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THE ANATOMY OF A MAJOR BUTTERFLY MIGRATION IN SOUTHERN INDIA

by
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Introduction

The purpose of this paper is to describe and to quantify a major, mixed butterfly migration event that took place in the Nilgiri Mountains of southern India in late May and early June of 1986. It was unfortunately not possible to follow the migrants for more than 45 km, so their origin and ultimate destination remain unknown. They did, however, leave the Nilgiri mountains. The paper thus presents a snapshot of a migration in process, but it must be one of the most detailed snapshots on record.

I do not, at present, wish to attempt to place this single event in the wider context of butterfly movement in southern India. I have, however, earlier published an account of butterfly migrations in the Nilgiris (LARSEN, 1978a) based on observations made during my childhood here in the period 1954 to 1958. These were chiefly in the opposite direction of the one now observed. According to local sources the timing of these migrations are likely to have been September or October. I had tentatively assigned them to spring.

Composition

At noon on 30 May 1986 the sun broke through what had been a dense cloud cover. Immediately a definite and relatively dense butterfly migration became appararent at my temporary base at Glenburn Bungalow, 1400 m. There had definitely been no migratory movements during the preceding three days where I had been collecting in the area. I tested the limits of the migration on the Kotagiri-Mettupalayam Road and made a count of passing butterflies. The next three days were spent making additional counts, collecting samples, and confirm the consistency and limits of the flight path. On 3 May I went to the neighbouring Biligiriranga Mountains, 45 km distant as the crow flies, in order to determine if the migrants left the Nilgiris (see fig. 1). On 4 May and during the following week mainly stragglers were seen. Indidual counts were made on 12 occasions as listed in the appendix. The following were recorded as definite members of the migration (table 1):

1) This paper has been written up under a general research grant kindly provided by the Danish Carlsberg Foundation.

Table 1: Migrants observed during twelve individual counts from 30 May to 03 June

Species*	No. seen	Species*	No. seen
Junonia lemonias L.	425	*Ixias marianne* L.	10
Catopsilia pomona F.	276	*Ariadne* sp.[2]	9
Tirumala septentrionis BTL.	173	*Appias* sp.[3]	8
Euploea sp.[1]	131	*Danaus chrysipus* L.	8
Cepora nerissa F.	123	*Danaus genutia* CR.	8
Ixias pyrene L.	36	*Libythea* sp.[4]	7
Catopsilia pyranthe L.	30	*Junonia orithya* L.	3
Papilio demoleus L.	26	*Hypolimnas misippus* L.	3
Papilio polythes L.	20	*Phalanta phalantha* DR.	2
Junonia hierta L.	14	Other	5
Precis iphita CR.	12	Total	1329

* A number of species cannot be identified in flight: 1) Both *E. core* and *E. sylvester* F. were present in more or less equal numbers. 2) Both *A. merione* CR. and *A. ariadne* L. were seen. 3) Only *A. albina* BDV. was positively identified. 4) Only *L. myrrha* GODART was positively identified.

Only the certain migrants are included in the list. Even of those species only recorded in a few cases during the formal counts, several dozen were seen at other times. Seven other species were seen in ones or twos, apparently also participating in the migration: *Papilio crino* F., *Pathysa nomius* ESPER, *Eurema hecabe* L., *Eurema brigitta* CR., *Acraea terpsicore* L., *Cirrochroa thais* F., and *Tirumala limniace* CR. All the species have previously been recorded as migrants and many are among those most consistently recorded as such. A possible exception is the Indian sub-continent endemic *Ixias marianne* L., which is lacking from WOODHOUSEs (1950) somewhat overgenerous list of „flighters" in Sri Lanka. Some known migrants were missing, though they were common enough in the area at the time. Of the species listed in my 1978 paper *Hebomoia glaucippe* L. and *Cupha erymanthis* DRURY are prominent absentees. *Euthalia nais* FORSTER and *Euthalia lubentina* CR. were also absent which is less surprising as these are very rare in the Nilgiris. *Anaphaeis aurota* F. was present neither in 1986 nor in the 1950ies though it is often very common in the dry tracts surrounding the Nilgiris. *Pachliopta aristolochiae* L. and *Pachliopta hector* L. were also absent, but their migratory patterns seem different from those included in the main flight (1978a).

The species included in the migration are largely those that are at home in relative dry plains country and which can survive in habitats modified by man, with only the *Libythea* as partial exceptions. This is hardly co-incidental.

Direction and extent of the migration

The migration was moving towards ENE on a compass course of 75°. It was measured on numerous occasions in many localities and never varied.

The main migration front covered only 4000 metres along the southern flanks of the Nilgiris (see fig. 1). In the area of observation the altitude of the main flight ranged from 600 to 1600 m, but in the course of their flight the main stream would have descended to as low as 250 m. In a belt stretching some 4000 metres to either side of the main stream a thin migration was also in progress. Some of these would pass the highest point of the Nilgiris at altitudes well in excess of 2000 m.

Behaviour

The behaviour of the migrants was the classical one onwards, onwards, onwards with such a determination that even non-naturalists are impressed. Obstacles are sumounted rather than circumvented. The *Junonia, Ixias* and *Cepora nerissa* flew with great consistency at 0.80 to 1.20 m above the ground with a rapid and direct flight, often in small clusters of three or four specimens of the same species. The Danaids and the Papilionids flew in a more diffident fashion at levels of 1.20 to 3.00 m, making rapid progress none-the-less. The *Catopsilia* flew fast, furious and direct at heights ranging from 1.00 to 8.00 m, usually lower than 4.00 m. Test runs, supplemented by observations from my car yielded the following estimates of true air speed (table 2).

Table 2: Estimates of air speed of migrants

Species	km/hour
Papilio sp.	15-20
Ixias, Cepora nerissa	15-20
Catopsilia sp.	25-30
Junonia, Precis	20-25
Tirumala septentrionis	15-20
Danaus ssp., *Euploea*	10-12

The speed estimates given in table 2 are some 5 km/hour faster than estimates given in my paper from Benin (Dahomey) for similar species. These were made without the benefit of a car and I believe the present estimates to be the better ones (LARSEN, 1978b).

As shown in the appendix the average density was about 50 specimens crossing a 100 m front per minute, though when conditions were best, the figure rose to 100 per 100 m.

Activity on a good day began at 08.00 with some feeding activity and generally aimless behaviour. By 09.00 the migration started, by 09.30 it had fully consolidated. It was difficult to say how long the migration lasted since the weather usually deteriorated towards the afternoon, and on some occasions I was away from the main stream when acitivity ceased. However, little migratory activity was seen after 15.30.

Weather conditions

Weather conditions were very variable during the period of observations. Clouds would often stop the migration. *Junonia lemonias* was usually the first to give up, with some of the Danaids continuing even in a light drizzle. However, from 30 May till 03 June the main stream had approximately one thousand minutes of good weather and a further 300 minutes of passable weather. These figures will be used for quantifiying the migration.

I was particularly interested in seeing whether wind conditions influenced the track of the migration. This proved difficult. Wind varied throughout, minute by minute and locally, but rarely were speeds significant. Topography made it impossible to observe the migrants over long distances. The general impression was that wind had only a marginal influence on the direction of the flight (see later).

Quantification of the migration

Based on the information already given the data in the appendix it is possible to arrive at a fairly precise estimate of the total numbers involved in the migration as shown in table 3 below.

Table 3: Estimate of total number of migrating butterflies

Dates/conditions	Front in metres	Minutes available	No. per m. per minute*	Total
30.V.-03.VI. Main stream, Good weather	4000	1000	0.80	3.200.000
Fringes, Good Weather	8000	1000	0.05	400.000
30.V.-03.VI. Main stream, Passable weather	4000	300	0.20	240.000
Fringes, Passable weather	8000	300	0.02	50.000
04.VI.-11.VI. Main stream, Stragglers	4000	1500	0.05	300.000
Fringes, Stragglers	8000	1500	0.01	120.000
Total				4.310.000

*Conservatively estimated from appendix and from interpretation of counts and observations from 04. to 11.VI.

Thus on a reasonably conservative estimate the migration is found to contain more

than four million individual butterflies, ranging in numbers from 1.4 million *Junonia lemonias* and 900.000 *Catopsilia florella*, down to 5.000-10.000 of the weakly represented species (using the percentage composition given in the appendix).

Origin and recruitment

The migration definitely originated outside of the observation area. Most of the species were not present in anywhere near the numbers necessary for the migration, and resident populations of most species were not affected. However, the low level Kallar area did lose most of its resident population of *Tirumala septentrionis* and the two *Euploea*. This, and the presence of small numbers of some species, might indicate some sort of „recruitment" by the migrant swarm. However, it is more than likely that the Kallar butterflies have simply received the same environmental cues that triggered the main migration.

The origin of the migration cannot have been very far from the Nilgiris. The Malabar coast is only about 110 km away to the west. Beyond that is the Indian Ocean.

The „extra" migration

On the fourth day of the main migration (02.VI.), at the Glenburn Bungalow, it became evident at 09.30 that a further migration had started up, this one flying due north. On that first morning it was quite strong, though the density was less than half that of the main migration. The front of this migration was relatively narrow, but the road network was not conducive to checking it fully. It rapidly thinned out drastically, though I saw traces of it during the nect nine days, including at Kotagiri (1900 m). The sight of two migrant streams crossing each others' paths without engendering the least confusion was an interesting one. While the species involved in the two migrations were the same, the species composition was different as illustrated in table 4 below. I have not done a chi-square test, but I suspect that the differences are statistically significant.

Table 4: Key species in the two migratory streams observed at Glenburn from 09.30 to 10.00 on 02.VI.1986*

Species	Main migration ENE		„Extra" migration N	
	No.	%	No.	%
Papilio polytes	1	0,8	5	5.0
Cepora nerissa	18	14.4	8	8.0
Appias sp.	0		0	
Catopsilia pomona	30	24.0	18	18.0
Tirumala septentrionis	19	15.2	16	16.0
Euploea sp.	14	11.2	28	29.0
Junonia lemonias	32	25.6	8	8.0
Other	11	8.8	11	11.0
Total	125	100	99	100

*The main migration was observed over a 10 m front, the „extra" migration over a 30 m front.

Orientation

The migrants maintained their direction and orientation throughout the day and throughout the period of observation. All compass checks confirmed this. Many of my observations were made in a wind sheltered spot at Glenburn Bungalow where a stretch of road, 100 m long, ran absolutely parallel to the migration track. This provided optimal conditions for confirming that there were no changes in direction during the day or from day to day.

Wind conditions were ever changing, varying locally, and never very strong. There may have been some drift, but my own impression was that the butterflies compensated for any drift. Unfortunately the topography was such that individual butterflies could not be observed for distances long enough to measure the effect of drift. What is quite certain is that wind would have had only marginal influence on the ultimate direction of the migration.

The precision of the directional flight reminds me of those migrations that I saw in my childhood. Here we had pickets stationed to inform us of incoming butterflies of particular interest: „Giant Orange Tip coming between the porch and the bedroom!", the cry would come, and it was never wrong.

So how do these butterflies navigate? Butterflies are known to lock onto the sun (BAKER, 1984) and then to maintain a direction related to the sun. This leads to a curved flight path as the sun moves, and BAKER does not believe this to be true for long range tropical migrants. It is certainly precluded in the current migration. The migrants would have been facing the sun as they set out, by noon the sun would be directly overhead, and in the after noon the sun would be will behind the migrants. Were they locked on the sun, they would be disorientated at midday, and then turn on thei tracks. This they obviously did not do.

I had been attracted to the idea that butterflies took a fix on the morning sun and then maintained their direction through topographical features, such as large trees, distant hill-tops, etc. Both elements in this suggestion can probably be discounted. On one of the main migration days, activity started only at noon, when the sun was directly overhead, having been totally blotted out by cloud till then. I also saw the migration progress through large expanses of featureless tea and coffee plantations where the evenly spaced shade trees precluded navigation by any long or short term fixed points. I also saw specimens migrating several hundred metres up nearly featureless, vertical forest.

In some cases butterflies have been known to use topographical features such as forest edges and roads for navigation. This seems to be the case for *Ascia monuste* in the Neotropical area (NIELSEN, 1961) and I have observed it in *Libythea labdaca* in Nigeria (LARSEN, 1981). There was no element of this in the current migration.

Ecological gradients of various types have been advanced as possible causes for direction of movement. In the widest sense the temporal rainfall gradient of the SW moonsoon is probably responsible for the direction of the observed migration. But it cannot be responsible for the navigation of the individual migrant. A butterfly observed below Coonoor will have had the stylized flight patterns shown in fig. 2 while travelling from Coonoor to the Biligiriranga. It will have passed through tropical evergreen forest and thorn scrub, at altitudes from 250 to 1700 m, through rainfall regimes of 400 to 3000 mm a year, and with mean maximum daily temperatures ranging from 40 to 15 centigrade. No butterfly could identify a gradient though such background noise.

But navigate the butterflies obviously do, and with very great precision. When I went to the Biligiriranga (40 km on the map. 50 km when vertical movements are also taken into account) I skirted the main migration front (see fig. 1). However, I rejoined the main flight within a few hundred metres of the spot predicted by projecting the flight path on a large scale map. So what mechanism is involved? I do not know, but it is difficult not to conclude that an internal, magnetic compass of some sort is involved, once the butterfly has become locked on its initial direction. WILLIAMS (1958) was convinced that this would eventually be proved to be the case. I have no proof, but I can think of no other mechanism.

Visual contact is essential for maintaining orientation within a locust swarm, but this is only a way of maintaining the cohesion of the swarm. The direction in which the locusts are facing have, at most, a marginal influence on where they eventually end up. This is decided by the wind patterns of the intertropical convergence zone (RAINEY, 1978), which must have had a major influence on shaping the locust life cycle. In the core area of the migration several butterflies must have been constantly within sight of others, but it is most doubtful whether this has had any influence on maintenance of direction. At the fringes of the migration, and during the days of stragglers, there was no visual contact, but no diversion. And the two separate migration streams at Glenburn led to no confusion. There was never any problem in assigning a given individual to one of the two streams.

Release experiments

I collected 37 individual migrants, stored them overnight in paper triangles, and released them the following morning. Of these 22 sat almost immediately. Eleven flew out of sight in the correct direction (± 10%), often after having made a full circle or a semi-circle. Only four flew out of sight in the wrong direction. However, after spending the night in paper triangles the butterflies seemed, not surprisingly, quite traumatised. More conclusive results would demand an improved storage and release technique. In many cases I collected specimens simply to determine sex or species. These were immediately released. Like specimens just missed with the net, they would often move some 10-15 metres in any direction as a result of the

Appendix

The twelve main observation series on which the quantifications are based

1. 30.V.1096. Glenburn, Bungalow, 12.30-12.45. Front of 10 metres. Weather good.
2. 31.V.1986. Konakarai, River 1, 10.40-10.55. Front of 30 metres. Semi-overcast.
3. 01.VI.1986. Glenburn Bungalow, 09.15-09.30. Front of 10 metres. Poorish weather.
4. 01.VI.1986. Glenburn Bungalow, 10.30-11.00. Front of 10 metres. Weather quite good.
5. 01.VI.1986. Hairpin 2/3, Kotagiri Ghat, 13.05-13.30. Front of 8 metres. Weather perfect.
6. 01.VI.1986. Foot of Kotagiri Ghat, 14.07-14.12. Front of 15 metres (this was a bit outside of the main stream).
7. 02.VI.1986. Glenburn Bungalow, 09.30-10.00. Front of 10 metres. Weather OK.
8. 02.VI.1986. Hairpin 2/3, Kotagiri Ghat, 11.30-11.45. Front of 6 metres. Weather OK.
9. 02.VI.1986. Kallar (6 km NW of Mettupalayam), 12.20-12.35. Front of 10 metres. Weather OK.
10. 02.VI.1986. Runnymede, below Coonoor, 1600 m, 14.00-14.15. Front of 20 metres. Weather good (this was to the north of the main stream).
11. 03.VI.1986. Foot of Biligiriranga, Dhimbam Ghat, 10.30-11.00. Front of 8 metres. Weather OK.
12. 03.VI.1986. Dhimbam, 1100 m, 11.30-11.45. Front of 10 metres. Weather closing down.

	1	2	3	4	5	6	7	8	9	10	11	12	Total	%
P. Polytes		5	3	6	3		1				2		20	1.5
P. Demoueus		2	1		3	2	3	2		3	8	2	26	2.0
C. Nerissa	11	12	3	36	6	4	18	9	4	6	5	9	123	9.3
Appias sp.[2]		2		2		2		1	1				8	0.6
I. Pyrene		8	1	2	2		1		7	2	11	2	36	2.7
I. Marianne		2		1				1		1	4	1	10	0.7
C. Pomona a a	43	67	9	39	34	3	30	4	9	9	8	21	276	20.8
C. Pyranthe		2		4		4	1		12		7		30	2.3
D. Chrysippus	2				4				1		1		8	0.6
D. Genutia		2	3					1	1		1		8	0.6
T. Septentrionis s	14	28	7	8	51		19	16	12	3	12	3	173	13.0
Euploea sp.[2]	8	5	16	9	57		14	5	5	2	8	2	131	9.9
J. Lemonias	54	6[1]	7	50	130	1	32	32	33	3	66	11	425	32.0
J. Hierta	1			2	3		1	1	1		2	3	14	1.1
J. Orithya								1			1	1	3	0.2
P. Iphita	3	2			2		3			1		1	12	0.9
H. Misippus					2						1		3	0.2
Ariadne sp.[2]	3			1	1	1	2	1					9	0.7
P. Phalantha			1									1	2	0.1
Libythea sp.[2]					5				1			1	7	0.5
Other[3]				2	2							1	5	0.4
Total	139	143	51	162	305	17	125	74	87	30	137	59	1329	100.0
M/Min/Obs[5]	150	450	150	300	200	75	300	90	150	300	240	150	2555	
Sp/M/Min[6]	0.93	0.32	0.34	0.54	1.53	0.23 4)	0.42	0.82	0.58	0.10 4)	0.57	0.39	0.52	

1) *Junonia lemonias* picked up in force shortly afterwards.
2) In these genera there are two or more species that cannot be identified on the wing. See table 1 for more details.
3) Includes observations of *Papilio crino, Pathysa nomius, Cirrochroa thais, Eurema* sp. and *Acraea terpsicore*.
4) These observations were outside of the main stream.
5) Metre/minutes/of observation. Thus if a 10 metre front is observed for 30 minutes, the total is 300.
6) Specimens/per minute/per metre. If 305 butterflies cross on 8 metre front in 25 minutes, the Sp/M/Min index becomes 1.53 (305:8:25).

disturbance. The flight direction would then be resumed.

Sex ratio and gonadal development

Throughout the observation period notes were made on the sex of passing and captured specimens when time permitted. This means that species with obvious sexual dimorphism are over-represented compared to those where capture was necessary for sex determination. Although the observations were not made within any strict observational framework, they leave no doubt that the sex ratio for all species was more or less normal (table 5).

Table 5: Sex of migrant butterflies consolidated from all observations and captures during the main flight

Species	Males	Females	Total
Papilio polytes	12	14	26
Papilio demoleus	2	1	3
Cepora nerissa	21	22	43
Appias sp.	5	6	11
Ixias pyrene	14	7	21
Ixias marianne	1	0	1
Catopsilia pomona	18	18	36
Catopsilia pyranthe	3	2	5
Danaus genutia	1	0	1
Tirumala septentrionis	13	8	21
Euploea core	1	0	1
Euploea sylvester	6	7	13
Junonia lemonias	6	8	14
Junonia hierta	2	0	2
Hypolimnas misippus	1	2	3
Totals	106	95	201

These observations are not limited to the formal counts listed in the appendix.

A number of female specimens were dissected, under very difficult working conditions so that I may have missed traces of very early egg development. Two female *Catopsilia pomona* contained much fatty tissue but no trace of egg development; I found no trace of eggs but little fat in migrating *Catopsilia florella* F. in West Africa (LARSEN, 1978b). Two *Cepora nerissa* showed incipent egg development, a third none. Five *Junonia lemonias* showed no trace of eggs at all. A single *Papilio polytes* had many developing eggs but none that were fully formed.

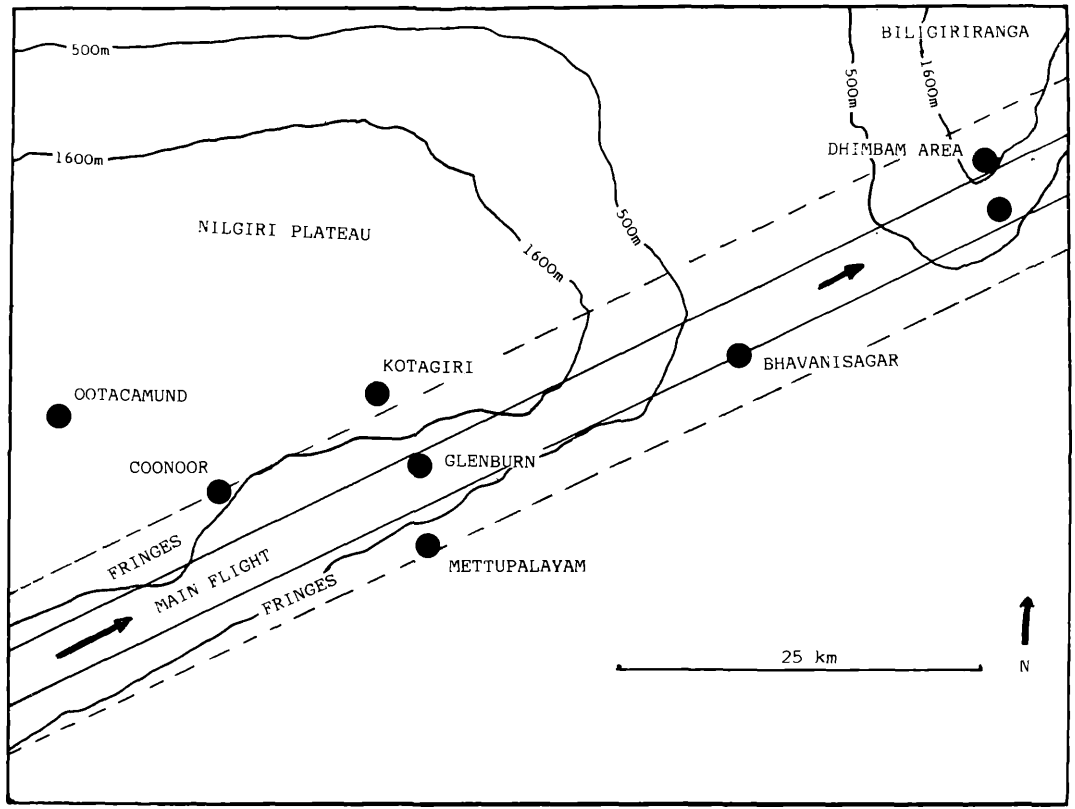

Fig. 1: A schematic map of the area where the observations were made (11.25 N, 76.45 E)

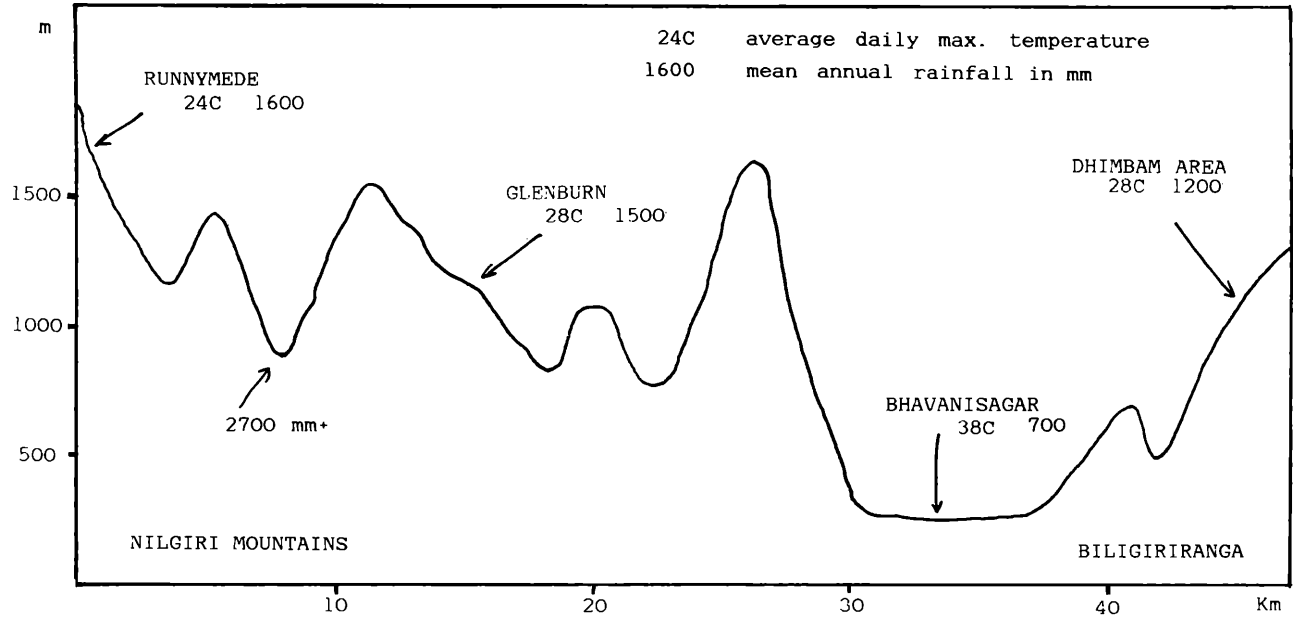

Fig. 2: Elevation and climatic conditions passed by the main migration within the area of observation.

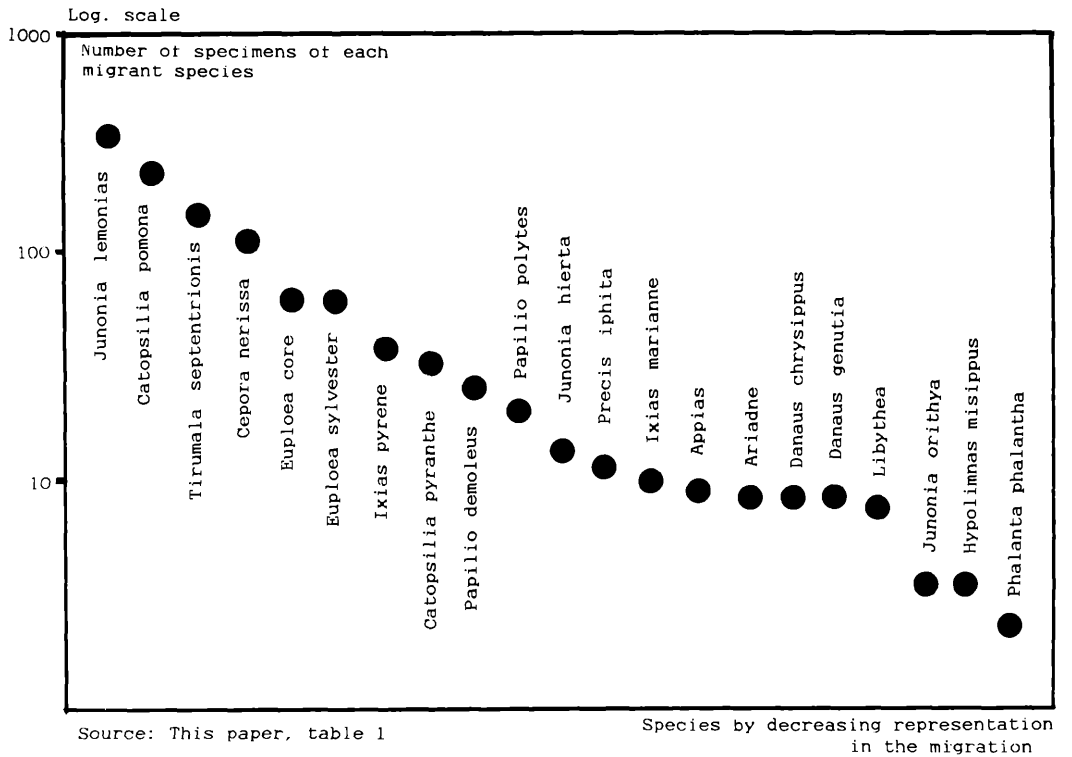

Fig. 3: Semilogarithmic plot of the numbers of individual specimens of each species revealing the classical linear relationship from studies of population densities (the two species of *Euploea* have each been assigned a value of 60).

Summary

This paper documents a major, mixed butterfly migration in southern India, involving more than four million specimens pertaining to more than twenty species. The dominant species composed about two thirds of the total. The relative frequency of the participating species fits a linear semi-logarithmic relationship (see fig. 3 - the linear fit would have been even better had it been possible to decompose the *Appias, Ariadne* and *Libythea*).

All specimens in the main migration, irrespective of species, maintained the same compass direction irrespective of weather, wind direction, sun position and absence of topographical navigation aids. These was a minor migration on a different heading, but this did not engender any confusion. The migrants were passing through an area of extreme ecological variability and ecological gradients cannot be a navigational aid. Some sort of magnetic compass is indicated, but prrof is wanting.

The migration co-incided with the onset of the SW monsoon, moving from the wet coastal areas of Kerala towards the arid zones of Tamil Nadu and Karnataka that were due to benefit from the advancing monsoon. All but one species are well established mass migrants, though some common migrants were absent. If the migration was part of a general monsoon-inspired event, the narrowness of the front is somewhat surprising (4 km core, 12 km all told). It is quite certain that during the main migration there were no flights within thirty kilometres to either side of the path.

Once again one is left with mixed feelings. Awe at the magnitude and consistency of such a major migration event; pleasure at having been able to document at least some facets of the event; and considerable frustration at not being able to get closer to an explanation.

References

BAKER, R.R. (1984): The dilemna: when and how to go or stay. In VANE-WRIGHT, R.I. & P. ACKERY (eds.). The biology of butterflies. London.

LARSEN, T.B. (1978a): Butterfly migrations in the Nilgiri Hills of South India (Lep.; Rhopalocera). – J. Bom. nat. Hist. Soc. **74**: 546-549.

LARSEN, T.B. (1978b): A mixed butterfly migration in West Africa (Benin). – Atalanta **9**: 191-198.

LARSEN, T.B. (1981): A migration of *Libythea labdaca* Westw. in Nigeria. – Atalanta **12**: 94-96.

NIELSEN, E.T. (1961): On the habits of the migratory butterfly *Ascia monuste*. – Biol. Meddlr. **23**: 1-81.

RAINEY, R.C. (1978): The evolution and ecology of flight; the oceanographic approach. In DINGLE, H. (ed.) Evolution of insect migration and dia-

pause. Springer, New York.
WILLIAMS, C.B. (1958): Insect migration. London.
WOODHOUSE, L.G.O. (1950): The butterfly fauna of Ceylon. Colombo.

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