Observations on the migrations of the Painted Lady (*Vanessa cardui* (L.)) in Denmark in 1996
(Lepidoptera: Nymphalidae)

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In June 1996, Denmark and the rest of N Europe was invaded by huge numbers of Painted Ladies (*Vanessa cardui* (L.)). The first butterflies were observed in Denmark on 1 June, but they were not seen in numbers until 7 June, when masses of *V. cardui* arrived in NW Jutland along a stationary front situated over the North Sea. On the following day the front disappeared and the butterflies were seen all over southern Scandinavia. Strong migratory flights were observed in Denmark until 14 June.

Mid- to late August massive re-migrations of *V. cardui* were observed in Denmark for the very first time. These flights contained far more individuals than in spring. The numbers of *V. cardui* declined rapidly during the first half of September but a scarce third generation was observed mid-October.

Meteorological data suggest that, during spring as well as fall migrations, the butterflies were subjected to significant wind drift. In easterly winds, migrations were observed in W Jutland, while in westerlies, migrations were only seen in E Jutland. In fall, the data indicate that the re-migration was initiated by the first cold night in a stable high pressure period.

The migrations in spring were highly wind-aided and the butterflies advanced rapidly towards N Europe. In fall, however, the flights were often into the wind. Still, the speed and range of the fall re-migrations remain unknown.

The arrival of *V. cardui* in spring was closely synchronized with *Vanessa atalanta* (L.) and *Autographa gamma* (L.). In fall, *V. cardui* was observed in mixed flights with *Inachis io* (L.), *V. atalanta, Aglais urticae* (L.) and *A. gamma.*

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Introduction

The Painted Lady *(Vanessa cardui* (L.)*)* is a well-known migratory butterfly which is distributed throughout the world. In the Western Palaearctic the source areas of migrations are the steppe areas in northern Africa, southernmost Europe and the Middle East (Williams, 1930). Due to a large clutch size and a short developmental period (about 7 weeks) (Stoltze, 1996), *V. cardui* rapidly takes advantage of favourable conditions and in years of large-scale migrations, the species finds its way all the way to the Polar Sea.

Williams (1930) presented a historical review of butterfly migration with main emphasis on *V. cardui.* His data revealed that the most remarkble invasion took place in 1879 when swarms containing millions of specimens of *cardui* were frequently observed in Europe. Since then, much work has been done on the migratory habits of European butterflies. In western and northern Europe annual reports have been published in England since 1931 (*Entomologist* and later in *Entomologist's Record and Journal of Variation*), in Holland since 1941 (*Entomologische Berichten*), in Denmark from 1961 to 1983 (*Flora & Fauna*), in Germany since 1963 (*Atalanta*), in Sweden since 1972 (*Entomologisk Tidskrift*) and in Belgium since 1972 (*Phegea*).

This huge entomological litterature contains thousands of reports on migrations of *V. cardui*, but detailed observations on the flights are scarce. At our latitudes large invasions are usually taking place within irregular intervals of 8-10 years, the most recent ones being in 1980, 1988 and 1995 (Münster-Swendsen, 1980; Kaaber, 1981; Stoltze, 1996). In 1996, only one year after the previous invasion, Europe was again invaded by vast masses of *V. cardui*, and the year turned out to be the best ever. For the very first time spring immigrations as well as huge fall re-migrations (cf. Baker, 1982) were observed in several places in Denmark.

The purpose of this paper is to present the Danish observations and to place them in a wider European perspective. For this reason, the presently available 1996 observations from other European countries have also been included. Based on the main material of observations, some factors obviously influencing nymphalid butterfly migration in northern Europe are discussed.

Material and methods

The present material consists primarily of observations from ornithologists visiting different migration watchpoints. Only a few Danish lepidopterists have contributed, as there is no systematized and coordinated collecting of data regarding migratory Lepidoptera at present. Information from other European countries has been obtained from the Internet via the newsgroups LEPS-L and UK-Birdnet. No attempts have been made to standardize the observations which are presented as reported by the observer. Meteorological data have been obtained online from the National Climatic Data Centre in the USA and from Deutscher Wetterdienst in Germany.

Course of the 1996 invasion

The Danish data from 1996 are presented in Table 1. During the cold May no butterflies were observed, but in the morning of 1 June *V. cardui* arrived in many places. A real invasion with huge numbers of migrating butterflies took place in the period 7-16 June. The first invasion into Europe had started around 20 April when massive flights were recorded in Italy (Tout, pers. comm.) and southern France (Dubois, pers. comm.). The following invasion into N Europe was initiated late May. In the beginning it most probably consisted of African descendants from the April generation, later evidently accompanied by the newly hatched butterflies from southern Europe (Tout, pers. comm.). During the next month *V. cardui* advanced towards northernmost Scandinavia. Already on 9 June they reached 64°N (Breistøl, pers. comm.), and the butterflies crossed the Polar Circle around 20 June (Gustafson, pers. comm.). In July the author observed several very worn butterflies ("blinkers"), which may have been new immigrants from the south. In this period distinct immigrations, though not invasions, took place on Shetland and the Faroe Islands (Kaaber, pers. comm.).

The eggs laid by the June butterflies gave birth to an exceptionally common second generation which hatched from late July to mid-August. During the first half of August scattered flights in a northerly direction were recorded in E Jutland and in the Swedish island of Öland as well (Funch, pers. comm.), but it is unknown if these butterflies were migrants from the south. Mid-August the direction reversed and massive southerly flights, containing far more individuals than in June, took place. Individuals which stayed in Denmark and the rest of N Europe probably all died out in the cold September. However, large southerly flights were still recorded in southern Europe medio September (Dixon, pers. comm.).

Table 1. Flights of *Vanessa cardui* in Denmark in 1996.

Date	Location (+ reference on map)	Numbers	Direction	Observer	Remarks
1/6	Tipperne (1)	1	–	Henrik Knudsen	in the early morning
4/6	Århus (2)	4/10 min	NNE	The author	3 *V. atalanta* ENE
7/6	Skårups Odde (3)	40/h	ENE	Jens Frimer	5 *V. atalanta* ENE, thousands of *A. gamma*
7/6	Vendsyssel (4)	~50/h	N	The author	No migration at all in Århus
7/6	Bjergby (5)	25/h	NE	Jens Kr. Kjærgaard	4 *V. atalanta* ENE
9/6	Århus	27/h in early morning	NE	The author	3 *V. atalanta* ENE
9/6	Kalø (6)	500/h over a 50 m. front	N	Michael Stoltze	
9/6	Skagen (7)		ENE	John Pedersen	4 *V. atalanta* ENE
9/6	Anholt (8)	at least 10000 feeding in Anholt town	–	Niels Willumsen	~1000 *V. atalanta*!
10/6	Moesgård (9)	61/h over a 5 m. front	NNW	The author	Thousands of *A. gamma*. 4 *V. atalanta* ENE
14/6	Århus	max. 270/10 min for 4 hours	NE	The author	
16/6	Hvidding Krat (10)	8/h	W	Svend Kaaber	
27/7	Æbelø (11)	1 fresh	–	Svend Kaaber	
13/8	Klitmøller (12)	1000/min. for 4 hours!	SSE	Jens Jørgen Andersen	Over a million butterflies recorded, including hundred thousands of *V. atalanta*, *A. urticae*, thousands of *I. io* and ~20 *N. antiopa*. *A. gamma* extremely common. No sign of migration in E Jutland.
15/8	Vejle Fjord (13)	10/h	N	The author	400 *I. io* and 600 *P. brassicae* migrating WSW.
16/8	Århus	max. 220/10 min over a 20 m. front for 5 hours	SW	The author	*V. atalanta* and *I. io* abundant
17/8	Vejle Fjord	15/h	WSW	The author	250 *I. io* WSW
17/8	Knudshoved Odde (14)	extremely numerous	SW	Lisbeth Petersen	
18/8	Begtrup Vig (15)	25/min	SE	Peter Gjelstrup	
19-21/8	Århus	migration seen	S	Svend Kaaber	
20/8	Bulbjerg (16)	500/h	W	Anonymous	
20/8	Hanstholm (17)	min. 500/min	SSE	Jakob Olesen	Millions of hoverflies, *Episyrphus balteatus*
22/8	Lønstrup (18)	50/min	SSW	National Danish Television, DR.	Thousands of *I. io* and *V. atalanta*
23/8	Agger Tange (19)	300/h	S	Jens Kr. Kjærgaard	4000 *V. atalanta* and 500 *I. io*
26/8	Skårups Odde	90/h	S	Jens Frimer	150 *V. atalanta*
2/9	Vejle Fjord	25/h	WSW	The author	1900 *V. atalanta*
10/10	Vejle Fjord	1 fresh	–	The author	
13/10	Gedser Odde (20)	1 fresh	–	Anonymous	

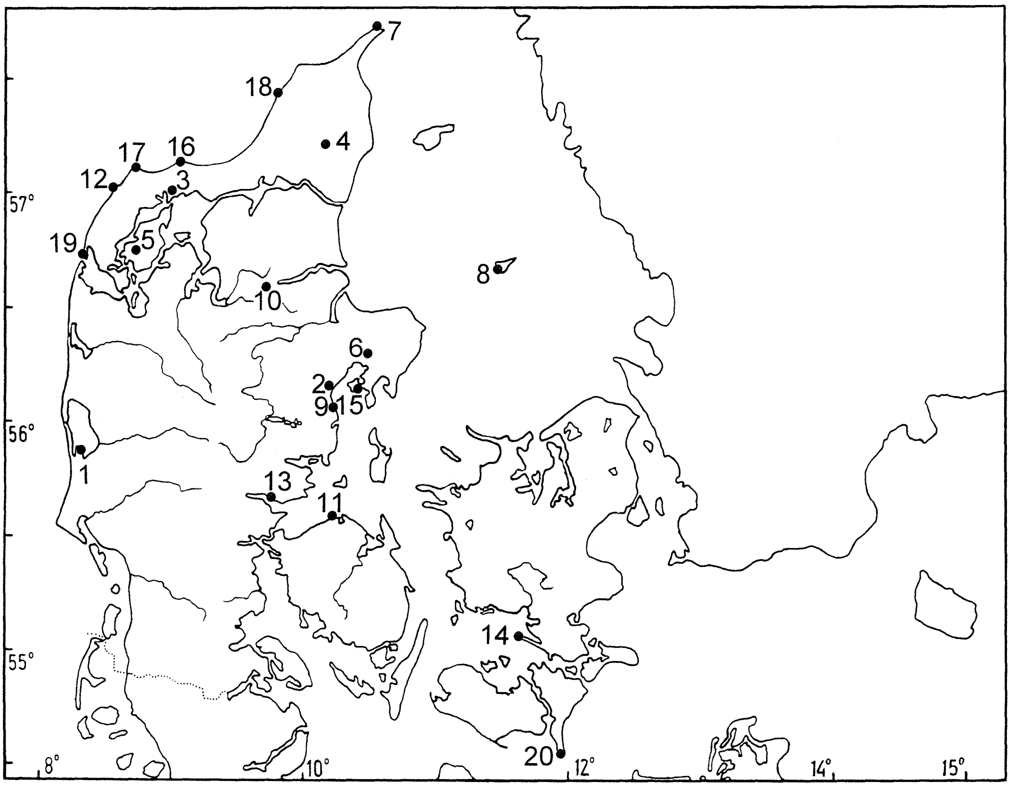

Fig. 1. Sites where migrations were recorded (note the references in table 1).

Phenology of Painted Ladies in Northern Europe

In western Europe large immigrations of *V. cardui* may occur from mid-April to late July (Williams, 1930). Such invasions usually originate in one area, i.e. North Africa or the Middle East, the latter being the case in 1995 (Ten Hagen, 1996). In normal years, independent and scattered immigrations originating in different source areas are observed in northen Europe throughout the summer. Outbreaks from the same source area in two successive years have never been reported. In 1996, observations from southern Europe show that *V. cardui* invaded Europe twice, both invasions undoubtedly originating in NW Africa. However, as proposed by Williams (1930), early immigrations of *V. cardui* might without any doubt originate even further south, from the Sahel area.

The strong southerly flights which were recorded in Denmark from mid- to late August are very remarkable and in strong contrast to the scattered flights normally reported (Kremer, 1969; Steineger & Eitschberger, 1979). In Alberta in Canada, however, massive southerly flights were observed in 1983 (Myres, 1985). Probably, massive re-migrations in August will occur in most years of early summer invasions.

An assessment between homebred butterflies and/or migrants from the north or from the south is very difficult. Thus, the origin of the second Danish brood which was observed mid-October is obscure, because it is uncertain whether *V. cardui* hatched in Denmark always need a reproductive diapause (including migration) (cf. Tauber,

1986) before breeding. In all probability, the October butterflies were descendants of a few fertile late July immigrants from the south.

It is worth mentioning that the course of the 1996 invasion closely resembles the famous one in 1879 described by Williams (1930).

Flight behaviour and direction

The Painted Lady is well known for its dispersal capacity. Mikkola (1986) reports that it can cover a distance of about 650 km in 24 hours! However, considering the advance of butterfly migrations, refueling stops must also be taken into account. Vanholder (pers. comm.) reports that in Belgium there was a break in migration on 2 June where the butterflies fed intensively, and on the island Anholt in Kattegat thousands of exhausted butterflies were feeding on 9 June (Willumsen, pers. comm). Yet it is unknown how often migrating *V. cardui* need to rest and "refuel". An "average" Monarch *(Danaus plexippus* (L.)*)* has a maximum active, flapping flight (flight speed 40 km/h) duration between successive refueling stops of approximately 11 hours (Gibo & Pallet, 1979) but when the butterfly enters a "cruising flight" a maximum flight duration of 44 hours may be reached. Even more energy can be saved if the butterfly flies at higher altitudes, uses tailwinds or soars in thermals (Gibo & Pallet, 1979). For instance, meteorological data suggest that thousands of Monarchs made a transatlantic migration in October 1995 (Vanholder, 1996), which lasted about 5 days. Contrary to Peacocks (*Inachis io* (L.)*)* (Stoltze, 1996; own obs.), Red Admirals *(Vanessa atalanta* (L.)*)* (Benvenuti, 1994; own obs.) and Small Tortoiseshells *(Aglais urticae* (L.)*)* (own obs.) which can also perform soaring flight in thermals, *V. cardui* has only been observed close to the ground in the energetically costly flapping flight. On one occasion, however, migrating butterflies including *V. cardui* were seen in all heights up to at least 200 meter, the visibility limit for binoculars.

A weather analysis which was performed on 1992 butterfly data from the Faroe Islands demonstrated that with the appropriate weather conditions *V. cardui* and *V. atalanta* might reach these isolated islands from NW Africa within 2 or 3 days (Kaaber et al., 1994). Under such conditions the butterflies have to fly at night and make use of tail winds where the flight speed may reach about 40 km/h. Indeed, night migrations of nymphalid butterflies, including *V. cardui,* in coastal areas have been reported several times (Williams, 1930; Kettlewell, 1956; Ryrholm & Källander, 1986; J.J. Andersen, pers. comm.). It is yet unknown whether such migrations are accidental or regularly occurring phenomenons. Also in 1996, high numbers of *V. cardui* reached the Faroe Islands (Kaaber, 1997).

In the spring of 1996, many observers reported first sightings of *V. cardui* in the early morning, indicating that the butterflies had arrived during the night. At the Skaw (Skagen) the first migrating *V. cardui* actually arrived at sunrise (03.30 Central European Standard Time) on 7 June and on at least one occasion migrating butterflies were seen until sunset (9 June in Århus). In the fall flights there were no indications of night migrations of *V. cardui,* and in the morning migrating butterflies were never observed until around 08.00 CET. The migrations peaked around 12.30 CET and ended around 16.00 CET. Such daytime distributions during the fall migration have often been recorded in *V. atalanta* (Benvenuti et al., 1994). In Denmark there are single reports on massive *atalanta* migrations around 16.00 CET (Grell, pers. comm.).

Weather conditions suitable for migration are usually associated with winds from southerly directions. Wind aided flights prevail in spring while flights into the wind are a common feature of fall migrations, the latter shown by detailed observations in Canada in August 1983 (Myres, 1985). In early June the butterflies were frequently using tail winds but they were also seen in calm weather or in crosswinds. During the fall remigrations in August and September *V. car-*

dui were only observed migrating in weak head- or crosswinds (Beaufort 2-3, occasionally 4-5).

The Painted Ladies were on several occasions observed using shores as guidelines. The observations show that the butterflies allow a considerable deviation in flight direction, as long as the main component (N or S) is maintained. This is consistent with observations on *D. plexippus* (Schmidt-Koenig, 1985) and *V. atalanta* (Benvenuti, 1994). Generally, observers have reported that butterflies and passerine birds tend to migrate in the same directions, indicating that they use the same topographical cues.

In accordance with the observations of several authors (Williams, 1958; Baker 1969), the direction of migrating *V. cardui* reversed mid-August. It is an intriguing question whether this reversal acts on an individual level, as claimed by Baker (1969), or whether it is just a shift in the direction ratio, i.e. the same amount of individuals are still heading north, but this migration is obscured by other groups of butterflies that have started moving south. Assuming that the single butterfly has only one migratory phase before reproduction, a 180 degree reversal of direction seems to be a waste of time and energy! A more likely explanation could therefore be that the north migrating individuals at our latitudes are fertile (extension of range) while the south migrating ones are not. Still, the only butterfly where individuals are known to reverse their direction is *D. plexippus* (Brower, 1996).

Recent laboratory studies have demonstrated, that the direction of migrating Large Cabbage Whites (*Pieris brassicae* (L.)) is different between successive generations (Spieth & Holtgrave, 1996). In many butterfly species, voltinism and reproduction is controlled by photoperiod and temperature as shown in *D. plexippus* (Barker & Herman, 1976; James, 1983; Malcolm et al. 1987) and *I. io* (Pullin, 1986). Taking the intimate coupling between reproduction and migration into account, migration must ultimately be controlled by the same factors as reproduction. Therefore, butterflies subjected to different temperatures and photoperiod might acutally arrive in an area where native individuals have not started migrating yet. This may indeed have been the case 13 August 1996, when millions of *V. cardui* arrived from the north in NW Jutland while native butterflies were still stationary.

Biometeorological aspects of the 1996 flights

According to Deutscher Wetterdienst, NW Africa experienced heavy rains in winter and early spring 1996. This situation probably caused an explosion in the regional *V. cardui* populations within one or two generations. However, without detailed information from southern Europe, it is at present difficult to correlate the progress of the 1996 invasion with synoptic scale weather conditions. In a Danish perspective, warm weather and tail winds are needed for the butterflies to advance towards Scandinavia.

The first major invasion of *V. cardui* in Denmark took place in NW Jutland on 7 June. A weather analysis suggests that the butterflies arrived from the North Sea along the edge of a stationary front (fig. 1). This is supported by the fact that no migrating butterflies at all were observed in E Jutland. Furthermore, the arrival of *V. cardui* and *V. atalanta* into neighbouring southern Norway did not take place until 8 June where the front over the North Sea had disappeared (Breistøl, pers. comm.). Migratory flights in association with fronts and thunder storms are indeed a regularly occurring phenomenon, especially in various moths (Mikkola, 1967). However, for *V. cardui* observations suggest that horisontal wind patterns rather than thermal upwinds make fronts favourable in northerly flights, e.g. winds are normally having a southerly component (tail wind) prior to a front passage.

On 9 June, a day with stable high pressure weather all over northern Europe, massive flights were recorded in Denmark (table 1), England (Whitehead, 1996), southern Norway (Breistøl, pers. comm.) and eastern

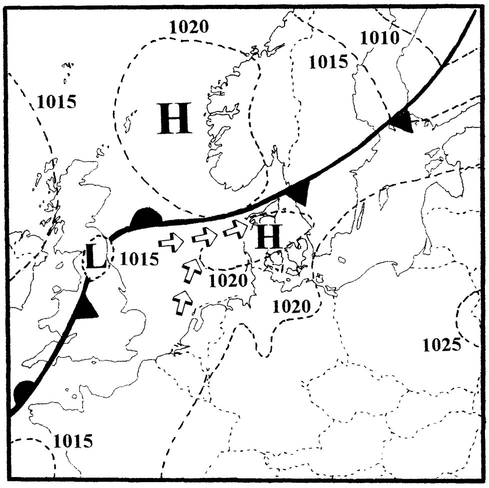

Fig. 2. Weather conditions in northen Europe at midnight 6-7 June. Arrows indicate the suspected route of migrating *Vanessa cardui*.

Sweden (Breistøl, pers. comm.). In Denmark winds had turned into westerlies after the passage of a major front system with heavy thunder storms on 8 June. Thus, the apparent concentration of *V. cardui* in E Jutland on 9 June may have been due to wind drift, but it is more likely that new butterflies had arrived from the south. Wind drift is however suspected to have accounted for the distribution of migrations in a period of stable high pressure weather in August. When the weather was calm or winds blew from W (fig. 3), migratory flights were recorded on Zealand and in E Jutland, but when the winds increased from SE (fig. 3), large migrations were only observed along the west coast of Jutland (table 1, figs. 1 and 2). Although *V. cardui* like *D. plexippus* (Schmidt-Koenig, 1985; Gibo 1986) and several neotropical butterflies (Srygley et al., 1996) may compensate for wind drift by turning their headings or even fly against the wind, they nevertheless experience significant displacements on a larger scale.

The Danish Painted Ladies emerged in the first 10 days of August but no significant migrations were observed in this period. Instead the butterflies were feeding. Fat supplies of newly emerged *D. plexippus* are insufficient for long-distance migrations (Gibo & McCurdy, 1993) but if the butterflies are not in danger of being overtaken by the Polar front, they will feed and hence accumulate large fat reserves before migration. Most probably, this has also been the case in *V. cardui* in 1996.

In E Jutland, heavy migrations of locally bred *V. cardui* started on 16 August and were observed during the rest of the month. What initiated this onset of migratory behaviour? Temperature and wind data from Tir-

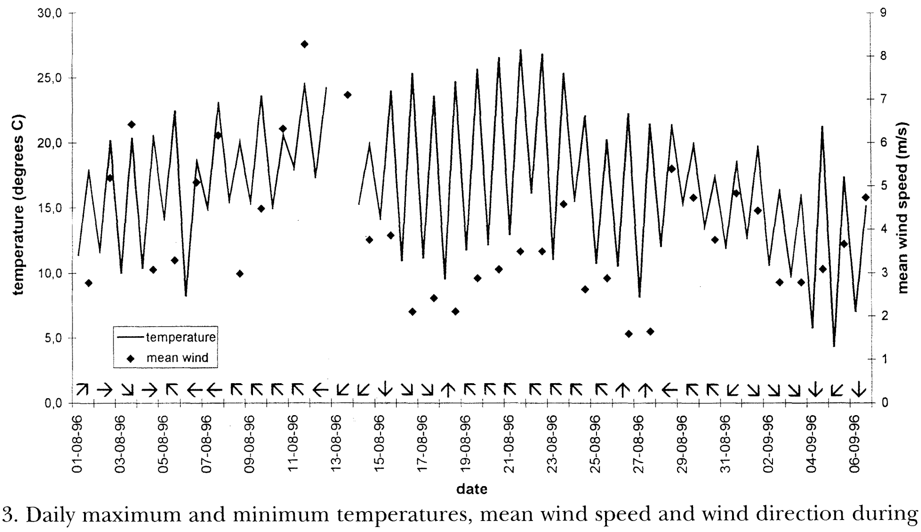

Fig. 3. Daily maximum and minimum temperatures, mean wind speed and wind direction during August and the beginning of September at Tirstrup, E Jutland.

strup, E Jutland (fig. 3) indicate that the releasing factor was the first cold night in a period of hot, sunny days. The cue tells the butterfly to leave Denmark before the, what Baker (1969) termed *onset of autumnal selective pressures.* During the rest of August and the beginning of September migrations continued whenever weather conditions were favourable (light winds, sunshine).

In 1996 many observers reported mixed flocks of migrating butterflies. The arrival of *V. cardui* in June was perfectly synchronized with Red Admirals and Silver Y's (*Autographa gamma* (L.)), indicating that these insects too had their origin in North Africa. In fall *V. atalanta* and *A. gamma* were again extremely common but surprisingly, migrating *V. cardui* were also accompanied by huge numbers of *I. io, A. urticae* and small numbers of Camberwell Beauties (*Nymphalis antiopa* (L.)). These resident species sometimes show strong migratory behaviour with spectacular flights. This was the case for *urticae* in 1991 (de Vos et al., 1993) and 1996 (J.J. Andersen, pers. comm.), *io* in 1995 (de Vos & Rutten, 1996) and 1996 (own obs., table 1), and *antiopa* in 1995 (de Vos & Rutten, 1996). The flights are generally towards W, but observations from 1996 showed that mixed flocks of butterflies tended to migrate in the same direction. Synchronized and unidirectional flights of these five nymphalid species indicate that flights depend upon the same meteorological factors although the ecological causation of the migratory behaviour (overwintering, reproduction, crowding etc.) may differ considerably among the species.

The distances covered by Painted Ladies during fall flights are unknown but in order to survive they must at least reach southernmost Europe. Unfortunately, no evidence exists whether they are capable of undertaking this long journey. Thus the fate of the millions of butterflies observed during fall migration in Denmark is still highly uncertain.

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References

Baker, R.R., 1982. *Migration: paths through time and space.* Hodder and Stoughton, London.

Baker, R.R., 1969. The evolution of the migratory habit in butterflies. – *Journal of Animal Ecology* 38: 703-746.

Benvenuti, S., P. Dall'Antonia & P. Ioalé, 1994. Migration pattern of the Red Admiral, *Vanessa atalanta* L. (Lepidoptera, Nymphalidae), in Italy. – *Bollettino di Zoologica* 61: 343-351.

Brower, L.P., 1996. Monarch butterfly orientation: Missing pieces of a magnificent puzzle. – *Journal of Experimental Biology* 199: 93-103.

Gibo, D.L., 1986. Flight Strategies of Migrating Monarch Butterflies (*Danaus plexippus* L.) in Southern Ontario. In: *Insect Flight: Dispersal and Migration,* ed. by W. Danthanarayana. Springer-Verlag, Berlin Heidelberg 1986: pp. 172-184.

Gibo, D.L. & J.A. McCurdy, 1993. Lipid accumulation by migrating monarch butterflies (*Danaus plexippus,* L.). – *Canadian Journal of Zoology* 71: 76-82.

Gibo, D.L. & M.J. Pallet, 1979: Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. – *Canadian Journal of Zoology* 57: 1393-1401.

Kettlewell, H.B.D., 1956: A southern migration of *Vanessa atalanta* L. – the Red Admiral butterfly. – *Entomologist* 89: 18-19.

Kaaber, S., P. Gjelstrup, D. Bloch & J.-K. Jensen, 1994. Invasion af admiralen (*Vanessa atalanta* L.) og andre sommerfugle på Færøerne i 1992. – *Fròdskaparrit* 41. bok 1994 (1993): 125-149.

Kaaber, S., 1981. Fund af migrerende og fluktuerende pyralider og storsommerfugle. – *Flora og Fauna* 87: 73-79.

Kaaber, S., 1997. Iagttagelser under tre sommerfugletræk over Færøerne i 1996. – *Entomologiske Meddelelser* 65: 109-118.

Lempke, B.J. & R. de Vos, 1990. Migrating lepidoptera in 1988 (forty-ninth report). – *Entomologische Berichten* (Amsterdam) 50: 37-41.

Mikkola, K., 1967. Immigrations of Lepidoptera, recorded in Finland in the years 1946-1966, in

relation to aircurrents. – *Annales Zoologici Fennici* 2: 124-139.
Mikkola, K., 1986. Direction of Insect Migration in Relation to the Wind. In: *Insect Flight: Dispersal and Migration,* ed. by W. Danthanarayana. Springer-Verlag, Berlin Heidelberg 1986: pp. 152-171.
Myres, M.T., 1985. A southward return migration of painted lady butterflies, *Vanessa cardui,* over southern Alberta in the fall of 1983, and biometeorological aspects of their outbreaks into North America and Europe. – *Canadian Field-Naturalist* 99 (2): 147-155.
Münster-Swendsen, M., 1980. Studies on migrating Painted Ladies *(Cynthia cardui* (L.)) (Lepidoptera: Nymphalidae) on a peninsula of West-Denmark. – *Entomologiske Meddelelser* 48: 9-10.
Rankin, M.A., M.L. McAnelly & J.E. Bodenhamer, 1986. The oogenesis-flight syndrome revisited. In: *Insect Flight: Dispersal and Migration,* ed. by W. Danthanarayana. Springer-Verlag, Berlin Heidelberg 1986: pp. 27-48.
Ryrholm, N. & C. Källander, 1986. Nattmigrerande dagfjärilar inom familjen Nymphalidae. – *Entomologisk Tidskrift* 107: 107-109.
Schmidt-Koenig, K., 1985. Migration strategies of Monarch butterflies. – *Contributions in Marine Science* suppl. 27: 786-798.
Spieth, H.R. & H. Kaschuba-Holtgrave, 1996. A new experimental approach to investigate migration in *Pieris brassicae* L. – *Ecological Entomology* 21: 289-294.
Srygley, R.B., E.G. Oliveira & R. Dudley, 1996. Wind drift compensation, flyways, and conservation of diurnal, migrant Neotropical Lepidoptera. – *Proceedings of the Royal Society of London B Biological Sciences:* 1351-1357.
Steineger, H. & U. Eitschberger, 1979. Nymphalidae. – *Atalanta* 10: 347-351.
Stoltze, M. 1996. *Danske dagsommerfugle.* Gyldendal. København.
Tauber, M.J., C.A. Tauber & S. Masaki, 1986. *Seasonal adaptations of insects.* – Oxford University Press, New York.
Ten Hagen, W., 1996. Massenvermehrung und Wanderungen von *Vanessa cardui* (Linnaeus, 1758) in Syrien. – *Atalanta* 27: 101-106.
Vanholder, B., 1996. The migration of *Danaus plexippus* (Linneaus, 1758) during October 1995 in the UK (Lepidoptera: Nymphalidae, Danainae). – *Nota lepidopterologica* 19: 129-140.
Vos, R. de & A.L.M. Rutten & B.J. Lempke 1993. Migrating lepidoptera in 1991 (fifty-second report). – *Entomologische Berichten* (Amsterdam) 53: 51-60.
Vos, R. de & A.L.M. Rutten 1996. Migrating lepidoptera in 1995 (fifty-seventh report). – *Entomologische Berichten* (Amsterdam) 56: 177-191.
Weise, W. 1996. Eine auffällige Wanderung des Tagpfauenauges *Vanessa io* (Linnaeus, 1758). – *Atalanta* 27: 99.
Whitehead, P.F., 1996. The 1996 immigration of *Vanessa cardui* (Linneaus) (Lepidoptera: Nymphalidae) in the English south Midlands. – *Entomologist's Gazette* 47: 226.
Williams, C.B. 1930. *The Migration of Butterflies.* Oliver & Boyd. Edinburgh.
Williams, C.B. 1958. *Insect Migration.* Collins, London.

Dansk resumé

Artiklen omhandler 1996-trækket af tidselsommerfuglen i Danmark og præsenterer et omfattende observationsmateriale (tabel 1). Store mængder af tidselsommerfugle ankom til Nordeuropa i de første dage af juni, og i Danmark sås kraftige nordgående trækbevægelser i perioden 7-14/6. Igennem resten af juni samt juli sås kun meget få tidselsommerfugle, men fra først i august optrådte artens 2. generation i uhyre mængder på alle egnede lokaliteter i landet.

Fra midten af august sås for første gang i Danmark et meget massivt returtræk mod syd omfattende langt flere eksemplarer end i foråret. Trækket var overstået først i september, og snart efter forsvandt de sidste tidselsommerfugle. Omkring den 10. oktober optrådte en meget sparsom 3. generation.

Observationerne viser, at træk af tidselsommerfugle minder om fugletræk m.h.t. vinddrift, trækretninger og udløsere af trækadfærd: I forsommeren sker tiltrækket således i lune sydlige vinde, hvorimod træk i efteråret favoriseres af svage modvinde fra sydlige retninger. Udløseren af trækadfærd i efteråret formodes at være den første kolde nat i en periode af varme, solrige dage.

Endvidere diskuteres trækkets rumlige struktur i forhold til fotoperiode samt meteorologiske faktorer.