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ECOLOGY OF LEISHMANIASIS IN THE SOUTH OF FRANCE
20. Dispersal of *Phlebotomus ariasi* Tonnoir, 1921 as a factor in the spread of visceral leishmaniasis in the Cévennes*

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SUMMARY. The dispersal of *Phlebotomus ariasi* was studied in mark-release-recapture experiments in the summer of 1980 in a valley on the north-eastern slopes of the Oiselette range in the Cévennes mountains, in the commune of Roquedur, Gard, 50 km north of Montpellier, France. More than 5,000 specimens of *P. ariasi* were marked with fluorescent powders and released in 9 batches at 3 different places. Seven batches were engorged females and two were unengorged females and males. From 1-29 days after release, 497 marked sandflies (approximately 9 %) were recaptured by active searches with UV lamps or in 58 CDC light traps set up in groups of 4 or 5 at 12 recapture stations.

Females released engorged generally remained within 250 m of the release point for the first eight days while the bloodmeal was being digested after which there was a tendency to disperse to distances > 350 m presumably in a search for oviposition sites or another bloodmeal. The furthest distance to which a female released engorged was shown to move was 925 m ; it was caught 12 days after release. Some of the females released unfed quickly moved away from release points, sometimes to distances of 1,000 m or more. One of these was caught 68.5 hrs after release at a station 2,200 m from the release point. Male sandflies tended to stay near the point of release and were not recaptured at distances > 600 m.

There was no evidence that the movement of the sandflies was assisted by wind. Observations on the dispersal of female sandflies confirm that leishmaniasis can be more widely spread than generally assumed by the movements of the vector.

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Écologie des leishmanioses dans le Sud de la France. 20. Dispersion de *Phlebotomus ariasi* Tonnoir, 1921 considérée comme l'un des facteurs de diffusion de la leishmaniose en Cévennes

RÉSUMÉ. Dans le cadre d'une étude de la dispersion de *Phlebotomus ariasi* en Cévennes, des opérations de capture-recapture ont été réalisées durant l'été 1980, sur les versants nord-est du massif de l'Oiselette (commune de Roquedur, Gard) à 50 km au nord de Montpellier, France. Plus de 5 000 exemplaires de *P. ariasi* ont été marqués à l'aide de poudres fluorescentes puis relachés, en neuf lots, dans trois lieux différents. Sept lots étaient composés de femelles gorgées et deux de femelles non gorgées et de mâles. Durant les 20 jours qui ont suivi le lâcher, 497 phlébotomes marqués (approximativement 9 %) ont été recapturés, soit à l'aide de lampes UV, soit en utilisant 58 pièges CDC placés par groupes de 4 ou 5 dans 12 stations.

Pendant les huit premiers jours les femelles gorgées ont généralement tendance à demeurer dans une zone ne dépassant pas 250 m autour du point de lâcher, jusqu'à ce qu'elles aient digéré leur repas sanguin. Ensuite, elles franchissent aisément des distances supérieures à 350 m, probablement pour trouver un gîte de ponte ou effectuer un autre repas sanguin. Une des femelles gorgées, recapturée 12 jours après le lâcher, a même été retrouvée à 925 m de son point de départ. Quelques femelles relâchées non gorgées se sont éloignées rapidement. Certaines ont franchi plus de 1 000 m. L'une d'entre elles a été recapturée après 68 h 5 dans une des stations situées à 2 200 m du point de lâcher. La dispersion des mâles reste faible et toujours inférieure à 600 m. Rien ne permet de préciser le rôle du vent dans la portée de vol du Phlébotome.

L'ensemble de ces observations confirme l'importance des phénomènes de déplacement vectoriel dans le processus de dispersion du parasite.

In preliminary observations on the dispersal of *Phlebotomus ariasi* in a valley in the Cévennes, southern France, marked female flies were recovered up to 750 m from the place of release (Rioux *et al.*, 1979). A few of the recaptured flies were found to have moved with blood in the midgut or while gravid. This sandfly is a proven vector of *Leishmania infantum* Nicolle, 1908 (see review by Killick-Kendrick & Rioux, 1981) and, from these findings, it was concluded that the movement of *P. ariasi* was perhaps a factor of greater importance than previously supposed in the spread of visceral leishmaniasis in the Cévennes focus.

In the summer of 1980, we carried out similar experiments in the same place to find out if the distance of dispersal of female flies was commonly greater than 750 m, to compare the dispersal of males and females and to examine the effect of wind on dispersal.

These studies were integrated with observations on the gonotrophic cycle and physiological age of female *P. ariasi* (Wilkes *et al.*, to be published in 1985), the host preferences of *P. ariasi* (Guy *et al.*, 1984) and the development of *L. infantum* in *P. ariasi* in natural conditions. In the present paper, accounts are given of the locality, the methods which were common to all the projects undertaken in 1980 and of the results of the observations on dispersal.

Materials and Methods

Time and place

The field experiments were undertaken from July 13 to August 25, 1980, a period which coincides with the peak population of *P. ariasi* in the Cévennes (Rioux *et al.*, 1969).

All releases and most captures and recaptures were done in a small valley in the Cévennes in the commune of Roquedur in the Department of Gard, about 50 km north of Montpellier *(fig. 1)*. The valley is situated on the northeastern slopes of the Oiselette range and is ringed by hills varying in altitude from 317-664 m above sea level. The catchment area formed by the valley is 2.2 km in length by 1 km at its widest point; it is drained by the Valat des Fabrègues, a tributary of the River Hérault.

There were only 26 permanent inhabitants in the work area but this number is more than doubled in the summer by holiday makers. Many of the steep slopes of the valley are terraced from previous farming activities *(fig. 2)* at the time the Cévennes were more heavily populated than at present. These abandoned terraces are covered in grass, weeds and brambles. The area is heavily wooded, the dominant trees being the Spanish chesnut *(Castanea vulgaris)* interspersed with the green oak *(Quercus ilex)*. There are also a few white oaks. *(Q. pubescens)*, some recently planted stands of cedars *(Cedrus atlantica)* and Douglas firs *(Pseudotsuga menziesii)*, and a few cherry, peach and pear orchards. A road (D 291) runs through the valley along the slopes of the northern side. An aerial photograph of the area is published in the preliminary report on the dispersal of *P. ariasi* (Rioux *et al.*, 1979).

Stations in the field

A field laboratory equipped for the handling, dissection and examination of recaptured sandflies was established in an abandoned farmhouse at Laumède *(fig. 1)*.

Meteorological stations were set up on a terrace 65 m east of Mas de Langlade ("Langlade East") and on another terrace by the side of the D 291 road below Laumède ("Laumède-le-Bas") *(fig. 1 and 2)*. Records were kept of temperature, relative humidity and wind speed and direction. Marked sandflies were released at these two places and also in cellars beneath the field laboratory at Laumède.

The positions of the recapture stations and release points are given in *figures 1 and 2*. Brief descriptions of the stations are given below. Guy *et al.* (1984) give a list of the hosts available to the fly at each station and map references.

1. *La Rabasse;* altitude 170 m; east end of valley at lowest point; water mill by stream; no other habitations nearby; occasionally inhabited.

2. *La Salle;* altitude 320 m; north east side of valley; inhabited hamlet.

3. *Mas d'Arboux;* altitude 350 m; north east side of valley; inhabited hamlet *(fig. 2)*.

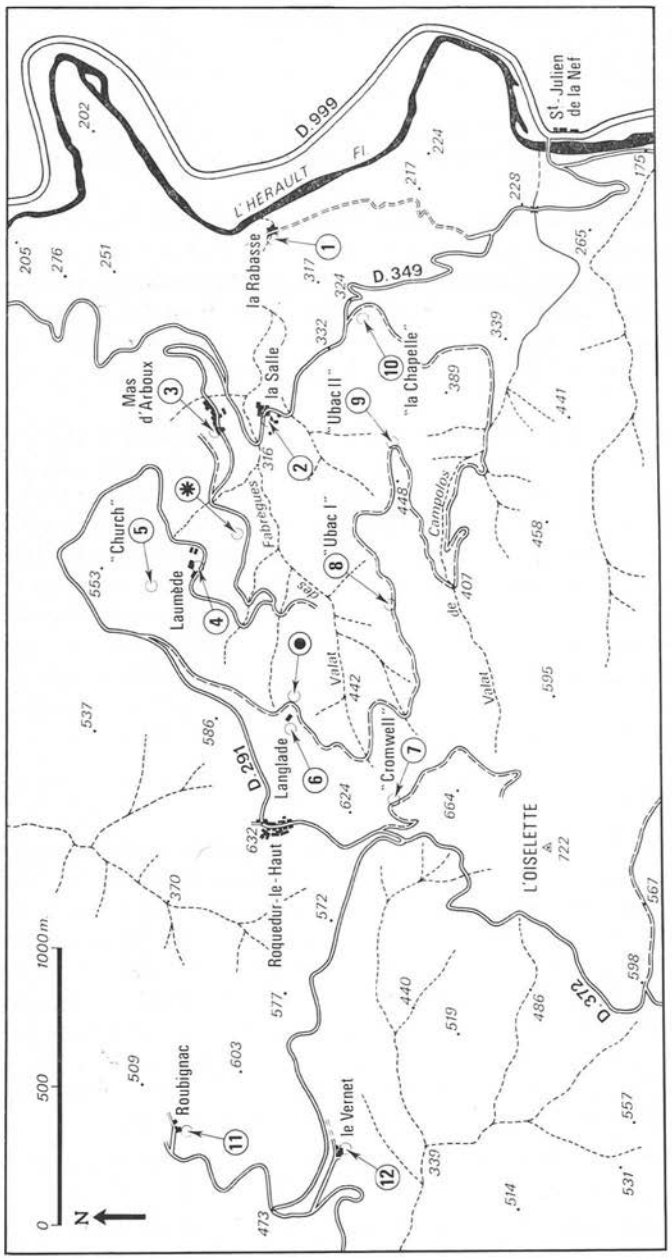

FIG. 1. — Release and recapture stations ; encircled numbers show recapture stations ; * shows the position of the meteorological station and release point "Laumède-le-Bas" ; • shows the position of meteorological station and release point "Langlade East" ; other releases were made at Laumède (4) ; numbers in italics are altitudes in metres above sea level.

FIG. 2. — Showing terrain on the north side of the valley in the study area including stations La Salle (2); Mas d'Arboux (3); "Laumède-le-Bas" release point and meteorological station (M2); Laumède release point and recapture station (4); Church (5); Mas de Langlade (6); "Langlade East" release point and meteorological station (M1); and "Cromwell" (7) (on the south side of the valley).

4. *Laumède;* altitude 450 m; north side of valley; inhabited hamlet *(fig. 2)*.

5. *"Church";* altitude 510 m; north west part of valley; station was on a terrace about 100 east of an abandoned church and ruined buildings on an uninhabited site *(fig. 2)*.

6. *Mas de Langlade;* altitude 540 m; isolated old house; occasionally inhabited; situated on a bluff projecting into the valley at the top, western end *(fig. 2)*.

7. *"Cromwell";* altitude 600 m; at the top of the valley at the western end; small isolated ruined house.

8. *"Ubac I";* altitude 470 m; by the southern side of a motorable track on the southern face of the valley.

9. *"Ubac II";* altitude 440 m; east of "Ubac I" on the northern side of the same track; firebreak from station in a northerly direction towards the bottom of the valley.

10. *"La Chapelle";* altitude 320 m; near a church by inhabited houses in the south eastern part of the valley.

11. *Roubignac;* altitude 520 m; a large inhabited farm with outbuildings and livestock; 2 km west of main work area.

12. *Le Vernet;* altitude 430 m; large isolated house; occasionally inhabited; 2 km west of main work area.

Distances between release and recapture points were calculated from map 2741 ouest Le Vigan of l'Institut géographique national with a scale of 1 : 25,000.

Mark-release-recapture techniques

Sandflies to be marked were caught with sucking tubes from resting places beginning at sunset and continuing until the early hours of the following day. Most were taken from walls at Laumède, Mas d'Arboux, La Salle or Roubignac but some were caught as they came to bite workers engaged in active searches. The pattern of the sucking tubes used was one described by Rioux *et al.* (1969) (fig. 20A, p. 34). This type causes little or no damage to sandflies which can be kept in the tubes for many hours without loss.

Flies to be released *engorged* were left for the remainder of the night in a mosquito net, in a cellar, with a tranquilized dog. On the following day, the freshly engorged females were caught individually in a tube, counted and transfered to a wood and plastic dusting box which is described and figured by Rioux *et al.* (1979). After dark on the evening following capture, the boxed females were taken to a release point and fluorescent powder was puffed into the box with a Pasteur pipette. The marked flies were left to settle for 15-20 mins and the box was then opened to allow them to escape. The open box was left at the release point for 24 hrs so that no marked flies could accidentally be taken into a vehicle and carried to another part of the valley. Flies to be released *unengorged* were similarly marked, but were released on the night of capture.

Six different coloured fluorescent powders were used *(table I)*, each with a separate box to avoid contamination of one colour by another. The powders were chosen from a range of Flame Fluorescent Pigments and were coded Magenta D (brick red under UV), Yellow L (yellow green under UV), Orange M (tangerine under UV), Orange L (lemon under UV), Red L (flame red under UV) and Blue L (blue under UV) (see Killick-Kendrick *et al.*, 1978 ; Rioux *et al.*, 1979). Three other colours (pink, silver and metallic green) were made by empirically mixing powders and examining the mixtures under UV light to ensure they were distinguishable.

Recaptures were made in two ways. Except for stations Roubignac and Le Vernet, groups of 5 CDC light traps were run nightly at each station from the night of the first release (20 July, 1980) until the end of the field work (25 August, 1980). At each of the other two stations, 4 traps were run nightly from 26 July, 1980 (after a marked fly had unexpectedly been found at Roubignac). The cages were taken off the traps each morning and flies were collected with aspirators and narcotized with CO_2. They were then screened under UV light and marked flies were removed for examination.

The second method of recapture was by active searches by teams of 2-5 workers with portable ultra violet lamps at the recapture stations 1-4 hours after sunset. Marked flies were caught, dissected and identified either on the night of capture or on the following day.

Identification of recaptured sandflies

After recapture, male flies were identified by their external genitalia. Female flies were identified by the characters of the spermathecae in freshly dissected spe-

TABLE I. — Numbers, places and days of releases and recaptures of 9 batches of marked *P. ariasi*, composition of batches and colours of marking powders.

Numbers of batches	Colours of marks under UV light	Composition of batches	Places of release	Nights of release(*)	Days of recapture after release	Numbers marked and released	Numbers and % recaptured	
1	yellow-green	engorged females	"Laumède-le-Bas"	20.7.80	7-22	500	31	*6.2*
2	brick red	engorged females	"Laumède-le-Bas"	22.7.80	1-21	307	17*	*5.5*
3	blue	unfed females (plus very few males)	"Laumède-le-Bas"	22.7.80	1-29	1,800+	151*	*8.4+*
4	flame red	engorged females	"Laumède-le-Bas"	24.7.80	2-20	350	45	*12.9*
5	tangerine	engorged females	cellars of ruined house, Laumède	26.7.80	1-16	250	53	*21.2*
6	lemon	unfed females males	"Langlade-East"	27.7.80	0-17 1-21	1,180+ 420+	61 29	*5.2+* *6.9+*
7	pink	engorged females	cellars of ruined house, Laumède	31.7.80	2-12	210	23	*10.7*
8	silver	engorged females	cellars of ruined house, Laumède	1.8.80	0-18	354	57*	*16.1*
9	metallic green	engorged females	cellars of ruined house, Laumède	7.8.80	0-17	200	27	*13.5*
				females marked and released engorged :		2,171	256	*11.9*
				females marked and released unengorged :		2,980+	212	*7.1+*
				males marked and released :		420+	29	*6.9+*
				total number of flies marked and released :		5,571+	497	*8.9+*

(*) Date of day preceding night of relase ; no account taken of differences between releases before and after midnight.

* Including one female specimen of *P. perniciosus*. + Estimated * Plus 3 males.

cimens examined with phase contrast illumination. Females of the four species of sandflies in the work area [*P. ariasi* ; *P. perniciosus* Newstead, 1911 ; *P. mascittii* Grassi, 1908 and *Sergentomyia minuta* (Rondani, 1843)] are separable by this character alone. All of 32 recaptured male flies were *P. ariasi*. Of 465 recaptured females, 456 were *P. ariasi*, 2 were *P. perniciosus* and 7 were not identified because their spermathecae were lost in dissection.

Results

Of the estimated 5,571 marked sandflies released in 9 batches, 497 (8.9 %) were recaptured 0-29 days after release. The proportions of flies of each batch which were recaptured ranged from 5.5 to 21.2 % *(table I)*.

Fed and unfed females released at « Laumède-le-Bas »

Three of the first four batches of marked sandflies (nos 1, 2 and 4) released at "Laumède-le-Bas" were engorged females released on the nights of 20 July (yellow green), 22 July (brick red) and 25 July, 1980 (flame red). The fourth batch (no. 3) was composed of unfed females, with very few males, released on the night of 22 July, 1980 (blue). For purposes of a comparison of the dispersal of female flies released engorged and unengorged, the results of the batches of flies marked and released after engorgement (nos 1, 2 and 4) are combined. The number of engorged females released in batch 1 was 500, in batch 2, 307 and in batch 4, 350 making a total of 1,107. Of these, 93* (8.0 %) were recaptured 1-22 nights after release.

The number of unfed females of batch 3 released unengorged on 22 July, 1980, was estimated at 1,800 of which 151 (8.4 %) were recaptured 1-22 nights after release.

The numbers of recaptured females of both fed and unfed groups caught at each station are shown in *figures 3 and 4*. Almost all recaptured females of both groups were found to have dispersed along the north side of the valley where the release point was situated *(fig. 2)* ; 91 of 93 (97.8 %) flies recaptured from the batches released engorged, and 148 of 151 (98.0 %) of the females recaptured from the batch which was released unfed had not crossed the valley.

About two thirds of the recaptured females of both groups were caught at the nearest station (Laumède) which lies 250 m uphill from the release point *(fig. 3 and 4)*. The numbers of recaptured females taken at this station were 56 (60.2 %) of 93 recaptured flies of the batches released engorged, and 105 (69.5 %) of 151 recaptured flies of the batch released unfed. Comparatively few marked flies were recaptured at station "Church", which is further uphill than Laumède *(fig. 2)* and 387 m from the release point [6 (6.5 %) of 93 and 7 (4.6 %) of 151].

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* One of these females was a specimen of *P. perniciosus* (no 240) which was caught by hand 9 days after release at Mas d'Arboux, 380 m from the release point ; it had laid eggs once, its ovaries were stage 2 and it had not taken a second bloodmeal.

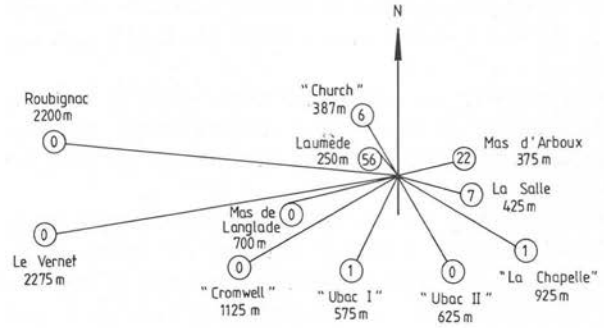

FIG. 3. — Numbers of recaptured *P. ariasi* at each recapture station out of 1,107 marked females released *engorged* at "Laumède-le-Bas" (batches 1, 2 and 4) on 20, 22 and 24th July, 1980 ; the total number of females recaptured was 93 (8.0 %).

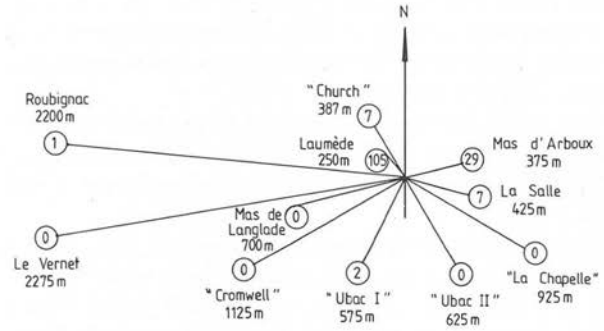

FIG. 4. — Numbers of recaptured *P. ariasi* at each recapture station out of an estimated 1,800 marked females released *unengorged* at "Laumède-le-Bas" (batch 3) on 22nd July, 1980 ; the total number of females recaptured was 151 (estimated 8.4 %).

In contrast, relatively high proportions of both groups were caught at station Mas d'Arboux, 375 m downhill from the point of release [22 (23.7 %) of 93 and 29 (19.2 %) of 151] *(fig. 3 and 4)*. Of the 93 recaptured females of the batches released engorged, one (no. 398) crossed the valley and was taken 12 nights after release at station "Ubac I", 575 m in a direct line from the release point. On dissection, it was found to be a primipar with ovaries in stage 2. Another female of this group (no. 397) was recaptured, also 12 nights after release, at station "La Chapelle" towards the bottom of the valley 925 m in a direct line from the point of release. At the time it was recovered, this female was also a primipar with ovaries at stage 2. This was the furthest distance at which a fly released engorged was recaptured.

Of the 151 recaptured females of the batch released unfed, two crossed the valley and were caught at "Ubac I" (575 m from the release point). One (no. 399) was a primipar with stage 2 ovaries recaptured 13 nights after release. The other (no. 438) was a bipar with almost mature eggs (stage 4/5) caught on the 16th night ; sometime between release and recapture it had fed on an infected animal and was found to have a heavy infection of promastigotes in the midgut but no parasites in the head (an infection judged to be of about 14 days duration suggesting that the fly became infected 2 days after release). A third female of this batch (no. 92) was recaptured

68.5 hrs after release at station Roubignac, 2,200 m in a direct line from the point of release. When dissected, this fly was found to have ovaries in stage 2 and was nulliparous and still unengorged.

The numbers of females recaptured at stations at distances > 390 m from the release point formed similar proportions of the total numbers of both groups recovered [15 (16.1 %) of 93 recaptured females of the group released engorged and 17 (11.3 %) of 151 recaptured females of the other group].

The times at which females released at "Laumède-le-Bas" were recaptured at each station are shown in *table II* (released engorged) and *table III* (released unengorged). Of the 93 recaptured females of the group released engorged, 62 (66.6 %) were caught 8-11 nights after release. *P. ariasi* is gonotrophically concordant, and the time from engorgement to oviposition of the marked flies is known to be 6-7 days (Wilkes *et al.*, to be published in 1985). The peak time of recapture was after the flies had oviposited and were, presumably, actively seeking a second bloodmeal. Such appetitive activity would be expected to increase the chances of the flies being caught in light traps or in active searches with UV lamps.

This suggestion is supported by the earlier peak times of recapture of the flies marked and released unfed *(table III)*. In this group, 103 (68.2 %) of the 151 recaptured females were caught 2-6 nights after release when it is presumed they would have been searching for a bloodmeal.

Among the females which were marked and released unengorged, there were a few males three of which were recaptured. One (no. 522) is of special interest because of its longevity. It was caught in a light trap at the station nearest to the release point (Laumède, 250 m) 29 nights after release. The other two were caught by hand at Laumède on the fourth night (no. 145) and at Mas d'Arboux (375 m from the release point) on the eleventh night (no. 342).

Fed females released in farm cellars at Laumède

Four batches of engorged flies (nos 5, 7, 8 and 9) were released in the cellars of a ruined house at Laumède on the nights of 26 July (250, tangerine), 31 July (210, pink), 1st August (354, silver) and 7 August, 1980 (200, metallic green). The recapture rates were 21.2 % on nights 1-16 after release (batch 5), 10.7 % on nights 2-12 (batch 7), 16.1 % on nights 0-18 (batch 8) and 13.5 % on nights 1-17 (batch 9). The total number of released females was 1,620 of which 160* (9.9 %) were recaptured 0-18 days after release *(table I)*.

Recaptures of flies in these batches were mainly near the point of release [137 (85 %) of 160]. The remaining 23 were caught at nearby stations on the same side of the valley as the place of release (north) [10 (6.3) at "Church", 9 (5.6 %) at Mas d'Arboux and 4 (2.5 %) at La Salle].

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* One of these females was a specimen of *P. perniciosus* (no 402) which was caught in a trap at the release point 4 days after release ; it had no blood in the gut, was nulliparous and contained fully developed eggs (stage 5).

TABLE II. — Days and places of recapture of 93 marked female sandflies *(P. ariasi)* out of 1,107 released *engorged* at "Laumède-le-Bas" on 20, 22 and 24th July, 1980 (batches 1, 2 and 4).

Days after release	Collection stations and distances from release point ("Laumède-le-Bas")						Totals and % of all recaptures	
	Laumède 250 m	Mas d'Arboux 375 m	"Church" 387 m	La Salle 425 m	"Ubac I" 575 m	La Chapelle 925 m		
1	.	.	.	.	.	.	.	.
2	2	.	.	.	.	.	2	*2.2*
3	4	.	.	.	.	.	4	*4.3*
4	.	.	.	.	.	.	.	.
5	1	1	.	.	.	.	2	*2.2*
6	.	.	.	.	.	.	.	.
7	7	2	.	.	.	.	9	*9.7*
8	14	7	3	2	.	.	26	*28.0*
9	5	3*	.	3	.	.	11	*11.9*
10	5	4	2	1	.	.	12	*12.9*
11	11	1	.	1	.	.	13	*14.0*
12	4	1	.	.	1	1	7	*7.5*
13	.	1	.	.	.	.	1	*1.1*
14	.	.	.	.	.	.	.	.
15	.	.	.	.	.	.	.	.
16	.	1	.	.	.	.	1	*1.1*
17	1	1	.	.	.	.	2	*2.2*
18	.	.	.	.	.	.	.	.
19	.	.	.	.	.	.	.	.
20	1	.	.	.	.	.	1	*1.1*
21	.	.	1	.	.	.	1	*1.1*
22	1	.	.	.	.	.	1	*1.1*
totals	56	22	6	7	1	1	93	
% of recaptures	*60.2*	*23.7*	*6.5*	*7.5*	*1.1*	*1.1*		

* One of these flies was a female *P. perniciosus* which was a primipar with stage 2 ovaries.

TABLE III. — Days and places of recapture of 151 marked female sandflies *(P. ariasi)* out of an estimated 1,800 released *unengorged* at "Lauméde-le-Bas" on 22nd July, 1980 (batch 3).

Days after release	Collection stations and distances from release point ("Laumède-le-Bas")						Totals and % of all recaptures	
	Laumède 250 m	Mas d'Arboux 375 m	"Church" 387 m	La Salle 425 m	"Ubac I" 575 m	Roubignac 2,200 m		
1	2	2	.	.	.	.	4	*2.7*
2	13	6	.	.	.	.	19	*12.6*
3	26	8	.	4	.	1	39	*25.8*
4	8	.	.	.	.	.	8	*5.3*
5	17	1	.	1	.	.	19	*12.6*
6	15	.	3	.	.	.	18	*11.9*
7	1	1	.	.	.	.	2	*1.3*
8	4	3	1	.	.	.	8	*5.3*
9	12	1	.	.	.	.	13	*8.6*
10	7	3	.	.	.	.	10	*6.6*
11	.	1	.	1	.	.	2	*1.3*
12	.	1	2	1	.	.	4	*2.7*
13	.	1	.	.	1	.	2	*1.3*
14	.	.	.	.	.	.	.	.
15	.	.	.	.	.	.	.	.
16	.	.	.	.	1	.	1	*0.7*
17	.	.	.	.	.	.	.	.
18	.	1	.	.	.	.	1	*0.7*
19	.	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.
22	.	.	1	.	.	.	1	*0.7*
Totals	105	29	7	7	2	1	151	
% of recaptures	*69.5*	*19.2*	*4.6*	*4.6*	*1.3*	*0.7*		

The short distances of dispersal compared to females released at "Laumède-le-Bas" is explained, firstly, by the suitability of Laumède as a habitat for *P. ariasi*; this hamlet lies 450 m above sea level on the slope of a hillside in a protected position, a typical place where high densities of *P. ariasi* are to be expected (Rioux *et al.*, 1980). Secondly, having oviposited, the marked females had opportunities easily to find another bloodmeal from several dogs and members of the team who were living in a house only 50 m from the release point. Thirdly, for much of the first half of August the weather was windy and thundery, conditions which do not favour the activity of sandflies.

Unfed females and males released at "Langlade East"

A large batch of unfed sandflies was caught, marked and then released at station "Langlade East" on the night of 27 July, 1980 (lemon). This release point lies on a promontory projecting into the top, western end of the valley in a position which permits easy access by sandflies to both sides *(fig. 2)*.

The total number of sandflies was estimated at 1,600. From the results of a dissection of a sample of 49, the rough composition of the batch was calculated as 1,180 (73.5 %) females and 420 (26.5 %) males. Of 36 females dissected, 27 were nullipars, 8 were primipars and 1 was a bipar. Of the estimated 1,180 females marked and released (unengorged), 61 (5.2 %) were recaptured 0-17 nights after release; of the estimated 420 males in the batch, 29 (6.9 %) were recaptured 1-21 nights after, release *(table IV)*. In the total of 80 recaptured flies of both sexes, the ratio of females to males was a little lower (2.1:1) than the ratio estimated from the control dissections (2.8:1).

Of the 61 recaptured females, 19 (31.2 %) were caught at the station only 65 m from the point of release (Mas de Langlade), 33 (54 %) on the north side of the valley and 8 (13.1 %) on the south side *(fig. 5)*. The comparatively high number (15, 24.6 %) recaptured at Laumède (600 m from release) may, in part, have been due to the optimal altitude and sheltered position of this station (Rioux *et al.*, 1980). Unexpectedly high numbers (12, 19.7 %) of females were caught at stations > 1 km from the release point. The furthest distance at which a female of this group was recaptured was at Roubignac, a farm situated in a neighbouring valley 1,575 m in a straight line from "Langlade East". This fly (no. 411) was caught in a light trap

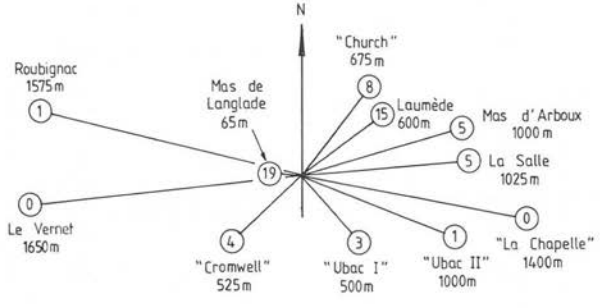

FIG. 5. — Numbers of recaptured *P. ariasi* at each recapture station out of an estimated 1,180 marked females released *unengorged* at "Langlade-East" (batch 6) on 27th July, 1980; the total number of females recaptured was 61 (estimated 5.2 %).

TABLE IV. — Days and places of recapture of 29 marked male sandflies and 61 marked female sandflies *(P. ariasi)* out of an estimated 1,600 released *unengorged* at "Langlade East" on 27th July, 1980 (batch 6).

Days after release	Collection stations and distances from release point ("Langlade East")																		Totals and % of all recaptures of each sex			
	Mas de Langlade 65 m		"Ubac 1" 500 m		"Cromwell" 525 m		Laumède 600 m		"Church" 675 m		"Ubac II" 1,000 m		Mas d'Arboux 1,000 m		La Salle 1,025 m		Roubignac 1,575 m		♀		♂	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂				
0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	*1.6*	1	.
1	8	.	2	.	.	1	.	.	3	.	.	.	.	.	.	.	.	.	13	*21.3*	1	*3.5*
2	2	.	.	.	1	.	3	.	.	.	.	.	1	.	3	.	.	.	10	*16.4*	.	.
3	.	1	.	.	.		1	1	2	.	.	.	1	.	.	.	.	.	4	*6.6*	2	*6.9*
4	2	1	.	.	.	.	4	.	1	.	.	.	1	.	1	.	.	.	9	*14.8*	1	*3.5*
5	.	7	1	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	4	*6.6*	7	*24.1*
6	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	*1.6*	.	.
7	.	1	.	.	.	.	1	.	.	.	.	.	1	.	1	.	.	.	3	*4.9*	1	*3.5*
8	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	*1.6*	2	*6.9*
9	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	*3.3*	.	.
10	.	3	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	2	*3.3*	3	*10.3*
11	2	4	.	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.	5	*8.2*	4	*13.8*
12	i	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	*1.6*	1	*3.5*
13	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	*1.6*	1	*3.5*
14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
15	.	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	*1.6*	3	*10.3*
16	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	*1.6*	3	.
17	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2	*3.3*	1	*3.5*
18	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	*3.5*
19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
21	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	*3.5*
Totals and % of total recaptures of each sex	19 *31.2*	26 *90.0*	3 *4.9*	0 *0*	4 *6.6*	1 *3.5*	15 *24.6*	2	8 *13.1*	0 *0*	1 *1.6*	0 *0*	5 *8.2*	0 *0*	5 *8.2*	0 *0*	1 *1.6*	0 0	61		29	

9 nights after release. When dissected, it was seen still to be nulliparous and it had not taken a bloodmeal.

As with the unfed females of batch 3 released at " Laumède-le-Bas ", the unfed, marked females released at "Langlade East" tended to disperse rapidly away from the place of release, presumably in a search for a bloodmeal *(table IV)*. In comparison with flies released at "Laumède-le-Bas" females released at "Langlade East", situated on a central bluff near the top of the valley, dispersed more widely to the south side of the valley.

The numbers of marked male flies and the days and stations of recapture are shown in *table IV*. The figures suggest that the males moved less than the females. Of the 29 males recaptured, 26 (89.7 %) were caught 65 m from the point of release. Two of the remaining three were recaptured at Laumède (600 m from the release point) on the 3rd and 8th nights respectively; the third fly was taken by hand at station "Cromwell", 525 m from " Langlade East " within 24 hrs of release.

The influence of weather on activity

The general movement of *P. ariasi* is greatly inhibited at temperatures < 15° C. At about 16° C, hungry females sometimes alight on human bait, but appear to be unable adequately to respond to the stimulus and to feed. From recent unpublished work on host-finding behaviour, we know that the optimal wind speeds for movement are < 0.6 m/sec. Females are, however, still active at speeds from 0.6 m/sec to about 1 m/sec. Above 1 m/sec, activity ceases but is regained in temporary lulls.

During the experiment, there was no evidence that dispersal of the sandflies was assisted by wind. For example, the recapture of large numbers of female flies at Laumède, 250 m from "Laumède-le-Bas", was not explained by prevailing winds from the SE at optimal speeds for the activity of the flies. Furthermore, wind records at night during the 68.5 hrs between the release of the unengorged female no. 92 at "Laumède-le-Bas" and its recapture at Roubignac, 2,200 m away, suggest that this distance was unlikely to have been achieved with the assistance of wind. Roubignac lies almost due west of the point of release *(fig. 1)*. Assuming that the fly was not active during the hours of daylight, it would have necessitated a noctural wind from the east at a speed sufficiently low to encourage activity for the fly to have been taken directly to the place of recapture. Wind records during the hours of darkness showed that, except for a brief period at sunset on one night, the direction of the nocturnal winds was always from the south west, west, north west or, briefly, the north. The exception was a wind from the south east, but this lasted for less than half an hour as night fell and the wind speed (1.0 m/sec) was at the point when activity is suppressed.

In the study area, there are normally storms in the middle of August. These are preceded by one or two warm, still nights which, in spite of apparently ideal conditions for the activity of sandflies, are notable because catches both by light traps and active searches are always low. It is probable, therefore, that the activity of the flies is inhibited by falling atmospheric pressure.

Discussion

In a preliminary study of the dispersal of *P. ariasi*, the maximum distance between release and recapture of female flies was 750 m (Rioux *et al.*, 1979). In the present work it is shown that this distance is often exceeded, and that distances > 1,000 m are not uncommon. The supposition that the dispersal is usually active and not dependent on wind is suggested but not proven by observations on the direction and speed of nocturnal winds from the time of release to recapture of the unengorged female (no. 92) released at "Laumède-le-Bas" and recaptured 68.5 hrs later at Roubignac, 2,200 m away. This assumption is supported by other general observations on the prevailing winds in the valley in relation to the places where flies were recaptured. Further evidence is found in the different patterns of dispersal of, firstly, males and females and, secondly, of females released either engorged or unengorged. The maximum distance from a release point at which males were recaptured was 600 m whereas, for females, it was 2,200 m. Most females released engorged remained near the release point until after oviposition, but unengorged females tended to move away without delay. If the dispersal had been mainly by wind, no such differences would have been expected. In spite of these observations, it cannot be said that sandflies are never carried by wind. The discovery of a male specimen of *P. perniciosus* on the island of Jersey (Marett, 1923), where sandflies are otherwise absent, suggests the contrary. Furthermore, the small size, high ratio of surface area to weight and comparatively poor flight ability or sandflies put them into the category of insects most likely to be found at heights of more than 500 m (Berland, 1935) which could not be achieved without the assistance of wind.

In 1983, we investigated the possibility that the distances of dispersal of *P. ariasi* may have been increased by an attraction to the lights of CDC traps used for recaptures (Killick-Kendrick *et al.*, 1984). It was shown that the flies are not drawn to the light at distances > 2 m and our use of CDC traps seems not to have distorted our results. An interesting observation in the work on the range of attraction was that, in suitable weather conditions, *P. ariasi* is remarkably mobile ; the results of the work reported here support this, although it is generally assumed that sandflies are relatively inactive insects.

Previous work on the dispersal of sandflies has not revealed distances of movement as great as those we recorded. Quate (1964) carried out mark-release-recapture experiments with *P. orientalis* Parrot, 1936 on flat terrain in open *Acacia* woodland in the Sudan. He marked the flies with fluorescent powders and recaptured them as they came to bite man. His recapture rate was low with only 17 (0.3 %) females recovered out of 6,300 released. Eleven were recaptured within 3 nights of release and the remaining 6 on nights 4-7. One female was caught 730 m from the release point only 24 hrs after release.

From the results of mark-release-recapture studies by a number of Soviet workers, Perfil'ev (1968) concluded that, although sandflies do not generally fly long distances, movement is occasionally as much as 1-1.5 km. The behaviour of the

desert sandflies was, however, different from that of *P. ariasi* in that only 1 % of marked sandflies moved as far as 25 m from a room in which they were released.

Foster (1972) investigated the dispersal of *P. longipes* Parrot and Martin, 1939 in stony farmland in the foothills of a mountain in Ethiopia. He marked and released 2,394 unfed females and a few males of which he recaptured 17 females and 1 male (0.8 %) 1-15 days after release. The two furthest recaptures, both uphill from the release point, were at 240 m (at 24 hrs) and 289 m ("3-4" days). Of 485 mostly male flies, Foster recaptured 51 at the release point 1-8 days later. Two nights after release, he caught one (? sex) in a light trap at 36 m and found another (? sex) resting in a tree hole at 20 m. Foster concluded that the potential distance that *P. longipes* can travel is considerable.

The only published observations on the dispersal of sandflies in a Neotropical rain forest are those of Chaniotis *et al.* (1974) who worked in Panama. They marked and released about 20,000 sandflies including male and unfed female specimens of, mainly, *Lutzomyia trinidadensis* (Newstead, 1922), *L. shannoni* (Dyar, 1929), *L. trapidoi* (Fairchild and Hertig, 1952) and *L. ylephiletor* (Fairchild and Hertig, 1952). The median recapture rate was 8.6 %. Four marked flies were recaptured at 200 m, the furthest recapture station from the point of release; 1 of these 4 (a female *L. shannoni*) achieved this distance within 24 hrs. Most attempts at recapture were made 24 hrs after release, and no searches were made for marked flies after 15 days.

Chaniotis *et al.* (1974) concluded that, in Neotropical forests, sandflies do not move far but this should be confirmed with observations made for more than 15 days, and with collection stations further than 200 m from the point of release. It is, however, difficult to find marked sandflies with a UV lamp in a forest by night and, moreover, displacement of many sylvatic sandflies may be mainly vertical rather than horizontal.

Our results suggest that, at least in some habitats, leishmaniasis may commonly be spread between reservoir hosts or from a reservoir host to man by the movement of female sandflies (Foster, 1972; Rioux *et al.*, 1979). The maximum distance of displacement of *P. ariasi* was more than 2 km but it is not yet known whether or not this is sufficiently common to be relevant to the spread of leishmaniasis. However, the "effective flight" (see Eyles, 1944), or the distance at which sufficient numbers of this species travel to be epidemiologically important, appears to be more than 1 km. The practical relevance of these findings is shown by an attempt to control endemic cutaneous leishmaniasis in a focus in Iran by a *cordon sanitaire* of 300 m around human settlements in which all rodent reservoir hosts and sandflies were destroyed (Seyedi-Rashti & Nadim, 1973). The transmission of disease to man was, however, not interrupted "either because the flight range of sandflies is more than 300 meters or transmission takes place in untreated areas".

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