

A COMPARISON OF THE BEHAVIOUR AND ECOLOGY
OF THE TASMANIAN BANDICOOTS, *Perameles gunnii*
(GRAY 1838) AND *Isoodon obesulus* (SHAW AND NODDER 1797)

by

DAMIEN JOHN MOLONEY B.Sc. (Melb.)

Thesis submitted to the University of Tasmania, Department of
Zoology, as partial fulfilment towards the degree of Bachelor
of Science with Honours

December 1982



Perameles gunnii



Isodon obesulus

ACKNOWLEDGEMENTS

I would firstly like to thank my supervisor, Mr. Othmar Buchmann, for his invaluable assistance and advice throughout the course of the study and also for his thorough reviewing of the manuscript.

Appreciation is also extended to the staff of the Zoology Department, University of Tasmania, in particular, Dr. I. Wilson for his assistance in the filming of the locomotion of bandicoots, Dr. A. Richardson and Dr. R. White for their help in statistical and computer analyses of data, Mr. R. Rose for advice, Dr. J. Hickman for identification of parasites and to the technical staff for providing equipment and a helping hand.

A permit for trapping bandicoots was obtained from the National Parks and Wildlife Service of Tasmania and Mr. G. Hocking, Mr. N. Mooney and Mr. D. Rounsevell, of the Service, allowed me generous access to records held by the latter. Two of the trapping programmes were conducted on privately-owned properties and therefore I am indebted to Mr. Dorney and Mr. J. Whitehouse for their cooperation and use of their land.

I am grateful to Dr. M. Maskrey and Colin Sthulel of the Physiology Department for the use of their equipment and Dr. B. Brown of the Mathematics Department for statistical advice. To all other honours students, in particular Mr. T. Clancy and Miss I. Jensen, I express my appreciation for their interest in the study. Thanks also to Dan, Janet and Shk for the use of their photographs.

For their support and encouragement, I am indebted to my family and Elizabeth Morrison. Finally, thanks are extended to Mrs. L. Wilson for her efforts in typing this thesis.

TABLE OF CONTENTS

	Page
CHAPTER 1 INTRODUCTION	1
1.1 Survey of the Behaviour and Ecology of Marsupials	4
1.2 General Biology of the Family Peramelidae	4
CHAPTER 2 CAPTURE AND MAINTENANCE OF BANDICOOTS	9
2.1 Methods of Capturing Subjects	9
2.2 Maintenance of Bandicoots in Captivity	22
CHAPTER 3 MAINTENANCE ACTIVITIES	27
3.1 Activity-Levels	27
3.1.1 Introduction	27
3.1.2 Materials and Methods	28
3.1.3 Results	36
3.1.4 Discussion	54
3.2 Nesting	57
3.2.1 Introduction	57
3.2.2 Materials and Methods	58
3.2.3 Results	58
3.2.4 Discussion	60
3.3 Grooming	60
3.3.1 Introduction	60
3.3.2 Materials and Methods	61
3.3.3 Results	61
3.3.4 Discussion	66
3.4 Locomotion	68
3.4.1 Introduction	68
3.4.2 Materials and Methods	69
3.4.3 Results	72
3.4.4 Discussion	78
CHAPTER 4 FEEDING BEHAVIOUR AND DIET	81
4.1 Foraging and Feeding	81
4.1.1 Introduction	81
4.1.2 Materials and Methods	82
4.1.3 Results	83
4.1.4 Discussion	99
4.2 Defaecation and Micturition	103
4.2.1 Introduction	103
4.2.2 Materials and Methods	103
4.2.3 Results	103
4.2.4 Discussion	105
4.3 Prey-Killing Behaviour	107
4.3.1 Introduction	107
4.3.2 Materials and Methods	107
4.3.3 Results	109
4.3.4 Discussion	117
CHAPTER 5 HOME-RANGE AND HABITAT-UTILIZATION	121
5.1 Description of Study Areas	121
5.2 Home-range and Movements	126
5.2.1 Introduction	126
5.2.2 Materials and Methods	128
5.2.3 Results	131
5.2.4 Discussion	139

TABLE OF CONTENTS (continued)

	Page
5.3 Habitat Utilization	143
5.3.1 Introduction	143
5.3.2 Materials and Methods	144
5.3.3 Results	144
5.3.4 Discussion	146
CHAPTER 6 INTRA- AND INTER-SPECIFIC INTERACTIONS	148
6.1 Introduction	148
6.2 Materials and Methods	149
6.3 Results	152
6.3.1 Intra-Specific, Monosexual Interactions	152
6.3.2 Intra-Specific, Heterosexual Interactions	156
6.3.3 Inter-Specific Interactions	159
6.4 Discussion	160
CHAPTER 7 GENERAL DISCUSSION	165
REFERENCES	167
APPENDIX A <i>I. obesulus</i> and <i>P. gunnii</i> Dying During the Course of the Study	i
APPENDIX B Road-Kill Surveys and the "TASPAWS" Biological Record Scheme	v

CHAPTER 1

INTRODUCTION

1.1 SURVEY OF THE BEHAVIOUR AND ECOLOGY OF MARSUPIALS

The study of the behaviour and ecology of marsupials has been a neglected area of research for a long time and few quantitative studies of this subject have been undertaken to date. However, recently (particularly during the past twenty years), there has been a recrudescence of interest in these spheres of investigation as the ensuing review of the relevant literature shall demonstrate, although the amount of this research-effort is still meagre in comparison with the volume of information published about many species of eutherian mammals.

This neglect of research on marsupials is both surprising and unfortunate, as marsupials are widely distributed, occupy all of the major habitats occurring in Australia and have adapted diverse modes of life almost, if not precisely comparable in variety to that of analogous eutherian mammals occupying comparable ecological niches. Earlier studies on marsupials were of a comparative nature often specifically dealing with differences between metatherian and eutherian mammals. In addition, these investigations mainly concentrated on only a few species, particularly the larger members of the family Macropodidae (the kangaroos and wallabies) and the Virginia opossum, *Didelphis marsupialis*. Research-activities were further limited by the fact that these studies were largely centred on reproduction, a process of considerable importance in view of its uniqueness in marsupials.

It is the above factors and the fact that the majority of other marsupials are nocturnal, timid and cryptic, (rendering investigations difficult, particularly in the field) that have resulted in the paucity of behavioural and ecological information available on the numerous diverse groups of the sub-class Metatheria.

As previously mentioned, *D. marsupialis* has received considerable attention, being the only specie of marsupial endemic to North America. Investigations have covered behavioural characteristics and seasonal

changes in behaviour (McManus 1970, 1971), the daily activity cycle (Bombardieri and Johnson 1969) and population density and movement patterns (Holmes and Sanderson 1965; Shirer and Fitch 1970).

Studies on the family Macropodidae have included observations on daily activities and social behaviour of *Macropus rufus* (Frith 1964; Russell 1970a; Croft 1981a), agonistic encounters and social behaviour in *M. giganteus* (Grant 1973; Kaufmann 1975) and locomotion in several species of the larger macropods (Windsor and Dagg 1971; Alexander and Vernon 1975). Locomotion has also been observed in the genus *Potorous* by Buchmann and Guiler (1974). Russell and Pearce (1971) studied the investigation of novel objects by selected species of four marsupial families, of which two species belonged to the family Macropodidae and one to the family Peramelidae. Observations have been made in captivity on the quokka (*Setonix brachyurus*), the pademelon (*Thylogale billardierii*) and the burrowing bettong (*Bettongia lesueuri*) by Packer (1969), Morton and Burton (1973) and Stodart (1966), respectively and Kitchener (1973) has investigated the home ranges and movements of *S. brachyurus* and *P. apicalis*.

By comparison, all of the other families of marsupials have received scant attention. Studies on the family Dasyuridae have been mainly concerned with prey-killing and feeding behaviour in *Dasyercus cristicauda* (Ewer 1969) and in *Sarcophilus harrisii* (Buchmann and Guiler 1977). Hutson (1975) investigated sequences of prey-catching in *Dasyuroides byrnei* and in 1976 he also presented an account of maintenance activities in the same species, as did Moss (unpubl.) in a study of *Dasyurus viverrinus*. The ecology of *S. harrisii* was described by Green (1967) and its home range and movements by Guiler (1970a). The smaller representatives of the family have received some attention in that investigations of certain aspects of the behaviour and ecology of *Antechinus stuartii*, *A. minimus* and *A. swainsonii* have been conducted by Marlow

(1961), Braithwaite (1974, 1979), Hocking (unpubl.) and Haynes (in press). Hall (1980) studied the diets of two sympatric species of *Antechinus*.

Finally, the family Peramelidae (bandicoots), forming the subject of the present investigation, has received a small amount of attention with respect to their behaviour and ecology. Lyne (1964a) and Stodart (1966a) studied the breeding of *Perameles nasuta* in captivity. Heinsohn (1966) and Braithwaite and Gullan (1978) investigated the ecology of *P. gunnii* and *Isoodon obesulus*. Reproduction was also studied in *I. macrourus* (Mackerras and Smith 1960; Lyne 1974) and observations on the behaviour of the same species were undertaken by Day, Kirkby and Stenhouse (1974) using an open field arena. Activity-patterns and social behaviour were analysed in *I. obesulus* (Watts 1974, O'Callaghan, unpubl.) as were ranging movements in *I. macrourus* (Gordon 1974). Discrimination-reversal learning in *I. obesulus* was investigated by Buchmann and Grecian (1974) and studies of other behavioural and ecological aspects undertaken included burrowing in *I. obesulus* (Kirsch 1968), feeding and foraging in *I. macrourus* (Anon. 1970), the status of *P. gunnii* in Victoria (Seebeck 1979) and grooming in *I. macrourus* (Clarke and Clarke 1969). Lyne (1951, 1952) described the external characters (particularly of pouch young) of *P. gunnii* and four other species of bandicoots and Stoddart and Braithwaite (1979) made a study of the utilization of regenerating heathland habitats by *I. obesulus*.

In view of the relative lack of detailed information on members of the family Peramelidae the present investigation was undertaken to examine two distinctive but comparable species of the family. Heinsohn (1966) described the same two species, *Isoodon obesulus* and *Perameles gunnii* as being sympatric. Consequently this study is an attempt to provide quantitative data on four specific aspects of their behaviour and ecology, in order to acquire a general appreciation of the relation-

ship of the two species to their environment and to each other. The aspects investigated were maintenance activities (Chapter 3), feeding behaviour and diet (Chapter 4), home ranges and habitat utilization (Chapter 5) and intra- and inter-specific interactions (Chapter 6).

It was hoped and is the avowed aim of this study, that a comparison of these aspects may assist in explaining why these two species are able to co-exist in the same habitat while presumably utilizing somewhat similar resources.

1.2 GENERAL BIOLOGY OF THE FAMILY PERAMELIDAE

The family Peramelidae consists of 8 genera, comprising 20 species. Four genera occur over continental Australia and two of these are also found in Tasmania. The remaining genera are situated in New Guinea and surrounding islands (Troughton 1965). The generally accepted or colloquial name for members of the family, bandicoots, is a corruption of a word in the Telugu language of India, meaning "pig-rat", a term originally applied to a large species of rodent, *Bandicota indica* (*B. bengalensis*), occurring in India and Sri Lanka (Walker 1964).

Members of the family are distinguished by having many incisor teeth (polyprotodont dentition) as do the carnivorous marsupials of the family Dasyuridae, and two combined (syndactylous) toes, a condition also present in the herbivorous groups of the family Macropodidae (Rayment 1954). The second and third digits of the pes are partly fused, leaving only the terminal joints and claws free. The fourth digit is elongated and this syndactylous condition is believed to have evolved as a specialised structure, functioning as a hair-comb, useful because the pelage of the animals usually harbours a number of small ectoparasites including fleas, fur mites and ticks. Heinsohn (1966) reported that both *P. gunnii* and *I. obesulus* carry large numbers of these, and noted that the fur is groomed by chewing and licking, as well as by the combing action of the hindfeet. Material adhering to the syndactylous toes is

subsequently removed by the incisors.

The forefeet of all genera of bandicoots, except *Chaeropus*, have five digits, the second, third and fourth being quite long and possessing sharp and strong nails for digging after invertebrate larvae - the principal food-source of bandicoots, in the soil. The first and fifth digits are vestigial (Walker 1964). Digging-actions are very rapid, as the forepaws scratch into the earth dislodging potential food items which are then quickly snapped up by the probing elongated and pointed snout. When procuring larger food items, digging is discontinued while the food is consumed. Excavations are usually conical in shape (Wood-Jones 1924).

The incisors are small, those of the upper jaws are flattened and unequal in size and those of the lower mandibles are procumbent. The crown of the last lower incisor has two lobes, a condition not found in related families. The canines are slender and pointed. The premolars are narrow and pointed and the molars are triangular in outline, with four external cusps. The dental formula is $i \frac{5}{3}, c \frac{1}{1}, pm \frac{3}{3}, m \frac{4}{4}$ (Walker 1964). Rayment (1954) considered bandicoots to be economically important because of their appetite for destructive insect larvae.

With respect to their general biology *P. gunnii* and *I. obesulus* appear to be very similar. In both species the pouch opens backwards presumably serving to prevent material from being thrown into the pouch during excavating. Both shelter in nests made of grass, leaves and sticks on the surface of the ground. Occasionally a small hollow is scratched out and the nests are then very difficult to detect due to the material of which they are composed blending in with the surroundings. The entrance of the nest is usually concealed upon emergence or entry (Ride 1970). Individuals of both species drink water in captivity although moisture obtained from their diets and from dew appears to be sufficient for their needs in the wild (Stanbury 1970).

Heinsohn (1966) reported that both species are solitary and their social interactions are generally restricted to reproductive activities and mother-offspring relationships. Breeding may occur throughout the year, with a peak usually just after the early winter rains when nearly all females of both species possess pouch young. Gestation is similar in these species, approximately thirteen days in length and the pouch life of the young is usually concluded after sixty days. Both species possess eight mammae arranged in a circular pattern and usually an average of three young are born at one time.

The genus *Isoodon* consists of three species of which *I. obesulus*, commonly known as the quenda, the southern short-nosed or brown bandicoot, is a sturdily built and compact animal. The pelage is short and harsh due to the presence of spiny, flattened guard-hairs. Beneath these guard-hairs is a coat of softer, greyish, shorter fur (Wood-Jones 1924). The fur detaches easily when the animal is handled. The ventral surface and distal parts of the limbs of the animal are greyish-white, whereas the dorsal and lateral surfaces are brown with a yellowish tinge associated with the ends of the guard-hairs. Ears are short and rounded. The rhinarium is naked, brown and tessellated. Eyes are black and the tail is long in comparison with that of *P. gunnii* (Hyett and Shaw 1980).

I. obesulus is known to emit a sneezing and spitting noise when disturbed and Heinsohn (1966) reported that cover is sought immediately upon disturbance. Here the animal will remain motionless for some time or until the disturbance has passed. Open forest, woodland, pasture and urbanized areas are the commonly recognized habitats of *I. obesulus* and they are quite common in these areas throughout Tasmania, as well as in the south-east and south-west of Australia. *I. obesulus* is terrestrial and nocturnal, although occasionally it has been seen to be active during daylight hours (Heinsohn 1966). Runway systems are made through dense undergrowth all over its home range and when walking,

locomotion involves the use of all four feet, the fore- and hind-limbs moving separately. When moving fast, a galloping action is employed (Walker 1964). Linear measurements for the species have been listed by Le Souef, Burrell and Troughton (1926): head and body = 275-300 mm, tail = 100-133 mm, pes = 53.59 mm, ear = 15-21 mm, muzzle to eye = 41 mm.

Two members of this species can seldom be maintained together in captivity, due to the intolerance and pugnacity shown towards conspecifics. Fights are frequent and the long claws of the animals appear to inflict most injuries (Walker 1964). Wood-Jones (1924) described the peculiar method of fighting common in this species. The aggressor tirelessly follows its victim until it wears it down and the assault is made by a jump or an endeavour to strike with claws of the hind feet. Each stroke that results in contact removes hair from the rump of the victim and scratches the thin skin. This continues until the antagonist is exhausted, then the stronger individual attacks with a rapid scrabbling motion of its forefeet, causing further serious damage by the strokes of the strong claws of the manus. This rapid scrabbling movement of the forefeet is also employed in dealing with live prey, such as earthworms or unusual objects apparently regarded as suspicious, such as dead mice. After this, the object is either eaten or rejected. Wood-Jones (1924) reported that when *I. obesulus* is given dead mice, only the head of the carcass is eaten.

The genus *Perameles* consists of five species, of which *P. gunnii*, commonly known as the barred or striped bandicoot, is a timid animal of slender form. The fur is yellowish-brown on the dorsal and lateral surfaces, and white to yellowish-white on the ventral surface and distal parts of the limbs. Behind the shoulders there is a distinct lighter band passing downward and backward fusing with the lighter colour of the ventral surface (Le Souef, Burrell and Troughton 1926). Four lighter

bands associated with the darker rump region give *P. gunnii* its descriptive colloquial name. The ears are long and pointed and the rhinarium is pink. The tail is short and predominantly white in colour but brownish at the base. No vocalizations have been described for *P. gunnii* and the habitats of the species include open forest, pasture and urbanized areas. This species is usually strictly nocturnal (Hyett and Shaw 1980). *P. gunnii* is distributed over most of Tasmania and one colony exists on the Australian continent, in southwest Victoria.

Locomotion employs the same methods as those described in *I. obesulus* but *P. gunnii* has the ability to jump into the air while moving and initiate rapid movement immediately in another direction upon landing (Walker 1964). Heinsohn (1966) believed this to be associated with escape from predators as *P. gunnii* is vulnerable to attack when it ventures into open fields under the cover of darkness to feed.

Le Souef, Burrell and Troughton (1926) also provided selected linear measurements for this species: head and body = 380-400 mm, tail = 80-90 mm, pes = 70-72 mm, ear = 31-34 mm, muzzle to eye = 60-65 mm. Males and females have similar length measurements, unlike *I. obesulus*, the males of which are heavier and correspondingly have larger length measurements.

Heinsohn (1966) also investigated the sizes of home ranges in both species and reported that female *P. gunnii* possessed ranges averaging eight acres in size whereas those of males averaged sixty-three acres, but there was considerable, if not extensive, overlap in the areas occupied. There was little evidence of overlapping home ranges in *I. obesulus*.

CHAPTER 2

CAPTURE AND MAINTENANCE OF BANDICOOTS

2.1 METHODS OF CAPTURING SUBJECTS

Both *Isoodon obesulus* and *Perameles gunnii* are distributed over most of Tasmania (Figure 2.1); consequently, for convenience, trapping was carried out at three localities situated in the vicinity of Hobart (Figure 2.2). These areas were recommended as suitable areas for a trapping programme by investigators who had previously pursued live-trapping operations there.

Removal-trapping for investigations of captive subjects was performed in the Blackmans Bay area (E. $147^{\circ}20'$, S. $43^{\circ}01'$), whereas non-removal trapping for studies of home range and habitat-utilization was undertaken at Porter's Hill, Mount Nelson (E. $147^{\circ}23'$, S. $42^{\circ}54'$), Lower Longley (E. $147^{\circ}10'$, S. $42^{\circ}58'$) and also in the Blackmans Bay area. A general description and the features of the vegetation of the trapping localities is presented in Chapter 5.

Information relating to weather conditions were obtained from the Commonwealth Bureau of Meteorology (Hobart Division). Mean monthly temperatures, based on maximum and minimum values, and rainfall recorded in the Hobart district during the current year (1982) and previous years are summarised in Tables 2.1a and b. Only moderate seasonal variations in temperature and rainfall were noted to occur. The highest temperatures were obtained in the summer (December to February) and the highest rainfall in spring and at the beginning of summer (October to December). A comparison of mean monthly temperatures and rainfall of the current year with those recorded in the Hobart district during the past 98 years indicates that temperatures have been generally higher and rainfall lower for most months during the period of the study. In fact, very large areas of the state have been declared drought-stricken, with recorded rainfall well below average and temperatures often soaring above the norm.

All trapping localities experienced similar weather conditions to

FIG. 2.1 DISTRIBUTION OF Perameles gunnii AND Isoodon obesulus
(Marlow 1965 ; Seebeck 1979).

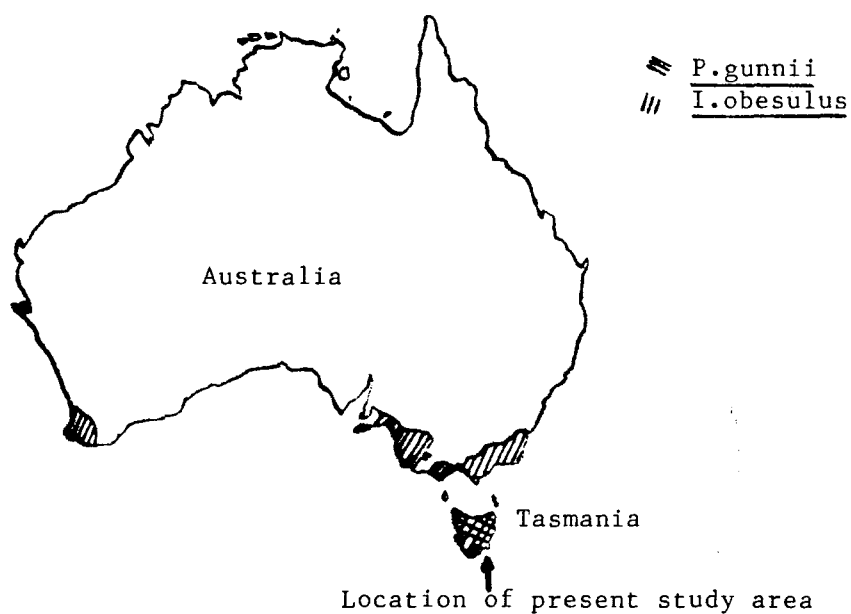


FIG. 2.2 LOCATION OF TRAPPING AREAS IN AND NEAR THE
HOBART DISTRICT.

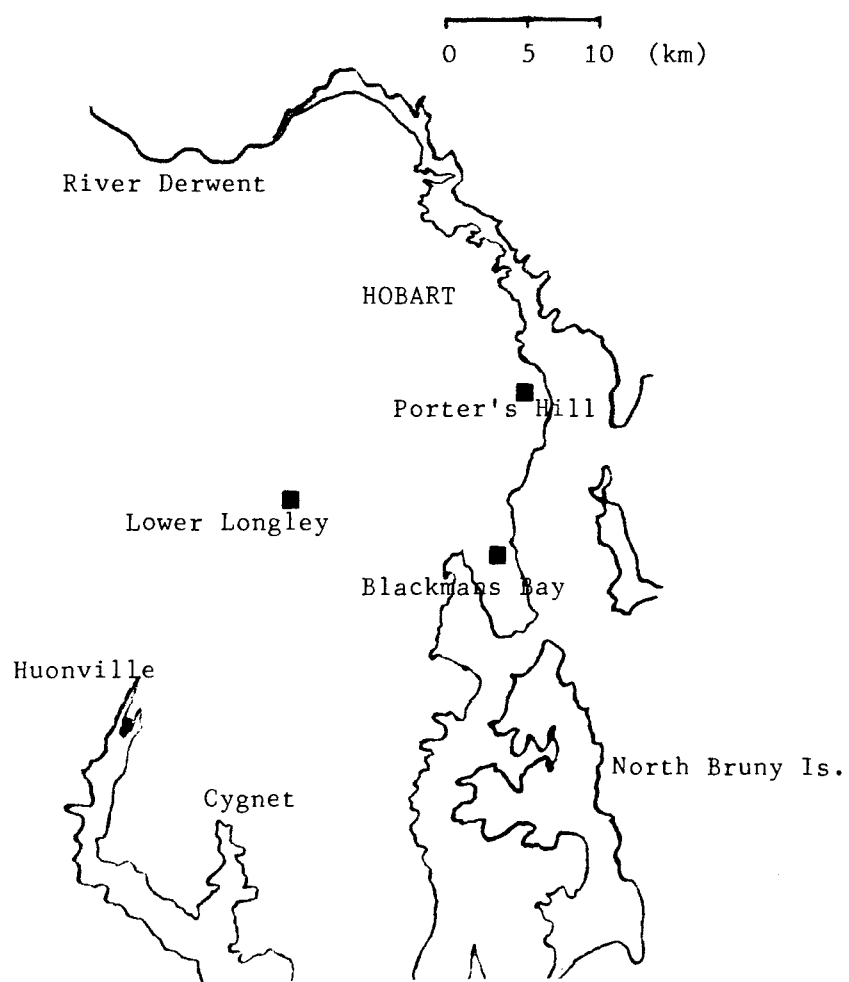


TABLE 2.1a Mean monthly temperatures ($^{\circ}\text{C}$) and rainfall (mm) in the Hobart district based on a record of 98 years (1882-1981).

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year
Temperature	16.5	16.6	15.2	12.9	10.5	8.5	7.9	9.0	10.6	12.2	13.7	15.4	12.4
Rainfall	48	41	47	54	48	58	53	51	52	63	56	56	627

TABLE 2.1b Mean monthly temperatures ($^{\circ}\text{C}$) and rainfall (mm) in the Hobart district for 1982.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct
Temperature	18.0	18.2	15.7	13.5	11.4	8.0	7.0	11.3	10.1	13.0
Rainfall	36	25	77	12	57	35	35	11	64	9

those recorded above, since the most distant area trapped, Lower Longley, is approximately only 20 miles from Hobart. Blackmans Bay is approximately 10 miles from Hobart and Porter's Hill is actually situated within the Hobart district.

The traps used in the present investigation were of two different designs. Each trap was of the dimensions 50 x 20 x 20 cm and one of the designs operated on the principle of a hook from which bait was suspended and animals entering the trap were confined by the closure of the door behind them when the baited hook was manipulated (Plates 2.1a and b). The releasing-mechanism of the other design was activated by the pressure of the weight of the animal on a treadle set in the floor of the trap. No springs were used to increase the speed of closure of the door in traps of either design and a locking tie falls with the door so that it cannot be pushed by the animal inside. All traps were made of heavy gauge wire mesh. A summary of the comparative efficiency of the two designs of traps is presented in Table 2.2.a and it is evident that the treadle design was less efficient at capturing bandicoots by almost 50%. Other factors may also have influenced trapping-success and these include the different types of bait used, placement of traps, the weather and other species present in the trapping areas. These factors and their effects on trapping-success are discussed in the following text.

Three different mixtures of baits were used throughout the period of trapping. These consisted of a quarter of an apple smeared with peanut butter, a combination of oats and peanut butter in half a slice of brown bread and a combination of bacon, oats and peanut butter in half a slice of brown bread. Bait was either attached to the hooks of the traps or placed on the floor of the treadle-activated traps. Table 2.2.b summarises the comparative efficiency of each bait used in the study. There was no significant difference in the capture-rates obtained with different baits. This is probably due to the fact that all types of bait contained peanut butter, an ingredient that has a

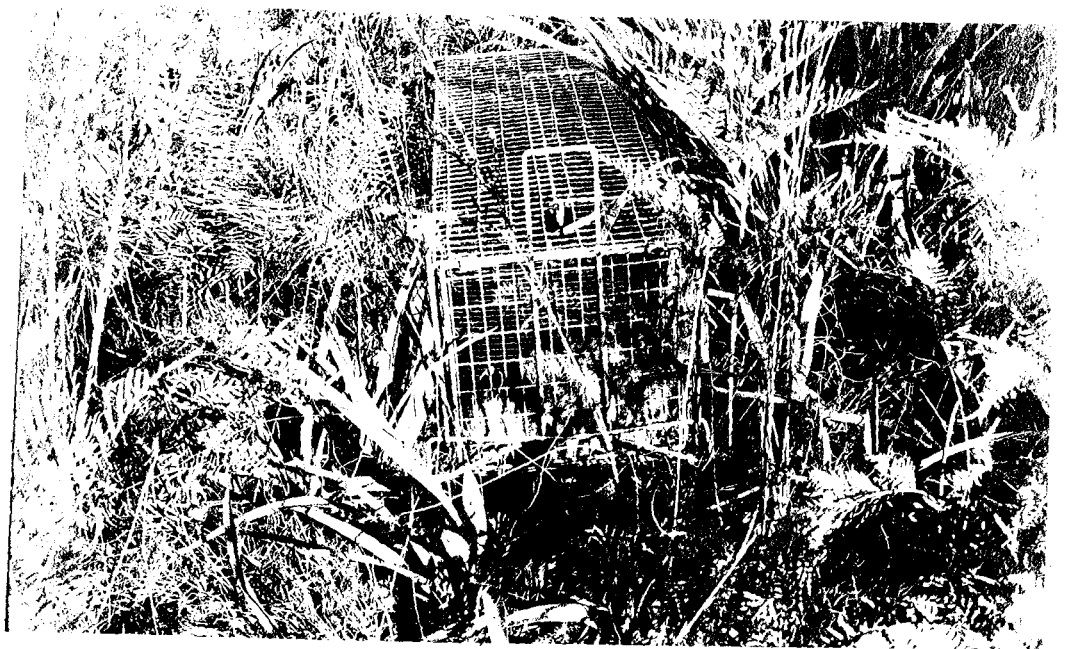
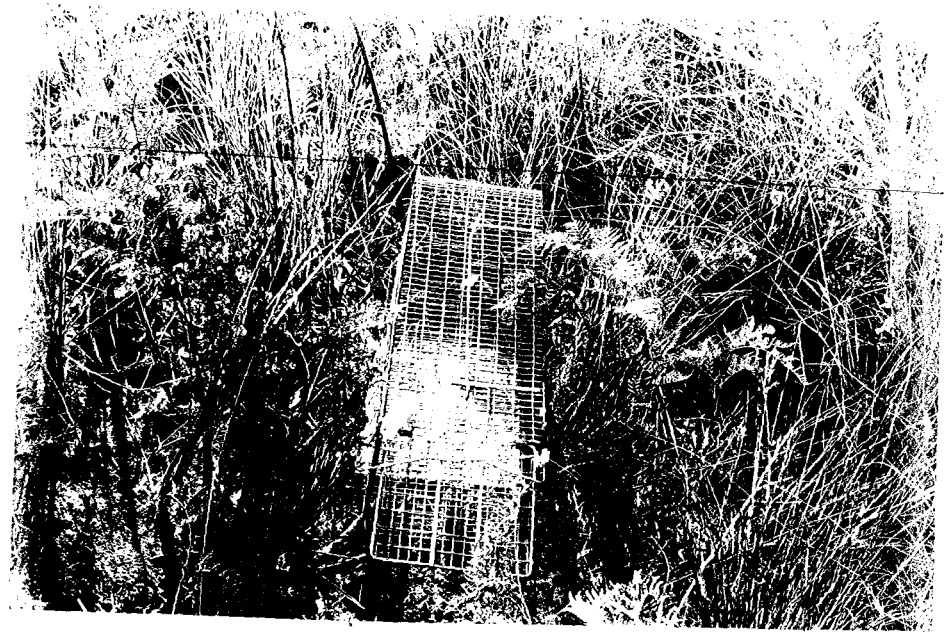


TABLE 2.2a Comparison of traps used in the present investigation (expected captures of bandicoots in parenthesis).

Type	Number	Bandicoots captured (observed)	d.f.	P	Other animals captured	Disturbed traps		
Hook	1372	82 (72)	1.39		362	287		
Treadle	418	12 (22)	4.55		73	56		
TOTAL	2	1790	94 (94)	5.94	1	0.025	435	343

TABLE 2.2b Comparison of baits used in the present investigation (expected captures of bandicoots in parenthesis).

Type	Number	Bandicoots captured (observed)		d.f.	P	Other animals captured	Disturbed traps	
Bread, oats & peanut butter	210	11 (11)	0			36	28	
Apple & peanut butter	1111	62 (58)	0.276			287	221	
Bread, oats, bacon & peanut butter	469	21 (25)	0.640			112	94	
TOTAL	3	1790	94	0.916	2	n.s.	435	343

strong and distinctive odour and is of considerable attraction to bandicoots. However, the bait was not merely used to attract bandicoots but was also intended to supply nutritional requirements, since trapped individuals are expected to spend prolonged periods of time in the traps. Successful recaptures of individuals indicated that none of the animals lost condition as a result of the restraint of normal activities and food deprivation.

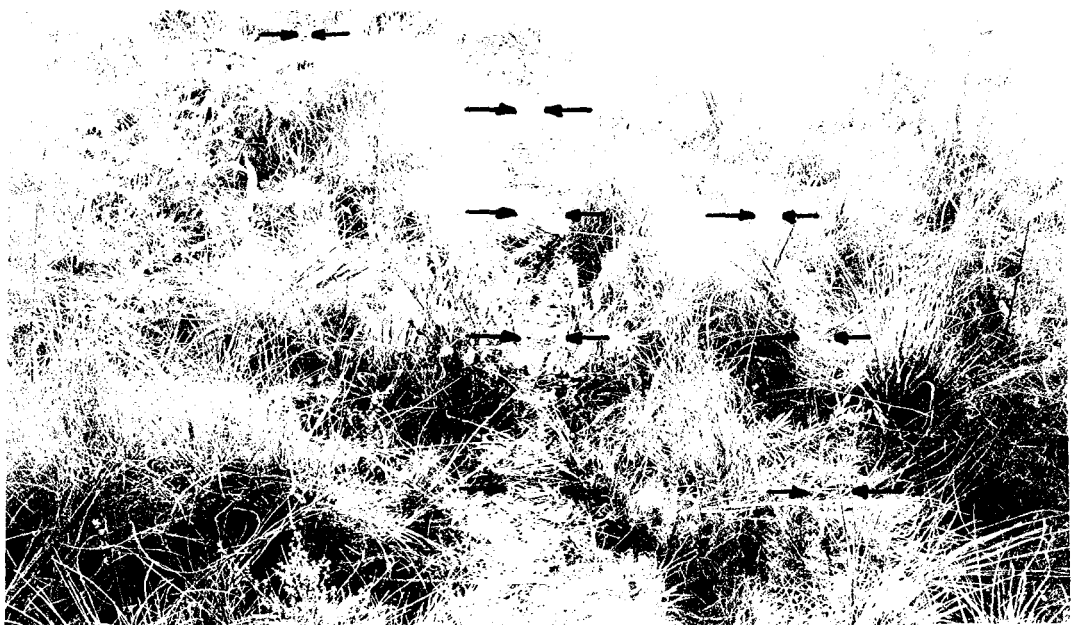
Items used as bait were firmly attached to the traps' hooks because bandicoots (and most of the other animals captured) appeared to have considerable manipulative skills and could easily remove baits without releasing the trap-doors. Evidence of this dexterity can be seen in Tables 2.2.a and b in terms of the high number of traps "disturbed", a term referring to traps from which the bait was removed but no capture was observed or bait was still attached to the hook but the releasing mechanism was activated. This evidence was further supported by the fact that bait was renewed daily because of the possibility that drying and crumbling bait may prejudice capture. In some instances, traps were found overturned and moved for distances of up to five metres from their original position. These were included in the "disturbed trap" category and are believed to have been caused by brush-tailed possums, *Trichosurus vulpecula*, since scat of this species was usually found in the disturbed trap in such instances. It is also suspected that the smaller mammals, *Rattus rattus*, *R. lutreolus* and *Antechinus swainsonii*, of which a total of only 20 specimens were captured, were largely responsible for the inevidence of high numbers of disturbed traps; in many of the latter the bait appeared to have been nibbled. In addition, numerous traps were covered with ice during the colder months of the year rendering the mechanism for the trap-door to be inoperative and permitting easy removal of the bait. In an attempt to reduce this effect, oil and grease were applied to the releasing mechanism of the trap-door and this procedure resulted in moderate success (in reducing the number of disturbed traps).

In addition to *P. gunnii* and *I. obesulus*, several other species were recorded and captured during the trapping programme. Those captured included the potoroo *Potorous tridactylus*, which accounted for 78 per cent of all other species captured, the brush-tailed possum *T. vulpecula*, the native cat *Dasyurus quoll*, *R. rattus*, *R. lutreolus*, *A. swainsonii*, feral domestic cats *Felis domestica*, the blackbird *Turdus merula* and the blue-tongued lizard *Teliqua nigrolutea*. Rabbits, *Orycholagus cuniculus*, were often sighted but none of this specie was captured. Trapping areas were also frequented by dogs and domestic (non-feral) cats and the presence of a copperhead snake, *Denisonia superba* was also noted. It is believed that *T. nigrolutea* was attracted into traps by insects around the bait. All of the animals captured were released. Larger domestic animals were absent from the trapping areas.

During the whole of the trapping programme, a capture-success rate of 30 per cent (for all animals) was recorded for all trapping nights. However, only 45 individual bandicoots were captured on a total of 94 occasions, yielding a capture-success rate of 5.25 per cent.

Traps were arranged in an irregular pattern, usually spaced 20-40 m apart. Trap-sites were selected on the basis of their proximity to signs of the bandicoots' presence such as excavations, scats and pathways (Plates 2.2.a, b, c and d). The placement of traps of the two types of design was random, as was the use of bait. Traps were usually placed under shrubs to facilitate locating them and for the protection of the captives from inclement weather and the early morning sun. All plants and loose material were removed from near the entrance of the trap to permit easy and complete closure of the trap-door. After the traps were set they were tested to ensure that the mechanism functioned correctly; they were then reset again. Plastic bags were placed beneath all traps for the collection of scats for subsequent analysis in determining the diet of the bandicoots.

Traps were examined for the presence of captive animals and reset



usually between 0700 and 1200 h each day. A total of 1790 trap-nights were used and each trap-station was numbered and recorded on maps. The locations of traps were easily recognised by the presence of two white paper cards, with the trap number printed on them, attached in conspicuous positions to nearby trees. Two markers were used at each site to minimize accidental loss and these were positioned at high levels on the trees in an attempt to reduce the possibility of alarming animals. Every individual trap was assigned its own metal tag with the trap number printed on it.

Since the number of traps available for the study was inadequate for simultaneous use over an entire trapping area, only a section of the latter was trapped in a given period. This sector was used for seven consecutive nights and the traps were then moved to an adjacent area; and this process continued until the whole trapping area was covered. This technique was selected for several reasons. Firstly, if bandicoots were present in the area trapped, it was considered unlikely that they would fail to come into contact with at least one trap. Secondly, the availability of several alternative traps within a restricted area may be expected to enhance the probability of capture (i.e. along trails and around excavation areas). Thirdly and finally, as no part of the locality was sampled continuously, it is possible that the method may reduce the trap-directed responses of animals, whether they are positive or negative.

Since the traps were made of heavy gauge wire mesh, the possibility existed that animals would injure themselves while trying to escape. However, the injuries thus sustained were usually only of the minor types, consisting of loss of fur (which was quickly regenerated) and abrasions to the snout, which also healed quickly. When captive bandicoots were approached they often became highly agitated and collided with the sides of the trap; consequently, it was of considerable importance to place the animals into hessian bags as rapidly as possible, in order to keep injuries to a minimum. When inside the bag the excitement of the subjects subsided

almost immediately and handling was then much easier. It was also noted that captive bandicoots often excavated a large hole immediately outside the door of the trap in their attempts to escape. The forepaws of the animal were able to reach outside the trap through a small opening between the end of the door and the bottom of the cage.

The hessian bag proved very useful in restraining animals while they were examined and marked. Marking was accomplished with the aid of a veterinary tattoo-kit. Tattoos, in the pattern of various numerals, were placed on the ears of the animals and provided easy recognition of individuals, as well as having no appreciable effect on mortalities, prerequisites that are considered essential in recapture studies. The routine linear measurements made on captive individuals were similar to the standards employed by Wood-Jones (1924) and Lyne and Verhagen (1957), and Vernier calipers were used for obtaining estimates. All measurements were recorded to the nearest mm and the means and standard errors for initial measurements of all adult bandicoots captured are summarised in Table 2.3. Individuals were also weighed to the nearest 5 grams in the hessian bags wherein they were placed after capture, using a spring balance. In addition, the pouch was examined for young and the size of the nipples noted. General notes were made of the general condition of the animal with particular reference to ectoparasites, injuries and state of the pelage. After the appropriate information on individuals was obtained, the animals were released at the site of capture, except those that were retained for investigations in captivity, and the directions in which the animals moved after their release were also recorded on maps of the study area.

Two specimens of *I. obesulus* were found dead in the traps and so in an attempt to prevent further deaths from occurring, particularly in the colder months of the year, dry straw was placed in the traps. Distinguishing features of the carcasses and possible causes of the death of subjects are presented in Appendix A.

TABLE 2.3 Comparison of the means and standard errors for initial measurements of all adult bandicoots captured.

	Males		P	Females		P
	<i>I. obesulus</i>	<i>P. gunnii</i>		<i>I. obesulus</i>	<i>P. gunnii</i>	
Weight (grams)	1079.4 ± 65.7	846.3 ± 44.4	Invalid	716.8 ± 46.4	670.0 ± 22.3	n.s.
Head (mm)	79.5 ± 1.7	84.9 ± 1.9	n.s.	73.7 ± 1.3	84.0 ± 1.4	0.01
Pes (mm)	61.0 ± 0.7	71.4 ± 0.9	0.001	54.9 ± 0.5	66.4 ± 1.0	0.001
Tail (mm)	110.9 ± 1.9	81.1 ± 3.2	0.001	96.6 ± 2.8	72.4 ± 1.4	Invalid
Scrotum/ Pouch (mm)	20.2 ± 0.8	22.0 ± 1.2	n.s.	18.3 ± 1.1	21.0 ± 0.7	n.s.
Ear (mm)	21.9 ± 0.6	39.3 ± 0.7	0.001	20.4 ± 0.5	35.2 ± 0.6	0.001
General Condition	14 possessed ectoparasites 4 were young individuals 6 had tail damage 1 was missing an eye	7 possessed ectoparasites		10 possessed ectoparasites No pouch young noted, although enlarged nipples present in 2	4 possessed ectoparasites 2 pouch young noted in one subject	
N	18	8		14	5	

The data shown in Table 2.3 indicates that there were numerous differences in the linear measurements between *P. gunnii* and *I. obesulus*, and students t-tests were used to detect these differences in the means. Males of *I. obesulus* had much longer tails than those of *P. gunnii* but had significantly smaller pes and ear lengths. It should be noted that only individuals with intact tails were used in the analysis of data. It is believed that the high proportion of male *I. obesulus* possessing some degree of tail damage may be due to intraspecific aggressive encounters because females appeared to be relatively unaffected by such minor injuries. *I. obesulus* were significantly heavier than *P. gunnii* but the test was not valid on account of the large variation of these measurements of individuals.

Female *P. gunnii* possessed significantly larger ear, head and pes lengths than female *I. obesulus*. These results are comparable to those noted by Heinsohn (1966) in his study of both species. Male *I. obesulus* were significantly heavier than female conspecifics and their corresponding linear measurements were also significantly larger. In *P. gunnii* there was no significant difference between males and females except for weight, the males being the heavier.

Seventy-eight per cent of all of the bandicoots captured possessed ectoparasites and only one subject, a female *P. gunnii*, had pouch-young but, unfortunately, both of its infants were dead. The young were estimated to be ca. two weeks old and weighed 3.5 g. The eyes were closed and no facial vibrissae were present. The linear measurements were head = 15.5 mm, pes = 5 mm, tail = 7 mm and ear = 2.5 mm. The absence of pouch young noted in both species may be a result of the very dry conditions experienced during the current year since breeding is known to occur predominantly after the beginning of the winter rains.

2.2 MAINTENANCE OF BANDICOOTS IN CAPTIVITY

A total of twenty bandicoots, consisting of ten individuals of each species (five males and five females) were captured for investigations in captivity, as this was considered a suitable number of subjects for statistical analysis, as well as being the maximum number that could be housed and maintained without difficulties.

All subjects were captured in the Blackmans Bay area and taken to the Department of Zoology, University of Tasmania, where they were measured, weighed and tattooed using the methods already described in Section 2.1. Individuals were accommodated in heavy-gauge wire mesh cages measuring 60 x 45 x 45 cm. Subjects were provided with water in glass dishes, *ad libitum*, and food was placed in plastic dishes within the holding cages. The food was a mixture of "Pal meaty bites", blood and bone pellets, mixed bird seed and an apple quarter or half a slice of brown bread. Subjects were fed this mixture, approximately 100 g in weight, daily, for four days and on the fifth day they only received water because some food usually remained uneaten. Meal worms were supplied with the regular food items once a week and occasionally earthworms were also added, when available. "Pentavite" infant drops were placed on the bread every month and after the success of the study dealing with the prey-killing behaviour, the diet was also supplemented by live lizards, snails and laboratory mice when these were obtainable.

Wood-shavings and straw were supplied as nesting material and wooden boxes measuring 25 x 20 x 20 cm were also provided; the subjects sheltered and built their nests in these. The holding cages were situated in an open, south-facing verandah; consequently, all animals were subject to normal Hobart daylight lengths and temperature regimes. All animals usually settled down after two days within their holding cages, constructing nests, eating regularly and, in general, apparently returning to the normal activity period of emerging after darkness. Subjects were held in these holding

cages until the end of the study and all animals were housed individually, in view of their pugnacity, described by Wood-Jones (1924), Heinsohn (1966), and Stodart (1966).

Holding cages were cleaned once in every two weeks and the wood-shavings and straw were replaced. Food and water were changed daily, usually in the late afternoon, before the emergence of the animals. Two subjects escaped during the course of the study.

Tables 2.4a and b summarise the initial and final measurements of animals used in behavioural investigations. Initially, all measurements were obtained weekly to check the condition of animals and to ascertain whether or not the animals were adjusting to captivity. As most subjects increased in weight throughout the study, measurements were restricted to only occurring before interaction experiments. In this way handling of subjects was minimal and the possibility of taming was also substantially reduced. Experimental sessions were preceded by a minimum of fourteen days acclimation-period to ensure that animals had adjusted to captivity without any undesirable effects such as behavioural disturbance and loss of weight. Mean weights and linear measurements increased in both species over the study period.

TABLE 2.4a Initial and final measurements of *Isoodon obesulus* used for behavioural experiments.

SEX	NUMBER	INITIAL MEASUREMENTS							FINAL MEASUREMENTS						
		WEIGHT (g)	PES (mm)	TAIL (mm)	EAR (mm)	HEAD (mm)	SCROTUM (mm)	Date of capture and condition of animal (e.g. ectoparasites, distinguishing features)	WEIGHT (g)	PES (mm)	TAIL (mm)	EAR (mm)	HEAD (mm)	SCROTUM (mm)	Date of final measurement and condition of animal (e.g. ectoparasites, distinguishing features)
MALES	1	775	59	110	20	70	20	22/2/82. No ectoparasites.	1020	65	68	22	78	25	Part of tail missing. No ectoparasites. 15/9/82.
	5	365	52	86	19	71	13	12/3/82. Young individual. Mites and fleas present.							Escaped from cage 13/3/82.
	0	940	58	-	16	82	23	14/3/82. No ectoparasites. No tail, but well healed at base. Only ca. one half of right ear present.	1010	61	-	18	82	25	Killed by <i>I. obesulus</i> , male, No. 1 on 14/9/82. Broken mandible, dorso-ventrally flattened and large patches of fur removed from rump.
	7	500	54	107	20	65	12	18/3/82. No ectoparasites.	860	57	108	22	76	17	No ectoparasites. 15/9/82.
	9	820	60	112	23	74	25	18/3/82. Mites, fleas and ticks present.	1120	62	113	24	81	28	No ectoparasites. 15/9/82.
	11	1120	62	61	23	80	16	19/3/82. Half tail missing. Mites and fleas present.	1210	63	65	24	82	18	No ectoparasites. Half tail missing. 15/9/82.
	12	360	52	90	20	63	12	21/3/82. Young individual. Fleas present.	330	52	90	20	63	12	Found dead in cage 23/3/82.*
	13	710	58	101	23	74	17	22/3/82. No ectoparasites.	1140	65	58	24	81	23	No ectoparasites. Half tail missing. 15/9/82.
	20	1175	60	118	20	79	20	2/4/82. Mites, ticks and fleas present.	1200	61	120	24	82	21	Died 12/9/82, after harassment by cat.
		752	57	103	20	73	19	MEAN	1080	62	114	23	80	22	MEAN
		300.7	3.7	11.8	2.3	6.6	4.8	S.D.	134.8	2.8	6.0	2.2	2.4	4.0	S.D.

TABLE 2.4a (continued)

INITIAL MEASUREMENTS								FINAL MEASUREMENTS							
SEX	NUMBER	WEIGHT (g)	PES (mm)	TAIL (mm)	EAR (mm)	HEAD (mm)	POUCH (mm)	Date of capture and condition of animal (e.g. ectoparasites, distinguishing features)	WEIGHT (g)	PES (mm)	TAIL (mm)	EAR (mm)	HEAD (mm)	POUCH (mm)	Date of final measurement and condition of animal (e.g. ectoparasites, distinguishing features)
FEMALES	3	620	53	75	21	75	13	8/3/82. No young. Fleas and mites present.	735	58	78	21	77	14	15/9/82. No ectoparasites. Part of tail missing.
	half circle	675	55	82	19	80	17	13/3/82. No young, but 4 enlarged nipples noted. Fleas, mites and ticks present. The end of the tail became detached when handled.	760	55	60	19	86	19	15/9/82. No ectoparasites. Part of tail missing.
	6	840	55	80	22	74	19	14/3/82. No young. Mites and ticks present.	960	59	95	23	81	19	No ectoparasites.
	8	930	52	113	24	83	24	14/3/82. No young. No ectoparasites.	1020	54	114	24	84	24	15/9/82. No ectoparasites.
	15	710	54	105	20	74	22	25/3/82. No young. No ectoparasites.							Escaped 2/4/82.
	16	675	56	100	19	73	21	25/3/82. No young. Mites and fleas present.	785	57	74	20	80	23	15/9/82. No ectoparasites. Part of tail missing.
	17	675	56	106	20	75	21	31/3/82. No young. Fleas present.	700	58	112	20	76	19	No ectoparasites.
		732	54	96	21	76	20	MEAN	827	57	107	21	81	20	MEAN
		110.8	1.5	14.0	1.8	3.7	3.6	S.D.	131.0	1.9	10.4	1.9	3.9	3.6	S.D.

Note: animals without intact tails were excluded from statistical analysis of tail-lengths.

* Measurements excluded from final measurements of statistical analysis.

TABLE 2.4b Initial and final measurements of *Perameles gunnii* used for behavioural experiments.

SEX	NUMBER	INITIAL MEASUREMENTS							FINAL MEASUREMENTS						
		WEIGHT (g)	PES (mm)	TAIL (mm)	EAR (mm)	HEAD (mm)	SCROTUM (mm)	Date of capture and condition of animal (e.g. ectoparasites, distinguishing features)	WEIGHT (g)	PES (mm)	TAIL (mm)	EAR (mm)	HEAD (mm)	SCROTUM (mm)	Date of final measurement and condition of animal (e.g. ectoparasites, distinguishing features)
MALES	2	665	68	79	41	88	15	5/3/82. No ectoparasites.	770	69	80	41	90	17	Escaped 21/7/82. Last measurement 20/7/82.
	18	1025	73	88	40	82	24	2/4/82. Fleas present.	960	76	87	40	86	26	15/9/82. No ectoparasites. Rash on neck.
	8	825	73	75	40	86	23	3/4/82. Fleas present.	880	75	75	41	88	24	15/9/82. No ectoparasites. Rash on neck.
	1	885	74	82	41	88	24	25/5/82. Fleas and ticks present.	920	76	82	42	89	24	15/9/82. No ectoparasites. Rash on neck.
	7	800	72	70	38	74	24	8/7/82. Ticks and fleas present.	860	72	71	40	76	25	15/9/82. No ectoparasites. Rash on neck.
	3	800	68	86	37	89	23	20/7/82. Fleas present.							Died 21/7/82.
	5	1020	74	97	41	90	24	22/7/82. Fleas present.	910	74	97	41	91	24	Died 22/8/82.
		860	72	82	40	85	22	MEAN	883	74	82	41	87	23	MEAN
		129.0	2.6	8.9	1.6	5.6	3.3	S.D.	65.3	2.7	9.2	0.8	5.5	3.2	S.D.
FEMALES	41	710	68	74	36	86	21	8/3/82. Fleas and mites present.	790	72	74	37	86	21	15/9/82. No ectoparasites. Rash on neck.
	4	665	67	74	37	84	19	12/3/82. No young. Ticks, fleas and mites present.	760	70	74	38	85	19	15/9/82. No ectoparasites. Missing claws on both fore- and hind-feet.
	14	600	69	75	34	80	22	22/3/82. No young. No ectoparasites.	710	71	76	36	82	22	15/9/82. No ectoparasites.
	2	725	64	67	34	88	23	20/7/82. Two young noted in pouch; however, both were dead. Pouch very red and moist. Fleas present.	750	64	67	34	89	23	Found dead in cage 21/8/82.
	30	650	64	72	35	82	20	25/7/82. No young. Fleas and ticks present.	740	68	73	37	84	21	15/9/82. No ectoparasites.
		610	66	72	35	84	21	MEAN	750	69	73	36	85	21	MEAN
		49.9	2.3	3.2	1.3	3.2	1.6	S.D.	29.2	3.2	3.4	1.5	2.6	1.5	S.D.

* For details of animals that died during the present investigation see Appendix A.

CHAPTER 3

MAINTENANCE ACTIVITIES

3.1 ACTIVITY-LEVELS

3.1.1 Introduction

In general, the majority of species of small marsupials are solitary, their social interactions being restricted to mating and mother-offspring relationships. Such forms of social contact comprise only a relatively small proportion of the time when the animals are active, by contrast with maintenance activities, which occupy most of their activity-period. It therefore seems surprising that research in this area of behaviour is scarce and fragmentary, particularly in view of the fact that information about maintenance-activities is an essential prerequisite to understanding the broader aspects of adaptation to the natural environment of a given species.

Studies of maintenance-activities in marsupials are few in comparison to studies on eutherian mammals, and in the majority of cases, observations have been of a qualitative nature. Most investigations have focussed on several members of the family Macropodidae (Stodart 1966; Packer 1969; Russell 1969, 1970b, 1976), and the American opossum, *Didelphimarsupialis* (McManus 1970). The bandicoots (Peramelidae) have received some attention and a few species have been investigated. Stodart (1966) observed the behaviour of *P. nasuta* in captivity and Heinsohn (1966) recorded selected activities of *P. gunnii* and *I. obesulus* both in captivity and in the field. He reported that both species are nocturnal, although *I. obesulus* is occasionally seen to be active during the day. After emergence from the nest, members of both species are very active during most of the night. A high proportion of the nocturnal activity-period is spent foraging and feeding. Other studies on the behaviour of bandicoots have included the observations on exploration of novel objects by *I. macrourus* (Russell and Pearce 1971), aspects of the general behaviour of the

latter species (Day et al. 1974) and the activity-rhythms of *I. macrourus* and *P. nasuta* in captivity (Lyne 1981). Exploratory behaviour has also been described in several other species of marsupials (Glickman and Scroges 1966; Russell and Pearce 1971) and Ewer (1968) conducted naturalistic studies on *Sminthopsis crassicaudata*.

Under natural conditions, the activity-patterns of many animals exhibit definite phase-relationships with the light-dark cycle (Lyne 1981). In view of this, an attempt was made in the present study to monitor the activity-patterns of *I. obesulus* and *P. gunnii* in a semi-natural environment (enclosure). Maintenance-activities were observed and recorded throughout the nocturnal activity-periods and, although this technique places the animal in a somewhat unnatural situation, it has the advantage of permitting the manipulation of variables difficult to control in the field, such as low lighting and the presence of dense vegetation which obstructs the visibility of subjects. Despite the obvious advantages of enclosure-based investigations, it is emphasised that the information obtained from these can only be related to what may occur, rather than what actually happens in the field (Orr 1959), since many potentially important environmental influences are excluded. However, it is still considered that such experimental situations may provide reasonable indications of what is expected to occur in natural conditions and enclosure studies similar in design to those used in the present investigation have been successfully employed by some of the investigators previously mentioned.

3.1.2 MATERIALS AND METHODS

Observations on the maintenance-activities and activity-levels of *Isodon obesulus* and *Perameles gunnii* were conducted in an outdoor enclosure situated on the campus of the University of Tasmania. Experi-

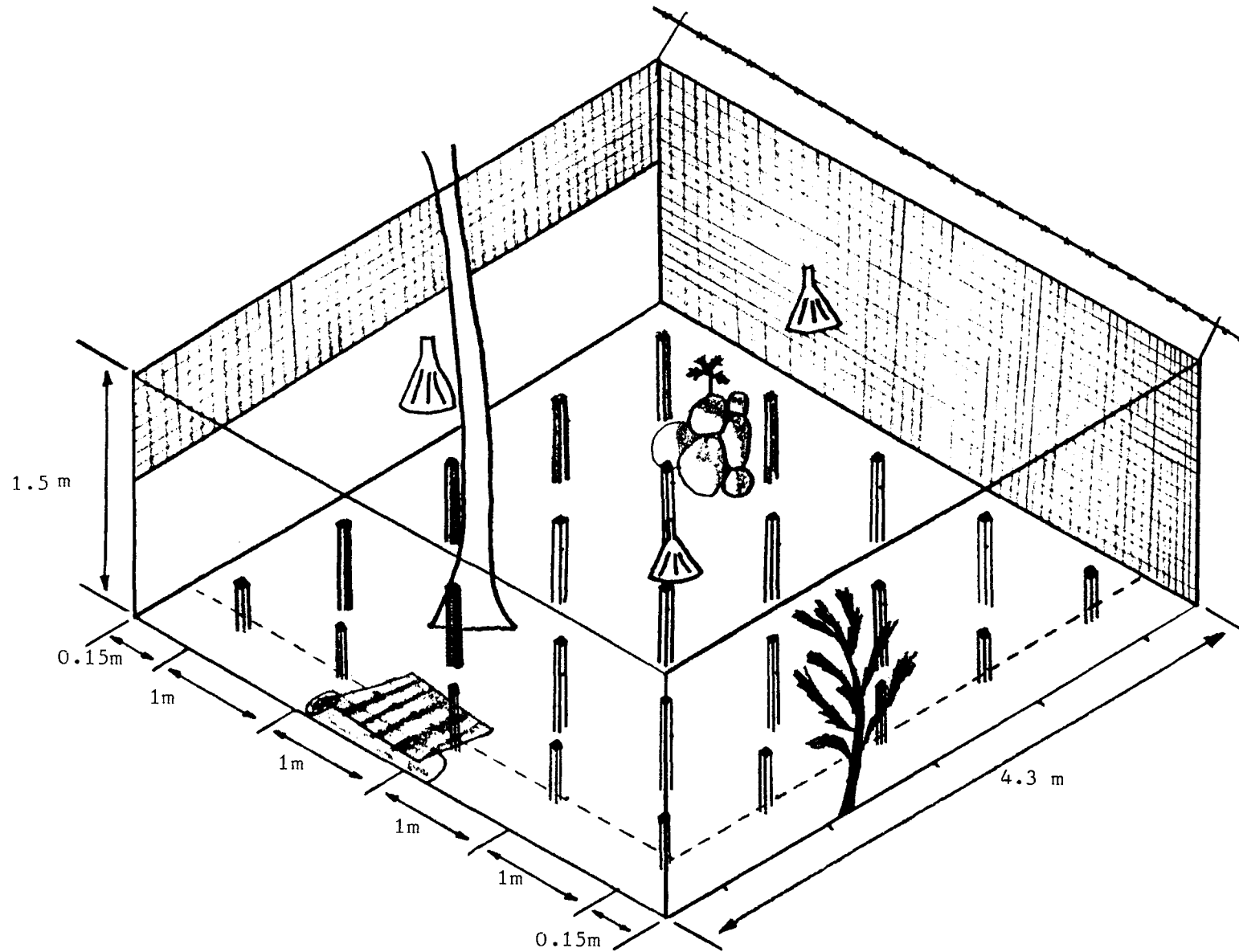
mental subjects captured in the Blackmans Bay area, were maintained in holding cages (Section 2.2) for a period of 14 days before they were used in behavioural observations. The reasons for this precaution and selected, salient features of individual subjects (i.e. weights, linear measurements and distinguishing features) are presented in Section 2.2.

A diagram of the observation-compound is shown in Figure 3.1.1. The dimensions of the enclosure were 4.3 x 4.3 x 1.5 m and the area was completely enclosed by 2 cm wire-mesh, which was securely attached to the structural framework. The latter consisted of steel posts set in the ground and metal tubing transecting the roof. The walls of the compound were anchored at the base in a trench, 15 cm in depth, completely encircling the periphery of the enclosure. These wire-mesh walls were embedded in concrete situated within the trench. Nevertheless, the seemingly secure arrangement did not prevent the escape of one subject (a male *I. obesulus*) which succeeded in excavating underneath the trench but, fortunately, it gained access only to an adjacent enclosure and was subsequently recaptured.

A hessian partition was suspended along the lower half of the wall of the adjoining compound to prevent visual contact between the bandicoots used in the present study and animals (*Bettongia gaimardii* and *Trichosurus vulpecula*) held in the nearest enclosure. Although this did not prevent vocal and olfactory cues from passing between the two compounds, aberrant behaviours resulting from these were not noticeable.

The enclosure was situated on a gradual, but well-drained slope, and access to it was gained by a gate set in the wall. The floor of the compound was subdivided into quadrats by wooden stakes embedded in the ground at the intersections of a system of grids. The stakes projected above the surface of the ground to a height of 30 cm and

FIG. 3.1.1 Schematic diagram of the observation-compound.
(The interrupted line represents the limits of the peripheral region).



Scotchlite reflective tape was attached to their distal ends. They were clearly visible at night and provided reference points for monitoring the spatial distribution of various activities, particularly ambulation. The grid-system was used to divide the floor of the compound into two zones: central and peripheral. The central zone consisted of 16 one m squares, which was surrounded by 16 rectangles, each with the dimensions 0.15 x 1 m designated as the peripheral zone. Consequently, the latter zone accounted for only 13.5% of the total area of the floor of the compound.

Vegetation present in the enclosure was generally scanty, consisting of sparse grass-cover, a small shrub, *Bayeria viscosa*, and one tree, *Acacia mollissima*, which projected through the roof of the compound. Wood-shavings and straw were distributed around the floor of the enclosure, to provide sufficient nesting material. During the preliminary studies, when various categories of behaviour and the terms used to describe them were selected, two types of shelter were provided. The first consisted of a wooden box (40 x 30 x 30 cm) and the second was simply a piece of corrugated iron draped over a wooden log. The latter was utilized by the majority of the subjects during the preliminary observation trials, therefore the boxes were subsequently removed. Water was always supplied *ad libitum* in plastic containers, located in the centre of the compound, as was food, whenever this was provided.

During observation periods, illumination of the compound was provided by three 100 Watt light-globes encased by red plastic funnels and suspended from the roof. Light was projected through red filter-paper attached to the funnels. This provided adequate visibility in all parts of the compound so that subjects were easily observed; yet the illumination so obtained was only slightly more intense than that provided by a full moon on a cloudless night. Davis (1961) and Southern (1965) recommended the use of red light for observing nocturnal

animals because the latter generally have poor cone-vision, consequently, disturbance of their normal behaviour by this factor is expected to be minimal.

Subjects were carried from their holding cages to the enclosure in hessian bags. Observations were performed through a glass window set in the side of an aluminium shed (1.5 x 1.5 x 2.0 m) which was positioned opposite the lower wall of the compound. The window provided excellent visibility of the subjects. Illumination in the observation shed was provided by a shielded 15 Watt globe. No attempts were made to alter either the natural photoperiod or the influence of climatic conditions during the present investigation. All subjects were initially maintained for two complete days in the enclosure in an attempt to habituate them to their novel surroundings and on the third night observations commenced. The amount of time spent in the enclosure by subjects before the collection of systematic records of their behaviour began was deemed to be an acclimatization period of suitable duration, since the preliminary observations had indicated that fence running, a common initial escape-response, and the possible effects of prior occupancy appeared to be greatly reduced in consequence.

Experimental tests conducted in the enclosure and involving individual subjects of *I. obesulus* and *P. gunnii*, were designed to ascertain if the animals utilized the total physical space available in the compound. At the same time, records of the diel activity-cycles and the principal maintenance-activities of the subjects were compiled. Utilization of the compound area was assessed in terms of both the ambulatory-scores (number of grids crossed) assessed for the peripheral and central zones and durations of time spent in the peripheral region. The tests were also used to assess possible modifications of activities and the utilization of space in relation to presence or absence of food in the enclosure.

In all observation periods, the investigator arrived at 1700 hrs (usually was 30 mins to 1 hr before sunset). Immediately after arrival, the red lights were switched on and remained so throughout the night. Recording of data was invariably concluded at 0800 hrs (usually 30 mins after sunrise). In some cases, recording ceased when animals entered and remained in their nests for more than one h after 0500 hrs. It was assumed to be unlikely in these instances that the subjects would re-emerge after that period. Some support for the validity of this assumption was provided by information obtained with the aid of a National Panasonic portable video recorder. This apparatus was able to operate at 10 min intervals for durations of 10 secs at a time. Presumably, if an animal had re-emerged, its activity would have been monitored by the recorder which was focussed on the central zone of the compound. Subsequent viewing of the video tapes so obtained on a screen failed to disclose the presence of the subjects in all instances when observations ceased earlier. This equipment also proved to be very useful in compiling behaviour elements considered to be important for the purposes of the study (described later).

After each observation period, the enclosure was manually raked thoroughly in attempts to oblivate existing excavations and cover any scat and fragments of food that were not eliminated from the enclosure by other means of removal. Nesting-material was also replaced and food and water were replenished.

Quantitative records of maintenance-activities and utilization of space by the subjects were obtained for every 60 mins of the observation period. The latter involved monitoring the frequencies with which different maintenance-activities were performed for each hour the subjects were active and tabulating the number of grids crossed in the central and peripheral areas of the compound. Data were recorded

on duplicated standard protocol-sheets. Two hand-counters and two manual stopwatches were employed for recording the numbers of grids crossed in each zone and the time spent in the peripheral zone and in different maintenance activities, respectively. At the end of every 60 min session of recording during the observation periods, the data recorded with the aid of all of the four devices were entered on the appropriate protocol-sheets. All instruments used in recording were then reset in preparation for the commencement of the ensuing period of observation. A subject was deemed to have traversed a given grid line if the whole of its body had passed across the latter. Appropriate provisions were made on all protocol-sheets for recording infrequent events or elements of behaviour not previously observed and identified.

The purpose of the preliminary observations were to identify the most commonly-occurring types of activities and to gain familiarity with the procedures of recording. The behavioural categories used in recording the activities of individual subjects in the enclosure are summarized in Table 3.1.1. The prerequisites suggested by Slater (in Colgan 1978) were taken into consideration for establishing the criteria for compiling inventories of behavioural events (i.e. all of the categories used must be discrete and homogenous). In addition, each category was given a name which was descriptive and based on the form of the behaviour under consideration not on causal or functional implications, as recommended by Altmann (1974). Some of the behavioural events such as eating, drinking, grooming, excavating and resting, were accurately timed to provide estimates of their durations (per h) in the records, whereas other activities were recorded in terms of their frequencies/h. These behavioural categories are further discussed in the relevant sections of this chapter and Chapter 4. The different types of observed locomotory gaits and behaviours associated

TABLE 3.1.1 Behavioural categories used in recording the
behaviour of individual subjects in an enclosure.

Eating

Drinking

Excavating

Grooming

Peripheral Grids Crossed

Central Grids Crossed

Lateral Movements of Forequarters and Head

Crouching

Tripedal Stance

Nosing Ground

Bipedal Stance

Full Stretch

Rearing up Fence

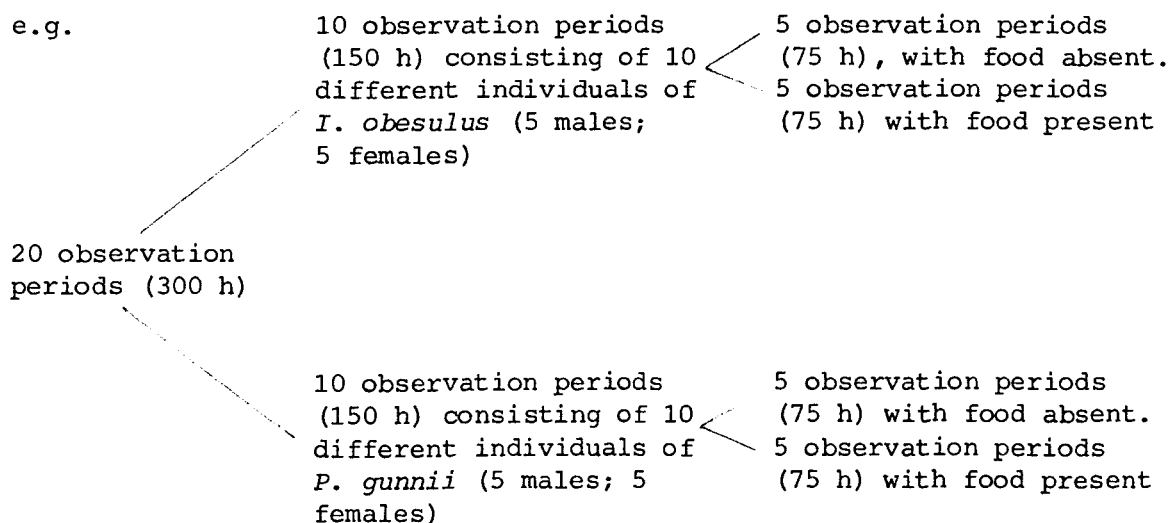
Climbing Fence

with them are described in Section 3.4.

The majority of the behavioural events recorded were visually represented on photographic prints, videotapes or sketches. Illustrations were traced from photographs and videotapes wherever this was possible. Sketches were considered to be preferable to photographs because they can be used to selectively emphasise the salient features of the behavioural events under scrutiny and irrelevant or confusing background-objects could be eliminated. The use of the videorecorder proved to be useful in that behavioural events could be taped at very low light intensities, to be subsequently viewed and analysed at the convenience of the observer.

3.1.3 Results

In all test situations (i.e. food absent or present in the enclosure), replicates of observations on five individuals of each species were performed. This may be clarified by stating that five observation periods, each of 15 h duration, were conducted on both *I. obesulus* and *P. gunnii* in the presence or absence of food.



The preliminary trials indicated that no significant difference with respect to the different behavioural categories existed between

the sexes of either species. Consequently, the use of individuals of different sexes in various test-situations was not selective and the results were not subjected to separate analysis. The compiled data were examined by three-way analysis of variance and the mean values (and standard errors) of the behavioural categories recorded hourly throughout the observation period were graphically illustrated. This method of examining the data provided opportunities for comparisons between all of the variables existing between the test-situations (i.e. species, the presence of food, time of night and individual differences). Student's t-tests were also used, in attempts to detect the differences between times of emergence after sunset and the durations of the time when individuals of *I. obesulus* and *P. gunnii* were active in both test situations (Table 3.1.2).

The times of emergence from nests and the durations of the active period varied between individual subjects of both species. However, significant differences pertaining to the latter were recorded between *I. obesulus* and *P. gunnii*. *I. obesulus* usually emerged approximately one hour after sunset and were active for over 6 h, whereas *P. gunnii* did not emerge until much later after sunset (2.5 hrs), and were active

TABLE 3.1.2 Mean values and standard errors of the times of emergence from the nest after sunset and the durations of the times of nocturnal activity in *I. obesulus* and *P. gunnii*.

Species	Time of emergence after sunset (mins)	Duration of time active (hrs)
<i>I. obesulus</i>	52.2 \pm 17.68	6.26 \pm 0.55
<i>P. gunnii</i>	165.0 \pm 21.31	7.56 \pm 0.82
t-test	3.99; d.f. = 17; P <0.001	2.29; d.f. = 18; P <0.05

for longer periods (8 h). It therefore appears that both species are essentially nocturnal, although one specimen of *I. obesulus* was active when the observer arrived at 1700 hrs, approximately 40 min

before sunset. It is not known whether or not the animal was disturbed, but apparently "normal" activities were performed by this individual.

The times of emergence were more regular than the times of cessation of activity (indicated by final return to the nest) in both species. Climatic influences such as rain and wind appeared to have little or no effects on activity. Only once did an animal retire to the shelter provided, following a period of heavy rain. However, this subject emerged again when the rain had ceased.

Tables 3.1.3 - 3.1.5 and Figures 3.1.2 - 3.1.4 presents the results of three-way analyses of variance, as well as the means and standard errors obtained in each hour of the observation periods, respectively, for the frequencies of crossing central and peripheral grids and the durations of activity periods spent by subjects in the peripheral region of the compound. The significant difference between *I. obesulus* and *P. gunnii* with respect to times of emergence and the durations of activity periods already described are graphically demonstrated by the figures and by the fact that the interaction between the species and the observation period in the three-way analysis of variance was highly significant ($P < 0.001$) in all cases. The presence of food in the enclosure significantly reduced the ambulatory-scores recorded in both the central and peripheral zones in both species ($P < 0.001$), although the amounts of time spent in each zone remained relatively unchanged. There was no significant difference between species with respect to the number of central grids crossed, in either test-situation, but *I. obesulus* traversed larger numbers of peripheral grids than *P. gunnii* ($0.01 < P < 0.001$). The latter feature may be associated with the greater amount of fence running practised by *I. obesulus*. The significant variation between data obtained in different hours during the observation period was, in all cases, probably an artefact

TABLE 3.1.3 Three-way analyses of variance of the frequencies of crossing central grids by subjects, using the following categories: *I. obesulus* - food absent, *I. obesulus* - food present; *P. gunnii* - food absent, *P. gunnii* - food present (using replicates of five subjects in each group).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects (influence of food)	1	29363.41	16.48	0.001
2. Within groups of subjects (differences between species)	1	2523.00	1.42	n.s.
3. Hour of observation period	14	11203.25	6.29	0.001
1 x 2 interaction	1	5275.21	2.96	n.s.
1 x 3 interaction	14	2767.38	1.55	n.s.
2 x 3 interaction	14	8514.38	4.78	0.001
1 x 2 x 3 interaction	14	2221.41	1.25	n.s.
Residual	240	1781.47		
Total	299	4228.80		

FIGURE 3.1.2 Mean values \pm one standard error of the frequencies of crossing central grids recorded in each hour of the observation period.

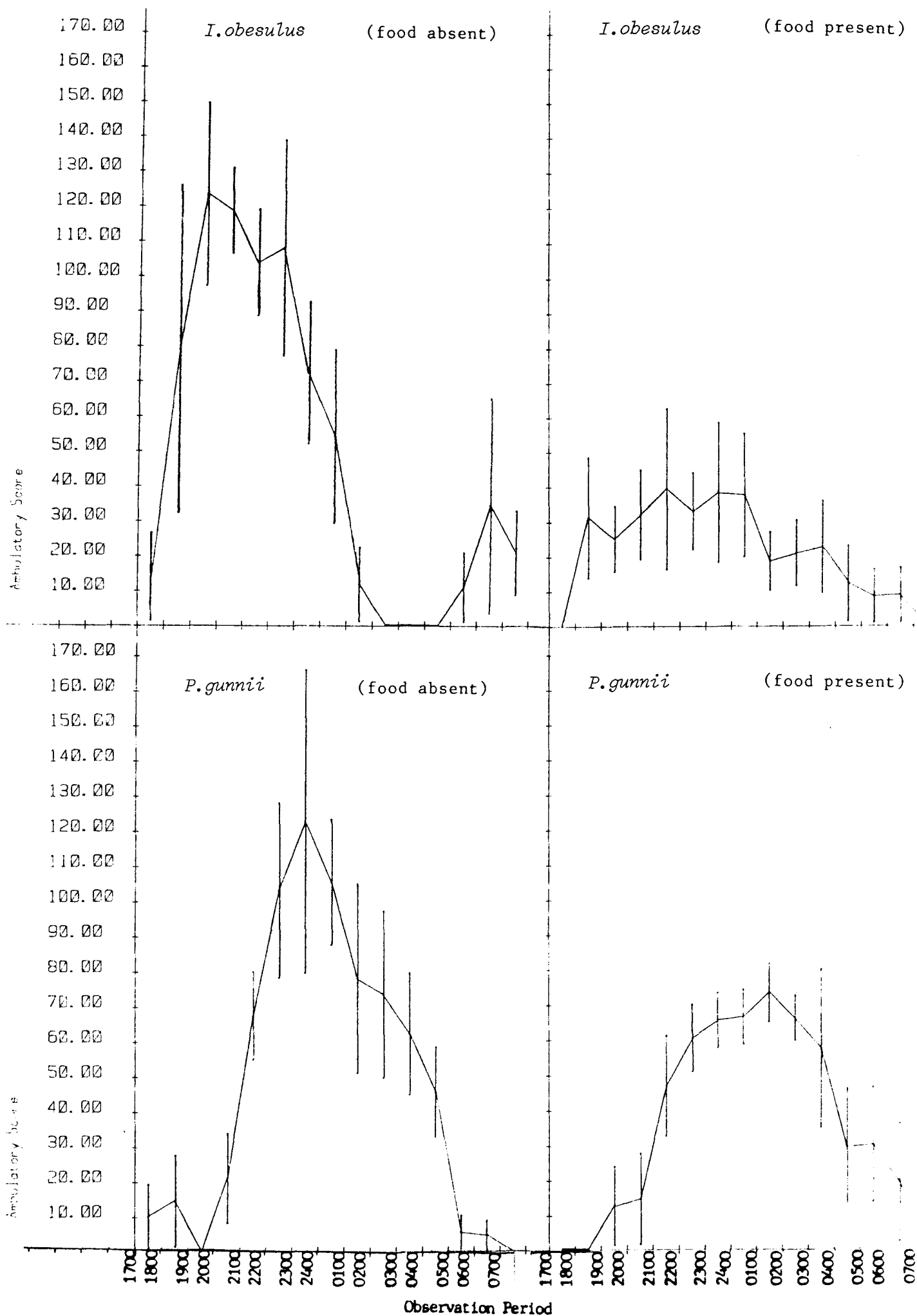


TABLE 3.1.4 Three-way analyses of variance of the frequencies of crossing peripheral grids recorded by subjects under the following categories: *I. obesulus* - food absent, *I. obesulus* - food present; *P. gunnii* - food absent, *P. gunnii* - food present (using replicates of five subjects in each group).

Source	d.f.	Variance (M.S.)	F-ratio	P
1. Between groups of subjects (influence of food)	1	54918.27	23.56	0.001
2. Within groups of subjects (differences between species)	1	15394.00	6.60	0.01
3. Hour of observation period	14	11180.11	4.80	0.05
1 x 2 interaction	1	3724.16	1.60	n.s.
1 x 3 interaction	14	3689.55	1.58	n.s.
2 x 3 interaction	14	10620.01	4.56	0.001
1 x 2 x 3 interaction	14	2883.44	1.24	n.s.
Residual	240	2331.43		
Total	299	4759.18		

FIGURE 3.1.3 Mean values \pm one standard error of the frequencies of crossing peripheral grids recorded in each hour of the observation period.

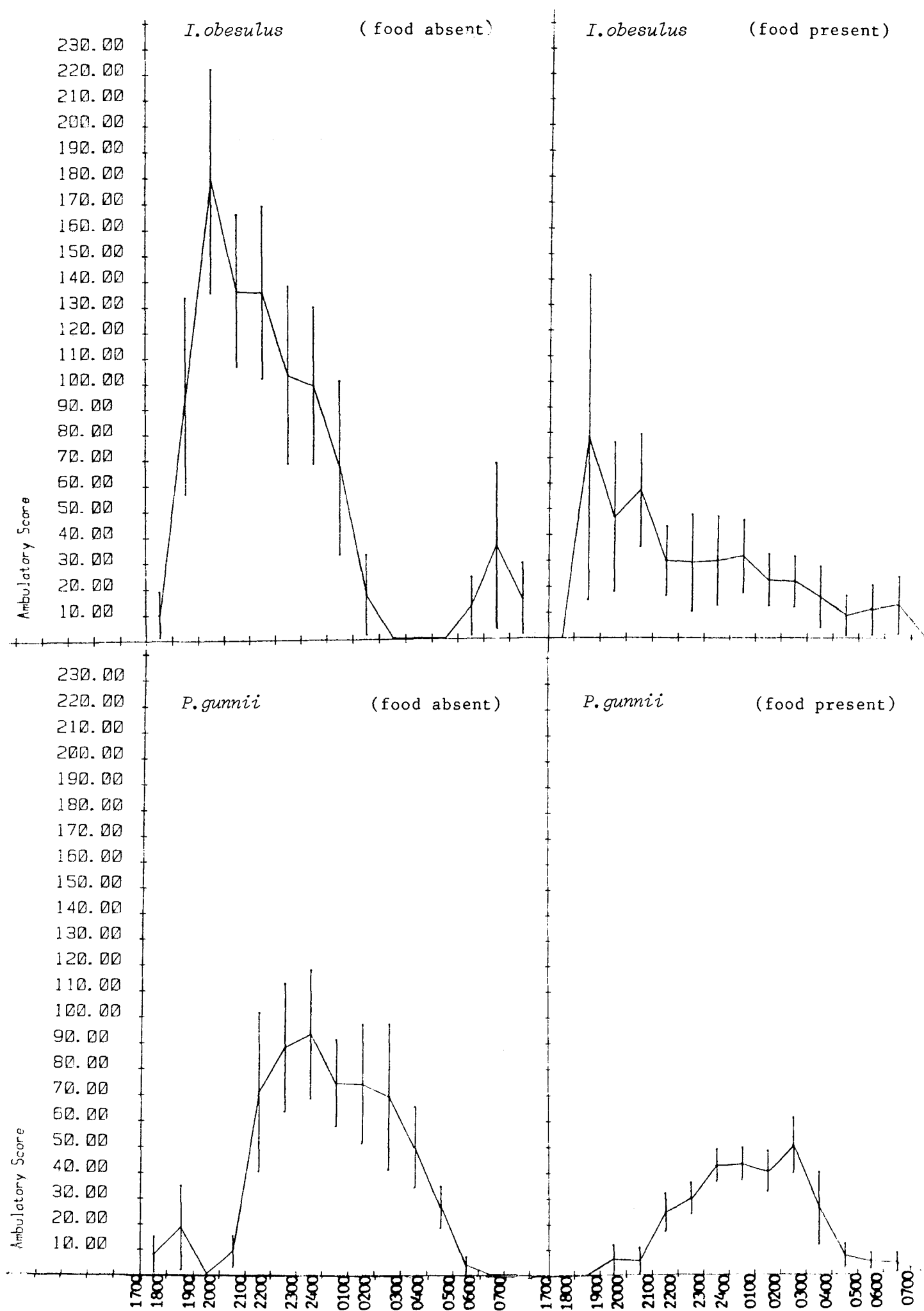
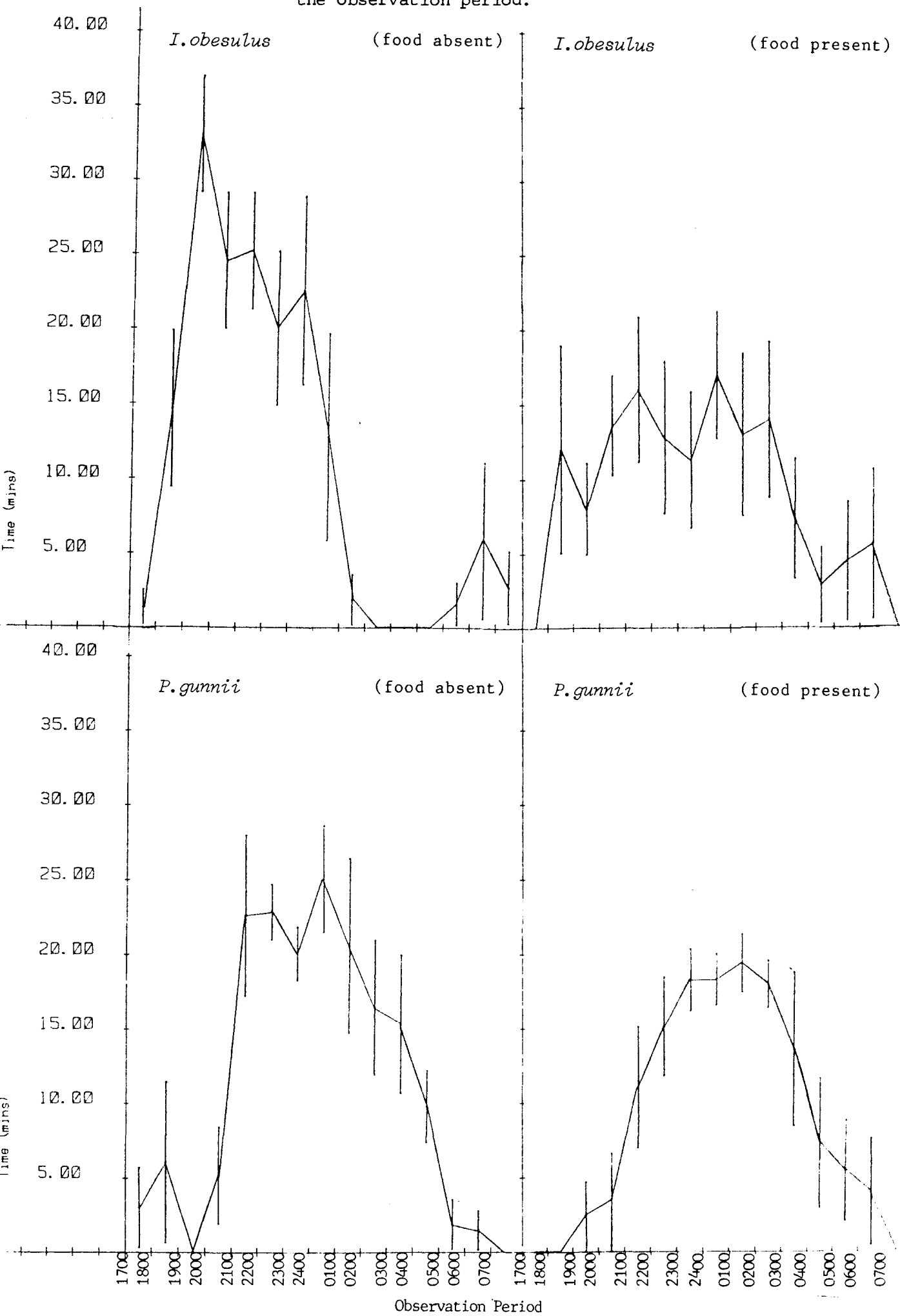


TABLE 3.1.5 Three-way analyses of variance of the times spent in the peripheral region of the compound, recorded in subjects under the following categories: *I. obesulus* - food absent, *I. obesulus* - food present; *P. gunnii* - food absent, *P. gunnii* - food present (using five subjects as replicates for each group).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects (influence of food)	1	322.96	3.80	n.s.
2. Within groups of subjects (differences between species)	1	0.74	0.01	n.s.
3. Hour of observation period	14	803.00	9.45	0.001
1 x 2 interaction	1	1.99	0.02	n.s.
1 x 3 interaction	14	157.40	1.85	0.05
2 x 3 interaction	14	432.60	5.09	0.001
1 x 2 x 3 interaction	14	133.83	1.57	n.s.
Residual	240	85.00		
Total	299	244.64		

FIGURE 3.1.4 Mean values \pm one standard error of the time spent in the peripheral zone recorded in each hour of the observation period.



of the actual number of subjects active at the times when observational samples were taken and was unlikely to be the result of major changes in activity throughout the observation-periods. However, a general decline of activity appeared to occur with respect to the numbers of grids crossed in both zones and the periods of time spent in the peripheral zone towards the end of activity-cycles when food was absent from the enclosure. This phenomenon was not noticeable when food was present.

The peripheral zone only accounted for 13.5% of the total area of the compound and yet the amount of time spent in this area by individuals of both *I. obesulus* and *P. gunnii* was far greater than expected ($\chi^2_1 = 17.48$; $P < 0.001$) in both test-situations.

Numerous behavioural elements, including postures (static) and acts (dynamic), were also recorded during the course of observations in the enclosure. However, only events that occurred frequently were used in quantitative analysis, although other, infrequently performed types of behaviour were also noted (Table 3.1.1). The methods of recording the elements of behaviour has been previously described, in Section 3.1.2. It should be noted here that the majority of behavioural events described were common to both *Isodon obesulus* and *Perameles gunnii*, and differences between the two species, if these were considered to exist, are mentioned in the text.

The observed postures were characterised and illustrated, in terms of the gross configuration of limbs in relation to the trunk and the disposition of the longitudinal axis of the body in relation to the substrate. Acts, which were essentially dynamic events, were described in terms of the actual movements involved. Components, associated with both of the preceding categories consisted of minor movements in the position of the appendages and were described accordingly.

The quadrupedal stance (Figure 3.1.5a) involved placement of all four limbs firmly on the substrate and the body elevated to a parallel position to the latter. Lateral movements of the head and sniffing were generally associated with the stance and it was commonly observed in both *I. obesulus* and *P. gunnii*. A slight variation in the form of this posture was observed in *P. gunnii* (Figure 3.1.5b). The modification consisted of lowering of the hindquarters of the animal, so that it actually established contact with the ground, while the forelimbs supported the forequarters away from the substrate. The angle of the body was approximately 30° to the surface of the ground.

Figure 3.1.6 presents an illustration of the crouched posture, which involved maintaining the body parallel to and in contact with the ground. The legs were retracted under the body, but the head was raised clear off the ground. This posture was usually adopted following some disturbance and both lateral movements of the head and tail and twitching of the ears were often associated with it. It therefore appears that the animals may have been alert or moderately aroused when they adopted this posture. Individuals of *P. gunnii* exhibited higher frequencies of the incidence of this behavioural element than those of *I. obesulus*, since members of the former species appeared to be very timid and hesitant, repeatedly adopting this posture at the slightest disturbance.

The bipedal stance and the full-stretch posture (Figures 3.1.7 and 3.1.8) both involved elevation of the trunk, with the body only supported by the hind limbs. In the former posture the entire length of the pes and tail rested on the surface of the ground and the head was approximately parallel to the latter. In the full-stretch posture, an almost vertical pose was assumed, with almost the entire body (hind legs, trunk, neck and head) extended upwards, and the hind legs braced so that only the digits were in contact with the ground (as was

FIG. 3.1.5a TWO VARIATIONS OF THE QUADRAPEDAL STANCE

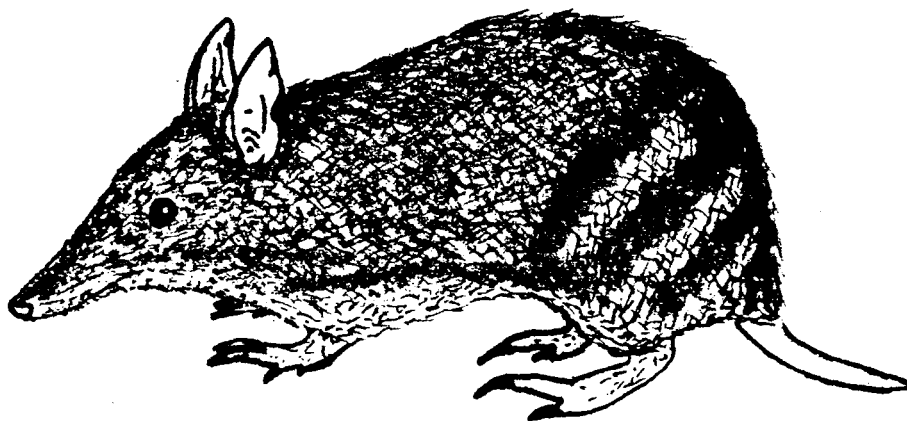


FIG. 3.1.5b

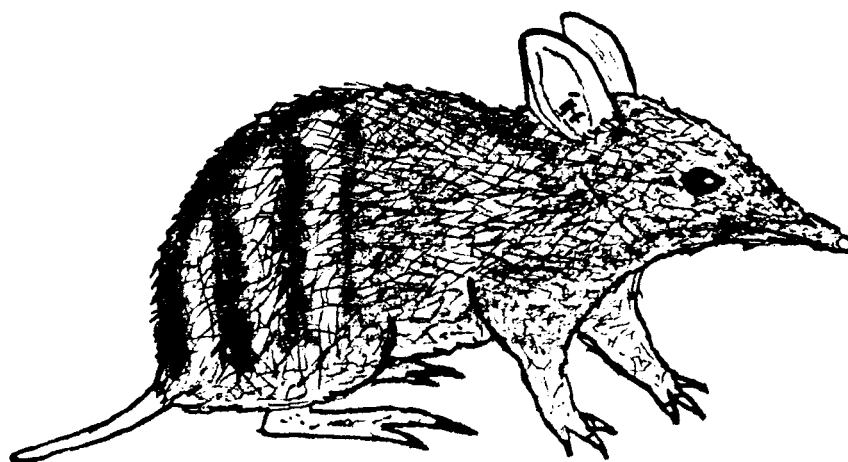


FIG. 3.1.6 CROUCHED POSTURE

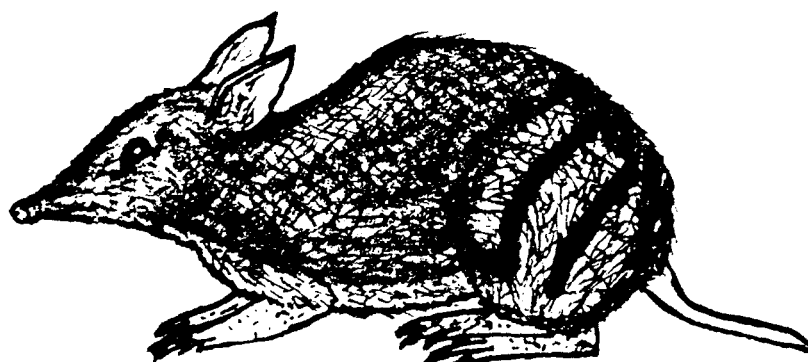


FIG. 3.1.7 BIPEDAL STANCE

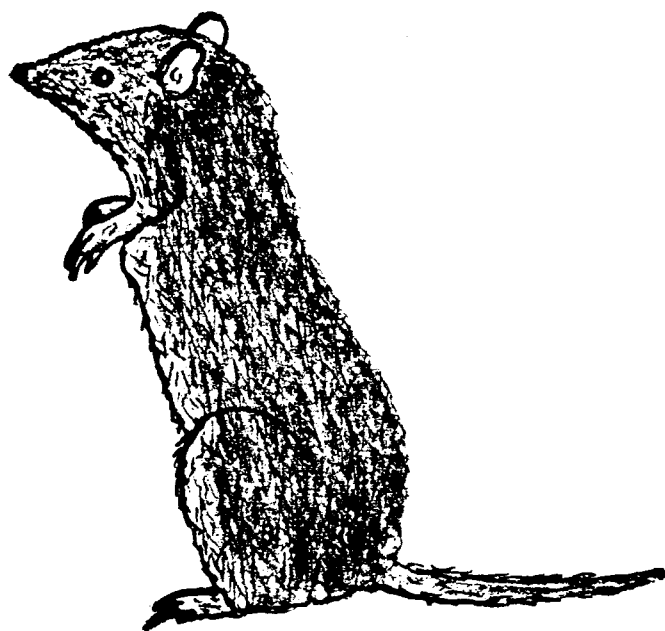
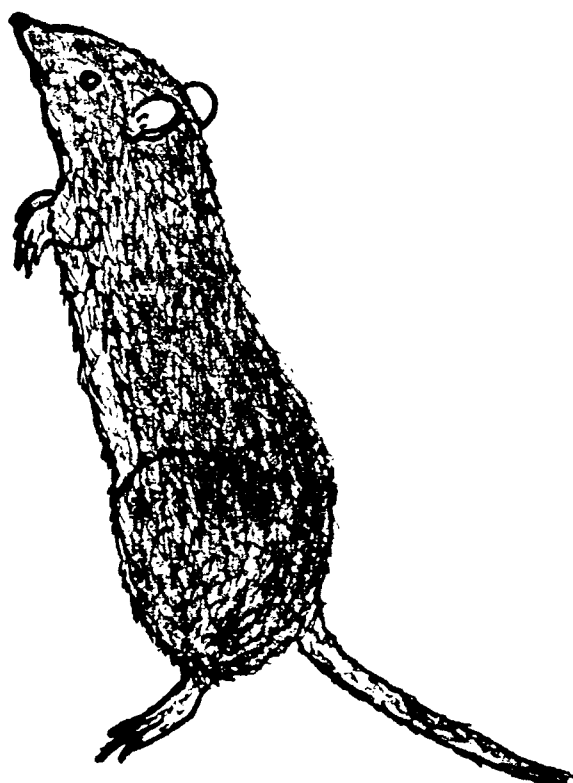


FIG. 3.1.8 FULL-STRETCH POSTURE



the distal end of the tail). Both postures were usually adopted when animals were in close proximity to various objects and the forelimbs were not extended. Sniffing, accompanied by irregular circular movements of the snout, was also frequently associated with both of these stances. Consequently, such postures may have been involved in exploratory and investigative behaviour.

Figure 3.1.9 summarizes the numbers of times per h when the bipedal stance was adopted by individuals of *I. obesulus* and *P. gunnii* and the frequencies with which the latter occurred throughout the ten observation periods in which each of the two species were studied. The most conspicuous feature of this distribution is the significantly greater frequency of large, rather than small numbers of times when the bipedal stance was adopted by individuals of *I. obesulus* (t-test; $0.01 < P < 0.001$; d.f. = 98). The mean number of bipedal stances per hour recorded in ten individuals of each of *I. obesulus* and *P. gunnii* was 52 and 29, respectively. The mean number of full-stretch postures occurring per hour was much lower in both species (i.e. 5 in *I. obesulus* and 4 in individuals of *P. gunnii*).

Another frequently-occurring behavioural element recorded during the observation periods was rearing against a fence of the compound (Figure 3.1.10). The form of this act was essentially a combination of the bipedal and full-stretch postures already described. The head and neck were extended, as in the latter, but the full length of the pes and most of the tail were in contact with the surface of the ground, as in the former stance. The forefeet rested on the fence and climbing (Section 3.4.3) often followed this act. There was no significant difference between the species with respect to frequencies of this event per hour (Figure 3.1.12), and the mean numbers occurring per hour were 33 and 23, in *I. obesulus* and in *P. gunnii* respectively. It is probable that this act was also associated with investigative behaviour.

FIGURE 3.1.9 The distribution of frequencies with which varying numbers of bipedal stances per hour were adopted by ten individuals of *I. obesulus* and *P. gunnii*.

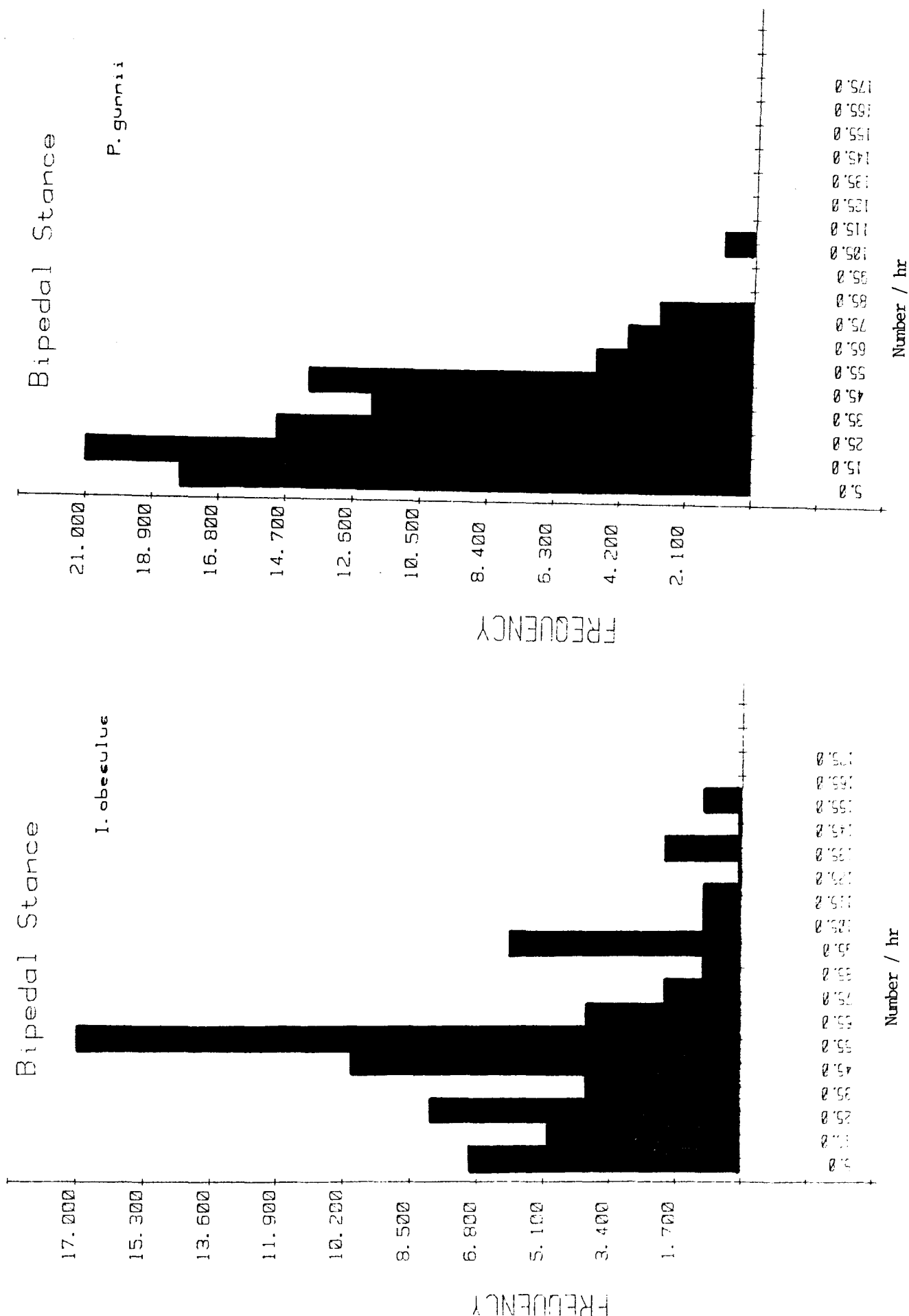


FIG. 3.1.10 REARING AGAINST A WALL

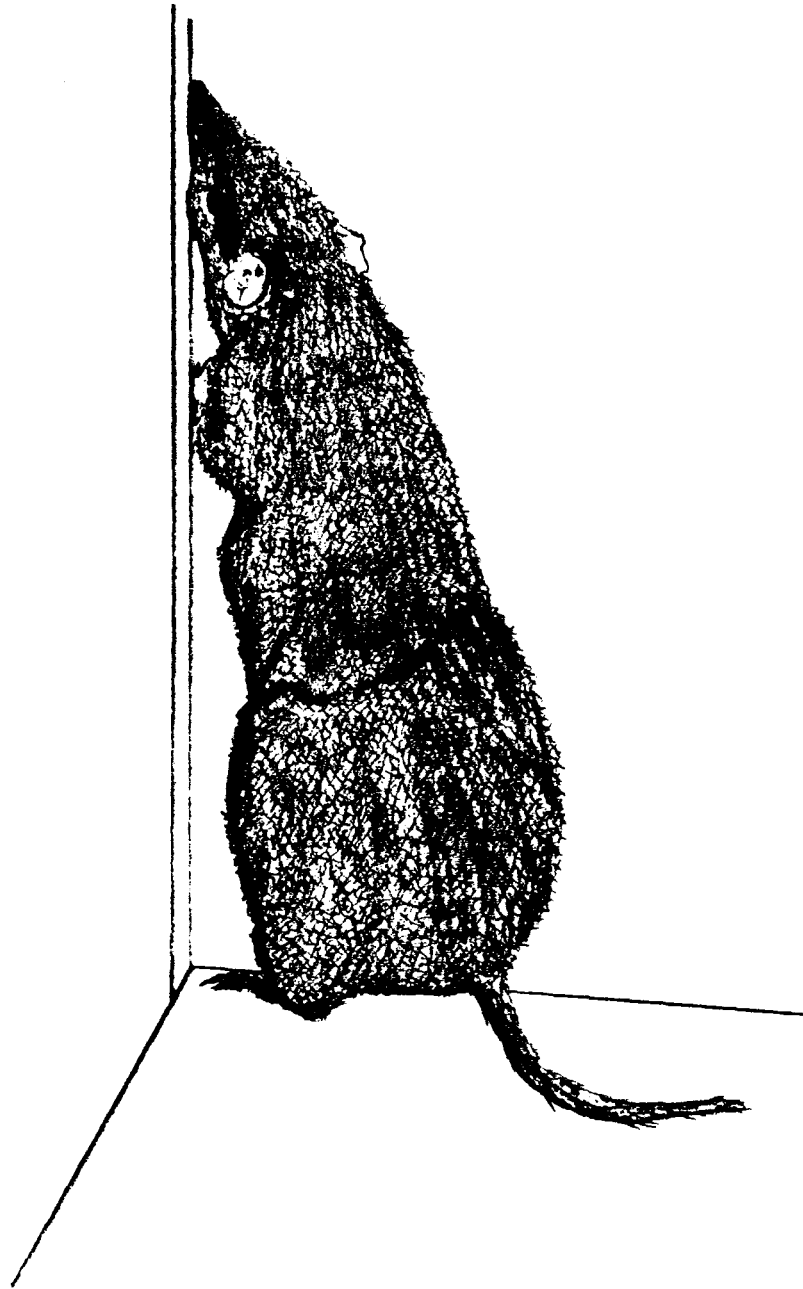


FIG. 3.1.11 TRIPEDAL STANCE

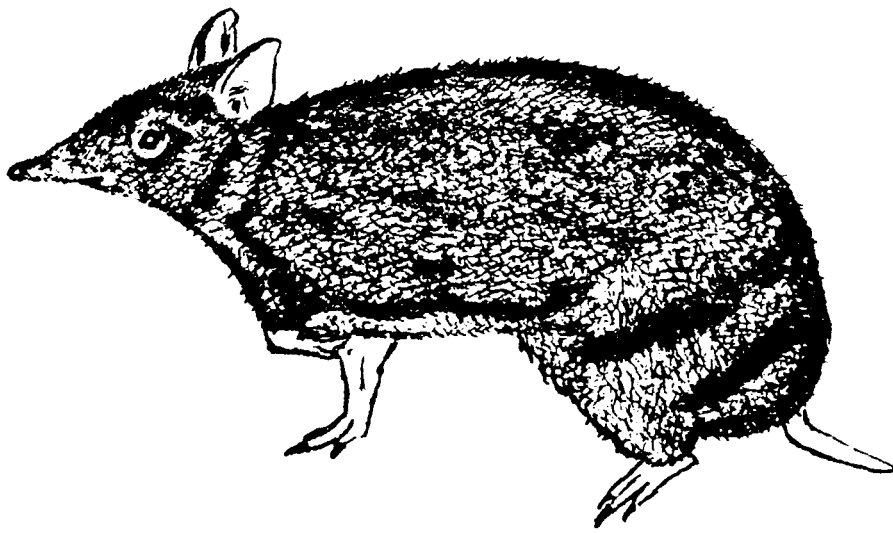


FIGURE 3.1.12 The distribution of frequencies with which varying numbers of rearing up the fence of the compound per hour were adopted by ten individuals of *I. obesulus* and *P. gunnii*.

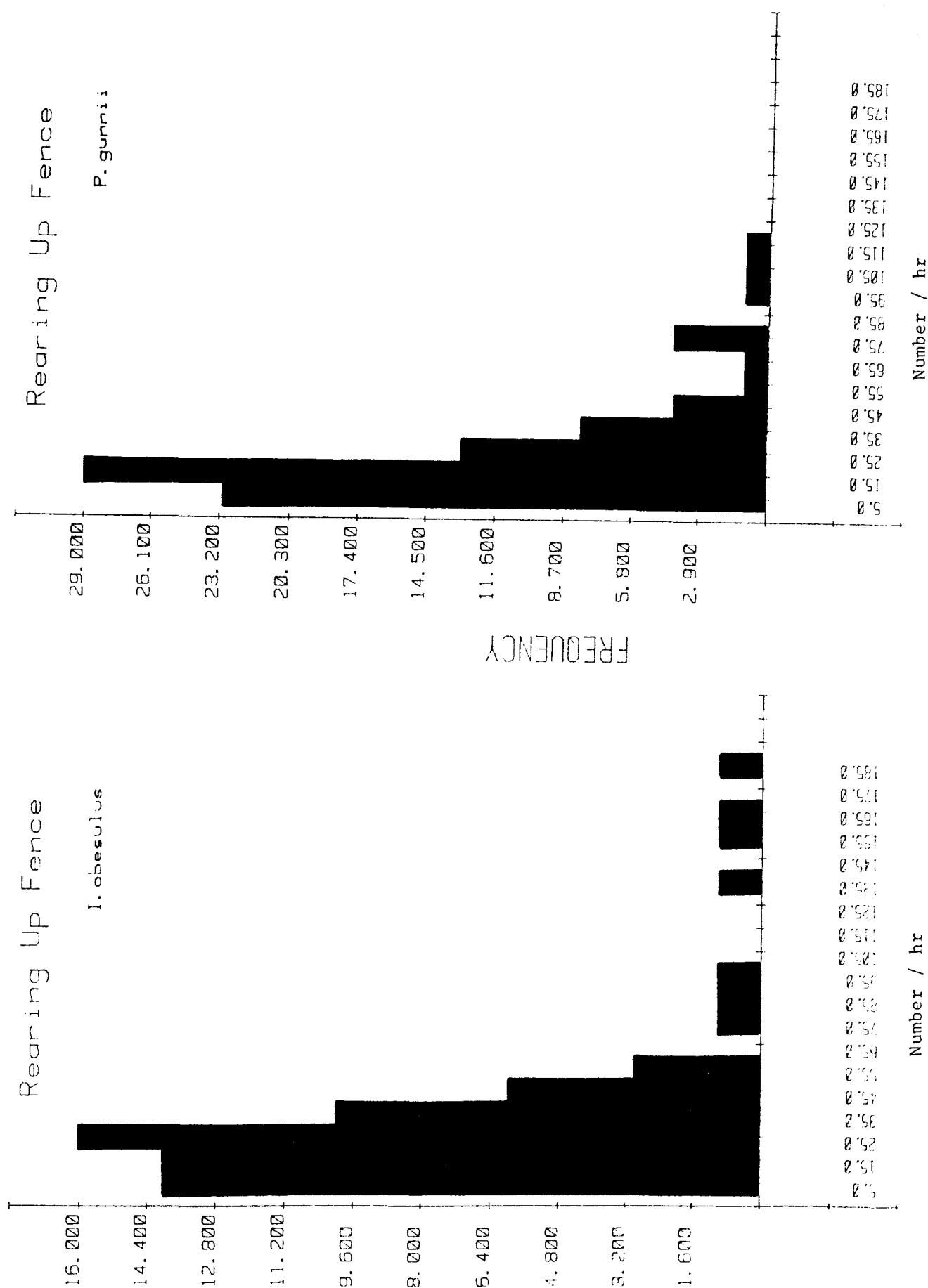
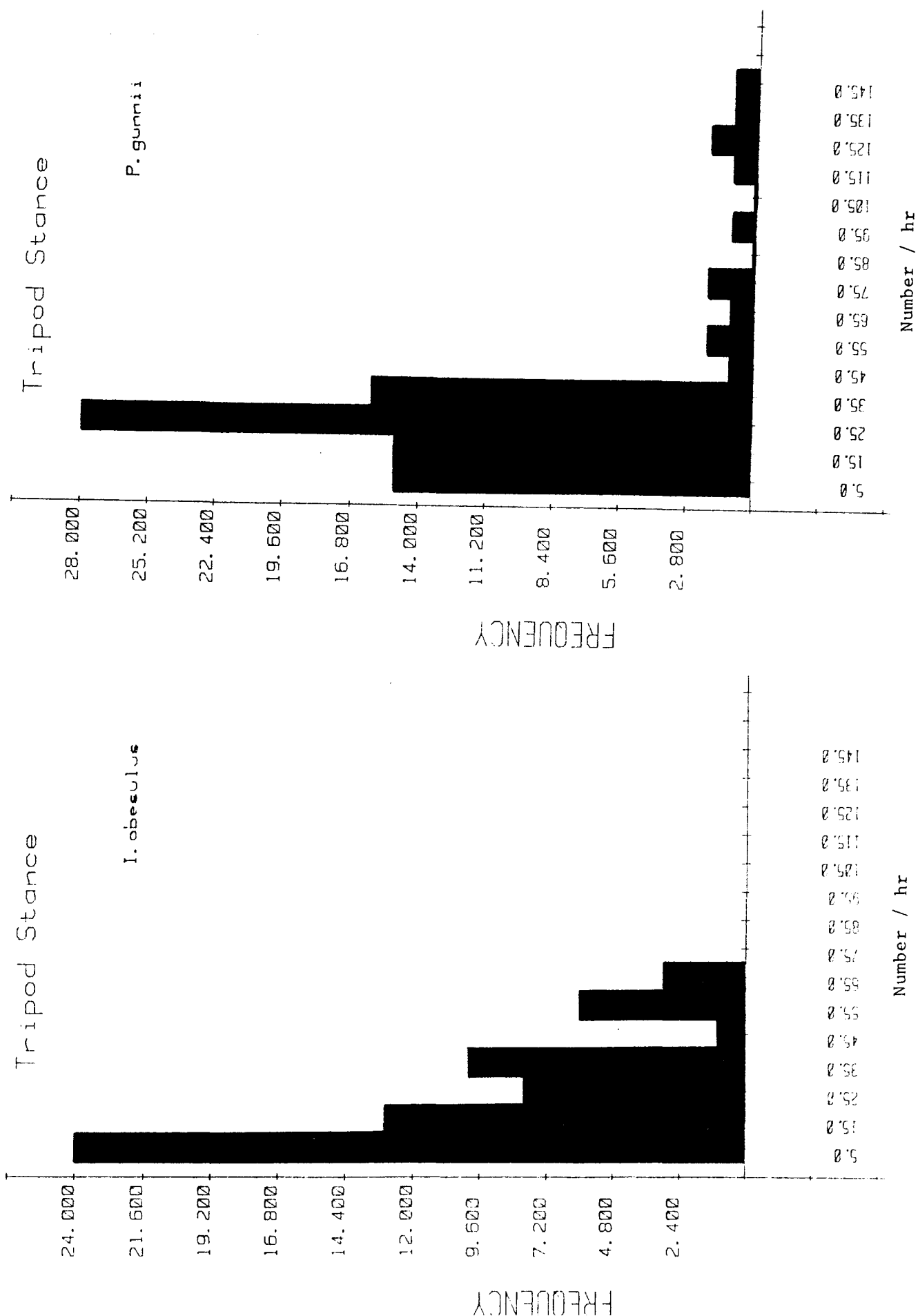


FIGURE 3.1.13 The distribution of frequencies with which varying numbers of tripod stances per hour were adopted by ten individuals of *I. obesulus* and *P. gunnii*.



The tripodal stance (Figure 3.1.11) involved the placement of three limbs in contact with the ground while one of the forelimbs was raised and extended but the forepaw was retracted backwards and in towards the body. The hindquarters were occasionally lowered and even contacted the ground several times while the posture was maintained. There was no apparent preference with respect to which of the forelimbs was elevated from the ground. Sniffing and lateral movements of the snout were conspicuous adjuncts of this event and the stance may represent an indecision-alert posture. No significant difference occurred between the two species with respect to the number of times it occurred per hour; this resulted from a high variability existing between individuals of the same species. The mean numbers of the tripodal stances adopted per hour by *I. obesulus* and by *P. gunnii* were 21 and 33, respectively (Figure 3.1.13).

Vocalizations were produced by both species and these were emitted in association with a number of behavioural events. *I. obesulus* made sneezing and spitting sounds and *P. gunnii*, a species in which no vocalizations had been previously recorded, uttered hissing and grunting sounds, in addition to those noted in *I. obesulus*. Descriptive accounts of these vocalizations and the contexts in which they were heard are described in Chapter 6, since they were most frequently recorded during observations of intra- and interspecific interactions.

3.1.4 Discussion

Both *I. obesulus* and *P. gunnii* appeared to be nocturnal, spending daylight hours in nests and emerging from the latter after darkness had fallen. Heinsohn (1966) observed some *I. obesulus* being active during the daylight hours, but this activity was restricted to darting between bushes, and he presumed that the animals had merely responded to disturbance.

Both species were very active from the time of their emergence to the final cessation of nocturnal activities. Stodart (1966) and Lyne (1981) reported regular withdrawal to the nest-sites for prolonged resting periods during the activity-period of both *P. nasuta* and *I. macrourus*. However, this was not observed in either species during the present investigation, except for occasional brief darting escapes into the nest following interference, such as the approach of brush-tailed possums (*Trichosurus vulpecula*), moving across the roof of the compound. After the cessation of disturbance the subjects soon re-emerged resuming activities immediately. A substantial proportion of the activity-cycle was concerned with the pursuit of maintenance activities (Chapter 4).

The significant differences established with respect to times of emergence and the durations of the times of activity between the two species may assist in reducing direct competition in localities where they occur sympatrically. Such allotonic activity-cycles may enable *I. obesulus* and *P. gunnii* to utilize the same habitats without overt confrontations. The later times of emergence and longer activity-periods recorded in *P. gunnii* may be associated with the movements of members of this species into open pastures to feed. Where these occur, the probability of being detected by predators is presumably greatly increased and this problem may be aggravated if the animals move into open areas soon after sunset, during the twilight period before total darkness supervenes. These considerations are unlikely to apply to *I. obesulus*, which remain in densely vegetated areas. The longer period of activity observed in individuals of *P. gunnii* may also be attributed to their regular visits to open fields, since during these, longer distances may be traversed while foraging for food supplies (Heinsohn 1966).

The significant reduction in the ambulatory score recorded in both species when artificial food supplies were placed in the enclosure

may have been due to a decreased motivational state associated with the need for foraging. The fact that *I. obesulus* generally traversed significantly higher numbers of peripheral grids than *P. gunnii* may indicate that members of the former species attempted to avoid and escape the exposed, open areas of the enclosure; the higher amounts of fence running observed in *I. obesulus* accords with this contention.

The majority of the observed behavioural events occurred at similar frequencies both in *I. obesulus* and in *P. gunnii*. However, significantly higher numbers of bipedal stances were recorded in *I. obesulus* during each hour of the observation period and may be attributed to the habitat in which individuals of the latter species utilize. Since the posture appears to be of an investigatory nature (suggested by the fact that it is regularly accompanied by sniffing and lateral movements of the snout), *I. obesulus* may be required to elevate its head above the low ground-cover, in order to scan its surroundings efficiently. This would not be an essential requirement for individuals of *P. gunnii* in open pastures, where visibility is less likely to be obstructed. Presumably, the utilization of open habitats recorded for *P. gunnii* (Heinsohn 1966) is also related to the tentative nature of the activities of individuals of this species. The subjects observed in the present study appeared to be very wary of even mild disturbances (i.e. noises from outside of the enclosure) and adopted the crouched or tripedal posture before resuming the activities pursued before the onset of the disturbing influence.

The postures regularly observed in both *I. obesulus* and *P. gunnii* are similar to those described in many other species of mammals. Betts (1976) observed the bipedal stance in several species of rodents and Ewer (1968) identified a similar posture in the marsupial mouse *S. crassicaudata* as did Haynes (unpubl.) in *A. swainsonii* and *A. minimus*. Sniffing and lateral movements of the snout associated with the posture

observed in these species led the authors to consider the stance to be investigative in nature.

The tripedal stance described for *I. obesulus* and *P. gunnii* in the present investigation is similar to that observed in *S. crassicaudata* (Ewer 1968) and terrestrial members of the family *Dasyurcus* and *Sarcophilus* (Buchmann and Guiler 1977; Ewer 1968). Ewer considered the posture to be an indecision-alert stance and Calaby (1960) described the same form of behaviour in the numbat (*Myrmecobius fasciatus*).

3.2 NESTING

3.2.1 Introduction

Numerous species of small mammals construct nests. The uses of these include incubation (particularly in cold climates), the maintenance of young and provision of refuges when extreme temperatures prevail. Nests are usually built in sheltered localities (i.e. under dense growth) and are generally well-camouflaged.

Bandicoots construct nests which consist of small mounds of grass and litter scratched together from the surrounding area (Wood-Jones 1924). Newly-constructed nests are relatively conspicuous because of patches of bare ground which surround them. However, following new growth around nest-sites, the shelter gradually blends with the surrounding vegetation and is well concealed. In dry situations, a hollow is excavated so that the summit of the nest is level with the surface of the ground. In wetter areas, the nest may be raised and form a distinct mound (Troughton 1965). Captive specimens of *I. obesulus* have been observed to excavate small shallow burrows which are used during hot weather (Kirsch 1968). These subterranean constructions do not contain nesting material and are not camouflaged in any way. Their features appear to indicate that burrowing may protect *I. obesulus* from excessive heat loss. However, no burrows of this type have been

observed in the field. Heinsohn (1966) did not report such burrowing in either *I. obesulus* or *P. gunnii* but he did observe the use of burrows made by other animals (e.g. rabbits) as refuges. He also reported construction and occupancy of temporary nest-sites when captured individuals were released during daylight.

3.2.2 Materials and Methods

Observations on the construction of nests were conducted while the animals were maintained in the enclosure (Section 3.1.2) and in their holding cages. Detailed records of the dimensions, shape and complexity of each nest were noted. Unfortunately, no nests were ever found in the field, presumably due to their inconspicuous appearance.

3.2.3 Results

All individuals of *I. obesulus* and *P. gunnii* constructed nests of the straw and wood-shavings provided. The nests of both species were very similar in appearance and consisted of an oval mound, of dimensions ranging from 20 x 15 x 12 cm to 35 x 25 x 20 cm. No visible entrance could be detected and nests were usually constructed within the nesting-boxes that were provided. However, nest-sites were occasionally abandoned and a new nest, consisting of material salvaged from the old one, was built in a different area of the holding cage. This phenomenon usually occurred after the animal had been disturbed in the nest (for example when it was removed from the holding cage for other observations) and immediately before the fortnightly cleaning of the cages. The reasons for this behaviour were obscure because the abandoned nest-sites were quite clean and devoid of faeces. On each occasion when the holding-cages were cleaned, all individuals quickly reconstructed their nests using the new material that was supplied.

Additional material was usually added to the nest on subsequent nights.

The time required for constructing a nest into its definitive form (2-3 days) permitted the investigator to observe subjects of both species sleeping in their nests, because the roofs of the latter were the last items added. *P. gunnii* generally slept on their sides and curled up in a ball with the snout tucked under the posterior part of the flanks, whereas *I. obesulus* adopted a crouched posture (Section 3.1.3) with the head lowered. Both species rested in the centre of nests and if disturbed, readily dashed out, in any direction. The nests of *I. obesulus* were usually more compact than those of *P. gunnii*, this presumably had the effect of reducing air-flow throughout the nest, resulting in greater insulation.

Individuals of *I. obesulus* and *P. gunnii* were observed constructing nests and adding material to them. This process normally occurred just after emergence or before the cessation of the nocturnal activity periods. Several heaps of straw and wood-shavings were scraped backwards with the forelimbs between the widely parted and extended hind limbs (Figure 3.2.1). The tail was raised and held parallel to the surface of the ground throughout the activity and the rump was elevated as a result of the extension of the hind limbs and the forelimbs moving caudad with the collected material. The tail and mouth were not

FIGURE 3.2.1 Movements involved in scraping materials in the direction of the nest-site (circle represents the position of the nest).



observed to play any role in the transport of materials, which were usually gathered within a 0.5 m radius of the nest-site. Occasionally an individual moved back into the nest for a few minutes after scraping material into it. This may have been related to lining the nest.

3.2.4 Discussion

The process of construction and features of the nests by *I. obesulus* and *P. gunnii* described in the present investigation were very similar to those reported by Heinsohn (1966) and other investigators who observed other species of bandicoots. Stodart (1966) and Mackeras and Smith (1960) reported nest construction in *P. nasuta* and *I. macrourus* and their observations paralleled those made on *I. obesulus* and *P. gunnii*.

The fact that several types of refuges are utilized by both *I. obesulus* and *P. gunnii* (i.e. hollow logs, rabbit burrows and crevices in the soil), as described by Troughton (1965), Heinsohn (1966) and Wood-Jones (1924) and also the fact that both species construct their own nests from a plentiful supply of available materials, appears to indicate that competition for such resources may be negligible. It also appears that both species can alter the features of their nests in accordance with currently prevailing climatic conditions (i.e. nests are constructed above the surface of the ground in wet situations and are positioned in depressions during warmer, drier periods).

3.3 GROOMING

3.3.1 Introduction

Various types of grooming behaviour exhibited by *P. nasuta*, *I. obesulus* and *P. gunnii* has been described by Stodart (1966) and Heinsohn (1966). All of these three species carry numerous ectoparasites, yet grooming was alleged by the authors to be normally

limited to only occasional, perfunctory scratching of the fore-quarters with one of the hind feet and gnawing and licking of the pelage with the teeth and tongue, respectively. The durations of bouts were very short and grooming-activity was generally infrequent, comprising only a small percentage of the total activity-period.

3.3.2 Materials and Methods

Observations of the grooming behaviour by individuals of *I. obesulus* and *P. gunnii* were recorded while subjects were maintained in their holding-cages and in the enclosure. The different types of grooming-elements were described and illustrated. Photographic methods and videotapes were employed to record the latter. The regions of the body that were groomed were also recorded by these methods. Durations of bouts of grooming and the total amounts of time spent in such activities in each hour of the observation periods were recorded and computed. Three-way analysis of variance was used to compare the results obtained for both species in different test situations.

3.3.3 Results

Grooming consisted of isolated bouts, as well as sequences of two or more grooming actions performed in succession. Bouts were considered isolated if more than 30 s elapsed between successive grooming events, or if some other type of activity was performed by the subjects between the bouts. The numbers of bouts occurring within a given sequence were recorded as single units if the subject subsequently proceeded to groom another region of its body.

Three types of grooming movements were identified in both *I. obesulus* and *P. gunnii* and the subjects used their snout and limbs in the course of these. Figure 3.3.1 provides a diagrammatic illustration of scratching-motions employing the hind claws. Rapid, raking movements of the hind feet served to scratch the snout, ears, chest, neck,

FIG. 3.3.1 SCRATCHING THE FOREQUARTERS WITH THE HIND CLAWS

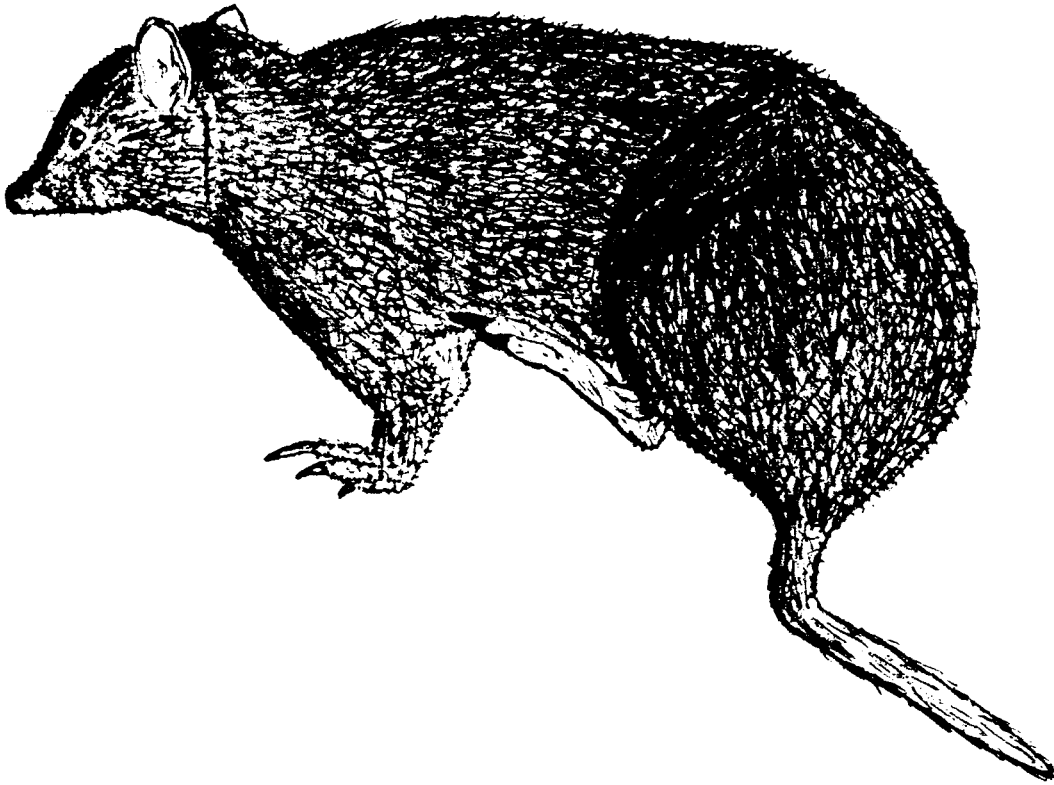


FIG. 3.3.2 WIPING THE SNOUT WITH
 LICKED FOREPAWS

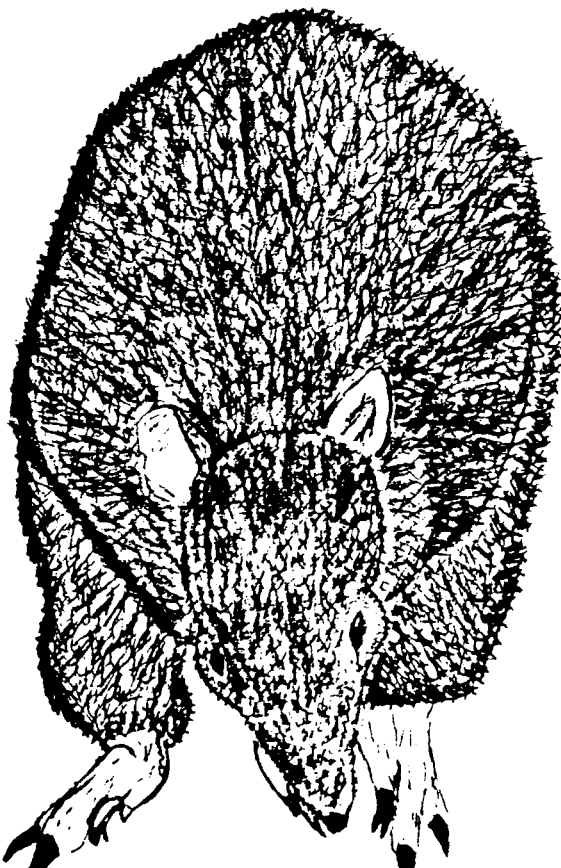


FIG. 3.3.3 GNAWING AND LICKING
 THE FUR WITH THE
 MOUTH



shoulders, dorsum and the flanks. Scratching actions were often interspersed with gnawing and licking of the syndactylous claws, possibly to remove fur, dirt and ectoparasites from the latter.

Wiping the snout with licked forepaws (Figure 3.3.2) was also frequently observed, particularly after feeding (Section 4.3; prey-killing behaviour). Grooming-actions were restricted to the muzzle only and did not extend behind the eyes. Subjects generally assumed a bipedal stance with the back and head arched downward, and stroked the snout with simultaneous actions of both forepaws, which were licked between every few strokes. Presumably, this action was employed to remove dirt (after excavating), food-particles (after feeding) and blood (after successful killing and eating of prey).

The final grooming element observed was gnawing and licking of the pelage (Figure 3.3.3). During this action, the head was turned towards the posterior end of the animal and intermittent licking with the tongue, as well as chewing with the incisors were performed. The forepaws were not used to manipulate the fur in any way, and one of the forelimbs was placed firmly on the ground while the other was held loosely by the side of the animal. Occasionally, the animals were seen to topple sideways during attempts to reach the most distal parts of the rump. The flanks, genitals, ventrum, back and rump were groomed in this manner. The frequency of licking was greatly increased when precipitation occurred and grooming of the tail and pouch was not observed in any subjects of either species.

Two types of comfort-activities were observed, both in *I. obesulus* and *P. gunnii*. The first of these involved shaking of the body and this was usually performed while running or jumping forward, with the body shaken in mid-air. This movement occurred more frequently when it was raining, presumably in order to dislodge water adhering to the pelage. The second type of comfort movement consisted of

stretching the body. The forefeet were moved forward while the hind limbs remained stationary. The head rested on the forelimbs and the back was arched downward. The trunk was concave but no contact was made between the abdomen and the ground. This activity usually occurred as the animal emerged from the nest and was often accompanied by yawning.

Table 3.3.1 and Figure 3.3.4 present the results of three-way analyses of variance, as well as the means and standard errors obtained in each hour of the observation-periods, for the times spent grooming. A highly significant difference occurred between *I. obesulus* and *P. gunnii*, with respect to the amount of time devoted to this activity ($P < 0.001$). *P. gunnii* spent considerably more time grooming (mean = 1.48 mins per hour) compared to *I. obesulus* (mean = 8 sec per hour) but the activity comprised only a small percentage of the total activity-period in both species. The longest recorded duration of a bout of grooming was 5 min 36 s; this was recorded in an individual of *P. gunnii*. A significant difference ($0.05 < P < 0.01$) also occurred in the times at which grooming occurred throughout the observation-period. *I. obesulus* generally groomed most often in the first few hours after emergence, whereas *P. gunnii* performed this activity mainly before the cessation of its nocturnal activity-period. The greater amount of time spent in grooming during the later period of the activity-cycle in *P. gunnii* was due to the increased durations of individual grooming-bouts.

The durations of grooming-bouts varied considerably, ranging from a few seconds to several minutes. Within the longer bouts, a definite order in the movements of the limbs appeared to exist, so that different regions of the body were groomed in succession. Such series of movements involved gnawing one side of the hindquarters of the animal, then scratching the more anterior areas of the same side,

FIGURE 3.3.4 Mean values \pm one standard error of the amounts of time spent grooming, recorded in each hour of the observation-period.

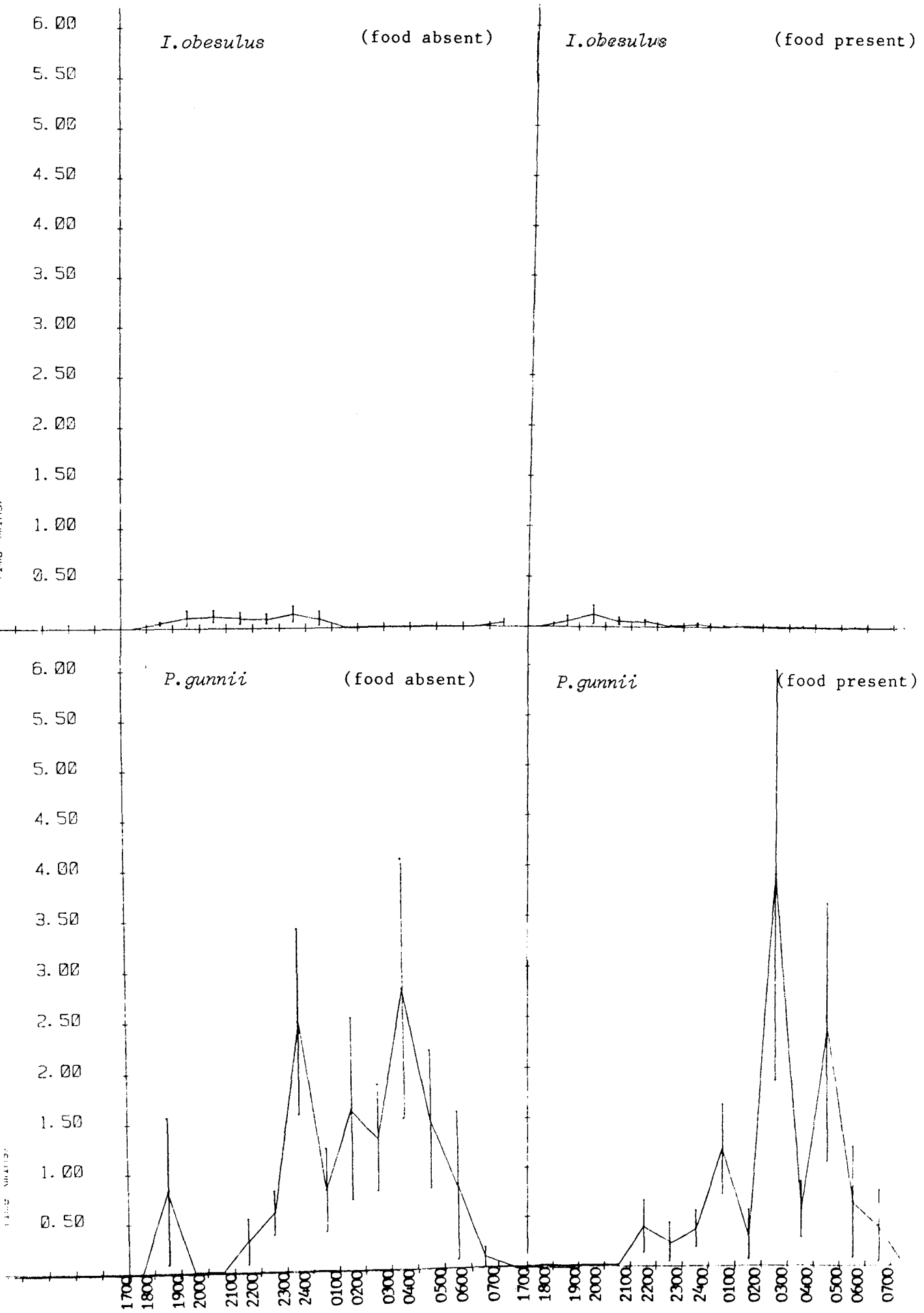


TABLE 3.3.1 Three-way analyses of variance of the times spent grooming, recorded in subjects under the following categories: *I. obesulus* - food absent, *I. obesulus* - food present; *P. gunnii* - food absent, *P. gunnii* - food present (using 5 subjects as replicates in each group).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects (influence of food)	1	0.88	0.70	n.s.
2. Within groups of subjects (difference between species)	1	41.96	33.05	0.001
3. Hour of observation period	14	3.15	2.48	0.01
1 x 2 interaction	1	0.51	0.40	n.s.
1 x 3 interaction	14	1.73	1.36	n.s.
2 x 3 interaction	14	3.38	2.66	0.01
1 x 2 x 3 interaction	14	1.67	1.32	n.s.
Residual	240	1.27		
Total	299	1.80		

followed by repeating the same sequence on the other side of the body.

3.3.4 Discussion

The different types of grooming movements described in the present study appear to be similar to those observed in *P. nasuta* (Stodart 1966) and what has already been reported about these events for *I. obesulus* and *P. gunnii* by Heinsohn (1966). Investigations regarding this type of activity have been made on several other species of marsupials, for example, *Dasyurus viverrinus* (Moss, unpubl.), *Dasyuroids byrnii* (Hutson 1976), *Antechinus swainsonii* and *A. minimus* (Haynes, unpubl.) and *Sminthopsis crassicaudata* (Ewer 1968). The

grooming movements described in the species used in these studies parallel those observed in *I. obesulus* and *P. gunnii* in the present investigation.

The bipedal posture adopted during face-grooming appeared to be similar to that used by *A. swainsonii* and *A. minimus* (Haynes, unpubl.) and by *S. crassicaudata* (Ewer 1968). This stance permitted free use of the forelimbs and they were employed simultaneously to groom the snout. This type of grooming was also observed in *Didelphis marsupialis* (McManus 1970) and is commonly employed in rodents belonging to the genus *Peromyscus* (Eisenberg 1968).

The intermittent licking of the forepaws during face-wiping and cleaning of the syndactylous claws after scratching has also been observed in *D. marsupialis* (McManus 1970) and in some of the larger macropods (Russell 1974). The action appears to be important in removing fur, ectoparasites and other material collected during grooming. Such substances were often detected in subsequent analyses of scats (Section 4.1.3).

The methods of scratching with the hind feet observed in this study were very similar to those described in the majority of marsupials and eutherians that have been investigated in detail (Ewer 1968; McManus 1970; Eisenberg 1968). The absence of pouch-grooming in bandicoots was not surprising, since Lyne (1964) has only observed this type of activity immediately before conception. The actions involved were licking the pouch by inserting the snout into the latter. The animal performed this in a sitting position, supported by one of the forelimbs as shown in Figure 3.3.3.

The limited amount of time devoted to grooming during individual activity-periods is rather unexpected since both *I. obesulus* and *P. gunnii* possess numerous ectoparasites. Presumably the actions of grooming serve to relieve irritation caused by the latter and to dis-

lodge such unwanted companions. However, captive animals continued to groom in the absence of heavy ectoparasitic infestations, therefore grooming may also function to remove dirt and other material adhering to the pelage. Heinsohn (1966) observed grooming occurring in the nest, in *P. gunnii*. This may explain the small amount of time employed in this activity in the open, as both species reside for long periods in the nests. However, grooming was also not observed to be performed in the nests by either species during the present investigation.

Increased frequencies of shaking the body during precipitation observed for both *I. obesulus* and *P. gunnii* have also been reported in *D. marsupialis* (McManus 1970) and was presumably also employed to dislodge water adhering to the pelage.

In conclusion, grooming functioned to cleanse and condition the pelage and remove ectoparasites or other materials which may have had irritating effects. The limbs, employed in grooming, were routinely cleansed, generally directly after they were used. Face-wiping usually followed feeding and excavating holes; in general, grooming activities appeared to be situation-specific. Bouts of grooming were considerably variable but most areas of the body received similar amounts of attention in grooming throughout the activity-periods.

3.4 LOCOMOTION

3.4.1 Introduction

Little research has been done to date on marsupial gaits. Windsor and Dagg (1971) studied the gaits of 19 species of Macropodinae, whereas locomotion in the potoroo was observed by Buchmann and Guiler (1974). Other investigations include an account of the mechanics of hopping by kangaroos (Alexander and Vernon 1975), locomotion of *Antechinomys* (Ride 1965) and a comparison of the gaits of two desert-living

Australian mammals, *Antechinomys spenceri* and *Notomys cervinus* (Marlow 1969). Locomotion in kangaroo-rats has also been observed (Bartholomew and Caswell 1951) and is of interest because of the characteristic bipedal gait employed by this group of eutherian mammals.

Locomotory behaviour in bandicoots has only been described briefly (Walker 1964). Therefore, the purpose of this section of the present study was to analyse the different types of locomotion employed by *P. gunnii* and *I. obesulus* and to determine the nature of any relationship existing between this type of behaviour and other maintenance activities.

3.4.2 MATERIALS AND METHODS

As it was not possible to observe the locomotion of bandicoots on natural terrain due to the ground often being uneven and vegetation obscuring the movements of the animals, it was decided to observe captive subjects in a semi-natural environment (Section 3.1.2), in an artificial arena (Section 4.3.2), and to film the different types of gaits by placing animals on a treadmill which could be operated at various velocities. Before the filming of locomotion was actually commenced, animals were tested for their ability to acquire a steady gait when placed in the treadmill. These tests were conducted on every second day for three weeks and animals that did not perform satisfactorily were excluded from the filming. It is for this reason that only two *P. gunnii* (a male and a female) and four *I. obesulus* (two specimens of each sex) were deemed suitable for use in filmed records; the remaining subjects were considered to be unacceptable. All of the subjects used were adults and the linear measurements of their forelimbs and hind limbs were recorded. It is clear from Table 3.4.1 that male subjects of both species possessed longer fore- and hind limbs than female conspecifics (presumably related to the

generally larger size of the males) and that individuals of both sexes of *P. gunnii* also yielded longer fore- and hind limb measurements than *I. obesulus*.

TABLE 3.4.1 Linear measurements (lengths) of fore- and hind limbs of the subjects used in obtaining filmed records of the different gaits.

Species	Sex	N	Forelimb (mm)	Hind Limb (mm)
<i>I. obesulus</i>	F	6	68	117
		16	66	109
	M	1	74	123
		7	68	119
<i>P. gunnii</i>	F	4	76	136
	M	7	80	140

Different gaits were filmed using 16 mm cine film (400 ASA) at a velocity of 64 frames/s. Adequate illumination was provided by a 250 W and a 500 W Philips Photoflood light used simultaneously. Filming was conducted from a distance of approximately 1 m, in order to obtain optimum conditions of image and field-size and it was performed through the Perspex wall of a box (100 x 50 x 75 cm) positioned over the treadmill in order to prevent subjects leaping from the latter. The opposite wall of the box contained a 1 cm² grid-pattern which was easily visible within each frame of the film. This provided a satisfactory index of the height and length of each stride (a full cycle of a given type of motion). Although the treadmill provided a reading of the velocity at which it was operating (a meter position at the side of the machine), these were checked by multiplying the length and rate of each stride (i.e. the number of frames).

Successive frames of the motion-picture were projected as life-

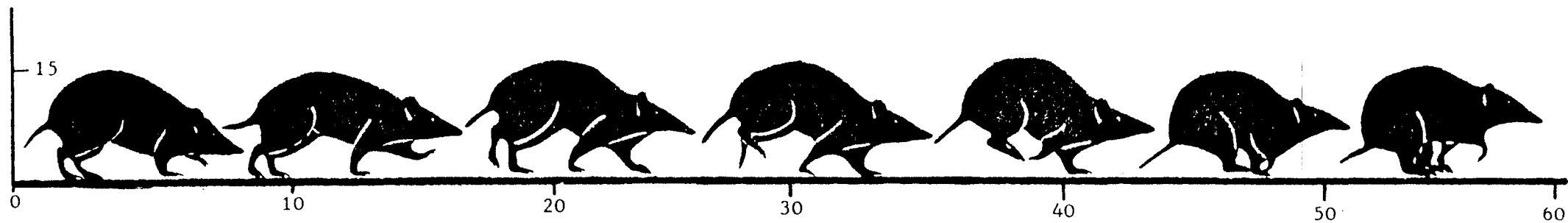
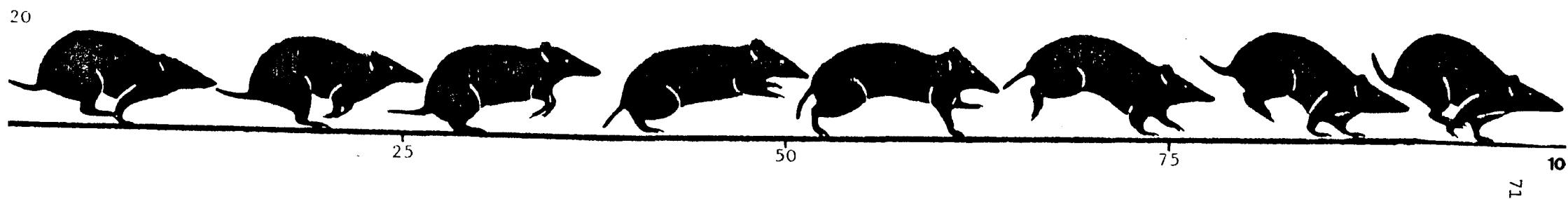


FIG. 3.4.1 Running

NOTE : all numerals represent cm.

FIG. 3.4.2 Galloping



sized images on tracing-paper; on this the dispositions of parts of the body in relation to one another and the substrate could be traced for purposes of subsequent analysis. These illustrations were later reduced in size.

3.4.3 Results

Based on filmed records of locomotion, as well as on observations in the enclosure and arena, four gaits were identified in each of the two species, and associated activities performed during these different locomotory bouts were also recorded. There was no variation between the sexes of either species, except in "prancing" (described later), and males had slightly higher velocities of locomotion because of their larger individual limb measurements, permitting greater lengths of stride. Consequently, all of the measurements and rates of locomotion presented are based on average values obtained for the males and females tested. Minor differences in the gaits were detected between species and these are described below.

The four gaits identified were categorised as slow quadrupedal motion (walking), galloping, fast quadrupedal motion (running) (a gait approximately intermediate of the two latter) and prancing; only observed in the females of both species during sexual interactions (Section 6.3.2). The most rapid form of locomotion recorded in both species was galloping (Figure 3.4.2). This gait was employed by subjects that were excited. This state of excitement was usually initiated by a disturbance such as being chased by an aggressive conspecific or the observer and, presumably predators, since this type of locomotion was employed by an individual of *I. obesulus* when pursued by a domestic dog. In locomotion the propulsion exerted by the hind feet elevated the whole body, particularly the hindquarters. As the hindfeet moved to their original position beneath the body, the weight of the body

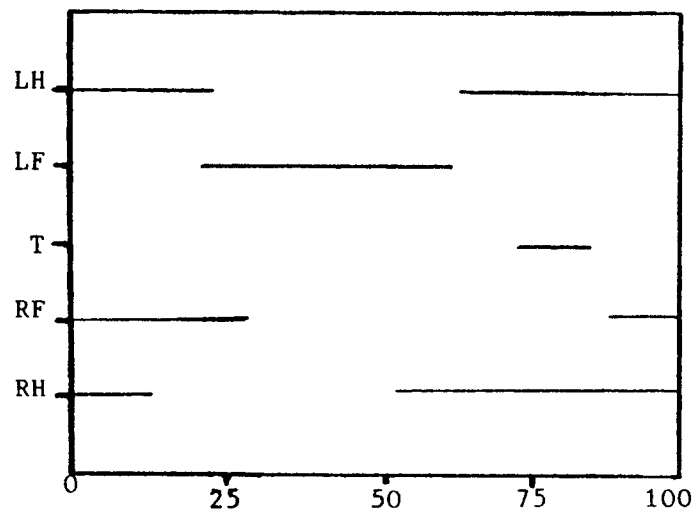
was supported by the forelimbs; sometimes only one of the forefeet was used. The hindfeet finally contacted the ground, with the heels almost aligned with the forefeet which moved caudad as the hindlegs were drawn forward. The animal then raised its forefeet from the ground (also simultaneously) and moved them forward under the lower jaw, at the same time beginning to raise the heels for another thrust from the ground. At this stage, the body was almost horizontal to the ground. The tail did not touch the ground in this form of locomotion and appeared to be used for acquiring improved balance and control in the movement.

The rate of galloping was 3.73 m/s (14.44 k.p.h.) and the length of each stride ranged from 85 - 100 cm (3-4 x body-lengths). *I. obesulus* was unable to increase its rate of galloping if the velocity of the treadmill was increased above the value mentioned. However, *P. gunnii* was able to achieve a rate of locomotion of 4.3 m/s (15.5 k.p.h.) in galloping. Even this is probably a conservative estimate and it is suspected that this species could attain even greater velocities. *P. gunnii* could not be filmed at greater speeds because of the erratic leaping and jumping performed by the individuals, described later. It should be noted here that an individual of this species escaped from the observer while its measurements were being recorded in the field. The observer was able to reduce the distance to the fleeing animal by vigorous pursuit through the dense heath where it was captured, but after the escapee made its way to a path, it was soon lost from sight, because the rate of its movements increased greatly, and its erratic leaping into the air (to an approximate height of 1.5 m) and resuming locomotion at approximately 90° to the direction of its initial progression after landing, rendered pursuit impossible. These unpredictable changes in the direction of progression appeared to be controlled since the stability of the animal upon landing was

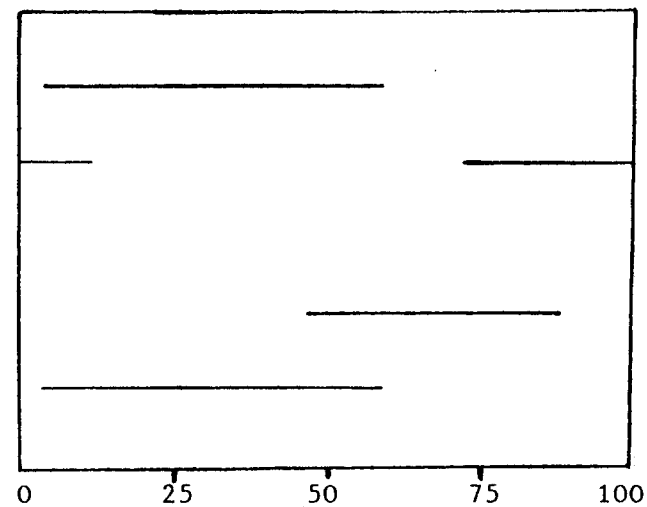
emphasised by the fact that it resumed locomotion in the turned direction immediately. The speed and agility in changing directions exhibited by this animal was most surprising and it appeared as if the gait was bipedal, although this cannot be confirmed. The faster speed of *P. gunnii* was probably less closely associated with an increased rate of the stride (6%) than with an increased length of the stride (20%); presumably due to the relatively longer limbs which members of this species possess and the more powerful thrusting action of their hind feet. A slight variation in the gait was observed at higher velocities. For approximately 5% of the time required to complete a stride, all limbs were elevated off the ground since both forefeet were raised before contact was established between the hind feet and the ground.

Figure 3.4.3 presents the relative amounts (per cent) of time that each limb was in contact with the ground during a full stride of each of the two gaits filmed. In galloping, both hind feet evidently moved synchronously, spending 56% of the time in contact with the ground, whereas the forefeet move asynchronously but both were in contact with the ground for the same period (39%). In the highest rate of galloping achieved by *P. gunnii*, the hind feet only made contact with the surface during 44% of the time and the forefeet in 33% of the time. Asynchronous movements of the forelimbs at higher velocities were not as pronounced as those of the forelimbs of *I. obesulus* at lower speeds.

The second most rapid type of locomotion observed in both species was "running" (fast quadrupedal locomotion). As in the preceding example, both species were quite similar and this gait was employed by subjects engaging in fence-running, pursuing conspecifics, in dense vegetation and moving around in familiar places. As previously mentioned in the context of galloping, the forelimbs moved asynchronously,



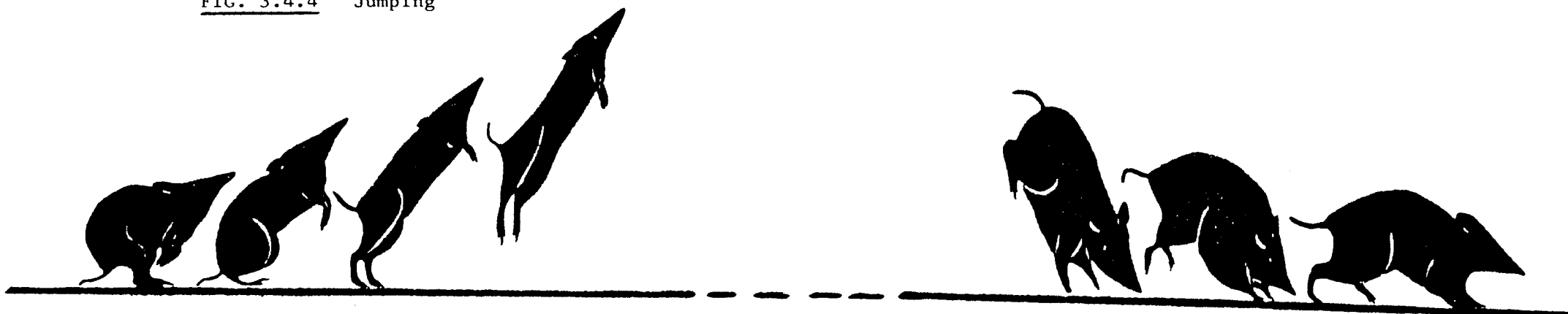
Fast quadrupedal run



Gallop

FIG. 3.4.3 The relative amounts (percent) of time of contact by individual limbs with the ground in each complete stride of the two gaits filmed.

FIG. 3.4.4 Jumping



although this was more pronounced (Figure 3.4.1). The hind limbs also moved separately but both made contact with ground synchronously. *P. gunnii* differed slightly from *I. obesulus* with respect to the latter action, in that the asynchronous movement of the hind limbs was less marked. During most (75%), of the stride at least three limbs were in contact with the ground. As one of the forefeet moved anteriorly and downward, the other moved caudad. At the same time, one of the hind feet was raised from the ground, soon followed by the other. Both hind feet moved forward, finally drawing together and establishing contact with the ground immediately behind the forefeet (which were also moving anteriorly and downward) currently in contact with the ground. At this stage, the caudad-moving forefeet were also moving forward for the next phase of the stride.

The rate of running was 1.86 m/s (6.70 k.p.h.) and the length of individual strides ranged from 50 - 65 cm (2-3 x body lengths). This value was almost precisely comparable in both species. The maximum height attained during the stride was approximately 15 cm, slightly less than that in galloping (17-21 cm); this was most probably attributable to the greater thrust provided by the hind limbs in this form of locomotion. The relative amount of time (per cent) while each limb was in contact with the ground was greater than in galloping (Figure 3.4.3). The longer period of surface contact in running was a result of the lower velocity of this gait. Both hind limbs were in contact with the ground for 62% of the time required to complete a stride, albeit at different times during the stride, and both forelimbs for 43%, also during different periods of the stride. The tail was observed to make contact with the ground in this gait, but only for a small proportion (19%) of the stride. It appeared to have no function since it was limp and hung downward during the process of locomotion.

The slowest type of locomotion observed was "walking" (slow quadrupedal motion). Unfortunately, the subjects of neither species appeared to maintain a steady gait on the treadmill at such low velocities; filming was therefore not attempted. Instead, individuals of both species were observed in the naturalistic conditions of the enclosure where rates of walking were calculated by timing subjects as they moved across the 1 m² grid-pattern of wooden stakes positioned around the enclosure. The duration of each stride varied considerably, as did recorded velocities (0.20 - 0.90 m/s; 1.08 - 3.24 k.p.h.). The strides ranged from 15 - 45 cm (0.5 - 1.5 x body-lengths). The gait was very similar to that employed in running, except that the asynchronous movement of both fore- and hind limbs was more pronounced. The alternating movements of forelimbs was followed by movements of contralateral-hind limbs. This asynchronous movement of the hind limbs in *P. gunnii* was also not as conspicuous as in *I. obesulus*. The gait was employed in foraging, approaching conspecifics and unfamiliar objects, and prey such as those used in studies of prey-killing behaviour (Section 4.3.3). The hind feet were usually in contact with the ground for longer periods during the stride than the forefeet and the tail was also dragged loosely behind on the surface for most of the stride. The body and lower jaws were positioned close to the ground.

A fourth and final gait observed, "prancing", was only observed in female subjects of both species. This gait was adopted by females when approached and followed by male conspecifics. Female individuals usually jumped in the air and landed on the digits of all four feet synchronously, almost immediately springing back in the air and subsequently landing again on the digits of each limb. The rate of prancing could not be determined, but it was more rapid than the walking already described (pers. obs.). As this gait was only observed in the context of sexual interactions and the male usually concluded

by mounting the female, it may be possible that it plays some role in courtship behaviour.

Some features of the jumping behaviour, described earlier, were also recorded on film. The initial propulsive action and landing of an individual *P. gunnii* are presented in Figure 3.4.4. Jumps were performed when approached or chased by conspecifics, individuals of *I. obesulus* or the observer. Both species performed this type of activity, but *I. obesulus* was only able to attain heights of approximately 0.5 m (only ca. a third of those achieved by *P. gunnii*). During jumping the powerful thrust of the hind limbs elevated the whole body from the ground. The hind limb was fully extended to provide this propulsion. The body was elevated vertically and projected forward. Before landing, the forefeet were extended to reduce impact and the snout almost made contact with the substrate upon landing. The tail appeared to play a more important role in jumping, than in any of the other types of locomotion. It was raised and curved upward distally during the process of launching and was not always held at the same position during the ensuing stages of the jump. The tail was maintained clear of the ground throughout the stride and appeared to be employed in a rudder-like fashion.

Climbing was also observed in captive subjects of both species and consisted essentially of the same movements that were described for walking, except that these were transposed to the vertical plan and were performed on the wire-mesh of holding cages and the enclosure. It is doubtful if this behaviour commonly occurs in natural situations.

3.4.4 Discussion

I. obesulus and *P. gunnii* were observed to exhibit generally similar gait-patterns. The gaits investigated in this study have not been described in detail previously. Minor differences between the species in the different types of locomotion were noted. The greatest difference

observed was the fact that *P. gunnii* was able to achieve higher rates of locomotion than *I. obesulus*.

High speed requires that long strides be performed at rapid rates. Longer limbs may be expected to be capable of longer strides, but this does not necessarily mean that speed can be increased merely by the enlargement of the animal; a larger animal is likely to have a lower rate of striding. Therefore, cursorial forms, capable of rapid running generally possess longer legs in relation to other parts of the body (Hildebrand 1960). In particular, the parts of the limbs that are distal to the body (the feet, shanks and forearms) are elongated by comparison to the parts proximal to the body (the thighs and upper arms). These relationships apply to the two species of bandicoot observed in the present study. *P. gunnii* has greater limb-measurements than *I. obesulus*; consequently it is able to attain greater lengths in its stride. It is also usually lighter than *I. obesulus*, and this feature permits increased rates of striding. The constallation of these two factors appears to endow *P. gunnii* with the ability to achieve greater velocities.

It also appears that the habitat which a given species utilises may influence the evolution of its gait. Woodland forms such as *I. obesulus* are probably slower since dense vegetation may obstruct rapid fast movement; therefore, camouflage and a cryptic nature may be more effective adaptations for defence against predators rather than speed and agility as possessed by *P. gunnii*, a form occurring in more open habitat. The high leaping and unpredictable changes in direction observed in *P. gunnii* may be useful strategies in evading predators and attacks from conspecifics. Erratic behaviour similar to this (protean phenomena) occurs widely throughout the Animal Kingdom, and has been described for a number of animals by Humphries and Driver (1970) and Chance and Russell (1959). It is believed that this type

of unsystematic motion could prevent a predator predicting in detail the position or actions of the prey. Sustained high-velocity locomotion may not be an essential requirement of *P. gunnii*. Heinsohn (1966) observed that individuals of *P. gunnii* usually seek cover if disturbed and this may explain why numbers of this species were trapped in woodland habitats adjacent to pastures (Section 5.3.3). An evasive locomotion following a rapid start and a short dash to cover or a refuge may be the most appropriate stratagem for avoiding predators by such species.

Although the gaits observed in both species appeared awkward, this is quite deceptive because both species were, in fact, very agile. The different gaits appear quite unique, particularly galloping and prancing. A survey of the relevant literature revealed that only a few species employ types of locomotion somewhat tenuously resembling those described. The crawling gait of the genus *Antechinus* (Haynes, in press) and the quadrapedal locomotion of eutherian kangaroo-rats of the genus *Dipodomys* (Bartholomew and Caswell 1951), appear to have some affinities with the walking and running gaits, respectively, of *I. obesulus* and *P. gunnii*, although the nature of the activity was different in both cases. The crawling gait of the genus *Antechinus* was employed while moving along a branch of a tree or narrow ledge and the quadrapedal locomotion of the genus *Dipodomys* was utilized in moving only short distances.

Further investigations are required in this area of behaviour, particularly based on field-records of subjects in natural situations. By this means, a full inventory of various locomotory activities may be acquired and subsequently analysed.

CHAPTER 4

FEEDING BEHAVIOUR AND DIET

4.1 FORAGING AND FEEDING

4.1.1 Introduction

Descriptive accounts of feeding activities are scarce in the literature pertaining to marsupials, although they are of considerable importance in understanding several of the broader aspects of the behaviour and ecology of the animals.

The digging-actions employed by bandicoots have been described by Troughton (1965) and Stodart (1966); this type of activity has also been recorded in smaller macropods, notably *Potorous tridactylus* (Le Souef *et al.* 1926) and *Bettongia lesueuri* (Stodart 1966). Ewer (1968) provided brief notes on the feeding behaviour of *Sminthopsis crassicaudata* and Hall (1980) investigated the diets of two sympatric species of the genus *Antechinus*. The digestive physiology and nutrition of several species of bandicoots have been described by Hume (1982) and Heinsohn (1966) made a detailed study of the diets and feeding methods of the two species of bandicoots investigated in the present study (*Isoodon obesulus* and *Perameles gunnii*). The major food items taken by the two species were similar and consisted mainly of earthworms, adult beetles, scarabid larvae as well as other larvae, moths and pupae. Occasionally small vertebrates such as frogs and skinks may have been eaten but these did not appear to be a very important part of the diet. The only plant-products extensively used by *P. gunnii* and *I. obesulus* were ripe blackberries and boxthorn berries, particularly in the warmer months of the year when other food sources (in the soil) were scarce.

Wood-Jones (1924) considered that *I. obesulus* scratched at the roots of vegetation with the objective of obtaining insects associated with the latter, rather than the roots themselves. In captivity, he provided individuals of *I. obesulus* with roots and fruit but these

were not eaten, whereas bread, meat, insects, snails, birds and mice were all readily devoured. Analysis of the stomach-contents and faeces of *I. obesulus* by Sampson (unpubl.) revealed a predominance of insect-cuticle remnants. Opie (1980) also inspected the faeces of *I. obesulus* and reported that the most important dietary item consisted of larvae of scarabid beetles. Other major items were tinebrionid larvae, earwigs, hemipterans, ant-pupae, adult scarabid beetles and fungi (Family Endoraceae).

Heinsohn (1966) reported that *I. obesulus* and *P. gunnii* spent most of their time foraging and feeding when active outside the nest and such behaviour involved digging in the soil with the forepaws to produce small, conical holes of barely sufficient dimensions to insert the snout. Olfactory stimuli were apparently utilised to locate food.

Studies on the drinking behaviour of marsupials have also been scarce and published accounts are generally concerned with the larger macropods (Ealey 1967; Russell 1974). Ewer (1968) made some observations on *S. crassicaudata* and Stanbury (1970) reported that although bandicoots drink water in captivity, sufficient moisture is obtained from their diets and from dew in the wild.

Unfortunately, the majority of the studies mentioned have not been based on quantitative information. Therefore, the present investigation included attempts to obtain quantitative records and descriptions of the feeding, drinking, and digging activities and the diets of *I. obesulus* and *P. gunnii*. The methods of prey-killing and associated forms of behaviour are discussed in Section 4.3.

4.1.2 Materials and Methods

Several methods were employed in the present study to monitor the foraging and feeding in *I. obesulus* and *P. gunnii*. Firstly, observations were made on the types of behaviour associated with eating

the regular rations of food supplied to subjects in their holding cages (Section 2.2). Secondly, quantitative data on the times spent eating, drinking and excavating were obtained of subjects placed in an outdoor enclosure, as described in Section 3.1.2. Data were analysed using three-way analyses of variance and graphic illustrations, showing the mean values (and standard errors) of the durations of particular activities in each hour of the observation period, were prepared. Thirdly, excavations located in the field were measured with the aid of vernier calipers. The depth and diameter of each excavation was recorded, in conjunction with its locality (i.e. pasture and grassland areas - open habitats or woodland and scrub areas - dense habitats). The dimensions of excavations in the enclosure were also measured by the methods described above. Fourthly, faeces were collected from the traps which held captive subjects, by placing plastic bags under the traps (Section 2.1). It was hoped that subsequent inspection of the scats may provide useful information about the diets of *I. obesulus* and *P. gunnii*, as such methods have been successfully employed by Kitchener (1967). However, few samples of faeces were obtained because the digging actions employed by captive specimens while attempting to escape from the traps usually resulted in the scats being damaged or buried and being rendered undetectable in the soil under the traps. However, analyses of the contents of the digestive tract were performed on the two subjects found dead in the traps.

4.1.3 Results

Both *I. obesulus* and *P. gunnii* appeared to locate food-sources mainly by olfaction. Items of food placed in the containers in the holding-cages and in the enclosure were regularly approached with frequent lateral movements of the snout and audible sniffing. However, subjects generally moved directly to the food containers after emergence

from the nests, whether food was present or not. This behaviour appears to indicate that the subjects may have learned to approach the food-containers without requiring guidance by olfactory stimuli thereafter, perhaps as part of their topographical-learning strategy.

While maintained in the enclosure, individuals of both species traversed the whole of the floor area, apparently unsystematically. During this process, the head was lowered and sniffing and lateral turns of the face to either side of the body were frequently observed. Nasal contact was often made with the ground (Figure 4.1.1). Figure 4.1.2 summarizes the frequencies (numbers of times per h) of such contact with the substrate in individuals of *I. obesulus* and *P. gunnii* and also the frequencies with which the latter type of tactile activity occurred throughout the ten observation periods in which each of the two species were studied. The most conspicuous feature of the distribution of these events is the significantly greater frequency of large, rather than small numbers of times when the nose made contact with the ground in individuals of *P. gunnii* (t-test; $P < 0.001$; d.f. = 98). The mean numbers of naso-substrate contacts per hour recorded in ten individuals of each of *I. obesulus* and *P. gunnii* were 10 and 19, respectively.

When regular food-sources were provided, subjects of both species usually approached the food-containers directly, without any apparent hesitation and immediately began to eat. The smaller food items such as blood and bone pellets, "Pal meaty-bites" and meal worms were taken in the mouth during eating but large food items such as quarter-portions of apples and slices of bread were braced against the substratum with both forepaws while pieces of the food were detached by backward jerks of the head. When mealworms were provided, they were quickly sought out from amongst the rest of the food material and devoured. Mixed bird seed was lapped up with the tongue. Food

FIG. 4.1.1 NOSING THE GROUND

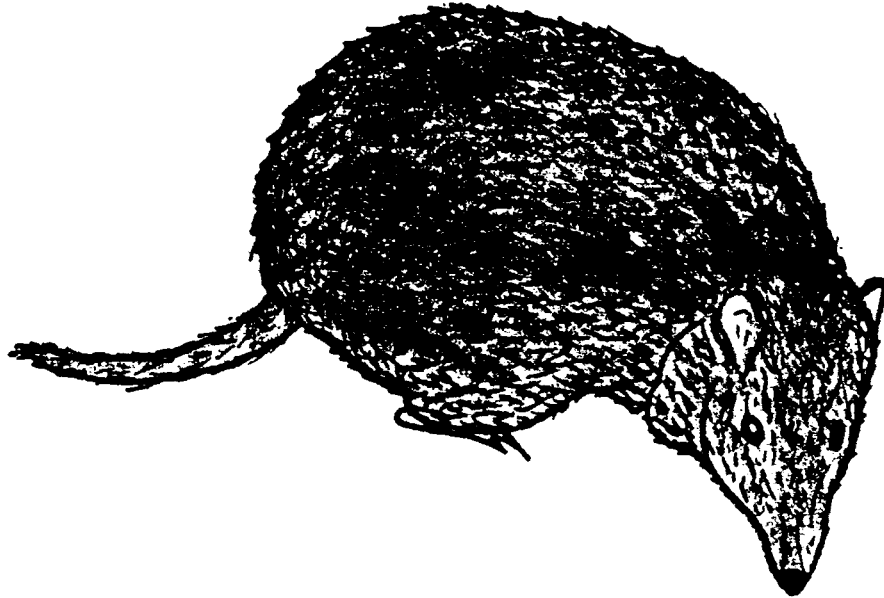


FIG. 4.1.3 Using the molars and premolars to crush large and hard food items (eg. "Pal meaty-bites").

Occasionally, the forepaw was employed to hold the food item in the mouth.

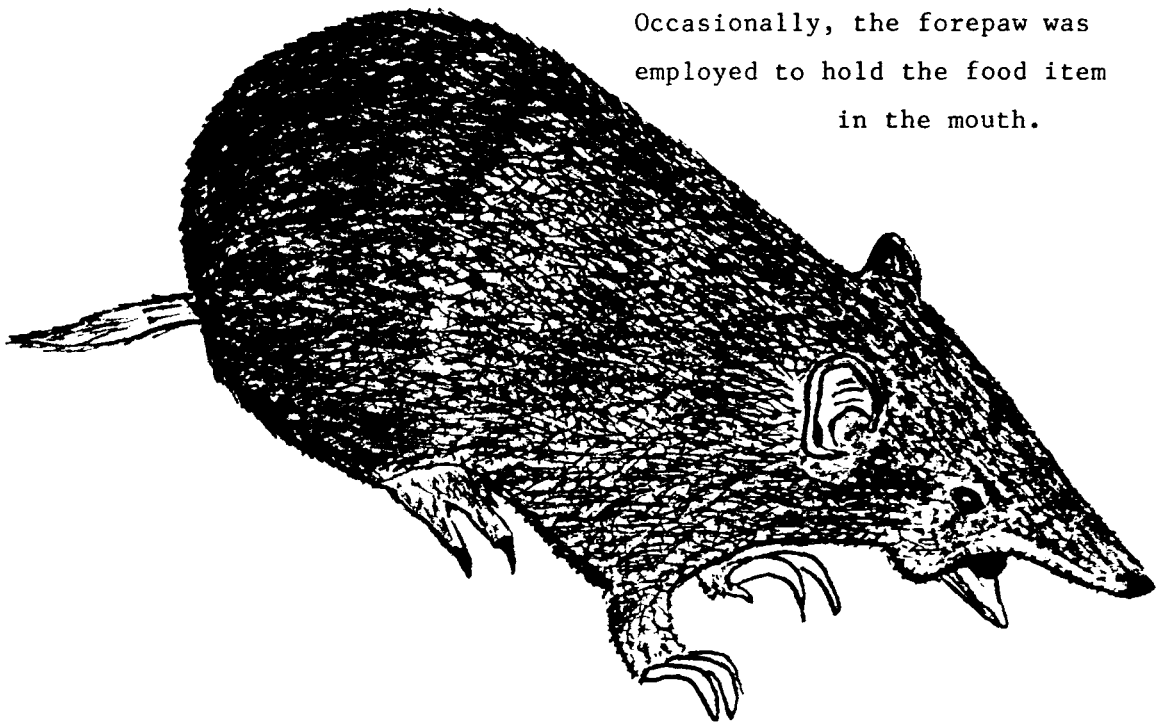
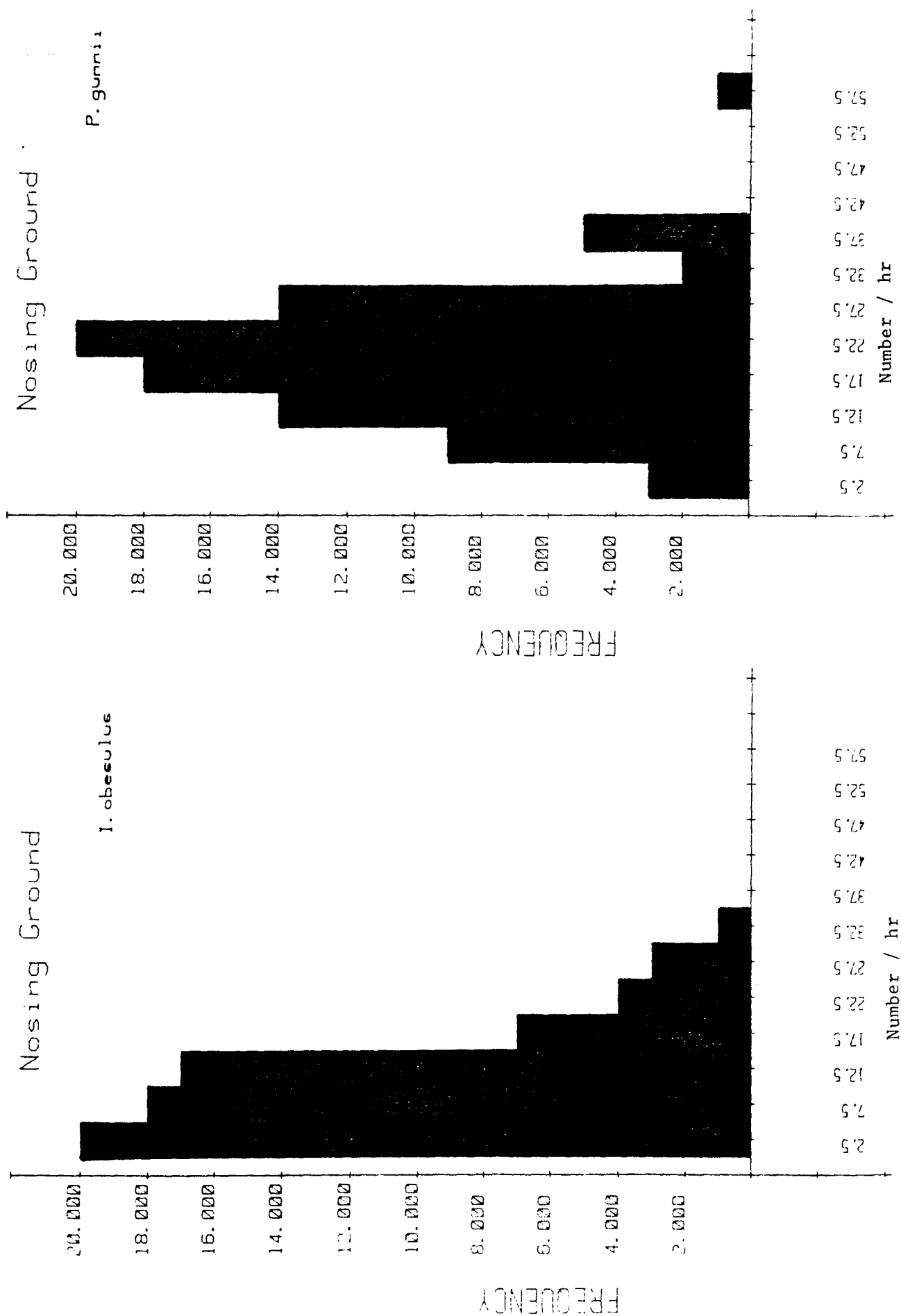


FIG. 4.1.7 EXCAVATING



FIGURE 4.1.2 The distribution of frequencies with which varying numbers of nosing the substrate per hour occurred in ten individuals of *I. obesulus* and *P. gunnii*.



was always eaten in a quadrupedal posture, with the dorsum slightly arched and the head lowered in the direction of the food. The forepaws were never observed to convey food to the mouth but they were occasionally employed to hold food items of very solid consistency ("Pal meaty-bites") in the mouth which were subsequently crushed with the molars and premolars. Only one forepaw was used at a time; this depended on which side of the mouth the food item was positioned. The head was inclined to one side while eating hard food items (Figure 4.1.3) and vertical, bobbing movements of the head were also associated with the activity. Hoarding or carrying of food items was never observed.

The methods of feeding described were very similar in individuals of both *I. obesulus* and *P. gunnii*. However, the times spent eating the artificial food items supplied differed significantly between the two species ($P < 0.001$). Table 4.1.1 presents the summarized results of analysis of variance applied to the times spent eating recorded in subjects of *I. obesulus* and *P. gunnii*. A highly significant difference between the amount of time spent eating during different hours of the observation period occurred ($P < 0.001$). After emergence from the nest, subjects of both species spent large amounts of time eating for the first few hours, then a gradual decline in this activity was observed. Figure 4.1.4 summarizes the mean values (and standard errors) of the times spent eating, recorded in five individuals of *I. obesulus* and *P. gunnii* in each hour of the observation period. The trend in generally decreasing eating-activity is easily discerned, although there was considerable variation among individuals of both species. The mean values obtained for the amounts of time spent eating in each hour of the observation period were 5.28 min and 10.12 min for *I. obesulus* and *P. gunnii*, respectively.

The interaction between the sources of variance (i.e. difference

TABLE 4.1.1 Two-way analyses of variance of the times spent eating, recorded in subjects of *I. obesulus* and *P. gunnii* (using replicates of five subjects of each species).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects (differences between species)	1	400.33	12.99	0.001
2. Hour of observation period	14	95.09	3.08	0.001
Interaction	14	93.12	3.02	0.001
Residual	120	30.84		
Total	149	54.33		

between species at different hours of the observation period) was also highly significant ($P < 0.001$), further illustrating the allotonic activity-cycles of *I. obesulus* and *P. gunnii*. Figure 4.1.5 summarizes the mean values (and standard errors) of the durations of bouts of eating. A general decline in the durations of bouts of eating during the observation period was evident in *P. gunnii* but not so for *I. obesulus*. There was also considerable variation between subjects of both species with respect to duration of bouts of eating and one individual, a male *I. obesulus*, ate for 22 min 5 s in the first hour after its emergence.

The behaviour associated with drinking was also observed while animals were maintained in their holding cages and in the enclosure. A quadrupedal posture was assumed by individuals of *I. obesulus* and *P. gunnii* while drinking. The head was lowered towards the water-container and the forefeet were generally placed on the rim of the latter. Water was lapped up with rapid thrusts of the tongue and the head was seldom raised until drinking had ceased. Although water was always available in all test-situations, drinking activity was negligible and often infrequent, occurring mainly after bouts of feeding.

FIGURE 4.1.4 Mean values \pm one standard error of the amounts of time 89 spent eating, recorded in five individuals of *I. obesulus* and *P. gunnii* in each hour of the observation period.

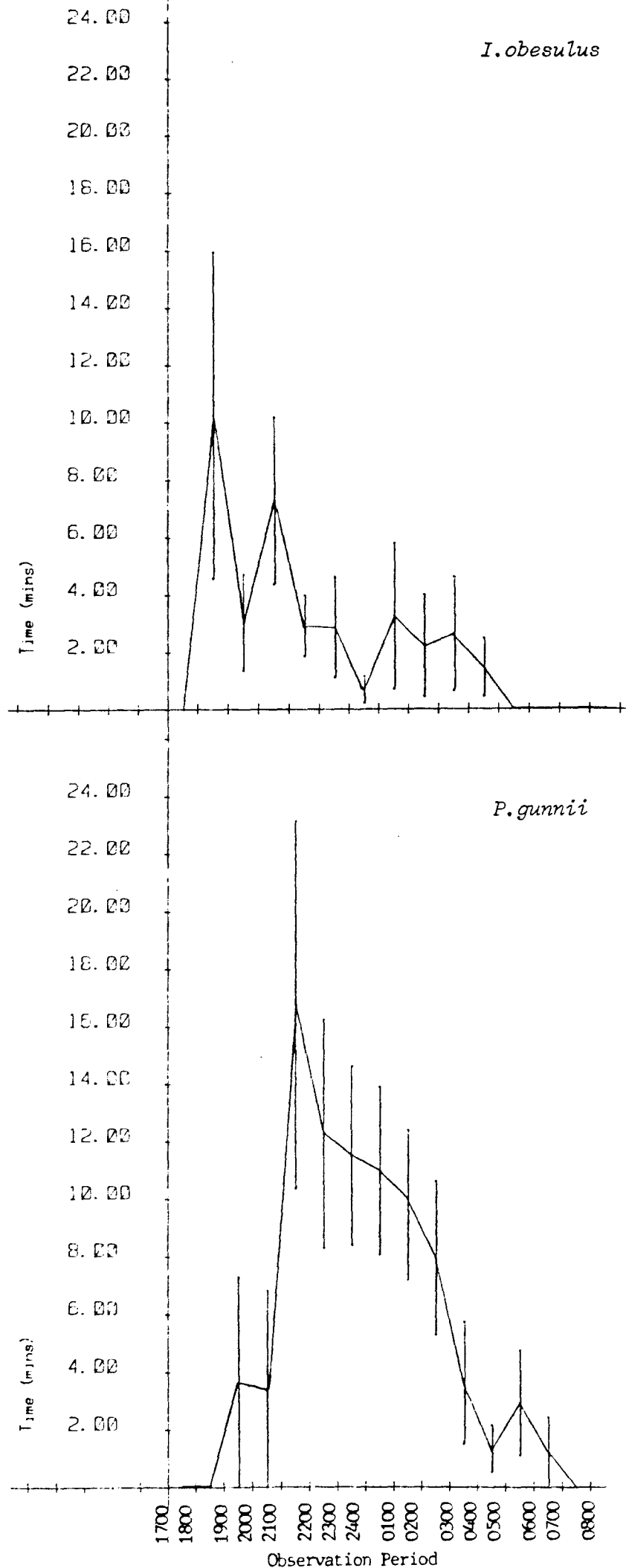


FIGURE 4.1.5 Mean values \pm one standard error of the durations of bouts of eating recorded in five individuals *I. obesulus* and *P. gunnii*, in each hour of the observation period.

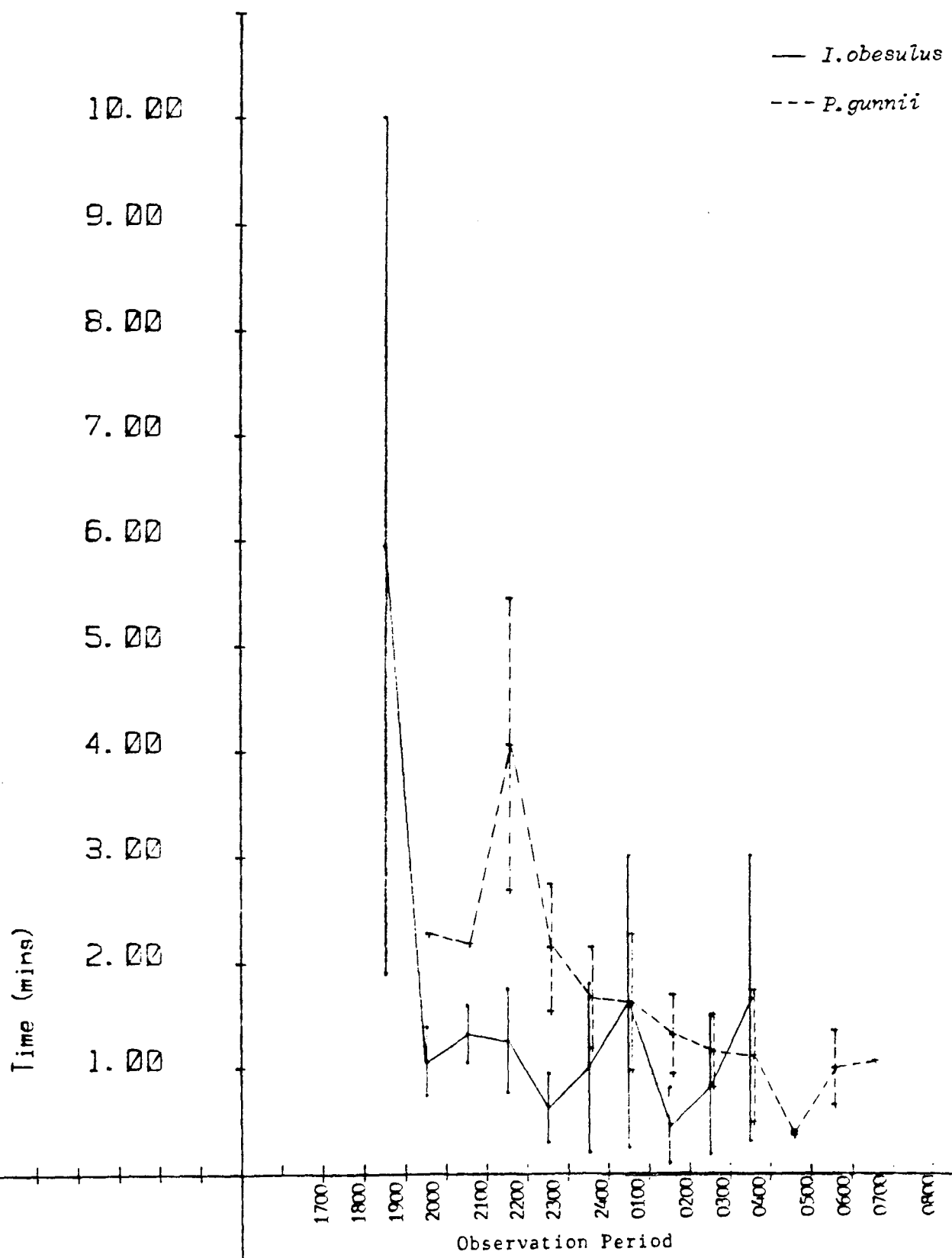


Table 4.1.2 and Figure 4.1.6 present the results of three-way analyses of variance and the mean values (and standard errors) of the amounts of time spent drinking, recorded in individuals of *I. obesulus* and *P. gunnii*, respectively. No significant differences existed between the two species with respect to the total amounts of time spent drinking per h (*I. obesulus*, mean = 46 s; *P. gunnii*, mean = 59 s) and this amount was relatively constant during each hour of the observation period, although considerable variation existed between subjects with respect to this parameter. The durations of bouts of drinking ranged from a few seconds to 2 min 48 s, the later value was recorded in an individual of *I. obesulus* when food was present. Drinking was sporadic and some individuals of both species frequently did not drink in every hour of the observation period. However, a significant difference ($P < 0.05$) was observed between the two test-situations, in that both *I. obesulus* and *P. gunnii* spent greater amounts of time drinking when food was present in the enclosure. This was presumably associated with the dry-food diet supplied to the subjects and the increase in the amount of time spent drinking recorded in both species was probably due to an increase in the duration of bouts, not an increase in the frequencies of drinking-bouts.

Digging behaviour was similar in all individuals of *I. obesulus* and *P. gunnii* observed and involved vigorous asynchronous scrabbling backward motions of the forefeet. The claws of these were used to scrape the surface of the soil and the dorsum was arched during the process (Figure 4.1.7). Nosing the ground, as previously described, almost invariably preceded digging attempts. The accumulated soil remained under the abdomen of the digging animal and was not kicked behind it. The head or snout were not seen to be employed for removing loosened material from the excavated hollow. Digging activities were accompanied by inserting the snout in the excavations, followed by

TABLE 4.1.2 Three-way analyses of variance of the amounts of time spent drinking, recorded in subjects under the following categories: *I. obesulus* - food absent, *I. obesulus* - food present; *P. gunnii* - food absent, *P. gunnii* - food present (using replicates of five subjects in each group).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects (food present or absent)	1	2.13	5.49	0.05
2. Within groups of subjects (difference between species)	1	0.92	2.39	n.s.
3. Hour of observation period	14	0.55	1.42	n.s.
1 x 2 interaction	1	0.05	0.14	n.s.
1 x 3 interaction	14	0.36	0.93	n.s.
2 x 3 interaction	14	0.47	1.22	n.s.
1 x 2 x 3 interaction	14	0.25	0.66	n.s.
Residual	240	0.39		
Total	298	0.47		

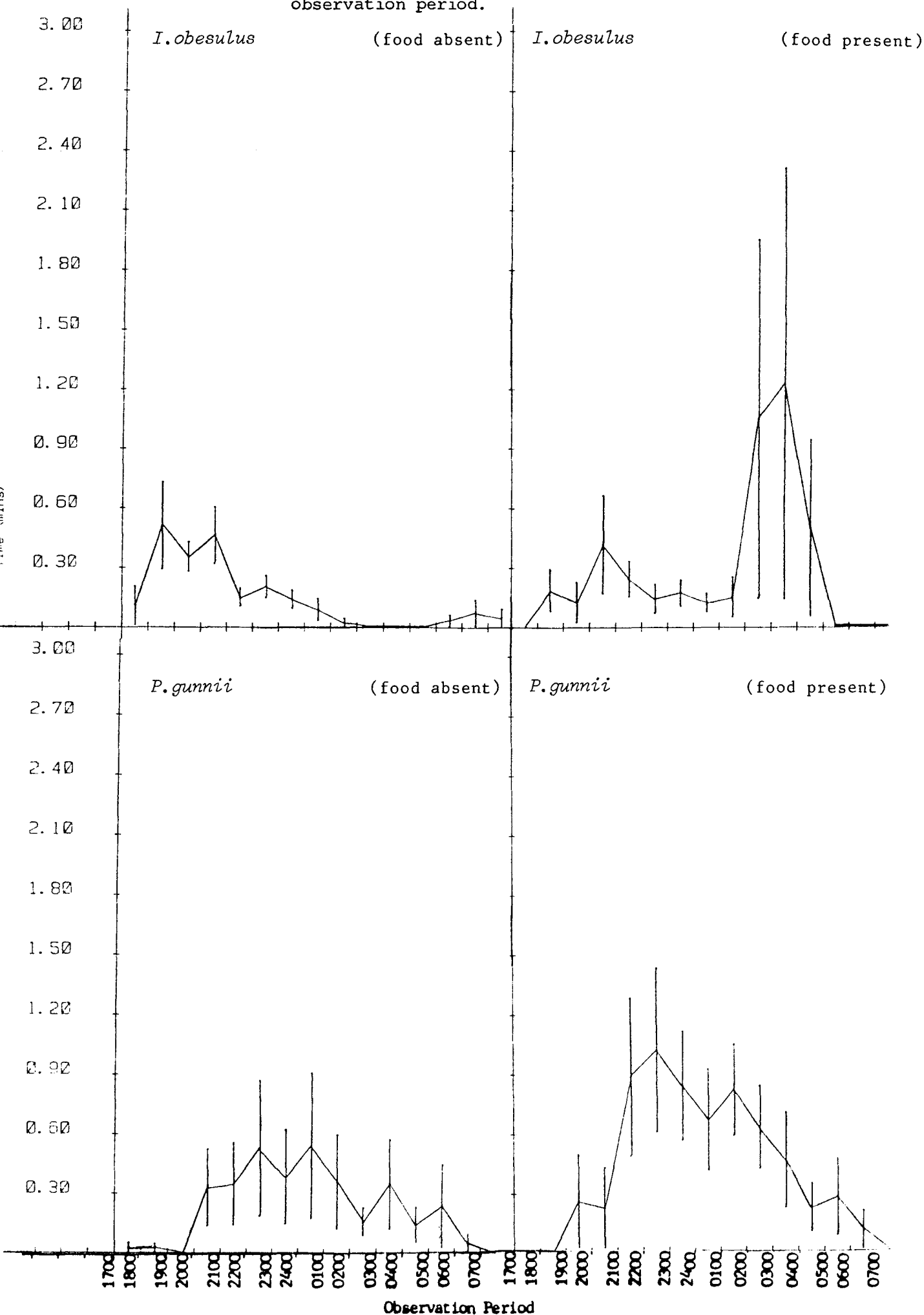
removal of food-items, using the mouth. Digging behaviour was not observed in the field but the excavations made by bandicoots were frequently encountered (Plate 2.2a).

Table 4.1.3 and Figure 4.1.8 present the results of three-way analyses of variance and the mean values (and standard errors) of the amounts of time spent excavating by individuals of *I. obesulus* and *P. gunnii*. Significant differences were recorded between the species and with respect to the presence and absence of food ($P < 0.001$ in both cases). Individuals of *P. gunnii* spent much greater amounts of time excavating than did *I. obesulus*. The presence of food in the enclosure resulted in a decrease in the digging activities of both species, particularly of *P. gunnii*. The mean values of the total durations of time devoted to digging per h in the test-situations

FIGURE 4.1.6

Mean values \pm one standard error of the amounts of time spent drinking, recorded in five individuals of *I. obesulus* and *P. gunnii*, in each hour of the observation period.

93



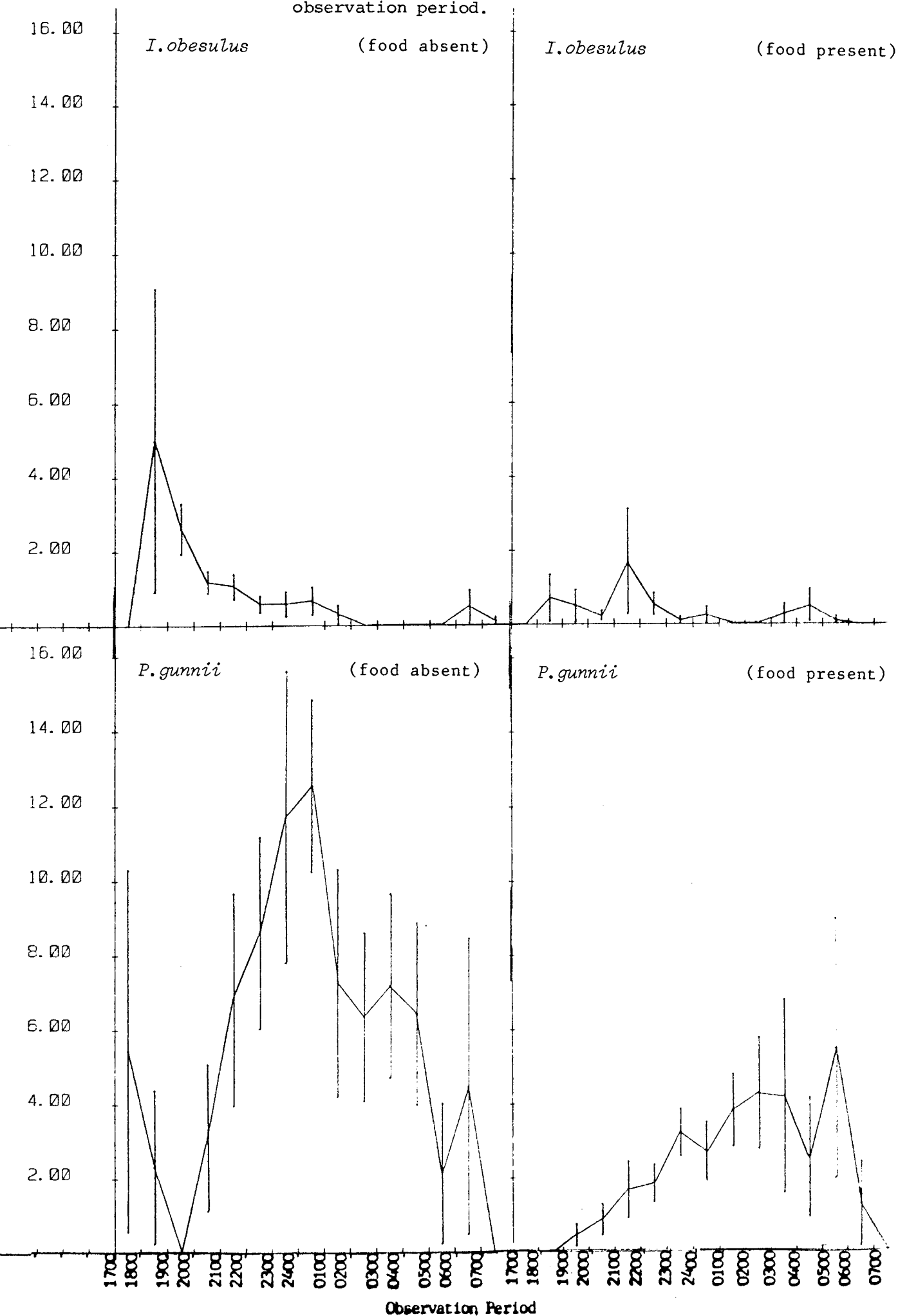
I. obesulus - food absent, *I. obesulus* - food present; *P. gunnii* - food absent and *P. gunnii* - food present were: 1 min 33 s, 1 min 12 s, 10 min 27 s and 3 min 17 s, respectively. The durations of bouts of digging were quite variable, ranging from a few seconds to 8 min 12 s; the latter value was recorded in an individual of *P. gunnii*.

TABLE 4.1.3 Three-way analyses of variance of the amounts of time spent excavating, recorded in subjects under the following categories: *I. obesulus* - food absent, *I. obesulus* - food present; *P. gunnii* - food absent, *P. gunnii* - food present (using replicates of five subjects in each group).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects (food present or absent)	1	414.00	15.32	0.001
2. Within groups of subjects (difference between species)	1	648.68	24.00	0.001
3. Hour of observation period	14	16.48	0.61	n.s.
1 x 2 interaction	1	92.79	3.43	n.s.
1 x 3 interaction	14	16.92	0.63	n.s.
2 x 3 interaction	14	61.67	2.28	0.01
1 x 2 x 3 interaction	14	34.09	1.26	n.s.
Residual	240	27.03		
Total	298	37.58		

It should be noted here that the soil in the enclosure was relatively hard and dry during the course of the study because of the weather conditions then prevailing; therefore, the recorded amounts of the times spent digging by subjects may have yielded conservative estimates. Presumably, this type of substrate supports few invertebrates suitable as food for bandicoots.

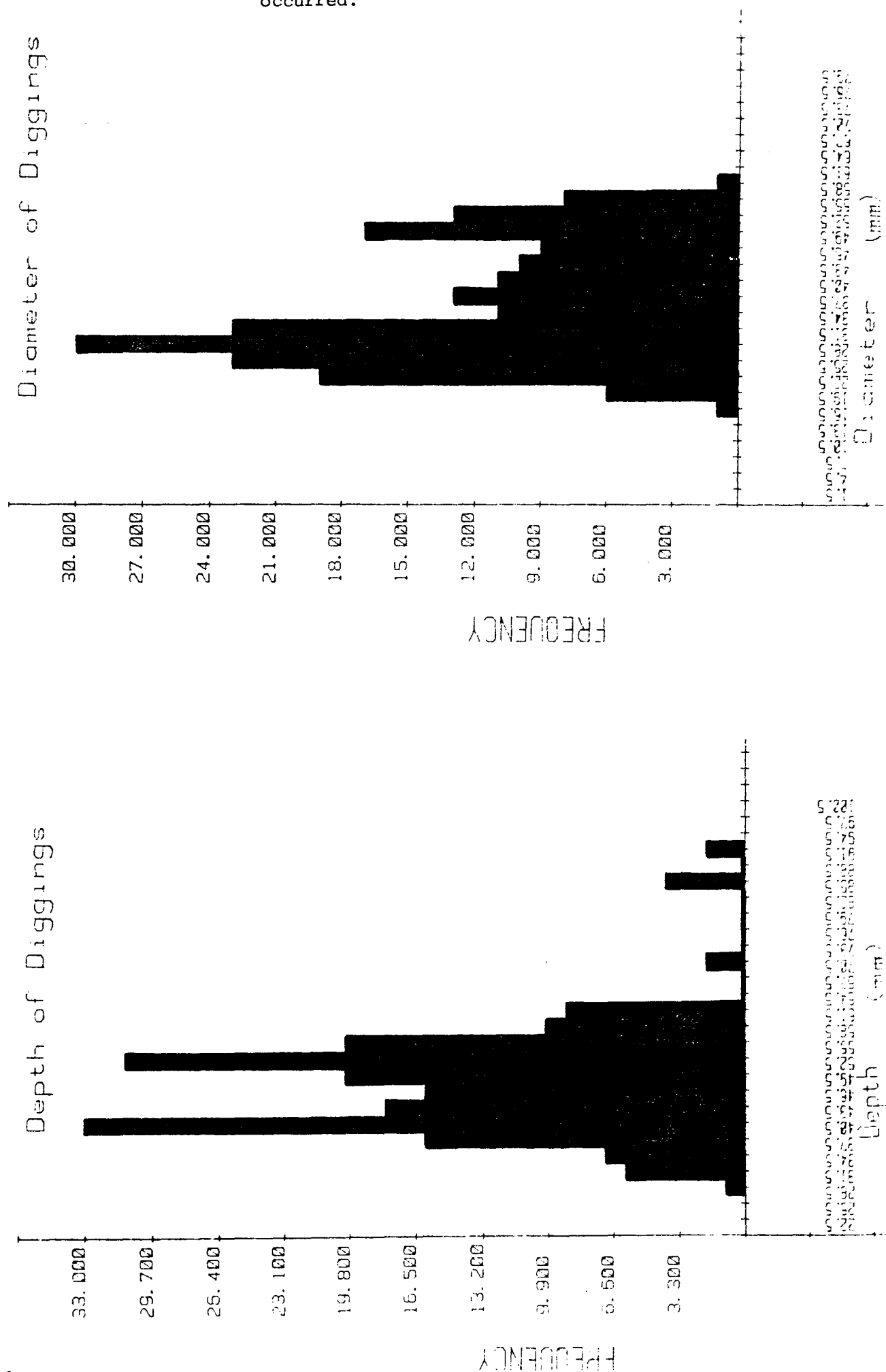
FIGURE 4.1.8 Mean values \pm one standard error of the amounts of time spent excavating, recorded in five individuals of *I. obesulus* and *P. gunnii*, in each hour of the observation period.



The excavations produced by individuals of *I. obesulus* and *P. gunnii* were relatively uniform in character and similar between the species. The majority of those observed and measured were shallow, conical-shaped hollows. Excavations measured in the field were generally smaller, at least judged by their depth and diameter, than those produced by subjects in the enclosure; the latter resulted from the activities of subjects revisiting previously excavated sites and subsequently extending the dimensions of the holes. The dimensions (depths and diameters) of 196 excavations, identified as those of bandicoots, were measured in the field. No attempt was made to differentiate between those made by *I. obesulus* and *P. gunnii*, but the location of each excavation was recorded using two categories - open habitat (pasture, grassland) and dense habitat (woodland, shrub-areas).

Figure 4.1.9 summarizes the dimensions of excavations observed and measured in the field and the frequencies with which the selected parameters were recorded. The depth and diameter of excavations were measured to the nearest 0.1 mm with the aid of vernier calipers. The mean values and standard deviations of the depths and diameters of excavations were 48.28 ± 10.68 mm and 35.25 ± 10.70 mm, respectively, but two peaks were evident with respect to each of the frequencies of the depths and diameters recorded. The larger frequencies of greater dimensions were mainly recorded in denser habitats (mean values and standard deviations of the depths and diameters were 51.6 ± 6.1 mm and 42.0 ± 9.2 mm, respectively; $n = 56$). The mean values and standard deviations of the depths and diameters of 139 excavations measured in open habitats were 46.9 ± 11.8 mm and 32.5 ± 10.1 , respectively. Therefore, deeper and wider excavations were generally observed in the denser habitats.

FIGURE 4.1.9 The depths and diameters of 196 excavations measured in the field and the frequencies with which they occurred.



In an attempt to limit possible bias produced by erosion of the excavations, only relatively recent ones were measured. The majority of excavations were recorded in the open habitat-types but this was probably due to the fact that they were more conspicuous in such areas than in denser habitats and does necessarily reflect greater differential utilization of the former for purposes of digging by the bandicoots, since few captures were recorded in these open areas. Two or three excavations often occurred in close proximity (Figure 2.2a) and in a 1 m² area, the presence of 76 excavations was noted. Faeces of domestic cattle and horses found in the area often bore evidence of bandicoot feeding and associated activities and numerous excavations were located immediately around them.

The diets of *I. obesulus* and *P. gunnii* have been extensively investigated by Heinsohn (1966). Inspection of the stomach contents revealed that similar food items were ingested by both species, consisting mainly of earthworms, elaterid larvae, scarabid larvae, adult beetles, hepialid larvae, phalaenid larvae, dipteran larvae, lepidoptera larvae and box-thorn berries. Small vertebrate animals (frogs and skinks) were also occasionally eaten.

Analysis of scat conducted in the present study also revealed essential similarities in the types of food items ingested by *I. obesulus* and *P. gunnii*. The food of both species consisted mainly of insects (dipteran larvae, adult beetles, earthworms, numerous species of ants, coleopteran larvae) and some plant material (seeds, pieces of grass). The faeces contained a large amount of soil, presumably ingested incidentally, while excavating for food items. Ants were the major food item and this may have been associated with the dry conditions prevailing during the study (possibly being the most abundant dietary item in the areas trapped). A specimen of *P. gunnii* was observed jumping at moths while maintained in the enclosure and

subjects of both species were seen to remove earthworms from the soil by grasping them and jerking the head backwards. While jumping at moths, the individual of *P. gunnii* showing this behaviour was observed to twitch its tail, possibly indicating a state of excitement. Hairs were also detected in the faeces of both species, presumably ingested during grooming activities.

4.1.4 Discussion

The foraging and feeding activities of *I. obesulus* and *P. gunnii* observed in the present study were very similar. Food sources were apparently mainly located by olfaction and the techniques employed in eating varied with the type of food items supplied. Presumably, such variability of the behavioural repertoire associated with feeding activities, is of considerable adaptive value in utilizing a wide range of food sources in natural conditions. Russell and Pearce (1971) observed that *I. macrourus* commonly used the forelimbs to hold food items while eating and this technique was also employed by individuals of *I. obesulus* and *P. gunnii* studied in the present investigation when bracing large food items against the substratum and eating prey (Section 4.3.3). However, food was not delivered to the mouth by the forepaws as described in some species of rodents (Ewer 1971).

Individuals of both *I. obesulus* and *P. gunnii* were very busy during their period of activity, and individuals of *P. gunnii* spent a large percentage of their activity period nosing the substrate and excavating, even when artificial food was supplied. Sniffing at the ground with the head lowered is also a characteristic of foraging opossums, *D. marsupialis* (McManus 1970) and Stodart (1966) observed that individuals of *P. nasuta* spent considerable amounts of time foraging and excavating in the soil. The fact that individuals of *I. obesulus* spent little time excavating may indicate that the species

do not subsist solely on items obtained by such activities and may also obtain substantial nourishment from other sources (Section 4.3); presumably, this may also reduce competition between the species. However, food of this type is generally abundant, hence competition for it may be negligible between *I. obesulus* and *P. gunnii* (Heinsohn 1966).

The principal types of food items recorded in the faeces of both *I. obesulus* and *P. gunnii* were generally similar and the two species were not ecologically separable on the basis of such criteria. Heinsohn (1966) obtained comparable results and the diets of both species appeared to reflect the seasonal and temporal availability of the various components (i.e. abundance of ants and box-thorn berries incorporated into the diet during the drier periods of the year). *D. marsupialis* has also been observed to utilize food which is seasonally or regionally abundant (McManus 1970). It therefore appears that both species exhibit a considerable amount of opportunism with respect to their dietary selection and other feeding habits. The utilization of a wide range of food sources may, in itself, reduce competition between *I. obesulus* and *P. gunnii*.

Plant materials recorded in the faeces of both species may indicate a partly omnivorous diet. Evidence for the latter has been presented by Schultz (1976) and Kerry (1969). Compared with carnivores, omnivores usually have a relatively large caecal cavity, and also longer small intestines, the length or diameter (or both) of the colon may, in addition, be increased. Schultz (1976) observed a specimen of *Perameles* sp. with a colon of large diameter and Kerry (1969) measured the activities of several disaccharidases in the mucosa of the small intestine of *P. nasuta* and *I. obesulus*. The levels of activity of trehalase and cellobiase were substantial in both species. Trehalose is a disaccharide found only in insects, whereas

cellobiose is formed during the katabolism of cellulose. Thus, the bandicoots appear to be adapted to utilizing sugars of both insect and plant origin. By comparison, *A. stuartii* and *Dasyurus maculatus* both exhibit high levels of trehalase, but not of cellobiase, reflecting their predominantly carnivorous/insectivorous dietary habits.

Water consumption was negligible in individuals of both *I. obesulus* and *P. gunnii*. Stanbury (1970) believed that bandicoots obtained adequate quantities of water from their diet and dew. Several other species of marsupials are known to obtain water from the metabolic breakdown of food; this apparently occurs in various species of macropodids (Frith and Calaby 1969). Water intake may be expected to increase when higher temperatures prevail, as has been observed in *S. crassicaudata* (Ewer 1968), but no evidence of such changes have been obtained during the present investigation. Both *I. obesulus* and *P. gunnii* may occur at considerable distances from bodies of free water, as noted in the course of the live trapping programmes (Chapter 5). Therefore, it appears that drinking may not be the principal method of obtaining water and the inferences offered by Stanbury (1970) are probably the most appropriate.

The digging activities exhibited by *I. obesulus* and *P. gunnii* were very similar to those described in other species of Peramelidae. Stodart (1966) described the digging behaviour of *P. nasuta* as consisting of repeated, alternate scratching movements of the forefeet. Presumably, the increased amounts of excavating recorded in the present study when food was absent from the enclosure was due to changes in the motivational states of the subjects (enhancement of the hunger drive).

The observed differences in the dimensions of excavations produced in open and dense habitats may indicate that *I. obesulus* and *P. gunnii* generally forage and feed in different habitats. Those of larger

dimensions were recorded in denser areas, the latter being "typical" of the habitats of *I. obesulus*. However, it should be noted that the dimensions of excavations are probably influenced by numerous and very diverse factors, varying considerably between the two broad categories of habitats, such as soil composition and the depths at which food items occur; these must be examined in detail before any reliable conclusions can be offered.

4.2 DEFAECATION AND MICTURITION

4.2.1 Introduction

Few studies of mammals have included observations on eliminative behaviour. Calhoun (1962) made some brief comments about defaecation and micturition in *Rattus norvegicus* and Ewer (1968) and McManus (1970) described these processes in the marsupials *Sminthopsis crassicaudata* and *Didelphis marsupialis*, respectively. Later investigations have been conducted on *Dasyuroides byrnei* (Aslin 1974), as well as *Antechinus swainsonii* and *A. minimus* (Haynes, unpubl.). The present investigation included some general observations of defaecation and micturition in *I. obesulus* and *P. gunnii*.

4.2.2 Materials and Methods

The behaviour of *I. obesulus* and *P. gunnii* during eliminative activities was observed throughout the course of the study. The behaviour was seldom seen clearly in animals held in the enclosure (Section 3.1.2) but detailed records were made of subjects maintained in their holding cages.

4.2.3 Results

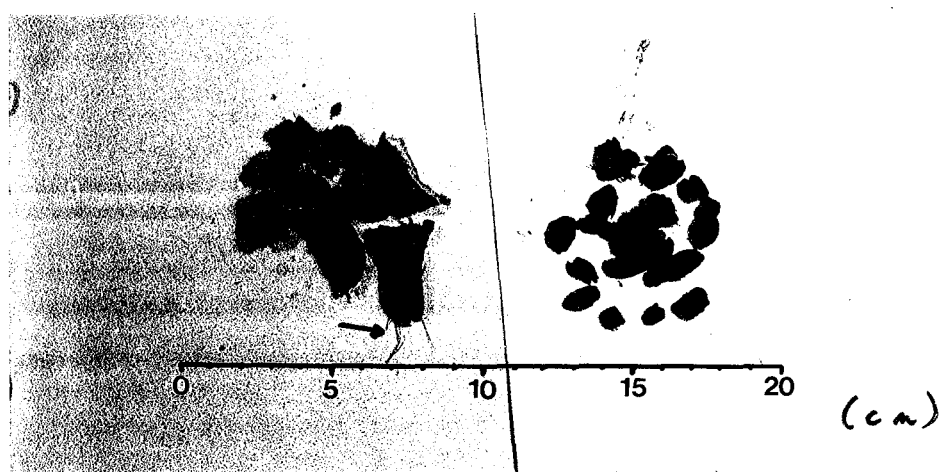
The quadrupedal stance was adopted by both *I. obesulus* and *P. gunnii* while the animals voided faeces and urine. The hind legs were partly separated and the hindquarters were slightly lowered. The tail was raised parallel to the ground and its distal end was occasionally raised. After elimination, the animals generally assumed the positions previously adopted. There was no investigation by the subjects of their faeces or excreta or bouts of dragging the anal area along the surface of the ground as observed in *Sarcophilus harrisii* (Buchmann and Guiler 1977) and *Dasyurus viverrinus* (Moss, unpubl.). Both defaecation and micturition occurred during short, temporary pauses

in locomotion or other maintenance activities.

Little fouling of nests was observed in either species and faeces and urine were generally distributed around the holding cages and enclosure, although there was a noticeable tendency for depositing wastes in and around the food and water containers. The method of elimination at these preferred sites involved turning around after feeding or drinking and elevating the hindquarters over the containers. There was also considerable deposition of faeces on the roofs of the nest boxes.

Faeces deposited in the holding cages and in the traps during capture-programmes were collected and examined. Scats obtained from field investigations were generally 0.5 to 1.2 cm long and 0.3 - 1.0 cm in diameter (Plate 4.2.1). They were usually solid and oval to cuboid in shape. The colour ranged from dark brown to black. Faeces collected from the holding cages were generally much larger, ranging from

PLATE 4.2.1 Faeces deposited in captivity (left) and in the wild (right). Arrow indicates hair present in faeces.



1.0 to 4.5 cm long and 0.6 to 1.4 cm in diameter. These were also solid and of similar form as scats collected in the field. However, the colour of faeces deposited in captivity was usually much lighter, ranging from fawn to brown. There were no differences with respect to the size, shape and colour of scats between *I. obesulus* and *P. gunnii*, either of those collected in the field and captivity. Presumably the

range in size, texture and colour of faeces examined was dependent on the size of the animal producing them and the actual diet of the subjects. The contents of faeces have been previously described, in Section 4.1.3.

No differences were observed between the sexes of either species in regard to the behaviour of elimination and the nature of scats and animals generally voided faeces and urine during handling (i.e. when routine measurements were taken).

4.2.4 Discussion

The elimination behaviour of *I. obesulus* and *P. gunnii* appears to be similar to that described in other mammals. Defaecation and urination in *R. norvegicus* also generally occurred when other activities were in temporary abatement (Calhoun 1962). Studies relating to marsupials in this area of research are limited but Ewer (1968) observed *S. crassicaudata* to simply drop scats while performing normal maintenance activities and during locomotion, although there was some evidence of "deliberate" defaecation in the corners of holding cages and around sources of food and water. No specialised posture was associated with the process, except for a slight lowering of the hind-quarters. There were no sexual differences in observed eliminative behaviours.

Grant (1974) and McManus (1970) also observed apparently deliberate defaecation near food- and drinking-sources in *Macropus giganteus* and *D. marsupialis*, respectively. The negligible extent of fouling of nests described in *I. obesulus* and *P. gunnii* was also evident in *A. swainsonii* and *A. minimus* (Haynes, unpubl.) and *D. viverrinus* (Moss, unpubl.). The fact that most bouts of elimination occurred in and around food and drink containers and on the roofs of the nest-boxes in *I. obesulus* and *P. gunnii* may indicate the use of such products in reassurance of frequently visited areas. Scats detected in the field

probably denote the presence of feeding-sites, since defaecation was usually performed after feeding. Differences in the sizes and colour of faeces between samples collected in the field and from holding cages were probably related to the longer duration of feeding-bouts in captivity and the nature of the artificial diet provided to captive subjects. After emergence, the animals fed for long periods in the first few hours (Section 4.1.3) and this may have resulted in the deposition of larger scats. The lighter colour of the faeces voided in captivity was presumably associated with the light colour of the artificial food supplied. Scats obtained from the field contained much soil (probably from excavating in the latter for food) which resulted in their darker colour.

Rodents of the genus *Peromyscus* (Eisenberg 1962) have also been observed to defaecate and urinate when frightened, in circumstances similar to those recorded in *I. obesulus* and *P. gunnii* when the bandicoots were handled.

4.3 PREY-KILLING BEHAVIOUR

4.3.1 Introduction

Methods of prey capturing and feeding have been described in several species of marsupials. Ewer (1969) provided information on the killing and eating of prey in *Dasycircus cristicauda* and *Sarcophilus harrisii*, as did Buchmann and Guiler (1977) in a study of the latter species. Hutson (1975) described the methods of capturing prey by *Dasyuroides byrnei* and Haynes (unpubl.) reported on killing of mice and associated feeding behaviour by *Antechinus swainsonii* and *A. minimus*.

The prey-killing behaviour of marsupial mice belonging to the genus *Planigales* has been observed by Van Deusen (1969) and Andrew and Settle (1981) and Heinsohn (1966) provided individuals of *I. obesulus* and *P. gunnii* with dead infant mice and noted that they ate such food readily. However, Wood-Jones (1924) reported that *I. obesulus* only ate the heads of carcasses of mice. The aim of the present investigation was to describe the prey-catching and feeding behaviour of *I. obesulus* and *P. gunnii* in captivity in response to different types of prey, activities not previously observed or recorded in insectivorous marsupials.

4.3.2 Materials and Methods

Observations on the prey-killing behaviour of *I. obesulus* and *P. gunnii* were conducted by placing subjects in a 2 x 2 x 1.2 m arena which was surrounded by glass walls for easy viewing and covered by a detachable wire mesh roof. The floor of the arena was constructed of synthetic material and illumination was supplied by a dull red, 25 Watt globe suspended above the arena. The temperatures within the observation room were similar to those prevailing outside and obser-

vations were made from behind a wooden partition with a glass inset.

The prey used were laboratory mice *Mus musculus*, infant domestic chickens *Gallus domesticus*, lizards *Leiopisma metallica*, and frogs *Litoria ewingi*. Larger prey such as laboratory rats *Rattus norvegicus*, a single specimen of wild *R. rattus* and an eighteen-day old domestic chick were also given to selected individuals in an attempt to gain some indication of the maximal possible size of prey that could be subdued.

Three specimens of each species of bandicoot (two males and one female) were individually removed from their holding cages and placed in the arena. All subjects were initially maintained for 30 min in the arena in order to permit them to habituate to their new surroundings before prey were introduced. The same three specimens of *I. obesulus* and *P. gunnii* received mice and chickens as prey, whereas three other subjects of each species received lizards and frogs. Bandicoots were supplied with one of the types of prey in five successive trials. However, two complete days were permitted to elapse between trials conducted on a given individual. All subjects were fasted for 24 h before each test-session and all trials were held between 1900 - 2400 h when the subjects were usually active. Observations were made in the first 30 min after prey were released into the arena. Details of the prey-killing behaviour and feeding were recorded on standard duplicated protocol sheets and various events of the relevant activities were timed, using a manual stop watch; such data included apparent awareness of prey, the commencement of attack, the killing process, the onset and termination of ingestion and apparent loss of interest in the site of killing and feeding. A National Panasonic video-recorder was also employed to film several trials of prey-killing and the activities comprising these were subsequently analysed.

After each test-session, the arena was manually cleaned with a

mop soaked in disinfectant liquid and all traces of scats, as well as parts of carcasses that had not been ingested were removed and subsequently weighed. If no successful attempts at capturing prey were observed in the 30 min trials, subjects were left in the arena over-night with the prey. In the morning, the arena was examined in order to ascertain whether or not the prey had been despatched.

4.3.3 Results

The weights of *L. ewingi* supplied as prey ranged from 1.45 to 4.52 g. No kills were recorded on the 30 occasions when frogs were given to individuals of *I. obesulus* and *P. gunnii*, but their regular ration of food was readily eaten by subjects at the end of each test-session. Specimens of species exhibited similar behaviour in all the trials and no apparent differences were observed with respect to the activities of individuals of different sexes. Bandicoots approached and sniffed at frogs; this behaviour appeared to be investigative in nature. Nasal contact occurred occasionally but the majority of subjects merely sniffed the prey, then proceeded to pursue other, normal maintenance-activities. Movements of frogs appeared to enhance further investigative behaviour, the bandicoots following the frogs and occasionally attempting to pin them to the ground with one or both forepaws. However, as soon as frogs were touched, they generally exhibited uncoordinated jumping and bandicoots thereupon rapidly lost sight of the prey and engaged in sniffing at the area of the floor of the arena previously occupied by the frogs.

Bandicoots that had successfully killed and eaten mice and chickens were also supplied with frogs under similar conditions in the arena, in order to test whether or not previous experience in killing resulted in modification of their prey-killing behaviour but the essential features of the behaviour observed in these subjects were similar to those described above. A single frog was placed in the holding cage

of a male *I. obesulus*. The animal pinned the frog to the substrate and subsequently ate the hind limbs of the prey. The bandicoot then released the carcass and did not return to consume it.

The weights of lizards supplied to bandicoots ranged from 2.14 to 2.76 g and individuals of both species rapidly killed and ate such prey during the first test-session (Table 4.3.1); therefore, subsequent trials of this type were not deemed necessary. The methods of killing and eating lizards were similar in all individuals of *I. obesulus* and *P. gunnii*. The bandicoots approached and sniffed at the prey almost immediately after the introduction of the lizard into the arena. The prey was seized in the mouth and ingestion commenced

TABLE 4.3.1 Durations (s) of the different stages of prey-killing recorded for individuals of *I. obesulus* and *P. gunnii* supplied with specimens of *Leiolopisma metallica*.

Species		<i>I. obesulus</i>			<i>P. gunnii</i>		
Sex		M	M	F	M	M	F
Number		7	13	17	1	7	2
Stages of Prey-killing (s)	"Awareness"	4	4	0	4	9	2
	Attack	5	5	2	5	12	6
	Kill	6	6	7	6	13	6
	Start of ingestion	6	8	7	6	13	6
	End of ingestion	32	14	26	31	27	36

immediately. Occasionally, the forepaws were employed to restrain the prey against the substrate, if it attempted to move away when approached, but there was no manipulation of the prey with the forepaws during the process of ingestion.

Table 4.3.2 summarizes the durations of the different stages of prey-killing and feeding recorded in individuals of *I. obesulus* and *P. gunnii* when the bandicoots were supplied with laboratory mice. Prey were killed only by individuals of *I. obesulus* (14 in 15 trials). Individuals of *P. gunnii* attacked mice by pouncing on them and striking with the forepaws, followed by biting but no successful killing of prey was observed in any of the 30 min observation periods. However, when individuals of *P. gunnii* were left in the arena with the prey overnight, two kills were recorded, although only one of the mice was eaten.

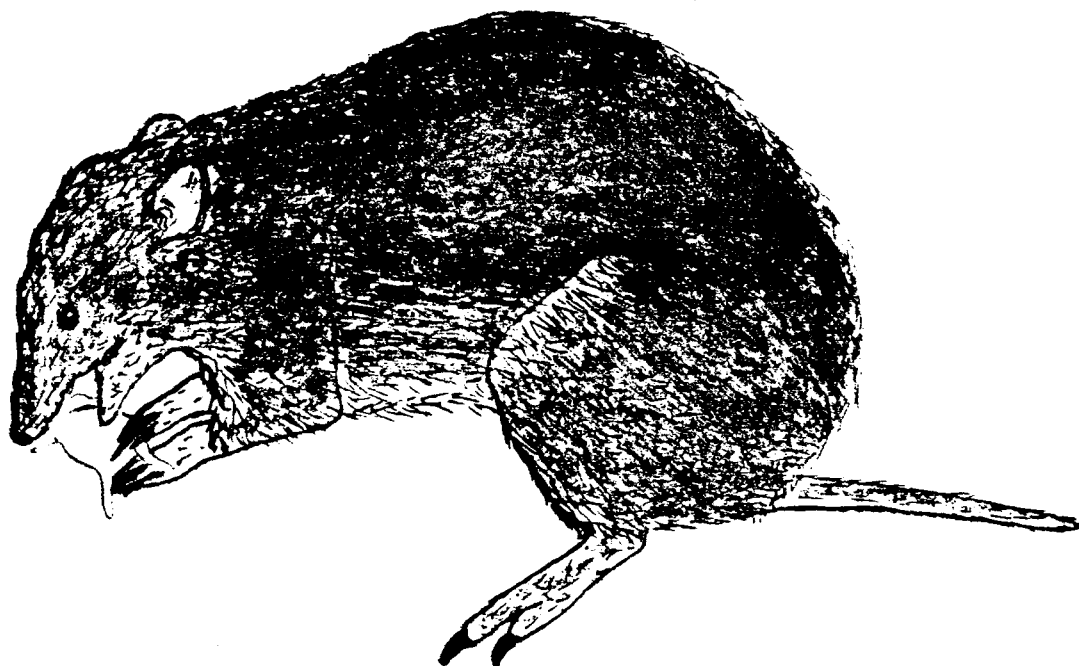
Methods of capturing, killing and eating mice were similar in all individuals of *I. obesulus*. Subjects approached and sniffed the prey almost immediately following its introduction and occasionally nasal contact was observed. Initial attempts to pin the mouse to the substrate by pouncing upon them, using the forepaws, were usually unsuccessful and the mice were able to escape. The bandicoots thereupon generally followed the prey, pouncing on it and biting it on the dorsum and tail. Eventually (usually within one minute after placing the mouse in the arena), the prey was captured and held to the substrate by the forepaws while a bite was delivered to the head region (Figure 4.3.1). This action generally resulted in the death of the mouse but occasionally the bandicoot ran around the arena with the head of the prey held in its mouth, presumably permitting further penetration of the teeth. There was no shaking of the head with the prey in the mouth. The mean value (and standard error) of the times taken to kill prey was 53 ± 10 s, and no correlation occurred between the weight of the mouse and this parameter. The female *I. obesulus* generally required a longer period of time to kill the prey in all test-sessions, apparently because its bites were not precisely oriented towards the anterior end of the mouse but were directed at the dorsum and abdomen.

TABLE 4.3.2 Durations (min) of the different stages of prey-killing recorded for individuals of I.obesulus and P.gunnii supplied with Mus musculus over five successive trials.

Species		<i>I. obesulus</i>														
Sex		M					M					F				
Number		0					1					6				
Trial No.		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Stages of prey-killing (min)	Awareness	0.11	0.01	0.01	0.03	0.02	0.01	0.00	0.01	0.00	0.00	0.05	0.02	0.01	0.00	0.01
	Attack	-	0.02	0.03	0.02	0.03	0.11	0.02	0.03	0.01	0.04	0.13	0.05	0.03	0.01	0.02
	Kill	-	0.23	0.44	0.24	0.22	0.24	0.32	0.15	0.16	0.15	2.03	1.02	1.01	0.56	0.58
	Start of ingestion	-	0.24	0.44	0.24	0.24	0.25	0.32	0.15	0.16	0.15	2.49	1.05	2.20	0.56	0.60
	End of ingestion	-	12.19	19.25	17.62	17.94	18.25	18.45	12.52	15.39	18.62	17.42	37.32	19.58	18.14	17.31
Weight of <i>M. musculus</i> (grams)		36.00	20.37	18.20	24.72	25.17	22.70	18.16	18.32	25.52	19.83	29.00	26.83	19.5	21.30	22.16

Species		<i>P. gunnii</i>														
Sex		M					M					F				
Number		18					1					4				
Trial No.		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Stages of prey-killing (min)	Awareness	0.09	0.25	0.01	0.05	0.02	0.02	0.00	0.09	0.01	0.02	0.05	0.10	0.02	0.02	0.04
	Attack	-	1.00	0.45	0.22	0.14	-	0.12	0.37	1.06	0.13	-	0.23	-	-	-
	Kill	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Start of ingestion	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	End of ingestion	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Weight of <i>M. musculus</i> (grams)		24.45	19.45	16.20	20.41	19.24	19.15	22.90	18.32	23.62	19.25	24.23	19.80	21.32	23.12	18.46

FIGURE 4.3.1 Killing bite directed to head and neck region of mouse. Note the use of the forepaws in holding down the prey.



Eventually a bite was delivered to the head, resulting in the death of the mouse.

Ingestion of the prey occurred almost immediately after the killing-bite was delivered but occasionally rapid, scrabbling movements of the forefeet were directed at the carcass before eating commenced. This activity also occurred during ingestion and the head was always eaten first; presumably as a consequence of the added stimulus of blood drawn from the site of the killing-bite. Prey were eaten at the location where they were killed and a crouched position was adopted during the process. The hind feet were braced and the dorsum was arched. The forepaws grasped the prey around the abdomen and oriented the anterior end of the mouse towards the mouth. The abdominal organs were subsequently eaten and, occasionally, the fur was peeled downwards by the forepaws to gain access to the muscles and viscera. However, the fur, tail and remaining fleshy parts were also eaten subsequently. The head was inclined to the side during ingestion, allowing the molars and premolars to crush and detach pieces from the carcass

(Figures 4.3.2a and b). The head was frequently jerked backwards while chewing at the dead prey, presumably assisting in tearing pieces from it. The variation recorded in the durations of feeding between subjects of *I. obesulus* may be associated with the different motivational state (the hunger of subjects), of these, since durations of feeding were not correlated with the weight of the prey. Subjects often interrupted eating to engage in short bouts of grooming which involved licking the forepaws and wiping the snout with these, presumably removing blood adhering to the muzzle after ingestion. The same type of grooming activity was observed after ingestion had been completed and the part of the floor soiled with blood, where the carcase had lain was also licked clean. In all test-sessions, the whole of a mouse was consumed and lack of interest in the kill-site (i.e. subjects ceasing to return to the latter and nosing the floor) ranged from approximately one to eight minutes. Rapid side to side shaking of the head with the mouse in the mouth was only observed in one test-session and occurred when a male *I. obesulus* bit the dorsum of the prey and the mouse bit the bandicoot on the leg. The subsequent shaking of the head and release of the mouse was so vigorous that the prey was hurtled across the floor of the arena.

The durations of the different stages of prey-killing and feeding recorded in individuals of *I. obesulus* and *P. gunnii* when the bandicoots were supplied with chickens are summarized in Table 4.3.3. In fifteen test-sessions on each species, 14 kills were recorded in individuals of *I. obesulus* but only 3 kills, by one individual of *P. gunnii*, were observed. The times required to kill chicks were longer (mean and standard error = 2 min 57 s \pm 49 s) than those taken by the same subjects in killing mice. This resulted from subjects being generally slower in finally achieving a killing-bite to the head. The behaviour of subjects in trials in which no killing was recorded

FIG. 4.3.2a Eating prey (mouse). Note that the hind feet are braced to support the body while the forepaws grip and position the carcass. The head is inclined, allowing the molars and premolars to crush and slice pieces from the dead prey.



FIG. 4.3.2b Orientation of the initial feeding response. The head of the mouse is eaten first. Note the arched dorsum.



TABLE 4.3.3 Durations (min) of the different stages of prey-killing and feeding recorded for individuals of I.obesulus and P.gunnii supplied with Gallus domesticus over five successive trials.

Species		<i>I. obesulus</i>														
Sex		M					M					F				
Number		0					1					6				
Trial No.		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Stages in prey-killing (min)	Awareness	0.03	0.06	0.01	0.02	0.02	0.02	0.01	0.00	0.01	0.00	0.04	0.08	0.02	0.01	0.03
	Attack	-	0.15	0.02	0.02	0.04	0.05	0.17	0.01	0.01	0.01	0.15	0.10	0.03	0.01	0.14
	Kill	-	2.40	4.09	2.36	2.18	0.09	0.52	1.51	0.46	0.53	10.08	0.40	1.15	1.36	1.21
	Start of ingestion	-	-	4.14	2.41	2.18	0.28	0.52	1.58	0.46	0.55	12.13	0.46	1.17	1.37	1.21
	End of ingestion	-	-	23.00	19.76	20.00	12.27	20.05	19.54	23.21	14.34	29.31	31.40	10.36	27.84	16.47
Weight of <i>Gallus domesticus</i> (grams)		35.22	32.24	36.00	42.16	44.18	52.27	33.61	58.20	47.26	37.74	37.88	43.70	39.40	50.22	42.06
Species		<i>P. gunnii</i>														
Sex		M					M					F				
Number		18					1					4				
Trial No.		1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Stages in prey-killing (min)	Awareness	0.06	0.15	0.03	0.36	0.14	0.02	0.01	0.01	0.00	0.03	0.31	0.01	0.21	0.32	0.00
	Attack	-	-	-	-	-	-	-	0.45	3.16	0.16	-	-	-	-	-
	Kill	-	-	-	-	-	-	-	6.52	4.42	4.46	-	-	-	-	-
	Start of ingestion	-	-	-	-	-	-	-	6.58	4.42	4.46	-	-	-	-	-
	End of ingestion	-	-	-	-	-	-	-	18.21	10.56	13.36	-	-	-	-	-
Weight of <i>Gallus domesticus</i> (grams)		29.43	36.37	52.92	46.63	37.48	32.20	35.70	37.80	66.4	39.31	47.52	35.50	23.24	49.95	59.70

consisted of approaches and sniffing, followed by retreating (quickly turning around and moving away from the prey). Nasal contact was rare and subjects often approached chicks with the mouth gaping. A tripedal stance was frequently adopted during the approach, possibly indicating hesitation or moderate arousal in the animal. When individuals of *P. gunnii* were left in the arena overnight with the prey, three kills were recorded but only two of the carcasses were ingested.

The methods of capturing, killing and eating chicks were very similar to those already described when mice were introduced as prey. Subjects approached and sniffed chicks and then proceeded to attempt to pin them to the floor by pouncing on them with the forepaws. The bandicoots began chewing on the wing or the abdomen while the chick was still alive. Eventually a killing-bite was delivered but not necessarily directed decisively at the head-region. Running around the arena, with the prey held in the mouth was also frequently observed. There was no correlation between the weight of the prey and the time required to kill it and the process of ingestion generally commenced at the head. Rapid, scrabbling movements of the forefeet was also directed at these carcasses and the technique of eating was essentially similar to that previously described for ingestion of mice. In the majority of cases, some parts of the prey remained uneaten (i.e. crop, wings, feet and feathers) and licking of the forepaws and subsequent wiping of the snout were frequently observed during and after ingestion. In one test-session, a male *I. obesulus* killed a chick but did not eat it. Rapid, scrabbling movements of the forefeet were directed at the abdomen of the carcass but then the bandicoot moved away from the site of killing, evidencing no further interest in the carcass except occasional approaches and sniffs. Regurgitation was observed in a single individual of *P. gunnii* after ingestion of the prey concluded. This activity consisted of spasmodic, convulsive movements of the flanks

and gaping. Presumably, this was the result of feathers irritating or obstructing the buccal cavity or throat and the regurgitated food was immediately reingested.

Chicks and mice were supplied to individuals of both species that had not previously received such prey, in their holding cages. In all of these cases, the prey was killed and eaten in the first trial.

Laboratory rats of different ages (sizes) were presented to the four individuals (three *I. obesulus* and one *P. gunnii*) which had previously killed and ingested chickens and mice. Only one of these, male *I. obesulus* (number 1), was successful at killing rats of up to the age of seven weeks after weaning. The remaining subjects were unable to kill rats, three weeks after the latter were weaned, and weighing approximately 40 g. Unsuccessful bandicoots appeared hesitant, approaching the prey and sniffing at it but retreating in all cases without attacking. The tripedal stance was frequently adopted during approaches and nasal contacts were rare.

Male *I. obesulus* (number 1) successfully killed rats of 3, 5 and 7 weeks of post-weaning age; the weights of these prey averaged 40, 96 and 137 g, respectively. The techniques employed in killing 3 and 5 week-old rats were essentially the same as those already described in mice and chicken kills and the time required to kill the rats were 23 and 27 s, respectively. However, the latency to kill a 7 week-old rat was much longer (4 min 36 s) and a different method was used in attacking this prey. The subject immediately attacked the prey after its introduction by biting the rat on the dorsum and the tail, then pouncing on it with the forepaws. After the prey was pinned, bites were directed to the neck, followed by raising the rat in the jaws and striking at its abdominal region with the hind claws. This action was presumably an attempt to stun or disembowel the prey and resulted in flinging it across the floor of the arena, while the bandicoot

toppled awkwardly on its side. However, it then immediately regained its balance and quickly moved over to the "stunned" rat to repeat the sequence of earlier actions. Such kicking movements with the hind feet have been previously described by Wood-Jones (1924) but they were stated to be directed at conspecifics during intense agonistic interactions. The kicks did not result in the death of the rat and a killing-bite was eventually directed at the head. Running around the arena with the head of the rat in the jaws was also observed. Methods of eating the prey were similar to those employed while ingesting mice and chickens but not all parts of the carcasses were eaten. Generally, the tail and the posterior half of the body remained unconsumed.

The same subject also received adult laboratory rats and a wild bush rat (approximately 250 and 175 g respectively) on three occasions. No kills were recorded and the behaviour observed in the presence of such prey indicated hesitation (approaching, sniffing and retreating). In one trial, the bandicoot pounced on a laboratory rat and bit it. However, the rat retaliated by biting the attacker and the latter then spent the remainder (ca. 25 min) of the 30 min observation period attempting to escape from the arena (repeatedly leaping high at the walls).

I. obesulus (number one) was also presented with a 19 day-old chicken weighing 374 g. The time taken to kill this was 5 min 27 s but no killing-bite was recorded. The prey died during the process of being eaten alive. The same technique was employed to disembowel the prey as described in the context of the attack on the 7 week-old rat and ingestion commenced with eating the exposed entrails.

4.3.4 Discussion

The techniques employed by individuals of *I. obesulus* and *P. gunnii* in killing different types of prey appear to be considerably diversified

and resemble many of the methods used by other species of marsupials. Attempts to pin the prey to the substrate with the forepaws is a characteristic of the genera *Dasycercus* and *Dasyuroides* (Ewer 1969; Hutson 1975) and has also been observed in *S. harrisi* (Buchmann and Guiler 1977). Stalking of prey as recorded in *D. viverrinus* (Eisenberg and Leyhausen 1972) was not evident in either of the species of bandicoots observed in the present study and Ewer (1969) did not detect such behaviour in either *D. cristicauda* or *S. harrisi*.

Running with the prey in the jaws has also been observed in *D. viverrinus* (Moss, unpubl.) and Fox (1971) believed this activity to serve the same function as the head-shake of the eutherian carnivores (i.e. securing the grip and ensuring deeper penetration of the teeth). Decisive killing-bites directed at the head of the prey are characteristic of the majority of eutherian predators and several species of marsupial carnivores of the genera *Dasycercus*, *Dasyuroides*, *Planigales* and *Antechinus* (Ewer 1969; Hutson 1975; Andrew and Settle 1981; Haynes, unpubl.) but *I. obesulus* and *P. gunnii* delivered bites towards the anterior region of the prey without any evidence of very accurate orientation and the same lack of accuracy was observed by Ewer (1968) in the eutherian rodent, *R. rattus* when these killed laboratory mice.

Ingestion of the prey beginning at the anterior end and peeling of the skin from the carcass using downward-strokes of the forepaws have been recorded in *S. crassicaudata*, *Dasyuroides*, *Dasycercus*, *S. harrisi* and *Antechinus* (Ewer 1968, 1969; Hutson 1975; Buchmann and Guiler 1977; Haynes, unpubl.).

The observations made in the present investigation suggest that both *I. obesulus* and *P. gunnii* are generalised carnivores/insectivores and may not rely exclusively on nourishment obtained from excavating in the soil. Presumably, the different techniques employed in forag-

ing, feeding and prey-killing (Section 4.1.3) enable both species to utilize a diverse range of dietary items, thereby being adapted at exploiting the seasonal abundance of different types of food-sources. The utilization of such a wide spectra may also be expected to reduce competition between the two species where they occur sympatrically.

The higher success-rates in killing different types of prey observed in individuals of *I. obesulus* and the significantly shorter periods of time they spent in digging during their activity periods (Section 4.1.3) appears to indicate that the specie is more adept at utilizing some types of food-items than *P. gunnii*. The latter species appeared to be unable to kill large prey (mice, rats and chickens) because individuals were less dexterous in holding down prey to deliver killing-bites; this may be associated with the less robust build of individuals of *P. gunnii*, particularly with respect to their weak forequarters.

Although prey were unable to escape from attacking bandicoots in the arena (a situation that would not be expected to occur in natural conditions), it should be noted that the larger prey supplied were not familiar to either species, yet hesitancy on the part of the bandicoots to attack was negligible and the recorded times for a kill were very short in duration. It is, therefore, possible that bandicoots, particularly *I. obesulus*, may take infant mice and chicks of ground-nesting birds when opportunities to do so arise in natural conditions.

The ease with which lizards were killed and ingested by individuals of *I. obesulus* and *P. gunnii* appears to indicate that this type of prey may normally be a regular constituent of the diet of both species, as lizards are relatively inactive and defenceless if excavated from the soil, e.g. around logs, during the night.

Heinsohn (1966) recorded the presence of remains of frogs among the stomach contents of individuals of both *I. obesulus* and *P. gunnii*.

However, no kills were observed during the present investigation when frogs were presented to the two species. The reason for this is unknown but it is possible that the specie of frog used (*L. ewingii*), was unpalatable, suggested by the fact that one subject ate the hind limbs of a frog but left the rest of the body uneaten.

CHAPTER 5

HOME-RANGE AND HABITAT-UTILIZATION

5.1 DESCRIPTION OF STUDY AREAS

Live-trapping activities were conducted at three localities within and near the Hobart area. The temperature, rainfall and positions of the localities are presented in Section 2.1.

Porter's Hill, Mt. Nelson, was selected as the site of the first trapping-study attempted. This area was approximately 62 ha and had previously been used in other investigations (Guiler 1958; Kitchener 1967; and Buchmann, unpubl.). These earlier studies indicated that the area is suitable for pursuing a live-trapping programme on bandicoots and provided useful information which could be the basis of comparisons with results obtained in the present study.

The vegetation of Porter's Hill consisted mainly of dry sclerophyll woodland, in turn comprising several distinctive plant-associations. A dense stand of *Eucalyptus globulus* covered the moist western slopes, whereas the drier eastern and southern slopes supported an open *E. viminalis* and *E. linearis* association. The dry, rocky northern slopes supported dense, low thicket of *Casuarina stricta*, and on the lower, less humid slopes, an open association of *Acacia dealbata*, *A. mollissima* and *C. stricta* was present. Much of the area was covered by a lower, dense scrub-layer comprised of *Correa speciosa*, *Lissanthe strigosa*, *Acacia verticillata*, *Epacris impressa*, *Dodonaea viscosa*, *Baeria viscosa* and *Bedfordia salicina*. There were also a few areas of low ground cover, particularly the bare, rocky northern slopes and a small number of grassy areas, consisting of *Poa australis* and *Lomandra longifolia*.

The site was covered by shallow soils and was poorly drained. Temporary ponds and a narrow creek were present but these were completely dry during the study period because of the somewhat atypically dry conditions prevailing at this time. Open pastures and urban housing-

estates surround most of the locality but these were outside the study area proper. The cover of natural vegetation was only interrupted by a fire-break and an unimproved road extending along the northern sector of the area to a private dwelling situated at the summit of the hill. A very large proportion of the study-area was damaged by bushfires in 1967, 1972 and 1979, but most of the vegetation present at the time of this investigation was very similar to that described by Kitchener, in 1967.

The second live-trapping programme was conducted at Lower Longley. Plates 5.1.1-5.1.4 show the major types of vegetation present in this area, namely open pastures and grassland, dense forest and a fire-affected dense forest. However, since 484 trap nights only yielded a total of four captures of two individuals of *I. obesulus*, a detailed description of this unproductive area is not considered essential. The captures of *I. obesulus* were recorded only in open grassland, although numerous excavations made by bandicoots were observed in the open pastures.

The third and chronologically the last trapping programme was situated at Blackmans Bay. The vegetation of the area was very similar to that described in relation to the Porter's Hill study-site, consisting of open, dry sclerophyll woodland interspersed with a low but dense understorey, predominantly composed of wattles (*Acacia* spp.), heath (*Epacris impressa*), teatree (*Leptospermum scoparium*), bracken fern (*Pteridium* spp.) and *Lomandra longifolia*. The dominant species of tree were blue gums (*E. globulus*) and white gums (*E. viminalis*), with specimens of the native cherry (*Exocarpos cupressiformis*) scattered over the area (Plates 5.1.5-5.1.7). Thickets of blackberries (*Rubus fruticosus*) were also distributed over most of the area, which was flat, with minor undulations and sandy soils. A narrow creek flowed to the west through the central part of the area and minor bodies of



PLATE 5.1.1 Open pasture



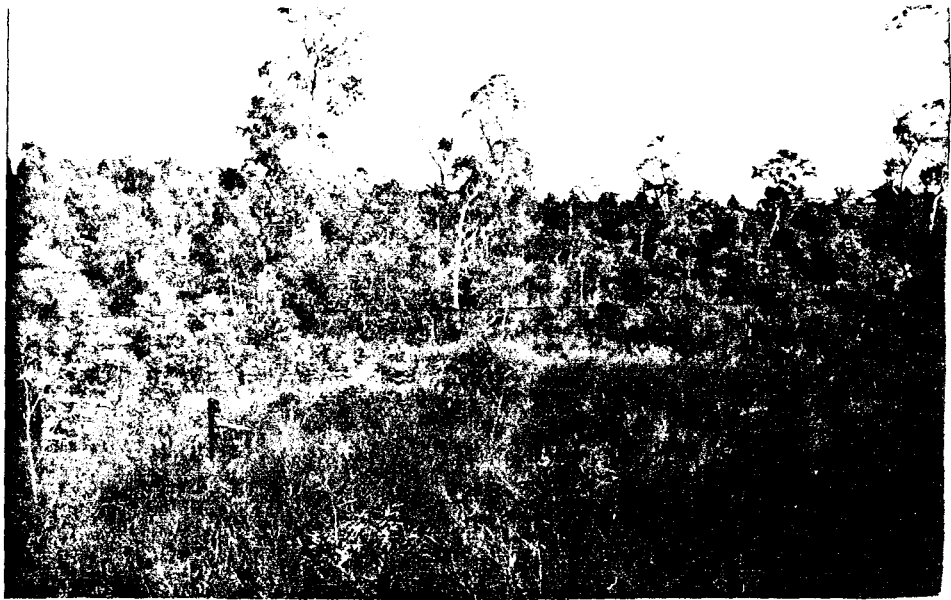
PLATE 5.2.2 Open grassland



PLATE 5.2.3 Dense sclerophyll forest. Note the trap-station marker on a tree in the approximate centre of the photograph.



PLATE 5.2.4 Fire-affected dense sclerophyll forest. Note the absence of a dense understorey.



standing water were noted to be present in depressions while the trapping programme was being conducted. A recently fire-affected area was located in the western part of the area and open pastures adjoined its eastern and south-western boundaries. Human interference was pronounced in this locality, indicated by large numbers of narrow, improved roads and paths transecting the area. The latter were formed by trail-motorcyclists and by horse riders. The peripheral regions of the trapping area (i.e. those close to sealed roads) were strewn with litter from the nearby human settlements.

Diagrams summarising the vegetation, altitude, slope and the positions of trap-stations pertaining to the Porter's Hill and Blackmans Bay study-areas are presented in Section 5.2.

5.2 HOME-RANGE AND MOVEMENTS

5.2.1 Introduction

A home-range, as the concept is applied to mammals, has been defined as the area with which an animal becomes thoroughly familiar and habitually patrols in the course of its normal activities of food gathering, mating and raising of young in natural conditions (Burt 1943); occasional sallies outside this area are usually specifically excluded from consideration. However, the latter may be incorporated to formulate the "total range" of an animal, as this is defined by Goin and Goin (1962). Longer forays, usually infrequent, may be important in achieving familiarity with larger areas and in extending the range of an individual (Stickel 1954). In many instances, parts of the home-range, if not all of it, may be defended by means of overt defense or advertisement (Noble 1939; Brown 1964; Wilson 1971b) resulting in the occupation of an area by an individual on a more or less exclusive basis. Such home-ranges may be defined as territories

(Noble 1939).

Within a home-range, some parts of the area may be subject to more intensive utilisation than others, e.g. feeding-sites and nests (Hayne 1949), and the selective use of these "core areas" (Kaufmann 1962) may change with varying conditions, as do the boundaries of the home-range. The attributes of populations of animals are usually continuously modified as new animals appear and older individuals leave or die; these changes affect the sizes, shapes and distribution of home-ranges (Stickel 1946; Blair 1940), in conjunction with seasonal variations and the availability of resource (Connell 1954; Layne 1954). These factors, as well as interference by the process of trapping (described in Section 5.2.2) militate against obtaining precise measurement of the sizes of home-ranges, since the boundaries of the range usually cannot be clearly or confidently demarcated. However, it is still considered that a live trapping programme, followed by delineation of areas around points of capture represented on a map provide useful indications of the home-range of a given species and several methods are available for estimating the boundaries of these areas, hence providing information about the spatial distribution of the activities of the animals. The uses of such techniques have been reviewed by Hayne (1949), Davis and Golly (1963), Mohr and Stumpf (1966), Ambrose (1969), Stickel (1954) and Sanderson (1966), and the authors have described the advantages and disadvantages associated with all of the principal methods employed in home-range studies. The procedures adopted for the estimation of home-ranges in the present study, and the attendant benefits and problems, are discussed in Section 5.2.2.

A survey of the relevant literature reveals that numerous methods of investigation are available for the purpose of estimating home-ranges, movements and densities of various species of small mammals. The majority of these studies were conducted on eutherian mammals,

and only a few shall be mentioned here because of their relevance and similarity to the techniques employed in examining home-ranges in the present investigation. Previous studies have included the home-range dynamics of populations of heteromyid rodents (e.g. Maza *et al.* 1973), population estimations of wood mice, *Apodemus sylvaticus* (Tanton 1965) and the assessments of the numbers of house-mice, *Mus musculus* (Smith 1968). Studies pertaining to marsupials in this area of research have included investigations of the movements of *Isodon macrourus* (Gordon 1974), home-ranges and movement in two small macropods, *Potorous apicalis* and *Setonix brachyurus* (Kitchener 1973), dynamics of spatial dispersion and estimations of population sizes in *Antechinus swainsonii* (Hocking unpubl.), as well as home range, movements and population densities of *P. gunnii* and *I. obesulus* (Heinsohn 1966).

5.2.2 Materials and Methods

The techniques employed in the placement and distribution of traps over the study area have been described in Section 2.1. A total area of ca. 50 acres was trapped in each of the two study areas examined (Porter's Hill and Blackmans Bay), and these estimates of area have included most of the types of vegetation mentioned (Figures 5.2.3 and 5.2.7). Initially, the directions of the movements of captured individuals after they were released from the traps were recorded on maps of each study site, in attempts to determine whether or not the animals consistently moved towards particular localities within the study-area (i.e. possibly indicating the positions of nest-sites). However, since the direction of movement from the trap was found to be highly variable, apparently lacking clear trends, this exercise was discontinued.

The home-ranges of individuals of *I. obesulus* and *P. gunnii* were demarcated by the "boundary-strip method". This method has been

employed by several investigators (Burt 1940, 1943; Haugen 1942; Evans and Holdanreid 1943; Stickel 1946a) and Stickel (1954) found that the technique produced results that were closest to the true (independently-assessed) home-range when compared with other methods, including the commonly employed "minimum-area method" (Dalke 1942; Mohr 1947) and the "inclusive and exclusive boundary-strip methods" (Blair 1940, 1941). The latter two methods yielded smaller and larger estimates, respectively, of the true home-range. The boundary-strip method is based on the reasonable assumption that animals may range, on the average, half way to the nearest trap positioned beyond their peripheral capture-sites and lines are then drawn connecting these outermost points to form a convex polygon. The area enclosed was then measured, as were the circumference of the polygon and the distances between recaptures. Linear measurements of distances between successive captures have been used by Davis *et al.* (1948) and Evans and Holdenreid (1943) because of the usefulness for comparative purposes. The method has some disadvantages, particularly because the animals do not normally travel in straight lines and the recapture-distances seldom approximate the known limits of the home-range.

As previously mentioned, the precise strategy of the trapping-programme may, itself, influence or bias estimates of home-range, movements and densities. For example, the act of capturing an animal *per se* prevents further movement of that specimen until it has been released, and the consequences of liberating a nocturnal animal during the daytime usually cannot be accurately determined, although some effect on its activity-rhythm may be expected (Justice 1961). In addition, numerous uncontrollable factors which affect trappability may exist. Figure 5.2.1 summarises some of these possible influences. However, the bias induced by such variables was believed to be negligible in the present study, since trapping was conducted for only brief

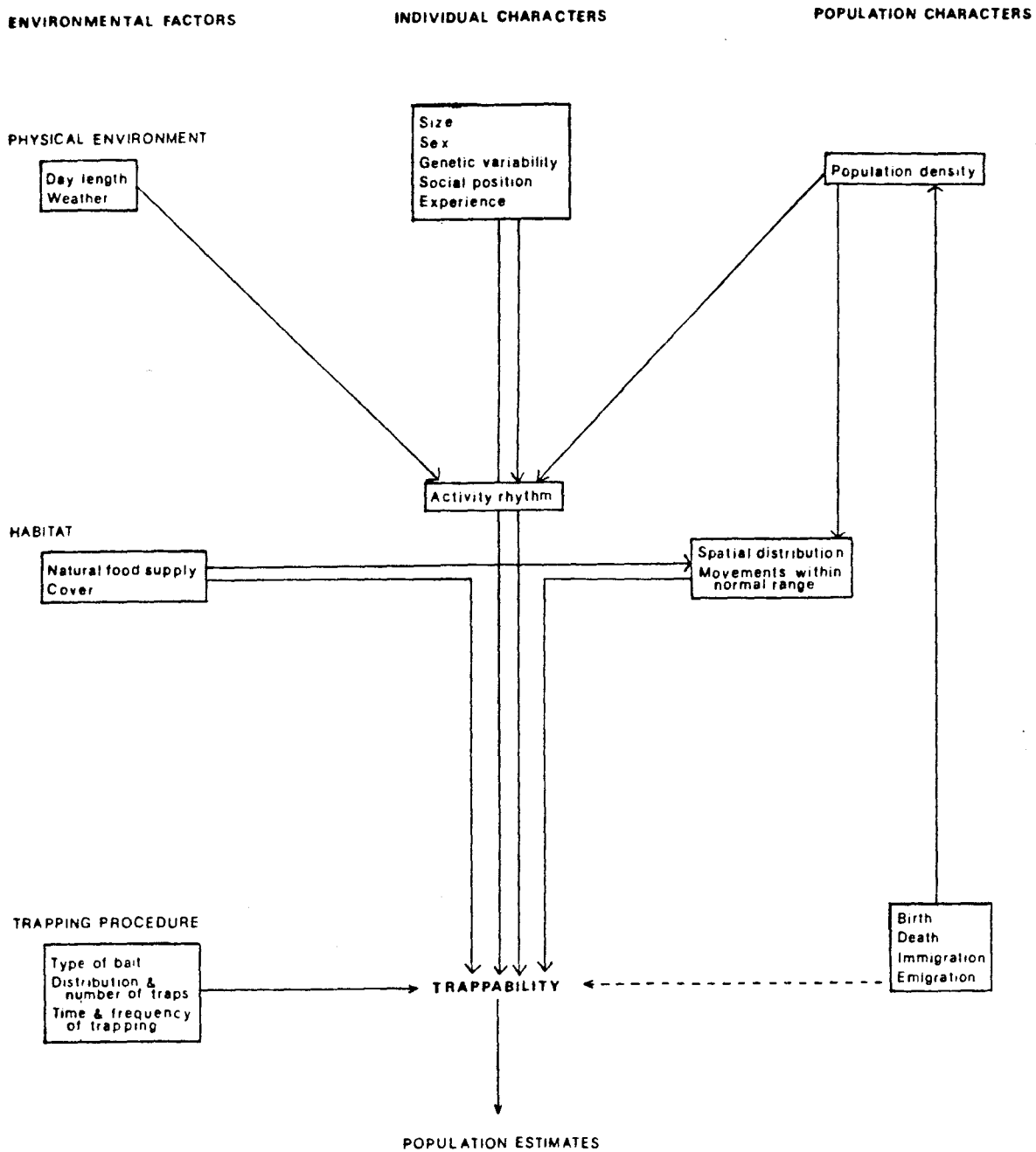


FIG. 5.2.1 Individual and population characteristics, and environmental parameters which may have influenced or biased the trapping programs. (Taken from Kikkawa, 1964)

Note: arrows indicate the directions of bias.

periods of time (ca. 6 weeks at each locality) and traps were moved to adjacent blocks of the study area after every 7 days. This method of trapping may be expected to reduce the effects created by variations in pertinent environmental factors and population characteristics since the influence of these would probably change very little over such a short period, and the bias produced by varying individual characteristics promoting differential trap-response as described by Chitty and Kempson (1949), Tanton (1965), Crowcroft and Jeffers (1961) and Smith (1968) are presumably partly compensated by the fact that all of the traps were moved to adjacent blocks of the study area every week.

5.2.3 Results

Plates 5.2.1 and 5.2.2 present aerial photographs of the two trapping-localities utilized for estimates of home-range and habitat utilisation. Other relevant information, including the types of vegetation present, the distribution of trap-stations and topography of the two areas is summarised in Figures 5.2.3, 4, 5, 7, 8, and 9. The home-range estimates obtained for resident individuals are presented in Figures 5.2.2, and 5.2.6. An individual was considered to be a resident if it was captured three or more times during the trapping-period. Although this may appear to be a very small number of captures for an animal to be deemed a resident, it should be remembered that only a restricted sector of the whole locality was trapped at one time and the trapping-period only encompassed 7 days within a given sector. Therefore, if individuals were captured three or more times in its sector in such a short period of time, it is most probable that the individual was a resident and was thus assumed. Presumably, if the trapping programme had continued over a longer period, more precise estimates of home-ranges would have been obtained. A greater number of captures would also probably have resulted in larger values

PLATE 5.2.1 Aerial Photograph of the Porter's Hill Area

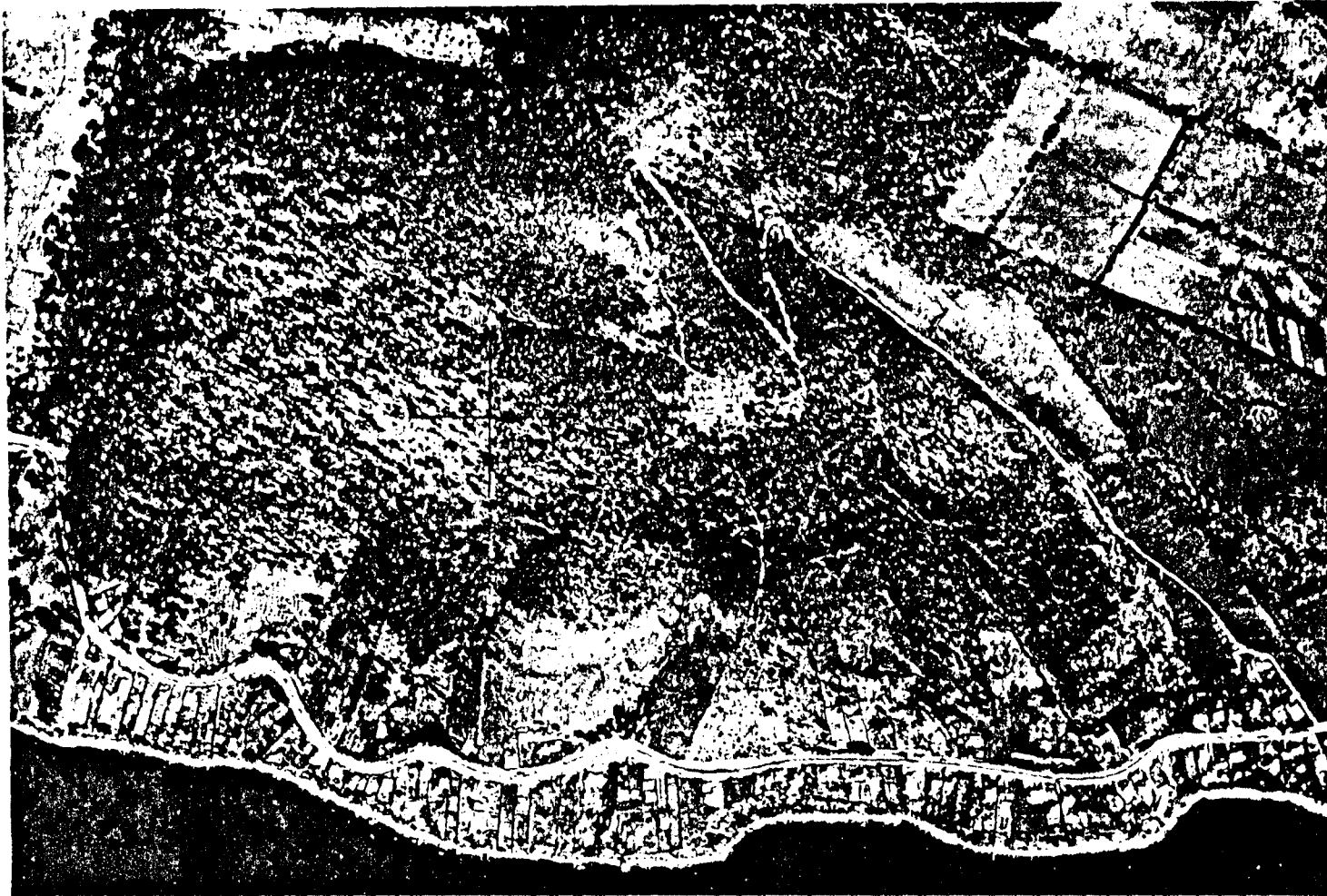


FIG. 5.2.2 HOME RANGES OF I.obesulus DISTRIBUTED OVER THE PORTER'S HILL STUDY AREA.



I.obesulus
M.1



I.obesulus
M.0



I.obesulus
F.2



I.obesulus
M.half circle

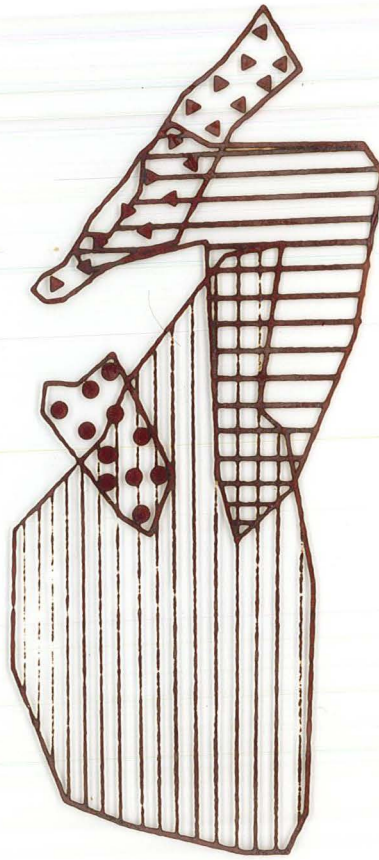


FIG.5.2.3 THE DISTRIBUTION OF VEGETATION TYPES OVER THE PORTER'S HILL STUDY AREA

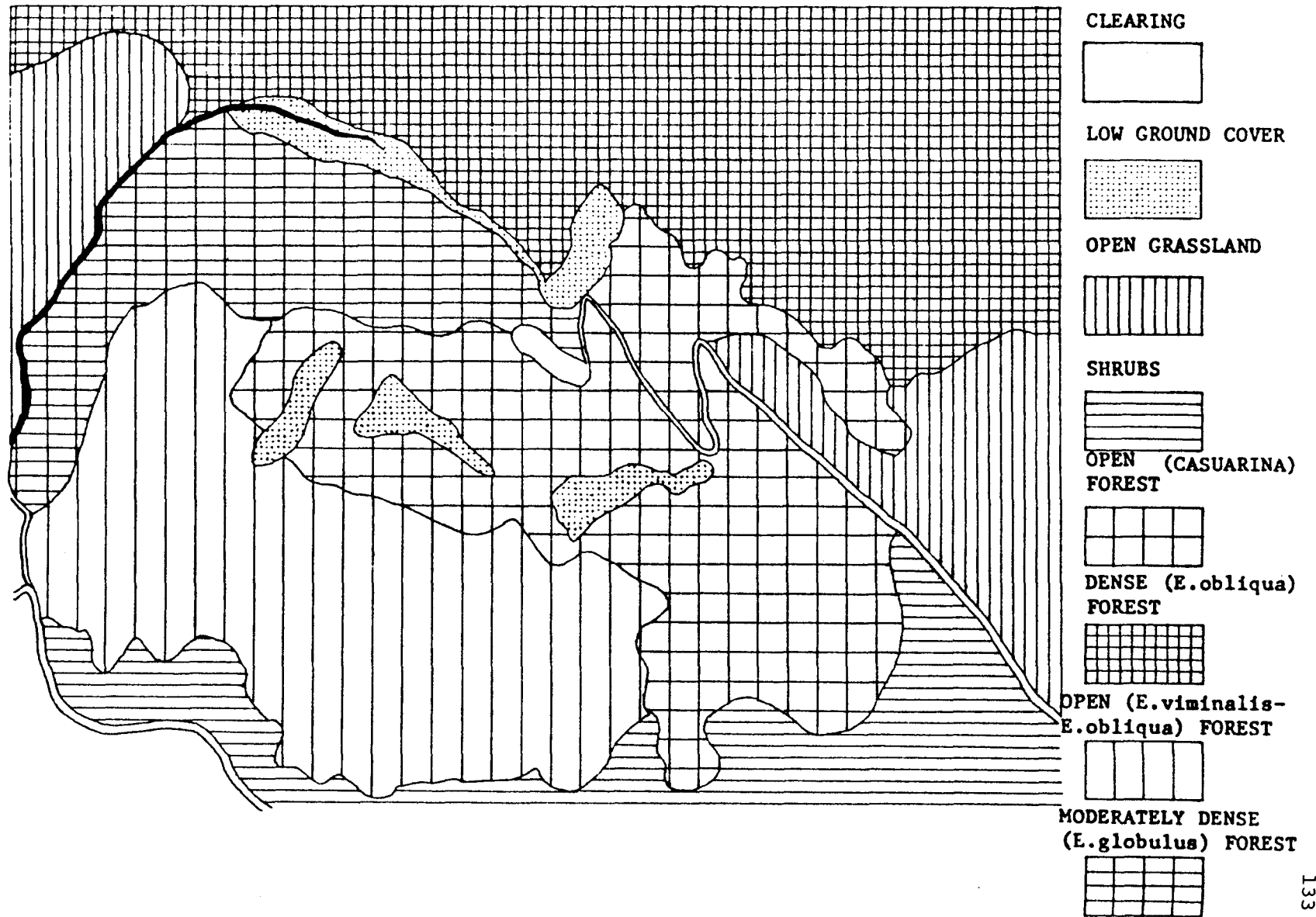


FIG.5.2.3 THE DISTRIBUTION OF VEGETATION TYPES OVER THE PORTER'S HILL STUDY AREA

FIG. 5.2.2 HOME RANGES OF *I.obesulus* DISTRIBUTED OVER THE PORTER'S HILL STUDY AREA.

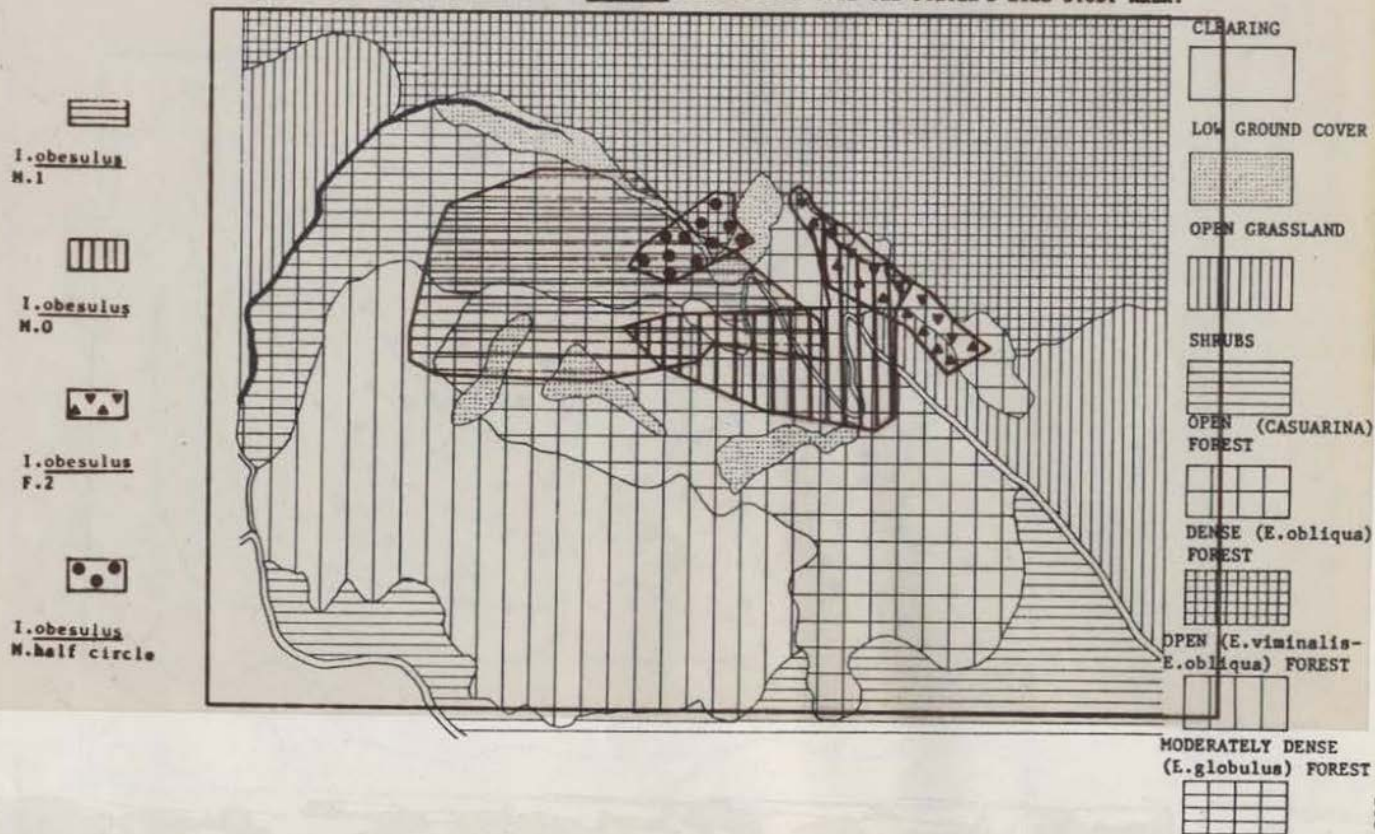


FIG. 5.2.4 THE DISTRIBUTION OF TRAP STATIONS OVER THE PORTER'S HILL
STUDY AREA.

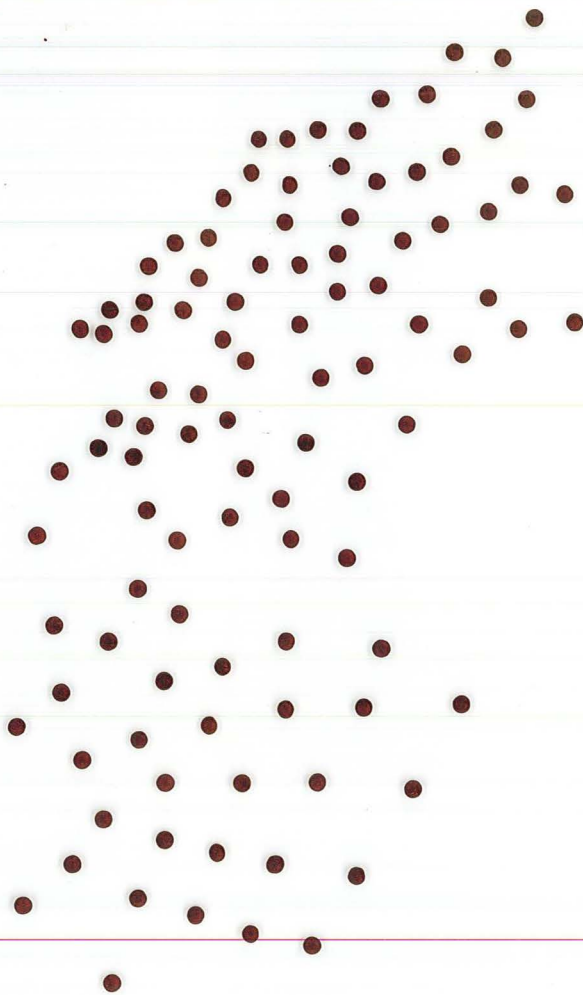


FIG.5.2.5 CONTOUR MAP OF THE PORTER'S HILL STUDY AREA SHOWING ALTITUDES IN FEET

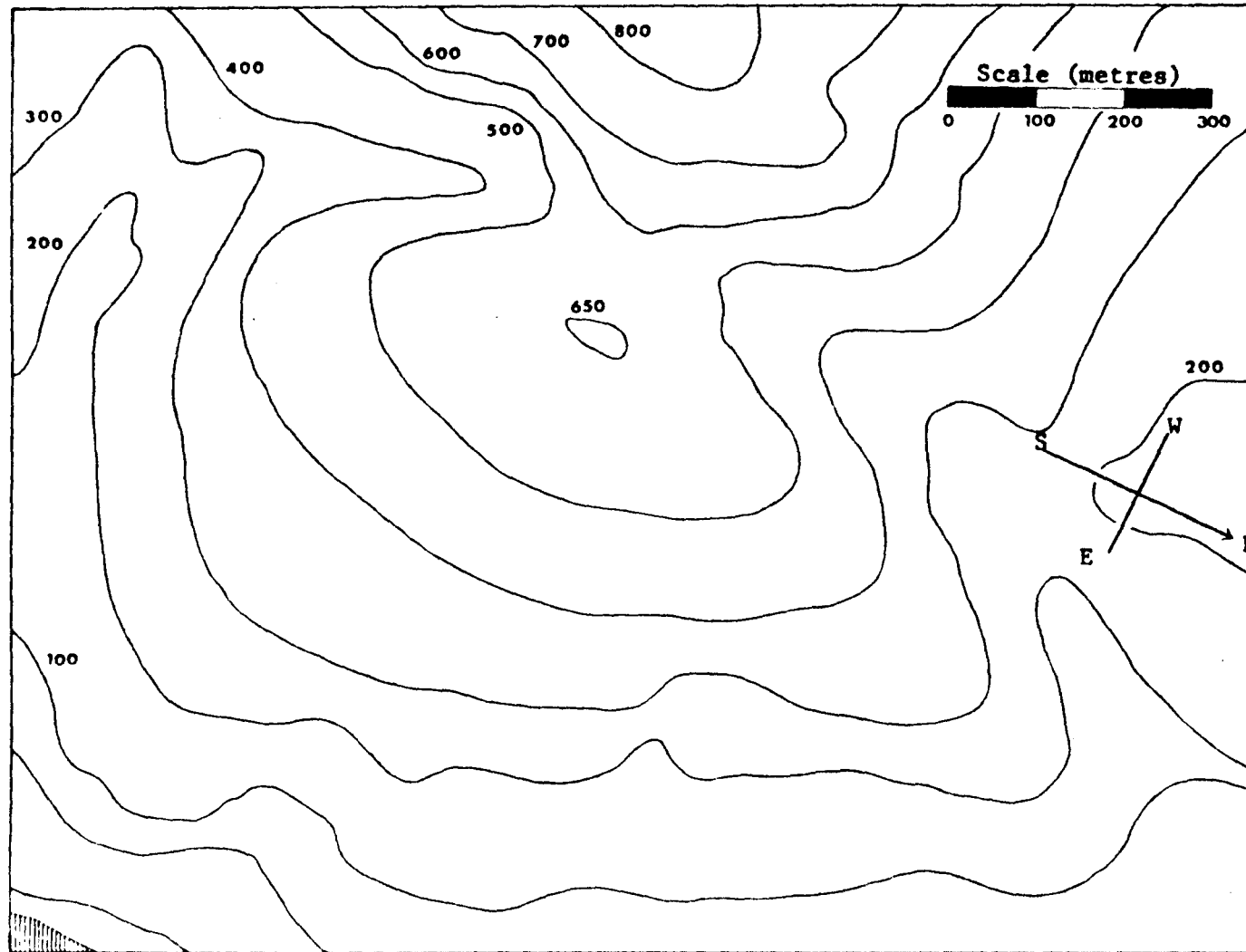


FIG.5.2.5 CONTOUR MAP OF THE PORTER'S HILL STUDY AREA SHOWING ALTITUDES IN FEET

FIG. 5.2.4 THE DISTRIBUTION OF TRAP STATIONS OVER THE PORTER'S HILL STUDY AREA.

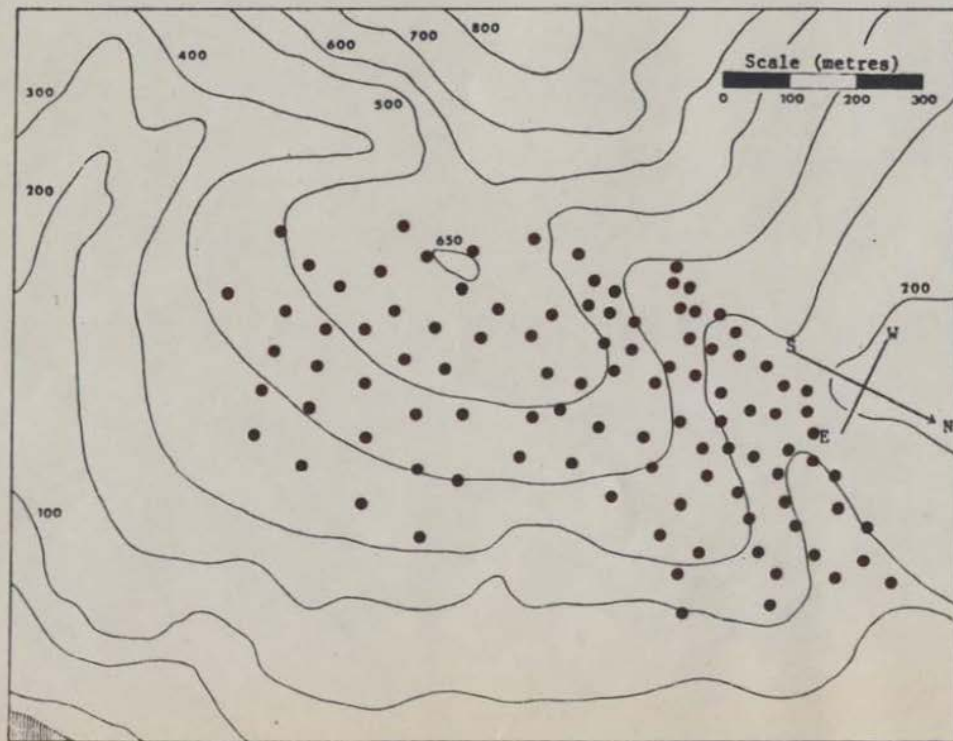


PLATE 5.2.2 Aerial Photograph of the Blackmans Bay study area.

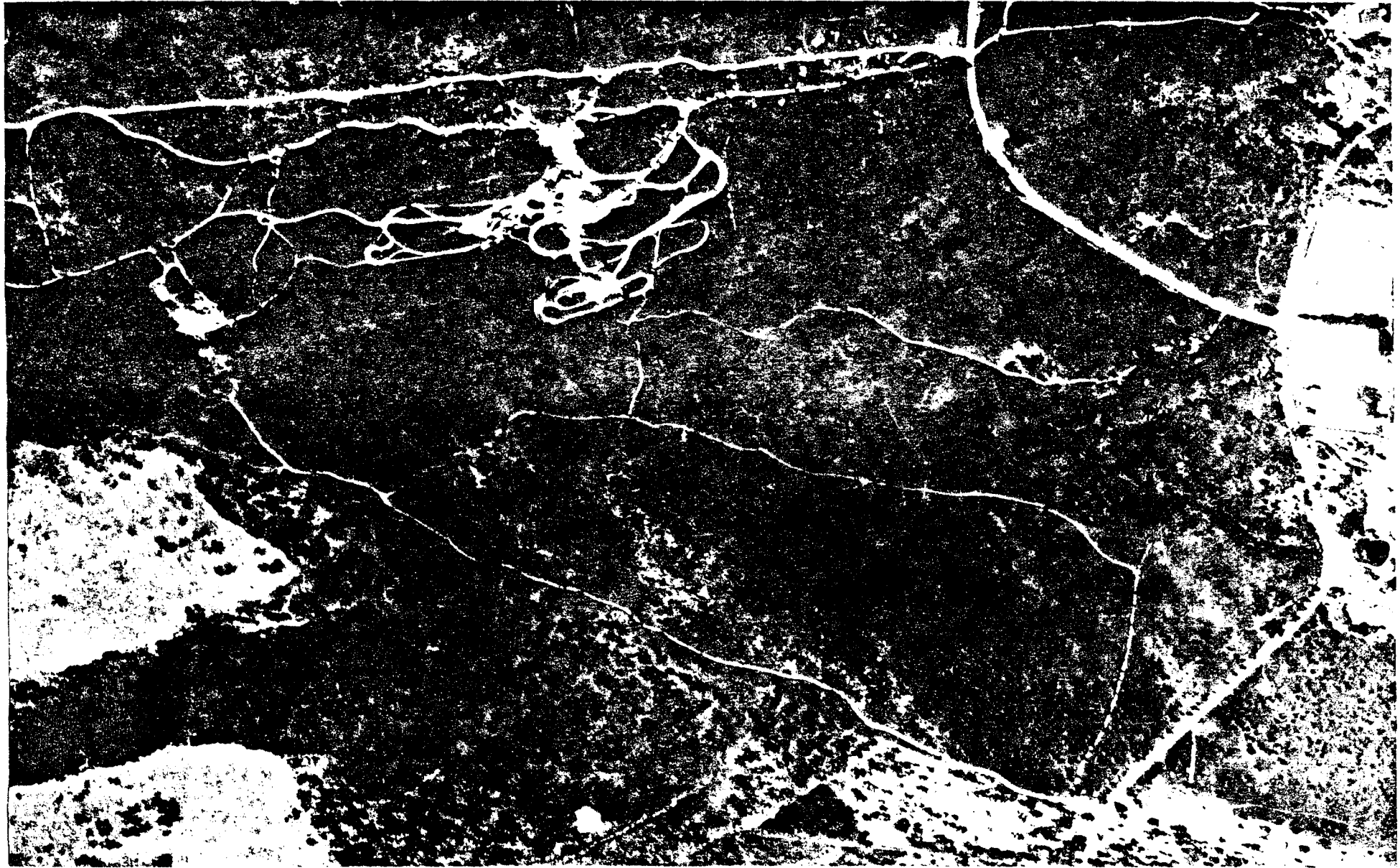


FIG. 5.2.6 HOME RANGES OF *I. obesus* AND *P. gunnii* DISTRIBUTED OVER THE BLACKMANS BAY STUDY AREA.

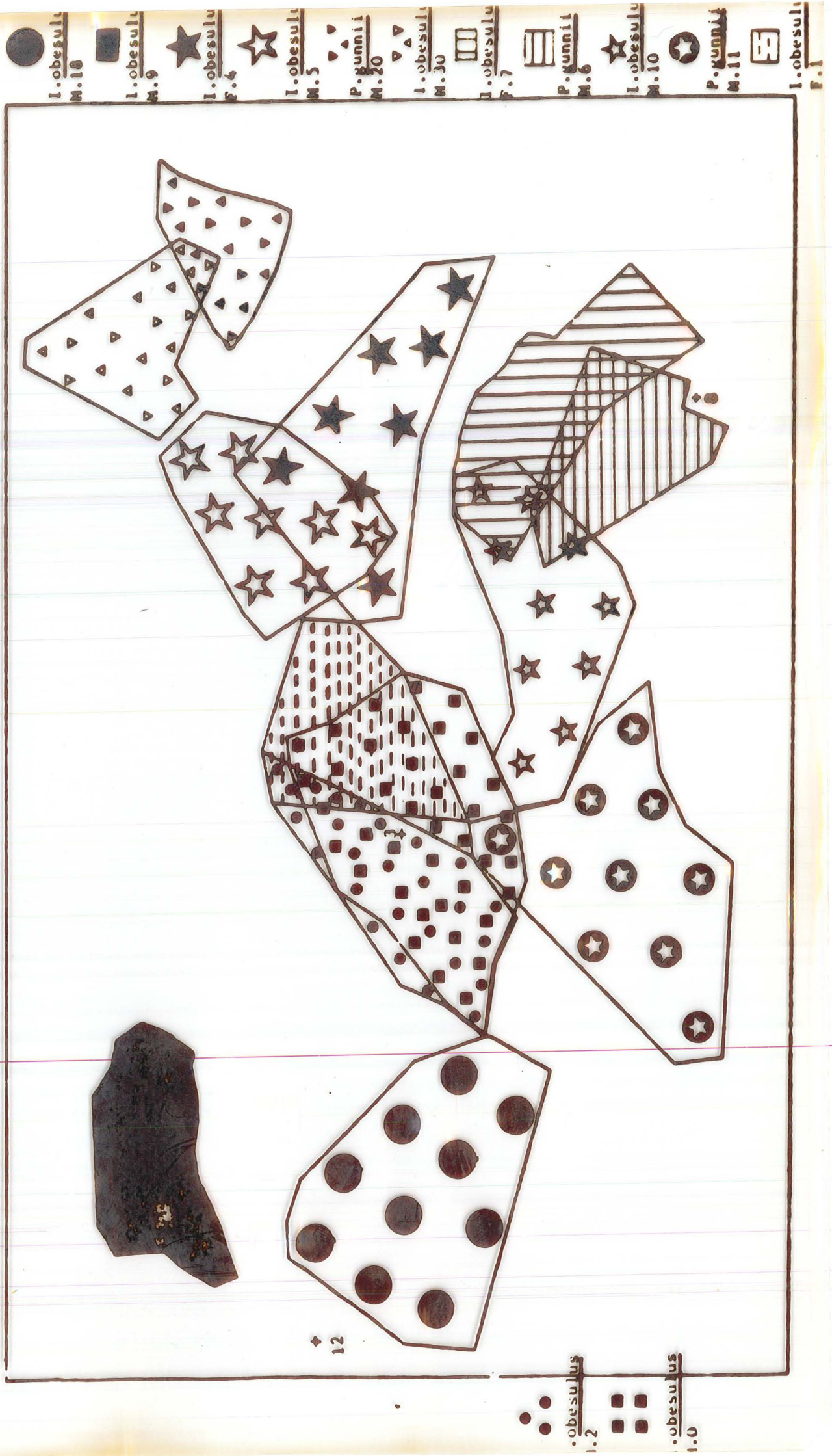


FIG.5.2.7 : THE DISTRIBUTION OF VEGETATION TYPES OVER THE BLACKMANS BAY STUDY AREA

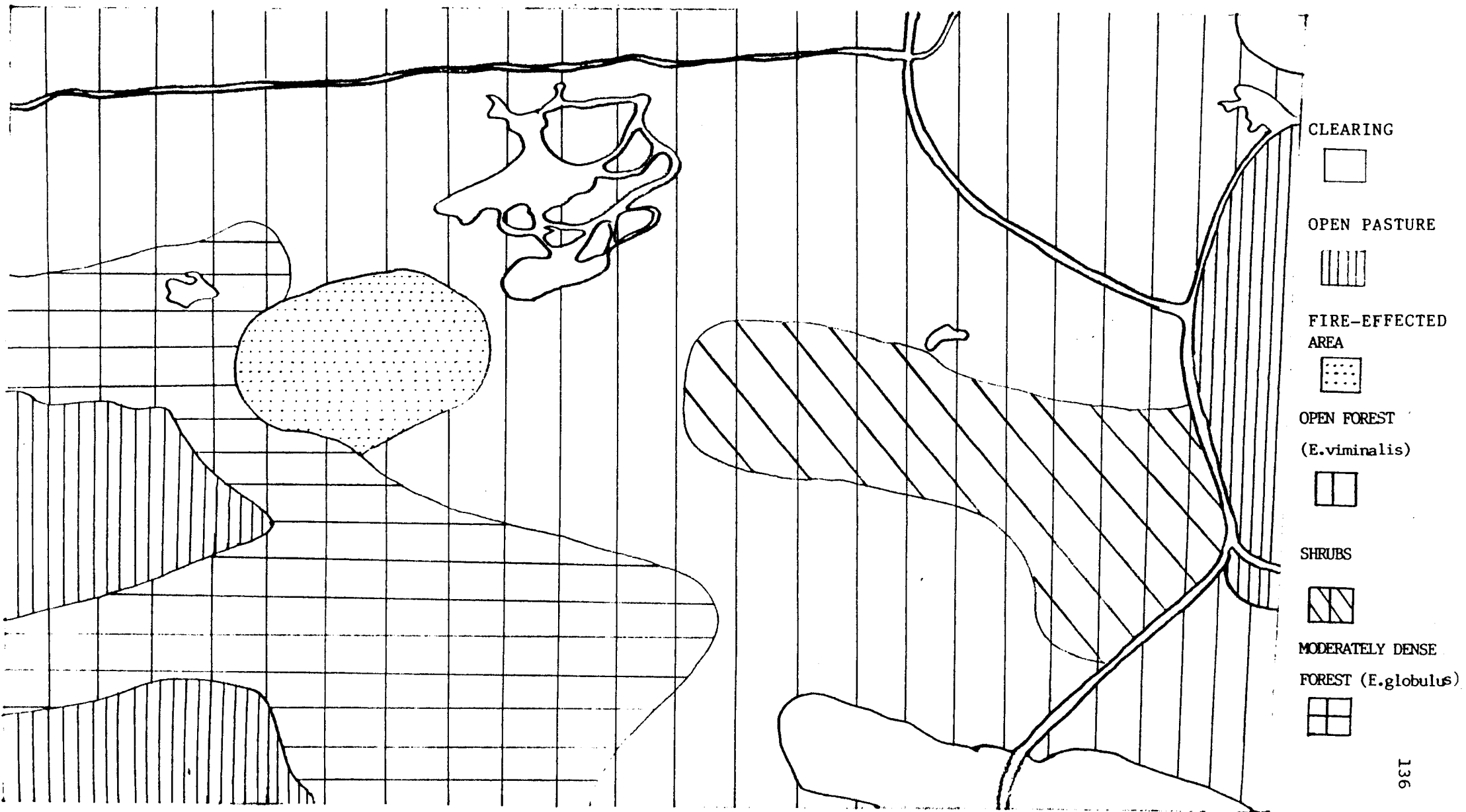


FIG. 5.2.6 HOME RANGES OF *I. obesus* AND *P. gunnii* DISTRIBUTED OVER THE

BLACKMANS BAY STUDY AREA.

FIG.5.2.7 : THE DISTRIBUTION OF VEGETATION TYPES OVER THE BLACKMANS BAY STUDY AREA

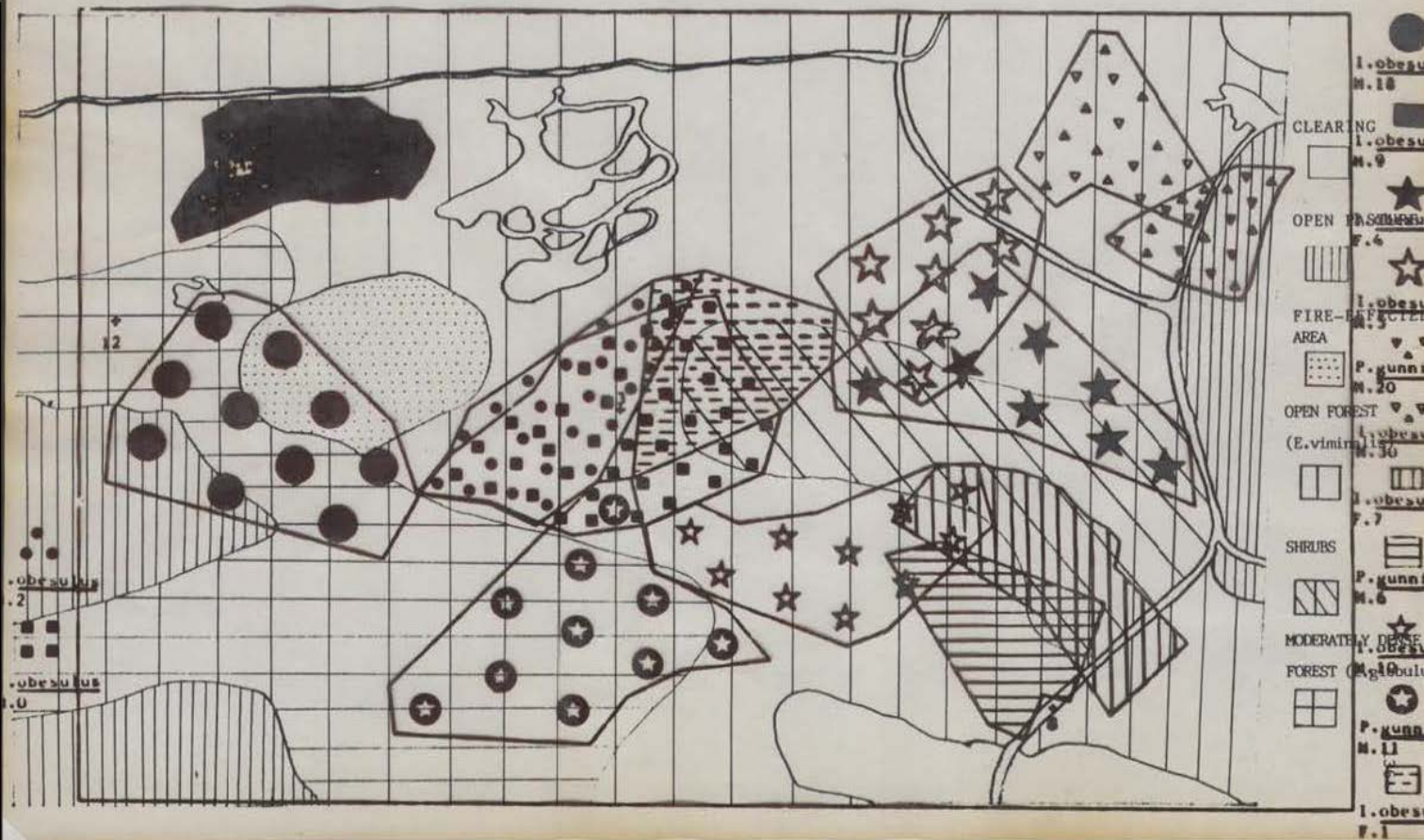


FIG.5.2.8 : THE DISTRIBUTION OF TRAP STATIONS OVER THE BLOOMING BAY STUDY AREA

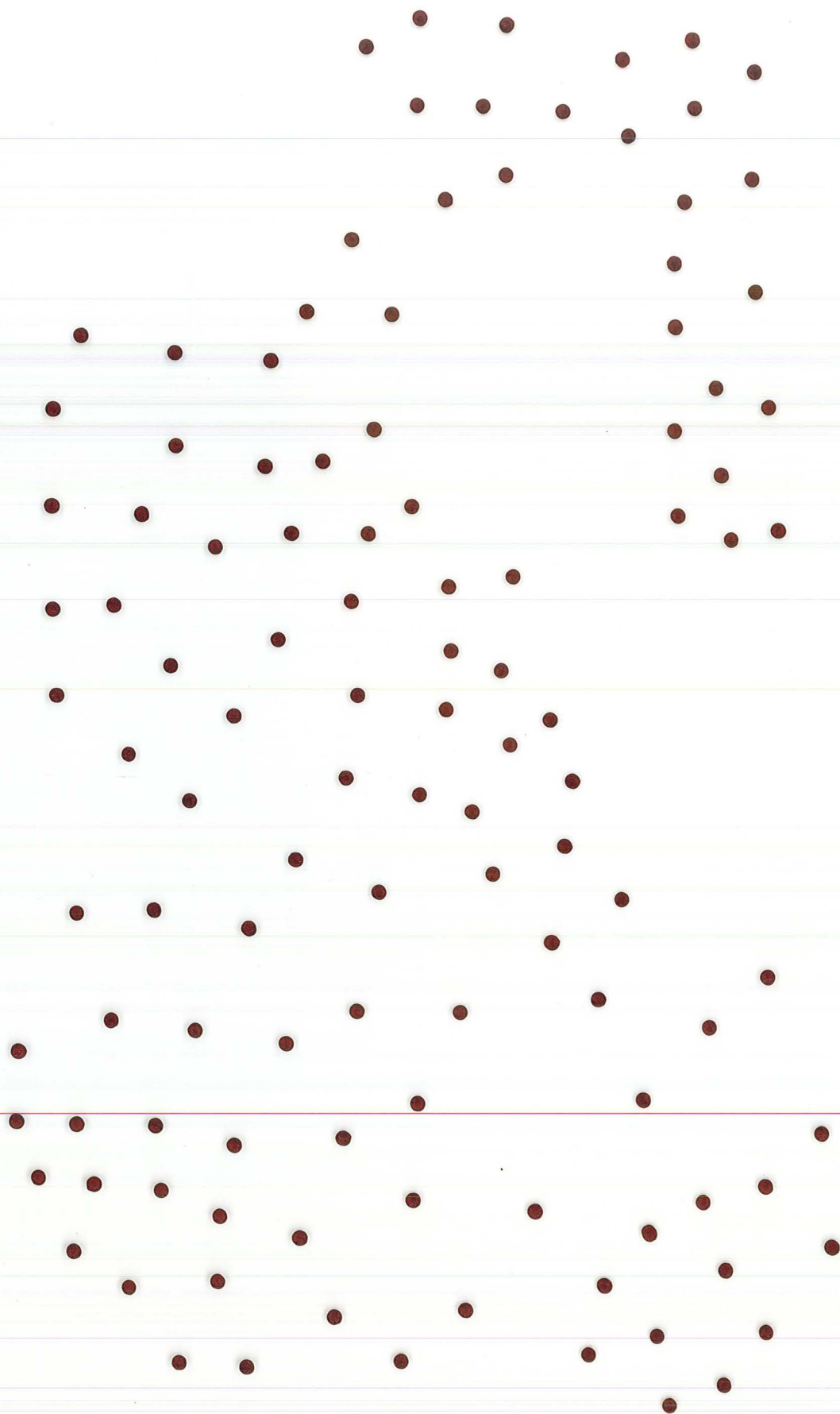


FIG. 5.2.9 : CONTOUR MAP OF THE BLACKMANS BAY STUDY AREA SHOWING ALTITUDES IN METRES

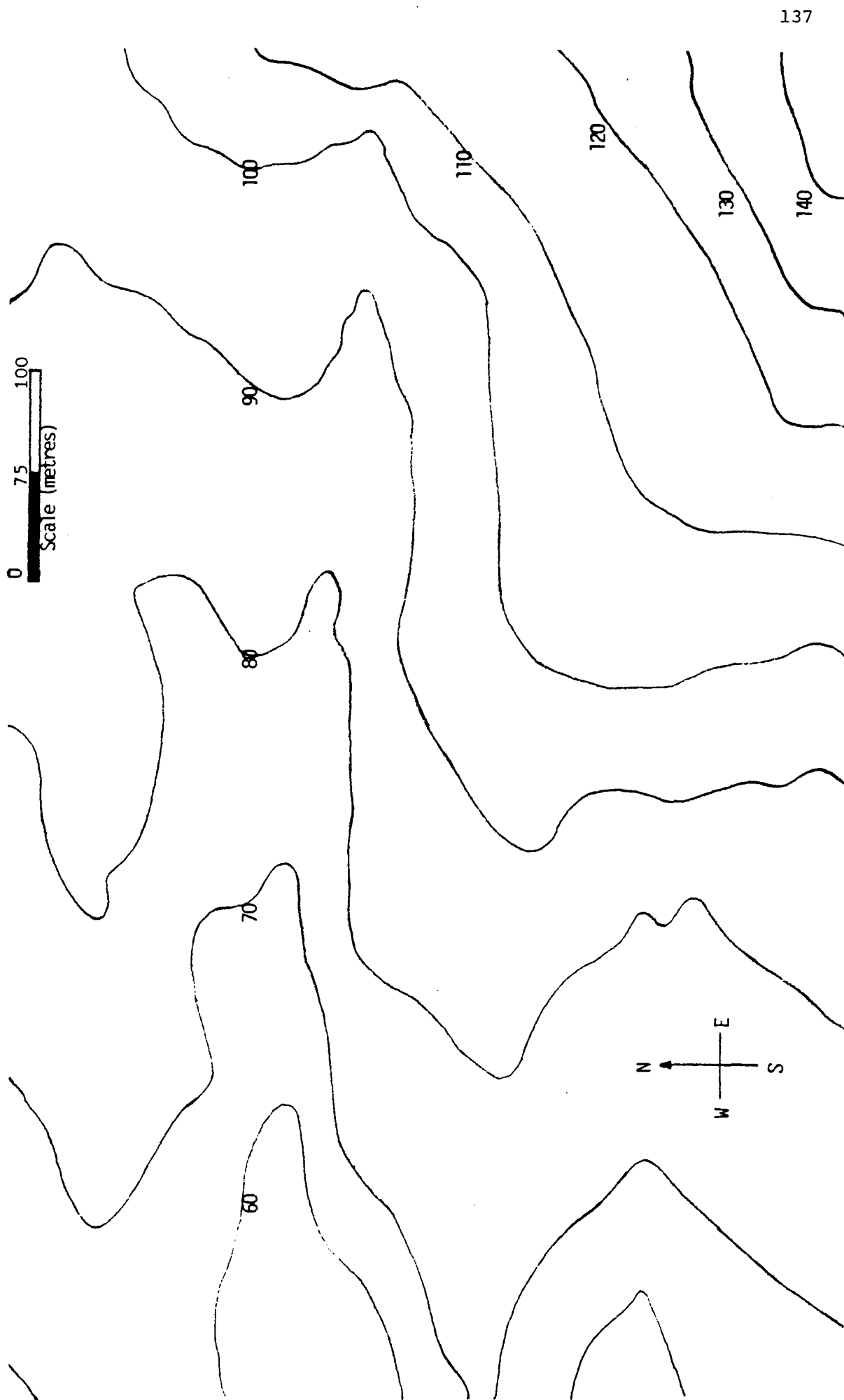
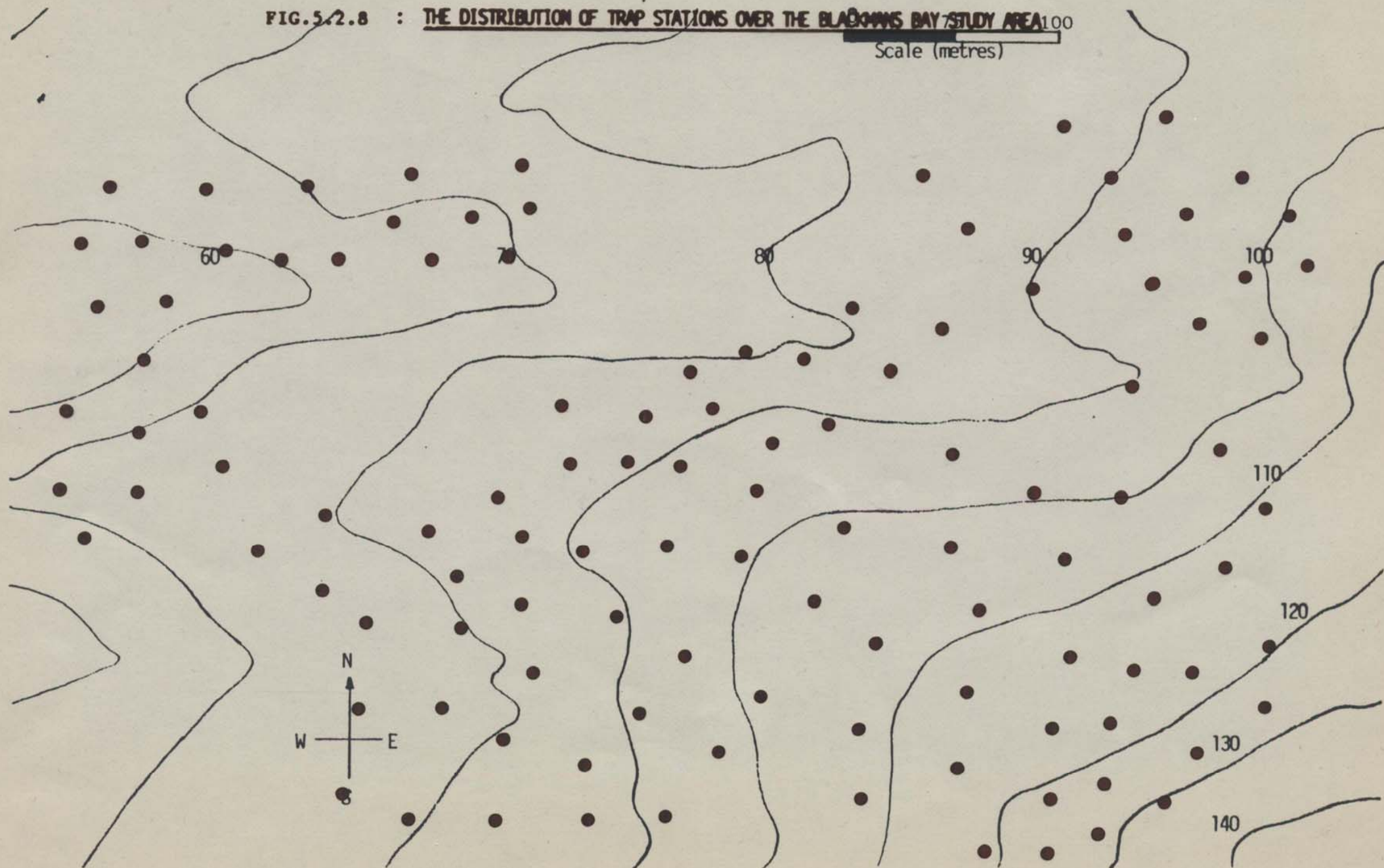


FIG.5.2.9 : CONTOUR MAP OF THE BLACKMANS BAY STUDY AREA SHOWING ALTITUDES IN METRES

FIG.5.2.8 : THE DISTRIBUTION OF TRAP STATIONS OVER THE BLACKMANS BAY STUDY AREA



of home-range estimation, since the spaces between mapped home-ranges such as those shown in Figure 5.2.6, would hardly be expected to remain unexploited and are probably used by the animals, albeit to a minor extent.

Table 5.2.1 provides details of the estimated areas and circumferences of home-ranges and the mean linear distances between successive captures of resident individuals of *I. obesulus* and *P. gunnii* located in the two study areas. The most conspicuous feature of the table is the large size of the home-range of two male individuals of *I. obesulus* trapped in the Porter's Hill study area. The mean range sizes computed for these two animals were approximately 500% larger than the mean home-range sizes obtained for all other resident bandicoots recorded in both localities. Presumably associated with this larger range size are the significantly ($0.01 < Pr < 0.005$, d.f. = 38) greater distances between successive captures recorded for these two individuals. The other major difference existing between the two study areas pertained to the actual numbers of bandicoots recorded; 4 resident *I. obesulus* in the Porter's Hill area contrasted with 10 resident *I. obesulus* and 3 resident *P. gunnii* in the Blackmans Bay area. It should be emphasised here that both areas were of approximately the same size (20.5 ha); consequently, the Porter's Hill area yielded a much lower overall density of bandicoots. There were no significant differences with respect to the sizes and circumferences of home-ranges between either species, and individual males and females of *I. obesulus* possessed home-ranges of similar sizes in the Blackmans Bay area. No significant correlation was found between the sizes of the home-ranges and the weights of the individuals associated with them.

Transient individuals were recorded only in the Blackmans Bay study area, and two of the latter were captured on the periphery of the area, presumably occupying ranges adjacent to the sectors trapped.

All three transients were *I. obesulus* (two males and a young female). Overlap of the ranges of individual *I. obesulus* was extensive in both study-areas, but no overlap existed between those of individual *P. gunnii* and conspecifics. However, home-ranges of individuals of the two species did overlap.

The commonly observed phenomena of animals being initially reluctant to enter traps (unfamiliar object-avoidance), as described by Chitty and Shorten (1946) and Chitty and Kempson (1949) was pronounced in the present investigation. The first night of trapping in a new area yielded considerably lower captures than the subsequent nights of captures. However, there was no evidence of animals learning to enter or avoid traps as described in rodents by Tanton (1965), because bandicoots were seldom captured on successive days but were usually trapped only every second or third day. This also appears to indicate that the placement of traps introduced little or no bias in estimates of home-ranges because animals were able to avoid or by-pass traps.

5.2.4 Discussion

A comparison of the results obtained in the present investigation with those reported by previous studies reveals several contrasting features with respect to the sizes of home-range and the densities of the two species of bandicoots observed (Table 5.2.2). Heinsohn (1966) recorded data about the home-ranges of the same species and these were considerably larger than the home-ranges measured in the present study. The higher estimates of the former author may have resulted from the fact that he conducted trapping in more open habitats such as natural grassland and introduced pastures where the movements of the subjects may have been relatively unrestricted. The movements of several individuals of both species were monitored by Heinsohn, and distances of over one kilometre were travelled by some individuals in a single night

TABLE 5.2.1 Estimated areas and circumferences of home-ranges, and mean linear distances between successive captures of resident individuals of *I. obesulus* and *P. gunnii* in the two study areas investigated.

Locality	Porter's Hill								Blackmans Bay								
Species	<i>I. obesulus</i>								<i>I. obesulus</i>							<i>P. gunnii</i>	
Sex	M		F						M		F				M		
Identification Number	1	0	half circle	2	0	2	18	10	9	5	30	1	7	4	20	6	11
Number of captures	6	5	3	5	7	5	4	4	4	4	3	5	4	4	4	3	4
Home-range (acres)	10.76	5.03	1.02	1.84	2.47	1.32	2.58	1.75	1.17	1.49	1.05	1.49	1.57	2.08	0.61	1.12	2.47
Circumference (m)	1577	1301	488	836	778	567	751	720	574	567	519	680	811	680	421	537	855
Mean linear distance between successive captures \pm S.E.	167 \pm 19.4		*	*	112 \pm 10.4				115 \pm 16.8				102 \pm 19.2				
Weight (g)	1415	1025	175	760	950	1025	950	1400	1125	1525	860	675	670	1025	720	750	820
Age category	Adult	Adult	young individual	Adult	ADULTS												

* Included in the category of mean linear distance between successive captures obtained for male and female individuals of *I. obesulus* in the Blackmans Bay area because of the similar home-range size.

TABLE 5.2.2 Comparison of the mean sizes of home-ranges and the densities of resident individuals of the two species, *I. obesulus* and *P. gunnii*, based on data from the present investigation and from other sources.

Source of Data	Present Investigation				Heinsohn (1966)				Buchmann (unpubl.)				Sampson (unpubl.)			
Locality	Porter's Hill; Blackmans Bay				Smithton (N-E Tas.)				Porter's Hill				Tuttaning (W.A.)			
Species	<i>I. obesulus</i>		<i>P. gunnii</i>		<i>I. obesulus</i>		<i>P. gunnii</i>		<i>I. obesulus</i>		<i>P. gunnii</i>		<i>I. obesulus</i>			
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Mean home range (acres)	3.65	1.8	1.4	-	13.2	5.7	63.4	8.0	1.27	0.88	0.96	0.86	49.2	4.4		
Density (number/50 acres)	7.0		1.5		2.5		17.0		13.7		3.7		8.25			

(mean = 200 m); these were also larger than the linear distances recorded between successive captures in the present investigation. Heinsohn further found that males occupied significantly larger home-ranges than females. Similar results were recorded by Sampson (unpubl.) in male but not female individuals of *I. obesulus* at Tuttanning Reserve located in the south-west of Australia. Sampson attributed the larger sizes of home-ranges of male *I. obesulus* to the more arid conditions existing at Tuttanning, causing individuals to forage over greater distances for food.

Buchmann (unpubl.) conducted a trapping programme at one of the localities used in the present investigation. His results showed smaller home-range sizes for both species than those recorded in the present investigation. However, a higher density of both species was registered in his study, and this may have resulted in the smaller estimates of home-range sizes recorded.

Density estimates have been highly variable between the different studies thus far undertaken, and this variability is presumably attributed mainly to the substantial differences occurring in the different study-areas, with respect to climate, abundance of food and vegetation. However, a direct comparison can be made between the results obtained by Buchmann and the present investigation, since both trapping programmes were conducted on Porter's Hill. The density (4/50 acres) of bandicoots registered in this area during the current study was much lower than corresponding estimates recorded by Buchmann ($\approx 21/50$ acres). In the twelve year interval that has elapsed between these studies, numerous changes appear to have occurred presumably resulting in the observed discrepancies in density estimates. Three bush-fires have affected most of the area and urban housing estate now surround three sides of the study-site. This encroachment of human settlement may have reduced recruitment from outside of the study-area proper, and perhaps also led

to increased predation-pressure as a result of the introduction of domestic cats and dogs, which were often observed in the area during the present study. Very dry conditions prevailing on the hill during the present study may also have resulted in the lower densities recorded, since suitable food was probably scarce. This is in accordance with the significantly larger sizes of the home-ranges of bandicoots on Porter's Hill and the low numbers of young individuals and lactating females recorded in the current investigation.

Extensive overlap of home-ranges was recorded both in the present investigation and in the previous studies. This appears to indicate that territoriality is absent or minimal in either of the species investigated. Heinsohn (1966) observed several individuals of *P. gunnii* feeding within a few metres of each other. However, the pugnacious behaviour of individuals of *I. obesulus* shown towards conspecifics, as described by Wood-Jones (1924) and the present investigation (Section 6.1), appears to imply that defence of home-range may be important. Although this may, indeed be the case, it should be recognised that animals such as bandicoots are most unlikely to be in a position to survey the whole of their individual home-ranges, and trespassers may go unnoticed. In fact, the animals may only be able to scan a very small area immediately surrounding them, because of the dense undergrowth present over most of the two study-areas. Therefore, it is most likely that territories, if they exist at all, are in the form of spatio-temporal systems, based on passive avoidance and reinforced by experience and learning (i.e. the animals may defend only the area where they happen to be at any given time). It is not known whether or not either species of bandicoot uses communicative signals, such as odour or scat, at the peripheries of their home-ranges to advertise the boundary. Considering the high degree of observed overlap, the latter proposition appears to be unlikely.

In conclusion, it appears that the home-range of an animal, whether defended or not, must be large enough to yield an adequate supply of food, refuges and mates. At the same time, it should not be very much larger than the size compatible with obtaining these requisites because excessive amounts of energy may be expended in traversing large tracts of ground. In general, the poorer the energy-yield of a given habitat, the larger the size of the home-range occupied, to compensate for the former. The anomalous data of the different studies cited in Table 5.2.2 appears to indicate that the sizes of home-ranges change under the influence of different pressures such as the abundance of food, population-densities and other factors.

5.3 HABITAT UTILIZATION

5.3.1 Introduction

Isoodon obesulus and *Perameles gunnii* are widely distributed throughout Tasmania and in southern Australia. A considerable variety of habitats are occupied by both species. These include open dry sclerophyll forest, woodlands, grasslands, heathlands, pastures and urbanized areas (Heinsohn 1966; Stoddard and Braithwaite 1979; Hyett and Shaw 1980).

The two species frequently appear to co-exist in the same areas, and there may even be extensive overlap of individual ranges between the species (Section 5.2.3). This may be expected to result in aggravated competition for food resources between the species in sympatric situations, since both have similar diets (Heinsohn 1966). However, in a heterogeneous environment, the possibility of direct competition may be greatly reduced, because *I. obesulus* and *P. gunnii* occupy different types of vegetation, as described by Heinsohn (1966). He found that *P. gunnii* utilized more open areas such as pastures, whereas *I. obesulus* was restricted to areas with more dense vegetation

such as woodlands. Such partitioning of selectively utilized habitat-types is presumably one of the factors permitting the species to co-exist without destructive competition.

Research in this area has been relatively active, although the majority of such studies have also concentrated on eutherian mammals. Some of the studies relevant to the present investigation have included assessments of the utilization of space and habitat-selection in small mammals (Myton 1974; Barnett et al. 1978; Braithwaite and Gullan 1978; Braithwaite et al. 1978; Suckling and Heislors 1978), as well as competitive interactions and microhabitat selection occurring between two genera of rodents, *Microtus* and *Clethrionomys* (Grant 1970, 1971; Cameron 1964; Douglass 1976; Morris 1969).

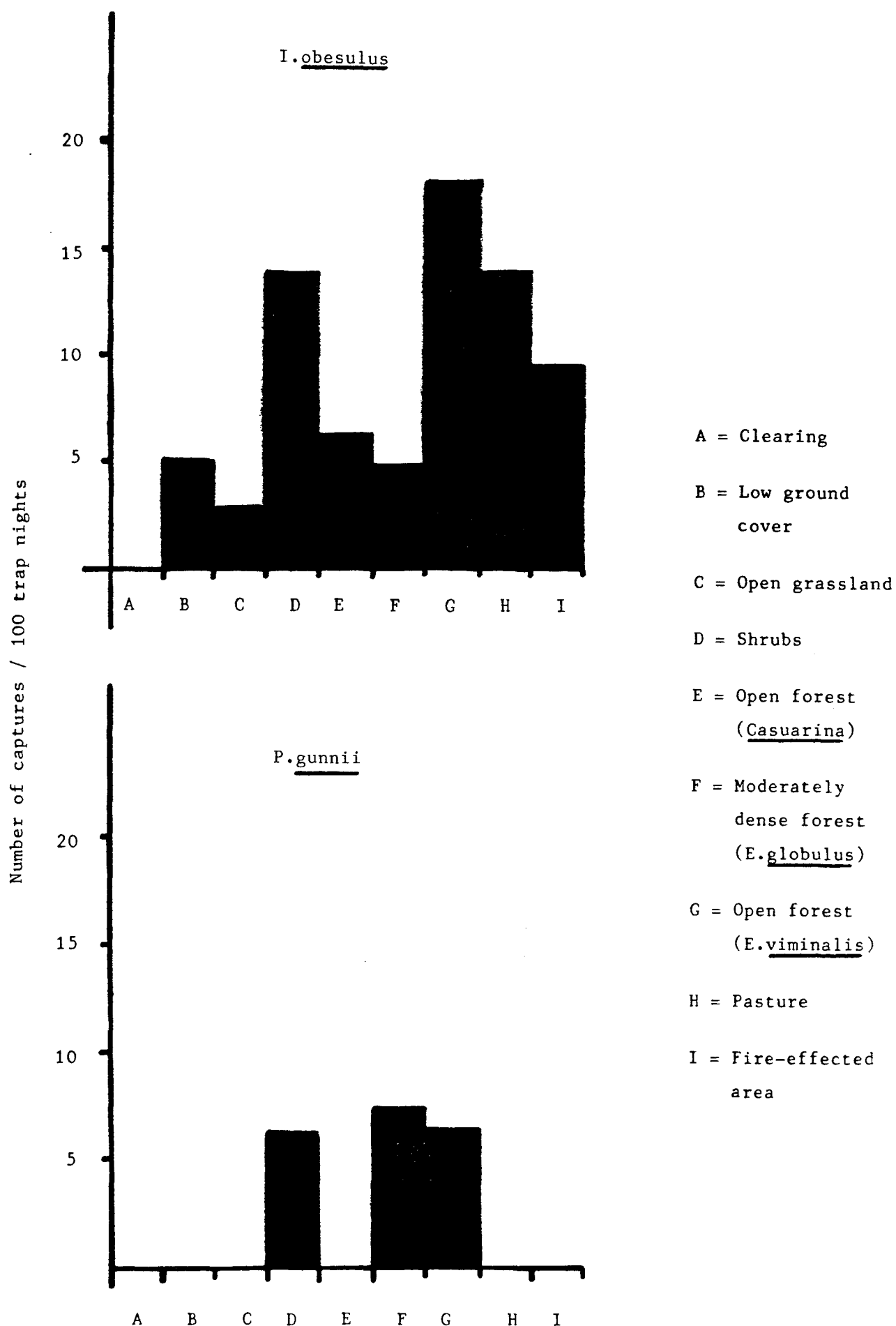
5.3.2 MATERIALS AND METHODS

The techniques used in trapping have been described earlier in Section 2.2 and 5.2.2. Indications of the habitat utilization in the two species were obtained by calculating the numbers of captures at trap stations situated in the different vegetation types. Rates of trapping were expressed as numbers of captures per hundred trap nights (i.e. the expected number of captures for traps positioned in that vegetation type on 100 nights). All records of captured individuals, including those trapped for use in behavioural investigations, were included in the analysis.

5.3.3 Results

Figure 5.3.1 summarizes the distribution of captures of *I. obesulus* and *P. gunnii* in relation to vegetation. The results indicate that *I. obesulus* utilized the majority of different habitats present in the trapping-areas. Higher levels of captures were recorded in both open forest and shrub areas; that which had good understorey cover. The high capture-rates recorded in pastures and fire-affected habitats

FIG. 5.3.1 DISTRIBUTION OF CAPTURES OF I.obesulus AND P.gunnii IN
RELATION TO VEGETATION.



are believed to be biased results since there were much lower aggregate numbers of trap-nights in these areas, in comparison with all the other vegetation-types. However, it is important to note that *I. obesulus* was recorded in these areas since previous investigations had indicated that the latter was restricted to dense habitat types.

Few clear conclusions can be drawn from the results obtained for individuals of *P. gunnii*, because of the low numbers of captures recorded. However, it should be stated that all animals of this species were trapped in relatively dense areas that were adjacent to pastures. This appears to indicate that individuals of *P. gunnii* seek shelter in densely-vegetated areas during the day and move out into the open fields at night to feed. However, it is essential to recognize that the utilization of the different habitats may also depend on the availability of food and on social interactions. Both species possess home-ranges that could, in principle, potentially result in the exclusion of other conspecifics from an occupied area. Therefore, the area in which an animal is captured may not necessarily represent its preferred habitats. The occurrence of competitive interactions between and within species may restrict individuals to different sub-optimal habitats.

5.3.4 Discussion

The results pertaining to habitat utilization obtained in the present investigation are comparable to those recorded in previous studies. Buchmann (unpubl.) found that both *I. obesulus* and *P. gunnii* were distributed over a variety of habitats present on Porter's Hill. No significant preferences in habitat type were recorded. Heinsohn (1966) found that *P. gunnii* showed a marked preference for open areas, whereas *I. obesulus* were restricted to the more dense woodland habitats. Stoddart and Braithwaite (1979) reported that *I. obesulus* exhibits a

preference for regenerating heathland, but this tendency was most clearly shown by juveniles. Similar phenomena were indicated by the present study but a substantial ground covering also appeared to be essential before substantial movements into a fire-affected area occurred. It appears, therefore, that *P. gunnii* utilizes more open habitats but dense areas may still be required for refuges during the day. *I. obesulus* occupies a wide variety of habitats, with a clear preference for areas having low, dense ground-cover. Movements are facilitated by the presence of pathways penetrating throughout the dense understorey.

CHAPTER 6

INTRA- AND INTER-SPECIFIC INTERACTIONS

6.1 INTRODUCTION

Bandicoots are generally considered to be socially intolerant and pugnacious animals (Walker 1964), and amiable interactions are restricted only to mating and mother-offspring relationships (Ride 1970). Wood-Jones (1924) reported severe fighting when several individuals of *I. obesulus* were maintained together in captivity and occasionally the death of one of the animals resulted as a consequence of this. The method of fighting commonly practised by this species consisted of the aggressor tirelessly following its victim and striking it with the claws of the hind feet and forefeet.

Stodart (1966) observed intra-specific interactions between individuals of *P. nasuta* and described the animals as highly aggressive. Fighting between male conspecifics was similar to that described above. O'Callaghan (unpubl.) attempted to present quantitative data of social interactions in *I. obesulus* and Heinsohn (1966) observed interactions between individuals of *P. gunnii* and *I. obesulus* in a 30 x 30 m enclosure and in the field.

Events relating to social behaviour have been investigated in very many other species of mammals; therefore, only those relevant to the present investigation shall be mentioned here. King (1957) observed intra- and inter-specific conflicts between members of the two eutherian genera *Mus* and *Peromyscus* and Murie (1971) reported some aspects of the behavioural relationships occurring between two sympatric voles of the genus *Microtus*. Eisenberg (1962) investigated the social behaviour between two species of the genus *Peromyscus* and social interactions between *Rattus rattus* have been observed by Ewer (1971).

Studies on communication in normally solitary species of marsupials have been conducted by Buchmann and Guiler (1977) and Haynes (unpubl.) on *Sarcophilus harrisii* and *Antechinus swainsonii* and *A. minimus*, respectively. Agonistic behaviour and dominance has been observed in

confined individuals of wallabies (LaFollette 1971) and Hocking (unpubl.) reported on aspects of olfactory communication in post-parous females of *A. swainsonii* and *A. minimus*.

The purpose of the present investigation was to relate various forms of social behaviour occurring within and between the species of *I. obesulus* and *P. gunnii* maintained in artificial conditions to corresponding behaviours that may be exhibited when individuals of either species confront each other in natural conditions.

6.2 MATERIALS AND METHODS

The social behaviour of individuals of *I. obesulus* and *P. gunnii* was observed by placing paired subjects in a 2 x 2 m open arena as described in Section 4.3.2. Tests involved intraspecific-monosexual, intraspecific-heterosexual and interspecific (monosexual and heterosexual) interactions. For clarification, see Table 6.1.1.

Three dyadic trials were conducted on each of the ten possible combinations of paired subjects, yielding in a total of 30 observation-sessions, each of 30 min duration. The aim of these trials was to obtain an indication of the influence of the presence of subjects on one another and to obtain quantitative data (frequencies) of the activities performed by each of the individuals. The behavioural categories used in recording the behaviour of each of the two subjects used in a trial are presented in Table 6.2.2; the data were recorded on duplicated standard protocol sheets using abbreviated symbols as codes. This involved noting the behaviour of one of the subjects, then recording the ensuing behaviour (response) of the other individual.

Before any dyadic trials commenced, the arena was cleaned as described in Section 4.3.2 and subjects were weighed to the nearest 5 g using a Salter 5 kg spring-balance. Tests were calculated after 1900 h when subjects were normally active and two days were permitted to elapse between consecutive sessions that involved a particular individual.

TABLE 6.2.1 Schematic format of the test-sessions involving paired individuals of *I. obesulus* and *P. gunnii*. The numbers of dyadic trials are shown in parenthesis.

Sex-composition of dyads	Intraspecific	Interspecific
Monosexual	(3) male-male	
	<i>I. obesulus</i>	<i>I. obesulus</i> - <i>P. gunnii</i>
	(3) female-female	
		(3) male-male
	(3) male-male	(3) female-female
	<i>P. gunnii</i>	
Heterosexual	(3) female-female	
	(3) male-female <i>I. obesulus</i>	(3) male-male
	(3) male-female <i>P. gunnii</i>	(3) female-male

Individuals were identified by their sizes and other distinguishing features such as tail-lengths (most males having lost some part of their tails) and patches of bare skin (resulting from removal of fur when subjects were handled). It was, therefore, unnecessary to mark animals by applying water-based paints to the pelage as employed by Haynes (unpubl.) for observations of interactions between species of the genus *Antechinus*. Except during dyadic trials, all animals were continuously maintained in isolation in their holding cages.

For the purpose of assessing agonistic interactions, the aggressor was defined as the individual which employed pouncing in its behavioural repertoire and an interaction was not deemed sexual unless mounting by the male was observed. A National Panasonic video-tape recorder was used to film the majority of dyadic encounters; these tapes were subsequently analysed.

In many of the aggressive interactions, the antagonists were removed after only 10 min of observations because of the accumulation of injuries being inflicted by the attackers (described later).

TABLE 6.2.2 Behavioural categories and associated abbreviations used in recording the activities of each member of dyads maintained in a 2 x 2 m open arena.

Crouched posture	CP
Tripedal stance	TS
Nosing floor	NF
Bipedal stance	BS
Full stretch	FS
Rearing up wall	RW
Jumping	J
Lateral movements (head or forequarters)	LM
Head in corner	HC
Rump in corner	RC
Approach	A
Retreat	R
Quadrupedal stance and gaping	QG
Following	F
Nosing other animal	NA
Rearing and standing over other animal with head down and gaping	RS
Forepaws on other animal	FA
Pouncing	P
Biting	B
Crawling under other animal	CU
Head over other animal	HO
Grooming	G
Genital investigation	GI
Mounting	M
Prancing and spitting vocalization	PS
Pelvic thrust	PT

Frequencies of the various types of behavioural events were summed for all encounters of this nature. The same process was employed in recording behavioural events observed during sexual interactions. Events occurring with frequencies less than five in both subjects were excluded from analysis (presumed unimportant).

After 30 dyadic trials had been completed, the trials were repeated, with the modification that one of the individuals was placed in the arena one hour before the introduction of the other subject. These tests were performed to observe whether or not prior occupancy of the arena by an individual had any influence on the social status of that subject. However, no relationship appeared to exist between these factors, therefore the results of such tests were excluded from subsequent analyses.

6.3 RESULTS

6.3.1 Intra-specific, Monosexual Interactions

Encounters between male conspecifics of both *I. obesulus* and *P. gunnii* were invariably aggressive and the forms of behaviour exhibited by the aggressor and its antagonist were very similar in all dyadic trials, and also comparable between species. After their release, subjects immediately appeared to become aware of the presence of each other, mutually approaching, sniffing and nosing but frequently retreating after contact was established. During approaches, subjects occasionally nosed the floor and adopted the tripedal stance, possibly indicating hesitancy. Eventually subjects nosed and sniffed the cloacal region of each other and one individual thereupon immediately adopted a quadrupedal agonistic posture (Figure 6.3.1), presumably recognizing the other animal as another male. The posture involved a slight lowering of the head, with the mouth gaping. The back was

arched and the tail was held rigid, parallel to the ground. From this moment to the time of the cessation of observations, the aggressor continually engaged in this type of posturing while approaching the antagonist. The majority of approaches were made from behind the opponent, since the latter endeavoured to move away from its attacker. When close proximity was obtained, the aggressor reared and stood over the other animal, with the mouth gaping and the head lowered towards the antagonist (Figure 6.3.2). The aggressor then fell on the dorsum of the opponent, striking with the forepaws; these actions apparently induced the antagonist to jump high at the wall and later to run around the arena, with the aggressor in pursuit. While running, the fleeing animal emitted sneezing noises and the aggressor attempted to pounce (usually unsuccessfully) upon it. When the escaping individual had ceased running, the aggressor generally approached it again (usually from behind) and the sequence of events described in the foregoing account was repeated. It therefore appears that the aggressor may tirelessly follow and harass the antagonist, perhaps until it is worn down. Biting or striking with the hind claws was not observed in aggressive encounters, but these highly aggressive acts may have been recorded if observations had not been terminated after 10 min.

A comparison of the frequencies of various behavioural events occurring between the aggressor and its antagonist during agonistic interactions is presented in Table 6.3.1. Chi-square tests were performed on the observed and expected values of these events. The majority of the latter were significant. Higher frequencies of the tripedal stance and nosing the floor, presumably associated with the greater number of approaches observed, were observed in the behaviour of the aggressor. Agonistic activities such as following, nosing other animal, quadrupedal stance and gaping, pouncing, forepaws on other animal and rearing and standing over the antagonist were recorded

FIG. 6.3.1 The quadrupedal agonistic posture.
Note the gaping mouth.



FIG. 6.3.2 Rearing and standing over the antagonist.
Note the gaping mouth and lowered head of
the aggressor.



TABLE 6.3.1 Comparison of the frequencies of the various behavioural events occurring between the aggressor and antagonist in aggressive interactions.

Behavioural event	Aggressor	Antagonist	fe	χ^2_1	P
Tripedal stance	48	13	30.5	10.04	0.01
Nosing floor	39	10	24.5	8.58	0.01
Bipedal stance	19	12	15.5	0.79	n.s.
Rearing up wall	33	75	54	8.17	0.01
Jumping up wall	12	63	37.5	17.34	0.001
Head in corner	3	10	6.5	1.88	n.s.
Rump in corner	7	4	5.5	0.41	n.s.
Approach	93	25	59	19.59	0.001
Retreat	33	70	51.5	6.65	0.01
Quadrupedal stance and gaping	78	0	39	39	0.001
Following	46	0	23	23	0.001
Nosing other animal	48	16	32	8	0.01
Rearing and standing over animal with head down and gaping	101	0	50.5	50.5	0.001
Forepaws on other animal	31	0	15.5	15.5	0.001
Pouncing	99	0	49.5	49.5	0.001
Crawling under other animal	0	13	6.5	6.5	0.02

at significantly higher frequencies in the behaviour of the aggressor. Rearing and jumping up the wall and retreating, presumably associated with escape-motivation, were recorded in the behaviour of the antagonist with significantly higher frequencies than the expected values, as was crawling under the aggressor. The latter activity was performed

by the antagonist when the aggressor approached headlong and may be a submissive act.

Injuries inflicted upon the antagonist by the aggressor during agonistic encounters consisted of removal of fur and lacerations of the skin of the dorsum. However, more severe injuries may have resulted from interactions if observations were not concluded after only 10 min in each session, as indicated by the episode when two male *I. obesulus* dug underneath a deeply implanted partition and occupied a confined space for 12 h. When the observer arrived, one of the bandicoots was dead and subsequent autopsy of this animal revealed extensive superficial damage to the musculature of the thoracic and lumbar regions (Appendix A). The body was dorso-ventrally flattened and large patches of fur were found to be removed from the posterior lumbar region, presumably resulting from pouncing on the stricken animal by the aggressor. It should be noted here that there was no significant correlation between the dominance-status of subjects and their weights.

Encounters between female conspecifics of *I. obesulus* and *P. gunnii* were characterised by mutual avoidance and the frequencies of the various behavioural events observed in the two subjects during each dyadic trial were very similar. Occasionally an individual approached another animal with its mouth gaping but generally both subjects avoided each other at all times, one jumping high at a wall or moving away when the other came close.

6.3.2 Intra-specific, Heterosexual Interactions

Interactions between male and female conspecifics of both *I. obesulus* and *P. gunnii* were generally similar to encounters between female conspecifics, already described (i.e. mutual avoidance). However, some of the dyadic trials involved sexual interactions and minor differences were observed between these and the behaviour of the two species.

Sexual encounters of *I. obesulus* with conspecifics consisted of the male and female approaching each other tentatively at first (indicated by tripedal stances and sniffing), and retreating, followed by nosing of the cloacal region of the female by the male (Figure 6.3.3). This usually resulted in the female moving away and the male persistently following. Eventually, the female was cornered and as the male approached to close quarters, it attempted to position its head under the body of the male. The female then pranced (Section 3.4.3) away from the male and the latter began to follow again. Sneezing vocalizations were associated with the prancing locomotion. Mounting was not observed until late in the course of the observation period and this involved the male rearing on its hind limbs with the body inclined slightly forward, and pressing the pelvic region towards the hind-quarters of the female. The forelimbs of the male were suspended loosely by its sides and pelvic thrusts occurred in rapid succession (Figure 6.3.4). The stance was maintained for a few seconds; the male then resumed a quadrupedal posture as the female moved away. Successive attempts at mounting occurred at intervals of approximately 30 s. However, in all such attempts, the female appeared unreceptive because its rump was always in contact with ground. It is, therefore, unlikely that intromission could have occurred.

Table 6.3.2 presents a comparison of the frequencies of the various behavioural events between male and female *I. obesulus* during sexual interactions. As expected, males exhibited significantly higher frequencies of following, nosing the female, mounting and pelvic thrusting, whereas in females significantly higher frequencies of prancing and placing its head under the male were recorded. However, males were also observed to perform activities associated with aggression. These consisted of pouncing, rearing and standing over the female or adopting a quadrupedal agonistic posture and such events

FIG. 6.3.3 Nosing the cloacal region of the female.



FIG. 6.3.4 Mounting the female.
Note the apparent lack of cooperation by the female, indicated by lowering the hindquarters to the ground.



were generally observed after mounting attempts had terminated. The male appeared to become intolerant of the female and continually harassed it (as described for agonistic encounters) until observations were concluded.

Similar forms of aggressive behaviour were recorded in sexual interactions of *P. gunnii* with conspecifics after mounting attempts had ceased. When attacked, the female repeatedly attempted to crawl under the male or to insinuate its head under the latter (Table 6.3.3). Although this behaviour appeared submissive in its motivation, the male generally bit the female when in close contact and emitted snorting sounds.

The course of events in the sexual behaviour of *P. gunnii* to conspecifics was essentially similar to that described in *I. obesulus* sexual interactions except that males approached significantly more often than females and when approached, females generally adopted a crouched posture, possibly indicating their wariness. While engaging in prancing, female *P. gunnii* emitted a spitting vocalization, not a sneezing sound as described in female *I. obesulus*. Female *P. gunnii* also appeared unreceptive when mounted, holding the rump in contact with the ground.

6.3.3 Inter-specific Interactions

Encounters between individuals of *I. obesulus* and *P. gunnii*, whether monosexual or heterosexual, were similar to those described for female conspecific interactions. Both subjects avoided each other and if one approached too close the other would jump high at a wall of the arena with both animals subsequently running and jumping around the arena, apparently in a frenzied state. The frequency of the various behavioural events recorded for both interacting individuals in each dyadic trial were also very similar.

TABLE 6.3.2 Comparison of the frequencies of the various behavioural events between male and female *I. obesulus* in sexual interactions.

Behavioural events	Male	Female	fe	χ^2_1	P
Tripedal stance	41	5	23	14.1	0.001
Nosing floor	53	46	48.5	0.13	n.s.
Bipedal stance	62	67	64.5	0.10	n.s.
Rearing up wall	54	72	63	1.29	n.s.
Jumping up wall	45	32	38.5	1.10	n.s.
Head in corner	4	9	6.5	0.96	n.s.
Approach	86	64	75	1.61	n.s.
Retreat	37	45	41	0.39	n.s.
Quadrupedal stance and gaping	67	13	40	18.23	0.001
Following	45	2	23.5	19.67	0.001
Nosing other animal	63	31	47	5.45	0.02
Rearing and standing over other animal with head down and gaping	28	3	15.5	10.01	0.01
Forepaws on other animal	35	16	25.5	3.54	n.s.
Pouncing	6	0	6	6	0.02
Head under other animal	5	20	12.5	4.5	0.05
Mounting	12	0	12	12	0.001
Pelvic thrust	10	0	10	10	0.01
Prancing	0	7	7	7	0.01

6.4 DISCUSSION

Although solitary animals such as bandicoots spend the majority of their lives with little direct contact between conspecifics,

TABLE 6.3.3 Comparison of the frequencies of the various behavioural events between male and female *P. gunnii* in sexual interactions.

Behavioural event	Male	Female	fe	χ^2_1	P
Tripedal stance	13	3	8	3.13	n.s.
Nosing floor	19	4	11.5	4.89	0.05
Bipedal stance	3	10	6.5	1.88	n.s.
Crouched posture	0	85	42.5	42.5	0.001
Rearing up wall	20	25	22.5	0.28	n.s.
Jumping up wall	28	38	33	0.76	n.s.
Approach	47	2	24.5	20.66	0.001
Retreat	0	56	28	28	0.001
Quadrupedal stance and gaping	16	0	8	8	0.01
Following	12	0	6	6	0.02
Nosing other animal	22	12	17	1.47	n.s.
Forepaws on other animal	27	0	13.5	13.5	0.001
Pouncing	30	0	15	15	0.001
Biting	32	0	16	16	0.001
Crawling under other animal	0	61	30.5	30.5	0.001
Head under other animal	0	42	21.5	21.5	0.001
Mounting	62	0	31	31	0.001
Pelvic thrust	49	0	24.5	24.5	0.001
Prancing	0	44	22	22	0.001

situations must arise in natural conditions when encounters are unavoidable or are an essential requirement of individuals (i.e. mating, mother-offspring and territorial defence). In order that social interactions may occur between conspecifics, there must be suitable channels of communication in the form of either visual, auditory,

tactile or chemical stimuli (Van Gelder 1969). Accordingly, the present investigation was aimed at examining the influence of individuals on one another, with particular reference to agonistic and sexual interactions, and to attempt to recognise the role of the aforementioned stimuli during such encounters.

Interactions between male conspecifics of both *I. obesulus* and *P. gunnii* were invariably agonistic and the behaviours observed in each dyadic trial were very similar to the aggressive encounters described in *P. nasuta*, *I. obesulus* and *P. gunnii* by Stodart (1966), O'Callaghan (unpubl.) and Heinsohn (1966), respectively. The aggressors performed activities that were contact-promoting (i.e. approaching, following, nosing, pouncing and striking with the forepaws) whereas the behaviour of the opponent was generally non-contact-promoting (i.e. retreating). However, when cornered and unable to retreat, the latter individual often altered its behaviour to a type promoting contact, e.g. by crawling under the aggressor. Presumably this activity was beneficial since it prevented the aggressor from pouncing and striking the antagonist with the forepaws.

Encounters were seldom conducted face-to-face. Instead, the antagonist exposed its rump to the aggressor. This may explain the high incidence of male subjects of *I. obesulus* lacking intact, complete tails that were captured during the course of this study (Section 2.2). Heinsohn (1966) recorded observations on the mauled tail on an antagonist after he observed an agonistic interaction between two male *I. obesulus* and loss of at least part of the tail is also a characteristic form of mutilation in the eutherian kangaroo rats, *Dipodomys panamintinus* during aggressive encounters (Bartholomew and Caswell 1951). The fact that the aggressor generally approaches from behind the antagonist appears to indicate that the role of visual stimuli is relatively unimportant in such interactions and that rearing and standing over the

antagonist with the head down and mouth gaping may merely constitute an activity assisting in the delivery of decisive blows to the dorsum of the antagonist with the foreclaws and not a threat-posture *per se*. However, in natural situations, an opportunity to inflict serious injuries may seldom exist because the antagonist usually flees rapidly from the attacker. Kicking with the hind feet as described by Wood-Jones (1924) was not observed in any of the dyadic trials.

The results are compatible with the view that male individuals of *I. obesulus* and *P. gunnii* may be territorial, exhibiting overt hostility to other male conspecifics. Presumably, individuals are unable to defend the whole of their home range (Chapter 5) but males may be aggressive towards male conspecifics whenever they meet (spatial-temporal territoriality). The generally amicable behaviour shown by males towards females and *vice versa* may be an advantage to both individuals since little time may need to be spent searching for mating partners in natural conditions (individuals of both sexes usually occupy adjacent or overlapping home ranges).

Olfactory communication between individuals appears to be important in recognising the sex of conspecifics. In all dyadic trials, subjects approached and sniffed the cloacal region of other individuals before the interaction became aggressive, sexual or amicable. This appears to be the most probable method of identifying the sex of conspecifics, since morphological differences between males and females are negligible and if any of these exist they may be expected to be more difficult to detect at night when the animals are normally active.

Sexual interactions observed in the present investigation were similar to those described by Stodart (1966) and Heinsohn (1966) in *P. nasuta* and *I. obesulus* and *P. gunnii*, respectively. The male persistently follows and attempts to mount the female. Both sexes of *I. obesulus* and *P. gunnii* possess subauricular cephalic skin-gland

complexes (Stoddart 1980). The complex lies immediately behind and slightly below the ear. It is approximately oval in shape and in adult males, during the breeding season, the complex expands, causing its upper surface to bulge outwards, and the secretion from the complex is sufficiently copious to impart a damp appearance to the fur of the neck. Two specimens of *I. obesulus* possessing these characteristics, were captured during the trapping-programmes. However, bandicoots maintained in captivity did not exhibit any complex activity. Stoddart (*op. cit.*) suggested that the pungent odour secreted by these complexes has a calming and reassuring role in the courtship behaviour of these solitary and pugnacious small marsupials.

The absence of activity of the complex in captive subjects used in studies of sexual encounters may explain the aggressiveness of the males directed towards females after mounting ceased. Both subjects appeared highly agitated and a male *P. gunnii* was observed biting the female, an activity not even recorded in agonistic encounters.

The mutual avoidance observed between individuals of *I. obesulus* and *P. gunnii* when the animals are placed together appears to indicate that neither species has any major effects on the behaviour or dispersal of members of the other species.

CHAPTER 7

GENERAL DISCUSSION

Bandicoots appear to be ecological equivalents of the eutherian hedgehogs and shrews (insectivora) in that they occupy similar niches, are small mammals that excavate in the soil during darkness, attempting to locate insects and rest during the day in nests.

The present investigation was conducted to establish differences in the behaviour and ecology of two sympatrically-occurring species of bandicoots, *Isoodon obesulus* and *Perameles gunnii*, considered to be of interest because both species have very similar requirements with regard to food and refuges. Live-trapping programmes revealed that a variety of similar habitat-types are occupied by both species, but it was noticeable that *P. gunnii* was associated with open areas while *I. obesulus* remained in dense scrub areas. Overlap in the areas of home ranges was extensive between and within the two species and the relative sizes of the home ranges appeared to represent the area needed to provide the food requirements of an individual. Food is abundant during most of the year and both *I. obesulus* and *P. gunnii* utilize a wide variety of food items. Consequently, competition between the two species for such a resource may be negligible.

Observations were conducted on individuals of *I. obesulus* and *P. gunnii* in captivity. The activity-patterns of the two species were significantly different; *I. obesulus* emerged shortly after sunset and was active for only a brief period in contrast to *P. gunnii* which emerged much later after sunset, then remained active until immediately before sunrise. Both species resided in nests during the day and since similar food items were utilized and home ranges between the two overlapped, this difference in their activity-schedules may reduce competition further.

The foraging behaviours of *I. obesulus* and *P. gunnii* were also significantly different. *I. obesulus* devoted considerably less time to excavating in the soil but appeared to be better adapted at capturing

and killing large prey (small vertebrates). This may indicate that *I. obesulus* is capable of utilizing a greater variety of food items.

The use of faeces and urine in marking by both species appears to have a reassurance value to the animals performing it. Deposits were mostly concentrated around food, drinking-sources and nest areas. However, the possible use of such substances in communication between individuals cannot be positively excluded.

Studies on locomotion revealed that both *I. obesulus* and *P. gunnii* possess four terrestrial gaits that are utilized in the contexts of different activities. *P. gunnii* is able to attain higher velocities than *I. obesulus* and this may be an essential attribute for animals utilizing open terrain where the probability of predation is presumably greater.

Intraspecific agonistic behaviour was frequent between males, but negligible between females and between members of the opposite sex. Tactile and olfactory stimuli appeared to be important in these interactions and males may be assumed to be territorial to the extent that they actively harass and expel an intruding male from an area that they concurrently or immediately occupied. However, there was no evidence to suggest that the weights of the interacting individuals was a predictive index to the outcome of encounters; a heavier individual was not always dominant over a lighter one. It also appears that both species are promiscuous with regard to mating and that the pair-bond lasts only as long as the duration of matings.

In conclusion, observations made in the present study suggest that ecological separation of the two species is associated with different activity-periods, foraging-strategies and selection of micro-habitats.

REFERENCES

- ALEXANDER, R.M. and VERNON, A. (1975). The mechanics of hopping by kangaroos. *J. Zool., Lond.* 177: 295-303.
- ALTMANN, J. (1974). Observation study of behaviour: sampling methods. *Behav.* 49: 227-267.
- AMBROSE, H.W. III (1969). A comparison of *Microtus pennsylvanicus* home range as determined by isotope and live-trap methods. *Amer. Mid. Nat.* 81: 535-555.
- ANDREW, D.L. and SETTLE, G.L. (1981). Observations on the behaviour of *Planigale* Dasyuridae, Marsupialia) with particular reference to the Narrow-nosed *Planigale* (*Planigale tenuirostris*). In: Archer, M. (ed.), *Carnivorous Marsupials*, Roy. Zool. Soc. of N.S.W.
- ASLIN, H. (1974). The behaviour of *Dasyuroides byrnei* (Marsupialia) in captivity. *Z.Tierpsychol.* 35: 187-208.
- BARTHOLOMEW, G.A. Jr. and CASWELL, H.H. Jr. (1951). Locomotion in kangaroo rats and its adaptive sign. *J. Mammal.* 32: 155-169.
- BLAIR, W.F. (1940). Home ranges and populations of the meadow vole in southern Michigan. *J. Wildl. Mgr.* 4: 149-161.
- BLAIR, W.F. (1941). Techniques for the study of mammal populations. *J. Mammal.* 22: 148-157.
- BOMBARDIERI, R.A. and JOHNSON, J.I. (1969). Daily activity schedule of captive opossums. *Psychon. Sci.* 17: 135-136.
- BRAITHWAITE, R.W. (1974). Behavioural changes associated with population cycles of *Antechinus stuartii*. *Aust. J. Zool.* 22: 45-62.
- BRAITHWAITE, R.W. (1979). Social dominance and habitat utilization in *Antechinus stuartii*. *Aust. J. Zool.* 27: 517-528.
- BRAITHWAITE, R.W. and GULLAN, P.K. (1978). Habitat selection by small mammals in a Victorian heathland. *Aust. J. Ecol.* 3: 109-127.
- BRAITHWAITE, R.W., COCKBURN, A. and LEE, A.K. (1978). Resource partitioning by small mammals in lowland heath communities of south-eastern Australia. *Aust. J. Ecol.* 3: 423-445.
- BUCHMANN, O.L.K. and GRECIAN, E.A. (1974). Discrimination-reversal learning in the marsupial *Isoodon obesulus* (Marsupialia:Peramelidae). *Anim. Behav.* 22: 975-981.
- BUCHMANN, O.L.K. and GUILER, E.R. (1974). Locomotion in the potoroo. *J. Mammal.* 55: 203-206.
- BUCHMANN, O.L.K. and GUILER, E.R. (1977). Recent behavioural and ecological studies on the Tasmanian Devil, *Sarcophilus harrisii* (Boitard) (Dasyuridae:Marsupialia). In: *Biology of Marsupials*, McMillan, London, pp.155-168.
- BURT, W.H. (1940). Territorial behaviour and populations of some small mammals in southern Michigan. *Misc. Publ. Mus. Zool. Univ. Mich.* 45: 1-58.

- BURT, W.H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24: 346-352.
- CALABY, J.H. (1960). Observations on the banded Anteater, *Myrmecobiacis fasciatus* Waterhouse (Marsupialia) with particular reference to its food habits. *Proc. Zool. Soc. Lond.* 135: 183-206.
- CHANCE, M.R.A. and RUSSELL, W.M.S. (1959). Protean displays: a form of allaesthetic behaviour. *Proc. Zool. Soc. Lond.* 132: 65-70.
- CAMERON, A.W. (1964). Competitive exclusion between the rodent genera *Microtus* and *Clethrionomys*. *Evol.* 18: 630-634.
- CHITTY, D. and KEMPSON, D.A. (1949). Pre-baiting small mammals and a new design of live traps. *Ecol.* 30: 536-542.
- CHITTY, D. and SHORTEN, M. (1946). Techniques for the study of the Norway rat (*Rattus norvegicus*). *J. Mammal.* 27: 63-78.
- CLARKE, J.H. and CLARKE, C. (1969). Scrub ticks and a bandicoot. *Qd. Nat.* 19: 81.
- CROFT, D.B. (1981a). Behaviour of red kangaroos, *Macropus rufus* (Desmarest 1822) in north-western New South Wales, Australia. *Aust. Mammal.* 4: 5-58.
- CROWCROFT, P. and JEFFERS, J.N.R. (1961). Variability in the behaviour of the wild house mouse to live traps. *Proc. Zool. Soc. Lond.* 137: 573-582.
- DALKE, P.D. (1942). The cottontail rabbits in Connecticut. *Connecticut State Geol. and Natur. Hist. Surv. Bull.* 65: 1-97.
- DAVIS, D.E., EMLEN, J.T. and STOKES, A.H. (1948). Studies on home ranges in the brown rat. *J. Mammal.* 29: 207-225.
- DAVIS, J.A.Jr. (1961). Exhibition of nocturnal mammals by red light. *Inter. Zool. Year.* 3: 9-11.
- DAY, B., KIRKBY, R. and STENHOUSE, E. (1974). The behaviour of marsupials III. The shortnosed bandicoot, *Isodon macrourus* (Peramelidae) in the open field. *Aust. Mammal.* 1: 255-259.
- DOUGLASS, R.J. (1976). Spatial interactions and microhabitat selections of two locally sympatric voles, *Microtus montanus* and *M. pennsylvanicus*. *Ecol.* 57: 346-352.
- EISENBERG, J.R. (1962). Studies on the behaviour of *Peromyscus maniculatus gambolii* and *Peromyscus californicus paraciticus*. *Behav.* 19: 177-207.
- EISENBERG, J.R. and LEYHAUSEN, P. (1972). The phylogenesis of predatory behaviour in mammals. *Z. Tierpsychol.* 30: 59-93.
- EVANS, F.C. and HOLDENREID, R. (1943). A population study of Beechey ground squirrel in central California. *J. Mammal.* 24: 231-260.

- EWER, R.F. (1968). A preliminary survey of the behaviour in captivity of the dasyurid marsupial *Sminthopsis crassicaudata* (Gould). *Z. Tierpsychol.* 25: 319-365.
- EWER, R.F. (1969). Some observations on the killing and eating of prey by two dasyurid marsupials: the mulgarn, *Dasyercus cristicauda*, and the Tasmanian Devil, *Sarcophilus harrisii*. *Z. Tierpsychol.* 26: 23-28.
- EWER, R.F. (1971). The biology and behaviour of a free-living population of black rats (*Rattus rattus*). *Animal Behaviour Monographs*. Vol. 4 Part 3.
- FOX, M.W. (1971). Behaviour of wolves, dogs and related canids. Cape, London.
- FRITH, H.J. (1964). Mobility of the red kangaroo, *Megaleia rufa*. *C.S.I.R.O. Wildl. Res.* 9: 1-19.
- FRITH, H.J. and CALABY, J.H. (1969). Kangaroos. F.H. Cheshire, Melbourne.
- GLICKMAN, S.E. and SCROGES, R.W. (1966). Curiosity in zoo animals. *Behav.* 26: 151-181.
- GORDON, G. (1974). Movements and activity of the shortnosed bandicoot *I. macrourus* (Gould) Marsupialia. *Mammalia* 38: 405-431.
- GRANT, P.R. (1970). Experimental studies of competitive interaction in a two-species system II. - the behaviour of *Microtus*, *Peromyscus*, *Clethrionomys*. *Anim. Behav.* 18: 411-426.
- GRANT, P.R. (1971). Experimental studies of competitive interaction in a two-species system III. *Microtus* and *Peromyscus* species in enclosure. *J. Anim. Ecol.* 40: 323-350.
- GRANT, T.R. (1973). Dominance and association among members of a captive and free-ranging group of grey kangaroos (*Macropus giganteus*). *Anim. Behav.* 21: 449-456.
- GRANT, T.R. (1974). Observations of enclosed and free-ranging kangaroos *Macropus giganteus*. *Z. Säugetierk.* 39: 65-77.
- GREEN, R.H. (1967). The murids and small dasyurids of Tasmania: Parts 1 and 2. *Rec. Queen Vict. Mus.* 28: 1-19.
- GUILER, E.R. (1958). Observations of a population of small marsupials in Tasmania. *J. Mammal.* 39: 44-58.
- GUILER, E.R. (1970a). Observations on the Tasmanian Devil, *Sarcophilus harrisii* (Marsupialia:Dasyuridae). 1. Numbers, home-range, movements and food in two populations. *Aust. J. Zool.* 18: 49-62.
- HALL, S. (1980). The diets of two coexisting species of *Antechinus* (Marsupialia:Dasyuridae). *Aust. Wildl. Res.* 7: 365-378.
- HAYNE, D.W. (1949). Calculations of size of home range. *J. Mammal.* 30: 1-18.

- HAYNES, M.A. (1982). Social behaviour of *Antechinus swainsonii* (Waterhouse 1840) and *A. minimus* (Geoffrey 1803) from the Cloudy Creek catchment area, Bruny Island, Tasmania. B.Sc. (Hons.) Thesis, University of Tasmania, Hobart, 217 pp.
- HEINSOHN, G.E. (1964). Ecology and reproduction of the two species of Tasmanian bandicoots, *Perameles gunnii* and *Isoodon obesulus*. *Calif. Publ. Zool.* 80: 1-107.
- HILDEBRAND, M. (1960). How animals run. *Sci. Amer.* 202(5): 148-157.
- HOCKING, G.J. (1975). Studies on the behaviour and ecology of *Antechinus swainsonii*. B.Sc. (Hons.) Thesis, University of Tasmania, Hobart, 167 pp.
- HOLMES, A.C.V. and SANDERSON, G.C. (1965). Populations and movements of opossums in east-central Illinois. *J. Wildl. Mgmt.* 29: 281-295.
- HUME, I.D. (1982). *Digestive physiology and nutrition of marsupials*. Cambridge Uni. Press, Cambridge.
- HUTSON, G.D. (1975). Sequences of prey-catching behaviour in the brush-tailed marsupial rat (*Dasyuroides byrnei*). *Z. Tierpsychol.* 39: 39-60.
- HUTSON, G.D. (1976). Grooming behaviour and birth in the dasyurid marsupial, *Dasyuroides byrnei*. *Aust. J. Zool.* 24: 277-282.
- HUMPHRIES, D.A. and DRIVER, P.M. (1970). Protean defence by prey animals. *Oecologia* 5: 285-302.
- HYETT, J. and SHAW, N. (1980). *Australian Mammals: a field guide for New South Wales, Victoria, South Australia and Tasmania*. Thomas Nelson Aust., Melbourne.
- JUSTICE, K.E. (1961). A new method for measuring home ranges of small mammals. *J. Mammal.* 42: 462-470.
- KAUFMANN, J.H. (1975). Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus*. *Anim. Behav.* 23: 214-221.
- KERRY, K.R. (1969). Intestinal disaccharidase activity in a monotreme and eight species of marsupials (with an added note on the disaccharidases of five species of sea birds). *Comp. Biochem. and Physiol.* 29: 1015-22.
- KING, J.A. (1957). Intra- and inter-specific conflict of *Mus* and *Peromyscus*. *Ecol.* 38: 355-357.
- KIRCH, J.A.W. (1968). Burrowing by the quenda, *Isoodon obesulus*. *West. Aust. Nat.* 10: 178-180.
- KITCHENER, D.J. (1967). The biology of the potoroo (*Potorous tridactylus apicalis*). B.Sc. (Hons.) Thesis, University of Western Australia.
- KITCHENER, D.J. (1973). Notes on home range and movement in two small macropods, the potoroo (*Potorous apicalis*) and the quokka (*Setonix brachyurus*). *Mammalia* 37: 231-240.

- LaFOLLETTE, R.M. (1971). Agonistic behaviour and dominance in confined wallabies, *Wallabia rufogrisea frutica*, (Bennett's wallaby). *Anim. Behav.* 19: 93-101.
- Le SOUEF, A.S., BURRELL, H. and TROUGHTON, E.G. (1926). The Wild Animals of Australasia. George G. Harrap and Co. Ltd., London, pp.297-317.
- LYNE, A.G. (1951). Notes on the external characters of the barred bandicoot (*Perameles gunni* Gray), with special reference to pouch young. *Proc. Zool. Soc. Lond.* 121: 587-598.
- LYNE, A.G. (1952). Notes on the external characters of the pouch young of four species of bandicoot. *Proc. Zool. Soc. Lond.* 122: 625-649.
- LYNE, A.G. (1964a). Observations on the breeding and growth of the marsupial *Perameles nasuta* Geoffroy, with Notes on other bandicoots. *Aust. J. Zool.* 12: 322-339.
- LYNE, A.G. (1974). Gestation period and birth in the marsupial *Isoodon macrourus*. *Aust. J. Zool.* 22: 303-309.
- LYNE, A.G. (1981). Activity rhythms in the marsupials *Isoodon macrourus* and *Perameles nasuta* in captivity. *Aust. J. Zool.* 29: 821-838.
- LYNE, A.G. and VERHAGEN, M.N. (1957). Growth of the marsupial *Trichosurus vulpecula* and a comparison with some higher mammals. *Growth* 21: 167-195.
- MACKERAS, M.J. and SMITH, R.H. (1960). Breeding of the shortnosed marsupial bandicoot *Isoodon macrourus* (Gould) in captivity. *Aust. J. Zool.* 8: 371-382.
- MARLOW, B.J. (1961). Reproductive behaviour in the marsupial mouse, *Antechinus flavipes* (Waterhouse) (Marsupialia) and the development of the pouch young. *Aust. J. Zool.* 9: 203-218.
- MARLOW, B.J. (1969). A comparison of the locomotion of two desert-living Australian mammals, *Antechinomys spenceri* (Marsupialia: Dasyuridae) and *Notomys cervinus* (Rodentia: Muridae). *J. Zool. Lond.* 157: 159-167.
- MAZA, B.G., FRENCH, N.R. and ASCHWANDEN, A.P. (1973). Home range dynamics in a population of Heteromyid rodents. *J. Mammal.* 54: 405-425.
- McMANUS, J.J. (1970). Behaviour of captive opossums, *Didelphis marsupialis virginiana*. *Amer. Midl. Nat.* 84: 144-169.
- McMANUS, J.J. (1971). Activity of captive *Didelphis marsupialis*. *J. Mammal.* 52: 846-848.
- MOHR, C.O. (1947). Table of equivalent populations of North American small mammals. *Amer. Midl. Nat.* 37: 223-249.
- MOHR, C.O. and STUMPF, W.A. (1966). Comparison of methods for calculating areas of animal activity. *J. Wildl. Mgmt.* 30: 293-304.

- MORRIS, R.D. (1969). Competitive exclusion between *Microtus* and *Clethrionomys* in the Aspen Parkland of Saskatchewan. *J. Mammal.* 50: 291-301.
- MORTON, S.R. and BURTON, T.C. (1973). Observations on the behaviour of *Thylogale billardierii* (Desmarest) in captivity. *Aust. Zool.* 18: 1-14.
- MOSS, V.N. (1978). Studies on the maintenance activities of the eastern native cat, *Dasyurus viverrinus*. B.Sc. (Hons.) Thesis, University of Tasmania, Hobart, 171 pp.
- MURIE, J.O. (1971). Behavioural relationships between two sympatric voles (*Microtus*). *J. Mammal.* 52: 181-186.
- MYTON, B. (1974). Utilization of space by *Peromyscus leucopus* and other small mammals. *Ecol.* 55: 277-290.
- O'CALLAGHAN, B.W. (1974). Studies on the behaviour of *Isoodon obesulus*. B.Sc. (Hons.) Thesis, University of Tasmania, Hobart, 246 pp.
- PACKER, W.C. (1969). Observations on the behaviour of the marsupial *Setonix brachyurus* (Quoy and Gaimard) in an enclosure. *J. Mammal.* 50: 8-20.
- RAYMENT, T. (1954). Australia's bandicoots. *Vict. Nat.* 70: 194-196.
- RIDE, W.D.L. (1970). A Guide to the Native Mammals of Australia. Oxford University Press, London, pp.95-100.
- RUSSELL, E.M. (1969). Summer and winter observations of the behaviour of the euro *Macropus robustus* (Gould). *Aust. J. Zool.* 17: 655-664.
- RUSSELL, E.M. (1970a). Observations on the behaviour of the red kangaroo (*Megaleia rufa*) in captivity. *Z. Tierpsychol.* 27: 385-404.
- RUSSELL, E.M. (1970b). Agonistic interactions in the red kangaroo (*Megaleia rufa*). *J. Mammal.* 51: 80-88.
- RUSSELL, E.M. (1974). The biology of kangaroos (Marsupialia: Macropodidae). *Mammal. Rev.* 4: 1-59.
- RUSSELL, E.M. (1976). The behaviour of red kangaroos (*Megaleia rufa*) on hot summers days. *Z. Tierpsychol.* 40: 396-426.
- RUSSELL, E.M. and PEARSE, G.A. (1971). Exploration of novel objects by marsupials. *Behav.* 40: 312-322.
- SAMPSON, J.C. (1971). The biology of *Bettongia penicillata* (Gray 1837). Ph.D. Thesis, University of Western Australia, Perth, 255 pp.
- SANDERSON, G.C. (1966). The study of mammal movements - a review. *J. Wildl. Mgmt.* 30: 215-235.

- SCHULTZ, W. (1976). Magen - Darm - Kanal der Monotremen und Marsupialier. In: Digestive Physiology and Nutrition of Marsupials. Hume, I.D. (ed.), Cambridge University Press.
- SEEBECK, J.H. (1979). Status of the barred bandicoot, *Perameles gunnii*, in Victoria - with a note on husbandry of a captive colony. *Aust. Wildl. Res.* 6: 255-264.
- SHIRER, H.W. and FITCH, H.S. (1970). Comparison from radio-tracking of movements and denning habits of the racoon, striped skunk and opossum in north-eastern Kansas. *J. Mammal.* 51: 491-503.
- SLATER, P.J.B. (1978). Data collection. In: Colgan, P.W. (ed.), *Quantitative Ethology*, John Wiley and Sons, New York, pp.7-24.
- SMITH, M.H. (1968). A comparison of different methods of capturing and estimating numbers of mice. *J. Mammal.* 49: 455-462.
- SOUTHERN, H.N. (1965). *The Hand-book of British Mammals*, Blackwell, Oxford, pp.24-25.
- STANBURY, P. (1970). *Looking at Mammals*, Oxford Uni. Press, London, pp.35-39.
- STICKEL, L.F. (1948). The trap line as a measure of small mammal populations. *J. Wildl. Mgmt.* 12: 153-161.
- STICKEL, L.F. (1954). A comparison of certain methods of measuring ranges of small mammals. *J. Mammal.* 35: 1-15.
- STODART, E. (1966). Observations on the behaviour of the marsupial *Bettongia lesueuri* (Quoy and Gaimard) in an enclosure. *C.S.I.R.O. Wildl. Res.* 11: 91-99.
- STODART, E. (1966). Management and behaviour of breeding groups of the marsupial *P. nasuta* (Geoffroy) in captivity. *Aust. J. Zool.* 14: 611-623.
- STODDART, D.M. and BRAITHWAITE, R.W. (1979). A strategy for utilization of regenerating heathland habitat in the brown bandicoot. *J. Anim. Ecol.* 48: 165-179.
- STODDART, D.M. (1980). Observations on the structure and function of cephalic skin glands in bandicoots. *Aust. J. Zool.* 28: 33-41.
- SUCKLING, G.C. and HEISTENS, A. (1978). Populations of four small mammals in *Radiata* pine plantations and *Eucalypt* forests of north-eastern Victoria. *Aust. Wildl. Res.* 5: 305-315.
- TANTON, M.T. (1965). Problems of live-trapping and population estimation for the wood mouse, *Apodemus sylvaticus* (L.). *J. Anim. Ecol.* 34: 1-22.
- TROUGHTON, E. (1965). *Furred Animals of Australia*. Angus and Robertson Ltd., Sydney, pp.60-78.
- VAN DEUSEN, H.M. (1969). Feeding habits of *Planigale* (Marsupialia: Dasyuridae). *J. Mammal.* 50: 616-618.

- WALKER, E.P. (1964). Mammals of the World. Vol. 1. John Hopkins Press, Baltimore, pp.49-55.
- WATTS, C.H.S. (1974). The Nuyts Islands bandicoot (*Isoodon obesulus nanticus*). *South Aust. Nat.* 49: 20-24.
- WINDSOR, D.E. and DAGG, A.I. (1971). The gaits of the Macropodinae (Marsupialia). *J. Zool. Lond.* 163: 165-175.
- WOOD-JONES, F. (1924). The Mammals of South Australia, Part II - the Bandicoots and Herbivorous Marsupials. A.B. James, Government Printer, Adelaide, pp.136-151.
- BROWN, J.C. (1964). Observations on the elephant shrews (Macroscelididae) of equatorial Africa. Proc. Zool. Soc. Lond. 143: 103-119.
- CALHOUN, J.B. (1962). The ecology and sociology of the Norway rat. U.S. Gov. Printing, Washington, D.C.
- DAVIS, D.E. and GOLLEY, F.B. (1963). Principals of Mammalogy. pp. 288-297. Reinhold Publ. Corp. U.S.A.
- EALEY, E.H.M. and MAIN, A.R. (1967). Ecology of the euro, Macropus robustus (Gould), in north-western Australia. 11 Behaviour, movement and drinking patterns. C.S.I.R.O. Wildl. Res. 12: 9-80.
- EISENBERG, J.F. (1968). Behaviour patterns. In: Biology of Peromyscus (Rodentia). King, J.S. (ed.).
- GOIN, C.J. and GOIN, O.B. (1962). Introduction to Herpetology. W.H. Freeman, San Francisco. 341pp.
- KAUFMANN, J.H. (1962). Ecology and social behaviour of the coati, Nasua narica, on Barro Colorado Island, Panama. Uni. Calif. Publ. Zool. 60: 95-222.
- LAYNE, J.N. (1954). The biology of the red squirrel, Tamiasciurus hudsonicus loquax (Bangs), in central New York. Ecol. Mono. 24: 227-267.
- NOBLE, G.K. (1939). The role of dominance in the social life of birds. Auk. 56: 263-273.
- RIDE, W.D.L. (1965). Locomotion in the Australian marsupial Antechinomys. Nat. Lond. 205: 199.
- WILSON, E.O. (1971b). Competition and aggressive behaviour. In: Man and Beast: comparative social behaviour. J.F. Eisenberg and W. Dillon (eds).
- VAN GELDER, D. (1969). The biology of mammals. Charles Scribers Sons, New York, 197pp.
- OPIE, A.M. (1980). Habitat selection and the diet of *Isoodon obesulus*. Aust. Mammal Soc. Bull. 6: 56.

APPENDIX A

APPENDIX A*I. obesulus* AND *P. gunnii* DYING DURING THE
COURSE OF THE STUDY

Autopsies were conducted on all subjects that died during the course of the study. The features of gross morbid anatomy were first noted before dissections were carried out. The spleen and adrenal glands of the corpses were removed for subsequent weighing, and the stomach and duodenum were examined for ulcerations under a dissecting microscope. The intestine was also inspected for the presence of parasites.

Possible explanations of the causes of death in subjects are particularly difficult to formulate. Table A.1 presents selected anatomical and morphological features of the carcasses autopsied, and the high degree of variation occurring between the subjects with respect to these is easily discerned; this probably indicates considerable differences in the causation of deaths.

Subjects M5 and F2 showed distinctive features probably associated with systemic stress. However, a low combined relative adrenal weight, a phenomenon usually associated with the exhaustion phase of stress, was only recorded in M5. Indeed, both relative adrenal and spleen weights were highly variable indicating that their usefulness as a measure of stress in *P. gunnii* and *I. obesulus* is somewhat dubious, assuming that stress was responsible for deaths.

Ulceration of the gastric lining was pronounced and five of the six captive animals experienced some of these symptoms, possibly associated with stress induced by confinement. The cause of deaths on subjects M.20 and M.0 were identified on the basis of personal observations. M.20 died, after harassment by a domestic cat (*Felis domesticus*), resulted in the subject leaping and thrusting itself into the steel bars of its holding cage with such violence that it caused the vertebral column to break. M.0 was killed by a male conspecific after the two subjects had dug underneath a deeply implanted partition (approximately twelve inches

TABLE A.1 Selected anatomical and morphological features of subjects that have died during the course of the study.

	SEX	NUMBER	RELATIVE COMBINED ADRENAL WEIGHT (mg/100 g of body wt.)	RELATIVE SPLEEN WEIGHT (mg/100 g of body wt.)	STOMACH AND DUODENUM	FEATURES OF GROSS MORBID ANATOMY
<i>I. obesus</i>	M	20	11.3	428.2	Small haemorrhagic ulcerations of stomach. No duodenal ulcerations.	Vertebral column broken and damage to ribs. Neither pair of limbs retracted. Massive haemorrhaging, particularly around the pectoral region.
	M	0	13.4	843.5	No ulcerations present.	Fur removed from posterior lumbar area. Tongue protruding but not cyanosed. Extensive superficial damage to internal thoracic and lumbar areas. Limbs contracted to body. Slightly anaemic. Fracture of mandibles. Body dorso-ventrally flattened.
	M	12	32.7	277.3	Stomach contained three small haemorrhagic ulcerated patches. Duodenum free of ulceration.	Forelimbs asymmetrically retracted. Hindlimbs directed forwards. Tail hung downwards. Slightly anaemic.
	M	half circle	30.9	199.4	No ulcerations present.	Forelimbs directed backwards. Hindlimbs and neck extended. Tail limp and distal end is damaged.
	M	22	10.4	90.6	No ulcerations present.	One forelimb and ipsilateral hindlimb retracted; other limbs extended. No evidence of myotonic contraction.
<i>P. gunni</i>	M	5	16.8	106.2	Massive ulceration of gastric lining. Local haemorrhagic ulcers, two perforated. Mucous membrane severely eroded. Duodenum devoid of ulceration.	Contact flattening of left ear. Eyes closed, tongue protruding internally and slightly cyanosed. Pronounced cyanosis of soft tissues of the nose and slight cyanosis of the rhinarium. Pronounced myotonic contractions of the anterior lumbar and cervical regions. Asymmetric anterior disposition of forelimbs, the left forelimb retracted towards the snout. Forefeet curved downwards. Hindlimbs extended posteriorly. Pes recurved towards the body and the tail extends downwards. Slight damage to posterior lumbar region but contraction of musculature of trunk not evident. Minor bruising over most of body and one rib broken.
	M	3	21.8	79.4	Duodenum contains one large ulcer. Stomach devoid of ulceration.	Extreme emaciation of lumbar area. Body curled downwards. No evidence of myotonic contractions. Slightly anaemic.
	F	2	29.7	127.1	Haemorrhagic ulceration of the stomach - duodenum junction.	Eyes closed. Slight cyanosis of rhinarium and protruding tongue. Myotonic contractions of the anterior lumbar area. Hindlimbs extended posteriorly and tail extends downwards. Forefeet curved downwards.

into the soil).

In the remaining subjects, causes of death could not be reliably determined. The characteristic features of the carcasses are summarised in Table A.1. The intestine of subject M5 was found to contain a cestode, *Hymenolepis peramelidarum* (Nybelin 1917). However, the identification of the specific identity is not 100% certain since the scolex and suitable material for measurements of organs was absent.