Fig. 1 (top). FIRST PRIZE — BUTTERFLIES: *Diaethria clymena* (Nymphalidae), Rondonia, Brazil, J. L. Nation, Jr. (Gainesville, FL). 2 (lower left). THIRD PRIZE — BUTTERFLIES: *Ornithoptera priamus poseidon* (Papilionidae), Irian Jaya (New Guinea), Indonesia, G. Deslisle (St. Raymond, Quebec, Canada). 3 (lower right). SECOND PRIZE — IMMATURES: *Remelana jangala mudra* (Lycaenidae) larva, Hong Kong, J. L. Young (Hong Kong).

FRONT COVER.– SECOND PRIZE — BUTTERFLIES [tie-winner]: *Aporia agathon moltrechti* (Pieridae), Taiwan, C. C. Lin (Yungho, Taiwan); FRONT COVER (inside).– FIRST PRIZE — IMMATURES: *Cerura* sp. (Notodontidae) larva, Taiwan, C. C. Lin (Yungho, Taiwan). BACK COVER (inside).– FIRST PRIZE — MOTHS: *Euchromia polymena formosana* (Arctiidae: Syntominae), Taiwan, C. C. Lin (Yungho, Taiwan); BACK COVER.– SECOND PRIZE — MOTHS: *Apsarasa radians* (Noctuidae), Vietnam, K. Spitzer (České Budějovice, Czechoslovakia).

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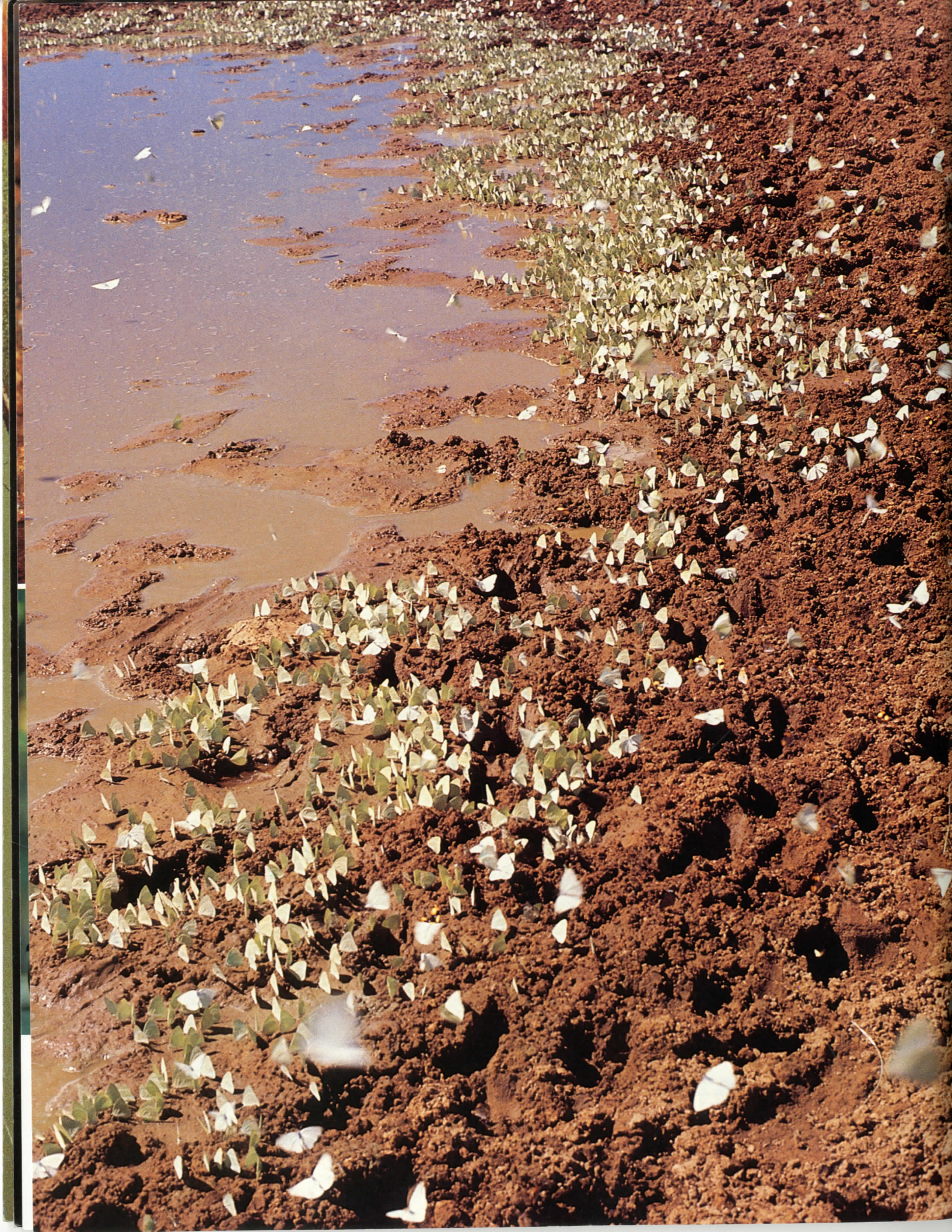
Fig. 4 (upper left). SECOND PRIZE — BUTTERFLIES [tie-winner]: *Phoebis* sp. (Pieridae), Rondonia, Brazil, J. L. Nation, Jr. (Gainesville, FL). 5 (upper right). THIRD PRIZE — IMMATURES: *Chlorocoma melocrossa* (Geometridae), South Australia, N. McFarland (Sierra Vista, Arizona). 6 (lower center). THIRD PRIZE — MOTHS: *Urania* sp. (Uraniidae), Rondonia, Brazil, D. Petr (Keene, TX).



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MIGRATION OF *CATOPSILIA FLORELLA* IN BOTSWANA (LEPIDOPTERA: PIERIDAE)

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ABSTRACT.– During March and April of 1991 a large migration of *Catopsilia florella* (Fabricius), comprising more than 1.5 billion individuals, crossed the whole of Botswana (about 1000km) with a direction just north of east-northeast. Numerically, this is one of the largest butterfly migrations ever documented. No major outbreak areas were identified and the evidence is consistent with breeding over a large part of the inner Kalahari and probably Namibia. The behaviour of the migrants was typical, though *C. florella* seems more ready to make small pauses at flowers or damp patches than is usual in migrants. The migrants unerringly resumed the migration even after several days of inactivity due to bad weather. The migrants were morphologically different from the parents and from non-migrant populations in the area. Migrant males were not sexually active while migrant females mated non-migrant males in some numbers, though these were always significantly outnumbered by migrants. The flight direction was maintained with great precision irrespective of wind conditions. Virtually all migrants left Botswana. The direction was the same throughout Botswana over nearly two months, precluding the possibility of spoke-like movement out of an out-break centre. A few cases of movement towards the northwest, presumably with an origin in the Orange Free State, were also noted. At times, half a dozen other species participated in the migration, but always at very low densities. Bushmen in the Kalahari use butterfly migrations as indicators of the imminent arrival of the vast herds of migratory ungulates from the same direction.

KEY WORDS: *Acraea*, Africa, *Belenois*, *Byblia*, *Colotis*, *Danaus*, Ethiopia, Ethiopian, *Eurema*, *Hypolimnas*, India, *Junonia*, Kenya, Labiatae, Lamiaceae, Leguminosae, migration, Nymphalidae, South Africa, *Vanessa*, Zimbabwe.

The purpose of this paper is to describe a major migration of the common migratory African Emigrant, *Catopsilia florella* (Fabricius), in southern Africa during the months of Mar and Apr, 1991. While making the observations it also became clear that there were strong morphological differences between non-migrant and migrant populations, though whether this may be some form of seasonal variation rather than strictly limited to migrant and non-migrant phases is still open to question.

I first observed migrations of *C. florella* and other *Catopsilia* in the Nilgiri Mountains of South India in the late 1950s (Larsen, 1978b), and I am struck by the great visual similarity between these and the event to be described below. In addition to personal observations throughout Botswana, telephone calls were made to people in Botswana and in the Republic of South Africa who might be in a position to assist, and some additional information came in response to a letter in some of the local newspapers.

Though found throughout the region, *C. florella* is not necessarily abundant, and at times it may even be quite scarce. Thus in 1989 and 1990 it was not numerous and only a very limited migratory movement was seen.

SUMMARY OF FIELD OBSERVATIONS

Between 11 and 28 Feb masses of non-migrant *C. florella* were seen at damp patches in the area stretching along the Molopo Valley from Werda to Tshabong and Bokspits, i. e., most of the southern border between Botswana and South Africa (Figs. 1 & 2). Similar conditions were found in the lower part of the Nosop Valley on the western border, while the species was not very common in the Gemsbok National Park as such. The species had not been common in the Gaborone area or elsewhere in eastern Botswana earlier in the year. Several residents in the Tshabong area emphasized that these numbers were exceptional and had seen nothing like it since before the great drought of the 1970s and 1980s.

As usual, males outnumbered females at the damp patches, though females of many butterflies are more frequently seen at damp patches in Botswana than they are in the equatorial area. Both sexes of many *Colotis* visit damp patches, which is only rarely seen in Kenya and Uganda. Most individuals in these assemblages were worn and virtually all females were of the white, male-like morph (f. *pyrene* Swainson); very few matched the light yellow morph (f. *hyblaea* Boisduval). Typical females are bright yellow and were almost entirely missing. Towards the end of February, as we made our way back to Tshabong, yellow females became slightly more frequent, and fresh males were seen.

On 1 Mar at the Mabuasehube Game Reserve, *C. florella* began to manifest migratory activity, and for the first time yellow females were seen in quantity. Between 16.50 and 17.10, in the middle of the main Mabuasehube Pan, there seemed to be movement in three different directions - ENE, just south of ESE, and N. All in all, it seemed that while movement was starting, it had not crystallized into a set pattern (and it was also very late

Fig. 1. Large numbers of the parent generation of the migrant *Catopsilia florella* assembled at water at a cattle post near Middelspits in the Molopo Valley, Botswana (26 Feb 1991).

Fig. 2. Large numbers of the parent generation of the migrant *Catopsilia florella* at a natural damp patch near Tshabong, Botswana (27 Feb 1991).

in the day for migratory movement).

The next day we camped 30km S of Tshane and when the sun came fully out at 14.00, the migration was both denser and firmer than at Mabuasehube. A directional count of 135 specimens showed 106 moving ENE (the final direction of the migration was about 60 degrees), 23 moving ESE, and 6 moving S. The density constituted more than 300 per minute per km of front (Table 1). In addition to making the density counts, the sex ratio was also checked; during the count of 228 individuals, 127 were males and 101 females. This is consistent with a sex ratio of 1:1, given that some females were possibly white (and therefore not identifiable in flight). Additionally, this was obviously the beginning of a migration, and some degree of protandry might be expected. It was noted that all the females were yellow and quite fresh (as was a sample of many females collected). A random sample of 27 males was also taken; 23 of these were completely fresh migrants, 1 was a damaged migrant, and 3 were worn non-migrant types. This confirmed the general visual observation that nearly all the migrants consisted of fresh specimens.

On the morning of 3 Mar, the migration started at about 10.00 with the general aspects of the previous day, though more firm in the ENE direction. However, the weather soon clouded over. At 11.00 in the village of Lokhwabe very large numbers of *C. florella* were seen on flowers of *Arctome inflatis* (Lamiaceae), a synanthropic weed. They constituted a mixture of mainly worn non-migrants and fresh migrants. The differentiation between non-migrants and migrants is given in a later section.

During breaks in the cloud cover (11.30) at Hukuntsi more than 100 per minute were seen on a 25m front in what was by far the densest seen so far (Table 1). The sex ratio was 50/50 and virtually all were fresh. Direction was now uniquely ENE. This was confirmed to us by a pilot from the Flying Mission who landed at Hukuntsi at 15.00 and said that 'the amount of butterflies made the final landing approach difficult'.

At 15km E of Tshane, on the road to Kang, thousands were feeding on flowers in a non-breeding area, making a pause during the strong phase of the migration. Ten minutes of observations here permitted confirmation that: (1) all migrants were fresh; (2) all migrant females were yellow; (3) average size of migrants was larger than that of non-migrants; (4) colour patterns of both sexes were constant; (5) only very few, if any, non-migrant males were caught up in the migration (less than 5 percent, not all of which need necessarily be migrating). We lost the migration about 14.30, about 50km W of Kang; it was probably being blocked by clouds and thunderstorms further west.

Just before reaching Kang, there was some sunshine and we saw hundreds *C. florella* at mud-puddles. These were almost exclusively very worn, non-migrant males. The two next days (4/5 Mar) saw almost no sunshine. Only very occasionally could

Table 1. Counts of migrants made at various points and estimates of numbers passing a one kilometre front per minute.

Locality* and date		Time	Minutes observed	Number passing	Front width	Number per km per minute
1	02 March	15.00	20	127	20 m	318
1	02 March	15.50	25	228	25 m	364
2	03 March	11.30	10	1000	25 m	4000
3	06 March	14.40	7	325	30 m	1548
4	11 March	10.50	4	104	25 m	1040
4	22 March	11.45	4	158	30 m	1317
4	22 March	14.58	12	456	30 m	1267
4	27 March	15.30	4	91	30 m	750
4	28 March	11.41	5	82	30 m	547
4	28 March	14.50	3	180	25 m	2400
5	29 March	13.45	4	104	25 m	1040
4	31 March	12.00	visual check		25 m	ca 300
4	01 April	13.30	visual check		25 m	ca 100
7	03 April	14.00	1	60	25 m	2400.**
6	04 April	14.00	4	80	20 m	500.***
8	07 April	14.00	visual check		25 m	ca 200
9	11 April	12.00	visual check		100 m	ca 300
10	12 April	14.00	visual check		100 m	ca 500
11	17 April	14.00	visual check		100 m	ca 200
12	21 April	15.30	10	110	100 m	110

* 1 = 30 km S of Tshane; 2 = Hukuntsi; 3 = Lehututu; 4 = Gaborone; 5 = Livingstone Mission, Kolobeng River; 6 = Serowe; 7 = Shashe; 8 = Victoria Falls; 9 = Kasane; 10 = Mababe Flats; 11 = Shakawe; 12 = Kubu Island, Sua Pan; ** observations by Dr. Richard Hartland-Rowe.
*** there seemed to be some channeling through low passes.

the migration be observed, and then only at very low density. However, the direction was still the same.

On 6 Mar between 09.00 and 12.00 in Kang, the weather was poor and little sign of the migration was seen. However, at 50km W of Kang we suddenly hit a major flight, which in dimensions seemed to be more than 1000 per km per minute. Weather then closed in till we reached Lehututu. Here the weather cleared and between 14.40 and 15.10 a very large flight was seen, at the rate of more than 1000 per minute per km. The sex ratio was checked to be roughly 1:1. There was a near headwind, pretty strong. When overcast occurred they immediately dumped into *Grewia* and *Acacia hebeclada* (Leguminosae) bushes, where they roosted very visibly. When the weather clouded over, observations were made on couples in copula and larvae were collected, to be discussed later.

On 7-9 Mar I went to Hukuntsi and then back to Gaborone via Kang, Takotakwane, and Letlhakeng. Weather was again poor to indifferent, but whenever the sun came out briefly, the migration picked up, at the same magnitude as at Lehututu. This was especially prominent near Duthlwe, at the de Beers cut-line, near Letlhakeng, and between Molepolole and Gaborone. On the afternoon of 9 Mar, Carol Tovee (personal communication) said that at the same time the migration had been very evident between Lobatse and Gaborone, a stetch of 70km.

The weather was still poor on 10 Mar, but the next day there was much activity, roughly stable during the day at 1000 migrants per minute per km. There was then ten days of bad weather, with only intermittent movement. But during most of 22 Mar, the migration again reached strong levels of more than 1000 per km a minute. The movement was fully solidified by 10.30 and began tapering off by 16.30.

Between 23 and 31 Mar, the weather was cool and on two days there was practically no movement. However, there were two full days of migration and several half days. On 1 April there was a strong tapering off and on 2 April the migration had stopped completely. I have to confess to an eerie feeling that somehow a mysterious, giant engine had suddenly been switched off.

Migratory activity still persisted north of Gaborone, though densities were generally less than in the Gaborone area. However, probably from 18 to 20 Mar a very dense stream passed through Maun, sufficiently dense to make driving difficult (Ursula Boyce and Doline Bridges, pers. comm.). I also received data from the same period that butterflies were a 'considerable nuisance for trucks' for several days at the Sua Soda Ash plant (Nigel Ashby, pers. comm.). Mark Vandewalle (pers. comm.) observed several days of strong movement in the Savuti area in the later half of Mar.

On 4 Apr, while driving north, the migration became very evident 30km north of Gaborone and continued till the Tswapong Hills and Serowe where it had been in evidence for more than a week, though generally only at half the density of the Gaborone stream (Per Forchhammer and the Macallum family, pers. comm.). This matches information from the Zanzibar area on the Limpopo, where Dierdre Kirby (pers. comm.) noted a strong flight for three or four days after 3 Apr, preceded by modest movement for a week before, and for some time after.

Fig. 3. A non-migrant male *Catopsilia florella* mating with a freshly hatched migrant female at Lehututu, Botswana (6 Mar 1991).
Fig. 4. A fresh male migrant *Catopsilia florella* stopping to sip moisture from a wet towel in camp at Tshane, Botswana (3 Mar 1991).

Around this time migration began quite strongly around Shashe, where I also saw it on 6 Apr. There were no observations around Francistown, where Catrien van Waarden (pers. comm.) never saw a noticeable movement. On 7 and 8 Apr the migration was evident between just north of Francistown all the way to Kasane and Victoria Falls.

For three good days very little migration was seen, but on 11 Apr a strong movement was seen at Kasane, and on the next day on the Mababe Flats. Between 16 and 18 Apr fairly consistent migration took place between Shakawe and Sepupa; according to Jan Drotsky (pers. comm.), this had been going on for some time.

Between Sepupa and Maun, and then between Maun, Nxai Pan, Nata, and the Sua Pan, only fairly sporadic migration was seen, though it solidified somewhat on the Sua Pan on 21 Apr. On the following day sporadic migrants were seen between Orapa and Shashe, while on 23 Apr none was seen between Shashe and Gaborone.

These observations seem to indicate that the main migration was later further north than it was in southern Botswana. Don Wilson (pers. comm.) says that in Kanye very dense flights stopped just after mid-Mar.

In this respect it is interesting to note that in Zimbabwe, Cockbill (1951) noted a peak of about 2900 per km per minute in a migration towards the southwest, or not far off the maximum seen in Botswana.

OBSERVATIONS FROM NEIGHBOURING AREAS

According to Steve Woodhall (pers. comm.), there was significant migratory movement in parts of Transvaal between Thabazimbi and Randburg, beginning with a few stragglers in the last week of February, being very firm between 3 and 24 Mar. He also noted migrants as far south as Port St. Johns in the Transkei between 1 and 10 Apr, but they were not many and he believed that the migration was petering out at the time.

M. W. Lunderstedt (pers. comm.) observed many migrants, moving towards the northeast, at Virginia and Welkom in the Orange Free State, beginning on 1 Mar. These localities are well south of Botswana.

Carol Tovee (pers. comm.) observed some migratory activity in Harare, Zimbabwe on 4 Apr, but it was so slight that she would not have noticed had she not become attuned to the migration in Botswana.

MORPHOLOGICAL DIFFERENCES BETWEEN MIGRANTS AND NON-MIGRANTS

During the first part of our trip, we had seen hundreds of thousands of worn *C. florella*. When the migration began at Mabuasehube and south of Tshane, it was most evident that only fresh specimens were involved and that the females were yellow. Nonetheless, I did some random sampling near Tshane, concentrating on migrating males (the females could be assessed with no collecting). The result was as follows: 23 perfect migrant males;

Table 2. Morphological differences between migrant and non-migrant populations of *C. florella* in Botswana, March 1991

Characters	Description	
	Non-migrant	Migrant
MALES	(n=45)	(n=34)
Length of forewing	31.6 mm	34.8 mm
Upperside colour	white	white
Underside pattern	weakly spotted little irroration	strongly spotted much irroration
Antenna colour	blackish	purplish
FEMALES	(n=13)	(n=17)
Size of forewing	31.0 mm	35.9 mm
Upperside colour	white/cream	yellow
Underside pattern	weakly spotted little irroration	strongly spotted much irroration
Antenna colour	blackish	purplish

1 damaged migrant male; 3 old non-migrant males, some of which may not have been migrating. The observations at Lokhwabe and 15km E of Tshane have already been mentioned, supporting the fact that old non-migrants and fresh migrants were clearly distinguishable. Genuinely transitional specimens were nearly absent, and none was contained in the random samples.

At Kang, both migrants and non-migrants came to mud-puddles and samples were caught at random. Pooling of all samples yielded the following results:

I have previously called attention to the fact that yellow females are characteristic of migrant populations in Ethiopia and Kenya (Larsen 1982, 1991), and this was the case also in a much smaller migration towards the northeast observed between Kang and Ghanzi on 14 Apr 1990 and at Etsha Six in the Okavango on 17 Apr 1990. Many of my informants on the present migration emphasized that all females seemed to be yellow. Trimen (1891) also pointed out that specimens from early in the season were smaller and lighter than those later in the season. Though he did not link it directly with migration, such would normally be expected late in the season, and certainly the variations are not parallel to the usual seasonal dimorphism or polyphenism of the Pieridae, which provides for camouflage during the dry season (Brakefield and Larsen, 1982). I also remember seeing a reference to a parallel situation in respect of migrant and non-migrant forms of *Catopsilia pomona* Fabricius, in India, but I have not been in a position to retrace it.

The question is whether there is a parallel to the phases of the migratory locust (*Shistocerca gregaria* (Forsskaal) (Orthoptera: Acrididae), as first discovered by Uvarov (1921). The locust has a migratory phase which is induced by crowding, and a morphologically very different non-migrant phase. The strongly migratory Caper White Butterfly (*Belenois aurota* (Fabricius)) has pupae which become almost black instead of white when living under crowded conditions, but there is no visible differences in adults hatched from black pupae (personal, unpublished data from Oman).

SEXUAL BEHAVIOUR

Migrant males did not appear to be sexually active. It was, fortunately, possible to test this at Lehututu, where a non-migrant population was outnumbered four to one by migrants. I was able to find no less than 70 couples in copula, with the results given in Table 3.

Table 3. Mating pairs observed (migrant and non-migrant morphs)

Mating	Observed	Expected*
Mig ♂ - Mig ♀	5	45
Mig ♂ - Non ♀	0	11
Non ♂ - Mig ♀	50	11
Non ♂ - Non ♀	15	3
Total	70	70

* based on random mating and the observation that 80% of all specimens present were migrant phase.

Most of the non-migrant males in the locality were very worn, but some females were fresh, and small numbers of non-migrants were still hatching. The table makes it clear than most migrant males are sexually inactive whereas the migrant females are receptive to courtship from sexually active non-migrant males (Fig. 3). Lines 1 and 3 are strongly significant on a binomial test.

EARLY STAGES

Large samples of the early stages could unfortunately not be procured, though the larval food plant, *Cassia italica* (Caesalpiniaceae), was plentiful and in good state of development. However, 3 pupae from Hukuntsi produced migrants, and 15 larvae from Lehututu produced non-migrants. Nowhere did I see larvae and pupae in sufficient numbers to indicate that we were in a major source area for the migration. That the Hukuntsi pupae resulted in migrants, and those from neighbouring Lehututu not, may indicate that the cues for migration, be they social or environmental, depend on local circumstances.

The fact that the Hukuntsi pupae produced migrants may indicate the source areas need not necessarily be very densely populated, though this is often the case in other butterflies. The long duration of the flight and the sometimes relatively low densities over a period of time may indicate the same. However, the dense three-day migration at Maun is more consistent with a true out-break area, and of a flight that had not been too disrupted by adverse weather.

BEHAVIOUR OF THE MIGRANTS

In Mar and Apr, nights in Botswana already begin to be relatively cool and butterfly activity begins only at 08.30-09.00. The migrants seemed to begin activity somewhat later than most resident butterflies, flying about at random, and feeding. By about 10.00 movement begins and by 10.30 movement will have attained the daily average intensity, which would continue till temperatures began to drop at 16.00-16.30.

The flight is the typical bounding one of the *Catopsilia*, timed from the car at just under 30km/hour, so the butterflies will be able to cover about 200km on a good day. The flight is between 1 and 3m above the surface. Large obstacles, such as houses, are surmounted rather than circumvented. In the tall Mopane woodland of the Mababe area in Chobe the migrants flew in between the trees under the level of the canopy. I could see no difference from the normal flight pattern, except that the course was dead straight. Fortuitously the migration was exactly parallel to our road in Gaborone; I saw many migrants keeping a straight line for nearly 500m. In contrast, *Danaus chrysippus* has a much more whirring flight than normal, making remarkably good progress compared to the usual, leisurely flight. Again, seeing *Byblia ilithyia*, which has a most irregular and weaving flight, suddenly proceed doggedly in the same direction, is a curious sight. This is also true for *Eurema brigitta* which is not usually associated with such determination. These three species were flying more slowly than the *C. florella*, while *Junonia hierta* kept up with them.

It must be emphasized that the direction of the migrants was maintained under all wind conditions (though most days they were flying more or less against a headwind). However, when the wind was very strong, the flight was lower down than usual, in the so-called 'boundary layer,' where wind influence is less. Nonetheless, there seems to be a genuine ability to compensate for drift, judging from observations made on our road in Gaborone. The ability to maintain the course in the face of differing wind directions has frequently been commented upon (see summary by Williams (1958) and Pennington (1967)).

One difference between the *C. florella* and most other migrants I have seen was their willingness to stop to feed whenever suitable flowers or damp patches were available (Fig. 4). When standing to the south of a large patch of flowers where thousands were feeding, hundreds could be seen arriving while other hundreds left the flower patch. Usually feeding behaviour of an individual would not last more than a few minutes. A favourite nectar source is *Leonotis* sp. as also observed in South Africa by Steve Woodhall (pers. comm.). Col. Bowker, about 100 years ago, described the same phenomenon in the mountains of Lesotho (quoted in Swanepoel, 1953).

In the evening, or when the sky became overcast, the migrants stopped to roost in bushes and small trees, in the evening usually after some flying about and feeding. There was no indication at all of any social element in the roosting.

It should be emphasized that as far as I could observe in eastern Botswana in Apr all migrants left Botswanan territory and that new populations were not building up. Virtually none was seen in and around Gaborone in May, Jun, and Jul.

PREDATION

This large quantity of butterflies should in principle be a bonanza for insect-eating predators, especially birds. Several of my informants spontaneously commented on the fact that the migrants did not appear to be preyed upon. I did in fact over the open Okavango River at Shakawe see several groups of Blue-cheeked Bee-eaters (*Merops persicus*) which had obviously specialized temporarily on the migrants (Larsen, Bartlett, and Drotsky, 1991). This had also been observed in Maun (Dawn Riggs and Doline Bridges, pers. comm.) and at the Gaborone Dam by M. Herremanns and D. Tonnoeyr. I have also seen the occasional migrant being taken by Fork-Tailed Drongoes (*Dicrurius adsimilis*) and by Lilac-Breasted Rollers (*Coracias caudata*), but these two birds, though common, are not very numerous and may well prefer to stick to their normal prey, which would be abundant at the time. However, the speed and the bounding flight of the migrants are such that they probably quite simply are suitable prey only for highly specialized, and quite large, aerial predators.

FELLOW TRAVELLERS

The migration began as one containing only *C. florella*, but towards 20 Mar other species began to get involved. First modest numbers of *Hypolimnas misippus* (Linnaeus) of both sexes appeared, easily recognizable since their migratory flight pattern is so different from the normal one. Then appeared modest numbers of *Eurema brigitta* (Stoll), *Belenois aurota* (Fabricius), *Danaus chrysippus* (Linnaeus), *Byblia ilithyia* (Drury), and rather larger numbers of *Junonia hierta* (Fabricius). At no time did the fellow travellers constitute more than 5 percent of the total, and mostly much less. These species are all known migrants, though in the case of *E. brigitta* and *B. ilithyia* they seem to take place at such low densities that actual records of migration are few.

In this case the proportion of species other than *C. florella* is so low that the migration can hardly be classified as a genuine mixed migration, where one species usually does dominate, though usually with a maximum of 50 to 60 percent of the total. However, *C. florella* has frequently been seen both as single species migrations and as participants in mixed migrations (Larsen, 1978a-b, 1982, 1985, 1988a-c, 1991; Pennington, 1967; Williams, 1930, 1958).

NUMBERS INVOLVED

In order to estimate the numbers involved in such a migration it is necessary to make some reasonably heroic assumptions, but the attempt is still worth doing. Though there were variations in pattern, not only mediated by weather, the total records indicate that the front stretched from at least Kimberley and Welkom in the Orange Free State right through to the northwestern corner of Botswana, a distance of 1100km, and records are available for virtually the entire front (Fig. 5). Densities were greatest south of Serowe, though the three day migration at Maun and the records from Sua Pan also indicate very high densities. Using an average of 1000 per km per minute would be a modest average for a good day for the country as a whole (see Table 1). In Gaborone the migration lasted some 20 days, though strongly broken up by weather conditions, but still adding up to at least five or six whole days, measured as six-hour days. In Maun a very dense migration lasted three days, but there were later stragglers as well, and densities were much higher than 1000 km/minute. Using an average of four full, good days of migration over the whole front would seem a reasonably modest assumption. For each of these four days the flight period would have lasted six hours (10.00-16.00), or 360 minutes.

Using these figures we arrive at the following equation:

1100km x 1000/minute x 4 days x 360 mins = 1,584,000,000

Thus, a minimum estimate of the numbers involved is about 1.5

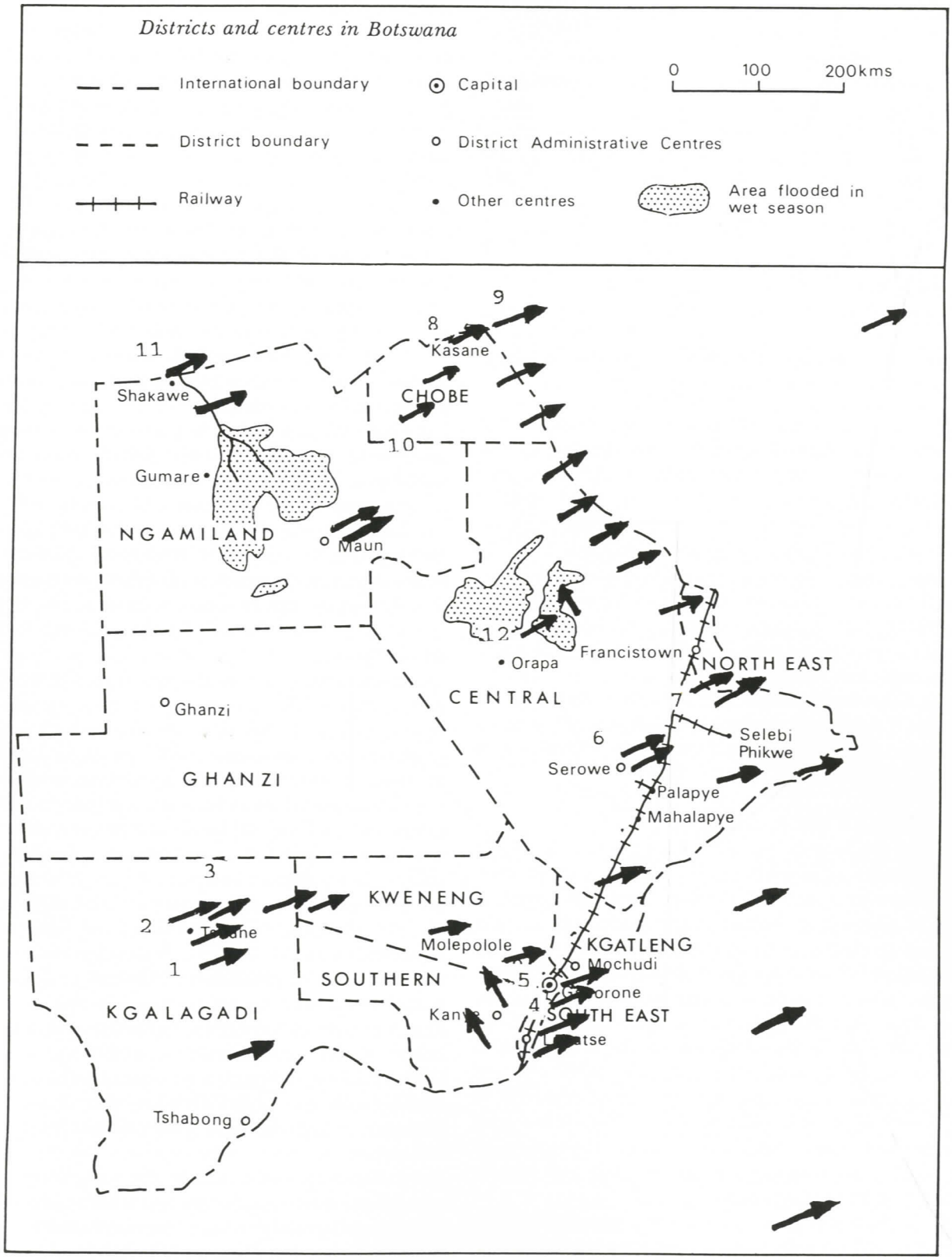

Fig. 5. Map of Botswana showing where major migration activity of *Catopsilia florella* was observed; arrows denote the flight direction. The numbers refer to the localities mentioned in Table 1.

Table 4. Summer rainfall by month in Tshabong and Tshane, 1965/66, 1990/1991, and mean monthly rainfall (millimetres per month)

Month	Tshabong 1965/66	Tshabong 1990/91	Tshabong Mean	Tshane 1965/66	Tshane 1990/91	Tshane Mean
Oct	4.0	23.1	15.3	2.2	0.0	18.3
Nov	16.9	6.2	27.1	16.9	2.2	34.3
Dec	1.5	41.4	35.1	35.1	10.7	34.9
Jan	17.1	174.8	50.6	88.5	174.9	83.3
Feb	81.2	25.9	53.7	221.2	68.5	65.8
Mar	3.0	124.7	53.4	0.3	24.8	63.8
Total	123.7	396.1	235.2	364.2	281.1	300.4

Source: Data kindly provided by the Rainfall Unit of the Department of Meteorological Services, Government of Botswana.

billion, but the true total may well have been much higher than that. The only higher previous estimate I remember having seen concerning butterfly migration was of three billion *Vanessa cardui* (Linnaeus) flying into the southwestern states of USA from Mexico, but this was based on less precise data than the present estimate (M'Gregor, 1924: quoted by Williams, 1930). In contrast, 'only' about 150 million monarchs (*Danaus plexippus* (Linnaeus)) from eastern Canada and United States reach their Mexican roosting sites every year (Monarca, pers. comm. — an anonymous reviewer suggested that studies by L. Brower would more than double this figure).

This also means that the numbers of fellow travellers were not insignificant. Even supposing that each of the species involved was represented only as half a percent of the total, this still leaves more than 7 million.

THE SECONDARY MIGRATION

On 23 Mar the weather was dull, but by 13.00 the clouds cleared and a major migration began in a northwesterly direction in the area between Diabo and Lobatse, some 70km south of Gaborone. Its composition, behaviour, and density was as in the later days of the migration in Gaborone, including the same 'fellow travellers.' Two counts gave a total of 966 and 1280 per kilometre per minute. The distance between Diabo and Lobatse was about 20km. At Lobatse the weather again deteriorated, but for a brief period we were privileged to see the ENE migration being intersected by the NW migration. I have previously seen two large migrations intersecting, with no trace of confusion, in the Nilgiri Hills of southern India (Larsen, 1988a). It is a great pity that time and weather did not allow further observations of this interesting phenomenon, but it was clear that both streams maintained their integrity and direction.

On 28 Apr there was minor northwesterly migration activity (no more than 100 per km/minute) in the same locality, and at least one case of northwesterly migration was reported from Kubu Island in the Sua Pan around 20 Mar.

THE 'GREAT MIGRATION OF 1966'

The 'Great migration of 1966' lasted about three weeks (peaking in mid-Apr), with individuals flying whenever there was sun, but with a peak activity of ten days in each location. It stretched from west of Pretoria to the Indian Ocean, a 400mi front, and ultimately reached Salisbury (Harare) and Umtali, and almost certainly Mozambique. Reports were received from Vryburg, Steynsburg, Queenstown, Stutterheim, and East London. At Umzumbi they went out to sea, and hundreds were found washed up on the coast. The direction of the migration was mainly northeast, and the course was maintained irrespective of wind direction. There were a few records of slight deviation from the main course. As was the case in the present migration *C. florella* was dominant, but small numbers of *Belenois aurota* and *Danaus chrysippus* were also involved, while *Eurema brigitta*, *Hypolimnas misippus*, and *Junonia hierta* were not reported. Other species were also involved: *Colotis subfasciatus**, *C. agoye**, *Acraea stenobea**, *A. lygus**, *A. anemosa***, and *A. neobule* (those marked * are mainly Kalahari-centred and not normally migrant; those marked ** are not normally migrant).

As the cause for such a large migration, Pennington (1967) advances the hypothesis that 'the Kalahari drought had reduced predators to a minimum, and the copious January rains brought an abundance of their foodplants to coincide with the normal emergence of larvae.' He believed the 1966 migration of *C. florella* to be the biggest such event ever in southern Africa, and emphasized that migrations of this species are much less frequent than the regular migrations of *B. aurota*.

DISCUSSION

Williams (1958) summarizes the migrations of *C. florella* in Africa. In Zimbabwe, in Nov-Jan, there are many records of migrations, chiefly SSW. They are often of large scale; Cockbill (1951) records a maximum of 2900 per m per minute. In Feb-Mar there are records chiefly of flights towards NE, mostly rather weak. Most records from Transvaal and Natal are towards NE in Feb and Mar. There are, however, a few anomalous records.

These dates would fit the explanation suggested by Pennington (1967). The southward migrations from Zimbabwe would reach the Kalahari in Dec and Jan, quite possibly in such small numbers that SW migrations through Botswana and Transvaal would not be noticed by casual observers. If there have been good rains in the inner Kalahari and Namibia, then two or three non-migrant broods could build up the potential for large-scale migration. Certainly the inner Kalahari received much above average rainfall in Jan of 1991, while February rainfall was low to normal. During the 1965/1966 season there was exceptionally high rainfall in Feb (Table 4), which matches the fact that the peak of the migration in 1966 was in mid-Apr, several weeks later than in 1991.

I cannot help suspecting that these migrations actually take place every year, but that in normal years conditions in the Kalahari do not permit a major population build-up and that the return migrations are too small to be noticed by anyone not specially studying the issue. R. Plowes (pers. comm.) certainly thinks that some NE migration is seen every year.

How the butterflies maintain their chosen direction so unerringly, almost certainly compensating for drift, remains unknown. Solar navigation, with compensation for the movement of the sun, is often suggested. However, at this time of the year the sun will be directly overhead the butterflies for part of the day, moving from east to west. Between at least 11.00 and 13.00, the peak time of migration, it surely cannot be used for navigation. Another suggestion is that after the direction is set, navigation is by use of major features in the terrain, like human beings would do when trying to maintain a straight line. However, much of the Kalahari, not to mention the Sua Pan, is so featureless as to make this practically impossible. There is also no question of a follow-the-leader explanation, since single stragglers follow the same course well out of sight of other migrants. Henning (1983) believes a pheromone to be a stimulus to migration, but this could not be responsible for setting and maintaining direction.

I personally have little doubt that navigation by use of the earth's electromagnetic field is the most likely solution. Williams (1958) virtually dismisses this option, but shortly before his death he told me that he was beginning to accept this solution. I believe there is evidence that some moths have electromagnetic sensors. How all butterflies in a population get coded with the same direction, while other populations all get coded with another, remains a mystery.

TRIBAL BELIEFS ABOUT BUTTERFLY MIGRATION

Finally, it must be mentioned that the San peoples (Bushmen) use the advent of butterfly migrations to predict the arrival of the vast ungulate migrations that take place in Botswana (Lea, in press), claiming that the animals will follow shortly from the same direction. The larger the butterfly migration, the larger the herd. The main migration is claimed to be west to east, with the opposite movement in summer. Certainly, the main zebra migration up through Chobe took place at the same time as the present migration passed through that area. However, it may be that the main indicator species for the San is *Belenois aurota*, which is a much more regular mass migrant in southern Africa than *C. florella*. However, both species often migrate together at the same time and in the same direction, though usually the main *B. aurota* migrations tend to be somewhat earlier than Mar and Apr.

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