THE ECOLOGY OF LACERTIDS AT GIBRALTAR

by JOHN E CORTÉS

ANIMAL ECOLOGY RESEARCH GROUP
DEPARTMENT OF ZOOLOGY
and
MAGDALEN COLLEGE

A THESIS SUBMITTED FOR
THE DEGREE OF DOCTOR OF
PHILOSOPHY, AT THE
UNIVERSITY OF OXFORD
HILARY TERM, 1984

TO THE BIRDS OF GIBRALTAR,
WHO MADE WAY FOR THE LIZARDS

CONTENTS

CONTENTS

CHAPTER 4 - MORPHOLOGY

ABSTRACT

THE ECOLOGY OF LACERTIDS AT GIBRALTAR

by JOHN EMMANUEL CORTES, MAGDALEN COLLEGE, OXFORD.

Submitted for the degree of Doctor of Philosophy

HILARY TERM, 1984.

ABSTRACT

Behavioural and ecological studies on southern European reptiles have been few. Knowledge even of the distribution and habitat requirements of the herpetofauna of southern Iberia is limited.

The reptile fauna of Gibraltar was studied in relation to the history of the habitats, and compared to that of the region. Habitats, climate, and relevant aspects of microclimate are described.

Work centred on the Iberian Wall Lizard *Podarcis hispanica* which where possible was compared to *Psammodromus algirus* with which it sometimes occurred.

Data were collected from lizards captured in the field and kept in captivity, which were used in experiments, and from transect and continuous observations in the wild. Morphology, use of microhabitat, height and substrate preferences, annual activity, emergence, temperature relations, metabolism and behaviour were investigated. Where possible, comparison was made between lizard size classes and sexes.

The observational and experimental data suggest that Gibraltar *P. hispanica* are well adapted to their environment. Using a variety of thermoregulatory methods they can maintain fairly uniform body temperature throughout the year.

They appear to change their distribution in the habitat seasonally in response to the need for food and shelter. Activity is most severely restricted during the hottest part of the day in summer and in overcast weather.

It is suggested that *P. hispanica* is an opportunistic feeder consuming a variety of small invertebrates during bouts of foraging which vary in length and frequency according to time of year.

Lizards are tolerant of each other outside the breeding season, when males become aggresive towards each other and females and juveniles show more appeasement behaviour.

The results for *P. hispanica* are discussed in relation to existing work on other lizards, especially lacertids from more northerly locations in Europe.

ACKNOWLEDGEMENTS

This work was partly financed with a grant from the Government of Gibraltar. I am endebted to my family, especially my late uncle Pepe Casellas,for their financial support. H.E. the Governor of Gibraltar authorised the collection of lizards under the Animals and Birds Ordinance (1964).

Gravediggers and mourners at North Front Cemetery, at first incredulous, showed great understanding, as did the Barbary Partridges at Bruce's Firebreak, who changed feeding grounds while I was there.

I am grateful to a great many others. My supervisor, Dr. Malcolm Coe,took me into the Animal Ecology Research Group in the first place and supported me throughout. Dr. Clive Finlayson rendered his usual moral support. Alan Bullock provided his Close.

Most of all I am endebted to my wife, Valerie. She has been field assistant, driver and secretary throughout the work. Above all, her patience and understanding, and her love of animals - including lizards - has helped me through the past four years.

CHAPTER 1

INTRODUCTION

1 INTRODUCTION

1.1.1 Historical - General

Most recent herpetological work has been carried out in the New World. The Anolis lizards of North America and the Caribbean are particularly well studied, especially with regard to ecology and niche relationships. Other lizard genera, such as Sceloporus and Dipsosaurus have also been the subjects of fairly intensive ecological, behavioural and physiological study (e.g. Porter et al., 1973). Schoener and Pianka especially have used examples from herpetology in formulating and expanding on general biological concepts such as optimal foraging and the evolution of communities. The work carried out in America, and also in Australia (refs. in Heatwole 1976), has not been matched in Europe in terms of quantity. However, the research of Saint-Girons & Saint-Girons, 1956; Saint-Girons & Duguy, 1970) on the Continent and of Avery (1971, 1973, 1975, 1976, 1978) in Britain, for example, have been useful contributions to the study of the European herpetofauna and has almost certainly inspired other workers.

Herpetology has never had the amateur backing that has made ornithology such a popular and well-studied science. This fact may well have contributed to the relatively slow growth of herpetological research. In recent years, amateur herpetologists in Europe have become progressively more organised and have established international contacts with other amateurs and with professional zoologists. This progress culminated in the holding of the 1980 European Herpetological Symposium, organised by the amateur Association for the Study of Reptilia and Amphibia (A.S.R.A.) but with participation of professional herpetologists. The Symposium led to the adoption of the International Strategy for the Conservation of the European Herpetofauna (Appendix 1), to the publication of Newsletters and to the holding, in 1981, of the International Herpetological Congress. Here a number of sessions were again dedicated to research and conservation in Europe (British Journal of Herpetology, December 1982). Together with the work of national herpetological societies and the Societas Herpetologica Europaea, the process has resulted in greater contact between herpetologists throughout Europe and should lead to a more co-ordinated approach to herpetological work.

1.1.2 Historical - Iberia

Apart from the research already mentioned, European herpetological papers have recently been published by other workers, including Bons (1974), Busack (1977, 1978) and Mellado (1980; Mellado *et al.*, 1975). *Lacerta vivipara* and to a lesser extent *L. agilis*, have been particularly well studied (e.g. Avery 1971, 1973, 1975, Cragg, 1978a & b, House *et al.*, 1980). The related Mediterranean lizard *Podarcis muralis* has also been the subject of some scientific research (e.g. Saint-Girons & Duguy, 1970; Boag, 1973; Avery, 1978).

Taking into consideration the relatively greater number of amphibian and reptile species found in the Iberian Peninsula compared to the rest of western Europe, there has been comparatively little work done in the region. Salvador (1974) produced a field guide to the species of the Peninsula which was used by Schall & Pianka (1977) to discuss the distribution of the Iberian herpetofauna in relation to the climate of the region. Mellado (1975) and other workers at the Estación Biológica de Doñana (e.g. Mellado *et al.*, 1980) have carried out some ecological work on the lizard communities of the Coto Doñana in southern Spain. This work has dealt mainly with niche relationships of a number of species in different habitats rather than with individual species biology, although some work of this type, particularly on *Psammodromus algirus* (Mellado & Martinez, 1974) has been done. Busack (1977, 1978) also worked in Andalucia. With few exceptions this other Spanish work has been short-term, almost exclusively in spring and summer. Work by visiting, mainly British, herpetologists has resulted in a number of interesting publications (e.g. Patterson & Davies, 1978, Davies *et al.*, 1981, Hailey *et al.*, 1982) but has again been restricted, as far as field work is concerned, to brief visits of several weeks' duration (McClelland, pers. comm.). Fairly extensive laboratory studies of *Podarcis hispanica* have been carried out by Patterson and McCelland (McClelland, pers. comm.).

There has been no previous attempt to study the ecology of any Iberian reptile in the field during the whole of the annual cycle.

A study of this type is particularly interesting in a region with such a markedly seasonal climate. Nor has any serious attempt been made in the past to accurately determine the habitat requirements of Iberian species.

1.2 Gibraltar - Introductory

1.2.1 Geology and topography

Gibraltar (36° 7'N, 5° 21'W), is situated at the eastern end of the Strait of Gibraltar, and together with the southern coast of the Spanish Province of Cadiz, forms the northern shore of the Strait (Figure 1.1). The Rock is a mass of Lower Jurassic limestone running approximately north-to-south along the greater part of a peninsula about 6 kilometres long and 1.2 kilometres across at its widest point. The northern end of the peninsula is a flat isthmus which connects the Rock to the Spanish mainland.

The northern and eastern faces of the Rock consists of steep cliffs rising to about 426 metres above sea level. The eastern cliffs are ascended to 290 metres along the northern half by accumulated sand slopes. The western slopes of the Rock are less steep and largely vegetated, although the town covers the lower parts. On the south of the peninsula a series of flat, stony terraces descend from the highest point to the sea.

The terms "Gibraltar" and "the Rock" are synonymous locally, but in this work "the Rock" will refer specifically to the limestone mass, in order to distinguish this from "the isthmus", which has a different geology and vegetation. The term "Upper Rock" refers to the vegetated areas above the town on the western slopes (Figure 1.2).

1.2.2 Climate

Gibraltar's climate is Mediterranean. Mean temperatures of the coldest and warmest months are 13°C and 24°C respectively for January and August (2.1.3). Mean annual rainfall is 797mm although there are considerable yearly variations (Cortés, 1979). Most rain falls between October and April. Due to its position close to the Atlantic Ocean, Gibraltar experiences less extreme temperatures and more rainfall than much of the surrounding area and locations further east around the Mediterranean (Cortés 1979).

Prevailing winds (88% of days in the year) are from the east or west sectors. Winds from north and south sectors are rare. Easterlies, coming over the Mediterranean and forced up sheer cliffs, cause condensation and produce an often dense cloud known as "Levanter". Usually - particularly during the summer - the cloud covers the Rock while the isthmus and extreme south remain clear. At other times the cloud will stretch several kilometres north and west from Gibraltar.

Features of climate thought to have a bearing on lizard activity are considered again in Chapter 2.

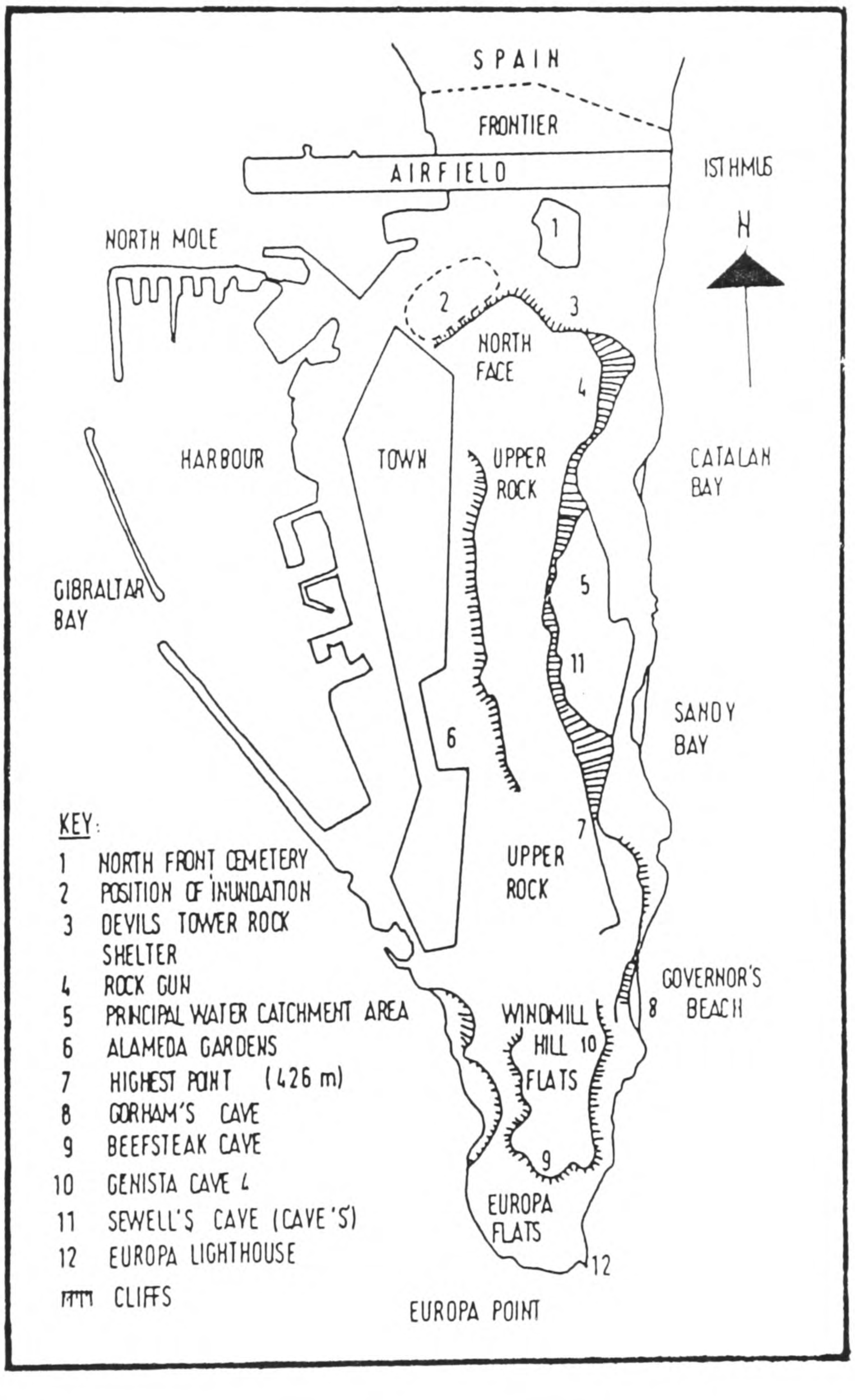
FIG.1.1a

GEOGRAPHIC POSITION OF CADIZ PROVINCE WITHIN IBERIA

FIG 1.1b

GEOGRAPHIC POSITION OF GIBRALTAR

FIG. 1.2
GIBRALTAR - SHOWING LOCALITIES MENTIONED IN THE TEXT



1.3 The herpetofauna of Gibraltar

1.3.1 Comparison with the herpetofauna of the region

Schall & Pianka (1977) summarised the number of amphibian and reptile species found in one degree grid squares over the whole of the Iberian Peninsula (based on the distribution maps in Salvador, 1974). Both works give totals for the Peninsula of 21 species of amphibian (8 salamanders and 13 frogs and toads) and 36 species of reptile (4 chelonians, 18 lizards, 1 amphisbaenian and 13 snakes). These are the highest numbers in any western European country or region. There is an even larger herpetofauna in Morocco, across the Strait from Gibraltar. Bons (1972) lists 90 species as definitely occuring, these being 10 amphibians (2 salamanders and 8 frogs and toads) and 80 reptiles (3 chelonians, 53 lizards, 3 amphisbaenians and 21 snakes). Bons (1972, 1973, 1975) and Busack (1977) discuss various theories accounting for the differences in the number of species in the two regions. The obstacle of the Strait of Gibraltar is thought to have been the major obstacle to the recolonising of Europe after the retreat of amphibians and reptiles during the glaciation. Although some colonisation has apparently occurred from eastern Europe around the Pyrenees, and rafting from North Africa is believed to have been likely (Busack, 1977) a considerable difference in number of species (= species density in Schall & Pianka, 1977) remains.

Gibraltar holds a number of species in its flora and fauna which are essentially North African and occur nowhere else in Europe. It is widely believed that the Barbary Partridge Alectoris barbara and the Barbary Macaque Macaca sylvanus were introduced by the Moors around A.D. 700 - 800 although this is by no means definitely established (Cortés et al.,1980, Cortés,1983). The case of the Gibraltar Candytuft Iberis gibraltarica is likewise unsolved. It is worth noting that no otherwise-exclusively North African reptile species occur on Gibraltar. It is unlikely that the Moors would have voluntarily introduced any such species or, with the possible exception of the Chameleon Chamaeleo chamaeleon have kept them as pets.

In comparison even to that of Spain, the herpetofauna of Gibraltar is limited. One amphibian, 6 lizards, 1 amphisbaenian and 6 snakes currently occur. Table 1.1 lists the number of species in each genus found in Iberia, Gibraltar and Morocco. Table 1.2 lists the species reported as occurring in Provincia de Cádiz, Spain, adjacent to Gibraltar (Figure 1.1) by Salvador (1974) and Busack (1977) and those attributed to Gibraltar by Busack (1977) and this study.

Some older records, which have been quoted in recent publications, require comment. Busack (1977) gives distribution maps for the herpetofauna of Provincia de Cádiz, and includes Gibraltar. The distributions are based on records at points along roads, general collecting and museum specimens (Busack pers. comm.). The records for Gibraltar were taken from the catalogues of the British Museum (Natural History) (Busack pers. comm.).

All the species given except four occur in Gibraltar today. Seven species which do occur are not reported by Busack (since there are no specimens in the British Museum (Natural History)). Of the four which are absent, two, Acanthodactylus erythrurus and Natrix maura occurred until recently (1.3.3.), the former species still occurring occasionally as a vagrant from Spain. The Psammodromus hispanicus record has not been traced and no other record of the species is known to me. The record for Chamaeleo chamaeleon is doubtful. The British Museum (Natural History) specimens consist of a group of embryos which formed part of a collection of different species from around the world donated to the Museum by a British serviceman returning from Gibraltar. There is no indication as to the exact point of collection. Experience has shown that old botanical and ornithological records attributed to Gibraltar have in many cases originated from anywhere within a wide area around Gibraltar in Cádiz Province, especially that part of it known as the "Campo de Gibraltar" (loosely translated as the "Ground (or Hinterland) of Gibraltar"). No particular care was taken to identify those species collected in Gibraltar itself (Cortés et al., 1980). Old herpetological records should be considered in this light, particularly since both Chamaeleo chamaeleon and

TABLE 1.1 Number of species in each amphibian and reptile genus found in Iberia (Salvador, 1974), Gibraltar (this work) and Morocco (Bons, 1972).

		No. of species		
		IBERIA	GIBRALTAR	MOROCCO
AMPHIBIANS				
CAUDATA				
Salamandridae				
Salamandra		1	0	1
Chioglossa		1	0	0
Pleurodeles		1	0	1
Euproctus		1	0	0
Triturus		4	0	0
	Totals	8	0	2
ANURA				
Discoglossidae				
Discoglossus		1	0	1
Alytes		2	0	1
Pelobates		1	0	1
Pelodytes		1	0	0
Bufonidae				
Bufo		2	0	3
Hylidae				
Hyla		2	0	1
Ranidae				
Rana		4	0	1
	Totals	13	0	8
REPTILES				
TESTUDINES				
Testudinidae				
Testudo		2	0	1
Emydidae				
Emys		1	0	1
Mauremys		1	0	1
	Totals	4	0	3

TABLE 1.1(contd.).

	No. of species		
	IBERIA	GIBRALTAR	MOROCCO
SAURIA			
Gekkonidae			
Gekonia	0	0	1
Hemidactylus	1	0	1
Ptyodactylus	0	0	1
Quedenfeldtia	0	0	1
Saurodactylus	0	0	3
Stenodactylus	0	0	2
Tarentola	1	1	5
Agamidae			
Agama	0	0	2
Uromastix	0	0	1
Chamaeleonidae			
Chamaeleo	1	0	1
Lacertidae			
Acanthodactylus	1	0	8
Eremias	0	0	5
Lacerta	6	1	3
Podarcis	2	1	1
Ophisops	0	0	1
Psammodromus	2	1	3
Algyroides	1	0	0
Varanidae			
Varanus	0	0	1
Scincidae			
Chalcides	2	2	6
Eumeces	0	0	2
Scincus	0	0	1
Sphenops	0	0	2
Anguidae			
Ophisaurus	0	0	1
Anguis	1	0	1
Totals	18	6	53

TABLE 1.1(contd.).

	No. of species		
	IBERIA	GIBRALTAR	MOROCCO
AMPHISBAENIA			
Amphisbaenidae			
Blanus	1	1	1
Trogonophis	0	0	2
Totals	1	1	3
SERPENTES			
Leptotyplopidae			
Leptotyphlops	0	0	1
Boidae			
Emyx	0	0	1
Colubridae			
Boaedon	0	0	1
Coluber	2	1	2
Coronella	2	1	1
Lytorhynchus	0	0	1
Elaphe	2	1	0
Macroprotodon	1	1	1
Malpolon	1	1	2
Natrix	2	1	2
Psammophis	0	0	1
Sphalerosophis	0	0	1
Elapidae			
Naja	0	0	1
Viperidae			
Bitis	0	0	1
Cerastes	0	0	2
Echis	0	0	1
Vipera	3	0	2
Totals	13	6	21

TABLE 1.2 Amphibians and reptiles attributed to Cadiz Province, Spain (Salvador, 1974; Busack, 1977) and Gibraltar (Busack, 1977; this study).

	CADIZ		GIBRALTAR	
SPECIES	Salvador	Busack	Busack	This study
Salamandra salamandra (L.)	-	+	-	-
Pleurodeles waltl MICHAHELLES	+	+	-	-
Triturus marmoratus (LATREILLE)	+	+	-	-
Discoglossus pictus OTTH	+	+	-	-
Pelobates cultripes (CUVIER)	+	+	-	(-)
Pelodytes punctatus (DAUDIN)	+	+	-	-
Bufo bufo (L.)	+	+	-	-
Bufo calamita LAURENTI	+	+	-	-
Hyla meridionalis BOETTGER	+	+	-	-
Rana ridibunda PALLAS	+	+	-	-
Emys orbicularis (L.)	+	-	-	-
Mauremys caspica (GMELIN)	+	+	-	-
Tarentola mauritanica (L.)	+	+	+	+
Hemidactylus turcicus (L.)	+	+	-	-
Chamaeleo chamaeleon (L.)	+	+	+	-
Psammodromus algirus (L.)	+	+	+	+
Psammodromus hispanicus FITZINGER	+	+	+	-
Acanthodactylus erythrurus (SCHINZ)	+	+	+	(-)
Lacerta lepida DAUDIN	+	+	+	+
Podarcis hispanica STEINDACHNER	+	+	+	+
Chalcides bedriagai (BOSCA)	+	+	-	+
Chalcides chalcides (L.)	+	+	-	+
Blanus cinereus (VANDELLI)	+	+	-	+
Malpolon monspessulanus (HERMANN)	+	+	-	+
Coluber hippocrepis L.	+	+	+	+
Elaphe scalaris (SCHINZ)	+	+	-	+
Natrix natrix (L.)	+	+	+	+
Natrix maura (L.)	+	+	+	(-)
Coronella girondica (DAUDIN)	+	+	-	+
Macroprotodon cucullatus (GEOFFREY)	+	+	-	+
Vipera latasti BOSCA	+	-	-	-

Notes: (-) indicates species which have recently disappeared from Gibraltar.

Systematic order follows Arnold, Burton & Ovenden (1978).

Psammodromus hispanicus occur in Provincia de Cádiz. There is one record of Chameleon found in an urban area of Gibraltar in 1979, but it is thought to have been an animal escaped from captivity.

The list of reptiles given in The Gibraltar Environmental Group Report (1980) is inaccurate.

The absence of certain typical and common Iberian species from Gibraltar(Table 1.2)can be explained in various ways. Some species, such as Psammodromus hispanicus and Vipera latasti (which is in any case rare in Cádiz (Busack 1977)) may never have colonised the Rock. There is habitat in Gibraltar which appears to be suitable for these species. In other cases, lack or scarcity of habitat is probably the main cause of absence.

Habitats of Gibraltar are described in Chapter 2, but a brief description and history of the vegetation of the Rock as it has affected the herpetofauna can be given in this introductory chapter.

1.3.2 History of the habitats of Gibraltar

(a) The vegetation of the Rock

The main vegetated area of the Rock at present consists of the upper western slopes (Figure 1.4). The City of Gibraltar covers the lower slopes. The area covered by the City has increased from 0•06 km^2 in the later Middle Ages, to about 0•4 km^2 in 1875 (Figure 1.3) and 1•3km^2 in 1984 (Figure 1.4). Although there has been some reclamation from the sea, most development has been at the expense of the vegetated areas. On the eastern side, touristic developments and water-catchment areas (corrugated iron sheets rivetted to the ground) have been the main cause of habitat loss. Elsewhere industrial and residential development has been most important.

The vegetation of Gibraltar, like that of the rest of the Mediterranean Region, probably reached its maximal development between twelve thousand and four thousand years ago as a cover of evergreen sclerophyllous forest and pine (Tomaselli, 1977). In Iberia the forests predominated until removed by successive civilisations, including that of the Moors. There are references to extensive woodland on Gibraltar and to the use

FIG. 1.3

GIBRALTAR - AROUND 1875

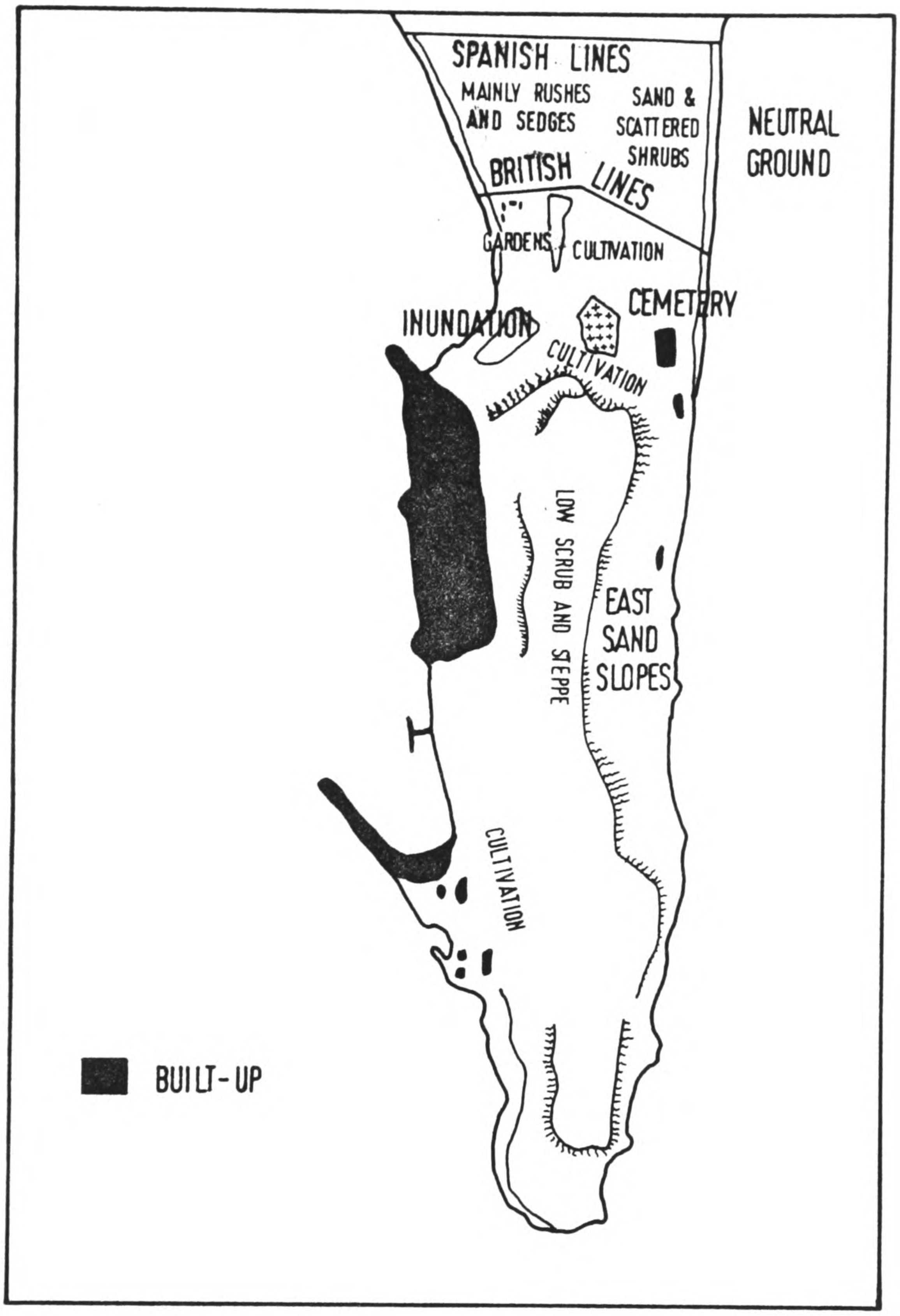
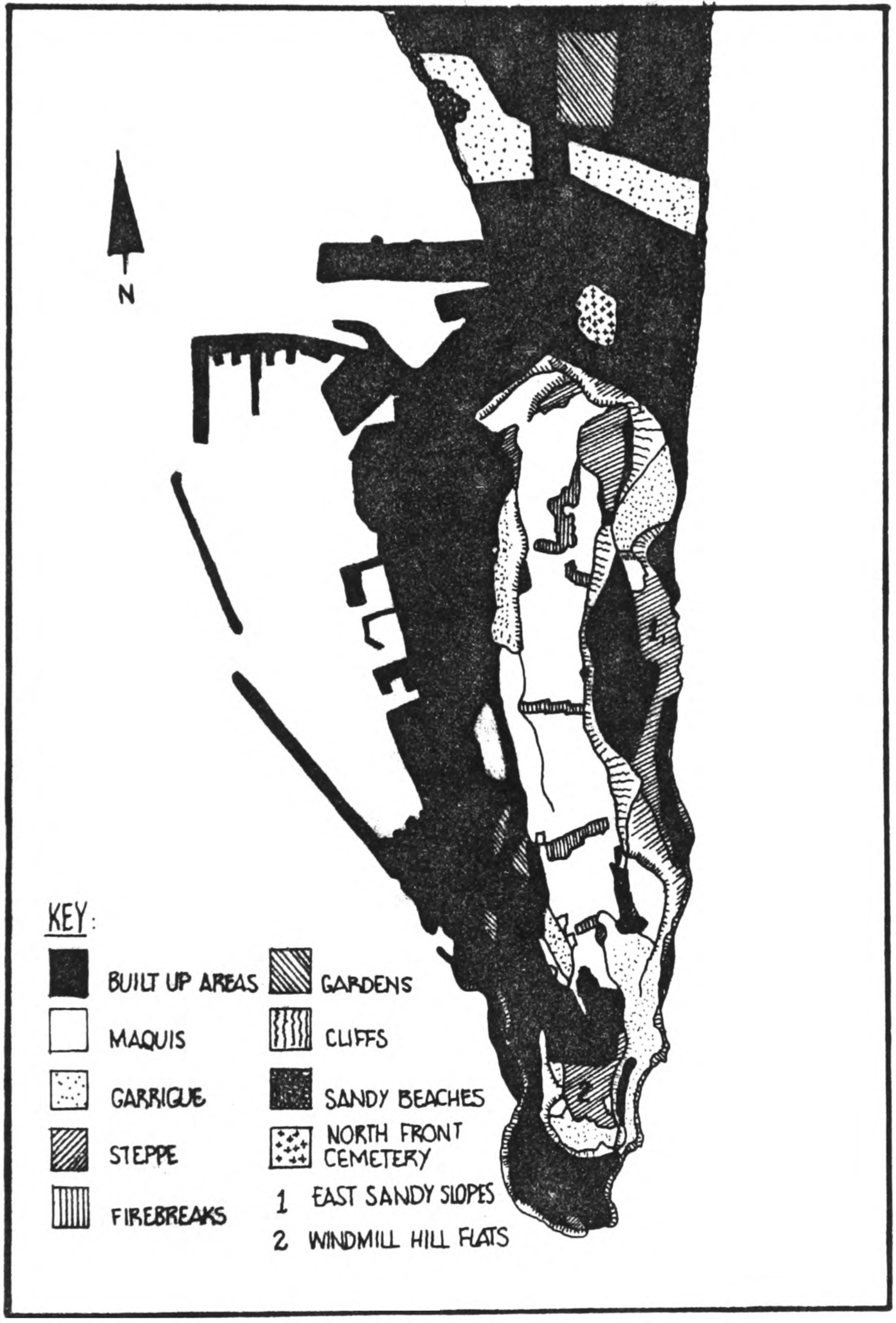


FIG 1.4

GIBRALTAR - Distribution of the major habitats 1984 (Adapted from Cortes et. al., 1980)



of the Rock as a port for the shipment of timber (Benady, in prep.) during the years of Moorish occupation (A.D. 711 - 1309). Some parts of the Rock and isthmus were under cultivation by Spanish times (1309 - 1333 and 1462 - 1704) (Ayala, 1782). The major part of the Rock was nevertheless under dense vegetation in the early 1600s (Euctemon quoted by Ayala, 1782). The cover was mainly Carob Ceratonia siliqua and lasted until 1704 (Governor's Order Book 1704) when trees and shrubs were removed to provide fuel for the British garrison (James, 1771). The vegetation, thus opened up, was maintained in this state by the grazing of goats and cattle (Gaudichaud, 1817 in Wolley-Dodd, 1914). There are numerous references around this time to "the barren rock" (Kelaart, 1846), the "general sterility of the place" (Ayala, 1782) and the vegetation of a "comparatively diminutive kind" (Kelaart, 1846).

By the early 20th Century livestock had been removed from most of the Rock and the development of vegetation encouraged. Pines Pinus and Eucalypts Eucalyptus were planted (Wolley-Dodd, 1914) and shrubs became evident above the "unclimbable fence" which delimited the upper level of grazing at around 150 to 200 metres above sea level.

Seral succession on the western slopes has resulted in the present cover of dense matorral between 2 and 8 metres tall. This is broken up by areas regularly cleared as firebreaks where the vegetation is that of garrigue or pseudosteppe (Chapter 2.2).

Windmill Hill Flats (Figure1.2) at the southern end of the Rock is largely covered by open steppe vegetation. The slopes of sand on the east of the Rock cover an area of 31 hectares, vegetated only over 8 hectares as a result of sand-quarrying and conversion to water catchments. The vegetation has apparently always been low, with scattered bushes, corresponding to garrigue and steppe.

(b) The vegetation of the isthmus

The isthmus, with a maximum height of several metres above sea level, stretches for about 3 kilometres from the base of the Rock to the foot of Sierra Carbonera on the Spanish mainland. As far as can be determined, the vegetation of the area has always been low within historical times (Ayala, 1782; Kelaart, 1846). The Spanish town of La Linea de la Concepción grew up during the 18th Century and today occupies all the land between Sierra

Carbonera and the northern end of the "Neutral Ground" (Figure 1.2) about 1·5 kilometres north of the cliffs of the Rock. All the area south of La Linea remained vegetated, with fields of cultivation nearest the Rock. After the beginning of the 20th Century, these fields were converted into gardens and rough sports grounds, and these and a cemetery occupied the land up to the British Lines (Figure 1.5). North of this the natural vegetation remained. This consisted of open sandy ground with scattered shrubs on the higher, eastern side where restharrows *Ononis* spp. were characteristic. The land fell towards sea level on the western side where the rush *Juncus acutus* and various sedges *Cyperus* spp. dominated. This area was subject to flooding with rainwater in winter and spring.

On the southwestern corner of the isthmus lay several semi-permanent fresh water lagoons (Figure 1.5) which were finally filled in around 1941. At this time the construction of the[1] airfield and associated buildings commenced, so that by 1945 virtually all the British side of the isthmus was concreted. The area north of the frontier retained its natural vegetation and was used for grazing horses.

After 1969 development began in the remaining vegetated area. Sports complexes, housing estates and roads were built and a garden of exotics planted. This together with erosion caused after opening of the area to the public, has resulted in a patch only about 300 metres long remaining in a more or less natural state. Drainage has caused a lowering of the water table (as suggested by the changes in the levels of wells on the Gibraltar side). This together with the dumping of rubble which has raised the level of the land, has resulted in a change of vegetation towards scrub, with *Inula viscosa* in parts now the dominant species. The area is now rarely flooded and what rainwater pools form do not last more than a few days. The only other significant vegetation surviving on the isthmus is the North Front Cemetery. This is largely planted with exotics, notably *Myoporum pictum* and *Lantana camara*, both shrubs which grow to several metres in

FIG. 1.5

THE ISTHMUS EARLY 20TH CENTURY

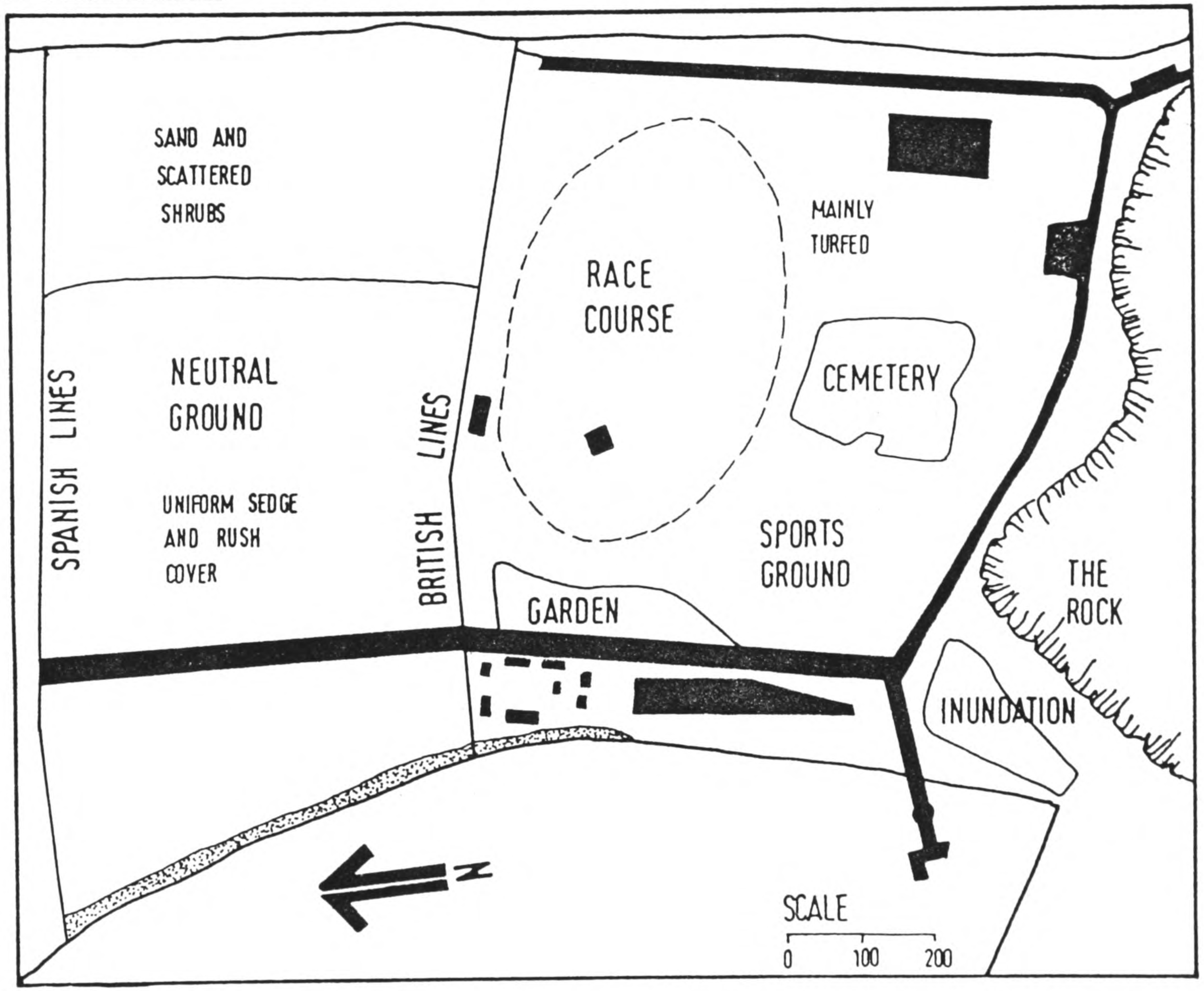
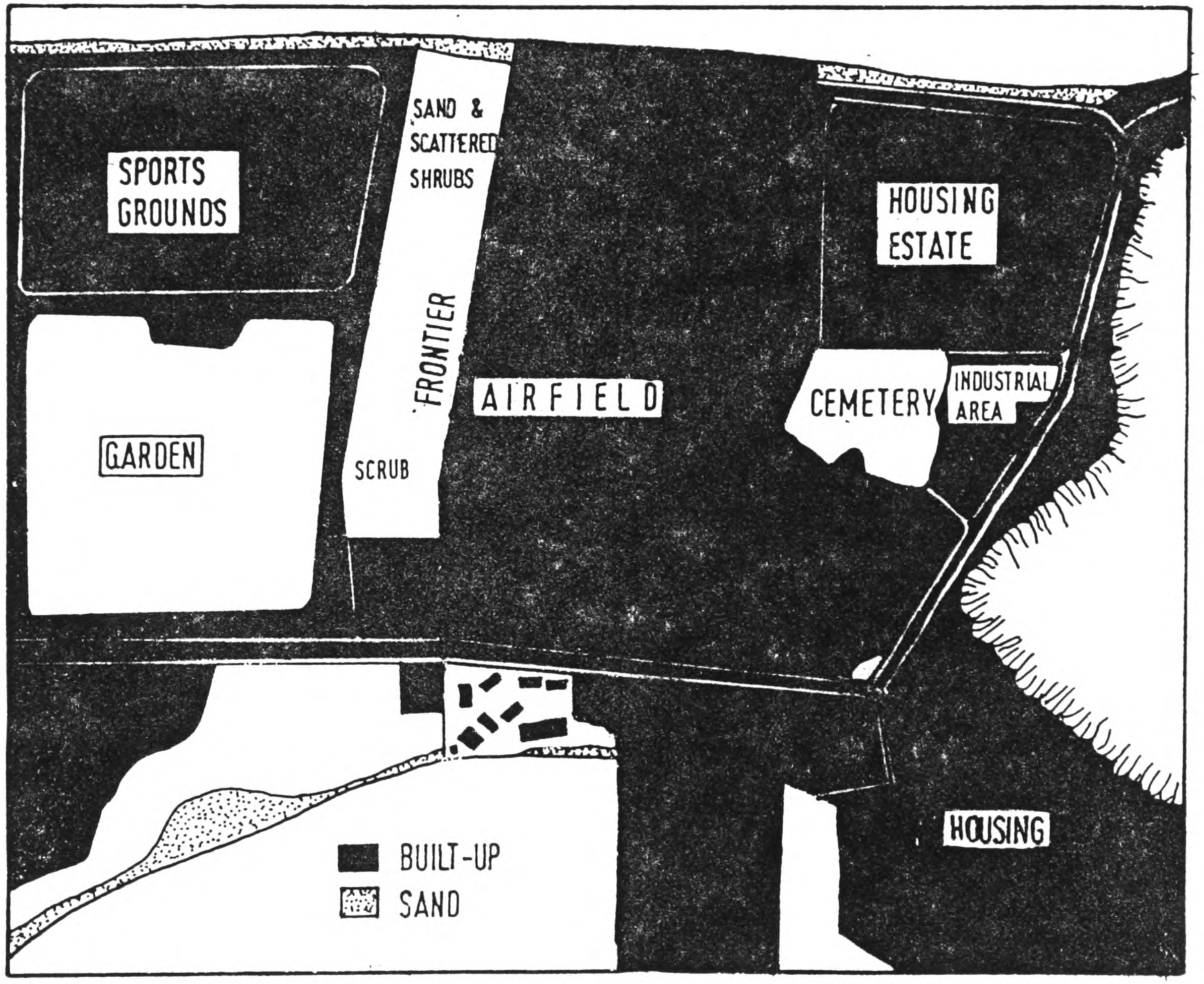


FIG. 1.6

THE ISTHMUS 1984



height. There is still some open vegetation with relict populations of the species which made up the former natural habitat of the isthmus.

1.3.3 History of the herpetofauna of Gibraltar

(a) Introduction

The effect on the fauna of the drastic change in the vegetation of Iberia as the forests were cut down, will have been considerable. This has been treated in some detail with regard to birds (Moreau, 1972).

Most of the present day reptile fauna of Iberia occurs in scrub and other degraded habitats, which in any case form the predominating cover of the region. It is not known whether reptiles were formally restricted to the relatively few open areas, such as steep or coastal zones, or whether they in fact had to adapt to present habitats from former forest-dwelling and perhaps more arboreal habits. The requirements of reptiles for basking sites suggests they may be more common than they were, or at least that the more heliothermic species are more widespread. One can do little more than speculate on this point, but it will be possible to discuss it further below in the light of evidence produced in this work. It is easier to attempt to follow the more recent history of the herpetofauna of a small area such as Gibraltar where changes in vegetation are more easily traced, at least over several hundred years, and to extrapolate from these.

The first known reference to the herpetofauna of Gibraltar is by Ayala (1782). Only a passing reference is made to snakes, and there are somewhat confusing descriptions of lizards, including one of a gecko which, it was claimed, spat poison. This gives some idea of the unpleasantness attached to reptiles, even today, by the people of the region. Some still believe that geckos have a poisonous "sting". Ayala (1782) gives a fair description of a lizard presumed to be Acanthodactylus erythrurus which he claims occurred on the "white soils" (either the east sand slopes or, more likely, the isthmus) and of Podarcis and Tarentola on roofs in the town. A vivid description is given of Lacerta lepida which was said to "abound on this hill".

(b) Recent history and present status

(i) Amphibia.

The Western Spadefoot Toad Pelobates cultripes was formerly common on the isthmus, breeding in the seasonal pools. Breeding since about 1979 is doubtful. No pools persisted during the drought years 1980 - 1982. Pools which formed after heavy rains in March 1982, and which attracted large numbers of calling toads, were filled in after several days, apparently to eliminate the noise following complaints from nearby housing estates. Some adults were observed in autumn 1982, but the continued survival of this population is in doubt due to the absence of the natural ponds. Breeding has not been confirmed in two artificial ponds in a nearby public park.

The newt Triturus marmoratus and Natterjack Bufo calamita have been reported (J. Bensusan, pers. comm.) but there are no recent records.

Reports of frogs breeding in the south of the Rock in the early part of this century may have referred to Tree Frogs Hyla meridionalis, but have been impossible to confirm.

(ii) Reptilia.

The Moorish Gecko Tarentola mauritanica is the most widespread lizard in Gibraltar. It occurs on walls of buildings, on cliffs and in rocky clearings throughout the vegetated areas. It is the best known reptile since it lives in houses in the town where it is often called the "chameleon".

The Turkish Gecko Hemidactylus turcicus, despite its littoral distribution in Iberia, has not yet been recorded in Gibraltar and is rare in Cádiz (Busack, pers. comm.).

The Spiny-footed Lizard Acanthodactylus erythrurus, formerly found in Gibraltar (Ayala, 1782) is common around La Linea on sandy ground (pers. obs.) and sometimes strays south to the Gibraltar side of the isthmus. It is likely to have been more widespread there and on the sand slopes where it does not now occur. The species does not occur at all south of the airfield. It appears that the runway, roads and housing estates of the area act as a barrier preventing movement of the lizards to the Rock.

Also present on the isthmus (including the Cemetery) are the Three-toed Skink Chalcides chalcides and Bedriaga's Skink Chalcides bedriagai, the latter having been confirmed also from the sand slopes. The Large Psammodromus or Algerian Sandracer Psammodromus algirus is common in the maquis and especially along its edges. This lizard is regularly encountered in firebreaks and open areas with scattered bushes, but avoids completely-bare ground. It is not found in the steppe vegetation of Windmill Hill Flats, the sand slopes or the isthmus. The present habitat provided by the Cemetery is similar in structure to that on areas of the Upper Rock where Psammodromus occurs. The open vegetation present there until recently was probably unsuitable for the species (and perhaps inhabited by Acanthodactylus erythrurus) and recent colonisation by Ps. algirus has apparently been impeded by the roads and other urbanisation that has isolated the Cemetery from other vegetated areas (Figure 1.6).

The Iberian Wall Lizard Podarcis hispanica is more widespread than the Large Psammodromus, but is not found over most of the town and is rarer in scrub, especially away from clearings. It is rare also in areas of low continuous vegetation (as in parts of the Cemetery) and was therefore probably rare over most of the isthmus. It is now very abundant in those parts of the Cemetery where the vegetation has been broken up by tombstones which provide basking sites and crevices.

The Ocellated or Eyed Lizard Lacerta lepida still occurs in the Cemetery, as an isolated and small population. Older labourers in the Cemetery recall times (about thirty years ago) when large lizards ("lagartos") were frequently encountered. Increasing human activity, allowing little undisturbed basking, may have contributed to the decrease in numbers of Lacerta both on the isthmus and on the Rock, particularly as available habitat shrunk. On the Rock there have been no confirmed records for at least ten years, despite regular searches. Here, seral succession may have been a main cause of the decrease.

Ocellated Lizards attract attention on open ground and are frequently pursued and quite easily captured. During the periods when the vegetation of the Rock was more open (1.3.2.) and the Upper Rock was heavily garrisoned, this may have additionally contributed to a drop in numbers. It is a fact that workers in the Cemetery still attempt to catch Ocellated Lizards whenever they encounter them - and they are often successful. The species is certainly no longer "abundant on this hill" (Ayala,1782) and is probably absent from most of the western slopes.

Snakes on Gibraltar are known from few observations, so the status of their populations is hard to determine. The Horseshoe Whip Snake Coluber hippocrepis is the species most frequently encountered in most habitats. It occurs both in dense scrub and open habitats, firebreaks, the Cemetery and gardens, sometimes venturing into houses. The Southern Smooth Snake Coronella girondica and the False Smooth Snake Macroprotodon cucullatus are also widespread but not encountered as frequently as the last species. The Ladder Snake Elaphe scalaris and Montpellier Snake Malpolon monspessulanus have only been recorded from the maquis, the latter as a single dead individual. The Grass Snake Natrix natrix has been recorded on the Upper Rock and the isthmus, while the more aquatic Viperine Snake Natrix maura, formerly found on the isthmus (J. Bensusan pers. comm.) no longer occurs.

1.4 Discussion

The reduction in size of areas available to the herpetofauna has resulted in a decrease in the populations of the different species, with the possible exception of Tarentola mauritanica. Some species have disappeared from certain areas or are in danger of doing so in other areas.

The herpetofauna has also been subjected to changes in habitat type. The habitat changes have caused changes in breeding species of birds (Cortés et al., 1980). Colonisation by new reptile species is obviously more difficult and necessarily a long-term process. The result of habitat change will often be a drop in numbers and ultimate local extinction with no new species initially taking the place of the old ones. This appears to be happening in the case of Lacerta lepida. It is not difficult to believe that in the course of centuries of often drastic vegetation change some species (perhaps Psammodromus hispanicus) may have been lost.

The problems faced by the herpetofauna of Gibraltar over the last few centuries have been and still are similar to those encountered by amphibians and reptiles in the rest of Europe: fragmentation of habitats, seral succession, disappearance of amphibian breeding sites, predation by feral cats and humans, disturbance, inadequate habitat protection and lack of law enforcement. (All wildlife is protected in Gibraltar under the 1964 Animals and Birds Ordinance. Enforcement is difficult, however, especially in the case of reptiles which are generally viewed with disgust and contempt.) The measures needed to combat these threats are also common to other countries. Public education in particular is essential, and this is gradually being achieved through the efforts of local natural history societies.

There is no protection in law against habitat loss, a matter which is currently being reviewed by the legal authorities. The difficulty lies in that there can only ever be small amounts of habitat available in a place of such a high density of population (30 000 inhabitants). Nevertheless, because of the political separation from the mainland, species of "local" importance have a "national" status. In this way species that may be common elsewhere in the the region could receive public support and protection. This could in time make Gibraltar an important refuge for a number of species.

Threats similar to those experienced in Gibraltar are currently increasing in neighbouring Spanish regions. Species which may not yet be in danger may suffer local reductions as they have done in Gibraltar. More specifically, the Campo de Gibraltar, already largely industrialised around the Bay of Gibraltar at the expense of coastal habitats, is earmarked for large scale development.

The problem of local extinction and difficulty of recolonisation of isolated patches of habitat is an important one, leading to fragmented distribution through the species' range. It has been shown that this has occurred in Gibraltar (whose history is better documented than that of most areas in the region). Short-term and local solutions - such as digging ponds for amphibians - can only meet with limited success, and do little to counteract the effect of the virtually total loss of the sensitive and rich coastal habitat of the area. This loss occurred at a time when conservationists in the area were even fewer than they are today. The danger, however, remains.

Having considered in general the herpetofauna of Gibraltar in relation to that of its hinterland, and to present and past habitats, we are in a position to look into the ecology of some of the component species of the community in more detail.

1.5 Present work and areas of study

1.5.1 Objects

The initial object of the present study was to investigate the interrelationships of the component species of the Mediterranean lizard community of Gibraltar. These were to be studied throughout the year in relation to seasonal variation and climate while lizard activity, preferred temperature ranges and seasonal variations in behaviour would be investigated. Soon after the study commenced, however, it was apparent that only three lizard species are sufficiently common in Gibraltar to allow detailed species comparison. *Tarentola mauritanica* is nocturnal for most of the year, which temporally separates this species from *Psammodromus algirus* and *Podarcis hispanica* which are diurnal. Since it would be difficult to study animals both at night and during the day it was felt that the study should be restricted to the comparative ecology of the diurnal lizard species.

Ps. algirus proved to be more difficult to observe than *P. hispanica* which was more widespread and allowed closer approach. *P. hispanica* occurs with and without *Ps. algirus* and allowed intraspecific comparisons between sexes and size classes as well as interspecific study throughout the year. This proved particularly interesting since unlike most western European reptiles *P. hispanica* in Gibraltar neither hibernates nor brummates, being active throughout the year. The bulk of the data collected and the subsequent discussion were therefore related to *P. hispanica*.

1.5.2 The study areas

Two main study areas were chosen which allowed the best direct field observation of lizards and of Podarcis hispanica in particular.

(a) Bruce's Firebreak (BFB)

This was an area of firebreak (1.3.2) above Bruce's Farm on the Upper Rock. The vegetation is reminiscent of garrigue, low plant cover, scattered bushes generally below 30cm in height, and open rock and soil. Green plant cover is almost absent between late May and the end of October, with the exception of stalks of young Jasminum fruticans and some hardy clumps of low Pistacia lentiscus. Plant growth usually commences at the beginning of November, but in 1981 was delayed until the latter half of the month by the lateness of the rains. Herbaceous annuals appear about this time, with Oxalis pes-caprae as the main species, and form a complete cover over the areas of soil by mid-December. At the same time the shrubs develop new shoots, so that by February they can reach a height of up to 50cm. Cover remains fairly continuous, except for rocky outcrops, although the predominant plant species change during the spring. The cover is never totally uniform however, once Oxalis dies back in February. After early April the rest of the herbaceous plants begin to die away so that little cover remains by early May. In either late May or early June, the vegetation is cut away in order to maintain the firebreak. This results in much dead plant material covering the ground throughout the dry summer and providing some shelter for lizards. There is often some growth of shrubs after this 'pruning', but nothing else grows until the onset of the autumn rains. This site slopes at an angle of about 45^{o} and covers an area of about 600 m^2. There is a narrow path at the bottom of the slope and beyond (west of) this a dry stone wall with many crevices between individual limestone blocks. Below the wall lies an overgrown garden where Olive trees

Olea europaea give much shade. Above the firebreak is an area of dense Maquis. The site is a part of a larger area of firebreak in the Maquis.
Bruce's Firebreak lies on the western slope of the Upper Rock. Because of this the area is in shade until several hours after sunrise when the sun crosses over the crest of the Rock. The trees below the firebreak cast a shadow over the lower area of the site (the wall and path) several hours before sunset. These factors affect the activity of the lizards. The species found in this site are T. mauretanica , Ps. algirus, and P. hispanica.

(b) North Front Cemetery (NFC)

The cemetery on the isthmus at North Front holds a number of habitats, and two main study sites were chosen there. A regular transect was made through different habitats, and one of the sites for observation was chosen within the transect route. This first site (NFC 1) is shown in Figure 5.1. The area is sandy, bare in the summer between May and October except for the bushes of introduced plants. The main shrubs are Pelargonium spp. (from South Africa) and Lantana camara (from the West Indies). The Pelargonium bushes reach a height of about 1m , Lantana about 2m. Ground cover starts to appear after the first autumn rains and consists largely of Oxalis pes-caprae, but other annuals grow later, notably Lotus spp. and Chrysanthemum coronarium. After most of the herbaceous species have dissappeared in May, low plants of straggling Centaurea bullata persist through the summer and when in flower attract large numbers of insects.
The site remained remarkably undisturbed, considering its position in a public cemetry, from the start of its use in September 1980 to September 1981 when disturbance and change of habitat were brought about by the trimming of vegetation and by grave digging. Observations were then moved to the eastern end of the cemetery.

Two adjacent areas constituted the eastern site (NFC 2). The first was known as 'NE Wall'(Figure 5.16). This is an area dominated by a stone wall, about 1.5m tall, sloping at an angle of about 60° to the vertical and running approximately south-west to north-east for 20 metres. The wall forms the eastern edge of a raised plateau of about 100 metres^2. Immediately below the wall and parallel to it, runs a narrow (1.5m wide) tarmac path separating it from an area of mainly grassy vegetation lined by a row of 2m tall bushes of Myoporum pictum. The site was chosen since it allowed a clear view of lizards using the area as they basked or foraged in the low (10 cm tall) vegetation which covers areas of the wall between October and May. The plants growing in the cracks in the wall were Oxalis pes-caprae, Lobularia maritima and Lotus spp. An added advantage of the site is the fact that a line of cracks ran along the tombstones on the top of the wall, which lizards use at night. Emergence in the morning and retreat when temperatures fell could therefore be seen.

The second area, continuous with 'NE Wall' was known as '+' ('cross'). It consisted of a flat 60 square metre patch bordered by 2m tall Myoporum bushes. The vegetation of the patch is almost exclusively of the grass Panicum repens reaching a height of about 50cm, which persisted throughout the year and did not die back to reveal bare ground in summer. Just off-centre of this patch is a marble cross (giving the site its name), standing on two concrete blocks (Figure 5.15). Cracks between these blocks provide refugia for lizards. The cross, with its stand and a small concrete cubic structure one metre to the south were the only basking sites available in the main area of grass, although a number of tombstones scattered around the patch were occasionally also used. The cross was an ideal location on which to observe lizard behaviour since the animals congregated on it both to seek shelter and to bask.

By far the commonest lizard species in the Cemetery was P. hispanica. T. mauritanica and some Lacerta lepida are also found, and Chalcides chalcides and C. bedriagai are occassionally encountered. Ps. algirus, however, is absent.

Both areas in North Front Cemetery are generally free from the influence of the Levanter Cloud (1.2.2.), especially during the summer months when the sun is high in the sky and is not obscured by the cloud over the Rock to the south. The Bruce's Firebreak site on the other hand is usually the first area of the Rock to be covered by the cloud.

Sites other than those described above were used occassionally. Some sites were used at first but were later abandoned after proving unsuitable for some reason (e.g., animals not easily observed, shaded during most of the day, etc.).

Most of the work that is discussed below was carried out on the main sites in particular North Front Cemetery, but occassional reference will be made in the text to other locations.

Appendix 2 contains photographs of the main study sites.

CHAPTER 2

ENVIRONMENTAL CONDITIONS

2 ENVIRONMENTAL CONDITIONS

2.1 Climate and microclimate

2.1.1 Introduction

A knowledge of the climatic conditions of the region in which the study sites are located is an essential background for the study of any species, particularly of an ectotherm. While much climatic information is superfluous in this case, data on temperature, sunshine and solar radiation are particularly relevant. The information given in this section will be a useful backdrop against which to consider the material in following chapters.

Several sources of climatological data were used. The main ones were the records and reports of the Royal Air Force Meteorological Office at Gibraltar. The R.A.F. recording station is situated only about 500m north-west of the North Front Cemetery study sites.

The Smithsonian Meteorological Tables and the Nautical Almanac (1982) were used as sources of astronomical data for calculation of solar radiation. Deacon (1969), Geiger (1969) and Escardó (1970) were also used as sources of data in particular for comparisons with climates of other areas in Iberia.

2.1.2 Methods

(a) Climate

Mean, maximum and minimum temperatures, sunshine and cloud cover were obtained from the meteorological data. Continuous recordings of air temperatures were made, using a thermograph, from December 1979 to November 1981, to supplement the meteorological office data. The thermograph was situated in a sheltered site in the Town of Gibraltar about 800m west of the Bruce's Farm Firebreak site.

Solar radiation at the surface (J_s), assuming perfectly clear skies, was calculated for hourly intervals for the 1st and 15th of each month using the following formula from Geiger (1969):

$$J_s = \frac{J_o}{e^2}(\cos\varphi \cos\delta \cos t + \sin\varphi \sin\delta) \quad J\ cm^{-2} min^{-1}$$

J_o is the solar constant (the radiation received at normal incidence at the outer limits of the earth's atmosphere corresponding to the mean distance of the sun from the earth) and is 8•08 $Jcm^{-2}min^{-1}$; e is the ratio of the actual sun-earth distance to the mean sun-earth distance (assumed here to be unity); δ is the declination (which varies through the year and is positive when the sun is north of the equator and negative when it is south of the equator); φ is the latitude (36° 7•292' N); and t is the hour angle (t = 0 at noon, is negative in the morning and positive in the afternoon). The values of these constants and variables were obtained from the Nautical Almanac.

(b) Microclimate

Temperatures of the air and ground were measured directly using thermistor probes, shaded when readings were being taken.

Air temperatures were taken before each transect or other field session. Substrate temperatures were taken during transects at points where lizards had been basking or foraging when first observed. In addition temperatures were taken at random under different heights of vegetation, morning and afternoon, to give indications of the temperature regimes to which the lizards were subjected in the field. Fifty recordings were made per area.

A multichannel thermograph recorder was used with six thermistor probes inserted in different points in and around vegetation during certain continuous observation sessions.

Microclimates are discussed in greater detail in Chapter 8.

2.1.3 Results

(a) Climate

The relevant climatological data are presented in Tables 2.1 to 2.4 and Figures 2.1 to 2. 21.

Figure 2.1 displays the data in Table 2.1 and shows monthly

Table 2.1 Mean, lowest and highest monthly air temperatures and lowest grass temperatures at Gibraltar; 1980 - 1982.

		Temperatures (°C)											
		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1980	Highest	18·0	21·5	25·6	31·6	26·4	32·4	34·7	38·8	35·2	27·8	23·4	21·6
	Mean	12·0	14·7	14·9	17·0	18·5	21·9	23·0	24·9	23·9	19·3	16·2	12·9
	Lowest	5·2	8·5	8·4	8·7	12·4	15·5	16·3	17·0	16·4	8·7	7·5	4·8
	Lowest grass	2·0	4·0	4·0	6·2	7·4	12·4	15·0	12·6	14·0	4·6	4·4	0·4
1981	Highest	20·4	20·6	26·1	23·7	25·8	30·4	32·4	34·3	31·4	27·3	24·3	21·2
	Mean	12·9	16·9	20·2	19·0	22·6	25·1	26·6	27·9	26·5	23·3	19·9	18·0
	Lowest	3·1	6·5	9·2	8·5	10·5	15·6	17·0	17·4	14·7	13·5	10·9	6·3
	Lowest grass	-1·3	2·3	5·5	7·6	9·8	10·0	12·4	14·5	12·4	10·6	9·3	4·1
1982	Highest	24·0	21·1	23·6	24·5	21·9	31·6	36·7	33·0	28·8	30·4	21·4	19·8
	Mean	14·3	14·4	15·7	16·3	20·9	22·5	24·1	22·7	23·1	18·7	15·8	13·0
	Lowest	8·5	5·5	9·5	10·8	13·0	16·1	15·8	16·9	16·5	10·9	9·0	6·5
	Lowest grass	5·5	4·0	4·8	7·5	9·8	13·9	14·0	14·2	15·0	7·0	5·5	3·5

Fig. 2.1 MEAN, LOWEST, HIGHEST AIR TEMPERATURES AND LOWEST GRASS TEMPERATURES FOR EACH MONTH IN 1980, 1981 AND 1982

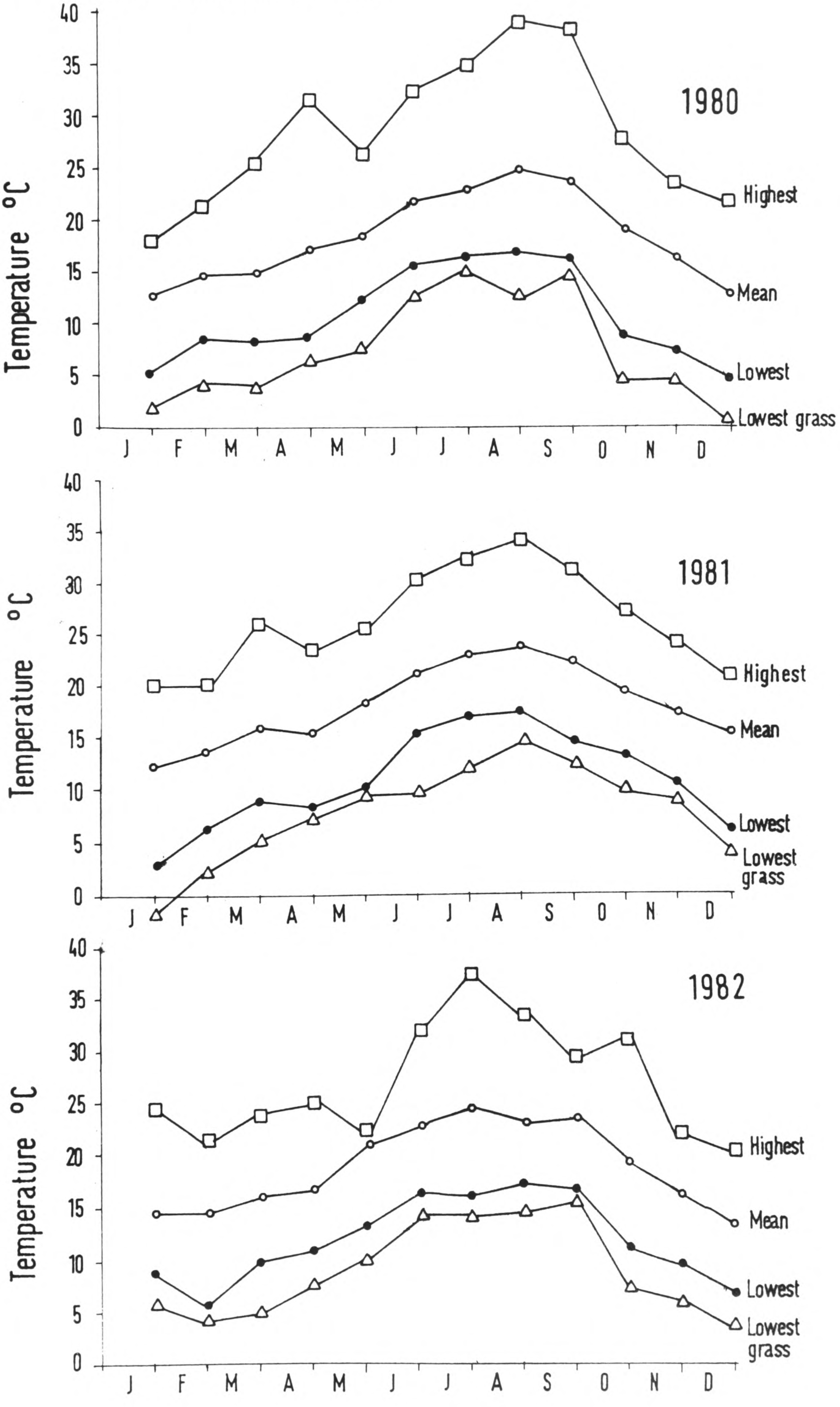


Fig 2.2 AVERAGE DAILY MEAN TEMPERATURES FOR TWO-WEEK PERIODS FROM DECEMBER 1979 TO APRIL 1982

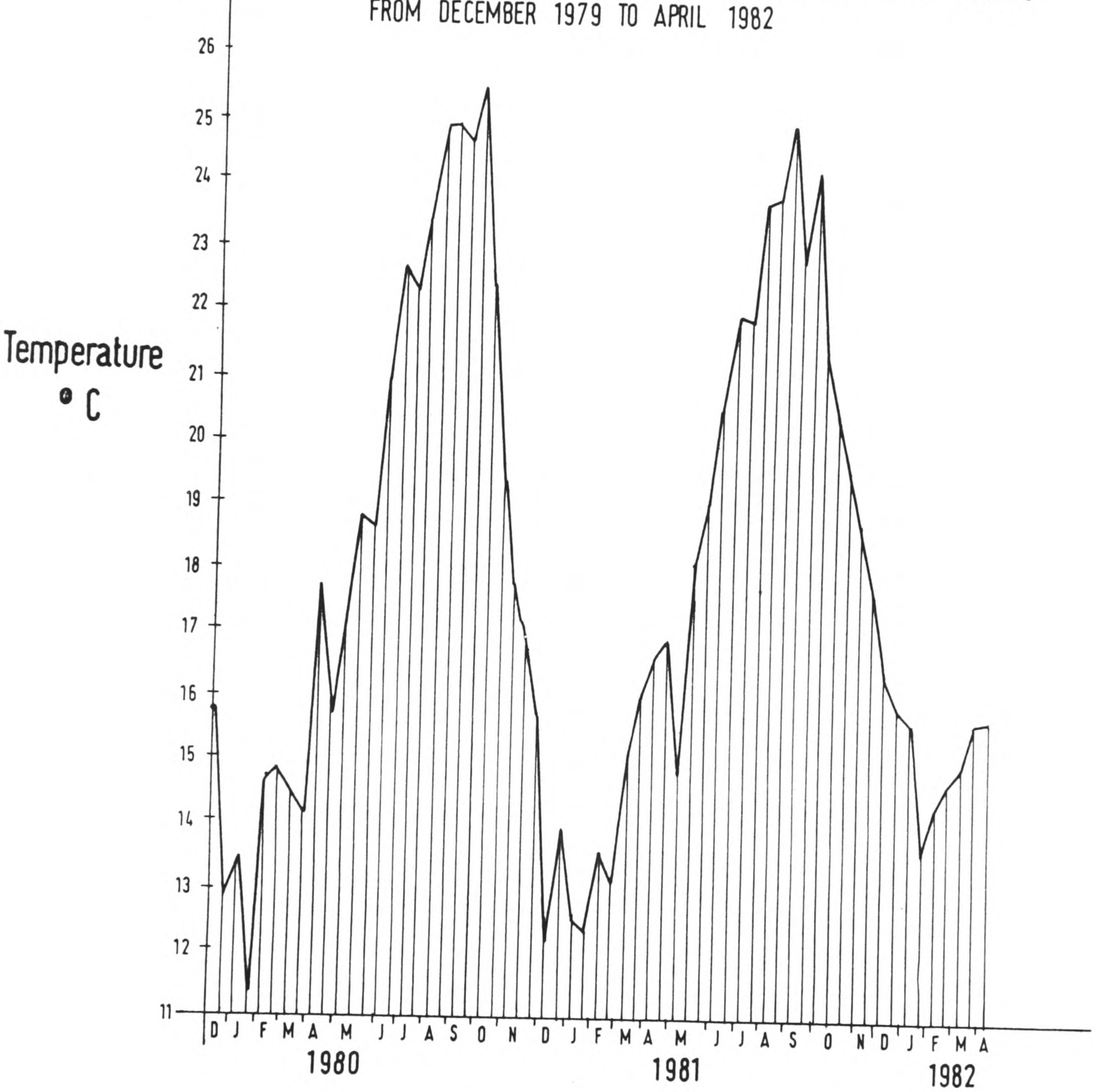


Table 2.2 Long term average mean temperatures and hours of sunshine per month at Gibraltar.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Temperature (°C)	13•1	13•5	14•7	16•4	18•7	21•2	23•6	24•2	19•2	16•3	13•3	10•5
Sunshine (hours)	155•5	153•0	196•6	246•5	245•3	320•6	344•5	325•9	259•3	208•1	151•7	144•4

Fig. 2.3 LONG TERM MONTHLY MEAN TEMPERATURES FOR GIBRALTAR

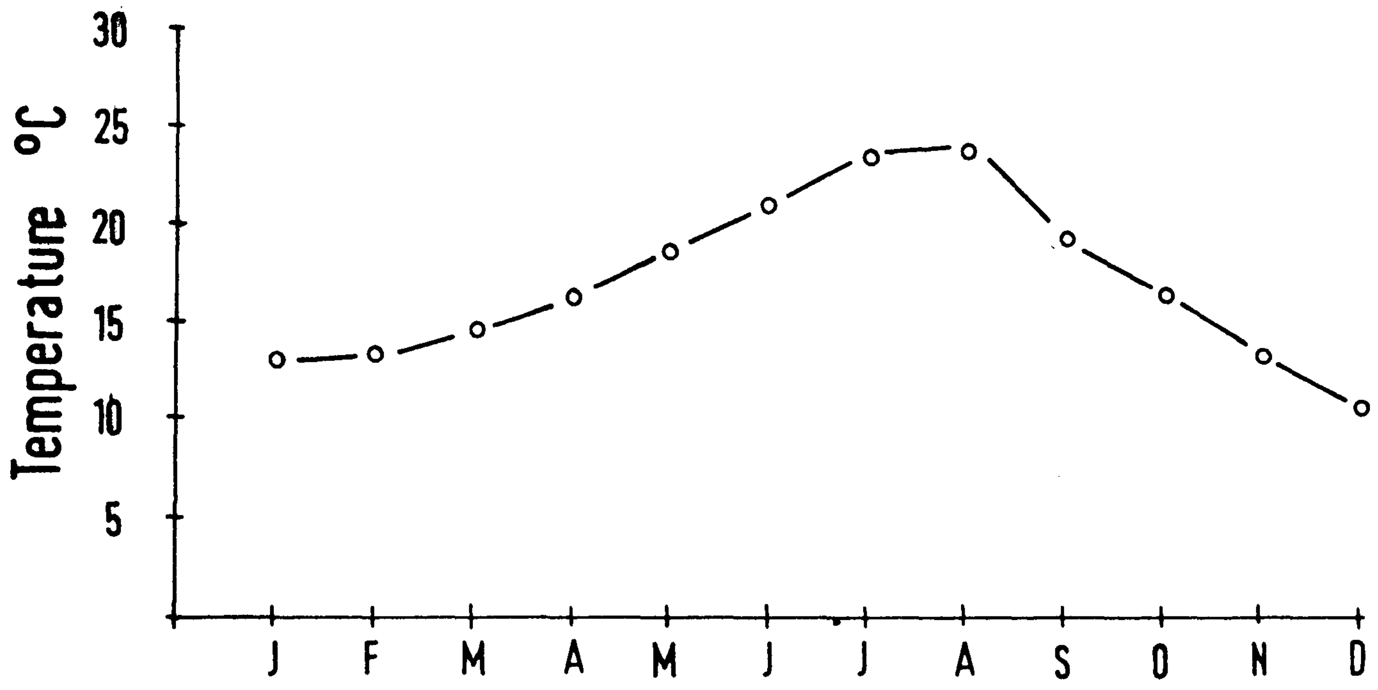


Table 2.3 Mean air temperatures at Gibraltar for fixed hours each month : 1980 - 1982. (°C).

	Time (GMT)				
Month	0200	0800	1400	2000	Year
JANUARY	11·2	11·4	14·6	12·3	1980
	11·1	11·3	15·2	12·6	1981
	12·7	12·7	16·8	13·6	1982
FEBRUARY	13·0	13·1	17·2	13·9	1980
	12·0	12·0	16·1	13·3	1981
	13·1	13·2	16·3	14·0	1982
MARCH	12·8	14·0	17·3	14·6	1980
	14·2	15·0	19·3	15·8	1981
	14·2	14·8	17·9	15·1	1982
APRIL	14·4	16·2	19·0	15·8	1980
	13·9	15·2	17·9	15·1	1981
	14·7	16·0	17·9	15·9	1982
MAY	16·2	18·2	20·8	17·5	1980
	15·7	18·0	21·3	17·1	1981
	16·9	18·8	21·1	18·1	1982
JUNE	18·7	20·9	24·5	20·4	1980
	18·8	21·4	23·9	19·9	1981
	19·9	22·1	24·9	21·1	1982
JULY	20·6	22·2	25·5	22·1	1980
	20·6	23·0	25·6	21·9	1981
	20·9	23·0	27·3	22·9	1982
AUGUST	21·8	24·0	27·7	23·4	1980
	20·9	22·9	26·4	22·6	1981
	20·6	22·2	25·0	21·6	1982
SEPTEMBER	21·7	22·9	25·3	22·1	1980
	20·5	21·8	25·2	21·5	1981
	21·1	22·4	24·8	21·6	1982
OCTOBER	17·5	18·6	21·2	18·4	1980
	18·0	19·3	22·2	19·2	1981
	16·6	17·5	21·3	17·9	1982
NOVEMBER	15·2	15·4	18·1	15·7	1980
	16·6	17·1	19·1	17·1	1981
	14·6	14·9	17·6	15·4	1982
DECEMBER	11·2	11·8	15·6	12·4	1980
	14·4	14·9	16·9	14·9	1981
	11·5	11·5	14·9	12·9	1982

Table 2.4 Hours of sunshine at Gibraltar: 1980 - 1982.

		JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1980	Total No. of hours	151·1	162·6	206·8	235·9	289·9	342·5	353·0	289·6	203·5	225·7	128·3	188·4
	% of possible	48·9	52·0	55·6	59·9	66·3	78·3	79·3	69·1	54·5	64·6	41·9	62·3
1981	Total No. of hours	178·6	188·5	219·5	188·8	345·9	322·8	333·6	313·1	276·0	220·0	123·7	126·1
	% of possible	57·8	62·0	59·3	48·0	79·2	73·9	75·0	74·8	74·0	63·0	40·2	41·6
1982	Total No. of hours	182·3	138·6	229·3	193·7	242·5	340·5	339·8	280·8	224·6	239·2	153·0	165·3
	% of possible	58·3	44·9	62·4	49·3	55·5	77·9	76·5	66·9	60·4	68·3	49·8	54·5

Fig. 2.4 MAXIMUM INCIDENT SOLAR RADIATION AT SURFACE AT GIBRALTAR

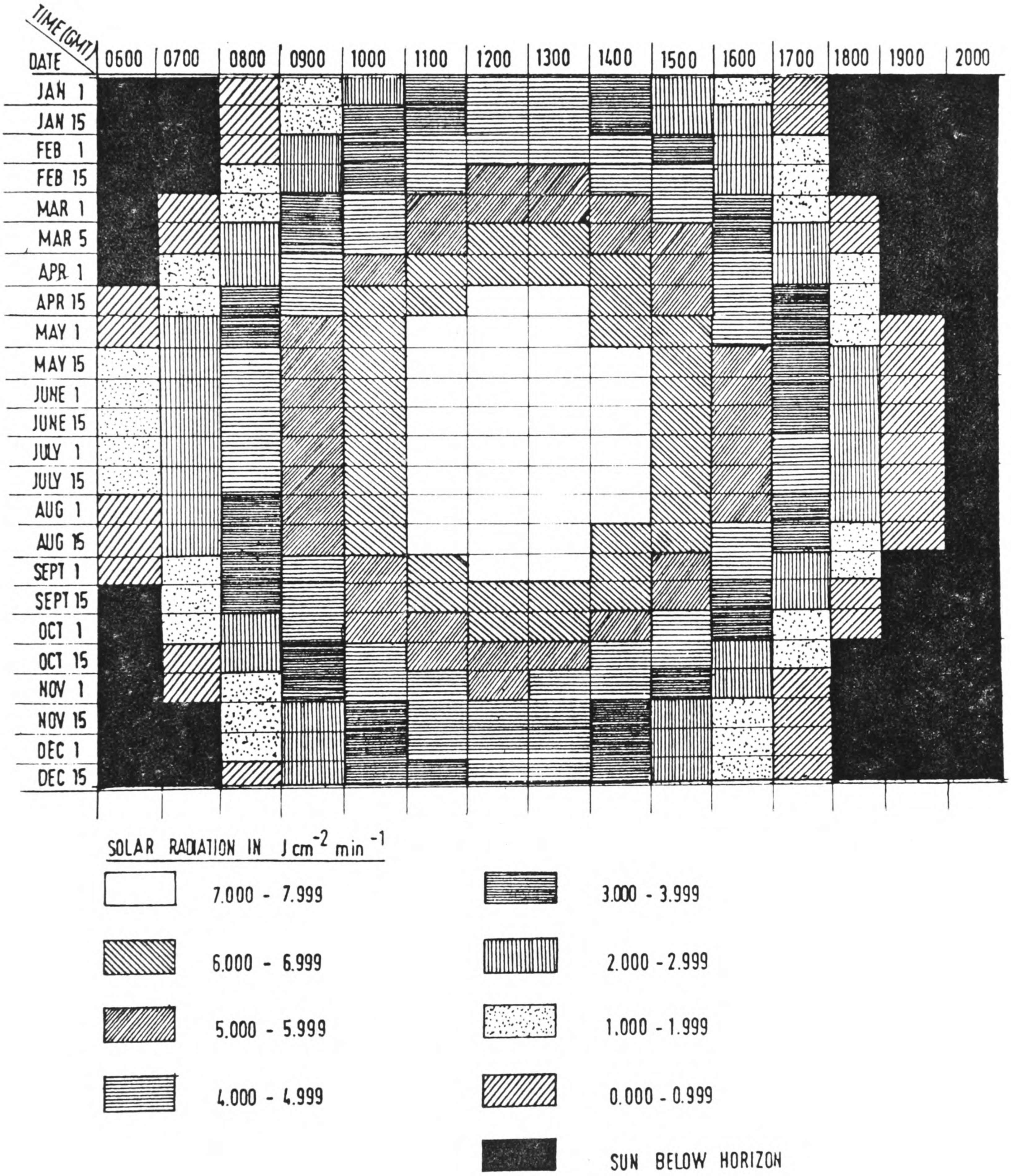


Fig. 2.5 PLOTS OF SOLAR RADIATION ($Jcm^{-2} min^{-1}$) AT THE SURFACE AT GIBRALTAR AGAINST TIME OF DAY FOR THE 1st & 15th OF EACH MONTH (VALUES ARE FOR 1982)

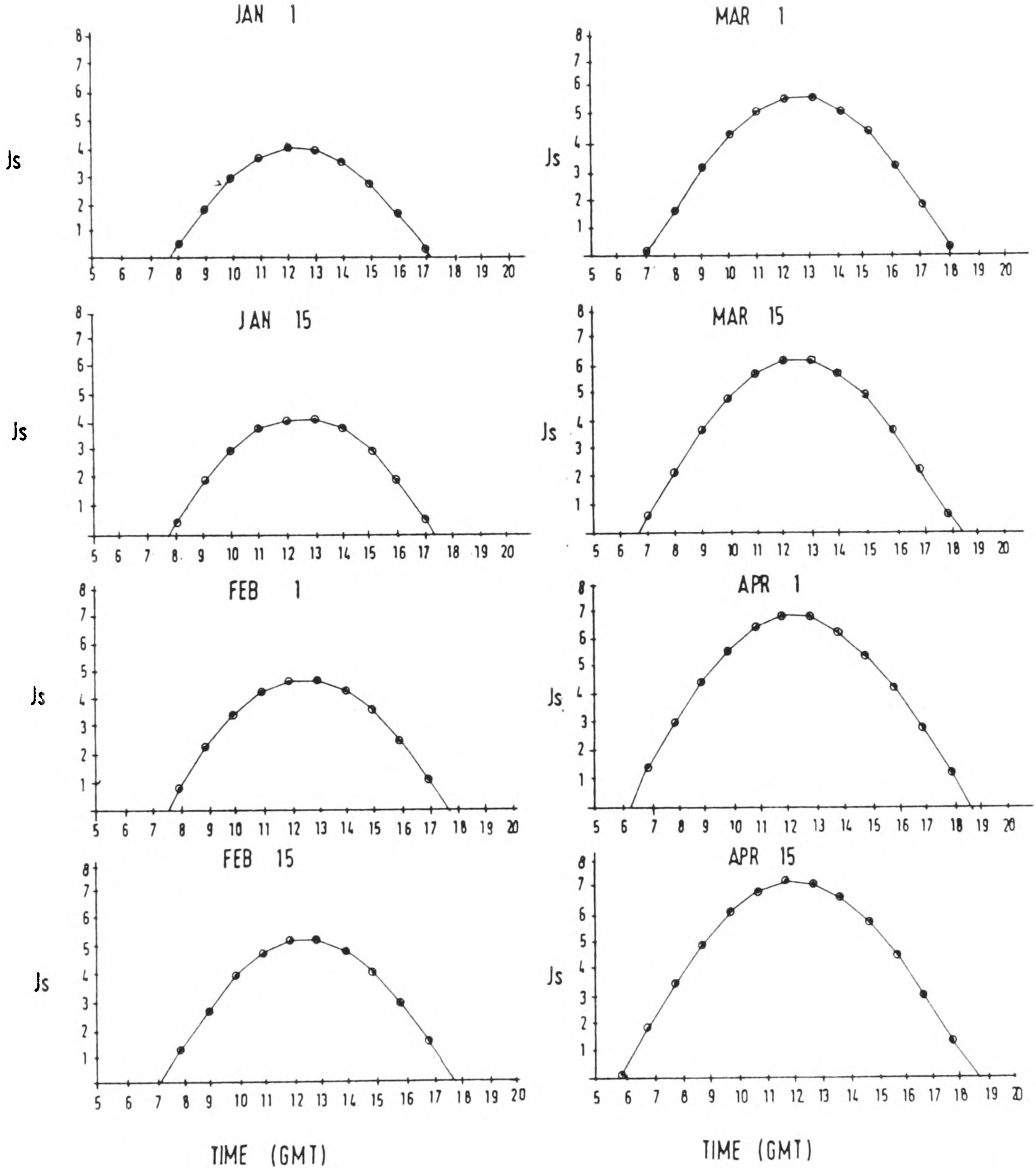


Fig. 2.5 (contd.)

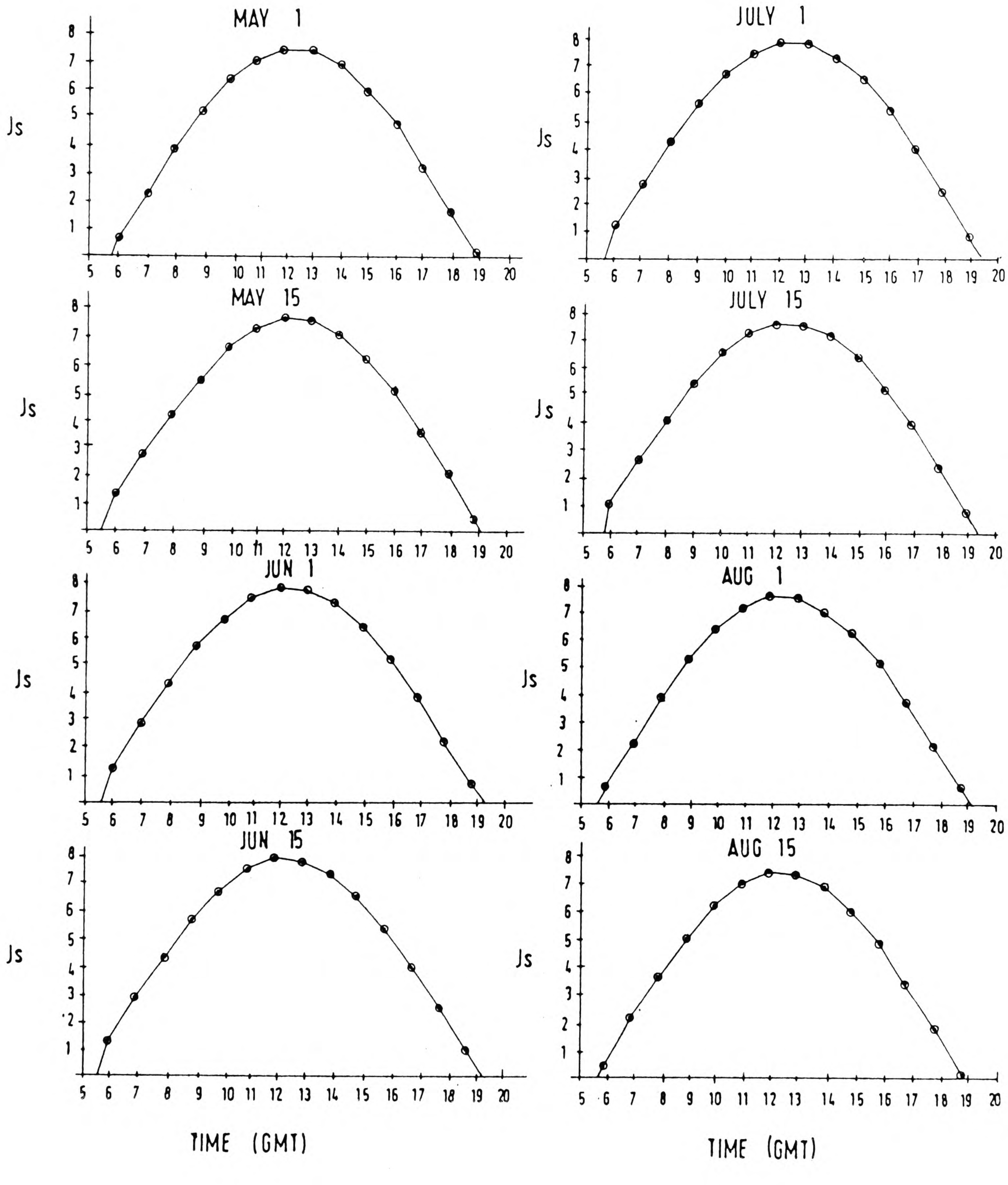

MAY 1
JULY 1
MAY 15
JULY 15
JUN 1
AUG 1
JUN 15
AUG 15
Js
1
2
3
4
5
6
7
8
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TIME (GMT)
TIME (GMT)

Fig. 2.5 (cont.)

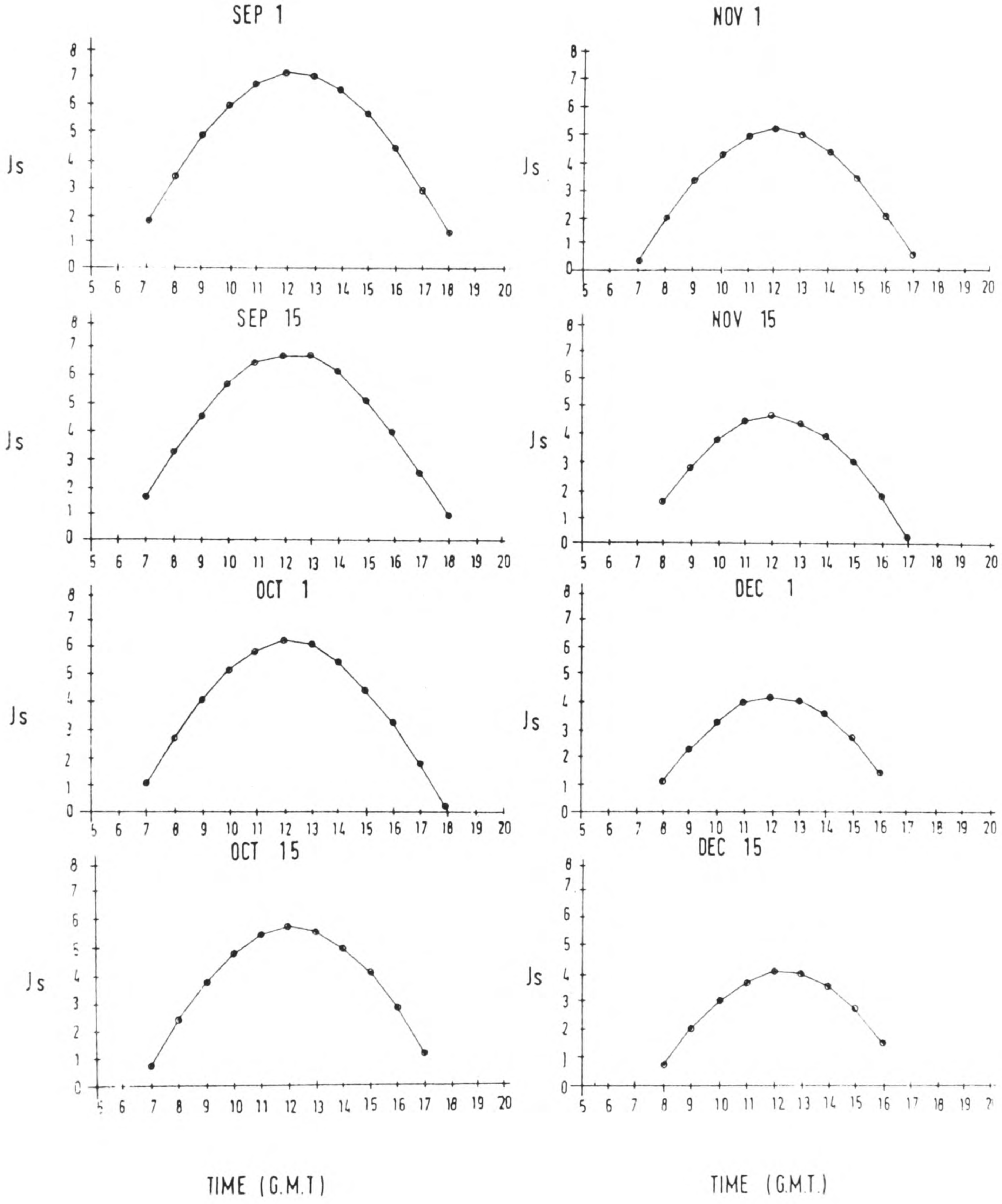

SEP 1
NOV 1
SEP 15
NOV 15
OCT 1
DEC 1
OCT 15
DEC 15
Js
0 1 2 3 4 5 6 7 8
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
TIME (G.M.T)
TIME (G.M.T.)

Fig. 2.6 HOURS OF SUNSHINE PER MONTH AS PERCENTAGE OF TOTAL POSSIBLE 1980 - 1982

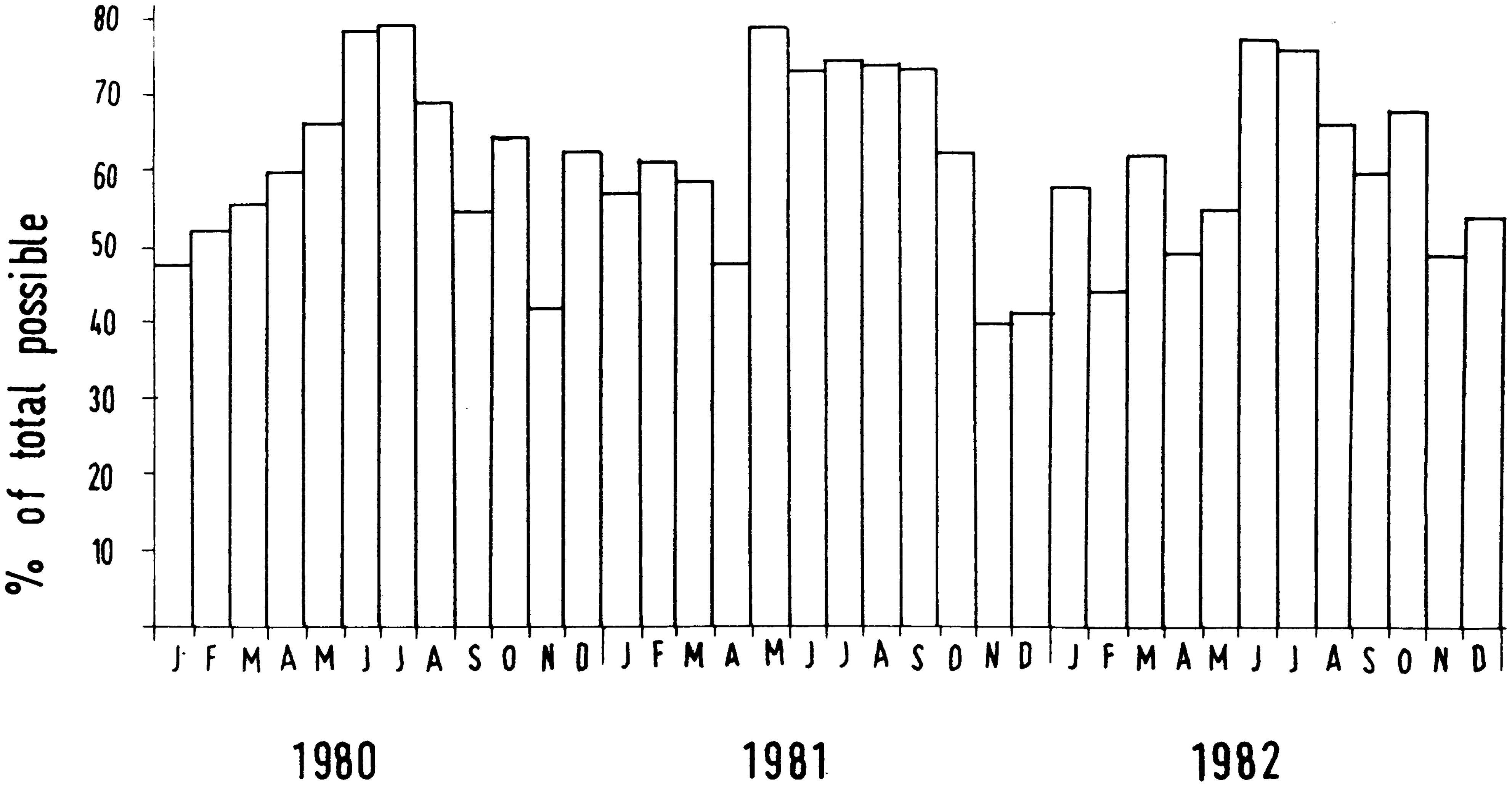
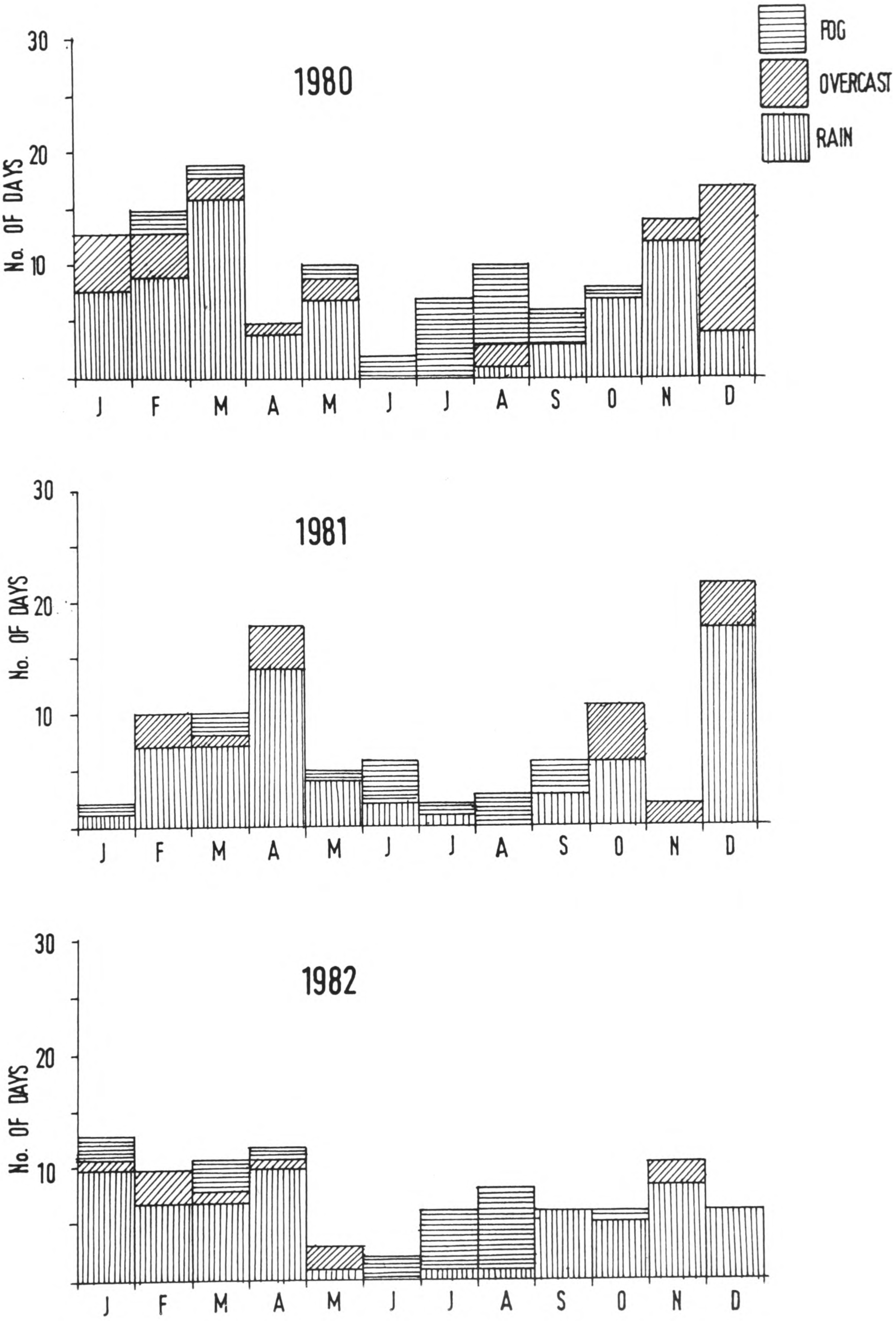


Fig. 2.7 No. OF DAYS OF RAIN, OVERCAST SKIES AND FOG EACH MONTH AT GIBRALTAR 1980 - 1982



mean temperatures ((mean minimum + mean maximum)/ 2) and the lowest and highest recorded temperatures for the years 1980, 1981 and 1982. As well as these air temperatures, the lowest grass temperatures are given. Figure 2.2 shows average daily mean temperatures in two-week periods for 1980 to spring 1982, showing the fluctuations possible within the general trend, shown in Figure 2.3, of the long-term mean temperatures for Gibraltar. Table 2.3 gives mean monthly air temperatures at 0200, 0800, 1400 and 2000 hours (G.M.T.).

Figure 2.4 shows the incident solar radiation levels at the surface for clear skies (J_s), calculated at hourly intervals as described in 2.1.2 above. Figure 2.5 displays these results graphically for the 1st and 15th of each month. The curves are symmetrical, and would be valid only for perfectly clear atmospheres. They are therefore over-estimations of incident radiation on even the clearest days. They will nevertheless give an indication of the way radiation varies on bright days. Cloud cover will affect radiation reaching the ground. Thus, cirrus or cirro-stratus clouds will reduce solar radiation to 75-85% of that for a cloudless sky, while at the other extreme, nimbo-stratus clouds and fog will reduce radiation to 15% (Deacon, 1969). Hours of sunshine for each month for 1980 - 1982 are given in Table 2.4 and represented diagramatically in Figure 2.6 as percentages of the total possible.

The number of days of rain or overcast each month are illustrated in Figure 2.7. A good number of overcast days, and all those in summer, are due to a local phenomenon, the 'Levanter'. Moist air from the Mediterranean is forced up the sheer east face of the Rock by easterly winds, causing the moisture to condense as the air cools, and forming a sometimes extensive cloud which causes air temperatures to drop, and reduces solar radiation. This reduction in radiation reaching the ground is probably similar to that caused by fog or thick cloud, i.e., to 15% of the value for clear skies (Deacon, 1969). This would reduce even midday solar radiation in summer (Figure 2.4) to no more than 1·2 J $cm^{-2} min^{-1}$, equivalent to that within two hours of sunrise or sunset in winter.

Fig. 2.8 THERMOGRAPHS ; GIBRALTAR TOWN - JANUARY

Fig. 2.9 THERMOGRAPHS , GIBRALTAR TOWN - FEBRUARY

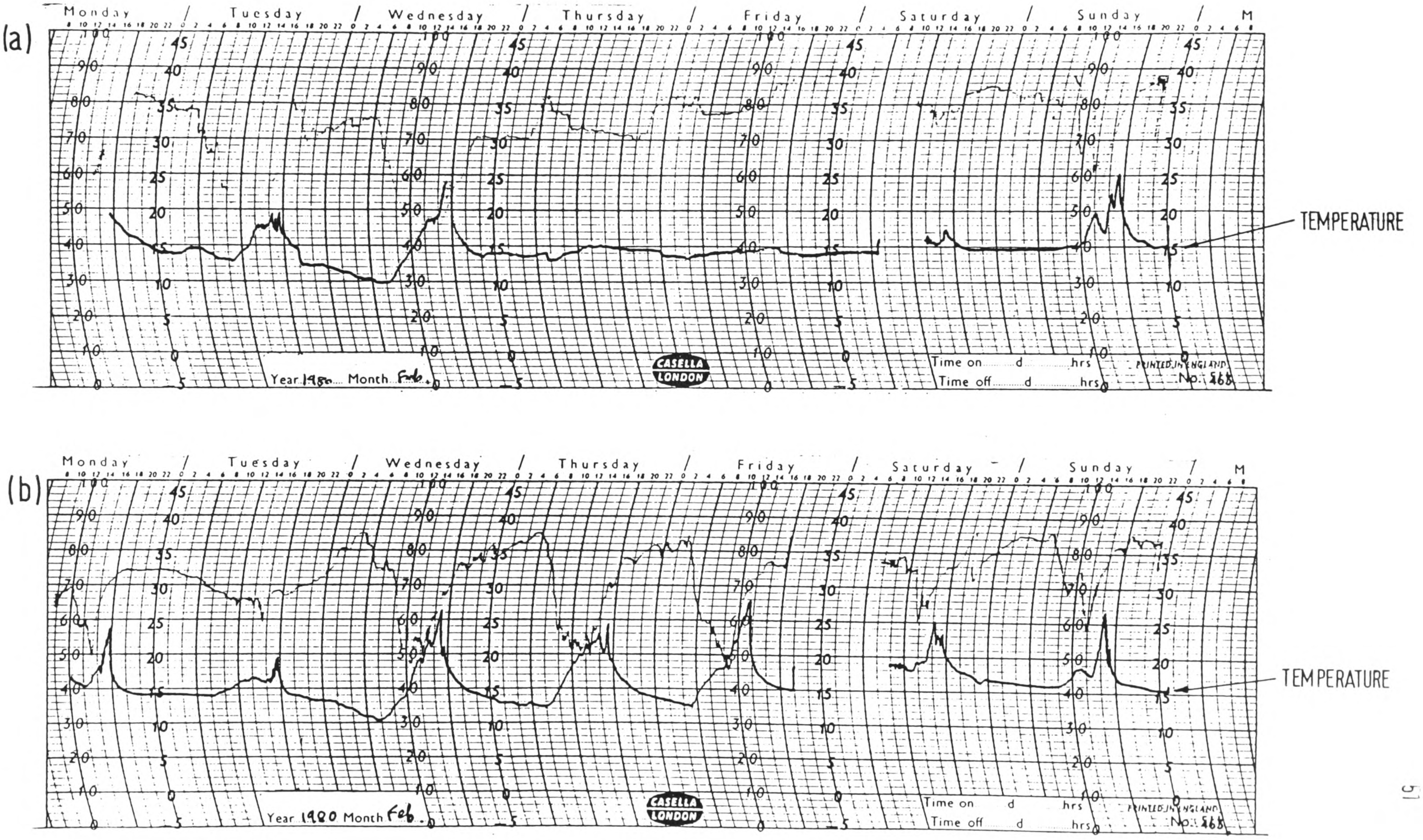
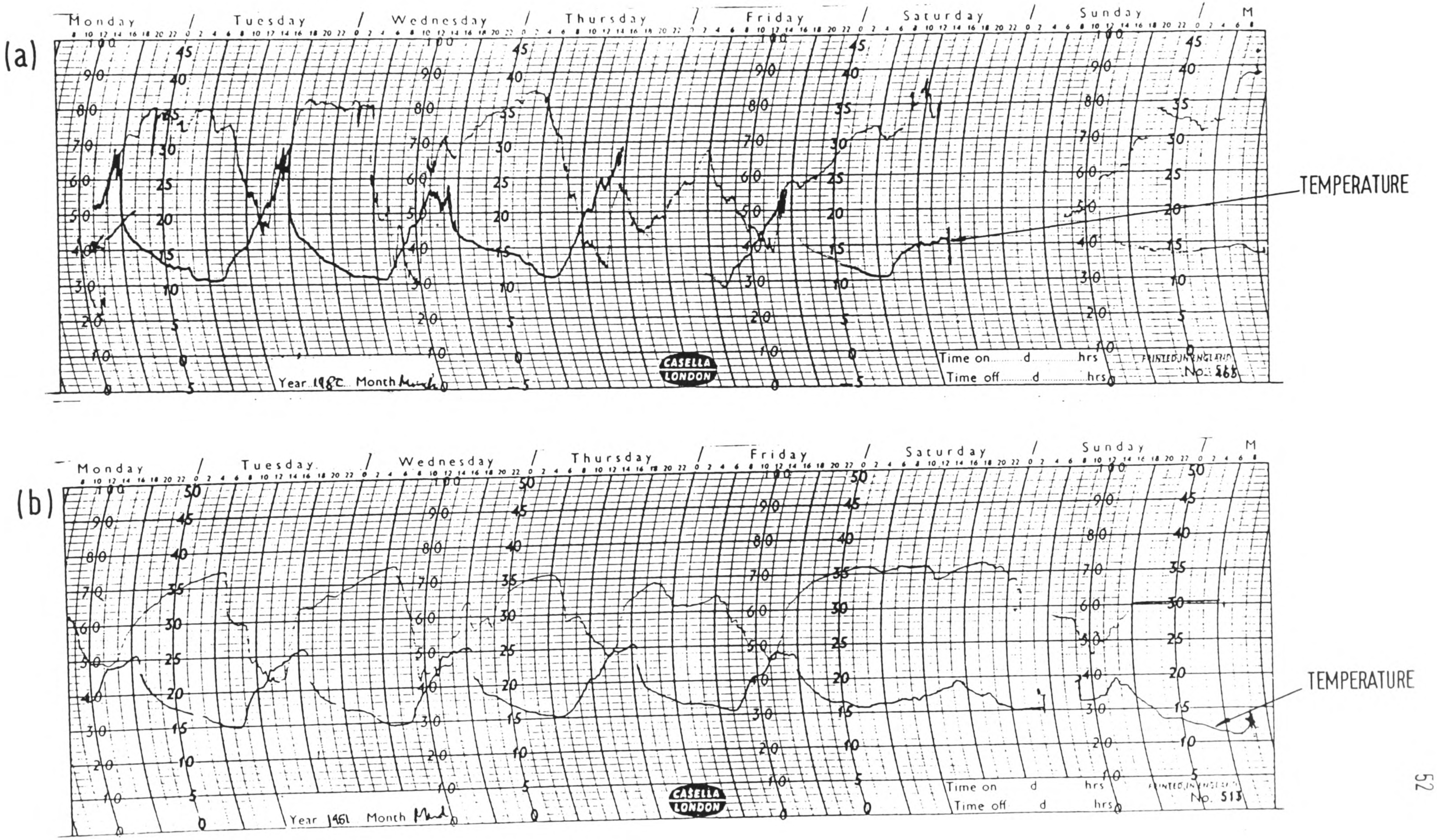
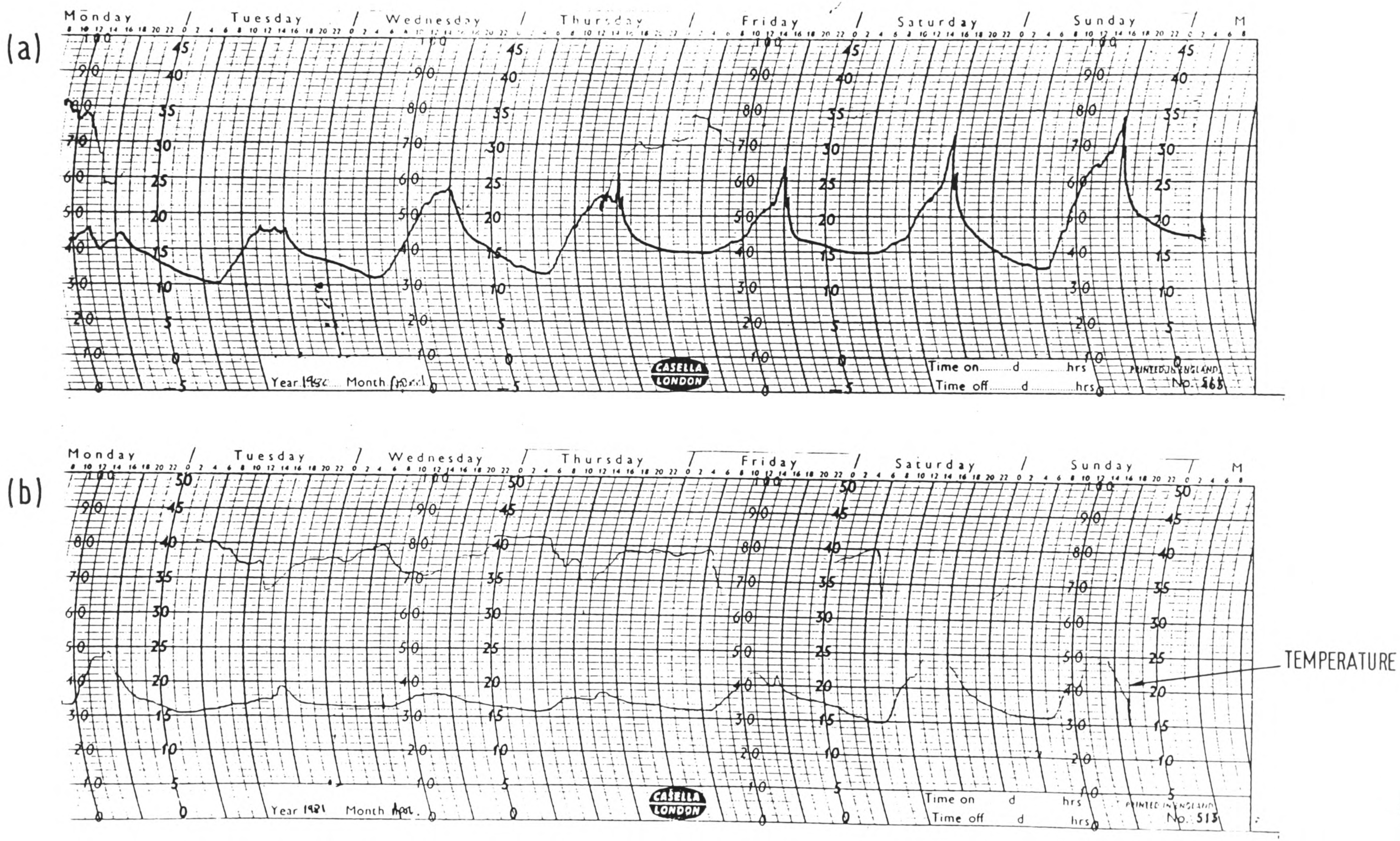


Fig. 2.10 THERMOGRAPHS, GIBRALTAR TOWN - MARCH





g. 2.11 THERMOGRAPHS, GIBRALTAR TOWN - APRIL

Fig. 2.12 THERMOGRAPHS, GIBRALTAR TOWN - MAY

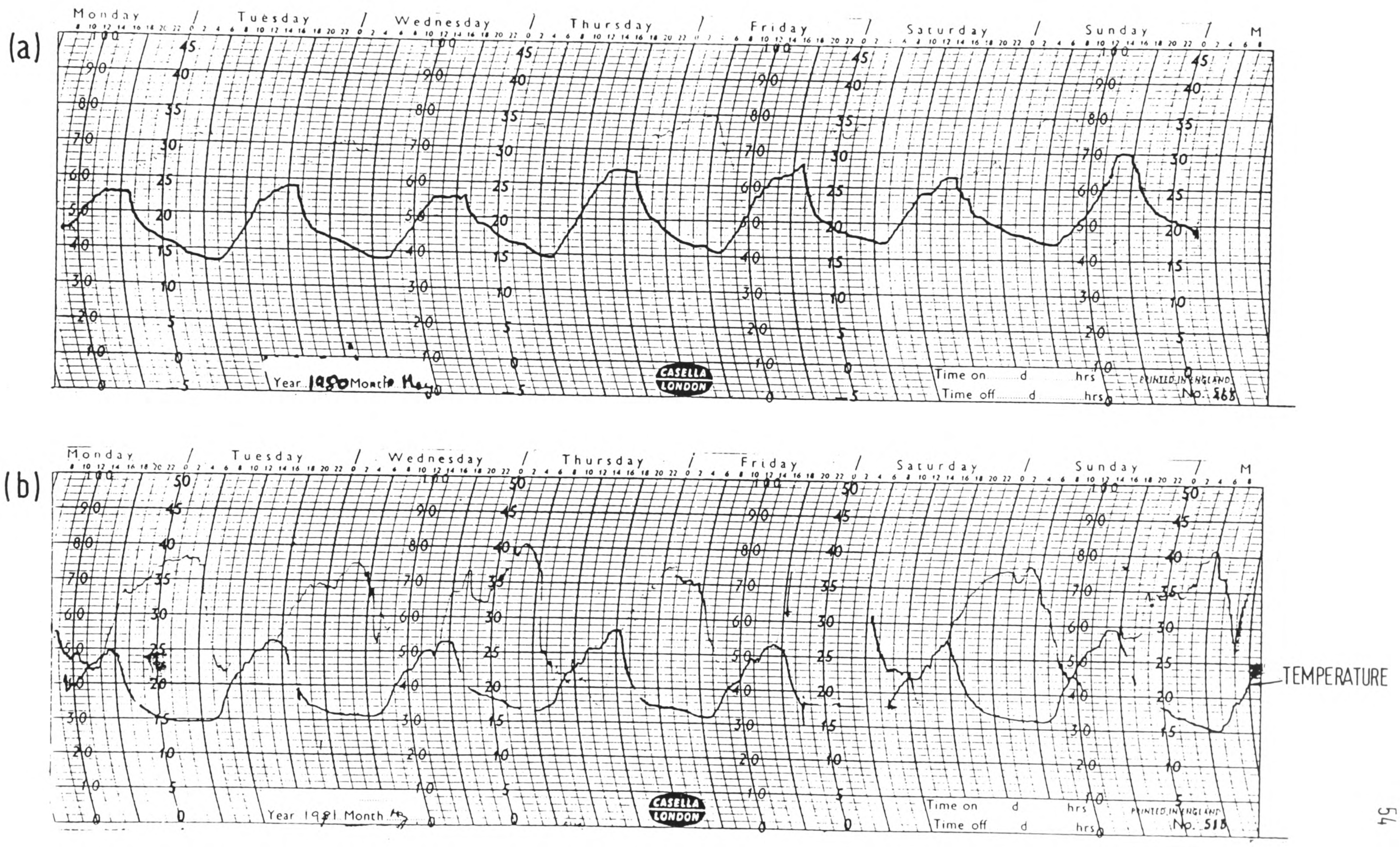


Fig. 2.13 THERMOGRAPHS, GIBRALTAR TOWN - JUNE

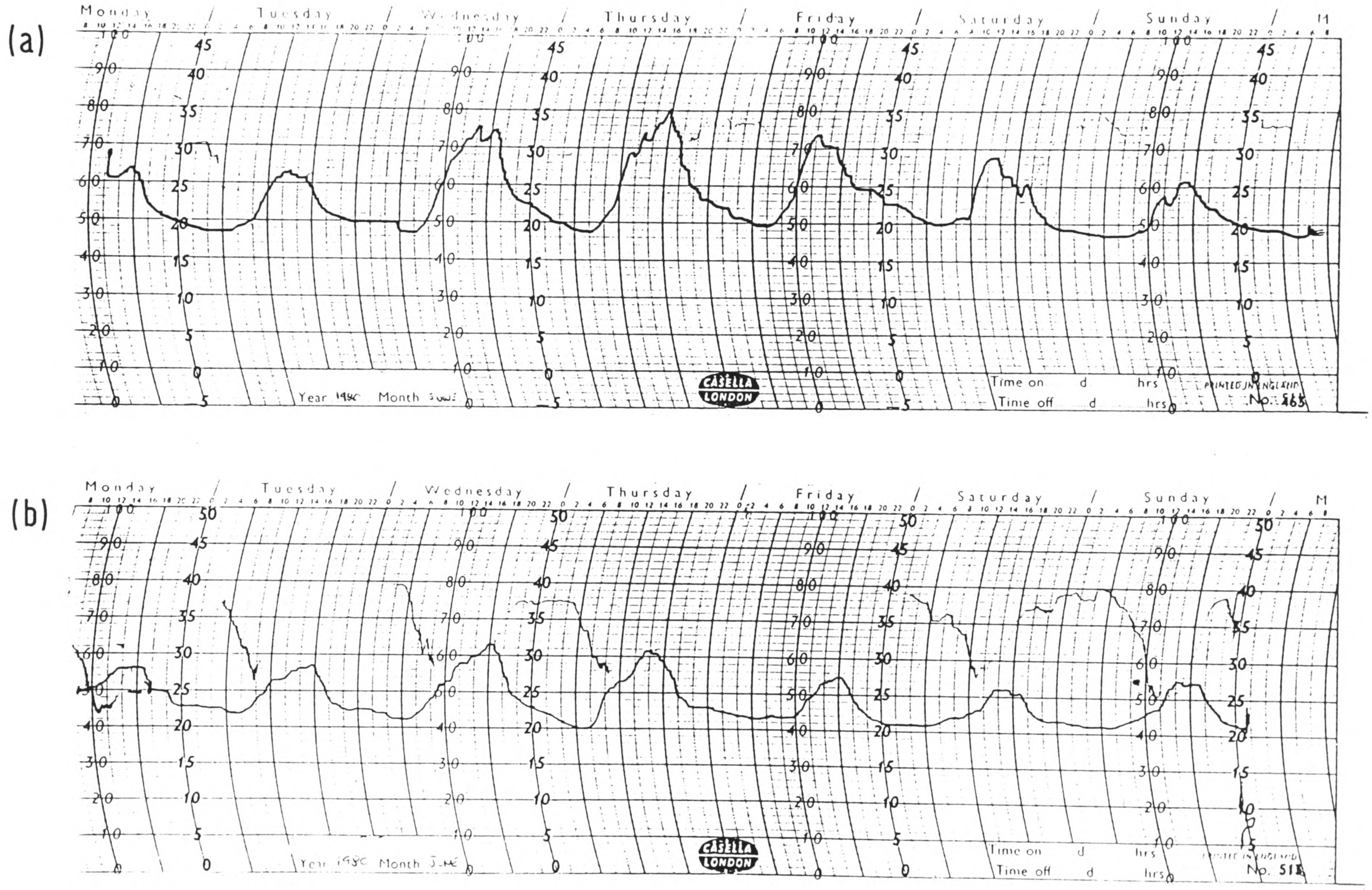


Fig. 2.14 THERMOGRAPHS, GIBRALTAR TOWN - JULY

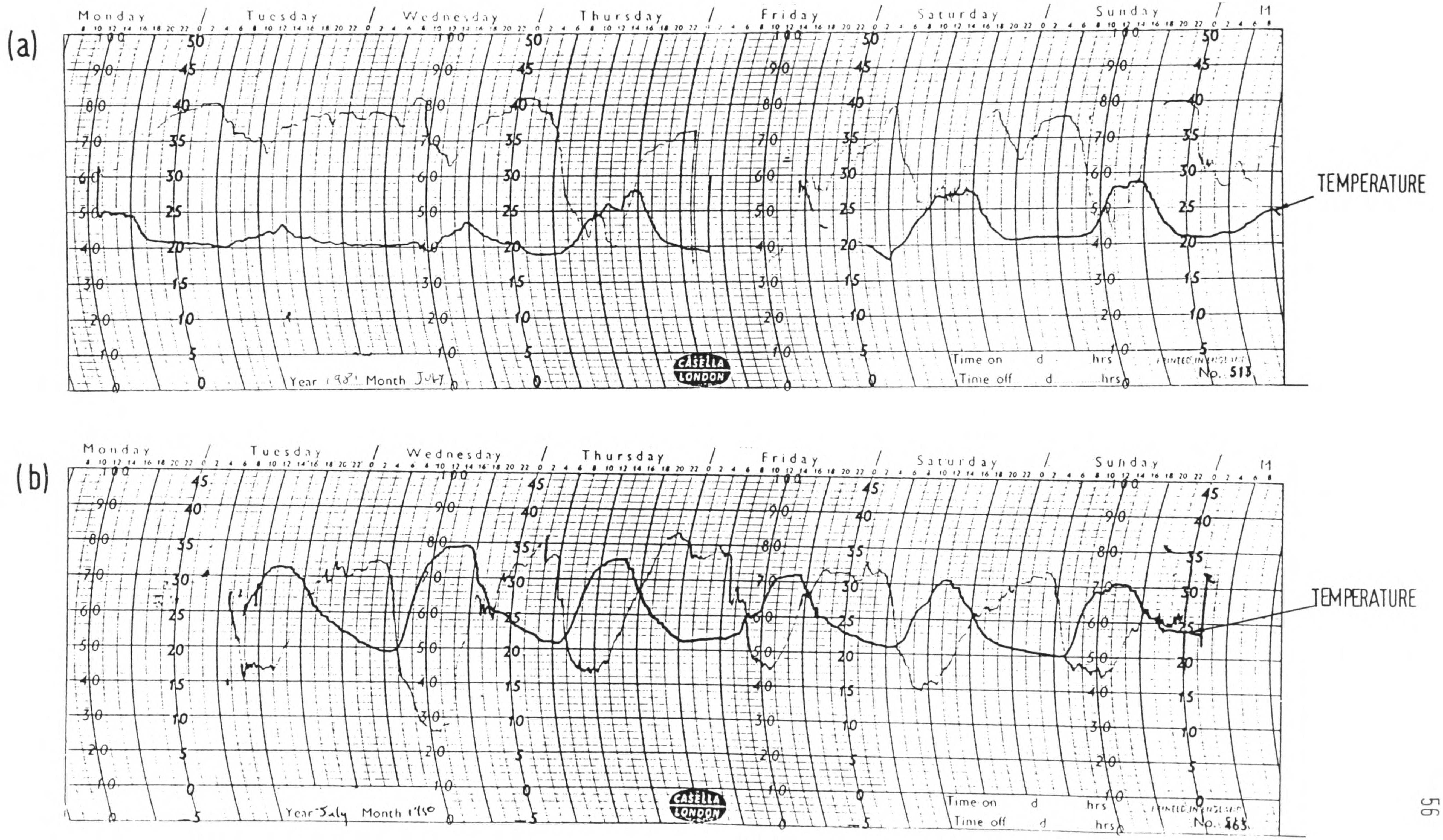


Fig. 2.15 THERMOGRAPHS, GIBRALTAR TOWN - AUGUST

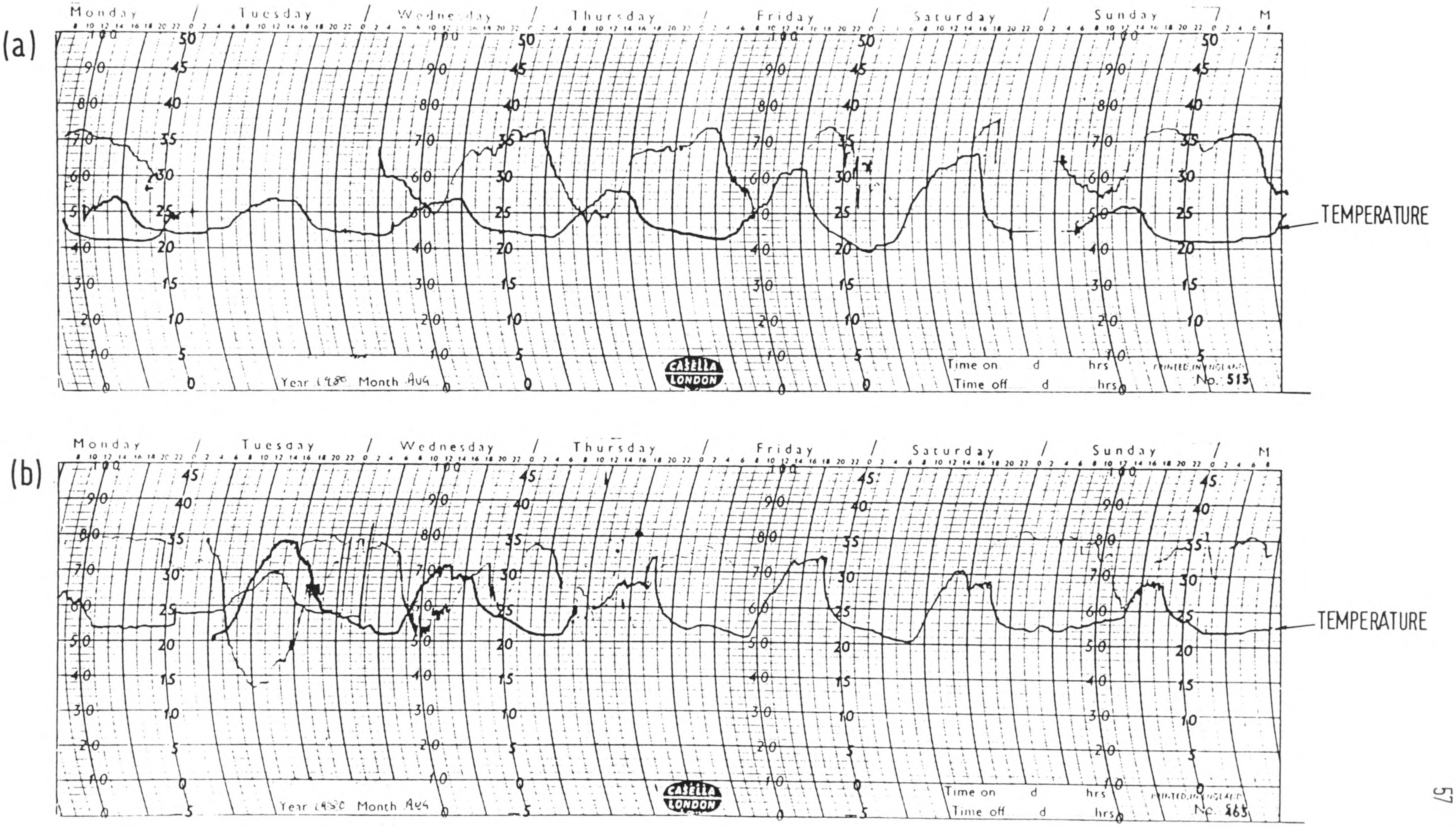


Fig. 2.16 THERMOGRAPHS, GIBRALTAR TOWN - AUGUST

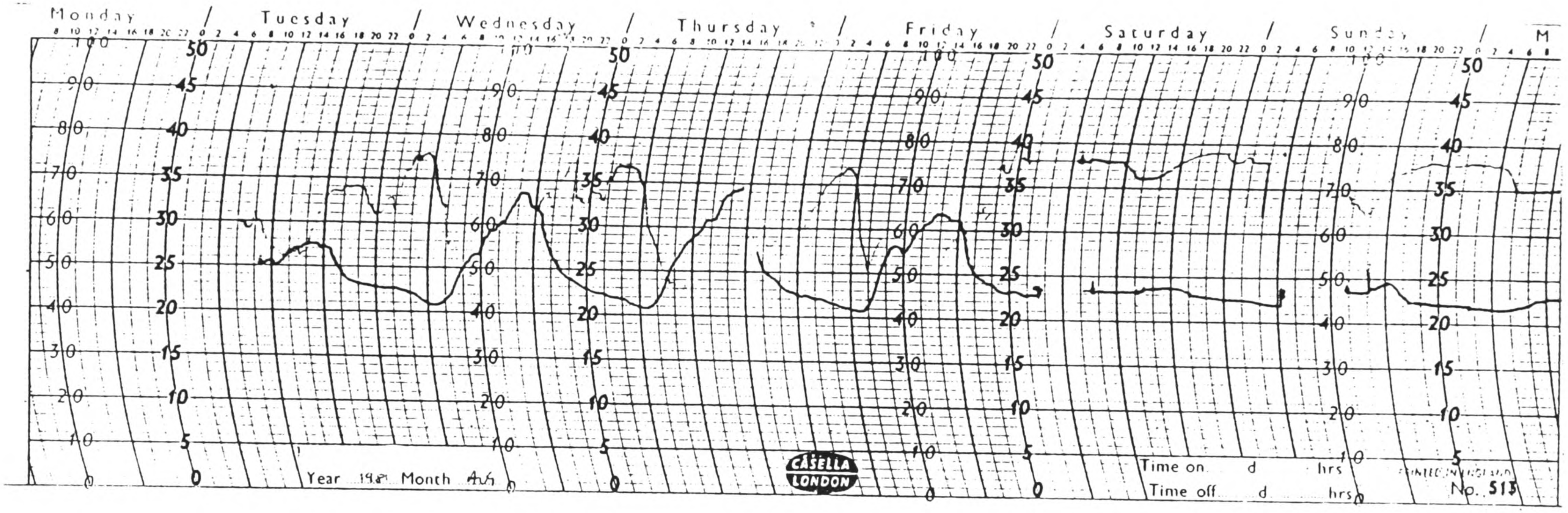


Fig. 2.17 THERMOGRAPH, GIBRALTAR TOWN - SEPTEMBER

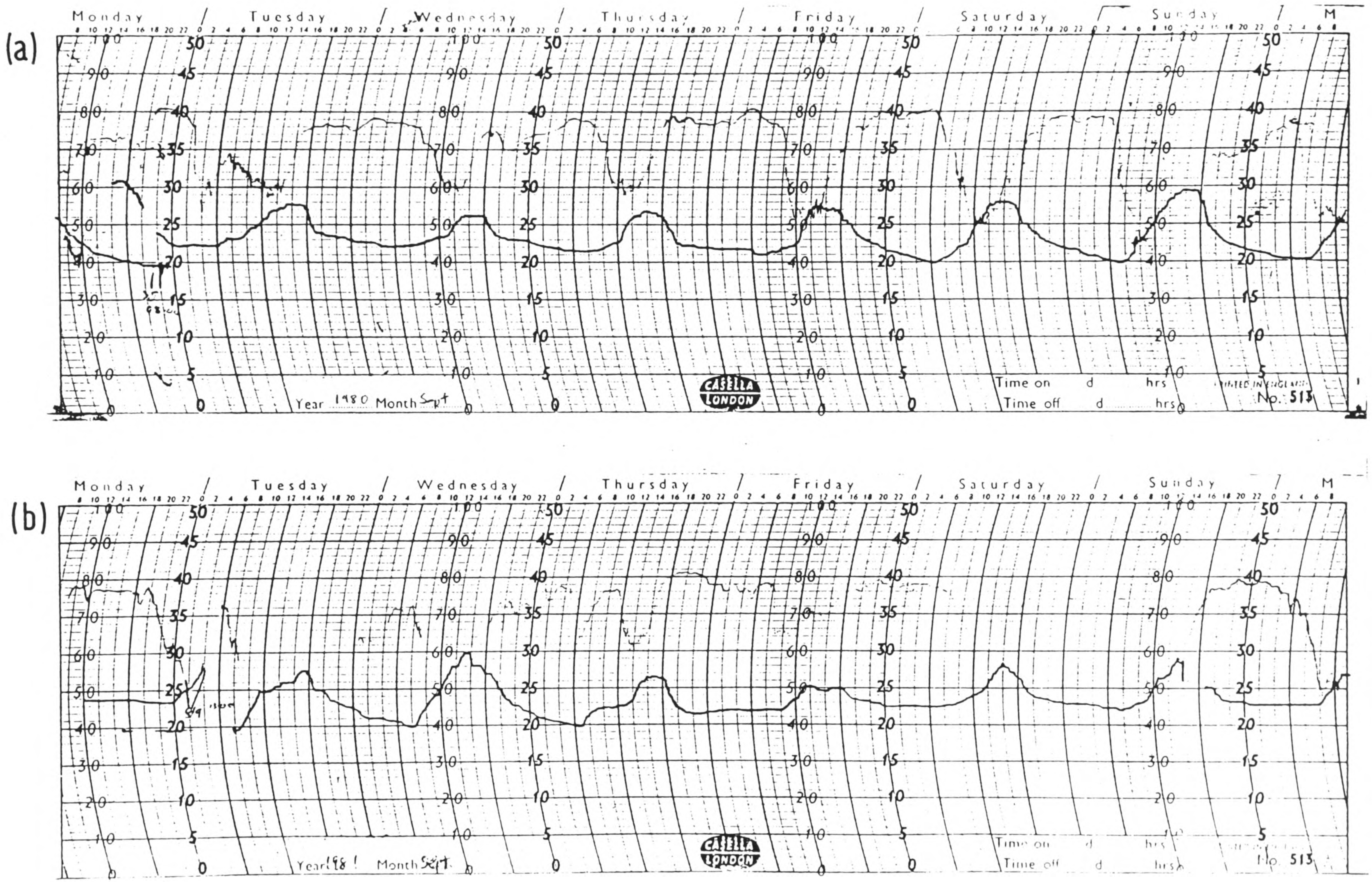


Fig. 2.18 THERMOGRAPHS, GIBRALTAR TOWN - SEPTEMBER/OCTOBER

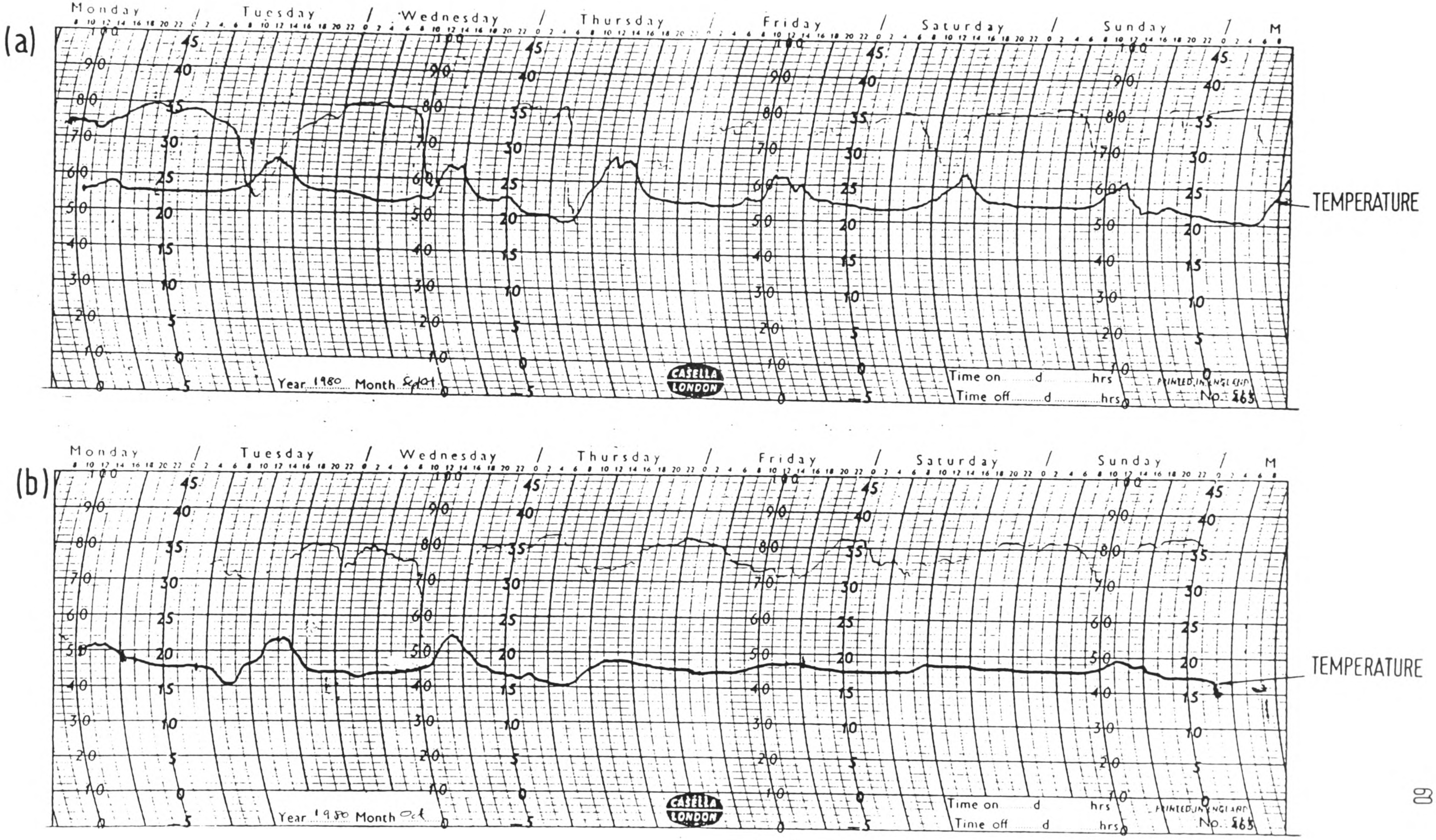


Fig. 2.19 THERMOGRAPHS, GIBRALTAR TOWN - OCTOBER/NOVEMBER

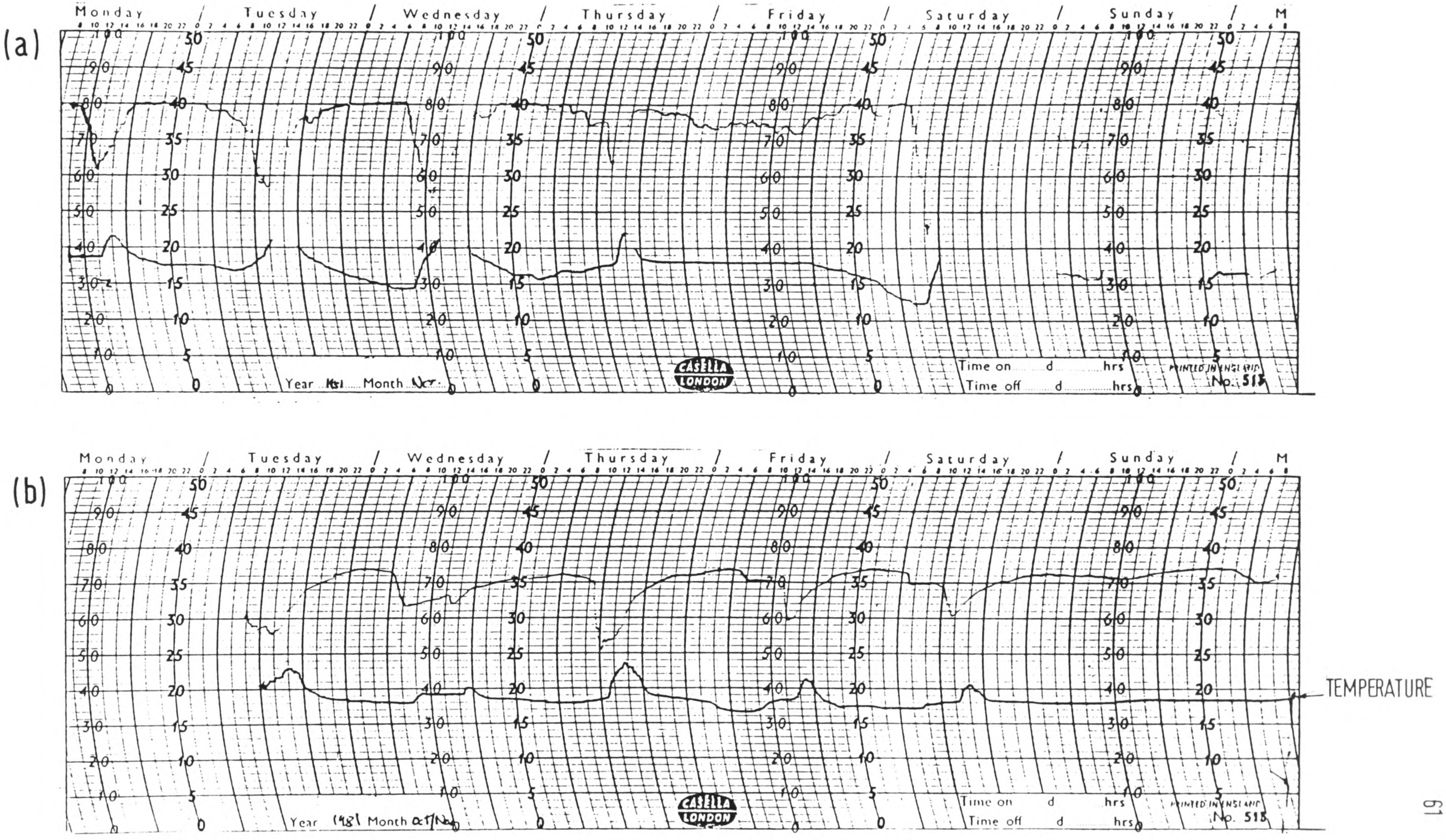
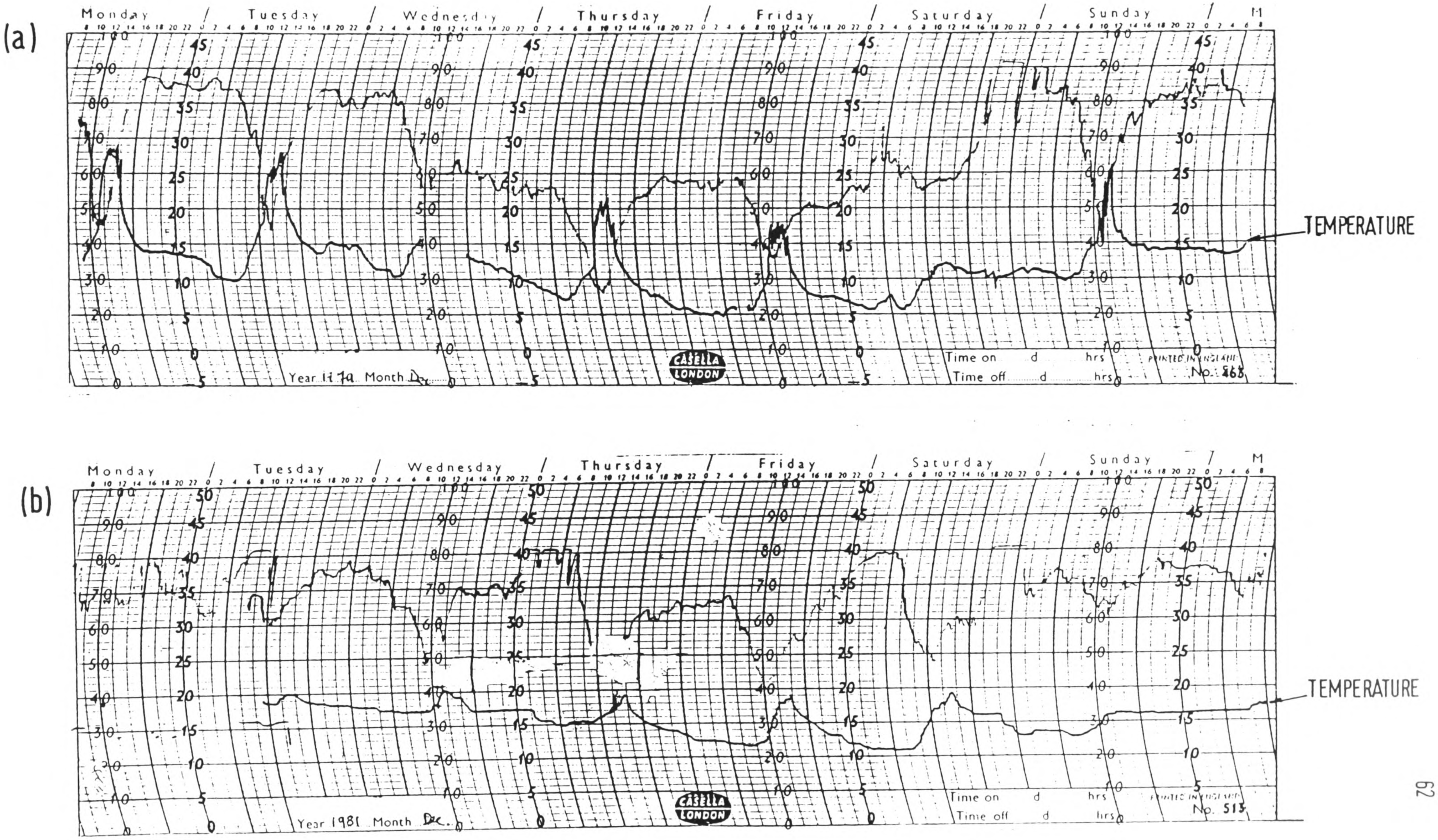


Fig. 2.20 THERMOGRAPHS, GIBRALTAR TOWN - DECEMBER



Figures 2.8 to 2.20 are examples of thermographs obtained at the site in the Town in different months. Figure 2.8 contrasts the daily fluctuation of temperature on bright days (Figure 2.8 a) to that on days of Levanter (Figure 2.8b) when range of temperature is markedly less. A similar contrast is seen between the early and middle parts of the week in Figure 2.9a, between Figure 2.11a and 2.11b, and in Figure 2.18b. It should be noted that during the summer months, night temperatures hardly drop below 20°C, and in winter, they rarely drop as low as 5°C. Grass temperatures can, however, be lower (Figure 2.1; Table 2.1).

Figure 2.21, taken from Escardó (1970), shows mean annual hours of sunshine, mean January and July temperatures, differences between the mean temperatures in the warmest and coldest months, and mean duration of the frost-free period for the Iberian Peninsula, with the values for Gibraltar given also below the maps. The hours of sunshine are within the range shown in Figure 2.21a. However, Gibraltar is warmer in January, cooler in July and has a longer frost-free period than expected from Escardó's (1970) diagrams. The difference between the mean temperatures of the coldest (December) and warmest (August) months (13·7°C) is within the given range.

(b) Microclimate

The results and discussion of the microhabitat temperatures will be left to Chapter 8 where they are considered together with lizard activity and temperature relations.

2.1.4 Discussion

The patterns of mean air temperature for the years 1980 to 1982 (Figure 2.1) were similar to the long term mean (Figure 2.3) except that autumn temperatures (September to December) were somewhat higher than usual. The 1981 mean temperature curve showed a slight increase in March, making temperatures for that month also slightly higher than usual. This may account for a similar slight increase in March microhabitat temperatures (Figure 8.9) since these were largely recorded in that year.

On the whole, the typical Mediterranean pattern of warm summers and cool winters can be seen.

The highest and lowest temperature curves are useful in that they give an idea of the extremes of air temperatures the lizards have to tolerate. These are of course not as directly relevant as the microhabitat temperatures discussed in Chapter 8. It should be noted, however, that the peak temperature of 38·8°C recorded in August 1980 (Table 2.1) was higher than the voluntary maximum temperature (35·5°C) and the absolute voluntary maximum (38·0°C) of P. hispanica (8.2). All other peak air temperatures are within the voluntary range of P. hispanica temperatures (17·3°C - 35·5°C) (8.2).

In the three years under consideration, only grass temperatures fell below 0°C, and then only on one occasion (-1·3°C on 12 January 1981). Most of the lowest grass temperatures (Figure 2.1; Table 2.1) were below P. hispanica's ~~critical~~ minimum temperature of 12·2°C (8.2). It is unlikely, however, that temperatures fell that low in nocturnal refugia, and temperatures will have risen rapidly after sunrise before emergence (8.4).

In Figure 2.2 air temperatures are shown as means for two-weekly periods. It shows more clearly than Figure 2.1 how reversals in air temperature can take place at different times of the year. Thus, for example, cloudy spells in April and May 1980 and 1981 resulted in drops of temperature of about 2°C. Similar effects can be seen at other times of year, e.g., in September 1981, when the mean two-weekly temperature dropped as a result of the preponderance of Levanter conditions. While mean temperature is only affected by several degrees, solar radiation can drop by as much as 85% (2.1.3) in cloudy weather.

Cloud will affect the levels of solar radiation given for the 'ideal' clear sky in Figures 2.4 and 2.5. These figures will be related to lizard activity and emergence in Chapter 8.

While the change in solar radiation through the year is fairly symmetrical with regard to spring and autumn, the temperature curves are skewed, showing higher values in autumn than spring. In autumn the sky is clearer than in spring, when the weather tends to be more unsettled (~~Table~~ 2.7) and when conditions are generally cooler following the winter.

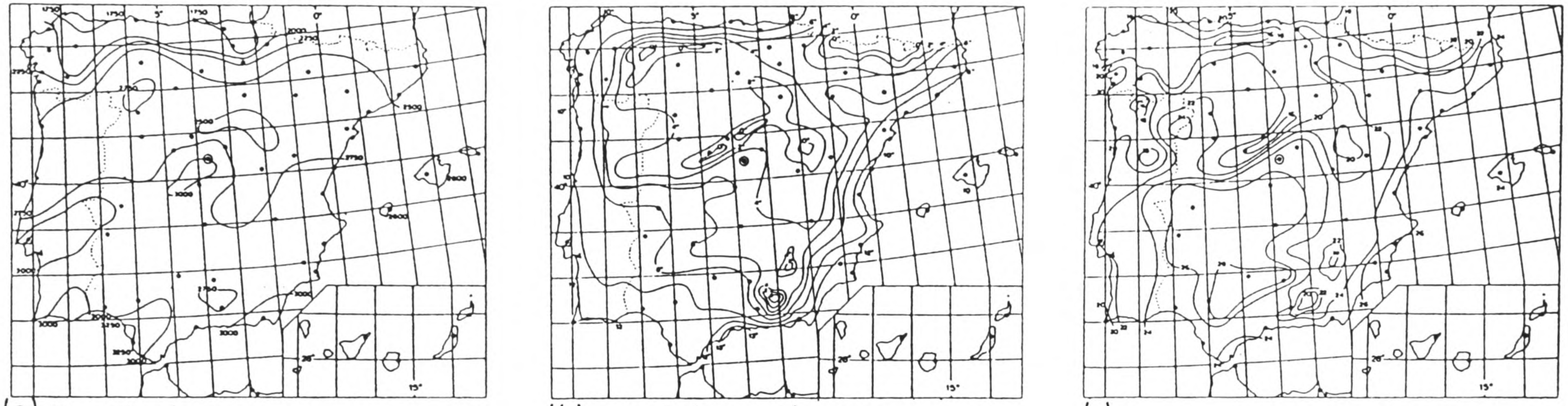
The percentage of hours of sunshine in relation to the total possible (Figure 2.6) shows that, as would be expected, there is more sunshine in summer than in the rest of the year, since there is a greater percentage of hours when the sun is not obscured. However, from year to year there is considerable variation in the percentage of sunshine hours for different months. Thus, in December 1980, the sunshine hours were 62·3% of those possible, while in 1981 the percentage for the month was 41·6% (Table 2.4). Similarly, from one month to the other in summer, there can be considerable differences in the percentage of hours of sunshine, e.g. 79·3% in July and 69·1% in August 1980.

Figure 2.7 shows that overcast days are extremely rare between July and August, although fog is most likely then. This fog normally moves from the Mediterranean on hot days with light easterly winds. Although it usually covers the isthmus (where North Front Cemetery is situated), it rarely affects the western slopes of the Rock, which are sheltered by the east cliff. The fog has almost invariably cleared by noon (1100 hrs G.M.T.). The effect on lizard activity at North Front Cemetery is to delay emergence (solar radiation can be reduced to 15% of normal; 2.1.3) until around midday. Temperatures can then rise quickly, however, so that activity time is curtailed.

Variation in the number of cloudy days can be seen for each month from year to year. Thus in December 1981 there were a total of 22 days of rain or overcast conditions, while only 6 days of rain occurred in 1982. Again, in January 1980 there were 13 days of rainy or overcast weather, while only 2 days were overcast in January 1981. There is therefore a low predictability of cloudy weather in any month, even in summer when cloud is comparatively rare.

Table 2.3, which gives air temperatures at six-hourly intervals, gives an indication of night-time temperatures. Thus, from May to October air temperatures at night can be within the voluntary range of P. hispanica, and between June and October can be higher than the minimum recorded field temperature of the species ($21{\cdot}9^{o}$) (8.2).

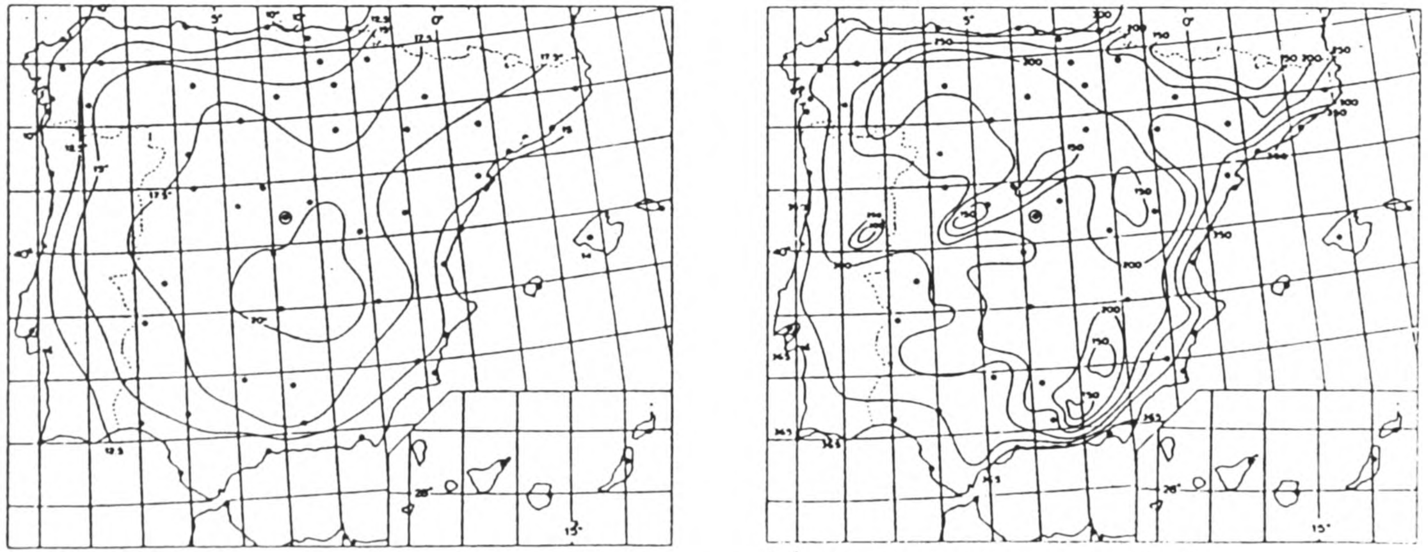
Fig. 2.21 CLIMATIC MAPS OF THE IBERIAN PENINSULA (FROM ESCARDÓ, 1970).



(a) Mean annual hours of sunshine (1931–1960).

(b) Mean temperature (°C) for January (1931–1960).

(c) Mean temperatures (°C) for July (1931–1960).



(d) Difference between the mean temperatures in the warmest and the coldest months

(e) Mean duration of frost-free period in days (1931–1960).

Values for Gibraltar

(a) MEAN ANNUAL HOURS OF SUNSHINE: 2805·4

(b) MEAN JANUARY TEMPERATURE: 13·1°C

(c) MEAN JULY TEMPERATURE: 23·6°C

(d) DIFFERENCE BETWEEN MEAN TEMPERATURES IN WARMEST AND COLDEST MONTHS: 13·7°C

(e) MEAN DURATION OF FROST-FREE PERIOD: 365 DAYS

Schall & Pianka (1977) compared reptile (and amphibian) species diversity with a number of climatic characteristics of the Iberian Peninsula. They suggested that lizards and reptiles in general diversified in Iberia in sunny, warm places. Hours of sunshine, frost free-period and mean July temperature contributed significantly to reduction in residual variance in species numbers when a stepwise regression procedure was used.

Schall & Pianka predict that at the latitude of Gibraltar there will be 11 species of lizard and 8 species of snake, when in fact there are 7 lizards and 6 snakes. Figure 2.21 shows that mean July temperature is lower in Gibraltar than in the surroundings (although mean January temperatures and frost-free period are greater), which may at first suggest that this may be a reason for the lower number of reptile species. However, for the mean July temperature for Gibraltar (23·6°C), Schall & Pianka (1977) suggest that 10 lizards and 8 snakes will occur. It is therefore likely that the lower number of species on the Rock are a result of habitat and historical limitations, as discussed in Chapter 1, and not of climatic considerations.

Figure 2.21 shows also that *P. hispanica*, the main species of this study, whose range includes the whole of Iberia south of the Pyrenees (Salvador, 1974) must tolerate a wide range of conditions. These range from those at Gibraltar and areas with warmer summers to those in regions with mean January temperatures of 0°C, over 100 days of frost and July temperatures of below 16°C (Figure 2.21).

2.2 Habitats

2.2.1 Introduction

The habitats of Gibraltar were considered briefly in Chapter 1. They were considered quantitatively as regards species composition and structure of vegetation by Cortés (1979). Observations at Gibraltar have shown that lizards were present in some habitats and absent or almost totally absent from others.

While the distribution of the lizards within the study sites is considered in some detail in Chapter 5, which includes discussion on the use of different microhabitats, it would be useful to describe the habitats as regards main constituent plant species and structure. This will serve as useful background information to the chapters which follow.

2.2.2 Methods

The vegetation of the Rock was studied using data from Cortés (1979).

Optimal quadrat size was determined at 15m x 15m using a species-area curve (Cortés,1979). Eighty-one quadrats were used, located in different vegetation types, and the cover provided by each plant species was given a Domin rating (Table 2.5). Domin ratings were also given to heights of vegetation, irrespective of species. The data were used in various association analyses and ordinations, but only two will be considered here. The first analysis was a Braun-Blanquet Association Analysis (Braun-Blanquet, 1932, 1951) which attributes 'degrees of presence' to each species in the different habitats (Table 2.5). These habitats, although chosen subjectively, contained quadrats grouped together by various statistical methods (e.g. Williams & Lambert (1959) Association Analysis). Secondly, the height data were used to define quadrats by means of scores on the Daget et al. (1968) scale (Table 2.6).

Transects along the Upper Rock helped determine qualitatively which lizards were present in different habitats.

2.2.3 Results

Table 2.5 lists the five main habitat types of the Rock: pseudosteppe (which has similar characteristics to steppe and open cliff as regards vegetation); garrigue; low maquis; high maquis and woodland. Plant species present in 60 - 100% of quadrats (4 - 5 on Braun-Blanquet scale) are listed also. The

TABLE 2.5 Habitats of Gibraltar and lizard presence

HABITAT TYPE	PLANT SPECIES WITH DEGREE OF PRESENCE = 4-5[1]	DOMIN RATINGS OF MAIN SPECIES IN SAMPLE QUADRAT[2]		HABITAT SCORE OF QUADRATS[3]	PRESENCE (+) or ABSENCE (-) of:[4] T.m.	Ps.a.	P.h.
Pseudosteppe	Pistacia lentiscus	Bare ground	5	8,8,5,5,4,0,0	+[5]	+[5]	+[5]
	Ferula tingitana	Grass	5				
	Smyrnium olusatrum	F. tingitana	3				
	Olea europaea	S. olusatrum	3				
	Phlomis purpurea	Asteriscus maritimum	3				
	Calendula spp.	Asphodelus aestivus	3				
	Oxalis pes-caprae	Gladiolus communis	2				
Garrigue	A. aestivus	Bare ground	5	8,8,8,8,8,6,6, 5,5	+	+	+
	Urginea maritima	O. pes-caprae	5				
	Phagnalon rupestre	Acanthus mollis	4				
	Grass	P. lentiscus	3				
	Geranium purpureum	A. aestivus	3				
	Lotus spp.	Chaemerops humilis	3				
Low Maquis	O. europaea	Teline linifolia	9	9,8,8,8,8,8,8,8, 8,8,8,8,8,4,4,4, 4,4,4,4,4,4,4,0	-	+	-
	Osyris lanceolata	Calicotome villosa	5				
	P. lentiscus	O. europaea	5				
	Rhamnus alaternus	P. lentiscus	4				
	A. mollis	O. lanceolata	3				
	F. tingitana	Coronilla valentina	3				
	O. pes-caprae						
	U. maritima						
High Maquis	O. lanceolata	O. europaea	8	9,9,9,9,9,9,7,7, 7,7,6,6,6,6,1,1, 1	-	+[6]	-
	R. alaternus	P. lentiscus	5				
	O. europaea	R. alaternus	5				
	Clematis cirrhosa	A. mollis	5				
	Asparagus albus	O. lanceolata	4				
	Aristolochia baetica	C. humilis	3				
	Lonicera implexa	C. villosa	2				
	Tamus communis	T. linifolia	2				
Woodland	O. europaea	O. europaea	9	9,9,7,7,7,7,7,6	+[6]	+[6]	-
	C. cirrhosa	C. cirrhosa	5				
	A. baetica	A. mollis	5				
	Vinca difformis	V. difformis	2				
	A. mollis	O. lanceolata	2				
	S. olusatrum						
	T. communis						

Notes: (1) Degree of presence values: 5 = in 80-100% of quadrats (constantly present)
(Braun-Blanquet, 1932, 1951) 4 = in 60- 80% of quadrats (mostly present)
3 = in 40- 60% of quadrats (often present)
2 = in 20- 40% of quadrats (seldom present)
1 = in 1 - 20% of quadrats (rare).

(2) Domin values for plant cover: 1 = 1 plant; 2 = occasional; 3 = frequent; 4 = 5 - 20% cover; 5 = 20 - 25%; 6 = 25 - 33% 7 = 33 - 50%; 8 = 50 - 75%; 9 = 75 - 90%; 10 = 90 - 100%.

(3) Habitat scores : see Table 2.6.

(4) T.m. = Tarentola mauritanica; Ps.a. = Psammodromus algirus; P.h. = P. hispanica.

(5) T.m. if rocks present; Ps.a., P.h. where cover available.

(6) Present where gaps in canopy allow sunlight through.

Table 2.6 Types of vegetation - criteria for division (from Daget *et al.*, 1968).

Score

SIMPLE TYPES

Simple woody communities

Tall woody vegetation : >2m; crown cover >50% of ground
low variant : 2 - 8m.

1 Dense > 75%
2 Fairly open 50 - 75%
3 Open 25 - 50%
4 Low woody vegetation : >10% at <2m height
<25% at >2m height
<10% herbaceous

5 Simple herbaceous communities

<25% at >2m height
<10% at <2m height
>10% herbaceous

Open <90% of ground
Closed >90% of ground

COMPLEX TYPES

6 Complex woody communities

25 - 50% tall woody
10 - 100% low woody
<10% herbaceous

7 Complex tall-woody/herbaceous communities

25 - 50% tall woody
<10% low woody
>10% herbaceous

8 Complex low-woody/herbaceous communities

<25% tall woody
10 - 100% low woody
10 - 100% herbaceous

9 Complex herbaceous/low woody/tall woody communities

25 - 50% tall woody
10 - 100% low woody
>10% herbaceous

0 Clear or bare communities

<25% tall woody
<10% low woody
<10% herbaceous

Domin ratings of plant species in a sample quadrat in the habitat are also given. The score on the scale of Daget et al. (1968) are given in the table for each quadrat attributed to the habitat. Consultation of Table 2.6 shows that pseudosteppe includes quadrats which can be defined as complex low woody/herbaceous communities, simple herbaceous communities and clear or bare communities, with one quadrat having low woody vegetation. Most of the garrigue quadrats were complex low woody/herbaceous communities. Low maquis was also largely of this type, but also prominent were quadrats of low woody vegetation, with the occasional clear area. High maquis quadrats were mainly complex herbaceous/low woody/tall woody, complex tall woody/herbaceous and complex woody communities, with some dense tall woody vegetation. Finally, woodland was categorised similarly to high maquis as regards vegetation structure.

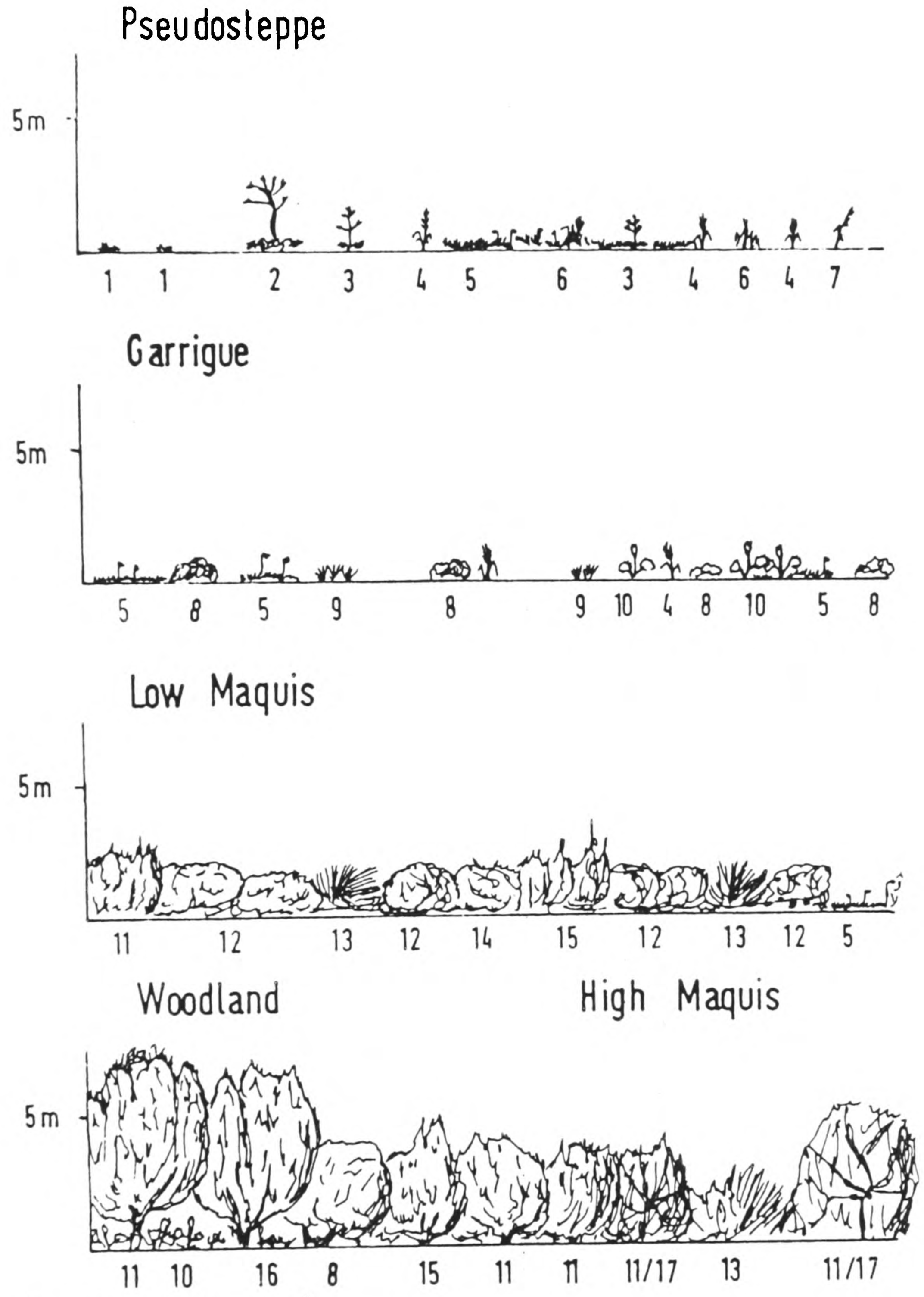
Using the above information, the main habitats of Gibraltar (some of which are represented diagrammatically in Figure 2.22) can be described briefly as follows:

Pseudosteppe

This vegetation type is caused by the action of man through the regular clearing of vegetation in the firebreaks. The vegetation of the firebreaks varies according to the regularity of cutting, to the former vegetation of the area, and to the effects of erosion. In general however, plant cover is low. There is much bare rock. The species growing in pseudosteppe are mainly herbaceous.

The steeper firebreaks have become almost denuded of soil, unlike those on gentler slopes (e.g., Bruce's Firebreak), which in general have greater plant cover. Firebreaks which are not regularly cleared tend to revert to maquis. Many roadside plants grow in the pseudosteppe areas which also support species, such as Acanthus mollis and Smyrnium olusatrum which are common in the undergrowth of surrounding taller vegetation.

Fig. 2.22 DIAGRAMMATIC REPRESENTATION OF THE MAIN HABITATS OF GIBRALTAR



Key to plant species

1. Asteriscus maritimus
2. Ferula tingitana
3. Smyrnium olusatrum
4. Asphodelus aestivus
5. Oxalis pes-caprae
6. GRASS
7. Gladiolus communis
8. Pistacia lentiscus
9. Chaemerops humilis
10. Acanthus mollis
11. Olea europaea
12. Teline linifolia
13. Calicatome villosa
14. Coronilla valentina
15. Osyris lanceolata
16. Vinca deformis
17. SCANDENTS (mainly Clematis cirrhosa).

Steppe

Steppe vegetation is similar to pseudosteppe, but is natural, and does not need to be maintained by man. Steppe is found on Windmill Hill Flats (Figure 1.2). It is an open herbaceous community with much bare, stony ground exposed. Plant cover is generally of low stature and the lack of woody plants makes the area become virtually devoid of vegetation in summer.

The most prominent species are *Chrysanthemum coronarium* and *Mantisalca salmantica*. A large number of herbaceous plants (largely therophytes) can be seen in spring. These include *Tetragonolobus purpureus*, *Lathyrus clymenum* and *Pisum elatius*, while geophytes include *Romulea clusiana* and *Iris sisyrinchium*.

The vegetation of the northern areas of North Front Cemetery is of a similar type.

Cliff

Although a major habitat in Gibraltar, and one which is relatively undisturbed, the cliffs are mostly inaccessible. Many plant species grow on the cliffs, including plants of maquis flora. Typically cliff-growing species, however, include *Ephedra fragilis*, *Iberis gibraltarica* and *Antirrhinum majus*.

Matorral and Woodland

Tomaselli (1972) defines Matorral as "a stand of xerophilous evergreen woody plants of which parts above the ground cannot be clearly differentiated as between trunk and foliage, but whose foliage generally extends to the base".

The vegetation of Gibraltar's western slopes falls almost entirely into this category. In some areas the matorral has develop ed into trees with distinguishable trunks. These areas are called Woodland in this work, although all are of limited extent. In most cases the tree canopies, rarely more than 8 m high, are continuous with the 'canopy' of the lower matorral.

The matorral can in fact be subdivided:

Maquis and Woodland

Maquis is a thick matorral (Macchia alta of Beguinot, 1922), described by Molinier (1959) as a stand of xerophilous non-deciduous bushes and sclerophyllous shrubs, evergreen, and generally so thick as to be impenetrable. Floristic composition is not taken into account in the definition of this term.

Figure 1.4 shows the extent of maquis vegetation in Gibraltar. The extent of Woodland is so small that this category has not been mapped. The maquis of Gibraltar is in fact a mosaic of patches of varying density and height of vegetation and, taken as a whole, can be considered to be a complex low woody/herbaceous community (Table 2.6). Within this, the following can be described.

- Woodland

The tallest trees on the Upper Rock, excluding the scarce introduced Eucalypts, are Pinus halepensis and P. pinea. Both species reach a height of 9 metres at present, the individual trees being of fairly uniform age (about 75 years). The Pines, however, have been planted mainly along roads where they are effectively separated from the main plant communities. Olea europaea will also grow to about 9 metres and form woodland with a fairly closed canopy. The undergrowth consists of annual shade-resisting species, such as Geranium purpureum, Acanthus mollis, Smyrnium olusatrum and Vinca difformis. Litter in woodland can be several centimetres thick.

- High Maquis

This is the maquis proper, a dense, tall-woody community. The main components of the high maquis, dominant in as much as they determine the appearance of the vegetation, are Olea europaea and Osyris lanceolata. Prominent also are Pistacia lentiscus and Rhamnus alaternus and the lianes Clematis cirrhosa, Tamus communis, Aristolochia baetica and Lonicera implexa.

There are areas of open maquis with clearings. These are found where the slope is steeper (consequently the soil is thinner), or on areas of scree or bare rock. Many plant species of more open communities enter the maquis here (as do lizards). Plants encountered in woodland undergrowth also occur in the high maquis.

- Low Maquis

As in the case of the high maquis, this vegetation varies on the Rock from closed to open in nature, for apparently similar reasons. As far as species composition is concerned, two main types of low maquis can be distinguished. The first is a low form of high maquis, having a similar species composition as the latter type, but not achieving the height. The second type predominantly contains different species, notably Teline linifolia, and is normally characteristic of areas regenerating vegetation after fire (Cortés, 1979).

There are more patches of open ground in low than in high maquis.

- Garrigue

Garrigue (Macchia bassa of Beguinot, 1922) is in appearance intermediate between pseudosteppe/steppe and low maquis. It is a discontinuous, low type of matorral. It occurs mainly where soil is thin or covered by scree or in firebreaks which are being allowed to revert back to maquis. The latter areas often have similar plant species to the maquis, with a greater number of open ground species in addition, such as Stipa gigantea, Cerastium gibraltaricum and Gladiolus communis.

Table 2.5 also gives an indication of the presence or absence of T. mauritanica, Ps. algirus and P. hispanica in the habitats. These were found in open habitats (as long as some cover was available). This included woodland, which had more open lower strata of vegetation than maquis, as long as some sunlight could reach the ground.

Ps. algirus was present in all the habitats (but not the North Front Cemetery), although mainly in lower vegetation. Both T. mauritanicus and P. hispanica occurred throughout on roadsides, etc. where the vegetation cleared and, in the case of the gecko, where there were vertical surfaces, provided usually by limestone or concrete.

The vegetation of Bruce's Firebreak can be categorised as pseudosteppe and garrigue. That of North Front Cemetery varied considerably, from closed simple herbaceous communities to complex low woody/herbaceous communities. In summer, the herbaceous communities become open as the annuals dry in the drought.

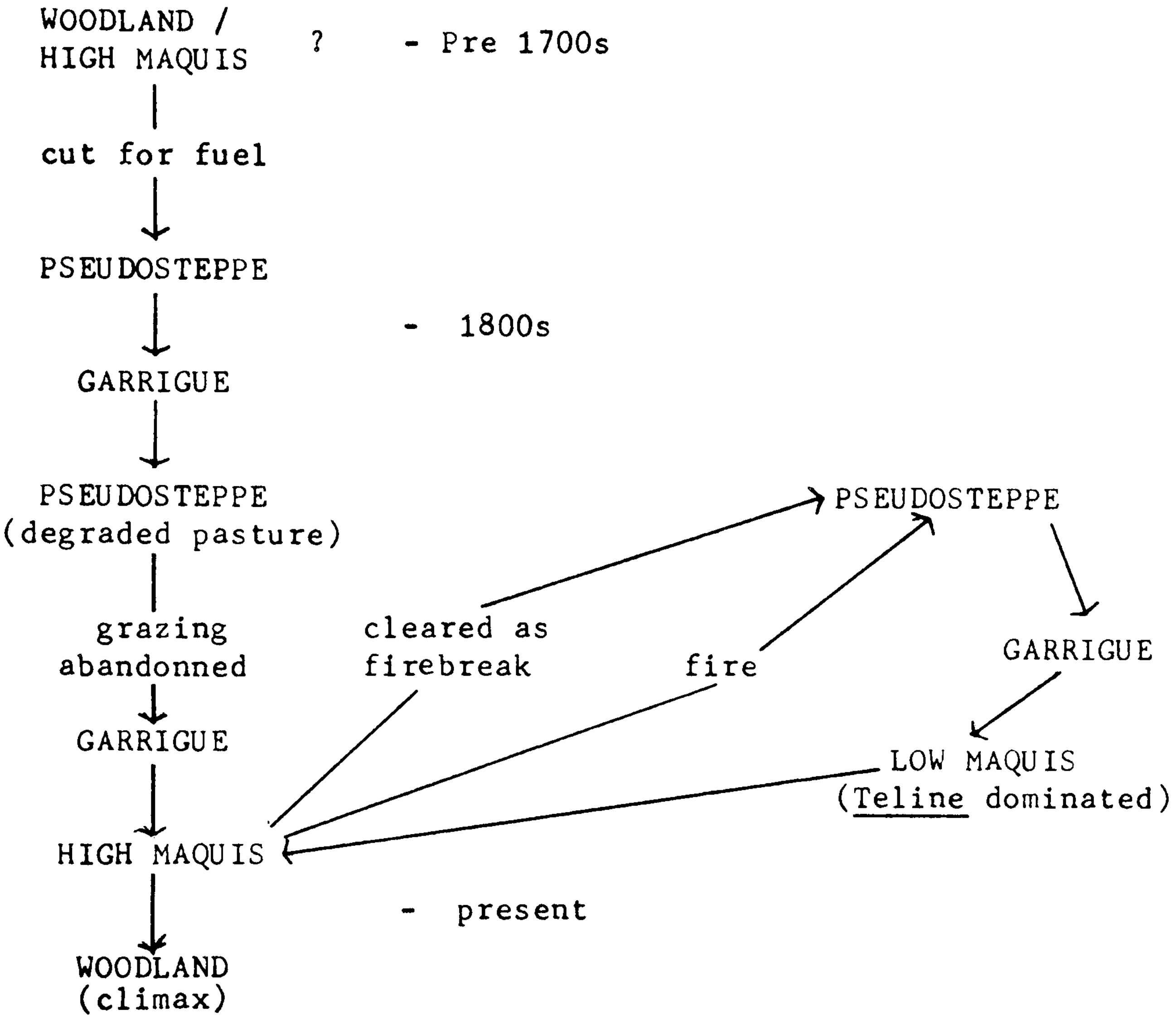
2.2.4 Discussion

Cortés (1979) concluded that habitats in Gibraltar could not be classified so much by plant species, as by structure of the vegetation. It appears, from this superficial approach, that vegetation structure is more important than plant species for lizards also. A similar conclusion is apparent from Mellado Camacho (1980) for lizards in Doñana, Spain.

The vegetation is represented diagrammatically in Figure 2.22, prepared from vegetation data collected around the Bruce's Firebreak site. The vegetation changed seasonally, and so lizards became more restricted in summer when ground cover virtually disappeared. Seasonal changes in habitat use are discussed, with particular reference to North Front Cemetery, in Chapter 5.

More long-term changes in vegetation were discussed in 1.3.2. These changes have been summarised in Figure 2.23, which gives a suggested pattern of seral succession at Gibraltar. From a consideration of the use of different habitats by lizards, it would appear that lizards will have increased in numbers in Gibraltar in the 1800s when vegetation was cleared, and later decreased again as it was allowed to regenerate. This pattern, on a smaller scale, is probably followed by the lizard community whenever vegetation is cleared artificially or by fire and is later allowed to regenerate.

Fig. 2.23 SUGGESTED SERAL SUCCESSION IN GIBRALTAR



CHAPTER 3

MATERIALS AND METHODS

3 MATERIALS AND METHODS

3.1.1 Trapping techniques

The technique most employed for catching lizards was the use of a noose, although in some few cases lizards were caught by hand.

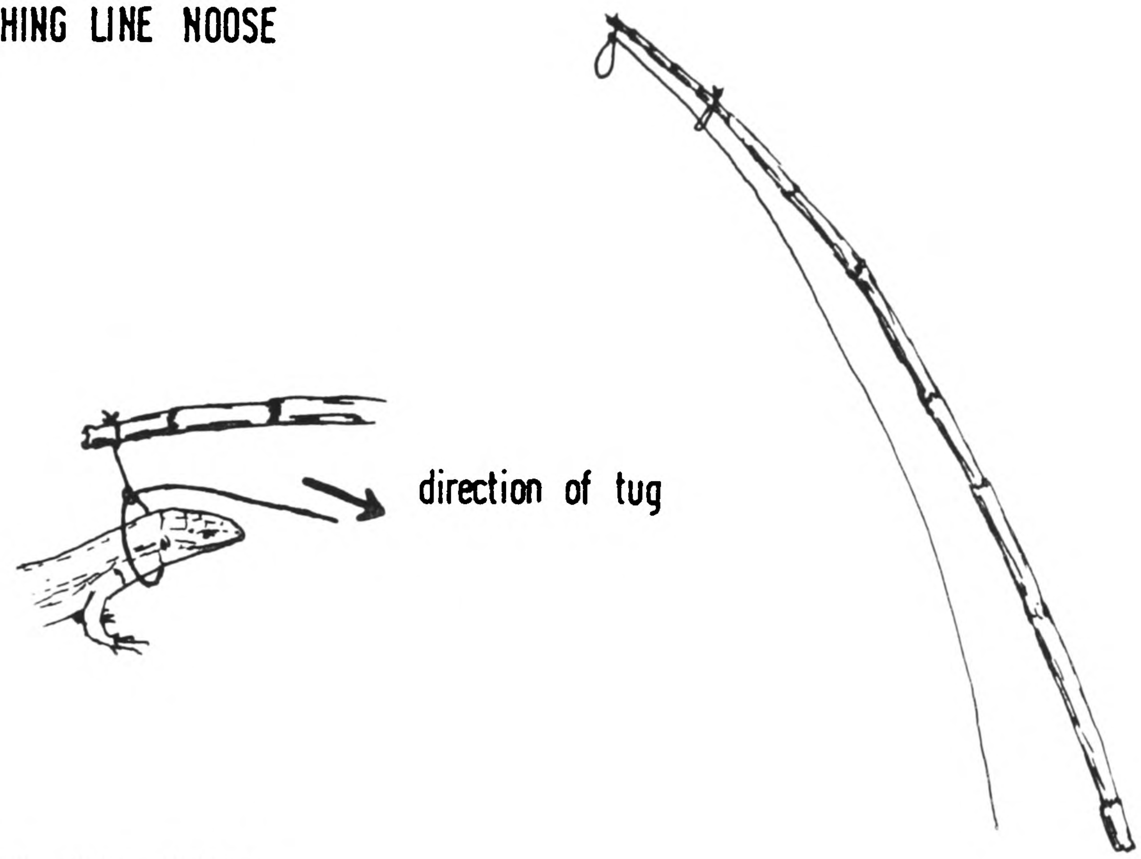
Two versions of noose were used. The first consisted of a length of about one metre of thin Giant Reed Arundo donax, with a loop of nylon fishing line tied on to one end, a length of the line continuing along the rod to the base. Once the lizard was noosed, the line was pulled sharply, and the loop closed around the lizard's neck (Figure 3.1.(a)). This procedure was found to be necessary since the weight of the lizards was not sufficient to close the loop if the noosed lizard was simply lifted quickly off the ground. The efficiency of this method was less than 50 per cent capture. The main reason for this was probably that the nylon line was too thick and visible. This assumption is supported by the observation that lizards often bit at the line.

Lizards were easier to catch in the morning just after emergence, (although not during emergence) than later on during the day. In many cases, the lizards fled at the approach of the noose, particularly after a failed attempt at noosing it. Even after the loop of the line was around the animal's neck, the latter frequently managed to escape in the time that it took to pull the noose tight. On several occasions the lizard ran through the noose, resulting in it being caught by the tail or escaping. On two out of four occasions when a lizard was thus caught, tail autotomy occurred.

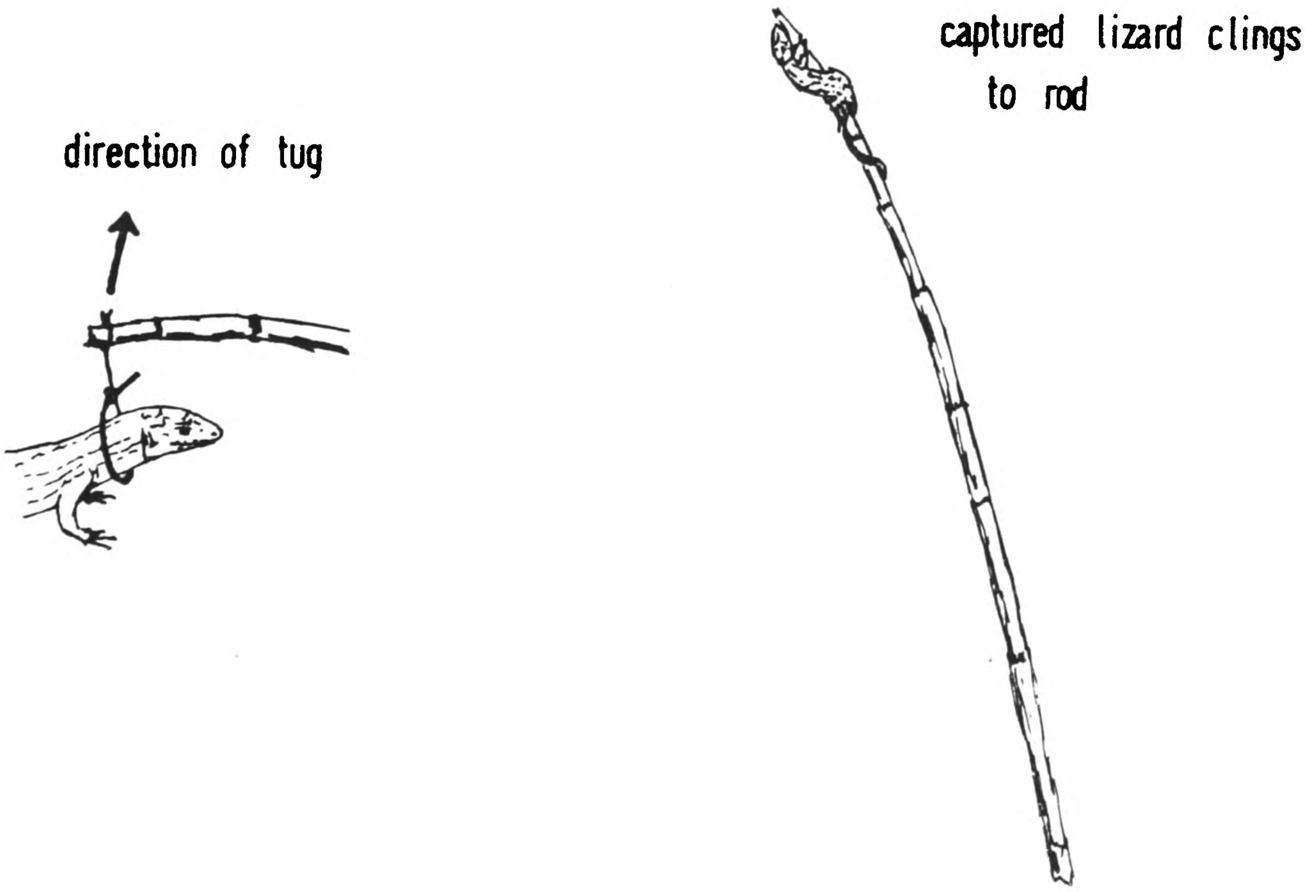
In October 1981, a second version of the noose was tried. It was made of Zebra-tail hair (from a Kenyan fly-whisk brought to Gibraltar as a souvenir - horse-hair was unobtainable in Gibraltar). The noose is depicted in Figure 3.1.(b). In this version, the end was not extended down the rod. Once the loop was around the lizard's neck, the rod was jerked upwards. Since the hair used did not have the same spring as the nylon previously employed, the weight of even the smallest lizards was enough to close the noose tightly. Moreover, since the hair was much thinner than the fishing line, it was generally not seen by the lizards, even if it touched them

Fig. 3.1. NOOSES

a) NYLON FISHING LINE NOOSE



b) ZEBRA-TAIL HAIR NOOSE



before they were noosed. None was seen to bite at the noose. This increased capture efficiency enormously. Since this technique was introduced quite late in the study, there is a bias in the morphometric data towards lizards caught during and after October 1981. Consequently also, there are relatively few data for Ps. algirus which were mainly caught during the early part of the study.

One disadvantage of the noosing technique is the fact that there is an unavoidable tendency to noose basking animals. Foraging animals are more difficult to detect and, since they are moving, to noose. There may therefore be a bias towards animals whose temperature may be lower than foraging ones, and towards animals caught at those particular times of day, and during those times of year, when basking is more intense.

3.1.2 Data collected

The following data were collected from captured lizards: date, time, species, sex, weight, cloacal temperature, head length, head-depth and width, hindleg and foreleg lengths, tail length (including length of new growth) and colours were recorded. Toes were clipped for permanent marking using the system of Marcellini (unpubl.; Figure 3.2) to take into consideration the possibility of natural toe loss (e.g. as a result of aggressive encounters with other lizards). Only on three occasions were lizards caught which had lost toes other than those clipped during the course of the study. The system of colour marking of lizards was an adaptation of that used by Jenssen (1970) and is illustrated in Figure 3.3.

The first measure to be taken was body temperature, taken as cloacal temperature for ease of measurement. This was measured with a thin thermistor probe inserted into the cloaca, and the temperature read off a scale. The ground temperature on the spot where the lizard was captured was recorded. Neither cloacal nor surface temperatures were taken when more than a few minutes had elapsed between capture and measuring. This occurred, for example, whenever there was any difficulty in removing the noose from around the lizard's neck. Excessive handling of these small ectotherms will affect their temperature. Date, time of capture, species and sex (in the case of Podarcis and Psammodromus which could be sexed by examining

Fig. 3.2 Code for marking lizards by toe-clipping. Symbol (1) represents an entire digit; the (0) represents a clipped toe.

	Fore Limbs		Hind Limbs	
Number	Left	Right	Left	Right
1	11110	10101*	11111	11111
3	11011	10101*	11111	11111
6	01110	11111	11111	11111
9	00111	11111	11111	11111
10	10101*	01111	11111	11111

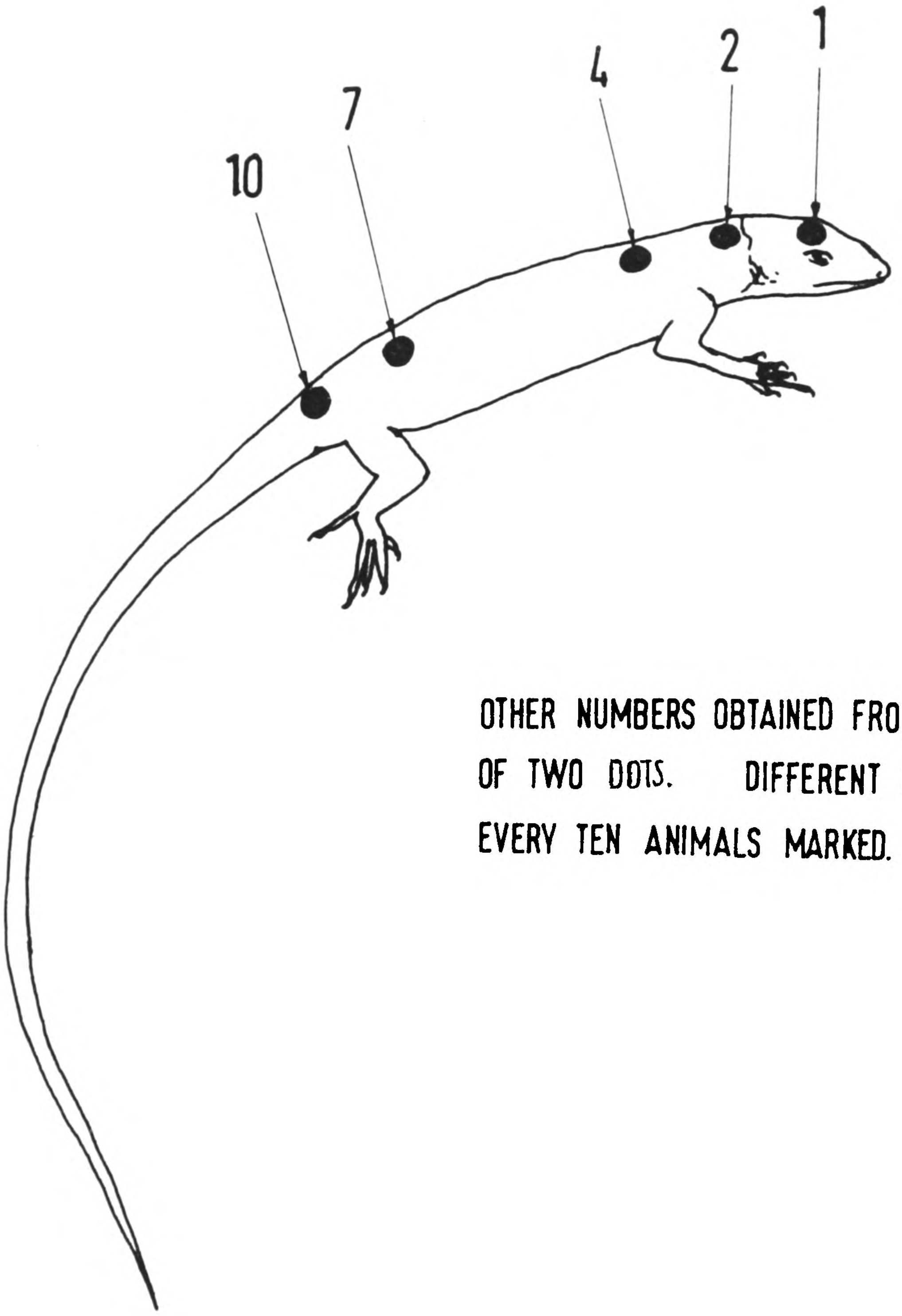
*Zero mark, used to prevent confusion that might arise with the capture of a lizard having a toe missing through natural causes.

the femoral pores, which are more developed in males (Arnold 1973, Mellado & Martinez, 1974)) were recorded. The location at which each lizard was caught and current weather conditions were noted. Lizards were weighed in small cellophane bags with Pesola scales. A 5g Pesola was used for P. hispanica and young Psammodromus, and a 10g Pesola for adult Psammodromus.

Measures of body and tail length (including lengths of regrown parts of the tail) were taken using a metal rule marked in 0·5 millimetre divisions. Measures of head and leg dimensions were made using callipers. Lizard measurements made in the field are illustrated in Figure 3.4.

Notes were made on colour, condition of femoral pores (in males), any scars or other unusual features, and, in the case of Ps. algirus the size of the spots on the neck (Figure 3.5; Table 4.8).

Fig. 3.3. COLOUR MARKING SCHEME USED ON LIZARDS



OTHER NUMBERS OBTAINED FROM COMBINATIONS OF TWO DOTS. DIFFERENT COLOURS USED AFTER EVERY TEN ANIMALS MARKED.

Fig. 3.4. LIZARD MEASUREMENTS TAKEN IN THE FIELD

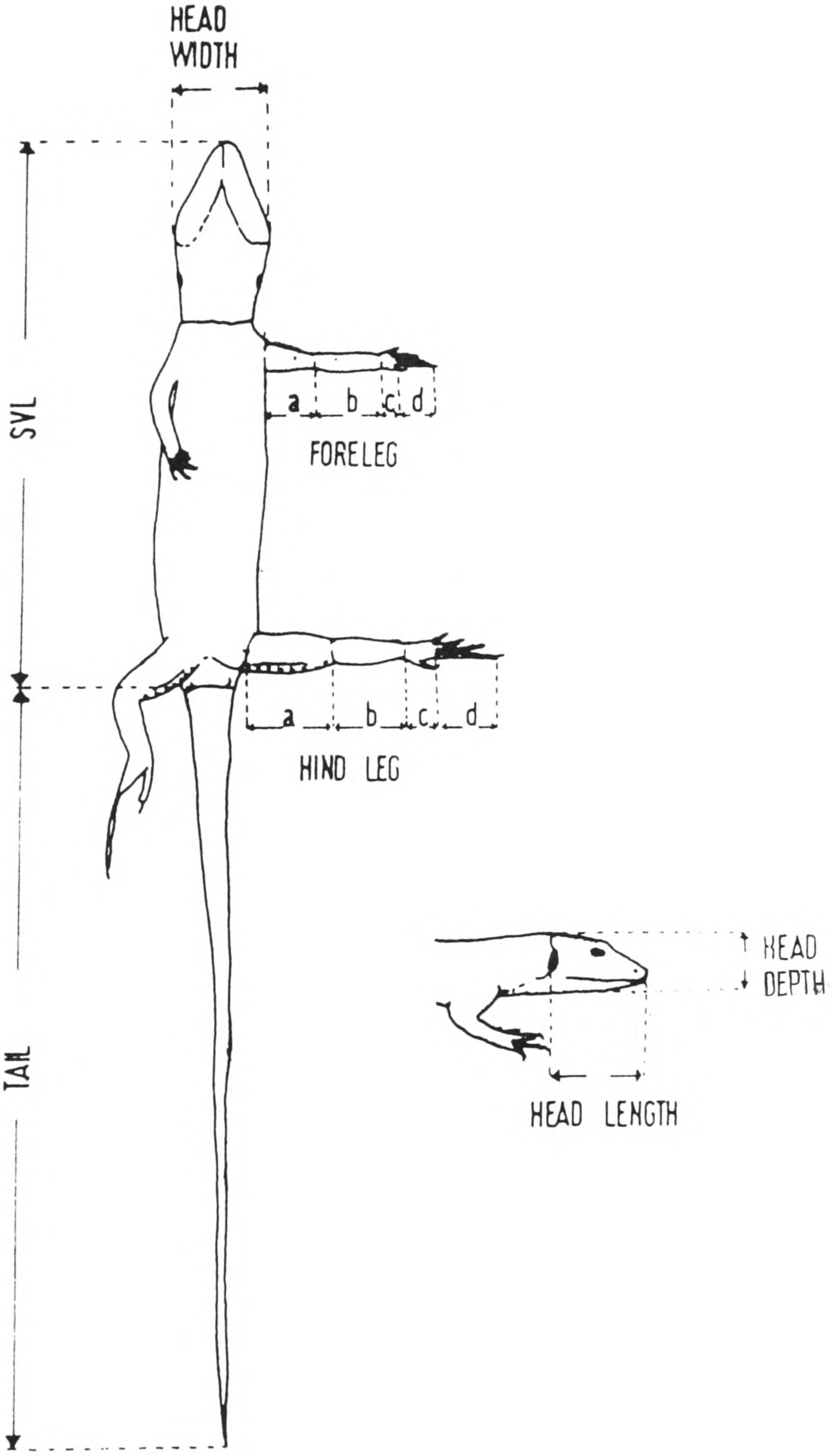
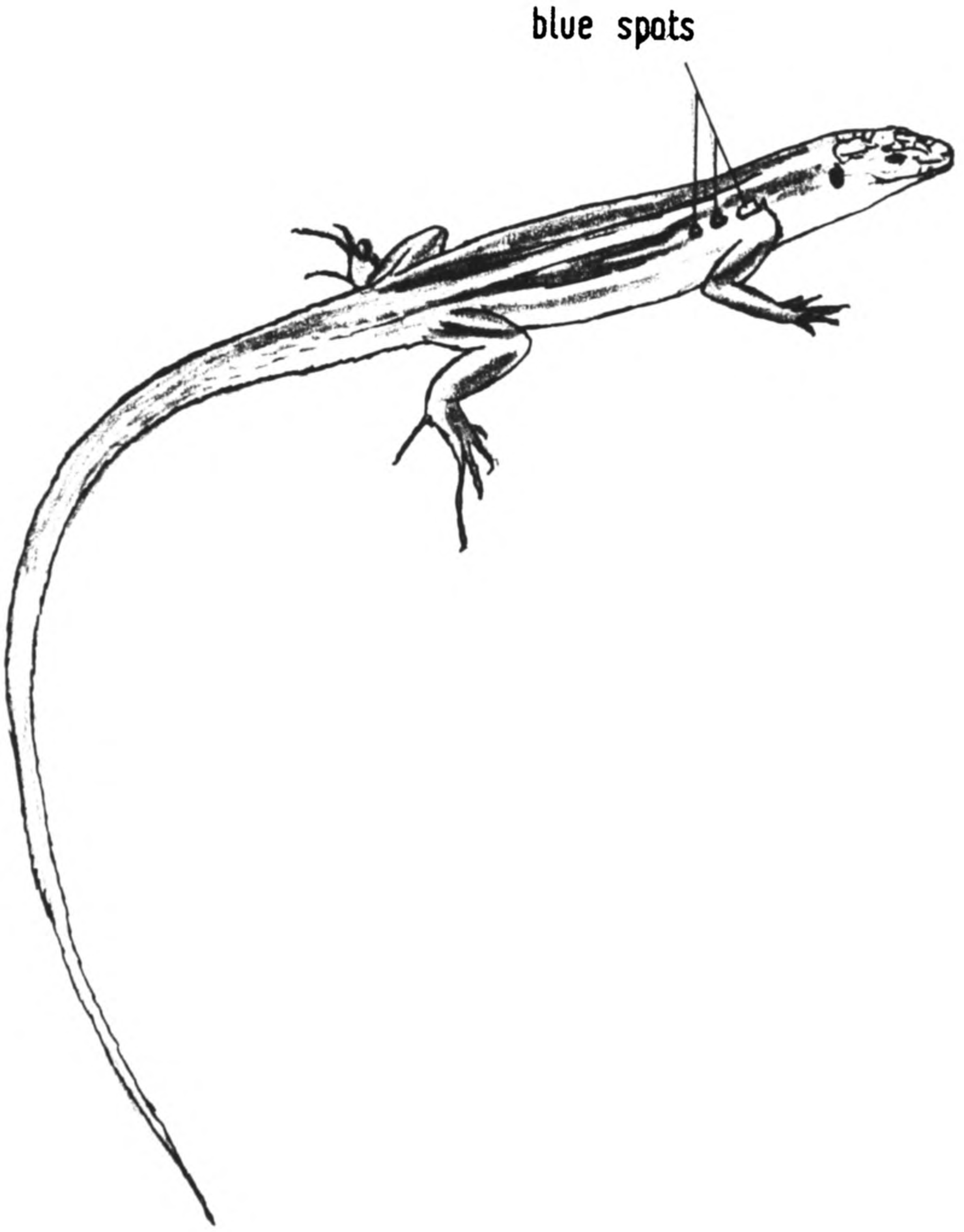


Fig. 3.5 Psammodromous algirus. SHOWING POSITION OF BLUE SPOTS.



3.2 Observational techniques

3.2.1 Transects

In order to determine the general habitats in which the lizards were found, the first few months of the study were dedicated largely to carrying out transects along a large stretch of the Upper Rock, from south to north along a road which crosses all the main habitat types of the area.

After specific sites had been chosen (1.5.) similar transects were carried out within these study areas, i.e. Bruce's Firebreak and North Front Cemetery. The data which were collected during these transects are listed in a sample page of the field notebook reproduced as Figure 3.6. Data headings were date, time, species, sex, microhabitat, substrate, orientation (with respect to compass direction and the ground) height above ground, cloud cover, whether in open or shade, activity, temperature at surface and 1cm above the surface, and any noteworthy remarks.

The original transects along the Upper Rock were made between December 1980 and March 1981, once daily during the middle of the day (commencing between 14•30 and 15•00 hrs). This, it was thought, would be the time when lizards would be most active at this time of year. The assumption was later proved to be correct (Chapter 8). Initially transects were made in all weathers, but it was soon realised that lizards were not active on other than clear days ($< \frac{3}{8}$ cloud cover). Subsequent observations were made on clear days only, except on a few occasions when the areas were visited on overcast days as a check on activity.

Transects in the sites were made at least every hour on most bright days (and some dull ones as a check). Long periods of dull weather (see Chapter 2) interrupted observations considerably, so the results for several days were pooled. This was generally done by months, so that all observations for each month were considered together and maxima for each hourly interval used. Observations were made from times of lizard emergence (determined by observations from sunrise) to times of submergence (again, determined through observation). Air temperature was recorded at the start of each transect. As was the case with

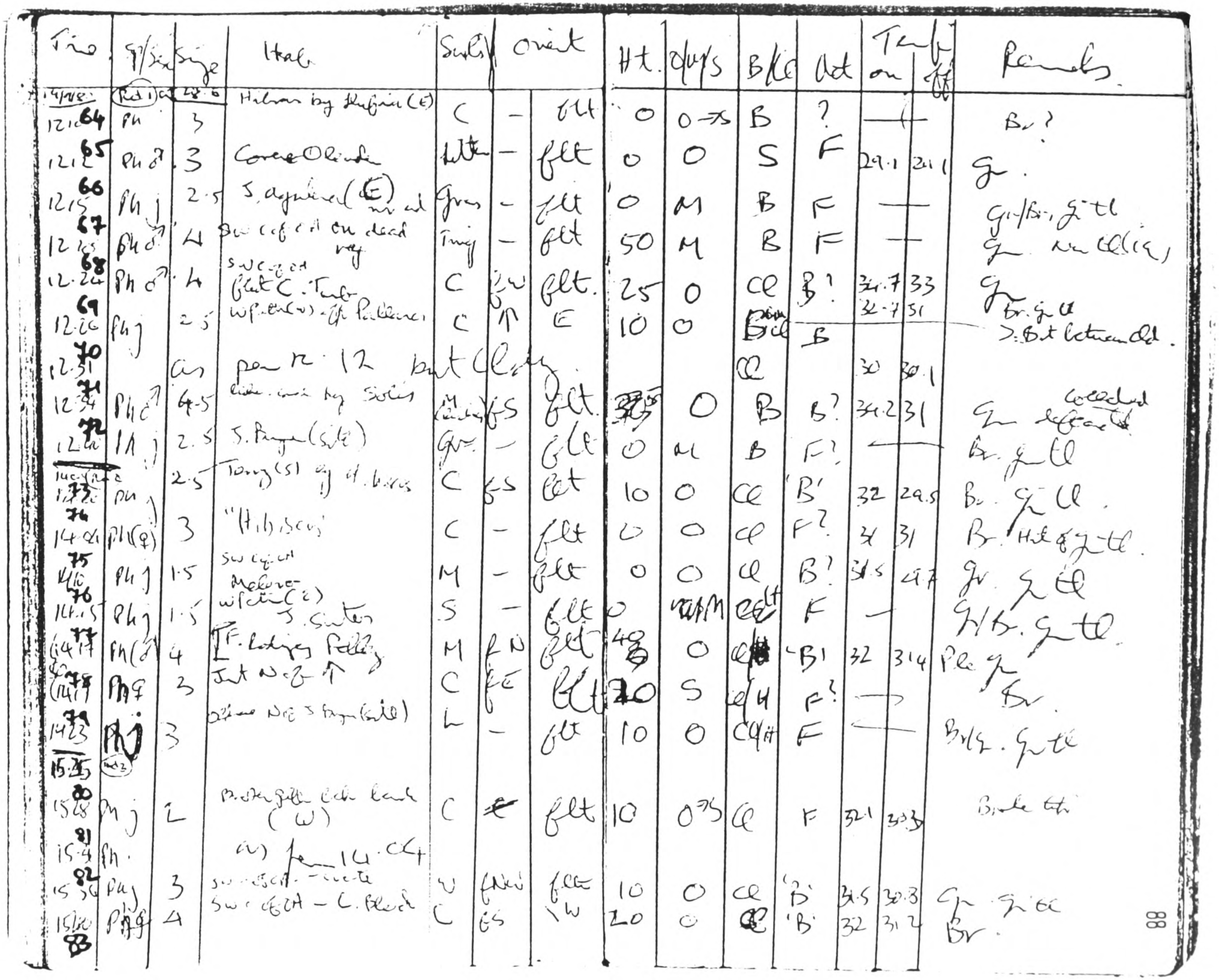


Fig. 3.6 SAMPLE PAGES FROM FIELD NOTEBOOK - NORTH FRONT CEMETERY TRANSECT.

Time	Sp/Sex	Size	Habitat	Substrate	Orient		Ht.	Clouds	Bkd	Act	Temp on	Temp off	Remarks
14/4/88	(Ref 1)	28.6	Habitat by [illegible] (E)										
12.10 64	Ph	3		C	–	flt	0	0→S	B	?	—		Br?
12.12 65	Ph ♂	3	Corner Oleander	[illegible]	–	flt	0	O	S	F	29.1	2?.1	Gr.
12.15 66	Ph j	2.5	S. [illegible] (E) [illegible]	Grass	–	flt	0	M	B	F	—		Gr/Br, [illegible]
12.18 67	Ph ♂	4	[illegible] on dead veg	Twig	–	flt	50	M	B	F	—		Gr [illegible]
12.24 68	Ph ♂	4	[illegible] flat C. [illegible]	C	f W	flt.	25	O	Cl	B?	34.7	33	Gr
12.26 69	Ph j	2.5	[illegible] Pallenis	C	↑	E	10	O	[illegible]	B	32.7	31	Br. [illegible] > [illegible]
12.31 70		As	per no. 12 but Cl[illegible]						Cl		30	30.1	
12.34 71	Ph ♂	4.5	[illegible] by Solis	M [illegible]	f S	flt.	35	O	B	B?	34.2	31	Gr [illegible] collected
12.[illegible] 72	Ph j	2.5	S. [illegible] (site)	Gr	–	flt	0	M	B	F?	←		Br. [illegible]
14c.4/88 1.33 73	Ph j	2.5	Tomb (S) [illegible]	C	f S	flt	10	O	Cl	'B'	32	29.5	Br. [illegible]
14.0[illegible] 74	Ph (♀)	3	"Hibiscus"	C	–	flt	0	O	Cl	F?	31	31	Br. [illegible]
14.10 75	Ph j	1.5	Sw [illegible]	M	–	flt	0	O	Cl	B?	31.5	[illegible]	Gr. [illegible]
14.15 76	Ph j	1.5	Malva [illegible] (2) J. [illegible]	S	–	flt	0	[illegible] M	Cl lt	F	—		Gr/Br. [illegible]
14.17 77	Ph (♂	4	F. [illegible] Felling	M	f N	flt	40	O	Cl	'B'	32	31.4	Ple. [illegible]
14.19 78	Ph ♀	3	Just N of ↑	C	f E	flt	20	S	Cl/H	F?	→		Br.
14.23 79	Ph j	3	[illegible] S. [illegible] (site)	L	–	flt	10	O	Cl/H	F	—		Br/Gr. [illegible]
15.25	(Ref 2)												
15.28 80	Ph j	2	[illegible] (W)	C	f	flt	10	0.75	Cl	F	32.1	30.3	[illegible]
15.4 81	Ph		As per 14 [illegible]										
15.3[illegible] 82	Ph j	3	Sw [illegible]	W	f NW	flt	10	O	Cl	'B'	31.5	30.3	Gr [illegible]
15.[illegible] 83	Ph ♀	4	Sw [illegible] – C. Black	C	f S	W	20	O	Cl	'B'	32	31.2	Br.

capture techniques, an observational bias towards basking lizards would be expected. It is true that basking lizards, being more prominent are easier to observe. However, foraging lizards could be seen, particularly in the more open vegetation where most observations were made. Moreover, foraging animals were frequently located by sound. The results demonstrate that despite this bias, differences in the number of lizards basking and foraging at different times of day and year can be seen from the data, and appear to reflect a natural pattern. This is discussed again in the section dealing with basking behaviour (Chapter 8). Although all lizards observed were recorded, data on activity and ground temperatures were only used if the lizard had been seen (or heard) before being disturbed. The treatment of the data collected is described in the pertinent sections.

3.2.2 Continuous observations

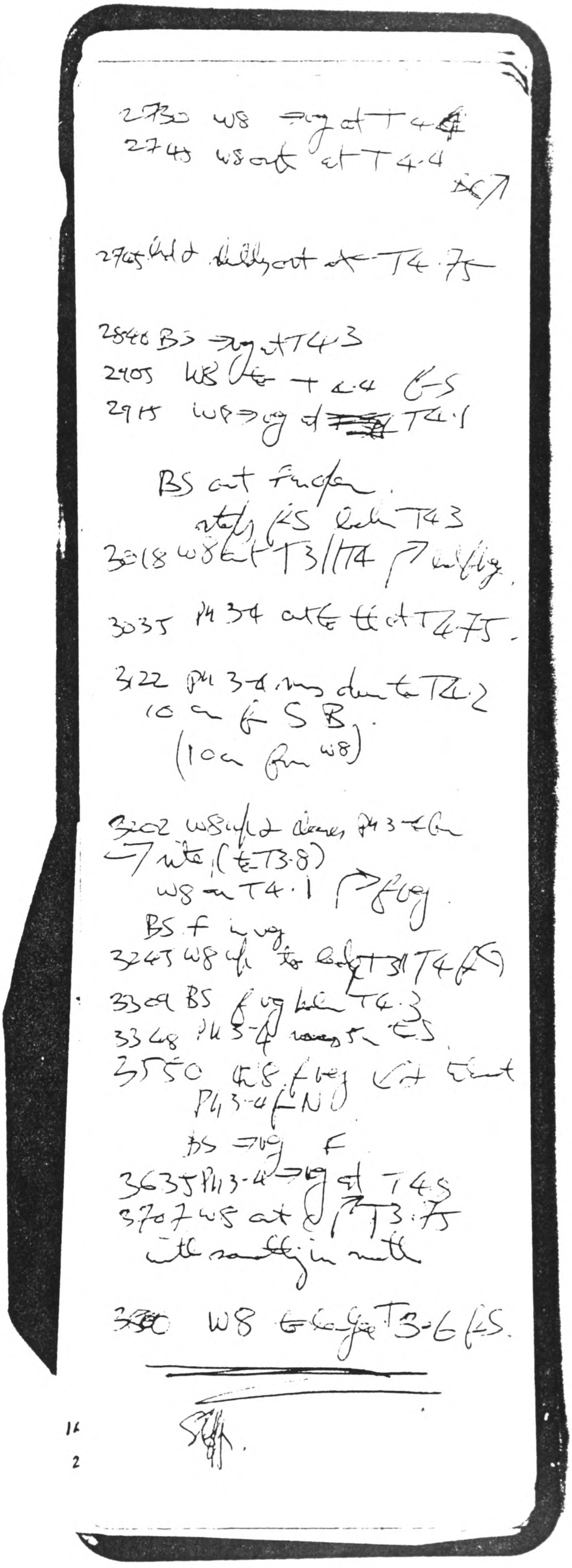
The transect method was alternated with direct and continuous observations of marked lizards. Towards the end of the field study (the end of 1981) continuous observations replaced transects completely, in order that I could relate the results of the transects, (which had been carried out for well over a year) with the behaviour of individual lizards. Continuous observations would have had to be interrupted in order to carry out a scheduled transect. Initially when a determination of activity periods was essential, transects took priority.

A marked lizard was observed and followed during all aspects of behaviour until it was lost for a period exceeding 10 minutes. Then attention was switched to another lizard. Lizards could on occasion be followed for over two hours.

Time was divided as much as much as possible between males and females and different age classes. However, when it appeared that it would be impossible to cover all sizes and sexes thoroughly, preference was given to adult males which in any case were easier to see throughout the year. All the activities of the lizards were recorded in a field notebook, together with the time in minutes and seconds read off a digital watch attached to the notebook. Directions of movement, distance covered, changes in direction, changes in orientation, height above ground and any particular activity, such as aggressive or other encounters with lizards, feeding, scratching and drinking were noted. (A sample page is reproduced in Figure 3.7.). Although much data had to be recorded, this did not prove as difficult as might appear, since much time was spent basking and changes in activity did not occur in rapid succession. There was generally time enough even to draw the occassional diagram in the field notes and, when several lizards were basking together, to record observations for more than one at a time.

Air temperatures were recorded every hour and continuous recording of temperature in different microhabitats was carried out as described in 2.1., simultaneously to the observation on the lizards.

Fig. 3.7 SAMPLE PAGES FROM FIELD NOTEBOOK - CONTINUOUS OBSERVATIONS.



2730 W8 → veg at T4.4
2745 W8 out at T4.4
[illegible] ↗

2765 [illegible] [illegible] out at T4.75

2840 BS → veg at T4.3
2905 W8 [illegible] T4.4 [illegible]
2915 W8 → veg at ~~[illegible]~~ T4.1

BS out [illegible]
[illegible] [illegible] [illegible] T4.3
3018 W8 at T3/T4 ↗ [illegible]

3035 Ph 3-4 out [illegible] at T4.75.

3122 Ph 3-4 [illegible] down to T4.2
10 m [illegible] S B.
(10 m from W8)

3202 W8 [illegible] [illegible] Ph 3-4 [illegible]
↗ [illegible] (to T3.8)
W8 on T4.1 ↗ [illegible]
BS f in veg
3245 W8 [illegible] to [illegible] T3/T4 [illegible]
3309 BS f veg [illegible] T4.3
3348 Ph 3-4 [illegible] [illegible] ES
3550 W8 f veg [illegible] [illegible]
Ph 3-4 f N
BS → veg F
3635 Ph 3-4 → veg at T4.5
3707 W8 at [illegible] ↗ T3.75
with something in mouth

[illegible] W8 [illegible] T3.6 [illegible].

3.3 Studies in Captivity

Lizards (*P. hispanica*) were kept in captivity during three periods.

(1) In Gibraltar out-of-doors.

(2) In the Zoology Department, Oxford from January to March (9 weeks) in 1981.

(3) In the Zoology Department, Oxford from April to July (15 weeks) in 1982.

3.3.1 Lizards kept in Gibraltar

Lizards were collected from NFC at different times of the year and kept in a terrace in the Town of Gibraltar (Figure 1.2). Several enclosures were made using a wooden frame and fine mesh. It however proved impossible to use these since feral cats which roam the rooftops in the area repeatedly damaged the mesh and allowed lizards to escape.

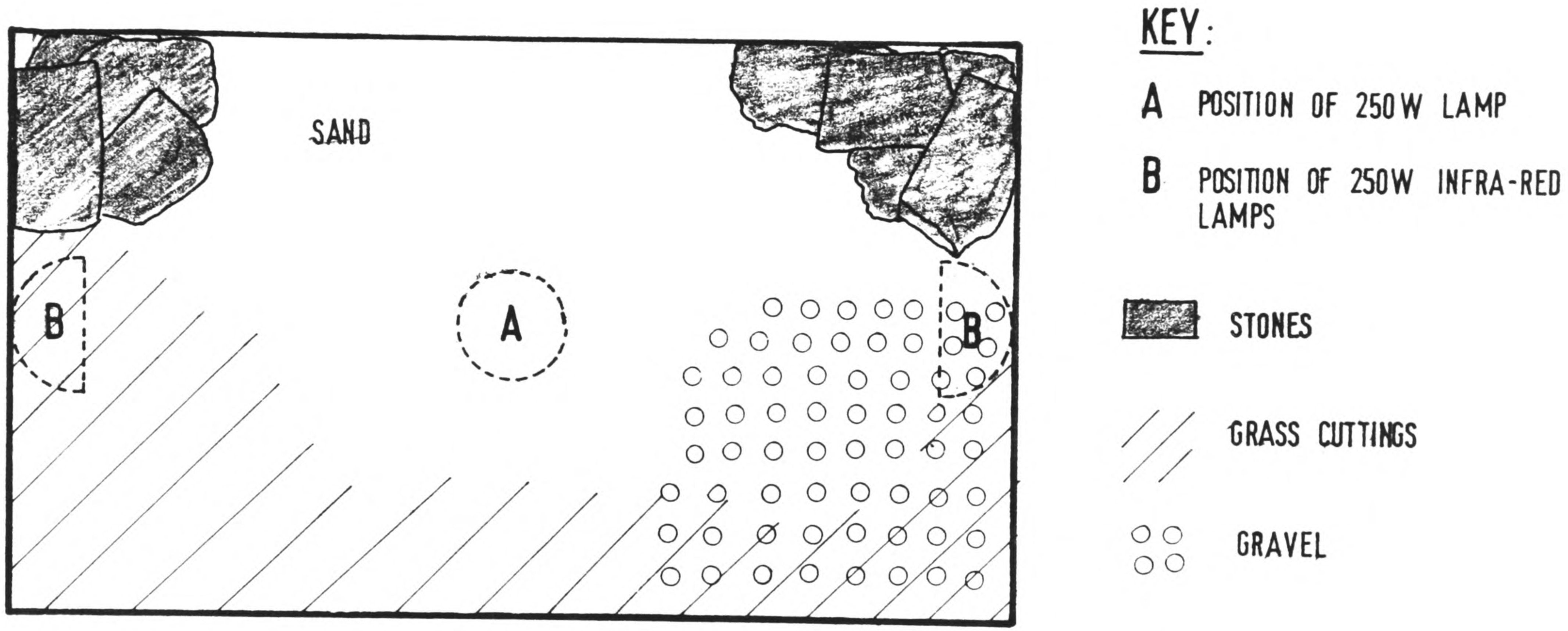
The lizards were subsequently kept in smaller glass (70 x 35 x 35cm) or plastic (35 x 25 x 25 cm)vivaria with a mesh as a lid and which were covered with wooden boards at night to prevent cat damage. Each vivarium was provided with a layer of earth and gravel, leaf litter and grass. Stones were arranged at either end of the tanks to provide basking sites and crevices for shelter. The lizards were fed on blowflies, houseflies, mealworms and other insects collected during sampling in the field. Two to three lizards were kept in the smaller vivarium and up to five in the larger one. These were kept temporarily before transfer to Oxford, so that few observations were made.

3.3.2 Lizards kept in Oxford: January to March 1981.

Nine lizards, (7 males and 2 females) collected in late December 1980 from NFC site, were kept during this time in a vivarium similar to that used in Gibraltar. The tank measured 70 x 40 x 40 cm and contained a layer of sand with grass litter and stones arranged as shown in Figure 3.8. The tank was fitted with a wooden lid with an attachment for a lamp. Lizards could not climb up the smooth sides of the tank.

The tank was kept in conditions simulating those found in the wild in winter. A light regime of 8 hours light: 16 hours dark was maintained. The temperature at night was allowed to drop to 7°C, that of the temperature - controlled room in which the vivarium was kept. During the hours of light heating was provided by a 250 W reflector lamp in the centre of the tank and two 250 W infra-red lamps attached at the sides preventing the sides of the tank from remaining at the room temperature of 7°C throughout the day. Temperatures in the tank were monitored using a maximum-minimum thermometer and were normally

Fig. 3.8 ARRANGEMENT OF LARGE VIVARIUM



maintained at around 15°C. Substrate temperatures were taken under lizards using thermistor probes.

Young cockroaches, crickets and mealworms were provided as food. Lizards were observed throughout the light hours. Interactions between individuals were recorded and notes were made on feeding and drinking behaviour.

3.3.3 Lizards kept in Oxford : April to July 1982.

Fifteen lizards (10males and 5 females) were kept in vivaria at Oxford between April and July 1982. Initially 10 were kept in the same vivarium used a year earlier, 2 and 3 lizards were kept respectively in vivaria measuring 35 x 25 x 25 cm and 45 x 30 x 30 cm, arranged similarly to that in Figure 3.8.

The lizards were collected from NFC mainly in the last fortnight in March. At Oxford they were kept in conditions approximating those found in the field in spring. A light regime of 10 hours light : 14 hours dark was maintained. Light and heat was provided by 60 W opaque light bulbs. The tanks were kept in a room at about 15°C. Temperature during the day rose to about 25°C. All other conditions were similar to those described in 3.3.2.

Observations on behaviour were again made. Growth was monitored by taking regular morphometric measurements. In addition adult males were used for respirometry.

CHAPTER 4

MORPHOLOGY

4 MORPHOLOGY

4.1 Morphometrics

4.1.1 Introduction

The main morphometric measurements taken for both *Podarcis hispanica* and *Psammodromus algirus* are given in Table 4.1. Values given by Mellado *et al.* (1975) and Busack (1978) are included for comparison. Neither work gives a breakdown of results in relation to the number of lizards of different sizes which were sampled. Busack (1978), whose sample size for *P. hispanica* is very small, does not distinguish between sexes. The sets of results are therefore not directly comparable and no conclusion can be arrived at as regards differences in the morphometric characteristics of the different lizard populations. The times of year during which the lizards were collected (year-round in this study, spring in Mellado *et al.*, 1975, summer in Busack, 1978) will also affect the results, since different sizes of lizard are predominant at different times of the year. Rather than absolute values, it is far more useful to investigate the relationship between the different dimensions and lizard snout-vent length (SVL). Unfortunately, neither of the two studies mentioned give this information, so no comparisons are possible.

4.1.2 Methods

The main morphometric measurements taken for both *P. hispanica* and *Ps. algirus*, given in Table 4.1., were weight (g); snout-vent length (SVL) (mm), head length (mm), and head width (mm). Values given by Mellado *et al.* (1975) and Busack (1979) have been included for comparison in Table 4.1.

Weights, head lengths and widths for *P. hispanica* were divided arbitrarily according to SVL. Regressions of $\sqrt[3]{\text{weight}}$ against SVL, head length against SVL and head width against SVL were calculated and compared using t-tests and analyses of covariance (ANCOVA) on pairs of regressions. This latter test calculates F-ratios for slope and intercept for the pairs of regressions.

Where sample sizes were too small for the t-test to be used with confidence (pairs marked with an asterisk in Table 4.3.) this test was not carried out. Data on male and female *Ps. algirus* were pooled due to small sample size.

A regression of head width against head length was also calculated. A comparison was made of pooled P. hispanica and Ps. algirus data.

To allow subdivision of data and therefore smaller sample size, the ratios $\sqrt[3]{\text{weight}}$ / SVL; head length: SVL; head width/ SVL and head width/ head length were compared for each pair of lizard category with the non-parametric Mann-Witney U-test. The subdivision of the data was according to sizes (SVL). Categories were for both male and female NFC P. hispanica as follows: >50mm (fully grown), 45-50mm, <45mm (juvenile). No differences could be found between the 45-50mm and >50mm NFC males for any of the ratios tested, so that these data were pooled into a >45mm category. For BFB lizards only data from males could be subdivided (into < 45mm and >45mm categories) since the sample size was small. The pairs of data compared are listed in Table 4.6.

The NFC P. hispanica weight data were divided according to time of year when they were collected. The year was itself divided according to the condition of the habitat (type of vegetation) at the time. Period A corresponds to the months of December and January (mainly low vegetation consisting of Oxalis pes-caprae), period B corresponds to the months of February, March, April and May, when there is a profuse growth of flowering annuals; period C to June, July, August and September when the ground cover is almost completely dry; and period D includes October and November, when vegetation begins to sprout after the autumn rains.

Kruskall-Wallis non-parametric tests were carried out on the $\sqrt[3]{\text{weight}}$ / SVL ratios for the four periods and for males, females and males and females together. Only where sample size was large enough was an analysis of covariance carried out. This was possible for data from males, females and males and females for periods A vs D, B vs D and A vs B. Data for males and females were compared for each of the four periods using the Mann-Witney U-test. For periods B and D, where $N_2 > 21$, the calculation of z (Siegel, 1956) was necessary. Season C was excluded from the ANCOVA and from one Kruskall-Wallis test since sample size was small.

4.1.3 Results

SVL measured in the field varied from 55·5mm to 30·5mm for males (n=95) and 55mm to 31mm for females (n=42) for P. hispanica and from 72mm to 36mm for Ps. algirus (males) (n=8) and from 73mm to 32mm for females (n=15).

Weights, head lengths and head widths for P. hispanica are presented in Table 4.2. according to arbitrary size classes (< 35mm, 36·0 - 39·9mm, 40·0 - 44·9mm, 45·0 - 49·9mm, >50mm).

Weights of P. hispanica range from a mean of 1·02g (S.D. = 0·30) and 1.04g (S.D. = 0·16) for females and males respectively of SVL up to 35·9mm, to 2·81g (S.D. = 0·74) and 3·38g (S.D. = 0·44) respectively for females and males of SVL greater than 50·0mm (Table 4.2.). Mean head lengths of the smallest size class are 9·34mm (S.D. = 0·92) and 9·20mm (S.D. = 0·50) for females and males respectively and range to 11·84mm (S.D. = 0·59) and 13·61mm (S.D. = 0·82) respectively in the largest size class. Head widths for the small size class were 5·76mm (S.D. = 0·41) and 5·65mm (S.D.=0·52)(means)for females and males and for the largest class were 7·42mm (S.D. = 0·50) and 8·57mm (S.D. = 0·49) for females and males.

The differences between males and females increased with SVL. Small (< 35·9mm) males were very similar in all dimensions to small females.

The results of the regression of $\sqrt[3]{\text{weight}}$ against SVL are given as follows: Male P. hispanica (North Front Cemetery) y= 0·145 + 0·026x r= 0·952 (Figure 4.1.). Female P. hispanica (North Front Cemetery) y= 0·262 + 0·22x r= 0·884 (Figure 4.2.) Ps. algirus, y= 0·239 + 0·026x r= 0·964 (Figure 4.3.). These three regressions, which are all significant, (P < 0·01) are shown together in Figure 4.4. The widest scatter of points was found for female P. hispanica (Figure 4.2) with both exceptionally heavy (gravid) and light animals featuring in the sample. If measured as rate of increase in the $\sqrt[3]{\text{weight}}$ /SVL ratio, the rate of growth is greatest in male P. hispanica, while Ps. algirus tend to be heavier per given SVL than either male or female P. hispanica. Plots of head length against SVL for male and female P. hispanica (North Front Cemetery) and for all Ps. algirus are shown in Figure 4.5 and the regression slopes in Figure 4.6. The equations of the regressions are, for male P. hispanica y = 1·597 + 0·231x (r= 0·907); for female P. hispanica y= 4·415 + 0·142x (r= 0·842) ; and for Ps. algirus y= 3·219 + 0·206x (r= 0·910). All the regressions are significant (P < 0·01).

Head length in *Ps. algirus* tends to be greater than that in *P. hispanica* (males or females) of the same SVL, although there is considerable overlap (Figure 4·5) between *P. hispanica* and young *Ps. algirus*. There is also overlap in the data between males and females although this decreases as the regression lines diverge with increasing SVL. Male *P. hispanica* achieve greater head lengths than females. Similar plots of points and regression lines for head width against SVL are shown in Figure 4.7 and 4.8 respectively. Regression equations are : male *P. hispanica*, $y= 0{\cdot}253 + 0{\cdot}159x$ ($r=0{\cdot}894$); female *P. hispanica*, $y= 2{\cdot}485 + 0{\cdot}088x$ ($r= 0{\cdot}458$) *Ps. algirus* $y= 1{\cdot}824 + 0{\cdot}123x$ ($r= 0{\cdot}925$). Again all are significant ($P< 0{\cdot}01$). A similar pattern to that seen in the head length vs SVL relationship is seen for head width. Male *P. hispanica* however have wider heads in relation to SVL than *Ps.algirus* in general after achieving a SVL of about 44mm. Male *P. hispanica* also achieve greater head widths than do females. Results are illustrated similarly for head width against head length in Figure 4.9 and 4.10 for male *P. hispanica* ($y= -0{\cdot}055 + 0{\cdot}622x$ $r=0{\cdot}879$), female *P. hispanica* ($y = 1{\cdot}426 + 0{\cdot}475x$, $r = 0{\cdot}670$) and *Ps. algirus* ($y = 1{\cdot}034 + 0{\cdot}524x$, $r = 0{\cdot}870$). There is a great deal of overlap in these data, male *P. hispanica* however achieving greater head widths and lengths than females. The regression for males has a steeper slope than that for females and for *Ps. algirus*. The latter species achieves greater head lengths and widths (they grow larger in any case).

The results of the t-tests and analyses of covariance on pairs of the above regressions are summarised in Tables 4.3 and 4.4. The t-test was used to compare the regression of $\sqrt[3]{\text{weight}}$ vs SVL between NFC male *P. hispanica* and NFC female *P. hispanica*, NFC male *P. hispanica* and BFB male *P. hispanica* , NFC male *P. hispanica* and *Ps. algirus*, NFC female *P. hispanica* and *Ps. algirus* and BFB male *P. hispanica* and *Ps. algirus*. Similar pairs of regressions of head length vs SVL and head width vs SVL (with the exception of the NFC female *P. hispanica* and *Ps. algirus* pair of head length vs SVL data where sample sizes were too small)were tested. All regressions tested were significantly different ($P<0{\cdot}001$) from the others.

The analysis of covariance of the $\sqrt[3]{\text{weight}}$ vs SVL regressions (Table 4.4) showed no significant differences between male *P. hispanica* from the two study sites (these data were then pooled for comparison with *Ps. algirus*). In the comparisons of NFC males with NFC females, NFC females with BFB males, NFC females with *Ps. algirus* and *Ps. algirus* with both all male P. hispanica and all P. hispanica, only the intercepts and not the slopes were significantly different. Similarly only the intercepts were significantly different in the comparison of head length vs SVL regressions between BFB and NFC male P. hispanica and pooled P. hispanica data and Ps. algirus. No difference was found between the Ps. algirus and all male P. hispanica regressions. Only the slope showed a significant difference in the comparison of head width vs SVL regressions of NFC male P. hispanica and Ps. algirus. Both slope and intercept differed significantly in the NFC male with NFC female and the NFC female with Ps. algirus comparisons of the similar regressions. Neither slope nor intercept were significantly different in the comparisons of BFB male with both NFC males and Ps. algirus. No significant differences were found between either slopes or intercepts in any of the pairs of regressions of head width vs head length compared, viz. NFC males with NFC females, NFC males with BFB males, NFC males with Ps. algirus, NFC females with Ps. algirus and BFB males vs Ps. algirus. The implications of these differences are given in 4.1.4.

The resultsof non-parametric Mann-Witney U-test on the main data are tabulated in Table 4.5, together with a summary of both t-tests and analyses of covariance. Significant differences were found between the following pairs: $\sqrt[3]{\text{weight}}$ vs SVL :- NFC male and BFB male P. hispanica ($P = 0{\cdot}0192$), Ps. algirus and BFB male P. hispanica ($P = 0{\cdot}0003$) Ps. algirus and NFC male P. hispanica ($P = 0{\cdot}0034$), Ps. algirus and NFC female P. hispanica ($P = 0{\cdot}0002$). Head length vs SVL :- NFC male vs NFC female ($P = 0{\cdot}00003$), NFC male and BFB male ($P = 0{\cdot}0119$), Ps. algirus and BFB male P. hispanica ($P = 0{\cdot}0033$), Ps. algirus and NFC male P. hispanica ($P = 0{\cdot}0495$); Head width vs SVL - NFC male and NFC female P. hispanica ($P = 0{\cdot}00003$), Ps. algirus and BFB males P. hispanica ($P = 0{\cdot}0007$), Ps. algirus and NFC male P. hispanica ($P = 0{\cdot}0003$); head width vs head length - Ps. algirus and BFB male P. hispanica ($P = 0{\cdot}0091$), Ps. algirus and NFC female ($P = 0{\cdot}0018$).

The Mann-Witney U-tests carried out on the data divided into size classes gave significant results for most of the comparisons of head dimensions between corresponding categories of males and females (Table 4.6). Both males and females showed differences between those lizards <45mm SVL and those >45mm SVL. More interesting than this apparent growth of the head in relation to SVL is the observation that the head length of large (adult) male BFB P. hispanica differs from that of Ps. algirus with which it occurs, while that of male NFC P. hispanica which are not in contact with Ps. algirus do not. (Large male P. hispanica from each site differ statistically from each other; small males do not.)

Table 4.1 Weights, snout-vent lengths (SVL), head lengths and head widths of *Podarcis hispanica* and *Psammodromus algirus*. (S.D. = **Standard deviation of sample**).

	Weight (g)			SVL (mm)			Head length (mm)			Head width (mm)		
	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n
Podarcis hispanica ♂												
This study	2·30	0·93	92	44·51	6·78	94	12·00	1·73	90	7·21	1·42	91
Mellado *et al.* (1975)	2·00	1·00	45	46·03	4·70	131	10·30	1·80	59	5·87	1·00	56
Podarcis hispanica ♀												
This study	1·91	0·85	42	42·88	6·69	44	10·44	1·16	42	6·45	0·83	43
Mellado *et al.* (1975)	2·16	0·91	139	43·97	6·75	139	11·43	1·74	134	7·10	1·16	135
Psammodromus algirus ♂ + ♀												
This study	6·22	2·82	24	55·33	18·77	27	15·48	2·63	25	9·14	1·59	25
Mellado *et al.* (1975)	7·70	2·40	65	58·88	14·60	41	15·90	2·20	39	10·60	1·90	39

Note: Busack (1979) gives the following results for male and female lizards together:

Podarcis hispanica Weight = 3·9 ± 0·03 g; SVL = 55·9 ± 1·1 mm; n = 19

Psammodromus algirus Weight = 7·7 ± 0·40 g; SVL = 63·3 ± 1·0 mm; n = 27

Table 4.2. Weights, head lengths and head widths of *Podarcis hispanica* at Gibraltar by arbitrary size classes.

Size class (SVL) mm		≤35·9		36·0-39·9		40·0-44·9		45·0-49·9		≥50·0	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Weight (g)	$\bar{x}$	1·02	1·04	1·15	1·37	1·76	1·82	2·42	2·61	2·81	3·38
	S.D.	0·30	0·16	0·23	0·23	0·27	0·26	0·52	0·40	0·74	0·44
	n	7	13	6	9	12	24	7	18	10	27
Head length (mm)	$\bar{x}$	9·34	9·20	9·18	10·60	10·35	11·16	11·11	12·85	11·84	13·61
	S.D.	0·92	0·50	0·69	0·74	0·42	0·74	0·51	1·02	0·59	0·82
	n	7	12	6	8	13	25	7	19	9	29
Head width (mm)	$\bar{x}$	5·76	5·65	5·35	6·27	6·42	6·92	6·76	7·87	7·42	8·57
	S.D.	0·41	0·52	0·79	0·60	0·31	0·52	0·28	0·77	0·50	0·49
	n	7	12	6	9	13	25	7	19	10	30

Fig. 4.1. REGRESSION OF $\sqrt[3]{\text{WEIGHT}}$/SVL FOR MALE *Podarcis hispanica* (NORTH FRONT CEMETERY SITE)

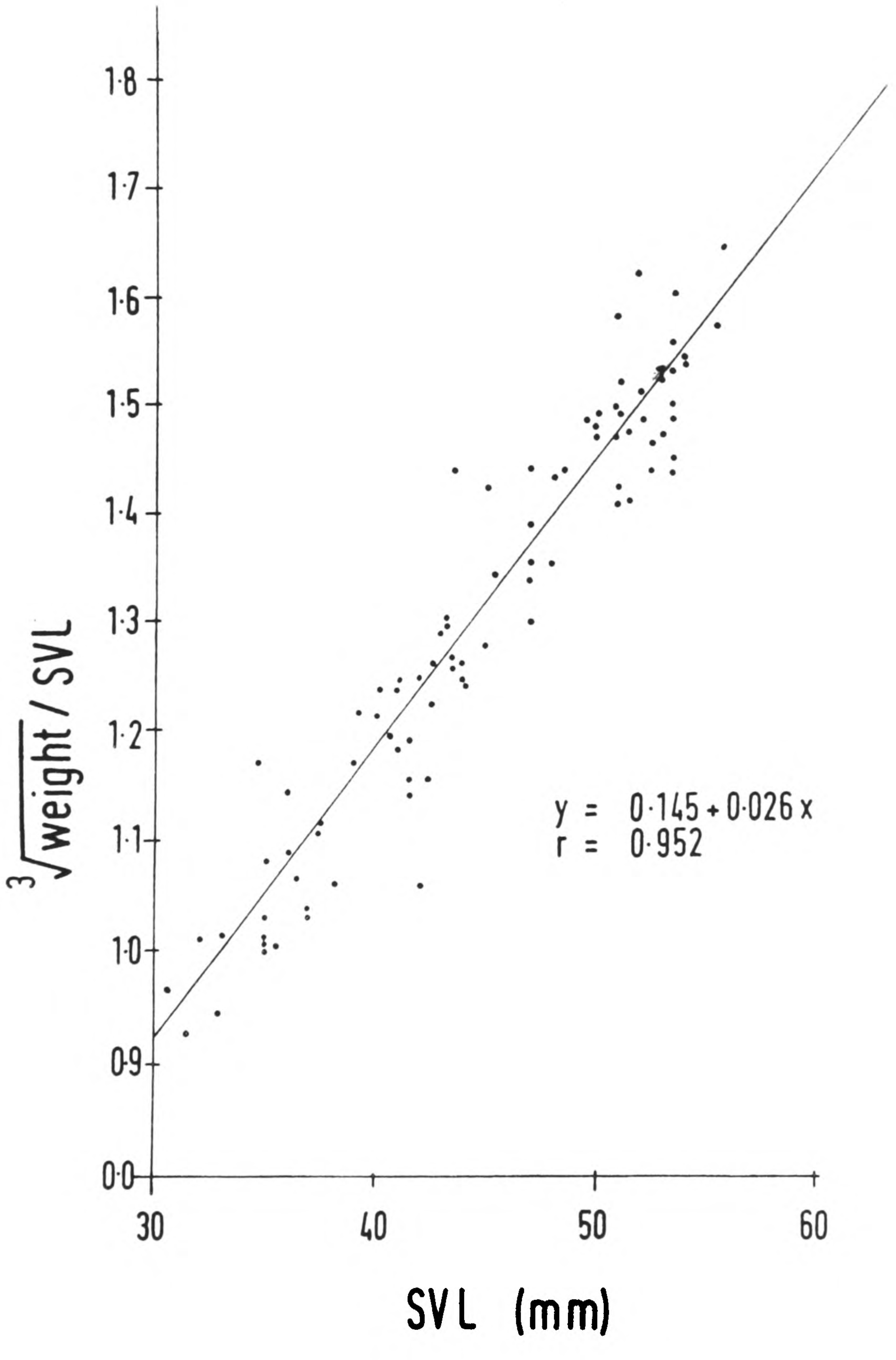


Fig. 4.2 REGRESSION OF $\sqrt[3]{\text{WEIGHT}}$/SVL FOR FEMALE *Podarcis hispanica* (NORTH FRONT CEMETERY SITE)

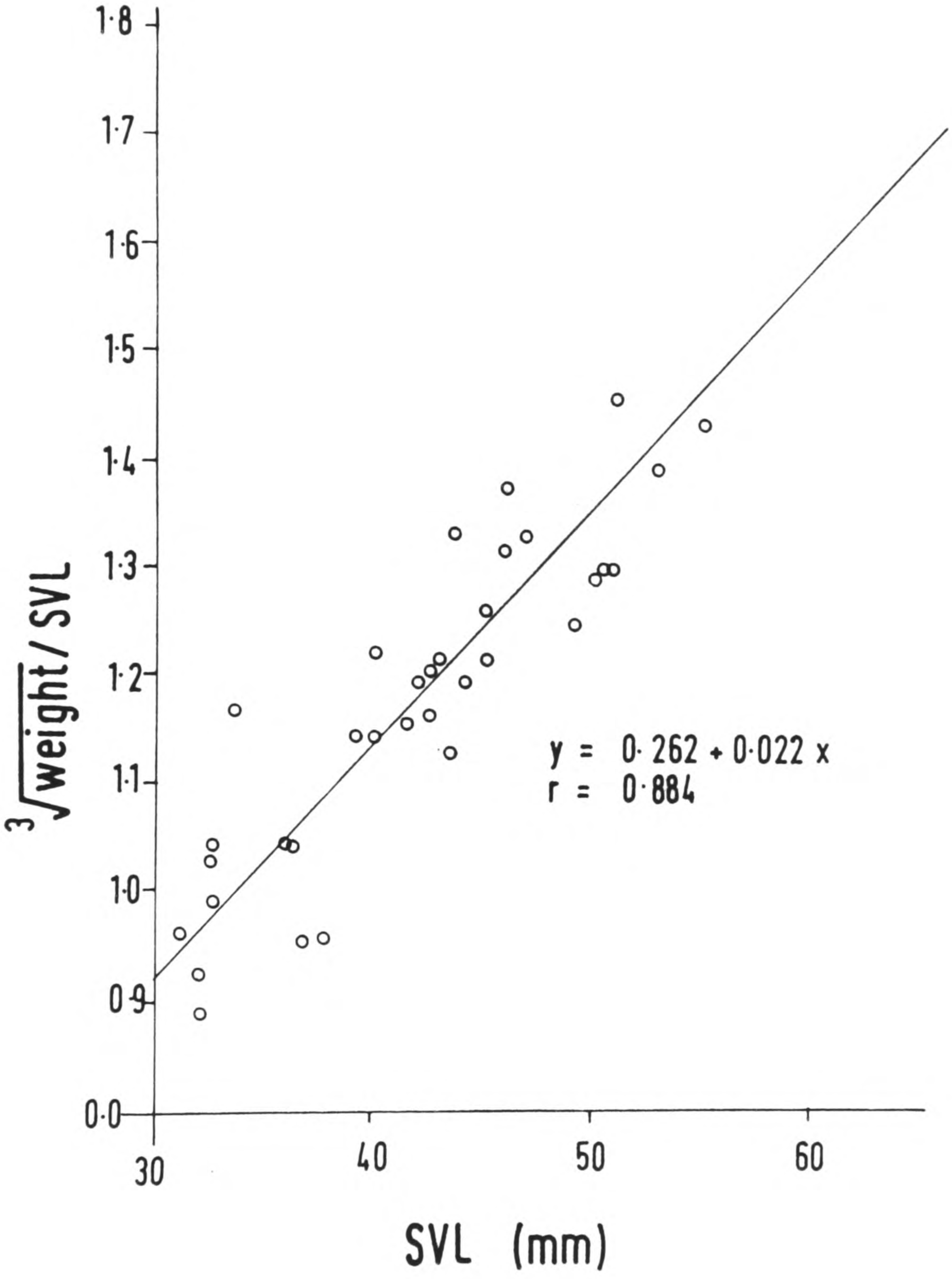


Fig. 4.3 REGRESSION OF $\sqrt[3]{\text{WEIGHT}}$/SVL FOR <u>*Psammodromus algirus*</u>

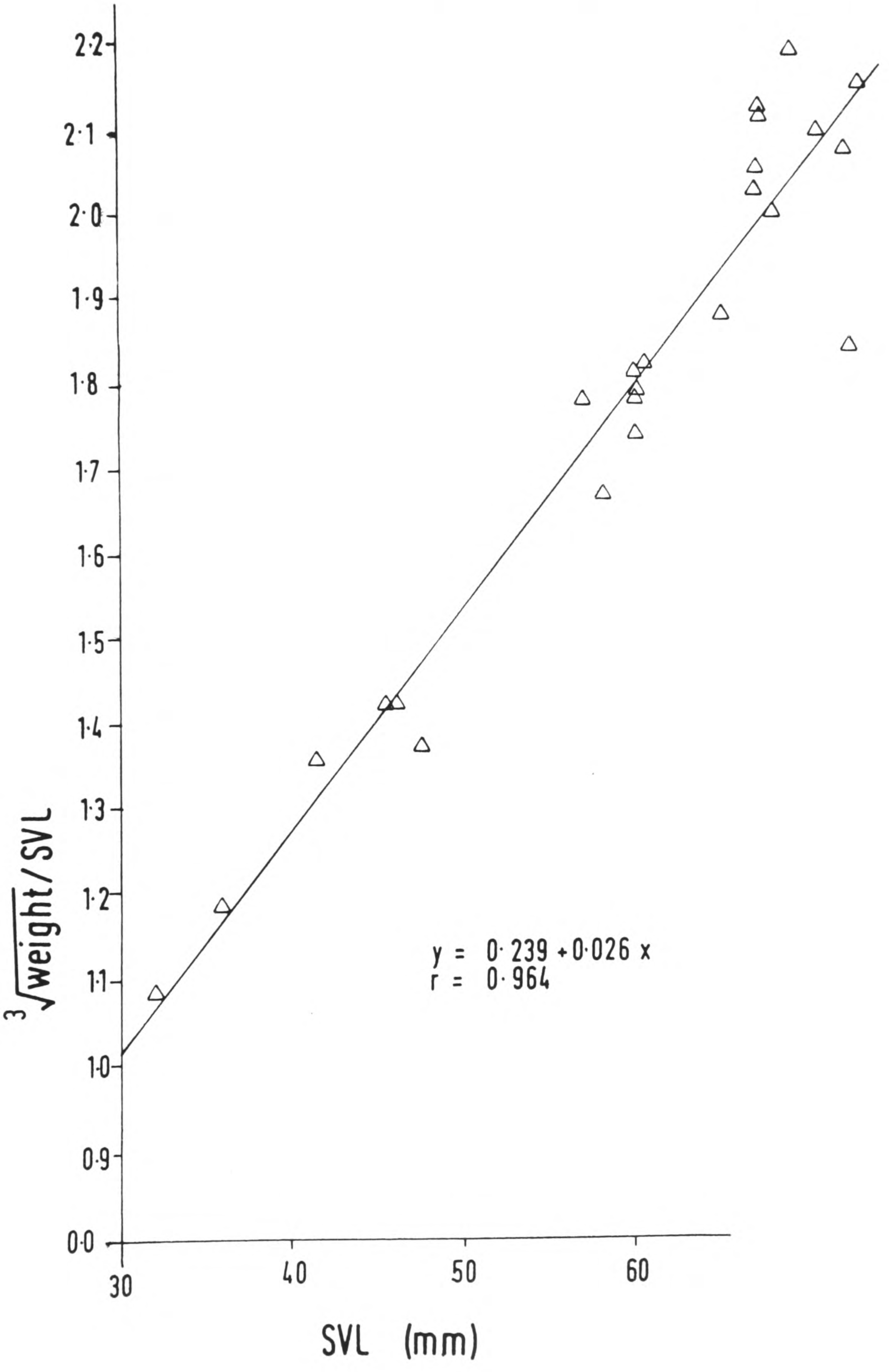


Fig. 4.4

REGRESSION OF $\sqrt[3]{\text{WEIGHT}}$ vs. SVL FOR *Podarcis hispanica* (MALE AND FEMALE, NORTH FRONT CEMETERY) AND ALL *Psammodromus algirus*.

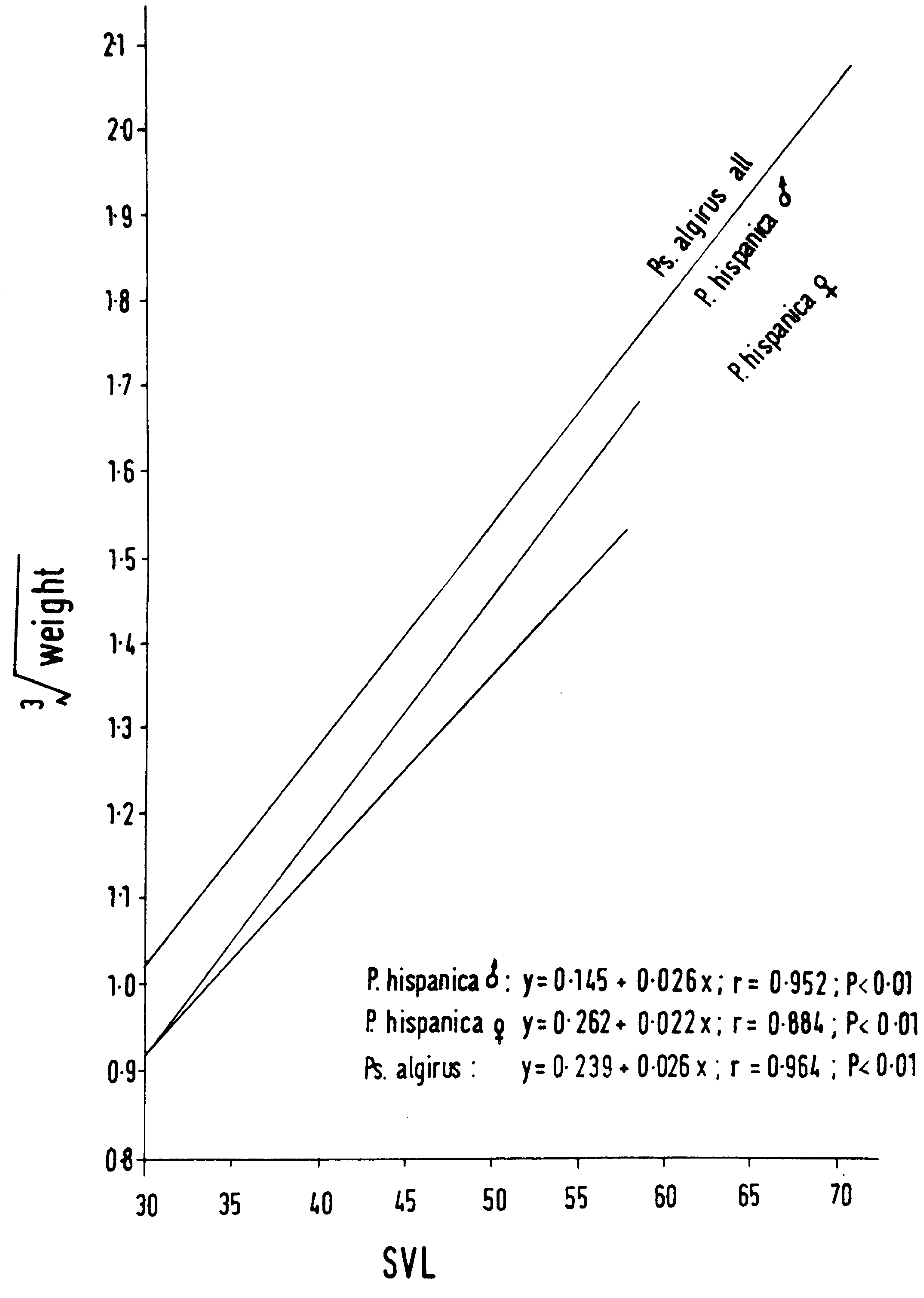


Fig. 4.5. PLOTS OF HEAD LENGTH vs SVL FOR MALE AND FEMALE *Podarcis hispanica* (NORTH FRONT CEMETERY SITE) AND ALL *Psammodromus algirus*

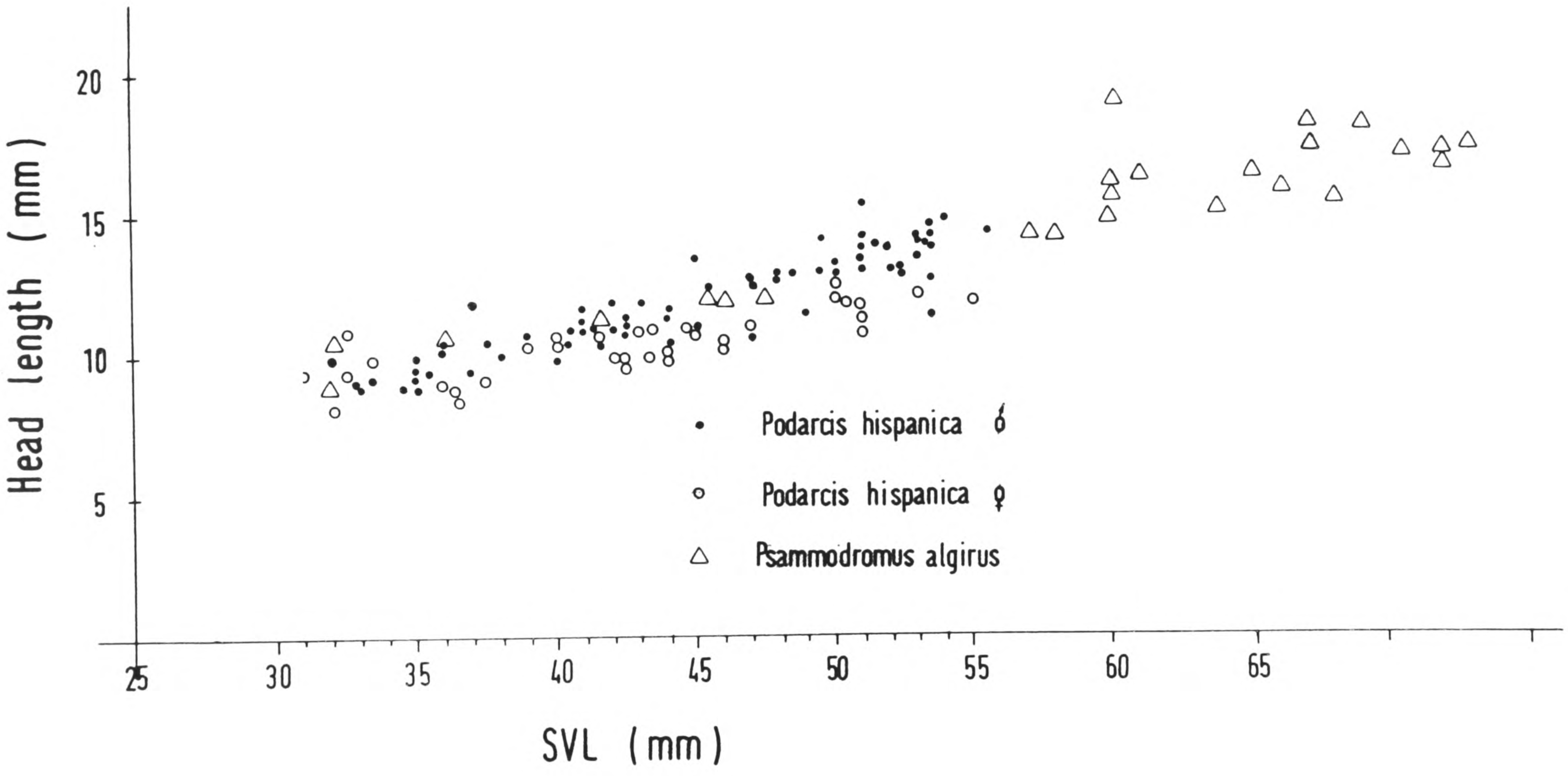
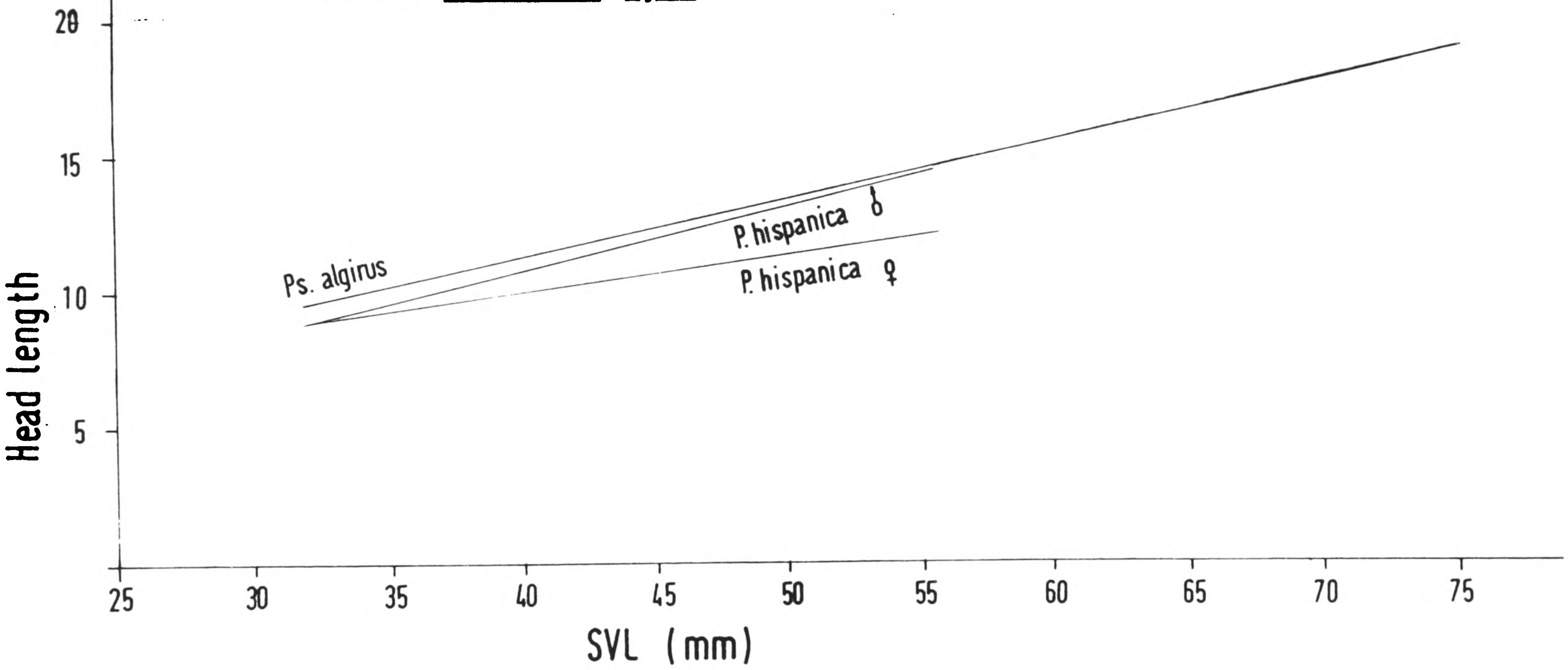


Fig. 4.6 REGRESSIONS OF HEAD LENGTHS vs SVL FOR MALE AND FEMALE Podarcis hispanica (NORTH FRONT CEMETERY SITE) AND ALL <u>Psammodromus</u> <u>algirus</u>



P. hispanica ♂ $y = 1{\cdot}597 + 0{\cdot}231x$

P. hispanica ♀ $y = 4{\cdot}415 + 0{\cdot}142x$

Ps. algirus $y = 3{\cdot}219 + 0{\cdot}206x$

Fig. 4.7. PLOTS OF HEAD WIDTH vs SVL FOR MALE AND FEMALE *Podarcis hispanica* (NORTH FRONT CEMETERY SITE) AND ALL *Psammodromus algirus*

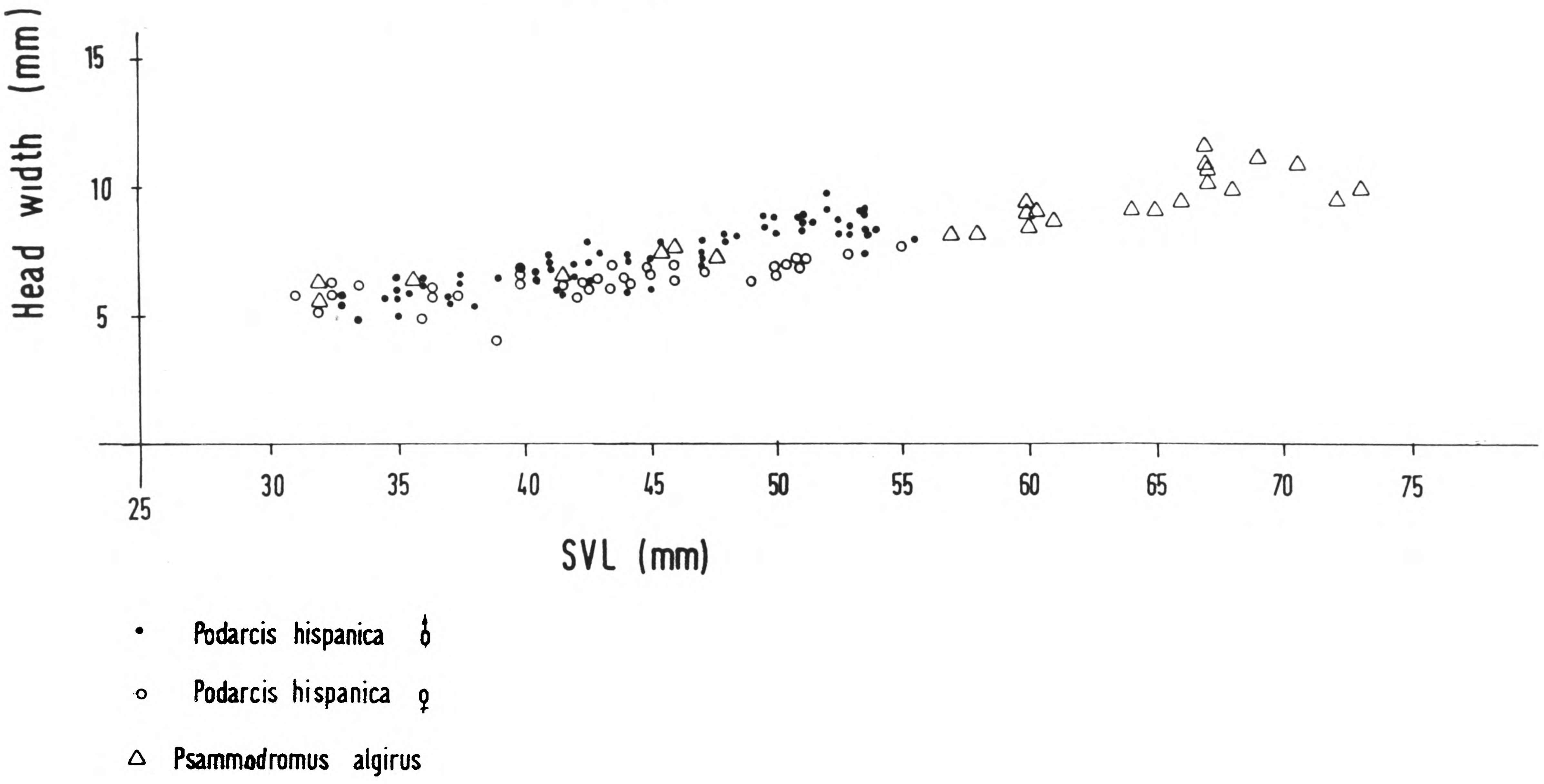
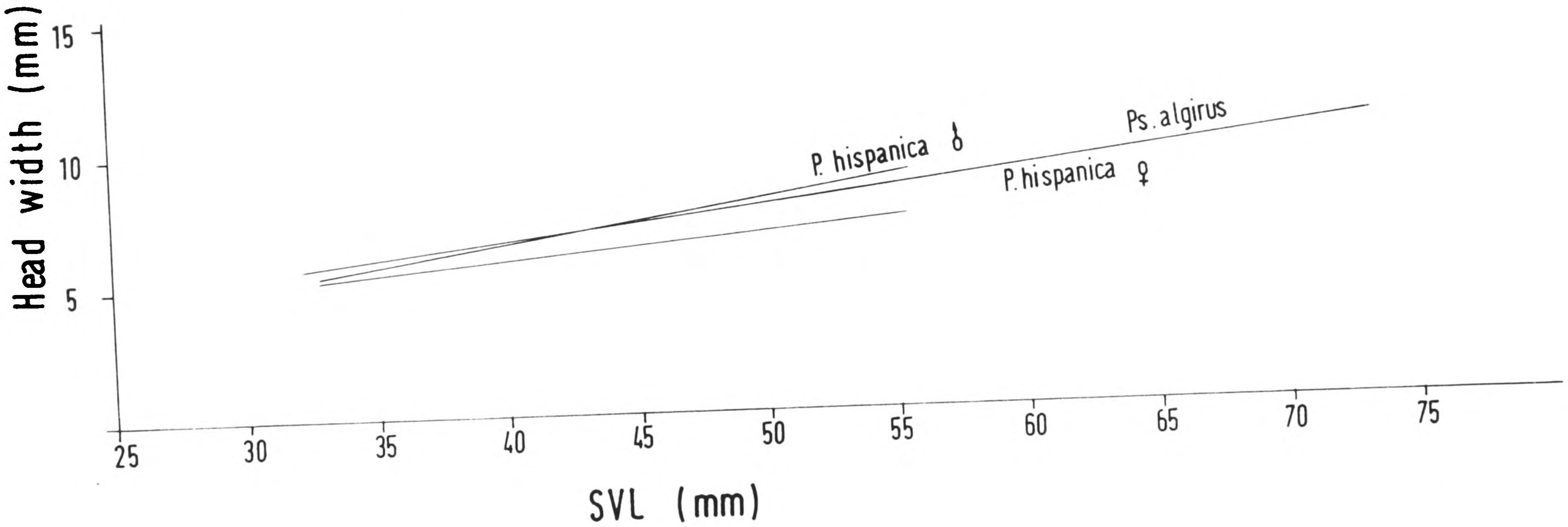


Fig. 4.8 REGRESSIONS OF HEAD WIDTH vs SVL FOR MALE AND FEMALE *Podarcis hispanica* (NORTH FRONT CEMETERY SITE) AND ALL *Psammodromus algirus*



P. hispanica ♂ $y = 0{\cdot}253 + 0{\cdot}159\,x$

P. hispanica ♀ $y = 2{\cdot}485 + 0{\cdot}088\,x$

Ps. algirus = $y = 1{\cdot}824 + 0{\cdot}123\,x$

Fig. 4.9 PLOTS OF HEAD WIDTH vs HEAD LENGTH FOR MALE AND FEMALE _Podarcis hispanica_ (NORTH FRONT CEMETERY SITE) AND ALL _Psammodromus algirus_

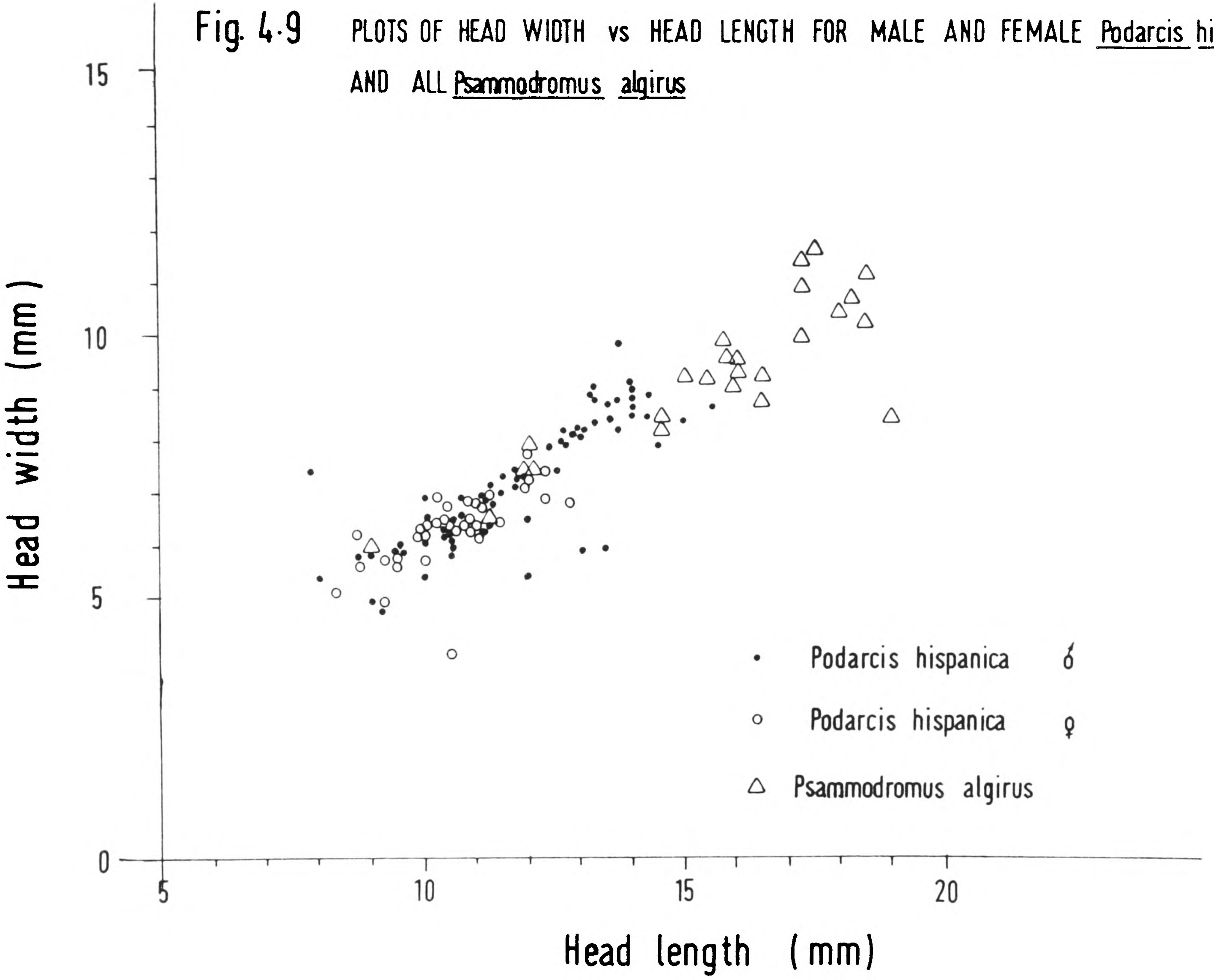
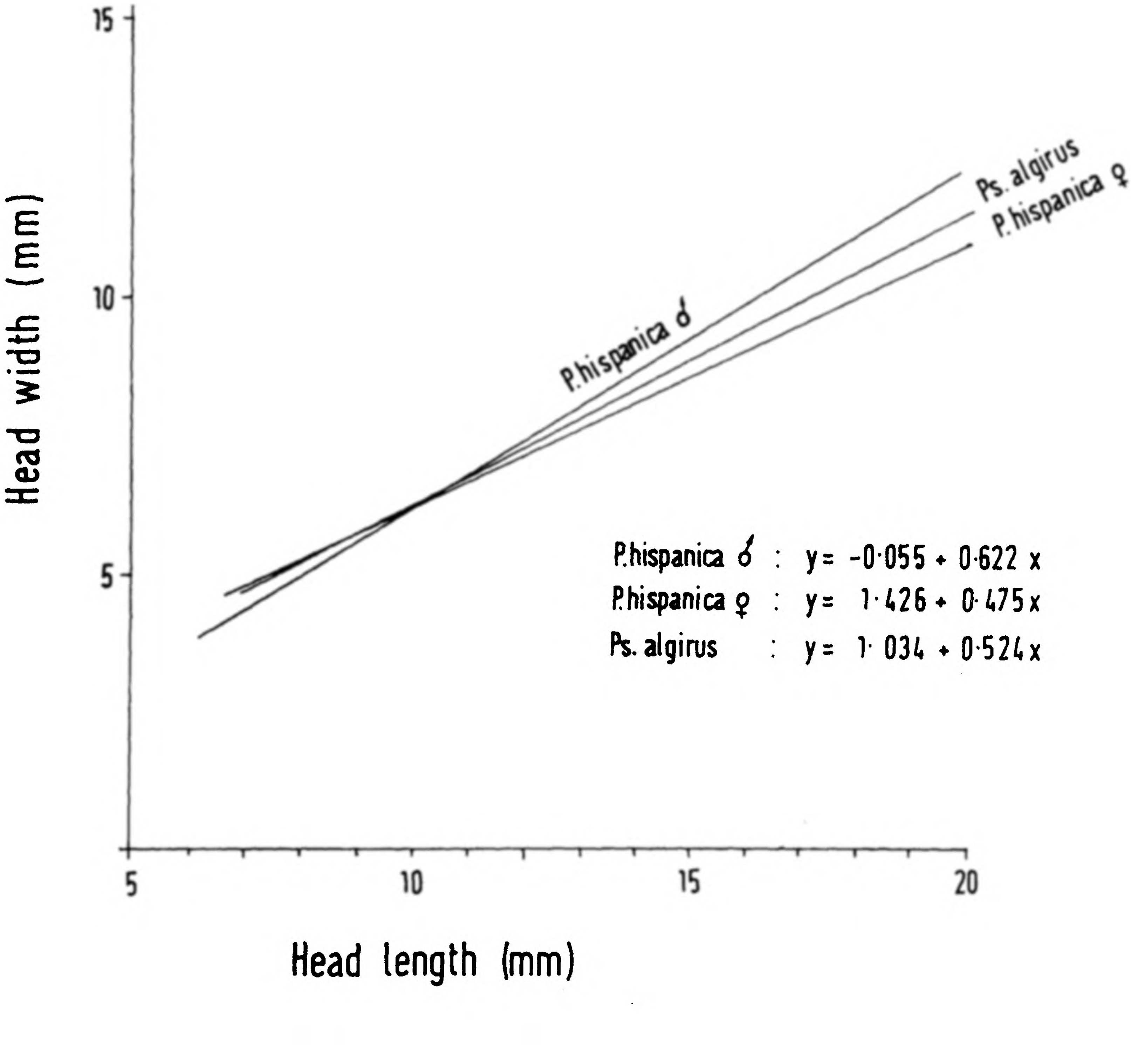


Fig. 4.10

REGRESSION OF HEAD WIDTH vs. HEAD LENGTH FOR MALE AND FEMALE *P. hispanica* (NORTH FRONT CEMETERY SITE) AND ALL *Ps. algirus*.



P. hispanica ♂ : y = -0·055 + 0·622 x

P. hispanica ♀ : y = 1·426 + 0·475 x

Ps. algirus : y = 1·034 + 0·524 x

Table 4.3 Results of t-tests on pairs of regressions of (a) $\sqrt[3]{\text{weight}}$ vs. SVL; (b) head length vs. SVL; (c) head width vs. SVL for different categories of lizards at Gibraltar.

Figures in the matrix represent values of t. * indicates that t was not calculated for the corresponding pair of regressions (explanation in the text).

NFC = North Front Cemetery; BFB = Bruce's Firebreak; *Ps.* = *P. algirus* (♂ + ♀)

(a) $\sqrt[3]{\text{weight}}$ vs. SVL

		Podarcis hispanica			
		NFC ♂	NFC ♀	BFB ♂	*Ps.*
Podarcis	NFC ♂	-			
	NFC ♀	-89·1	-		
	BFB ♂	-69.7	*	-	
	Ps.	-88·9	-51·7	-36·3	-

P < ·001, in all cases

(b) head length vs. SVL

		Podarcis hispanica			
		NFC ♂	NFC ♀	BFB ♂	*Ps.*
Podarcis	NFC ♂	-			
	NFC ♀	-71·8	-		
	BFB ♂	-50·7	*	-	
	Ps.	-63·4	*	-32.0	-

P < ·001, in all cases

(c) head width vs. SVL

		Podarcis hispanica			
		NFC ♂	NFC ♀	BFB ♂	*Ps.*
Podarcis	NFC ♂	-			
	NFC ♀	-42·8	-		
	BFB ♂	-41·5	*	-	
	Ps.	-66·5	-30·1	-28·8	-

P < ·001, in all cases

Table 4.4 Results of analyses of covariance on pairs of regressions of (a) $\sqrt[3]{\text{weight}}$ vs. SVL; (b) head length vs. SVL; (c) head width vs. SVL; (d) head width vs. head length; for different categories of lizard at Gibraltar.

(NFC, BFB refer to P.hispanica at North Front Cemetery and Bruce's Firebreak respectively. Ps. refers to Ps. algirus. sl. = slope; int. = intercept.)

Figures in the matrix represent values of F (upper figure) and P (lower figure) where P < 0·05.

(a) $\sqrt[3]{\text{weight}}$ vs. SVL

	NFC ♂		Ps.	
	sl.	int.	sl.	int.
NFC ♀	3·91	10·75 0·01	1·96	30·50 0·01
BFB ♂	1·67	3·67		
All P.h.			0·46	41·75 0·01
All P.h. ♂			0·22	35·24 0·01

(b) Head length vs. SVL

	NFC ♂		Ps.	
	sl.	int.	sl.	int.
BFB ♂	1·45	6·74 0·025		
All P.h.			0·43	7·80 0·01
All P.h. ♂			1·73	0·25

(c) Head width vs. SVL

	NFC ♂		Ps.	
	sl.	int.	sl.	int.
NFC ♂			7·15 0·01	2·79
NFC ♀	18·42 0·01	31·78 0·01	4·37 0·05	17·21 0·01
BFB ♂	0·31	2·33	0·02	2·90

(d) Head width vs. head length

	NFC ♂		Ps.	
	sl.	int.	sl.	int.
NFC ♂			2·02	1·77
NFC ♀	1·94	0·42	0·16	0·32
BFB ♂	0·36	0·49	0·0002	1·04

Table 4.5 Summary of statistical tests on morphometric data from *Podarcis hispanica* and *Psammodromus algirus* at Gibraltar.

(NFC, BFB refer to *P.hispanica* at North Front Cemetery and Bruce's Firebreak respectively. *Ps.* refers to *Ps. algirus*.)

(a) $\sqrt[3]{\text{weight}}$ vs. SVL

		Ancova		
P	t-reg	slope	int.	U-test
NFC ♂ vs. NFC ♀	0·001	x	0·01	*
NFC ♂ vs. BFB ♂	0·001	x	x	0·0192
Ps. vs. BFB ♂	0·001	*	*	0·0003
Ps. vs. NFC ♂	0·001	*	*	0·0034
Ps. vs. NFC ♀	0·001	x	0·01	0·0002

(b) Head length vs. SVL

		Ancova		
P	t-reg	slope	int.	U-test
NFC ♂ vs. NFC ♀	0·001	*	*	0·00003
NFC ♂ vs. BFB ♂	0·001	x	0·025	0·0119
Ps. vs. BFB ♂	0·001	*	*	0·0033
Ps. vs. NFC ♂	0·001	*	*	0·0495
Ps. vs. NFC ♀	*	*	*	*

(c) Head width vs. SVL

		Ancova		
P	t-reg	slope	int.	U-test
NFC ♂ vs. NFC ♀	0·001	0·01	0·01	0·00003
NFC ♂ vs. BFB ♂	0·001	x	x	x
Ps. vs. BFB ♂	0·001	x	x	0·0007
Ps. vs. NFC ♂	0·001	0·01	x	0·0003
Ps. vs. NFC ♀	0·001	0·05	0·01	*

(d) Head width vs. head length

	Ancova		
P	slope	int.	U-test
NFC ♂ vs. NFC ♀	x	x	x
NFC ♂ vs. BFB ♂	x	x	x
Ps. vs. BFB ♂	x	x	0·0091
Ps. vs. NFC ♂	x	x	0·0018
Ps. vs. NFC ♀	x	x	*

Notes: int. = intercept; x indicates $P > 0\cdot05$; * indicates test not carried out (see text).

Table 4.6 **Results** of Mann-Witney U-tests on lizard morphometric data. (NFC, BFB refer to *P.hispanica* at North Front Cemetery and Bruce's Firebreak respectively. *Ps.* refers to *Ps. algirus*.)

		P	$\frac{\sqrt[3]{\text{weight}}}{\text{SVL}}$	$\frac{\text{Hd length}}{\text{SVL}}$	$\frac{\text{Hd width}}{\text{SVL}}$	$\frac{\text{Hd width}}{\text{Hd length}}$
NFC ♂	vs.	NFC ♀		≪0·00003	≪0·00003	0·123
NFC ♂	vs.	*Ps.*	0·0034	0·0495	<0·0003	0·0018
NFC ♂	vs.	BFB ♂	0·0192	0·0119	0·1515	0·4247
Ps.	vs.	BFB ♂	0·0003	0·0033	<0·0007	0·0091
NFC ♂ >50 mm	vs.	NFC rest		0·0192	0·4168	0·0136
NFC ♂ >50 mm	vs.	NFC ♂ <45 mm		0·0207	0·4268	0·0051
NFC ♂ 45-50	vs.	NFC ♂ >50 mm		0·1401	0·4325	0·3409
NFC ♂ >50 mm	vs.	*Ps.*		*	*	0·0010
BFB ♂ <45 mm	vs.	NFC ♂ <45 mm		0·4522	*	*
BFB ♂ >45 mm	vs.	NFC ♂ >45 mm		0·0024	0·3520	0·1003
BFB ♂ >45 mm	vs.	*Ps.*		0·0052	0·0027	0·0516
NFC ♂ >45 mm	vs.	*Ps.*		0·2389	0·0009	0·00016
NFC ♂ >45 mm	vs.	NFC ♂ <45 mm		0·0329	0·4641	0·0013
NFC ♀ >45 mm	vs.	NFC ♀ <45 mm		*	0·0011	*
NFC ♀ <45 mm	vs.	NFC ♂ <45 mm		*	0·0446	0·1539
NFC ♀ >45 mm	vs.	NFC ♂ >45 mm		*	≪0·00003	0·0132

Notes: spaces and * indicate tests not carried out (see text).
lengths (mm) refer to snout-vent lengths (SVL)

Table 4.7 Results of tests on $\sqrt[3]{\text{weight}}$ vs. SVL data from P. hispanica (North Front Cemetery Site), divided into seasons.

(Period A = December-January; B = February-May; C = June-September; D = October-November)

(a) Kruskal-Wallis test:

♂ Seasons A, B, C, D

H = 6·3459 P = 0·1

♀ Seasons A, B, C, D

H = 3·4367 P = 0·5

♂+♀ Seasons A, B, C, D

H = 8·5085 P = 0·025

♂ Seasons A, B, D

H = 6·2014 P = 0·1

♀ Seasons A, B, D

H = 0·1282 P = 0·975

♂+♀ Seasons A, B, D

H = 5·7156 P = 0·01

(b) Analysis of Co-variance:

No differences found for ♂, ♀, or ♂ + ♀, for the following pairs of seasons investigated:

A vs. D
B vs. D
A vs. B

(c) Mann-Witney U-test : (♀ vs. ♂)

		♀	♂		
	U	N_1	N_2	z	P
Period A	60	9	18	-	not significant (from tables)
Period B	201·5	21	22	-0·717	0·2358
Period C	2	2	3	-	not significant (from tables)
Period D	54·5	7	30	-1·958	0·0250

Note: Mean values of the ratio $\sqrt[3]{\text{weight}}/\text{SVL}$

	Season			
	A	B	C	D
♂ + ♀	0·0291	0·0285	0·0350	0·0295
♂	0·0292	0·0284	0·0299	0·0297
♀	0·0289	0·0285	0·0315	0·0285

The results of the tests on the $\sqrt[3]{\text{weight}}$ / SVL data which were divided according to periods of the year are given in Table 4.7. The only significant result in the Kruskall-Wallis analysis was for combined male and female data (P = 0·05 for ABCD, P = 0·01 for ABD). No differences were found in the Analysis of covariance for the season pairs compared, viz. A and D, B and D, A and B. Males and females were only different in the $\sqrt[3]{\text{weight}}$ / SVL ratio in Period D (October and November) according to the results of the Mann-Witney tests. Data from this season give mean values for $\sqrt[3]{\text{weight}}$ / SVL of 0·0297 for males and 0·0285 for females.

4.1.4 Discussion

(a) Relationship between lizard weight and snout-vent length

Figures 4.1 to 4.4 illustrate the direct relationship between weight and SVL. The greatest variation was seen for female *P. hispanica*. The slopes for male and female *P. hispanica* diverge with increasing SVL. The slopes meet at the 30mm SVL point corresponding to 0·9 on the $\sqrt[3]{\text{weight}}$ axis (weight =0·73 g). This is the size at which *P. hispanica* first appear, when the sexes are indistinguishable by sight. Field observations show that adult males are heavier in relation to length than females.

The weight of a lizard will vary according to its condition, while its snout-vent length will not change. The relationship between $\sqrt[3]{\text{weight}}$ and SVL can therefore be used as an indication of the condition of the animal. Data on captive lizards (Chapter 6) supports this observation - the heavier animals were more active and lived longer. The results given in Table 4.4 (a) indicate statistically significant differences between NFC and BFB males. Differences in morphology between lizards in the different populations may account for this, so that conclusions on differences in condition between the sites cannot be arrived at. Lack of significant differences between data from lizards collected at different times of the year when tested parametrically (ANCOVA) and non-parametrically (Kruskall-Wallis test) (Table 4.7) indicates that lizards maintain a fairly constant weight/length ratio through all the seasons. This suggests the animals were able to remain in a fairly constant condition throughout the year.

There is a significant result, when females are considered together with males.

The lizards are heaviest per unit length during period C (May to September) (mean $\sqrt{\text{weight}}$/ SVL = 0·030), and least heavy in B (February to May) (mean $\sqrt[3]{\text{weight}}$ / SVL = 0•0285(male + female), 0•0287 (male), 0•0285 (female)). When C is excluded from the analysis (sample size is small), lizards captured during period A (December to January) are heaviest (mean $\sqrt[3]{\text{weight}}$ / SVL = 0•0291 (male and female), 0•0292 (male), 0•0289 (female), but the significance of the Kruskall-Wallis test remains. Aspects of the life history of P. hispanica support the assumption that these results reflect lizard condition. This could be worst in season B (spring) when males are spending more time in territorial and other reproductive behaviour (Chapter 5 and 6). Gravid females, which would tend to increase the value of the ratios are rarely seen and do not feature in the sample. Contrary to this is the fact that food is most abundant in spring (7.4). Weight increases at season C.

The Mann-Witney U-test used to compare males and females in each of the chosen seasons give a difference between these only in season D (October to November). This is the time when least behavioural difference is apparent between the sexes, when males in direct competition with females, will do better at the expense of the latter (mean $\sqrt[3]{\text{weight}}$ / SVL female = 0•0285).

(b) Relationship between lizard head size and snout-vent length

The results show that males have a significantly larger - longer and wider - head than females of the same SVL, although two-dimensional head shape (head width/head length) is not significantly different. Males use their head in display and in other mating behaviour - they sieze females with the jaws around the hind-quarters. A wide jaw and hence a wide head is necessary for a good grip. These reasons may contribute towards the significant difference in head dimensions between the sexes.

There is a significant difference in head length / SVL between males from NFC and BFB (Table 4.5). Lizards with larger heads will be able to take larger prey (Pianka, 1973). If head dimensions are so associated with feeding, this suggests that males in NFC take smaller prey than similar sized BFB males (mean head length NFC = 11•8mm, BFB =12•9mm). Females would then take smaller prey than males. Failure to successfully carry out stomach flushing made it impossible to put this suggestion to the test, but observations on captive lizards tended to support this assumption (7.2).

(c) Differences between size classes

The most interesting result to emerge from the Mann-Witney U- test on head dimensions according to size classes, are those which show differences between adult male *P. hispanica* from NFC and BFB and differences in these dimensions between males from BFB and *Ps. algirus* but not between NFC males and the latter species. This suggests the possibility of character displacement of *P. hispanica* in the presence of *Ps. algirus*.

4.2 Coloration and scaling

4.2.1 *Psammodromus algirus*

Mellado & Martinez (1974) describe the coloration of *Psammodromus algirus*, in particular the nuptial colour of the males. Arnold *et al.* (1978) describe the species' colour as being fairly constant: metallic brown with two conspicuous white or yellowish stripes on each side, the upper ones bordered above by dark dorsolateral stripes. This constitutes a good description of the *Psammodromus* observed and caught at Gibraltar. Underparts also conform with Arnold *et al.* (1978) and are whitish. Both males and females have an orange venter throughout the year, a fact reported by neither Mellado & Martinez (1974) nor Arnold *et al.* (1978). Arnold (1973) reports a brightly-coloured venter in breeding males of other species of *Psammodromus*, including *Ps. hispanicus*. Young lizards have a bright orange tail. The head and throat of breeding males are also orange, although in Gibraltar the orange has not been observed to extend as far down the throat as illustrated by Mellado & Martinez (1974) for their extreme cases. Both males and females (as stated by Mellado & Martinez, 1974, but not by Arnold *et al.* (1978) who claim this to be a male characteristic) can have blue spots in the shoulder region. These consist of two to three bright blue spots on each side, covering from two to nine scales (Table 4.8 ; Figure 3.5). The spots are most prominent in adult male *Ps. algirus*.

The body scales of this species are, on the back and flanks, large and pointed with a prominent keel. These, and the belly scales, overlap strongly. The possible significance of this with regard to thermoregulation is best considered together for both *Psammodromus algirus* and *Podarcis hispanica* in section 4.3.

4.2.2 *Podarcis hispanica*

Podarcis hispanica, like many other small lacertids, has been reported as showing considerable variation in colour between and within populations (e.g. Arnold, 1973; Arnold *et al.*, 1978). Colour differences were observed between individuals within sites during the early part of this study which were difficult to describe. There appears to be continuous variation in such aspects of coloration as the prominence of dorso-lateral stripes and amount of blotching.

Table 4.8 Blue spots on captured *Ps. algirus* (Figure 3.5).
(Total number of blue scales given as indication of prominence of blue.)

sex	SVL	No of scales covered by spots anterior spot	middle spot	posterior spot	Total blue scales	month of capture
♂	67•0	5	3	1	9	April
♂	67•0	3	3	1	7	April
♂	45•5	4	2½	0	6½	May
♂	69•0	2	3	0	5	April
♂	70•5	2	1½	1	4½	April
♀	46•0	3	1½	0	4½	April
♀	58•0	3	1	0	4	July
♀	60•0	3	1	0	4	July
♀	32•0	2½	½ ½	0	3½	April
♀	64•0	1	½	½	2	September
♀	68•0	0	0	0	0	April
♀	57•0	0	0	0	0	July
♂	36•0	0	0	0	0	April
♀	32•0	0	0	0	0	September

There are also differences in the shades of the ground colour of the lizards' backs, throats and bellies and in the number of spots on the ventral scales. The basic pattern, however, is similar and fairly constant although even in this there is definite sexual dimorphism (Figures 4.11 and 4.12).
Both males and females have a dark lateral band on either side running the length of the body from the head to the base of the tail. The appearance of the bands varies from solid black to paler grey, when the black is concentrated in blotches. The variation occurs within individuals and appears to depend on thermal conditions (4.4). Immediately above the band, again in both sexes, is a pale stripe which usually lacks all dark blotches. Directly above the pale stripe is a more or less-well defined line of dark blotches, always more prominent in males where they often form a definite black stripe. The blotches are smaller and fewer along the centre of the back, allowing more of the ground colour to be seen and giving the area a paler appearance. Most females lack blotches along this central region, or have very few small ones. From close-up the females look more uniform in colour than the males. These females resemble the 'concolor mutants' described in Arnold (1973)(Figure 4.14).

The ground colour of the lizards also varies between the sexes. Females are almost invariably browner and duller than males. Males usually look green. However, there is considerable variation within these general rules. Some females have been seen looking almost as bright as males. Some males are brighter green than others, although large males (about 5cm SVL or longer) are brighter green than smaller ones, and more so during the breeding season (February to May). Very young males (about 3cm SVL or shorter) are indistinguishable from females by sight. Hatchlings of both sexes invariably have a bright bluish-green tail, which colour is retained until about December, when the brownish colour of the tails of the adults is assumed.

The variation in the colour (and blotching) of the backs of individual lizards is such that captive lizards (up to 15 of them) could be indentified individually even without reference to their clipped toes or paint marks.

Fig. 4.11 MALE *Podarcis hispanica*

Fig. 4.12 FEMALE *P. hispanica*

Table 4.9 Colour of underside of *P. hispanica* sample (North Front Cemetery Site, Gibraltar).

	♂		♀	
COLOUR	TOTAL	%	TOTAL	%
White	35	48	21	50
White with yellow chin	8	11	4	10
Buff	10	14	3	7
Pale green	4	6	0	0
Pale yellow	6	8	11	26
Orange	9	12	3	7
Pale blue	1	1	0	0

$\chi^2 = 45{\cdot}36 \quad P < 0{\cdot}001$

X^2 test for data from male lizards (pale green + pale blue pooled):

$X^2 = 49{\cdot}70$; D of F = 5; $P < 0{\cdot}001$

X^2 test for data from female lizards :

$X^2 = 26{\cdot}35$; D of F = 4; $P < 0{\cdot}001$

The colour of the throat and belly is variable, but usually off-white. There is great variability in the number of spots in these areas, but some are always present, especially on the throat. Individuals of both sexes are found throughout the year with lemon-yellow throats, and all lizards have at least some hint of yellow on the throat in the breeding season.

Lizards with orange undersides have been seen in November (once) and in the breeding season although these have been few in number (Table 4. 9). Males with pale bellies have been seen chasing females and copulating, indicating that the orange colour does not necessarily indicate male breeding condition. One female with a bright orange underside has been observed copulating in March. A number of males with pale bluish undersides have also been seen. There is obviously great variability in the coloration of the undersides and apparently little correlation between this and breeding condition, except perhaps in the amount of yellow on the throat (of both males and females) (see 5.5).

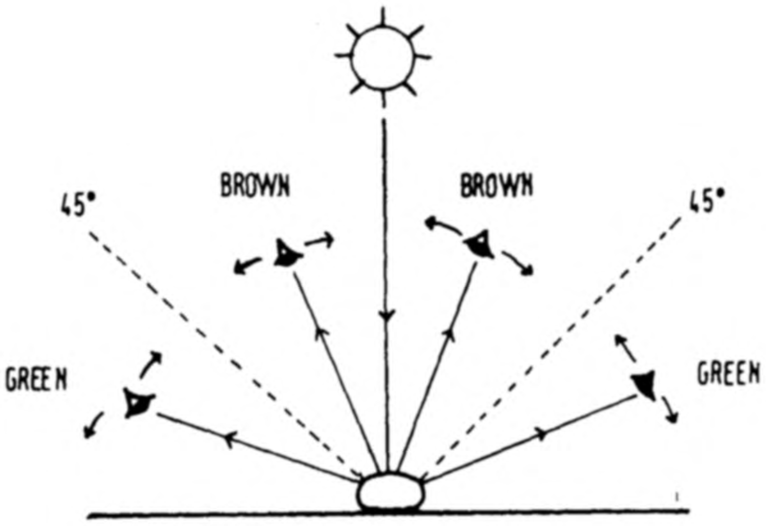
4.2.3 Angular colour change in Podarcis hispanica

(a) Introdution

The picture of variability is further confused by the fact that both males and females show within-individual differences in apparent overall dorsal colour at the same point in time. The colour that is most obvious when a lizard is observed from more than two metres is the ground colour of the back, when the blotches cannot be distinguished. This observed colour depends on the angle between the sun (or other light source), the lizard, and the observer. This phenomenon is evident in all individuals studied from the Gibraltar *Podarcis hispanica* population. Lizards viewed from the same direction as the incident light appear brown (Figure 4. 13); lizards viewed at an angle greater than 45° from the incident light appear green (Figure 4. 13). This is true for males and females. In the case of males, the brown colour seen often has a reddish tinge. This is most obvious on the neck, which often appears reddish when the rest of the body looks green.

Fig. 4.13 ANGULAR COLOUR EFFECT OF *P.hispanica*

(a) SUN OVERHEAD



(b) SUN AT ANGLE < 90°

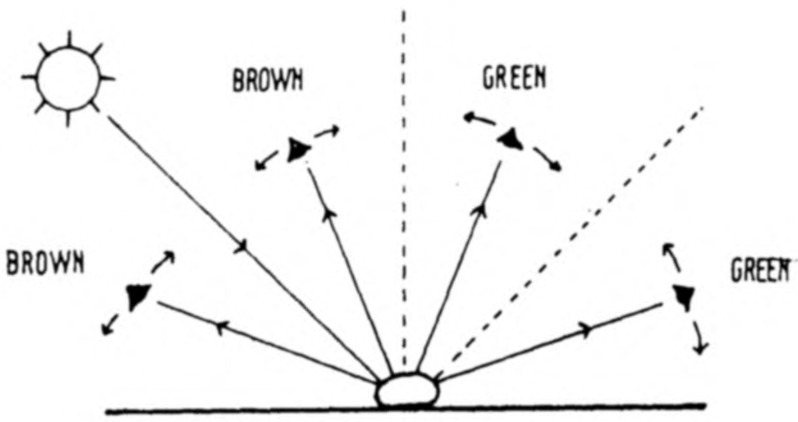


Fig. 4.14 FEMALE P. hispanica "CONCOLOR MUTATION" (ARNOLD, 1973)

Fig. 4.15 MARKED MALE P. hispanica. NAPE APPEARS RED-BROWN AT THIS ANGLE

Fig. 4·16 BASKING YOUNG MALE *P. hispanica*

Fig. 4.17 MALE *P. hispanica* POSTURING (PHOTOGRAPH TAKEN FROM SAME SIDE AS INCIDENT LIGHT.)

Fig. 4·18 MALE P. hispanica (PHOTOGRAPH TAKEN AT APPROXIMATELY 90° TO DIRECTION OF INCIDENT LIGHT.)

Fig. 4·19 ONE COLOUR OF UNDERSIDE OF MALE P. hispanica.

In the case of females, the brown colour is dull and fairly dark, while the green is also dull, often bottle-green. Colour photographs of various lizards are shown in Figures 4. 14 to 4.19. A lizard can therefore appear to be of two different colours at the same time to two observers each viewing it from different angles (Figure 4. 13b) This has been confirmed in the field.

The effect was first noticed when observing captive lizards and attempting individual recognition through colour and patterning. It was noticed that on several occasions the same lizard (previously marked with paint spots) was of a different colour. It was at first thought that the effect was due to differences in temperature. However, on one occasion a green lizard was observed through the side of the vivarium. When the lid was raised in an attempt to catch it from above so as to take routine measurements, it was seen to be brown. Moving the captured lizard around in front of a lamp caused the colour changes to be noticed again. It was decided to look at the phenomenon in more detail and an experiment was carried out:

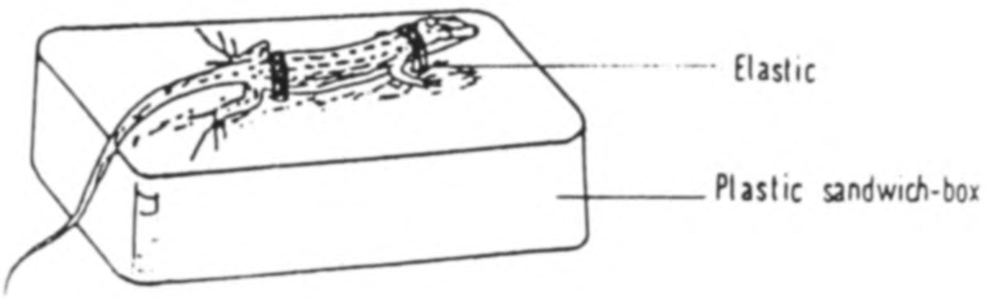
(b) Angular colour experiment

A holder was made for the lizards using a plastic sandwich box and elastic threaded through it (Figure 4. 20). A lizard was held in place by the elastic around its neck and in front of its hind legs. White light from a microscope external lamp was focussed to provide as parallel a beam as possible. This beam was directed at the lizard along the face of a semi-circle of white card marked at ten degree intervals, at various positions, and the lizard's back was observed from different positions along the circumference for each position of the beam (Figure 4. 20) The observed colour, whether predominantly green or brown, was noted at each pair of positions of incident and reflected light. Sample results are shown in Table 4. 10 . The general rule was confirmed to be that any part of the lizard appears brown when observed from the direction of incident light, and green when observed away from the incident light. However, when seen from the front, the lizard appeared shiny, particularly when the light was from behind.

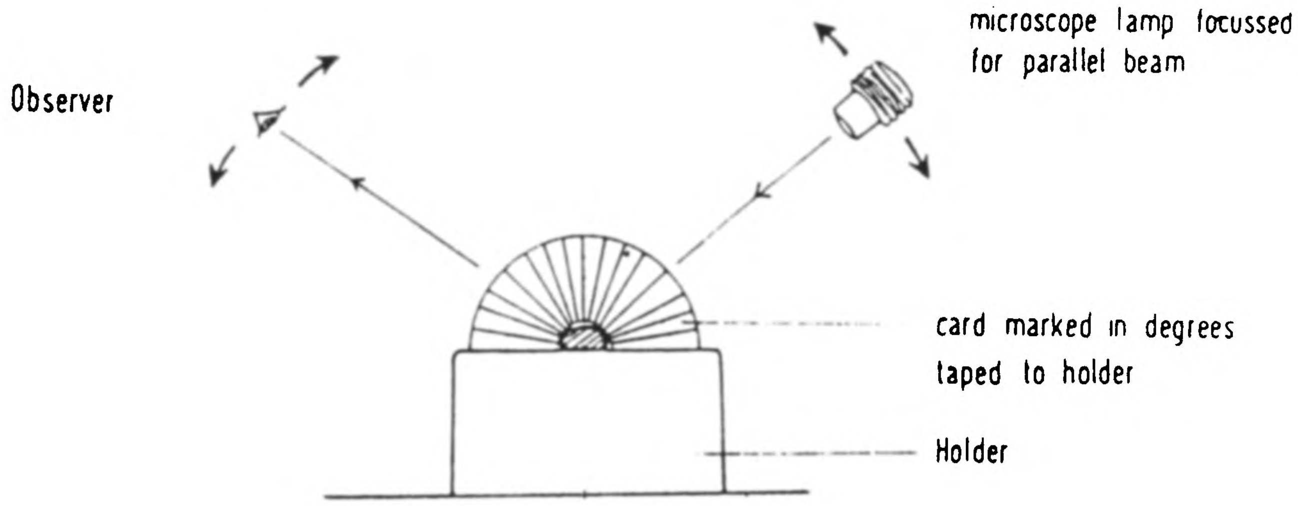
These observations have all been confirmed when observing lizards from various angles in the field.

Fig. 4.20 COLOUR ANGLE EXPERIMENT

a) LIZARD HOLDER



b) ARRANGEMENT FOR COLOURS ACROSS BODY



c) ARRANGEMENT FOR COLOURS ALONG BODY

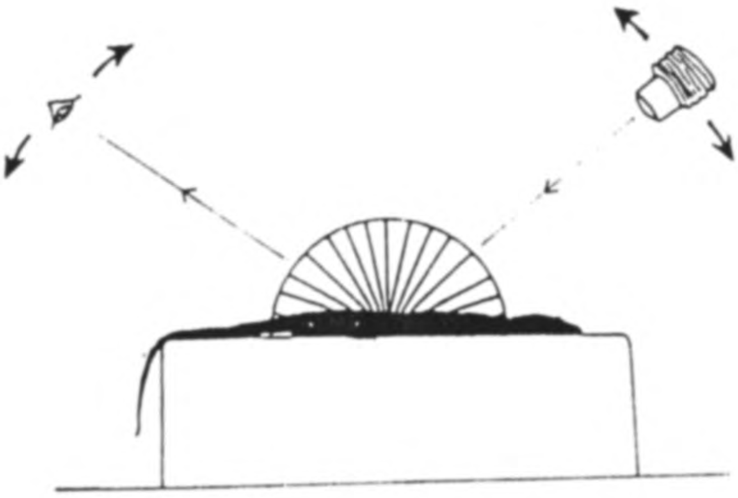


Table 4.10 Sample result of colour angle experiment.

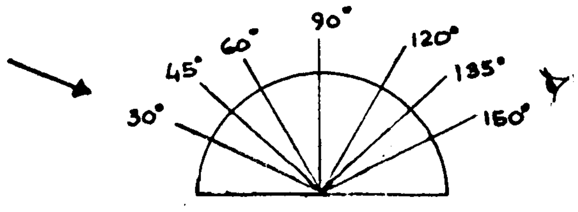
(<u>Note</u>: The exact transition between colours was difficult to determine. The following code was therefore used:

G = green; g = predominantly green, with a hint of brown;
B = brown; b = predominantly brown, with a hint of green;
r = 'reflective', the lizards appearing shiny;
bg = brownish green (browner than g);
gb = greenish brown (greener than b).

The colour given is the ground colour of the lizard's dorsal surface.)

	Position of eye						
Position of incident beam of light	30°	45°	60°	90°	120°	135°	150°
30°	Gr	Gr	Gr	G	G	G	G
45°	Gr	bg	bg	bg	G	G	G
60°	bg	b	b	b	bg	G	G
90°	G	b	b	b	b	bg	G
120°	G	b	b	b	b	b	gb
135°	G	G	bg	b	b	b	b
150°	G	G	G	bg	b	b	b

<u>N.B.</u> (1) lizards gave similar results, although exact colour and angle of change varied slightly;
(2) when light was anterior, lizards were reflective and generally appeared green.
(3) angles given above are as in the following diagram:



Position of light beam = 30°;
Position of eye =150°.

(c) Discussion

No reference describing this effect in reptiles has been found in the literature. Fox (1953) deals in some detail with the different types of colouring shown by reptiles. These are given as:

(i) Tyndall (=diffraction) colours - "no irridescence or conspicuous changes of colour occur over wide variations in the angle of reflection".

(ii) Interference colours (=irridescence) - which depend on the disintegration of light by structures whose unit dimensions are of the order of visible light (0·7mμ or less) The basic units are thin films or laminae arranged in uniform layers by periodic secretion and deposition. Melanin often underlies it, absorbing transmitted light and intensifying the irridescence of the reflected fraction. Melanin does underlie the skin of Podarcis, which has a black peritoneum (see 4.5.).
According to Fox (1953) keratins on reptile scales can cause irridescence. However, he also states that true irridescence should have a "metallic lustre", which is absent in the case of the Podarcis hispanica studied.

(iii) Selective reflection - the surface reflects one colour while the approximately complementary colour is transmitted by a thin layer.

Time and the broad subject-matter of the study did not allow a full examination of the colour effect, which would in any case have called for expensive equipment to measure reflectivity etc., if it was to have been made fully worthwhile. However, it is possible to speculate on the causes of the colour-phenomenon.

Fox & Vevers (1960) state that the colour green in reptiles, as well as in amphibians and birds, can be due to Tyndall scattering, and not to green pigments. In these cases, yellow pigment filters much of the short-wave radiation out of the incident white light, while minute air spaces scatter the remaining (longer) short waves, principally those giving the sensation of green. This makes the animal appear green. Below these air spaces (or crystals of guanine, guanophores, in frogs - and possibly reptiles) melanophores prevent the long-wave light that has passed the yellow filter but has hardly been scattered by the guanine from being reflected as yellow and red and so masking the green (and making it appear brown).

In Tyndall colouring seen by transmitted white light, the green disappears to be replaced by dull brown. Several characteristics of the colour-effect of Podarcis hispanica suggest that the Tyndall effect might be responsible - e.g. the green colour seen in reflected light is replaced by brown in diffuse (i.e. transmitted) light; there is a black melanin layer. One further piece of circumstantial evidence is the observation by Fox & Vevers (1960) that in Hyla arborea if melanin granules are concentrated into compact groups at the base of the xanthophores of yellow pigment, the melanin has little effect and the skin appears yellow. There has been one observation of a male P. hispanica in the field seen to look almost totally yellow, but which later appeared to change to the more normal green. An extension of the melanin granules in the melanophores would, following Fox & Vevers' (1960) argument, make this change occur.

If the Tyndall Effect is the cause of the angular colour phenomenon in P. hispanica, it must work on a scale-by-scale basis, since the overall colour is the summation of the colours of the individual components (Norris & Lowe, 1964).

More detailed investigation of scale structure may reveal how the Tyndall Effect could produce the angular-colour phenomenon. If, for example, the yellow and red components of light incident at a glancing angle were reflected before reaching the melanin due to some property of the scale, these would mask the green and make the lizard appear brown.

4.3 Colour and Camouflage

4.3.1 Effect on predation

The characteristics of the lizards' coloration, including the angular effect, will have a bearing on predation, since most of the species which prey on the lizards hunt by sight (see 6.6).
In general, the brown seen in both males and females, and the dark green of females resembles to a lesser or greater degree the dull colouring of leaf litter in the species' habitat, as well as of the dry dead grass and other vegetation characteristic also of these habitats. The bright green of the male is more similar to that of the living grass, Oxalis and other low plant species characteristic of winter and spring vegetation.

P. hispanica basks mainly on stones and rocks close to low vegetation and in spots of sunlight in and between bushes. In summer, lizards bask horizontally when the sun is high in the sky (8.2). From directly above they appear brown - which is the colour of the surrounding vegetation at this time of year. This effect will be especially important for an aerial predator (e.g. a Lesser Kestrel or a Blue Rock Thrush perched above the ground) and for any other if it has been successful enough to approach the lizard closely (Figures 4.21 and 4.22).

In winter and spring the vegetation is green and lizards bask (or 'sit and wait') at an angle to the horizontal, their bodies perpendicular to the sun, which in these seasons is lower in the sky. In the situations outlined above, the lizard will appear green to the predator (Figure 4.21). This is again the colour of the vegetation in the vicinity of the lizard.

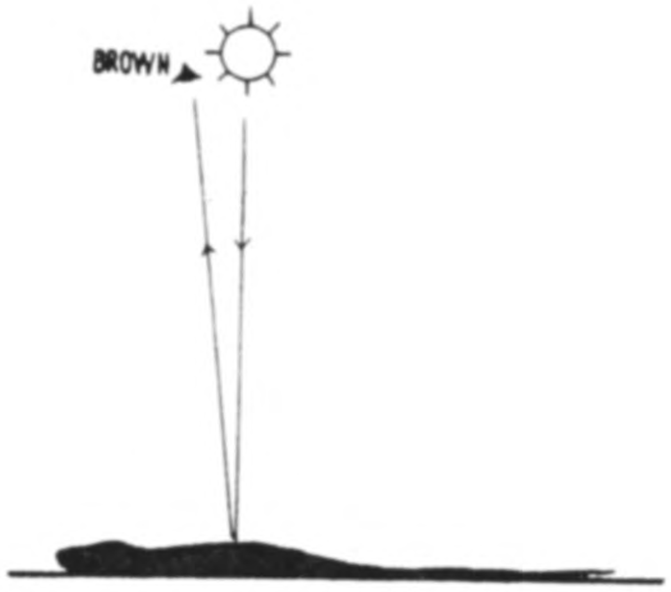
When lizards are foraging in vegetation, they are less visible to predators, although more noticeable (by sound and movement) if they are moving in low grass. Colour will not be as important while they are in close cover. Foraging however also takes place in leaf litter where the lizard is exposed. In such cases light is usually diffuse, and animals generally appear duller.

Predating birds are thought to use a specific search image (Croze,1970). Polymorphism has therefore been proposed as an anti-predator adaptation.

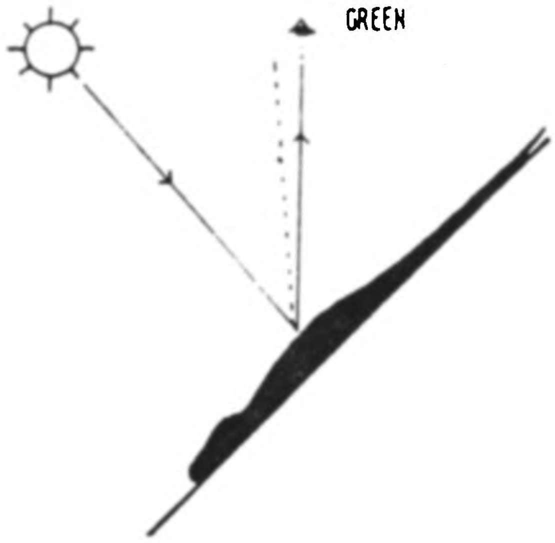
The observer-oriented colour change exhibited by individual P. hispanica is such that predators foraging on the ground (e.g. Blackbirds and Feral Cats) will see individuals in different colours depending not only on sex, but also on the angle at which they are observed - thus increasing the effective polymorphism.

Fig. 4.21 APPEARANCE OF LIZARD TO AERIAL PREDATORS

(a) SUMMER - BASKING HORIZONTALLY; SUN HIGH IN SKY



(b) WINTER AND SPRING - BASKING AT ANGLE TO HORIZONTAL; SUN LOW IN SKY.



In any event, a lizard will at any one time be camouflaged in relation to a certain area of space around it from which a predator can approach, thus reducing total potential predation. A ground predator approaching a lizard will observe a change in colour as the angle of reflected light is reduced. This change may cause the predator some confusion, making it hesitate and allowing the lizard more time to escape (see Figure 4.22).

Equipment was not available to examine the reflectivity of lizard skin under different conditions, in comparison to that of the environment. However, we cannot assume that the reflectivities of both surfaces throughout the visual spectrum are any closer to the eye of a predator than to human sight. We shall assume therefore, that the appearance of the lizards to the human eye closely resembles the appearance to the eye of the lizards' predators.

4.3.2 Flight distances

Norris & Lowe (1964) state that the human ability to discriminate a disc of uniform colour superimposed on a large area of a slightly different uniform colour is related to the arc subtended by the central disc in relation to the viewer and its wavelength difference from the background area in millimicrons. This is known as the 'just noticeable difference' (j.n.d.) (Wright, 1944). The match between two colours, each involving the entire visible spectrum requires an arbitrary system (the C.I.E. chomaticity diagram, Norris & Lowe, 1964) to quantify, so that for these purposes, the system employed by Norris & Lowe (1964) will be used, and colour difference will be considered in terms of wavelength difference.

Norris & Lowe (1964) state that background colour-matching in small lizards tends to continue to be effective at shorter ranges than that of large lizards, since the arc subtended by them in the eyes of a predator is very small until the predator is quite close, whereas the same arc is achieved by the large lizard at a much greater distance.

Assuming the wavelength discrimination of a predator is like that of a human, a prey animal subtending an arc of 2° and having a wavelength variation from the background of 1mμ (according to Norris & Lowe (1964) a close match not unlike that achieved across the entire spectrum by some well-matched animals) will just reach the j.n.d. in the yellow-orange and blue-green parts of the spectrum. Using the Figure in Norris & Lowe (1964) adapted here in Figure 4.23,

Fig. 4.22 COLOUR CHANGE DISTANCE FOR DIFFERENT PREDATORS

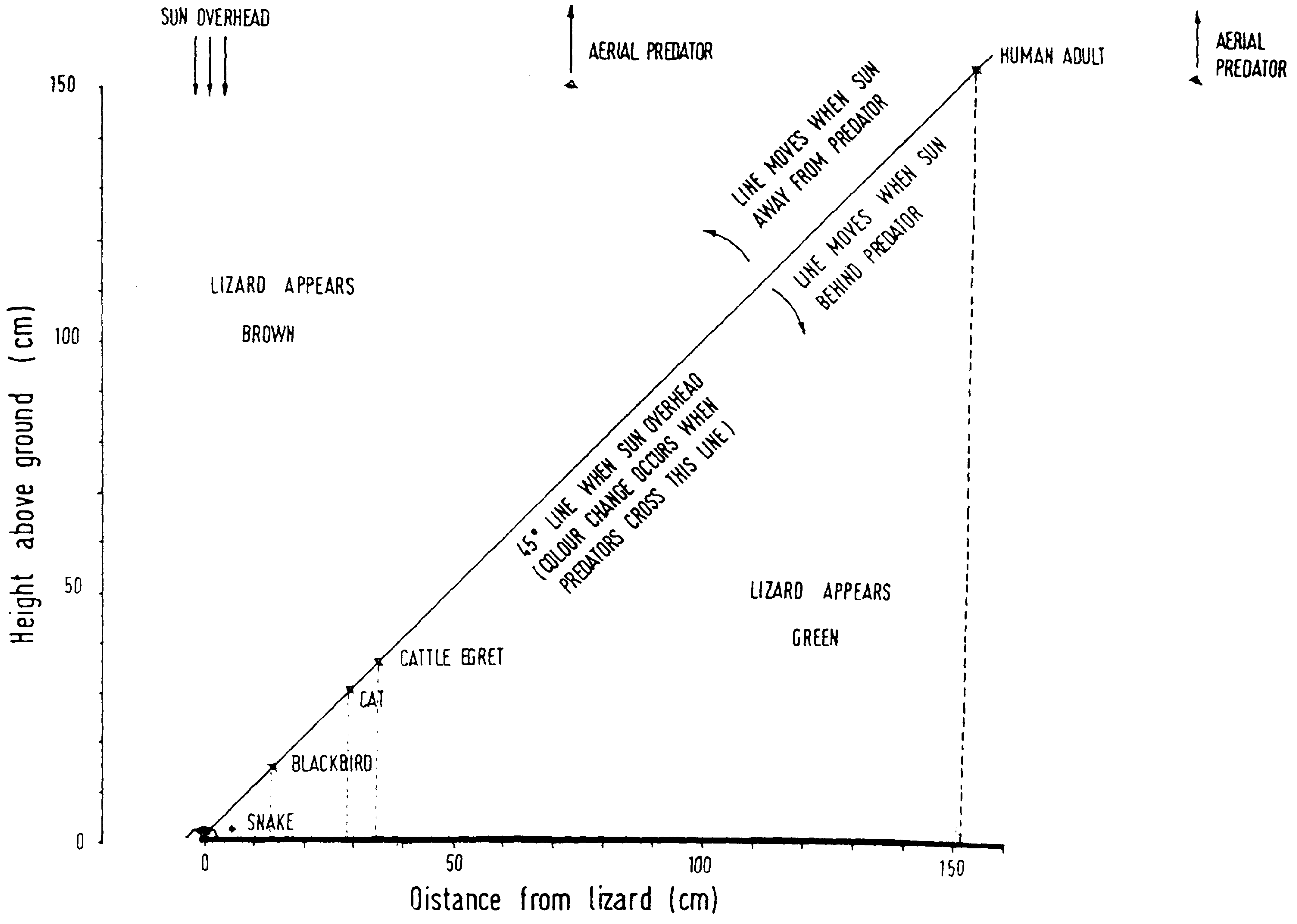
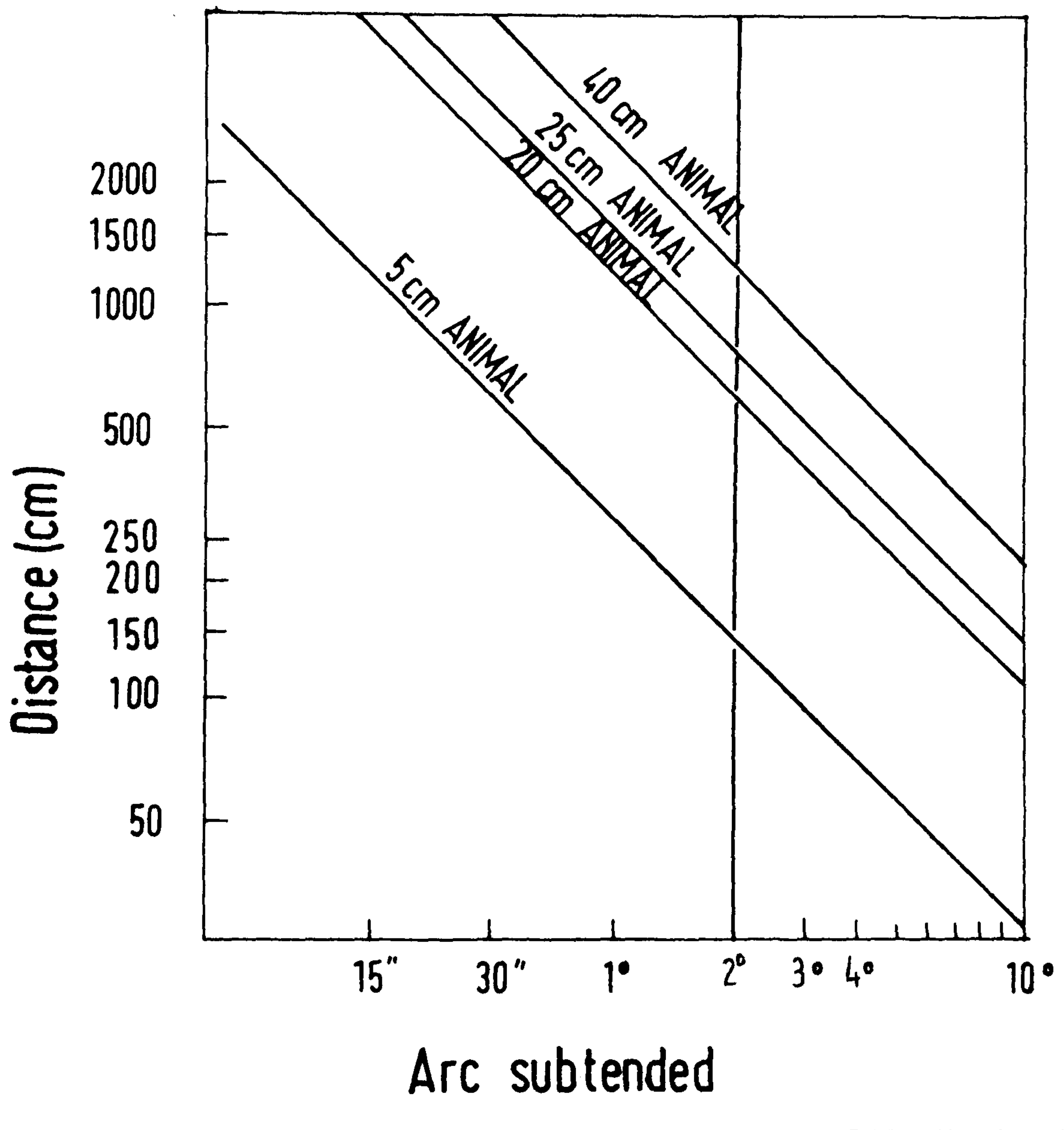
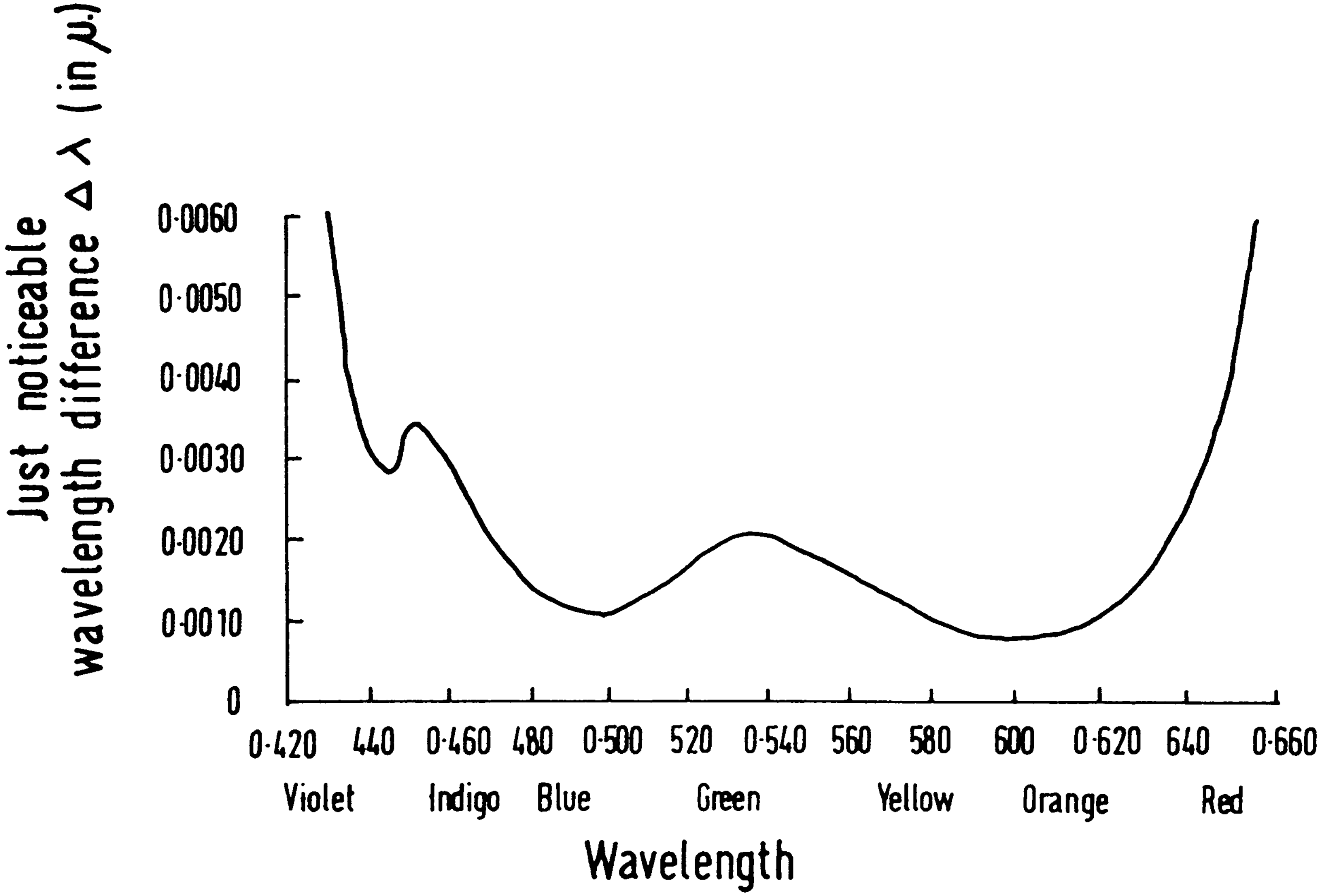


Fig. 4.23



THE RELATION OF ANIMALS OF VARIOUS LENGTHS TO THE VISUAL ANGLE THEY SUBTEND, ON LOG LOG COORDINATES. THE VERTICAL LINE AT 2° INDICATES THE POINT AT WHICH ANIMALS OF VARIOUS SIZES BECOME DISTINGUISHABLE FROM THEIR BACKGROUNDS IF THEY DIFFER FROM THAT BACKGROUND BY ONE mu AT THE POINT OF MAXIMUM DISCRIMINATION ABILITY FOR HUMANS. (FROM NORRIS & LOWE, 1964)

Fig. 4.24 TYPICAL WAVELENGTH DISCRIMINATION FOR A NORMAL HUMAN OBSERVER USING A 2° FIELD (FROM NORRIS & LOWE, 1964)



we find that a 5cm lizard would become visible on the basis of colour at a distance of about 1·5 metres. Should a predator approach undetected to within less than that distance (see below), the lizard would be in danger of being caught. A shift towards the end of the visual spectrum, however, provided there is still a background colour match, would increase the j.n.d. and make the lizard less visible (Norris & Lowe, 1964) (Figure 4.24). This is in fact what occurs as a predator approaches a lizard basking or foraging on flat ground. As the angle between the incident light, the lizard and the eye of the predator decreases, the lizard's colour will change from green to brown, and the lizard thus becomes less visible. This may allow the lizard an extra opportunity to escape predation. Figure 4.22 shows the distance from the lizard at which the colour change will appear to occur for different predators.

Lizards' flight distances (the distance from a predator at which a lizard takes flight) have been considered by some authors in relation to the thermal condition of the animals.
Norris & Lowe (1964) attempt to relate it to the j.n.d. and size of the lizard, and state "escape distance may often reflect the distance at which colour matching breaks down". The escape distance for P. hispanica was investigated in the field. Lizards seen undisturbed were approached at a slow steady pace and the distance at which they showed flight reaction was recorded. Results are given in Table 4.11. The mean flight distance corresponds closely to that of 1.6m taken from Norris & Lowe (1964) (Figure 4.23). The smaller lizards could be approached closer than the larger ones.
Lacerta lepida (SVL = 200mm + , Arnold et al, 1978) was too rare to allow comparative data collection, but on no occasion when these lizards were seen were they approached openly without flight to a distance of less than 5m. Psammodromus could be approached more closely, but again no quantative data were collected.

Norris & Lowe (1964) state that the sizes of pattern components possessed by colour-matched lizards generally vary in direct relation to the animals' size. In keeping with this general principle, the blotches and spots of P. hipanica represent a much more fine-grained pattern than the blotches and ocelli of Lacerta lepida which form a markedly bold pattern. Norris & Lowe (1964) consider that these pattern elements are disruptive patterns affording concealment from predators that approach closer than the minimal distance for the j.n.d. of background colour-matching. The observer-oriented angular colour change of P. hispanica would then serve as

Table 4.11 Mean escape distances of P. hispanica sample (North Front Cemetery, Gibraltar).

	n	$\bar{x}$ (m)	S.D.	var.
Total sample	208	2·06	1·07	1·13
30mm SVL	39	1·65	0·73	0·52
30-40mm SVL	31	2·08	1·29	1·61
40mm SVL	54	2·14	0·90	0·79
40-50mm SVL	31	2·02	0·93	0·84
50+mm SVL	41	2·51	1·33	1·73

Results of t-tests on escape distance data:

30mm SVL : 40mm SVL samples: $t = 1\cdot07$; $P > 0\cdot05$

40mm SVL : >50mm SVL samples: $t = 0\cdot76$; $P > 0\cdot05$

30mm SVL : >50mm SVL samples: $t = 3\cdot91$; $P < 0\cdot001$

Notes:

SVL was estimated by sight and lizards classified according to size. Individuals which were not placed in firm groups were excluded from the statistical test.

Estimated SVL agreed well with measurements where lizards were captured.

Note largest lizards have significantly greater escape distance than smallest.

an additional protection. The disruptive effect would be more important in the more brightly coloured males which are more obvious particularly when basking in the open in the spring on bare rock. This may account for the fact that males are more blotched than females which spend more time concealed in vegetation during the course of the year than males (6.3). It is interesting to note here that a general trend in lizards (Porter, 1972) is for species or populations living in dense vegetation to be dark. In P. hispanica females tend also to be dark.

As is normally the case, one must assume that the various aspects of lizard coloration and patterning will have a combined effect on escape from and avoidance of predation. However, in a small ectothermic animal thermal considerations must also be borne in mind where colour is concerned.

4.4 Colour and thermoregulation

Many authors (e.g. Atsatt, 1939, Norris, 1967, Porter, 1972) have reported that lizards are darker in the cold and lighter in heat. This is assumed to be a thermoregulatory response:(dark lizards will absorb heat and light ones will reflect more heat;)and is especially noted in desert lizards. Colour has been proved to affect thermal flux in some species at least (Norris,1967). In fact, Porter (1972) states that lack of ability to change colour restricts a lizard's capability to regulate its temperature.

There is some enlargement of blotches on the backs of P. hispanica, possibly in response to temperature. (The greater prominence of the blotches in males may counteract the fact that the females are darker in colour.) In this species there is however no obvious overall colour change, as does occur in such desert lizards as Uma, Callisaurus and Dipsosaurus (Norris,1967). There is a change in colour of the dark lateral bands below the dorsolateral stripes which is noticeable when lizards are observed closely, and is not generally evident in the field. The area of black on these bands increases as a lizard cools, and contracts on warming. In addition, lizards which are warming up in cool conditions, such as after morning emergence, or during periods of hazy cloud cover, press their bodies down against the substratum, flattening the lateral bands so that they lie horizontally and receive solar radiation normally (Figure 4.25). This will increase the absorption of solar radiation, at least in the visible part of the spectrum.

The angular colour phenomenon of P. hispanica may have thermoregulatory effects. While lizards in any case thermoregulate by posturing (e.g. Heatwole,1976) the change in colour with regard to posture in relation to incident light can increase the potential for thermoregulation through posturing. The positions adopted by P. hispanica at different times of the day and year are treated later in 8.3. In simplified terms, it would appear that lizards are darker and hence less reflective at least to visible light, when this light is normal to any part of its surface, and is brighter, and hence more reflective, when the light strikes at an angle to the normal. This would mean that when the light is more intense per unit area of skin, more of it is absorbed, while when it is less intense, it is reflected. This would appear to be

Fig. 4.25 P. hispanica LATERAL BANDS

TOP VIEW OF LIZARD
WHEN FLATTENED - LATERAL
BANDS OBVIOUS

NORMAL POSITION OF BANDS
IN CROSS SECTION

POSITION OF BANDS WHEN
BODY FLATTENED

a good compromise between thermoregulation and protective coloration, since the reflected light which will give it a good colour match is that which in any case can be less efficiently used to warm up the body. Therefore, all scales, whether dorsal or dorso-lateral, will absorb more normal radiation and reflect proportionally more of that incident at an angle (including diffuse radiation from the atmosphere and surroundings) than if the effect did not exist. Pressing the body to make it flat will present a greater area of body wall to normal light and thus increase absorption. In addition, when more heat is required, the lateral bands will be darkened and brought into play.

The shape of the scales and the way they are arranged can also have an effect on thermoregulation (Regal, 1975). Figures 4.26 and 4.27 shows the arrangement of scales on the back of a male P. hispanica. The scales are rounded and slightly raised, lying on those posterior to them. For this reason, and following Regal's (1975) argument, a beam of light perpendicular or normal to the body cannot strike each scale(or part of a scale) at a normal angle. Since the transmission of light into a medium is greatest at the normal angle, transmission decreases and reflectivity increases towards those parts of the scale where the light is incident at angles less than perpendicular to the surface. The light can be adjusted (e.g. by the lizard's posturing) so that it no longer strikes the lizard's body wall at a normal angle, but does strike the main part of a body scale at a normal angle. Absorption will be maximal for the light that does strike the scale, but the shadow cast by each scale is longer and a greater proportion of the more vascularized base of each scale is shaded. Furthermore, the energy per unit area falling on the lizard's skin is less. This can make the scale act as a heat shield. However, the colour effect will probably maximise the energy absorbed even at this angle, and the scales are in any case only slightly raised and are rounded, minimising shade when compared, for example, with the raised keeld scales of Ps. algirus. These rounded scales present a perpendicular surface to the sun's rays at most positions (Figure 4.26), although the amount of scale surface that is perpendicular will vary with the animal's posture. There will be least perpendicular scale surface when the

Fig. 4.26 INCIDENCE OF LIGHT FROM VARIOUS ANGLES ON LIZARD SCALES

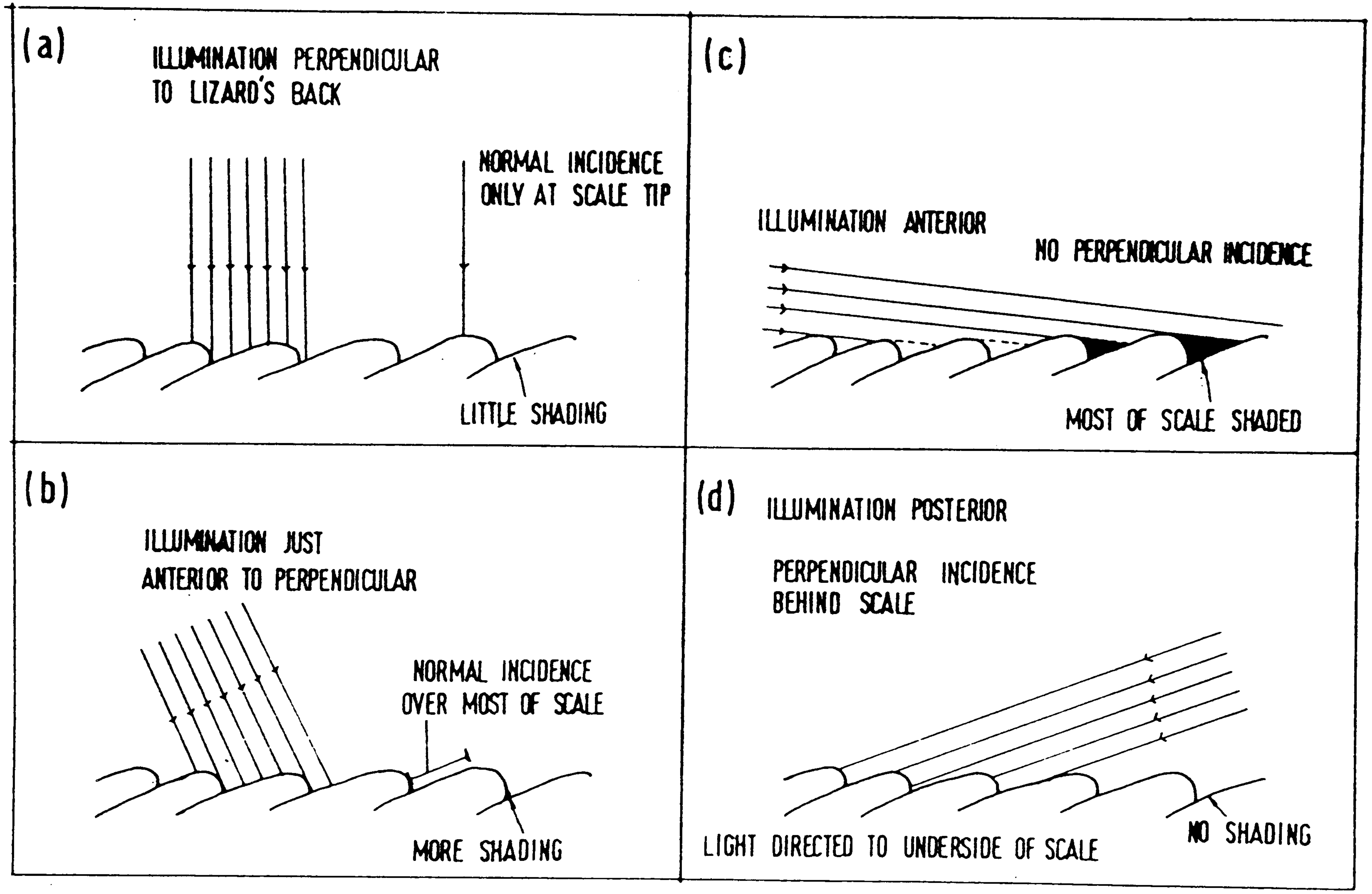
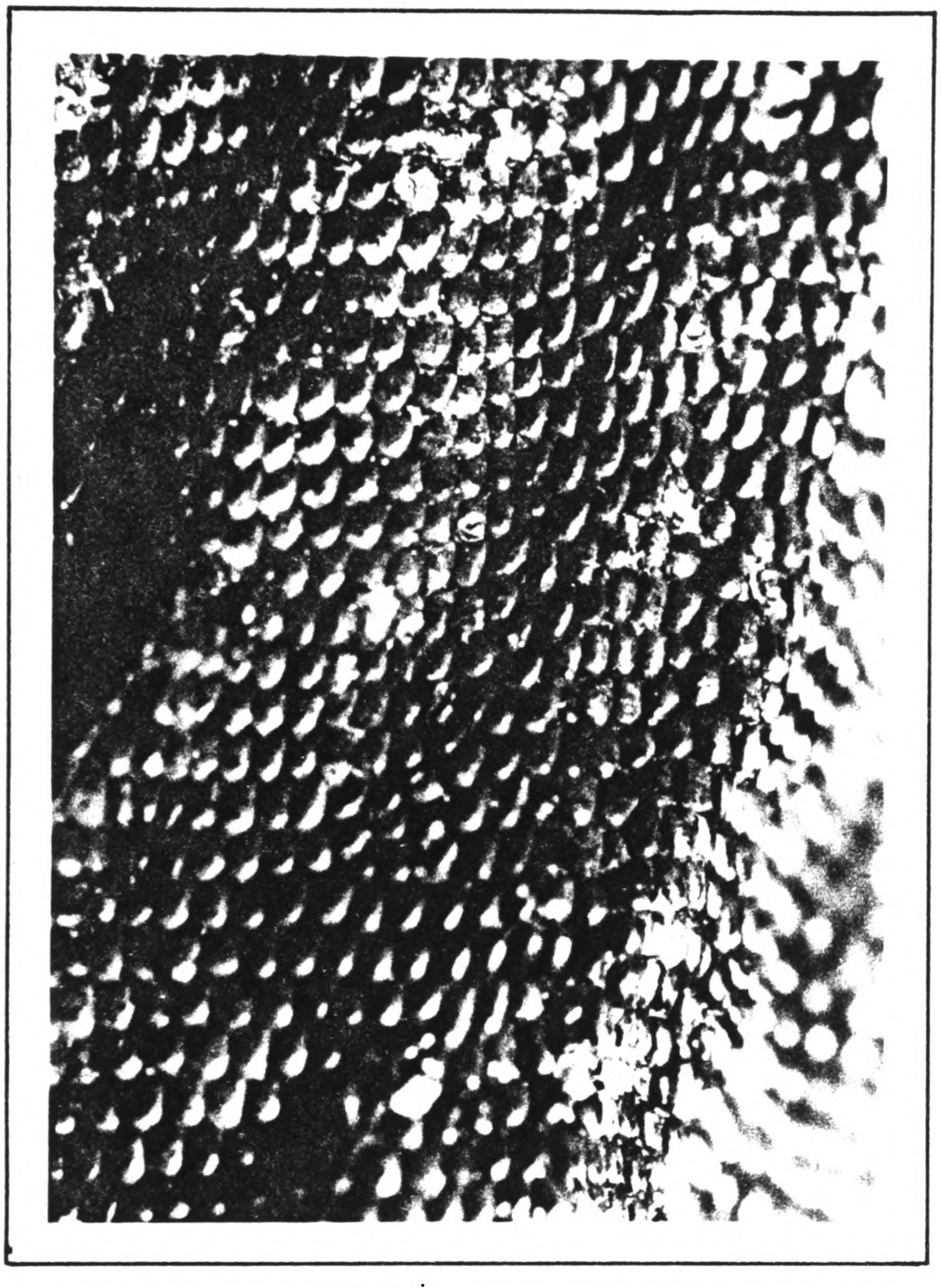


Fig. 4.27 SCALES FROM BACK OF P. *hispanica*

anterior



posterior

light is anterior, which additionally is the position where the lizard looks more shiny and therefore seems to reflect most light. Most scale surface will be perpendicular when the light source is just anterior of the perpendicular (Figure 4. 2 6). From a posterior direction light will behave quite differently (Regal,1975). As the angle of incidence flattens, the reflected light begins to be directed to the undersides of the anterior scales. Radiant energy then tends to be channelled to the bases of the scales from where it can be transferred to the internal tissues of the lizard. The scales thus act as a trap to light originating from a posterior direction. Regal suggests,using experimental evidence, that this is indeed a side effect of scale arrangement. The effect is probably increased by the angular colour effect, and all reflected light is absorbed under the scales. All the adaptations discussed theoretically above appear to be for the maximisation of heat gain, rather than for its minimisation. Regal (1975) suggests that flat scales are better for conserving heat than raised scales. The flattened scales of P. hispanica therefore support the hypothesis that the species predominantly needs to keep warm rather than cool. This implies that the lizard will more effectively increase its active period by being able to warm up in cold conditions (cooler parts of the day or year) than by being able to remain cool in warm or hot conditions. The lizards' activity periods are discussed later (Chapter 8), but in general lizards are more often seen active during cool winter months and during the morning than during the midday heat of summer. This is probably of added advantage since insect food is least abundant in the summer. It is also likely to be more a characteristic of lizards originating in temperate climate such as are those in the genus Podarcis, than of tropical lizards.

4.5 Colour as a radiation shield

The position and shape of scales can create a heat shield as we have seen above. Porter (1972) considers that colour can itself act as a shield to radiation. In particular, Porter (1967) found that the black peritoneum found in many lizard species (including *P. hispanica*) excludes significant amounts of ultra-violet radiation at 290 to 400 mμ . This could well be significant in thermoregulation. The effect, however, is unclear - energy absorbed by the peritoneum could, for example, be transmitted to internal organs as heat while dangerous radiation is stopped. If the peritoneum was absent, ultra-violet light of wavelengths of around 300 mμ could penetrate the internal organs. This is sufficient to cause mutations (Porter, 1967). Since the peritoneum only absorbs about 5% of incident solar energy, whereas skin absorbs 60 - 70% and muscles 10 - 20% , it is likely that its main value is in fact as a radiation shield (Porter, 1967).

4.6 Discussion

Norris (1967) considered that a small lizard, about the size of P. hispanica, is at a selective advantage if it is highly absorptive (dark), allowing it to reach temperature equilibrium in most environmental situations. According to Norris (1967), under certain circumstances, protective coloration can take precedence over temperature control aspects of reptile colour. This appears to be so in desert reptiles during their activity periods (Norris, 1967), but just after emergence there is a time during which the skin is darkened that represents the reverse relationship.

P. hispanica appears to compromise between the two, combining, with its angular colour effect, both anti-predator and thermoregulatory properties. This has probably been possible due to the small size of the species, which allows rapid changes in and fine control of temperature, and to the small size of the dorsal and lateral scales which permit the colour effect. This fine control of temperature was considered possible by Norris (1967) with respect to colour change. He stated that when body temperatures oscillate about equilibrium points, both when heat supplies are low and when activity levels have been reached, colour change capability could be responsible for the animal's entire temperature change. The subtle colour angle effect could well have a similar function.

The phenomenon may in fact occur in other similar species, since it will probably give lizards a selective advantage over larger types which may not be able to develop such a system.

CHAPTER 5

USE OF SPACE

5 USE OF SPACE

5.1 Introduction

Pianka (1969, 1973) and others have pointed out that species can divide resources along three dimensions: food type, habitat and time. Resource partitioning may reduce competition, increase feeding efficiency, and increase carrying capacity (Simon & Middendorf, 1976). More recently, attention has been paid to resource partitioning within species (e.g. Simon & Middendorf, 1976; Mellado Camacho, 1980; Schoener & Schoener, 1982). These latter studies have usually dealt in detail with a specific aspect of intraspecific resource partitioning. Thus Simon & Middendorf (1976) concentrated on temporal and microhabitat aspects and Schoener & Schoener (1982) on home ranges.

Mellado Camacho's (1980) study was of a more general nature, and dealt with three Mediterranean lizards, Acanthodactylus erythrurus, Psammodromus algirus and Podarcis hispanica. The field work was carried out in March and April in Doñana, Spain. The author did not distinguish between ages or size classes of P. hispanica. His conclusions of the species' habitat preferences were that it is a generalist, but requires the proximity of cover in the form of dense matorral (scrub) or trees. Salvador (1974) considered the species to be an inhabitant of rocky and wooded areas (vertical surfaces).

In this chapter I attempt to describe the preferred microhabitat of P. hispanica in Gibraltar and determine whether there is a partitioning of space resource between different sizes of lizards. Related to the use of space are social interactions between individuals (Brattstrom, 1974) which are also discussed in this chapter.

5.2 Microhabitats

5.2.1 Methods

Apart from the many incidental observations during field work, which will be referred to in the course of discussion, the main sources of data for this section were the transects made through the habitats (3.2.1). The habitats and microhabitats themselves have been described in Chapters 1 and 2.

The two transect areas differed considerably in layout and vegetation and so have been treated differently. The North Front Cemetery transect site (Figure 5.1) was larger and covered a more heterogenous area. The main ground cover was Oxalis pes-caprae and grasses in winter and spring. During these seasons cover varied between 50% and 100%. This ground cover disappeared in late spring. The route was lined with gravestones of various sizes. Most were constructed of marble and concrete. One length of the transect route (the northernmost part) passed through an open area several metres away from any gravestones. Along the path were a number of bushes of various species, notably Lantana camara and Cupressus sempervirens.

The Bruce's Firebreak transect path was shorter and consisted of two parts - a lower track along an old stone wall, and an upper track through garrigue vegetation (2.2.3) consisting of low Oxalis pes-caprae and Jasminum fruticans ground cover with scattered clumps mainly of Catharmus arborescens and Pistacia lentiscus.

For the North Front Cemetery transects, the results have been plotted on a plan of the area as numbers of lizards observed at each point. No distinction has been made in this case between sexes or size classes. This method is subject to bias since some individuals will have been seen more often than others.

Because the Bruce's Firebreak area consisted clearly of two main types of habitat, the two types have been compared without further division.

In both sites approximate heights above the ground (usually on rocks or gravestones, but sometimes on bushes or trees) were divided into height classes as shown in Table 5.1. The use made of heights by different categories of P. hispanica

Table 5.1 Table of height classes used.

Height class	Height
9	150+
8	130/140 cm
7	110/120 cm
6	90/100 cm
5	70/ 80 cm
4	50/ 60 cm
3	30/ 40 cm
2	15/ 25 cm
1	5/ 10 cm
0	Ground

Note : Heights were estimated by eye, allocated to the nearest round figure under the 'height' column, and then given the appropriate height class.

according to sex and to size (SVL), as well as time of year, have been compared using χ^2.

A similar analysis was made of data collected on substrates used for basking. This is considered in Chapter 8.

In addition to the above, a morphological method was used to try and determine whether differences in use of space indicated either by the results of the above analyses or inferred from direct observation were reflected in a particular morpholigical adaptation (Pianka, 1973). Thus the ratio of hind leg to foreleg length was calculated for all captured lizards, *P. hispanica* and *Ps. algirus* from Bruce's Firebreak, and *P. hispanica* from North Front Cemetery. The fourth toe of both foreleg and hind leg is the longest and probably most used in climbing. *P. hispanica* climbs more than *Ps. algirus* on vertical surfaces (5.2.2). The purpose of the analysis was to determine the ratio as it relates to the microhabitat in which the lizards forage (Pianka, 1973). In order to reduce bias related to climbing, it was decided to exclude the length of the fourth digits from these calculations. All data used were from right-hand limbs.

Data sets of small sample size (e.g. Bruce's Firebreak samples) were compared using the Mann-Witney U test. Larger samples were compared using an F-test since it was felt it should not be assumed that variances between the samples being compared were identical (Sokal & Rohlf, 1969). A regression was made of the hindleg:foreleg ratio against SVL for North Front Cemetery data in order to try to determine whether there was a relationship between the ratio and the ages of the lizards.

Fig. 5.1 PLAN OF NORTH FRONT CEMETERY MAIN TRANSECT SITE SHOWING VEGETATION. (GRASS, *Oxalis pes-caprae* AND *Chrysanthemum coronarium* ARE EVIDENT ONLY FROM NOVEMBER TO APRIL/MAY.) AND TOMBSTONES.

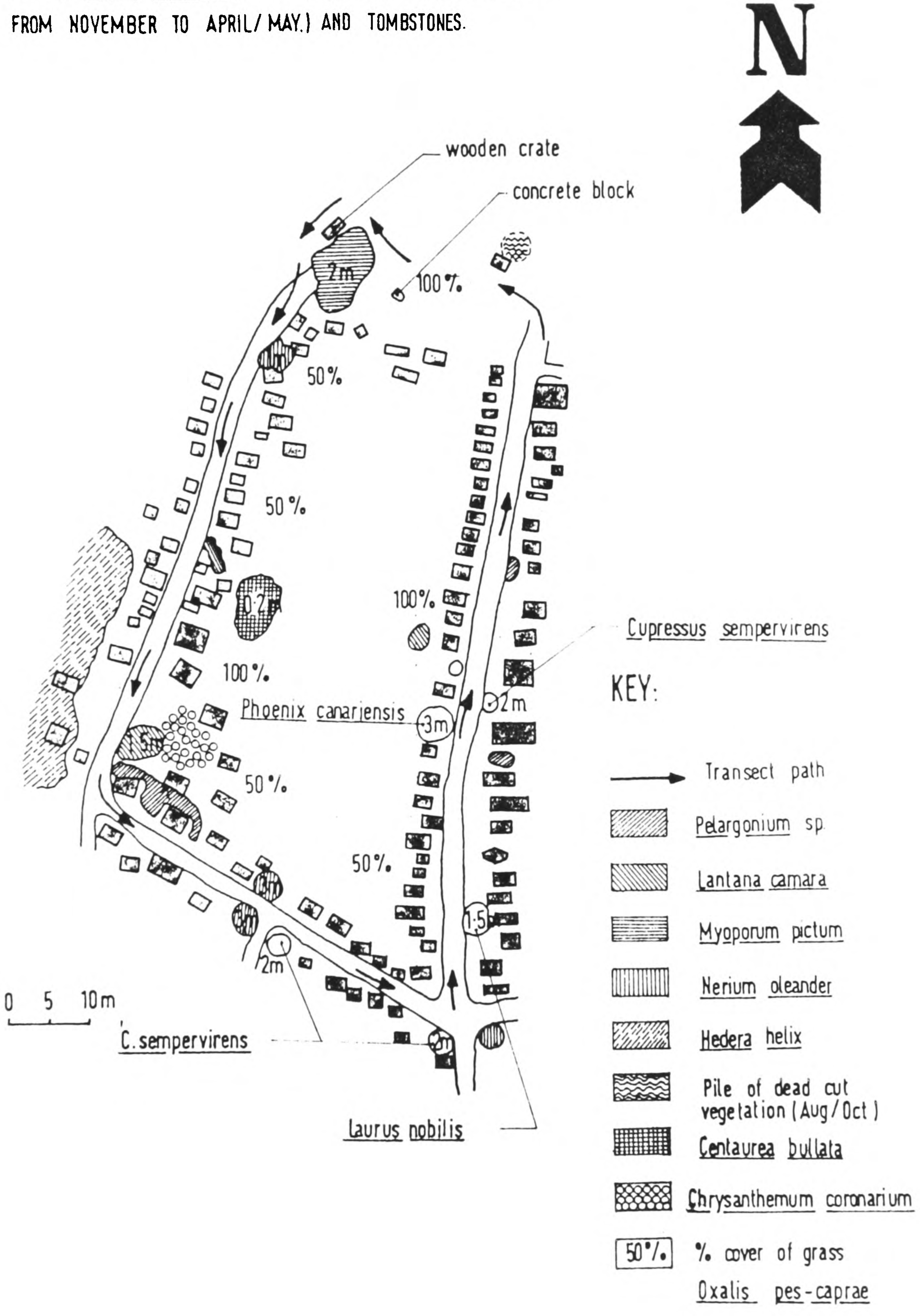


Fig. 5.2 LOCATIONS OF OBSERVATIONS OF P. hispanica DURING TRANSECTS AT NORTH FRONT CEMETERY, GIBRALTAR (VEGETATION MAP AT Fig. 5.1.) (DATA FROM 164 TRANSECTS. OBSERVATIONS ARE OF LIZARDS WITHIN SIGHT OF THE TRANSECT PATH.)

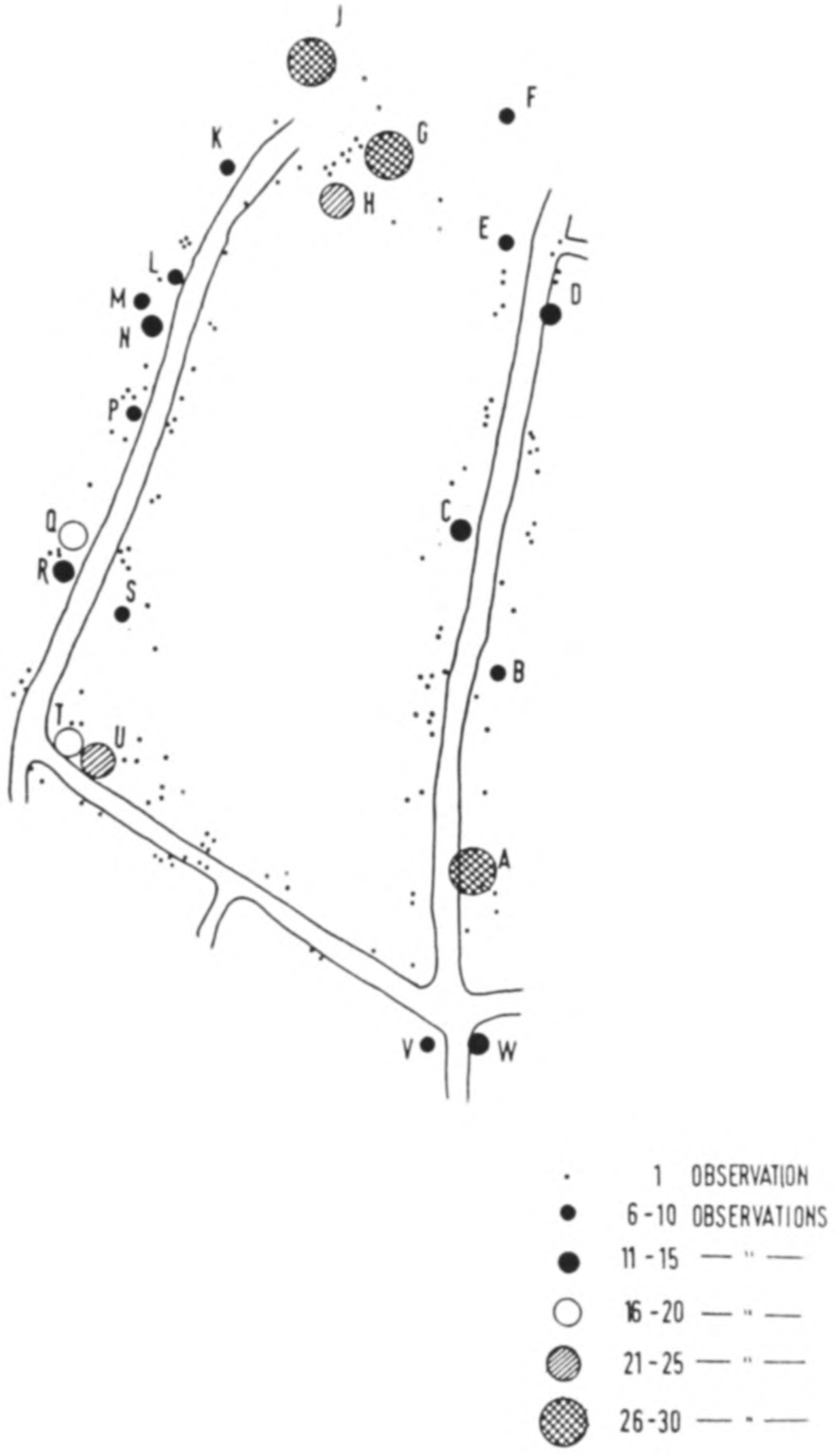


Fig. 5.3 LOCATION OF OBSERVATIONS OF *P.hispanica* AT NORTH FRONT CEMETERY GIBRALTAR TRANSECT SITE DURING FEBRUARY/MAY (PERIOD A) (DATA FROM 23 TRANSECTS).

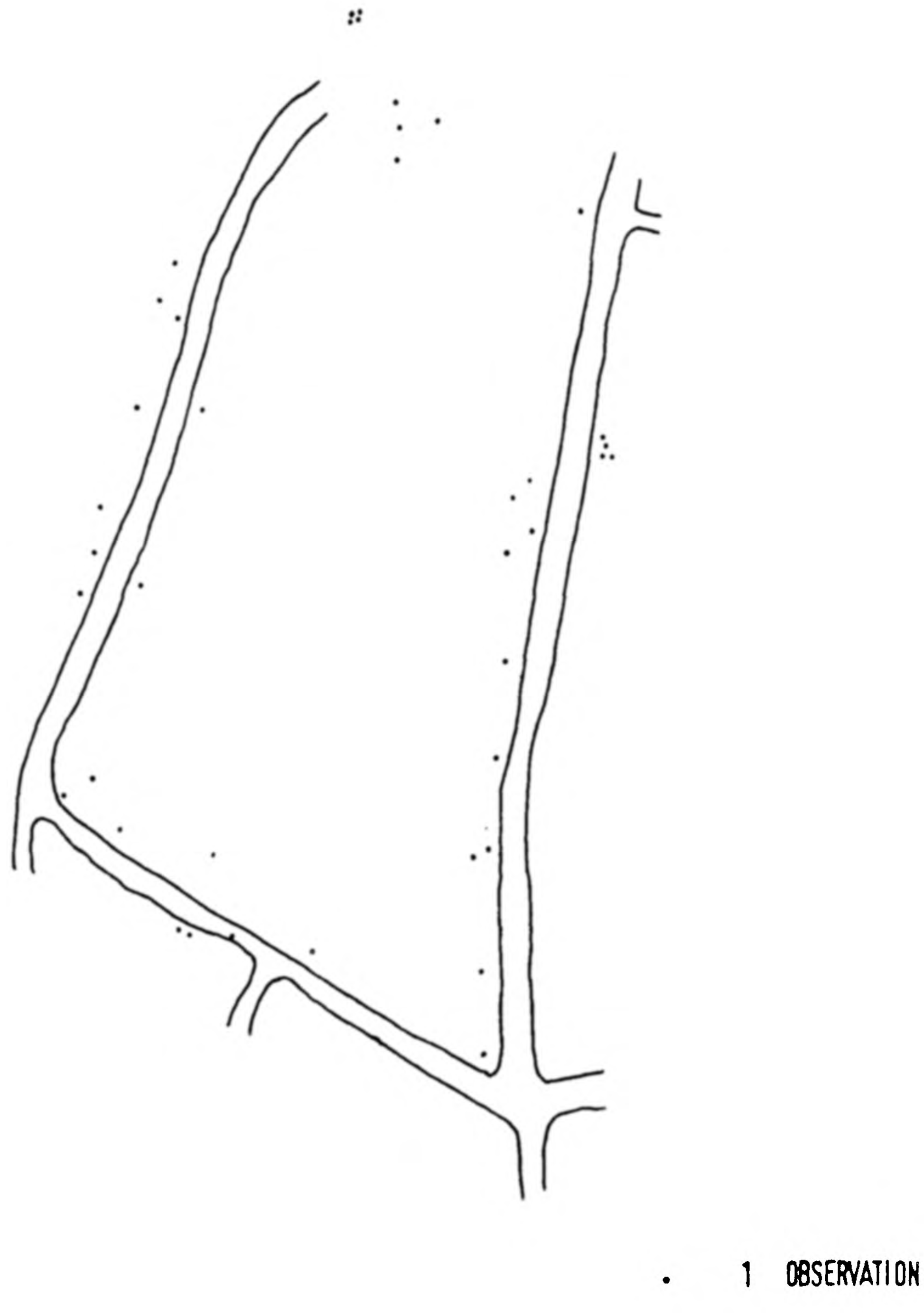


Fig. 5.4 LOCATION OF OBSERVATIONS OF *P.hispanica* AT NORTH FRONT CEMETERY, GIBRALTAR TRANSECT SITE DURING JUNE TO SEPTEMBER (PERIOD B) (DATA FROM 89 TRANSECTS)

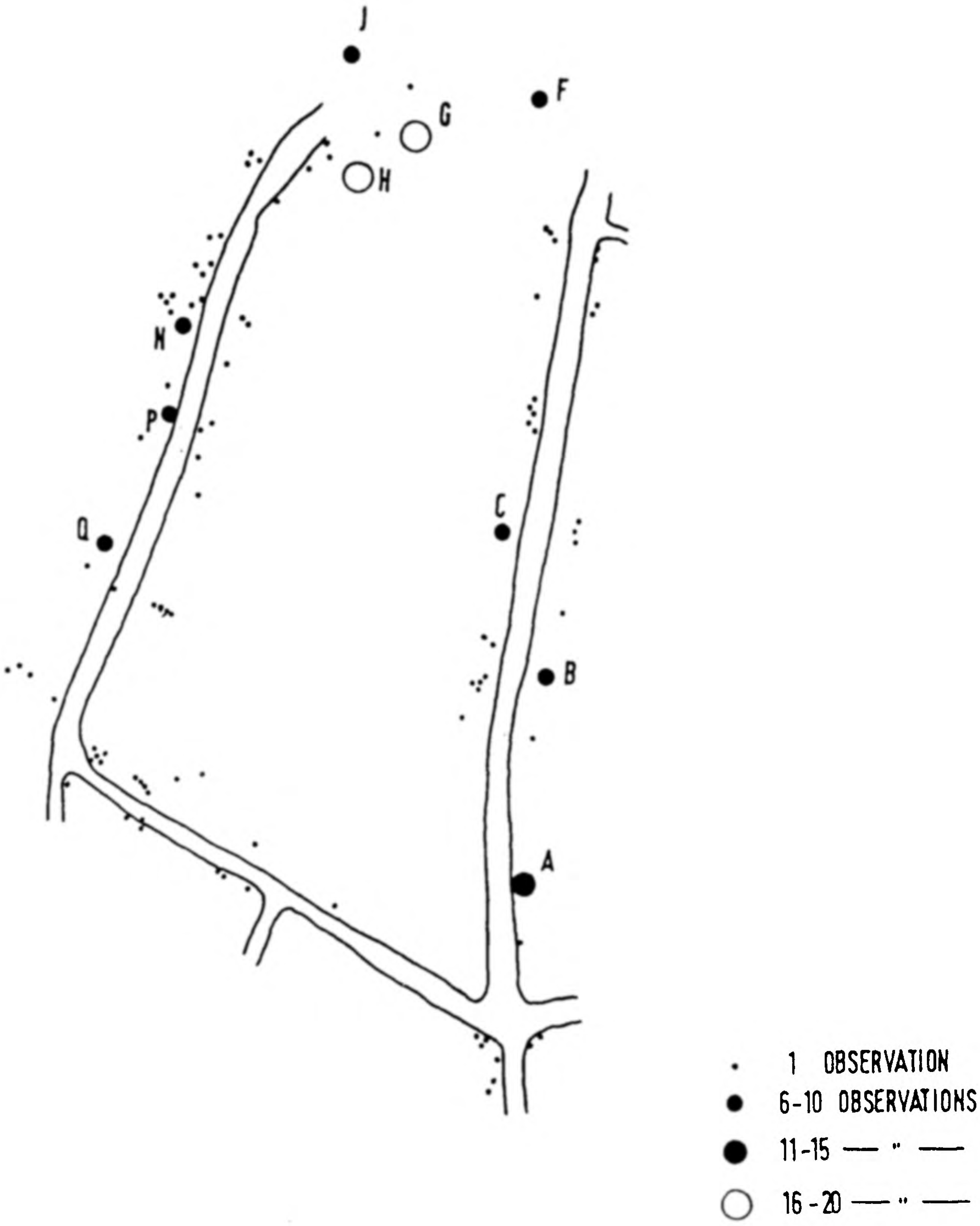


Fig. 5.5 LOCATION OF OBSERVATIONS OF *P. hispanica* AT NORTH FRONT CEMETERY GIBRALTAR TRANSECT SITE DURING OCTOBER AND NOVEMBER (PERIOD C.) (DATA FROM 39 TRANSECTS).

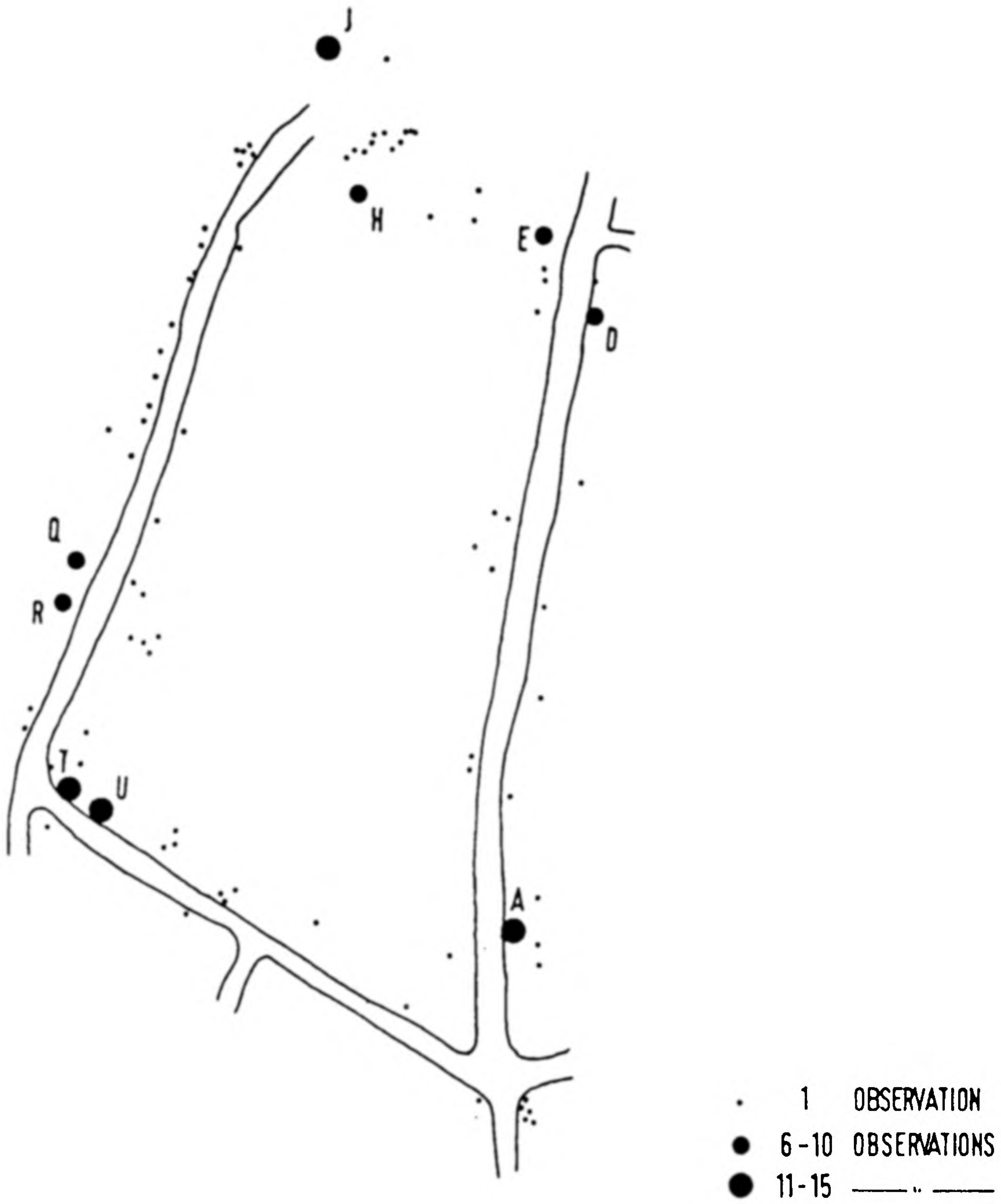
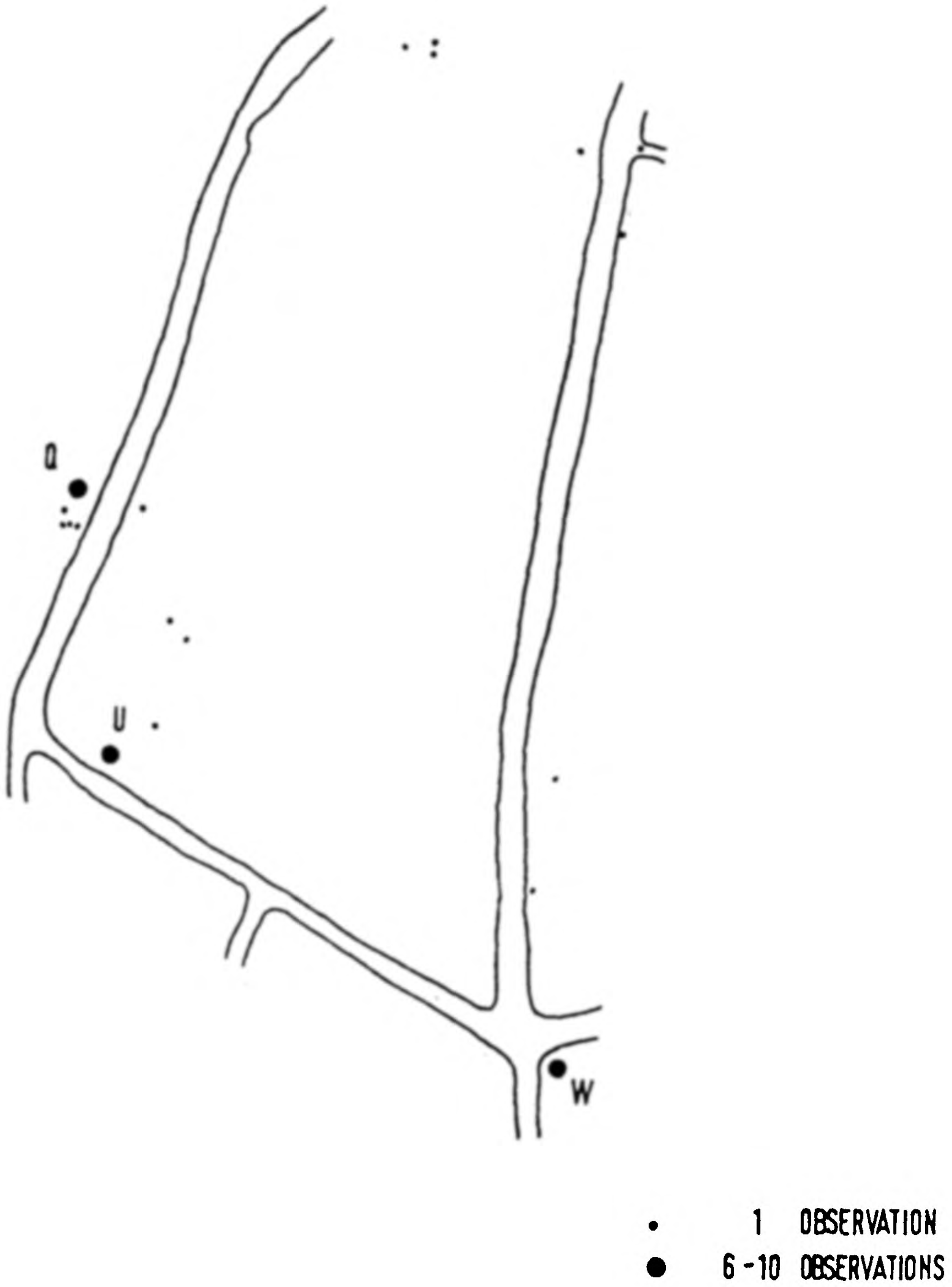


Fig. 5.6. LOCATION OF OBSERVATIONS OF P. hispanica AT NORTH FRONT CEMETERY, GIBRALTAR TRANSECT SITE DURING DECEMBER AND JANUARY (PERIOD D) (DATA FROM 13 TRANSECTS).



5.2.2 Results

(a) Transect observations

Figures 5.2 to 5.6 show the numbers of lizards seen in North Front Cemetery during transects in 1980 and 1981. Although sampling was not carried out with equal regularity during all periods of the year, the whole transect path was covered during each transect so that relative occurence in different parts of the area should reflect relative abundance from area to area in the field.

The data represented in the figures are from a total of 164 transects with actual observation of lizards, i.e. excluding rounds during cool conditions when no lizards were seen.

Figure 5.2 shows the overall year-round result. There are a number of sites with concentrated sightings and large areas of the transect path where very few or no lizards were seen. Fewest lizards overall were seen during period A (February - May), when the vegetation is most lush. Numbers were well distributed throughout the area with no obvious aggregations (Figure 5.3).

More lizards (including hatchlings) were seen during period B (June to September) when observations seemed to be more frequent in certain parts of the transect (lettered in Figure 5.4).

Aggregations of observations were also evident during period C (October - November) in similar areas (Figure 5.5). In winter (period D, Figure 5.6) numbers of observations were again low, but concentrated in certain areas in the south of the transect site. They were notably absent from areas in the north of the site where observations were frequent during the rest of the year.

At Bruce's Firebreak 82% of the year-round observations of P. hispanica were along the lower wall and adjacent area, while 91% of observations of Ps. algirus were among the low shrubs of the garrigue.

(b) Heights

The proportions of P. hispanica from North Front Cemetery seen at different heights above the ground throughout the year are shown in Figure 5.7 for all lizards together, and for male, female and juvenile lizards. The ground was most used in all cases, least so by adult males (34•4% of observations compared to 43% for females and 42•5% for juveniles). Over 50% of observations were of lizards within 10cm of the ground (height classes 0 and 1) (55•4% of males, 60•7% of females and 72•9% of juveniles). Contingency table analyses show a significant difference in the proportions of heights used between adult males and juveniles ($P<0\cdot01$) and all adults and juveniles ($P<0\cdot01$). No juvenile lizards were seen more than 80cm from the ground.

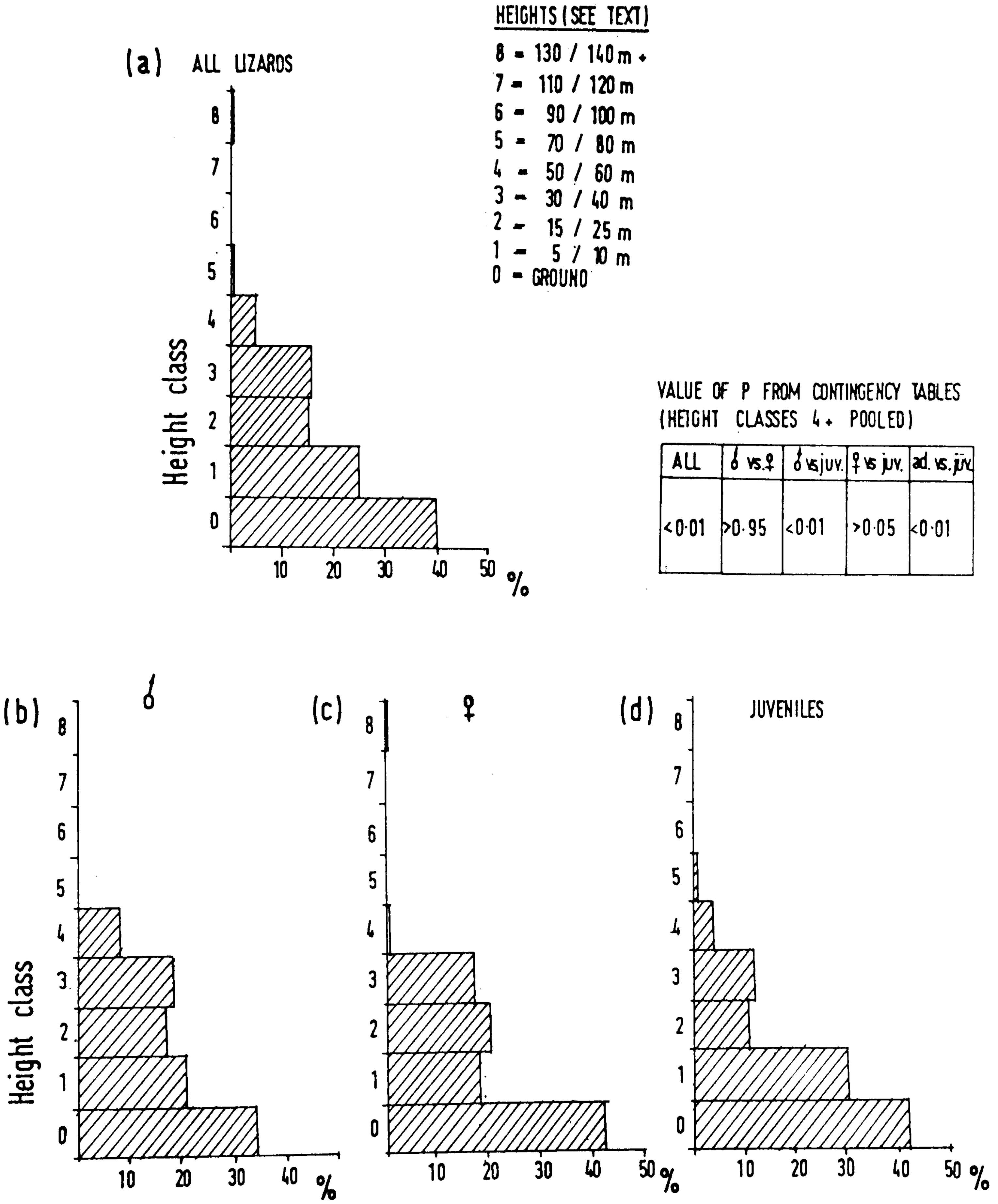
These data, in turn subdivided according to size class (Figure 5.8), again show that young lizards made more use of the ground (69% of observations of size class 1) than did larger lizards. In fact, no size class 1 lizards were seen above 40cm and only 2% of size class 2 lizards were seen above this height. All size classes of lizard did use the ground more than any other single height class.

The heights at which young lizards were seen during the months of August to November, the time of year when they were most numerous, are illustrated in Figure 5.9. The diagrams suggest there was an increase in the preferred height of young lizards during this period. In the November sample, the 15/25 cm height was that most used by these wall lizards. The proportions of lizards at different heights are significantly different at $P < 0\cdot01$ (χ^2 test).

Similar trends for all lizards considered together in the late summer/autumn are seen represented in Figure 5.10 which gives a month by month breakdown of heights used. Over 50% of the observations during the summer months were on the ground (or just above, in August). Heights were more evenly used in winter and spring, with an intermediate height (15/25 cm) being significantly most used in March ($P< 0\cdot05$, χ^2 test).

In Figure 5.11, the data from Figure 5.10 are grouped according to 'season'. This breakdown again suggests greatest use of the ground during summer (period B), and more even use of different heights

Fig. 5.7 PERCENTAGE OF LIZARDS SEEN AT DIFFERENT HEIGHTS ABOVE GROUND LEVEL AT NORTH FRONT CEMETERY GIBRALTAR



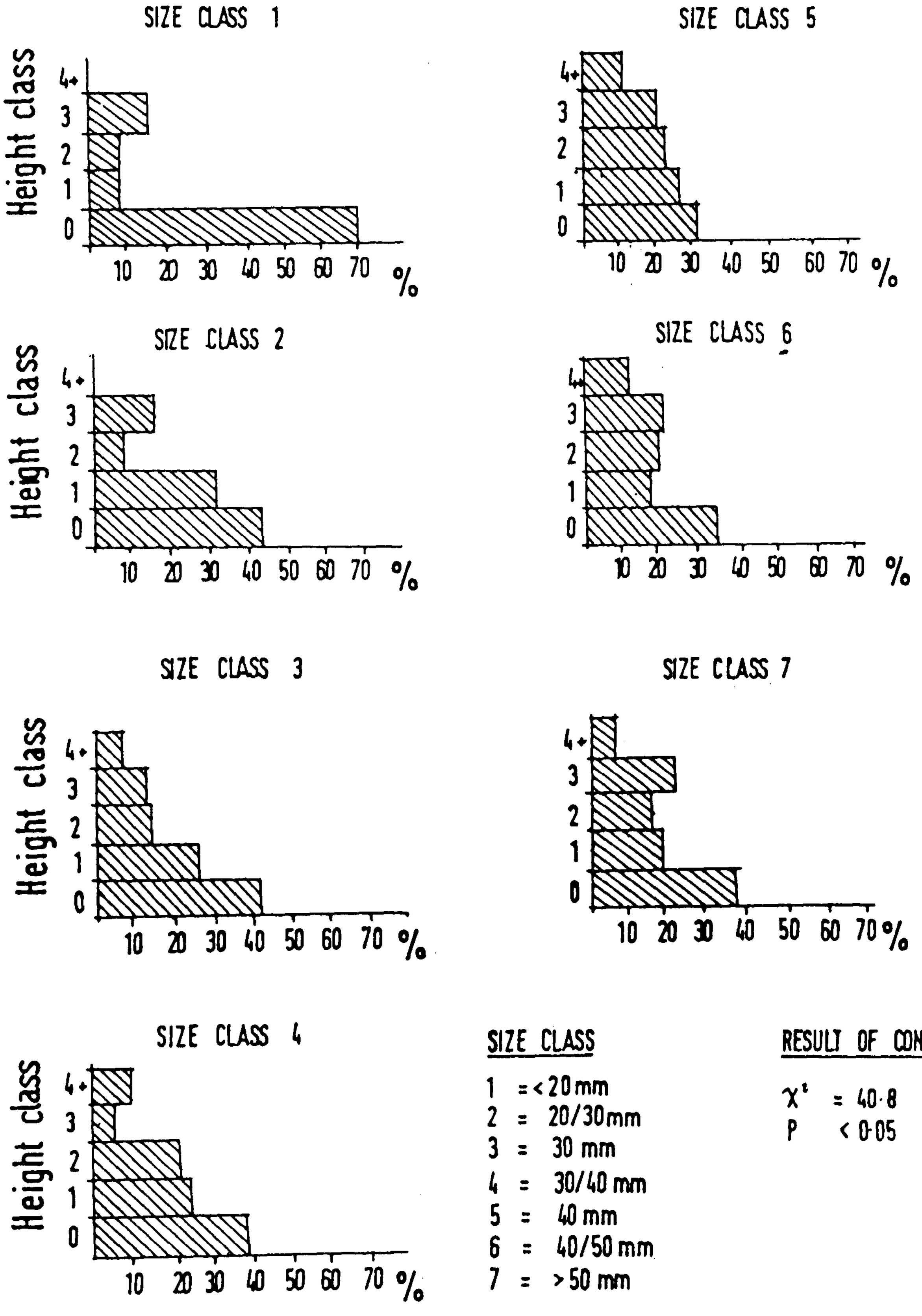
HEIGHTS (SEE TEXT)

8 = 130 / 140 m +
7 = 110 / 120 m
6 = 90 / 100 m
5 = 70 / 80 m
4 = 50 / 60 m
3 = 30 / 40 m
2 = 15 / 25 m
1 = 5 / 10 m
0 = GROUND

VALUE OF P FROM CONTINGENCY TABLES (HEIGHT CLASSES 4+ POOLED)

ALL	♂ vs. ♀	♂ vs. juv.	♀ vs juv.	ad. vs. juv.
<0·01	>0·95	<0·01	>0·05	<0·01

Fig. 5.8 PERCENTAGE OF P.hispanica OF DIFFERENT SVL SIZE CLASSES SEEN AT DIFFERENT HEIGHTS AT NORTH FRONT CEMERY GIBRALTAR.



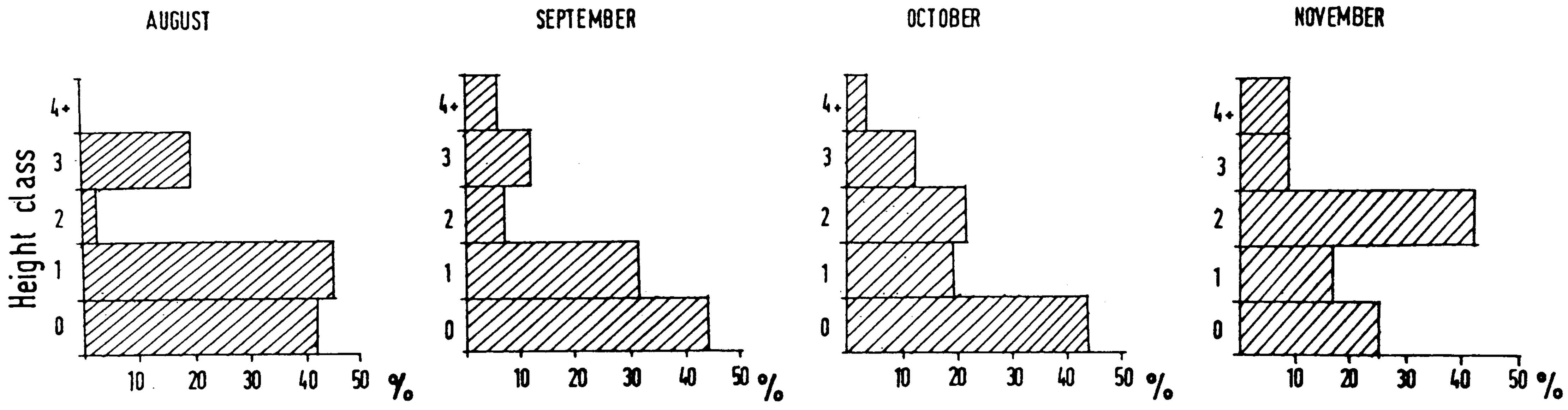
SIZE CLASS

1 = < 20mm
2 = 20/30mm
3 = 30 mm
4 = 30/40 mm
5 = 40 mm
6 = 40/50 mm
7 = > 50 mm

RESULT OF CONTINGENCY TABLE

$\chi^2 = 40{\cdot}8$
$P < 0{\cdot}05$

Fig. 5.9 PERCENTAGE OF JUVENILE LIZARDS SEEN AT DIFFERENT HEIGHTS ABOVE THE GROUND BETWEEN AUGUST AND NOVEMBER 1981
NORTH FRONT CEMETERY, GIBRALTAR.

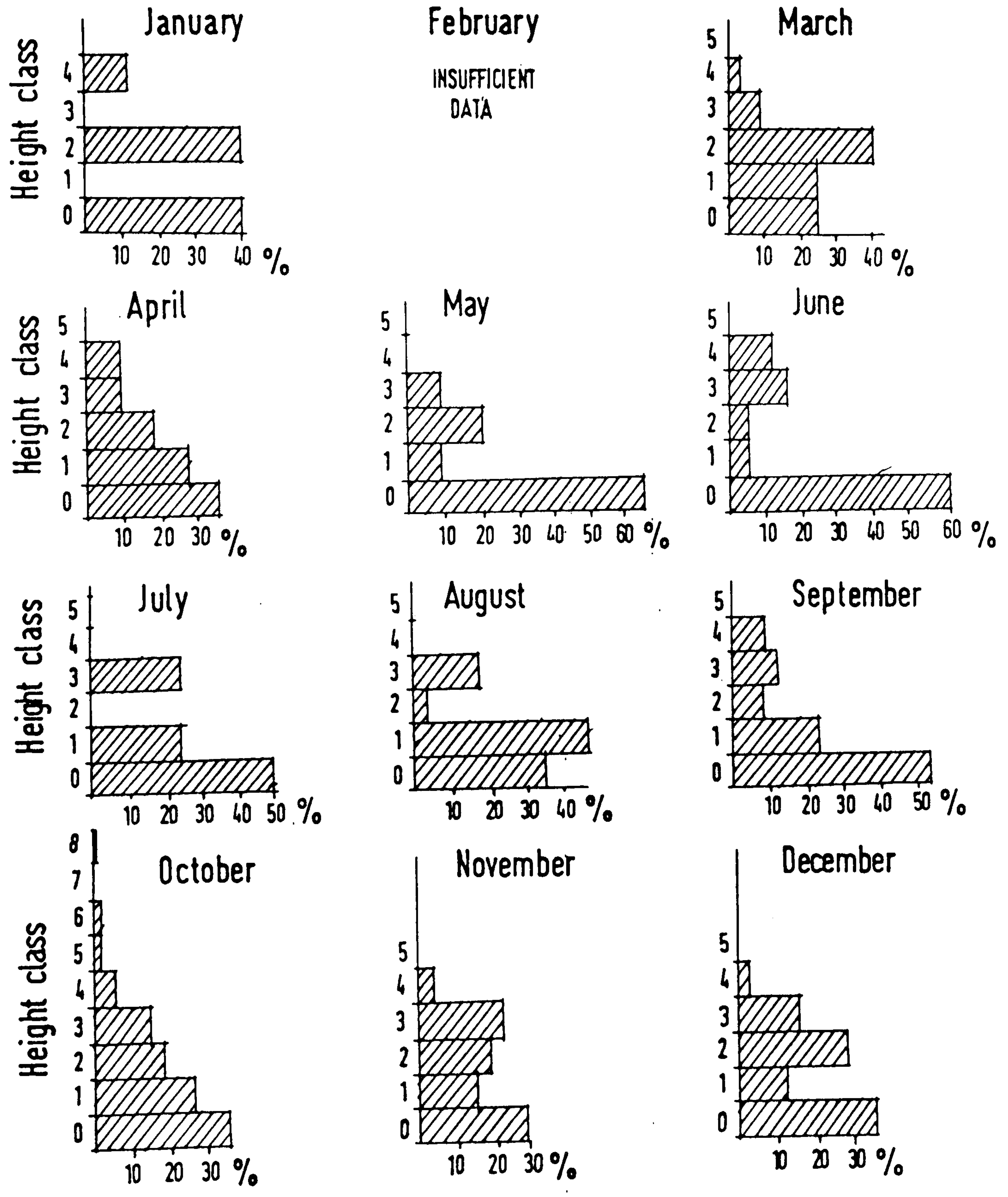


RESULT OF CONTINGENCY TABLE ANALYSIS

$\chi^2 = 28{\cdot}97$

$P < 0{\cdot}01$

Fig. 5.10 PERCENTAGE OF ALL LIZARDS SEEN AT DIFFERENT HEIGHTS ABOVE GROUND EACH MONTH AT NORTH FRONT CEMETERY, GIBRALTAR.

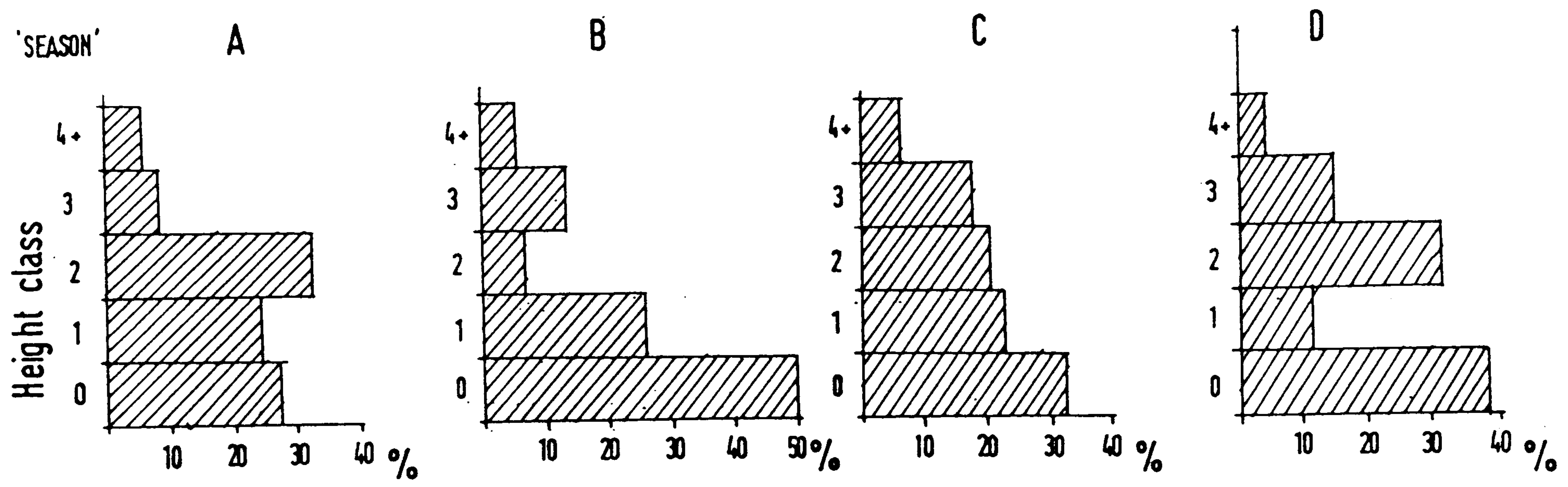


CONTINGENCY TABLE RESULTS:

HEIGHT CLASS 4+ POOLED : $\chi^2 = 105{\cdot}18$ $P \ll 0{\cdot}001$

HEIGHT CLASS 3+ POOLED : $\chi^2 = 94{\cdot}84$ $P \ll 0{\cdot}001$

Fig. 5.11 PERCENTAGE OF LIZARDS SEEN AT DIFFERENT HEIGHTS ABOVE THE GROUND DURING DIFFERENT PERIODS OF THE YEAR

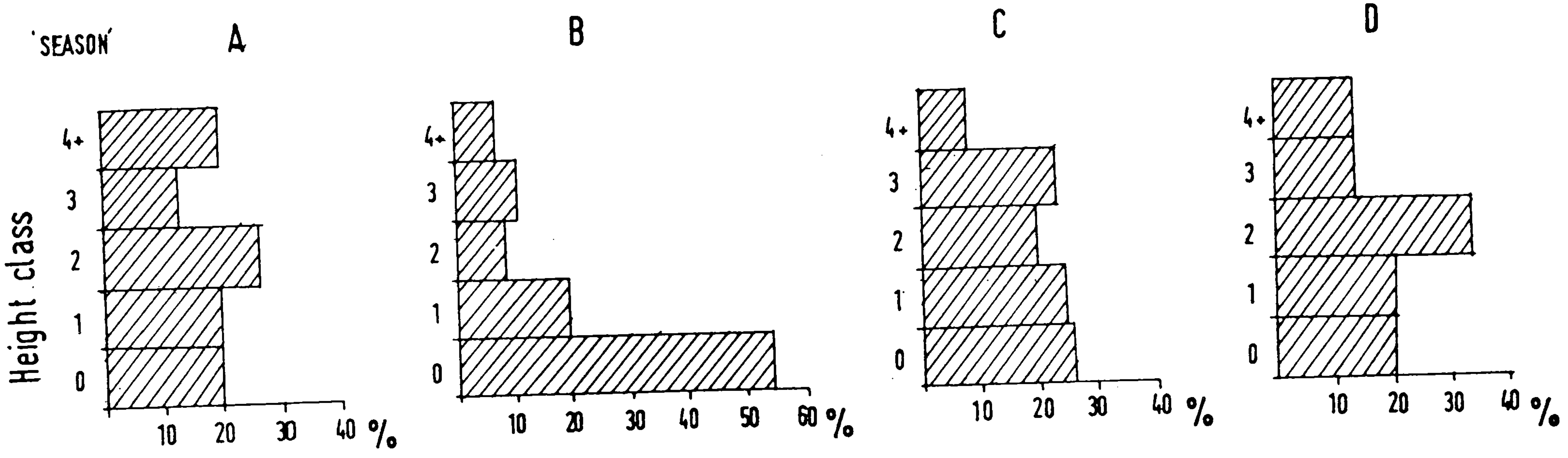


A = FEBRUARY, MARCH, APRIL.
B = MAY, JUNE, JULY, AUGUST, SEPTEMBER.
C = OCTOBER, NOVEMBER.
D = DECEMBER, JANUARY.

RESULT OF CONTINGENCY TABLE

$\chi^2 = 55{\cdot}9$
$P < 0{\cdot}001$

Fig. 5.12 PERCENTAGE OF MALE *P. hispanica* SEEN AT DIFFERENT HEIGHTS ABOVE THE GROUND DURING DIFFERENT PERIODS OF THE YEAR AT NORTH FRONT CEMETERY GIBRALTAR.



A = FEBRUARY, MARCH, APRIL.

B = MAY, JUNE, JULY, AUGUST, SEPTEMBER.

C = OCTOBER, NOVEMBER.

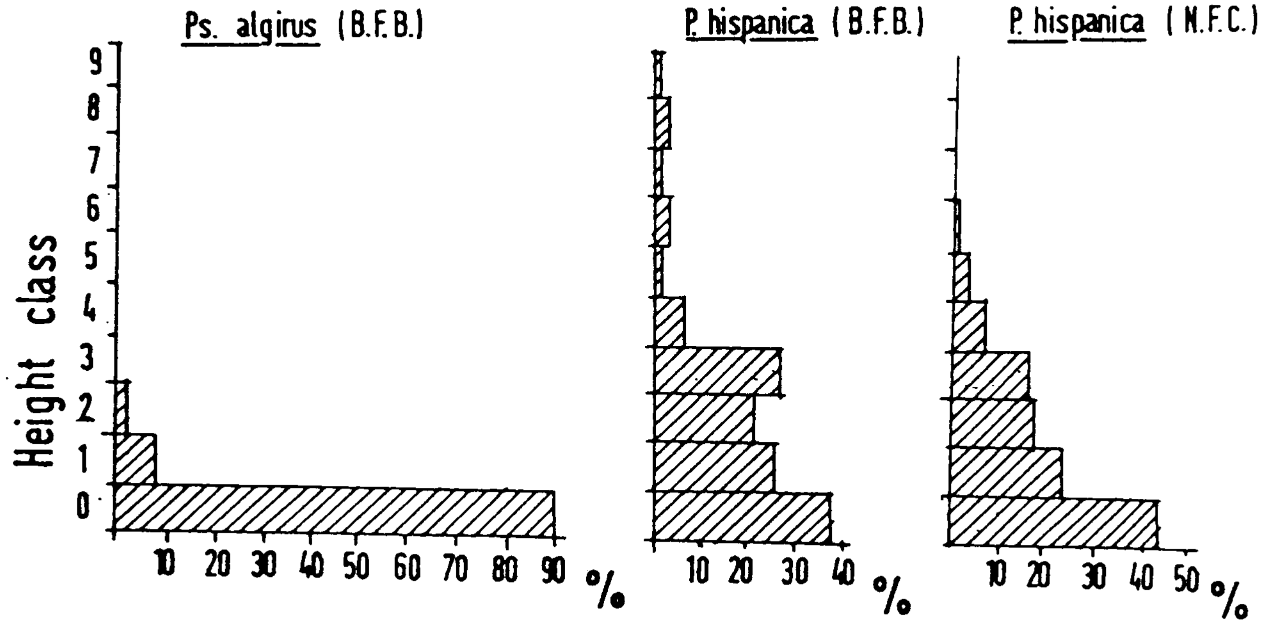
D = DECEMBER, JANUARY.

RESULT OF CONTINGENCY TABLE

$\chi^2 = 21{\cdot}12$

$P < 0{\cdot}05$

Fig. 5.13 PERCENTAGES OF P.hispanica AND Ps.algirus SEEN AT DIFFERENT HEIGHTS ABOVE THE GROUND AT BRUCE'S FIREBREAK (B.F.B.) AND NORTH FRONT CEMETERY (N.F.C.)



HEIGHT CLASS	HEIGHT
9	150 + cm
8	130/140 cm
7	110/120 cm
6	90/100 cm
5	70/ 80 cm
4	50/ 60 cm
3	30/40 cm
2	15/ 25 cm
1	5/ 10 cm
0	GROUND

RESULTS OF CONTINGENCY TABLES

Ps. algirus vs. P.hispanica (B.F.B.)
(HEIGHT CLASSES USED : 0/1, 2+)
$\chi^2 = 28{\cdot}88$
$P \ll 0{\cdot}001$

Ps. algirus vs. P.hispanica (N.F.C.)
(HEIGHT CLASSES 0/1 2+)
$\chi^2 - 29{\cdot}73$
$P \ll 0{\cdot}001$

P. hispanica (N.F.C.) vs. P.hispanica (B.F.B)
(HEIGHT CLASSES USED : 0,1,2,3,4,5+)
$\chi^2 = 16{\cdot}46$
$P < 0{\cdot}01$

during the other seasons, with a predominance of the 15/25 cm height during spring. Results for males only are similar, with less use of the ground in winter (Figure 5.12).

The overall results for P. hispanica at North Front Cemetery and at Bruce's Firebreak and those for Ps. algirus at Bruce's Firebreak are illustrated in Figure 5.13. The heights at which Ps. algirus were observed clearly differed from those for P. hispanica at both sites ($P \ll 0{\cdot}001$). Ps. algirus were observed more often on the ground (89·9% of observations). P. hispanica from both sites differed from each other in the use of heights ($P < 0{\cdot}01$). The Bruce's Firebreak lizards were seen at heights above 100 cm which North Front Cemetery lizards were never seen to use. Only 37·4% of Bruce's Firebreak lizards were observed on the ground compared to 50·7% of North Front Cemetery wall lizards.

(c) Hindleg/foreleg ratio

Table 5.2 gives the mean hindleg/foreleg ratios for Ps. algirus and P. hispanica for both sites and shows which sets of results are significantly different.

The ratio for Ps. algirus differs from all the P. hispanica results. ($P < 0{\cdot}05$ for Bruce's Firebreak wall lizards; $P < 0{\cdot}02$ for North Front Cemetery males; $0{\cdot}02 < P < 0{\cdot}05$ for females; $P < 0{\cdot}02$ for all Cemetery adults). There is no significant difference between male and female North Front Cemetery lizards nor between wall lizards from each site. The mean ratio is, however, greater for North Front Cemetery lizards (1·39; SD =0·14) than for Bruce's Firebreak lizards (1·33; SD = 0·15). It is greater for Cemetery females (1·41; SD = 0·15) than males (1·38; SD = 0·14). The mean ratio for Ps. algirus (1·50; SD = 0·22) is greater than all the P. hispanica ratios.

When the hindleg:foreleg ratios were compared to snout-vent lengths for the North Front Cemetery sample (which was the largest) the correlation coefficient ($r = 0{\cdot}095$) was found not to be significant ($P > 0{\cdot}05$). However, a Mann-Witney U test was used to test the difference between the ratios for lizards of SVL above 50 mm ($\bar{x} = 1{\cdot}39$) and those below 40 mm ($\bar{x} = 1{\cdot}34$). This test showed significance at the $P = 0{\cdot}01$ level.

Table 5.2 Hindleg:Foreleg ratios for *Psammodromus algirus* and *Podarcis hispanica* at Gibraltar.

(a) Mean Hindleg:foreleg ratios

	Bruce's Firebreak (BFB)		North Front Cemetery (NFC)		
	Ps. algirus	*P. hispanica*	*P. hispanica* ♂ + ♀	*P. hispanica* ♂	*P. hispanica* ♀
$\bar{x}$	1·50	1·33	1·39	1·38	1·41
n	22	9	104	65	36
SD.	0·22	0·55	0·14	0·14	0·15

(b) Comparison of Hindleg:Foreleg ratios

	Ps. algirus (BFB)	*P. hispanica* NFC ♂	*P. hispanica* NFC ♀	*P. hispanica* NFC all
Ps. algirus (BFB)	-	$P < 0.02^{*}$	$0\cdot02 < P < 0\cdot05^{*}$	$P < 0\cdot02^{*}$
P. hispanica (BFB)	$P < 0\cdot05^{**}$	$P > 0\cdot05^{*}$	-	$P > 0\cdot05^{*}$

Note : * denotes result of F-test

** denotes result of Mann-Witney U-test

5.2.3 Discussion

Mellado Camacho (1980) stressed the importance of cover in the form of bushes or trees for P. hispanica in Doñana, Spain. This requirement seems to be shared by the Iberian Wall Lizards observed in North Front Cemetery, where most were concentrated in particular areas with bushes (Figure 5.2). Taller trees with trunks and without foliage close to the ground did not appear to be as attractive. Thus sightings were concentrated around bushes of Myoporum pictum, Pelargonium spp., Lantana camara, Laurus nobilis and Nerium oleander, but not around the taller Cupressus sempervirens. Valverde (1967) and Salvador (1974) stress the need for this species to have access to vertical surfaces, usually in the form of trees. While vertical surfaces are clearly available throughout North Front Cemetery, there is evidently no necessity for trees.

The need for vertical surfaces may be supported by the fact that P. hispanica are noticeably absent from the flatter stretches of North Front Cemetery (the northern part of the transect, except where flat gravestones at ground level provide an open area for basking) and also from sites such as Windmill Hill Flats (2.2.3). In the latter area, ground cover is low and uninterrupted in winter and spring, and absent in summer and autumn. A lack of basking sites in the former seasons and of cover and food in the latter may account for the absence. Wall lizards also appeared scarce in dense matorral, however, while this was not the case in Doñana (Mellado Camacho, 1980).

Seasonal differences in vegetation as well as in lizard behaviour and requirements may also result in different distributions within the North Front Cemetery transect site. Figures 5.3 to 5.6 suggest this is so. During period A (spring) relatively few lizards were seen, possibly because the vegetation was at its densest. Those that were seen during transects were well distributed throughout most of the area, with the exception of the north-east section, particularly that part away from gravestones (Figure 5.3). Figure 5.4 shows the distribution of the lizards during the summer (period B). More lizards overall were seen, in particular observations being concentrated around a number of sites. These were mainly in the vicinity of bushes (Figure 5.4 A, B, G, H, J, P and Q) or cut dry vegetation (F). Site C was adjacent to persistent grassy vegetation (Panicum repens). These aggregations of lizards were seen at a time when vegetation is otherwise dry and most of the ground is exposed, achieving high daytime temperatures (8.4) and providing little invertebrate food (7.4). Bushes provide both shelter and a food supply (7.4) and would be expected to attract lizards.

These requirements begin to change during the autumn. Temperature and insolation decrease (2.1), and the ground vegetation begins to grow. Some aggregations of lizards near bushes remained (Figure 5.5 A, J, H and Q), and a number of additional sites of regular occurence were found. Of these sites D, E, R and U were on or near gravestones with cracks which were seen to be lizard refugia. Refugia became increasingly important with the onset of winter when lizards spent much time basking close by.

During the winter period (period D) fewer lizards overall were again seen (Figure 5.6). The three areas where there were most observations (Q, U and W) were sites combining the presence of refugia with the proximity of dense perennial vegetation in the form of Hedera helix, Pelargonium and Nerium oleander respectively.

When the overall year-round results are considered (Figure 5.2) the sites of lizard aggregation can perhaps be attributed to the factors listed in Table 5.3, which are a combination of the need for the cover of vegetation - to provide food and shelter from heat in summer - and for suitable refugia with adjecent basking sites and vegetation (again) for foraging. In spring when food is most abundant (7.4), suitable foraging habitat in the form of ground vegetation is widespread, and the need for continuous periods of basking is reduced, the wall lizards can spread through the habitat. Indeed this is necessary since lizards are then least tolerant of each other.

The habitat at Bruce's Firebreak was not varied enough to allow the above type of comparison. It is clear, however, that P. hispanica was more restricted to the area of stone wall and its proximity while Ps. algirus kept to the areas of garrigue (and particularly the low bushes therein). The observations of lizards varied through the year. It should be noted that few P. hispanica were observed in the open firebreak or stone wall during the dry summer months. Although systematic transects were not made through more wooded areas of the Upper Rock (partly due to the difficulty of access and of seeing lizards), incidental observations suggest lizards were more common there during this season. The sighting of individual wall lizards foraging in litter under taller trees in areas of North Front Cemetery outside the transect site reinforces the suggestion that these animals shift habitat in response to seasonal changes in environmental conditions.

Table 5.3 Possible factors contributing to lizard aggregations in North Front Cemetery, Gibraltar, transect area (Figures 5.1 to 5.6).

Site	Environmental factor(s)
A	Proximity of Laurus nobilis bush.
B	Proximity of Pelargonium bush.
C	Persistent Panicum repens (grass) cover.
D	Cracks providing refugia.
E	Cracks providing refugia.
F	Proximity to cut vegetation and flat basking site.
G, H, J	Basking site next to Myoporum pictum bush.
K	Cracks providing refugia.
L, M, N	Proximity to area of Giant Reeds Arundo donax just outside limit of map (Figure 5.1) ?
P, Q, R	Cracks providing refugia; proximity to Hedera helix cover.
S	Cracks providing refugia.
T	Proximity to Pelargonium bushes.
U	Cracks providing refugia; adjacent Pelargonium bushes.
V	Proximity to young Cupressus sempervirens.
W	Cracks providing refugia; proximity to Nerium oleander bush.

Figures 5.7 to 5.13 show quite convincingly that P. hispanica predominantly uses the ground and the bottom 10 cm from the ground, both for foraging and basking (Chapters 7 and 8). This observation contradicts published work on the species which associates the Iberian Wall Lizard primarily with vertical surfaces above ground level (Mellado Camacho, 1980). Few lizards were seen in Gibraltar above 40 cm despite the fact that most of the gravestones at the Cemetery site were at least 60 cm tall and there were trees in the area above 300 cm in height.

Smaller lizards used lower levels more than did larger lizards. This deployment downwards of smaller size classes is found in other lizards (e.g. some species of Anolis (Schoener & Gorman, 1968)). Smaller lizards forage more than larger ones in the summer (7.3.2). This would tend towards their spending more time on the ground. The deployment of adults at higher levels may reflect the greater need adults have of basking and of being more visible during the mating season. Assuming lizards prefer to bask higher within a certain maximum height (perhaps around 40 - 50 cm), larger individuals would be able to displace smaller ones (5.3).

During the months when least basking takes place lizards tend to keep to the ground even more than during the rest of the year (Figures 5.10 and 5.11). This is so before and after the appearance of the young in August. The general trend towards higher perches largely follows the growth of the herbaceous vegetation in the autumn. This development of ground cover will require lizards, which now need to bask more as temperatures and solar radiation decrease, to rise higher, above the vegetation, in order to bask. Vertical and sloping surfaces will then become more important as the sun gets lower in the sky (8.3). The 15/25 cm height (height class 2) which is the most used in March (Figure 5.10) and by juveniles in November (Figure 5.9) and in periods A and L (Figures 5.11 and 5.12) is in fact just around the maximum height of the Oxalis/grass vegetation predominant in the habitat.

Wall lizards were never seen high in trees in the transect area and only rarely elsewhere. Where rocks or gravestones were absent the lizards could be seen on tree trunks at similar heights to those recorded here.

In Bruce's Firebreak the distribution of available heights was similar to that in North Front Cemetery. The stone wall, which has cracks to provide refugia,was about 60 cm tall, similar to the height of the gravestones at the Cemetery. Rocky outcrops to 200 cm and trees to 300 cm added vertical extent to the habitat. *P. hispanica* again made considerable use of the ground, but only close to the stone wall, and rarely in the vegetation away from this. This effectively reduced the ground available to the wall lizards, which may have contributed towards their making use of higher areas on the walls and on tree trunks. There are records for this site of lizards above 150 cm and 34·4% of observations were above 30 cm from the ground (Figure 5.13) as opposed to 20·4% for North Front Cemetery *P. hispanica*.

It is likely that this restriction of the species to the wall area and the consequent use of higher surfaces (perhaps more typical 'wall lizard' behaviour : Salvador, 1974) is due to the presence of *Ps. algirus*. The latter species is restricted to the lower areas below 25 cm (Figure 5.13). *Ps. algirus* can compete for food with *P. hispanica*. Young *Ps. algirus* have similar head dimensions to *P. hispanica* (4.1). Large *Ps. algirus* can take items of food which can also be used by adult *P. hispanica*. Adult *Psammodromus* have been seen cannibalising their young and so presumably can eat young *P. hispanica* also. They have on occasion been seen chasing adult wall lizards. While an even larger lizard, *Lacerta lepida*, is found in North Front Cemetery, this species is so rare there that direct or indirect competition between this and *P. hispanica* is likely to be negligible.

Both adult and juvenile *Ps. algirus* were seen regularly in the garrigue vegetation of the firebreak. Mellado Camacho (1980) found that in Doñana adults kept to dense matorral while juveniles shifted to other more open areas. *Ps. algirus* in the firekreak was found mainly in and around the scattered low shrubs although, especially but not exclusively in spring when vegetation was more dense, they could be seen foraging throughout the area. A close watch was kept for the species in adjacent matorral, but sightings were few.

Historically, no matorral existed on the Rock for about 200 years from the early 18th Century (1.3.2), a fact which may have forced *Ps. algirus* here to adapt to living in open areas of vegetation as still exist in the firebreaks.

The differences in the relative lengths of the hind leg can give an indication of different ways of exploiting space. Thus terrestial species that forage in the open between shrubs and/or grass clumps generally have longer hind legs (Pianka, 1973). This suggests that Ps. algirus (hindleg:foreleg ratio = 1·50) does in fact exploit open spaces rather than dense vegetal cover (Mellado et al., 1975). Those species that forage closer to cover or within dense clumps have proportionally shorter hind legs. This supports the observation that P. hispanica forages within the cover of vegetation, its hindleg:foreleg ratio (1·33 - 1·41) being smaller than for Ps. algirus. Although the difference is not statistically significant, the indication is that Bruce's Firebreak wall lizards have a smaller ratio than those in North Front Cemetery (Table 5.2(a)). This may suggest a shift in this species towards greater use of dense cover due to the presence of Ps. algirus in the open areas.

The result which shows large P. hispanica have greater hindleg: foreleg ratios than smaller ones suggests that the larger lizards make more use of open spaces than do young ones. This is supported by observations discussed in Chapter 7 .

Ps. algirus elsewhere are lizards of dense vegetation (Mellado et al., 1975) and slightly arboreal (Andrada, 1979). In Gibraltar I have only once observed an individual (an adult) climbing a tree. Pianka (1973) states that arboreal lizards tend to have slender, long-tailed forms. In fact, the Spanish name for Ps. algirus is 'Lagartija Colilarga' or 'Long-tailed Lizard'. The mean tail:SVL ratio for the Bruce's Firebreak sample is 2·62 (SD = 0·17), compared to 2·01 (SD = 0·40) for P. hispanica from the same site ($P < 0{\cdot}05$, Kolmogorov-Smirnov test). Unfortunately there are no published data giving this ratio for either species to allow comparison. It would be interesting to know whether the Gibraltar population, which appears to climb less, shows a smaller ratio than do mainland populations.

5.3 Social behaviour

5.3.1 Introduction

Lizard social behaviour has only recently begun to receive serious attention (Brattsrtom, 1974). Work has included some on Gekkonid lizards (Marcellini, 1977) and on Anolis species (Stamps, 1976, 1977; Stamps & Crews, 1976; Stamps & Tanaka, 1981). Relatively little work has been done on social behaviour in lacertids (e.g. Boag, 1973).

Stamps & Tanaka (1981) found changes in aggressive and other social behaviour in *Anolis aeneus* according to season (wet vs dry). An alternation of wet and dry seasons exists in Gibraltar also, which additionally has a seasonal change between warm and cool conditions. Changes in social behaviour in response to environmental changes could therefore be expected.

5.3.2 Methods

Because of the large range of topics on which data were required in this study, it was considered most realistic if detailed observations on social behaviour were carried out during one of the transition periods between the seasons. Because of the additional interest of lizard reproductive behaviour, it was decided that these observations be carried out during the winter-to-spring transition (cool-to-warm, scarce food-to-abundant food). Thus, between December 1981 and March 1982, all types of social behaviour occurring between lizards during continuous observations were noted (Table 5.4).

Captive lizards were also observed, one group under winter conditions and another under springtime conditions (3. 3).

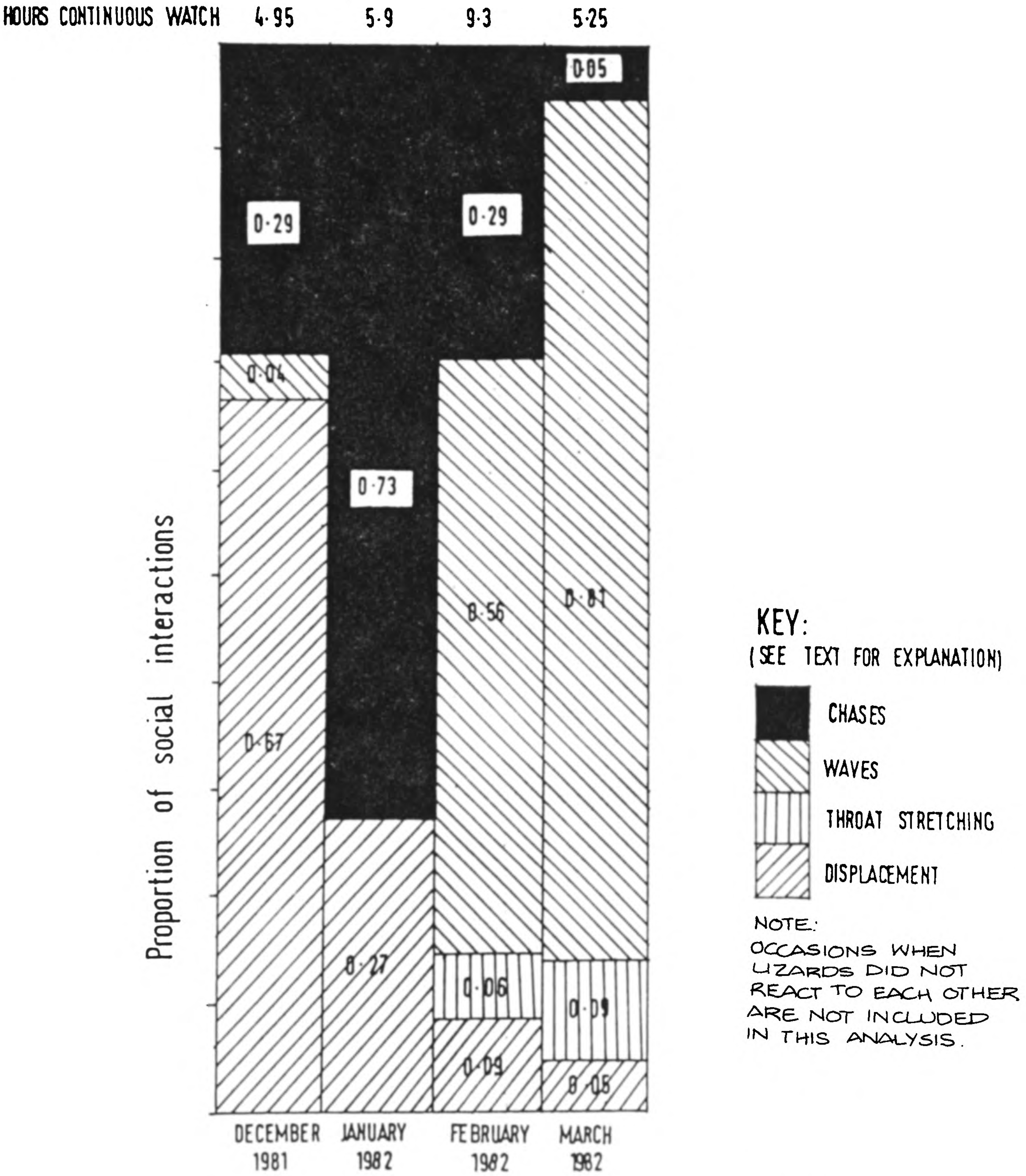
In addition other less-detailed observations will be considered in the discussion section below (5.3.3).

5.3.3 Results and Discussion

(a) Winter

During the initial set of captive lizard observations (January/February 1980) in conditions simulating those in the field in winter (3. 3) lizards showed no aggressive behaviour. The only social interaction was the passive displacement of smaller lizards by larger ones under the heating lamps. Lizards spent the night communally under the stones provided and did not display or attack each other even when active during the day.

Fig. 5.14 BREAKDOWN OF SOCIAL INTERACTIONS OF P.hispanica AT NORTH FRONT CEMETERY SITE GIBRALTAR DECEMBER 1981 - MARCH 1982



$\chi^2 = 61{\cdot}39$

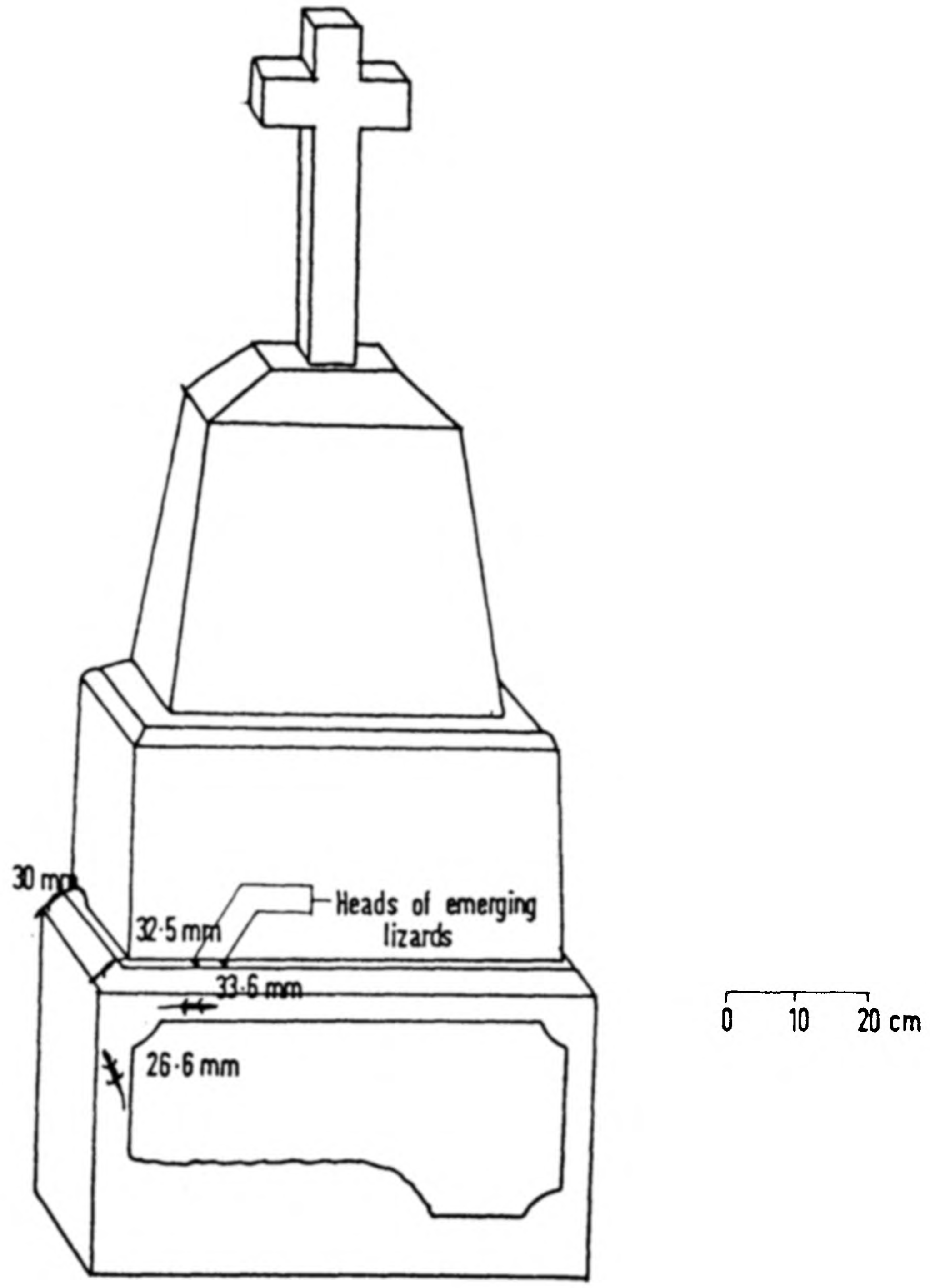
$P < 0{\cdot}001$

This behaviour was comparable to that observed in wild lizards at North Front Cemetery, where conditions on occasion did become somewhat warmer than in the Oxford vivaria. Figure 5.14 (explained fully below) shows that the most frequently observed social interactions between lizards in the field in December were passive displacements (67% of observations).

At the N.E. Wall site (3.1.4) up to five lizards were seen emerging each morning from the same crack. At the 'Cross' site (3.1.4) up to six lizards were seen emerging from the same crack (Figure 5.15). These included individuals of SVL 30-40 mm up to 50+ mm. There was no aggressive behaviour observed during the early hours when basking was in progress, lizards sometimes basking one upon the other (this was also observed at other sites, in the evening, and in captivity). Passive displacements, always of smaller lizards by larger ones, irrespective of sex, did take place. Chasing was observed during the warmer periods of the day once the lizards had started to forage. On the coldest days, lizards would not enter the foraging stage, but remain basking close to their refugia throughout most of the day. It would seem to follow that during cold months, lizards will congregate in areas where refugia in exposed open areas allow basking close by (and warming of the refugia by the sun in the morning). The proximity of good foraging ground should also be an advantage since the lizards will not have to move far from the refugia. This may be of additional importance at a time of year when clouds could obscure the sun and cause a drop in temperature which would force the lizards to return to their refugia.

There appear therefore at this time to be no defended home ranges, and lizards are tolerant of each other around the basking site early in the morning. The social structure of the lizards is hierarchichal, the dominance relationship being related to the snout-vent length of the lizard. Such hierarchies are normally induced by crowding (Brattstrom, 1974). Aggregations in "winter retreats" have been mentioned by Brattstrom (1974) (see Appendix 4).

Fig. 5.15 POSITION OF EMERGING AND RECENTLY-EMERGED LIZARDS AT 'CROSS SITE' AT NORTH FRONT CEMETERY GIBRALTAR AS AT 10·50 HRS ON 2ND DECEMBER 1981.
(FIGURES GIVEN ARE SNOUT-VENT LENGTHS)



(b) Spring

As the spring approaches, the number of chases as a proportion of total social interactions (Figure 5.14) increases to 73% in January as opposed to 27% passive displacements. This may result either from a change in tolerance of the lizards (with increasing temperatures ?) or as a result of a decrease in basking time and an increase in foraging time (8.3), which leads to a greater number of aggressive encounters. However, the impression is that there is an increase in the number of chases taking place at the initial basking sites. This increasing aggression would tend to result in the spreading out of the lizards away from the winter communal refugia (see 5.2). By the end of January a maximum of only three lizards were to be seen emerging from the N.E. Wall crack, and two from the 'Cross' site crack.

The captive lizards kept in April and May under conditions simulating the spring (3.3) also showed some reluctance to spending the night communally, unlike the winter captives. No regular sleeping sites were noticed for individual lizards, but some tended to sleep away from the main stones (under which the larger lizards usually slept), under loose pebbles or among dry grass elsewhere in the vivarium.

When lizards were first introduced into the large vivarium (70cm x 40cm x 40cm) in early April, there was no clear ranking between the adult males. Females and immature males displaced each other according to SVL. Interactions between adult males were noticed during the first three days. Males UM (SVL = 54mm) and 07 (SVL = 50mm), for example, were seen to meet and both to retreat; UM displayed its throat at male 06 (SVL = 52•5mm) which retreated; male 06 later displayed its throat at 07 and male W6 (SVL = 45mm), both of which withdrew. Similar interactions between the adult males continued for some days. By the fourteenth day, male 06 was established as the dominant male or tyrant (Brattstrom, 1974). Thus 06 chased the other males and did not tolerate them within his sight. The subordinate males tolerated the presence of each other.

The females rarely showed aggressive behaviour, and continued to displace each other, and smaller males, according to snout-vent length.

After six weeks as tyrant (8 weeks after entering the tank), 06 was removed. Male 07, which had on two occasions been seen to have been tolerated close by (< 5 cm) 06, assumed the tyrant role almost immediately, mating with the females and chasing males. It was also able to increase body weight (6.4).

In another vivarium, males 01 (SVL = 51mm) and W5 (SVL = 51mm; with bright orange underparts) were placed together. In this case, despite W5's bright underparts, 01 soon imposed its authority. This was, however, after considerable fighting. Fighting continued after this since 01 would chase W5 whenever it came into sight and the latter was not always able to hide. On one occasion W5 lost its tail and was almost killed, apparently as the result of a bite on the side of the chest. W5 them became extremely submissive, hiding under stones, and was eventually removed to another tank.

It is a common observation that lizards become hierarchical in the laboratory even if they are not so in the field (Carpenter, 1967; Brattstrom 1971). The situation is somewhat similar to that in the field in winter when lizards become crowded in suitable areas. The difference is that, as was clearly observed, males are much more aggressive in the spring.

A number of specific behaviours were seen in P. hispanica particularly at this time. The proportions of the different interactions observed from December to March in the field are given in Figure 5.14.

(i) Displacement

These were the passive displacements of individuals by larger ones. A small lizard would move away on the approach of a a larger one, either into vegetation, or some distance away. This behaviour usually avoided any aggression and therefore minimised the expense of energy. It may be disadvantageous to the displaced lizard if it is a prime basking site that is ceded to a larger individual.

Displacements of this type were observed throughout the year. It was used throughout by females and usually by younger males. This behaviour was also typical of adult males in winter (December) (few adults were seen in summer).

Figure 5.14 shows that displacement was the most common form of interaction observed in December (67% of observations) and became progressively less important through January (27%), February (9%) and March (5%). Alternative forms of behaviour increased in importance.

(ii) Chasing

In December displacement was effective in preventing open aggression. On 29% of the observed lizard-lizard contacts however, a chase occurred. Chases were initiated either when a larger lizard approached a smaller one unseen (the smaller one therefore failed to move away), or when the larger lizard actually chased the displaced lizard after the latter had moved away. The chase was usually short, of under 50 cm, and ended when the chased lizard had disappeared into vegetation. The larger lizard usually returned to the site vacated by the smaller one when this had been basking. Chases became more frequent in January (73% of observations). They were always of larger animals chasing smaller ones.

(iii) Waving

Carpenter et al. (1970) and Brattstrom (1971) reported what they considered to be a unique waving submissive behaviour in Amphibolurus barbatus and related Australian Agamids. P. hispanica shows a similar submissive behaviour. Lizards encountering or approached by a larger lizard will stop and rapidly (not slowly as in A. barbatus) wave either or both forelegs directed towards the specific individual. Waving behaviour has also been observed in a lizard while moving around a basking larger lizard.

This behaviour was observed 62 times and was successful in preventing aggressive behaviour on all but five occasions. The waving was usually followed by the smaller individual moving away, and its effect seemed to include the preventing of a chase following displacement.

Some waving was observed in December, but there was a great increase in the incidence of this behaviour in February (56% of observations) and at the same time a reduction in the frequency of chases (29% of observations). The trend continued into March when 81% of observed social interactions were waves with only 5% each of chases and passive displacements.

It would appear that waving is an efficient method of avoiding intraspecific aggression. On one occasion a young lizard was seen to wave - unsuccessfully - at a large Tarentola mauritanica. On another occasion, another young P. hispanica waved as I approached it to within 5 cm.

Waving is therefore more widespread than previously thought

(I have observed it in <u>Gallotia gallotia</u> in Tenerife also) as a submissive gesture in lizards.

(iv) <u>Throat-stretching</u>

Lizards would sometimes show aggression by laterally compressing the throat region, stretching the throat downwards, and raising the neck to display the throat. The displaying lizard would then approach the other slowly. This display was used most evidently by adult males, towards other adult males or towards females but was twice seen to be used between two similar-sized immature males in captivity. In captivity also a female was seen to display her throat in this way at a smaller female in an apparent attempt to displace her from a prey item.

It should be noted that the throat is the only part of the underparts of male and female <u>P. hispanica</u> at Gibraltar that is generally coloured (4.2).

Throat displays were never frequent, but most were observed in March. In all cases observed they resulted in the lizard being approached moving away.

(c) <u>Summer and autumn</u>

Observations in summer did not result in any record of throat-stretching or waving. This may have been partly due to the fact that few adult lizards were seen during this time. Hatchling lizards show little aggression towards each other. What interactions were seen during summer and autumn months were displacements, parallelling the behaviour of the lizards in winter (despite the much higher temperatures).

Aggressive behaviour, then, occurs throughout the year, but is most marked in males in the mating season (late winter-early spring). It is at a minimum when the lizards are aggregated, especially during the cold winter months (and times of day, as when they are basking early in the morning).

As aggressive behaviour in the form of chases and throat stretching increases with the arrival of spring, so submissive behaviour - waving - increases also.

Such submissive behaviour, rarely seen in males, reduces aggression. Young lizards and females will therefore be able to remain close to males while other males, to which aggression is largely directed, will be kept away. Adult males would therefore be expected to keep fairly exclusive home ranges in the spring, while tolerating females and young lizards within these.

5.4 Home ranges

5.4.1 Introduction

Most species of lizard are territorial to some extent during the breeding season even if, when crowded, hierarchical systems can be set up (Brattstrom, 1974). In the non-breeding season, most species use home ranges as feeding areas. The size of home range and territory may depend on a number of factors, such as density of lizards and food abundance (Simon, 1975) and may change in response to changes in these factors. Density of lizards may in turn depend on the degree of aggression between lizards and on the availability of suitable areas of microhabitat within the lizard's habitat.

The results of the preceding section led to a suggested home range structure for P. hispanica (5.3.3) similar to that recorded in spring and summer for other lizards, including Podarcis muralis (Boag, 1973). The continuous observations being made at this time (late winter/spring 1982) on marked lizards (3.2) provided an opportunity to investigate whether this was in fact so.

5.4.2 Methods

Transect observations were unsuitable for attempting to establish the area of lizard home ranges. Few lizards were marked and those that were were not frequently seen. Therefore data from continuous observations of marked lizards were used. Those most suitable for this study were the N.E. Wall lizards (1.5) which were often visible for long periods, were relatively easy to catch, and could be approached to within several metres. Somewhat greater difficulty was encountered in following the 'cross' site lizards, which foraged in dense grassy vegetation.

At N.E. Wall, six marked lizards, four males (SVL = 53•5mm, 47•0mm, 41•5mm and 33•5mm) and two females (SVL = 36•5mm and 36•0mm) were followed (Table 5.4). A number of other lizards were only seen briefly after marking. Unmarked lizards were also followed when marked ones were not visible, but the data from these could not be reliably used since subsequent observations could never be attributed to the same individual. In addition, there was always doubt on these occasions as to whether a similar lizard emerging from a patch of vegetation where another had disappeared was in fact the same individual.

The marked lizards were followed from when first observed until lost from sight for over 10 minutes. The N.E. Wall site was conveniently divided by the gravestones above (Figure 5.16) which were numbered T1 to T8 ('Tombstone 1' to 'Tombstone 8') from left to right. The width of each gravestone was mentally divided into ten equal divisions. Thus a lizard seen midway along gavestone 4 was recorded as being at T4•5. Similarly the wall was divided downwards into ten, providing a full set of co-ordinates. If the above imaginary lizard at T4•5 was three-quarters of the way down the wall, it would be recorded at being at T4•5,D0•75 (Tombstone 4•5, Downwards 0•75). This allowed quick and accurate annotation of the position of lizards after each movement.

These records were then plotted on a scale plan of the wall. The area covered by each lizard was calculated using the convex polygon method (reviewed in Ford & Myers, 1981).

Ford & Myers (1981) evaluated and compared the four main techniques for estimating home ranges. They found that the probabilistic techniques of Jennrich & Turner (1969) and Ford & Krumme (1979) gave results closer to their 'real' estimates than did the minimum convex polygon technique. A main failing of the last technique was considered to be the large number of observations required before accuracy could be approached in the estimates of home range.

In this study, the observations on P. hispanica used were continuous and not disjunct. The paths used to move between each point were largely known, and included within the home range polygon. Ford & Myers (1981) obtained a relationship between estimated area and the number of observed locations necessary to approach a uniform realistic value for home range. For the convex polygon method, the true area was approached at 200 observed locations at one-minute intervals. Lizards W6 and W8 were seen for 295 and 455 minutes respectively (Table 5.4), with about 200 locations plotted for them on the N.E.Wall map. It can be assumed therefore that the results approached the actual value of area covered during the periods of observation.

An additional point to note is that the Jennrich-Turner method would produce an elliptical home-range estimate which may be realistic in size (but probably too large - Ford & Myers, 1981), but in shape

Table 5.4 Observed home ranges for six P. hispanica at N.E.Wall site, North Front Cemetery, Gibraltar (1982).

(Home range estimated by convex polygon method, corrected for slope (see text).)

Lizard code No.	Sex	SVL(mm)	No. of continuous observations	Range of dates of observations	Time seen (min)	Corrected Home Range(m^2)	Rank of Home Range
B6	♂	53•5	3	28.2- 3.3	62	7•79	1
W8	♂	47•0	8	28.1-28.2	455	4•86	3
W6	♂	41•5	9	9.1-11.3	295	5•72	2
B4	♀	36•5	5	24.2- 2.3	176	2•56	5
B5	♀.	36•0	1	24.2-26.2	60	2•76	4
B3	♂	33•5	1	31.1	32	1•55	6

would probably approach reality only in an area of uniform habitat. In the N.E. Wall site, the area of suitable habitat is delimited by unusable bare areas above and below the wall. Bearing in mind all the above, it was considered that the direct-observation convex polygon method would be suitable in this case.

Since the wall was not vertical, but at a gradient of 1·3:1, the values of the areas calculated from the maps were multiplied by 1·3 to give a corrected estimate of surface area covered.

5.4.3 Results

The convex polygons used to estimate the home range of the lizards listed in Table 5.4 are illustrated in Figure 5.17. These have been superimposed on each other in Figure 5.18 which gives also the location corresponding to T4 in Figure 5.16. A crack ran along the top of this 'Tombstone 4' (T4) which provided refugia for a number of lizards.

Table 5.4 summarises the results of the calculations of home ranges. The largest value was for the large male B6 (7·79m^2), despite it having been tracked only on three occasions (total 62 minutes). The immature male B3, only once followed, showed the least area covered (1·55m^2; 32 minutes). Females B4 and B5, tracked for 176 and 60 minutes respectively, had small ranges also (2·56 and 2·76 m^2 respectively). Small males W6 and W8 despite being watched for 295 and 455 minutes respectively, had smaller home range estimates than B6 (5·72 and 4·86 m^2).

Figure 5.18 shows that all the home ranges included the communal refugium at T4. (The corner of T4 also dripped water for some days after rain, and lizards could be seen drinking from the wet stonework.) The area used by B6 included most of the N.E. Wall. Those used by the other lizards fell almost totally within this area and overlapped largely, especially around T4.

Observations at the 'cross' site did not allow similar treatment to the above. Lizards in vegetation were not visible, and so marked animals could only be seen at their basking sites, within 1·5 m of the central Cross (1.5). It was obvious however that here also there was total overlap in basking sites and great overlap in foraging areas around this main basking site.

Fig. 5.16 N.E. WALL SITE, NORTH FRONT CEMETERY GIBRALTAR.

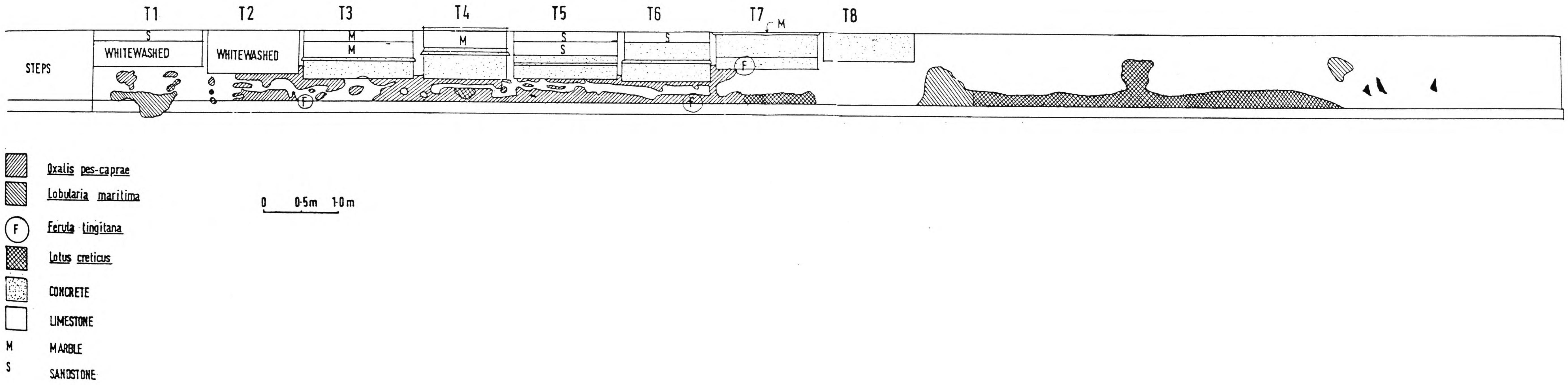


Fig. 5.17 HOME RANGES OF 6 LIZARDS AT N.E. WALL NORTH FRONT CEMETERY, GIBRALTAR. (LOCATION OF T4 OR T6 GIVEN - FIG. 5.16)

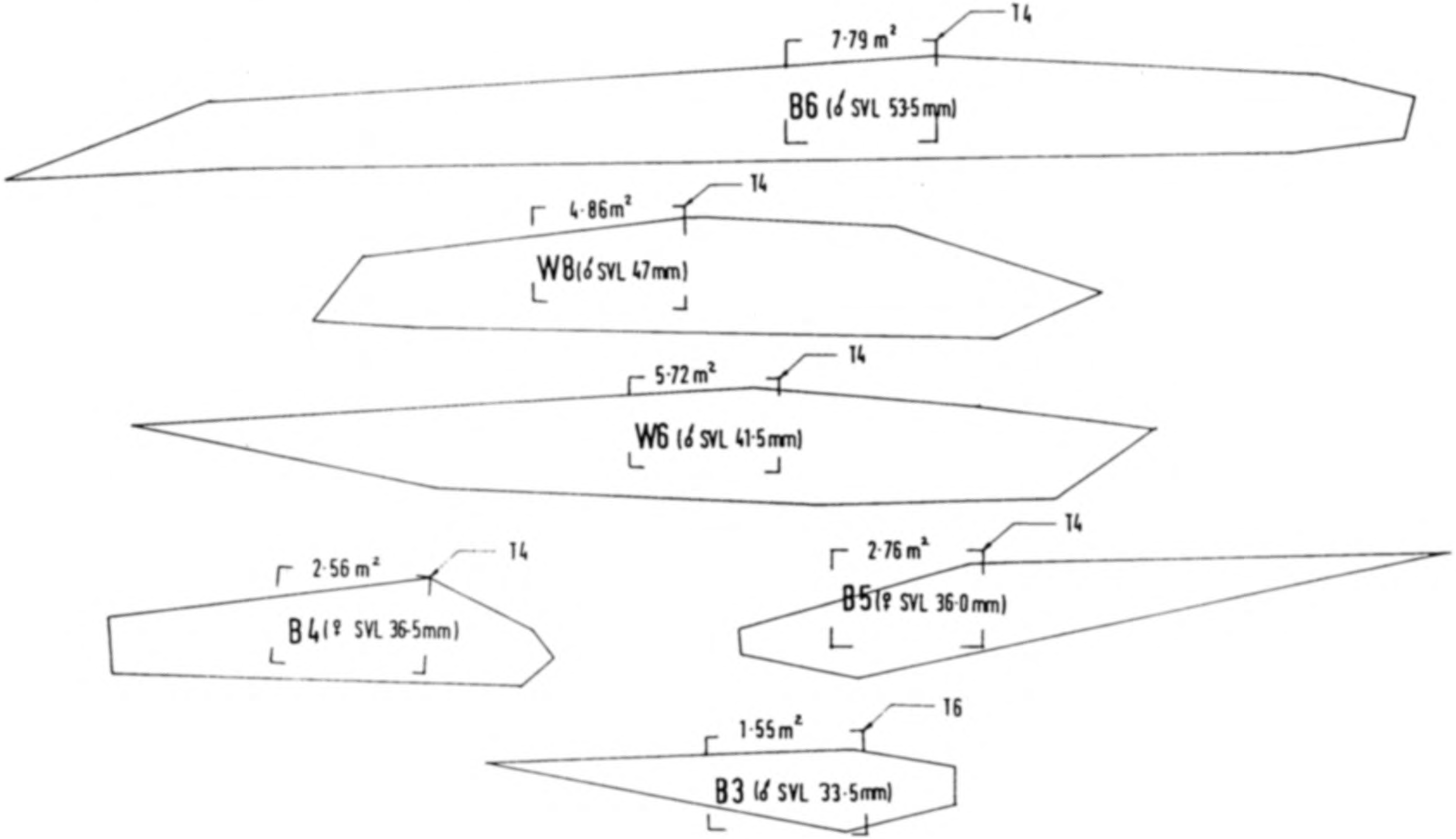


Fig. 5.18 HOME RANGES OF 6 LIZARDS AT N.E. WALL SITE NORTH FRONT CEMETERY GIBRALTAR (SUPERIMPOSED)

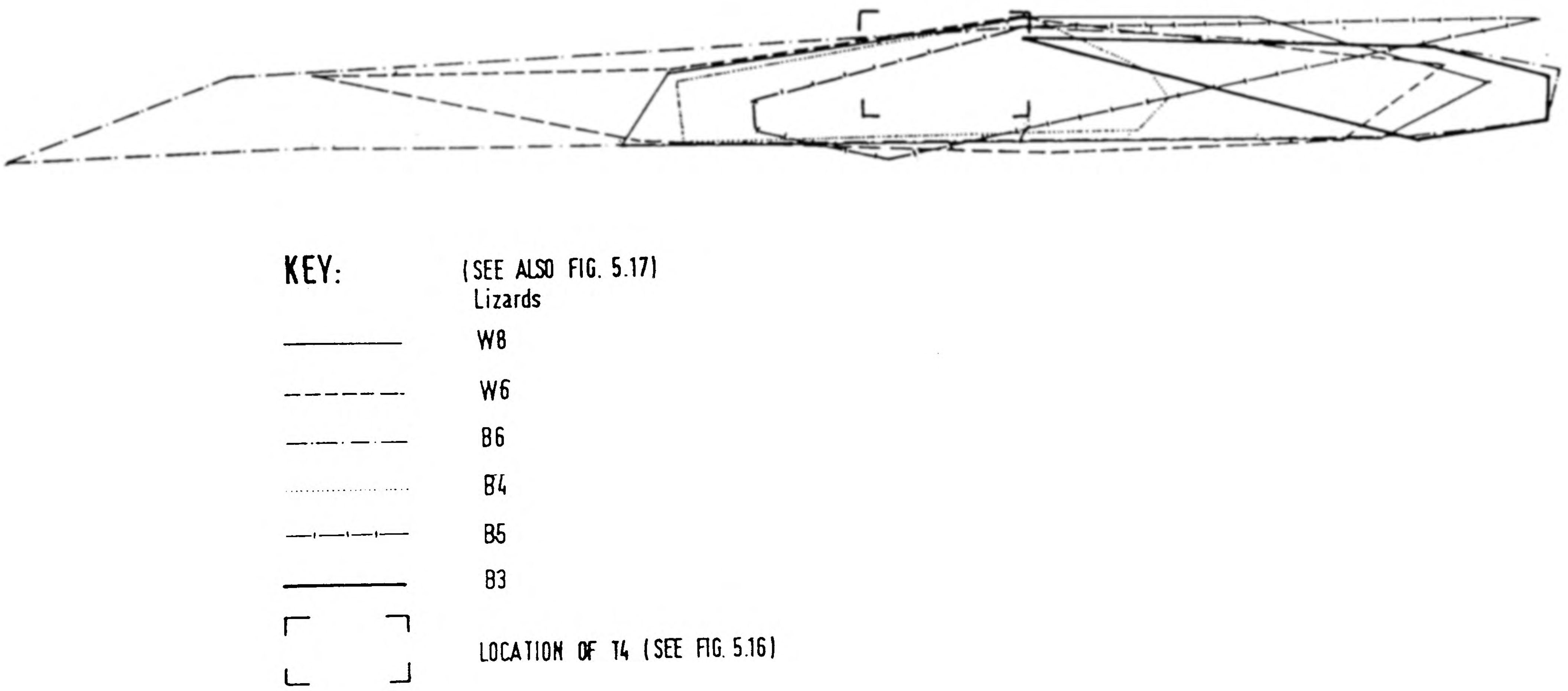


Table 5. 5 **Estimated** number of <u>P. hispanica</u> at N.E. Wall site, North Front Cemetery, Gibraltar between 11.00 and 14.00 hrs, January - March 1982.

Date	No. of lizards of approximate SVL 30	30-40	40	40-50	50+	Total No. of lizards
20.1.82	0	2	4	1	1	8
21.1.82	6	5	2	1	0	14
23.1.82	1	1	1	2	0	5
28.1.82	0	0	1	1	2	4
3.2.82	0	1	2	0	0	3
17.2.8	0	1	1	2	0	4
18.2.82	1	0	2	0	1	4
3.3.82	0	1	2	1	1	5
12.3.82	0	1	1	0	1	3

Observations at the cross site were mainly in November and December, while those at N.E. Wall were from January to early April.

The marked lizards at N.E.Wall were seen for different lengths of time during the study period (Table 5.4). This did not necessarily mean that after a lizard stopped being seen it had left the study area. Colour marks would be shed on sloughing.

There was an apparent drop in the number of lizards using the N.E. Wall as the season progressed. An indication of this is given in Table 5.5. Up to 14 lizards were seen at a time in the site in January, while not more than 5 were seen on days in February and March.

In total 50 lizards were caught and marked within a 200 metre radius of N.E. Wall between November 1981 and March 1982. Despite this, on no occasion were marked lizards seen more than 10 metres away from their point of capture. This was true also at other sites, including the North Front Cemetery main transect site and Bruce's Firebreak.

5.4.4 Discussion

Several types of home ranges and territories have been described for lizards. In some species adults and juveniles defend territories against lizards of the same species, size and sex (Simon, 1975). In other species, males keep harems (Stebbins et al., 1967; Berry, 1971). Some lizards show a strong relationship between home range and body size, explained by different authors as being due to food needs, costs of obtaining food, and food densities (McNab, 1963; Schoener, 1968; Turner et al., 1969; Harestad & Bunnell, 1979). Schoener & Schoener (1982) related home range to body size differences within four species of Anolis.

Boag (1973) provides the only published study of home range in a Podarcis lizard. His work on P. muralis during several summers in a garden in Italy suggests males keep overlapping terrirories with defended sunning sites which include territories of several females. The average territory size of males and females combined was $25m^2$. This was considerably greater than the largest home range estimated for Gibraltar P. hispanica. P. muralis is larger than P. hispanica with a mean snout-vent length of 73mm for males and 64mm for females (Boag, 1973).

In fact the home ranges calculated for P. hispanica are smaller than those recorded for most lizards. They are close to the mean home range size of Anolis sagrei (Schoener & Schoener, 1982) ($3{\cdot}7m^2$, SD = 1·5 for A. sagrei; $4{\cdot}2m^2$, SD = 2·3 for P. hispanica). Home ranges of island lizards are small. Minimum convex polygons for adult male Anolis lineatopus in Jamaica average between 2·5 and $16{\cdot}8m^2$ for adult males and 0·56 to 3·3 m^2 for adult females (Rand, 1967). This phenomenon, common to other small island anoles, is generally accompanied by higher lizard density. The P. hispanica population of Gibraltar, and specifically of North Front Cemetery, is effectively an island one, since the Cemetery is surrounded by unsuitable habitat (1.3). Lizard density increases when the quality of the habitat increases, so that home ranges will be reduced provided there is sufficient food. Food is at a maximum in February - March when the home ranges were calculated (7.4). It is also locally abundant in isolated bushes in the summer (7.4). This would then tend to produce small, overlapping home ranges in the vicinity of these bushes, leading to the concentrations of animals described in 5.2. Local 'abundance' of another resource - refugia - could, provided foraging grounds are available, lead to similar concentrations in the winter.

Intraspecifically, it appears that large male P. hispanica have the largest home ranges. Unfortunately, it was impossible to determine whether B6 (Table 5.4), caught on 28.2.82 was the same large male seen on N.E. Wall since January (Table 5.5) and after 3.3.82. Thus, it was only definitely seen in the area for four days. Nevertheless, in 62 minutes of watching it covered the greatest area of all the lizards. This suggests a truly large home range (Figure 5.17) in relation to the other lizards. The other males (W6 and W8) had smaller home ranges calculated despite considerably longer watches (295 and 455 minutes). All the males' areas overlapped each other . Male B6 used all the available habitat on the wall while the smaller lizards used only part of it. This could reflect food requirements (the larger lizard requiring more food or rarer (larger) food items) or could be a result of greater aggressive behaviour on the part of the larger lizards.

The females B4 and B5, observed for shorter total periods

(176 and 60 minutes respectively) had smaller home ranges than the males (2·56 and 2·76 m^2). Female home ranges have been known to be smaller than, and fall within male home ranges, in a number of species, including P. muralis (Boag, 1973).

Of all the lizards marked, only four were followed on more than one occasion and, except for B6, were seen to remain on the Wall for some considerable time (at least 2 months for W6). Some lizards were only seen on the day they were caught, or for only several days after this. While they may have shed their marks and remained on the site, the impression created, both on N.E. Wall and at the 'cross' site, was that there were a number of resident lizards as well as a number of wandering lizards which just passed through the area. This was observed by Boag (1973) in P. muralis.

The above results and discussion suggest an overall pattern of use of space by P. hispanica. During spring they use all available micrphabitat, foraging mainly on or close to the ground. The distribution of the lizards through the habitat is aided by an increased aggression between individuals. In summer, as productive areas are reduced to the vicinity of bushes and shrubs, animals tend to emigrate to areas of high resource abundance (Stamps & Tanaka, 1981). On the appearance of hatchlings in mid-to-late summer, these tend to use the ground more than the adults do. This division of the space resource remains noticeable throughout the year.

Division of resources into use of more dense areas by juveniles is suggested by the latter's smaller hindleg:foreleg ratio. This division of resources may be especially important in summer when food supplies are restricted.

Aggression is low in summer. As conditions get cooler and wetter, lizard aggregations are found in areas which provide refugia, as long as these are close to foraging areas (e.g. lizards were rarely seen at the N.E.Wall in the summer before the Oxalis vegetation recommenced its growth after the autumn rains). The lizard's basking sites get higher and there may be displacement of juveniles downwards. Lizards are tolerant of each other in winter, particularly during early morning basking.

Chasing of lizards, especially by large males, increases as spring approaches. Submissive behaviour becomes more important and is probably partly responsible for allowing smaller males (and females) to remain within adult male home ranges. This may even allow them to mate with females, as young males have been seen to do in captivity (6.5).

Dominance of males appears to be most commonly determined by snout-vent length and not by belly colour. It does appear, however, that dominant males, in the field and in the laboratory, look a brighter green than subordinate ones. The lizards may be able to control their body colour, and dull colour may in itself be a form of submissive behaviour.

P. hispanica has a small but notable repertoire of social behaviours which have not been described in any detail for other similar lizards from further north in Europe. Social behaviour may in fact be more important for P. hispanica in general and specifically at Gibraltar, being at the extreme south of Europe. Here the species is active for long periods during the day and throughout the year. This is not the case in the rest of Iberia where P. hispanica is rarely seen in winter and then does not appear to feed (Andrada, 1979). More time is therefore available for social interaction than is the case in lizards in more northerly latitudes which need to spend more time basking (Avery, 1981).

North Front Cemetery is virtually an area with one lizard species. Lacerta lepida is extremely rare and Tarentola mauritanica is nocturnal in summer and almost totally inactive in winter. In spring and autumn, T. mauritanica comes into contact with P. hispanica. A number of aggressive encounters have been observed, invariably resulting in the wall lizard running off. However, at the Bruce's Firebreak site, P. hispanica shares the habitat with another diurnal lizard, Ps. algirus. Results suggest that in the presence of the latter species, P. hispanica, while still foraging in vegetation, is restricted to the proximity of stone wall and uses the vertical dimension to a greater extent - it behaves more like a 'wall' lizard.

CHAPTER 6

POPULATION STUDIES

6 POPULATION STUDIES

6.1 Introduction

Recent work on small European lacertids has suggested these animals live for a maximum of four years (Pirloge, 1982). To arrive at these results cohorts of lizards have been followed over several years using snout-vent length data collected from field samples. Since lizards hatch within a few weeks of each other every year, the cohorts are fairly easy to identify. The data on the size structure of the population have been used in this study as in previous ones to provide information on the population's age structure, growth and the lifespan of individual lizards.

Similar procedures were used in this study to look at the age and sex structure of the population of lizards in question. *P. hispanica* kept in captivity were used to give indications of growth rates and reproductive behaviour.

6.2 Population age structure

6.2.1 Methods

The data used in this section are derived from *P. hispanica* at the North Front Cemetery sites.

Snout-vent lengths were estimated and recorded for lizards seen during transect observations in NFC Site 1. Since accurate measurements were not made, SVLs were recorded according to the following size classes:

Size Class 1 : 20mm
Size Class 3 : 30mm
Size Class 5 : 40mm
Size Class 7 : 50mm

The observed lizards were placed into the size class which was thought to be closest to their true size. In addition, three intermediate size classes were used into which lizards which were thought to fall between two of the above size classes were placed. These were:

Size Class 2 : 20/30mm
Size Class 4 : 30/40mm
Size Class 6 : 40/50mm

Classes 3 to 7 correspond approximately to classes A to E used in 6.5. In the latter section, however, most observations were carried out during months when the smaller size classes were not in evidence.

A χ^2 test was carried out on the size class data arranged according to month of observation. Months were also grouped into December/January; February/March/April/May; June/July; August/September; and October/November. A χ^2 test was carried out on the re-arranged data.

Snout-vent length data from captured lizards were used as a check on the purely observational data and were plotted on a frequency diagram.

Observations were made to cover all times of day (subject to weather conditions).

Table 6.1 Frequency of *P. hispanica* size classes*at NFC Site 1 per month.

Month	Size Class* 1	2	3	4	5	6	7
January	0	2	0	4	0	0	1
February	insufficient data						
March	0	0	4	2	4	7	0
April	0	0	1	2	3	3	4
May	0	0	0	3	6	9	10
June	0	0	0	0	0	5	9
July	0	0	0	0	0	5	5
August	0	24	18	7	6	2	4
September	10	48	59	13	20	8	16
October	2	18	37	18	40	13	28
November	0	5	10	5	31	13	7
December	1	4	5	8	14	3	9

* Size Class	SVL
1	20mm
2	20-30mm
3	30mm
4	30-40mm
5	40mm
6	40-50mm
7	50+mm

Fig. 6.1 PERCENTAGE OF LIZARD SIZE CLASSES OBSERVED AT NFC SITE 1 EACH MONTH (SEE ALSO TABLE 6.1.)

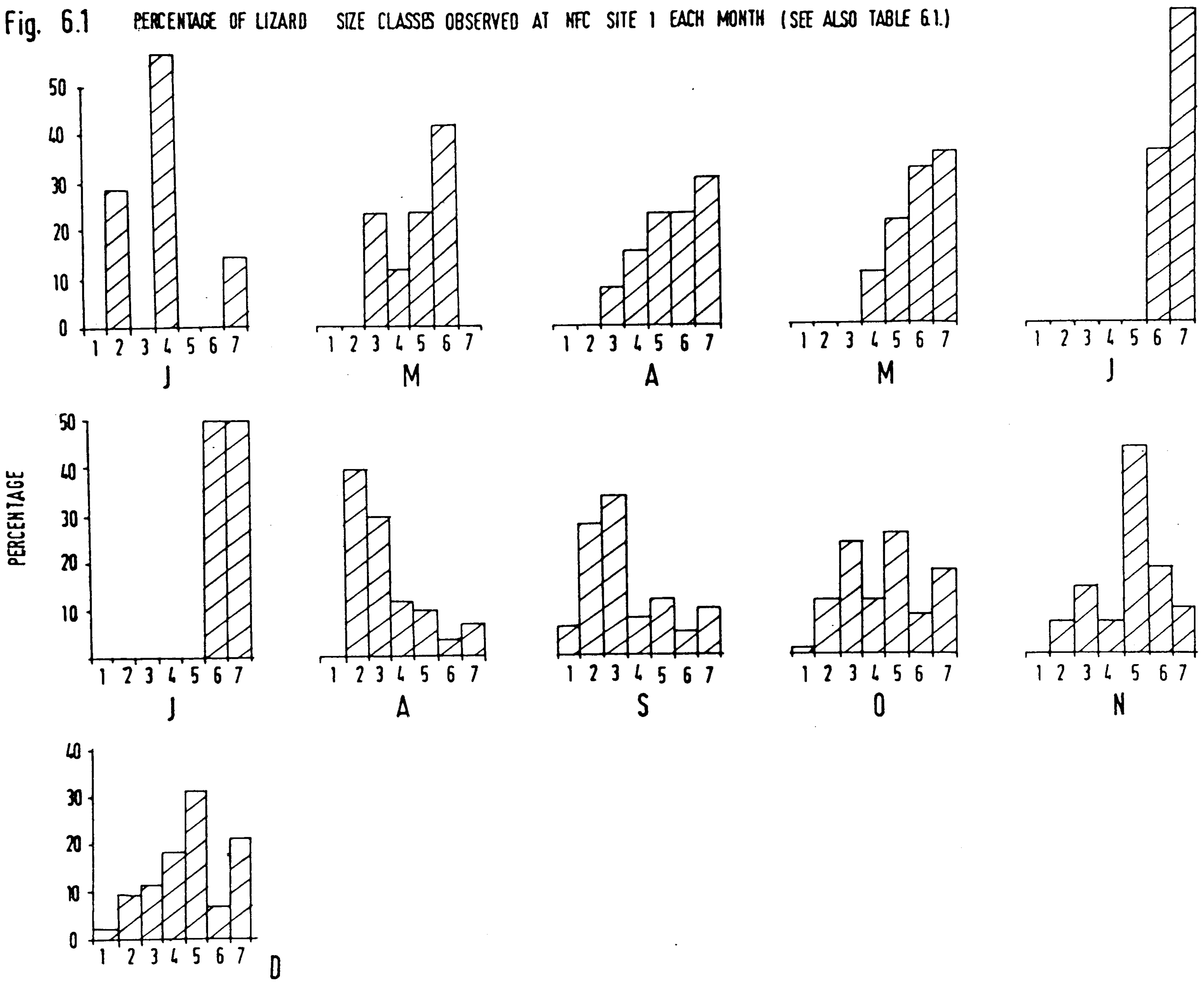


Table 6.2 Frequency of P. hispanica size classes at NFC site per season (see text).

Season*	Size Class 1	2	3	4	5	6	7
A	1	6	5	12	14	3	10
B	0	0	5	7	13	19	14
C	0	0	0	0	0	10	14
D	10	72	77	20	26	10	20
E	2	23	47	23	71	26	35

$\chi^2 = 242.604$

df = 24

$P < 0{\cdot}001$

* Season	Months
A	December/January
B	February/March/April/May
C	June/July
D	August/September
E	October/November

Fig 6.2. PERCENTAGE OF LIZARD SIZE CLASSES OBSERVED AT NFC SITE 1 EACH SEASON (SEE ALSO TABLES 6.3 & 6.4.)

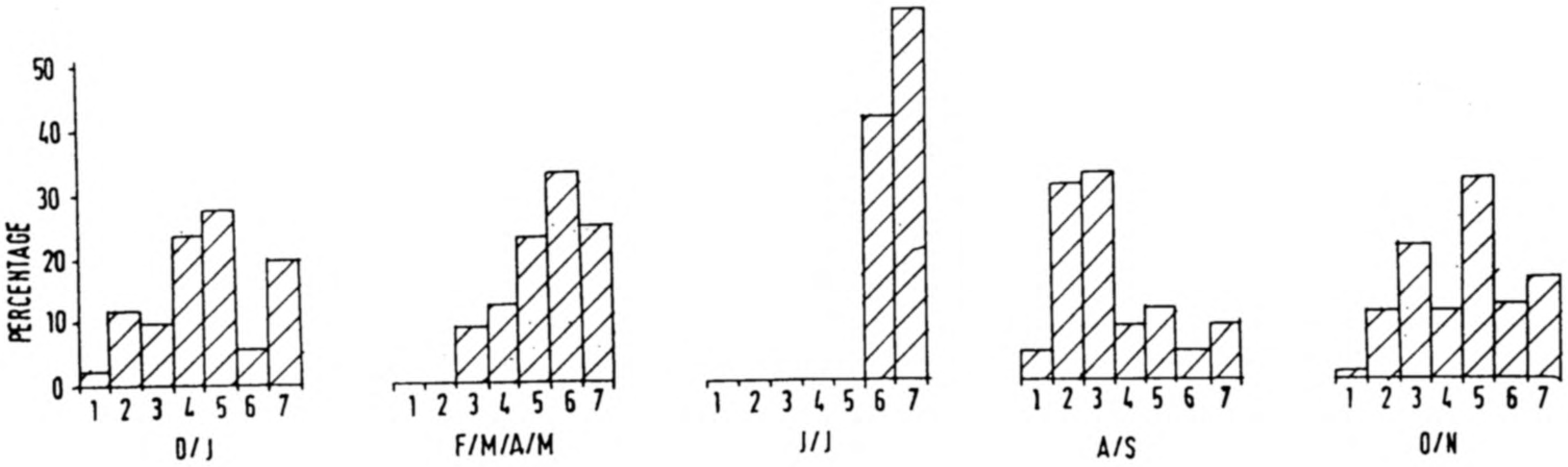


Fig 6.3. PERCENTAGE OF INDIVIDUAL SIZE CLASSES OBSERVED AT NFC SITE THROUGH MONTHS

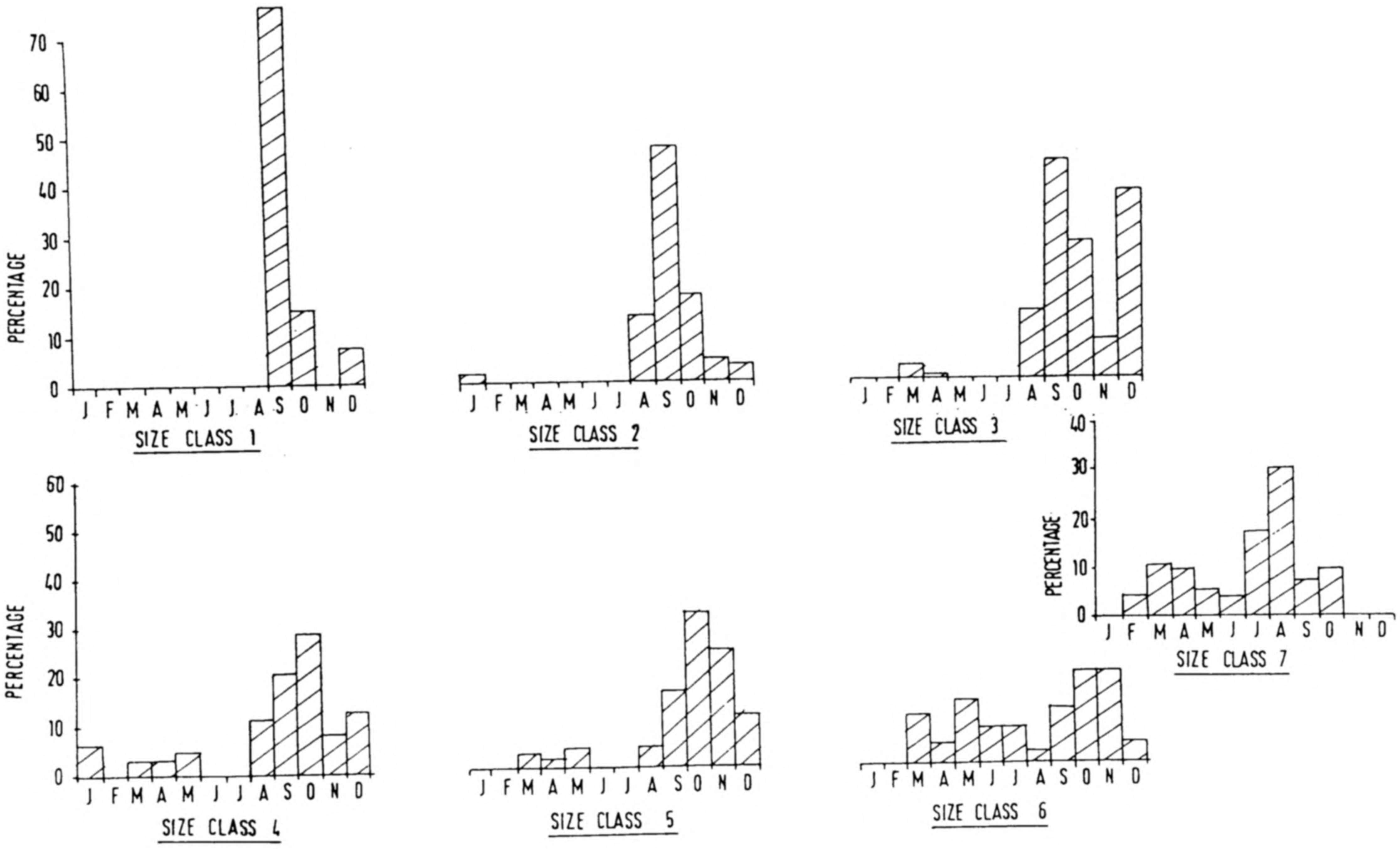
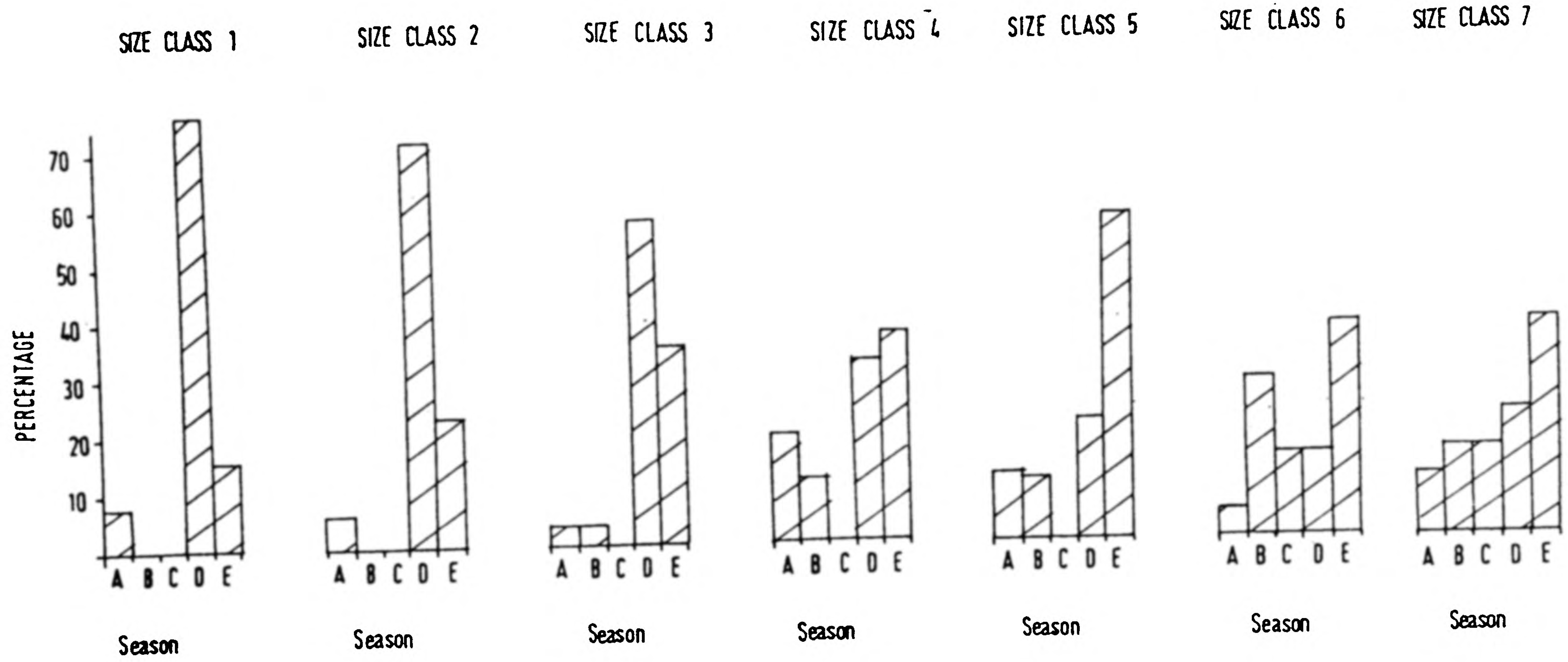


Fig 6.4. PERCENTAGES OF INDIVIDUAL SIZE CLASSES OBSERVED AT NFC SITE 1 THROUGH THE SEASONS

SEASON	MONTHS
A	December / January
B	February / March/April /May
C	June / July
D	August / September
E	October / November



6.2.2 Results

Table 6.1. lists the numbers of lizards allocated to each size class observed in NFC Site 1 during transect observations in 1981/82. Figure 6.1. illustrates these results as histograms showing each size class as a percentage of the total number of lizards seen in the transects each month.

Size Class 1 does not feature prominently in any month. The other small-size classes, 2 and 3, are the most abundant in August and September. Classes 5 and 3 are the most common in October , 5 in November and December when also the proportions of the smaller classes are lower. The pattern in March, April and May is similar in each case, with a predominance of the larger classes but also a presence of smaller lizards. In June and July only size classes 6 and 7 are evident, the situation reverting to a predominance of juveniles in August.

Results for months are grouped and represented in Table 6.2. and Figure 6.2. These reflect the pattern noted from the monthly data - the smaller lizards appear in August and September, there is an increase in the middle size classes in October/November and December/January, and the larger classes increase in relative abundance in February and May. All lizards smaller than those in Class 6 disappear in June/July .

The results of the χ^2 tests are significant both for the data arranged in months ($P < 0{\cdot}005$, Table 6.1) and in grouped months ($P < 0{\cdot}001$, Table 6.2).

Figures 6.3 and 6.4 illustrate the same results as above but for each size class in turn through the year as percentages of the total number of lizards of the size class seen. In all these cases males and females are considered together.

The small size classes were seen to be most common in September and October. Size Class 1 and Size Class 2 decreased towards the end of the year while Size Class 3 remained more common into December. Classes 1, 2 and 3 were seen to be almost totally absent from January to July. Size Class 4 and Size Class 5 increased later than the smaller classes and were more evident during the spring months. The largest lizards are least common in relation to the others during the winter months, and most common in the summer (August for Class 7) and the autumn (October/ November for Class 6).

Fig 6.5. NUMBERS OF LIZARDS CAUGHT AT NFC AGAINST SVL

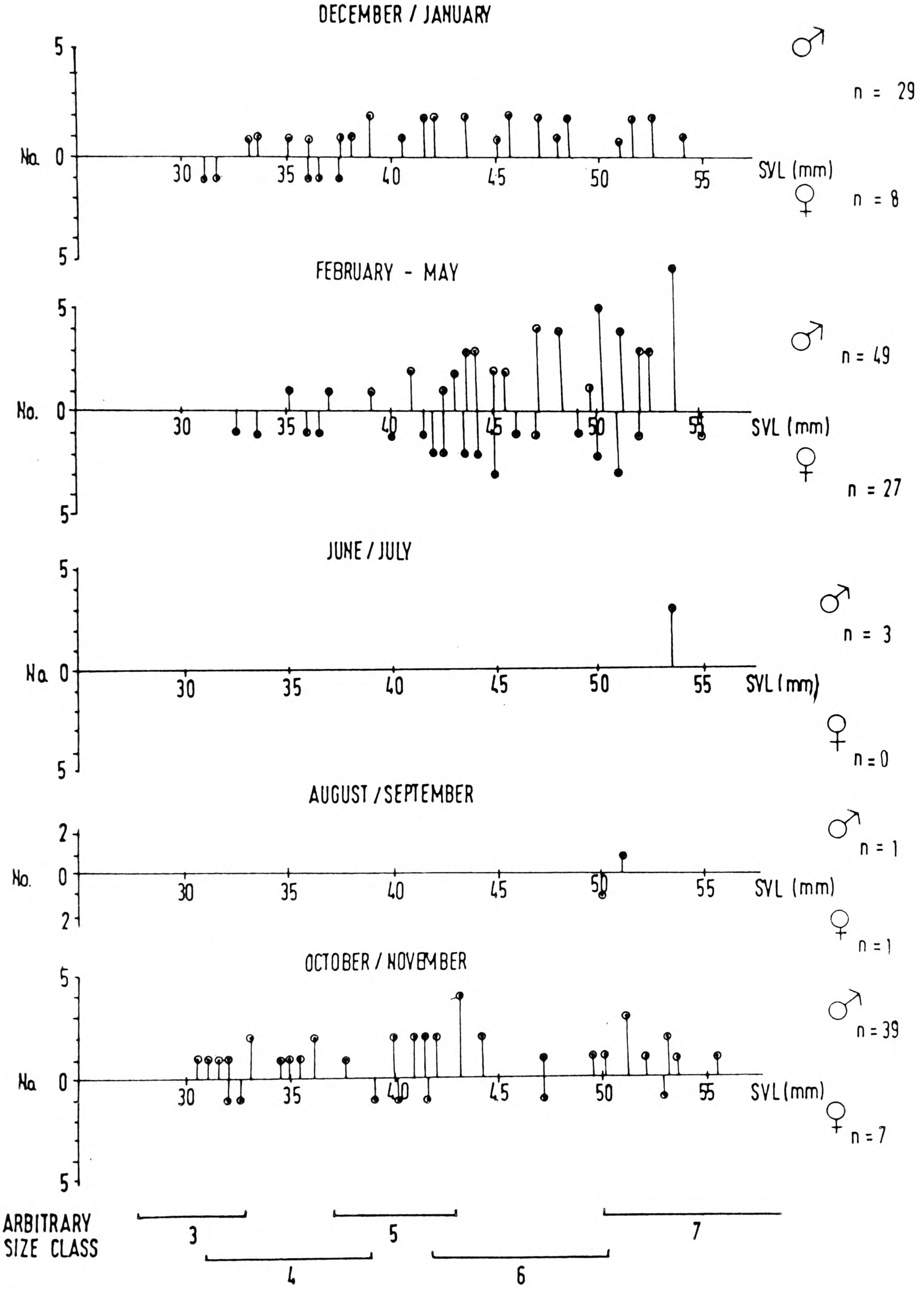


Figure 6.5 gives the number of lizards of each size captured using the snaring techniques described in 3.1.1. No lizards of size classes 1 or 2 were caught and the technique as a whole was subject to bias as described in 3.1.1. However, and despite the fact that sample sizes were too small for conclusive statistical analysis, comparison with Figure 6.2 shows similarity in the distribution of size classes between the purely observational and the trapping data. The exception to this is the August/September sample, when very few lizards were caught.

6.2.3 Discussion

The discrepancy between the size class distribution in the observational and capture data in August/September can be attributed to the fact that lizards are difficult to catch at this time. The predominance of elusive hatchlings, which were impossible to noose, further prevented the capture of a large number of animals.

Inspection of Figures 6.1 to 6.4 shows how the smallest size classes progressively decrease in relative abundance from the time of their appearance in late summer until they disappear altogether in March by which time Size Class 3 is the smallest in size. The shift in predominance to the middle size classes in the spring and to the large size classes (6 & 7) in June and July suggests full size can be attained in one year, at least in favourable habitats. However, thermal considerations may affect the activity of different size classes. This last point will be discussed in Chapter 8.

Observations on captive lizards suggest that at least some of the young lizards of one year have not attained full adult size the following summer (lizard W3, Table 6.3 and Figure 6.16). These may be young that hatch late in late September or October, or those that have not grown more due to environmental reasons (e.g., poor habitat, cold or rainy winter). Those lizards that hatch early can presumably grow to full adult size (and sexual maturity) in one year (e.g. lizards 04, 07, Table 6.3, Figures 6.10 & 6.13).

Adults are in fact seen throughout the year. Therefore some mature animals survive from one year to another side by side with growing hatchlings. Lizards which were obviously mature animals when captured in March 1982 survived to be released back into the wild in July 1982. These lizards will have been adult (or at least almost fully grown) in summer 1981 and therefore hatched at the latest in 1980. The minimum age for lizards 05 and 06 must therefore have been approaching two years when released in July 1982: i.e., hatched in summer 1980, fully grown in summer 1981, caught in spring 1982 and released in summer 1982. Lizard UM was first caught in the wild on 19 June 1981 as an adult (SVL = 53.5mm, Table 6.3b). UM therefore hatched at least in summer 1980, and possibly in summer 1979. On its release in July 1982 it will have been at least two, and possibly three years old.

Observational data include a record of a male P. hispanica, caught as a fully-grown adult in October 1980, observed regularly until March 1982 (and identified by observing clipped toes). It would then have been approaching at least three years of age.

6.3 Sex structure of the population

6.3.1 Methods

Methods used in this section were similar to those described in 6.2.1 with reference to lizard size.

Lizards were sexed during transect observations at North Front Cemetery. The sexing was done mainly by sight. Females on the whole are browner and smaller than males, with shorter and notably narrower heads. Juvenile lizards could not be sexed in this way.

The sexes of captured lizards were determined by reference to the prominence of the femoral pores, which are much better developed in males than in females (Arnold et al., 1978).

Only adult lizards which could be confidently sexed in the field were used in the X^2 test on the data.

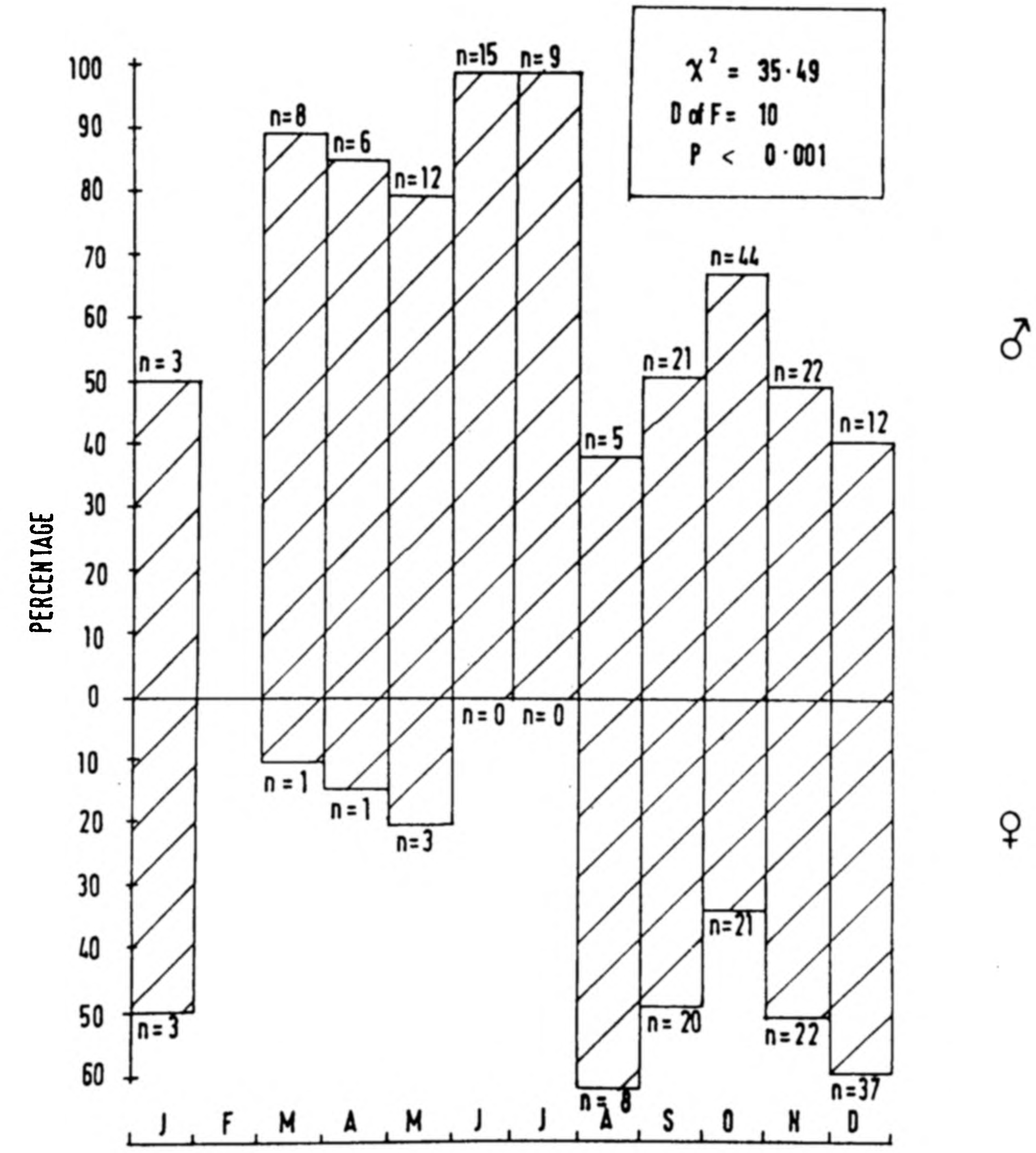
6.3.2 Results

The histogram in Figure 6.6 illustrates the proportion of male and female adult lizards in NFC Site 1 during each month. Numbers are low for some months due to days of inclement weather which restricted days of observation.

Figure 6.6 shows a marked predominance of males over females from March to July (perhaps also February). During the rest of the year there are almost equal numbers of males and females observed. The X^2 test on the data gives a significant result ($P < 0{\cdot}001$; Figure 6.6).

Figure 6.5 shows the numbers of males and females caught by noosing. Males are seen to predominate, but females feature more than in the observational samples in February-May.

Fig. 6.6 PERCENTAGE ADULT MALE AND FEMALE *P.hispanica* OBSERVED AT NFC SITE 1 PER MONTH (♂+ ♀ = 100 %. EACH MONTH): INSUFFICIENT DATA WERE AVAILABLE FOR FEBRUARY.



6.3.3 Discussion

The trends in the proportion of males and females are of course superimposed on the overall seasonal trends in activity of the species at the site (Chapter 8).

The results from the captured samples show a greater proportion of females between February and May than the observational results (Figures 6.5 and 6.6). Most of these lizards were captured at their site of emergence and also included females basking in gaps in vegetation and which may not have been noticed during transect observations. Some lizards were also caught in their refugia (under loose stone slabs). These results may reflect more closely the actual relative numbers of males and females in the population, while the observational data give a better idea of their relative conspicuity.

It is clear from the observational results that female *P. hispanica* are seen less in the spring and early summer than in late summer, autumn and winter. This does not necessarily imply lower activity, but does mean that female lizards at this time of year spend less time in the open than males do at that time of year.

Mating behaviour of lizards was observed between February and July (6.5.) the same months when the female lizards were less conspicuous. At this time males are prominant baskers (8.3) and will attempt to mate with any female emerging from vegetation in their proximity. This accosting of females may contribute to the absence of females from basking sites. Females may also keep away from prominent sites in order to avoid repeated copulations. However females do appear to be able to prevent copulation taking place even after having been caught by males (6.5.1). It may in any case be futile for a female to attempt to emerge to bask if she will not be able to remain basking for any length of time before being approached by a male.

Female lizards once gravid, appear not to attract males (6.5.3). However, at this time they are more susceptible to predators, being slower and less agile than males or unmated females. Moreover since they are carrying young, their survival is more important in evolutionary terms. The avoidance of open areas may therefore be adaptive anti-predator behaviour during the time they are carrying eggs.

Since females are generally smaller than males, it is necessary to consider as a possible alternative explanation of less conspicuous behaviour that their need to bask is smaller than that of the larger males. That is, they can achieve preferred body temperatures more quickly or spend less time in the open before overheating. The converse is also true, however, and they will cool more quickly in a cool environment. The explanation is also unlikely to be valid since it would hold true throughout the whole year, not just in the spring. Also, there is a marked difference in the percentage of females seen in July (when mating behaviour is still observed and many females may not have laid) to the percentage of females seen in August (when mating has ended and most females have laid), despite temperature and radiation regimes being similar (2.1).

It is therefore possible that during the mating season females are predominantly thigmothemic, or bask in small spots of sunlight within vegetation where they are less conspicuous to predators (and to male lizards). Males at this time are predominantly heliothermic and bask more prominently, to attract females and warn off rival males.

6.4 Growth of lizards

6.4.1 Methods

Lizards were rarely caught more than once (Table 6.3c). Although marked lizards were observed repeatedly, these observations could not provide precise morphometric data. An estimate of snout-vent length made by eye is not sufficient for comparison with a directly measured value. Therefore wild lizard data contributed little to the calculation of growth rates.

Growth of lizards was followed mainly in the laboratory. Male and female P. hispanica were kept under the conditions described in 3.3 and were weighed regularly (usually every two days) using a 5-gram Pesola scale. The snout-vent length was measured every 10 days. Records were kept of weight, SVL and $\sqrt[3]{\text{weight}}$ / SVL (calculated from each weight value using the previous value for SVL) for 96 days from capture in the field (27 March 1982) to release. Less-detailed records were kept for the lizards in captivity in January - March 1981.

6.4.2 Results

The increases in SVL, together with the rates of growth in 1982 during the captive period for the lizards are given in Table 6.3a. It is clear from the table and from Figures 6.7 and 6.8 that the lizards which were smallest (SVL) at the time of capture grew at the fastest rate (average of 0·62mm/week for O4), and those which were largest (approaching maximum size) grew slowest (average of 0·04mm/week for O6). With the exception of the small male(W3),the rate of growth of females was greater than that of the larger males.

Figure 6.8 suggests there are two relationships of rate of growth with SVL, one for SVL $<$ 45mm, and another for SVL $>$ 49mm. This suggests that the growth rate of lizards is similar between 45mm and 49mm SVL.

Figures 6.9 to 6.19 display plots of weight vs. day (0 = day of capture) and $\sqrt[3]{\text{weight}}$ / SVL vs. day for captive lizards (spring 1982). The lizards were labelled according to the colour code used to identify them (e.g. O7 means the lizard marked in orange paint in the pattern representing the number 7, Figure 3.3; W = white; 'UM' = 'unmarked'). Lizards ommitted

Fig. 6.7

PLOT OF MEAN GROWTH RATE OVER 96 DAYS vs INITIAL SVL FOR CAPTIVE <u>P. HISPANICA</u> FOR GIBRALTAR.

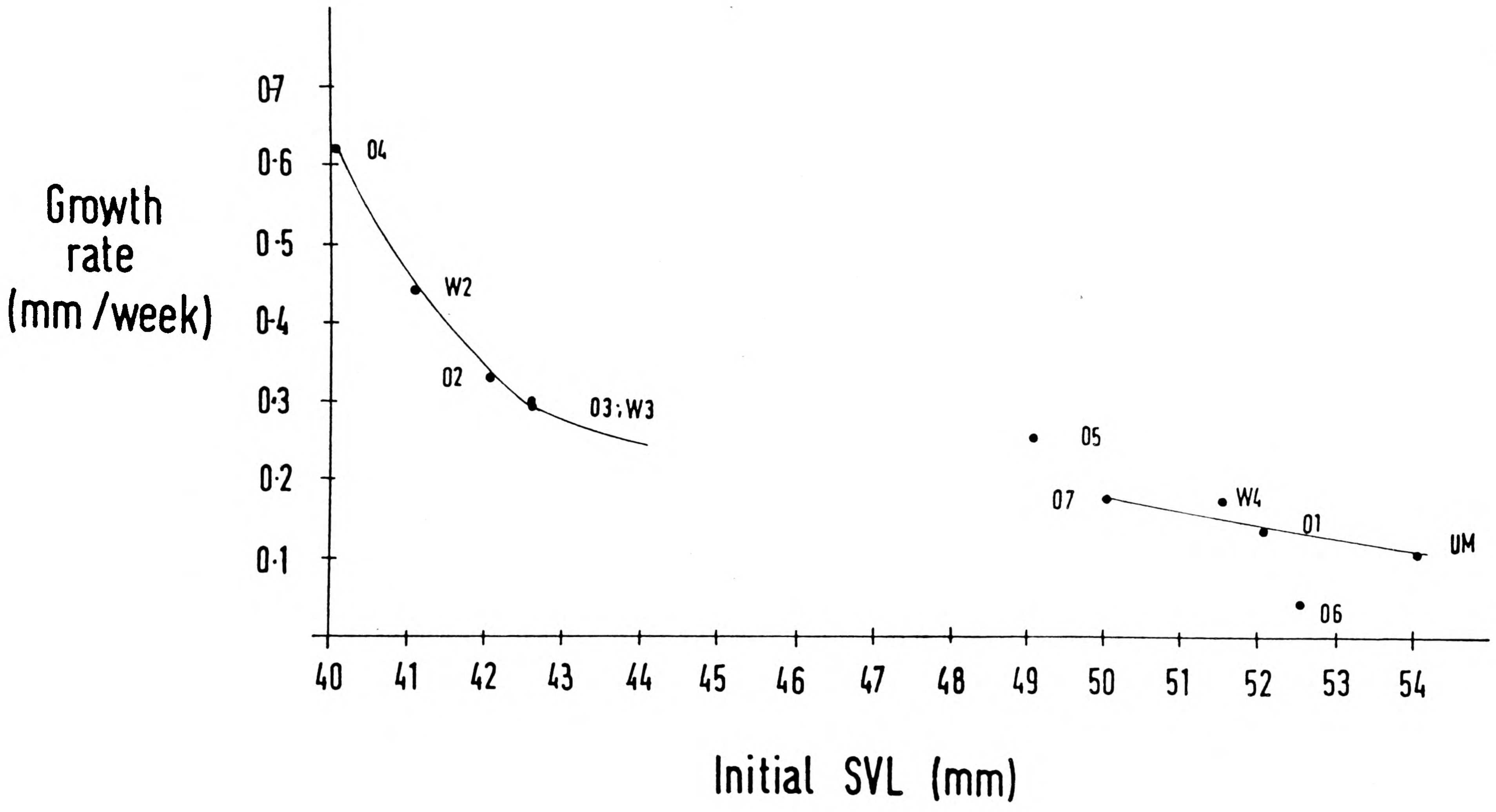
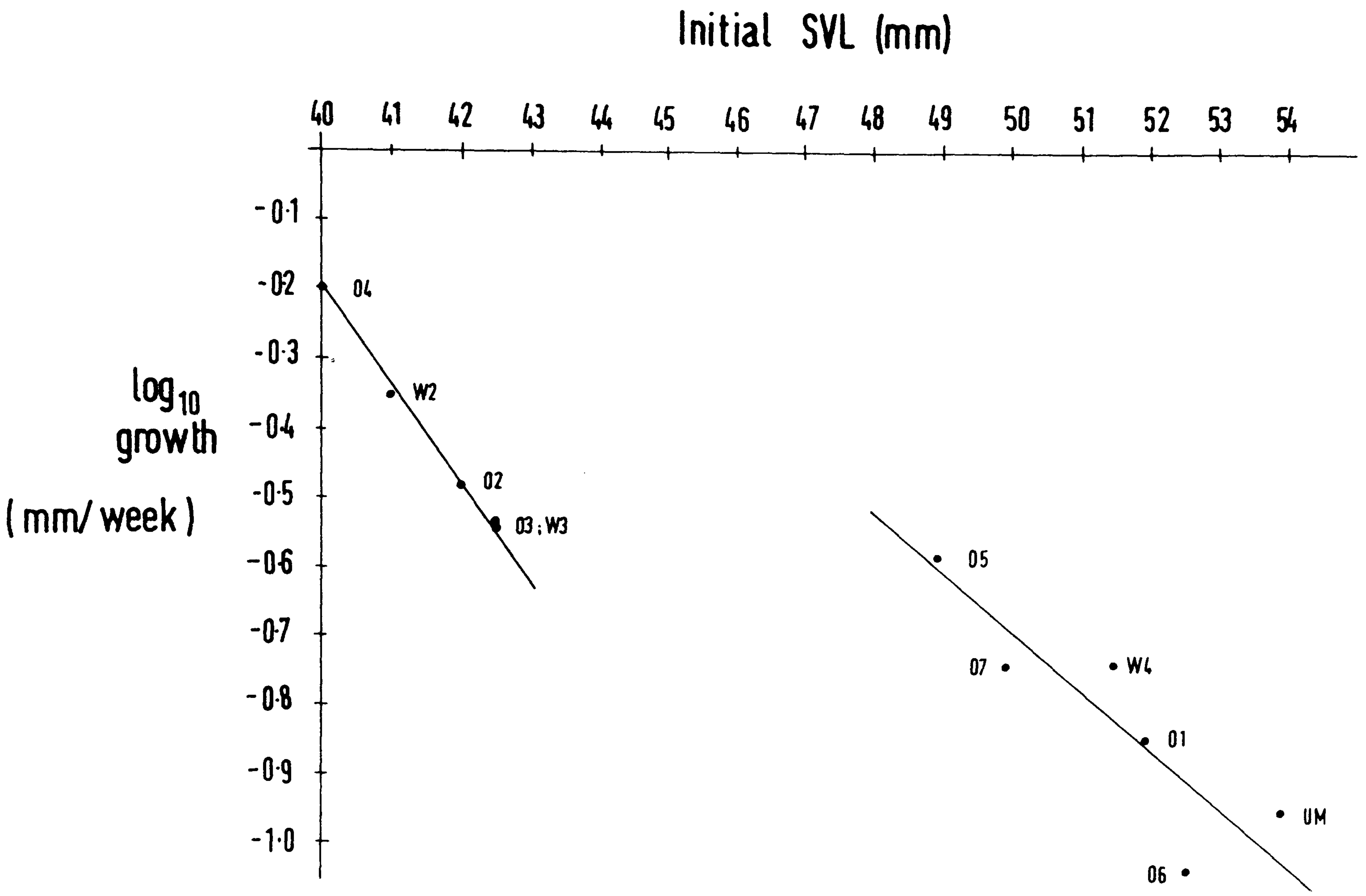


Fig. 6.8

PLOT OF LOG_{10} MEAN GROWTH RATE OVER 96 DAYS vs INITIAL SVL FOR CAPTIVE P. HISPANICA FOR GIBRALTAR.



from the figures were those which only survived several days in captivity.

In most cases, after a slight initial drop, the weight of the lizard, and the $\sqrt[3]{\text{weight}}$ /SVL ratio, increased. The latter stabilized and remained fairly constant for most of the lizards.

Inspection of Figures 6.9 to 6.19 shows the following:
01 (♂): After an initial drop in weight the lizard tended to increse in weight, with the $\sqrt[3]{\text{weight}}$ / SVL ratio remaining fairly constant although increasing slightly.

02(♀): an overall increase in weight was observed, with fluctuations, especially at around 60 days. The $\sqrt[3]{\text{weight}}$ ratio also increased overall, but remained fairly steady after about day 32.

03(♀): both weight and $\sqrt[3]{\text{weight}}$ / SVL fluctuated. The ratio was similar at day 96 to that at the beginning. There was one notable drop in weight at day 54, similar to that experienced by 04, although no eggs were found at this stage in 03's tank. There was an obvious drop in weight on laying which began to be recovered after 5 days.

04(♀): fluctuations observed similar to those of 03. Again the ratio $\sqrt[3]{\text{weight}}$ / SVL was similar at start and finish, fluctuations in both this and weight depending on the point in the egg laying cycle. Again weight loss seemed to be recovered in about 5 days after laying.

05(♀): this large female showed fewer fluctuations than 03 and 04. There was a steady increase in weight from the time of first mating to the day of laying, with a slower rate of recovery than the preceding, smaller females. The $\sqrt[3]{\text{weight}}$ / SVL ratio varied similarly to the weight and increased slightly overall.

06(♂): there was a slight increase in $\sqrt[3]{\text{weight}}$ / SVL and a steady overall increase in weight, with some fluctuations, however.

07(♂): a fluctuating increase was observed in weight and $\sqrt[3]{\text{weight}}$ / SVL until the dominant male (06) was removed from the vivarium, at which point 07 increased in weight more steadily. The weight of this lizard began to decrease after 91 days in captivity and the animal died soon afterwards.

W2(♀): a steady increase in both weight and $\sqrt[3]{\text{weight}}$ / SVL was observed until day 68, when a decrease in weight began, culminating in the death of the lizard on day 80 (weight = 1·95g; $\sqrt[3]{\text{weight}}$/SVL = 2·71).

W3(♂): there was a steady increase in both variables after fluctuations up to day 40. A notable increase in weight was observed after the removal of the dominant male on day 58. Weight decreased again after day 84.

W4(♀): there is an overall increase in weight and $\sqrt[3]{\text{weight}}$ / SVL with a number of fluctuations.

UM(♂): a large drop in weight and $\sqrt[3]{\text{weight}}$ / SVL was noted during and immediately after the commencement of a high mating and aggressive activity in the vivarium where UM was the dominant male. After being taken away from other males weight increased and, although with fluctuations, remained high in comparison with initial weight.

Table 6.3b shows the growth rates and change in $\sqrt[3]{\text{weight}}$ / SVL for the captive lizards kept from 20 January to 7 March 1981 under conditions described in 3.3. The overall trend again appears to be that of the data in Table 6.3a - an inverse relationship between growth rate and initial SVL. The $\sqrt[3]{\text{weight}}$ /SVL ratio increased in almost every case.

The limited data for recapture in the field are shown in Table 6.3c. No definite relationship is seen in these cases between initial SVL and growth rate, despite most of the data having been collected during the same time of year - autumn 1981/ spring 1982.

Table 6.3a Growth in SVL of captive P. hispanica from Gibraltar (arranged according to growth rate): April - July 1982.

Lizard	Initial SVL (mm)	SVL after 96 days (mm)	Increase in SVL (mm)	Rate of Growth (mm/week)
04 (♀)	40•0	48•5	8•5	0•62
* W2 (♀)	41•0	46•0	5•0	0•44
02 (♀)	42•0	46•5	4•5	0•33
03 (♀)	42•5	46•5	4•0	0•29
W3 (♂)	42•5	46•5	4•0	0•29
05 (♀)	49•0	52•5	3•5	0•26
07 (♂)	50•0	52•5	2•5	0•18
W4 (♂)	51•5	53•0	2•5	0•18
01 (♂)	52•0	54•0	2•0	0•14
UM (♂)	54•0	55•5	1•5	0•11
06 (♂)	52•5	53•0	0•5	0•04

* W2 growth rate calculated for 80 days to death.

(Note: Result of regression of rate of growth vs. initial SVL:

$y = 1{\cdot}515 - 0{\cdot}027x$; $r = -0{\cdot}876$; $P < 0{\cdot}01$)

Table 6.3b Growth in SVL and change in $\sqrt[3]{\text{weight}}$/SVL of captive P. hispanica from Gibraltar (arranged according to growth rate): January - March 1981.

Lizard	Initial SVL (mm)	SVL after 46 days (mm)	Increase in SVL (mm)	Rate of Growth (mm/week)	Initial $\frac{\sqrt[3]{\text{weight}}}{\text{SVL}}$ ($\times 10^{-2}$)	Final $\frac{\sqrt[3]{\text{weight}}}{\text{SVL}}$ ($\times 10^{-2}$)
R2 (♂)	33•0	37•5	4•5	0•68	3•03	3•02
FT (♂)	36•0	39•5	3•5	0•53	3•61	3•29
T (♂)	31•0	33•0	2•0	0•30	2•72	3•22
RW (♀)	42•0	43•5	1•5	0•22	3•36	3•00
Y2 (♂)	48•0	49•0	1•0	0•15	2•82	3•07
B1 (♀)	49•0	49•5	0•5	0•01	2•61	2•95
R1 (♂)	43•0	43•0	0•00	0•00	2•72	3•07
Y1 (♂)	49•0	49•0	0•00	0•00	2•90	3•07

(Note: Result of regression of rate of growth vs. initial SVL:

$y = 1{\cdot}405 - 0{\cdot}028x$; $r = -0{\cdot}803$; $P < 0{\cdot}05$)

Table 6.3c Growth in SVL of wild *P. hispanica* at North Front Cemetery, Gibraltar (arranged according to growth rate).

Date of first capture	Date of subsequent capture	Initial SVL (mm)	Subsequent SVL (mm)	Time Interval (days)	Rate of Growth (mm/week)
28/10/81	8/ 1/82	36·0	42·0	72	0·58
9/ 1/82	1/ 4/82	45·5	50·0	82	0·38
6/ 1/82	28/ 2/82+	51·5	53·5	53	0·33
9/ 1/82	6/ 3/82	41·5	43·5	56	0·25
6/ 1/82	10/ 4/82	48·5	51·5	94	0·22
28/10/81	29/11/81*	42·0	43·0	32	0·22
28/10/81	6/ 1/82*	42·0	43·5	70	0·15
17/12/80	27/10/81	38·0	43·0	314	0·11
29/11/81	6/ 1/82*	43·0	43·5	38	0·09
31/10/81	23/ 1/82	51·0	52·0	84	0·08
(UM) 19/ 6/81	10/ 4/82	53·5	54·0	294	0·01
23/ 1/82	24/ 2/82	47·0	47·0	32	0·00
28/ 2/82	27/ 3/82+	53·5	53·5	27	0·00

Notes:

1. All lizards were male.
2. Entries marked * were all for the same lizard, recaptured twice.
3. Entries marked + were all for the same lizard, recaptured once.
4. '(UM)' refers to the lizard taken into captivity on 27/ 3/82 (see Table 6.3b).
5. Result of regression of rate of growth vs. initial SVL:

$y = 0{\cdot}870 - 0{\cdot}015$; $r = -0{\cdot}508$; $P > 0{\cdot}05$.

Fig. 6.9 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND WEIGHT / SVL vs DAY FROM CAPTURE FOR CAPTIVE LIZARD 01 (♂)

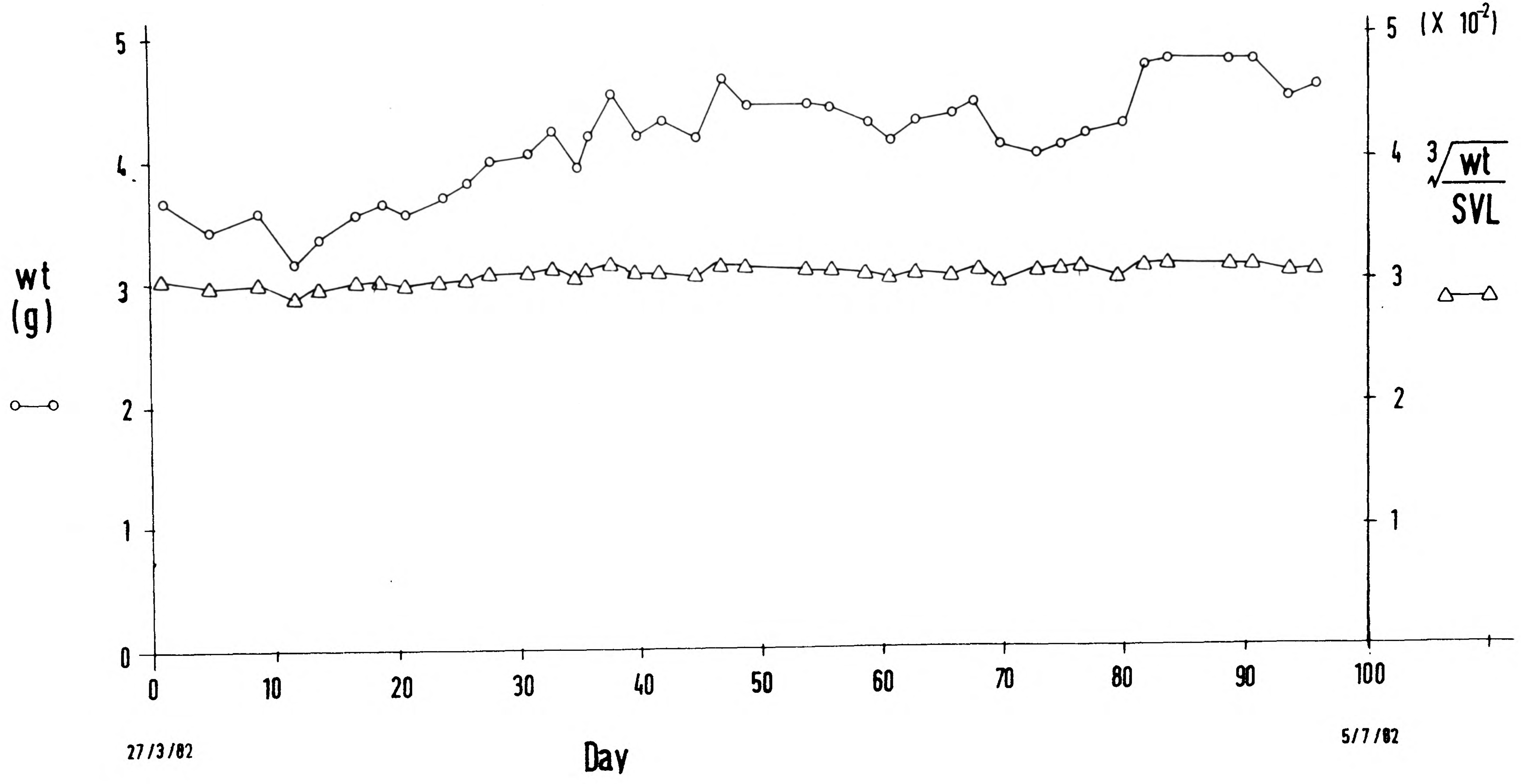


Fig. 6.10 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT/SVL}}$ vs DAY FROM CAPTURE FOR CAPTIVE LIZARD 02 (♀)

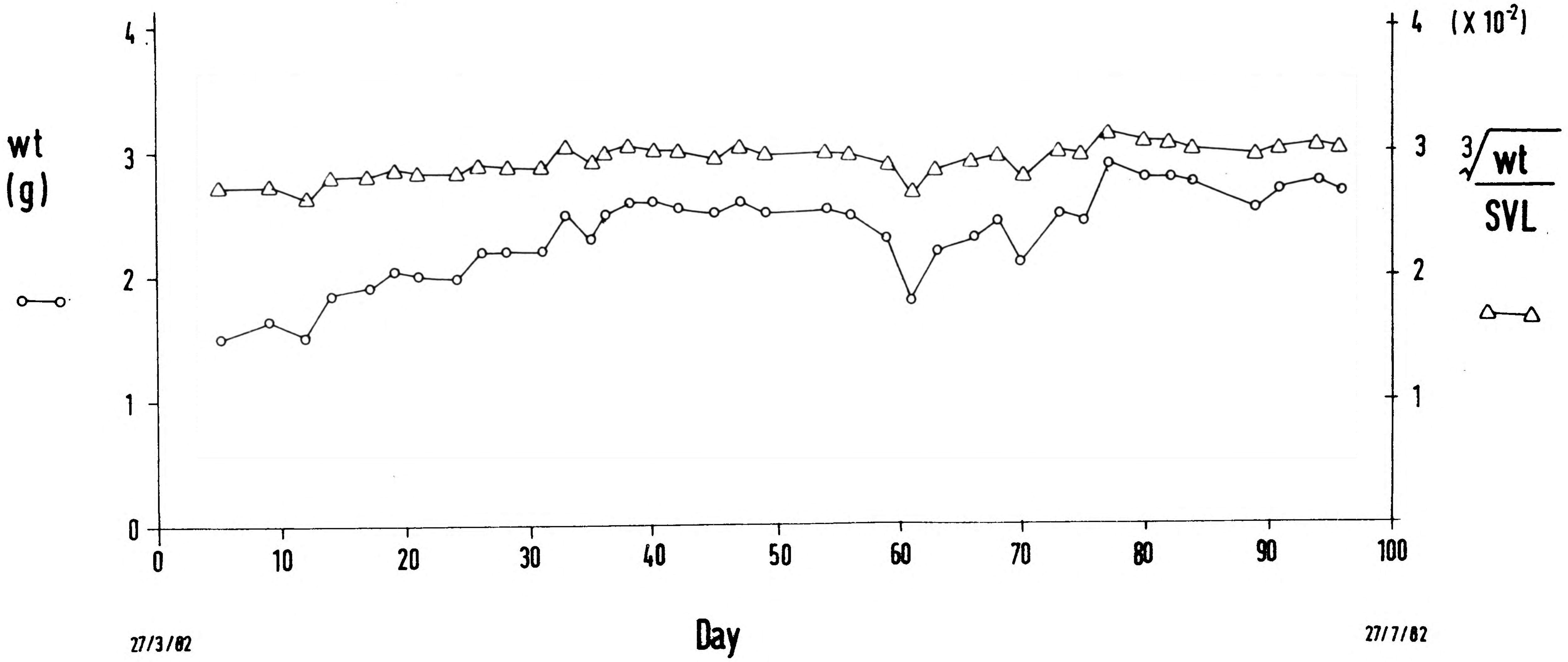


Fig. 6.11 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND ^{3} WEIGHT / SVL vs DAY FROM CAPTURE FOR CAPTIVE LIZARD 03 (♀)

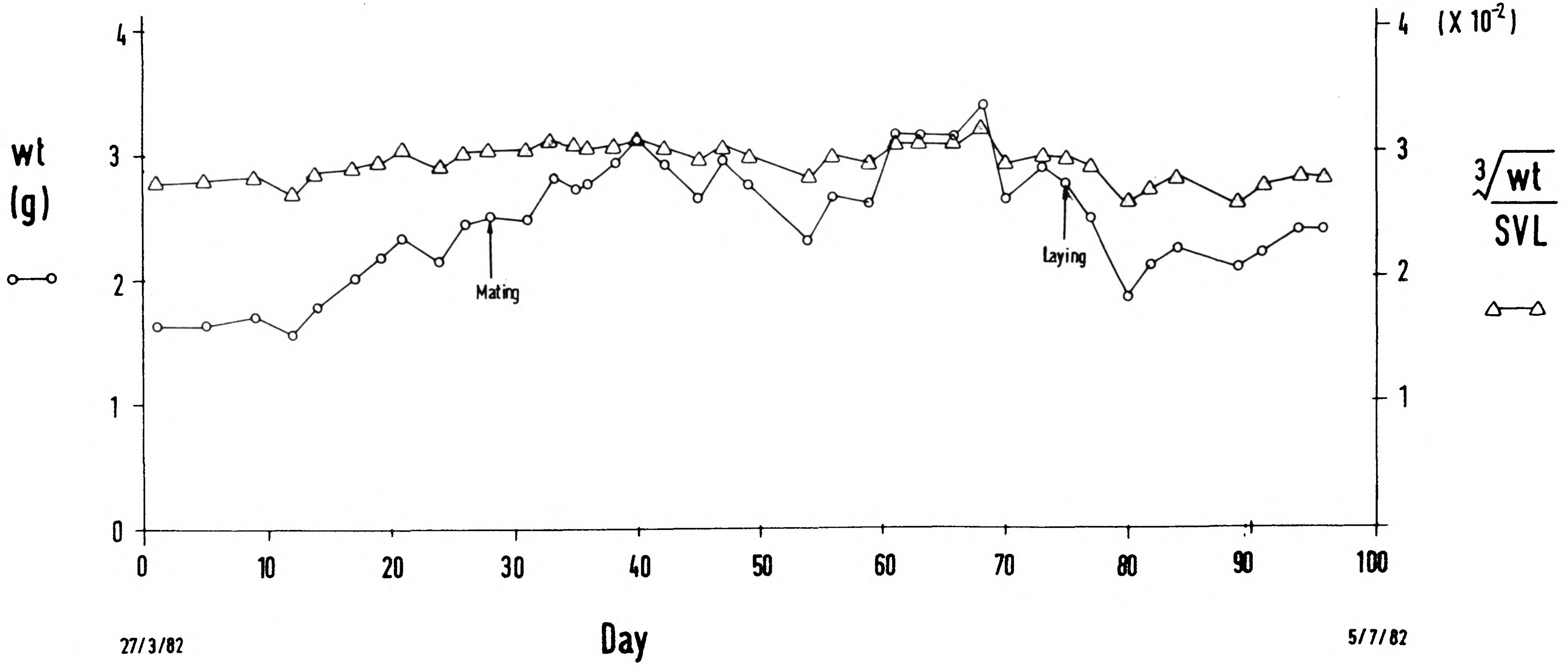


Fig. 6.12 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT}}/\text{SVL}$ vs DAY FROM CAPTURE FOR CAPTIVE LIZARD 04 (♀)

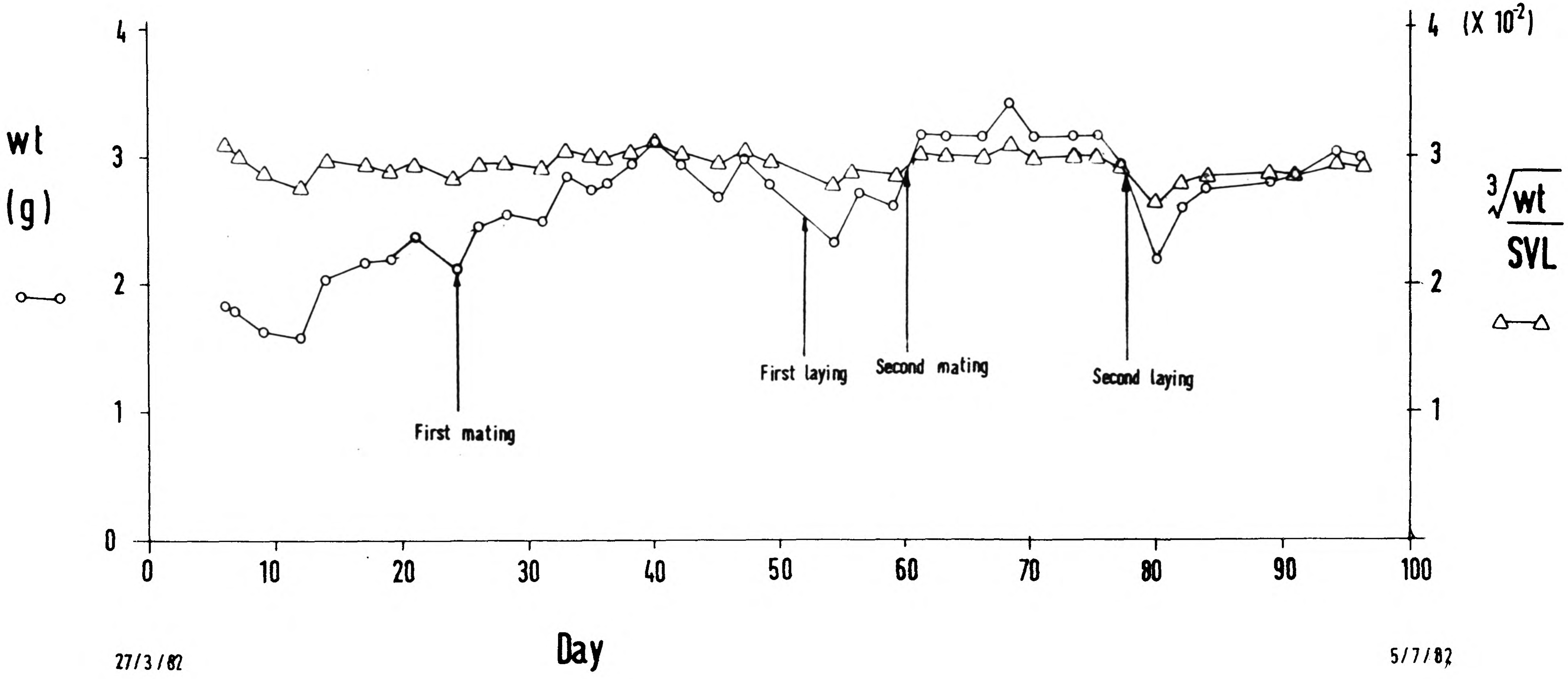


Fig. 6.13 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT}}$/SVL vs DAY FROM CAPTURE FOR CAPTIVE LIZARD 05 (♀)

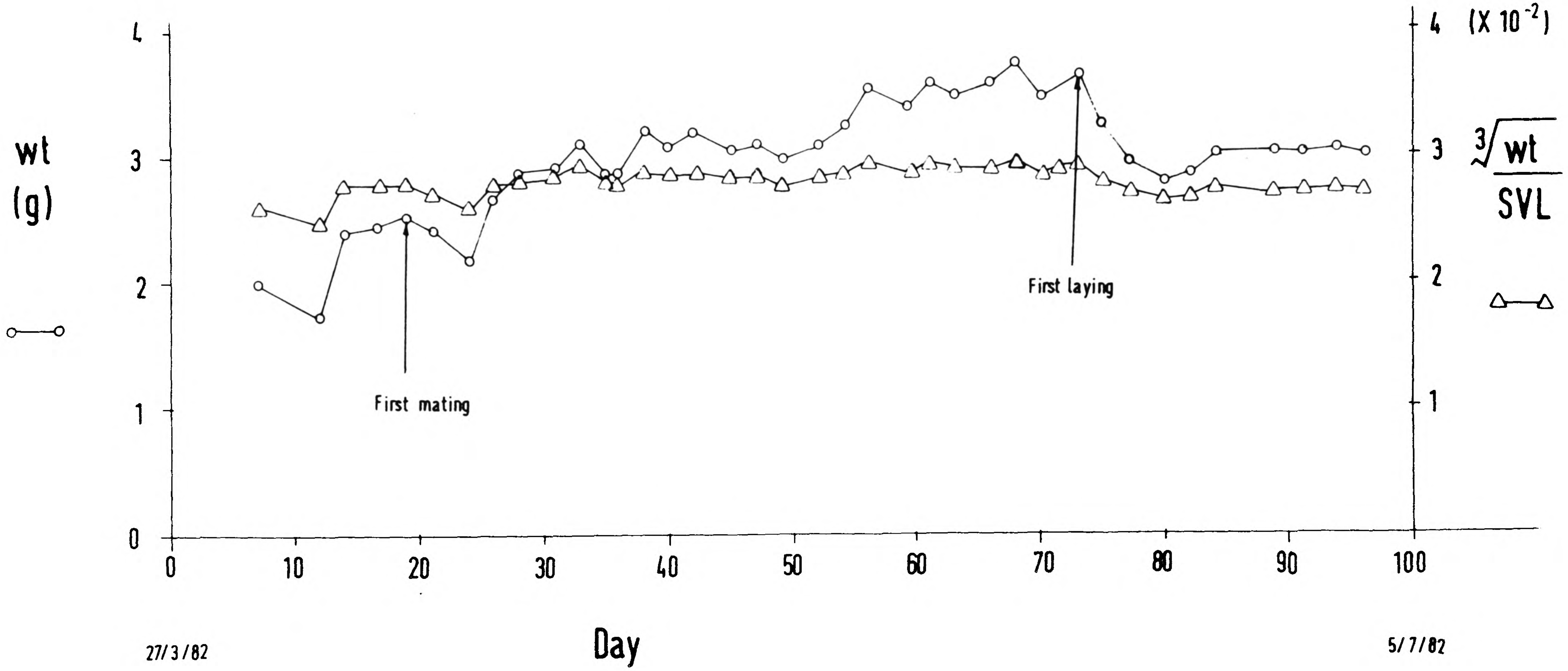


Fig. 6.14 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT}}/\text{SVL}$ vs DAY FROM CAPTURE FOR CAPTIVE LIZARD 06 (♂)

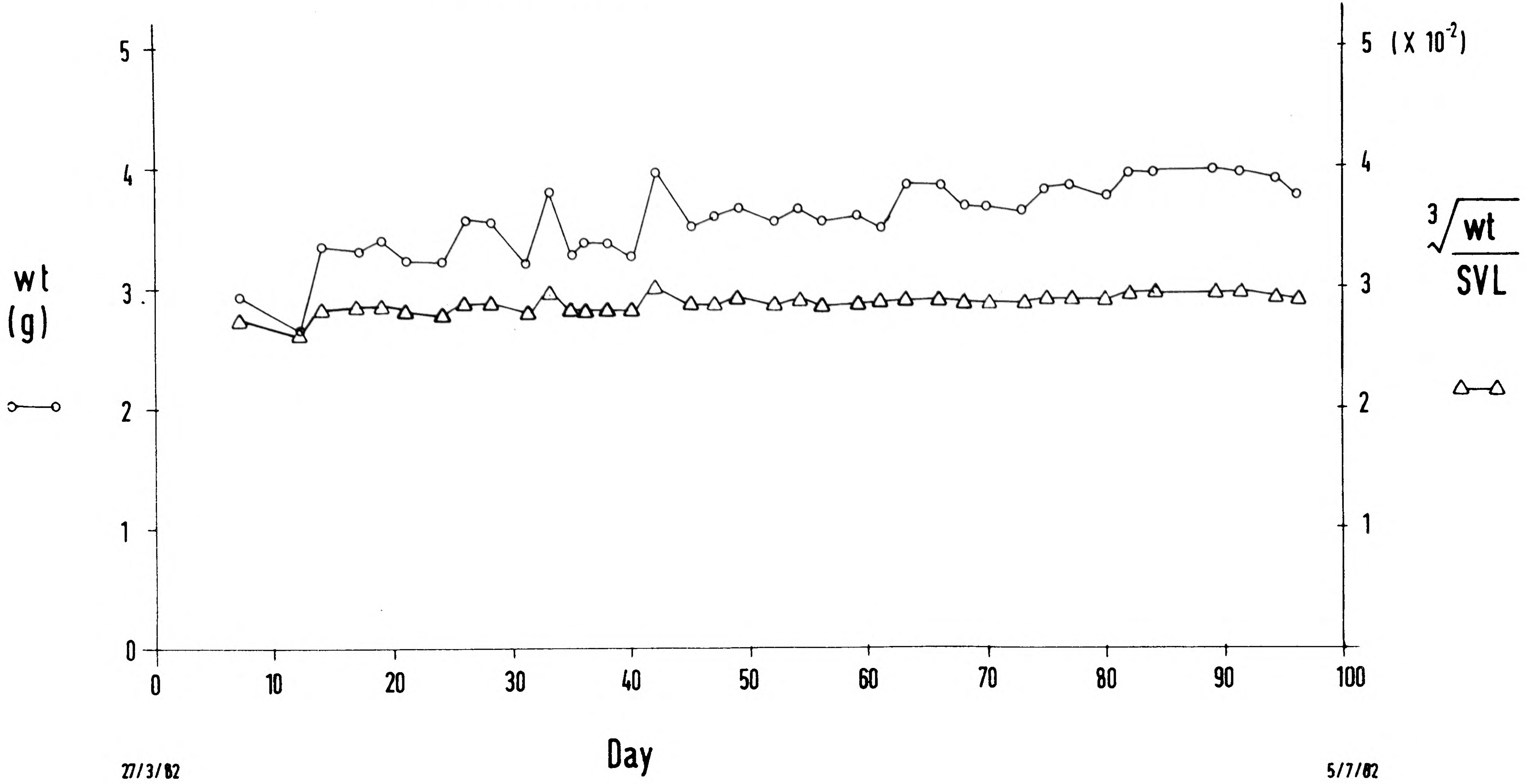


Fig. 6.15 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT}}/\text{SVL}$ vs DAY FROM CAPTURE FOR CAPTIVE LIZARD 07 (♂)

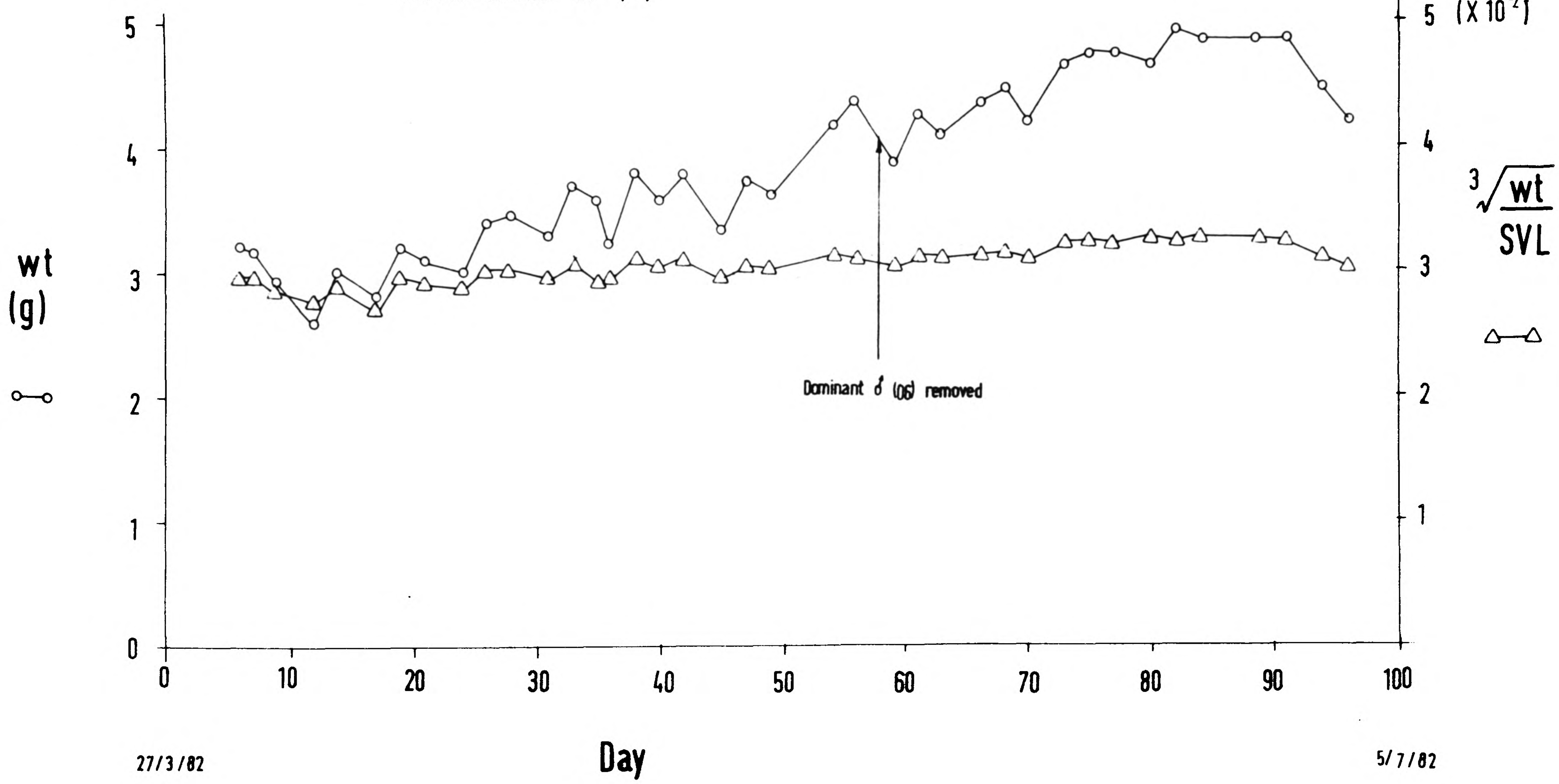


Fig. 6.16 PLOT OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT/SVL}}$ vs DAY FROM CAPTURE FOR CAPTIVE LIZARD UM (♂)

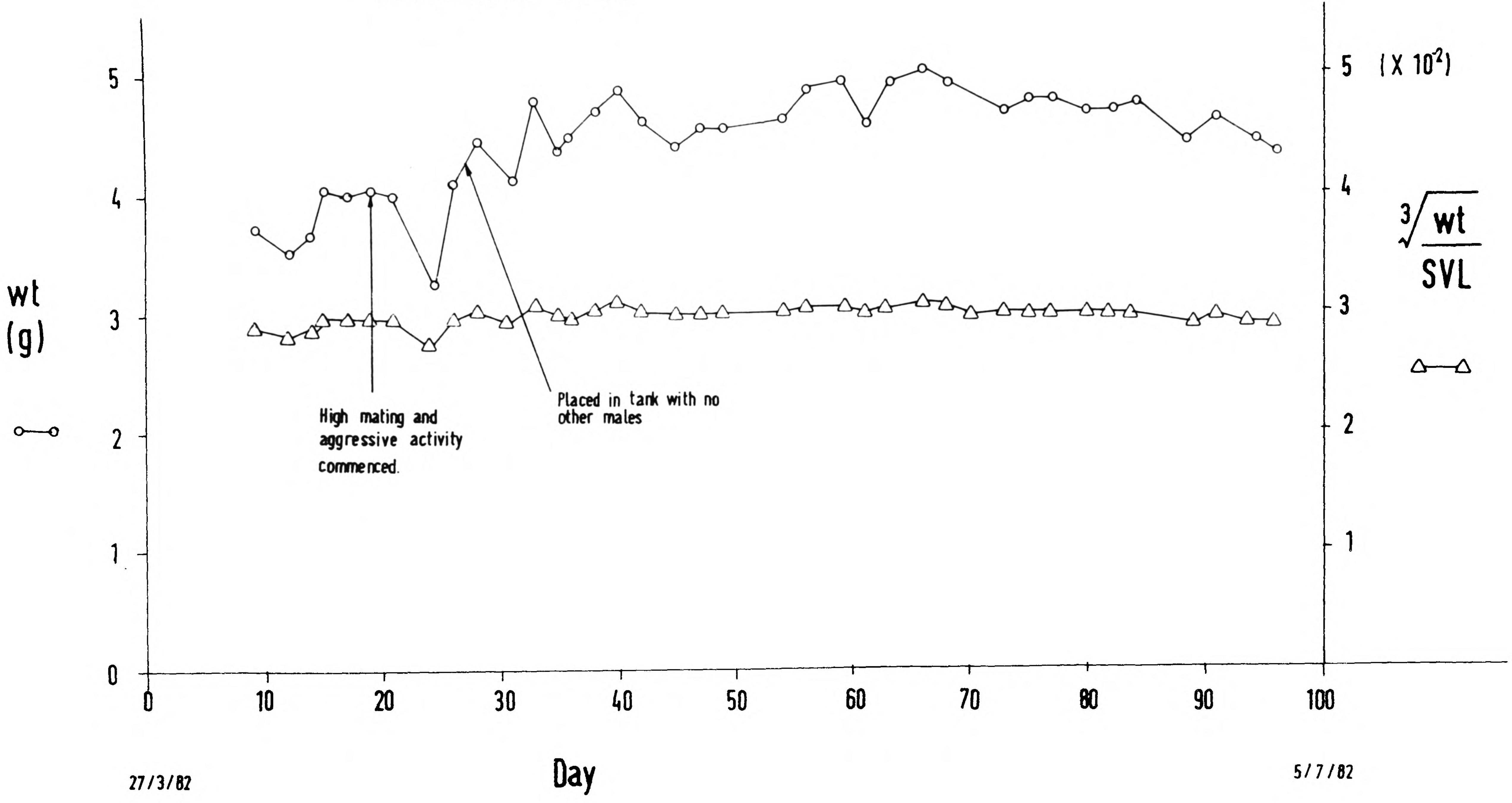


Fig. 6.17 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT}}/\text{SVL}$ vs DAY FROM CAPTURE FOR CAPTIVE LIZARD W 2 (♀)

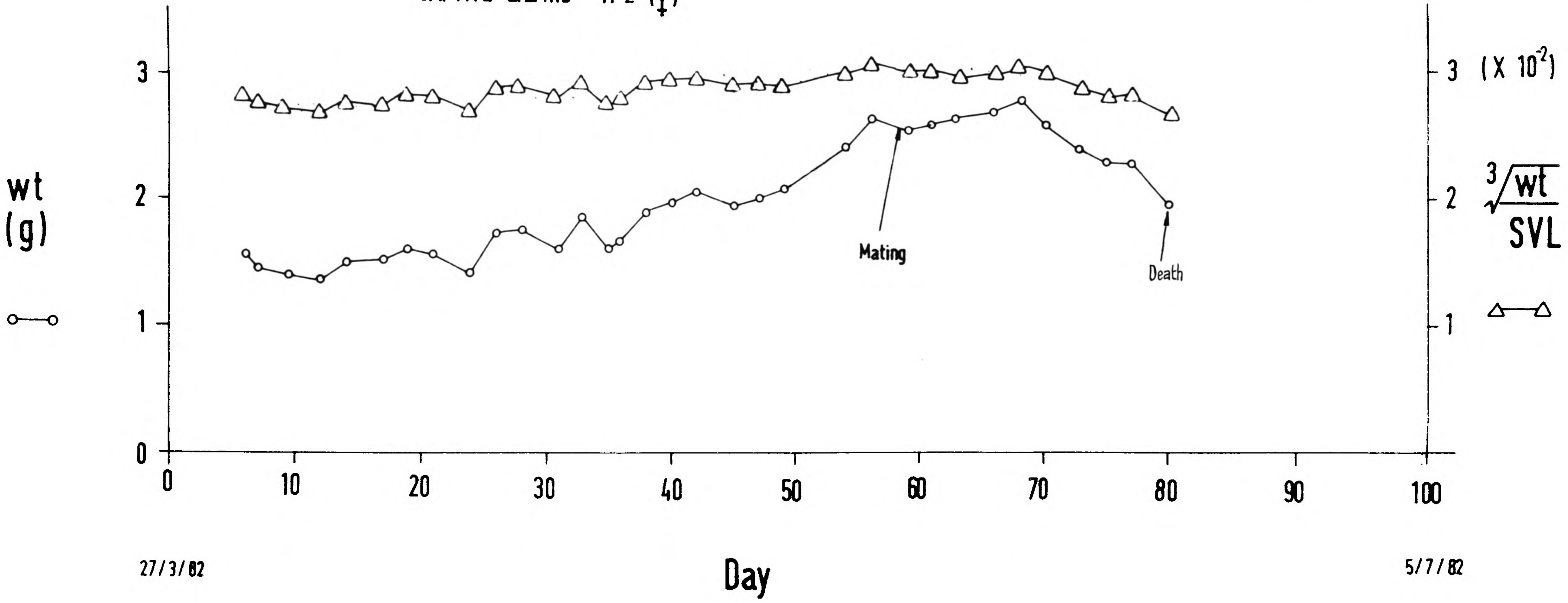


Fig. 6.18 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT}}/\text{SVL}$ vs DAY FROM CAPTURE FOR CAPTIVE LIZARD W3 (♂)

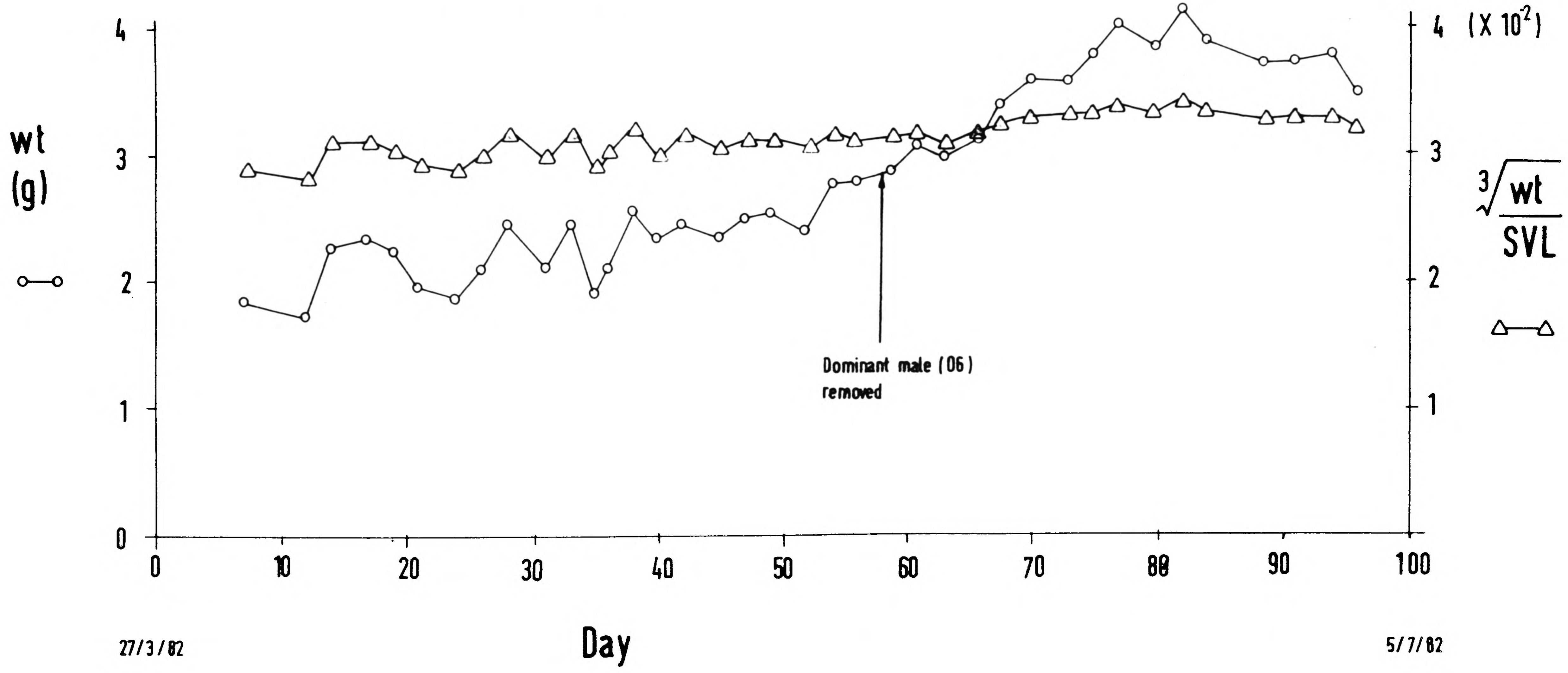
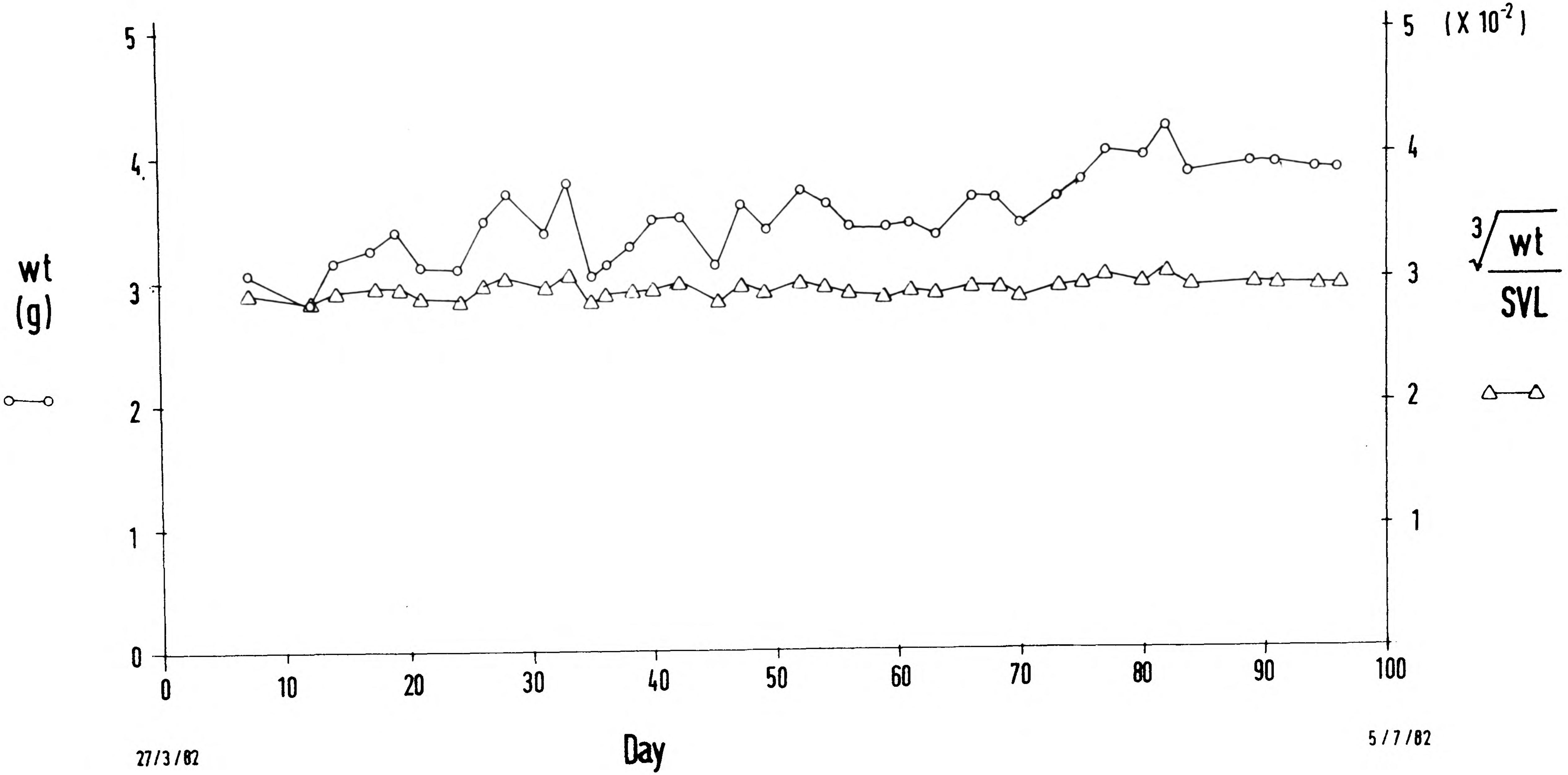


Fig. 6.19 PLOTS OF WEIGHT vs DAY FROM CAPTURE AND $\sqrt[3]{\text{WEIGHT}}$/SVL vs DAY FROM CAPTURE FOR CAPTIVE LIZARD W4 (♂)



6.4.3 Discussion

Growth rate in lizards will be affected by environmental factors such as food availability. Temperature may also play a part in this.

In the vivaria environmental factors also influenced weight in the short term and growth in the long term. For example, the weight of UM fell when sexual and aggressive activity increased and fluctuated less when it was removed from other males. The rate of growth of 01, only male in one vivarium, was greater than that of 06, of a similar initial SVL, which had been placed in a tank with five other males.

Table 6.3a and Figure 6.7 suggest an exponential relation between initial SVL and growth rate during the 96 day period in which the lizards were in captivity (where conditions of temperature were similar in all cases and food was superabundant at all times). Figures 6.7 and 6.8 suggest two trends in increase in rates of growth - one for lizards of SVL less than 45 mm and another for lizards of SVL greater than 49 mm. Once lizards have achieved adult size, therefore, growth is much slower.

The only exception to the initial SVL vs. growth rate trend concerns lizards UM and 06, whose expected positions are reversed. Again the fact that UM was isolated from other males while 06 was in a vivarium with others may have accounted for the difference.

The captive lizards kept in winter 1981 in conditions resembling those operative in the field at that time of year (see 3.3) showed a similar growth rate vs. SVL relationship to that of the spring 1982 sample (Table 6.3c). Lizards T and R1 showed lower growth rates than would be expected. In this case, all the lizards were kept in a single tank (3.3). Lizard T, being the smallest (SVL = 31mm), was repeatedly displaced by all the other lizards, and R1, the smallest of the larger males, was similarly repeatedly displaced by the latter. The lizards' social status may again explain their reduced growth rates. It appears that the lower temperatures to which these lizards were subjected did not lower the growth rate at least of the smaller lizards (maximum growth rate = 0·68 mm/week compared to a maximum of 0·62 mm/week for the spring 1982 sample). The small sample sizes, however, did not allow statistical analysis.

This relationship of growth rate and size is not shown by the wild lizard data (Table 6.3b). Differing environmental conditions between captures (weather conditions or microhabitats) and different social status will almost certainly affect growth in the wild. In most cases growth rates in the wild will tend to be lower and more variable than in the more stable conditions of captivity with regular superabundant food. The results shown in Table 6.3b support this suggestion. Thus, maximum growth rate in the wild was 0•58 mm/week, compared to 0•68 mm/week for the captive samples. Mean growth rate in the wild was 0•18 mm/week compared to 0•26 mm/week for the captive lizards. Only three out of 13 growth rates in the wild sample were greater than the average for captive lizards. In the wild UM grew 0•5mm in 294 days (Table 6.3c), whereas in captivity it grew 1•5mm in 96 days (Table 6.3a) - a tenfold increase in growth rate.

Potentially, a small lizard can grow quickly. This will be advantageous to it since a large lizard can compete more favourably with other lizards (Chapter 5) for basking sites (Chapter 8) and food (Chapter 7) as well as for mates. It will probably also have fewer predators. Whether or not the lizard grows quickly will depend on a number of environmental factors, probably limiting the amount of food the lizard can consume. Some of these factors will control the amount of time the lizard can spend feeding (e.g. the inclemence of the weather), others will affect the amount of food available (e.g. the microhabitat in which the lizard lives) and others will relate to the interaction between lizards.

6.5 Breeding

6.5.1 Mating behaviour

Mating was observed in the field on five occasions and 13 times in captivity. The behaviour was broadly similar in all cases.

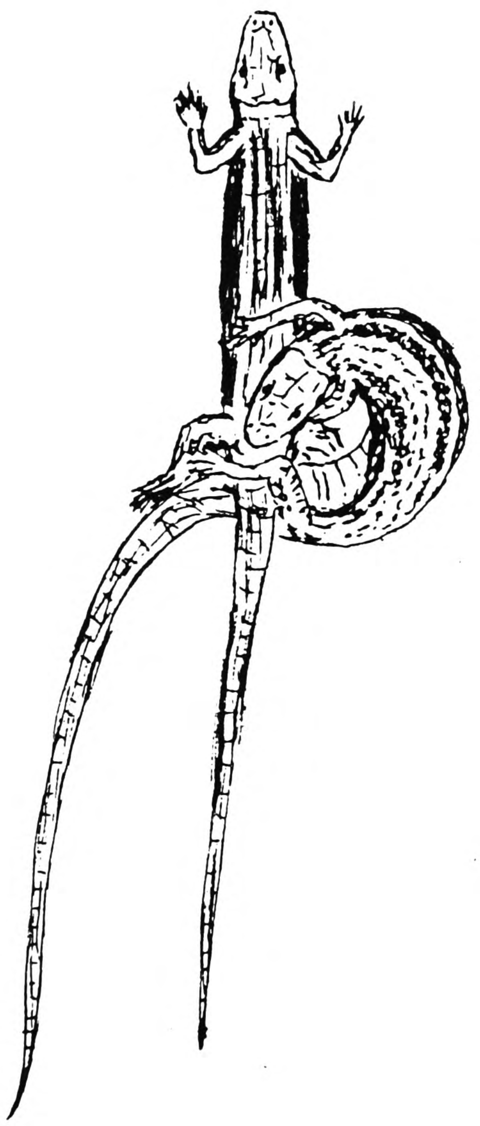
There is no display of coloured throat or belly preceding mating. Males encounter females either when the latter emerge onto a site where a male is basking, or while both are foraging. The male then approaches the female which moves away. The male follows the female. When successful the male catches the female by biting in the area of the hind legs (sometimes the tail), on or just above or below the thigh. The female will drag the male after it, until the latter manages to turn its body round under the female's, straddling it and copulating (Figure 6.20). The male continues to bite the female's hindquarters until the end of copulation. The female will periodically struggle as if attempting to get free. Should the male release its hold (for example if a rival male approaches and interferes) the female will run off.

On the seven occasions when a captive male caught a female lizard by the tail instead of the hindquarters, mating did not occur, nor was the tail autotomised. However the male was unable to assume the copulatory position.

On three occasions in captivity the male gripped the female by the hindquarters. The female did not drag the male along and the male in each case released the bite on the thigh. On two occasions the female, grabbed by the thigh, turned to face the male which promptly released. On one occasion the female actually turned and bit the head of the male, causing the latter to release its hold. On another occasion the female, once caught by the male, 'waved' the right foreleg (5.3.3) and was again released. It therefore seems clear that a female, even if caught by a male can prevent copulation.

Lizards in the wild have been seen to remain in the copulatory position for up to 64 minutes. In captivity the longest period observed in which the lizards remained in this position was 78 minutes. However, in all other cases in captivity when copulation lasted less, this was interrupted by interference from other lizards in the vivarium.

Fig. 6.20 P. hispanica IN COPULATORY POSITION



In the wild, only adult males of SVL greater than 50mm were seen chasing females or successfully copulating with them. Only adult females of SVL greater than 45mm were chased or mated. In captivity, however, a male of SVL 44•5mm (W6) has been seen copulating as have females of SVL 40•0mm, 41•0mm and 42•5mm. The particular conditions in captivity, particularly since there was a limited number of available females, would influence mating preferences.

6.5.2. Mating cycle

No mating-related behaviour (e.g. following of females by males) was observed during the winter months even though contact between lizards sharing refugia and basking sites was frequent. Such behaviour was similarly not observed in captive lizards in winter.

Wild males were first seen to follow females in February. The earliest date on which copulation was observed was 18 February (despite some males having strongly-coloured bellies in the winter). The latest date on which mating was seen in the wild was 10 July.

Mating was not observed on sufficient occasions to allow determination of a peak mating period in the wild. Peak mating in the captive lizards was on 16 April when six matings by four males and two females were observed. This would have depended on the condition of the limited number of males and females in the vivaria and cannot be taken as reflecting a true time of peak mating behaviour.

Lizards were introduced into the large vivarium (3.3) on 2 April. Males in the wild were already exhibiting sexual behaviour. In the vivarium, males started showing an interest in the larger female (05) on 13 April. On all mating attempts on that date the female did not drag the male, but avoided copulation in one of the ways described above. On 14 April, however, 05 spent two hours before any mating occurred moving around the tank and so coming into contact with males. On the following day this female was mated by three males. After mating, males ignored females and each other even though they had shown aggression beforehand.

No further mating or attempts at mating were observed with previously-mated females after 16 April until these had laid. The captive females in fact laid on several occasions, although the eggs were all infertile or otherwise failed to hatch. Table 6.4 lists mating and laying dates for these lizards.

Female 04, for example, laid on 18 May. Mating was attempted with her on the same day, four hours after laying. Copulation was observed 8 days later on 28 May and then not again (she lay for a second time on 13 June) (Figure 6.10.). It appears then that males do not respond to gravid females.

The range of dates on which matings were observed suggests the possibility of P. hispanica at Gibraltar laying two clutches a year. This is at least possible for females first mated in February. Lizard 04, which lay twice, possibly did so prematurely. 04 showed gestation periods of 28 and 18 days (Table 6.4.), always assuming that the first mating resulted in the clutch. Females 03 and 05 had gestation periods of around 50 days each (Table 6.4). The conditions in which the lizards were kept only approximated natural conditions so that these times cannot be taken as being true for the population.

In the absence of more conclusive data, and of any indication as regards hatching times, it may be assumed that lizards mated in the wild in late February would lay about 50 days later in mid-April. These probably result in the young lizards seen in August. The April layers could presumably mate again in April, lay in June and produce the young in August/September.

Table 6.4 Mating and egg-laying of captive P. hispanica from Gibraltar.

Mating date	lizard code	No. of matings	laying date	No. of eggs	maximum interval (days)
15/4/82	05	4 with 3♂♂	8/6/82	1	54
16/4/82	05	5 with 4♀♀	10/6/82	2	56
20/4/82	04	1	18/5/82	3	28
26/5/82	04	1	13/6/82	4	18
24/4/82	03	1	10/6/82	2	47
			13/6/82	1	50
24/5/82	W2	1	Died on 15/6/82		

6.6 Predation

A number of species are potential predators on P. hispanica and at least on juvenile Ps. algirus.

Blackbirds Turdus merula and Blue Rock Thrushes Monticola solitarius are present throughout the year in both sites. Like the other avian predators these species hunt by sight, usually from a perch above the ground although the Blackbird often forages in leaf litter. Both species have been observed with captured P. hispanica.

Lesser Kestrels Falco naumanni are summer residents and hunt from the air. They occur over the Cemetery between February and September while they nest on the adjacent North Face of the Rock. Towards the end of their stay they also hunt over Bruce's Firebreak. Adults have been seen taking lizards up to the size of adult Ps. algirus to the nest.

Cattle Egrets Bubulcus ibis are visitors to the Cemetery from October to March. They walk in the vegetation and along edges of grassy areas feeding on invertebrates and presumably lizards also.

Woodchat Shrikes Lanius senator occur in both sites during both migration periods from late March to early June and again from late July to September (Cortés et al., 1980). These have been seen taking adult P. hispanica.

Ocellated Lizards are active in the Cemetery between March and November and have been observed chasing adult P. hispanica. Adult Ps. algirus, which show year-round activity, have been seen eating hatchling lizards.

Praying Mantises Mantis religiosa are common in the Cemetery between July and October and are known to prey on young P. hispanica (Andrada, 1979).

Feral cats are present at both sites throughout the year. Humans also use the sites all year round. They are more likely to see (and thus attempt to catch) lizards in the Cemetery where they are more common. Disturbance is particularly intense in the Cemetery during the religious feasts of Holy Week in March or April and during the weeks preceding the Feast of All Souls (2nd November) when families (including children who are most likely to chase lizards) renovate the graves.

6.7 Tail breakage

6.7.1 Introduction

Data on fequencies of autotomy (tail breakage) in lizard populations in nature have been used as indirect estimates of the predator pressure on these populations (e.g. Rand, 1954, Blair 1960, Tinkle and Ballinger, 1972, Willis et. al., 1982). Vinegar (1975) found that in Sceloporus, females of populations in areas with the least protective cover displayed both the lowest survivorship and the highest autotomy frequency. Tinkle (1972, 1976) also demonstrated consistency of divergence in the proportion of broken tails with differences in survivorship.

The assessment of predator load through the use of tail autotomy frequency is complicated by a number of factors when different populations are being compared. Prey behaviour (e.g. perch height and vulnerability), prey density and predator efficiency may serve to complicate the situation.

Highly efficient prdators cause few injuries and many deaths and will therefore not contribute to increasing the proportion of lizards with autotomised tails. Intraspecific agonistic encounters can also cause tail autotomy, masking the effect of predation.

Data on tail loss collected during the course of this study were used in comparing predator pressures on the sexes and size classes of the lizard population in the study sites and discussing other possible causes of autotomy.

6.7.2 Methods

Records were kept of the occurence of autotomised or regenerated tails of all captured and captive lizards. Lengths of old or regrown parts as well as of unbroken tails were recorded.

The lizards were grouped according to snout-vent length as follows:

Class A : $\leqslant$ 35mm; Class B : 36 - 40mm; Class C : 41 - 45mm;
Class D : 46 - 50mm; Class E : 51 + mm.

Numbers of lizards with broken or regenerated tails were also recorded during transects.

Sexual and site effects on frequencies of tail autotomy were tested using 2 x 2 and N x N contingency tables and X^2 distribution.

Rate of regrowth of tails was monitored in captive animals.

6.7.3 Results

Behavioural observations including 45 hrs of continuous field observation did not result in any evidence of tail breakage through agonistic encounters. In captivity tail breakage was observed on one occasion only when a dominant adult male caused the loss of the tail of another male kept in the same small (45 cm x 30 cm x 30 cm) vivarium. On one occasion in the field an adult male P. hispanica was observed swallowing a P. hispanica tail (not its own) although it was impossible to tell whether it had been itself responsible for the breakage or it had stumbled across the recently autotomised tail.

Agonistic behaviour was not seen in the field other than between adult males and then only rarely (5.3). Therefore it can be assumed that tail loss and other injuries resulted exclusively from encounters with predators and not from intraspecific agonistic behaviour, particularly in young lizards.

Proportions of P. hispanica males and females from NFC having autotomised (recently broken or regenerated) tails are presented in Table 6.5. These were tested in a 2 - way contingency table of sex and tail condition. The effect of sex is not statistically significant ($X^2 = 0{\cdot}04$; 1df; $P > 0{\cdot}9$). Proportions of males from BFB having autotomised tails are also given in Table 6.5. The effect of site on male tail breakage is not statistically significant ($X^2 = 0{\cdot}14$; 1df ; $P > 0{\cdot}9$) although sample size for BFB is small.

Frequencies of tail breakage have been reported to increase with body size (Pianka and Parker, 1972; Parker and Pianka, 1973; Vitt, 1974; Vitt et. al., 1974; Brown and Ruby, 1977; Schoener and Schoener, 1980; and others).

The lizards sampled from NFC were grouped into size classes on the basis of SVL. The numbers of individuals and the proportions with autotomised tails are presented in Table 6.6. These were tested in a 5 x 2 contigency table of size class and tail condition. There is a statistically significant effect of size class on tail breakage when both sexes are considered together ($X^2 = 11{\cdot}54$; 4df; $P < 0{\cdot}025$) and when males are considered alone ($X^2 = 13{\cdot}06$; 4df; $P < 0{\cdot}025$), but not when females alone are tested ($X^2 = 1{\cdot}71$; 4df; $P > 0{\cdot}5$).

Table 6.5

Variation in the frequency of autotomy in Gibraltar *Podarcis hispanica*. Presented is the proportion of autotomy for each group. Sample sizes are tabulated in parentheses.

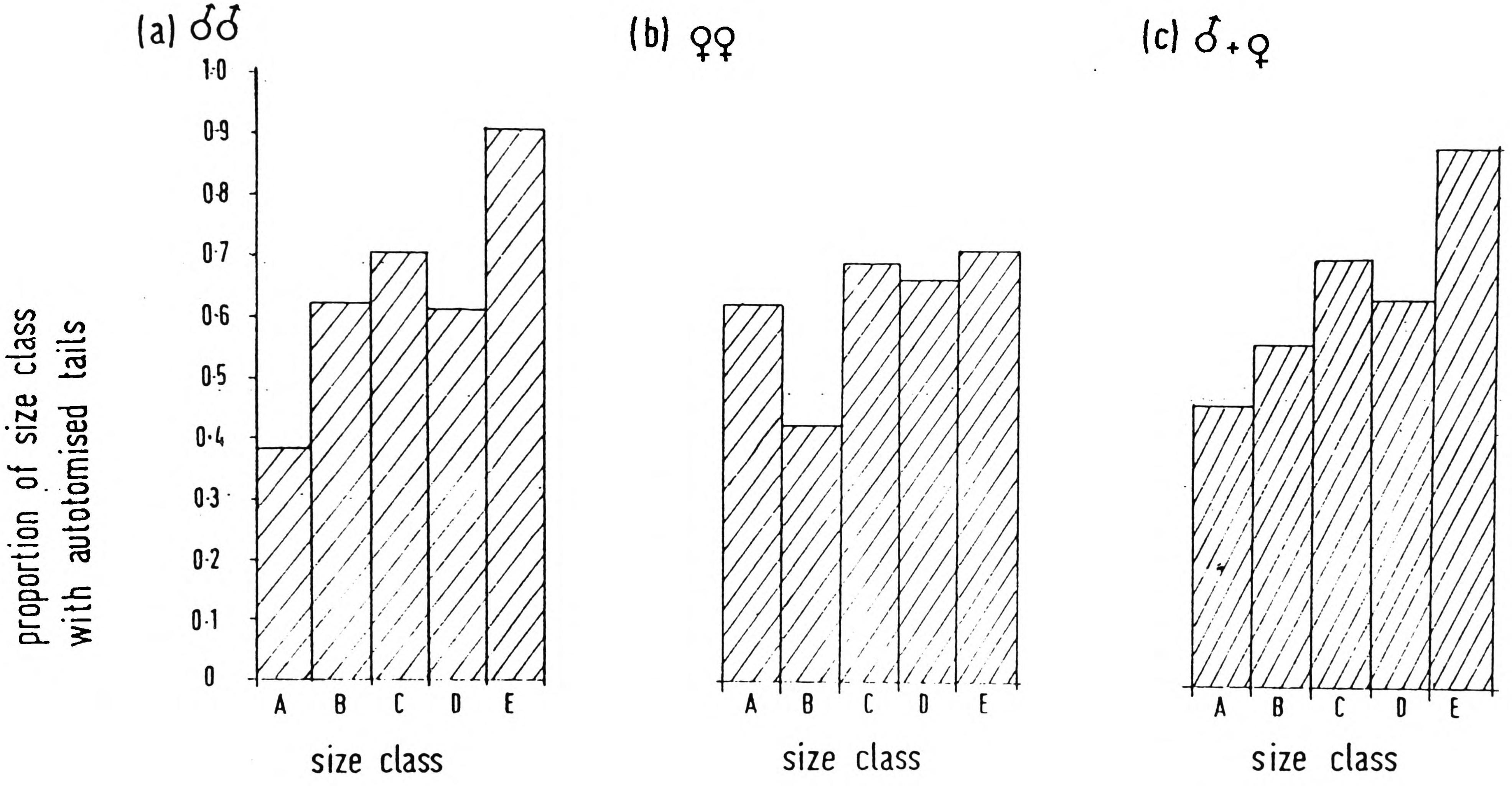
Area	♂♂	♀♀	Total
NFC	0·670 (63)	0·651 (28)	0·659 (91)
BFB	0·588 (10)	-	-
Total	0·657 (73)	-	0·652 (101)

Table 6.6

Variation in size class and in associated autotomy in Gibraltar (NFC) *Podarcis hispanica*. Proportions of autotomy and sample sizes presented as in Table 6.5. (Size classes as in 6.7.2.)

Size class	♂♂	♀♀	Total
A	0·389 (7)	0·625 (3)	0·462 (12)
B	0·625 (10)	0·429 (4)	0·565 (13)
C	0·708 (17)	0·692 (4)	0·703 (26)
D	0·615 (8)	0·667 (3)	0·636 (14)
E	0·913 (21)	0·714 (2)	0·887 (26)

Fig. 6.21 PROPORTIONS OF SIZE CLASSES OF P.HISPANICA (NFC, GIBRALTAR) WITH AUTOTOMISED TAILS (FROM TABLE 6·6)



The frequencies of tail breakage are presented as histograms in Figure 6.21. For P. hispanica there is a marked increase in these frequencies between size classes A and B and again between D and E. Even the smallest lizards show some autotomy.

Overall tail breakage frequencies (0•67 for males; 0•65 for females) are comparable to those of lizards in other studies. Table 6.7 gives the results of Vitt et al.(1977)in their review of the adaptive value of tail autotomy. The data for P. hispanica most resembles those of Coleonyx variegatus and Gerrhonotus multicarinatus, those with the highest tail loss frequencies in their study and both of which like young P. hispanica, move their tails during active foraging. Since attacks on tailless lizards by snakes always results in captures in some species (Congdon et. al. 1974), and since a high frequency of adults with regenerated tails is coincident with low adult mortality (Vitt et. al.,1977) it is suggested that tail autotomy is effective for predator escape.

6.7.4 Discussion

Male P. hispanica show slightly (though not significantly) more tail breakage than females. When the data are divided into size classes however, there is a significant trend in increasing tail breakage frequencies for males (and males and females together) but not for females considered alone. These data may reflect a higher frequency of predator encounters for adult males than for adult females. This may be true since males are more often seen in the open than females and tend to perch more prominently in the open, particularly during the mating season (see 6.3). Females may be less likely to escape predation than males when they are gravid since they are burdened with developing young. This would decrease their chance of escape, increasing predator efficiency and decreasing the proportion of autotomy recorded.

Low proportions of tail breaks can result from the injury-causing agent being particularly effective in causing death in injured individuals (Willis et al., 1982). A possibility therefore is that males are as a whole exposed to less-efficient predators than are females. Males would seem to be more exposed to aerial predators (birds) which hunt by sight. Females, which tend to remain in

Table 6.7

Variation in frequency of autotomy in Gibraltar (NFC) Podarcis hispanica compared with results in Vitt et. al. (1977).

Species	Immatures	Adults
Coleony variegatus	0·40	0·77
Eumeces skiltonianus	0·17	0·62
Eumeces gilberti	0·50	0·52
Gerrhonotus multicarinatus	0·43	0·74
Podarcis hispanica	0·51*	0·74**

* Size classes A,B and C

**Size classes D and E

vegetation may be more exposed to snakes and praying mantises which do not hunt in the open. It is conceivable that these latter predators are more efficient in capturing lizards without allowing them to escape by autotomisung the tail than are birds (or humans). It was unfortunately impossible to determine this experimentally. P. hispanica is active throughout spring, when males are much more evident than females (6.3) so that males may be exposed to predators for longer during the year than females. Sexual differences in behaviour could therefore be important in explaining the sex-associated patterns of tail autotomy (Brown & Ruby,1977).

The results presented in Figure 6.21 suggest high predation occurs between lizard size classes A - B and size classes D - E. Young lizards (class A) will tend to be subjected to a greater number of potential predators due to their small size. These will include smaller birds and notably praying mantises which are most common in the habitat during the time of hatching of the lizards. The predator load on hatchling lizards is further suggested by the bright green tails of P. hispanica at this age, and which act to distract attention from the body. Such a characteristic is generally believed to have an anti-predator function. In addition to the colour, the tail tip is often twitched during foraging, presumably also to distract predators. Adult lizards of size class E, and males in particular, for which the increase in tail break frequency is greater, are more obvious than younger subadults and therefore more open to predatory attack. Agonistic encounters between adult males is also more likely than between juveniles and subadults, so that there may be an intraspecific effect. This is however unlikely when the field observations are considered.

A reverse trend - a drop in tail loss frequency after the juvenile class - was observed by Willis et al. (1982) in Thamnophis species. This was attributed by the authors to death of injured individuals as a result of physiological stress during their first-year hibernation. P. hispanica does not hibernate in Gibraltar.

There is a difference between male and female P. hispanica in that female tail breakage frequency does drop between size classes A and B.

Frequencies of autotomy can be related to predation pressures directly even if qualitatively, only in species and size classes which show little tail breakage due to intraspecific fighting. Avoidance rather than fighting is the natural condition, as seen during hours of observation of *P. hispanica*. Few tails should therefore be lost intraspecifically. This would be selected against if it gives the tailless lizard a disadvantage in any case (Vitt *et al.*, 1977). Schoener & Schoener (1980) found that in Bahamian *Anolis* lizards tail-break (and back toe) injury rates are frequently negatively correlated with conspecific density - most likely a result of predation in which case the correlation may reflect a depressive effect of predation on population size. Front-toe injury rates were positively correlated with conspecific density. No front toe injuries were seen in the *P. hispanica* studied in Gibraltar, supporting the observational evidence of lack of fighting between lizards. I suggest therefore that tail loss frequency in *P. hispanica* can serve as an indication of predatory pressure in the absence of any direct method of determining such pressure.

6.8 Discussion

Pirloge (1982) found that the limited activity time and the variability of climatic conditions experienced by Lacerta vivipara in Puy-de-Dôme, France, affected growth rates of some categories of lizards, i.e., males and sub-adult females, in which growth rates fell considerably during adverse weather conditions. Growth also appeared to cease altogether during winter hibernation.

In P. hispanica it is likely that growth is also restricted during periods of inclement weather, or when food intake is otherwise restricted. However, growth was evident through the winter, as the proportion of size classes varied, and as the captive lizards kept in winter conditions showed. The L. vivipara in Pirloge's (1982) study achieved secondary sexual characteristics during their second summer, but breeding did not take place until the following year. P. hispanica in captivity mated and lay in their first year, although in the field this may not have been so easy due to the dominance of larger lizards.

There was no evidence, as there was in L. vivipara (Pirloge, 1982) and in other species (Bradshaw, 1971) of two types of sub-adults, a group of small individuals with low growth rates, and one of larger lizards, of recognisable sex and higher growth rates.

Both this division of the year's cohort and the temporal separation of activity of male and female L. vivipara (not seen in Gibraltar) are attributed by Pirloge (1982) to the need to use limited resources profitably. In Gibraltar, in contrast, activity is not so seriously curtailed during most of the year (Chapter 8), and these adaptations may not be necessary.

Other adaptations may have become necessary, for example, to allow activity during lower temperature conditions in winter (e.g. 8.5).

CHAPTER 7

FOOD AND FEEDING BEHAVIOUR

7 FOOD AND FEEDING BEHAVIOUR

7.1 Introduction

A subject that has been thoroughly covered in at least one European species (*Lacerta vivipara*) is food consumption (e.g., Avery 1971, 1973).

It was felt that in order to make an attempt at such a study of *P. hispanica*, a great deal of time, particularly in the laboratory would have been required. Since this was not possible, other aspects of the feeding ecology of the species were investigated, and laboratory work was limited. Thus, emphasis was given to time spent foraging at different times of year and to different foraging methods employed. This, together with a knowledge of the invertebrates available in the foraging microhabitat and an idea of food items being taken, allowed discussion of the activity of the species in relation to feeding behaviour.

7.2 Laboratory observations

7.2.1 Methods

The feeding behaviour of the lizards kept in captivity in Oxford (3.3) was observed and recorded. Notes were taken on the method of capture of prey by the lizards, on prey size, and the time taken to consume prey.

The food used in the vivaria were mealworms of two sizes (named "large" - approximately 30mm; and "small" - approximately 20mm) and crickets Atheta domestica of three sizes (5mm, 10mm and 15mm approx.).

An experiment was carried out to attempt to determine whether lizards of different sizes showed a preference for different-sized prey. Due to the limited time available, only three lizards were used in these experiments. These were two males (SVL 48•0mm and 42•5mm) and one female (SVL 42•5mm), giving a range of head dimensions (4.1). Each was placed in a small vivarium (35cm x 25cm x 25cm) which was heated and illuminated with a 40W light bulb 20cm from the floor of the tank. A thin layer of sand was placed on the floor of each vivarium. A stone provided shelter and an elevated platform for basking. Two young cockroaches Periplaneta americana of each of five different size classes (see Table 7.1) were released into each tank. Numbers of cockroaches remaining in the tanks were recorded each evening and the number eaten by the lizards found by subtraction. A control tank with no lizard was used to confirm that cockroaches were not escaping up the sides of the tank. The cockroaches that had been consumed were replenished the following morning before the lizards had emerged.

7.2.2 Results

Table 7.1 lists the results of the food choice experiment, which are represented in Figure 7.1. The results for each lizard do not differ significantly from each other (Kolmogorov-Smirnov test). They suggest a preference for the larger cockroaches, but a wide range of sizes was taken. The large male was the only lizard to take the smallest cockroaches.

Lizards in the main vivaria usually attacked prey which they encountered while moving around the tank. Once seen, prey was normally attacked immediately. Handling time as summarised in Table 7.2 included the time from catching the prey to once it had been completely swallowed. Usually the lizards continued to flick their tongues after this.

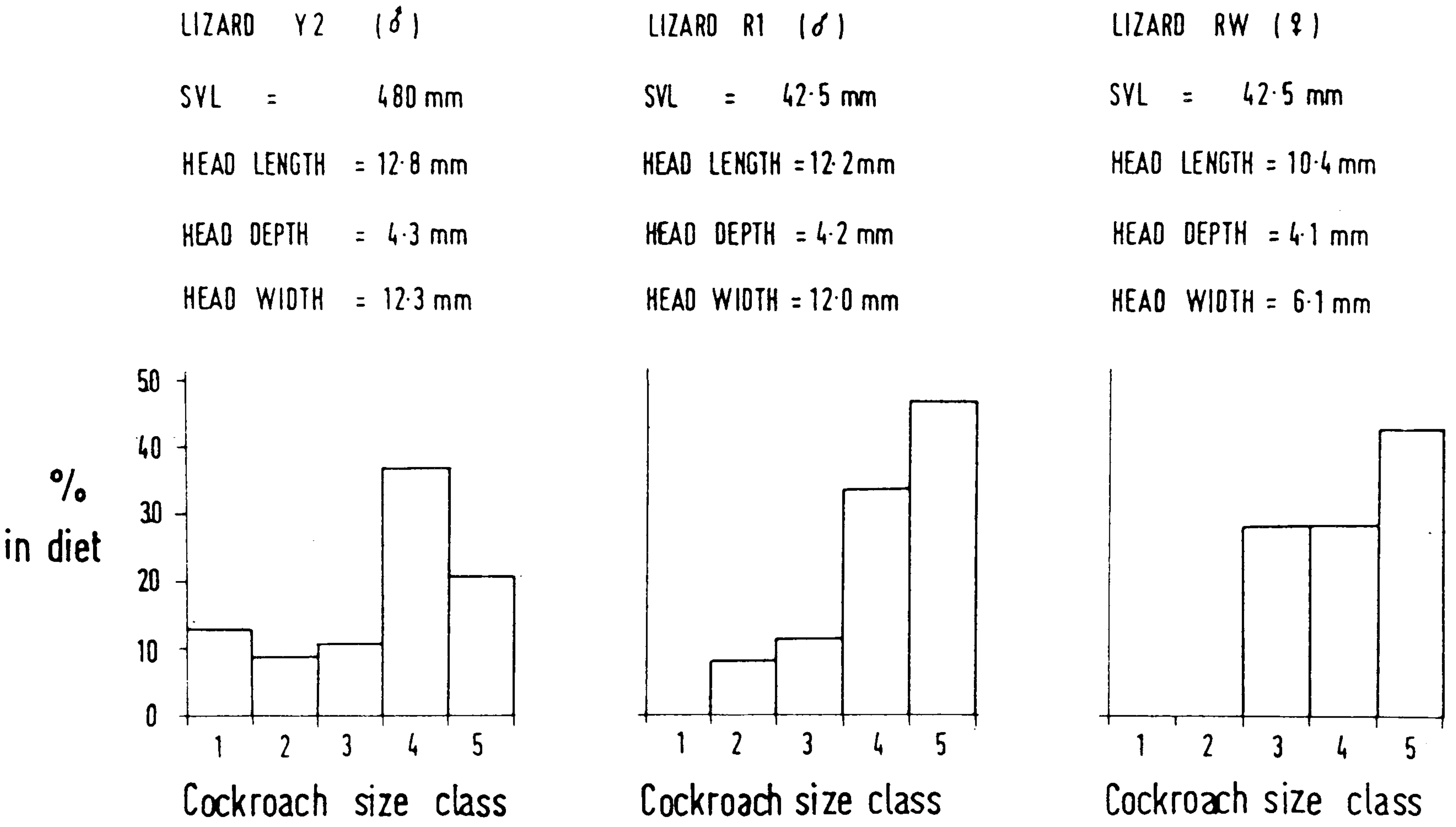
Table 7.1 Proportion of cockroaches <u>Periplaneta americana</u> eaten by marked lizards.

Lizard code	SVL	sex	Proportion of cockroaches taken by cockroach size class* 1	2	3	4	5	No. of days of experiment
Y2	48•0	♂	0•13	0•09	0•11	0•37	0•30	13
R1	42•5	♂	0•00	0•08	0•11	0•34	0•47	20
RW	42•5	♀	0•00	0•00	0•29	0•29	0•42	8

*The length of cockroaches of each size class was determined by measuring 10 individuals of each instar. Results were:

Size class	1	2	3	4	5
mean length (mm)	4•3	7•0	10•6	13•0	15•9
S.D.	0•3	0•7	0•5	0•9	0•3

Fig. 7.1 SELECTION OF COCKROACH SIZE CLASSES BY *P. hispanica* (SEE TABLE 7.1)



LIZARD Y2 (♂)
SVL = 480 mm
HEAD LENGTH = 12·8 mm
HEAD DEPTH = 4·3 mm
HEAD WIDTH = 12·3 mm

LIZARD R1 (♂)
SVL = 42·5 mm
HEAD LENGTH = 12·2 mm
HEAD DEPTH = 4·2 mm
HEAD WIDTH = 12·0 mm

LIZARD RW (♀)
SVL = 42·5 mm
HEAD LENGTH = 10·4 mm
HEAD DEPTH = 4·1 mm
HEAD WIDTH = 6·1 mm

SAMPLES NOT SIGNIFICANTLY DIFFERENT (KOLMOGOROV - SMIRNOV TEST)

Table 7.2 Prey handling times of captive *P. hispanica*

	mean handling time (seconds)	standard deviation	range	No. of observations
All lizards: 10mm crickets	64•0	39•80	13 - 120	8
All lizards: small mealworms	58•7	45•94	5 - 171	11
All lizards: 15mm crickets + large mealworms	97•2	84•35	34 - 306	12
All lizards: 10mm crickets + small mealworms	60•95	42•38	5 - 171	19
♂ lizards > 52•5mm: 10mm crickets + small mealworms	42•56	34•59	5 - 120	9
♀ lizards < 50mm: 10mm crickets + small mealworms	90•80	56•49	13 - 171	5

The results for 10 mm crickets and for 'small' mealworms have been pooled (the ranges of time taken overlap completely : 13s to 120s and 5s to 171s respectively). The data for 15mm crickets and large mealworms were similarly pooled. There is no significant difference (Kolmogorov-Smirnov test) between either the handling times of different foods by all the lizards or of all the food sizes between lizard size groupings. There is a tendency however for more time to be taken over handling larger than smaller prey (mean handling time was 97•20s and 60•95s respectively) and for females to take longer than males over similar-sized prey (mean handling times were 90•80s and 42•56s respectively).

7.2.3 <u>Observations</u>

After three days of being transported without food, the lizards were placed in different vivaria. Those that encountered young crickets took them quickly without hesitation. Three lizards, however, were only presented with mealworms. All three closely examined the mealworms for up to one minute before proceeding to attack them. This hesitant behaviour was not observed on any subsequent occasion.

On three occasions lizards were seen to investigate and then consume dead insects, including some larger than those normally taken live. One female (SVL = 42•5mm) was seen to eat the leg of a large dead cricket, and then return at intervals to swallow the rest in small pieces torn off by biting and shaking its head to and fro. The cricket was completely consumed in a total of seven minutes.

On one occasion (and once also in the field) a lizard was seen to eat the recently-deposited faecal pellet of another lizard.

The capture of a live prey item (other than of a relatively inactive mealworm) usually followed a short chase of up to 30cm. Longer chases were abandoned almost invariably. If the captured prey struggled, it was shaken . This appeared to be particularly necessary when large mealworms were caught.

Crickets larger than 15mm were almost invariably ignored.

7.2.4 Discussion

The sizes of food items eaten by P. hispanica individuals (i.e. about 15mm or less)are similar to those taken by Anolis lizards of similar head length (4. 1)(Schoener & Gorman,1968).

Adult P. hispanica can feed on a range of prey sizes. Larger lizards will be able to cope with larger prey items in relatively short handling times. Small prey will require negligible handling, especially if chanced upon while foraging or basking, so that the ratio of food value to handling time will be favourable (Pyke et al.,1977). This advantage may be lost to smaller lizards which would tend to drop these smaller items from their diet if larger ones (below a certain threshold size) are available (Figure 7.1).

The eating of dead insects allows a larger item (probably of higher food value) to be consumed with reduced difficulty, since the prey will not struggle nor escape. Since once the dead item is located searching time will also disappear, the total time taken to consume the dead insect will probably be less than if a number of live prey items of smaller size were taken instead. In the case in question, a live cricket of over 20mm length would almost certainly have been impossible to handle.

A lizard will remember the site of prey capture. In the field, lizards disturbed from recently-caught prey have been seen to return to the site to search for the dropped prey item.

The behaviour of lizards towards a newly-encountered potential food (mealworms) was cautious, but the food item was soon accepted and incorporated into the diet. A non-specialist opportunistic feeder (Pianka,1973) would be expected to be able to include a new item readily in its diet.

7.3. Field observations

7.3.1 Methods

The methods used in collecting field data were described in general in Chapter 3.

Observations were of two types, transects and continuous.

Transect data collected relevant to this chapter were the activity of each lizard when first observed, viz. whether it was foraging or basking. Unfortunately, since each lizard was observed only briefly, and was often disturbed as I moved through the habitat, it was difficult to recognise other types of behaviour. The proportions of lizards of different size classes seen foraging and basking at different times of year and during the day were calculated.

Continuous observations allowed individual lizards to be followed for various lengths of time and the time spent in each activity (Table 5.4) to be recorded. This provided the opportunity of comparing individual behaviour with the observations on the wider section of the lizard population sampled during the transects. Only data relating to foraging activity is discussed in the present chapter. Basking is considered in Chapter 8.

One source of bias in the continuous observations arose from the recording of incomplete intervals. On a number of occasions a timed interval on an individual lizard did not include the time of commencement or ceasing of the activity. In particular, since observations usually ended when lizards were lost while foraging in vegetation, the length of time spent in that activity was under-estimated by an unknown amount.

A second source of bias arose from some individual lizards contributing more than others to the data.

The total overall lengths of time spent in each activity were calculated. These results were subdivided into those for different lizard size categories. The numbers and lengths of intervals spent by the lizards in each activity were also extracted from the data.

Continuous observation allowed clearer separation of basking and 'sit and wait' behaviour (Pianka,1973). In the latter cases, lizards were seen, usually in the open or in 'mosaic' or patterned sunlight, facing into vegetation with head often raised above the surface of the ground or wall. The head was sometimes turned as if the vegetation, always within about 10cm of the lizard, were being 'scanned' for prey. In contrast, when a lizard was basking or otherwise at rest, it was seen to lie flat, usually in full sun away from vegetation, with its chin on the surface of the ground or wall. On occasions, a lizard in such a pose would react to a passing insect, which might be attacked if close enough, but which would not normally be chased. Lizards in 'sit-and-wait' posture, however, would run or jump into the vegetation after prey. Lizards in 'sit-and-wait' posture are illustrated in Appendix 3.

Data from each individual session of observation were analysed separately. Total time spent basking, foraging, in 'sit-and-wait' posture and carrying out other activities was determined and proportions of time spent in each activity calculated. These 'other' activities were 'social' (including chases, displaying and mating), feeding, drinking, and periods during which lizards were at rest out of direct sunlight (i.e. in shade or 'mosaic' and therefore not basking).

Individual session results were added for all observations made in each month and overall monthly proportions were calculated.

The lengths of intervals of foraging and sit-and-wait activity for lizards of various snout-vent lengths were extracted from the data for the period 28 January - 4 April 1982. This was the period during which sit-and-wait activity was most in evidence.

A comparison was made of the angles to the horizontal at which lizards lay during sit-and-wait intervals. Note was made of whether the lizard was facing vertically down or up, horizontally, or angled upwards or downwards. Both number and duration of intervals in each position were recorded. Percent number of intervals and of length of time spent in each position were calculated.

7.3.2 Results

(a) Transect observations

The overall proportion of basking and foraging observed in adult male, adult female and juvenile P. hispanica during transects is displayed in Figure 7.2. These results are significantly different from each other ($P < 0.001$). Although the proportions of foraging males and females were not significantly different, all combinations of juveniles with adults show statistically significant differences ($P < 0.001$). Over the whole year, juveniles were seen foraging less often than were adults.

The above results,sub-divided according to time of year are presented in Figure 7.3. There is a significant trend when adults and juveniles are considered together ($P < 0{\cdot}001$) and when adults only are considered ($P < 0{\cdot}05$), but not when adult males or adult females are compared alone. On the whole, more foraging was observed in the spring and summer than during the cooler months.

Since the differences observed were between adult and juvenile lizards, an analysis of activity (basking vs. foraging) was carried out for pooled data from the months of August and September, when juveniles are most in evidence. As suggested by the overall results, during these months a significantly higher proportion of juveniles were seen foraging ($P < 0{\cdot}001$; Figure 7.4).

The proportion of foraging and basking lizards according to size class (6.2) only varies significantly during these months (Figure 7.5). Proportionally more of the small lizards were seen foraging during these months.

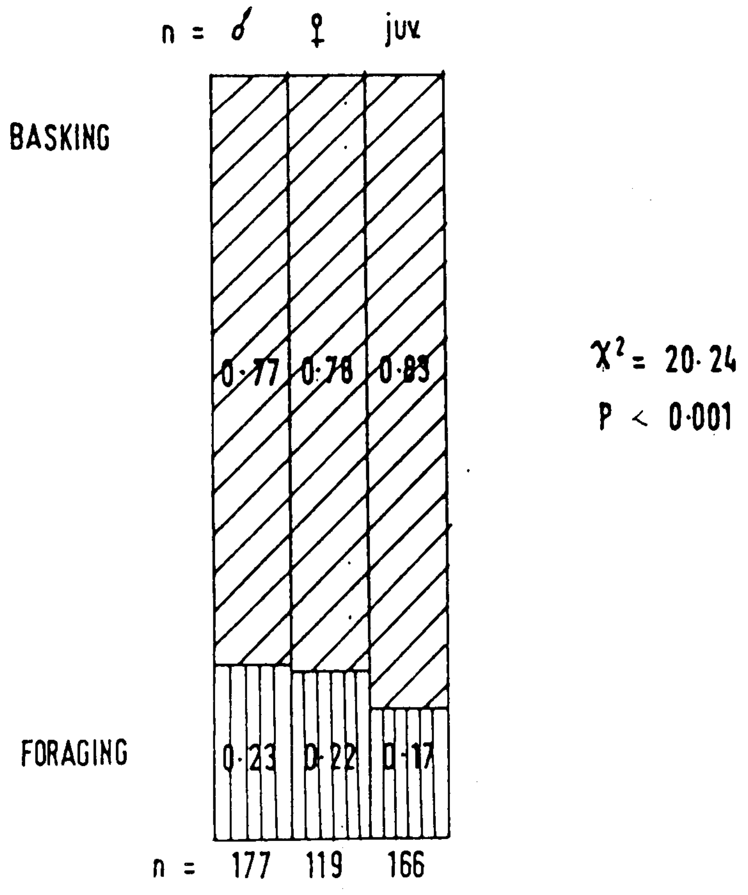
September was the only month during which a significant trend was seen in the proportions of lizards foraging or basking during different times of the day. There was a peak in foraging activity during the early hours of the afternoon. Few lizards were recorded from 12.00hrs to 13.00 hrs (see 8.3).

(b) <u>Continuous observations</u>

The overall proportion of time spent basking,in 'sit-and-wait' posture, foraging, and in 'other' activities, calculated for each month, is shown in Figure 7.7. Of the total 43 hrs 30 min of continuous observation included in this analysis (observations of less than 10 minutes or where lizards were disturbed were not included) the greatest proportion were spent basking. From the results it appears that the lizards spend proportionally more time in sit-and-wait posture in early spring (30% in February). They forage least in September and December (2% and 5% of the time respectively) and most in late spring and summer (46% in April, 30% in June, 26% in July and 39% in August).

In order to allow some comparison with the results of the transect observations given in Figure 7.3, the data in Figure 7.7

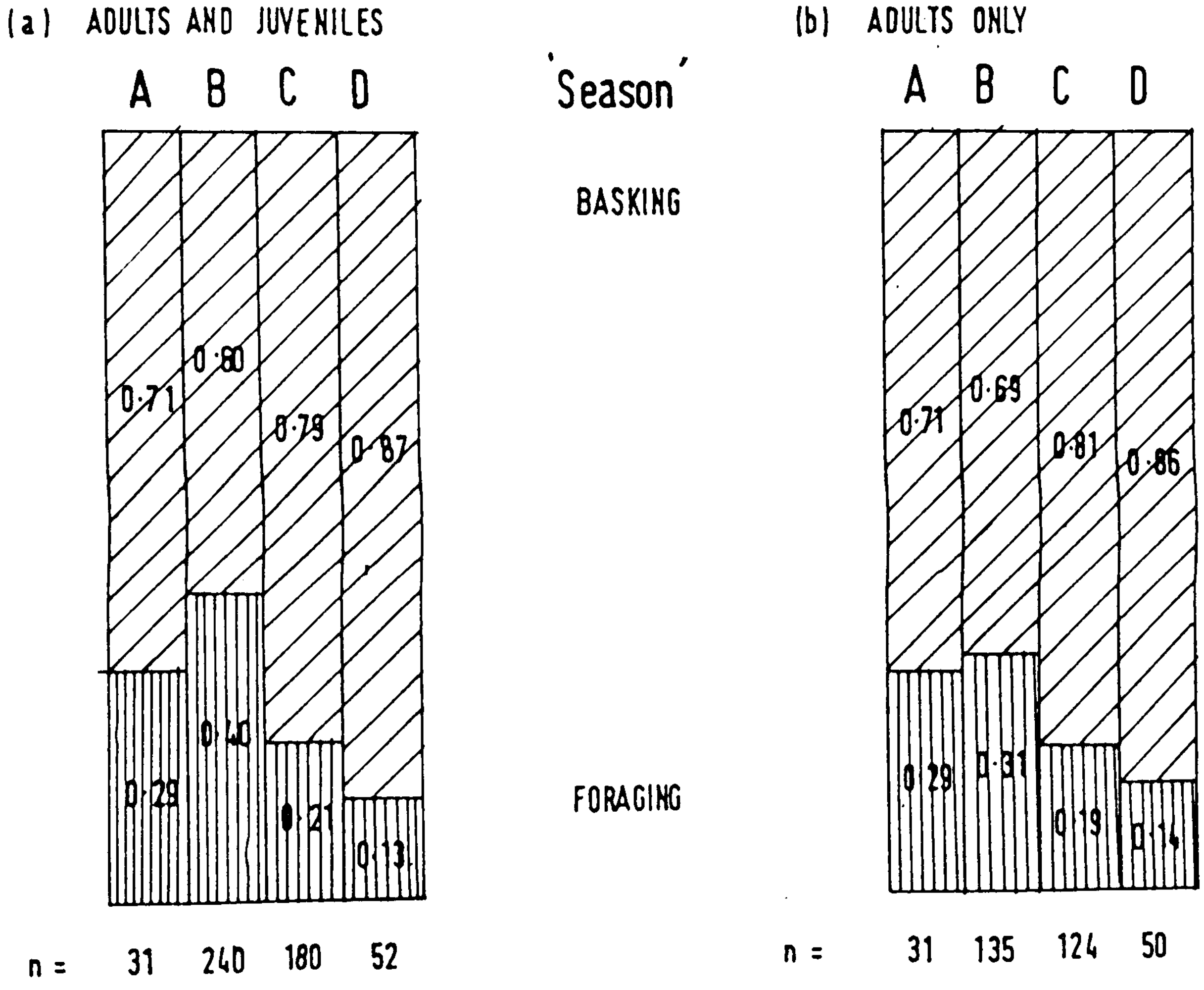
Fig. 7.2 OVERALL ACTIVITY OF P. hispanica AT GIBRALTAR.
(PROPORTIONS OF LIZARDS OBSERVED DURING TRANSECTS)



RESULTS OF CONTINGENCY TABLES.

	♂ vs ♀	♂ vs juv.	♀ vs juv.	adult vs juv.
DF	1	1	1	1
χ^2	0·02	15·06	12·81	20·32
P	Not significant	< 0·001	< 0·001	< 0·001

Fig. 7.3 SEASONAL ACTIVITY OF P.hispanica AT GIBRALTAR (PROPORTIONS OF LIZARDS SEEN DURING TRANSECTS)



(a) $\chi^2 = 26{\cdot}02$

$P < 0{\cdot}001$

(b) $\chi^2 = 8{\cdot}35$

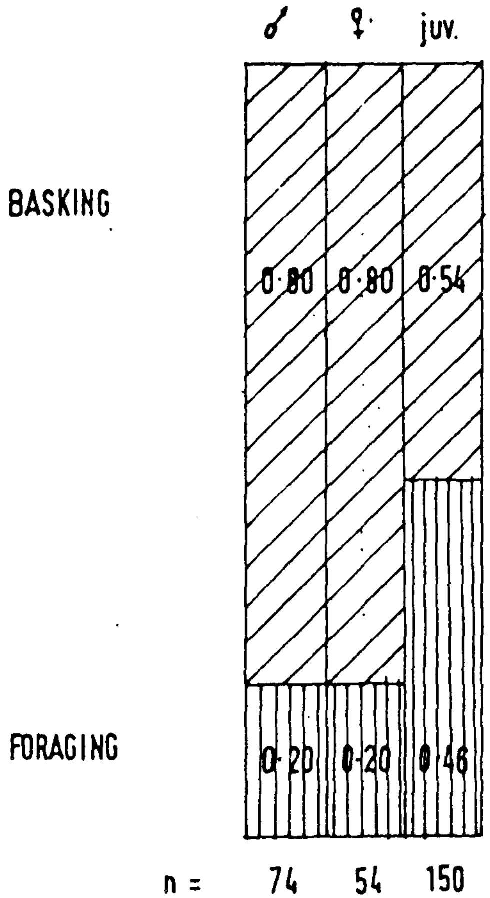
$P < 0{\cdot}05$

A = FEBRUARY, MARCH, APRIL.
B = MAY, JUNE, JULY, AUGUST, SEPTEMBER.
C = OCTOBER, NOVEMBER.
D = DECEMBER, JANUARY.

(THERE IS NO SEASONAL SIGNIFICANT DIFFERENCE IN ACTIVITY OF MALES OR FEMALES CONSIDERED ALONE.)

Fig. 7.4 BASKING AND FORAGING ACTIVITY OF *P. hispanica* IN GIBRALTAR IN LATE SUMMER / EARLY AUTUMN.

(PROPORTIONS OF LIZARDS SEEN DURING TRANSECTS.)



$\chi^2 = 20{\cdot}26$

$P < 0{\cdot}001$

RESULTS OF CONTINGENCY TABLES

	♂ vs ♀	♂ vs juv.	♀ vs juv.	adult vs juv.
D of F	1	1	1	1
χ^2	$1{\cdot}93 \times 10^{-4}$	14·90	10·94	20·26
P	Not significant	< 0·001	< 0·001	< 0·001

Fig. 7.5 PROPORTION OF P. hispanica OF DIFFERENT SIZE CLASSES BASKING AND FORAGING (NORTH FRONT CEMETERY GIBRALTAR) IN AUGUST AND SEPTEMBER

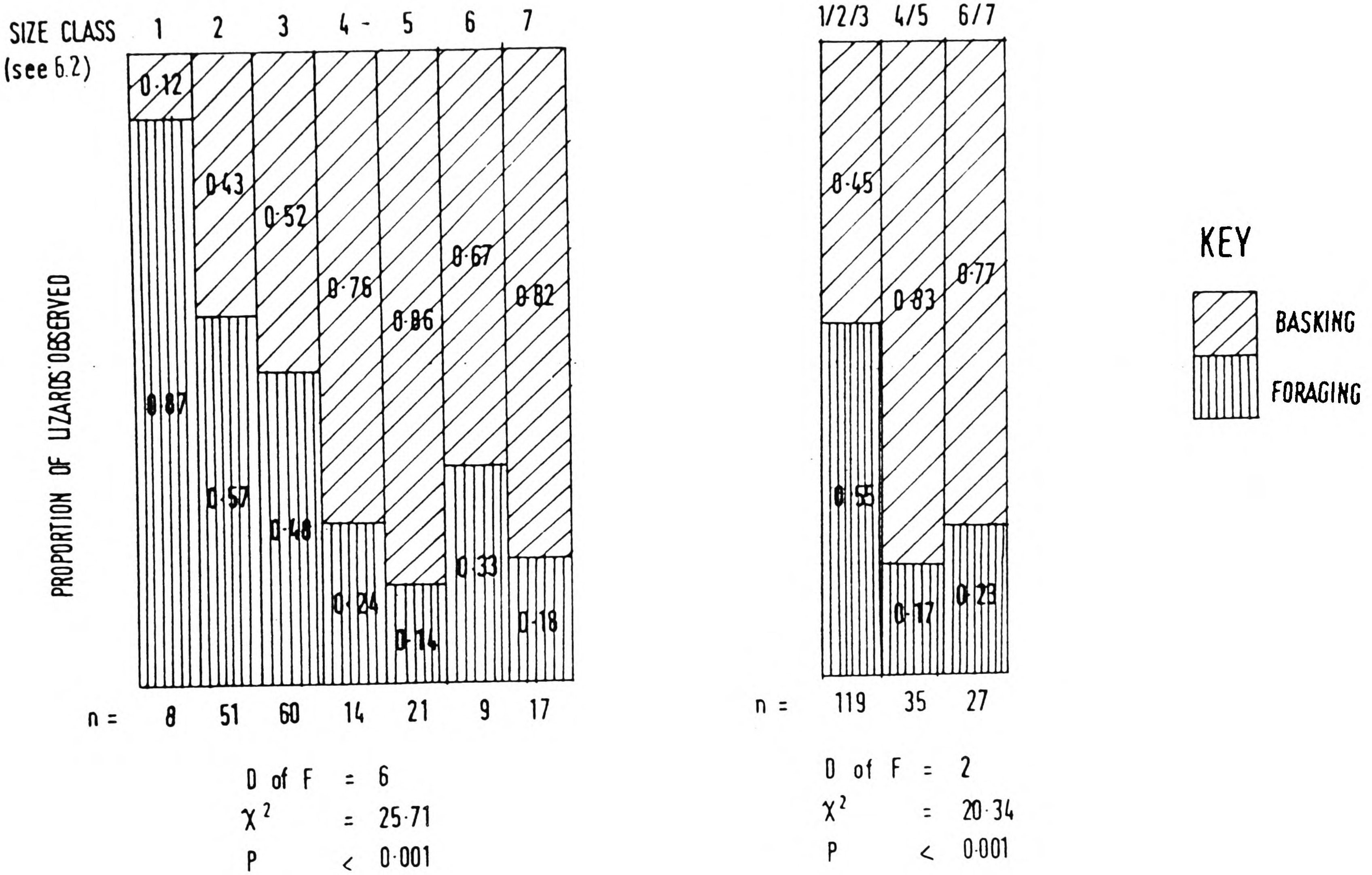
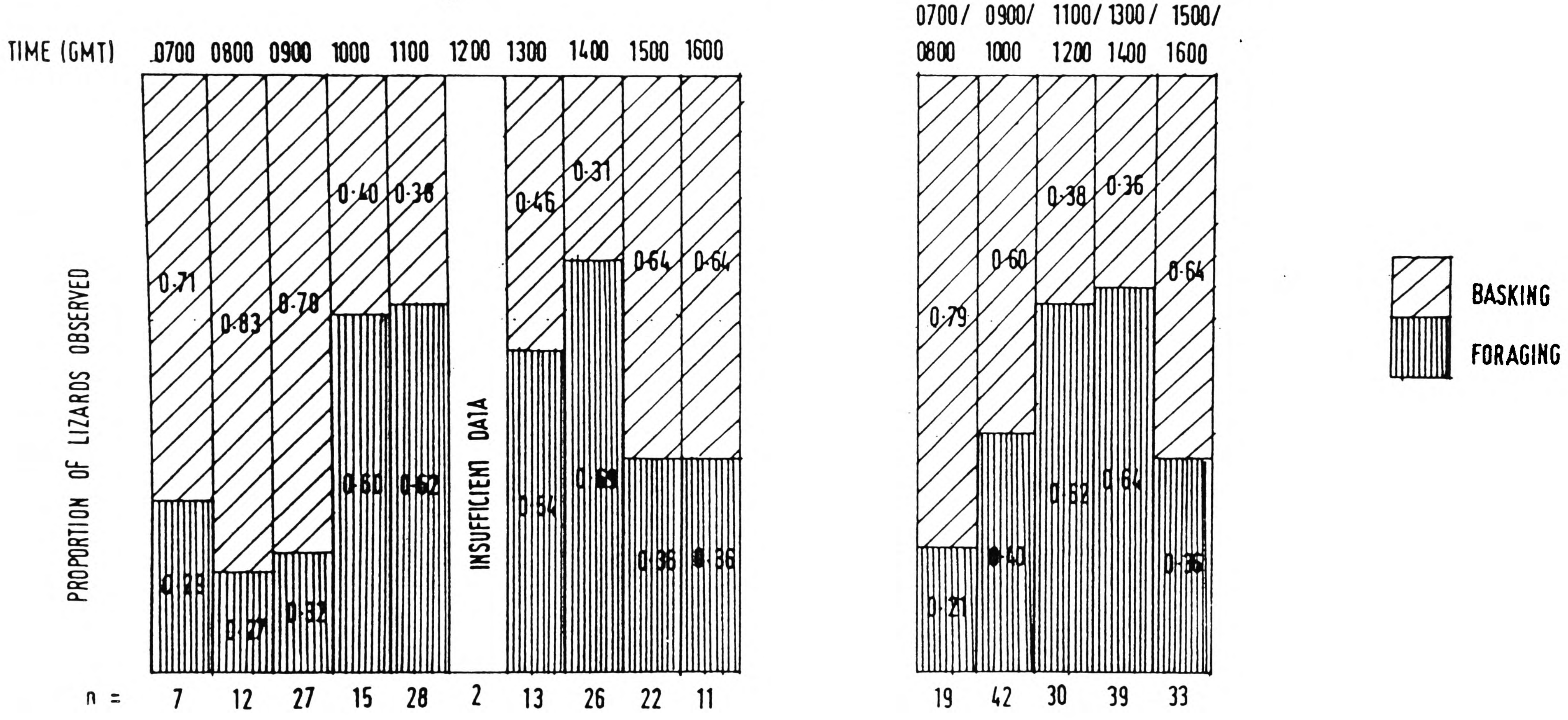


Fig 7.6 PROPORTIONS OF P.hispanica BASKING AND FORAGING AT DIFFERENT TIMES OF DAY (NORTH FRONT CEMETERY GIBRALTAR) IN SEPTEMBER.



D of F = 8
χ^2 = 17·18
P < 0·01

D of F = 4
χ^2 = 12·50
P < 0·05

Fig. 7.7 - PROPORTION OF TIME SPENT IN DIFFERENT ACTIVITIES BY *P. hispanica* AT NORTH FRONT CEMETERY GIBRALTAR

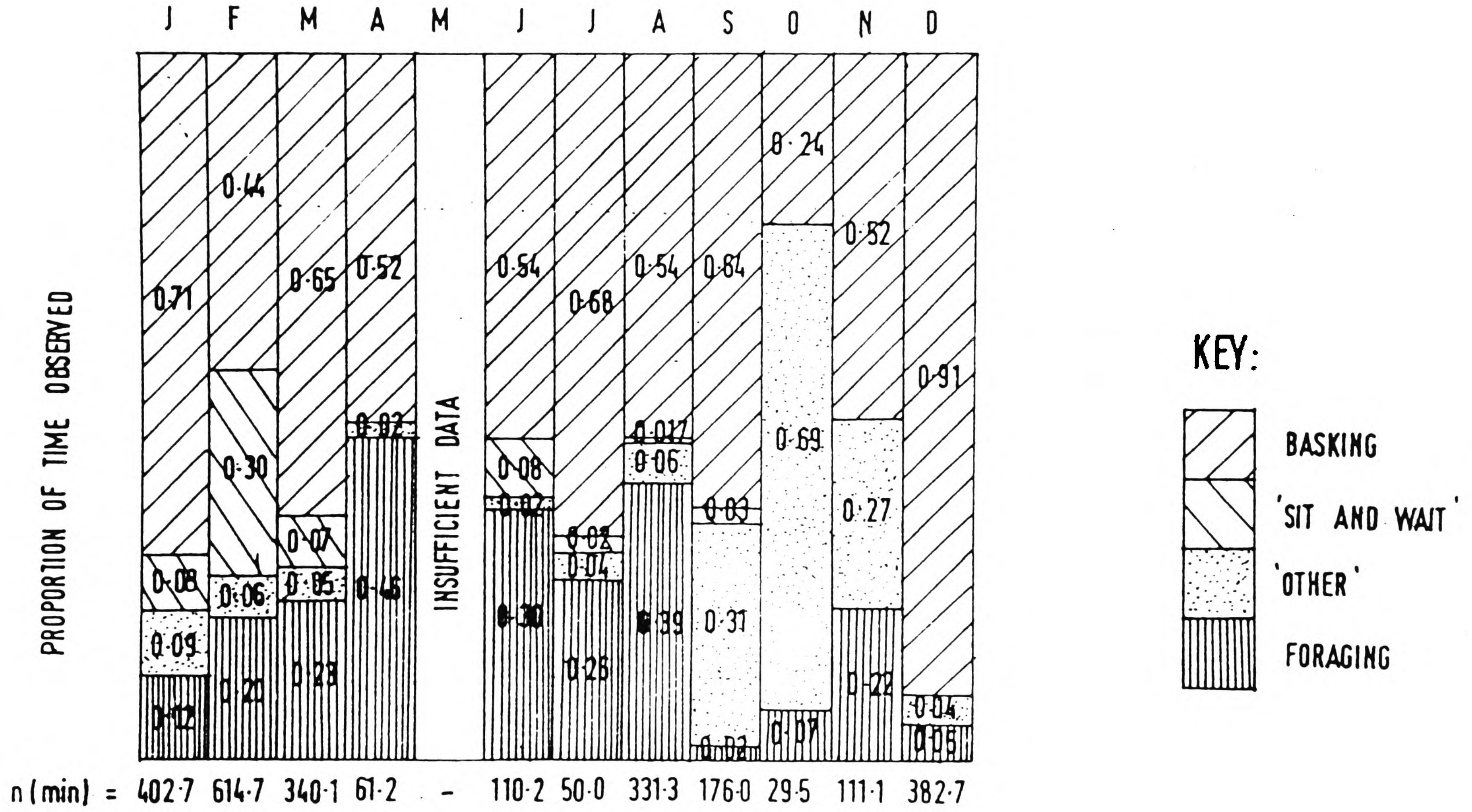


Fig 7.8 SEASONAL ACTIVITY OF P.hispanica AT GIBRALTAR (PROPORTION OF TIME SPENT IN DIFFERENT ACTIVITIES)

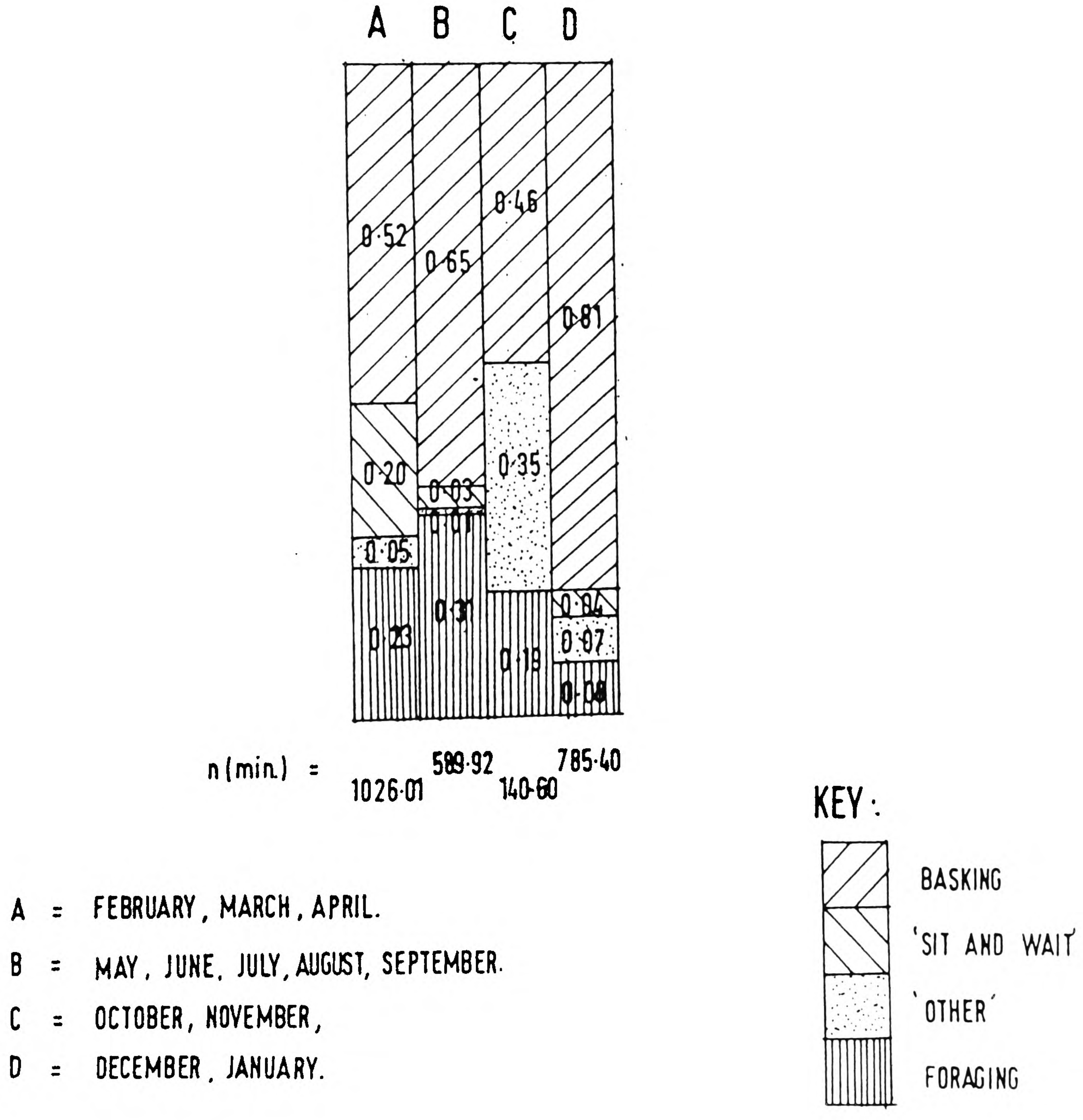
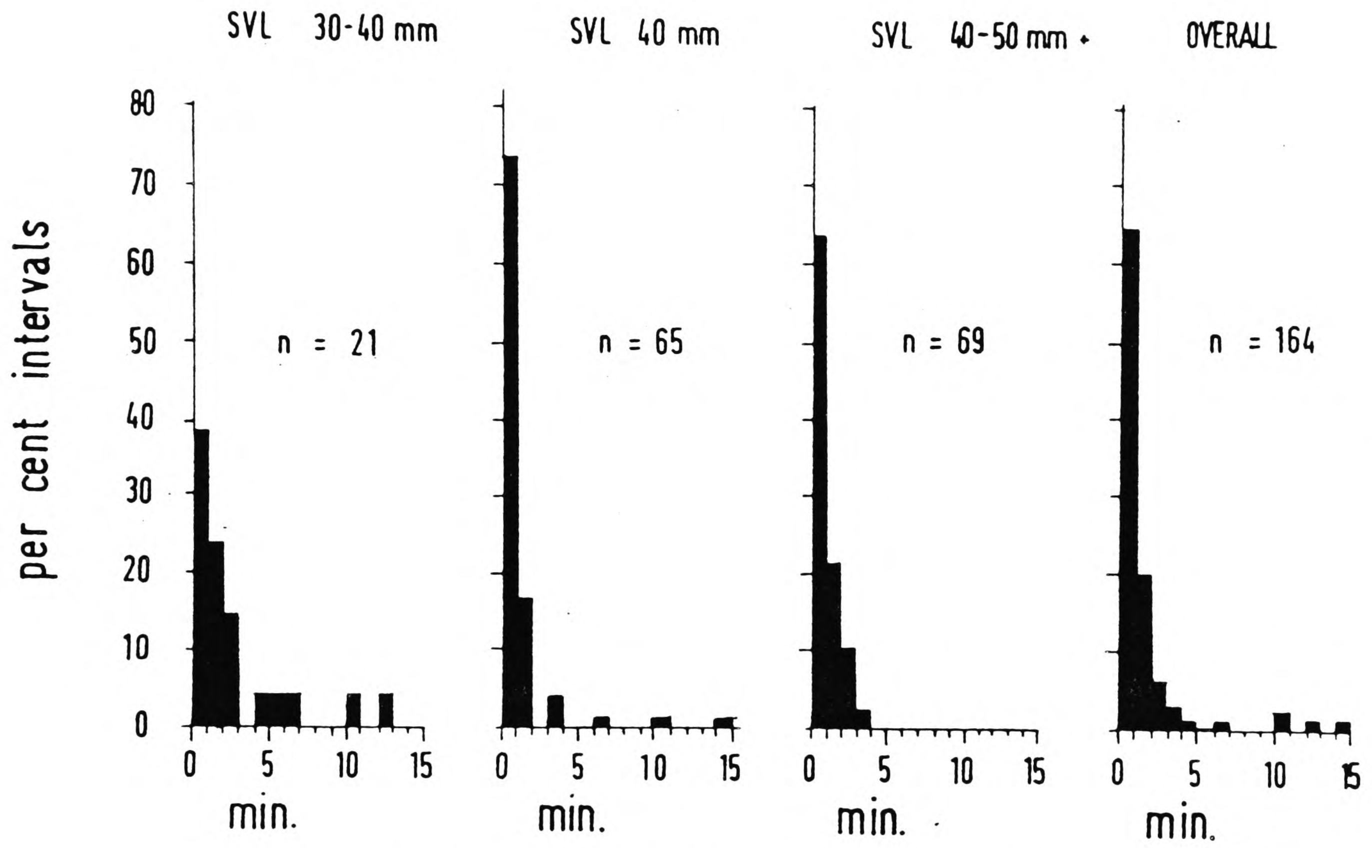
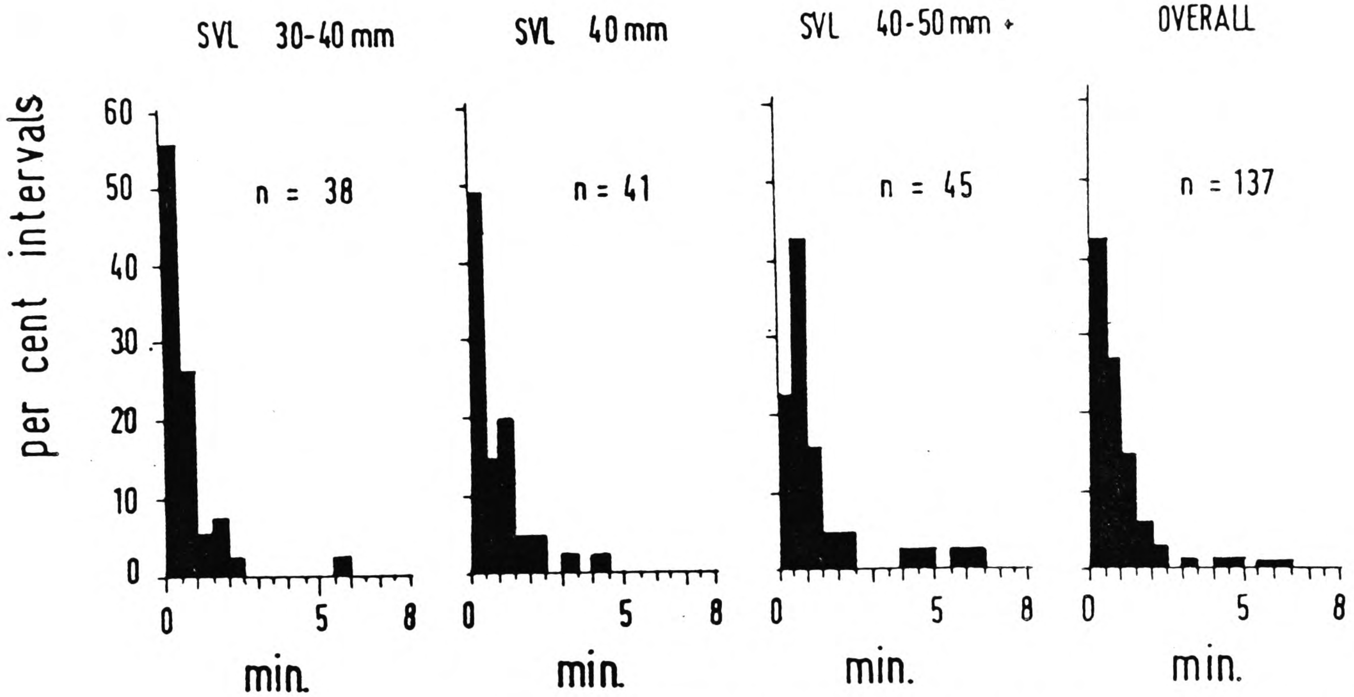


Fig. 7.9 DURATION OF 'SIT AND WAIT' INTERVALS.



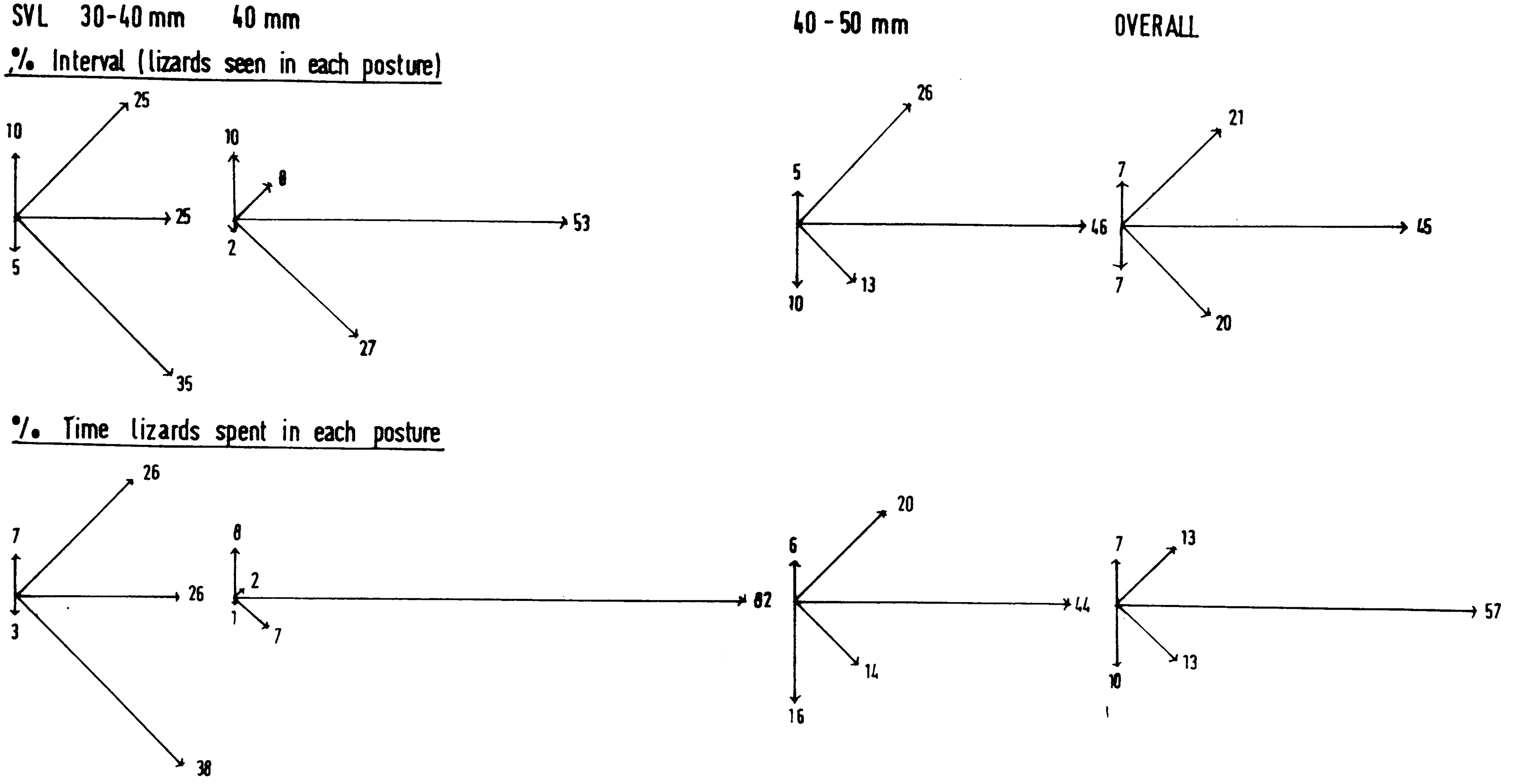
WAITING INTERVAL DISTRIBUTIONS FOR DIFFERENT SIZES OF P. hispanica AT NORTH FRONT CEMETERY.
INTERVALS LONGER THAN 15 MINUTES NOT SHOWN.
ONLY SIZES 30-40 mm AND 40mm ARE SIGNIFICANTLY DIFFERENT AT $P < 0{\cdot}05$ (KOLMOGOROV - SMIRNOV TEST.)

Fig. 7.10 DURATION OF FORAGING INTERVALS (IN VEGETATION).



FORAGING INTERVAL DISTRIBUTION IN VEGETATION FOR DIFFERENT SIZES OF <u>P. hispanica</u> AT NORTH FRONT CEMETERY.
INTERVALS LONGER THAN 8 MINUTES ARE NOT SHOWN.
ONLY SIZES 30-40 mm AND 40-50 mm ARE SIGNIFICANTLY DIFFERENT AT $P \leq 0{\cdot}05$ (KOLMOGOROV-SMIRNOV TEST).

Fig. 7.11 POSTURE ANGLES DURING 'SIT AND WAIT' ACTIVITY FOR *P. hispanica* AT NORTH FRONT CEMETERY, GIBRALTAR.



were re-arranged and pooled according to 'seasons' A, B, C and D (Figure 7.8). Except for the result for season C, where sample size was small, the sum of basking and sit-and-wait activity in Figure 7.8 and of basking in Figure 7.3 are very similar. The proportion of time spent foraging (Figure 7.8) is similar also to the proportion of lizards seen foraging during these times of the year (Figure 7.3).

The frequency of intervals of different lengths spent in a sit-and-wait position was plotted in Figure 7.9 for the period period 28 January to 4 April 1982, the time when this behaviour was most evident. Sit-and-wait intervals were normally short (under 1 minute). On three occasions only out of 155 intervals observed did capture of prey result from a sit-and-wait session.

Only the samples of lizards of SVL 30 - 40mm and 40mm differ significantly from each other ($P < 0{\cdot}05$; Kolmogorov-Smirnov test).

A similar graphical representation was prepared for lengths of foraging intervals. These foraging bouts were mainly in the cover of vegetation. Again these intervals normally lasted less than one minute. The larger lizards (SVL 40 - 50mm +) spent more intervals of 0·5 to 1·0 minutes foraging in vegetation while the smaller lizards spent more intervals of less than 0·5 minutes foraging. The lizards of SVL 30 - 40mm and those of 40 - 50mm + differ significantly in the lengths of foraging intervals ($P < 0{\cdot}05$; Kolmogorov-Smirnov test).

The angles of sit-and-wait posture for three size groupings of P. hispanica are compared in Figure 7.11. The upper diagrams show the percentage of intervals recorded in which the lizard 'sits-and-waits' at each angle. The lower diagrams show the percentage of time spent facing in each direction.

7.3.3. Discussion

The results outlined above and illustrated in Figures 7.2 to 7.7 will be discussed again in relation to activity cycles in Chapter 8. It is worth bearing in mind at this stage, however, that it is not easy to decide whether it is the need to feed or the necessity to bask that determines the proportion of a lizard's time spent in each activity.

The results shown in Figure 7.2 for transect data over the whole year suggest in fact that juveniles need to forage less and consequently bask more. However, juvenile lizards, being smaller, will warm up more quickly than adults and need to spend less time in the open. Figure 7.4 shows that this is true in the summer. During the months of August to October a prominence of juvenile lizards coincides with high temperatures. The results for this period will therefore be more directly indicative of the conditions governing the foraging behaviour of young lizards exposed to high temperatures. Clearly, juveniles spend less time basking than adults then, and more time foraging. During this time they will shuttle in and out of vegetation as they search actively for small items of prey. During cooler times of the year, small lizards, despite warming up relatively quickly in the sun, will also cool down quickly in the shade. This fact may account for there being a greater proportion overall of basking juveniles than adults.

Adult lizards spend relatively less time foraging. They can tolerate sunshine for longer than juveniles. During the summer adult lizards are active earlier in the day when temperatures are lower (8. 3). Basking time must therefore be increased at the expense of foraging time.

The seasonal trend is more clearly interpreted from Figure 7.3 which divides the year into four periods. The amount of foraging time increases during summer (period B), probably as the need for long periods of basking decreases. It is at a minimum in the winter when lizard activity is greatly reduced and most time is spent basking (8. 3). Foraging activity at that time is restricted to warm afternoons. Food requirements at this time of inactivity and predominant low temperatures must be low in any case.

Only in August, and September was there a significant relationship between proportion of foraging lizards and their size class. The trend suggested above is once again seen, with smaller lizards foraging more than larger ones.

Both Figures 7.2 and 7.4 suggest that there is no difference in proportion of basking and foraging lizards between adult males and adult females. Different head dimensions (4. 1) suggest different prey sizes and different prey handling times for similar sized food items (7.2.2). Despite this, it appears from the results that malea and females spend similar lengths of time in active foraging.

September is the only month when there is a significant trend in the percentages of lizards seen foraging and basking according to time of day. There was more foraging (and less basking) during the middle hours of the day than early in the morning or in the evening. The exception is the hour between 12.00hrs and 13.00hrs when lizard activity was too low to allow comparison.

It should be stressed that these differences in activity between both size classes and times of day are seen at the time of year when the population of lizards is highest due to the presence of hatchlings. While reaction to time of day is probably due to thermal trends, the large differences between the size classes may be related to the increased density of the animals. Competition for food will be greater, and comes at a time of year when food is scarce (7.4). Young lizards may be forced to forage for longer periods in order to obtain sufficient prey items for their needs. At this time of year, large lizards will take small prey. They have been seen picking ants from ant trails in the vicinity of ant nests. Schoener & Gorman (1968) state that large animals are forced to eat small items when larger food is not available for a length of time. Thus, competition for small prey items - the sole food of the smaller lizards - will be greater.

A disadvantage of the method used to gather the data used in the analyses discussed above is that all lizard activity was divided into 'basking' or 'foraging'. Thus all lizards at rest in the open were considered to be 'basking'. All those lizards moving in or around vegetation were recorded as 'foraging' (lizards were rarely seen moving actively in the open other than going to or from basking sites or refugia). No account was taken of sit-and-wait behaviour (therefore included under 'basking'),nor of mating or other 'social' behaviour (probably included under 'foraging') nor of feeding, which was rarely observed. Lizards out of sight temporarily in cracks or other shelter, including some of those foraging, were not included in the data since they will have been missed during the transects.

These disadvantages are not shared by the continuous observation method. The analysis of results from these observations is set out in Figure 7.7. From the figure it can be seen that the amount of time spent foraging fluctuates considerably, with a maximum in spring and summer and a minimum in winter. Sit-and-wait behaviour seems to be most important in early spring. At this time lizards looking into vegetation may be able to spot potential mates as well as prey. Also, prey is more abundant at this time of year (7.4.3) which would make this strategy more rewarding than during the months when prey is scarce. No increase in the low capture rate resulting from sit-and-wait sessions was observed, however. Nevertheless, despite similar intensity of solar radiation in the autumn, when it could be argued the need for basking is similar (but see Chapter 8) no sit-and-wait activity was observed. In autumn, food is scarce.

These results are shown in Figure 7.8 grouped into the same periods of the year as were the results of the transect observations (Figure 7.3). Comparison of these diagrams shows that when 'basking' and 'sit-and-wait' are taken together - since they both involve the lizards sitting exposed to the sun - the results for periods A, B and D coincide closely. When the 'other' category (made up in this case mainly of periods of inactivity in 'mosaic' sunlight) is included period C in figures 7.3 and 7.7 are also similar. When the proportion of foraging shown by both figures is considered, the similarity remains. This suggests that the trends seen in the transect data do in fact reflect the true activity of individual lizards. Conversely, it suggests that the data obtained from the individuals observed during continuous observations are representative of the lizard population as sampled in the transects.

It should be noted that the length of activity time of the lizards varies during the year with daylength and temperature. Therefore similar proportions of time as represented in the diagrams cannot be considered as corresponding to similar absolute lengths of time.

Figures 7.9 and 7.10 show that intervals of sit-and-wait activity and of foraging are **mainly** of short duration. The amount of time spent in sit-and-wait activity, which is mainly in the open and therefore involves basking, ranges up to over 15 minutes. Foraging **intervals range** up to about 7 minutes. Foraging takes place mainly in the shade of vegetation, so that, particularly at cooler times of day or year, foraging bouts will result in a lowering of body temperature, forcing the lizard to emerge once more to bask. The length of foraging intervals will then depend not only on success in prey capture, as optimal foraging theory suggests (Pyke *et al.*, 1977) but also on thermal conditions.

Thermal constraints on sit-and-wait behaviour will act differently. The limit on this behaviour (as on basking) will be an excessive rise in body temperature. This will tend to occur during the warmer part of the year, when temperature drop while foraging in the shade will be at a minimum. Both these factors will tend to reduce a lizard's basking time in favour of time in the shade, and to reduce sit-and-wait activity in favour of active foraging in vegetation. Sit-and-wait intervals will therefore be reduced in duration and frequency and foraging time will increase during the summer months (Figures 7.7 and 7.8).

Since few sit-and-wait intervals were seen to result in captures, it must be assumed that most prey captures are effected out of sight in vegetation as a result of active foraging. Sit-and-wait must therefore be considered a poor alternative to the latter. When a lizard's temperature is below its preferred level but its food requirements have not been met, it will be more advantageous for the lizard to assume a sit-and-wait posture, facing vegetation, where this is possible, since there is then a greater chance that a prey item will be spotted. As soon as the preferred body temperature is achieved, the lizard will be expected to enter the vegetation and forage.

In early spring, when mating begins, lizards are more likely to spot or be spotted by potential mates when in the open than hen in vegetation. This consideration may then tip the balance ore towards staying in the open and sit-and-wait as an alternative o active foraging. At the same time, prey is most abundant uring this period and the likelihood of spotting prey is greater. his suggests that -as is in fact the case - the sit-and-wait trategy would be most used in early spring (Figures 7.7 and 7.8). hus, *P. hispanica* can bask and search for mates or for prey ithout a loss in fitness from lack of time to participate in these ctivities (Schoener, 1971).

Lizards observing vegetation when in a sit-and-wait position casionally move their heads but do not actively scan the area fore them. The lizards actually wait for prey moving through. *hispanica* differs in this way from *Anolis* lizards (Moermond, 1979) which scan the area in front of them and move to another scanning site once the area has been investigated. In the case of these tropical anoles, temperature conditions will not play such an active part in determining lengths of sit-and-wait activity, while predator avoidance and social interaction will probably play a more prominent part (Moermond, 1979).

The most frequently held position and that held for the longest by all but the smallest lizards while in sit-and-wait activity is seen from Figure 7.11 to be the horizontal, with the vertical postures being the least used. These results support the observation already made in Chapter 5 that *P. hispanica* spends most of its time on the ground, particularly when feeding, and definitely when foraging. The data in Figure 7.11 do however include horizontal posture on a vertical surface as horizontal , since in these cases the lizards were observing flat ledges adjacent to these surfaces. There is a similarity between these results for *P. hispanica* and those given by Moermond (1979) for *Anolis koopmani* and *A. semilineatus*, both of which, like *P. hispanica* tend to spend most time on the ground or on low vegetation.

P. hispanica shows mainly a widely foraging strategy (Pianka, 1973) in which it actively searches out prey in low vegetation. The sit-and-wait strategy appears to be of secondary importance. It may be successful when energy requirements are low (Pianka, 1973), as during December and early January when lizards bask at the entrance to their refugia during cold weather, and may eat an insect that chances by. The method may be a more rewarding alternative to basking alone, especially when prey is denser and more mobile (as it is in spring), when low temperatures or levels of solar radiation make basking necessary. Increased prey density will also increase the efficiency of the widely foraging lizard, and foraging is also important in spring (Figures 7.3, 7.7 and 7.8). But in this case the searching ability of the lizard as a predator will take on considerable importance (Pianka, 1973). Unfortunately, since foraging is in cover, this cannot be easily studied.

7.4 Food availability

7.4.1 Introduction

In order to determine whether lizard activity is related to food availability, it was necessary to attempt to obtain an indication of relative food abundance through the year. Several methods were considered. The first was the method used by Finlayson (1981) in which the numbers of arthropods seen in foliage or on the ground per minute were recorded. This method yielded poor results, especially during times of the year when arthropods were scarce. Moreover, it excluded invertebrates hidden in litter or within vegetation where the lizards did most foraging. Sweeping vegetation with a sweep-net had similar limitations.

A method was attempted for flying insects which involved the laying out of strips of sticky fly-paper in the open. This also proved unsatisfactory. Few insects were caught and the paper rapidly dried out in the sun. The method was finally discarded when observation revealed that lizards fed mostly as a result of active foraging inside vegetation.

Eventually it was decided that a method which allowed extraction of most prey items in a given area of vegetation would be most suitable, since a foraging lizard would be able to seek out most items.

7.4.2 Methods

A portable UNIVAC vaccuum pump, powered by a two-stroke engine was used. An area of the ground measuring 1 metre x 1 metre was marked off with a wooden frame to prevent escape and worked systematically with the 10cm diameter nozzle. Since all areas sampled were of low grass and Oxalis pes-caprae vegetation, where most foraging took place, and up to 20cm height, problems associated with sampling highly stratified vegetation did not arise.

From October to May, sampling was carried out on dry, bright days between 1100hrs and 1300hrs. From June to September, sampling was done between 0900hrs and 1200hrs. These times corresponded approximately to those of highest lizard activity. This choice, to sample during similar weather, was made in order to reduce biases due to differing weather conditions.

These timings did however restrict the frequency at which sampling could be carried out. On clear days separated by long periods of adverse weather conditions, a choice had to be made between sampling invertebrates and conducting observations on the lizards. The latter was the inevitable choice. This was especially so because mechanical problems with the UNIVAC and transport difficulties resulted in days of sampling allowing little time for other field work. Despite this enough samples were obtained to give an indication of trends in availability of invertebrates.

After attempting to sample as wide a range of habitats as possible and finding that the method was time consuming and cumbersome and that lizards were in fact restricted to certain areas, I chose to restrict sampling to these areas only. The grass/Oxalis pes-caprae vegetation of North Front Cemetery (1.5) was chosen. This was sampled at least once, and usually twice a month (depending on prevailing weather conditions). The area of microhabitat in question was small (20m x 20m) so that five 1m x 1m patches were sampled on each occasion. However, because the lizards under study were largely restricted to these areas the sampled patches made up about 1.25 % of their foraging grounds.

Between May and September, additional samples were taken from Centaurea bullata shrubs which, in contrast to the rest of the vegetation, were in flower and attracted insects.

The samples collected in the UNIVAC were transferred to polythene bags which were then sealed. The contents were examined on the same evening by sifting through the collected vegetation and identifying all the invertebrates found and measuring them to the nearest 0·5mm.

7.4.3 Results

The results obtained from the sampling are given in Table 7.3 and illustrated in Figures 7.12 and 7.13.

Since numbers of invertebrates obtained in each sample were small in most cases, the results of all five samples from each sampling session were added to give a total for 5 m^2 of habitat. Results for each month were averaged to give the data in Table 7.3

Table 7.3 Average number of invertebrates collected in $5m^2$ of grass/Oxalis pes-caprae vegetation per day of sampling in North Front Cemetery, Gibraltar, by months.

	J	F	M	A	M	J	J	A	S	O	N	D
Gastropoda	4	3	2	20	23	18·5	10	1·5	9	8	6	4
Miriapoda			0·5									
Araneae	2	9	12	17	3		1	1·5	2	1	3	3
other Arachnida		1	2·5									
Collembola		1			1							
Orthoptera	0·5	1		1	1	3	1	1·5			2	1
Dermaptera	0·5	1										1
Hemiptera	5·5	2	7·5	9	14	2		0·5	1	2	5	4
Lepidoptera				1		0·5		1		1	1	
Diptera	1·5	4	3·5	2	6	1·5	1				2	3
Formicoidea	12·5	56	164	116	20	3·5						5
other Hymenoptera		1	2·5	2	3	1						2
Coleoptera	3	1	3·5	4	24	5	8	3·5		2	5	10
Lepidoptera larvae					1	0·5		1				
other larvae						0·5			1		1	
others	2·5		0·5		2							1
TOTALS	32	80	198	172	98	36	21	10·5	13	15	25	34

Fig. 7.12 AVERAGE NUMBER OF INVERTEBRATES COLLECTED IN 5m² OF GRASS / Oxalis VEGETATION IN NORTH FRONT CEMETERY GIBRALTAR.

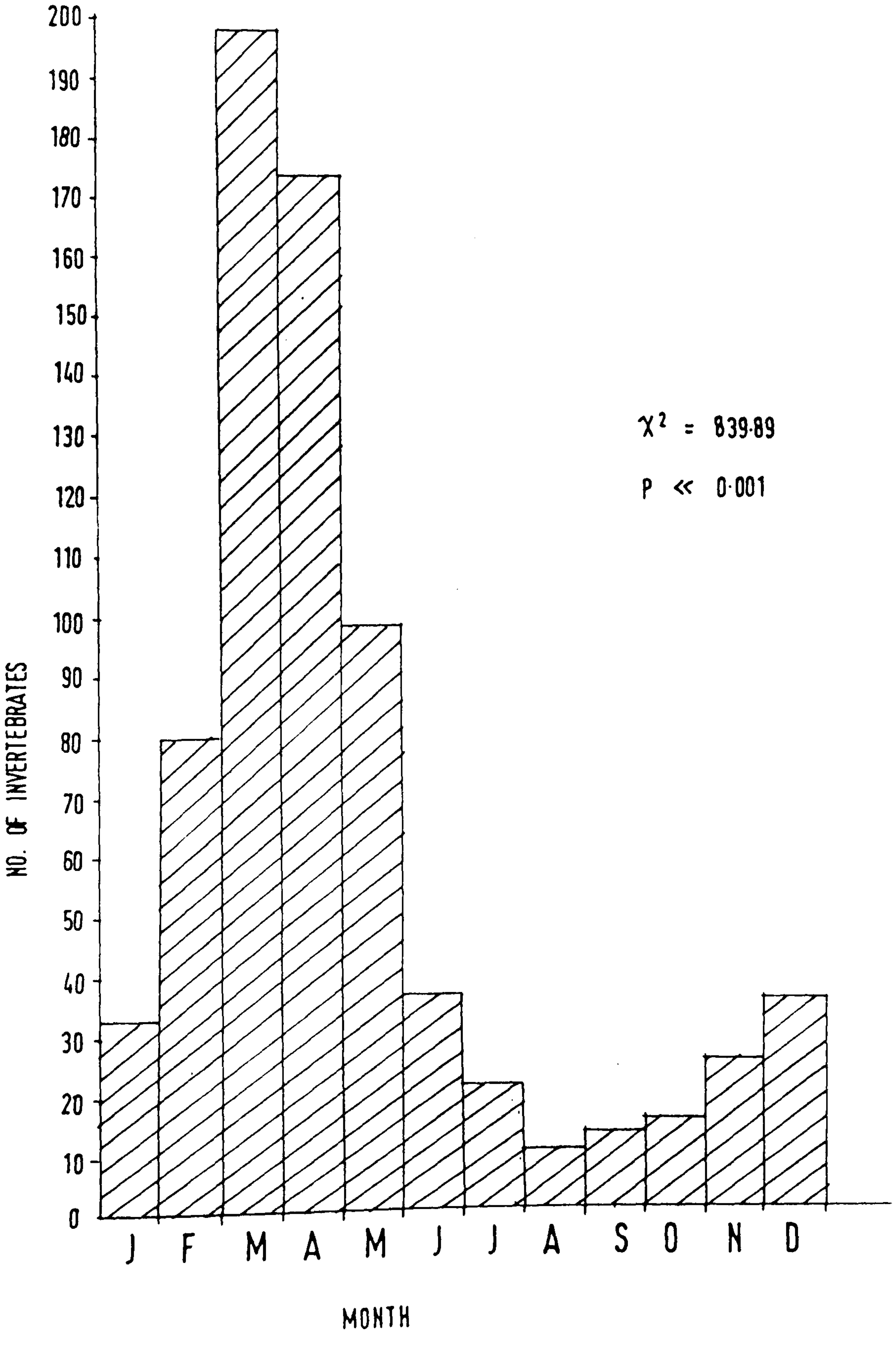
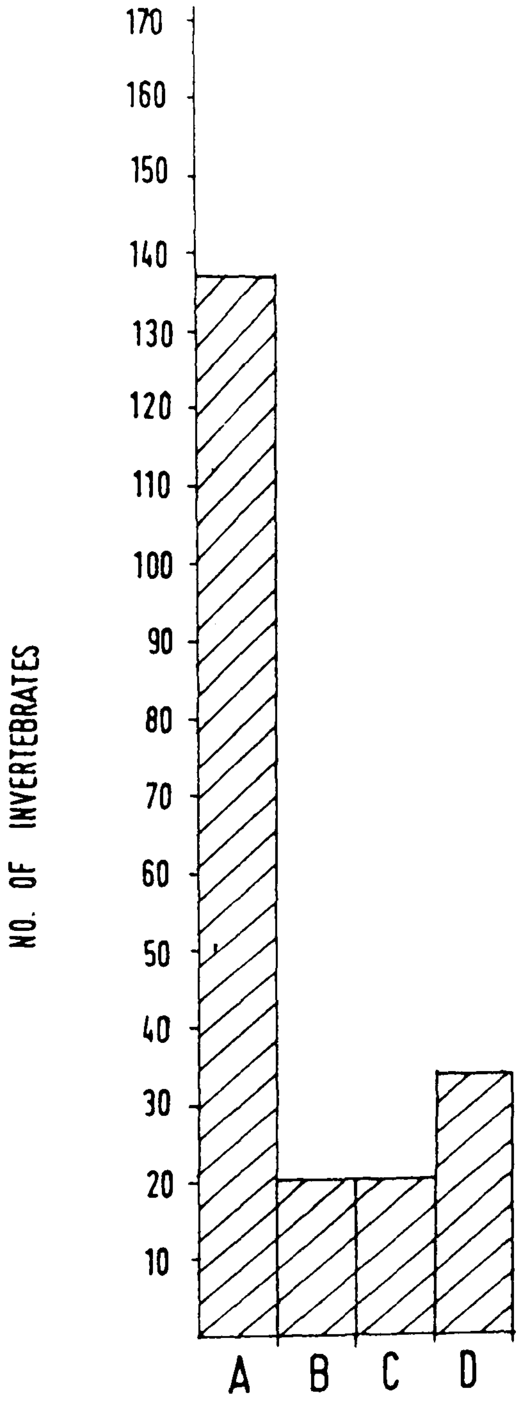
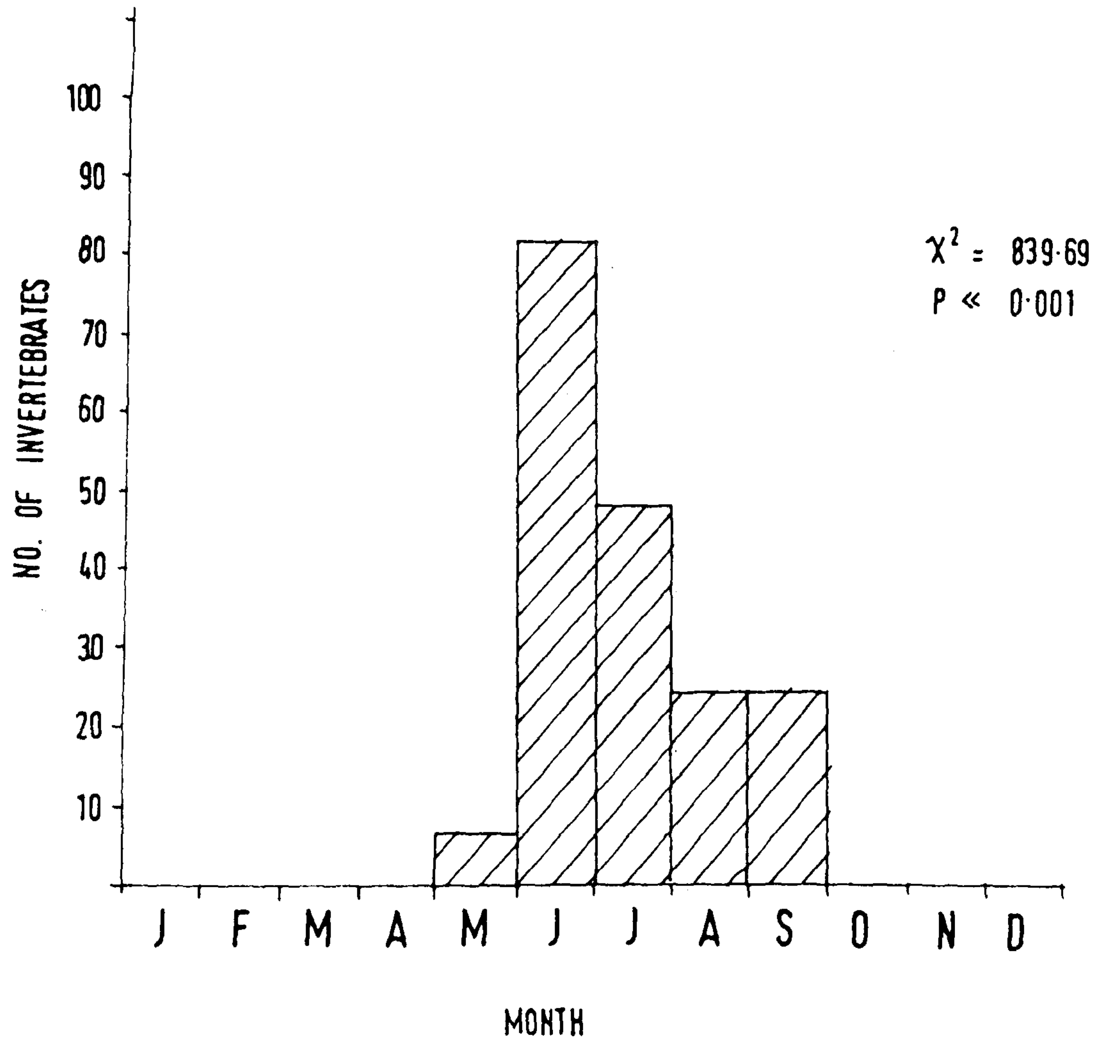


Fig. 7.13 AVERAGE MONTHLY NUMBER OF INVERTEBRATES COLLECTED IN 5 m^2 OF GRASS / <u>Oxalis</u> VEGETATION IN NORTH FRONT CEMETERY GIBRALTAR.



A = SPRING (FEBRUARY, MARCH, APRIL, MAY.)
B = SUMMER, BEFORE RAINS (JUNE, JULY, AUGUST, SEPTEMBER)
C = AUTUMN, AFTER RAINS (OCTOBER, NOVEMBER)
D = WINTER (DECEMBER, JANUARY)

Fig. 7.14 AVERAGE NUMBER OF INVERTEBRATES COLLECTED IN 2m^2 OF Centaurea bullata SHRUBS IN NORTH FRONT CEMETERY GIBRALTAR.



used in preparing Figure 7.12. Monthly results were averaged to provide the data represented in Figure 7.13 in which the year is divided into four periods: spring (A); summer before the rains (B); autumn during and after the rains (C); and winter (D). These data include all the invertebrates caught, since all are included in the diet of P. hispanica (7.5).

This pooling of data was felt to be the best way of obtaining an indication of changes in food availability in the microhabitat in question.. Unfortunately published data on invertebrate diversity and density in southern European grassland is non-existent. Only Finlayson's (1981) estimates, already discussed above, allow some comparison. His results for foliage also give the spring as the period with most arthropods, followed by winter, autumn (after rains) and summer (before rains).

The results in Figure 7.13 show few invertebrates in summer and autumn (20 in $5m^2$) (rainfall was low in 1981 when the samples were taken), somewhat more in winter (33 in $5m^2$) , and most in spring (136 in $5m^2$).

The results for Centaurea bullata shrubs show a late peak of invertebrate numbers in June, with a drop towards September when flowering ends for the plant (Figure 7.14).

7.4.4 Discussion

The trend in invertebrate numbers in the samples through the year (Figures 7.12 and 7.13) closely follows the cycle of vegetation. Greenery appears after the summer drought with the rains in the autumn. Plant growth continues through the winter to the peak of the flowering period from March to May. The herbaceous vegetation begins to die back by mid-May and by the end of the month is totally dry again.

There are exceptions to this general pattern, which in any case is not followed by the woody species of the scrub. Centaurea bullata, notably, flowers through the summer and retains green foliage throughout. Insects and other invertebrates are found in clumps of the shrub (which grows no taller than about 20cm) when they are scarce in the surrounding bare areas.

Lizards are attracted to such localised food supplies. P. hispanica have been seen active in these patches of C. bullata when they are absent from surrounding areas. They have also been seen to be more common on occasion around exotic bushes of Laurel Laurus nobilis which were attracting flies Drosophila sp. Similarly, lizards are attracted to flies which concentrate around flowering Smyrnium olusatrum.

Psammodromus algirus have been seen concentrating in patches of cut vegetation in areas otherwise cleared as firebreaks. The need for cover may also play an important part in this.

Seasonal isolated patches of vegetation which hold invertebrate food will prove of value to lizards during otherwise lean periods. If such a source of food allows a lizard to grow during a period when others cannot do so due to scarcity of prey, it may give the lizard an advantage in mating in the following spring (6.5). There is no direct evidence of this, however. Although some lizards have been seen using the same patch of C. bullata for several weeks, there is no evidence either of active defence of such patches. Continued investment in a patch of C. bullata can be explained with reference to Parker & Stuart's (1976) emigration threshold*. Expected future fitness due to continued investment in the existing resource (side (a) of the equation) will be greater than the expected future fitness due to withdrawal from the patch (side (b) of the equation). The lizard will therefore remain. The matter can be seen also from the point of view of the 'marginal value theorem' (Charnov, 1976), which predicts that an animal will leave a patch when its rate of food intake in the patch drops to the average rate for the habitat. This will only happen in the present situation when flowering of C. bullata ends and/or the surrounding vegetation grows and invertebrates become more abundant there. When this happens lizards are no longer more noticeable in Centaurea than elsewhere.

---

* Parker & Stuart (1976) describe 'I_{opt}', the emigration threshold, as being specified by the balance

(a)		(b)
Expected future fitness due to continued investment with an existing resource	=	Expected future fitness due to withdrawal (emigration) from the existing resource, to start a new search phase.

When (a) > (b), the animal should continue; when (a) < (b), it should withdraw.

Table 7.4 Mean sizes of invertebrates sampled in grass/*Oxalis* and *Centaurea* vegetation at North Front Cemetery, Gibraltar.

(Sizes for Gastropods are diameters; all other sizes are lengths. One Coleopteran of 19mm length was excluded).

	mean size (mm)	standard deviation	range (mm)	n
Gastropoda	4•93	1•68	1•0 - 14•0	122
Miriapoda	7•00	-	-	1
Araneae	2•44	1•52	0•5 - 7•0	54
other Arachnida	0•80	0•27	0•5 - 1•0	5
Collembola	2•00	0	-	2
Orthoptera	5•57	2•62	4•0 - 14•0	21
Dermaptera	7•00	1•00	6•0 - 8•0	3
Hemiptera	3•56	2•53	1•0 - 12•0	54
Lepidoptera	3•60	0•97	3•0 - 6•0	10
Diptera	2•36	1•30	1•0 - 6•0	29
Formicoidea	1•65	1•16	0•5 - 13•0	455
other Hymenoptera	6•48	4•97	1•0 - 15•0	26
Coleoptera	2•45	1•26	1•0 - 7•0	101
Lepidoptera larvae	6•92	4•67	1•5 - 14•0	6
other larvae	2•83	1•04	2•0 - 4•0	3
others	2•11	0•60	1•0 - 3•0	9

All the invertebrate groups collected in the samples (Table 7.3) have been seen to feature in the diet of P. hispanica either in this study (7.5) or by Mellado et al. (1975). With the exception of one Coleopteran Pimelia bipunctata, 19mm in length, all the invertebrates caught measured less than 15mm (Table 7.4) and therefore were potential prey of P. hispanica (7.2). Other large insects were seen in the habitat, including Locusta migratoria, Mantis religiosa and another large Coleopteran Blaps mucronata, but did not feature in the samples. The beetles kept to more open areas and the locusts and mantises escaped the nozzle of the UNIVAC.

The data in Table 7.3 show that ants were the most numerous insects in the samples. Snails, spiders and beetles were also prominent.

7.5 Faecal analysis

7.5.1 Methods

Lizard faeces are often deposited prominently on basking sites and dry quickly in the sun. On several occasions lizards have been seen ingesting fresh faecal pellets, but in general these lie exposed for up to several days before they are dislodged by passing lizards, rain, etc.

Faecal pellets of P. hispanica were collected from basking sites in the study area (mainly North Front Cemetery). Some faecal pellets known to have been produced by one individual Lacerta lepida were also collected. These pellets were examined under various magnifications with a binocular microscope. The pellets were teased open and the the fragments identified, using a key based on Pernetta (1973, unpubl.) (Appendix 5). Reference was also made to Chinery (1972) and to the invertebrates which were caught in the vaccuum samples (7.4). In general, the most common types of material became instantly recognisable and could be assigned with certainty to a particular group, e.g. coleopterous elytra or arachnid chelicera.

A disadvantage of the method was that the faecal pellets could not be attributed to lizards of different size classes.

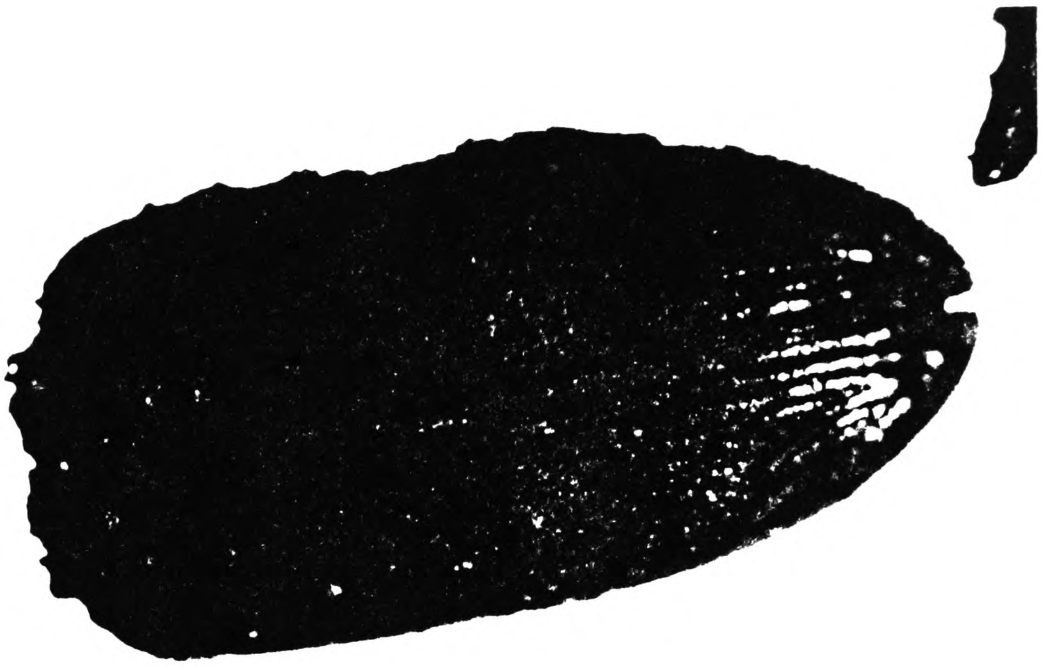
7.5.2 Results and Discussion

The fragments found in the often compact faecal pellets ranged from small pieces which could not be identified to complete elytra, heads, thoraxes and sections of abdomen. In many cases, whole insects could be 'pieced together' from the remains, so that approximate lengths (measured on a millimetre scale) could be estimated.
On other occasions, the pieces (particularly elytra) could be confidently attributed to insects caught in the sampling, so that a length could also be attributed to the specimens. Numbers of invertebrates in each pellet were only decided when it was obvious that different particles of the same individual were not being attributed to more than one. Thus, for example, one elytra was taken to represent one coleopteran, as were two paired elytra; three elytra or two similar elytra, were taken as representing at least two beetles, and so on.

Figure 7.15 shows photographs of some arthropod remains from faecal pellets of P. hispanica.

Fig. 7.15 INVERTEBRATE FRAGMENTS FROM *P. hispanica* FAECAL PELLETS

(a) COLEOPTERAN ELYTRA



(b) COLEOPTERAN ELYTRA

(c) CHELICERA OF ARACHNID

In many cases, lengths could not be estimated. Arachnids, in particular, left no remains large enough to allow this. Snail shells were found completely crushed in some pellets, and intact in others.

Small grains of sand were found in 57% of the pellets sampled. These may have been ingested incidently with the food items. However, since the lizards were seen to swallow food with little or no chewing, the grains may have been ingested to aid grinding of food.

One hundred and eighteen pellets were examined. Some showed clear evidence of only one invertebrate, others contained remains of up to seven food items (mean = 3·4 per pellet).

The numbers of different invertebrates identified from pellets collected at different times of year are shown in Table 7.5. This excludes particles which could not be identified. It should be noted that no vegetatble matter was found in any P. hispanica faecal pellet.

The mean size of food items in the diet overall was 5·8mm (S.D. = 2·34), with a range of 2·5mm to 10·0mm.

Comparison of Table 7.5 with Tables 7.3 and 7.4 suggests P. hispanica fed on a wide variety of invertebrates available in the habitat. Coleoptera, Gastropods and Araneae featured prominently in the faeces, and were among the commonest in the vaccuum samples (7.4). Notably, ants were not common in faecal pellets despite often being plentiful in the vegetation. When they did occur, their heads were characteristic, so it is unlikely that they were missed.

Herrera (1976) proposed an index of 'trophic diversity' to measure the diversity in the diet of a species. The index (Appendix 6) was to be used, for example, using data from stomachs. In the absence of such data in this study, data from the faecal pellets have been used. The value of the index, D, for the pellets was -0·398. This index reflects the variety of prey items in the diet of a population and the variety of ways in which populations are using them (Herrera, 1976) - the greater the uniformity, the lower is D (i.e. the greater the number of presences in the faecal pellets). In the

Table 7.5 Numbers of invertebrates identified from faecal pellets of P. hispanica (unidentifiable particles excluded).

	J	F	M	A	M	J	J	A	S	O	N	D	Tot	%total inverts.	in % of pellets
Gastropoda	3	2	12	15	2	5	3	1	3	4	1	2	53	13·2	17·8
Isopoda	2	1	2	1	1				1	3	1	2	14	3·5	12·7
Araneae	10	2	5	12	8				1	4	3	8	53	13·2	39·0
Orthoptera		1	1	1						1		1	5	1·2	4·2
Dermaptera		5	16						3	5		4	33	8·2	10·2
Hemiptera		1	13				3	7					24	6·0	17·0
Diptera	3	1		1		1	1	1	3			2	13	3·2	5·9
Formicoidea			1			1	3	1					6	1·5	4·2
other Hymenoptera		3	2		1	2							8	2·0	4·2
Coleoptera	15	8	50	15	21	9	2	8	19	4	4	10	165	41·0	65·3
Larvae			1						2	1			4	1·0	3·4
others	1		18			1	1		2			1	24	6·0	20·3
No. of pellets	10	8	21	12	8	8	5	5	20	6	7	8	402 118		

Table 7.6 Contents of 6 faecal pellets of Lacerta lepida

	No.
Seed of Lantana camara*	12
Seed of Myoporum pictum*	3
Gastropoda	6
Grillotalpidae	3
other Orthoptera	1
Hymenoptera (Bee)	1
Coleoptera	3

*Shrubs with fleshy fruit.

absence of data from other populations, D can be compared to the Shannon-Weaver index H' (Appendix 6) which considers the proportions of individual items in the diet rather than the frequency of occurence in different samples. H' in this case is - 0•0439. The ratio D/H = 9•045. This high value (although again there are no comparable data) suggests that overall, the members of the population show appreciable individual differences in food choice, or, as has already been suggested for P. hispanica, that they are opportunistic feeders (Herrera, 1976).

Table 7.6 lists the contents of six faecal pellets of L. lepida. The Coleopterans were Pimelia bipunctata (c. 20mm in length). Snails were important, and remains of fruit were common. This partial herbivory of L. lepida is not unexpected. The greater energy requirements of the Ocellated Lizard compared to P. hispanica means that L. lepida would need to feed on a large number of insects, and would have to expend large amounts of energy to capture small food items (Pough, 1973). This difficulty is circumvented by herbivory. A similar argument could be used to explain the apparent importance, even in this small sample, of snails in the diet.

7.6 Discussion

The results and discussion so far in this chapter have indicated that P. hispanica lives in a habitat where prey are predominantly of utilisable size. Feeding, it is suggested, is opportunistic, most small invertebrates being taken. The limit on what is taken is probably large size for the smallest lizards. The small items may be avoided by medium-sized lizards if handling time is such that the food value to handling time ratio is unfavourable.

There is a marked seasonality of the vegetation and also, it appears, of the supply of invertebrates therein. The fluctuations in food supply would be expected to have an effect on the degree of food specialisation of the lizards (Pyke et al., 1977). Thus, increased food abundance in the spring should lead to greater food specialisation. There is no direct evidence of this from faecal analysis. Lizards stomachs would have to be examined in order to establish whether this in fact is the case.

Lizards of temperate regions, including P. hispanica, have other factors influencing their feeding ecology and feeding behaviour. Thus, thermal conditions and changes throughout the year will affect the time a lizard can spend foraging.

During cooler parts of the year (Figures 7.3, 7.7 and 7.8) and times of day (Figure 7.6) most time is spent basking. Thus, as far as foraging is concerned, and particularyly in winter, P. hispanica would tend to behave as a 'time minimiser' (Schoener, 1971). Long periods of foraging would result in temperature loss and therefore a loss of fitness - onset of torpidity, inability to catch prey, increased susceptibility to predators. The activity of invertebrates would also be lower in colder weather.

In spring, when prey is more abundant, basking and foraging are combined in the sit-and-wait strategy, and foraging time is again minimised. When ambient temperature and solar radiation are greater, as in the summer, more time will be available for foraging. At these times, food is scarcer and lizards would be expected to be even more catholic in their diet. This period further coincides with the emergence of hatchlings which will increase competition for smaller prey.

An interesting observation, already mentioned, is the sudden increase in sit-and-wait activity in the spring. This can be considered again using Parker & Stuart's (1976) model for 'emigration threshold' (see 7.4.4). The proposed cycle of activity is represented diagrammatically in Figure 7.16.

In cool conditions, such as occur in December and January, when a lizard's temperature is below its preferred body temperature (PBT) (Chapter 8), its expected fitness (Parker & Stuart, 1976) while it is exposed to the sun and able to pose in order to maximise insolation will be greater than if it were in a flat posture facing vegetation (the most common sit-and-wait posture - Figure 7.11). It will certainly be greater than if it were foraging in the shade. The tendency will therefore be to remain basking. Once PBT has been achieved (provided thermal conditions make this possible), and since prey is not abundant (Figure 7.12), the expected future fitness while foraging will be greater than that while basking or than it would be in a sit-and-wait situation. The lizard will therefore move from basking to foraging and, on cooling, back to basking. The length of foraging intervals will depend on rate of heat loss and would tend to be shorter for smaller lizards (Figure 7.10).

In spring, a lizard below its PBT will again bask. At or around its PBT its fitness would increase on moving to a sit-and-wait position where, because prey is plentiful, it would increase its chance of feeding while remaining exposed to sunshine. This is more intense in spring than in winter. With the sun higher in the sky, moreover, a flat pose will not be as great a disadvantage to a basking lizard. If food were not obtained in this way, or if the lizard's body temperature increased so as to enable it to spend more time in the shade, it should 'emigrate' from the sit-and-wait situation and start to forage actively. On cooling, the lizard will emerge and revert to a basking or sit-wait position.

In hot summer weather, basking in the middle of the day is only necessary for short periods (Figure 7.6). More time can be spent foraging. Fitness is reduced by overheating, so that a foraging lizard will withdraw to the cover of its refugium.

The feeding behaviour of P. hispanica appears to result from a combination of reactions of the need to feed and the necessity to thermoregulate.

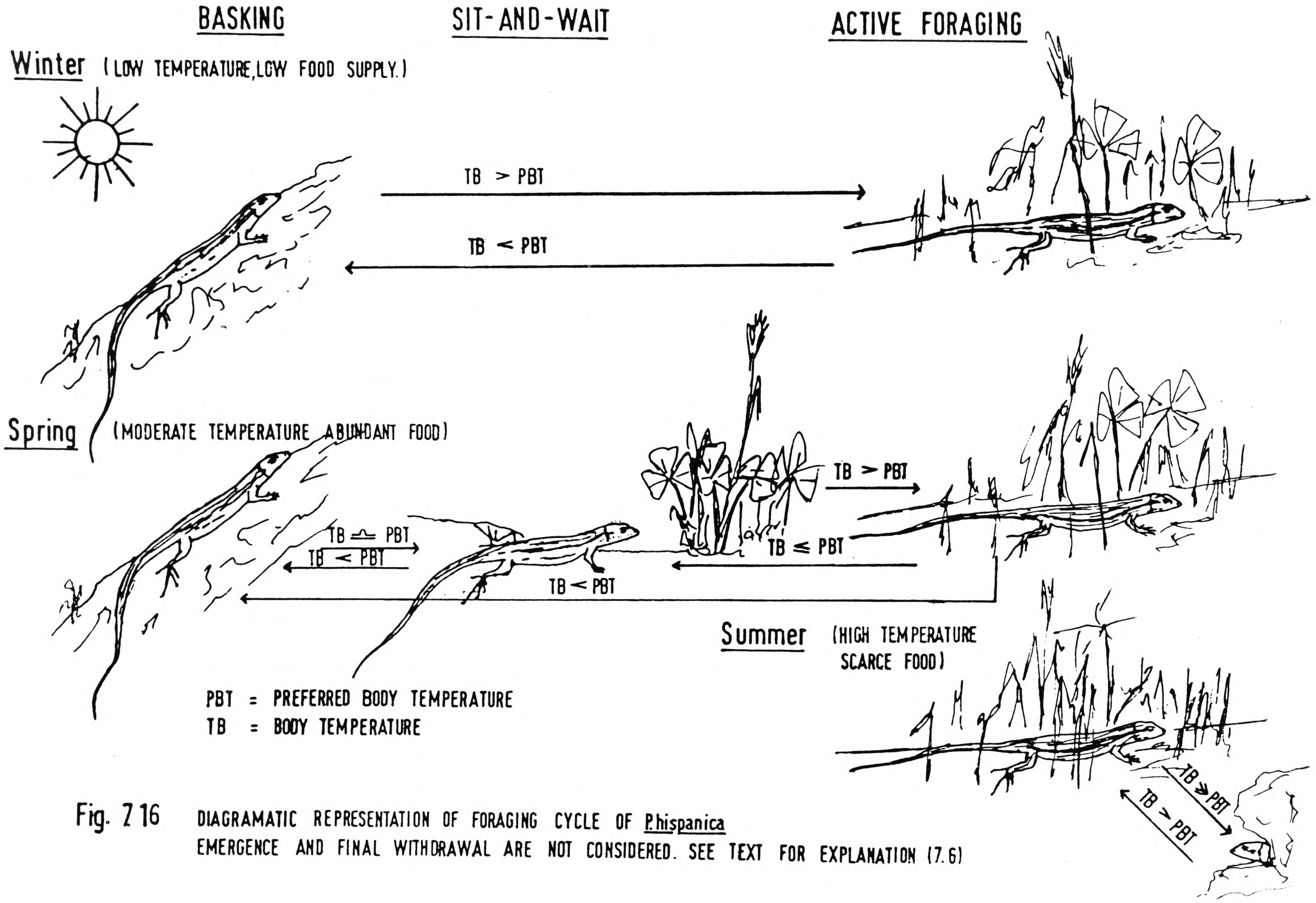


Fig. 7.16 DIAGRAMATIC REPRESENTATION OF FORAGING CYCLE OF *P. hispanica*
EMERGENCE AND FINAL WITHDRAWAL ARE NOT CONSIDERED. SEE TEXT FOR EXPLANATION (7.6)

CHAPTER 8

PATTERNS OF ACTIVITY

8 PATTERNS OF ACTIVITY

8.1 Introduction

Reptiles are well known for their patterns of activity. Lizard activity in particular shows definite patterns during the course of a day (e.g., Busack, 1976; Avery, 1978; House et al., 1980) which in turn vary during the course of a year (e.g., St - Girons & St -Girons, 1956; Porter et al., 1973; Huey & Pianka, 1977). While there are seasonal trends in activity in tropical lizards, for example in response to changes in food abundance (Stamps & Tanaka, 1981), the greatest seasonal changes in activity are found in desert lizards (e.g., Huey & Pianka, 1977; Porter et al., 1973) and lizards of temperate and cooler regions (e.g., Spellerberg, 1972b, 1972c, 1976; Avery, 1976).

These patterns of activity are related largely to the thermal conditions of the lizards which relate to thermal conditions of the environment. Solar radiation and temperature show a fairly regular cycle in temperate latitudes (2.1.3), reflected by lizard activity patterns.

The thermoregulatory abilities of a lizard (most obvious in low cost environments according to Huey & Slatkin, 1976) will be reflected in the body temperatures it can achieve under different conditions. Thermoregulatory behaviour tends to reduce the impact of variation in ambient conditions (Huey & Pianka, 1977). Lizard temperatures will nevertheless fluctuate during the course of a day and through the year. Metabolic rates will also vary (Nielsen, 1961; Bennett & Dawson, 1976).

Work on any aspect of activity patterns and temperature relations of Mediterranean lizards has not been plentiful (e.g. Avery, 1978; Patterson & Davies, 1978; Pough & Busack, 1978). There is no published year-round study of the activity of a European Mediterranean lizard to serve as a basis for further, more detailed studies of specific aspects of their ecology.

8.2 Temperature relations

8.2.1 Introduction

There has been considerable ambiguity in reptile thermoregulatory terminology. The terms used here follow Spellerberg (1976) and are defined below (8.2.2).

The value of knowing the tolerance limits of a reptile has been questioned (Huey & Stevenson, 1979), values such as thermal performance breadths being preferred. What are in fact of greatest interest are the temperatures - both environmental and body temperatures - at which a lizard can be active in the field. The temperature relations determined experimentally or by observation should therefore be compared with field temperatures and with the behaviour of lizards in the field if they are to be of true value.

This Chapter will therefore include information on substrates and environmental temperatures in the field as well as on body temperatures.

8.2.2 Methods and definitions

Cloacal temperatures of 112 lizards captured in the field were taken using a thin thermistor probe inserted in the cloaca. The temperatures recorded were used as measures of lizard internal temperatures. Where this was possible, a note was made of the activity of the lizard when caught, and the temperature of the surface on which the lizard was perched was also recorded, using a thicker thermistor probe.

Temperatures were taken in a similar way for captive lizards, active and at rest in their vivaria, under winter and spring conditions (3.3).

In addition to surface temperatures taken under captured lizards, random samples of 50 ground temperatures were taken throughout the year under different heights of vegetation: <30cm; >30cm; and in litter under bushes (>100cm). This sampling was carried out using a thermistor probe. The sampling was time-consuming, each session taking 20 to 30 minutes. Ground temperatures were seen to change rapidly as sampling progressed, particularly in the morning. Results have been used from data gathered 1 to 2 hours after sunrise and again between 1200 and 1500 hrs G.M.T.

In addition, temperatures in refugia and on adjacent concrete basking sites and vegetation were taken during December and January, the time of year when use of refugia was most evident (5.4).

During transect observations, the substrates on which lizards were basking were recorded, for both sexes and different size classes throughout the year.

Body temperature terms are as defined in Spellerberg (1976). Thus: Critical minimum temperature : the lower body temperature at which locomotory ability is disorganised (or lost) and the animal loses its ability to escape from conditions that may lead to its death (Cowles & Bogert, 1944). Voluntary mean temperature: the arithmetic mean of body temperatures recorded during the animal's normal activity (Brattstrom, 1965). Voluntary maximum temperature : that body temperature at or above which the animal moves away from conditions that would further raise its temperature (Cowles & Bogert, 1944). Voluntary minimum temperature: that body temperature at or below which the animal moves toward conditions that will raise its temperature, or to conditions that will shelter it from decreasing ambient temperatures (Cowles & Bogert, 1944). Voluntary range (normal activity range): the range of body temperatures between the voluntary minimum and the voluntary maximum (Brattstrom, 1965). The 'Preferred Body Temperature' referred to elsewhere (7.6) will lie within this voluntary range, but is probably impossible to determine accurately.

A number of other terms will be used below. These again are defined by Spellerberg (1976): Posturing heliotherm : an animal which uses heat energy from solar radiation for thermoregulation, chiefly by means of a series of postures. Shuttling heliotherm : an animal which thermoregulates chiefly by movement back and forth between sunlit and shaded areas. Thigmotherm : an animal which warms itself chiefly by contact with warm solid substances in the environment (Spellerberg, 1972a).

The field voluntary mean temperature was obtained from the field temperatures of captured lizards.

Other temperatures were determined using captive lizards kept under winter conditions (3.3). Individual lizards were taken from the vivarium and placed in a blackened chamber at 7°C, with a thermistor probe fixed inside the cloaca with tape. The lizards were observed until they became inactive and lost the righting response (only lizards with full tails were used since lack of tail hinders the ability of a lizard to turn itself over: Spellerberg, 1973). Note was taken of the body temperature at the point when the lizard first moved into shelter (under a stone provided). This temperature was recorded as the voluntary minimum temperature. The temperature at which the lizard became inactive was recorded as the critical minimum temperature.

Individual lizards were also placed in similar containers with heating lamps shining onto them. The temperature at which the lizard first sought shelter (maximum voluntary temperature) was recorded. This shelter was then removed. As temperature increased, the lizard became hyperactive, frantically moving around the container and trying to bury itself in the floor of the tank. The temperature at this point was called the 'absolute voluntary maximum temperature'. Finally, a critical maximum temperature was recorded when the lizard ceased all activity and appeared unable to move.

All lizards used in these experiments recovered after being returned to their vivaria and suffered no apparent ill effects apart from slight bleeding from the cloaca at high body temperatures.

The restricted experimental facilities at Gibraltar limited these experiments to the captive lizards at Oxford. Again the limited number of these and their being used for other observations and experiments meant that only the winter-captive lizards could be used in the above determinations. However, body temperatures of lizards active in their vivaria were recorded during both winter and late spring.

The various statistical methods used in analysing data from the above observations are given below in the Results section (8.2.3).

Table 8.1 Temperature relations of Gibraltar *P. hispanica* (definitions in text).

	mean	S.D.	range	n
Critical minimum temperature	12·2°C	0·51	11·5-12·7°C	7
Voluntary minimum temperature	17·3°C	1·83	14·0-20·0°C	7
Voluntary mean temperature	30·8°C	3·49	21·9-36·0°C	112
Voluntary maximum temperature	35·5°C	4·11	31·7-41·5°C	4
Absolute voluntary maximum	38·0°C	1·14	36·2-39·3°C	5
Critical maximum temperature	40·3°C	2·65	37·7-43·0°C	3

(Voluntary mean temperature ♂♂ : 30·9°C 3·01; n = 79
Voluntary mean temperature ♀♀ : 30·7°C 4·29; n = 33)

Fig. 8.1 BODY TEMPERATURES AND SURFACES FOR SPRING CAPTIVE AND WILD *P.hispanica*

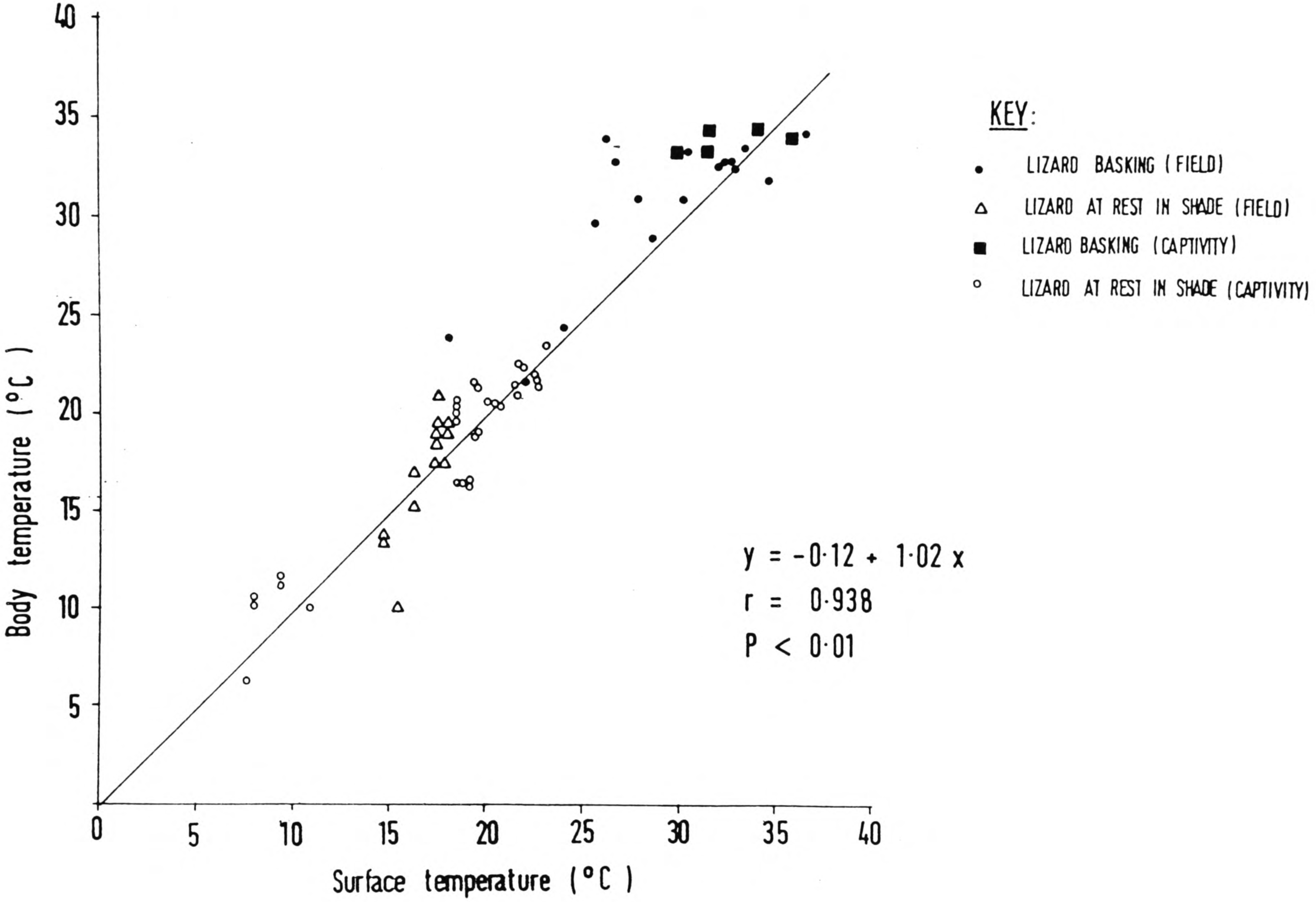


Fig. 8.2 BODY TEMPERATURES AND SURFACE TEMPERATURES FOR WINTER CAPTIVE *P. hispanica*.

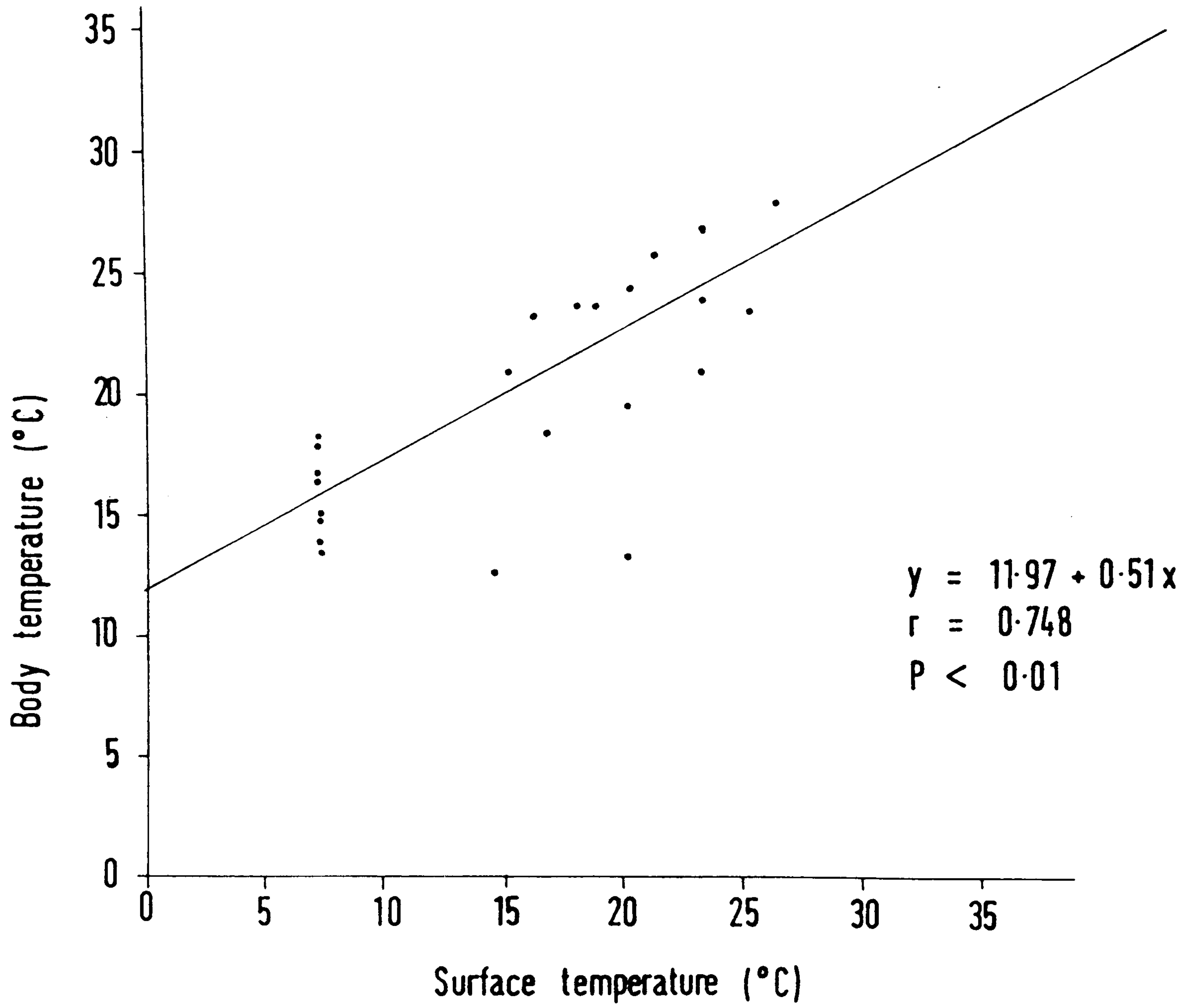


Fig. 8.3 REGRESSIONS OF BODY TEMPERATURES vs. SURFACE TEMPERATURES FOR WILD AND CAPTIVE *P. hispanica*

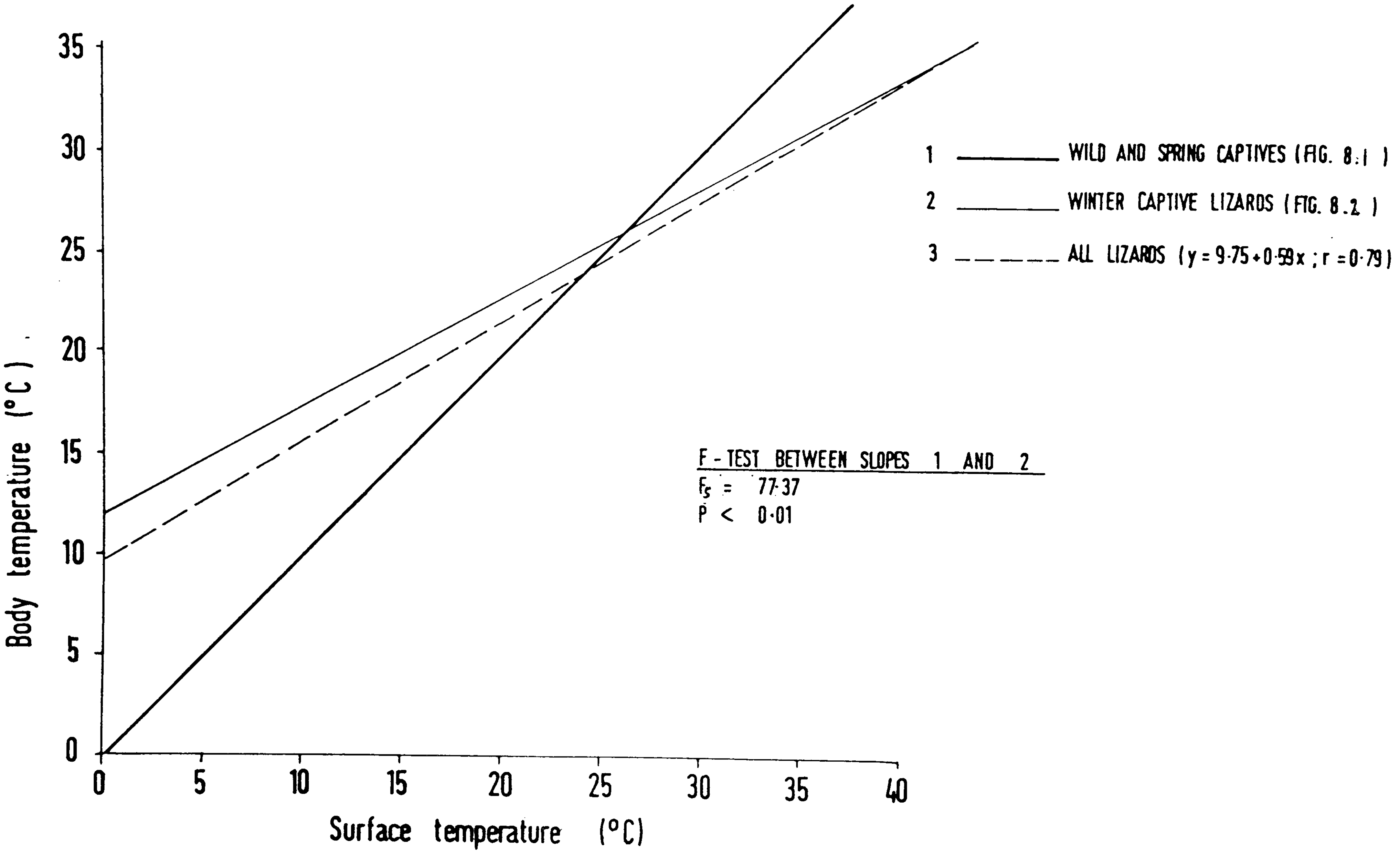
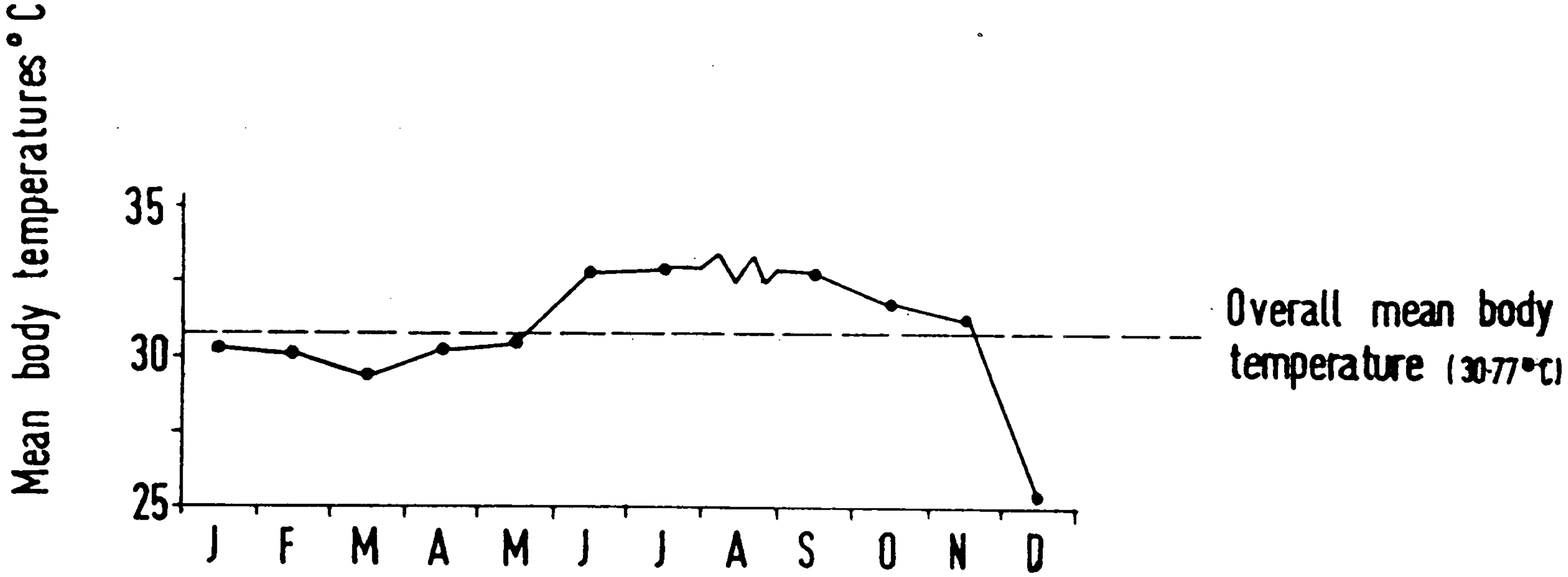


Table 8.2 Field voluntary mean temperatures of Gibraltar _P. hispanica_ by months.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
mean(°C)	30·43	30·20	28·50	30·34	30·64	32·98	33·00	-	32·89	31·84	31·25	25·12
S.D.	2·59	2·49	2·10	3·17	3·35	1·52	-	-	1·48	2·42	2·09	3·69
range (°C)	25·1-34·1	26·6-33·7	24·2-31·5	24·0-34·4	24·4-34·0	31·5-35·1	-	-	31·1-35·1	27·0-36·0	28·0-33·7	21·9-31·2
n	19	7	17	7	7	4	1	0	4	18	20	6

Fig. 8.4 MEAN FIELD TEMPERATURES OF LIZARDS (SEE ALSO TABLE 8.2)



P < 0·001 (Kruskall-Wallis test)

8.2.3 Results

Temperature relations

The temperature relations of P. hispanica are listed in Table 8.1. The critical minimum temperature was estimated as 12·2°C (S.D. = 0·51). The voluntary minimum temperature was determined to be 17·3°C (S.D. = 1·83). The voluntary mean temperature of P. hispanica in the field was 30·77°C (S.D. = 3·49) with a range of 21·9°C to 36·0°C. The voluntary maximum temperature was found to be 35·5°C (S.D. = 4·11) and the absolute voluntary maximum was 38·0°C (S.D. = 1·14). The critical maximum temperature was 40·3°C (S.D. = 2·65). The voluntary mean temperature for males only was 30·9°C (S.D. = 3·01) and for females alone was 30·7°C (S.D. = 4·29).

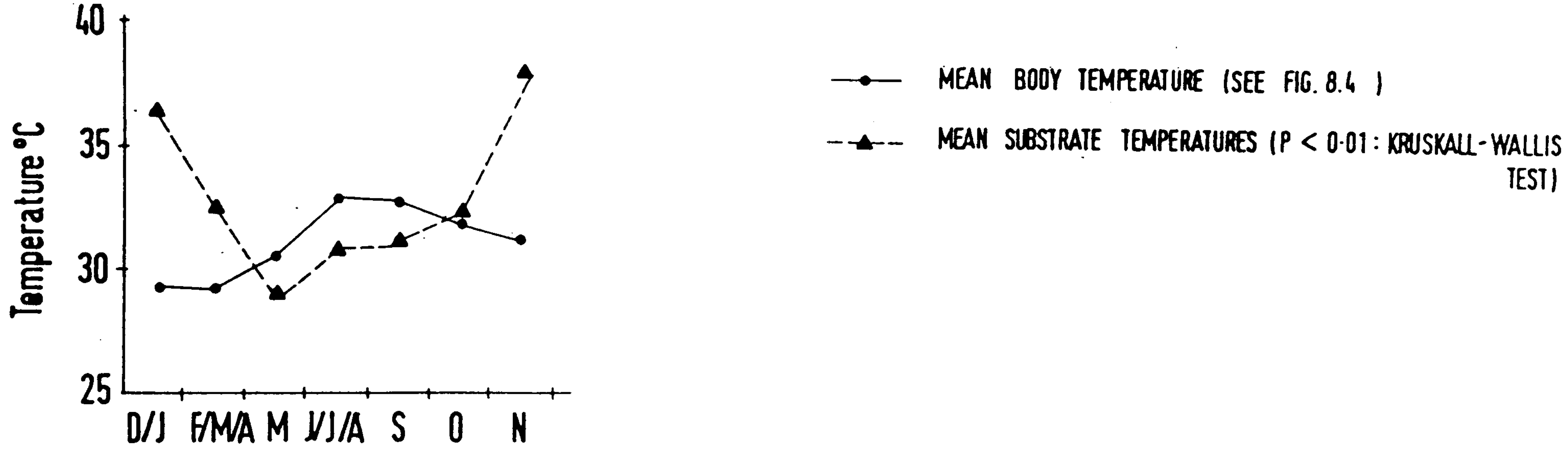
The voluntary mean temperature for Ps. algirus was found to be 30·9°C (S.D. = 2·95; n = 22).

Figure 8.1 shows the relation between body and ground surface temperatures for basking wild P. hispanica and for the spring captive lizards. There is a good correlation ($r = 0·938$; $P < 0·01$) between body temperature and surface temperature. The regression slope ($b = 1·02$) goes almost through the origin ($a = -0·12$). Most lizards basking at higher surface temperatures had body temperatures somewhat greater than the surface temperature. This suggests the use of solar radiation to warm up.

A significant correlation is found also for lizards kept captive in winter conditions ($r = 0·748$; $P < 0·01$) (Figure 8.2). However, the slope ($b = 0·51$) is significantly different from that for the other lizards in Figure 8.1 ($F_s = 77·37$; $P < 0·01$). These slopes are compared in Figure 8.3. The slope of the winter lizards is less steep. This suggests better control of body temperatures at low environmental temperatures in the winter than in spring/summer.

The mean temperatures by months of P. hispanica caught in the field are shown in Figure 8.4 and listed in Table 8.2. The overall differences are significant ($P < 0·001$; Kruskall-Wallis test). The lowest temperatures recorded were in December, with a mean of 25·1°C (S.D. = 3·69) and a range of 21·9°C to 31·2°C. This was considerably lower than the next lowest monthly mean, that for March (28·5°C: S.D. = 2·10; range : 24·2°C to 32·1°C).

Fig. 8.5 MEAN BODY TEMPERATURES OF MALE *P.hispanica* AND BASKING SURFACES AT NORTH FRONT CEMETERY GIBRALTAR



The highest temperature recorded was in October (36·0°C). Apart from the December data, the mean monthly temperatures were within three degrees Centigrade of the overall voluntary mean temperature of 30·77°C.

The mean temperature of active lizards kept in captivity in winter conditions was 26·7°C (S.D. = 3·76; n = 32). The mean for lizards kept in spring was 30·6°C (S.D. = 4·61; n = 13). These values were significantly different ($P < 0·01$; Kolmogorov-Smirnov test).

The monthly data have been grouped together into December/January, February/March/April, May, June/July/August, September, October and November. This grouped together months with few observations and allowed comparison with substrate temperatures. Thus Figure 8.5 shows a plot of mean lizard temperatures and mean temperatures of the surfaces on which lizards were basking. There is a significant trend in surface temperatures through the year ($P < 0·01$; Kruskall-Wallis test), but it is the reverse of the trend in lizard body temperatures, and indeed for ground surface temperatures (Figure 8.9).

In December and January the mean surface temperature of basking sites was 36·4°C (S.D. = 4·39), with a range of 31·9°C to 42·8°C. The lowest mean basking surface temperature was calculated for May as 29·1°C (S.D. = 3·89; range = 23·4°C to 36·0°C). In the summer (June/July/August) when lizard body temperatures were highest, the mean basking site temperature was 30·7°C (S.D. = 2·69) with a range of 27·0°C to 34·4°C.

There was no significant difference between the surface temperatures under basking lizards according to size class (Kruskall-Wallis test) nor according to sex (Mann-Witney U-test), whether considered overall or with the data divided by month.

Microhabitat temperatures

Figures 8.6 to 8.8 show the results of the random ground temperatures taken under vegetation of different heights. These results are summarised in Figure 8.9. Afternoon temperatures were higher than morning temperatures under all vegetation heights. The highest temperatures were recorded in low (<30cm) vegetation, the highest mean value for a sampling session being 51·6°C (S.D. = 4·95). During summer, this low vegetation was dry and much sunlight reached the ground. Even morning temperatures in low

Fig. 8.6 MEAN GROUND TEMPERATURES IN < 30cm VEGETATION, MORNING AND AFTERNOON, NORTH FRONT CEMETERY, GIBRALTAR. (95% Confidence limits given)

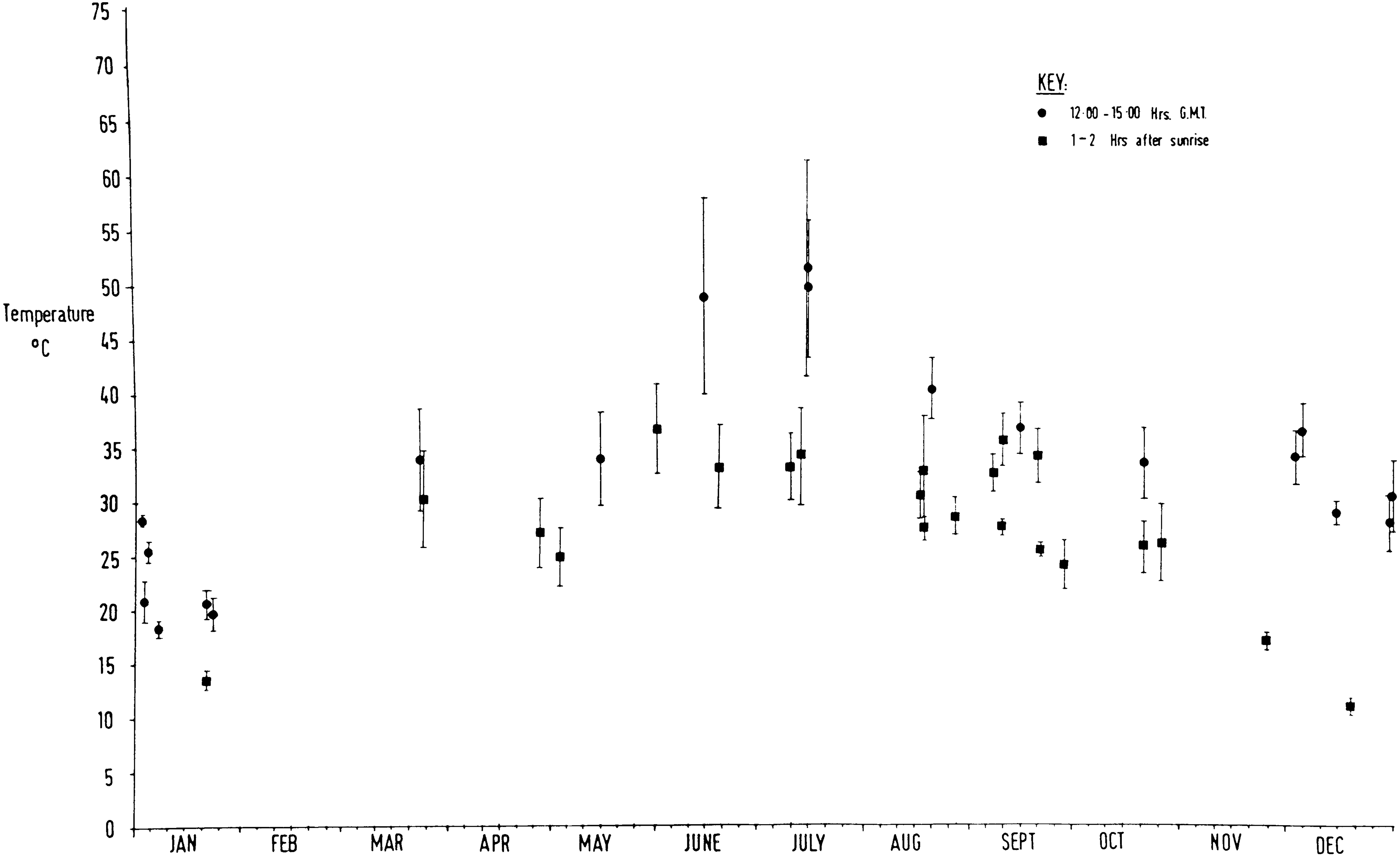


Fig. 8.7 MEAN GROUND TEMPERATURES > 30 cm VEGETATION, MORNING AND AFTERNOON, NORTH FRONT CEMETERY, GIBRALTAR (95% Confidence limits given)

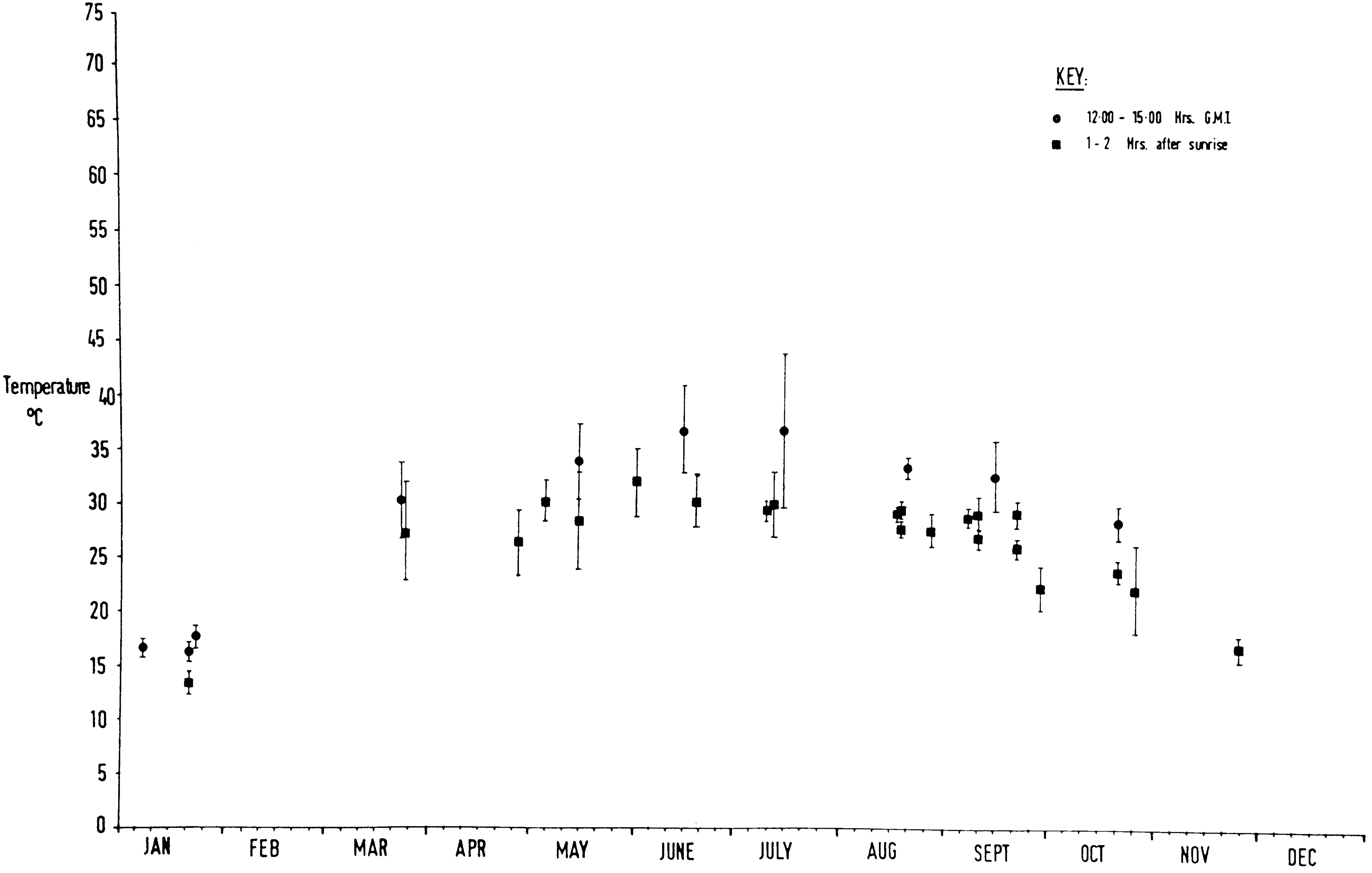


Fig. 8.8 MEAN GROUND TEMPERATURES IN LITTER UNDER BUSHES > 100 cm, MORNING AND AFTERNOON, NORTH FRONT CEMETERY, GIBRALTAR (95% Confidence limits given)

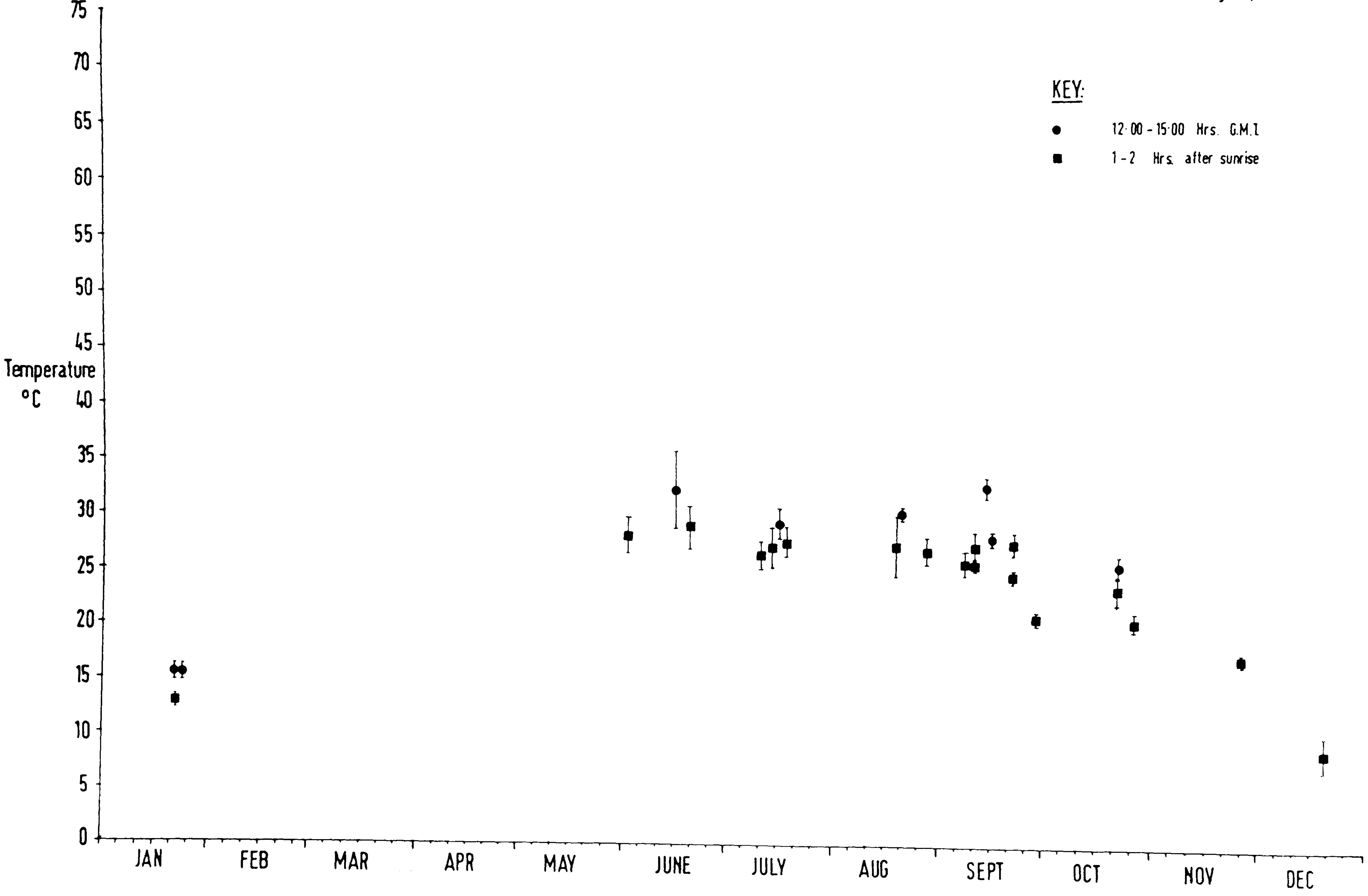
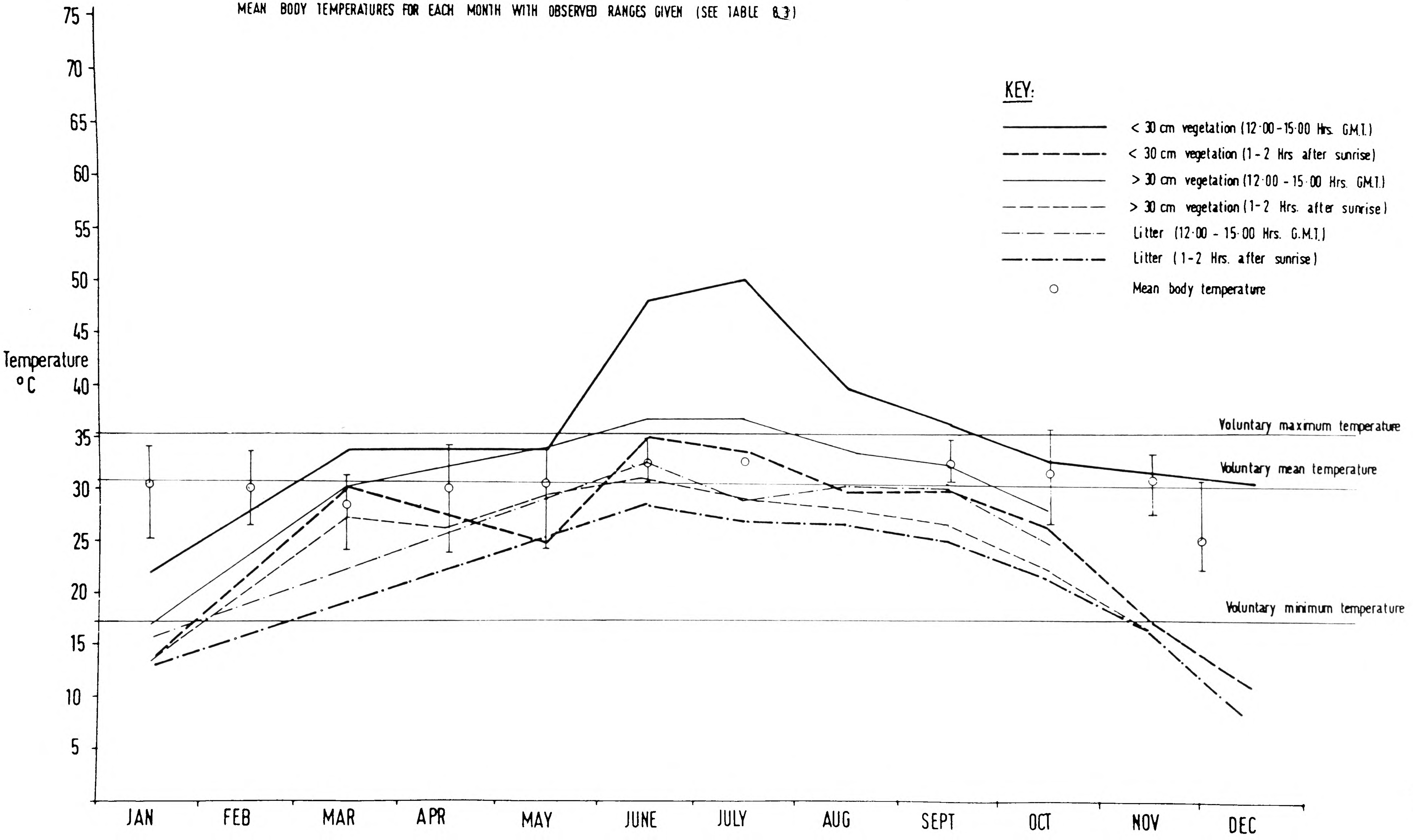


Fig. 8.9 LINES JOINING MEAN MONTHLY SURFACE TEMPERATURES UNDER DIFFERENT HEIGHTS OF VEGETATION; NORTH FRONT CEMETERY, GIBRALTAR MEAN BODY TEMPERATURES FOR EACH MONTH WITH OBSERVED RANGES GIVEN (SEE TABLE 8.3)



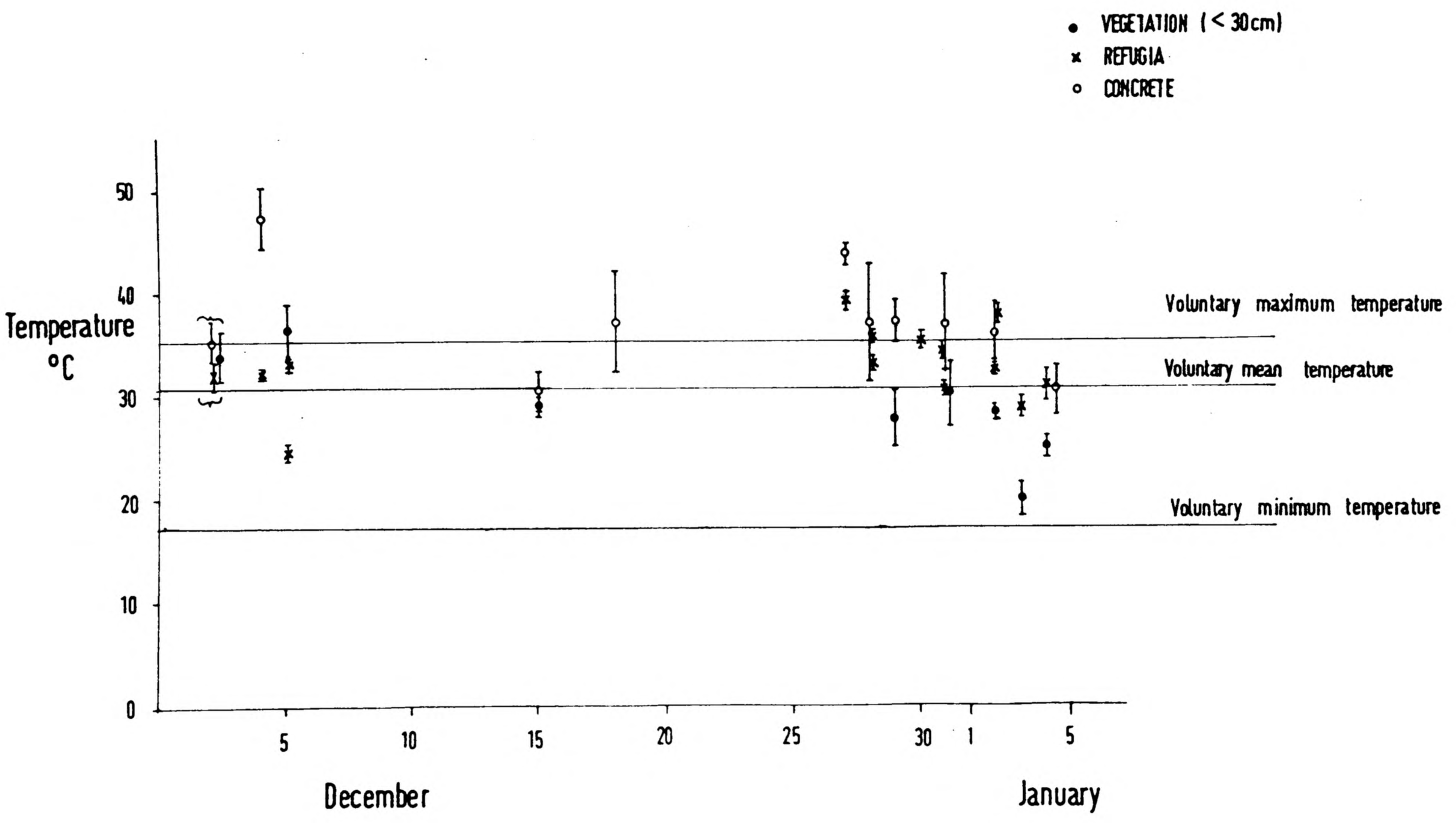
vegetation in July were above the voluntary mean temperature of P. hispanica (30·77°C), at a mean of 34·4°C (S.D. = 2·29). In winter (January), 'open' ground temperatures were at a minimum of 20·7°C (S.D. = 0·62) in the afternoon, and of 13·7°C (S.D. = 0·51) in the morning. The lowest mean temperature recorded was in December (11·3°C; S.D. = 0·47). Mean temperatures in the low (< 30cm) vegetation in spring and autumn ranged between 31°C and 34°C in the afternoon and 25·3°C in the morning.

Summer temperatures on the ground below taller vegetation (30cm - 100cm) rose to 36·9°C (S.D. = 3·61) in the afternoon and 29·5°C (S.D. = 0·53) in the morning. Maximum temperatures in this microhabitat in January were 17·8°C (S.D. = 0·43) in the afternoon and 16·6°C (S.D. = 0·36) in the morning. Spring and autumn temperatures were again similar to each other, between 25°C and 30°C. There was less variability in the winter temperatures than in those at other times of year.

Temperature in litter under bushes (> 100cm) were the lowest of those recorded. The highest temperatures were recorded in June, when mean afternoon temperatures were 32·5°C (S.D. = 1·80), with a mean of 28·3°C (S.D. = 0·85) in the morning. January temperatures were similar in the morning for all the microhabitats. For litter the mean temperature recorded in the morning was 12·8°C (S.D. = 0·17). In the afternoon, 15·7°C (S.D. = 0·40) was the mean temperature. The lowest microhabitat temperatures were recorded in December in the morning in litter, with a mean of 8·9°C (S.D. = 0·84).

Figure 8.10 depicts temperatures in refugia (samples of 20) and on concrete walls (south-facing) and in low (< 30cm) vegetation (samples of 30 readings), in mid-afternoon in December and January 1980/81. There ~~was~~ great overlap in the temperatures, although concrete temperatures tended to be highest and those in vegetation lowest. Vegetation temperatures tended to be below the voluntary mean temperature of P. hispanica, while those of refugia and concrete tended to above this temperature (30·77°C).

Fig. 8.10 MEAN MID-AFTERNOON TEMPERATURES ON DIFFERENT SURFACES AT NORTH FRONT CEMETERY, GIBRALTAR DECEMBER/JANUARY 1980/81 (95 %. Confidence limits given)



Use of substrates

The use of different substrates at the North Front Cemetery site throughout the year is shown in Figure 8.11. The surface most used by all the lizards (53·3% of the observations) was concrete, and that least used was grass/other vegetation (1·3% of observations). This does not reflect the relative abundance of the substrates in the habitat. The total surface areas were not measured, but it is estimated that sand covered the greatest surface area (although accounted for only 5·5% of the observations of lizards), followed by grass/other vegetation, marble, with concrete fourth and smaller proportions of limestone, wood, leaf litter, and others. There was no difference (X^2 test) between sexes or between adults (of both sexes or considered separately) and juveniles in substrate choice.

In Figure 8.12 the above data are shown sub-divided according to time of year. Concrete remains the most important substrate, although less markedly so in the autumn (51·3% of observations) and summer (57·0%) than in spring (68·8%) and winter (66·7%). These differences are not in themselves significant (X^2 test), but when taken together with the other substrates, the differences are significant ($X^2 = 49{\cdot}85$; $P < 0{\cdot}05$).

Figure 8.13 shows similar histograms for the whole year for lizards of different size classes. Concrete remains the most frequently used substrate, but not notably so for the smallest lizards (sample size was small also) (size class 1 : SVL < 20cm). The overall differences in substrate use between the size classes are significant ($X^2 = 62{\cdot}97$; $P < 0{\cdot}025$).

When the months of August to December, which represent the transition from barren open ground to green low plant cover, are taken alone (Figure 8.14), there appears to have been a slight decline in the use of concrete in November in comparison to the other months. However, in general concrete was clearly the substrate most used for basking by North Front Cemetery P. hispanica of all sizes and both sexes.

In areas where concrete was absent, limestone was most used, although wood appeared also to be important (pers. obs.).

Fig. 8.11 PERCENTAGE OF *P.hispanica* BASKING ON DIFFERENT SUBSTRATES, NORTH FRONT CEMETERY, GIBRALTAR. (KEY AS AT FIG. 8.13)

RESULT OF CONTINGENCY TABLE

$\chi^2 = 755$

$P \ll 0{\cdot}001$

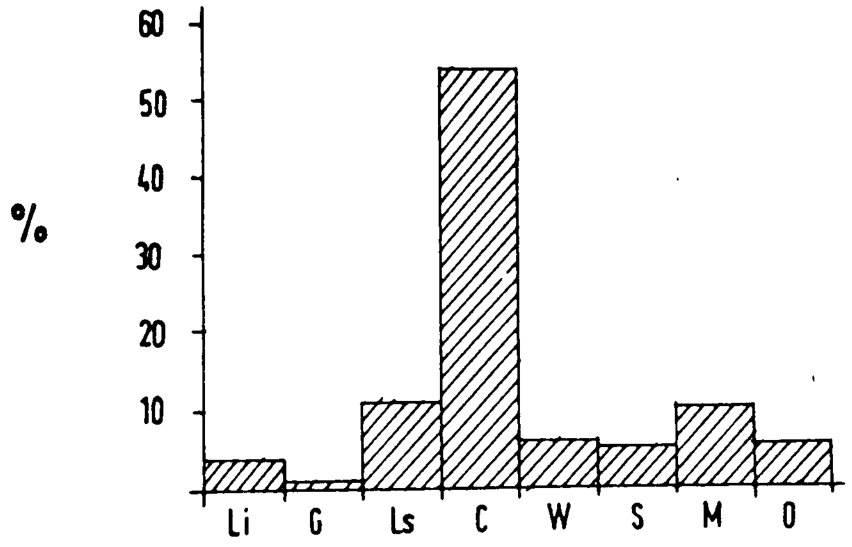
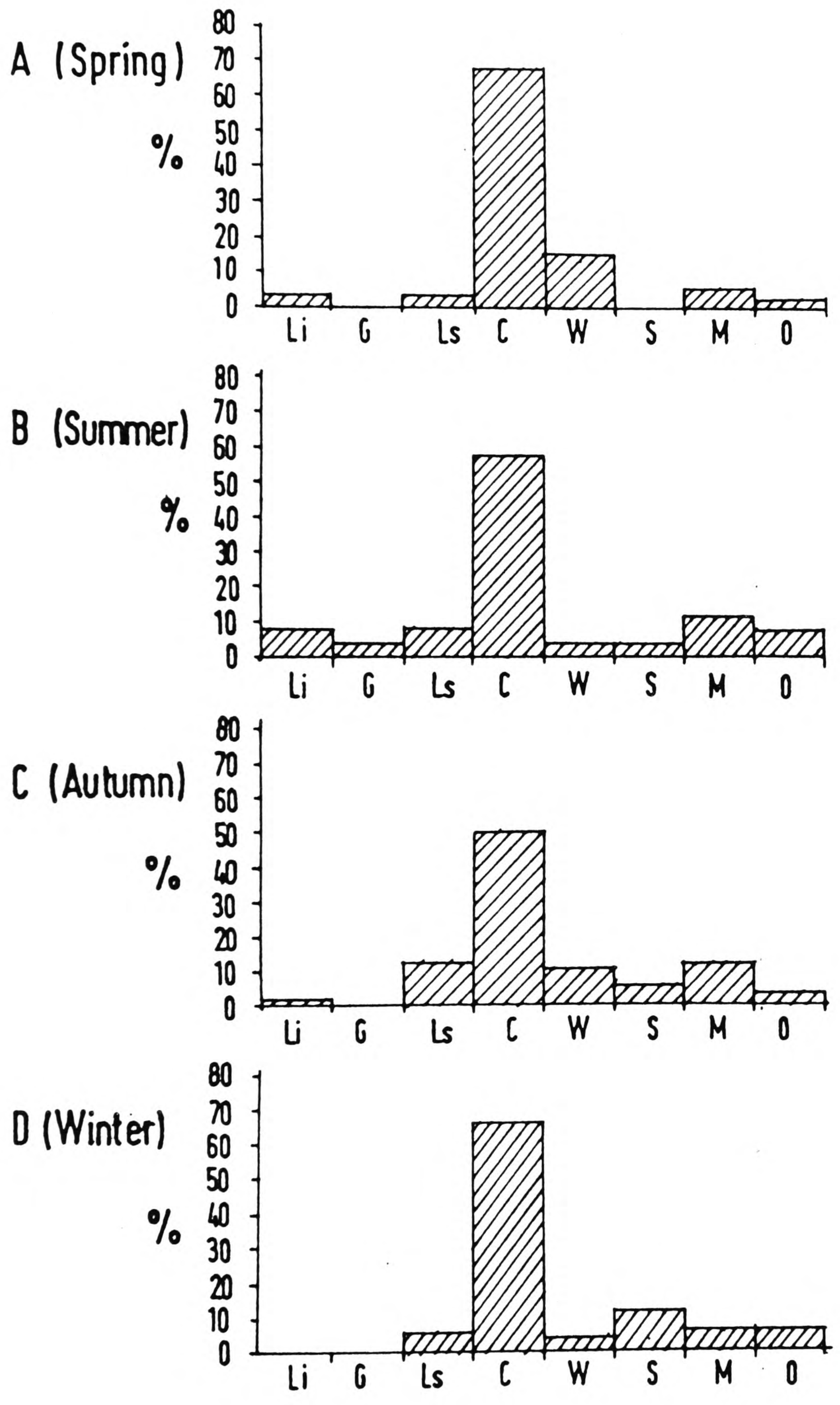


Fig. 8.12. PERCENTAGE OF P. hispanica BASKING AT DIFFERENT TIMES OF THE YEAR, ON DIFFERENT SUBSTRATES, NORTH FRONT CEMETERY, GIBRALTAR. (KEY AT 8.13)

SEASON

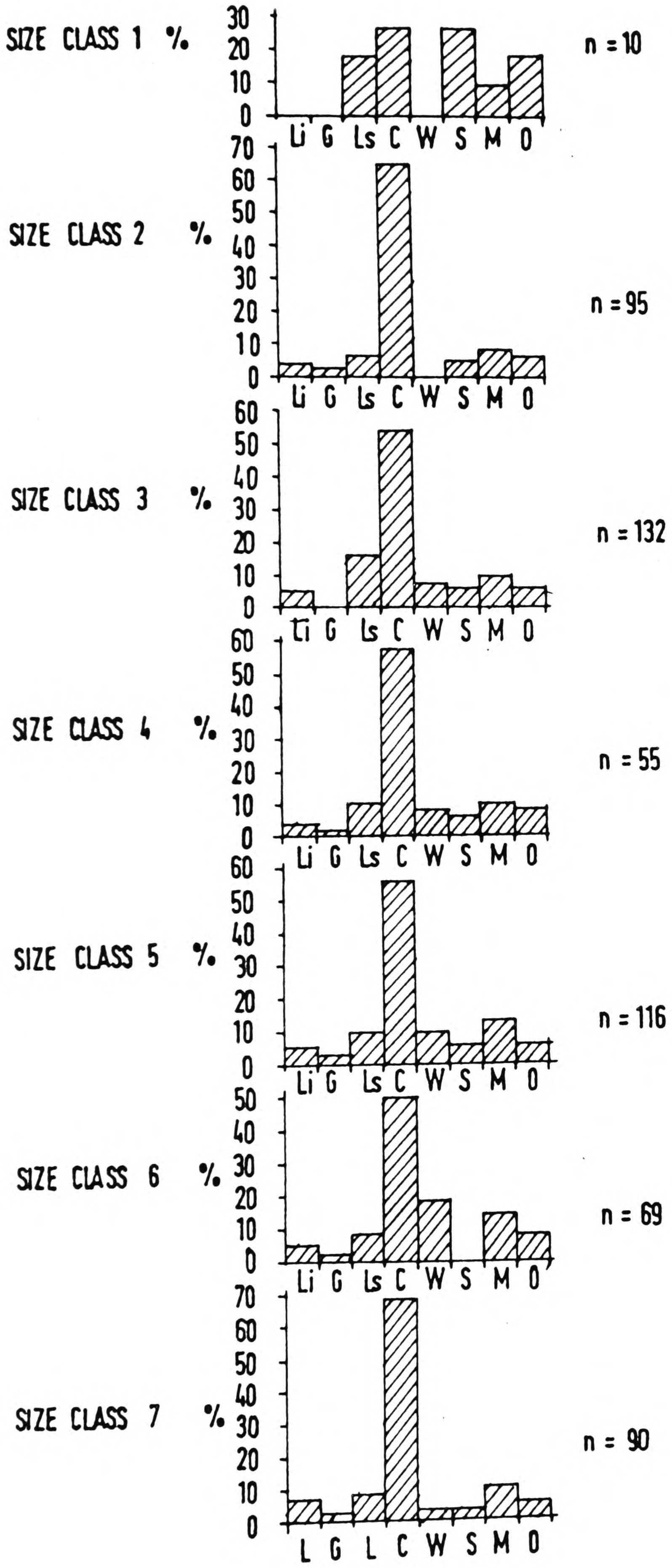


RESULT OF CONTINGENCY TABLE

$\chi^2 = 49{\cdot}85$

$P < 0{\cdot}001$

Fig. 8.13 PERCENTAGE OF *P. hispanica* OF DIFFERENT SIZE CLASSES OBSERVED BASKING ON DIFFERENT SUBSTRATES IN NORTH FRONT CEMETERY, GIBRALTAR.



SUBSTRATES:

Li = Litter
G = Grass
Ls = Limestone
C = Concrete
W = Wood
S = Soil
M = Marble
O = Other

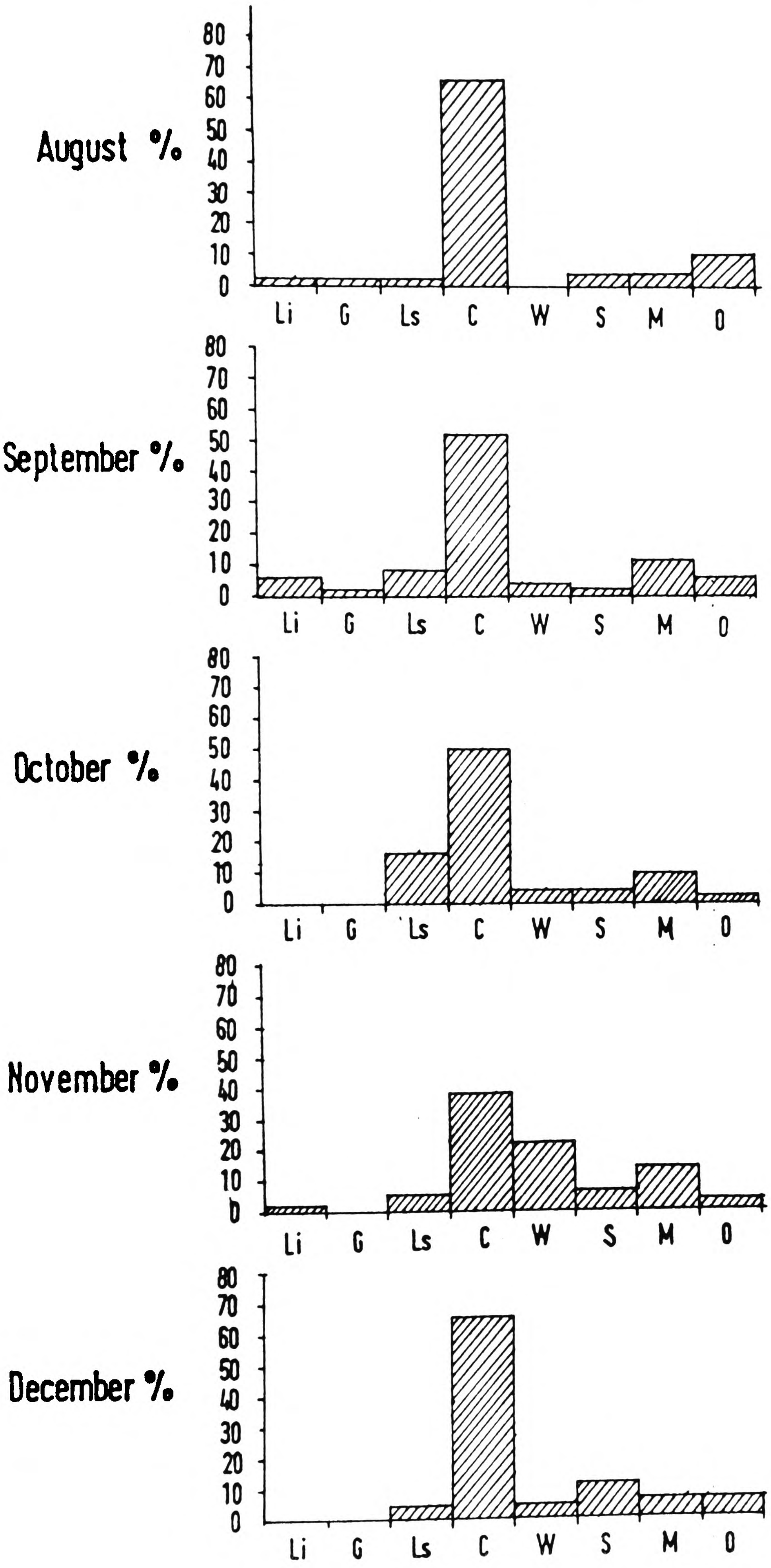
SIZE CLASSES

	SVL
1	< 20 mm
2	20 - 30mm
3	30 mm
4	30 - 40mm
5	40 mm
6	40 - 50mm
7	≥ 50 mm

RESULT OF CONTINGENCY TABLE

χ^2 = 62·97
P < 0·025

Fig. 8.14 PERCENTAGE OF *P. hispanica* BASKING ON DIFFERENT SUBSTRATES AUGUST TO DECEMBER 1981, NORTH FRONT CEMETERY, GIBRALTAR. (KEY AS IN FIG. 8.13)



RESULT OF CONTINGENCY TABLE

$\chi^2 = 77.58$

$P < 0.001$

8.2.4 Discussion

Temperature relations

The temperature relations of P. hispanica, listed in Table 8.1, can be used to predict the reactions of lizards at different body temperatures. A lizard can be expected to become slightly active at a body temperature just above the critical minimum temperature (12·2°C). Activity would be expected to increase with increase in body temperature, the lizard moving towards warmer conditions (or conditions that will raise its temperature) at around the voluntary minimum temperature of 17·3°C. The lizard will be active at around its voluntary mean temperature of 30·8°C (field range of 21·9 - 36·0°C). Cooling to significantly below this temperature, and certainly to close to 17·3°C would lead to the lizard either seeking warmth (e.g. by emerging to bask) or to its withdrawing to its refugium. The lizard would be expected to seek cooler conditions on reaching a body temperature above the voluntary maximum (35·5°C) and certainly above its 'absolute voluntary maximum' of 38·0°C. If shelter were not available, it would lose mobility at around the critical maximum temperature of 40·3°C, and eventually die.

The voluntary mean temperature recorded in this study (30·8°C) is low in comparison with those values recorded by other workers (Brattstrom, 1965) and specifically for other European reptiles (Spellerberg, 1976; Avery, 1978; Busack, 1978), although in most of those cases sample sizes have been considerably smaller than in this study (n = 112).

Only Busack (1978) gives a mean temperature for field P. hispanica. His value was 34·0°C ± 0·8SE, with a range of 25·4 - 38·4°C. The data, from 16 individuals, were all collected on one day in August and would therefore be expected to be higher than the overall value for Gibraltar P. hispanica. The voluntary mean temperature for Gibraltar lizards in summer (June to September) is 32·9°C (S.D. = 1·39), higher than the overall mean, and closer to Busack's (1978) value. A similar explanation may account for the voluntary mean temperature of Ps. algirus having been calculated as being 30·9°C in this study and 35·4 ± 0·4SE in Busack (1978).

P. hispanica, being a southern European species, would be expected to have higher active body temperatures than more northerly species (Avery, 1976). Unfortunately no data exist on *P. hispanica* to allow comparison of mean body temperatures at different latitudes. Avery (1978) gave the voluntary mean of *Podarcis muralis* as 33·57°C and that of *P. sicula* as 35·16°C. These mean temperatures of Italian lizards are higher than that of *Lacerta vivipara*, a more northerly species, given by Spellerberg (1976) as 32°C. The temperatures of Avery's (1978) two Mediterranean species are again similar to those of *P. hispanica* in Gibraltar in summer. Overall, however, the temperature mean for *P. hispanica* is lower than that for *L. vivipara* and than most of the other lizards listed in Table 8.3. The northern European species hibernate, and are only active during the summer. They may require higher temperatures during this time in order to reproduce successfully in a short season. *P. hispanica* in Gibraltar, active year-round, may be able to do so at slightly lower temperatures. The relatively low voluntary mean temperature may be an adaptation allowing activity during the cool winter months, when temperatures around 30°C are reached in the species' microhabitat. Other Mediterranean species have generally been studied only during some weeks in the summer. This may account for their higher recorded voluntary mean temperatures.

The critical minimum and critical maximum temperatures were determined using lizards kept in winter conditions. These temperatures would therefore be expected to have been lower than if other conditions had been operative, since acclimation would take place (Spellerberg, 1973). In fact, the critical minimum temperature obtained (12·2°C) is higher than all those given by Spellerberg (1972) (the highest value was 9·8°C (range 9·5 - 10·1°C) for the skink *Egernia inornata*). However the rate at which cooling takes place together with the method employed in determining these critical temperatures will affect their value (Heatwole, 1976), so that these results are not all comparable. *P. hispanica* can certainly tolerate temperatures below the 'ecological death point' (the critical minimum temperature). Captive lizards have been seen to recover fully after spending 60 hours at 5°C , at which temperature they were totally immobile and appeared to be dead.

The critical maximum temperature was closer to those given by Brattscrom (1965) and Spellerberg (1972). Again it must be remembered that critical maximum temperature is influenced by thermal acclimation and photo-period (e.g., Ballinger & Schrank, 1970; Corm, 1971) and time of day (Webb & Witten, 1973).

The critical temperatures, which are avoided in the field, are of little ecological value and certainly less important in that sense than tolerance limits and thermal performance breadths (Huey & Stevenson, 1979). The range of field temperatures of P. hispanica is 21·9°C - 36·0°C (compared to 29·9°C - 36·6°C for P. muralis and 33·9°C - 36·6°C for P. sicula; Avery, 1978). These values were all taken in the field and will therefore tend to be more indicative of the true tolerance range of the species. The suggestion therefore is that voluntary temperatures of P. hispanica are lower than expected. The field conditions through the year need to be considered in order to determine whether the estimates of temperature appear in fact to be too low or are such that they will enable the lizards to exploit the resources of their habitat successfully, in keeping with field observations of activity.

Mean field body temperatures during different months as given in Table 8.2 and represented in Figure 8.4 are, with the exception of the December result, within a range of 3°C, and suggest good thermoregulation by P. hispanica, with perhaps more difficulty during that month. Voluntary mean temperature for December was 25·12°C (S.D. = 3·69), and the lowest recorded field temperature, also in that month, was 21·9°C.

Figure 8.1 shows that there was a good correlation between lizard body temperature and surface temperature for captive lizards in spring and for animals in the field. Basking lizards had body temperatures up to 8°C higher than that of the surface on which they were resting. Again good thermoregulation is suggested, allowing lizards to maintain a temperature above ambient temperature (in all cases temperatures one centimetre above the surface were lower than surface temperatures). Lizards at rest in the shade usually had temperatures closer to the surface temperatures.

Lizards kept under winter conditions had resting temperatures considerably higher than those of the substrates (Figure 8.2). Spring captive lizards cooled to ambient temperatures of 7°C to 10°C did not attempt to raise their temperatures significantly. Body temperatures in winter could therefore be brought to within the voluntary range. This suggests less careful thermoregulation under spring conditions when in practice temperatures in the field never drop to below the critical minimum in daytime. It could also imply more basking will take place in winter. The winter body temperatures of captive lizards also suggest that in winter *P. hipanica* may have to be active at the lower half of the voluntary range of temperatures. This would reflect a seasonal variation in temperature tolerance (Ballinger *et al.*, 1970; Huey & Stevenson, 1979).

Figure 8.5 illustrates the mean temperatures under basking lizards compared to the mean body temperatures of the animals throughout the year. (No differences were found in temperatures of basking sites between sexes or size classes.) The figure suggests that lizards chose warmer surfaces in winter and cooler ones in summer. This choice contrasts with the results, shown in Figure 8.9, which indicate that substrates are warmest in summer. *P. hispanica* therefore appears to seek out warmer surfaces when in winter it needs to raise body temperature. The observations of basking lizards in summer, when differences between body and surface temperatures were not so great, were generally made early in the morning so that surface temperatures tended to be low. Since solar radiation is intense (around 7·9 $\text{Jcm}^{-2}\text{min}^{-1}$ at noon in mid-June) the reliance on surface temperatures for warming is probably negligible later in the day at this time of year.

Microhabitat temperatures

The microhabitat temperatures obtained and extrapolated from the random sampling of ground temperatures in the field are shown in Figure 8.9 and related to the mean voluntary, voluntary maximum, and voluntary minimum temperatures. The temperatures of all these microhabitats - vegetation $<$ 30cm, $>$30cm and litter under bushes taller than 100cm - within which lizards were seen to forage, were within the voluntary range of temperatures of P. hispanica during most of the year. Conversely, it could be said that lizard temperatures followed closely those of the environments in which the animals foraged.

The summer afternoon temperatures in vegetation > 30cm and particularly in the lowest category (<30cm), were above the voluntary maximum. Temperatures in the low vegetation rose to above the critical maximum temperature of the species (40·3°C). Although this maximum is probably higher in summer (Huey & Stevenson,1979), low activity would be expected during this period. In low and open vegetation during the afternoon lizards should be inactive or absent. Their activity is in fact restricted to the morning or evening, or, in the afternoon, to the litter layers under tall bushes or trees (5.2; 8.3). Lizards above their critical maximum temperature should seek shade. This would contribute to the redistribution of the reptiles in the habitat discussed in 5.2.

Temperatures in January and December fell below the voluntary minimum in the morning in all the microhabitats and in litter during the afternoon also. Thus lizards under tall vegetation, even if able to bask, will lose heat while foraging. When active, they will generate some heat, but the rate of loss will depend on the the difference between body and ambient temperatures. Lizards will therefore tend to favour warmer, open microhabitats in winter provided nocturnal refugia and morning basking sites are available, allowing them to increase temperature and maximise foraging time. Foraging will take place in low vegetation, close to the refugia. There, lizards will be able to maintain temperatures within their voluntary range in the afternoon and be close to shelter should cloudy conditions suddenly arise. On particularly cold days, these lizards will be able to remain basking close to the entrance to the refugia. This behaviour is precisely what is observed at this time (5.2).

In order to maintain body temperature in a cool environment, basking will be most necessary in winter. Foraging lizards, or those having recently emerged to bask, will have body temperatures at the lower end of the voluntary range (Table 8.3). Lizards will not be able to forage for long periods (Figure 7.10). Basking will tend to be on warm surfaces to aid increase in temperature and avoid loss of heat through the ground (Figure 8.5). Concrete

Table 8.3 Temperature relations of some western European reptile species

SPECIES	CLIMATIC REGION	VOLUNTARY MEAN (°C)	VOLUNTARY RANGE (°C)	n	SOURCE
Anguis fragilis	ACMS	23	14 - 29	2	(1)
Lacerta agilis	AC	31	23 - 38	8	(1)
L. viridis	AM	33	23 - 38	8	(1)
L. vivipara	ACS	32	22 - 38	7	(1)
Podarcis muralis	AC	36	31 - 40	2	(1)
		33·57	29·9 - 36·6*	24	(2)
P. sicula	M	34	24 - 38	11	(1)
		35·16	33·9 - 36·6*	7	(2)
P. hispanica	M	30·77	17·3 - 35·5	112	(3)
		34·0	25·4 - 38·4*	16	(4)
Psammodromus algirus	M	36	28 - 40	1	(1)
		35·4	30·4 - 40·6*	27	(4)
		30·9	25·0 - 37·0*	22	(3)
Ps. hispanicus	M	34	24 - 39	2	(1)
Coronella girondica	M	30	22 - 37	2	(1)
Natrix maura	M	29	20 - 38	2	(1)

*range of field temperatures
Climatic regions: A, Atlantic; C, Continental; M, Mediterranean; S, Subarctic (Spellerberg, 1976).
Sources: (1) Spellerberg, 1976; (2) Avery, 1978; (3) this study; (4) Busack, 1978.

provides such warm surfaces, in some cases warmer than the voluntary maximum (Figure 8.10).

Use of substrates

The marked preference of all P. hispanica for basking on concrete (Figures 8.11 to 8.14) is therefore probably related to surface temperature relations (c.f. House et al., 1980). Concrete readily absorbs heat radiation and releases it slowly. It feels warm even when windy or after the sun has been obscured. It was the warmest surface available (Figure 8.10) except in summer, when sand appeared to be hotter under dry vegetation (Figure 8.9).

Warm surfaces will be most useful to lizards in winter and spring (when in fact most use was made of concrete). In summer and autumn, when lizards spend more time on the ground (5.2) in the proximity of bushes, more of the ground substrates will be used (Figure 8.12). The smallest lizards, which use the ground most, will be seen basking on ground surfaces also (Figure 8.13). They may also be displaced from more favourable basking sites by larger lizards (5.3). Apart from the obvious preference for concrete, there was a fairly uniform use of the other substrates through the year by the different size classes (Figure 8.13).

While a lizard will be able to prolong its activity in winter by basking and chosing warm surfaces, cooling in summer will be more difficult. Summer is therefore expected to be the time of least lizard activity. Temperatures in spring and autumn are the closest to the voluntary mean temperature of the species. The temperatures of all the microhabitats fall between the voluntary minimum and maximum (17·3°C and 35·5°C) and the field range of temperatures (21·9°C to 36·0°C). This should facilitate the spread of individuals through the habitat in spring (5.2). Basking will still be necessary to increase temperatures towards the voluntary mean temperature. Temperatures in the lower vegetation should allow longer periods of foraging at this time of year.

P. hispanica, being active year-round, has to be able to cope with low as well as high temperatures. Its thermoregulatory behaviour - choice of microhabitat, basking surfaces, etc. - serves to reduce the impact of variation in ambient conditions (Huey & Pianka, 1977). A low voluntary mean temperature (if close to the preferred body temperature) will allow activity in winter at times when P. hispanica and other species from more northerly populations will be hibernating (Mellado, 1982). The lizards then adapt to being active in the cold (as opposed to hibernating) by modifying voluntary temperature levels (Spellerberg, 1976).

Shifts in preferred body temperature, as reflected in the voluntary mean, can be evidence of seasonal acclimation of optimal body temperature (Huey & Stevenson, 1979). A lower activity range in winter can be adaptive if it reduces costs associated with attempting to maintain a high body temperature (Huey & Stevenson, 1979). Since excessive basking will reduce foraging time, it will be favourable to forage at lower body temperatures. This is possible again, as long as foraging ground, basking sites and refugia are close together.

The observed temperature relations of P. hispanica at Gibraltar correspond well to the temperatures of the environment throughout the year. The adaptation of lizards to cold conditions in particular will be discussed in relation to morning emergence in winter in 8.4 and 8.5.

8.3 Activity patterns

8.3.1 Introduction

Having considered the temperature relations of P. hispanica, it is now possible to look at the diel and annual patterns of activity as observed in the field.

It is well known that activity patterns in many species of diurnal heliotherms are determined by climate and weather (Avery, 1978). Lizards in Mediterranean regions are known in some cases to show bimodal activity in the summer (e.g., Busack, 1976), while others show unimodal activity (Avery, 1978). Activity in winter is generally held to be low (St. Girons & St. Girons, 1956; Andrada, 1979) but has not been the subject of detailed study.

In order to discuss the activity of P. hispanica, its behaviour must be examined in order to determine whether or not it can be considered to be a heliothermic species, as a number of related species appear to be (Spellerberg, 1976). Overall activity can then be considered in the light of these conclusions, and of the temperature relations discussed earlier in this chapter (8.2).

8.3.2 Methods

Observations made during transects at North Front Cemetery were used to find the proportions of the different sexes and size classes basking and foraging at different times of the day and year. For basking lizards, note was made where possible of whether the lizard was facing towards or away from the sun and whether it was basking horizontally, vertically, or at some other angle.

The lengths of basking and foraging intervals recorded from continuous observations were compared for different times of the year also.

In order to gain an overall picture of year-round lizard activity, the maximum number of lizards seen during a transect within each hourly period each month was used. This gives an idea of the maximum number of lizards active each hour in the transect route. A mean value would be an underestimation, since there were transects when few or no lizards were seen due to disturbance or inclement weather.

8.3.3 Results

Basking activity

The proportions of basking and foraging lizards have been shown diagramatically in Figures 7.2 to 7.8.

Over the year as a whole, juvenile lizards were seen basking more and foraging less than adults (X^2 test; $P < 0{\cdot}01$). There was no difference in the proportion of basking males and females (Figure 7.2). Seasonally (Figure 7.3) the least proportion of basking lizards was in period B (May - September), and the greatest proportion was in period D (December and January) (X^2 test for four periods: $P < 0{\cdot}001$ for all lizards; $P < 0{\cdot}05$ for adults only). When basking and foraging were again compared for late summer to early autumn (Figure 7.4), the warmest time of year when most juveniles were to be found, there were again significant differences (X^2 test; $P = 0{\cdot}001$) between adult and juvenile lizards. Juveniles now basked markedly less (54% of observations) than adults (80% for males and females).

During this time, when juveniles were common, a comparison was made between the proportion of lizards of different size classes basking and foraging. Once again the smaller size classes were seen basking less often than the larger ones (12% of observations for size class 1, 43% for size class 2, 82% for size class 7) (Figure 7.5).

Although the proportions of P. hispanica seen basking and foraging varied significantly through the year (Figure 7.3), significant differences were not observed in most cases when these proportions were tested (X^2) for significant differences according to time of day. The exception was the month of September, when the greatest number of lizards was seen. During this month, there were significantly fewer lizards basking in the afternoon (40% at 1000 to 1100 hrs; 38% at 1100 to 1200 hrs; 46% at 1300 to 1400 hrs; 31% at 1400 to 1500 hrs G.M.T) than early in the morning (71% at 0700 to 0800 hrs; 83% at 0800 to 0900 hrs) and in the evening (64% at 1500 to 1600 hrs and 1600 to 1700 hrs)(Figure 7.6).

The results for the whole year are supported by those of the continuous observations (Figures 7.7 and 7.8) which give the proportion of time spent in various activities. Most basking was observed in December (91% of the time), with less between April and October. While in October only 25% of the time was spent basking in the open (Figure 7.7), most of the 69% spent in 'other' activities was in fact spent resting in partial ('mosaic') sunlight, which could be considered thermoregulatory behaviour.

When Figures 7.3 and 7.8 are compared and in the latter 'basking' and 'sit-and-wait', both of which involve sitting in the open, are taken together, there is a remarkable similarity between proportions of P. hispanica seen basking and the proportion of time spent basking by lizards observed continuously (71% and 72% respectively for period A; 60% and 68% for period B; 79% and 81% in period C; 87% and 85% in period D).

The percentage of time spent basking for continuous observations was plotted on a three-dimensional graph against time of year and time of day (G.M.T.) for observations of more than 30 minutes' duration in Figure 8.15. Of those lizard observations included in the diagram the smallest proportions of basking time were observed in the early-afternoons of the first quarter of the year, with the largest proportions in the morning, particularly during winter.

Mean lengths of basking intervals are given in Table 8.4. These monthly means were compared over the year by a single factor analysis of variance (Model II) which gave a significant result ($P \ll 0{\cdot}01$). The results are illustrated in Figure 8.19 as frequencies of basking intervals of different lengths. The greatest mean interval length (8 min 24sec) and the greatest number of intervals of more than 10 minutes duration were recorded in December, followed by January (mean = 4 min 36 sec) and November (mean = 3 min 33 sec). Intervals were shorter during spring and summer, with the greatest number of intervals of less than one minute (73·5%) and the shortest mean interval length (40 sec) was in April.

Fig. 8.15 PERCENT TIME SPENT BASKING AT DIFFERENT TIMES OF DAY AND YEAR, NORTH FRONT CEMETERY AND BRUCE'S FIREBREAK, GIBRALTAR.

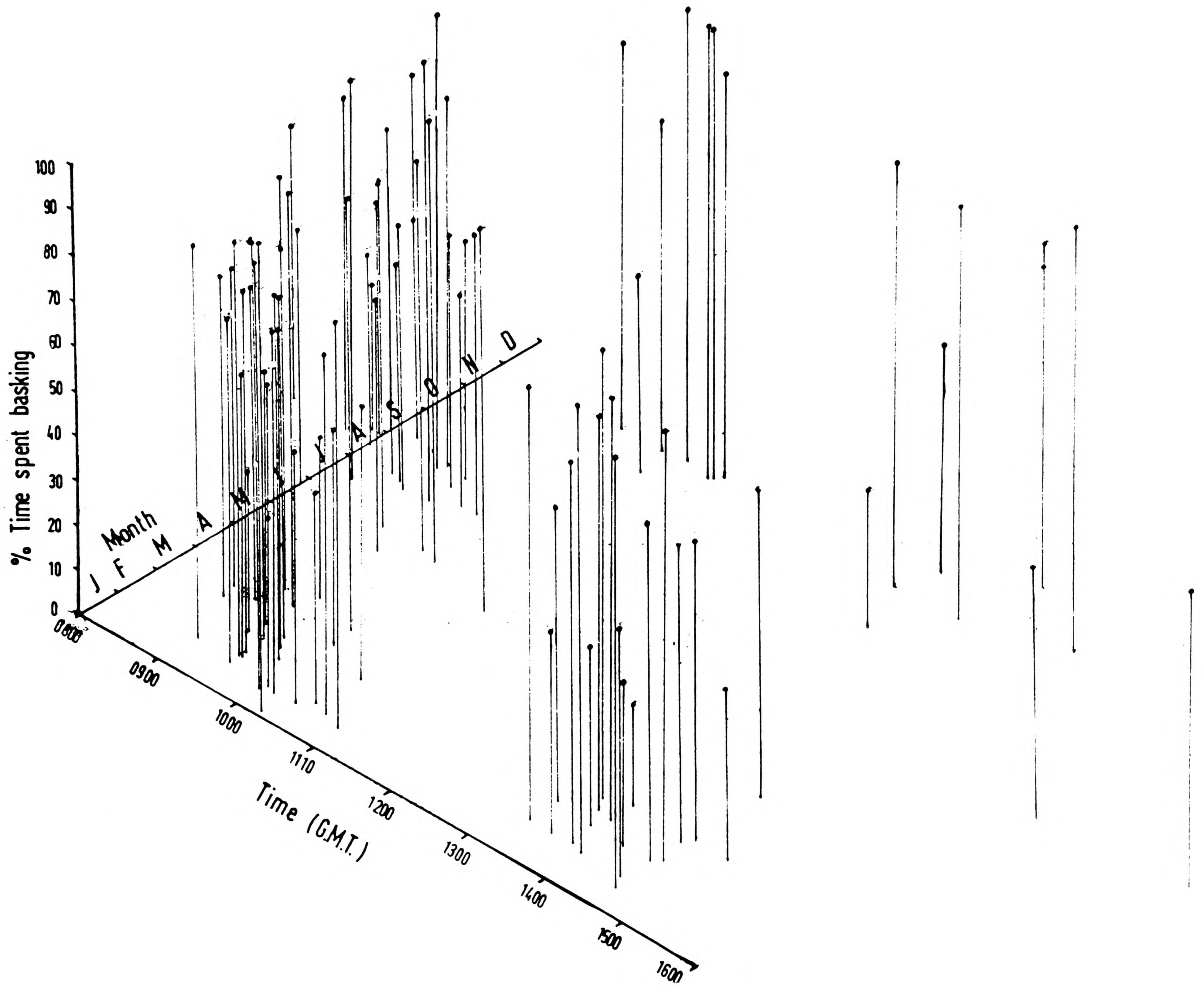
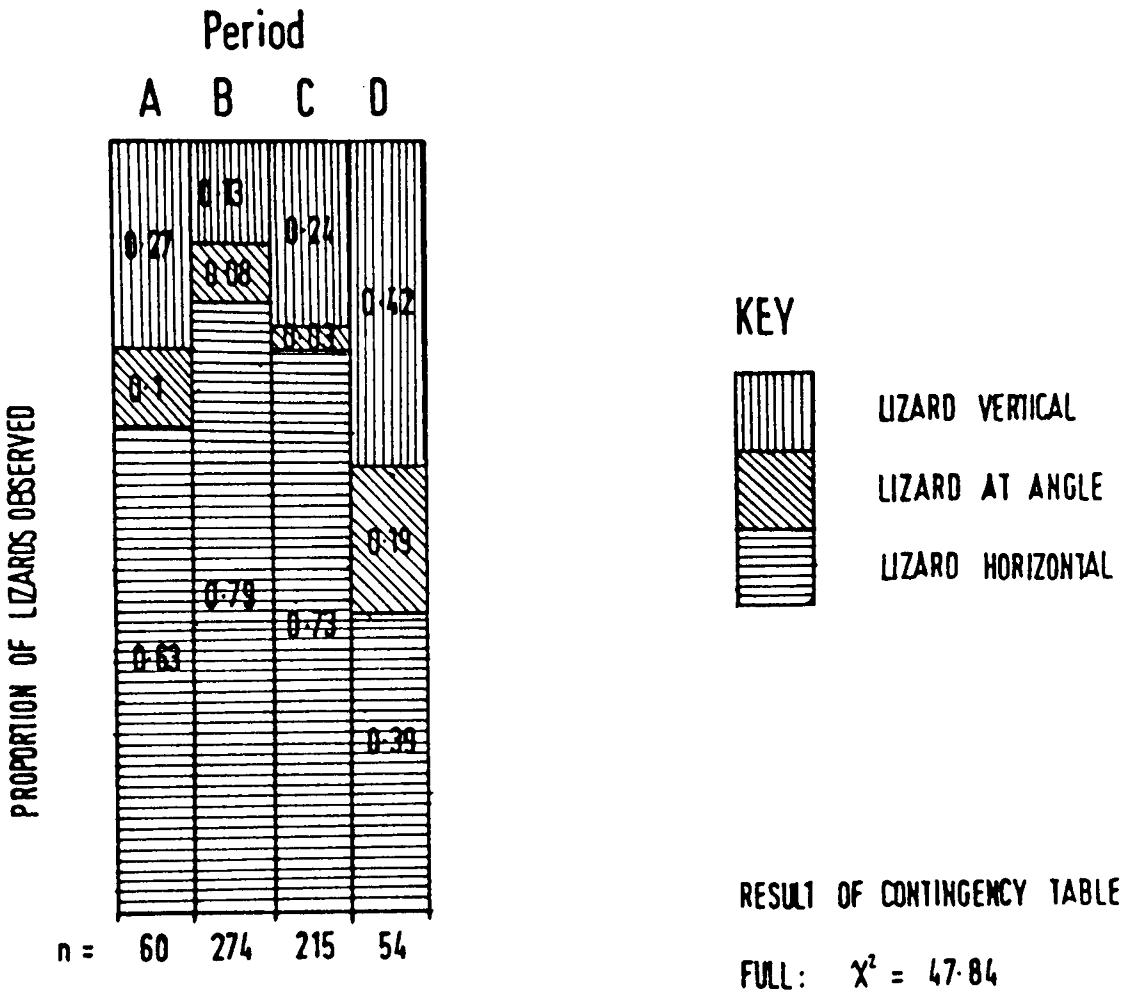


Fig. 8.16 PROPORTIONS OF LIZARDS SEEN BASKING AT DIFFERENT ANGLES



RESULT OF CONTINGENCY TABLE

FULL: $\chi^2 = 47{\cdot}84$

$P \ll 0{\cdot}005$

HORIZONTAL

VS

VERTICAL $\chi^2 = 35{\cdot}25$

$P \ll 0{\cdot}005$

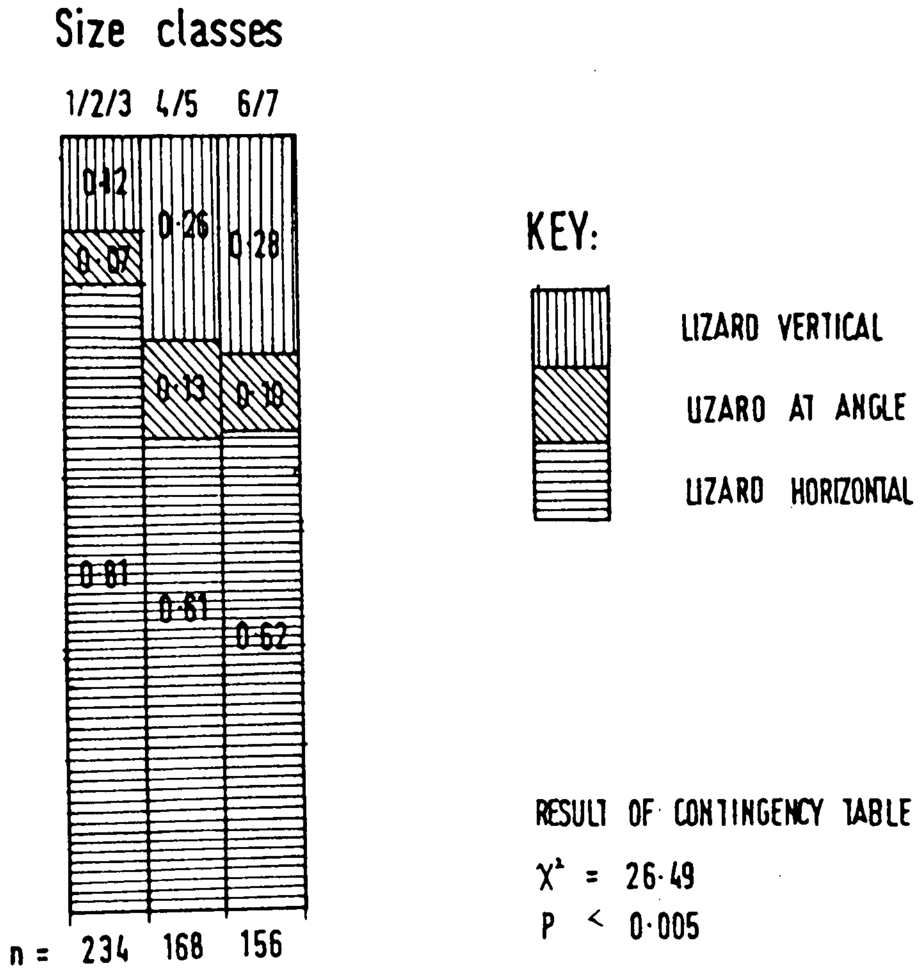
A = FEBRUARY, MARCH, APRIL, MAY.

B = JUNE, JULY, AUGUST, SEPTEMBER.

C = OCTOBER, NOVEMBER.

D = DECEMBER, JANUARY.

Fig 8.17 PROPORTION OF LIZARDS OF DIFFERENT SIZE CLASSES BASKING AT DIFFERENT ANGLES



RESULT OF CONTINGENCY TABLE

$\chi^2 = 26{\cdot}49$

$P < 0{\cdot}005$

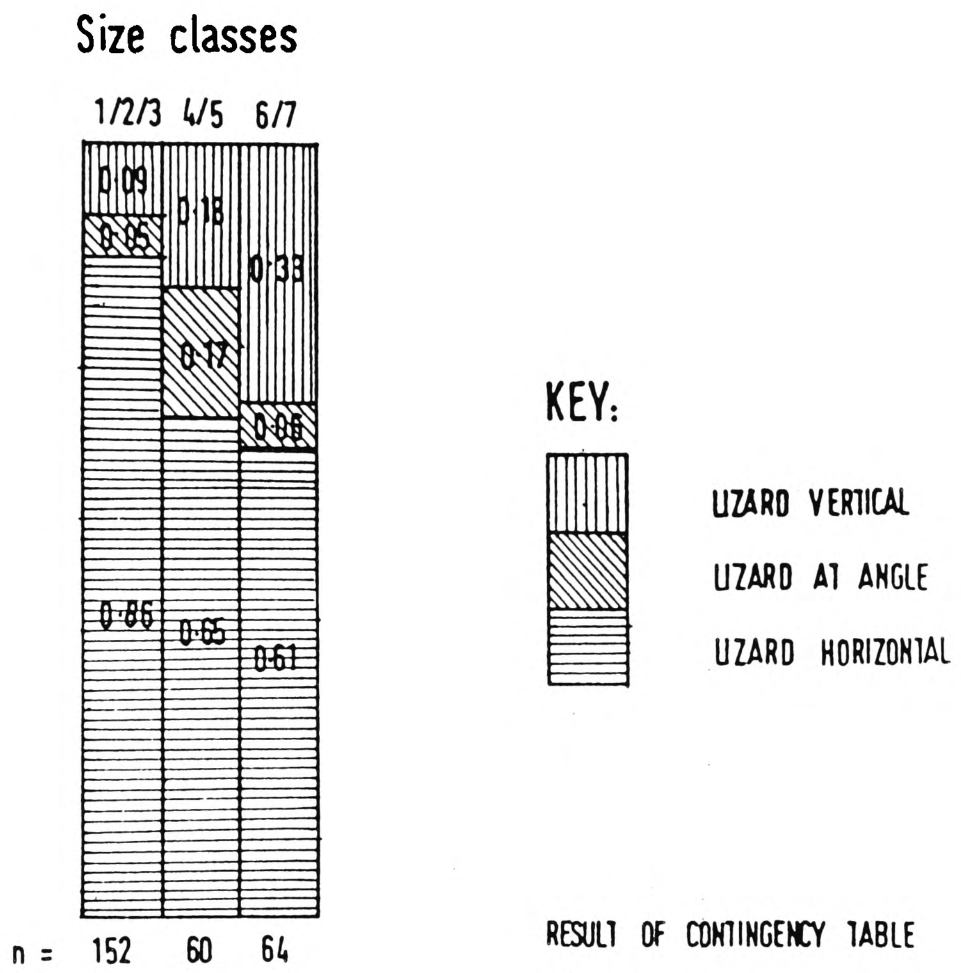
Size classes

1/2/3 = < 30 mm

4/5 = 30-40 mm

6/7 = 40 mm +

Fig.8.18 PROPORTIONS OF LIZARDS OF DIFFERENT SIZE CLASSES BASKING AT DIFFENT ANGLES (PERIOD B - JUNE, JULY, AUGUST, SEPTEMBER)



RESULT OF CONTINGENCY TABLE

$\chi^2 = 27{\cdot}21$

$P < 0{\cdot}005$

Size classes

1/2/3 = < 30 mm

4/5 = 30-40 mm

6/7 = 40 mm +

Fig. 8.19 DURATION OF BASKING INTERVALS OF *P. hispanica* BY MONTHS AT NORTH FRONT CEMETERY.
(INSUFFICIENT DATA FOR MAY AND OCTOBER)

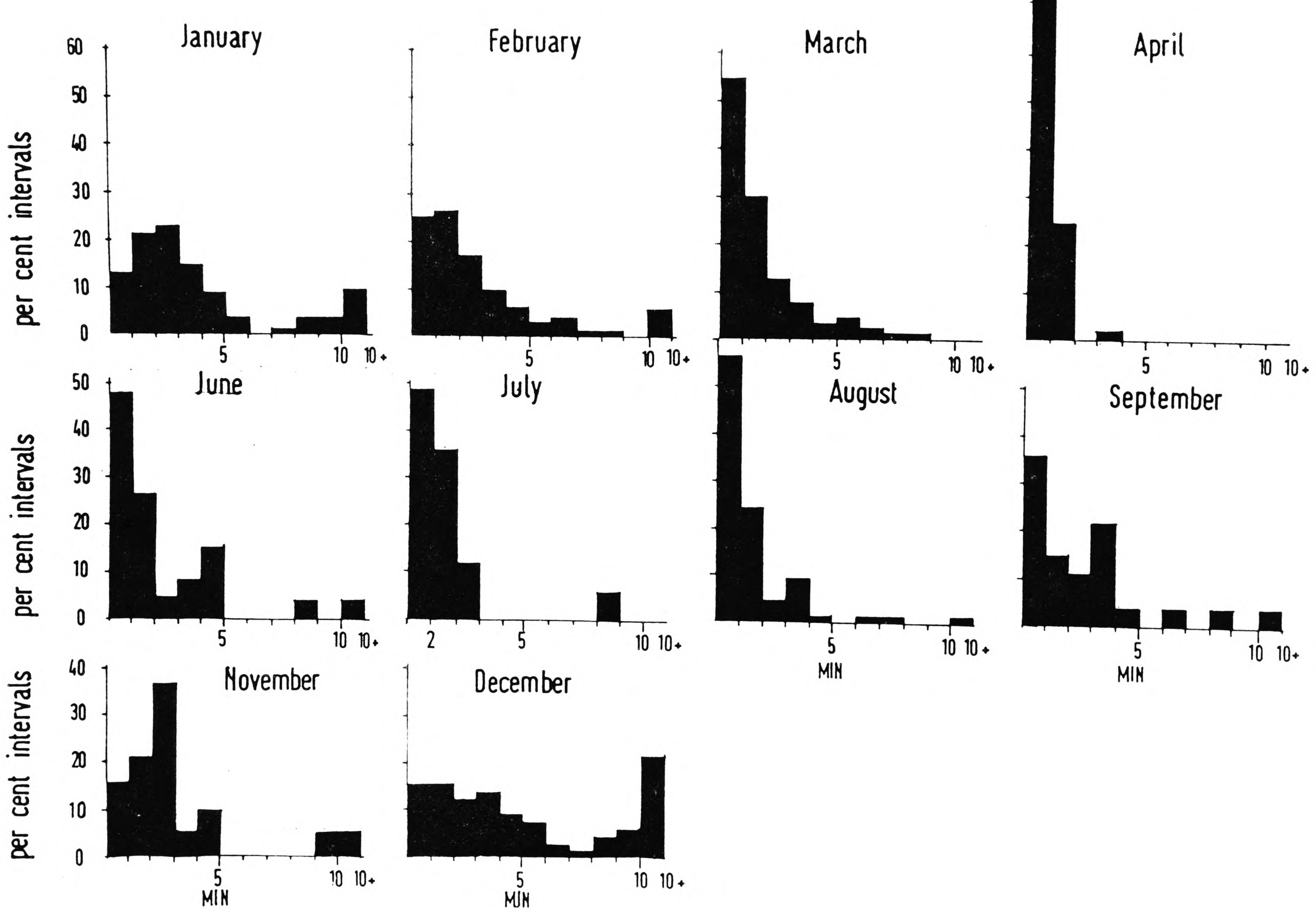
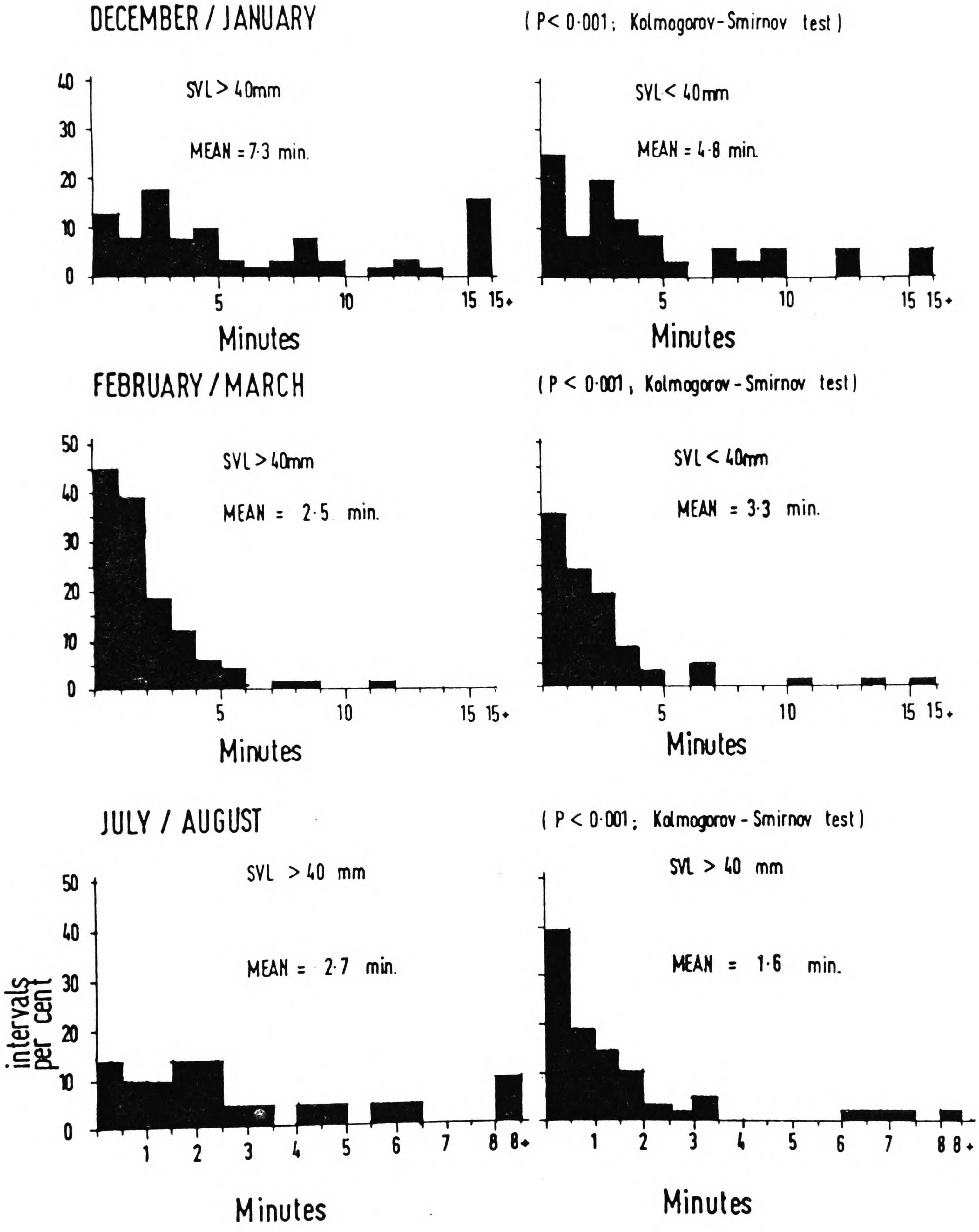


Table 8.4 Lengths of basking intervals of P. hispanica at North Front Cemetery, Gibraltar.

Month	Mean length of intervals (min.)	S.D.	n	Range (min.)
JANUARY	4·62	5·95	63	0·34 - 31·27
FEBRUARY	3·55	5·17	89	0·10 - 39·31
MARCH	1·67	1·73	113	0·03 - 7·68
APRIL	0·67	0·64	49	0·15 - 15·42
MAY	INSUFFICIENT DATA			
JUNE	2·49	3·35	27	0·30 - 16·12
JULY	1·57	1·93	17	0·12 - 2·53
AUGUST	1·93	2·52	76	0·07 - 15·42
SEPTEMBER	2·91	3·33	27	0·17 - 13·05
OCTOBER	INSUFFICIENT DATA			
NOVEMBER	3·60	3·93	22	0·29 - 15·58
DECEMBER	8·41	10·07	70	0·22 - 46·00

Fig. 8.20 LENGTH OF BASKING INTERVALS OF *P.hispanica* IN WINTER, SPRING AND SUMMER.



The lengths of basking intervals of lizards of SVL greater than 40mm were compared with those of lizards of SVL less than 40mm. Figure 8.20 gives frequency diagrams of the lengths of intervals for each group. The winter and summer samples showed significantly shorter basking periods for the smaller lizards, but the reverse was true for the spring sample ($P < 0{\cdot}001$; Kolmogorov-Smirnov test).

Posture

There were no significant differences found between the angles at which lizards were seen to bask when males, females and young lizards were compared.

When all basking lizards were considered together, there was a significant difference between the proportions of lizards basking horizontally and vertically during the course of the year (χ^2 test; $P < 0{\cdot}005$; Figure 8.16). Thus, in summer (period B) fewer lizards used vertical (13%) or sloping (8%) surfaces for basking than in winter (period B) (42% and 19% of observations respectively). Results for spring (period A) and autumn (period C) were intermediate between these, tending towards the use of horizontal surfaces (63% and 73% of observations respectively). There was a difference between the use of surfaces at different angles according to size class, both overall (Figure 8.17) and for late summer, the months of most numbers and diversity of sizes (Figure 8.18). Thus, smaller lizards (SVL < 30mm) used vertical surfaces less for basking (12% of observations) than larger ones (26% for SVL 30-40mm; 27% for SVL 40mm+; $P = 0{\cdot}005$; χ^2 test). The differences were more marked in the September sample (9%, 18%, 33% respectively for SVL <30mm; 30-40mm and 40mm+).

Data on the direction being faced by lizards while basking were too few to give significant results for different months of the year. However, results for the whole year were pooled into two categories - lizards seen within three hours of sunrise, and those seen during the three hours 1300-1600hrs. In the morning, 34·5% of lizards were facing sunwards. In the afternoon 62·5% were facing towards the sun. The difference was significant (G-test; $P < 0{\cdot}005$; $n = 167$).

No significant difference (χ^2 test) was found between size classes of lizards active at different times of day.

Fig. 8.21 MAXIMUM NUMBER OF P. hispanica SEEN IN TRANSECTS EACH MONTH; NORTH FRONT CEMETERY, GIBRALTAR.

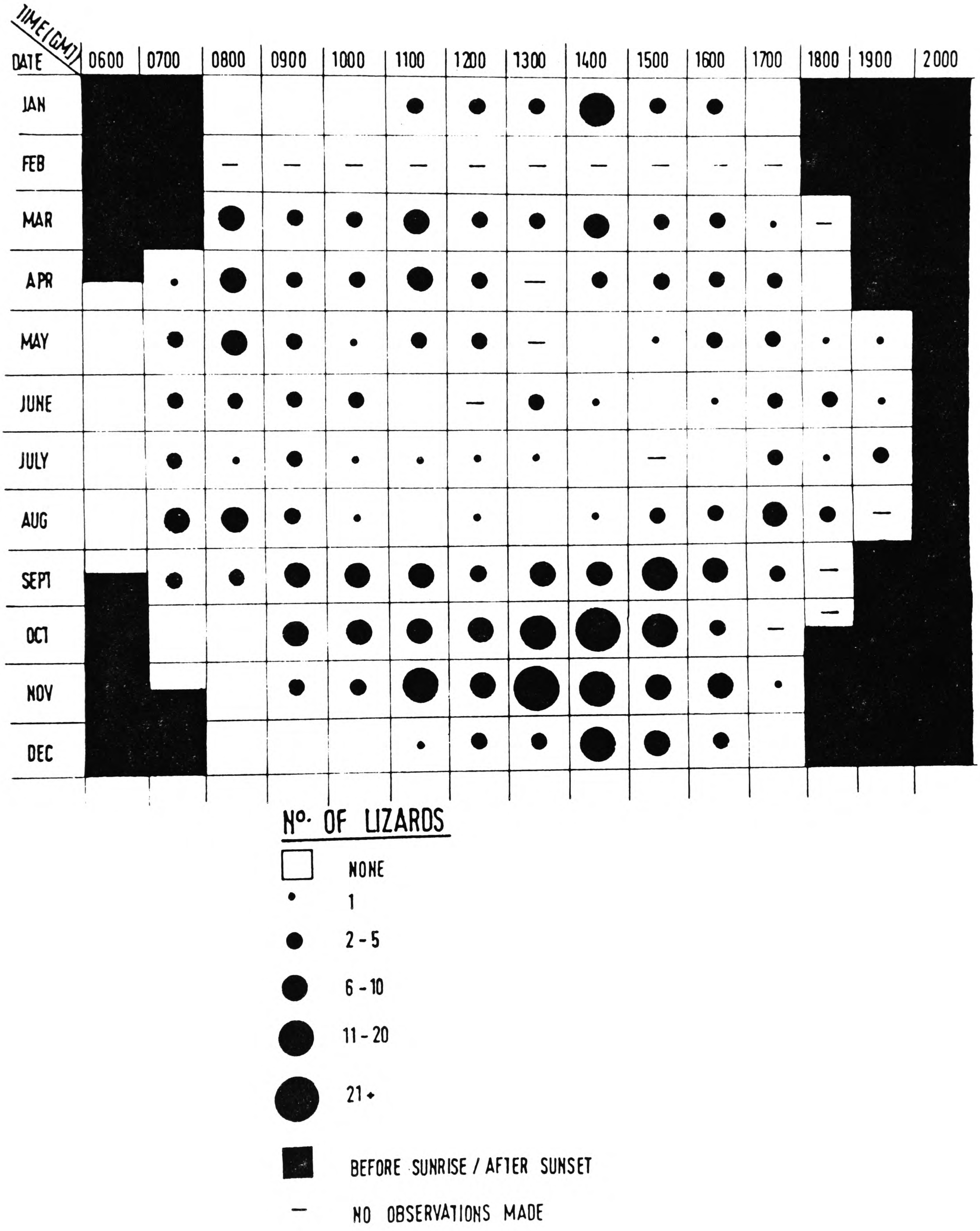
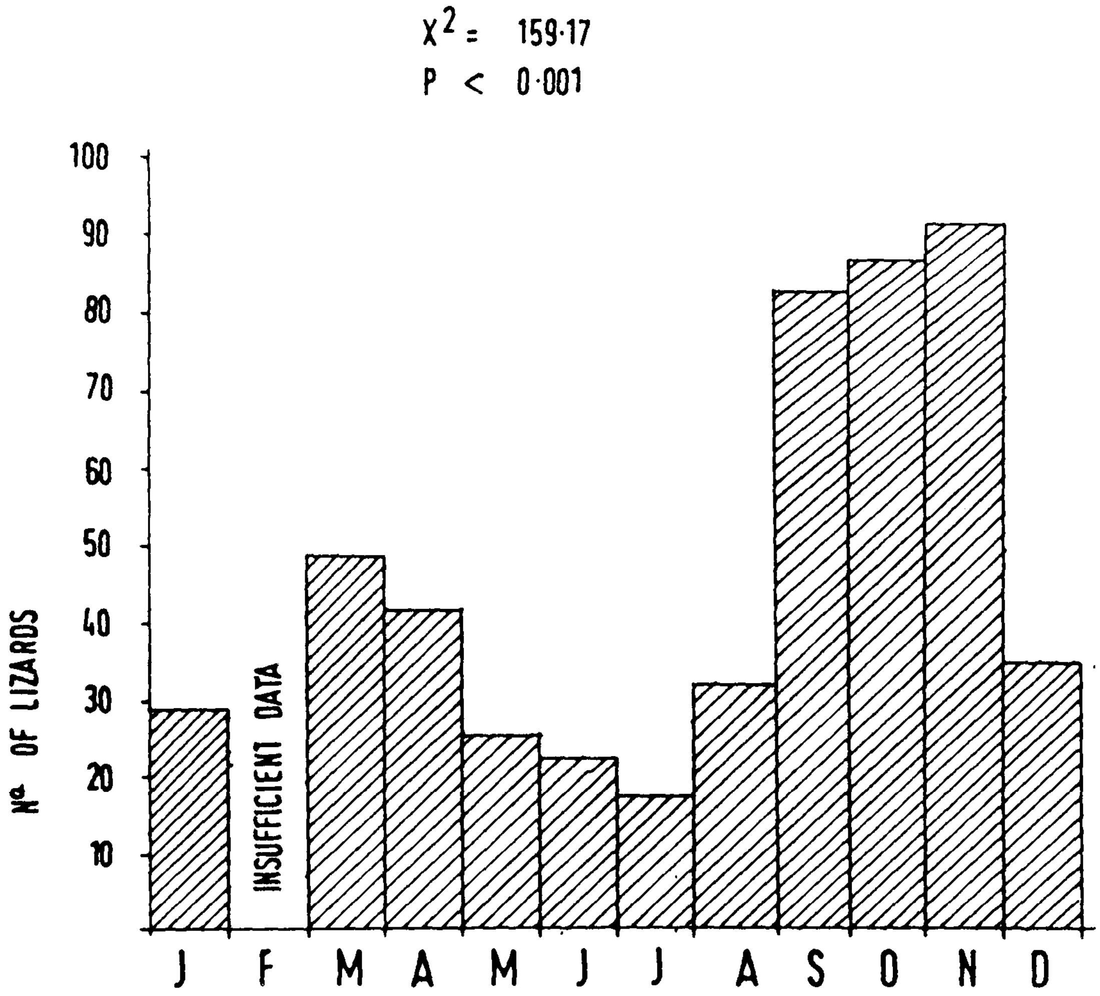


Fig. 8. 22 MONTHLY TOTALS OF MAXIMUM NUMBERS OF *P. hispanica* SEEN IN TRANSECTS EACH HOUR AT NORTH FRONT CEMETERY, GIBRALTAR.



Activity

Figure 8.21 illustrates the maximum number of lizards seen in the transect site each hour through the year. Activity is clearly unimodal between October and March, with most activity taking place after midday, and a shift of daytime activity towards the evening. The activity in April, May and September seems to be transitional between the unimodal spring and winter activity and the clearly bimodal pattern seen between June and August. During these months there are a potential 13 hours of activity but this is severely reduced during the middle of the day so that the total number of activity hours is lower.

The largest number of lizards were seen in the autumn. These included young lizards hatched in the summer.

A comparison with Figure 2.4, which shows the incident solar radiation at the surface through the year, suggests lizards are most obvious when this radiation is between 3 and 6 $Jcm^{-2}min^{-1}$. Activity is lowest below 2 $Jcm^{-2}min^{-1}$ (although there is some activity at this insolation value in the evening), and above 7 $Jcm^{-2}min^{-1}$. Activity at 6-7 $Jcm^{-2}min^{-1}$ is greater in the morning than in the afternoon.

Figure 8.22, prepared from values obtained by adding the hourly totals per month, gives an overall picture of lizard activity through the year, with peaks in spring and autumn, the latter being greater due to the presence of young, and minima in winter and summer.

8.3.4 Discussion

The relation of the amount of basking to time of year (Figures 7.3, 7.7 and 7.8) and, in some cases to time of day (Figure 7.6) is typical of that of a heliotherm (Spellerberg, 1976; Avery, 1978). The alternation of periods of basking, usually of short duration (Figures 8.18, 8.19) and intervals of foraging (Figure 7.10) is typical of the behaviour of a shuttling heliotherm. The use of flat surfaces in the summer when the sun is high in the sky, and of progressively more sloping and then vertical surfaces in spring and winter (Figure 8.16) suggests lizards are attempting to maximise insolation by presenting a perpendicular surface to the suns rays during the times of day when basking is important in the different seasons. However, the posture of the lizard in relation to the sun seems also to play a part in thermoregulation. In its simplest form, it was observed that morning baskers tended to face away from the sun when basking fully exposed. This will maximise the warming effect of the sun,due to the structure of the scales (4.4). A greater proportion of afternoon baskers whilst still basking fully exposed tended to face towards the sun. This will tend to reduce the warming effect. A similar behaviour has been observed in *Amphibolurus minima* (Bradshaw & Main, 1968). This behaviour, which may be used by lizards wanting to remain active in sunlight, or to maintain a preferred body temperature for metabolic purposes without overheating, is suggestive of that of a posturing heliotherm. However, the temperature relations of *P. hispanica* considered in 8.2, in particular the low voluntary mean temperature (30·77°C), the closeness of body to environmental temperatures, and the differences in voluntary temperatures between winter and summer, are close to those of thigmothermic reptiles (e.g., *Coronella girondica*, labelled a thigmotherm/shuttling heliotherm in Spellerberg, 1976).

The true thermoregulatory characteristics of *P. hispanica* are probably a combination of all these strategies, depending on environmental conditions. When conditions are cool, a lizard will try to maximise heat absorbtion by basking in the posture that will best do this, perpendicular to the sun's rays and/or facing away from the sun. When conditions are warmer, a lizard which needs to feed will shuttle in and out of vegetation, basking for short periods to boost body temperature for another foraging bout. During these bouts, the lizard's temperature will drop towards that of the surroundings, giving the impression of thigmothermic behaviour. This last method of thermoregulation will be most important when the sun is periodically obscured. During such periods lizards are seen flattening themselves close onto the warm surface. If food needs have been satiated after foraging, or if a lizard wishes to remain exposed for mating or other purposes, it may be able to maintain a suitable temperature, without overheating, by posturing. The discussion in section 4.4 suggests that this is possible, since lizards show different reflectivities depending on the angle of incident light. In particular, when light is anterior, the head appears shiny as it reflects much of it. If infra-red radiation is similarly reflected, head temperatures may be maintained low while the lizard remains exposed. If this is so, the temperature recorded from a basking lizard is not necessarily below preferred body temperature, but may be close to this. This is more likely in Gibraltar than in more northerly latitudes where microhabitat temperatures are cooler (e.g., "as high as 30 - 32°C in Calluna" in Britain (House et al., 1980), compared to 50+°C in low vegetation in summer in Gibraltar). Solar radiation is also less in Britain (Avery, 1976).

It is unlikely that a reptile will restrict its behaviour to any one type of thermoregulation when a selection of alternative strategies are available to it. Shuttling heliotherms can prolong activities in varied environments and by spending less time warming or cooling, an individual can spend longer periods foraging, feeding and digesting food at the required body temperature (House et al., 1980). If in addition the thermoregulatory strategy can be varied, activity can be prolonged even further. In this way also, the impact of variation in ambient conditions can be reduced (Huey & Pianka, 1977). A seasonal variation in the species' temperature tolerance (Ballinger et al., 1970; Huey & Stevenson, 1979) will also increase activity. It appears that a combination of all the above may be successful in allowing P. hispanica to be active during most diurnal conditions at Gibraltar, with the exception of the hottest hours in the summer and cloudy or cold conditions in the winter. This is in contrast to the situation further north in Europe where, because of levels of solar radiation are frequently reduced by cloud cover, the time available for feeding is limited by the ability of animals to maintain a high body temperature (Avery, 1971). Even in summer, a shift in habitat (5.2; 8.2) to denser vegetation may allow some individuals to prolong activity during the day. St. Girons (1976) reported this in Lacerta viridis, and House et al.(1980) suggested lizards use environments according to their thermal requirements.

There are several points within these general arguments that need further discussion.

Figure 7.2 for example, shows that on the whole small lizards bask more than adults during the year. In general, large lizards are known to bask more than juveniles due partly to their smaller surface area to volume ratio (e.g., House et al., 1980). P. hispanica juveniles basked less than adults in summer and autumn (Figures 7.4, 7.5, 8.20) and also in winter (Figure 8.20). Lengths of basking intervals were also shorter in winter and summer. However the reverse appears to be true in spring (Figure 8.20). A possible explanation is the greater food requirement of larger lizards, particularly at a time of reproduction when females are developing eggs and males are involved in aggressive and reproductive behaviour. Larger lizards may therefore need to forage more than young ones (the foraging intervals of larger lizards are significantly longer than those of smaller ones in spring; Figure 7.10), which may spend more time in the open regulating their temperature as suggested above. Avery (1971) suggests Lacerta vivipara may be able to satiate themselves in the field at times. It would follow that P. hispanica, with longer activity periods and a habitat productive in spring (7. 4) could do likewise, particularly small lizards. These could then bask, maintaining a suitable body temperature for the digestion of food.

Figure 8.19 shows that on the whole basking intervals tend to be shorter in the summer months than in the winter. The highest proportion of basking intervals of less than one minute was found in April, however (73•5%). This month combines warm conditions with a continuation of reproductive behaviour, which may account for fewer long basking intervals (and more foraging, as shown in Figure 7.7).

When the September data in particular are considered, the expected pattern of most basking in the morning and evening and least during the middle of the day is seen. That this is not as evident at other times of year could be due to smaller sample size, but could also indicate that, in general, the amount of basking time is determined more by the time of year than by the time of day. Since lizards are seen to be actively foraging shortly after emergence, even on relatively warm winter days, their basking/foraging behaviour during the rest of the day may be regulated by the use of various thermoregulatory strategies and microhabitats of different temperatures. This may mask the effect of time of day on basking.

The importance of posture in thermoregulation is suggested by the use of surfaces of different angles for basking and by variation in these through the year (Figure 8.16). The differences according to lizard snout-vent length (SVL) may be indicative of young lizards needing to maximise intake of solar radiation less than lizards of progressively larger size classes. However, it could also be a result of displacement of smaller lizards by larger ones from preferred basking sites.

The activity of the closely related Wall Lizard P. muralis at Florence (44°N) was seen to be unimodal in summer (Avery 1978), while that of P. hispanica at Gibraltar (37°N) is clearly bimodal. By reason of latitude solar radiation is greater at Gibraltar, which may account for the inactivity in midsummer during the day. However, it is probable that P. muralis hibernates in winter. A marked increase in activity was noticed by Avery (1978) on 17 April, while activity in Gibraltar, never very low in winter, showed a marked increase as early as February (pers. obs.). P. hispanica, in adapting to being active at lower temperatures through winter may have had to compromise its summer activity (when food is scarcer than in winter). Alternatively the fact that transects were mainly in open vegetation, may account for a lower activity indicated in Figure 8.21 for midsummer when activity may be greater under taller vegetation.

A comparison of Figure 8.21 with Figure 2.4 was made in section 8.3.3. Activity seemed to be limited by higher levels of solar radiation, which are coupled with high environmental temperatures (Figure 8.9). Activity appears limited also by low levels of solar radiation coupled with low temperatures. When solar radiation is low, but temperatures remain high, as in the evening in summer, some lizards can still remain active. Although no data were gathered due to low overall activity, the majority of lizards seen in the middle of the day in summer were adults.

The pattern seen was on clear days only. Rain, cloud or wind changed the pattern in a way that was difficult to categorise, as has been observed with other lizard species (Avery, 1978; House et al., 1980). No lizards were seen on cloudy days, and lizards seemed to bask more on hazy days, when solar radiation is reduced (2.1.3).

Figure 8.21 can be used to give an idea of the overall potential activity time for P. hispanica at Gibraltar on bright days; 6 hours of daily activity in January; 7 (?) hours in February; 10 to 11 hours in March; 11 hours in April; 12 hours in May; 10 to 11 hours in June; 10 to 11 hours in July; 8 to 9 hours in August; 11 to 12 hours in September; 8 to 9 hours in October; 9 hours in November; 6 hours in December. Peak activity would therefore appear to be possible between March and May, and September. This is reflected in Figure 8.22.

8.4 Morning emergence

8.4.1 Introduction

The limited number of authors who have published work dealing with lizard morning emergence have concluded that emergence is determined by temperature (Heath, 1962; Bradshaw & Main, 1968; Avery, 1978), or by the amount of solar radiation at the time of emergence which should allow the temperature of the lizard to rise quickly (Avery & McArdle, 1973; House et al., 1980). Work on emergence of European lizards has been largely limited to northern species, in particular L. vivipara (Avery & McArdle, 1973; House et al., 1980), or Mediterranean species in spring and summer (Avery, 1978).

Morning emergence of P. hispanica in winter was therefore considered to be worthy of study.

8.4.2 Methods

The first source of data was the transect observations (as illustrated in Figure 8.21) in which the time when lizards were first observed in the area were recorded. These were compared to the values of solar radiation discussed in Chapter 2 and illustrated in Figure 2.4.

Emergence was observed in captivity in winter, after heating lamps were switched on. The temperatures under the rocks where the lizards spent the night were recorded using thermister probes, when the first lizard head was seen emerging from the pile of stones (3. 3). Heating was continued, and cloacal temperatures of the lizards when they had fully emerged were also recorded. The procedure was repeated with only heating lamps and no lights switched on. Temperatures on full emergence in the dark were taken and compared to those for light emergence using the Mann-Witney U-test.

In addition, emergence of lizards was followed closely at the N.E. Wall and Cross sites at North Front Cemetery on separate occasions between December 1981 and February 1982. On six of these occasions concurrent continuous recordings of temperatures of the refugia, concrete surfaces, litter and Oxalis/grass vegetation were made (Appendix 4).

Submergence was more difficult to observe since it did not occur simultaneously. (Lizards were seen returning to refugia however, after shade had reached the area of their home range, regardless of time of day - i.e., earlier on E-facing slopes.)

8.4.3 Results

The times at which lizards were first seen during transect observations at North Front Cemetery can be found on Figure 8.21. These times are listed in Table 8.5 together with the corresponding incident solar radiation in Joules per square centimetre per minute (J cm^{-2} min^{-1}), assuming perfectly clear skies. Although in fact the radiation reaching the ground will be less, these figures are suitable for comparative purposes.

The times when lizards were first observed in the transects were somewhat later than those found for the continuous observations (Figures 8.23 to 8.28). It is likely that lizards will be seen away from their refugia some time after first emergence (Avery & McArdle, 1973). In any case, the continuous observations were on east-facing surfaces, which will tend to warm up more quickly in most cases (Figures 8.23 and 8.24), while transects included a large variety of sites, giving an overall picture for the habitat.

Table 8.5 shows that lizards emerged at higher levels of solar radiation in autumn and winter (2·765 - 4·126 J cm^{-2} min^{-1}) than in spring and summer (1·338 - 2·882 J cm^{-2} min^{-1}).

The mean refugium temperature at which winter-captive lizards were seen to show their heads outside shelter in the morning in light was 13·9°C (S.D. = 2·64) with a range of 12·0°C to 21·0°C. These differed significantly ($P < 0{\cdot}05$; Mann-Whitney U-test) from the mean temperature for lizard emergence in the dark. In dark conditions, the mean temperature at which lizards first appeared was 20·25°C (S.D. = 1·92), within the mean voluntary range. The range of first emergence temperatures was 16·5°C to 21·5°C. Since no thermoregulation was possible before emergence, it was assumed that body temperatures were equal to the temperatures of the refugia.

Temperatures at which lizards left the shelter of the stones and emerged fully (these were actual body temperatures) did not vary significantly between light and dark conditions. In the light, the mean temperature was 23·4°C (S.D. = 6·29), with an observed range of 18·2°C to 34·5°C. In the dark, the mean temperature for full emergence was 24·02°C (S.D. = 1·73), with a range of values between 22·3°C and 26·0 °C).

Table 8.5 Solar radiation at time of first observation of P. hispanica during transects at North Front Cemetery, Gibraltar.

MONTH	TIME (GMT) (to nearest hour)	INCIDENT[1] SOLAR RADIATION ($J\ cm^{-2} min^{-1}$)
January	1100	3·737 - 3·895
February[2]	1000	3·455 - 3·898
March	0800	1·729 - 2·289
April	0700	1·338 - 1·866
May	0700	2·361 - 2·666
June	0700	2·859 - 2·882
July	0700	2·784 - 2·619
August	0700	2·354 - 2·105
September	0700	1·779 - 1·488
October	0900	4·126 - 3·726
November	0900	3·229 - 2·765
December	1100	4·015 - 3·787

Notes 1. Values given are those at stated hours on 1st and 15th of each month.

2. Time of emergence in February is from casual observations, not from transect data.

Figures 8.23 to 8.27 show graphically the results of the continuous monitoring of temperatures and of lizard emergence on six days between December 1981 and February 1982. Temperatures of refugia at the time when lizards first showed their heads were 10°C, 12°C, 13°C, <11·5°C, 14°C and 12·5°C (mean <12·2°C). These were close to the figures obtained from captive lizards. Foraging commenced when temperatures of the basking surface were above the voluntary minimum temperature (17·3°C), with lizard body temperatures presumably higher than these.

Typically, on emergence, the snout of the lizard was seen first. Progressively more of the lizard became visible. The whole head emerged, then half the body, all bar the hind legs and tail, and then only the tail remained in the refugium. Finally the whole of the lizard became exposed and the animal moved away from the refugium for a further period of basking before moving into adjacent vegetation. Often the lizard was seen to defaecate during this period of basking.

8.4.4 Discussion

The figures in Table 8.5 suggest *P. hispanica* emerges at higher levels of incident solar radiation in winter than during the rest of the year. Avery & McArdle (1973) found that emergences of *Lacerta vivipara* were at higher radiation levels in midsummer (c. 4·5 J cm^{-2} min^{-1}) than in spring (c. 3·75 J cm^{-2} min^{-1}). The time spent by an emerging lizard with a temperature below its voluntary mean is believed to be a compromise between the need to become active as early as possible and the risk of being exposed to predators for too long a period (House *et al.*, 1980). It is possible, therefore, that *L. vivipara* emerges at lower levels of radiation in spring and autumn in order to increase possible activity time. Using a similar argument, it is suggested that *P. hispanica* in Gibraltar will emerge at lower levels of radiation in summer in order to lengthen its activity period towards the early part of the day, when thermoregulation can still be effective, since activity is curtailed by high midday and afternoon temperatures. Emerging early when solar radiation is relatively low will mean considerable basking will be necessary.

Fig. 8.23 MORNING TEMPERATURES OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, GIBRALTAR, AT LIZARD EMERGENCE
2/12/81 (CROSS SITE)

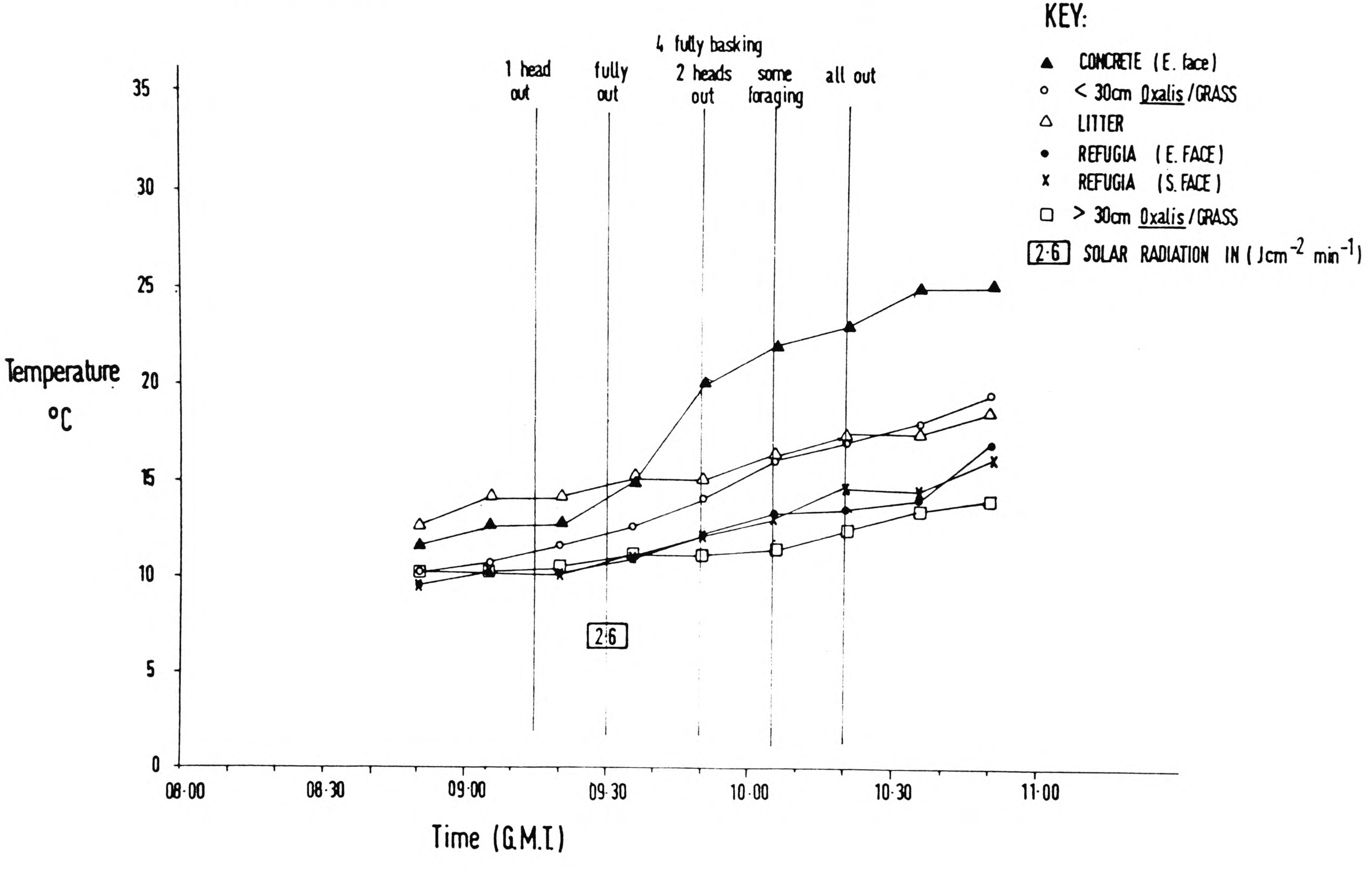


Fig. 8.24 MORNING TEMPERATURES OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, AT LIZARD EMERGENCE. 5/1/82 (CROSS SITE)

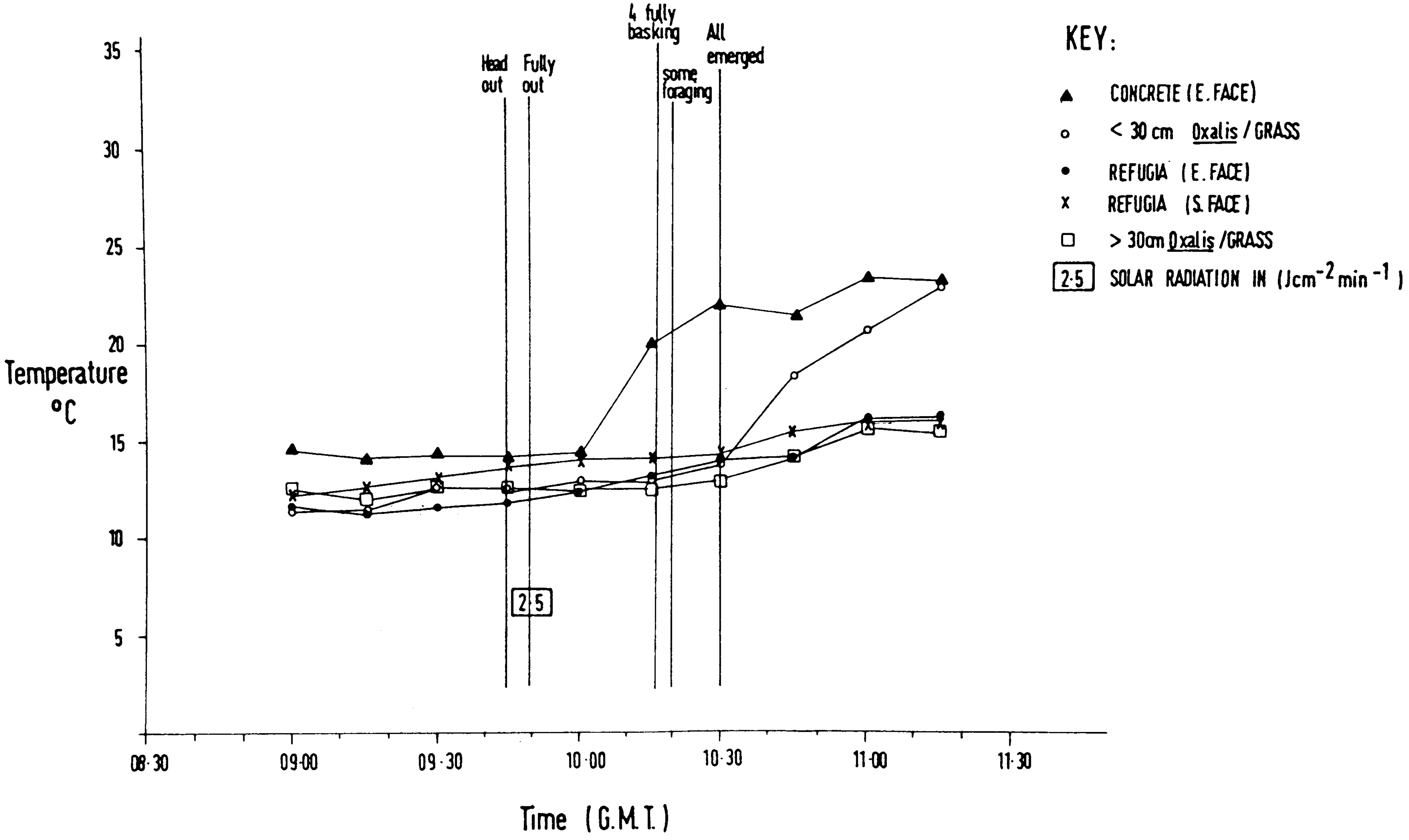


Fig. 825 MORNING TEMPERATURES OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, GIBRALTAR, AT LIZARD EMERGENCE.
9/1/82 (CROSS SITE)

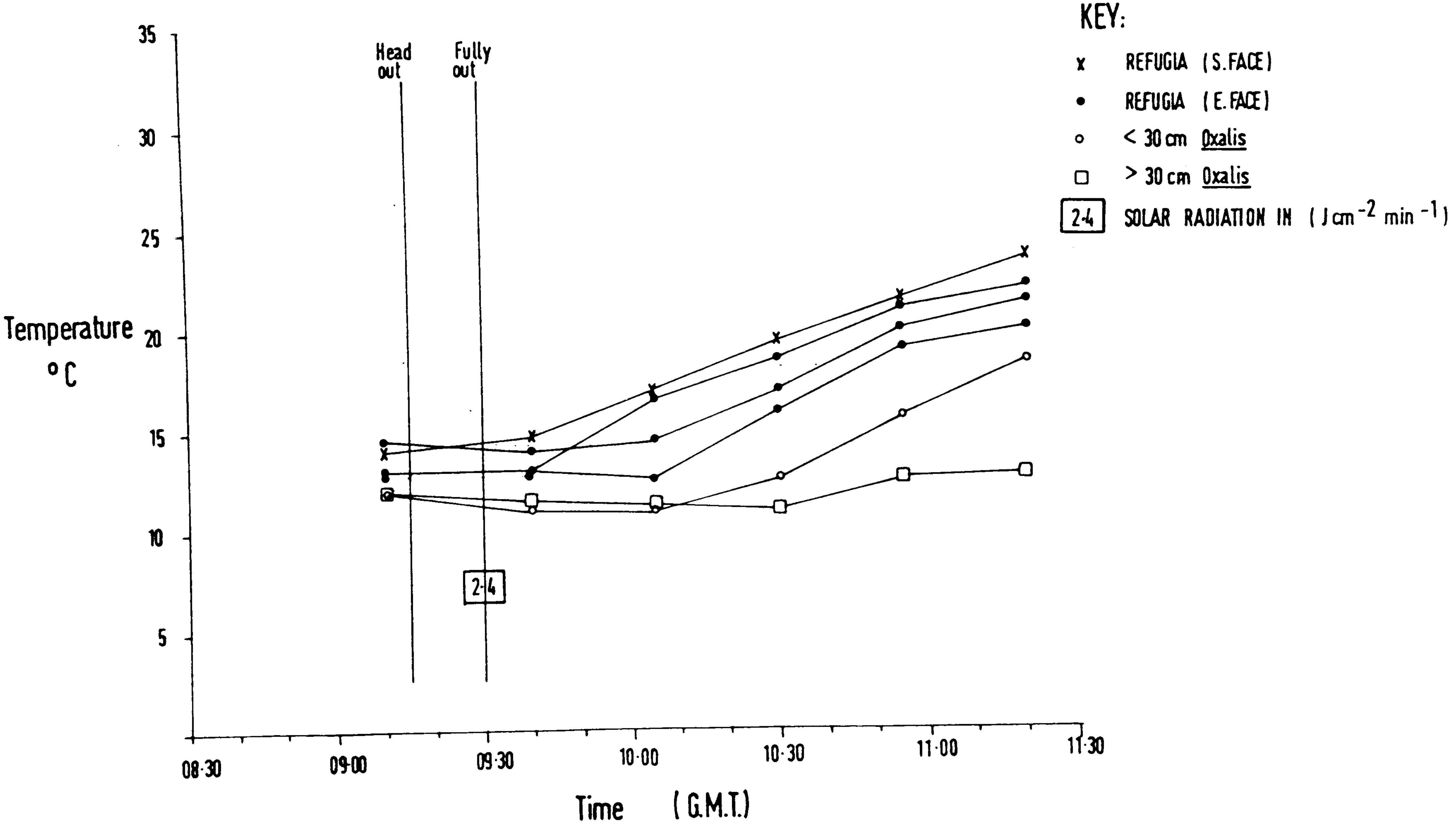


Fig. 8.26 MORNING TEMPERATURES OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, AT LIZARD EMERGENCE. 30/1/82 (N.E. WALL)

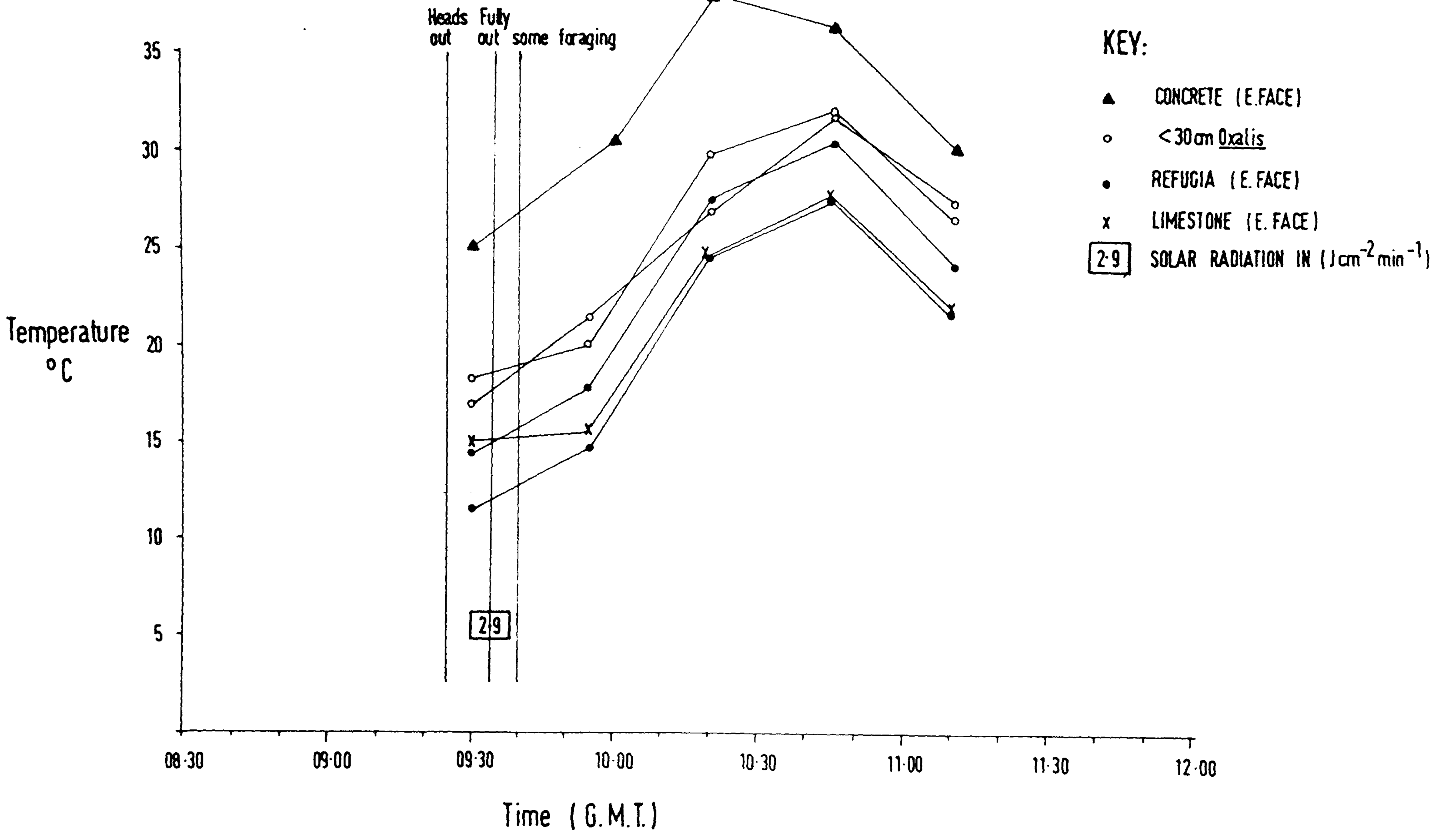


Fig. 8.27 MORNING TEMPERATURES OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, GIBRALTAR, AT LIZARD EMERGENCE.
31/1/82 (N.E. WALL)

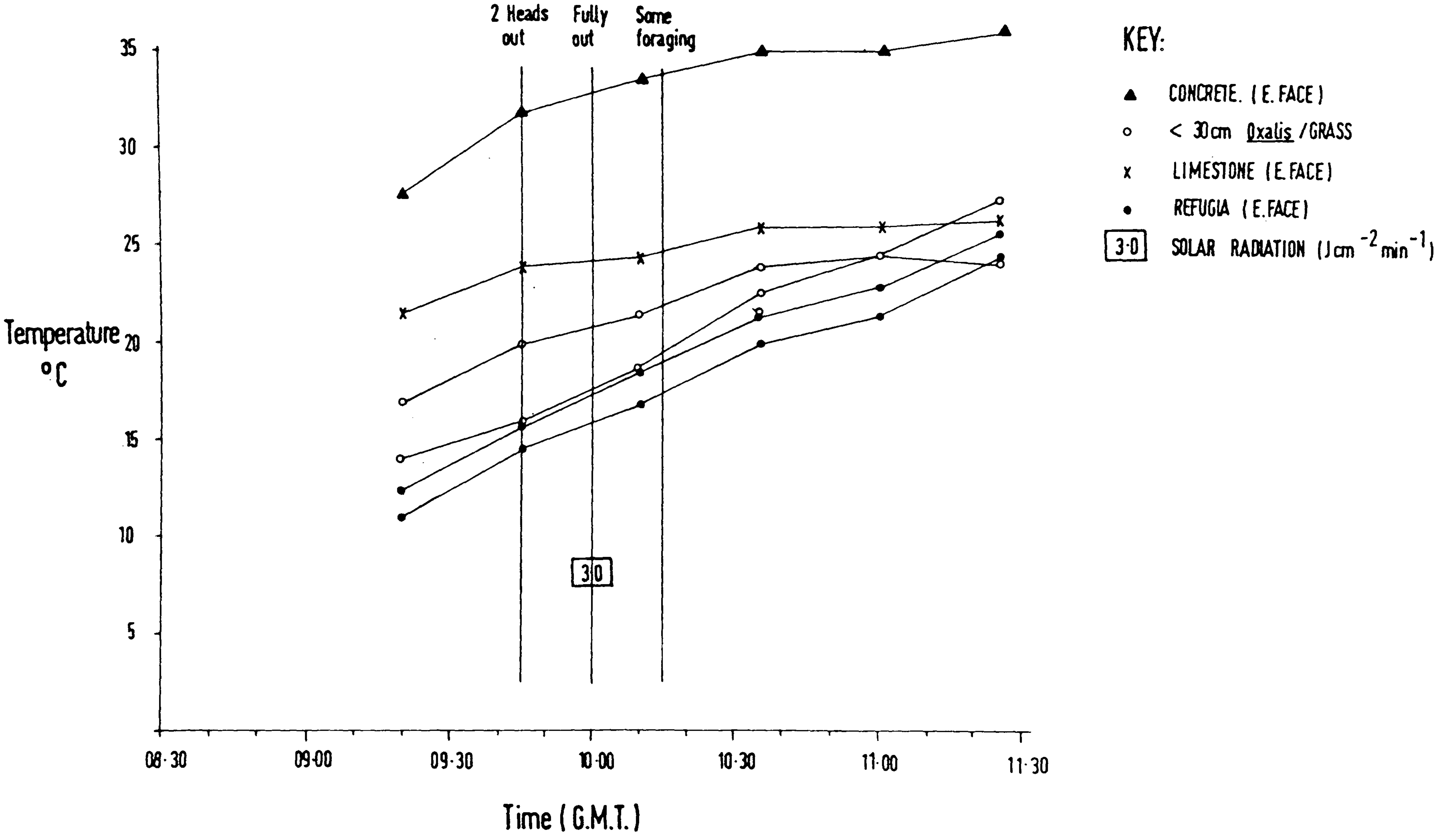


Fig. 8.28 MORNING TEMPERATURES OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, AT LIZARD EMERGENCE.
26/2/82 (N.E. WALL)

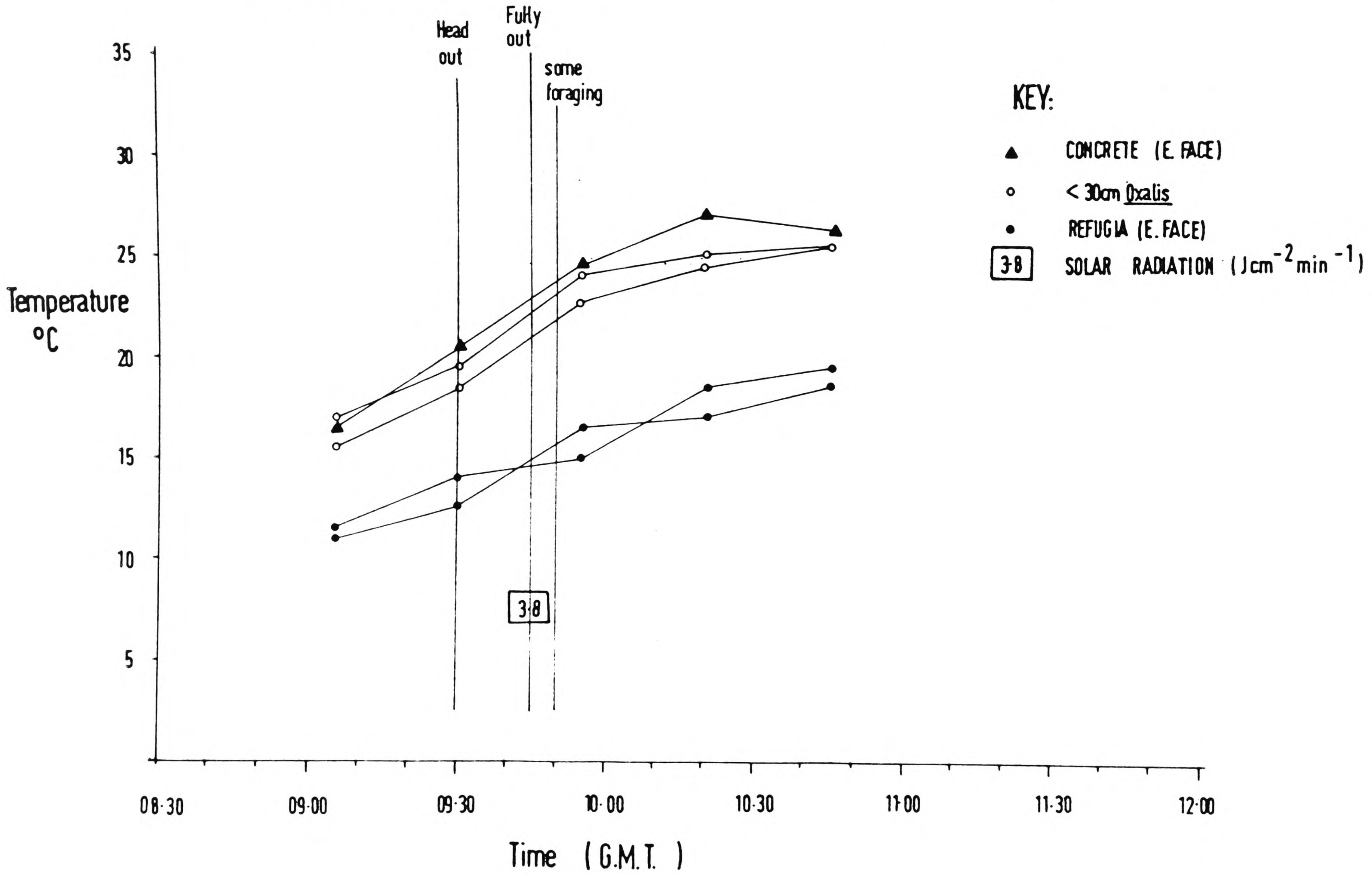


Fig. 8.29 MORNING TEMPERATURE OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, GIBRALTAR.
17/3/81

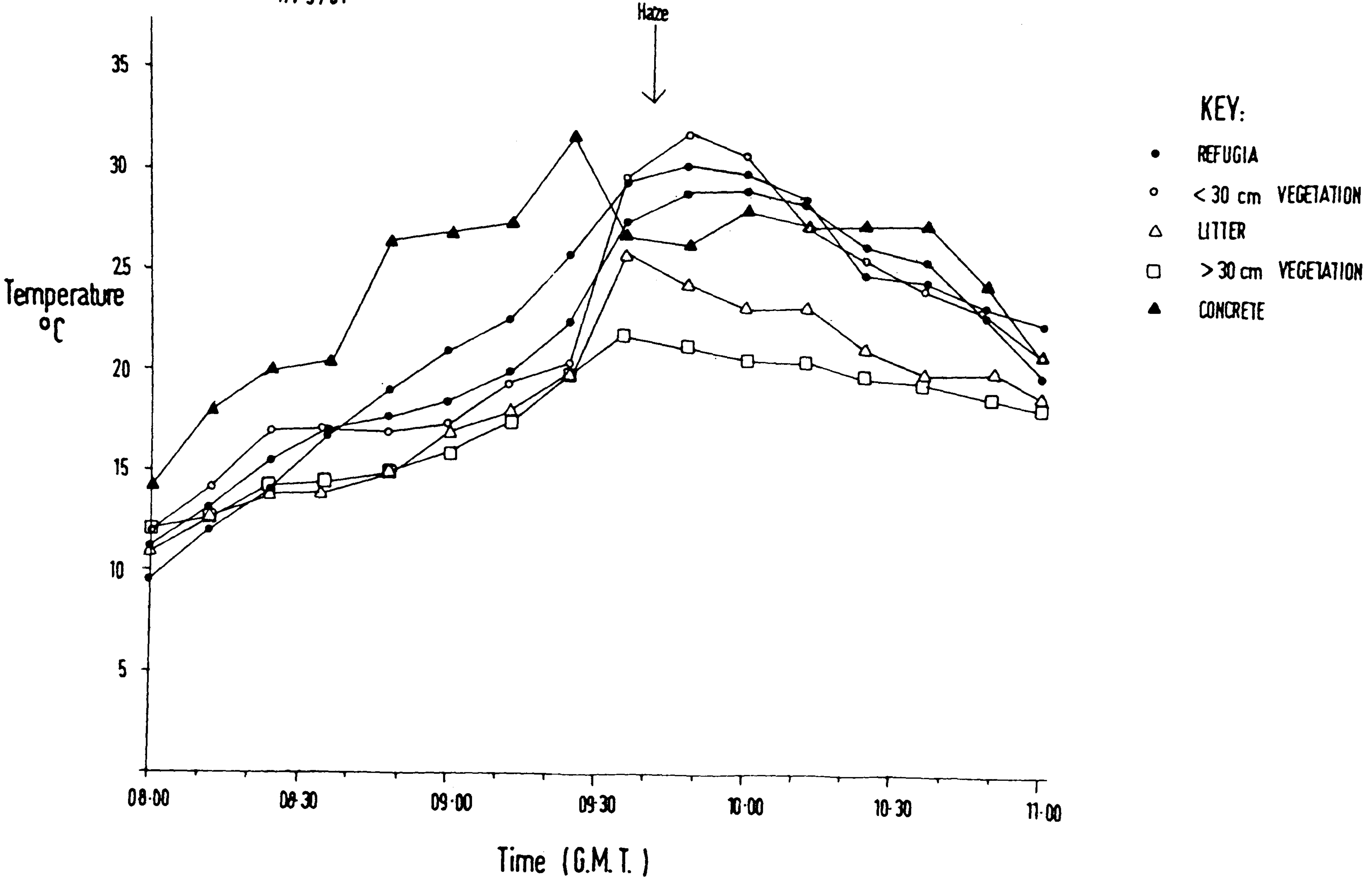
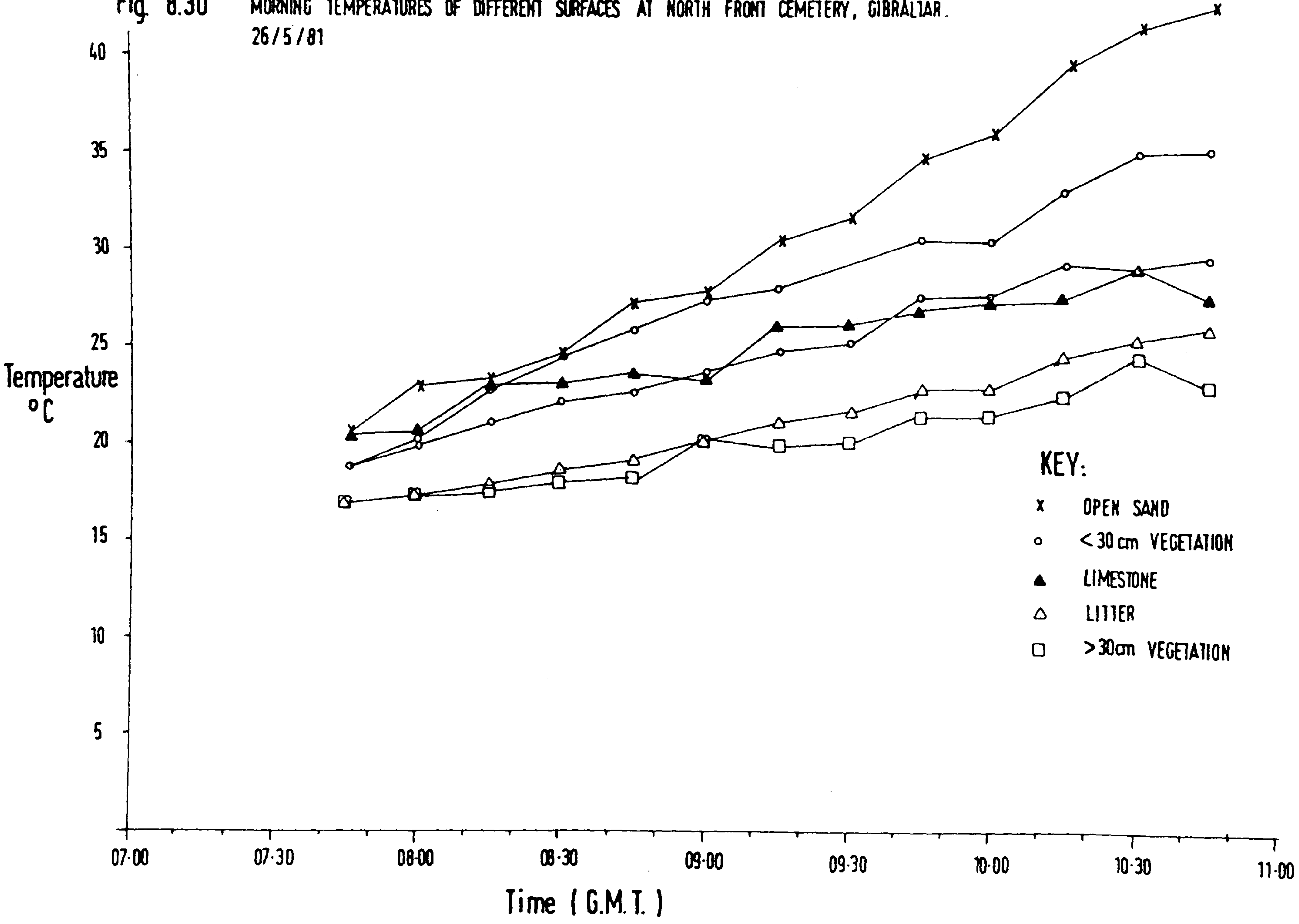


Fig. 8.30 MORNING TEMPERATURES OF DIFFERENT SURFACES AT NORTH FRONT CEMETERY, GIBRALTAR. 26/5/81



A large proportion of observed time was in fact spent basking, particularly in July, according to the results of continuous observations (68% of observed time; Figure 7.7).

Solar radiation on emergence was as a whole higher in Britain (Avery & McArdle, 1973) than in Gibraltar. Microhabitat temperatures in Gibraltar are within the voluntary range of the lizards throughout the year from early in the morning. Starting at a relatively high temperature, less intense radiation will be necessary for an adequate temperature to be attained, and it will then usually be relatively easy to maintain. In late autumn and winter, morning temperatures do fall below P. hispanica's voluntary minimum temperature. At this time, emergence of lizards at Gibraltar is at levels of solar radiation approximating those for emergence of L. vivipara in Britain (Avery & McArdle, 1973).

In east-facing refugia adjacent to concrete basking sites (such as the 'cross' site and N.E. Wall site), where body temperatures can be raised more quickly due to rapid warming of the surface (Figures 8.23 - 8.28), emergence appears to be possible at times when levels of solar radiation are lower (Figures 8.23 to 8.27). Thus in the examples of continuous observations in December and January, emergence was at solar radiation levels averaging 2·7 J $cm^{-2} min^{-1}$, compared to a range of 3·8 to 4·0 J cm^{-2} min^{-1} obtained from the transect data (Table 8.5).

Data from both captive and wild lizards in winter show that emergence seems to begin at a refugium temperature (and presumably body temperature) close to the critical minimum of 12·2°C and below the voluntary minimum of 17·3°C - i.e., virtually as soon as the lizards are able to move. Full emergence takes place after the lizard has attained a temperature within its voluntary range. Lizards then bask for a further period before proceeding on other activities. On some cold winter days this phase appears not to be reached and basking continues during most of the day.

Emergence, then, is possible at low body temperatures, allowing the lizards to prolong activity time.

Emergence seems to be triggered off by temperature, and completed by light. Thus lizards warmed in the dark did not emerge until they had attained temperatures under cover similar to those acquired by basking during the initial stages of light emergence. After lizards had finally emerged in the dark they could be attracted by a beam of light from a torch. Lizards kept briefly in outdoor vivaria in Gibraltar were seen to emerge during night-time when a terrace light was switched on. This was seen in summer, when night-time air temperatures were within the lizards' voluntary range (2.1.3).

It would appear, then, that once the lizard body temperature is within this voluntary range, emergence is effected as a response to a light stimulus. From a consideration of Figures 8.29 and 8.30, giving refugium temperatures in March and May, it would be expected that lizards could emerge as early as 0800 hrs in March and 0730 hrs in May. Figure 8.21 confirms this for March, and suggests this may be so in May, assuming emergence could be earlier than when first observed during transects.

Since environmental temperatures quickly rise to within the voluntary range of the species during most of the year, emergence can be soon after sunrise for all lizards. No difference was observed in time of emergence of young and older P. hispanica. If the sunrise is delayed due to an obstacle (e.g. on a west-facing wall or slope), emergence would be expected to be almost immediately after the sunlight reached the site. This was seen to be so. Emergence in the species is independent of temperature when the animals are warm enough to move, and provided there is light. The level of solar radiation is probably important also - lizards did not emerge on cloudy days even when, in summer, air temperatures were within their voluntary range.

8.5 Adaptation of P. hispanica to winter

The critical and voluntary minimum and maximum temperatures were determined using lizards kept in conditions similar to those in the field in winter. Since lizards will have an acclimation range for these temperatures (Spellerberg, 1973), the estimated values are probably lower than if they had been obtained from lizards acclimated to other conditions. The method used to obtain these temperatures will also affect results.

Bearing in mind the above limitations, it will be obvious that the temperature relations listed in Table 8.1 will be most useful in considering the activity of P. hispanica in the field in winter.

Table 8.6 compares the critical minimum of P. hispanica with those of other European reptiles. These temperatures were determined in summer, so that they are expected to be higher than winter critical minima. Spellerberg (1972b) found this to be so in Sphenomorphus species in Australia. Of the values given in Table 8.6, the closest critical minima to that of P. hispanica (12·2°C) are those of Psammodromus hispanicus (8·8°C) and Podarcis muralis (8·3°C), both Mediterranean species. Spellerberg (1976) suggests that within single species physiological races may exist with different critical minimum temperatures , as appears to be the case in Lacerta agilis. If this can be true for races, it is conceivable that in the species P. hispanica, or specifically in those in Gibraltar, there is in fact a high critical minimum temperature. Being the southernmost population of Iberian Wall Lizards, in a warm climate, could account for this.

The more ecologically meaningful temperature, however, is the voluntary minimum (17·3°C). Lizards will not be active below this temperature, so that they will not be exposed to predators (or continuing lowering temperatures) at the lower ecologically lethal temperature (the critical minimum). Lizards were never caught in the field at temperatures below 21·9°C (Table 8.1) and only once did a lizard fully emerge in captivity at a body temperature below 21·2°C. Thus, the critical minimum temperature, which will only be reached

Table 8.6 Critical minimum temperatures of some western European reptile species (from Spellerberg, 1976).

	Species	Mean critical minimum temperature (°C)	Season	n
	Anguis fragilis	4·0	summer	4
	Lacerta agilis	5·9	summer	7
	L. viridis	5·9	summer	6
	L. vivipara	2·8	summer	4
	Podarcis muralis	8·3	summer	4
	P. sicula	7·3	summer	16
*	P. hispanica	12·2	winter	7
	Psammodromus algirus	7·0	summer	1
	Ps. hispanicus	8·8	summer	2
	Coronella girondica	5·0	summer	2
	Natrix maura	4·0	summer	3

*data from this study

once the lizard has submerged, is ecologically irrelevant.

Very low ambient temperatures are rarely reached in Gibraltar (2.1), with never more than a few hours below 0°C in several years. The "emergence mortality" of Spellerberg (1976) in which a reptile could be susceptible to high mortality as a result of a sudden deterioration in weather conditions, is unlikely. P. hispanica forage close to refugia in winter (5. 2) and have been seen to return to them within 15 minutes of the sky becoming overcast, both in winter and in summer when 'Levanter' conditions have suddenly developped.

P. hispanica in Gibraltar therefore need no adaptation to cold stress, such as supercooling abilities, nor is it likely that lizards in Gibraltar will die of cold, as L. vivipara in Britain have been known to do (Spellerberg, 1976). Iberian Wall Lizards kept captive in Gibraltar in winter survived a night when temperature fell to 3°C in the vivarium for several hours. A male accidentally placed in a constant-temperature room at 5°C survived at this temperature for 60 hours without any apparent ill effects. The ultimate minimum temperature then appears to be considerably lower than the critical minimum and will allow lizards to survive brief cold periods as do occur in the wild.

P. hispanica has a low mean voluntary temperature (30·8°C), particularly in winter (25·1°C in December), which allows it to be active when environmental temperatures are relatively low (Figure 8.9). A reptile with a high critical minimum temperature, in an environment with fairly warm winters when, even on the colder days, solar radiation and environmental temperatures may be enough to allow foraging at a time when food is fairly abundant (7.4), will be at an advantage if, by having a lower minimum voluntary temperature, it can emerge and feed at mean body temperatures below the annual mean. This will be preferable to remaining in or just outside the refugium, using up energy in metabolism, but unable to replenish it by feeding.

Spellerberg (1976) believed reptiles adapt to the cold by modifying voluntary temperature levels and range. Lizards of colder climates 'switch-off' in winter and avoid the coldest weather, exceptionally emerging on the warmest days to the entrance to their refugia. P. hispanica at Gibraltar cannot hibernate, since temperatures remain relatively high, and must adapt themselves to the cool conditions of the winter. This may account for the low voluntary mean temperature. It may in this way also compromise high summer activity temperatures, restricting its summer activity to a few hours, morning and evening.

8.6 Principal Components Analysis of transect data

8.6.1 Introduction and method

Principal components analysis transforms data. Each measured variable will have a variance, and usually variables will be associated with each other so that there will be a covariance between pairs of variables. The data set as a whole will have a total variance which is the sum of the individual variances.

According to Daultrey (1976), in Principal Components Analysis (PCA) data are transformed to describe the total variance with the same number of axes, the same number of variables, but in such a way that:

- the first axis accounts for as much of the total variance as possible;
- the second axis accounts for as much of the remaining variance as possible, whilst being uncorrelated with the first axis;
- the third axis accounts for as much of the total variance remaining as possible, after that accounted for by the first two axes, whilst being uncorrelated with either;
- and so on.

The result is that a few large axes account for most of the total variance, and a larger number of small axes account for very small amounts of the total variance. This reduces the data set from having many correlated variables to a set having fewer uncorrelated axes.

Often the most useful result obtained from the analysis is the possibility of determining the relationship of the principal components to the original variables - i.e., which of the axes of variability contributed most variance to each of the principal components. Each scored value is given co-ordinates on the new axes, allowing them to be plotted in relation to these.

Program HCD:PCA, Forestry Department, Oxford, was used to carry out principal components analysis on the transect data collected at North Front Cemetery.

Table 8. 7 Seventeen variables included in Principal Components Analysis of *P. hispanica* observations from North Front Cemetery.

Variable	Description/score	
(i) Date	December/January	1
	March/April/May	2
	June/July	3
	August/September	4
	October/November	5
(ii) Time	- Table 8. -	
(iii) SVL	$<$30 mm	1
	30 mm / 40 mm	2
	40 mm	3
	40 mm - 50 mm	4
	50 mm +	5
(iv) Height	Ground	0
	10 mm	1
	15 / 25 mm	2
	30 / 40 mm	3
	50 / 60 mm	4
	70 mm +	5
(v) Air temperature	21·1 - 24·0 °C	1
	24·1 - 26·9 °C	2
	27·0 - 29·8 °C	3
	29·9 - 32·7 °C	4
	32·8 - 35·6 °C	5
(vi) Surface angle	Flat	1
	slope $< 45^{\circ}$	2
	slope $\simeq 45^{\circ}$	3
	slope $> 45^{\circ}$	4
	vertical	5

Table 8.7 (contd.)

Variable	Description/score	
(vii) Horizontal orientation	Vertical	0
	facing sun	1
	facing < 90° to sun	2
	facing 90° to sun	3
	facing > 90° to sun	4
	facing away from sun	5
(viii) Vertical orientation	Horizontal	0
	vertically up	1
	angled upwards	2
	parallel to horizontal	3
	angled downwards	4
	vertically down	5
(ix) Limestone/Marble	No	0
	Yes	1
(x) Concrete	No	0
	Yes	1
(xi) Wood	No	0
	Yes	1
(xii) Other surface	No	0
	Yes	1
(xiii) Exposure	In open	0
	in mosaic	1
	in shade	2
(xiv) Sky cover	Clear	0
	Partly cloudy	1
	Overcast	2

Table 8.7 (contd.)

Variable	Description/score	
(xv) Foraging	No	0
	Yes	1
(xvi) Basking	No	0
	Yes	1
(xvii) Other activity	No	0
	Yes	1

Table 8.8 Scoring codes used for times of day in Principal Components Analysis.

	Times (hrs G.M.T.)			
Code	January	March	April	May
1	0730-0930	0630-0855	0550-0825	0515-0805
2	0930-1130	0855-1120	0825-1100	0805-1055
3	1130-1330	1120-1345	1100-1335	1055-1345
4	1330-1530	1345-1610	1335-1610	1345-1635
5	1530-1730	1610-1835	1610-1845	1635-1930

	Times (hrs G.M.T.)			
Code	June	July	August	September
1	0505-0800	0515-0805	0540-0820	0605-0835
2	0800-1055	0805-1055	0820-1100	0835-1105
3	1055-1350	1055-1345	1100-1340	1105-1335
4	1350-1645	1345-1635	1340-1620	1335-1605
5	1645-1940	1635-1925	1620-1910	1605-1835

	Times (hrs G.M.T.)		
Code	October	November	December
1	0630-0845	0700-0900	0725-0920
2	0845-1100	0900-1100	0920-1115
3	1100-1315	1100-1300	1115-1310
4	1315-1530	1300-1500	1310-1505
5	1530-1745	1500-1700	1505-1700

Seventeen variables were measured and coded as shown in Table 8.7 for 319 observations of P. hispanica, made during transects, in which all the variables had been recorded.

Scoring values of variables have generally been attributed to data subdivisions similar to those already used elsewhere. In addition time of day has been subdivided into five equal periods of time between sunrise and sunset for the 15th of each month (Table 8.8). In a similar way, the range of observed air temperatures (21·1°C - 35·6°C) has also been divided into five.

The PCA was repeated using 104 data from the months of August and September. The date variable (i) was obviously excluded from this analysis. The analysis was carried out since a good number of observations were available from this period. Also, since most observations of lizards at this time were on the ground, the analysis would reduce somewhat the effect of variables (vi), (vii) and (viii) which, like variable (i), scored highly in the main components of the first analysis (8.6.2).

8.6.2 Results and discussion

Table 8.9 gives the absolute values of the component loadings for the first three components of the first analysis. Table 8.10 gives the relative loadings for the first four components of this analysis. Tables 8.11 and 8.12 give similar results for the August/September data.

These coefficients can be used to interpret the meaning of the components, using the sign and relative size of the coefficient as an indication of the weighting to be placed on each variable in the four indices of variability (Jeffers, 1978).

The first component of the first analysis using the 319 observations (Tables 8.9 and 8.10) is essentially a contrast between surface angle and actual vertical orientation of the lizards with their angle to the sun. It represents a measure of the posturing of the lizards, of 'verticality' and facing towards the sun. The second component is an index of the

Table 8.9 Component loadings of seventeen variables for 319 observations of P. hispanica at North Front Cemetery, Gibraltar.

Variable	Component I	Component II	Component III
(i) Date	-0•1303	0•6007	0•6254
(ii) Time	-0•0954	0•3256	-0•0267
(iii) SVL	0•0981	-0•2620	-0•1043
(iv) Height	0•2083	0•3055	0•0846
(v) Air temperature	-0.0000	0•0879	-0•1776
(vi) Surface angle	0•7052	-0•0663	0•0735
(vii) Horizontal orientation	-0•3189	-0•5821	0•6227
(viii) Vertical Orientation	0•5635	-0•1113	0•3961
(ix) Limestone/Marble	-0•0163	0•0501	0•0162
(x) Concrete	0•0373	-0•0327	-0•0224
(xi) Wood	-0•0202	-0•0003	-0•0034
(xii) Other surface	0•0002	-0•0182	0•0113
(xiii) Exposure	0•0062	-0•0226	-0•0142
(xiv) Sky cover	0•0477	-0•0574	-0•0852
(xv) Foraging	-0•0018	-0•0032	-0•0026
(xvi) Basking	0•0007	-0•0039	-0•0039
(xvii) Other activity	0•0011	0•0071	0•0065
VARIANCE EXPLAINED :	34•2%	13•3%	10•6%

Table 8.10 Relative component loadings of seventeen variables for 319 observations of *P.hispanica* at North Front Cemetery.

	Component			
Variable	I	II	III	IV
(i) Date	-0·1847	1·0000	1·0000	-0·0189
(ii) Time	-0·1353	0·5420	0·0427	0·4827
(iii) SVL	0·1391	-0·4361	-0·1675	0·8468
(iv) Height	0·2953	0·5085	0·1352	0·6591
(v) Air temperature	-0·0000	0·1444	-0·2839	1·0000
(vi) Surface angle	1·0000	-0·1104	0·1176	-0·0966
(vii) Horizontal orientation	-0·4522	-0·9690	0·9958	0·3764
(viii) Vertical orientation	0·7991	-0·1852	0·6334	0·0228
(ix) Limestone/Marble	-0·0231	0·0834	0·0259	0·0454
(x) Concrete	0·0528	-0·0544	-0·0359	-0·0609
(xi) Wood	-0·0286	-0·0006	-0·0055	0·0188
(xii) Other surface	0·0003	-0·0302	0·0180	0·0025
(xiii) Exposure	0·0087	-0·0377	-0·0228	0·0049
(xiv) Sky cover	0·0677	-0·0956	-0·1363	0·0380
(xv) Foraging	-0·0025	-0·0054	-0·0041	-0·0000
(xvi) Basking	0·0010	-0·0065	-0·0062	-0·0067
(xvii) Other activity	0·0015	0·0119	0·0103	0·0067
VARIANCE EXPLAINED :	34·2%	13·3%	10·6%	8·5%

Table 8.11 Component loadings of sixteen variables for 104 observations of *P. hispanica* in August/September at North Front Cemetery, Gibraltar.

Variable	Component I	Component II	Component III
(i) Time	-0·1969	-0·4108	0·7616
(ii) SVL	-0·0840	0·4475	0·0629
(iii) Height	0·1661	0·0496	0·4394
(iv) Air temperature	-0·0783	-0·0774	0·2008
(v) Surface angle	0·6957	0·0791	0·0201
(vi) Horizontal orientation	-0·3944	0·7106	0·2411
(vii) Vertical orientation	0·5220	0·3214	0·3389
(viii) Limestone/Marble	-0·0075	0·0404	0·0027
(ix) Concrete	0·0163	-0·0622	0·0561
(x) Wood	-0·0184	0·0216	-0·0146
(xi) Other surface	0·0096	0·0002	-0·0441
(xii) Exposure	0·0013	0·0430	-0·0057
(xiii) Sky cover	0·0840	0·0139	0·0051
(xiv) Foraging	-0·0086	-0·0048	0·0192
(xv) Basking	-0·0101	-0·0016	-0·0503
(xvi) Other activity	0·0187	0·0064	0·0311
VARIANCE EXPLAINED :	32·9%	16·4%	13·3%

Table 8.12 Relative component loadings of sixteen variables for 104 observations of *P. hispanica* in August/September at North Front Cemetery, Gibraltar.

Variable	Component I	II	III	IV
(i) Time	-0•2830	-0•5780	1•0000	-0•2626
(ii) SVL	-0•1208	0•6297	0•0826	0•8770
(iii) Height	0•2388	0•0698	0•5770	1•0000
(iv) Air temperature	-0•1125	-0•1090	0•2637	-0•0935
(v) Surface angle	1•0000	0•1113	0•0264	-0•2658
(vi) Horizontal orientation	-0•5669	1•0000	0•3165	-0•5889
(vii) Vertical orientation	0•7504	0•4523	0•4450	-0•3914
(viii) Limestone/Marble	-0•0108	0•0569	0•0035	0•1145
(ix) Concrete	0•0434	-0•0875	0•0736	-0•0105
(x) Wood	-0•0264	0•0303	-0•0192	-0•0243
(xi) Other surface	0•0138	0•0003	-0•0579	-0•0798
(xii) Exposure	0•0019	0•0605	-0•0075	0•0530
(xiii) Sky cover	0•1208	0•0196	0•0067	-0•0793
(xiv) Foraging	-0•0124	-0•0067	0•0252	-0•0082
(xv) Basking	-0•0145	0•0023	-0•0661	0•0025
(xvi) Other activity	0•0269	0•0090	0•0408	0•0057
VARIANCE EXPLAINED	32•9%	16•4%	13•3%	11•7%

time of year contrasting with angle to the sun, with height and time of day also contributing positively. Again posturing appears important here. (The component contrasts progression through the year with increase in lizards facing away from the sun.) The third component combines time of year with horizontal oreintation. The fourth component represents air temperature, snout-vent length and height above the ground. Most of the other variables score close to zero and contribute little overall to the lizard observations.

The analysis suggests that a limited number of variables is sufficient to account for the major variability in the observations of P. hispanica at North Front Cemetery. In this case four components account for 66·6% of the total variability.

It is not easy to interpret the components in environmental terms, particularly in components I and III, since the relationship between time of year and angle to the sun is somewhat abstract. However it appears that posture is important in P. hispanica and that the nature of observations in terms of the variables measured varies during the course of the year.

The first component in the analysis of the summer data, as given in Tables 8.11 and 8.12, again combines surface angle and vertical orientation contrasting these with horizontal orientation. Once again this component is a measure of 'verticality'. The second component, with the date variable now removed, is describing the general trend of correlation resulting from horizontal orientation, SVL and vertical orientation. Again this component contains a large element of posture variables.

The third component contains most influence from time of day, height above ground and vertical orientation (again).

The fourth component essentially combines height and SVL contrasting this with vertical orientation.

Together these first four components account for 74·3% of the total variability for these data. The importance of posture in P. hispanica observed is again highlighted in these summer data, this time together with height above ground and SVL. Most of the other variables gave scores close to zero.

The importance of the posturing of *P. hispanica* in the transect data stresses the importance of basking and therefore thermoregulation in the species, at least in those lizards seen during transects.

8.7 Metabolism

8.7.1 Introduction

Work on metabolic rates in reptiles has been building up gradually in recent years (e.g., as reviewed by Bennett & Dawson, 1976). There has been considerable discussion on the conditions necessary in order to standardise values determined experimentally. Discussion has also been considerable on the significance of the different metabolic rates and how these are affected by temperature (e.g., Aleksiuk, 1971) and by time of day and body weight (e.g., Cragg, 1978a). Studies have included measurement of metabolic rates of resting fasted lizards (Cragg, 1978a) as well of unrestrained ones (e.g., Avery, 1971).

Diurnal observations on animals resting in the dark have generally been used as the comparative base for Standard Metabolic Rate (SMR). SMR was measured in these conditions at temperatures encountered by resting lizards in the field.

8.7.2 Methods

A Noyons Diaferometer, an open system respirometer produced by Kipp and Zonen, was used to measure oxygen consumption. In this system a steady stream of air is pumped continuously through the metabolic chamber and the diaferometer. The operating principles are summarised briefly below.

When a stream of gas passes over a heated platinum wire (if the temperature is low enough to render radiation losses negligible) the cooling of the wire depends on the thermal conductivity of the gases in the stream - for example, carbon dioxide has a thermal conductivity ten times greater than oxygen. If the current is held constant the electrical resistance of the wire as it cools can be detected with a galvanometer, as a change in potential difference.

The diaferometer has four channels - two for detecting carbon dioxide and two for the detection of oxygen. The system is comparative: the oxygen in the room air is compared with the oxygen in the respired air and similarly room carbon dioxide is compared with that in the respired air.

In practice voltage changes were read from the inbuilt galvanometers, at one minute intervals for four minutes per channel. The galvanometer readings (on a millimeter scale) were plotted against time as on the sample graph (Figure 8.31).

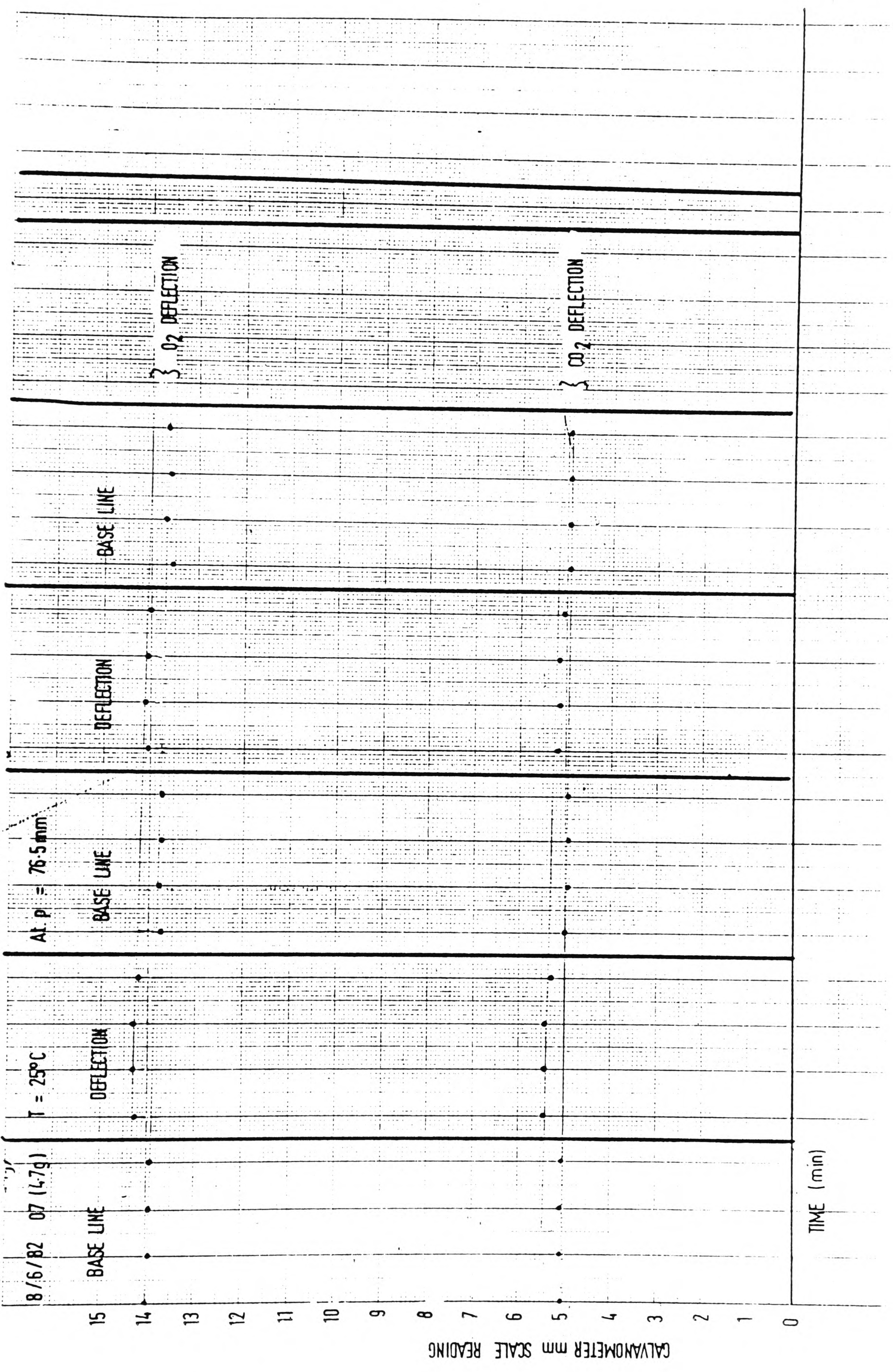
The diaferometer was first adjusted to draw room air through all four channels, thus comparing room O_2 with room O_2 and room CO_2 with room CO_2. When readings became stable, the diaferometer was adjusted so that room air passed through two channels and respired air through the other two. For alternate four minute intervals the galvanometer readings for the base lines for O_2 and CO_2 and for the respired air were recorded. The deflections thus obtained represented the O_2 decrease ($\triangle O_2$) and the CO_2 increase ($\triangle CO_2$) in the respired air. Using the appropriate correction factors, these deflections were converted to actual values of oxygen consumption.

The diaferometer was set up in a draught-free constant temperature room. Lizards which had been kept for at least two months in vivaria with conditions simulating those found in the field in late spring were used in the experiment. Only adult male lizards which were the largest and of which most were available were used. All lizards used were in a healthy condition and had not fed for twenty-four hours.

The experimental animals were placed in a small chamber (c. 225cm^3) which was air tight. This chamber contained a stone under which the lizard invariably withdrew after some exploration. The chamber was then placed in a blackened tank and connected to the diaferometer. Once the lizard had been at rest for one hour the recording of readings commenced.

Several problems were encountered with the equipment. Other electrical equipment in the vicinity sometimes resulted in large deflections of the galvanometer. Difficulty with temperature control also limited experiments and resulted in some data having to be discarded.

Fig. 8.31 PLOT OF DIAFEROMETER GALVANOMETER READINGS



In the end, data on a total of 49 experiments on six lizards were accepted. These were: 1 at 8°C; 4 at 9°C; 1 at 20·5°C; 2 at 21°C; 4 at 21·5°C; 9 at 22°C; 3 at 23°C; 1 at 24·5°C; 2 at 25°C; 2 at 25·5°C; 10 at 26°C; 8 at 28°C; 2 at 29°C.

In order to facilitate interpretation of data, the results were grouped into 8 - 9°C; 20·5 - 21·5°C; 22 - 23°C; 24·5 - 25·5°C; 26°C; 28 - 29°C.

8.7.3 Results

The scatter of points of SMR against the temperature in the chamber (assumed to be equal to lizard body temperature) is shown in Figure 8.32. There is an overall increase in SMR between the low temperatures (8°C and 9°C) and the higher temperatures. The regression line is shown in Figure 8.33 and the correlation is significant ($r = 0{\cdot}5073$; $P < 0.01$). When the mean results for the grouped data (Table 8.13) were plotted (Figure 8.33), there appeared to be two inverse translations of the metabolic rate curve after the mean values of the 20·5 - 21·5°C and 24·5 - 25·5°C groupings. Because of the great range of results, which may have been due to different levels of activity of the lizards within the shelter of the provided stone, the maximum and minimum rates recorded for each temperature grouping were also plotted on Figure 8.33. The maximum graph shows peaks at similar points to the mean graph. The minimum graph, however, which may reflect the true resting metabolism, showed a peak at the 22°C - 23°C grouping, a low at the 24·5°C - 25·5°C grouping, and an increase above this temperature. Even if the reversals in the slope were not real, all three curves suggest a levelling off of oxygen consumption as the mean voluntary temperature is reached (Jacobson & Whitford, 1970).

Aleksiuk (1971) found that in <u>Thamnophis</u>, although there was great variability in the overall curve of SMR against body temperature, in particular in the position of a shift (or shifts) in oxygen consumption, each individual had a characteristic curve. Individual curves have been plotted for lizards 01 and 06 in Figures 8.34

Table 8.13 Mean standard metabolic rates (SMR) of *P. hispanica* at different temperatures.

Temperature (^{o}C)	Mean SMR ($cm^3 O_2 g^{-1} hr^{-1}$)	S.D.	Range ($cm^3 O_2 g^{-1} hr^{-1}$)	n
8•0- 9•0	0•071	0•042	0•034-0•134	5
20•5-21•5	0•328	0•150	0•106-0•550	7
22•0-23•0	0•242	0•065	0•133-0•360	12
24•5-25•5	0•569	0•271	0•063-0•610	5
26•0	0•284	0•137	0•098-0•471	10
28•0-29•0	0•234	0•097	0•113-0•424	10

Table 8.14 Values of the Respiratory Quotient (RQ) of *P. hispanica*.

Temperature grouping (°C)	mean RQ	S.D.	n	range
All lizards	0•53	0•51	49	0•02 - 2•44
8•0 - 9•0	0•74	0•98	5	0•06 - 2•44
20•5 - 21•5	0•42	0•44	7	0•14 - 1•35
22•0 - 23•0	0•53	0•33	12	0•06 - 1•18
24•5 - 25•5	0•85	0•91	5	0•02 - 2•16
26•0	0•40	0•41	10	0•09 - 1•32
28•0 - 29•0	0•48	0•27	10	0•16 - 0•88

Fig 8.32 PLOT OF STANDARD METABOLIC RATES AGAINST TEMPERATURE

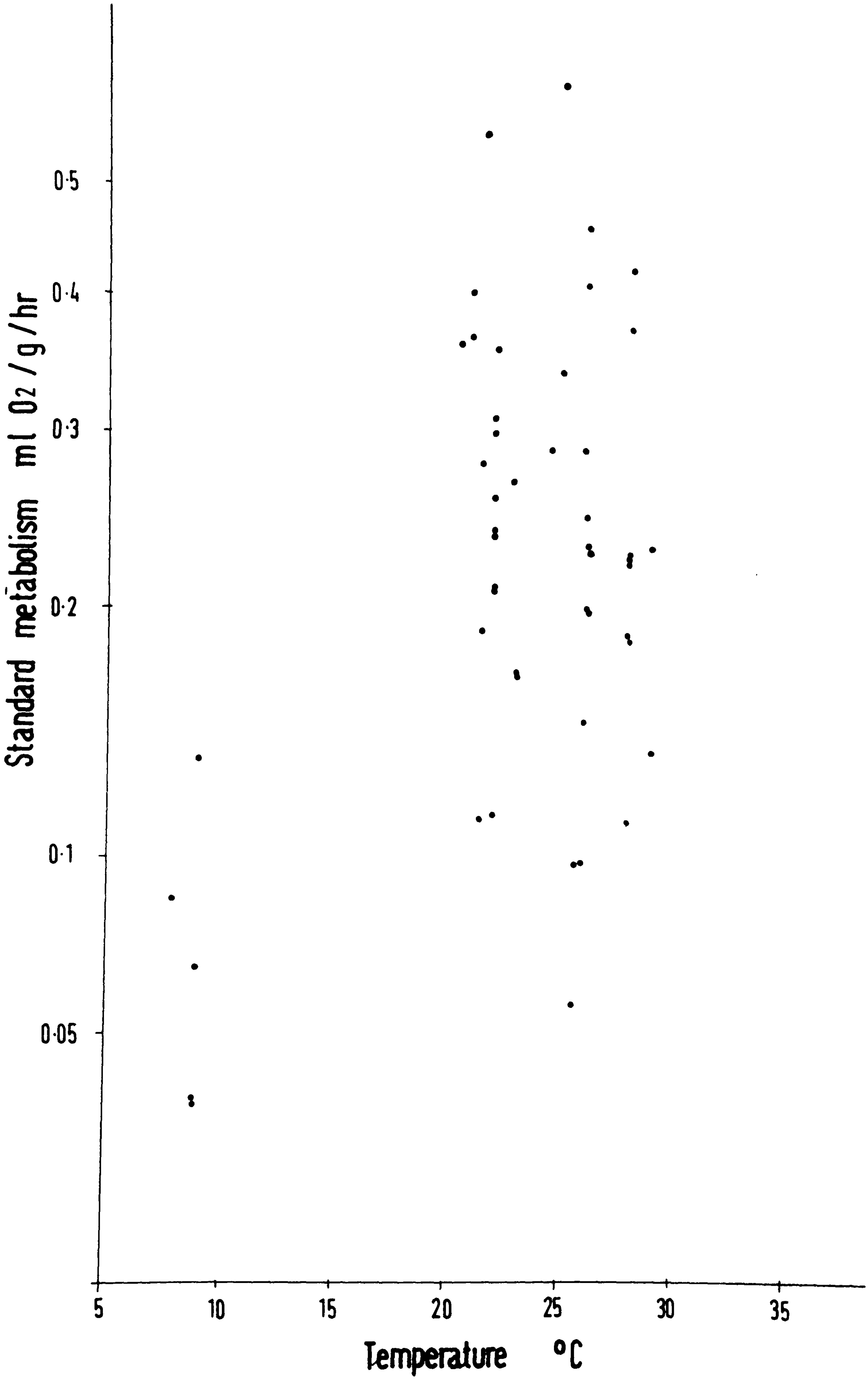


Fig. 8.33 THE RELATIONSHIP OF STANDARD METABOLISM TO TEMPERATURE IN <u>P. hispanica</u>

(MEAN VALUES: SEE TABLE 8.)

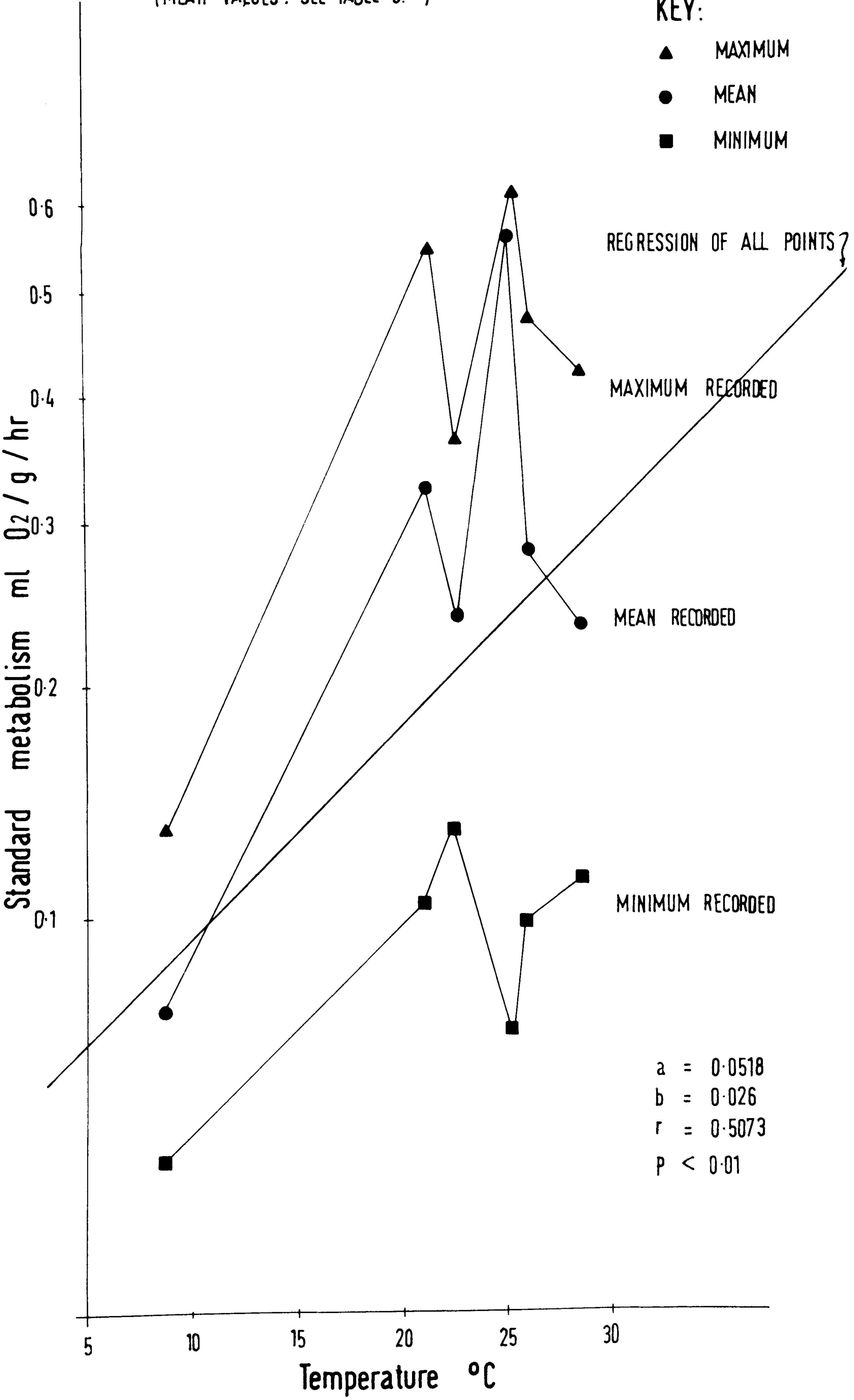


Fig. 8.34 STANDARD METABOLIC RATE OF LIZARD 01.

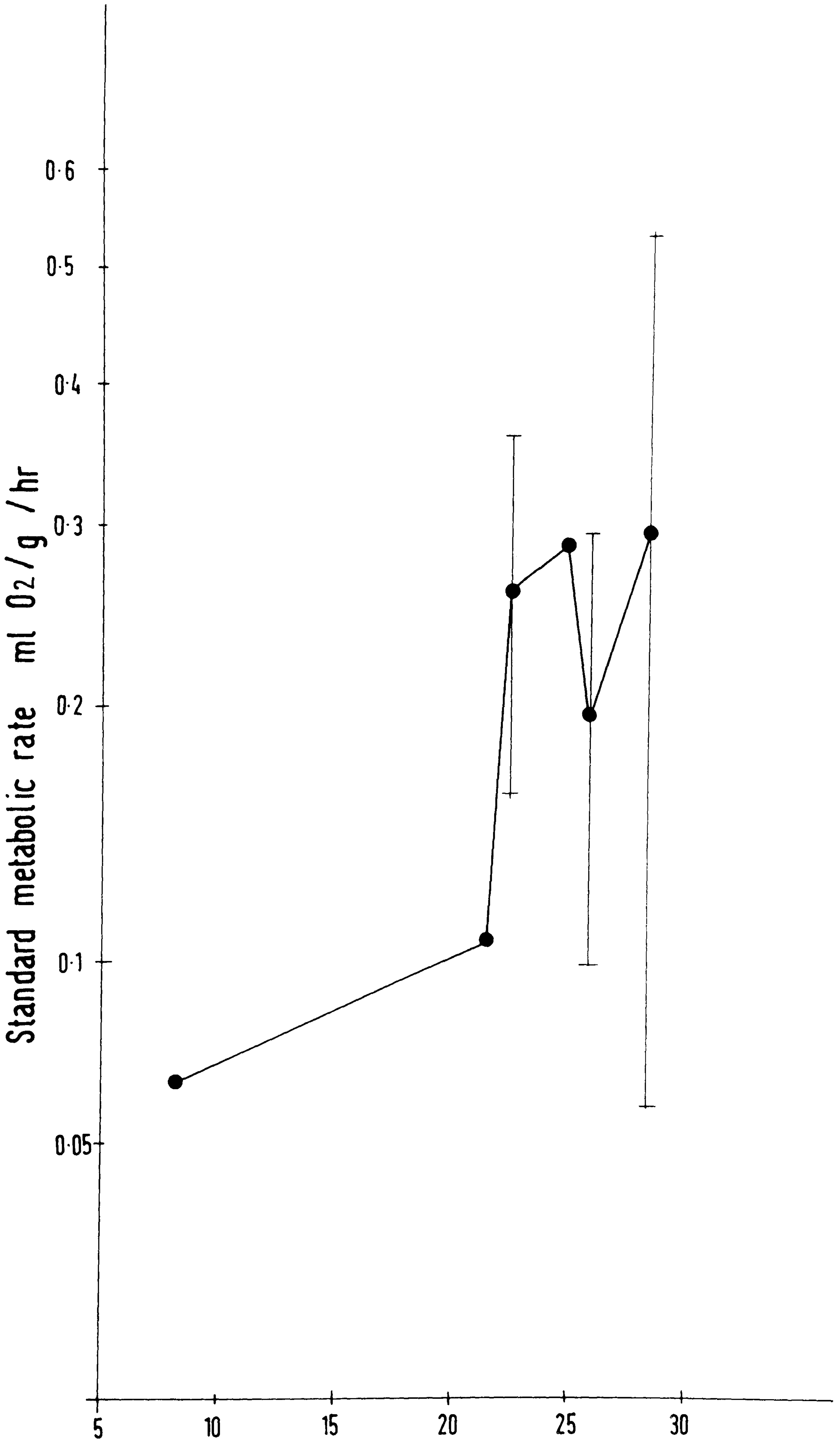
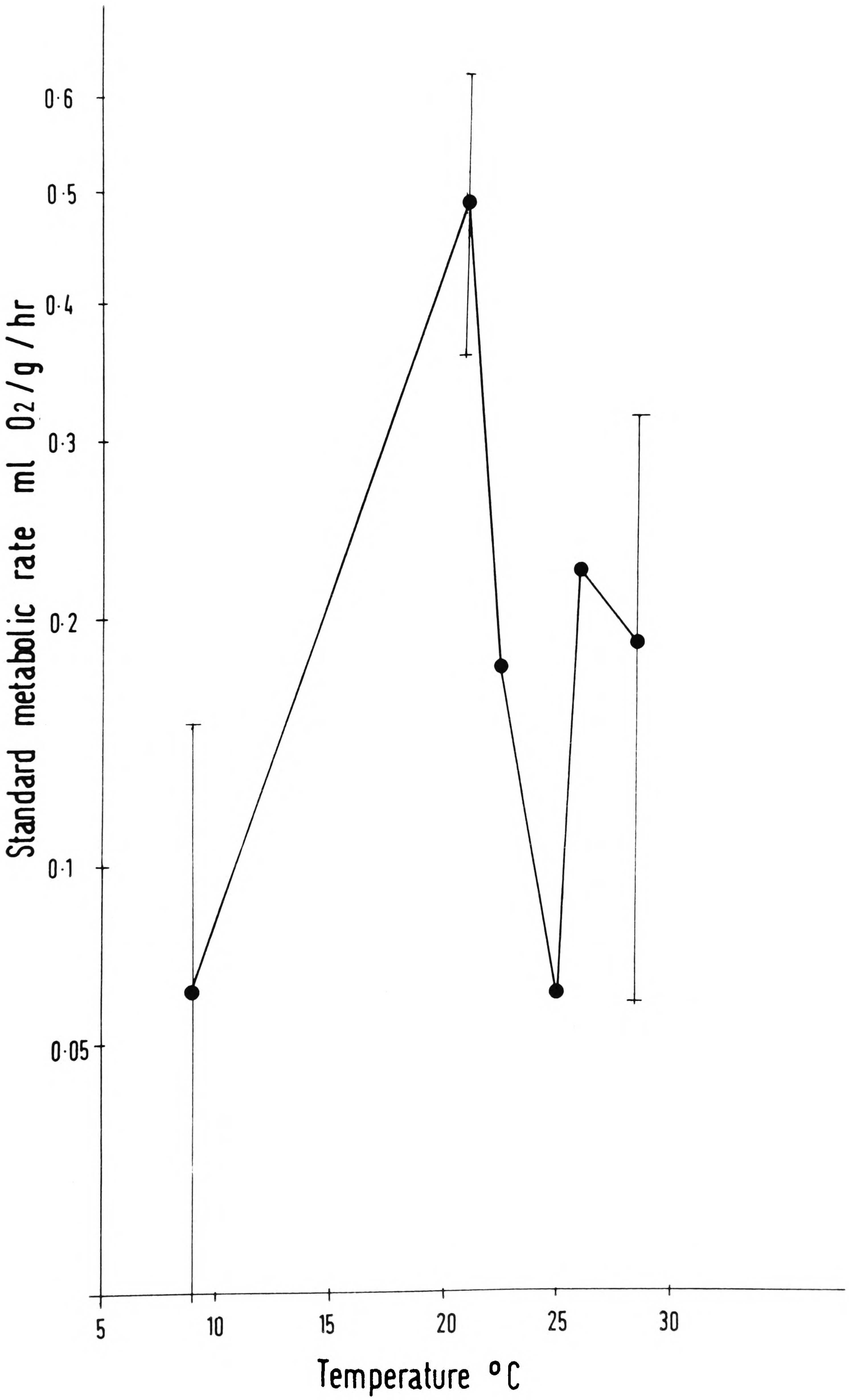


Fig. 8.35 STANDARD METABOLIC RATE OF LIZARD 06.



and 8.35. The curves differ considerably, although in both cases there is a drop in SMR after an initial increase and, noticeably in the case of O1, a levelling off of the curve above 22·5°C.

Values of SMR ranged from 0·034 to 0·610 $cm^3 O_2 g^{-1} hr^{-1}$, within ranges published by other workers for reptiles (see 8.7.4).

Table 8.14 shows mean values of the Respiratory Quotient (RQ) for all the 49 determinations and for each of the temperature groupings. The mean value was 0·52 (S.D. = 0·53) with a large range from 0·024 to 2·436. The highest RQ value was for the 24·5 - 25·5°C sample (0·85; S.D. = 0·91) and the lowest for the 26°C sample (0·40; S.D. = 0·41).

8.7.4 Discussion

Several factors may have contributed towards the large range of values of SMR obtained at the different temperatures. The possibility of different levels of activity of the experimental lizards has already been mentioned. Circadian cycles have also been known to affect oxygen consumption (Roberts,1968a,Gratz & Hutchinson 1977). This effect is lost in continuously dark conditions in certain species (e.g., *Lacerta vivipara*, *L. viridis*; Cragg,1978a). The experiments on *P. hispanica* were carried out between 0900 and 1600 hrs, so a range of values was possible. Bartholomew (1972) states that there will be fluctuations in metabolic rates if the lizard is under thermal stress, a condition which is probably only totally avoided when the lizard is close to its preferred body temperature (Cragg, 1978a).

The different values obtained for SMR (Figure 8.32) fall within the range of published values for reptiles (e.g., Bennett & Dawson, 1976) and have a similar range to those values given for *Acanthodactylus erythrurus* by Pough & Busack (1978), and perhaps more important for *P. hispanica* by Patterson & Davies (1978). This suggests the variability is probably real, and not due to experimental error. It also suggests that the maximum result may indeed be values of metabolic rate for more active lizards, the minima representing those of resting lizards.

Avery (1971) obtained metabolic rates of unrestrained L. vivipara of $0{\cdot}15\mathrm{cm}^3\ O_2\ g^{-1}hr^{-1}$ at 10°C; $0{\cdot}4\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$ at 20°C and $0{\cdot}75\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$ at 30°C (approximately). In the present study the following were the maximum values for metabolic rates for P. hispanica at temperatures close to these; $0{\cdot}13\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$ at 8 - 9°C; $0{\cdot}55\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$ at 20·5 - 21·5°C and $0{\cdot}42\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$ at 28 - 29°C (maximum values at 24·5 - 25·5°C was $0{\cdot}61\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$). Bartholomew and Tucker (1964) obtained values as high as $0{\cdot}9\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$ in Uta stansburiana. The elevated values of metabolism obtained for P. hispanica may have been due, then, to the failure of animals to reach standard conditions in the course of the experiments (Bennett & Dawson, 1976).

The minimum values in this study compare with those of summer-acclimated P. hispanica given by Patterson & Davies (1978) as follows:

Metabolic rate ($\mathrm{cm}^3 O_2 g^{-1}hr^{-1}$)

Temperature(°C)	Minimum:this study	Mean:Patterson & Davies (1978)
8·0 - 9·0	0·03	
10		0·025
20		0·12
20·5 - 21·5	0·1	
25		0·18
28·0 - 29·0	0·12	
30		0·2

Standard metabolic rate is related to the weight of the lizard and is lower the heavier the animal. (Cragg (1978a) found the relationship for 1 day-starved Lacerta at 30°C to be $0{\cdot}328W^{0{\cdot}756}$). Bennett & Dawson (1976) present a list of metabolic rates of the variety of lizards at different temperatures. As would be expected, the levels closest to those recorded in this study for P. hispanica (mean weight = 4·19g) are those of the smallest lizards.

Thus, at 20°C (metabolism for P. hispanica at 20·5 - 21·5°C = 0·1, 0·3, 0·5$cm^3 O_2 g^{-1} hr^{-1}$, minimum, mean and maximum values respectively), values for Anolis carolinensis (4·5g) and Scincella lateralis (1·0g) were 0·11 and 0·12$cm^3 O_2 g^{-1} hr^{-1}$ respectively. At 30°C (results in this study were: minimum = 0·12; mean = 0·23; maximum = 0·42$cm^3 O_2 g^{-1} hr^{-1}$ at 28 - 29°C) values given by Bennett & Dawson (1976) were (in $cm^3 O_2 g^{-1} hr^{-1}$); 0·19 for A. carolinensis, 0·31 for S. lateralis, 0·16 for Sceloporus graciosus (5·0g), 0·17 for U. stanburiana (3·0g), 0·13 for Xantusia vigilis (1·1g) and Eumecis fasciatus (7·0g). (A. carolinensis has a preferred temperature of 31°C, similar to the voluntary mean temperature of 30·8°C of P. hispanica.)

It has been noted above that there is a levelling off of increase in metabolic rates with temperature above about 20°C. Jacobson & Whitford (1970) suggest that the levelling off of oxygen consumption they observed in Thamnophis proximus may be "the results of reduced locomotor activity as the preferred body temperature is reached". The rapid increase in metabolic rates upto about 20°C will allow activity levels to be reached quickly and maintained (possibly with a drop towards higher temperatures) throughout the lizard's voluntary range.

There appears also to be a shift in the metabolic rate curve around 20 - 25°C, both overall (Figure 8.33) and for individual lizards 01 (Figure 8.34) and 06 (Figure 8.35). The reversals in slope are similar to those observed for Thamnophis by Aleksiuk (1971). Tromp & Avery (1977) also reported a shift in L. vivipara metabolic rates between 15 and 20°C. Bartholomew & Tucker (1963) found that in Amphibolurus barbatus the peak metabolic rate was recorded at 20°C (0·299$cm^3 O_2 g^{-1} hr^{-1}$) with a drop after this. The authors believed this pattern was useful in allowing lizards at this temperature to actively seek out areas in which they could reach eccritic temperatures and to avoid enemies. The same phenomenom may be reflected here. In addition, a peak at the lower end of the range of activity temperatures (Table 8.1) may allow food digestion, growth and gestation to take place while lizards are in shelter (Aleksiuk,1976).

Figure 8.32 shows a high metabolic rate value at 9°C, of $0{\cdot}13\text{cm}^3 \text{O}_2 \text{g}^{-1} \text{hr}^{-1}$. If this is due to activity of the lizard at this low temperature it shows an impressive ability to sustain metabolism at low body temperatures. Pough & Busack (1978) suggested a similar phenomenon in A. erythrurus. Whether due to a shift or a plateau, the possibility of having high metabolic rates at low temperatures is a valuable temperature dependent method of metabolic compensation which offsets the depressive effect of low temperature on metabolism (Aleksiuk, 1971). Plateaux occur in thermal ranges over which animals are normally active in nature (Bennett & Dawson, 1976).

A rapid reduction in metabolic rate below a lizard's voluntary range will be advantageous since it will minimise expense of energy when in shelter before emergence and during cold weather.

Classical cold compensation by acclimation, as Patterson & Davies (1978) found in their P. hispanica, may not be necessary if preferred body temperature can be maintained through the year. An instantaneous method would be more adaptive, especially if the predictability of low temperatures in the environment were low. Thus, while preferred body temperature (reflected in voluntary mean temperature) can be maintained through the year in Gibraltar (except, apparently, in December; Figure 8.4), cool conditions can arise unpredictably at any time of year with the onset of the Levanter (2.1.3). The onset of cool weather could immediately induce a cold-compensated state (Aleksiuk,1971), as opposed to what is the case in the majority of poikilotherms where compensation takes days or weeks to appear (Bullock, 1955; Fry, 1958). The onset of warm weather would "turn off" the cold compensated state (Aleksiuk, 1971).

Night temperatures in the summer in Gibraltar (2.1.3), and in the vivaria in which the experimental lizards were kept in Oxford, were in the low twenty degrees Centigrade range. It was around these temperatures that the 'troughs' in the metabolic rate vs temperature graph occurred. These troughs, if characteristic of the lizards, could allow a drop of metabolic rate at night which might not otherwise be possible. Lizards handled at night at these temperatures were indeed lethargic (unless light was shone on them : 8.4.4).

The ability to be active at low temperatures, whether or not sustained by a metabolic shift, will be a valuable feature of a lizard's physiological adaptation (Pough & Busack, 1978), allowing activity and reasonable levels of metabolism to persist through the winter and permitting lizards to emerge at low ambient temperatures (8.4). If,in addition, a lizard can reduce metabolism at times of inactivity when temperatures are still within the lower range of its voluntary range, it will be able to save energy at a time when food is scarce. These two adaptations will contribute to the success of the species in the climatic conditions of Gibraltar.

8.7.5 Respiratory Quotient (RQ)

The number of molecules of carbon dioxide produced divided by the number of molecules of oxygen consumed during respiration is called the Respiratory Quotient, RQ. According to Bennett & Dawson (1976) a resting, fasting reptile should have an RQ of about 0·7; higher values being found in reptiles equilibrating to high temperatures, lower values in those equilibrating to low temperatures. Cragg (1978a) considers that low values may be a result of leakage of carbon dioxide in closed circuit respirometry.

In mammals, an RQ of 0·7 is indicative of fat metabolism, 0.82 of protein or mixed diet, and 1·0 of carbohydrates (Mountcastle, 1974). In uricotelic animals, RQ for protein metabolism is also close to 0·7 (Roberts, 1968b). The lizard diet of mealworms corresponds to a mixed/protein diet, and RQ should approximate to 0·7 (Cragg, 1978a). Anaerobic metabolism can also result in a higher value of RQ (Mountcastle, 1974).

The range obtained in this study (0•02 - 2•44) is greater than that of 0•65 to 1•46 given by Bennett & Dawson (1976), and we must look at another possible source of error. Values of carbon dioxide and oxygen exhaled and inhaled over short time periods may not represent exactly the ratios in which they were used and produced in respiration.

It appears that the RQ measured in this study was somewhat bogus. Fortunately admission of error in RQ figures does not throw doubt on the accuracy of the oxygen consumption values, since it is well accepted that CO_2 output is an unreliable indicator of metabolism since, for example, it can be retained dissolved in the blood (e.g., Hall, 1924; Kayser, 1940) and then released.

CHAPTER 9

DISCUSSION

9 DISCUSSION

9.1 Summary

The data presented, the results and the discussions in the preceding chapters allow certain conclusions to be drawn.

It is clear, for example, that for lizards at Gibraltar, stress due to extremes of temperature, in particular low temperature, is almost totally absent. Thus, although inclement weather can occur and restrict activity at all times of year (by reducing solar radiation), favourable weather which allows lizard activity can also occur throughout.

Lizards behave in such a way as to maximise activity time. P. hispanica in Gibraltar do not hibernate, and in winter can be active at lower body temperatures than during the rest of the year, allowing activity in microhabitats which are also cooler. Activity is unimodal in winter and bimodal in summer. In summer, activity starts earlier in the day and at lower levels of solar radiation than during the cooler times of year, since restriction in activity is greatest in the middle of the day at this season.

P. hispanica temperatures correspond closely to those found in their environment throughout the year. The lizards appear to be able to thermoregulate well, and in various ways. Warm surfaces are chosen when temperatures are lower or when the sun is temporarily obscured. Lizards are seen to shuttle between open sunlight and the shade of vegetation. Posturing seems to be of particular importance . It may serve both to maximise energy uptake on warming and to reduce this when lizards want to remain exposed. The different reflective properties of the scales of P. hispanica may well play a part in this temperature control.

The small size of the Iberian Wall Lizard may be particularly significant in thermoregulation since small lizards can control their temperature by minor adjustments in behaviour (Norris, 1967). Larger lizards fail to regulate since factors tending to produce additional heating once preferred temperatures have been reached (e.g., metabolism, failure to dissipate heat) remain strongly predominant (Norris, 1967). Conversely, there will be resistance to quick uptake of heat when cold. Small lizards on the other hand are thermolabile, allowing finer control of temperature.

The success of temperature control in P. hispanica is suggested by the fact that mean body temperatures vary only slightly in the course of the year (except, in those sampled, in December) - which may suggest that the lizards are usually well nourished (Lee, 1980). Indeed, if the ratio $\sqrt[3]{\text{weight}}$ / SVL is taken as a comparative measure of lizard condition, it is true to say that the data suggest little variation in this through the year.

Activity throughout the year means exposure to predators through the year also. The angular colour effect observed in this lizard, which may be useful in thermoregulation, can also have a role to play in predator-defence.

Adult lizards are most evident at the start of summer. Hatchlings appear during the second half of that season and, provided food is available, can grow quickly. Sexual maturity is reached in the first summer and mating is possible then. Growth will probably depend on the productivity of the lizard's environment (captive lizards with superabundant food grow more quickly than wild ones).

The productivity of the habitat as a whole changes seasonally. In summer invertebrates are scarce except in localised areas, and lizards tend to congregate there. As food becomes gradually more plentiful and temperatures lower, congregations will tend to be encountered in areas with suitable refugia. At these times, aggression is minimal. As spring approaches, the lizards will spread more evenly through the habitat, now more productive, into areas where low vegetation provides foraging ground and there are outcrops for basking. The actual amount of basking decreases, while 'sit and wait' behaviour becomes more prominent. Aggressive behaviour also grows in importance, particularly between adult males. At the same time, appeasement behaviour (waving) is more often recorded, allowing females and young males to live within the larger home ranges of the fully-grown males. Females, while remaining in the habitat, become less obvious during the breeding season and are markedly less prominent in the transects.

P. hispanica are opportunistic feeders. They can feed on a wide range of invertebrates below 10 - 15mm in length. These seem to be those most frequent in their habitat. The food resource available to P. hispanica is therefore greater than if it were a specialist. Aggression occurs when there is competition for resources (Stamps, 1977). The broad food niche may contribute towards reducing aggression when lizards are congregated.

Intraspecific competition for food resources is probably reduced as a result of sexual dimorphism in head size (not in head shape). Schoener (1977) suggested that active foragers are more dimorphic than sit-and-wait specialists. (Indeed, in Gibraltar, T. mauritanica is almost exclusively a sit-and-wait feeder, and appears to show no dimorphism.) Partitioning between sexes should, according to Schoener (1977) be mainly with regard to macro- and microhabitat, and also to daily and seasonal activity. In fact, differences between male and female P. hispanica in Gibraltar are not many. In spring, females are more secretive and appear to spend more time in denser vegetation, however.

Adult/juvenile differences are predicted by Schoener (1977) to be mainly in food type and also in microhabitat. In P. hispanica there are differences in the use of heights - juveniles use the ground more than adults - which may reflect such a difference. However, it is more likely that the ability of juveniles to eat smaller food, and the limited activity of adults at most times of day in the summer is more important.

Variability in a species is expected to be greatest where the species occurs on its own (Lister, 1976). Unfortunately variability in P. hispanica, although considerable in the morphometric data, cannot be compared to that in other areas due to lack of published work.

There is some evidence, however, of a shift in habitat of P. hispanica in the presence of Ps. algirus. Thus the hindleg/foreleg ratio of P. hispanica is somewhat lower in the presence of Ps. algirus than when it occurs alone. The wall lizard also climbs more in habitats where it occurs with the Psammodromus, which in Gibraltar seems to be much less arboreal and to use the ground more than elsewhere. Similar shifts have been observed to occur in other lizard species (e.g., Jenssen, 1973). Conversely, we can interpret the observations as representing a spread of P. hispanica, in the absence of competitors, into microhabitats from where they are generally excluded. The heads of P. hispanica are longer in relation to snout-vent length in the presence of Ps. algirus. Although larger heads will tend to make these lizards more similar to Ps. algirus, they will also increase the maximum size of prey and effectively increase the amount of food available to the species.

The amount of time spent foraging, basking and in other activities by P. hispanica will depend not only on food requirements, but also on thermal conditions. Basking will be less frequent and for shorter periods when it is warmest. In some cases, sit-and-wait behaviour provides a compromise.

9.2 Conclusion

This study of the Iberian Wall Lizard, Podarcis hispanica STEINDACHNER, at Gibraltar, has allowed an overall picture of the year-round ecology and behaviour of the species to emerge. It has certainly made it possible to predict with certain accuracy the activity of the lizard in the field at Gibraltar, as I have had opportunity to observe.

Unfortunately, work on the species elsewhere has been too limited to allow comparison which would have made this study more valuable. In effect, comparisons have had to be made largely to related species of more northerly latitudes.

Even within the population of lizards in Gibraltar there is great scope for further work, particularly in the laboratory. Of definite interest would be research on the reflectivity of the skin of P. hispanica. Further comparisons of the North Front Cemetery population with that from other areas would also be of interest. Determination of temperature relations and metabolic rates under different conditions, and further work on food choice and food consumption are all aspects worth pursuing. However this more detailed work would be of limited value only if a basic knowledge of the field biology of the lizards did not exist.

At the European Herpetological Symposium (1980), Avery (1981) mentioned the desirability of a 'Synoptic Model' of European Lacertidae, taking into account all the existing work on the group and pointing out the need for more research in certain areas.

Avery (1981) summarised the various north-south trends in morphology, physiology, activity, ecology and behaviour of Lacertids in Europe. Most of his examples however, like mine, were taken from northern European species. There are many gaps in our knowledge of the ecology and behaviour of southern European lizards. Unfortunately the level of research in Iberia, although increasing, remains low. In this light, it is hoped that the present work has gone some of the way towards increasing our basic knowledge of the field biology of a small Lacertid lizard at the southernmost end of Europe.

APPENDIX 1

APPENDIX 1

Text of the International Strategy for the Conservation of the European Herpetofauna, passed at the European Herpetological Symposium, Oxford, 1980:

"With the increasing pressure on all species of European herpetofauna, the time for a concerted and unified European initiative by those most active in the field of herpetological conservation and field research has arrived.

"The intention is to present, as soon as possible, a single succinct plan for the conservation of European herpetofauna, which incorporates the ideas, data, information, criticisms and suggestions put forward by active field herpetologists. The plan will then be presented to those European bodies capable of offering substantial funds."

APPENDIX 2

A NORTH FRONT CEMETERY (NFC) MAIN TRANSECT SITE; EARLY SUMMER

B NORTH FRONT CEMETERY (NFC) MAIN TRANSECT SITE; SPRING

C NORTH AREA OF NORTH FRONT CEMETERY ; SPRING

D NORTH AREA OF NORTH FRONT CEMETERY ; EARLY SUMMER

E "CROSS SITE"; SPRING

F " NORTH-EAST WALL SITE"; SPRING

G BRUCE'S FIREBREAK SITE ; LATE SPRING

H BRUCE'S FIREBREAK SITE ; LATE SUMMER

APPENDIX 3

I LIZARD IN 'SIT AND WAIT' POSITION IN VEGETATION.

J LIZARD IN 'SIT AND WAIT' POSITION IN OPEN.

APPENDIX 4

K P. *hispanica* EMERGING AT N.E.WALL SITE ; THERMISTER PROBES IN REFUGIA.

L FOUR LIZARDS BASKING ON LOG IN WINTER.

APPENDIX 5

APPENDIX 5

GUIDE TO IDENTIFICATION OF FRAGMENTS FROM FAECAL PELLETS

1. Certain types of material were immediately recognisable:

Shell fragments ---- Gastropods
Chelicera ---- Araneae
Elytra ---- Coleoptera

2. The following Keys (from Pernetta, 1973 (unpubl.)) were also used, but not all the groups of invertebrates included were encountered in the faeces samples.

KEY A The Legs of Arthropoda

1.a. Generally pale in colour with a simple tarsus ending in a single claw. ---- 2

b. Pale, glabrous, with a multi-jointed tarsus, which is moniliform or filiform. ---- 3

c. Legs heavily chitinised with a variable tarsus, ---- Insecta ad.

2.a. Single tarsal joint equal in length to preceding two joints. ---- Isopoda

b. Tarsal joint 1½ - 2 times as long as the preceding two joints, pale, colourless or with a grey/black core. ---- Diplopoda

c. Generally pale yellow or brown, more heavily chitinised than a and b. ---- Chilopoda

3.a. Pale, often spiny and/or hairy, proportionally elongate, frequently with an elongate filiform or moniliform tarsus. ---- Opiliones

b. Darker than the above, with proportionally shorter moniliform or filiform tarsus rarely exceeding ten joints. ---- Araneae

The division of insect legs into further subgroups is not possible by means of a single key since there is great variability in shape and form within any one group. In general it may be said that:

Orthopteran legs show stridulatory pegs or other similar adornments and are long.

Coleopterous legs are heavily chitinised, not normally hairy and with one or two claws.

Dipterous legs are hairy, and with variable feet that usually include some form of pad.

Hymenopterous legs are generally thin and delicate when compared with those of coleoptera.

Hemipteran legs are generally lightly chitinised and are often comparatively long.

KEY B

Body Cuticle

1.a. Pale, translucent, thin and recognisably form a plate, colour patchy. ---- 2

b. Transparent and/or entirely coloured, ranging from pale yellow through to black. ---- Insects and Chilopoda

2.a. Inner surface with patches, or largely covered in a grey/black patina. Outer surface glaucous - Diplopoda

b. Outer surface patterned in some way, inner surface with small irregularly shaped areas of colour.-- Isopoda

c. Extremely thin, transparent at least in part, often large pieces with little or no apparent structure, colour patchy. ---- Arachnida excl. Acari

KEY C

Insect Wings

1.a. Wings with scales. ---- Lepidoptera

b. Wings with stigma. ---- Hymenoptera

c. Wings membranous, no stigma. ---- Orthoptera

d. Wings wholly or partially chitinised or leathery. ---- 2

2.a. Wings still membranous in the distal region. ---- Hemiptera fore-wing

b. Wings reduced to a leathery tegmina with no membranous portion. ---- Dermaptera fore-wing

c. Wings heavily chitinised. ---- Coleoptera fore-wing

d. Venation simple, often reduced. ---- 3

3.a. Highly specialised venation, radially disposed. ---- Dermaptera

b. Venation reduced. ---- Hemiptera hind-wing

c. Primitive veins normally all present. ---- 4

4.a. Alula often present, accessory and intercalary veins absent, chief cross veins present. ---- Diptera

b. Wings not as above. ---- 5

5.a. Principal veins developed, oblong cell present. ---- Coleoptera (Adephaga)

b. All cross veins absent, proximal portion of M_1 atrophied. ---- Coleoptera (Staphilinid type)

c. M_1 and M_2 coalesced, from point of junction one vein continues to the wing margin. ---- Coleoptera (Cantharid type)

APPENDIX 6

APPENDIX 6

INDICES OF DIVERSITY

Herrera (1976) proposed the following 'trophic diversity index':

$$D = -\sum_{i=1}^{s} \log \hat{p}_i$$

where p_i are the frequencies of occurence of the various prey categories; i.e.

$$\hat{p}_i = \frac{n_i}{N}$$

where n_i = number of occurences of the i^{th} prey type;

N = number of stomachs (faeces in this study)

i = 1, 2, ... s.

This is compared by Herrera (1976) to the Shannon-Weaver index of diversity H', given by :

$$H' = -\sum_{i=1}^{s} q_i \log q_i$$

where q_i is the frequency of the i^{th} food category with respect to the total number of prey items in the analysis.

REFERENCES

REFERENCES

ALEKSIUK, M. 1971. Temperature-dependent shifts in the metabolism of a cool temperate reptile, Thamnophis sirtalis parietalis. Comp. Biochem. Physiol.,39A, 495-503.

ALEKSIUK, M. 1976. Metabolic and behavioural adjustments of temperature change in the red-sided garter snake (Thamnophis sirtalis parietalis): an integrated approach. J. Thermal Biol.,1, 153-156.

ANDRADA, J. 1979. Los reptiles insectívoros de la España Mediterránea. Vida silvestre, 29, 1-17.

ARNOLD, E.N. 1973. Relationships of the Palaearctic lizards assigned to the genera Lacerta, Algyroides and Psammodromus (Reptilia: Lacertidae). Bull. Br. Mus. Nat. Hist.,(Zool.), 25, 291-366.

ARNOLD, E.N., BURTON, J.A. & OVENDEN, D.W. 1978. A field guide to the Reptiles and Amphibians of Britain and Europe. Collins: London.

ATSATT, S.R. 1939. Colour changes as controlled by temperature and light in the lizards of the desert regions of southern California. Publ. Univ. California Los Angeles Biol. Sci., 1, 237-276.

AVERY, R.A. 1971. Estimates of food consumption by the lizard Lacerta vivipara Jacquin. J. Anim. Ecol., 40, 351-365.

AVERY, R.A. 1973. Morphometric and functional studies on the stomach of the lizard Lacerta vivipara. J. Zool., Lond., 169, 157-167.

AVERY, R.A. 1975. Clutch size and reproductive effort in the lizard Lacerta vivipara Jacquin. Oecologia (Berl.), 19, 165-170.

AVERY, R.A. 1976. Thermoregulation, metabolism and social behaviour in Lacertidae. In Bellairs, A. d'A. & Cox, C.B. (Eds.), Morphology and Biology of Reptiles. Linnaean Society Symposium Series no. 3. Academic Press: London & New York.

AVERY, R.A. 1978. Activity patterns, thermoregulation and food consumption in two sympatric lizard species (Podarcis muralis and P. sicula) from Central Italy. J. Anim. Ecol., 47, 143-158.

AVERY, R.A. 1981. Ecophysiology and behaviour of lacertid lizards - towards a synoptic model. In Coborn, J. (Ed.), European Herpetological Symposium. Cotswold Wild Life Park: Oxon.

AVERY, R.A. & McARDLE, B.H. 1973. The morning emergence of the common lizard Lacerta vivipara Jacquin. Br. J. Herpetol., 5, 363-368.

AYALA, I.L. de 1782. Historia de Gibraltar. La Sancha: Madrid.

BALLINGER, R.E. & SCHRANK, G.D. 1970. Acclimation rate and variability of the critical thermal maximum in the lizard Phrynosoma cornutum. Physiol. Zool., 43, 19-22.

BALLINGER, R.E., MARION, K.R. & SEXTON, O.J. 1970. Thermal ecology of the lizard Anolis limifrons with comparative notes on three additional Panamanian anoles. Ecology, 51, 246-254.

BARTHOLOMEW, G.A. 1972. Energy Metabolism. In Gordon, M.S. (Ed.), Animal Physiology: Principles and Adaptation, 2nd edn. MacMillan: New York.

BARTHOLOMEW, G.A. & TUCKER, V.A. 1963. Control of changes in body temperature, metabolism and circulation by the agamid lizard, Amphibolurus barbatus. Physiol. Zool., 36, 199-218.

BARTHOLOMEW, G.A. & TUCKER, V.A. 1964. Size, body temperature, thermal conductance, oxygen consumption and heart rate in Australian varanid lizards. Physiol. Zool., 37, 341-354.

BEGUINOT, A. 1922. La macchia-foresta nella Sardegna settentrionale ed i suoi principali tipi. Bull. Ist. Bot. R. Univ. Sassari, 1, 1-35.

BENADY, M. in prep. A History of Gibraltar.

BENNETT, A.F. & DAWSON, W.R. 1976. Metabolism. In Gans, G. (Ed.), Biology of the Reptilia, vol. 5. Academic Press: London.

BERRY, K.H. 1971. Social behaviour of the Chuckwalla, Sauromalus obesus. Amer. Soc. Ichthyol. Herpetol. Ann. Meeting (Abstr.).

BLAIR, W.F. 1960. The Rusty Lizard, a population study. University of Texas Press: Austin.

BOAG, D.A. 1973. Spatial relationships among members of a population of wall lizards. Oecologia (Berl.), 12, 1-13.

BONS, J. 1972. Herpetologie Marocaine. I. Liste commentée des amphibiens et reptiles du Maroc. Bull. de la Société des Sciences Naturelles et Physiques du Maroc, 52, 107-126.

BONS, J. 1973. Herpetologie Marocaine. II. Origines, évolution et particularités du peuplement herpetologique du Maroc. Bull. de la Société des Sciences Naturelles et Physiques du Maroc, 53, 63-110.

BONS, J. 1974. Mise en place du peuplement herpetologique actuel dans le basin mediterranéene occidental. Bull. de la Société Languedocienne de Geographie, 8, 385-392.

BONS, J. 1975. La faune herpetologique du Maroc. Bull. de la Société Zoologique de France, 100, 670-673.

BRADSHAW, S.D. 1971. Growth and mortality in a field population of Amphibolurus lizards exposed to seasonal cold and aridity. J. Zool., Lond., 165, 1-25.

BRADSHAW, S.D. & MAIN, A.R. 1968. Behavioural attitudes and regulation of temperature in Amphibolurus lizards. J. Zool., Lond., 154, 193-221.

BRATTSTROM, B.H. 1965. Body temperatures of reptiles. Am. Midl. Nat., 73, 376-422.

BRATTSTROM, B.H. 1971. Social and thermoregulatory behaviour of the Bearded Dragon, Amphibolurus barbatus. Copeia, 1971, 484-497.

BRATTSTROM, B.H. 1974. The evolution of reptilian social behaviour. Am. Zoologist, 14, 35-49.

BRAUN-BLANQUET, J. 1932. Plant Sociology. McGraw Hill: New York.

BRAUN-BLANQUET, J. 1951. Pflanzensoziologie, 2nd. edn., Springer: Wien.

BROWN, C.K. & RUBY, D.E. 1977. Sex associated variation in the frequencies of tail autotomy in Sceloporus jarrovi (Sauria: Iguanidae). Herpetologica, 30, 182-183.

BULLOCK, T.H. 1955. Compensation for temperature in the metabolism and activity of poikilotherms. Biol. Rev., 30, 311-342.

BUSACK, S.D. 1976. Activity cycles and body temperatures of Acanthodactylus erythrurus. Copeia, 1976, 826-830.

BUSACK, S.D. 1977. Zoogeography of amphibians and reptiles in Cadiz Province, Spain. Annals of Carnegie Museum, 46, 285-316.

BUSACK, S.D. 1978. Body temperatures and live weights of five Spanish amphibians and reptiles. J. Herpetol., 12, 256-258.

CARPENTER, C.C. 1967. Aggression and social structure in Iguanid lizards. In Milstead, W. (Ed.), Lizard ecology, a symposium. Univ. Missouri Press: Columbia.

CARPENTER, C.C., BADHAM, J.A. & KIMBLE, B. 1970. Behaviour patterns of three species of Amphibolurus (Agamidae). Copeia, 1970, 497-505.

CHARNOV, E.L. 1976. Optimal foraging: the marginal value theorem. Theor. Pop. Biol., 9, 129-136.

CHINERY, M. 1972. A Field Guide to the Insects of Britain and Northern Europe. Collins: London.

CONGDON, J.D., VITT, L.J. & KING, W.W. 1974. Geckos: adaptive significance and energetics of tail autotomy. Science, 184, 1379-1380.

CORM, M. 1971. Upper thermal limits and thermal preferenda for three sympatric species of Anolis. J. Herpetol., 5, 17-21.

CORTES, J.E. 1979. (unpubl.) The vegetation of Gibraltar. B.Sc. Thesis, The Royal Holloway College, London.

CORTES, J.E. 1983. The Rock of Gibraltar - man-induced changes and conservation importance. Alectoris, 5, 10-20.

CORTES, J.E., FINLAYSON, J.C., GARCIA, E.F.J. & MOSQUERA, M.A.J. 1980. The Birds of Gibraltar. The Gibraltar Bookshop: Gibraltar.

COWLES, R.B. & BOGERT, C.M. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Am. Mus. Nat. Hist., 83, 261-296.

CRAGG, P. 1978a. Oxygen consumption in the lizard genus Lacerta in relation to diel variation, maximum activity and body weight. J. Exp. Biol., 77, 33-56.

CRAGG, P. 1978b. Ventilatory patterns and variables in rest and activity in the lizard, Lacerta. Comp. Biochem. Physiol., 64A, 399-410.

CROZE, H. 1970. Searching image in Carrion Crows. Zeits. Tierpsyche, Bleikeft 5. Verleg Paul Parey: Berlin & Hamburg.

DAGET, Ph., GODRON, M., LONG,G. & POISSONET, J. 1968. L'occupation de la station. In Godron, M., Daget, Ph., Long, G., Sauvage, C., Emberger, L., Le Floch, E., Poissonet, J., Wacquant, J-P. Code pour le rélevé méthodique de la végétation et du milieu. C.N.R.S.: Paris.

DAULTREY, S. 1976. Principal Components Analysis. Concept and Techniques in Modern Geography, no. 8. Geo Abstracts: Norwich.

DAVIES, P.M.C., PATTERSON, J.W. & BENNETT, E.L. 1981. The thermal ecology, physiology and behaviour of the viperine snake, Natrix maura: some preliminary observations. In Coborn, J. (Ed.), European Herpetological Symposium. Cotswold Wild Life Pary: Oxon.

DEACON, E.L. 1969. Physical processes near the surface of the earth. In Flohn, H. (Ed.), World Survey of Climatology, vol. 2, General Climatology. Elsevier: Amsterdam.

ESCARDO, A.L. 1970. The climate of the Italian Peninsula. In Flohn, H. (Ed.), World Survey of Climatology, vol.5. Elsevier: Amsterdam.

FINLAYSON, J.C. 1981. Seasonal distribution, weights and fat of passerine migrants at Gibraltar. Ibis, 123, 88-95.

FORD, R.G. & KRUMME, D.W. 1979. The analysis of space-use patterns. J. Theor. Biol., 76, 125-155.

FORD, R.G. & MYERS, J.P. 1981. An evaluation and comparison of techniques for estimating home range and territory size. Studies in Avian Biology, 6, 461-465.

FOX, D.L. 1953. Animal Biochromes and Structural Colours. Cambridge Univ. Press: Cambridge.

FOX, H.M. & VEVERS, G. 1960. The Nature of Animal Colours. Sidgewick & Jackson: London.

FRY, F.E.J. 1958. Temperature compensation. Ann. Rev. Physiol., 20, 207-224.

GEIGER, R. 1969. Topoclimates. In Flohn, H. (Ed.), World Survey of Climatology, vol. 2, General Climatology. Elsevier: Amsterdam.

GIBRALTAR ENVIRONMENTAL GROUP 1980. Environmental conservation in Gibraltar. Gibraltar Environmental Group: Gibraltar.

GRATZ, R.K. & HUTCHINSON, V.H. 1977. Energetics for activity in the diamondback water snake Natrix rhombifera. Physiol. Zool., 50, 99-114.

HAILEY, A., DAVIES, P.M.C. & PULFORD, E. 1982. Lifestyle and ecology of natricine snakes. Br. J. Herpetol., 6, 261-268.

HALL, F.G. 1924. The respiratory exchange in turtles. J. metab. Res., 6, 393-401.

HARESTEAD, A.S. & BUNNELL, F.L. 1979. Home range and body weight - a re-evaluation. Ecology, 60, 389-402.

HEATH, J.E. 1962. Temperature-independent morning emergence in lizards of the genus Phrynosoma. Science, 138, 891-892.

HEATWOLE, H. 1976. Reptile Ecology. Univ. Queensland Press: St. Lucia.

H.M. NAUTICAL ALMANAC OFFICE 1981. Nautical Almanac 1982. H.M. Nautical Almanac Office: London.

HERRERA, C. 1976. A trophic diversity index for presence - absence food data. Oecologia (Berl.), 25, 187-191.

HOUSE, S.M., TAYLOR, P.J. & SPELLERBERG, I.F. 1980. Patterns of daily behaviour in two lizard species, Lacerta agilis L. and Lacerta vivipara Jacquin. Oecologia (Berl.), 44, 396-402.

HUEY, R.B. & PIANKA, E.R. 1977. Seasonal variation in thermoregulatory behaviour and body temperature of diurnal Kalahari lizards. Ecology, 58, 1066-1075.

HUEY, R.B. & SLATKIN, M. 1976. Costs and benefits of lizard thermoregulation. Quart. Rev. Biol., 51, 363-384.

HUEY, R.B. & STEVENSON, R.D. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zoologist, 19, 357-366.

JACOBSON, E.R. & WHITFORD, W.G. 1970. The effect of acclimation on physiological responses to temperature in the snakes, Thamnophis proximus and Natrix rhombifera. Comp. Biochem. Physiol., 35, 439-449.

JAMES, T. 1771. History of the Herculean Straits. Rivington: London.

JEFFERS, J.N.R. 1978. An Introduction to Systems Analysis: with ecological applications. Edward Arnold: London.

JENNRICH, R.I. & TURNER, F.B. 1979. Measurement of non-circular home range. J. Theor. Biol., 22, 227-237.

JENSSEN, T.A. 1970. The ethoecology of Anolis nebulosus (Sauria, Iguanidae). J. Herpetol., 4, 1-38.

JENSSEN, T.A. 1973. Shift in the structural habitat of Anolis opalinus (Sauria, Iguanidae) due to congeneric competition. Ecology, 54, 863-869.

KAYSER, C. 1940. Les échanges respiratoires des hibernants réveillés (Deuxieme Partie). Le quotient respiratoire chez quelques espèces poikilothermes. Annls Physiol. physicochim. Biol., 16, 1-68.

KELAART, E.F. 1846. Flora Calpensis. John van Voorst: London.

LEE, J.C. 1980. Comparative thermal ecology of two lizards. Oecologia (Berl.), 44, 171-176.

LISTER, B.L. 1976. The nature of niche expansion in West Indian Anolis lizards: I. Ecological consequences of reduced competition. Evolution, 30, 659-676.

McNAB, B.K. 1963. A model of the energy budget of a wild mouse. Ecology, 44, 521-532.

MARCELLINI, D.L. 1977. Acoustic and visual display behaviour of Gekkonid lizards. Am. Zoologist, 17, 251-260.

MARCELLINI, D.L. unpubl. Ethoecology of Hemidactylus frenatus with emphasis on acoustic behaviour. Dissertation Univ. Oklahoma.

MELLADO CAMACHO, J. 1980. Utilización del espacio en una comunidad de lacertidos del matorral mediterráneo en la Reserva Biológica de Doñana. Doñana, Acta Vertebrata, 7, 41-49.

MELLADO, J. 1982. Anfibios y reptiles: la salida del letargo invernal. Quercus, 2, 29-30.

MELLADO, J. & MARTINEZ, F. 1974. Dimorfismo sexual en Psammodromus algirus. Doñana, Acta Vertebrata, 1, 33-42.

MELLADO, J., AMORES, F. PARRENO, F.F. & HIRALDO, F. 1975. The structure of a Mediterranean lizard community. Doñana, Acta Vertebrata, 2, 145-160.

MOERMOND, T.C. 1979. The influence of habitat structure on Anolis foraging behaviour. Behaviour, 70, 147-167.

MOLINIER, R. 1959. Etude des groupements vegetaux terrestres du Cap Corse. Bull. Mus. Hist. Nat. Marseille, 19, 5-75.

MOREAU, R.E. 1972. The Palaearctic-African Bird Migration Systems. Academic Press: London & New York.

MOUNTCASTLE, V.B. 1974. Medical Physiology, vol.2, 13th edn. C.V. Mosby Company.

NIELSEN, B. 1961. On the regulation of respiration in reptiles. I. the effect of temperature and CO_2 on the respiration of lizards (Lacerta). J. exp. Biol., 38, 301-314.

NORRIS, K.S. 1967. Colour adaptation in desert reptiles and its thermal relationships. In Milstead, W. (Ed.), Lizard ecology, a symposium. Univ. Missouri Press: Columbia.

NORRIS, K.S. & LOWE, C.H. 1964. An analysis of background colour-matching in amphibians and reptiles. Ecology, 45, 565-580.

PARKER, G.A. & STUART, R.A. 1976. Animal behaviour as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. Amer. Nat., 110, 1055-1076.

PARKER, W.S. & PIANKA, E.R. 1973. Ecology of the iguanid lizard, Sceloporus magister. Herpetologica, 29, 143-152.

PATTERSON, J. & DAVIES, P. 1978. Thermal acclimation in temperate lizards. Nature, Lond., 275, 646-647.

PERNETTA, J.J. 1973 (unpubl.). Field and laboratory experiments to determine the feeding ecology and behaviour of: Sorex araneus (L.) and Sorex minutus (L.). D. Phil. Thesis, Department of Zoology, Oxford.

PIANKA, E.R. 1969. Habitat specificity, speciation and species diversity in Australian desert lizards. Ecology, 50, 498-502.

PIANKA, E.R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst., 4, 53-74.

PIANKA, E.R. 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci., 71, 2141-2145.

PIANKA, E.R. 1975. Niche relations of desert lizards. In Cody, M. & Diamond, J. (Eds.), Ecology and Evolution of Communities. Harvard Univ. Press: Cambridge Mass.

PIANKA, E.R. & PARKER, W.S. 1972. Ecology of the iguanid lizard Callisaurus draconoides. Copeia, 1972, 493-508.

PIRLOGE, T. 1982. Strategie adaptive d'une population de montagne de Lacerta vivipara. Oikos, 39, 207-212.

PORTER, K.R. 1972. Herpetology. W.B. Saunders: Philadelphia.

PORTER, W.P. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. Ecological Monogr., 37, 237-296.

PORTER, W.P., MITCHELL, J.W., BECKMAN, W.A. & DeWITT, C.B. 1973. Behavioural implications of mechanistic ecology - thermal and behavioural modelling of desert ectotherms and their micro-environment. Oecologia (Berl.), 13, 1-54.

POUGH, F.H. 1973. Lizard energetics and diet. Ecology, 54, 837-844.

POUGH, F.H. & BUSACK, S.D. 1978. Metabolism and activity of the Spanish fringe-toed lizard (Lacertidae: Acanthodactylus erythrurus). J. Thermal Biol., 3, 203-205.

PYKE, G.H., PULLIAN, H.R. & CHARNOV, E.L. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol., 52, 137-154.

RAND, A.S. 1954. Variation and predation pressure in an island and a mainland population. Copeia, 1954, 260-262.

RAND, A.S. 1967. Ecology and social organisation in the iguanid lizard Anolis lineatopus. Proc. U.S. National Mus., 122, 1-79.

REGAL, P.J. 1975. The evolutionary origin of feathers. Q. Rev. Biol., 50, 35-66.

ROBERTS, L.A. 1968a. Oxygen consumption in the lizard, Uta stansburiana. Ecology, 49, 809-819.

ROBERTS, L.A. 1968b. Water loss in the desert lizard Uta stansburiana. Comp. Biochem. Physiol., 27, 583-589.

ST-GIRONS, H. & DUGUY, R. 1970. Le cycle sexuel de Lacerta muralis L. en plaine et en montagne. Bull. Mus. natn. Hist. nat. Paris, 42, 609-625.

ST-GIRONS, H. & ST-GIRONS, M.C. 1956. Cycle d'activité et thermoregulation chez les reptiles (lezards et serpents). Vie et Milieu, 7, 133-226.

ST-GIRONS, M.C. 1976. Relations interspecifiques et cycle d'activité chez Lacerta vivipara et Lacerta agilis (Sauria, Lacertidae). Vie et Milieu, 26, 115-132.

SALVADOR, A. 1974. Guia de los Anfibios y Reptiles Españoles. I.C.O.N.A., Madrid.

SCHALL, J.J. & PIANKA, E.R. 1977. Species densities of reptiles and amphibians on the Iberian Peninsula. Doñana, Acta Vertebrata, 4, 27-34.

SCHOENER, T.W. 1968. Sizes of feeding territories among birds. Ecology, 49, 123-141.

SCHOENER, T.W. 1969. Models of optimal size for solitary predators. Am. Nat. 103, 277-313.

SCHOENER, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst., 11, 369-404.

SCHOENER, T.W. 1977. Competition and the niche. In Gans, C. & Tinkle, D.W. (Eds.), Biology of the Reptilia, vol. 7. Academic Press: London.

SCHOENER, T.W. & GORMAN, G.C. 1968. Some niche differences in three Lesser Antillean lizards. Ecology, 49, 819-830.

SCHOENER, T.W. & SCHOENER, A. 1980. Ecological and demographic correlates of injury rates in some Bahamian Anolis lizards. Copeia, 1980, 839-850.

SCHOENER, T.W. & SCHOENER, A. 1982. Intraspecific variation in home range size in some Anolis lizards. Ecology, 63, 809-823.

SIEGEL, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw Hill: New York, Toronto & London.

SIMON, C.A. 1975. The influence of food abundance on territory size in the iguanid lizard Sceloporus jarrovi. Ecology, 56, 993-998.

SIMON, C.A. & MIDDENDORF, G.A. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. Ecology, 57, 1317-1320.

SOKAL, R.R. & ROHLF, F.J. 1969. Introduction to Biostatistics. W.H. Freeman: San Francisco.

SPELLERBERG, I.F., 1972a. Temperature tolerances of southeast Australian reptiles examined in relation to reptile thermoregulatory behaviour and distribution. Oecologia (Berl.), 9, 23-46.

SPELLERBERG, I.F., 1972b. Thermal ecology of allopatric lizards (Sphenomorphus) in southeast Australia. I. The environment and lizard critical temperatures. Oecologia (Berl.), 9, 371-383.

SPELLERBERG, I.F. 1972c. Thermal ecology of allopatric lizards (Sphenomorphus) in southeast Australia. II. Physiological aspects of thermoregulation. Oecologia (Berl.), 9, 385-398.

SPELLERBERG, I.F. 1973. Critical minimum temperatures of reptiles. In Wieser, W. (Ed.), Effects of temperature on ectothermic organisms. Springer Verlag: Berlin.

SPELLERBERG, I.F. 1976. Adaptations of reptiles to cold. In Bellairs, A. d'A. & Cox, C.B. (Eds.), Morphology and Biology of Reptiles. Linnaean Society Symposium Series no. 3. Academic Press: London & New York.

STAMPS, J.A. 1976. Rainfall, activity and social behaviour in the lizard Anolis aeneus. Anim. Behav., 24, 603-608.

STAMPS, J.A. 1977. The relationship between resource competition, risk and aggression in a tropical territorial lizard. Ecology, 58, 349-358.

STAMPS, J.A. & CREWS, D. 1976. Seasonal changes in reproduction and social behaviour in the lizard Anolis aeneus. Copeia, 1976, 467-476.

STAMPS, J.A. & TANAKA, S. 1981. The relationship between food and social behaviour in juvenile lizards Anolis aeneus. Copeia, 1981, 422-434.

STEBBINS, R.C., LOWENSTEIN, J.M. & COHEN, N.W. 1967. A field study of the lava lizard (Tropidurus albemarlensis) in the Galapagos Islands. Ecology, 48, 839-851.

TINKLE, D.W. 1972. The role of environment in the evolution of life history differences within and between lizard species. Univ. Arkansas Mus. Occ. Pop. no. 4: 77-100.

TINKLE, D.W. 1976. Comparative data on the population ecology of the desert spiny lizard Sceloporus magister. Herpetologica, 32, 1-6.

TINKLE, D.W. & BALLINGER, R.E. 1972. Sceloporus undulatus: a study of the intraspecific comparative demography of a lizard. Ecology, 53, 570-584.

TOMASELLI, R. 1972. Sulla nomenclatura della vegetazione mediterranea sempreverde dal punto di vista fisionomico-structurale ad ecologico. Atti. Ist. bot. Univ. Lab. crittogam, Pavia, ser. 6,7, 3-8.

TOMASELLI, R. 1977. Degradation of the Mediterranean maquis. M.A.B. Technical Notes 2. U.N.E.S.C.O.

TRAMP, W.I. & AVERY, R.A. 1977. A temperature dependent shift in the metabolism of the lizard Lacerta vivipara. J. Thermal. Biol., 2, 53-54.

TURNER, F.B., JENNRICH, R.I. & WEINTRAUB, J.D. 1969. Home ranges and body sizes of lizards. Ecology, 50, 1076-1081.

VALVERDE, J.A. 1967. Estructura de una comunidad mediterranea de vertebrados terrestres. C.S.I.C. Madrid.

VINEGAR, M.B. 1975. Demography of the Striped Plateau Lizard, Sceloporus virgatus. Ecology, 56, 172-175.

VITT, L.J. 1974. Winter aggregations, size classes and relative tail breaks in the tree lizard, Urosaurus ornatus (Sauria: Iguanidae). Herpetologica, 30, 182-183.

VITT, L.J., CONGDON, J.D. & DICKSON, N.A. 1977. Adaptive strategies and energetics of tail autotomy in lizards. Ecology, 58, 326-337.

VITT, L.J., CONGDON, J.D., HULSE, A.C. & PLATZ, J.A. 1974. Territorial aggressive encounters and tail breaks in the lizard Sceloporus magister. Copeia, 1974, 990-993.

WEBB, G.J.W. & WITTEN, G.J. 1973. Critical thermal maxima of turtles: validity of body temperature. Comp. Biochem.Physiol. 45A, 829-832.

WILLIAMS, W.T. & LAMBERT, J.M. 1959. Multivariate methods in plant ecology. I. Association analysis in plant communities. J. Ecol., 47, 83-101.

WILLIS, L., THRELKELD, S.T. & CARPENTER, C.C. 1982. Tail loss patterns in Thamnophis (Reptilia: Colubridae) and the probable fate of injured individuals. Copeia, 1982, 98-101.

WOLLEY-DODD, A.H. 1914. A flora of Gibraltar and the neighbourhood. J. Bot. (Supplement), 52.

WRIGHT, W.D. 1944. The Measurement of Colour. Adam Hilger Ltd.: London.