

Life history and body size of the introduced millipede *Ommatoiulus moreleti* (Lucas, 1860) (Diplopoda: Julidae) at different altitudes on Tenerife (Canary Islands)

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Synopsis: The life histories, body sizes and gonopod morphologies of the introduced millipede *Ommatoiulus moreleti* in four populations at different altitudes on Tenerife (Canary Islands) were compared with those of other populations in Portugal (native distribution), Madeira and Australia. The gonopod morphologies suggest that the Tenerife populations originated from southern Portugal. The life history of *O. moreleti* at high altitudes on Tenerife differs from that reported elsewhere, notably in the rarity of intercalary males in summer. Body size is inversely related to population density in all countries.

Keywords: millipede, *Ommatoiulus moreleti*, life history, body size, altitude, Tenerife

INTRODUCTION

The millipede *Ommatoiulus moreleti* (LUCAS, 1860) (DIPLOPODA: JULIDAE) is a native of Portugal which has been introduced to several Atlantic islands (e.g. Madeira, Azores, Bermuda, Canary Islands, St Helena), South Africa and Australia (BAKER, 1984). In Australia, *O. moreleti* is a significant nuisance pest entering houses in large numbers in autumn and spring (BAKER, 1978a, 1979). Previous studies in Australia, Portugal, Azores and Madeira (e.g. BAKER, 1978a, b, c, 1979, 1980, 1984, 1985a, b, c, 1988; CAREY & BULL, 1986; BAILEY, 1989) have been aimed at obtaining a sound understanding of the life history, behaviour and ecology of *O. moreleti* in order to develop appropriate methods of control for this pest.

The life cycle of *O. moreleti* consists of an egg, pupoid and up to sixteen stadia (BAKER, 1978b, 1984). Development is anamorphic. Maternity is variable with respect to stadium, but most millipedes in Australia and southern Portugal are mature by stadia X or XI when they are two years old. The breeding season is

autumn to early winter. *O. moreleti* is periodomorphic. That is, two forms of adult male occur, copulatory and intercalary. Intercalary males possess rudimentary gonopods and are incapable of mating. Copulatory males moult to intercalary males and vice versa. In Australia and southern Portugal, most adult males are copulatory during autumn and winter and intercalary in spring and summer. The fecundity of females is directly related to their size.

The life histories of several species of millipede vary between habitats (HALKKA, 1958; COTTON & MILLER, 1974; CRAWFORD *et al.*, 1987). Geographic variations in life histories have been attributed to climatic influences (FAIRHURST, 1974; MEYER, 1989). BAKER (1984) and READ (1985) gave limited evidence that the life history of *O. moreleti* varies with altitude, and hence habitat and climate, on the island of Madeira. They found different stadia age distributions for populations at different altitudes on the island in spring and summer. This paper describes in more detail changes in the life history and size of *O. moreleti* that occur with variation in altitude on the island of Tenerife, Canary Islands. Comparisons are then made with the life history and size of *O. moreleti* in other parts of the world and possible reasons for observed differences are discussed.

The gonopods of copulatory male millipedes are of primary importance in taxonomy (DEMANGE, 1981). Sub-specific variations in gonopod morphology have been used to trace the origins of introduced populations of *O. moreleti* (e.g. in Australia, South Africa and Madeira) back to southern Portugal as opposed to northern Portugal (BAKER, 1984). The morphology of the gonopods of *O. moreleti* from the Canary Islands is reported here and the origin of this island population is determined.

I. - MATERIALS AND METHODS

A) Canary Islands

Each month from April 1986 to April 1987 millipedes were collected by hand from beneath loose stones, logs, tins, boxes and other surface debris on random walks in three sites on Tenerife: Bajamar (20 m altitude), Jardina (600 m) and Las Lagunetas (1400 m). The habitat at Bajamar was an open grassland in which *Mulva* sp., *Erodium* sp., *Patellifolia procumbens*, *Plantago lagopus*, *Galactites tomentosa*, *Calendula* sp., *Sinapis alba*, *Cenchrus ciliaris* and *Avena* sp. were common. At Jardina an open shrubland with *Aeonium* sp., *Pteridium aquilinum*, *Silene vulgaris*, *Aspalathium bituminosum*, *Oxalis pes-caprae*, *Hyparrhena hirta* and *Origanum virens*, and at Las Lagunetas a pine forest (*Pinus canariensis*) with a sparse undergrowth of *Erica arborea*, *Cynosurus echinatus*, *Briiza minor*, *Agrostis* sp., *Festuca* sp. and *Bromus* sp. At each site, the first several hundred millipedes (stadium VI and older only) seen were collected by hand and preserved in 70% ethanol. Smaller millipedes could not be collected efficiently by hand. *O. moreleti* was consistently more difficult to find at Las Lagunetas than at the other two sites and therefore probably less abundant there. The stadium, sex and maturity (females with and without mature eggs in their oviducts; juvenile, copulatory or intercalary male) of each individual were recorded. Stadia were determined by the ocular field method (MAYR, 1978b).

In April, September and December 1987 and June 1988, *O. moreleti* was also collected beneath stones at Fuente Joco (1910 m), another pine forest (*Pinus canariensis*) with an undergrowth dominated by Gramineae and also *Levula linkii* and *Cheiranthus scoparius*. *O. moreleti* was particularly scarce at this site.

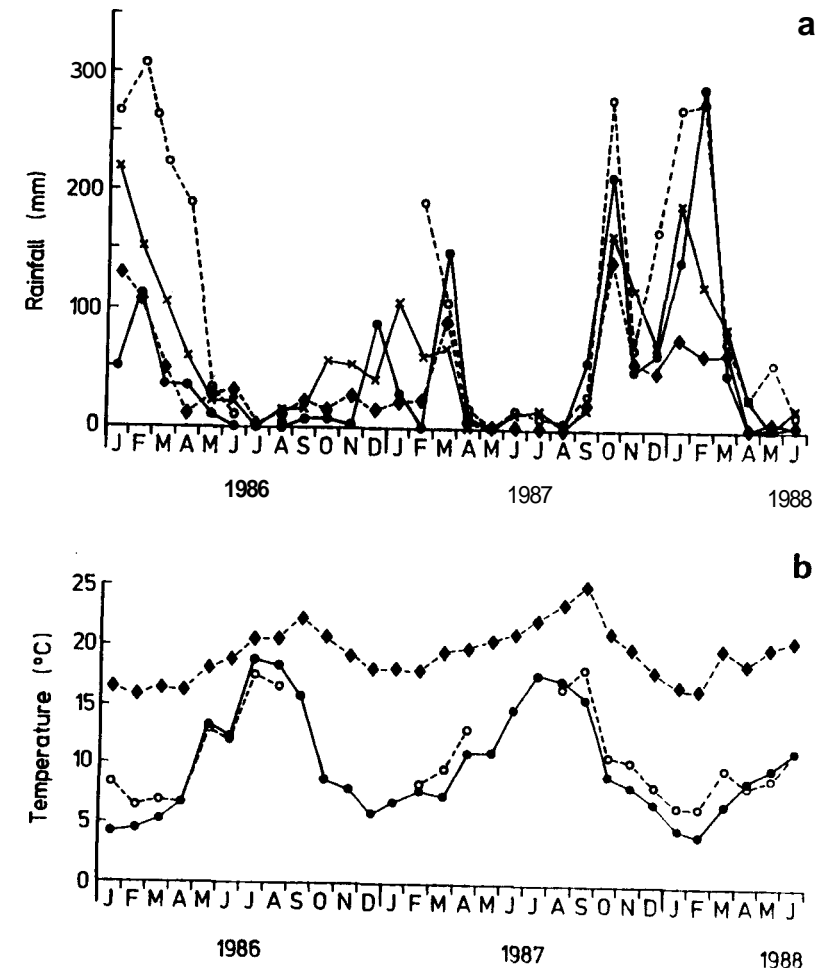


FIG. 1. - Monthly rainfalls (a) and mean monthly temperatures (b) recorded on Tenerife near Bajamar (station "Los Pajalillos", Valk Guerra) (◆), Jardina (×), Las Lagunetas (station "La Matanza") (○) and Fuente Joco (station "Izaña", 2386 m) (●).

Weather data recorded by the Tenerife Meteorological Office near the four sites on Tenerife during the period of sampling for *O. moreleti* are given in figure 1. No temperature data were available for Jardina and temperature and rainfall records for Las Lagunetas were incomplete. There was no obvious, consistent change in rainfall with increased altitude. Temperatures were much cooler at Fuente Joco and Las Lagunetas than at Bajamar, except for a brief period in mid-summer.

The total numbers of segments (including collum and excluding telson) and widths of the body at the twentieth segment were recorded for 20 female *O. moreleti* in stadium IX collected at each of Bajamar, Jardina and Las Lagunetas in June 1986 and also at each of these sites plus Fuente Joco in April 1987.

The widths at the twentieth segment and the numbers of mature eggs in the oviduct were recorded for 70 gravid females in stadia XI and XII that were collected at each of Bajamar and Jardina during November and December 1986 (35 in each month at each site). At Las Lagunetas, widths and numbers of eggs were similarly recorded for 40 females (20 in November, 20 in December). Fewer gravid females were collected at this site (c.f. Bajamar and Jardina) thus limiting the measurements that could be made. At Fuente Joco, body widths and numbers of eggs were also recorded for 40 females collected in December 1987. Females which contained < 50 mature eggs were not included in the analysis. Such females had either already laid and a few mature eggs were left in their oviducts or they contained many developing eggs and were clearly far from fully gravid.

The morphologies of the gonopods of 20 copulatory males from each of the four Tenerife sites were compared with those already reported for *O. moreleti* from southern and northern Portugal (see Fig. 4 in BAKER, 1984).

B) Portugal, Madeira and Australia

The widths of the body at the twentieth segment were recorded for female stadia IX *O. moreleti* collected by hand from beneath leaf litter at 15 sites in Portugal, Madeira and Australia between 1975 and 1987 (see Tab. V for sites). The millipedes were collected in spring. Some sites were sampled more than once (in different years). The numbers of females measured at each site varied between 13 and 33. Habitats included *Pinus*, *Quercus*, *Eucalyptus* and *Laurus* woodlands, a *Quercus/Ulex* shrubland and a *Trifolium/Lolium* grassland. Fuller descriptions of many of the sites are given in BAKER (1978b, 1984). Densities varied greatly between sites and with time at individual sites. For the purpose of this paper, populations are classed as (1) rare if more than 15 minutes was necessary for one person to collect 100 individuals of stadium VI or older by hand from beneath leaf litter, logs and loose surface stones during spring and (2) abundant if less than 15 minutes was required.

The widths of the body at the twentieth segment were also recorded for 312 female stadium X *O. moreleti* collected by BAKER (1984) at 15 sites at different altitudes (20-1600 m) on Madeira during spring 1982. Sites included *Laurus* and *Eucalyptus* woodland, herbaceous roadside wastelands and rocky slopes interspersed with heathers, grasses and ferns. Whilst *O. moreleti* was abundant at several sites and rare at a few, measures of density were not kept for all sites. The numbers of females measured at each site varied between 11 and 25. For consistency within this paper it would have been preferable to have measured stadium IX rather than stadium X females at the different altitudes on Madeira. However, stadium IX females were too rare in the Madeiran collections at the lowest and highest altitudes to allow adequate comparisons between sites.

II. - RESULTS

A) Canary Islands

At all sites, mature eggs were found in females in stadium X and older stadia (Tab. I). Some females in stadium IX at Bajamar and Fuente Joco also contained mature eggs. Most males were adult (copulatory or intercalary) by stadium X (Tab. I). Overall, slightly fewer males than females were collected. Males were particularly scarce in the youngest and oldest stadia.

Tab. I. - Stadia age distributions, maturities and sex ratios of the total *Ommatoiulus moreleti* collected on Tenerife.

	VI	VII	VIII	IX	X	Stadia XI	XII	XIII	XIV	XV	Tota
Fuente Joco (1910 m)											
Female											
No eggs.....			24	100	136	62	42	43	22	8	437
With eggs.....				2	39	34	10	13	12	3	113
Male											
Juv.....		3	11	45	22						81
Cop.....				47	127	56	20	12	9	1	272
Int.....					7	3	1	1	1		12
% males.....			31.4	47.4	47.	38.1	27.8	18.8	22.7	8.3	39.5
Las Lagunetas (1400 m)											
Female											
No eggs.....	33	244	299	629	608	261	95	22	4	1	2196
With eggs.....					31	59	53	26	7	3	179
Male											
Juv.....	16	204	232	488	138	13					1091
Cop.....			10	114	273	198	57	16	1	2	671
Int.....				1	34	5					40
% males.....	32.7	45.5	44.7	48.9	41.	40.3	27.8	29.6	8.3		43
Jardina (600 m)											
Female											
No eggs.....	04	89	255	845	1074	919	242	39	1	1	3669
With eggs.....					103	311	81	14			509
Male											
Juv.....	86	30	216	754	367	54	3				1610
Con.....			3	38	652	281	56	4			1034
Int.....				2	29	127	36	5			199
% males.....	45.3	40.8	46.2	48.4	47.1	27.3	22.7	14.5			40.
Bajamar (20 m)											
Female											
No eggs.....	190	82	301	676	850	435	150	8			2693
With eggs.....				27	370	395	49	6	1		847
Male											
Juv.....	112	55	252	771	408	32	2				1632
Con.....			1	119	906	331	47	6			1410
Int.....					34	239	37	5			315
% males.....	37.1	40.1	45.7	55.9	52.5	42.0	30.2	44.0			48

Females with mature eggs (stadium IX and older) were most common in autumn-winter (Fig. 2). They were found later into winter at Bajamar than at Jardina and Las Lagunetas. Data for Fuente Joco were too scarce to allow comparisons with other sites. At Bajamar and Jardina, most adult males were copulatory in autumn and winter and intercalary in spring and summer (Tab. II). Copulatory males predominated in autumn and winter at Las Lagunetas and in all seasons at Fuente Joco. Intercalary males were never predominant at Las Lagunetas.

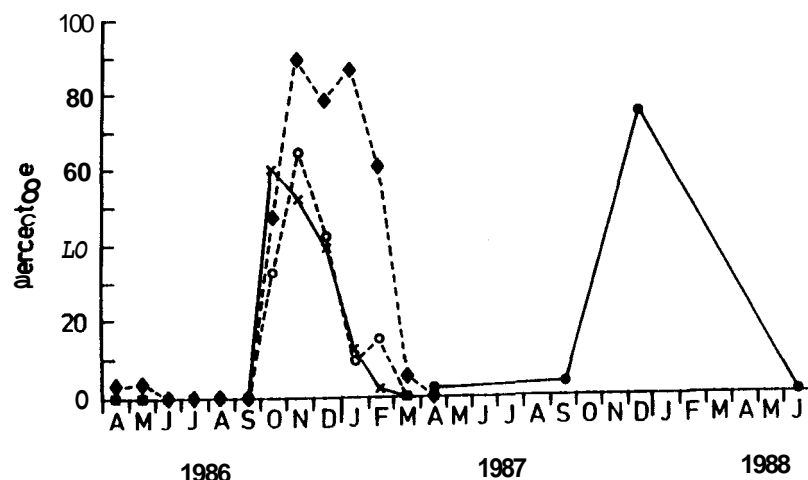


FIG. 2. — Percentages of female *O. moreletii* containing mature eggs at Bajamar (◆), Jardina (×), Las Lagunetas (○) and Fuente Joco (●).

TABLE II. — Numbers of Copulatory (C) and Intercalary (I) male *Ommatoiulus moreletii* collected on Tenerife.

Month	Bajamar		Jardina		Las Lagunetas		Fuente Joco	
	C	I	C	I	C	I	C	I
April (1986)	1	24	0	26	3	0	-	-
May	3	88	0	26	4	4	-	-
June	0	53	0	25	2	2	-	-
July	1	8	0	5	10	10	-	-
August	3	34	1	13	9	7	-	-
September	23	24	108	1	13	6	-	-
October	144	5	106	0	113	2	-	-
November	212	0	262	0	87	0	-	-
December	328	0	213	0	53	0	-	-
January (1987)	327	1	196	0	240	0	-	-
February	268	0	109	0	118	0	-	-
March	92	28	37	43	8	2	-	-
April	8	50	2	60	11	7	30	1
September							28	2
December							184	3
June (1988)							70	6

In summer (July to August) two cohorts of *O. moreletii* were recognizable at Bajamar (Appendix Tab. 1), a young cohort mostly in stadium VI and older cohort mostly in stadia IX-XI. In late autumn (November) and late winter (February),

these two cohorts were still evident as peaks in the numbers of millipedes in stadia VII and VIII and X and XI respectively. Similarly, two cohorts were recognizable at Jardina (Appendix Tab. 11), the stadial growth of the younger cohort being slightly advanced on that at Bajamar. The appearances/disappearances of the peaks in numbers of the younger cohorts in Appendix Tabs. I & II probably correspond to periods of surface activity (and hence likelihood of collection) and underground moulting.

Separating cohorts was more difficult at Las Lagunetas. If males and females were grouped together, separation of cohorts was impossible, but if females were considered alone, two cohorts were recognizable during spring 1986 (May); one cohort mostly in stadium VII, the other mostly in stadium X (Appendix Tab. 111). In autumn 1986 (November), most females were in stadium XI and carrying mature eggs but in spring 1987 (April) most were in stadium IX and had immature eggs. It seems probable that these latter females belong to the same cohort as that in stadium VII in spring 1986. In autumn 1986, they may have been moulting underground and therefore not collected. Most of the males in spring 1987 (April) were juveniles (89.7%) and in stadium IX. Most males in the previous autumn (November) were copulatory (86.1%) and in stadia X and XI. Again, it seems probable that the majority of males present in spring 1987 were in a younger cohort than most of those collected in autumn 1986 and originate from individuals that were mainly in stadium VII in spring 1986.

Two cohorts could not be identified at Fuente Joco, even if males and females were separated (Appendix Tab. IV).

Millipedes from Las Lagunetas and Fuente Joco were larger (wider) than those from Jardina and Bajamar and had slightly more segments (Tab. III).

TABLE III. — Numbers of segments and widths (mm) of stadium IX female *Ommatoiulus moreletii* ($\bar{x} \pm S.E., n = 20$).

Site and date	Segments	Widths
June 1986		
Bajamar	44.5 ± 0.4	2.29 ± 0.04
Jardina	43.6 ± 0.4	2.15 ± 0.03
Las Lagunetas	46.5 ± 0.2	2.73 ± 0.03
F.	19.8	78.3
Probability	<0.05	<0.05
April 1987		
Bajamar	45.2 ± 0.3	2.37 ± 0.04
Jardina	44.5 ± 0.3	2.11 ± 0.1
Las Lagunetas	46.1 ± 0.3	2.95 ± 0.06
Fuente Joco	45.7 ± 0.4	2.97 ± 0.08
F.	4.8	48.5
Probability	<0.05	<0.05

At all sites, the numbers of mature eggs found in females increased with female width (Fig. 3). There were no significant differences between sites in the slopes of the regression lines (e.g. $t = 1.79, p > 0.05$ for Bajamar c.f. Jardina; $t = 1.49, p > 0.05$ for Bajamar c.f. Las Lagunetas; $t = 1.74, p > 0.05$ for Bajamar c.f. Fuente Joco). BAKER (1984) measured the widths of 71 females (stadia IX-XIII) and the numbers

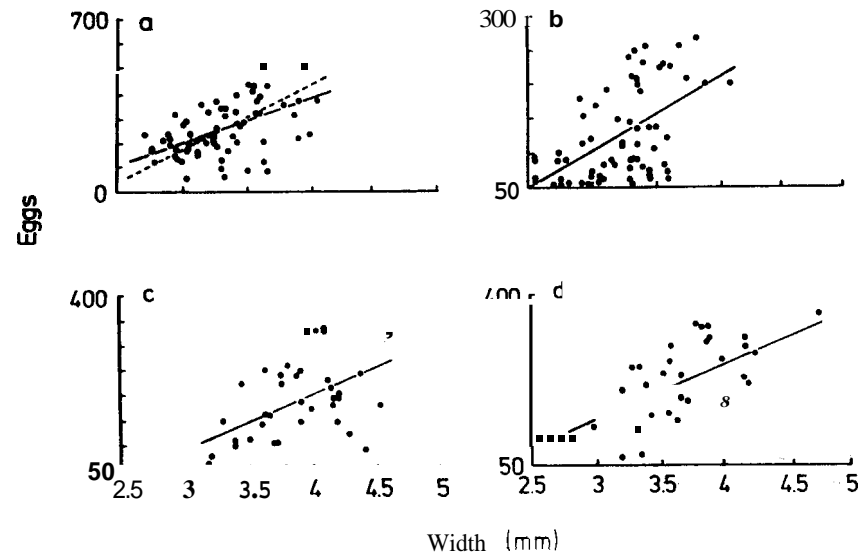


FIG. 3. — Numbers of mature eggs as a function of body width in female *O. moreleti* from Bajamar (a), Jardina (b), Las Lagunetas (c) and Fuente Joco (d). Equations of the regression lines are: $y = 183.5x - 356.7$, $r_{20} = 0.492$, $p < 0.05$ (Bajamar); $y = 104.8x - 213.5$, $r_{10} = 0.527$, $p < 0.05$ (Jardina); $y = 108.6x - 232.0$, $r_{40} = 0.491$, $p < 0.05$ (Las Lagunetas); $y = 1039x - 166.6$, $r_{40} = 0.584$, $p < 0.05$ (Fuente Joco). For comparison, the regression line $y = 261.3x - 614.5$, $r_{11} = 0.847$, $p < 0.05$ for Portugal (---) is included in (a).

TABLE IV. — Widths (mm) of stadia XI and XII female *Ommatoiulus moreleti* and numbers of mature eggs in their ovitubes ($\bar{x} \pm S.E$)

Site	Widths	Eggs
Bajamar	3.32 ± 0.04	251.5 ± 14.5
Jardina	3.22 ± 0.04	124.1 ± 8.1
Las Lagunetas	3.91 ± 0.06	192.6 ± 13.0
Fuente Joco	3.65 ± 0.07	213.1 ± 12.3
F.	38.33	23.04
Probability	< 0.05	< 0.05

of mature eggs these females contained at 5 sites in Portugal during autumn 1982. The widths of the females varied between 2.8 and 2.0 mm. The sites were at Cascais, Grandola, Santa Susana, Albarraque and Mendiga, all within 150 km of Lisbon and all < 400 m in altitude [see Tab. V and BAKER (1984) for further habitat descriptions and a map of site locations]. The regression line for numbers of eggs on widths, calculated from BAKER'S (1984) Portuguese data, is included in figure 3. There was no significant difference between the slopes of the regression lines for Portugal and Bajamar ($t = 1.77$, $p > 0.05$). However, there were differences between

the slopes for Portugal and the other Tenerife sites ($t = 5.53$, $p < 0.05$ for Portugal *c.f.* Jardina; $t = 4.13$, $p < 0.05$ for Portugal *c.f.* Las Lagunetas; $t = 5.15$, $p < 0.05$ for Portugal *c.f.* Fuente Joco).

The numbers of mature eggs per female varied between sites on Tenerife, as did the widths of the females that were dissected (Tab. IV). Although females were smaller at Bajamar than at Las Lagunetas ($t = 8.46$, $p < 0.05$) and Fuente Joco ($t = 4.28$, $p < 0.05$), fecundities were higher at Bajamar ($t = 3.02$, $p < 0.05$ for Bajamar *c.f.* Las Lagunetas; $t = 2.01$, $p < 0.05$ for Bajamar *c.f.* Fuente Joco). There was no significant difference in the size of females from Bajamar and Jardina ($t = 1.64$, $p > 0.05$) but the females at Bajamar contained more mature eggs ($t = 7.65$, $p < 0.05$).

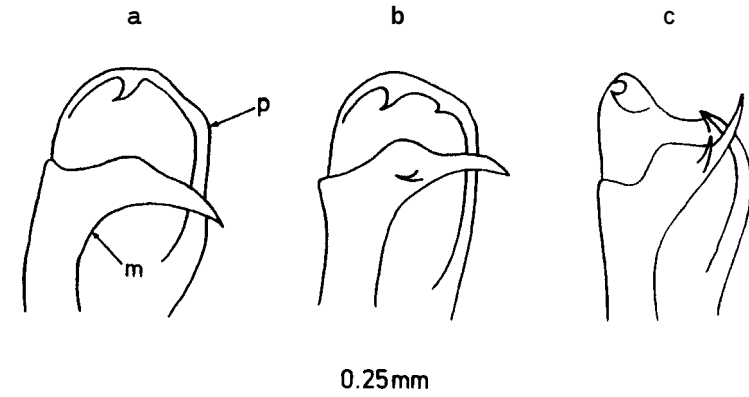


FIG. 4. — Posteroventral view of the promerites (p) and mesomerites (m) of the gonopods of copulatory male *O. moreleti* from Las Lagunetas, Canary Islands (a), Cascais, southern Portugal (b) and Braga, northern Portugal (c). The spike illustrated on the mesomerite of the male from Cascais is not always present.

Figure 4a illustrates the gonopods of a copulatory male from Las Lagunetas. The gonopods of all copulatory males at all four sites on Tenerife were similar in morphology. The gonopods of *O. moreleti* from Tenerife more closely resembled those from southern rather than northern Portugal (Fig. 4).

B) Portugal, Madeira and Australia

Females from abundant populations of *O. moreleti* in Portugal, Madeira and Australia were generally smaller than females from rare populations (Tab. V). Exceptions occurred at Bridgewater C and Heathfield in Australia in 1983. Female widths changed in time at individual sites in Australia, increasing as population density decreased at Bridgewater A from 1975 to 1983 ($t = 3.90$, $p < 0.05$) and decreasing as population density increased at Longwood from 1983 to 1987 ($t = 9.41$, $p < 0.05$). Widths also decreased at Bridgewater C and Heathfield from 1983 to

TABLE V. — Diameters (mm) (\bar{x} S.E.) of stadium IX female *Ommatoiulus moreleti* in rare and abundant populations in varying habitats in spring. Data taken from Baker (1985 c) are indicated by (*). Years of collection are given in parentheses.

Site	N	Diameter	Dominant plant genera
Rare			
Portugal:			
Braga (1982)	17	2.97 ± 0.05	<i>Pinus</i>
Mendiga (1982)	25	2.83 ± 0.04	<i>Quercus</i>
Cascais (1982)	25	2.78 ± 0.05	<i>Pinus</i>
Grandola (1982)	25	2.83 ± 0.05	<i>Quercus</i>
Madcira:			
Vasco Gil	22	2.63 ± 0.05	<i>Eucalyptus</i>
Canary Islands:			
Las Lagunetas (1987)	20	2.95 ± 0.06	<i>Pinus</i>
Fuente Joco (1987)	20	2.97 ± 0.08	<i>Pinus</i>
Australia:			
Bridgewater A (1983) (*)	25	2.71 ± 0.05	<i>Eucalyptus</i>
Bridgewater A (1987)	25	2.70 ± 0.03	<i>Eucalyptus</i>
Longwood (1983) (*)	25	3.05 ± 0.04	<i>Eucalyptus</i>
Abundant			
Portugal:			
Albarraque (1982)	25	2.36 ± 0.04	<i>Quercus/Ulex</i>
Madcira:			
Quinta Grande (1982)	23	2.45 ± 0.05	<i>Eucalyptus</i>
Ribeiro Frio (1982)	33	2.47 ± 0.05	<i>Laurus</i>
Queimadas (1982)	32	2.34 ± 0.04	<i>Laurus</i>
Canary Islands:			
Bajamar (1987)	20	2.37 ± 0.04	Serval Gramineae
Jardina (1987)	20	2.11 ± 0.1	<i>Aeonium</i>
Australia:			
Uridgewaier A (1975)	13	2.47 ± 0.04	<i>Eucalyptus</i>
Bridgewater B (1975)	15	2.31 ± 0.06	<i>Trifolium/Lolium</i>
Bridgewater C (1983) (*)	25	2.94 ± 0.04	<i>Eucalyptus</i>
Bridgewater C (1987)	25	2.34 ± 0.04	<i>Eucalyptus</i>
Heathfield (1983) (*)	25	2.85 ± 0.02	<i>Eucalyptus</i>
Heathfield (1987)	15	2.30 ± 0.04	<i>Eucalyptus</i>
Longwood (1987)	25	2.57 ± 0.03	<i>Eucalyptus</i>
Crafer (1987)	15	2.38 ± 0.04	<i>Pinus</i>

1987 ($t=11.01$, $p<0.05$ and $t=11.25$, $p<0.05$ respectively) although *O. moreleti* was abundant at both sites in both years.

The widths of the females collected at different altitudes on Madeira varied between sites (Fig. 5), but there was no correlation between width and altitude ($r=0.071$, $p>0.05$).

III. DISCUSSION

The morphologies of the gonopods of *O. moreleti* on Tenerife suggest that the populations there originated from southern rather than northern Portugal, as did populations of this species in Madeira, South Africa and South Australia (BAKER, 1984).

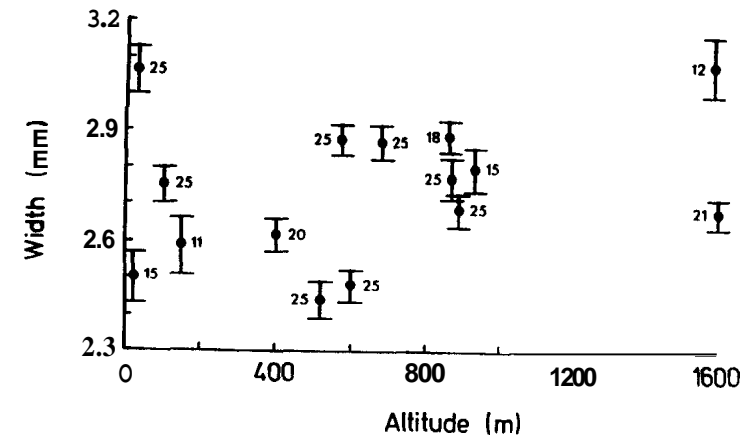


FIG. 5. — Widths (mm) ($\bar{x} \pm$ S.E.) of stadium X female *O. moreleti* at varying altitudes (m) on Madeira (n given adjacent to \bar{x}).

The autumn-winter breeding season of *O. moreleti* on Tenerife generally resembled that recorded in South Australia and southern Portugal (BAKER, 1978 b, 1984). Mature eggs were found in females later in winter at Bajamar than at Jardina and Las Lagunetas, suggesting a delay in oviposition at the former habitat. Rainfall during autumn and early winter (1986-1987) was much less at Bajamar compared with Jardina and may account for this delay. Insufficient weather data are available for Las Lagunetas to enable adequate comparisons with Bajamar.

At low altitudes on Tenerife (Bajamar and Jardina), most adult males were copulatory in autumn and winter and intercalary in spring and summer. Similar seasonal patterns in the form of the adult male of *O. moreleti* have been found in southern Portugal, South Australia and near Cape Town, South Africa (SCHUBART, 1966; BAKER, 1978 b, 1979, 1984). At high altitudes on Tenerife, different patterns were observed. At Las Lagunetas, copulatory males predominated in autumn and winter. Similar numbers of intercalary and copulatory males were collected in spring and summer. At Fuente Joco, copulatory males predominated in all seasons. H. READ (pers. comm.) found copulatory males ($n=36$) more often than intercalary males ($n=11$) on Madeira and the nearby islands of Porto Santo and Deserta Grande in summer. Most of READ's copulatory males ($n=30$) were collected at altitudes of 600+ m; most of her intercalary males ($n=10$) were collected below 500 m. These results suggest that intercalary males of *O. moreleti* become less predominant in summer at high altitudes on these Atlantic islands.

SAHJI (1985) has suggested that the intercalary males of *Cylindroiulus nitidus* are more resistant to environmental extremes than copulatory males. In several species of millipedes, intercalary males predominate in unfavourable seasons (e.g. Mediterranean summers (HALKKA, 1958)). It is therefore tempting to suggest that the high frequencies of intercalary males at low altitudes on Tenerife in summer are responses to the prolonged, high temperatures that occur there then (c.f. high

altitudes). However, the climate in parts of South Australia (e.g. Bridgewater), where intercalary males also predominate in summer (BAKER, 1978b), is similar to that recorded at the high altitudes on Tenerife (e.g. mean monthly temperatures of 16-19°C in summer and 8-9°C in winter). It thus seems improbable that variation in temperature explains the altitudinal variation in frequency of intercalary males on Tenerife.

The development of maturity in both male and female *O. moreleti* on Tenerife, generally by stadium X, is in agreement with findings elsewhere in the world (BAKER, 1978b, 1984). The bimodalities in stadial age distributions in autumn at Bajamar and Jardina and the inference that a similar bimodality also occurred in autumn at Las Lagunetas (although it was not obvious in the surface active millipedes that were collected there then) are consistent with two age groups found at this time in other habitats in southern and central Portugal and Australia; one year old millipedes mostly in stadia VII-IX (mostly immature) and two year olds mostly in stadia X-XI (mostly mature). Because of the inability to recognize separate cohorts at Fuente Joco, the generation time of *O. moreleti* remains unknown there.

Similar numbers of male and female *O. moreleti* were collected in stadia IX and X at all sites on Tenerife but males were rarer than females in older stadia, probably due to poorer survival of males compared with females as has been demonstrated elsewhere (BAKER, 1978c). Males were also relatively rare in the youngest stadia collected on Tenerife. Similar scarcities of males in young stadia have been recorded before (BAKER, 1976, 1978b). The reason for this scarcity is not known. Possibly, it is related to sexual differences in surface activity. The sexes of *O. moreleti* are not discernible (from external morphology) until stadium VI.

Prior to that stadium all animals look like females. It is possible that some males do not complete their differentiation until after stadium VI and that the low numbers of males in the youngest stadia collected on Tenerife reflect this.

O. moreleti was larger in body width and number of segments at the two highest altitude sites on Tenerife than at the two lowest altitude sites. This difference seems better explained by the low abundance of *O. moreleti* at high altitudes than by better conditions for growth, mediated for example by more suitable climate or difference in vegetation. No increase in size of females could be found with altitude on Madeira where more sites were sampled over a comparable altitudinal range. In a variety of habitats in Portugal, Madeira and Australia, the sizes of *O. moreleti* were generally greatest at sites where millipedes were rarest.

A negative relationship between population density and body size in *O. moreleti* was demonstrated temporally as well as spatially in Australia. Large body size was found in a population of low density at Loigwood in 1983. This was the first year that *O. moreleti* had been found at this site, invading it from nearby areas (BAKER, 1985c). By 1987, the density of *O. moreleti* had increased and the size of the millipedes had decreased. At Bridgewater A, which was first invaded by *O. moreleti* in 1967 (BAKER, 1985c), there was a dense population of millipedes in 1975 and their sizes were small. As population numbers decreased by 1983 (see BAKER (1985c) for a more precise demonstration of change in population numbers than provided here), body sizes increased.

Exceptionally large *O. moreleti* were found at Bridgewater C and Heathfield in 1983, considering the dense populations present there at the time. Both sites were invaded by *O. moreleti* only a few years before 1983 (1977 for Bridgewater C

and 1979 for Heathfield) (BAKER, 1985c). Possibly, insufficient time had elapsed since invasion to allow for the effect of high density to be expressed in small body sizes by 1983 at these particular sites. Densities remained high at both sites until 1987, and the sizes were then reduced to those commonly found in dense populations.

Competition for limited food might reduce the growth of *O. moreleti* at high densities. BERNES & KEETON (1968) and CHOTKO (1977) have shown that millipedes which are fed less, grow less. The food requirements of *O. moreleti* are not known. Dissections of gut contents reveal a variety of decomposing litter fragments. Probably, only a small portion of these fragments (e.g. fungi growing on decomposing plant material) are relevant to the millipede's nutrition. Through their feeding, other millipedes are known to cause marked qualitative changes in the litter microbial community, such as a shift from fungal to bacterial dominance (NICHOLSON *et al.*, 1966; MCBRAYER, 1973; INESON & ANDERSON, 1985). The possibility of negative interactions between food availability and the size and abundance of *O. moreleti* merits attention. MCKILLUP *et al.* (1988) have suggested that the collapse in numbers of *O. moreleti* which occurs several years after its invasion and rapid increase in abundance in new habitats in Australia (BAKER, 1985c) is due to a rhabditid nematode, a parasite of native Australian millipedes, which multiplies with *O. moreleti*, killing it when sufficiently abundant in the millipede's haemocoel. Reduced growth might also be caused by this nematode.

Fecundity, as measured by the numbers of mature eggs in female oviducts, increased with body width at all sites on Tenerife. Similar increases in fecundity with increased body width have been reported for *O. moreleti* in Portugal and Australia (BAKER, 1978b, 1984). However, the fecundities of *O. moreleti* were not greatest at high altitude sites on Tenerife although females were largest there. Greatest fecundities were recorded at Bajamar (20 m altitude) where females were small. The reason for the reduction in fecundity of *O. moreleti* at high altitudes on Tenerife is not known. Density dependent factors seem unlikely to be important. Density was high at Jardina (as for Bajamar) but low at Las Lagunetas and Fuente Joco. Possibly, the quality of food available to females was significantly better at Bajamar than at other sites.

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SUMMARY

The life histories, body sizes and gonopod morphologies of the introduced millipede, *Ommatoulus moreleti* (Diplopoda, Julidae), were studied at four sites of different altitude on Tenerife (Canary Islands) and compared with those of other populations within Portugal (native distribution), Australia and Madeira. The morphologies of the gonopods suggest that the Tenerife populations originated from southern Portugal, as did the other introduced populations. On Tenerife and Madeira, the life history of *O. moreleti* changes with altitude

In particular, copulatory males are common and intercalary males are rare at high altitudes in summer, whereas the reverse occurs at lower altitudes and in southern Portugal and Australia. Body size is inversely related to population density in all countries. Fecundity is positively related to body size within populations on Tenerife but not between them.

Résumé

Cycle biologique et taille, à différentes altitudes, d'un millipède introduit sur Tenerife (Îles Canaries), *Ommatoiulus moreleti* (Lucas, 1860)

Le cycle biologique, la taille et la morphologie des gonopodes d'un millipède introduit sur Tenerife (Îles Canaries), *Ommatoiulus moreleti* (Diplopoda: Julidae), ont été étudiés dans quatre sites de différentes altitudes et comparés avec ceux caractérisant d'autres populations répandues au Portugal (distribution d'origine), en Australie et sur Madère. La morphologie des gonopodes suggère que les populations de Tenerife sont originaires du sud du Portugal, comme le sont les autres populations introduites. Sur Tenerife et sur Madère, le cycle biologique de *O. moreleti* change suivant l'altitude. En particulier, à haute altitude, les mâles copulateurs sont courants et les mâles intercalaires sont rares en été alors que c'est l'inverse à basse altitude, comme aussi au sud du Portugal et en Australie. Dans toutes les régions, la taille est inversement proportionnelle à la densité de population. Sur Tenerife, la fécondité est proportionnelle à la taille au sein d'une même population, mais cette relation n'est pas conservée entre populations différentes.

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APPENDIX

TABLE I. - Monthly stadia age distributions of *Ommatoiulus moreleti* collected at Bajamar.

Month	Stadia										Total	
	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV		
1986												
April			10	113	177	55	8					363
May			2	56	113	138	45	4	1			359
June	135	9	6	106	145	85	23	1				510
July	96	9	4	89	116	24	3					341
August	19	1	26	220	206	57	13	2				444
September	14		17	201	190	68	21	4				515
October	3		6	65	235	167	37	9				522
November	18	77	59	41	207	165	30					597
December	2	2	4	53	374	162	13	1				571
1987												
January	13	18	28	74	340	147	12					632
February		16	95	46	264	125	17	3				566
March		3	177	176	116	141	39					652
April	2	2	120	353	125	74	24	1				725

TABLE II. - Monthly stadia age distributions of *Ommatoiulus moreleti* collected at Jardina.

Month	Stadia										Total	
	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV		
1986												
April		2	77	276	88	48	11	2				463
May	51		7	172	137	41	4	1				413
June	32	2	5	220	281	48	5	1				594
July	8	23	5	150	183	19		1				389
August	32	114	11	127	216	37	2					539
September	43	105	26	82	185	181	57	1		1		680
October		13	28	1	143	228	44	16				473
November	1	24	15	30	271	233	41	1				616
December			40	6	256	260	36	6				604
1987												
January		1	30	23	210	150	28	4				446
February		11	167	137	108	71	47	7				548
March	5		89	250	46	125	52	14				581
April	18	24	14	165	101	252	91	9	1			675

TABLE III - Monthly stadia age distributions of *Ommatoiulus moreleti* collected at Las Lagunas. (a) Males and Females combined (b) sexes separated for three months.

Month	Stadia										Total	
	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV		
(a)												
1986												
April	17	28	12	27	12	6	1	1				104
May	10	164	66	72	69	36	5					422
June	2	28	49	65	55	12	5					216
July	2	38	81	99	55	15	7					297
August	6	64	91	123	100	30	6					420
September	8	89	69	145	168	36	11	1				527
October		5	39	59	115	61	33	6	1	1		320
November		2	11	19	60	73	25	22	4	2		218
December	2	2	24	30	52	42	13	J				169
1987												
January		8	31	102	161	104	50	15		1		472
February		2	5	19	64	76	38	14	5	1		215
March		2	12	203	68	19						14
April	2	16	51	269	105	26	12			2		483
(b)												
1986												
May												
females	5	82	30	34	55	30	5					241
males	5	82	36	38	14	6						181
November												
females		1	4	9	21	38	20	19	4	1		117
males		1	7	10	39	75	5	3		1		101
1987												
April												
females	2	9	28	162	72	26	5			1		309
males		7	23	107	33		3			1		174

TABLE IV - Monthly stadia age distributions of *Ommatoiulus moreleti* collected at Fuente Joco. (a) Males and Females combined (b) Sexes separated.

Month	Stadia										Total
	VII	VIII	IX	X	XI	XII	XIII	XIV	XV		
(a)											
1987											
April	2	14	33	28	26	22	17	5	1		152
September	1	19	49	45	31	28	28	12	8		205
December		2	66	159	69						346
1988											
June			46	99	29	10	14	10	4		212
(b)											
1987											
April											
females		10	21	18	16	17	14	6	1		103
males	2	4	12	10	10	5	3	3			49
September											
females		12	34	37	22	16	19	8	3		151
males	1	7	15	8	9	6	3	4	1		54
December											
females		2	20	51	37	11	12	11	3		147
males			46	108	32	7	4				199
1988											
June											
females			27	69	21	8	11	9	4		149
males			19	30	8	2	3	1			63