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Oxford Expedition to the Sierrania de Macuira, Colombia, 1975

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DEDICATION

14th October, 1976. *We have just heard with great sadness of the recent death of Peter Knappett. His introduction to this acount is filled with the enthusiasm, originality and sense of humour for which his friends loved him. We dedicate the remaining parts of this report to his memory.*

JIM MALLET, ANDREW SUGDEN

PRINCIPAL AIMS

1. To compile representative collections of plant material and selected insect groups (Lepidoptera and Orthoptera) from the little studied and remote area of cloud forest in the Serranía de la Macuira, Guajira Province, Colombia.
2. To undertake a survey of the epiphytic vegetation in the cloud-forest zone.
3. To investigate the macrofauna associated with large tank bromeliads in the cloud-forest.

PERSONNEL

C. Peter Knappett, B.A., Leader (22), Zoologist, Trinity College, Oxford.
Jim Mallet, Treasurer (20), Zoologist, Balliol College, Oxford.
Andrew Sugden, B.A., Secretary (21), Botanist, Wadham College, Oxford.
Henry Bernal M., and Jaime Umaña A., Botanists, Insituto de Ciencias Naturales, Universidad Nacional, Bogotá.
Home Agent: Dr. P. Brunet, Department of Zoology, Oxford.

INTRODUCTION (C.P.K.)

Care and Maintenance of a Small OGRE

The 1975 Oxford–Guajira Research Expedition was planned as a short exercise in practical biogeography which would produce interesting and useful results.

OGRE matured rapidly under the beneficial influence of previous visitors to the South Caribbean coast lands. Richard Robins, leader of the Oxford expedition to the Sierra Nevada de Santa Marta (1974), had heard of a patch of moist forest on the Colombian coastal desert mountains, and in March 1974 raised the subject in conversation with me. He emphasised that Dr I. Hernandez of INDERENA, Bogotá, had declared that these hills were largely unexplored. The idea lay dormant until Jim, Andrew and I contacted Dr Enrique Forero of the Instituto de Ciencias Naturales (ICN), Bogotá, after deciding that here was a unique opportunity for gathering some useful and original data.

We could find very little information on the region of Alta Guajira beyond the fact that there existed a village – Nazaret – with a Capucchin mission (The Intermado Indigine de Guajira). Its connections with the outside world were said to be tenuous. An area of humid forest on a small range of hills, the Serrania de la Macuira, was marked on some vegetation maps of Colombia (Espinal and Montenegro, 1963), but besides a reference to some marsh birds existing in the area (Marinkelle, 1970), no other evidence of moist forest could be found. However, Enrique Forero's enthusiasm and a generous offer of help from the British Vice-Consul in Bogotá, David Lloyd, convinced us that an expedition was a practicable proposition. The possibility that we might arrive in Guajira and find nothing but empty desert became the subject of numerous horrifying jokes, though we suspected that our main difficulties would lie in successfully bringing back and identifying biological specimens.

Itinerary

So it was with slightly mixed feelings that OGRE left Dover for Brussels, with 85 kg of equipment, on the morning of 8th July. The three-day journey, arranged by the Colombian Travel Club, was cheap, complicated and exhausting, but the money saved and the glimpses of some

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truly ghastly American television in Miami were probably worth the weariness at the end of the journey. Janet and David Lloyd made us welcome on our arrival in Bogotá and invited us to stay with them while we sought official permission and collecting permits from INDERENA, the relevant government department. We were also able to discuss our plans with Enrique Forero, and to search the herbarium records. Andrew discovered that an Argentinian had briefly visited the Serranía de Macuira about ten years previously, but had unpredictably returned to Buenos Aires taking his field notes with him, and leaving behind an unlabelled and therefore useless collection of herbarium specimens; we were relieved to find that some of them were bromeliads of the genus *Guzmania*, which are fairly sure indicators of moist conditions.

A week after our arrival we took an internal flight to Barranquilla, armed with a great many 'permisos' and letters of introduction. There the British Honorary Consul, G. N. Hutchinson Esq., put us on an air-conditioned bus to Riohacha, the capital of Guajira Province. In unexpected luxury we arrived in the middle of the night, and the next morning requested an audience with the governor of Guajira, Senor Lorenzo Solano Pelaez. We waited, accumulating additional stores, for the whole of a stiflingly hot weekend, made bearable only by the frequent 'gaseosas' – the tapwater of Riohacha was brackish and interestingly soupy. Senor Pelaez helped us to hire a taxi – a square open-backed Ford – at a cost of $90. It was a fantastic eight-hour ride through Indian country to the end of the peninsula; beyond the salt mountains and flamingo lagoons of Manaure, the cactus and thorn woodland gradually gave way to white lunar mirage flats and red martian dust country. Isolated shimmery hills rose ahead of us, were passed, and sank down again behind us. There was great excitement when Luco, the driver, pointed out the narrow Serranía de Macuira, for unlike the dry grey slopes and gullies of the other peninsula ranges, its upper slopes were noticeably green.

Nazaret, reached late in the evening, was visible from some distance away; attention was drawn to it below the westward silhouette of the Serranía due to a cluster of curiously bright-coloured lights. These, it transpired, belonged to the Internado, an impressive white structure built in the style of an Italian monastery with a huge courtyard facing east. Although our letters had not reached him, Padre Pio showed us to rooms set aside for wandering geologists, INDERENA officials and other visitors. He insisted that we make ourselves at home – not difficult in view of the two rooms, worktables, shower, lavatory and hammock hooks. We owe a large part of our success to the generous help of Padre Pio, Apolinar Deltoro, Cyrillo, Hermana Ofelia and many others at the mission. Cooked meals were served in the village at the local inn, while cloth, corned beef, eggs, paraffin, rice, sardines, spaghetti, string, and other essentials were available in the village's four general stores. A small army barracks, a twelve-bed hospital and scattered Indian fincas complete the description of Nazaret. We arrived there on the 21st of July, 14 days after leaving England.

Fieldwork

It took us a week to find the moist forest areas we were looking for. The Serranía rises to three main summits 750–850 m in height, none of them clearly visible from Nazaret, and the twenty square kilometres of cloud forest is shared between them as three green 'islands'. On the windward side of the Serranía the green appears grey at noon, and is lost in clouds early and late in the day. Steep slopes, dry forest and impenetrable thorny scrub defend the humid zones on the more obvious lines of approach. The forest thick with the epiphytes we needed in order to fulfil our scientific programme was reached only after the hazardous ascent of about fifteen forty-foot waterfalls in the steep Arroyo Chichimahu. At the place where the Chichimahu stream began its descent from the Huararech (central 'island') plateau we found an overgrown clearing, on the edge of which stood a dilapidated hut infested with giant bees. Finca Uincua sat right on the edge of a 600 m scarp, the wall on that side consisting of only air and trees; enquiries in Nazaret revealed that it had been abandoned for three years, the subject of an ownership dispute between two Indian families. It would have made a perfect advanced base even without its freshwater supply and sweet potato patch, so in a four-hour struggle we lugged our belongings up the zigzag track from the lower Hudrapunu valley and moved in.

During the month of August we conducted an intensive survey of the Huararech island. As the plateau is densely forested and geographically confusing a proportion of each week had to be spent seeing *what* was present and *how* to get to it. The bewildering changes of vegetation type as one crossed the sharp-boundaried mosaic of parallel and antiparallel ridges and valleys made exploration essential. It was very easy to get lost. An irregular network of tracks linked with the 'Unfriendly Finca', whose occupants were beginning to devastate the further side of the 'island', greatly aided our elementary survey programme as well as travel to and from our sampling sites.

While Andrew's epiphyte survey took him round his endless quatrat circuit, Jim flitted about in the woods swearing at skippers (Hesperiid butterflies). An attempt at pitfall trapping had to be abandoned before the zoological programme settled down to day butterfly and Orthoptera netting, and evening Tilley lamp collections. With the arrival of Jaime and Henry more time became available for bromeliad faunal analysis to get under way.

Typical days began in cold mist at seven o'clock, and it was unpleasant to get up before this had lifted. The first to rise shivering from his hammock would light a fire to brew coffee and porridge, and by half past nine with equipment and lunchtime sardines rattling around in our pack we would be heading for our study areas. It was always necessary to be back by dusk, in order to avoid missing the way and to leave enough time to dig up potatoes for Andrew's remarkably palatable stews. These would be gulped as we crawled around the lamp with specimen tubes, catching insects while the air was still warm enough for them to fly to us.

Jaime and Henry

It was while purchasing sardines that Jim met reinforcements in Nazaret. Enrique Forero had hoped to send a student with us, but for various reasons there was nobody available at the time we left Bogotá for Guajira. Jim wrote to Dr. Forero as soon as we discovered our first bromeliads, and Enrique asked two of his botany students, Jaime Umaña A. and Henry Bernal M. if they would like to join us. Jaime and Henry possessed wide experience of expeditioning in Colombia, and they worked as a formidable team. They arrived after five days' travel and set out vigourously for the hills with Jim in the lead. Unfortunately they missed the indistinct lower reaches of the path up the escarpment to the hut, and tried to force their way up the Hudrapunu waterfalls. Jaime and Henry took the climb very seriously and produced about a hundred feet of rope by which they scrambled up a cliff on the wrong side of the Hudrapunu gorge. Realising their mistake as dusk fell the intrepid three bivouacked on top of what was thenceforth known as Jim's peak, and fought their way through the bush into Uincua the next morning. In spite of this, Jaime and Henry were not to be discouraged from cooking us a meal that evening while they improvised songs in honour of Andrew's twenty-first birthday and OGRE's presence in the Macuira. The Colombians' phenomenal work rate and practical knowledge of field methods enabled us to get through our schedule faster than we could have hoped for even in our most optimistic moments. It was with great regret that we had to bid them farewell only two weeks after their arrival, for their university course restarted early in September.

Shortly before we came down from Uincua a multinational party of postgraduate South American geologists arrived at the Internado. (The Alta Guajira is structurally highly diverse and is frequented by oilmen, uranium prospectors and field geologists.) Back in Nazaret we shared our quarters and our evening meals with this good-natured crew; they lent us some aerial photographs which showed that the cloud forest had not changed appreciably in extent since 1960, despite the recent inroads of the finceros' cattle. Andrew occupied himself with caring for and extending his moist forest collection, and beginning a dry forest analysis. Jim continued his insect netting and we were able to extend our light trapping programme to the dry forest and the intermediate forest zone just below the cloud level. To my intense annoyance I had to repeat one of my bromeliad animal replicates on far away Huararech summit and spent a night out in a very damp windstorm – the rains were clearly not far off. A brief but highly profitable visit to Cerro Uray, the highest of the three summits in the Serranía (and the furthest from Nazaret), brought our field adventures to a close on September 6th.

Return Journey

Being unwilling to risk our samples and equipment on the weekly bus to Uribia, we sought the advice of 'el Teniente', the officer in charge of the army barracks. He felt we might be able to take the military aircraft which flew every few weeks from Puerto Estrella to either Buenavista, Barranquilla or Bogotá. His immediate superior gave us his permission. Padre Pio feasted us magnificently the evening before the DC_3 was due, but September 8th brought no news of any aircraft. We were little worried about being marooned until, on the morning of the 9th, el Teniente's dilapidated jeep roared up to the Internado in a cloud of dust and we had to load our belongings in indecent haste. The DC_3, we were told, was due to leave any moment after being delayed by unusually heavy cloud cover. The flight was arranged in exchange for several vast papayas – produce of the Internado. Fortune was with us again, for two days later violent storms cut off the Alta Guajira and the peninsula was reported as being 'mostly under water'. We were flown directly to Buenavista, an airstrip fifty kilometres from Valledupar; there we were informed that we could not continue the flight to Bogotá. It so happened, however, that a bus ran from Buenavista directly past the civil airport at Valledupar, from where, after a four-hour wait, we were able to catch a direct flight to the capital. The whole journey lasted only ten hours, but was marred by the loss of a camera and a pair of binoculars at Eldorado Airport, Bogotá.

Conclusion

The rest of the tale concerns the hospitality of the Lloyds and their friends during the final week in Bogotá, and some confusion over the Colombian regulations concerning the export of biological collections from the country; the latter was resolved with the help of Enrique, David Lloyd and Patricia Londoño. The expedition held a farewell dinner in honour of David and Janet, Enrique, Jaime and Henry and we began our long flight home on September 18th, wishing that we could have prolonged our stay. September 20th saw the return to Oxford of an OGRE wiser and considerably fitter than the one that had set out twelve weeks earlier.

THE GUAJIRA AND ITS PEOPLE (J.M.)

'La Guajira' is virtually unknown outside Colombia and Venezuela. Bizarre myths about the region circulate even in these countries, so we feel it is worth giving our subjective account of life in the Guajira peninsula. For more detailed accounts see Weston (1937), Bolinder (1957), Chaves (1953), Crist (1957) and Useche (1974).

Geoffery Crossley, H.M. Ambassador in Bogotá, was the first to warn us of the dangers of Guajira. He had been touring the lower, southernmost regions of the Guajira when heavy rain forced him back. We quote from his letter: '. . . the rains were torrential and the desert was turned into a quagmire within hours . . . . Last week the young occupants of a jeep were kidnapped by gunmen

but later escaped, though shot at, when their kidnappers got drunk . . . my personal bodyguard carried a machine-gun and a revolver.' Weston and Bolinder, who had earlier travelled widely in Guajira, presented a rather different picture – of Indians largely friendly to foreigners, Indians who had been unchanged by the influences of conquistadores or missionaries. However, gloom descended on us in Bogotá when we were again reminded of possible difficulties in the lower Guajira. Friends told us we would probably be shot for no reason and certainly robbed in either Maicao or Riohacha – before we had ever seen Nazaret. Perhaps we were lucky, but our impression is that the guns carried openly in Riohacha are used, mainly against those who interfere with the rather dubious trade of the area; a traveller is more likely to be mugged in New York than in Maicao.

Guajira has very little in the way of industry, except for the extensive salt flats at Manaure, which lies on the coast to the north-east of Riohacha. Rumour has it that there is oil in the Guajira, and coal is a distinct economic possibility, while natural gas has recently been tapped for the first time. Otherwise the country is desert with a surprisingly high population. Many Guajiros obtain dual nationality and work for periods in Maracaibo, and for this reason prices are often quoted in Venezuelan bolívars. Food prices are high by Colombian standards, as much of it is imported from Venezuela. Riohacha, a small, ancient Caribbean port, is the capital of Guajira. Maicao is the centre for trade (much of which is contraband) and consists almost exclusively of shops where otherwise unobtainable or expensive goods can be bought duty-free. Maicao is visible for miles across the desert as it boasts Guajira's highest building – a thirteen-storey hotel; in Uribia the women's jail is reputedly the tallest landmark. In all of these towns education is run by Italian Capucchin monks at the 'Internados', or boarding schools.

The chief problem faced by the Guajiros is the lack of water during the dry periods; the rainy seasons are variable (October and November, and sometimes in April). Traditionally, deep wells were dug from which could be extracted a brackish liquid that was barely drinkable, but more recently the government has installed windpumps in many areas. Only in the Serranía de Macuira is fresh water available all the year round. Unfortunately the availability of water in recent years has resulted in an increase in stock-raising in the naturally dry areas, thereby increasing the rate of erosion; Cloudsley-Thompson has observed the same effect in the Sudan Savannah region of the southern Sahara. Bolinder, in the 1930s, noted that large herds of cattle were common signs of wealth among the Guajiros; today the cattle have been largely replaced by goats, and there is little vegetation save candelabra cactus and acacia scrub on the plains.

When Bolinder visited the Guajira, the Indians were apparently loth to learn Spanish or to have much to do with Christianity; now, however, most are bilingual and profess to be Roman Catholics. A facet of Christianity that must appeal to a Guajiro is that a wife can be married without the payment of the traditionally high bridal price. Cyrillo, the Guajiro driver at the Internado in Nazaret, had married five wives; the first he had married in church, but the most recent had cost him 80 goats, 2 cows, 2 gold medallions and a mysterious wooden object. The bridal price is paid to the woman's maternal uncle in accordance with the unwritten Guajiro laws. As Cyrillo put it, this is a business agreement rather than slavery, and is similar to the desire of most European parents to ensure that their daughter's fiancé has a certain financial status.

The Guajiros are a practical race for whom the mysticism of the nearby Kogis of the Sierra Nevada holds little interest. Herbal medicines are still used by the older Indians, but knowledge of these is rapidly dying out. They do not, as far as we know, resort to the use of drugs, but alcohol, both home-brewed and imported, is very popular. *Chicha*, a ferment made traditionally from maize which was chewed by the women and then spat out into a large vat, is now more usually prepared in a large metal grinder. A local fiery rum is produced from Heath Robinson-like stills.

All of the Guajiros we met were extremely generous, even though there was little we could give them in return. One family, whose finca we passed through and rested at frequently during our journeys to and from Uincua, suggested that we might mend their ancient Singer sewing machine in return for the fruit and meat that they gave us. This proved to be a great mistake, for although the machine plainly had but a minor fault, after several visits (which turned into ritual half hours with a pair of pliers and a broken screwdriver) it was quite obvious that it would never be used again. Gifts would always be received by the Indians with a nod, and in fact there is no Guajiro equivalent of 'Thank you'; in a land where giving and receiving are taken for granted, gratitude becomes redundant.

The Guajiros have recently adopted those features of Western civilization which they find useful, but the peace of the desert appeals to them more than the large towns in which they may work. They will always laugh at some of the West's strange and earnest habits; it was embarrassing for us to be greeted with giggles wherever we went, until we learned that it was acceptable to laugh at *their* strange habits in return. At least one member of OGRE is returning to Guajira, and we look forward to meeting once again the very good friends we made in the Serranía de Macuira.

SCIENTIFIC RESULTS

Botanical Sections (A.S.)

Since it is intended to publish the results of this survey elsewhere only a brief summary is presented here. A further more detailed botanical study is planned for 1976–77 and it is expected that this will provide answers

to many of the questions raised during the first expedition. Our botanical aims were as follows:

1. To ascertain whether a moist forest zone existed at all in the Serranía de Macuria, as the information given in various vegetation maps was somewhat conflicting (Fig. 1);
2. To account for the existence of a moist forest zone, given the very arid conditions prevailing in all other parts of Guajira, and to ascertain the extent of the zone;
3. To investigate the range of habitat types within the moist forest zone, placing particular emphasis on the quantification of epiphyte populations.
4. To make representative collections of herbarium material for the National Herbarium in Bogotá, for the Royal Botanic Gardens at Kew, and for the Fielding Herbarium at Oxford.

These aims were satisfactorily accomplished, and the groundwork on which to build future investigations was laid down.

It is apparent that the moist forest zone owes its existence entirely to the clouds which cling to the mountains from the early evening until the following morning; all precipitation onto the Serranía, except during the brief rainy seasons, occurs directly from clouds at ground level. The lower cloud limit is at about 550 m, and there is a sharp discontinuity in the vegetation at this level. Below 550 m the trees are deciduous, the soil is dry, epiphytes are virtually absent and the forest density is low (approximately 30 trees per 100 m^2); above 550 m the trees are evergreen, the soil is quite moist, epiphytes are abundant and the forest density is high (50–100 trees per 100 m^2). The canopy height of the moist forest, in common with other elfin cloud forests, rarely exceeds 5 m. It is reasonable to assume that annual primary production is greater in the cloud forest than in the dry forest.

In the course of the epiphyte sampling programme, some 16,000 bromeliads and many other epiphytes (mainly orchids and ferns) were counted on nearly 1,000 trees. The data acquired indicate that epiphytes in the Serranía de Macuira, and bromeliads in particular, exhibit strong zonations according to the following physical factors:

(i) distance below the canopy;
(ii) altitude;
(iii) degree of exposure to wind;
(iv) degree of exposure to precipitation from ground-level clouds.

(The last three factors are interdependent to varying degrees.)

As a result of the epiphyte survey, it has been possible to suggest that there are at least four distinct habitat types within the moist forest zone – windward slope, leeward ridge, leeward slope and gully – which have characteristic floristic and physiognomic features; however, it is expected that the next expedition will show this to be an oversimplification. It is possible that the structurally diverse nature of the cloud forest-zone provides more favourable circumstances for adaptive radiation resulting in a greater degree of endemism than would occur in a uniform environment. We have evidence that the division of the zone into three major 'islands' of cloud forest – isolated from one another by distances of 3–4 km – has led to differences between the three localities in certain aspects of their vegetation: for instance, two very different forms of the cycad *Zamia* are found to be mutually exclusive on the northern and central 'islands'.

As a final note, it is important to mention that the future of the cloud forest in the Serranía de Macuira is precarious. Already a number of farmers in the area are raising cattle, and felling large areas of the forest in order to grow vegetables and cereals; as the population expands it becomes necessary to utilise the rich, but very limited, resources of the upper slopes of the Serranía. It would not be pessimistic to predict that in 10–15 years there will be little or nothing left of the 20 km^2 of virgin cloud forest. It is essential that further botanical investigations – quite apart from next year's expedition – are undertaken in the Serranía de Macuira before the face of the mountain is radically and inevitably altered.

Zoology Section

1. *Species Diversity of Insects in the Serranía de Macuira* (J.L.B.M.)

Since we were collecting insects as part of our research programme, a study of species diversity was seen as both practicable and likely to produce reasonable results in the short time available. The questions we have tried to answer are as follows:

(i) How does insect species diversity change with the pronounced ecological gradient of the hill-sides?
(ii) What are the reasons for any observed change?

Field Methods: A large amount of data can be collected in a short space of time using a light-trap sampling method. Certain species of flying insects do not come to light; in other species only one sex is attracted, but a light trap has the advantage of sampling effectively at random the habitats of which the trapping area is composed.

The light-trap apparatus consisted of a Tilley pressure paraffin lamp, which was placed on a 1 m^2 linen sheet.

Insects were collected at Uincua (cloud-forest) at an altitude of 600 m on 22nd, 23rd and 24th August 1975. The two sites were selected carefully; both had a N-E aspect, and were on low hummocks inside clearings bordered by primary forest. To land close by either site was actually cultivated at the time, and both clearings had been invaded by secondary scrub.

Peter assisted in making the collections. Only flying species landing on the sheet or lamp were collected, and

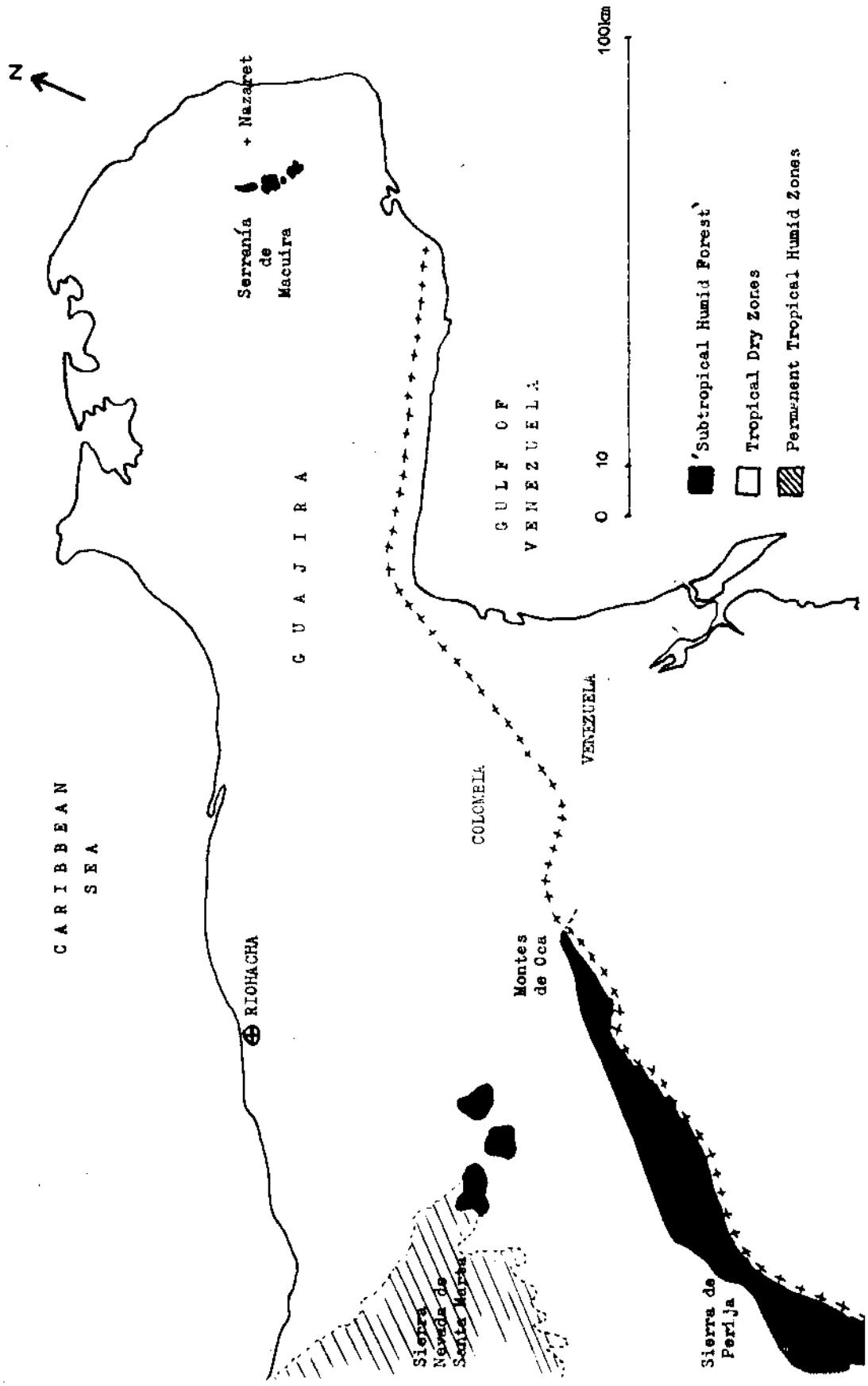

Figure 1: GUAJIRA – VEGETATION
(From Espinal and Montnegro – Ecological Map of Colombia, 1963)

all were killed. Moths were killed in a cyanide bottle; all other insects were asphyxiated with ethyl acetate.

The numbers of insects flying to the light fell off dramatically after about 1930 hours; accordingly we trapped from before dusk (1830 hours) until 2000 hours in each site.

Laboratory Work: Lepidoptera were pinned onto 'Plastozote' immediately after collection as suggested by Cogan and Smith (1974), with wings spread to enable identification. Other insects were put into 70 per cent alcohol.

The insect collection was identified to the specific level, with an estimated error of less than 10 per cent. The number of insects of each species was obtained. It should not matter if some species are grouped together providing that there is no weighting between the sample sites.

Results: Lepidoptera are arranged in order of abundance in Tables 1a and 1b. Social species (ant and termite alates) were omitted from the final data as their clumped distribution in both space and time could have caused unnecessarily large fluctuations in the data. Drosophilids, which were numerous in species and individuals at Uincua, were also omitted from the data because of my inability to separate them precisely into species. The records for all other insects can be found in Tables 2a and 2b. Summed records for all flying insects species (apart from those excluded above) are in Tables 3a and 3b.

Species Diversity: Most of the species collected were small to minute. No noticeable differences in size range were observed. On the other hand the two areas are composed of almost completely distinct communities, only eight species of insect being caught in both trapping sites.

In every case more species and fewer individuals were found at Uincua than at Nazaret. Eighty-four spp of Lepidoptera were caught among 272 individuals at Uincua; at Nazaret 58 spp among 566 individuals. For all other insects the same trend is evident; at Uincua there were 107 spp among 227 individuals, while at Nazaret only 83 species were found from among 292 individuals.

A histogram of species of all insects arranged according to octave abundance classes is shown in Fig. 2. The octave abundance scale is the simplest (× 2) geometric scale of abundances. Class 1 contains those species represented in the catch by one individual; Class 2, 2–3 individuals; Class 3, 4–7 individuals; Class 4, 8–15 individuals and so on. From Fig. 4 it can be seen that

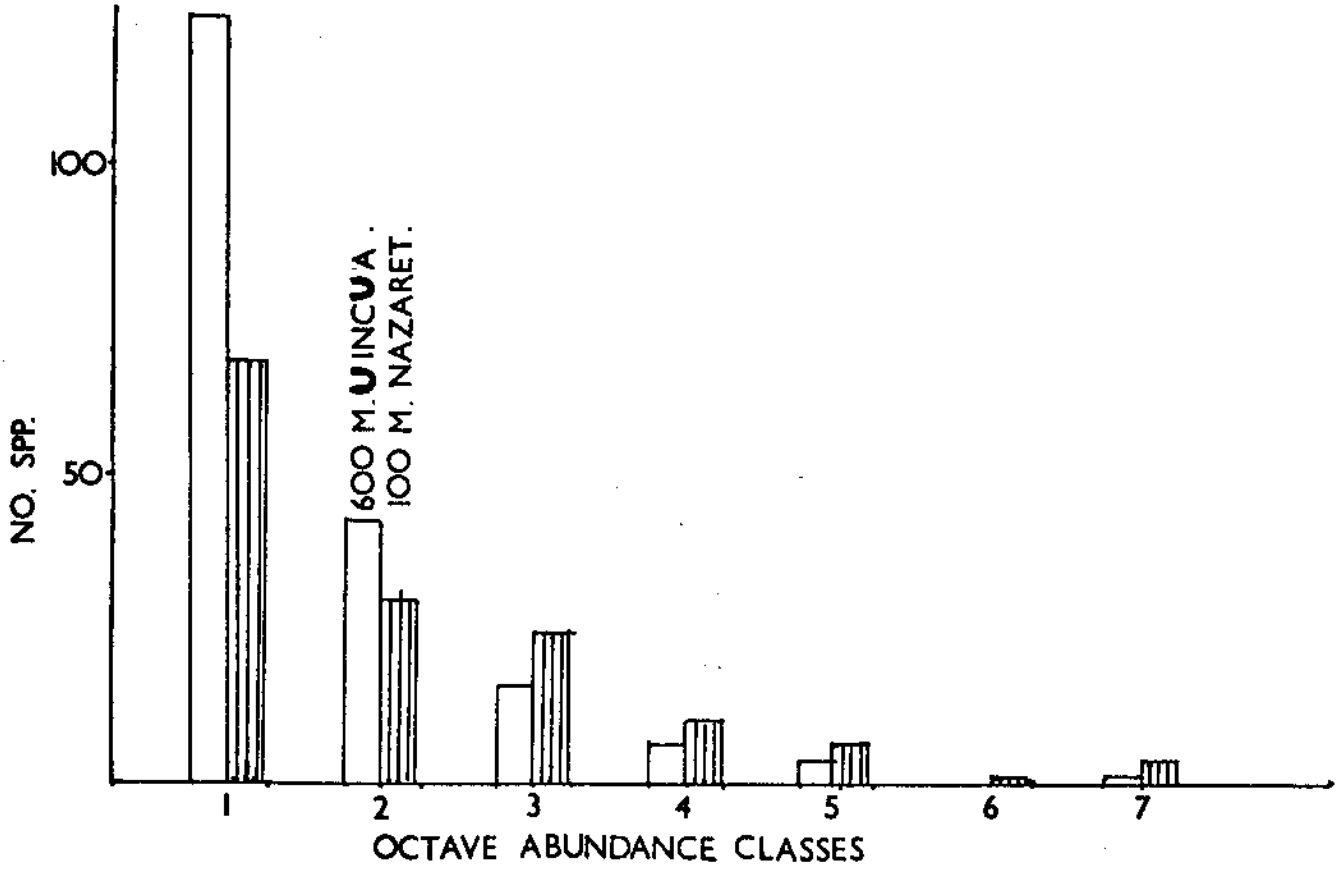

Figure 2: Species of nocturnal insects arranged to 'octave abundance classes'. See text for full details.

TABLE 1: Lepidoptera in order of abundance at different sites

(a) Uinca (600 m) (summed over three days)		(b) Nazaret (100 m) (summed over three days)	
Number of individuals per species (N)	Number of species with 'N' individuals	Number of individuals per species (N)	Number of species with 'N' individuals
1	45	1	23
2	17	2	6
3	8	3	4
4	4	4	8
5	3	5	3
6	1	6	2
7	1	8	3
10	1	9	1
11	1	10	1
15	1	11	1
16	1	19	1
73	1	23	1
		43	1
		91	1
		106	1
		124	1
272	84	566	58
H=5·0858 E=0·7955		H=3·9724 E=0·6784	

TABLE 2: All other insects arranged in order of abundance at different sites

(a) Uinca (600 m) (summed over three days)		(summed over three days) (b) Nazaret (100 m)	
Number of individuals per species (N)	Number of species with 'N' individuals	Number of individuals per species (N)	Number of species with 'N' individuals
1	78	1	45
2	10	2	13
3	7	3	6
4	3	4	2
5	2	5	6
6	1	6	1
7	1	7	2
8	1	8	1
9	1	12	1
10	1	14	2
19	1	19	1
27	1	22	1
		25	1
		31	1
227	107	292	83
H=5·9278 E=0·8883		H=5·3922 E=0·8457	

proportionally more rare species (Classes 1 and 2) were caught at Uincua than a Nazaret, but that more abundant species were commoner at Nazaret.

Shannon-Wiener indices of diversity (H) and equitability ($E=H/H_{max}$) were calculated for the samples, and are shown on the abundance tables. Within the groups, H and E were higher in every case at Uincua than at Nazaret.

Thus for night-flying insects, excluding social species and drosophilids, species diversity and both of its components, species richness and equitability, are higher at Uincua at 600 m than at Nazaret at 100 m.

Why a Greater Species Diversity in the Humid Forest? As we have estimates of species diversity from only two very different sampling sites, the analysis of the causes of the diversity gradient can proceed using non-parametric data. But the analysis suffers for the same reason; accurate correlations cannot be made with the various causal factors because of the lack of diversity points, and the lack of 'hard' data on causal factors.

A number of interdependent hypotheses have been put forward to explain diversity gradients (excellent reviews are Pianka, 1966; Krebs, 1972; Pianka, 1974). Parts of these hypotheses will be used in this discussion, but only in relation to the Serranía de Macuira. A full discussion of the relative merits of each hypothesis would be fruitless for this purpose and only key references are given (for more detailed bibliographies see Pianka, 1966; Krebs, 1972).

Causes of animal diversity gradients can be divided into abiotic factors, factors relating to plant production and factors due to animals.

Abiotic Influences on species diversity. Nazaret at 100 m receives more *insolation* than Uincua at 600 m, because of the near-permanent cloud bank above the higher parts of the mountains. *Windspeed* appeared higher to us at Uincua, and in some places the forest was reduced to a dense mat about 1 m tall because of it. This factor probably caused the low number of insects that was caught at 600 m. All this and the *lower temperature* of the humid forest would be expected to favour animal and plant production at Nazaret. However, the lower temperature at Uincua causes a *higher relative humidity* (Fig. 3), so that at night the saturation point is reached causing *precipitation.*

The dry forest is *less isolated* than the humid forest; there are a number of hills in Guajira which are clothed with dry forest, whereas the nearest humid forest is 200 km to the south-west. The dry forest takes up a *larger area* than the 20 km^2 of humid forest. Biogeographical theory leads us to expect more species on large islands close to regions of similar habitat, were these factors limiting (MacArthur and Wilson, 1967).

TABLE 3: Total aerial insect species arranged in order of abundance at different sites

(a) Uinca (600 m) (summed over three days)

Number of individuals per species (N)	Number of species with 'N' individuals		Octave Class
1	123	123	1
2	27	42	2
3	15		
4	7	16	3
5	5		
6	2		
7	2		
8	1	6	4
9	1		
10	2		
11	1		
15	1		
16	1	3	5
19	1		
27	1		
73	1	7	

Total 191 species

499 individuals

H=6·4731

$E=H/H_{max}$ =0·8542

(b) Nazaret (100 m) (summed over three days)

Number of individuals per species (N)	Number of species with 'N' individuals		Octave Class
1	68	68	1
2	19	29	2
3	10		
4	10	24	3
5	9		
6	3		
7	2		
8	4	10	4
9	1		
10	1		
11	1		
12	1		
14	2		
19	2	6	5
22	1		
23	1		
25	1		
31	1		
43	1	1	6
91	1	3	7
106	1		
124	1		

Total 141 species

858 individuals

H=5·3215

$E=H/H_{max}$ =0·7474

The hypothesis that a *longer evolutionary time period* leads to a greater species diversity can be applied here, although no glaciations or other climatic traumata are known to have taken place in either moist or dry forest zones. This hypothesis combined with the hypothesis of *climatic stability* may explain some of the observed differences in diversity between the forest types. If a climate is stable and not stressful, organisms can make use of available resources more easily. Thus production can be high, reproduction can occur all the year round, and hence evolution can proceed more rapidly.

The influence of primary production on species diversity. The lowered production of the dry forest when compared with the cloud forest is in part due to the absence of certain plant growth forms – notably epiphytes and herbs – and this lowers both *spatial* and *species diversity* of plants. *Production 'stability'* in the dry forest is also low because of the seasonality of plant growth. All these characteristics have been suggested in the literature to cause a depression of species diversity in animals.

The influence of animals on species diversity. A high production permits greater specialisation among higher trophic levels (MacArthur and Pianka, 1966; Pianka, 1974), and this permits a greater species diversity (MacArthur, 1965; Orians, 1969; Pianka, 1974). This would seem to be the case in the Serrania de Macuira.

Higher trophic levels may increase the species diversity of lower trophic levels by means of predation or cropping (Painka, 1966; Janzen, 1970). Thus animals may increase the diversity of plants, or predators may regulate prey which would otherwise outcompete less competitive species. At Uincua 21 spp (21 individuals) of Hymenoptera – excluding ants – were found, while at Nazaret only 10 spp (15 individuals) were caught.

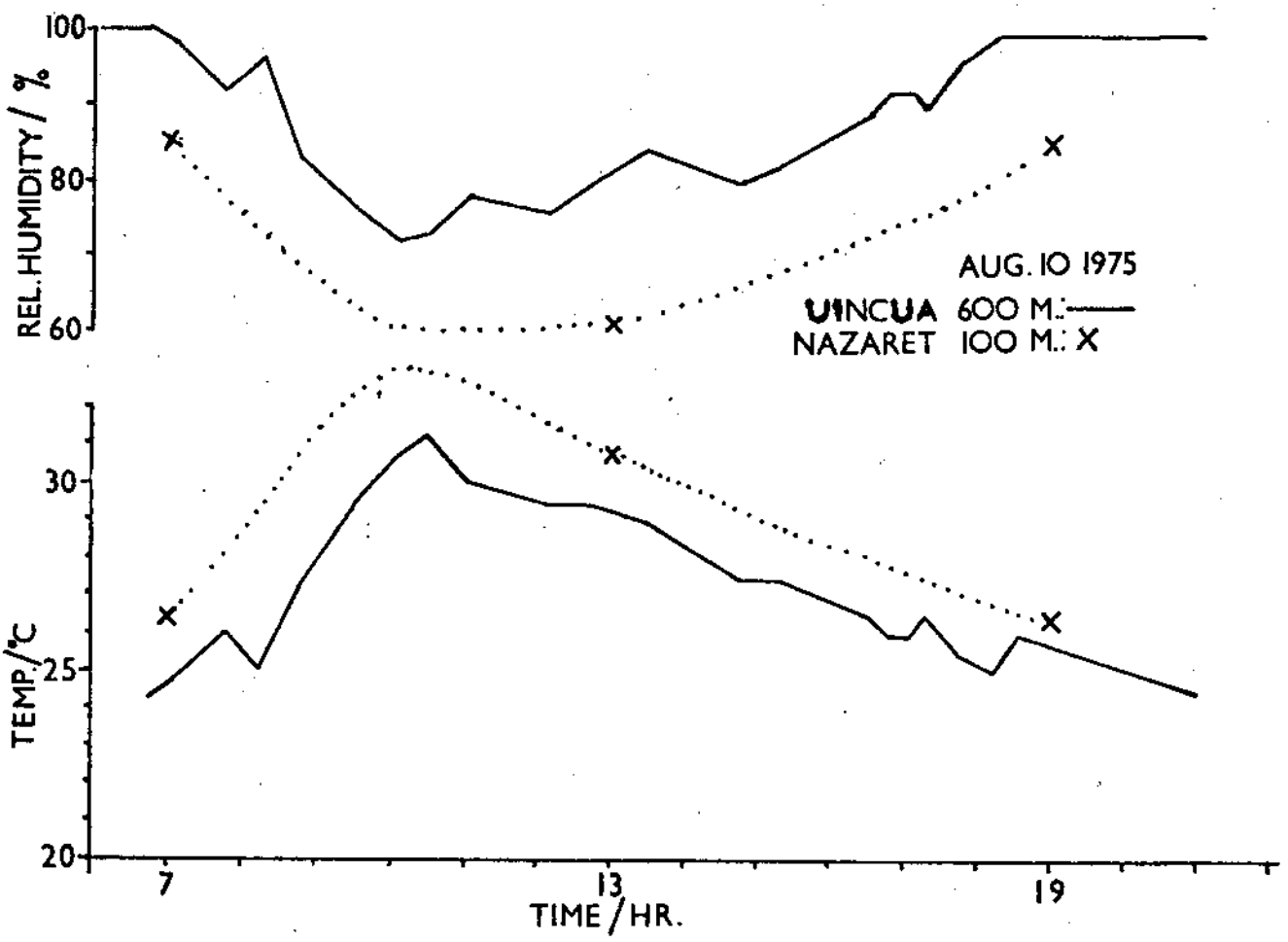

Figure 3: Diurnal variations of temperature and humidity in the Serranía de la Macuira. Solid lines connect actual measurements made at 600 m on 10th August while the dotted lines have been included merely to draw the eye between Nazaret weather data for that day. These differences, especially the nightly saturation of the air at 600 m determine the differences between the dry deciduous forest and the humid forest.

These Hymenoptera were mainly small parasitic forms. Ants showed a similar trend: 11 spp (51 individuals) of alates were caught at Uincua, while only 3 spp. (14 individuals were trapped at Nazaret. Thus there is some evidence for higher predation levels in the area of greater species diversity, but, as Paine points out, predation must themselves be partially controlled by primary production.

Competition for light and space may be important among plants in the dense humid forest, but it is quite probably less important among the insects of the humid forest on the Serranía due to *rarefaction* by wind (see above).

Conclusions. A causal chain can now be established for species diversity changes in the Serranía. Gradients in the abiotic environment can be related directly to species diversity gradients as follows: a more favourable climate permits a higher primary production, and in various ways this tends to cause a higher plant species diversity. Herbivorous insects, often specific feeders, are able to become more diverse, and thus the insect community as a whole can be more diverse.

2. *Insect Collections* (J.M.)

Many orders of insects were collected, and these are being identified at the British Museum (Natural History). A named set will be returned to the Instituto de Ciencias Naturales in Bagotá.

Butterflies

TYPE	LOCALITY
Morphidae (Morphos)	
Morpho peleides (Koll.)	Not similar to the Colombian sub-species; nearer to *M. hyacinthus*
	400–700 m. Semideciduous and humid zones
Danaidae (Milkweeds)	
Danaus plexippus (Linn.)	100 m. Dry forest
Papilionidae (Swallowtails)	
Battus polydamas (Linn.)	400 m. Secondary scrub

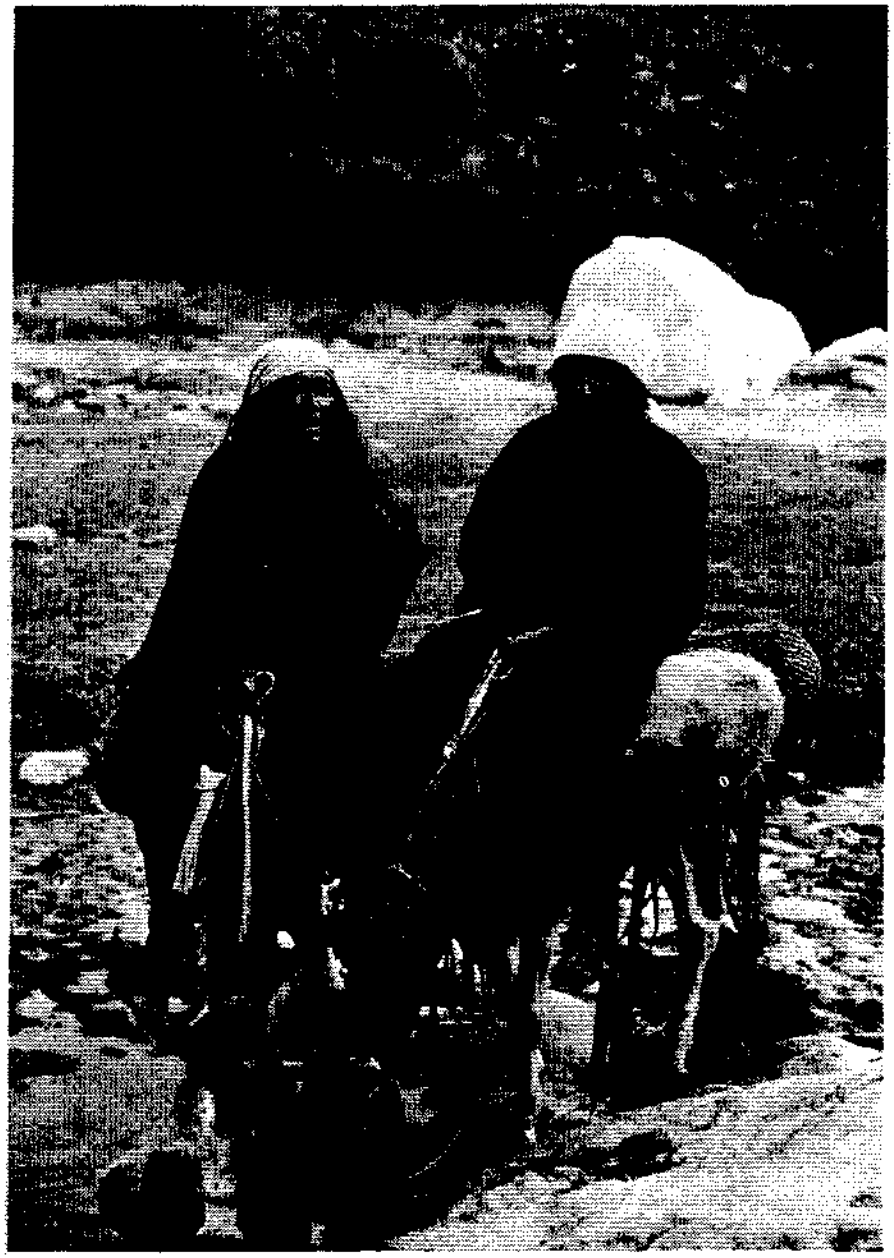

PLATE I
Indian women on the Arroyo Nazaret.

PLATE II
Dry forest at 200 m altitude.

PLATE III
Cloud forest at 700 m altitude.

Nymphalidae	
Myscelia leucocyana	250–350 m. Semideciduous woodland
Hamadryas februa (Hbn.)	300 m. Semideciduous woodland
Phyciodes leucodesma (Fldr.)	600 m. Humid forest
Anartia jatrophae (Johanss.)	150 m. Moist riverbed cultivated bank
Hypna rufescens (Bltr.)	100 m. Dry woodland
Agraulis (Dione) vanillae vanillae (Linn.)	300–600 m. Clearings
Heliconiidae	
Dryas julia (F.)	600 m. Clearings
Heliconius erato hydara (Linn.)	150–170 m. Riverside vegetation, moist forest
Ithomiidae	
Hypoleria andromica (Hew.)	600 m. Humid forest
Pieridae (Whites and Yellows)	
Phoebis sennae (Linn.)	100–600 m. Clearings
Itaballia pandosia pandosia (Hew.)	300–600 m. Semideciduous and humid zones
Itaballia demophile calydonia (Bdv.)	600 m. Humid forest
Ascia monuste (Linn.)	600 m. Humid forest
Euremarbele gratiosa (Hubn.)	100–600 m. Dry, semideciduous and humid zones
Satvridae (Browns)	
Pareuptychia metaleuca (Bsd.)	250 m. Riverside vegetation 600 m. Humid forest
Euptychia 'sp nov' (Venezuela, Panama)	600 m. Humid forest
Euptychia sp.	200–600 m. Dry deciduous and humid zones
Euptychia sp.	600 m. Humid forest
Lycaenidae (Blues)	
Polyniphes dumenlii (Godt.)	600–700 m. Humid forest clearings
unidentified	600 m.
unidentified	300 m.
unidentified	300–600 m.
unidentified	100–600 m.
Nemeobiidae	
Caliociasma lilina (Bltr.)	250–600 m. Semideciduous woodland
Lephelisca virginiensis ? (Holl.)	300 m. Stream bank
Nymphidium albina	600 m. Humid forest
Audre erostratus (Ww.)	100–300 m. Dry thorn scrub
Emesis sp.	300–600 m. Semideciduous and humid zones
Hesperiidae (Skippers)	
Heliopetes laviana (Hewitson)	200–300 m. Semideciduous forest
Corticea sp.	600–650 m. Humid forest
unidentified	100 m. Streamside vegetation
Panoquina silvicola (Herrich Schaffer)	100–600 m. Internado garden – humid
Heliopetes domicella (Erichson)	300 m. Scrub (most similar to subsp. *margarita* (Bell), only otherwise found on Margarita Is., Venezuela)
Chiomara asychis (Stoll.)	300–600 m. Clearings
Zopyrion sp.	300–600 m. Woodland (similar to *satyrina* (Felder), but apparently not in B.M. collection)
Bolla (?) *spp.*	600 m. Humid forest
Hylephila phylaeus phylaeus (Drury)	100 m. Internado garden
Timochares trifasciata (Hew.) subsp. nov.?	300 m. Scrub
unidentified	600 m. Humid forest
Urbanus dorantes dorantes (Stoll.)	600 m. Clearings in humid forest
Urbanus proteus proteus (Linn.)	100 m. Garden at Internado
Urbanus carmelita trebia (Maschler)	600 m. Humid forest
Codractus carlos arguta (Evans)	150–600 m. Riverside and humid forest
Chioides catillus catillus (Cramer)	600 m. Humid forest
Talides sp.	600 m. Humid forest. Not like any spp. in B.M. collection. Attracted to light at dusk
Autochton zarex (Hubner)	600 m. Humid forest
Oxynthes corusca (Herrich Schaffer)	600 m. Humid forest

3. *Tank Bromeliad faunal community analysis* (C.P.K.) One hundred and ten specimens of *Guzmania cylindrica* were dissected and the 15,327 animals recorded therein were scored as belonging to either the leaves and leaf axils, or the roots and dead leaves of each plant. Specimens were sampled in 10 replicates of 10 plants each at five altitudes on the Huararech massif, with two different levels of exposure to wind. These 10 replicates were composed of individual plants one metre or less from ground level; an additional replicate of 10 plants at canopy height (3 m approx.) was included. Thirty-eight categories of animals were recorded and await identification. A Spearman Rank Correlation matrix for these has been constructed using a programme supplied by Charlie Gibson. The results are as follows:

Faunal distribution patterns indicate that the Macuira bromeliad tank communities are overwhelmingly decomposer-based. Community structure and population density is decisively influenced by quantity and quality of input of organic material, usually in the form of dead leaves. High bromeliad density on the more exposed peaks of the Huararech massif provides alternative accommodation for at least two stream-dwelling animal species, particularly where the input of organic material is not unduly great. Further investigation of the Serranía's extensive system of isolated streams is essential; faunal comparisons between the streams and the bromeliad tanks, between the Macuira streams themselves, and between the Macuira streams and those of other Colombian and Venezuelan mountains would be fascinating. An Oxford expedition *must* make use of this opportuniy before 1980.

Joint publication with Charlie Gibson and Richard Robins is planned, since OGRE has approximately doubled the number of tank bromeliad faunal community data gathered by recent Oxford expeditions to Colombia.

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Income	£	**Expenditure**	£
The University of Oxford	25.00	Travel:	
Alexander Allan Paton Trust	350.00	London–Brussels–London x 3	60.92
Anonymous donor	650.00	Brussels–Bogotá–Brussels x 3	963.08
Mrs B. Ashley	5.00	Bogotá–Nazaret–Bogotá x 5	219.40
Balliol College, Oxford	50.00	Equipment (including film)	165.89
R. Dickins Esq.	15.00	Provisions	285.80
Drapers' Guild	150.00	Insurance at £25 each plus £35 for equipment	110.00
Oxford Society	40.00	Gifts	53.69
Poulton Fund	100.00	Accommodation	29.22
Albert Reckitt Trust	200.00	Administration	85.95
Slater Foundation	100.00	Report publication	196.05
Wadham College, Oxford	35.00		
Personal contributions	450.00		
Total	£2170.00	Total	£2170.00