight. Nature, Lond. 186: 348-350. – [44].
JOHNSON, C.G., 1965. Migration. *In*: M. Rockstein, The physiology of Insecta. II. Academic Press, New York. – [45].
JOHNSON, C.G., 1969. Migration and dispersal of insects by flight. Methuen, London. – [46].
KARSCH, F., 1900. Eine Invasion von Libellen (in Antwerpen). Ent. Nachr. 26: 253. – [47].
KEILHOLZ, 1925. Massenzüge von Libellen. Ent. Z. Frankf. a. M. 39: 38-39. – [48].
KENNEDY, J.S., 1961. A turning point in the study of insect migration. Nature, Lond. 189: 785-791. – [49].
KIAUTA, B., 1964. Over een trekvlucht van *Libellula quadrimaculata* L. (Odonata-*Libellulidae*). Levende Nat. 67: 59-63. – [50].
KIAUTA, B., 1965. Een trekvlucht van *Libellula quadrimaculata* L. in Nederland in 1964. Levende Nat. 68: 71. – [51].
KLIMEK, L., 1949. Ważki (Odonata) Wojewodztwa Pomorskiego. Studia Soc. Sci. Torun 2: 13. – [52].
KÖHLER, K., 1927. Der Libellenzug durch Schlesien im Jahre 1925. Mitt. naturw. Ver. Troppau 33: 26-30. – [53].
KOLOSOV, J.M., 1916. Sur l'apparition en masses des Odonates aux environs de Petrograd et de Novaja Alexandrija, gouvernement de Ljublin, au mois de mai 1914. Russk. ent. Obozr. 15: 413-419. – [54].
KÖPPEN, F.T., 1871. Einige Fälle von Massenerscheinen verschiedener Insekten und speziell der Libellen. Stettin. ent. Ztg. 32: 183-190. – [55].
KORMONDY, E.J., 1961. Territoriality and dispersal in dragonflies (Odonata). Jl N.Y. ent. Soc. 69: 42-52. – [56].
KRULL, W.H., 1930. The life history of two North American lung flukes. J. Parasit. 16: 207-212. (et ref. al., vide J. Timon-David, 1965). – [57].
LAMARQUE, H., 1923. Note sur les convois de Libellules. P.-v. Soc. linn. Bordeaux 75: 224. – [58].
LANCASTER, A., 1900 a. Migrations de Libellules. Ciel Terre 21: 196. – [59].
LANCASTER, A., 1900 b. Les passages de libellules du commencement de juin 1900. Ciel Terre 21: 246-270.
LANDWEHR, F., 1881. Der Zug von *Libellula quadrimaculata*. Ent. Nachr. 7: 180. – [60].
LARSEN, A., 1950. Guldsmedetraek over Danmark. Fauna Flora 56: 105-124. – [61].
LICHTENSTEIN, J. & P. GRASSÉ, 1920. Une migration d'Odonates. Bull. Soc. ent. Fr. 1920: 160-163. – [62].
LONGFIELD, C., 1950. Notes on the British Odonata in 1949. Entomologist 83: 203-206. – [63].
LORENZ, K.A., 1958. The evolution of behaviour. Scient. Am. 199: 67-68. – [64].
LUCAS, W.J., 1900. Migration of dragonflies. Entomologist 33: 210-211. – [65].
MORREN, M.C., 1853. Sur une émigration de demoiselles. Bull. Acad. r. Belg. Cl. Sci. 20: 323-324 (*Note*: this was probably *L. quadrimaculata*, not *depressa* as stated). – [66].
MULDER, C., 1855. Aanteekening over groote zwermen van glazenmakers in Nederland, in 1855. Alg. Konst Letterb. 67: 410-411. – [67].

MUSPRATT, V.M., 1947. Migrations d'insectes dans le sud-ouest de la France. Feuille Nat. 2: 28-29. – [68].

NEWTON, A., 1883. An extraordinary flight of dragonflies. Nature Lond. 28: 271. – [69].

NORDMAN, A., 1935. Über Wanderungen der *Libellula quadrimaculata* L. bei der zoologischen Station Tvärminne in S.-Finland in Juni 1932 und 1933. Notul. ent. 15: 1-8. – [70].

NORDMAN, A., 1937. Further observations on the migrations of *Libellula quadrimaculata* at the zoological station of Tvärminne, S.-Finland, in June 1936. Notul. ent. 17: 24-28. – [71].

NORDMAN, A., 1945. Vandrande skaror av *Libellula quadrimaculata* i Helsingfors. Notul. ent. 25: 185. – [72].

NORDMAN, A., 1957. Cordulia aenea L. och Somatochlora arctica Zett. på migration i Skärgårshavet i SW-Finland (Odonata). Notul. ent. 37: 30-31. – [73].

OWEN, D.F., 1958. Dragonfly migration in South West Portugal, Autumn 1957. Entomologist 91: 91-95. – [74].

PENDER, S., 1889. Migratory swarm of *Libellula quadrimaculata* off the Essex coast. Ent. Mo. Mag. 25: 93 (with additional note by R. Mc. Lachlan). – [75].

RITSEMA, C.C. 1884. Libellentrek. Tijdschr. Ent. 28: 21-22. – [76].

RIVEAU, C., 1882. Migration de libellules. Feuille jeun. Nat. 12: 123. – [77].

SAJO, K., 1897. Insektenreisen. Illte Wschr. Ent. 2: 229. – [78].

SCHAITER, H.J., 1880. Libellenschwärme in Galizien. Ent. Nachr. 6: 133, 167. – [79].

SCHNABL, 1880. Uber Libellenschwärme. Ent. Nachr. 6: 167. – [80].

SCHNEIDER, G., 1910. Libellenzug in Riga. KorrspBl. Naturf. Ver. Riga 53: 110. – [81].

SUOMALAINEN, H., 1937. Uber die Wanderungen von *Libellula quadrimaculata* L. Suom. hyönt. Aikak. 3: 3. – [82].

TARNUZZER, C., 1921. Wanderungen in der Insektenwelt im Sommer 1921. Naturw.-tech. Jb. 3: 185-187. – [83].

THORPE, W.H., 1966. A discussion on ritualization of behaviour in animals and man. (J. Huxley ed.). Phil. Trans. R. Soc. (B) 251. – [84]. 85

THIJSSE, J.P., 1925. De libellentrek van mei 1925. Levende Nat. 30: 114-119. – [86].

TIMON-DAVID, J., 1965. Trématodes parasites des Odonates. Biologie et Cycles. Annls Fac. Sci. Marseille 38: 15-41, – [86].

TRYBOM, F., 1894. Masswandring af Trollsländor. Ent. Tidskr. 15: 178. – [87].

TULLOCH, J.B.G., 1929. Dragonfly migration. Entomologist 62: 213. – [88].

TUTT, J.W., 1899. Migration and dispersal of insects: Dragonflies. Ent. Rev. Wash. 11: 153-55, 181-83, 213-15, 231-33. – [89].

VIEWEG, K., 1897. Libellenflug. Illte Wschr. Ent. 2: 464. – [90].

WAGNER, W., 1897. Der Libellenflug in Hamburg. Illte Wschr. Ent. 2: 479. – [91].

WEDTS DE SWART, J.C., 1971. Sterke libellentrek over Zeeland. Levende Nat. 74: 176-177. – [92].

WEIDINGER, G., 1881. Libellenschwarm. Ent. Nachr. 7: 187:188. – [93].

WEISSENBORN, W., 1839. Great migration of dragonflies, observed in Germany. Nat. Hist. Mag., (N.S.) 3. – [94].

WILLIAMS, C.B., 1929. Some records of dragonfly migration. Entomologist 62: 145-148. – [95].

WILLIAMS, C.B., 1958. Insect migration. Collins, London. – [96].

WRIGHT, M., 1946. The economic importance of dragonflies. J. Tenn. Acad. Sci. 21: 60-71. – [97].

This paper. – [98].