ASPECTS OF THE BEHAVIOUR AND ECOLOGY OF

THE POTOROO, *POTOROUS TRIDACTYLUS*

(MARSUPIALIA: POTOROIDAE)

by

S. D. Johnson, B.Sc. (Syd.)

Being a thesis submitted in fulfilment of the

requirements for the degree of Bachelor of

Science with Honours, University of Tasmania,

May, 1987

ACKNOWLEDGEMENTS

ABSTRACT

Aspects of the behaviour of captive potoroos, *Potorous tridactylus*, were examined with particular emphasis on quantitative differences in the behaviour of non-parous and pouch-gravid individuals and the behavioural interactions that occur within the context of the mother-young relationship. The ontogenetic development of the young was described, and the temporal distribution of adult and juvenile behaviour was compared. In addition, a program of capture-recapture trapping was conducted in order to examine the home ranges and habitat utilization of this species.

The durations of feeding activity in pouch-gravid females were shown to be significantly higher than those of non-parous subjects. In addition, pouch-gravid females engaged in resting behaviour for significantly longer periods than animals without young and, furthermore, were shown to exhibit significantly lower levels of locomotory activity. These observations were discussed in relation to the strategy of foraging which may be employed by free-living *P. tridactylus*.

The nature of the mother-young relationship was described. Following the initial vacation of the pouch at 112 days of age, young *P. tridactylus* spent increasingly longer periods of time out of the pouch until the time of its final vacation at 128 days. The mother was instrumental in the maintenance of proximity between herself and her young for the two weeks following initial vacation of the pouch; however, after this time the young assumed the responsibility for proximity. The mean distances between the mother and her young were shown to increase with the age of the young. Young continued to suckle until the age of ca. 139 days, after which time all attempts were prevented by the mother. Although the levels of agonistic behaviour between the mother and young were generally low, an increase in the frequencies of agonistic acts by the mother toward the young was observed. Allogrooming was a major component of the behavioural interaction between mother and young; however, the levels of this behaviour decreased with increasing age of the young. These observations were discussed with respect to the process of weaning in *P. tridactylus*.

The development of the young was described in relation to the first observed

occurrences of maintenance behaviours and several morphological traits. Juveniles were shown to engage in locomotory activities significantly less frequently than adults; conversely, juveniles spent more time engaged in resting. The temporal distribution of behaviour over the activity period was shown to be similar in both adults and juveniles. These observations were discussed with reference to the adaptive value of juvenile behaviour patterns.

The mean area of the home range of male *P. tridactylus* was 4.36 ha; the area of the home range of a single resident female was 0.94 ha. The home ranges of males were noted to overlap considerably (mean=62.6%). *P. tridactylus* was shown to preferentially utilize areas with a dense cover of vegetation. These observations were discussed with reference to results obtained in previous investigations of the ecology of this species.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

GENERAL INTRODUCTION

"The marsupials are as low in the scale of
mammalian intelligence as they are in that of
mammalian structure; so that.... I have met with
no fact connected with the psychology of this
group that is worth quoting........". (George J.
Romanes, Animal Intelligence, 1883).

The Marsupialia comprise a distinctive and diverse assemblage of species occupying
virtually every terrestrial habitat and exhibiting an adaptive radiation comparable to
their eutherian counterparts (Kirsch and Calaby 1977). Although differing from
eutherian mammals with respect to a small number of skeletal and morphological
features (Wood-Jones 1923; Young 1950; Barbour 1977), marsupials are primarily
characterised by their unique reproductive anatomy and physiology (Tyndale-Biscoe
1973) and the production of very immature young which remain attached to the teat for
a prolonged period (Eisenberg 1981). In the majority of species, the young continue
development within a pouch. This unique reproductive strategy, recognised in the
New World didelphids as early as the sixteenth century (Strahan 1983), has provided the
impetus for a long tradition of zoological research, particularly within the disciplines
of physiology, anatomy and taxonomy.

Unfortunately, ethological and ecological research has not enjoyed the advantages
of a long tradition and comprehensive investigations revealing the behavioural
diversity of marsupials are of recent development.

As the following survey suggests, marsupials, unlike eutherians, have generally
been neglected by ethologists and by comparative psychologists in particular (Kirkby
1977). The majority of studies undertaken to date have been descriptive, often
anecdotal or couched in the terminology of natural history with little scientific
objectivity. Consequently they have limited relevance to contemporary ethological
concepts (Brereton 1966).

Despite a recent trend toward a more quantitative approach to research, the
behaviour of many species remains known only through the antiquated and, indeed,
often erroneous accounts of standard natural history texts.

Behavioural investigations of marsupials, generally of limited scope, are often contained within documented accounts of broadly-based ecological research. However, few of these have attempted to relate behavioural processes to environmental adaptation (Myers 1967), particularly with respect to the relationship between conspecifics and sympatric species (Russell 1974a,b).

In contrast to eutherians, little is known of the social behaviour of marsupials (Russell 1974a, 1984). As Kaufmann (1974b) noted, this paucity of information has impeded attempts to develop a generalised theoretical model of the nature and evolution of mammalian social behaviour.

New World Marsupials

Perhaps not surprisingly, *Didelphis virginiana*, the only didelphid species commonly occurring in North America, has been the subject of a considerable amount of behavioural research (Reynolds 1952; McManus 1967, 1970, 1971; Bombardieri and Johnson 1969; Franq 1969; Hopkins 1977). Although brief descriptive accounts are available for other genera, including *Marmosa* (Beach 1939; Barnes and Bartold 1969), *Caluromys* (Bucher and Fritz 1977), *Monodelphis* (Hayssen 1980; Trupin and Fadem 1982) and *Caenolestes* (Kirsch and Waller 1979), the behaviour of the majority of New World Marsupials remains virtually unknown (Hunsaker and Shupe 1977).

Family Peramelidae and Thylacomyidae

Bandicoots exhibit features of reproductive biology which are unique among marsupials (Lee and Cockburn 1985), yet only a few studies have commented upon their reproductive behaviour (Mackerras and Smith 1960; Lyne 1964, 1974; Stodart 1966a, 1977). Activity patterns and social behaviour have been studied in *Perameles nasuta* (Stodart 1966a; Lyne 1981), *P. gunnii* (Moloney 1982; Heinsohn 1964), *Isoodon macrourus* (Gordon 1974) and *I. obesulus* (Heinsohn *op. cit;* O'Callaghan 1974; Lyne 1981). Buchmann and Grecian (1974) have investigated discrimination-reversal learning in *I. obesulus* and Stodart (1977) has compiled a review of behavioural studies on Australian peramelids.

The endangered bilby, *Macrotis lagotis* has been investigated briefly by Watts (1969) and subsequently in detail by Johnson and Johnson (1983).

Family Notoryctidae

The remarkable similarity of the marsupial mole, *Notoryctes typhlops,* to the golden moles (*Chrysochloris stuhlmanni*) of Africa is an excellent example of evolutionary convergence, yet only brief and fragmentary descriptions of its behaviour have been published (Wood-Jones 1923; Howe 1975).

Family Myrmecobiidae

The behaviour of the now endangered numbat, *Myrmecobius fasciatus,* is poorly documented. However, descriptive accounts of its myrmecophagous feeding habits (Calaby 1960), reproductive behaviour (Christensen 1975) and activity patterns (Christensen *et al.* 1984) have been published.

Family Phascolarctidae and Vombatidae

A series of behavioural studies have been carried out on the koala, *Phascolarctos cinereus* by Smith (1979 a,b; 1980 a,b,c,d). These, as well as studies by Eberhard (1978) and Robbins and Russell (1978) have provided considerable information on numerous aspects of the behaviour of this highly specialised marsupial.

Various aspects of the behaviour of one species of wombat, *Lasiorhinus latifrons* have been described by Wunschmann (1966), Gaughwin (1978) and Wells (1978 a,b).

Families Phalangeridae, Petauridae and Burramyidae

Of the three genera of aboreal phalangerids, only the behaviour of the common brushtail possum, *Trichosurus vulpecula* is well documented (Kean 1967; Biggins and Overstreet 1978; Wemmer and Collins 1978; Molnar and Goldfinch 1981; MacLennan 1984). How (1981) has provided a brief description of social organisation in *T. caninus.* Little is known of the behaviour of cuscuses, *Phalanger* spp. (Wemmer and Collins *op.cit.;* Menzies and Pernetta 1986).

The diverse forms of arboreal ringtail possums and gliders have received somewhat more attention. Behavioural observations have been made on *Pseudocheirus* spp (Thomas and Owen 1964; Winter and Atherton 1984) and *Hemibelideus lemuroides* (Winter and Atherton *op.cit.*). Social organisation and activity patterns have been investigated in *Gymnobelideus leadbeateri* (Smith 1984), *Petauroides volans* (Henry 1984; Kerle and Borsboom 1984), *Petaurus breviceps* (Suckling 1984; Goldingay 1984) and *P. australis* (Russell 1984; Henry and Craig 1984). Communication in the last two species has been investigated by Schultze-Westrum (1965) and Kavanagh and Rohan-Jones (1982) and a general review of communication in the superfamily Phalangeroidea was recently compiled by Biggins (1984).

Little is known of the behaviour of the pygmy-possums. However, feeding behaviour and activity patterns have been documented in *Cercartetus nanus* and *C. lepidus* by Hickman and Hickman (1960) and Wakefield (1970). The feeding behaviour of *Burramys parvus* has been described by Dimpel and Calaby (1972) and general notes on the behaviour of the same species were compiled by Dixon(1971). The thermoregulatory behaviour of *Acrobates pygmaeus* has been described by Frey and Fleming (1984) and its feeding habits studied by Turner (1984).

Family Tarsipedidae

The specialised feeding habits of the monotypic honey-possum, *Tarsipes rostratus* have been investigated by Vose (1972, 1973) and an extensive and quantitative behavioural study by Russell (1986) has recently been published.

Family Dasyuridae

In contrast to the above groups, the carnivorous dasyurids have received considerable atttention from ethologists, particularly with respect to their dynamic prey-killing behaviour (e.g. Ewer 1969; Eisenberg and Leyhausen 1972; Hutson 1975; Buchmann and Guiler 1977).

The largest extant representative of the family, the Tasmanian devil, *Sarcophilus harrisii* has been studied in some detail (Ewer 1969; Guiler 1970a,b; Eisenberg *et al.*

1975; Buchmann and Guiler 1977) Species of the genus *Dasyurus* have received considerably less attention (Green 1967; Archer 1974; Moss 1978; Blackhall 1980)

The smaller members of the Dasyuridae are well represented in ethological literature Detailed behavioural studies have been made on the kowari, *Dasyuroides byrnei* (Sorenson 1970; Aslin 1974; Hutson 1975, 1976, 1982; Meissner and Ganslosser 1985) and the mulgara, *Dasycercus cristicauda* (Ewer 1969; Sorenson 1970), the planigales, *Planigale tenuirostris* (Andrew and Settle 1982) and *P. maculata* (Van Dyck 1979), the kultarr, *Antechinomys laniger* (Marlow 1969; Happold 1972) and species of the genus *Sminthopsis*, the dunnarts, particularly *S. crassicaudata* (Ewer 1968a; Crowcroft and Godfrey 1968; Morton 1978).

Although much of the interest in the several species of *Antechinus* has been directed at the phenomenon of post-reproductive mortality of the males (e.g. Lee and Cockburn 1985) a number of detailed behavioural studies have been documented, particularly in *A. stuartii* (Rigby 1972; Braithwaite 1974, 1979; Dickman 1982; Settle and Croft 1982a,b; Vestal *et al* 1986). The reproductive behaviour of *A. flavipes* has been investigated by Marlow (1961) and the social behaviour of *A. swainsonii* and *A. minimus* was studied in detail by Haynes (1982). *Phascogale tapoatafa* has been investigated by Cuttle (1982).

Superfamily Macropodoidea

The macropodoid marsupials have undoubtedly been the focus of the great majority of behavioural studies undertaken in Australia. Yet, possibly as a consequence of pragmatic considerations, research has generally concentrated upon the larger, partly diurnal kangaroos, wallabies and wallaroos of the family Macropodidae at the expense of the numerous, smaller nocturnal species, particularly those comprising the family Potoroidae (Russell 1984). This unfortunate disparity has impeded a full understanding of the behavioural diversity of the group.

A disproportionate amount of attention has been given to the study of social interactions despite the paucity of information available for normal maintenance activities. This bias is unfortunate as these activities comprise the greater part of the

behavioural repertoire of macropods, and indeed most marsupials.

Family Macropodidae

Economic factors have been responsible for a large proportion of the research conducted on Macropodids (Frith and Calaby 1969; Lavery 1985). Concern about actual or potential competition with sheep has resulted in investigation of diet and feeding activities, particularly in the larger species, *Macropus rufus*, *M. giganteus* and *M. robustus* (Griffiths and Barker 1966; Ealey and Main 1967; Dawson *et al.* 1975; Ellis *et al.* 1977; Taylor 1980, 1983a; Priddel 1986).

The red kangaroo, *M. rufus* (= *Megaleia rufa*) has been the subject of a considerable amount of behavioural research, particularly with regard to social interactions (Caughley 1964; Frith and Calaby 1969; Russell 1970a,b 1979; Croft 1981a, 1985; Ganslosser and Wilhelm 1986). Detailed studies of behavioural thermoregulation (Russell 1971; Russell and Harrop 1976), drinking behaviour (Russell and Nicholls 1972), sleeping patterns (Cicala *et al.* 1970), movements and home range (Frith 1964) have been made on this arid-zone dwelling species. Reproductive behaviour and mother-young interactions have been investigated by Sharman and Calaby (1964), Russell (1973) and Russell and Nicholls (1974).

The eastern grey kangaroo, *M. giganteus*, has similarly received considerable attention. Social behaviour has been investigated in detail (Caughley 1964; Kirkpatrick 1966; Grant 1973, 1974; Kaufmann 1975); in addition Grant (1974) has described the general maintenance activities of this species and Poole and Pilton (1964) have described mating behaviour.

The western grey kangaroo, *M. fuliginosus* has received less attention. Stewart and Setchell (1974) have briefly described activity patterns in this species, and Coulson (1977) has compared its social behaviour with that of *M. giganteus*.

The social behaviour of the wallaroo, or euro, *M. robustus* has been studied in considerable detail by Ealey (1967), Croft (1981b, 1985) and Taylor (1983b). Drinking behaviour (Russell and Nicholls 1972), reproductive behaviour (Russell and Richardson

1971) and behavioural thermoregulation (Russell 1969) have also been described in this species.

Aspects of the behaviour of the antilopine wallaroo, *M. antilopinus* have been described in studies by Russell and Richardson (1971) and Croft (1982).

Kaufmann (1974a) has made an extensive survey of the social behaviour of the whiptail wallaby, *M. parryi*, which provided the basis for subsequent discussion of the evolution of social organisation in the Macropodoidea (Kaufmann 1974b,c).

Agonistic interactions (LaFollette 1971) and home range and movements (Mooney and Johnson 1979) have been documented in the Bennett's or red-necked wallaby, *M. rufogriseus*.

The tammar wallaby, *M. eugenii* is one of the few species in which detailed accounts of maternal behaviour are available (Russell 1973; Russell and Giles 1974; Giles and Russell 1975), yet little else is known of its behaviour (Andrewartha and Barker 1969).

The remaining representatives of the genus *Macropus* have received little attention. Reproductive behaviour, social organisation and activity patterns have been briefly noted in the parma wallaby, *M. parma* (Maynes 1973, 1977) and group-composition was described in the agile wallaby, *M. agilis* by Johnson (1980a). Similarly, the swamp wallaby, *Wallabia bicolor*, has been the subject of few behavioural investigations (Edwards and Ealey 1975).

The pademelons, *Thylogale* spp. have also received only limited attention, but various aspects of behaviour were described in *T. billardierii* (Morton and Burton 1973; McCartney 1978; Clancy 1982; Ganslosser and Werner 1984) and in *T. thetis* (Johnson 1980).

The rock wallabies, *Petrogale* spp. and *Peradorcas* spp. have been generally neglected, with only brief accounts of social organisation available for *Petrogale inornata* (Dwyer 1972), *P. puella* (Davies 1979) and *P. penicillata* (Joblin 1981); also a study of agonistic behaviour in female *Peradorcas concinna* has been made by Goldstone and Nelson (1986).

Similarly brief behavioural studies have been made on the nail-tail wallabies,

Onychogalea spp. (Gordon 1983), the hare wallabies of the genera *Lagorchestes* and *Lagostrophus* (Hughes 1965; Bolton and Latz 1978) and the aboreal tree kangaroos, *Dendrolagus* spp. (Ganslosser 1977, 1980, 1983).

In contrast, the remaining member of the family, the quokka, *Setonix brachyurus* is one of the most extensively studied of all marsupials, and the only small macropod for which comprehensive and detailed behavioural studies have been made. Activity patterns have been investigated in this species by Packer (1965), movements and home range by Dunnet (1962), Packer(1963), Holsworth (1967), Nicholls (1971) and Kitchener (1973), utilization of shelters by Kitchener (1972), reproductive behaviour by Shield (1968) and aspects of solitary and social behaviour by Packer (1969).

Family Potoroidae

Representatives of the Potoroidae are among the least well known of the macropod marsupials, possibly as a consequence of their cryptic, nocturnal habits. For similar reasons, behavioural investigations of potoroids are scarce; the existing literature on the subject consists mainly of descriptive accounts from the last century.

Behavioural studies on the musky rat-kangaroo, *Hypsiprymnodon moschatus*, are almost non-existent. Brief notes within the context of broader taxonomic studies provide the few fragmentary details currently available (Woods 1960; Johnson and Strahan 1982).

The bettongs, *Bettongia* spp. have received somewhat more attention. Stodart (1966b) has described maintenance activities and social interactions among captive burrowing bettongs, or boodies, *B. lesueur*. The nest-building habits of the brushtail bettong, or woylie, *B. penicillata* have been investigated by Christensen and Leftwich (1980) and Sampson (1971); the latter author has also provided brief notes on home range and longevity. Descriptions of various aspects of the behaviour of the Tasmanian bettong, *B. gaimardi* are contained within broader ecological and reproductive studies (Johnson 1978; Mooney and Johnson 1979; Rose 1986a,b). Social interactions and maintenance activities have been investigated in the rufous bettong *Aepyprymnus rufescens* (Johnson 1980b).

As early as 1924, Wood-Jones recognised the importance of studying the Tasmanian representative of the genus *Potorous, P. tridactylus,* but apart from brief descriptions or incidental observations (Guiler 1958, 1960; Hughes 1962; Heinsohn 1968), there has been only one major study on the behaviour of this species (Buchmann, in prep.)

Although the last-mentioned investigation has done much to elucidate numerous types of maintenance and social activities of *P. tridactylus,* there still remain certain aspects of the behaviour of this small nocturnal marsupial which are poorly understood *viz* maternal behaviour, mother-young interactions and behavioural ontogeny.

The present study aims to address those areas, and in addition, examine the spatial use of environment in this species.

CHAPTER 2

GENERAL BIOLOGY OF *POTOROUS TRIDACTYLUS*

The long-nosed potoroo, *Potorous tridactylus*, was among the first of the Australian mammals to be recorded by European man, the original description and illustration having been produced by Surgeon-General White in 1790 (Strahan 1981). The specific name *tridactylus*, given by Kerr in 1792, erroneously refers to the pes as possessing only three toes, the syndactylous second and third toes being counted as one. The common name, potoroo, is of Aboriginal derivation (Troughton 1943).

Potoroos comprise one of four extant genera within the family Potoroidae, these being distinguished from the Macropodidae by numerous dental features (Wood-Jones 1924; Strahan 1983) Potoroids are generally considered representative of a conservative branch of the evolutionary line leading to modern macropodids (Strahan 1983).

Several authors have recognised two subfamilies of potoroids (Troughton 1943; Kirsch and Calaby 1977; Strahan 1983):

1. Hypsiprymnodontinae, comprising a single living species, the musky rat-kangaroo, *Hypsiprymnodon moschatus*, a diurnal and omnivorous inhabitant of the rainforests of north-eastern Queensland (Johnson and Strahan 1982).

2. Potoroinae, comprising four genera; *Bettongia* (three species, two of which are endangered), *Aepyprymnus* (one species), *Caloprymnus* (one species, presumed extinct) and *Potorous* (three species).

Although *H. moschatus* retains a number of conservative characters, Johnson and Strahan (1982) suggested that subfamilial distinction is unwarranted unless the macropods are "elevated to a superfamily Macropodoidea comprising the families Macropodidae and Potoroidae" (p.27). This option was subsequently adopted by Strahan (1983) in a compendium on Australian mammals and provides the basis of the nomenclature used throughout the present study.

The genus *Potorous* (Desmarest 1804) has undergone numerous taxonomic revisions as a result of the considerable morphological variation exhibited by its constituent species (Johnston and Sharman 1976). Hope (1969) incorporated the previously separated *P. gilbertii* within *P. tridactylus*. However, her proposal that *P. tridactylus* be split into two separate species, *P. tridactylus* and *P. apicalis* was subsequently

contested by Johnston and Sharman (*op. cit.*) Morphometric analyses used by the latter authors have revealed the existence of clinal variation and has led them to propose that all potoroos belong to a single, albeit highly variable species, *P. tridactylus,* the exception being the broad-faced potoroo, *P. platyops,* formerly of south-west Western Australia, and now presumed to be extinct (Burbidge and Jenkins 1984).

In a subsequent investigation (Johnston and Sharman 1977) based on electrophoretic, chromosomal and breeding studies, *P. tridactylus* was further subdivided into the subspecies *P. t. tridactylus,* from mainland Australia and *P. t. apicalis* from Tasmania and the Bass Strait Islands.

Seebeck and Johnston (1980) recently described a third species, the long-footed potoroo, *P. longipes,* from east Gippsland in Victoria. It is distinguished from *P. tridactylus* by its larger size, its relatively longer pes and its different chromosomal characteristics (Johnston *et al.* 1984). The two species may be sympatric (Seebeck and Johnston *op. cit.*).

P. tridactylus is the only member of the genus which enjoys a relatively secure status. Early accounts of its distribution suggested that this species was formerly widespread and common over much of continental Australia but had declined in number (Wood-Jones 1924; Troughton 1943; Marlow 1958). However, Calaby (1971) has suggested that this supposed rarity was merely a consequence of lack of observation and subsequent studies have extended the known range of the species in Victoria (Seebeck 1981), coastal New South Wales (Calaby 1966) and Queensland (Frauca 1969; Amos 1982).

Fortunately, the species has remained widespread and numerous in Tasmania (TASPAWS Biological Records Scheme, Tasmanian N.P.W.S.), including the south-western corner of the state (Hocking 1978; White 1985; Taylor *et al.* 1985). It is rare, however, on Flinders Island and King Island (Johnston and Sharman 1976). The species status in Tasmania is in contrast to the restricted distribution of mainland populations and may be due to the absence of predation by European foxes (*Vulpes vulpes*).

The external morphology of the potoroo has been reviewed by Wood-Jones (1924) and Guiler (1961) *P. tridactylus* displays a sexual dimorphism in which the male is slightly larger than the female (Table 2.1).

Table 2.1. Comparison of means (± one standard error) of measurements of adult male and female *P. tridactylus* based on unpaired Student's t-tests(presentstudy) and previous descriptions (references given).

	MALES	FEMALES	P	REFERENCE
Head and Body Length (mm)	4 380	- 340	- -	Wood-Jones (1924) Johnston (1983)
Weight (g)	1437 ± 51 (n-20) 1180 (740-1640)	1148 ± 27 (n-22) 1020 (660-1350)	<.0005 -	Present study Johnston (1983)
Head (mm)	94.4 ± 1.7 (n-17)	92.1± 0.7 (n-21)	N.S.	Present study
Pes (mm)	84.2 ± 0.7 (n-17) 81 82	80.1 ± 0.6 (n-22) - 79.5	<.0005 - -	Present study Wood-Jones (1924) Guiler (1961)
Ear (mm)	40.8 ± 0.5 (n-17) 35	40.3± 0.4 (n-19) -	N.S. -	Present study Wood-Jones (1924)
Tail (mm)	230 235 (204-262)	- 228 (198-254)	- -	Wood-Jones (1924) Johnston (1983)
Albino tail-tip (mm)	24.9 ± 4.3 (n-16)	31.7 ± 3.3 (n-20)	N.S.	Present study

The pes (digital formula: 4>5>2.3) shows the syndactylous condition typical of macropods. The manus (digital formula: 3>4>2>1>5) possesses long claws used in the exploitation of subterranean food items (Guiler 1971a).

The dentition follows the typical potoroid pattern of relatively large canine teeth, elongated and grooved premolars and a decrease in the size of molars in the

antero-posterior direction (Wood-Jones 1924; Troughton 1943). The dental formula is

$$\text{I.} \frac{1.2.3}{1.0.0.}; \text{ C. } \frac{1}{0}; \text{ P.M. } \frac{0.0.3.4.}{0.0.3.4.}; \text{ M. } \frac{1.2.3.4.}{1.2.3.4.}$$

The pelage is brown and grizzled by the admixture of white-tipped hairs, particularly in older individuals. The ventrum is greyish-white and grades into darker shades on the flank. Clinal variation in coat colour occurs across northern Tasmania and may be related to climatic and vegetational gradients (Johnston and Sharman 1976). The latter authors have found a positive correlation between latitude and the proportion of individuals possessing albino tail-tips. Guiler (1958) noted that this feature was present in 85% (n=41) of the Tasmanian population. Similarly, in the present study a figure of 87% (n=45) was recorded. The length of the unpigmented area is highly variable (Guiler 1961).

Various aspects of the physiology of *P. tridactylus* have been documented including thermal balance (Hudson and Dawson 1975), thyroid function (Nicol 1977), the effects of hypoxia and carbon dioxide on sleep-waking patterns (Ryan *et al.* 1983), neurological aspects of sleep-waking patterns (Astic *et al.* 1976; Astic and Saucier 1978), lactation (Crowley 1984; Smolenski 1986) and gastrointestinal anatomy (Frappell and Rose 1986). Several investigators (e.g. Walen and Brown 1962; Cisar 1969) have attested to the value of *P. tridactylus* as a convenient subject for cytological research due to the low number ($10 \text{ X X } Y_1 Y_2$) and large size of its chromosomes (Sharman and Barber 1952).

As in many other marsupials, the reproductive physiology of the potoroo has received considerable attention. Hughes (1962) reported *P. tridactylus* to be polyeostrus and monovular, with an oestrus cycle of 42 days and gestation period of 38 days, the longest known in any macropodid marsupial. In common with the majority of macropods, *P. tridactylus* exhibits embryonic diapause. The delayed gestation period is 29 days (Shaw and Rose 1979).

Parturition has been described by a number of authors (e.g. Flynn 1922; Hughes 1962) and probably occurs in the manner characteristic of marsupials in general, via

the median vagina (Shaw and Rose 1979) The subsequent ontogeny of the young is described elsewhere (Section 6)

Broad descriptive accounts of habitat requirements, home range and movements (Guiler 1958; Heinsohn 1968; Kitchener 1973) suggest that *P. tridactylus* inhabits areas of dense vegetation and occupies relatively stable home ranges. These, and other considerations of the ecology of the species are discussed in the context of a live-trapping program undertaken in the present study (Section 7).

CHAPTER 3

ACQUISITION AND MAINTENANCE OF SUBJECTS

3.1 Acquisition of Subjects

A total of six non-parous and 11 pouch-gravid adult potoroos, *Potorous tridactylus* were used for the investigation of maternal behaviour in the course of the present study (Section 5.2). Three female juveniles, the offspring of the above adults, were used in the investigation of mother-young interactions (Section 5.3). Following weaning, these juveniles and a further three (one male, two female) were used in the investigation of quantitative differences between adult and juvenile behaviour patterns (Section 6.3). A further five pouch-gravid females held in a reversed daylight facility were used to obtain information about the ontogeny of behaviour and external features in *Potorous tridactylus* (Sections 6.2 and 6.4, respectively). In summary, a total of 22 adult females and their young (8 male, 11 female) were used for varying periods of time during the course of the present study. These numbers were considered adequate for the purposes of statistical analysis; however, due to the limitations of available holding facilities, no more than 14 adults were held in captivity at any one time.

With the exception of two adult females which were donated by another investigator, all subjects were obtained from various localities situated in dry sclerophyll forest in the vicinity of Hobart, by a regular program of removal trapping (Appendix A). The traps immediately available for this purpose were of heavy gauge wire mesh construction and were activated by either a hook or treadle mechanism. The dimensions of traps of each design were 56 x 22.5 x 22.5 cm and 55 x 20 x 20 cm, respectively. Each of the two designs accounted for approximately 50% of the total number of trap nights accrued. Advantage was taken of the high number of trap nights accumulated during both removal trapping (1221 trap nights) and a program of capture-recapture trapping (3116 trap nights; Section 7) which enabled the efficiency of the two trap designs to be compared. These results, in addition to a summarised list of all species captured, are presented in Appendix A.

Traps were set 20-30 m apart at sites which revealed indirect signs of the activity of *P. tridactylus*. These signs included the presence of characteristic diggings, trails

through dense vegetation and the presence of scats (Triggs 1985). Each trap was regularly relocated to avoid the repeated capture of resident male potoroos.

In order to maintain captured animals in a dry and unstressed condition, each trap was covered with liberal quantities of grass and leaf litter, or, when these materials were not available, green plastic garbage bags. During the initial stages of removal trapping several brown bandicoots *(Isoodon obesulus)* were found dead within the traps. Subsequent autopsy of one of these revealed signs of systemic stress, including ulceration of the gastro-intestinal and peritoneal lining (P. Clunie, pers. comm.). For further trapping it was considered expedient to provide each trap with sufficient quantities of grass in order to facilitate nesting. This appeared to be an effective measure, as subsequent mortality was substantially reduced. No deaths of potoroos occurred while the animals were within the traps.

Quartered slices of bread, liberally coated with peanut butter, constituted the bait used during the initial stages of removal trapping; however, this practice was quickly discontinued as the soft consistency of the bread allowed it to be easily removed from the hook without activating the release mechanism. Subsequently, apple coated with peanut butter was used as bait and appeared to be considerably more effective.

All traps were inspected, rebaited, and when necessary, serviced each morning between 7 and 11 am. A record was maintained of species captured in relation to the type of trap design. In addition, any evidence of disturbance of traps was noted.

Potential subjects were removed from the traps and held in hessian bags for subsequent examination. In addition to facilitating handling, potoroos restrained in this way usually remained calm and were, presumably, subject to relatively less stress. Males were released at the site of their capture after measurements of weight, head, pes, ear and albino tail-tip had been taken. Females were retained within the hessian bags and promptly transported to holding facilities situated on the campus of the University of Tasmania.

3.2 Identification and Measurement of Subjects

Adult female potoroos which were used for behavioural observations were individually marked on the right ear with either a numbered tattoo or a metal fingerling tag. Both methods proved effective in allowing individual recognition of subjects for the period during which they were retained for observation (3-32 weeks).

Standard measurements were taken of head, ear and pes following the methods employed by Wood-Jones (1923). In addition, the length of the unpigmented tip of the tail was recorded when this feature was present. All measurements were made with the aid of Vernier calipers and were recorded to the nearest 1mm. Weight was measured to the nearest 50g with a spring balance.

Regular weighing of adult subjects throughout the course of study revealed that in the majority of instances subjects maintained or increased their initial weight. One animal which lost more than 15% of its initial body weight and exhibited signs of hypophagia was released ca. two weeks following its capture. Another individual which had sustained damage to the snout while within the trap was not used for behavioural observation; however it was maintained in captivity and its offspring was used to provide data pertaining to the ontogeny of behaviour.

At the time of their acquisition, 17 of the subjects (77%) carried pouch young. A further four were born in captivity. The pes and head lengths of pouch young were measured to the nearest 1mm and young not attached to teats were weighed to the nearest g. In addition, notes were made on the general condition of the pouch and the apparent utilization of teats by young. Age-estimation of young was made on the basis of pes and head lengths, utilizing growth curves provided by Bryant (1982) and a nomogram provided by Guiler (1960a). The median of the estimates thus obtained was taken as the estimate of age. In the few cases where estimates disagreed by greater than four days, measurements were retaken until agreement of within four days was reached. The resulting degree of accuracy obtained (±4 days) was considered sufficient for the purposes of the present study.

3.3 Maintenance of Subjects in Captivity

Potorous tridactylus has been a common and popular subject in a number of experimental studies; consequently there is a considerable literature pertaining to the maintenance and husbandry of this species in captivity (Cisar 1969; Guiler 1971b; Bates *et al* 1972; Collins 1973; Seebeck 1982).

The subjects observed during the course of the present study were housed in one of the two following conditions:

1. Semi-natural outdoor enclosures

These comprised three relatively large (9 x 5 x 2 m; 11 x 3 x 3 m; 14 x 3 x 3 m) outdoor enclosures of galvanised wire mesh construction, each housing a maximum number of three subjects. Females housed together exhibited few signs of agonistic behaviour; however on one occasion a female was noted with considerable loss of fur from the posterior flanks and rump, presumably as the result of fighting. This apparent amiability of females is in sharp contrast to the "pugnacious and intolerant" behaviour exhibited by captive males (Buchmann, unpublished observations). The substrate of each enclosure consisted of natural soil and supported a dense undergrowth of grass and a variety of endemic and introduced species of vegetation, including *Bedfordia linearis*, *Beyeria viscosa*, *Clematis aristata*, *Westringia violaceae* and *Thrystomene* sp.

Captive subjects rarely utilized the separate nest boxes provided; preferring instead to nest together in tussocks of grass, as previously noted by Seebeck (1982).

Behavioural observations were conducted only on subjects which had been held within these enclosures for a minimum of two weeks. This was in order to ensure that potential subjects had adjusted to the conditions of captivity and were not exhibiting signs of abnormal behaviour.

2. Indoor holding cages

Due to the limited availability of large outdoor enclosures, and in order to facilitate daily examination of young, several subjects were held separately for varying periods of time in small (60 x 50 x 50 cm) galvanised wire cages situated within a reversed

daylight facility. In order to alleviate the effects of restraint experienced by these animals and to allow exercise, each subject was regularly allowed access to one of two indoor arenas (3 x 3 m; 3.5 x 4 m)

Each cage was provided with a triangular metal nest box (35 x 20 x 25 cm) and was lined with straw which was renewed weekly. Metal trays were placed beneath each cage in order to collect fallen detritus. These were emptied once a fortnight.

No behavioural observations were conducted on these subjects while they were housed indoors, although regular examination was made of any pouch young present. The majority of these subjects were eventually released into outdoor enclosures (described above) and, after a minimum period of two weeks, were used in behavioural observations.

Subjects housed under both of these conditions were provided with water *ad libitum* This was supplied in plastic containers held down by the weight of a rock or in small, cylindrical metal cups attached to the side of the holding cage. Water was regularly replenished as subjects frequently defecated within the containers. Only shallow containers were used in order to reduce the risk of the young drowning (Guiler 1971b). A vitamin supplement, "Pentavite", was occasionally added to the water to ensure that vitamin requirements were being satisfied.

Initial observations of food consumption were made on six subjects held in the small holding cages described above. Each subject was given a known weight of a standard diet comprising apple, bread, "Pal Meaty Bites" and carrot. The daily intake, determined by weighing back the uneaten portion and correcting for dehydration, ranged from 136-283 g (mean = 186.3 ± 21.4 g). In a similar investigation, albeit based on slightly different food items, Buchmann (in prep.) quoted the daily intake of female potoroos to be 146 g, considerably lower than that obtained in the present study. This discrepancy, however, is possibly attributable to the different body weights of the subjects used, as both Buchmann (*op. cit.*) and the present study found very similar values for mean food intake when expressed as a percentage of body weight (16.0% and $16.3 \pm 2.0\%$; range 11.8-24.6%, respectively). Apples constituted the greater part of the daily intake (mean $62.6 \pm 2.3\%$; range 53-71%), reinforcing their value as a bait in

trapping programs. Bread comprised 25.5 ± 1.8% (range 14-30%) of the daily intake, followed by "Pal Meaty Bites" (mean 6.3 ± 3.7%, range 0-40%) and carrots (mean 5.8 ± 1.6%; range 3-12%).

With the exception of carrots, the above food items comprised the main components of the diet of captive subjects. These were regularly supplemented or replaced by tomatoes, rat pellets, cooked meat, boiled rice and wheat biscuits. As noted by Guiler (1971b), vegetables and fruit were generally eaten in preference to dry cereals, neccessitating the occasional withdrawal of the former in order to maintain a high protein diet. On infrequent occasions, pears, plums, apricots, dandelions (*Taraxacum officinale*) sunflower seeds, rockmelon, mealworms, (*Tenebrio molitor*), berries of native cranberry (*Astraloma humifusum*) and avocado were given and eaten. In agreement with Guiler (*op. cit.*), cabbage, and in addition, fennel and lettuce were given but were never observed to be eaten. Food was provided daily, usually in the late afternoon. Two or more food sites were used for animals held within the outdoor enclosures in order to eliminate the possibility of monopolisation by a dominant individual, as recommended by Guiler (1971b).

CHAPTER 4

GENERAL ASPECTS OF METHODOLOGY AND

QUALITATIVE INVENTORY OF BEHAVIOUR

4.1 The Study of Behaviour in Captive Animals

The study of animal behaviour under conditions of captivity is often necessitated as a result of insurmountable difficulties encountered in obtaining comprehensive or even sufficient data from free-living populations. The nocturnal, cryptic habits of many species of small mammals, such as *Potorous tridactylus,* make field observation prohibitively difficult. Consequently, full information relating to the behavioural repetoire of these species can only be practically gained if observations conducted on captive subjects are considered in conjunction with information obtained in the wild.

Captive subjects have formed the basis of many of the behavioural studies conducted on macropodid marsupials (e.g. Sharman and Calaby 1964; Stodart 1966b; Packer 1969; Russell 1970b, 1973; Grant 1973; Morton and Burton 1973; Johnson 1980b; Clancy 1982; Ganslosser and Welhelm 1986). Provided care is exercised in the extrapolation of results to the situation in the wild, enclosure studies provide a useful basis for comparison with the results of investigations conducted on wild populations. Enclosure and field studies undoubtedly complement each other (Eibl-Eibesfeldt 1975) and information resulting from both sources is of greater value than that obtained by either approach alone. In view of this, the results obtained during the present study are, as much as possible, discussed with reference to the results of a concurrent capture-recapture trapping program (Section 7).

4.2 The Observation Enclosure

The majority of behavioural observations conducted during the present study were made on subjects held within an outdoor enclosure (4.6 x 4.6 x 1.6 m) situated on the campus of the University of Tasmania. The enclosure was built on a gently sloping (ca. 15 $^{\circ}$) natural substrate and was surrounded by galvanised iron wire mesh embedded in a concrete foundation. A roof of wire mesh prevented the entry of domestic cats and brushtail possums (*Trichosurus vulpecula*). An abundant covering of straw was provided along one margin of the enclosure to facilitate nesting. This measure

supplemented three straw-lined wooden nest boxes (each 60 x 40 x 40 cm). These were positioned in the centre, along one wall and in one of the corners of the enclosure. Two species of *Acacia* grew within the enclosure and blackberries, *Rubus fruticosus*, grew along the exterior of one wall, partially protruding through the wire mesh. Blackberries were occasionally eaten by subjects. A small area of grass and occasional growths of aerial fungi were also present, but were never observed to be eaten. Wooden stakes set 1m apart divided the enclosure into 25 one m^2 quadrants. Each stake projected ca. 30 cm from the substrate and bore a strip of white "Scotchlite" reflective tape at its free end to enhance visibility at night. These stakes provided a frame of reference for the investigation of the spatial distribution of activities and calculation of locomotory scores.

Illumination was provided by 4 x 75 W light bulbs suspended from the roof of the enclosure. Each bulb was covered by a red filter in order to reduce disturbance of subjects (Davis 1961; Southern 1965). Lights were switched on prior to sunset and switched off following the termination of observations. Observations were made through the window of a hide positioned 1.2m from the enclosure and illuminated by a 15W red light bulb. When necessary, binoculars were used to aid observation, however visibility of subjects was generally excellent. A second enclosure was utilized for investigation of the activity patterns of adult and juvenile subjects and is described in Section 6.3.1.

Subjects scheduled for behavioural observations were placed within the enclosure during daylight hours. In order to minimize stress and the risk of eviction of pouch young, subjects were transported between holding enclosures and the observation enclosure in hessian bags, from which the animals were permitted to emerge spontaneously.

4.3 Methods of Recording Behaviour

Intensive preliminary observations of the behavioural repertoire of *Potorous tridactylus* were made in order to test and refine suitable techniques for data collection

and to allow the investigator to gain familiarity with the methods selected. These observations permitted the development of an inventory of behavioural elements which were amenable to subsequent analyses (Section 4.5). Further, in an attempt to minimize the influence of extraneous variables, data were collected of the behavioural responses of captive subjects to rainfall and ambient temperature (Section 4.4).

Although numerous techniques for sampling behaviour are available (Altmann 1974; Dunbar 1976; Slater 1978; Lehner 1979; Martin and Bateson 1985), many of these provide only an incomplete record of the behavioural repertoire of animals. In a review of behavioural sampling methodology, Altmann (*op.cit*) discussed the relative merits of a number of techniques and concluded that, given conditions of continuous visibility of subjects, "focal-animal sampling" provides the most comprehensive record of the behaviour of a given animal. This method involves the focus of attention upon a single individual, although social interactions are capable of being recorded by use of an appropriate behavioural inventory which takes into account behaviours directed toward and received from a second individual (Lehner 1979). As Martin and Bateson (1985) have noted, several authors, including Altmann (*op.cit.*), have confusingly used "focal-animal sampling" as a synonym for continuous recording. Whereas the former method determines which animals are observed, the latter determines what technique is used to record the behaviours exhibited. "Scan sampling", the alternative to "focal-animal sampling", is used as a sampling strategy to record the behaviour of a relatively large number of individuals and this, similarly, has been confused with the instantaneous sampling method of recording observed behaviours (Martin and Bateson *op.cit.*).

Throughout the present study, the number of subjects observed at any one time did not extend beyond the mother-young dyad; consequently all observations were based on "focal-animal sampling". However, in order to reduce the limitations imposed by reliance upon a single technique, and in an attempt to obtain a complete record of observed behaviours, a number of additional methods of behavioural recording were employed.

4.3.1 Continuous Recording

This method involves the recording of all occurrences of behaviours observed during a given period of time and provides information about the sequence, durations and frequencies of behavioural elements. During the present study, continuous recording was employed during discrete one hour observation periods in order to collect data on aspects of the maternal behaviour and mother-young interactions of captive subjects (Section 5). A pre-recorded audio-tape of "clicks" occurring at 2s intervals was used in conjunction with a stopwatch to provide a time base for recording the duration of behavioural elements. Durations were recorded to the nearest 2s, as this was considered to be both manageable and to allow an acceptable degree of accuracy. Following the recommendation of Martin and Bateson(1985), all behavioural elements were subsequently analysed with respect to total duration, i.e. the total length of time for which all occurrences of the behaviour lasted over the 1h observation period. In addition, feeding and grooming behaviour were analysed with respect to the duration of bouts (defined in Section 4.5) and their frequency over the 1h observation period. Behaviours of short duration (<2s), such as jumping or shaking, were recorded within parentheses and subsequent analyses of these were based on their frequencies of occurrence. In order to facilitate recording, observed occurrences of behavioural elements were written sequentially on protocol sheets, using a shorthand notation.

Although continuous recording provides the most complete record of an animal's behaviour, it places a heavy demand on the concentration of the observer; consequently it is ultimately of dubious value for extended periods of time. Further, the number of behavioural elements able to be recorded is restricted by the pragmatic consideration of manageability.

4.3.2 Instantaneous Sampling

Instantaneous sampling requires the observer to record the behaviour of an animal at predetermined points in time and provides data both on the time distribution of behavioural elements and estimation of the proportion of time spent performing particular behaviour patterns (Dunbar 1976). However, durations and frequencies are

not measured and no record of the sequence of behaviours is obtained. It is, nevertheless, useful for extended periods of observation.

This method was employed in order to obtain information about the activity patterns of both adult and juvenile potoroos (Section 6.3) and the spatial proximity of mother-young dyads (Section 5.3.2). Further details of this method of behavioural recording are given in the relevant sections.

4.4 The Influence of Extraneous Variables on Behaviour

During the course of behavioural observations a number of measures were taken in an attempt to reduce the influence of extraneous variables on the behaviour of captive subjects.

In both field and enclosure studies, the presence of the observer may have profound or subtle effects on the behaviour of the animal under consideration (Martin and Bateson 1986). In order to reduce bias resulting from observer effects, all observations were made from within a hide and a period of at least ten minutes allowed to elapse before the commencement of observations. Noise was kept to an absolute minimum during each observation period.

All observation periods were distributed randomly between the hours of 10pm and 2am in an effort to reduce bias reulting from temporal variation in levels of activity. Such quantitative variation has been recorded in *Potorous tridactylus* by Buchmann (unpublished data) and was noted during all night observations conducted during the present study (Section 6.3.3).

In addition, Buchmann (*op.cit.*) has noted quantitative variation in the behaviour of *P. tridactylus* across successive nights of observation, which may be attributable to the effects of habituation. In an attempt to reduce such potential bias, all observation periods for each subject were conducted between a limited number of successive nights (minimum 2 - maximum 4) following their introduction to the observation enclosure.

4.4.1 The Effect of Rainfall on the Behaviour of *Potorous tridactylus*

A series of preliminary observations, employing the continuous recording method previously described, provided information relating to the effect of rainfall on the behaviour of captive potoroos. These were conducted in order to assess the validity of carrying out subsequent observations during periods of rainfall. Observations were made on four subjects during conditions of light and heavy rainfall and compared with data obtained for the same subjects during clear weather. No attempt was made to quantify precise levels of precipitation.

The results of these observations are summarised in Figure 4.4.1. They revealed substantial decreases in activity during periods of both light and heavy rainfall and a concurrent increase in the amount of time spent resting, particularly within the nests. The only other behaviours that showed an increase were shaking and grooming. Each of these were presumably used to free the pelage of accumulated water.

Similar decrease in activity has been noted in behavioural studies conducted on *Setonix brachyurus* (Packer 1965), *Bettongia lesueur* (Stodart 1966) and *Aepyprymnus rufescens* (Johnson 1980b).

Acting on the basis of these observations, subsequent behavioural observations were not made on wet nights.

4.4.2. The Effect of Temperature on the Drinking Behaviour of *Potorous tridactylus*

Studies of the effect of ambient temperature on the behaviour of macropodid marsupials have almost solely been based on the behavioural thermoregulatory responses of the larger species to hot and arid environments (Russell 1969, 1971; Russell and Nicholls 1972; Russell and Harrop 1976). The nocturnality and distribution of *P. tridactylus* throughout the temperate regions of south-eastern Australia undoubtably reduces the need for elaborate mechanisms of behavioural thermoregulation in this species. However, it may be predicted that the durations and frequencies of drinking behaviour should increase at high ambient temperatures. In order to test this, a sample of 25 one h observation periods were randomly selected from the data obtained during the course of the present study. The temperature at the onset of each of these was
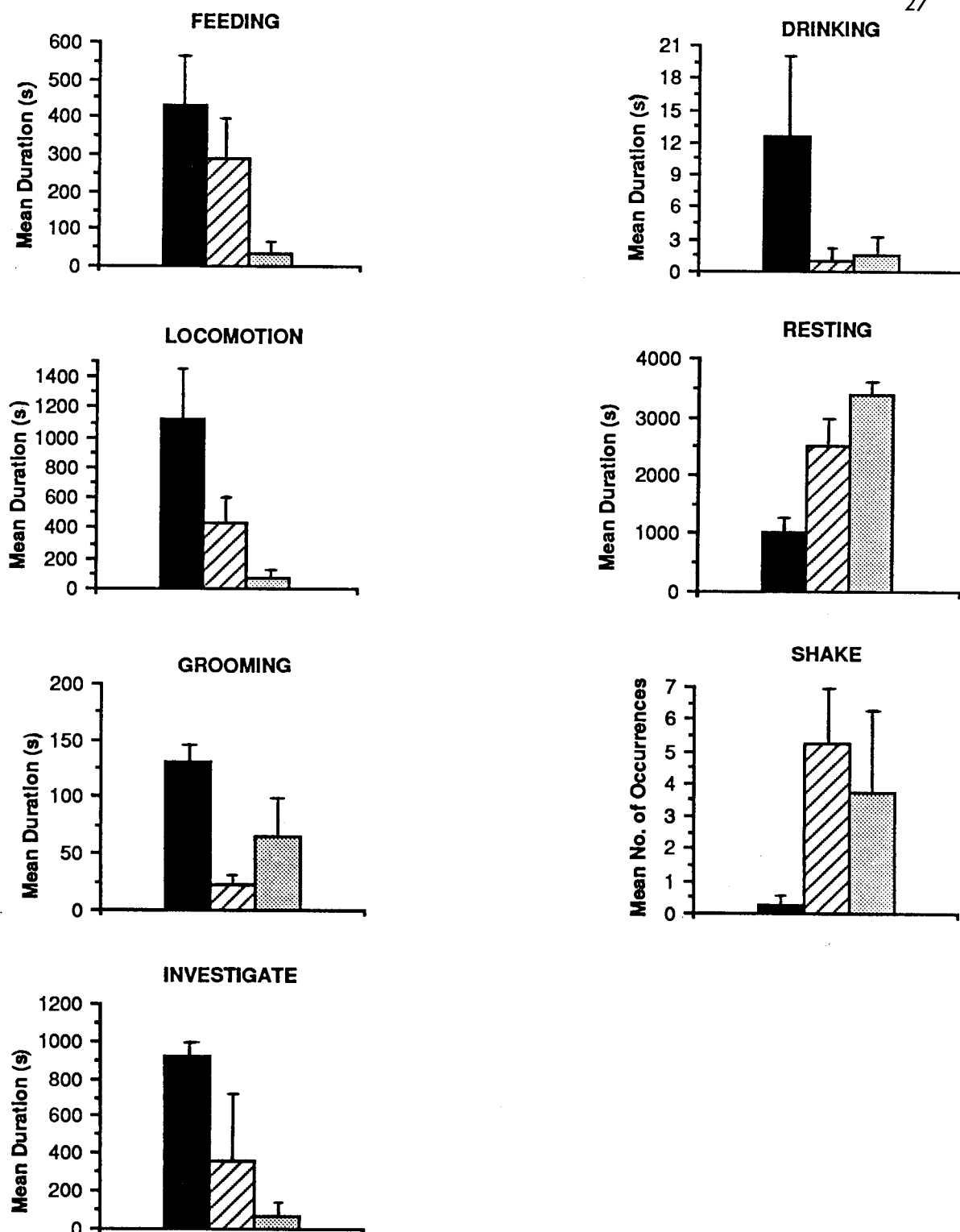
Figure 4.4.1 Quantitative variations (mean±one standard error) in the behaviour of captive *P. tridactylus* during periods of no rain (solid), light rain (striated) and heavy rain (grey).

obtained from records held by the Hobart Bureau of Meteorology   The total durations of drinking behaviour recorded in the observation periods were then correlated with the respective ambient temperatures

Perhaps surprisingly, the results of the analysis revealed a negative, albeit slight, correlation between ambient temperature and the amount of time subjects spent engaged in drinking behaviour (Pearson's $r = -0.285$).   This result, however, is perhaps not surprising when one considers that the maximum ambient temperature recorded was 19.1^0 C (mean $= 12.6\pm0.6^0$ C).   Hudson and Dawson (1975) have shown that the thermoregulatory response of *P. tridactylus* does not result in marked respiratory or cutaneous water loss until the ambient temperature exceeds ca. 33^0 C.   It is highly unlikely that such high temperatures would be experienced by potoroos during the course of their nocturnal acitivities.

4.5. Qualitative Inventory of Behavioural Elements

As a preliminary measure in any ethological research, a qualitative inventory of behaviour, or ethogram, must be delineated (Lehner 1979). Using methods similar to those employed by Slater (1978), the behaviours exhibited by captive female potoroos and their young during the present study were assigned to discrete and exclusive categories comprising homogenous acts. Wherever possible, strictly descriptive nomenclature was used in preference to terms carrying implicit aprioristic functional or causal connotations.

The categories that were established are summarised in Figure 4.5 and are described and illustrated below. In addition, the mean proportions of the 1h observation periods during which subjects engaged in each behaviour is given. These figures are based on combined data obtained for 17 subjects over a total of 59 observation periods. Values are only given for adult subjects, as juvenile individuals were shown to differ with repect to the temporal patterning of their behaviour (Section 6.3).

Figure 4.5 Qualitative Inventory of Behavioural Elements Exhibited by Captive Adult Female *Potorous tridactylus* during the Present Study (parameters used to quantify respective behaviours are given in brackets).

1. Ingestive Behaviour
    a) Feeding (mean total duration; mean duration of bouts; mean frequency of bouts)
    b) Drinking (mean total duration)
    c) Regurgitation

2. Digging Behaviour (mean total duration)

3. Locomotion
    a) Total Locomotory Activity (mean total duration)
    b) Quadrupedal Crawl (mean total duration)
    c) Bipedal Hop (mean total duration)
    d) Jumping (mean no. of occurrences)
    e) Climbing
    f) Swimming
    g) Number of Grids Crossed (mean no. / h)

4. Resting and Immobility
    a) Total Resting (mean total duration)
    b) Quadrupedal (mean total duration)
    c) Bipedal (mean total duration)
    d) Lying Down

5. Grooming and Comfort Behaviour
    a) Grooming the Body (mean total duration; mean no. of bouts; mean frequency of bouts)
    b) Grooming the Pouch (mean total duration)
    c) Shaking (mean no. of occurrences)
    d) Stretching

6. Investigative Behaviour (mean total duration)

7. Out of Sight (mean total duration)

4.5.1 Ingestive Behaviour

a) Feeding

The methods of feeding practiced by captive potoroos were determined largely be the consistency of the food provided. Food items of soft consistency, such as boiled rice, were consumed while subjects adopted a quadrupedal posture, with the head inclined downward. The food was taken directly with the mouth. It is doubtful, however, whether the diet of the potoroo frequently occasions such a method of feeding under natural conditions. Particulate food items were secured by varying degrees of forward extension of the trunk and subsequent grasping with the forefeet. The animal then assumed a sitting posture and brought the food to the mouth with the forefeet (Figure 4.5.1a). Food items were frequently rotated between successive bites, revealing the considerable dexterity of the potoroo and negating the disparaging remarks of early investigators who described the manner of feeding as "pig-like" (Troughton 1943).

In agreement with the observations of Buchmann (in prep.), food was almost invariably consumed *in situ* although on infrequent occasions both adults and were observed to carry even unwieldly items of food such as slices of bread and small, whole apples in the mouth while engaging in bipedal locomotion. Feeding comprised 13.3% 0.83% (range 0 - 27.38%) of all observation periods.

The postures assumed by potoroos while feeding bear some similarities to those described in other small macropodid marsupials, including *Bettongia lesueur* (Stodart 1966b), *Aepyprymnus rufescens* (Johnson 1980b), *Hypsiprymnodon moschatus* (Johnson and Strahan 1982) and *Setonix brachyurus* (Packer 1969). However, the behavioural repertoire of the potoroo did not appear to include the "pentapedal" posture often assumed by the larger, grazing macropods.

For the purposes of the present study, the frequencies and durations of feeding bouts were considered in addition to their total duration. Discrete bouts were defined as periods of feeding in excess of 10s duration and interrupted by other activities for periods not exceeding 6s. Hence, while subjects frequently engaged in acts of investigation and slow quadrupedal locomotion during the course of feeding, these were generally of less than 6s duration and not considered to be motivationally distinct.

b) Drinking

Captive subjects lapped water with rapid movements of the tongue whilst adopting a quadrupedal posture with the head inclined downward. The forefeet were frequently used to grip the rim of the water dish (Figure 4.5.1b). Drinking was infrequently observed in captive potoroos and several subjects were never observed to drink. This behaviour comprised only 0.63±0.16% (range 0 - 6.27%) of all observation periods.

c) Regurgitation

Regurgitation, or merycism was observed on only four occasions, in both adults and recently weaned subjects, and involved violent and conspicuous contractions of the flanks followed by the expulsion of the bolus. In all cases, reingestion immediately followed.

Regurgitation has been previously recorded in *P. tridactylus* (Buchmann, in prep.) and numerous other macropodid marsupials (Mollison 1960; Barker *et al.* 1963) and may aid digestion by stimulating salivary secretions (Hume 1982).

Due to its infrequent occurrence, regurgitation is not considered in the subsequent analyses of the present study.

Figure 4.5.1a Feeding

Figure 4.5.1b Drinking

4.5.2   Digging Behaviour

Potoroos frequently exploit subterranean food items, including fungi and invertebrates (Guiler 1971a) by digging irregular, crescentic holes in the ground (Buchmann, in prep.). However, digging was not a conspicuous activity of the captive subjects observed during the present study, comprising only 0.08±0.03% (range 0 - 1.33%) of the total observation period. Digging was possibly rendered superfluous by the *ad libitum* provision of ample food.

Digging was characterised by forward inclination of the body toward the substrate as a result of the raising of the hindquarters. The forefeet frequently alternated between a synchronous scratching of the substrate and synchronous raking of dislodged material toward the body. Food items were removed from the excavation with the mouth and, occasionally by the forefeet. None of the excavations made by captive potoroos were very deep, possibly due to a lack of subterranean food items within the observation enclosure.

Digging has been noted in several related species, including *Potorous longipes* (Seebeck and Johnston 1980), *Bettongia gaimardi* (Johnson and Rose 1983), *B. lesueur* (Stodart 1966b) and *Aepyprymnus rufescens* (Johnson 1983) and appears to be an activity characteristic of the members of the Potoroidae.

4.5.3   Locomotion

Although the locomotory activities of the larger macropods have been investigated in considerable detail (Badoux 1965; Windsor and Dagg 1971; Alexander and Vernon 1975), little such quantitative information is available for members of the Potoriodae.

Contrary to the anecdotal accounts of previous authors (Le Souef and Burrell 1926; Troughton 1943) the potoroo employs the well known ricochet gait typical of the larger kangaroos (Guiler 1958; Buchmann and Guiler 1974). This is one of two commonly used gaits described in detail by Buchmann and Guiler (*op. cit.*) and observed consistently throughout the present study. Locomotory activities comprised 21.75±1.49% (range 2.27-46.44%) of the observation period. The present terminology follows that of Buchmann and Guiler (*op. cit.*)

a) Quadrupedal Crawl

The quadrupedal crawl was achieved by the synchronous forward movement of the forefeet to support the body while the hind feet provided the thrust and were brought forward synchronously and placed outside the forefeet. This form of locomotion was commonly associated with investigative behaviour and comprised the great majority (98.3%) of all locomotory activity. The mean total proportion of this form of locomotion was $21.38 \pm 1.46\%$ (range 2.27 - 45.38%)

b) Bipedal Hop

The bipedal hop was achieved by synchronous digitigrade thrusts of the hind limbs. The forefeet were held close to the body and the trunk inclined forward, almost parallel to the substrate. Unlike the quadrupedal crawl, the tail is not trailed along the ground but is held horizontally and acts as a counterpoise to the body (Buchmann and Guiler *op.cit.*). This form of locomotion comprised only 1.7% of all locomotory activity and frequently followed disturbances. The total proportions of the observation periods subjects spent engaged in bipedal locomotion ranged from 0 - 1.94% (mean $0.37 \pm 0.05\%$).

The durations of both quadrupedal and bipedal locomotion were typically short (ca. 4 and 2s, respectively). It is possible that the constraints of the enclosure inhibited the full expression of locomotory activity, particularly bipedal hopping.

c) Jumping

Jumping was infrequently observed (1.56 ± 0.55 occurrences per observation period; range 0 - 24) and was achieved by the downward flexion and subsequent thrust of the hindlegs. The forefeet were extended to break the fall. Captive subjects frequently jumped onto the top of the nest boxes during the course of investigative behaviour.

d) Climbing

Climbing was observed only once and involved the slow and apparently awkward progression up the vertical wire mesh walls of the observation enclosure to a height of ca. 0.4m. It is doubtful if climbing occurs under natural conditions (Buchmann and Guiler 1974). Due to its infrequency, climbing is not considered in the subsequent analyses. In contrast to the observations of the present study, Seebeck (1983) reports that, in captivity, the related *Potorous longipes* frequently climbs with apparent ease.

e) Swimming

The potoroo is a capable swimmer (pers. observation) and utilizes the asynchronous movements of both pairs of limbs as described in the larger macropods (Wilson 1974).

f) Number of Grids Crossed

In addition to scores of total durations, locomotory activity was also assessed on the basis of the total number of grid-lines crossed during a 1h observation period. As described earlier, each grid line was represented by means of wooden stakes set 1m apart. The total number of grids crossed per observation period ranged from 28 - 774 (mean 306.88±8.47) and were, not unexpectedly, correlated with total durations of locomotory activity (Pearson's r = 0.913).

4.5.4   Resting and Immobility

Apart from the casual observations described below, diurnal resting in captive potoroos was not investigated in the context of the present study. Accounts of nesting and sleeping behaviour in the potoroo have been given by Buchmann (in prep.), Astic and Saucier (1978) and Astic *et al.* (1976).

During daylight hours, subjects were frequently observed to nest together in rudimentary nests of their own construction rather than in the nest boxes that were provided for them. Depressions in the straw within the enclosure were formed as a result of wriggling motions performed by the animals. The mouth was then used to pull the straw over the animals head and back to form a thin arch. Prolonged resting within the nest was associated with hunching of the back and marked downward inclination of the head. The eyes were usually only partially closed. Despite their apparent inattentiveness, the animals remained vigilant and promptly decamped from the nest when disturbed.

Nesting has been described in several members of the subfamily Potoroinae, including *Aepyprymnus rufescens* (Johnson 1980b), *Bettongia lesueur* (Stodart 1966b), *B. gaimardi* (Johnson 1979; Rose 1986a) and, in detail, in *B. penicillata* (Christensen and Leftwich 1980). In all these species, as in *Hypsiprymnodon moschatus* (Johnson and Strahan 1982), the prehensile tail is used to transport nesting material. *Potorous*

tridactylus appears to be conspicuously different in this respect as the tail of the adult is not prehensile; consequently nesting material is not carried in the above manner.

Prolonged nesting, as described above, was observed only once during night-time observations. Resting and periods of immobility during the nocturnal activity period were typically of shorter duration and were almost invariably characterised by the adoption of one of two postures.

a) Quadrupedal Resting

The quadrupedal posture was frequently assumed following quadrupedal locomotion or investigative activities and consisted of the adoption of a semi-sitting posture with the forefeet in contact with the substrate (Figure 4.5.4a). Periods of immobility and resting while assuming this posture comprised $13.90 \pm 1.70\%$ (range $4.0 - 19.58\%$) of the total observation period.

b) Bipedal Resting

The bipedal posture consisted of a semi-sitting posture with the hind legs supporting the animal, the forelimbs held loosely to the chest and the tail extended posteriorly in contact with the substrate (Figure 4.5.4b). This posture was typically assumed between bouts of locomotory activity and was frequently associated with investigative behaviour. It comprised $18.84 \pm 0.93\%$ (range $1.5 - 33.94\%$) of the observation period.

Both quadrupedal and bipedal resting postures were highly variable with respect to duration and ranged from brief pauses between ongoing activities to prolonged periods of resting often accompanied by partial closure of the eyes and "noticeable" arching of the back. Although it is difficult to assess whether brief pauses are motivationally distinct from the activities they punctuate, all periods of immobility exceeding 4s were included in the calculation of total time spent resting, regardless of their duration. Using this criterion, both forms of resting comprised $32.74 \pm 1.93\%$ (range $6.27 - 66.44\%$) of the observation period.

c) Lying down

In addition to the above postures, lying down was observed twice in an adult female. This posture involved the forward extension of the forelimbs and posterior extension of the hindlimbs resulting in contact between the ventrum of the animal and the substrate.

Although each observed instance of this behaviour was of relatively long duration (8min 42s and 14min 10s), its infrequency precluded it from subsequent analyses.

Figure 4.5.4a Quadrupedal resting

Figure 4.5.4b Bipedal resting

4.5.5 Grooming and Comfort Behaviour

a) Grooming the Body

The potoroo utilizes several methods to groom the body depending on the area to be cleansed (Figure 4.5.5a). Scratching of the flanks with the syndactylous claws of the hindlimb was frequently observed. This was usually performed while the animal assumed a sitting posture. Less often, the animal assumed a quadrupedal posture and raised the trunk by flexion of the hindlimbs, facilitating access of the hindlimb to the posterior portions of the trunk. These forms of grooming often punctuated other activities, particularly quadrupedal locomotion, and were generally of short duration (ca. 3-4s). Similarly, cleansing of the forefeet and muzzle (described below) frequently followed feeding and these acts were often performed independently of other forms of grooming. Their duration was also typically short (2-10s).

Prolonged bouts of grooming often resulted in cleansing of the entire body surface. Such bouts typically began with cleansing of the muzzle with synchronous strokes of the forefeet. This was occasionally interspersed with scratching of the region of the head

posterior to the eyes with the hindlimbs, the head being turned toward the hindlimb. Subsequently, the chest and abdomen were licked or rubbed with the mouth or, occasionally, scratched with the forefeet. The flanks were groomed in the manner desribed above, although occasionally the animal turned its head around to nibble or lick the anterior flanks whilst holding the fur with the forepaws. The cloacal region was licked with the snout pressed deeply between the hind limbs. Finally, the tail was nibbled while it was being held with the forepaws. The forefeet and hindfeet were frequently licked between successive scratching actions. The sequential patterning of grooming in adults appeared quite labile and was not investigated in the present study. The subject has been studied in considerable detail by Buchmann (in prep.). Prolonged bouts of grooming occasionally followed periods of bipedal resting. Based on an analysis of total durations, grooming the body comprised $6.09 \pm 0.86\%$ (range $1.5 - 33.94\%$) of the observation period. For the purposes of the present study, discrete bouts were defined as periods of grooming the body exceeding 10s duration and interrupted by other activities of no greater than 6s duration.

Grooming behaviour has been described, albeit briefly, in the potoroids *Bettongia lesueur* (Stodart 1966b), *Aepyprymnus rufescens* (Johnson 1980b) and *Hypsiprymnodon moschatus* (Johnson and Strahan 1982). The methods of grooming the body utilized by subjects observed during the present study were essentially similar to those employed by the above species, and appear to be typical of the pattern exhibited by macropodid marsupials in general (Buchmann, in prep.).

b) Grooming the Pouch

The pouch was cleansed while the animal assumed an upright sitting posture with the tail usually extended posteriorly. Both forefeet were used to hold the pouch open and to permit the insertion of the snout (Figure 4.5.5b). The interior of the pouch, and presumably in the case of pouch-gravid subjects, the young was licked with the tongue.

Pouch grooming was occasionally observed in isolation, but usually occurred as an integral component of extended bouts of grooming the body, particularly prior to cleasing of the cloacal region. Total proportions averaged $0.57 \pm 0.09\%$ (range $0 - 3.55\%$). For the purposes of the present study, pouch grooming was considered as a discrete

behaviour.

Pouch grooming has attracted only brief mention in studies conducted on the potoroids *Aepyprymnus rufescens* (Johnson 1980b) and *Bettongia lesueur* (Stodart 1966b). Among the macropodid marsupials, however, pouch grooming has been the subject of several comprehensive studies. Pouch grooming was described in *Macropus rufus* by Sharman and Calaby (1964) and subsequently investigated in considerable detail by Russell (1973). The latter author also provided detailed and quantitative descriptions of pouch grooming in *M. eugenii* and Russell and Giles (1974) have examined quantitative variation in pouch cleaning throughout the course of pouch occupancy in the latter species.

Figure 4.5.5a Grooming the body

i) Grooming the muzzle
   with the fore feet

ii) Grooming the muzzle
    with the hind feet

iii) Nibbling the flanks
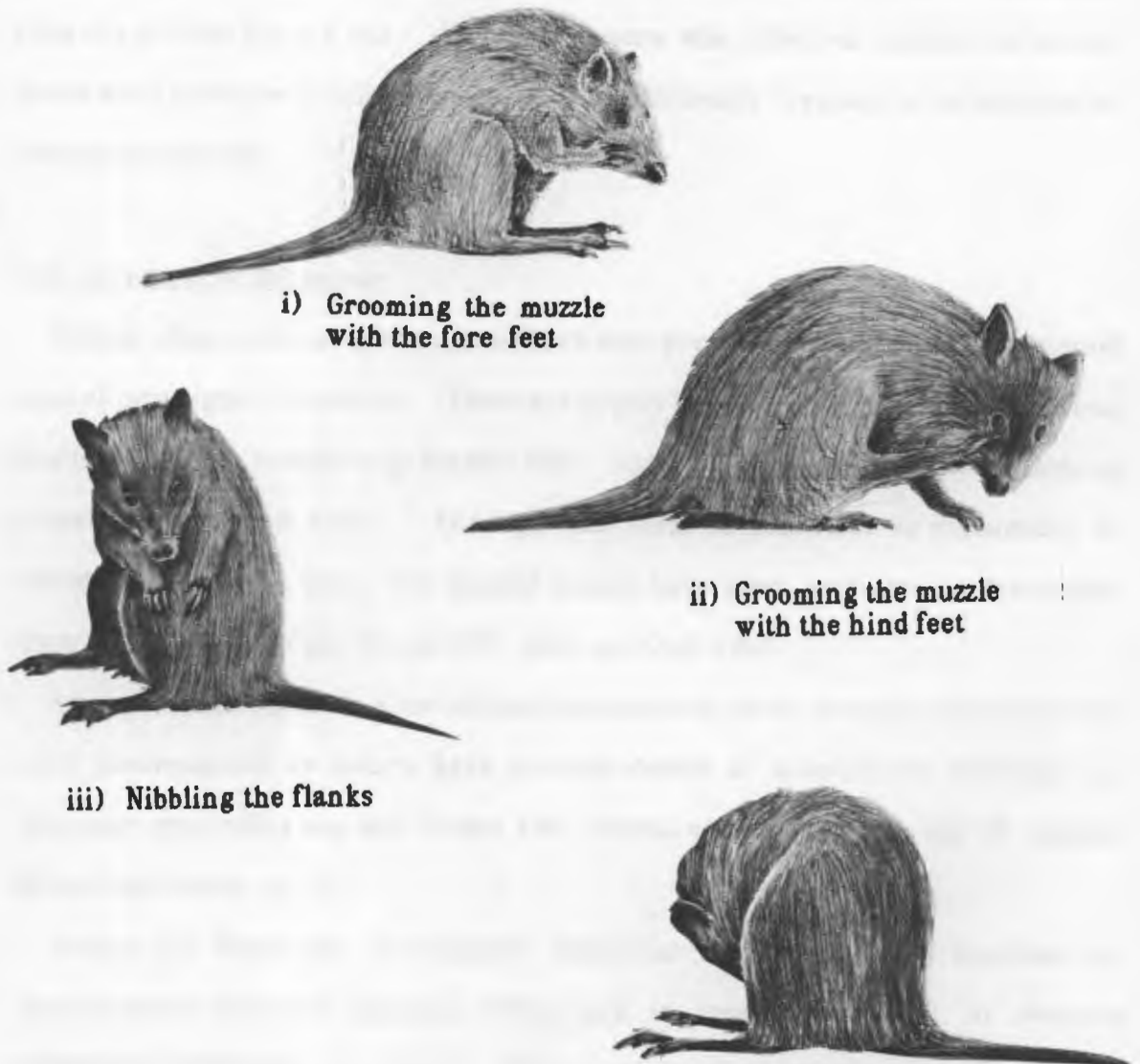
Figure 4.5.5b Grooming the pouch

c) Shaking

The most frequent comfort behaviour observed comprised the rapid shaking of the entire body, less often the head only. Shaking was of brief duration and consequently was analysed with respect to frequencies of occurrences during the observation period. For all adult subjects combined, these values ranged from 0 to 5 (mean 1.20±0.21) occurrences per observation period.

d) Stretching

Stretching was observed only twice during periods of data collection, and in both cases followed prolonged periods of resting. The hindlimbs were extended posteriorly to the trunk, the latter being similarly extended. The forelimbs were extended anteriorally. Stretching was frequently noted during casual observations at the time of emergence from the diurnal nesting site. However, because data collection commenced several hours after emergence, this behaviour was insufficiently frequent to be included in subsequent analyses.

4.5.6 Investigative Behaviour

Several, often conflicting hypotheses have been proposed to explain the motivational bases of investigative behaviour. These are largely based on information obtained from detailed studies on rodents (e.g. Barnett 1958; Shillito 1963) and, to a lesser extent, on primates (e.g. Menzel 1962). Although this form of behaviour is presumably of considerable adaptive value, few detailed studies have been conducted on marsupials (Ewer 1968a; Hunsaker and Shupe 1977; Settle and Croft 1982).

Among the Macropodidae, a few studies concentrating on the response of an animal to novel environments or objects have provided details of investigative behaviour in *Macropus rufus* (Glickman and Sroges 1966; Russell and Pearce 1971) and *M. eugenii* (Russell and Pearce *op. cit.*).

Among the Potoroidae, investigative behaviour has been briefly described in *Aepyprymnus rufescens* (Johnson 1980b) and, in considerable detail, in *Potorous tridactylus* (Buchmann, in prep.). Unfortunately, there is a noticeable lack of standardisation of the criterion used to define investigative behaviour. For the purposes

of the present study, criteria similar to those used by Baenninger (1967) and Buchmann (*op.cit*) were employed. Hence, an animal was recorded as exhibiting investigative behaviour if it engaged in sniffing whilst maintaining a stationary posture.

Three postures were typically associated with sniffing. A quadrupedal posture, accompanied by varying degrees of extension of the neck, a bipedal sitting posture and, less frequently, a bipedal upright posture accompanied by near-vertical extension of the neck were all assumed by animals engaged in investigative behaviour (Figure 4.5.6) Periods of investigative behaviour were typically of short duration (ca. 2-20s.) and frequently punctuated slow quadrupedal locomotion. This form of behaviour comprised 21.10±1.31% (range 1.83-43.05%) of the total observation period. Although potoroos undoubtedly receive information about their immediate environment through sensory modalities other than olfaction, these may prove difficult to identify in practice, and are presumably of secondary importance.

Figure 4.5.6 Postures associated with investigative behaviour
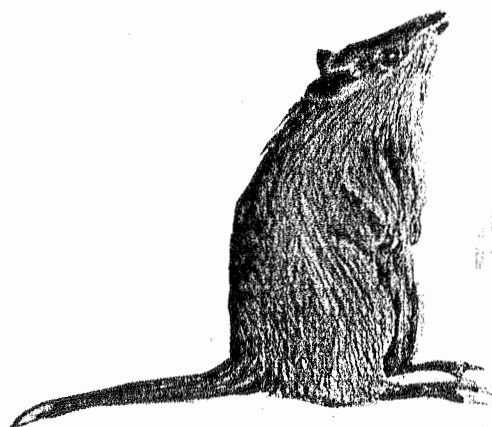
i) Vertical extension of the neck

ii) Bipedal posture

4.5.7   Out of Sight

An additional category designed to account for periods when subjects were not visible to the observer was included in the subsequent analyses.   This situation arose infrequently and was often a consequence of the animal being concealed behind a nest box. This category comprised only 0.23±0.08% (range 0 -4.22%) of observation periods.

CHAPTER 5

MATERNAL BEHAVIOUR AND MOTHER-YOUNG

INTERACTIONS

5.1 Introduction

The unique reproductive strategy of the Marsupialia has, traditionally, been considered to exemplify an intermediate stage of evolutionary development between prototherians and eutherians (Parker 1977). Given such a theoretical framework, it is perhaps not surprising that many early accounts of the reproductive biology of marsupials have emphasised the simplicity and primitiveness of their reproductive strategy. It is only in recent years that this strategy has been considered a viable and alternate means of producing offspring (Tyndale-Biscoe 1974). Parker (*op. cit.*) and Low (1978) have suggested that the reproductive strategy of marsupials is an adaptive response to environmental uncertainty, however their accounts were based largely on macropodid marsupials and as Russell (1982) has suggested, their conclusions do not take into account the diversity of patterns of parental care and investment exhibited by marsupials. Furthermore, such generalisations may be premature in view of the paucity of information available on the maternal behaviour of marsupial species. It is with this neglect in mind that the present study has sought to elucidate aspects of the maternal behaviour of a marsupial for which few details are available - the potoroo, *Potorous tridactylus.*

The factors involved in the initiation and maintenance of maternal behaviour have remained obscure despite an increasing amount of research devoted to this aspect of mammalian biology (Rosenblatt *et al.* 1979). Numerous studies, largely based on eutherian mammals, have implicated the importance of both hormonal factors (Lisk *et al.* 1969) and direct stimuli from the young (Rosenblatt and Lehrman 1963; Ross *et al.* 1963). In one of the few studies considering the factors involved in the initiation and maintenance of maternal behaviour in macropodid marsupials, Russell and Giles (1974) have suggested that direct stimuli from the young are important in the initiation and maintenance of pouch grooming in the tammar wallaby, *Macropus eugenii.* Their suggestion is further considered in the light of observations made during the course of the present study.

Behavioural interactions between a parent and its offspring constitute one of the most important aspects of mammalian social behaviour and, accordingly, have received considerable attention from ethologists. However, while a substantial literature is available for numerous eutherian species, particularly primates (e.g. Klopfer and Klopfer 1970; McKenna 1982), little is known of this aspect of marsupialian social behaviour. As Russell (1973) has noted, this dearth of information renders consideration of the function and devlopment of mother-young relations in marsupials premature and suggestions of "primitiveness" unfounded.

Marsupials exhibit a diversity of strategies of parental care. Russell (1982, 1984) has distinguished three broad patterns based on the degree of development of the pouch and the size of the litter.

Pattern A involves species possessing reduced or absent pouches and large litters. The young are carried firmly attached to the teat before being left in a nest at a relatively early stage of development. Numerous studies have indicated such a strategy in *Marmosa robinsoni* (Hunsaker and Shupe 1977), *Dasyuroides byrnei* (Aslin 1974), *Antechinus stuartii* (Marlow 1961; Settle and Croft 1982b), *Ningaui* spp. (Fanning 1982), *Antechinomys laniger* (Happold 1972) and *Phascogale tapoatafa* (Cuttle 1982) and may be considered the typical pattern of parental care practised by many small dasyurids (Russell 1984).

Pattern B involves species with well developed pouches, that utilize nests and generally have more than one young. While this strategy is similar to pattern A, it differs in that young are carried within the pouch for a relatively longer period and are deposited in the nest at a relatively more advanced stage of development. Further, the young remain in the pouch after releasing the teat and return to the pouch intermittently after being left in the nest. A number of studies, not specifically concerned with maternal behaviour, suggest that such a pattern occurs in *Didelphis virginiana* (Reynolds 1952; Hunsaker and Shupe 1977), the peramelids *Perameles nasuta* (Stodart 1966a; Lyne 1974), *P. gunnii* (Heinsohn 1966), *Isoodon obesulus* and *I. macrourus* (Stodart 1977), the petaurids *Pseudocheirus peregrinus* (Thomson and Owen

1964), *Petaurus breviceps* (Suckling 1984) and *Gymnobelideus leadbeateri* (Smith 1984),
the phalangerid *Trichosurus vulpecula* (Winter 1977, cited in Russell 1984), *Tarsipes
rostratus* (Russell 1986) and *Lasiorhinus latifrons* (Crowcroft and Sudenlund 1977,
cited in Russell 1984).

The third pattern of parental care, pattern C, occurs in species possessing large
pouches and only one young.   The period of permanent attachment to the teat is
followed by a period of intermittent attachment until the young first vacate the pouch
at a relatively advanced stage of development.   The young subsequently re-enter the
pouch at decreasingly frequent intervals.   Following final vacation of the pouch, the
young remain in association with the mother, at least until weaning.   Such a pattern
has been identified in *Phascolarctos cinereus* (Smith 1979a,b) and is typical of the
macropodoid marsupials (Russell 1984).

Among the Macropodidae, detailed studies of maternal behaviour *per se* are scarce,
with much of the information available having been derived from physiologically or
ecologically orientated research.   A number of studies have concentrated upon aspects
relating to maternal behaviour in *Macropus rufus,* including behaviour associated with
parturition (Sharman and Calaby 1964),   the distress vocalisations of young (Russell
and Nichols 1974),   inter- and intra-specific cross fostering (Merchant and Sharman
1965) and mother-young interactions (Russell 1970b, 1973); yet only the last mentioned
study has provided detailed information on maternal behaviour and mother-young
interactions in this species.

Russell (1973) has investigated in detail the mother-young interactions of *M.
eugenii* and additionally, has provided cursory information on the behaviour of adult
females of this species in relation to the presence or absence of pouch young. Russell
and Giles (1974) have investigated quantitative variations in pouch grooming in *M.
eugenii* with respect to the age of pouch young, yet make no mention of variations in
other, perhaps less obvious, behaviours.

Few detailed studies of maternal behaviour and mother-young interactions are
available for other macropodid species. Ealey (1967), Russell and Richardson (1971) and

Croft (1981b) have mentioned aspects of mother-young interactions in *M. robustus*, and brief notes within broader reproductive investigations have been published for *M. giganteus* (Poole and Pilton 1964; Kaufmann 1975; Poole 1975), *M. fuliginosus* (Poole *op. cit.*) and *M. parma* (Maynes 1973). Kaufmann (1974a) has described mother-young interactions during the course of a field study of the social behaviour of *M. parryi*. Clancy (1982) investigated mother-young interactions in *Thylogale billardierii* and Johnson (1983) has provided brief notes on *T. thetis*. Despite the considerable amount of information available on various aspects of the biology of *Setonix brachyurus*, little is known of its maternal behaviour or mother-young interactions.

To date, no extensive or detailed studies of maternal behaviour or mother-young interactions are available for members of the family Potoroidae, although brief descriptions or passing comments have been made in the context of broader behavioural or reproductive investigations. Rose (1986b) has provided notes on vacation of the pouch in *Bettongia gaimardi* and Delroy *et al.* (1986) have briefly described breeding in *B. penicillata*. Brief and descriptive accounts of mother-young interactions in *Aepyprymnus rufescens* have been given by Johnson (1980b). From the preceding account, it can be seen that the maternal behaviour and mother-young interactions of marsupial species is a relatively neglected area of mammalian biology. This neglect is both surprising and unfortunate in view of:

1. the unique and distinctive reproductive strategies employed by marsupials;
2. the relative abundance of information available on physiological and anatomical aspects of marsupial reproductive biology;
3. the relevance of maternal behaviour to social organisation; and
4. the evolution of an alternative and viable means of producing offspring.

In view of this neglect, the present study was undertaken in order to examine quantitative differences in the behaviour of adult *Potorous tridactylus* in relation to the absence or presence of pouch young (Section 5.2) and, further, to examine the behavioural interactions between mother and young following vacation of the pouch (Section 5.4).

5.2 Quantitative Differences in the Behaviour of Adult Subjects in Relation to the Presence or Absence of Pouch Young.

5.2.1 Methods

During the course of the present study, data were collected on captive *Potorous tridactylus* in order to determine if quantitative differences existed in the behavioural repertoire of pouch-gravid and non-parous females. In contrast to Russell (1973) and Russell and Giles (1974), *all* behavioural elements, as identified in the previously given inventory (Section 4.5), were considered. The parameters used to quantify each behaviour were as given in Section 4.3. All observations were made on animals held within the enclosure previously described (Section 4.2) and adhering to the precautions outlined in Section 4.4.

The continuous recording method, described in Section 4.3.1, was employed over 11 observation periods to collect data on six female subjects known, in retrospect, to be non-parous. A further 43 observation periods provided data on 11 females which carried pouch young of varying ages. The distribution of the body weights of the adult subjects across both groups was relatively uniform, as was the distribution of the ages of the pouch young of pouch-gravid females. Subjects with pouch young of 0-4, 4-8, 8-12 and 12-16 weeks of age were observed for 11, 12, 11 and 9 observation periods, respectively.

In order to test for differences in the levels of behaviour between non-parous and pouch-gravid subjects, the resulting data was analysed by use of unpaired Student's t-tests, with d.f.= 52 and $p<0.05$ as the selected level of significance. Figures 5.2.1-5.2.4 summarise the results with respect to mean values ± one standard error.

5.2.2 Results

Pouch-gravid females spent significantly greater periods of time engaged in feeding behaviour than did females with no young (t = 2.582; $0.005 < p < 0.01$), as

indicated by the greater value obtained for the mean total duration of feeding over the 1h observation period (Figure 5.2.1a). However, this difference was shown not to be the result of an increased frequency of feeding bouts (Figure 5.2.1b), but rather an increase in their mean duration (t = 2.956; $0.0005 < p < 0.005$; Figure 5.2.1c).

There were no significant differences between pouch-gravid and non-gravid subjects with respect to the total duration of drinking behaviour. In both groups, mean total durations were low and comprised only a small proportion of the one hour observation period (0.57% ± 0.17% and 0.94% ± 0.55%, respectively; Figure 5.2.1d).

As previously mentioned, captive potoroos were supplied food *ad libitum*, thereby reducing the neccessity for them to obtain their own food items. Consequently, it is not surprising that digging behaviour comprised, on average, only 0.12 ± 0.12% and 0.08% ± 0.03% of the observation period for non-gravid and pouch-gravid females, respectively. No significant difference between these two groups was found (Figure 5.2.1e). Further, of the 18 subjects observed throughout the present study, only six were observed to exhibit this behaviour.

The total locomotory activity of pouch-gravid females differed significantly from that of females with no young (t = 3.983; $p < 0.0005$; Figure 5.2.2a). This was true of both quadrupedal (t = 3.77; $p < 0.0005$; Figure 5.2.2b) and bipedal (t = 8.682; $p < 0.0005$; Figure 5.2.2c) forms. In addition, pouch-gravid females engaged in jumping significantly less frequently than did those without young (t = 2.811; $0.0005 < p < 0.005$; Figure 5.2.2d). In view of the result that pouch-gravid females showed a considerable reduction in the time spent engaged in locomotion, it is not surprising that the mean number of grids crossed by pouch-gravid females was significantly less than the value obtained for non-gravid subjects (t = 3.774; $p < 0.0005$; Figure 5.2.2e).

Pouch-gravid females spent significantly more time engaged in resting behaviour than did females with no young (t = 1.997; $0.025 < p < 0.05$; Figure 5.2.3a). However, although pouch-gravid subjects assumed both quadrupedal and bipedal resting postures for total durations exceeding those of non-gravid females (Figures 5.2.3b and 5.2.3c,

(a)

(b)

(c)

(d)

(e)
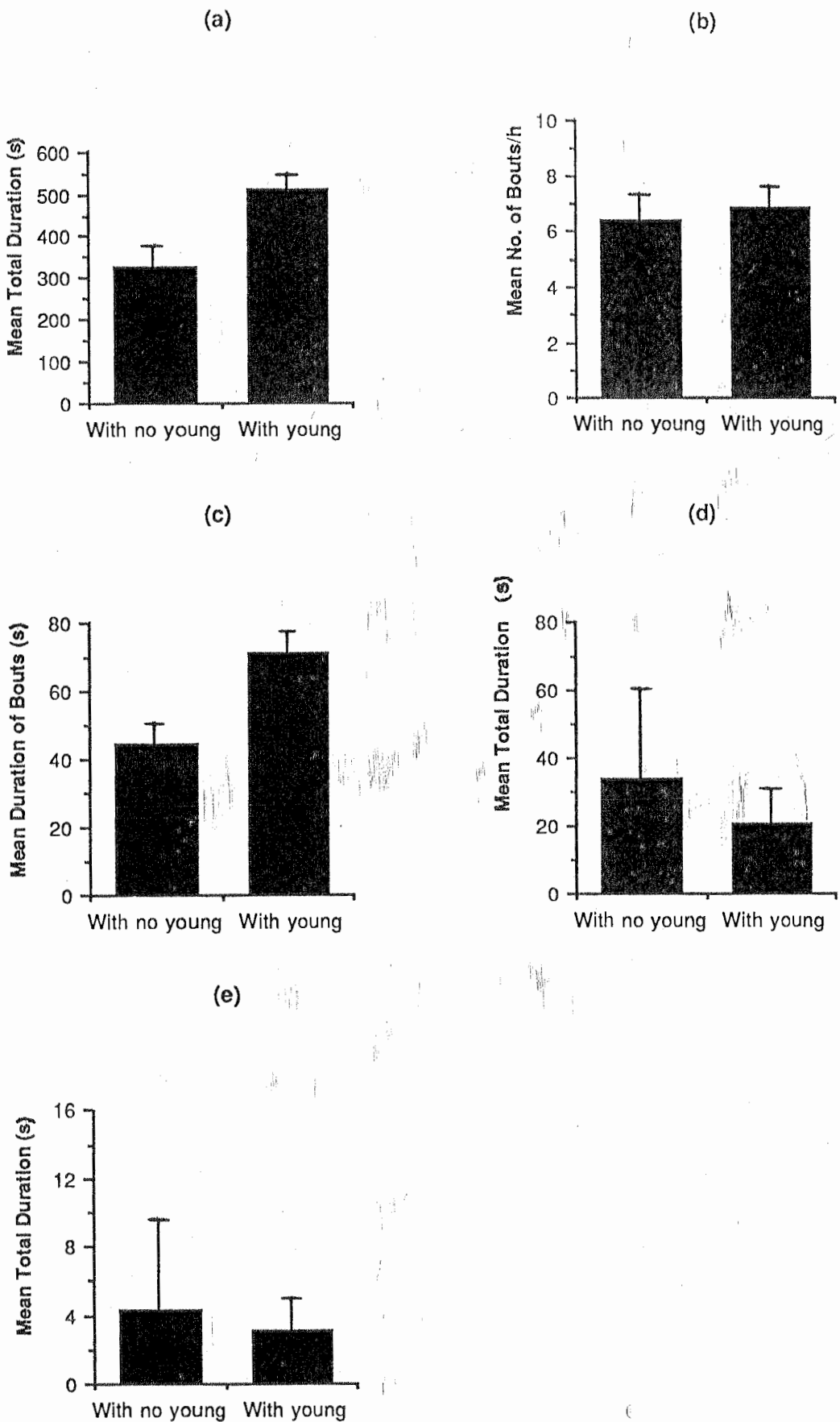
Figure 5.2.1　Mean (± one standard error) values for non-parous and
pouch-gravid subjects for: a) total duration of feeding;
b) frequency of feeding bouts; c) duration of feeding
bouts; d) total duration of drinking behaviour; e) total
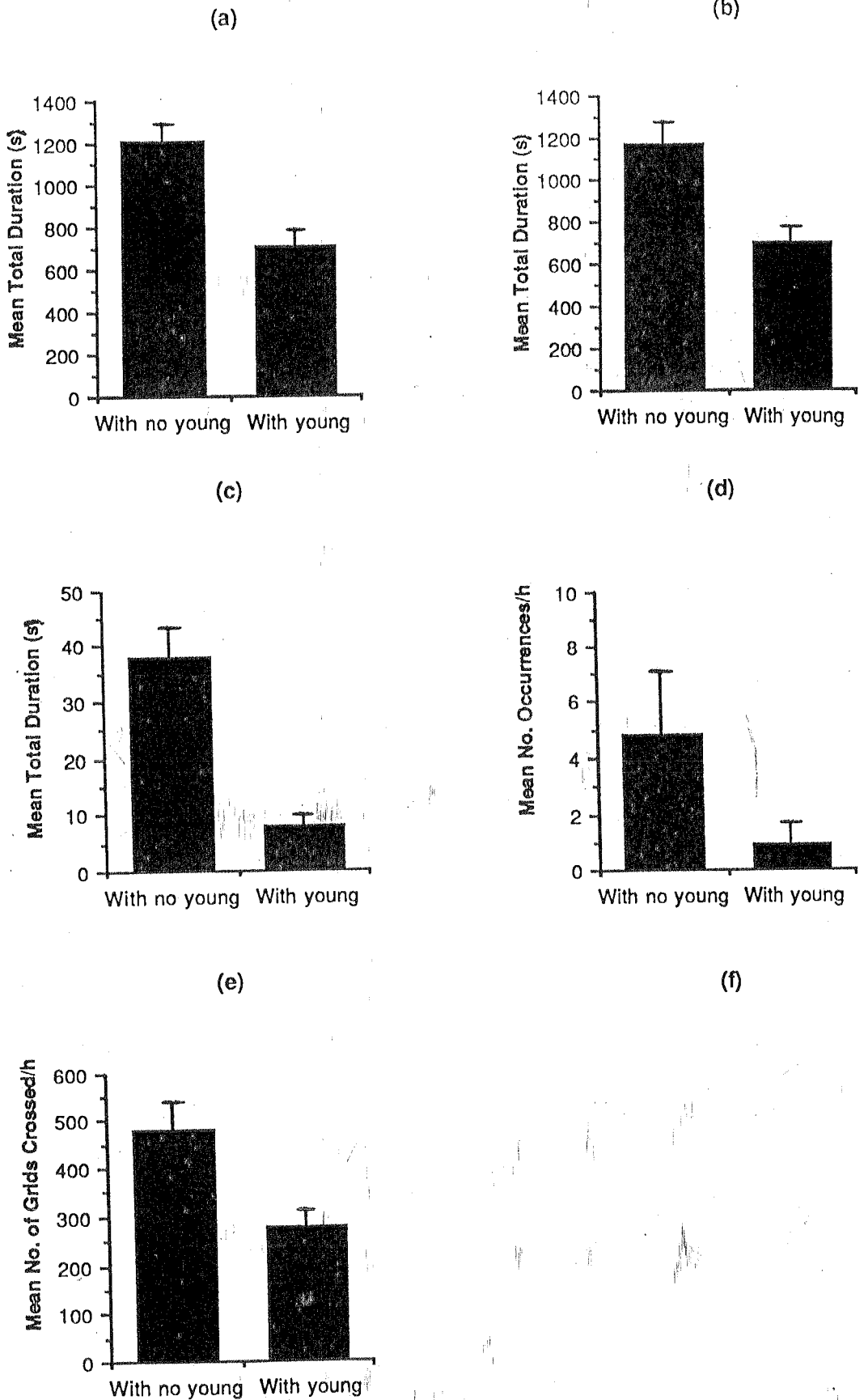
Figure 5.2.2   Mean (± one standard error) values for non-parous and
pouch-gravid subjects for: a) total duration of all locomotory
activity; b) total duration of quadrupedal locomotion; c) total
duration of bipedal locomotion; d) no. of occurrences of jumps;
e) no. of grids crossed
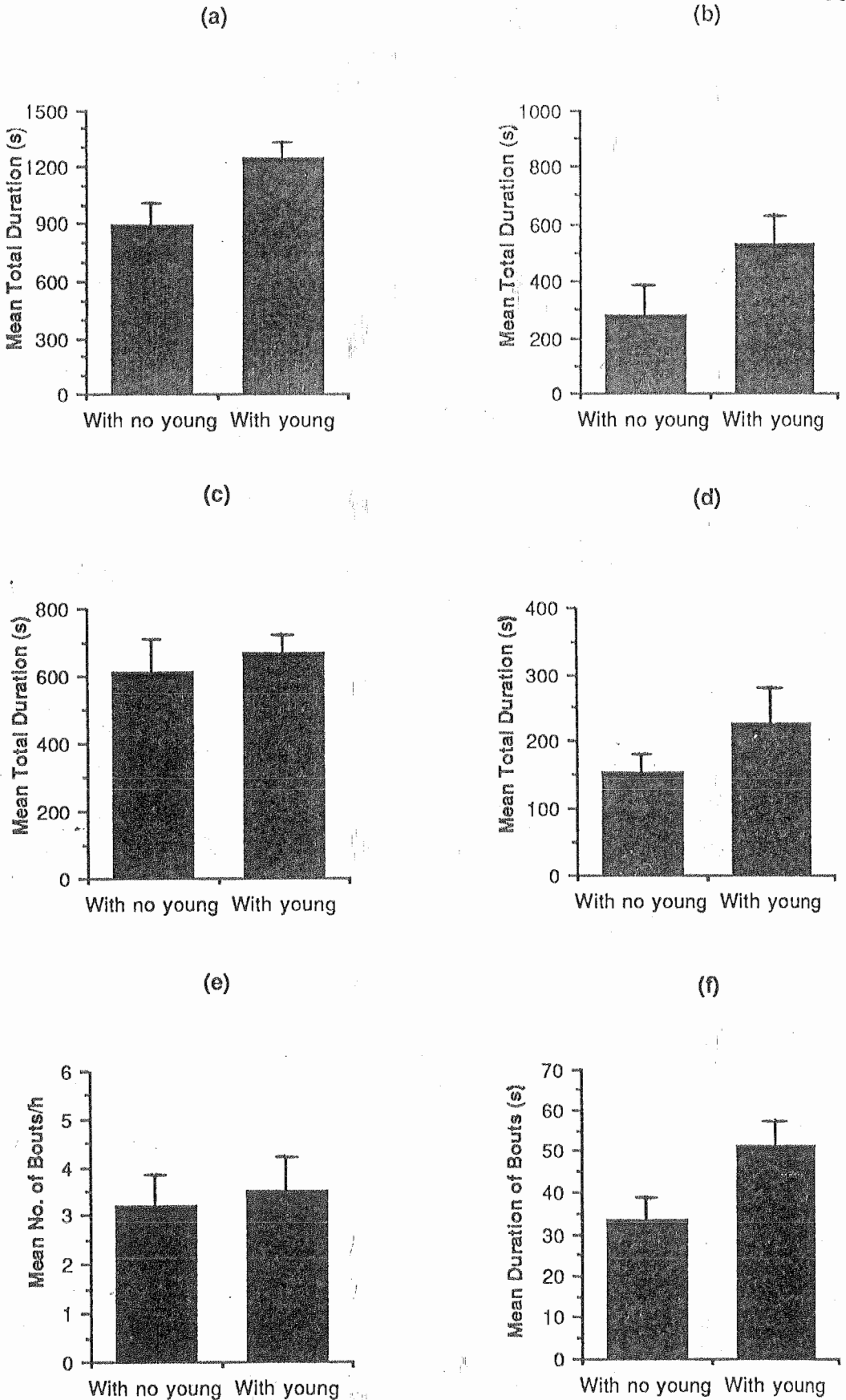
Figure 5.2.3 Mean (± one standard error) values for non-parous and pouch-gravid
subjects for: a) total duration of resting; b) total duration of resting in
quadrupedal posture; c) total duration of resting in bipedal posture; d)
total duration of grooming the body; e) frequency of bouts of
grooming the body; f) duration of bouts of grooming the body
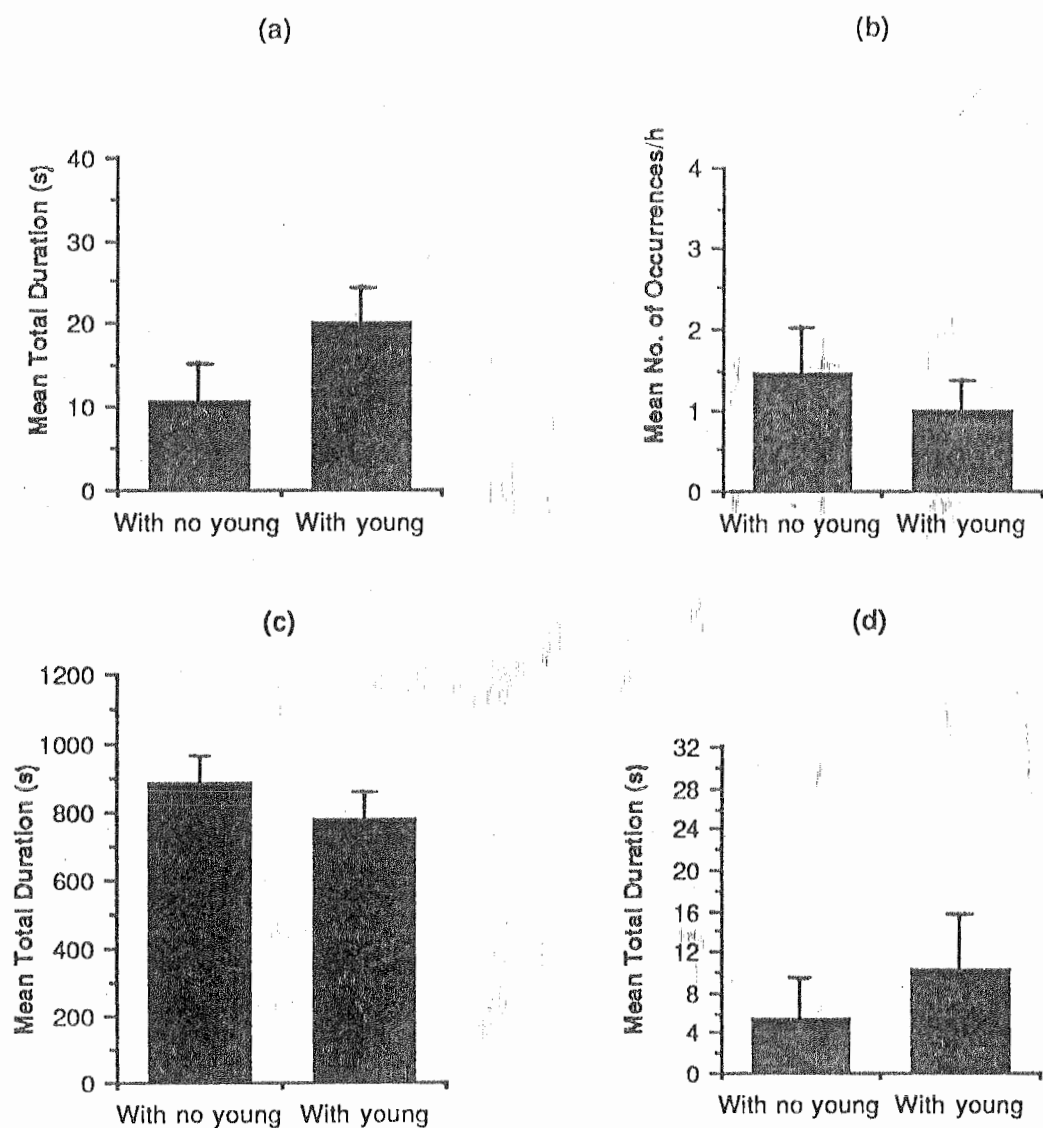
Figure 5.2.4 Mean (±one standard error) values for non-parous and pouch-gravid subjects for: a) total duration of grooming the pouch; b) frequency of shaking; c) total duration of investigative behaviour; d) total duration of time subject was out of sight of the observer.

respectively), the mean duration of these postures were not found to differ significantly between pouch-gravid and non-parous subjects.

No differences were found between pouch-gravid and non-gravid subjects in relation to levels of grooming of the body (excluding the pouch). This was true of mean total durations, mean frequency of bouts per observation period and mean bout duration (Figures 5.2.3d, 5.2.3e and 5.2.3f, respectively). Similarly, and perhaps surprisingly, no differences between the two groups were found with respect to mean total durations of pouch grooming (Figure 5.2.4a). There was no significant difference in the frequency of occurrences of shaking(Figure 5.2.4b). No significant differences were found between pouch-gravid females and non-gravid females with respect to mean total duration of investigative behaviour (Figure 5.2.4c). Similarly, there was no significant difference in the amount of time each group was out of sight of the observer (Figure 5.2.4d).

5.2.3 Discussion

Many authors have commented on the low levels of energy expenditure associated with intra-uterine development in marsupials, relative to the high costs of chorio-allantoic placentation in eutherian species (e.g. Tyndale-Biscoe 1973; Russell 1982; Lee and Cockburn 1985). However, one might suppose that this apparent energetic advantage is negated by the high metabolic cost of lactation, which, in marsupials, extends for a relatively longer period of time than it does in eutherian species of comparable weight (Tyndale-Biscoe *op.cit*; McNab 1978). As several authors have noted, lactation is the most energetically expensive period of the breeding cycle in both eutherian and marsupial species (Millar 1975, 1977; Lee and Cockburn 1985). For example, Fleming *et al.* (1981) have recorded a 92% higher metabolic rate in lactating female *Didelphis virginiana*, relative to non-reproductive adults and Lee and Nagy (1984, cited in Lee and Cockburn 1985) have reported that the active metabolic rate of free-living *Antechinus swainsonii* shows an increase of 76% during the later stages of lactation. In the potoroo, the metabolic demands of lactation

are further augmented by the burden of pouch young, particularly during the later stages of pouch occupancy. This consideration is presumably applicable for all macropodoid marsupials, as the proportion of the maternal body weight of young at the time of vacation of the pouch is similar in all species for which information is available (Maynes 1976; Russell 1982).

It is not unreasonable to assume that, in smaller species in particular, the metabolic demands of the period of lactation would be met by appropriate behaviourial strategies of increased feeding and energetic restraint. Subjects observed during the course of the present study exhibited a number of changes in various aspects of their behaviour which may be indicative of such behavioural strategies.

An increase in the dietary requirements of lactating females is well known in a number of eutherian species, particularly domestic stock (Brockway *et al.* 1963; Schmidt 1971) and rodents (Nelson and Evans 1961; Millar 1975, 1979; Randolph *et al.* 1977; Mattingly and McClure 1982; Lochmiller *et al.* 1982; Behrends *et al.* 1986). Nelson and Evans (*op. cit.*) have found that the food consumption and calorific intake of rats during the period of lactation is 2-3 times that of non-lactating females. They suggest, not unreasonably, that this increase is attributable to the maternal need to produce sufficient milk for both the dietary requirements of the young and the mother's own body maintenance.

Pouch-gravid *Potorous tridactylus* which were observed in the present study were shown to spend a significantly greater period of time engaged in feeding behaviour than were non-parous females, and it is reasonable to assume that this is correlated with an increased intake of food. Confirmatory evidence of this has been provided by Buchmann (unpublished data). In an extensive study of the feeding behaviour of this species, the latter author has shown that the weight of food consumed is significantly correlated ($p<0.001$) with the total durations of feeding in both males and females.

The observed increase in the duration of feeding behaviour in pouch-gravid subjects is in contradiction to the reports of Buchmann (*op. cit.*), who found no significant difference between the feeding activities or food-intake of non-parous and

pouch-gravid *P. tridactylus*. However, as Buchmann noted, the sample of individuals he examined did not include females with advanced pouch-young.

Among the few relevant observations which have been made on other marsupials, Hunsaker and Shupe (1977) have suggested that the increased activity levels observed in New World didelphids parallel an increased food intake in order to meet the high metabolic demands of raising young. Lactating female *Caluromys philander* have been shown to increase the duration of their nocturnal foraging by 38%, relative to that of non-lactating females. (Atramentowicz 1982, cited in Lee and Cockburn 1985). Similarly, Ewer(1968a) has noted an increase in the food consumption of the small dasyurid, *Sminthopsis crassicaudata*, although her observations were apparently based on a single individual.

An increase in food consumption is, perhaps, an obvious means of ameliorating the problems associated with the increased metabolic demands of lactation. Interestingly, however, pouch-gravid subjects achieved this increase by consistently extending the duration of feeding bouts at a given food site, rather than by increasing the frequency of feeding bouts. Buchmann (in prep.) has suggested that females, in general, "apply themselves to eating with greater diligence and economy". The results of the present study tend to suggest that such economy in feeding is more pronounced during the period of lactation and is the result of a strategy which extends beyond a mere increase in the amount of food ingested.

An increased efficiency in the exploitation of a food source would tend to reduce the need for widespread foraging and its associated high levels of locomotory activity. The slow quadrupedal crawl, which was frequently observed to accompany feeding, has been shown to be an energetically expensive form of locomotion (Dawson and Taylor 1973). It is clear that a foraging strategy which allows an increase in food consumption, but does not nesessitate increased locomotion, is energetically superior to widespread foraging. For a small mammal which must endure the metabolic burden of both a relatively long period of lactation and transportation of the young, such a strategy is to be preferred. It is proposed that *P.tridactylus* may employ such a

strategy. The lower levels of locomotory activity observed in pouch-gravid subjects further support this hypothesis. However, it should be noted that the subjects observed in the present study were provided food *ad libitum*, a situation which is undoubtedly not encountered in free-living populations. Nonetheless, the proposed factors operating to reduce energy expenditure during lactation presumably apply to both situations and, indeed, the adaptive advantage of efficient foraging would be expected to be more pronounced in free-living populations where food is not so readily available.

Although no attempt was made during the present study to assess potential qualitative variations in the diet, it is recognised that such factors may be of relevance to the feeding strategies of pouch-gravid *P. tridactylus*. Newsome (1980) has noted that female *Macropus rufus* ingest a significantly higher proportion of nitrogen-rich forbs than do males, and has tentatively suggested that this difference is related to the burden of reproduction. However, further detailed studies of the effect of diet quality are required before any conclusions are able to be made.

Drinking was not a conspicuous behaviour of either non-parous or pouch-gravid females observed during the present study. Similarly, Stodart (1966b) and Wood-Jones (1924) both failed to observe drinking in captive *Bettongia lesueur*. Troughton (1943) reported that captive *B. cuniculus* (=*B. gaimardi*) held in the London Zoo drank a "great quantity of water" (p. 160), however Kershaw (1971) has suggested that this species appears to have minimal water requirements. Sampson (1971) has proposed that free-living *B. penicillata* do not require free-standing water. Johnson (1980b) has reported that captive *Aepyprymnus rufescens* drink freely, however he did not provide an indication of the frequency of this behaviour. Smith (1983) reported that the desert-dwelling *Caloprymnus campestris* appeared to have been "quite independent of surface water, and, moreover, to have shunned... succulent plants" (p. 192).

The limited water intake of *Potorous tridactylus* observed in the present study has similarly been noted by Buchmann (unpublished data). The latter investigator has

suggested that, under natural conditions, this species is able to meet water requirements through the diet. Frauca (1969) has suggested that the potoroo obtains considerable water through the occasional ingestion of snails. Further, *P. tridactylus* may benefit from feeding at night by ingesting moisture in the form of dew, as has been suggested to be the case in *Macropus rufus* and *M. fuliginosus* (Priddel 1986). In subjects observed in the present study, it is likely that water requirements were at least partly met through the the provision of dietary items (e.g. apples) which have a high water content. Further observations on the effect of a diet comprised of dehydrated food items would provide interesting results.

The observation that pouch-gravid and non-parous subjects showed no significant difference with respect to drinking behaviour is in agreement with the observations of Buchmann (unpublished data); however these observations are in contrast to the findings of investigations made on a number of other species. Ewer (1968a) has reported that lactating *Sminthopsis crassicaudata* drank considerably more than individuals without young. Similarly, Ealey (1967) has shown that lactating female *Macropus robustus* engage in drinking behaviour more frequently than non-lactating females, at least during dry conditions. However, if the suggestion that *Potorous tridactylus* is able to obtain sufficient quantities of water in the diet is valid, then it may be reasonable to assume that the higher levels of feeding observed in pouch-gravid subjects may concurrently meet the water requirements associated with lactation.

In contrast to the larger, arid-dwelling macropods, the nocturnality and distribution of *Potorous tridactylus* throughout temperate south-eastern Australia undoubtedly ameliorates the problems of water-balance associated with high ambient temperatures. However, these are not the only avenues of thermal stress. As Dawson *et al.* (1974) have noted, hopping incurs considerable heat production, which in the potoroo, as in the larger macropods, is alleviated by copious sweating, albeit from a limited area (Hudson and Dawson 1975). As a response to cutaneous water loss, one might expect that water intake would increase with elevated levels of locomotory

activity. In the subjects observed in the present study, however, total durations of drinking behaviour showed no correlation with total durations of locomotion (Pearson's $r = -0.013$; d.f.$=52$), however, it is not considered that these animals were predisposed to atypically high levels of locomotory activity.

Happold (1972) has noted that female *Antechinomys laniger* burdened with large pouch young walked with notable "splayed and stiff" hind limbs While such an unfortunate predicament was not observed in pouch-gravid *P. tridactylus* the results of the present study did, however, clearly indicate significant differences between non-parous and pouch-gravid subjects in all locomotory parameters. The observed decrease in the frequency of jumping behaviour may serve to lessen the risk of the young being dislodged from the pouch. In addition, a concurrent increase in the mean total duration of resting behaviour was associated with the observed decrease in locomotory activity. Comparable results have been recorded in *Sminthopsis crassicaudata* by Ewer (1968a), who noted that with the increasing age of young, "the swelling pouch causes increasing locomotory embarrassment" (p. 352).

Fleay (1932) has commented that pouch-gravid *Antechinus swainsonii* are easier to catch than their non-parous conspecifics and similar observations have been reported for *Sminthopsis* (LeSouef and Burrell 1926). These observations suggest that, during the period of pouch-occupancy, these animals are more vulnerable to predation and it is reasonable to assume that a similar consideration applies to pouch-gravid potoroos. Hence, while decreased locomotory and increased resting behaviours may be proximally mediated by the burden of extra weight, it could be considered that these are adaptive behavioural responses which act to lessen the risk of predation during this important stage of the species life-history.

The present study revealed no significant quantitative differences between pouch-gravid and non-parous females with respect to the total duration, bout duration and frequency of grooming actions directed towards parts of the body other than the pouch. These findings are in agreement with those of Buchmann (in prep.) and are

consistent with relevant observations made on *Sminthopsis crassicaudata* (Ewer 1968a) and *Macropus eugenii* (Russell and Giles 1974). Perhaps unexpectedly, however, there were no significant differences in the levels of pouch grooming exhibited by non-parous and pouch-gravid subjects. These results contradict the findings of several previous investigators.

Russell and Giles (1974) have investigated in considerable detail the effects of young in the pouch on the levels of pouch grooming in *Macropus eugenii*. These authors found a significant increase in the levels of pouch grooming as the young matured. Russell (1973) has similarly reported increased levels of pouch grooming in pouch-gravid *M. eugenii*. In addition, Ewer (1968a) noted an increase in the levels of pouch grooming in pouch-gravid *Sminthopsis crassicaudata*.

In contrast to the present study, which disclosed a higher, albeit insignificant level of pouch grooming in pouch-gravid subjects, Buchmann (in prep.) has found that the total duration of pouch grooming in pouch-gravid *P. tridactlyus* is less than that of non-parous females, although his sample did not include subjects with advanced pouch young.

It is difficult to account for these differences, as one would expect levels of pouch grooming to increase when young are present in the pouch. It is not considered that the absolute size of the pouch and the pouch young has an effect, as levels of pouch grooming have been shown to increase in both large and small marsupial species. A further observation, made during the course of casual daily inspections is of relevance, as subjects were observed on two occasions to engage in pouch grooming while within the nest. Grooming is generally a sedentary activity, and may be motivationally associated with resting behaviour. It is therefore possible that the use of data derived from night time sampling would fail to fully disclose any potential increase in the levels of pouch grooming of pouch-gravid subjects.

A final observation, based on information obtained during the course of daily examination of subjects housed within a reversed daylight facility (Section 6), is of relevance to the present discussion of pouch grooming. Russell and Giles (1974) have

suggested that an increase in the levels of pouch grooming is initiated by direct stimuli eminating from the presence of the young in the pouch. However observations of parous adult *P. tridactylus* indirectly suggest that levels of pouch grooming increase *prior* to parturition. The condition of the pouch was examined in four subjects which had lost their initial pouch young and were parous with a reactivated blastocyst. In each case, the pouch was initially observed to be considerably dirty; however, at 1-2 days prior to parturition, a marked increase in pouch cleanliness was noted, and the pouch remained clean throughout subsequent pouch occupancy. It is reasonable to assume that this marked increase in pouch cleanliness was a direct result of the increased levels of pouch grooming. In one subject, no such change in the condition of the pouch was observed, and the neonate was obliged to enter a considerably dirty pouch. However, as this young died at 11 days of age, it is reasonable to assume that the apparent lack of pouch grooming by its mother was atypical and possibly a consequence of the confined conditions.

An increase in pouch grooming prior to parturition has been observed in *M. rufus* (Sharman and Calaby 1964; Sharman and Pilton 1964) and *M. parma* (Maynes 1973). These observations, in conjunction with Shaw and Renfree's (1984) report that oestrogen levels are elevated near birth in *M. eugenii* suggest that hormonal factors are important, at least in the initiation of pouch grooming. However, pouch grooming is not invariably a precursor of parturition, as the levels of this behaviour have been noted to increase only after birth in several dasyurid and paramelid species (Russell 1984). Clearly, further physiologically and behaviourally orientated investigations of marsupial species are required.

5.3 Mother-Young Interactions

Due to difficulties encountered in making observations on potential behavioural interactions between adult female *P. tridactylus* and their young while the latter remain wholly within the pouch, the present investigation sought to concentrate on those interactions which took place following initial vacation of the pouch. Except where otherwise stated, pertinent data were obtained from observations of three mother-young dyads from the age when they initially vacated the pouch to well after weaning. All three adult females were multiparous, as indicated by the presence of regressing mammary glands, and their current young were, in each case, females. Age estimation of young was made in accordance with the methods described in Section 3.2. Observations were made on mother-young pairs held in the enclosure previously desribed (Section 4.2). Each observation period was of one hour duration and was conducted in adherence to the precautions outlined in Section 4.4. Overall, a total of 26 observation periods were amassed. The methods of recording behaviour varied with respect to the information sought and are outlined in the relevant sections.

5.3.1 Exit from and Entry to the Pouch

During the course of observations, notes and sketches were made of the methods by which young first vacated the pouch. The durations of these initial excursions were timed to the nearest s with a stopwatch and the attempts of the young to regain the pouch were described.

Observed initial incidents of the vacation of the pouch occurred when young were at the ages of 112, 114 and 120 days, respectively, and in each case exit from the pouch appeared to be initiated by the young. Similarly, of 13 subsequent observations of vacation of the pouch, ten (77%) resulted from the young climbing out while the mother was resting. In two instances (15%) the young was observed to fall from the

pouch while the mother was engaged in bipedal locomotion and in one instance (8%) the young was spilled from the pouch during the course of pouch grooming by the mother. The observed initial excursions from the pouch were invariably of brief duration -: 22, 362 and 42s, respectively, in the three subjects observed. Not unexpectedly, the mean proportion of the one hour observation period in which young were observed out of the pouch increased with the age of the young (Figure 5.3.1a).

Young potoroos regained the pouch with considerable rapidity. On several occasions, entry to the pouch appeared to occur in response to disturbance from domestic cats on the outside of the observation enclosure. In order to facilitate re-entry, the mother adopted an upright bipedal posture and noticeably retracted her abdomen. The young held the rim of the pouch open with both forepaws, inserted its head and, by means a pulling action with the forelimbs and a simultaneous pushing action with the hindlimbs, re-entered the pouch (Figure 5.3.1b). In most observed instances the young appeared to perform a complete somersault within the pouch, occasionally with the result that the forelimbs and nose protruded.

By the age of 128, 129 and 134 days, respectively, the young were no longer observed to enter the pouch. Nevertheless, even beyond this age the young continued to make repeated attempts to regain the pouch. However, it should be noted that, in practice, it was difficult to distinguish between attempts at entering the pouch and attempts at suckling. To avoid ambiguity, all attempts to either regain the pouch or engage in suckling were treated as a single category. The frequency of these unsuccessful attempts greatly increased at the age of final vacation of the pouch, as shown in Figure 5.3.1c, and was invariably the result of a lack of cooperation on the part of the mother, as witnessed by either the mother moving away or failing to adopt a posture which allowed the young to gain access to the pouch (or teat).
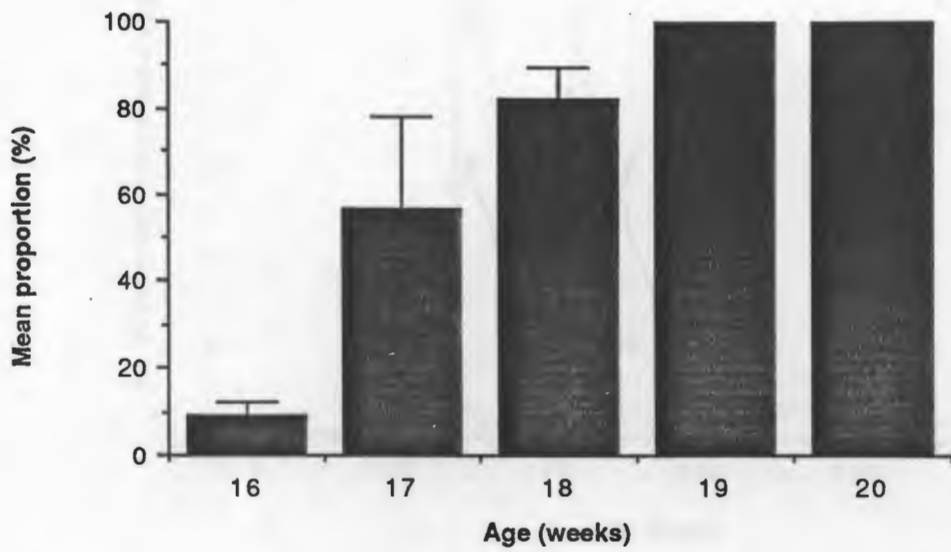
Figure 5.3.1a   Mean proportion (± one standard error) of the 1h observation period for which young (n=3) of 16-20 weeks of age were observed out of the pouch.

Figure 5.3.1b   Re-entry to the pouch
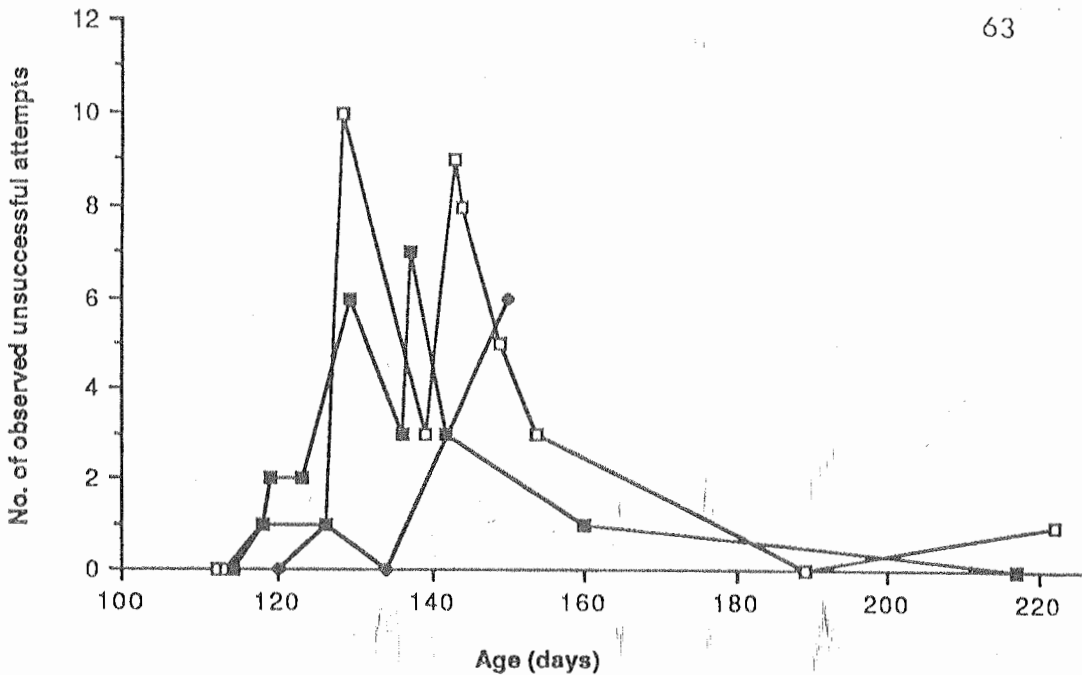
Figure 5.3.1c The number of observed attempts at pouch entry (or suckling) which were unsuccessful. Subjects 1, 2 and 3 are represented by the solid square, open square and solid diamond, respectively.

5.3.2 Spatial Proximity of Mother and Young

Data pertaining to the spatial relationship between mother and young with increasing age of the latter were obtained by the use of instantaneous sampling (Section 4.3.2) at two min intervals, yielding a total of 30 observations per observation period. The distance between a mother and her young was determined by reference to a series of grids delineated by stakes set 1m apart (Section 4.2). These allowed subjects to be scored (0-4) on the basis of the distance between them:

> 0 - physical contact
>
> 1 - > 0m but ≤ 1m
>
> 2 - > 1m but ≤ 2
>
> 3 - > 2m but ≤ 3m
>
> 4 - > 3m

For the purposes of the present study, distance was scored as 0 if the young was in the pouch at the time of observation.

The initial excursions from the pouch typically resulted in the young standing rather shakily no more than 1m away from the mother and, in most cases, in physical contact with her. However, with increasing age and duration of periods spent out of

the pouch, the distance between the two individuals progressively increased until ca. 150-160 days of age, after which time the mean distance between the two individuals remained relatively constant (Figure 5.3.2a).

The number of observations during which the mother and young were in physical contact was initially quite high, largely because the young spent considerable time in the pouch during observation periods. From the time of initial vacation of the pouch, the number of observations in which the mother and her young were in physical contact declined until by the 19th-20th week physical contact was consistently observed to occur at low levels (Figure 5.3.2b).

5.3.3   The Role of the Mother and Young in the Maintenance of Spatial Proximity

In order to assess the relative responsibilities of the mother and young in the maintenance of mutual spatial proximity, the continuous recording method was employed (Section 4.3.1). An individual was considered responsible for uniting the dyad if that individual entered a quadrant (as delineated by a series of stakes - Section 4.2) that was occupied by the other. Conversely, an individual was considered responsible for separating the dyad if that individual departed from a quadrant originally occupied by both individuals. Approaches that did not result in the simultaneous occupancy of a quadrant were excluded from consideration, as were departures that did not result in occupancy of separate quadrants.

The resulting data were analysed in accordance with a method prescribed by Martin and Bateson (1985) which determines a measure of the extent to which an individual (in this case the mother-M) is responsible for the maintenance of proximity between itself and a second individual (the young -/Y):

M's responsibilty for proximity $= [U_m / (U_m + U_y)] - [S_m / (S_m + S_y)]$

where U_m = number of occasions when the dyad was united by the mother's movements; U_y = number of occasions when the dyad was united by the young's movements; S_m = number of occasions when the dyad was separated by the mother's
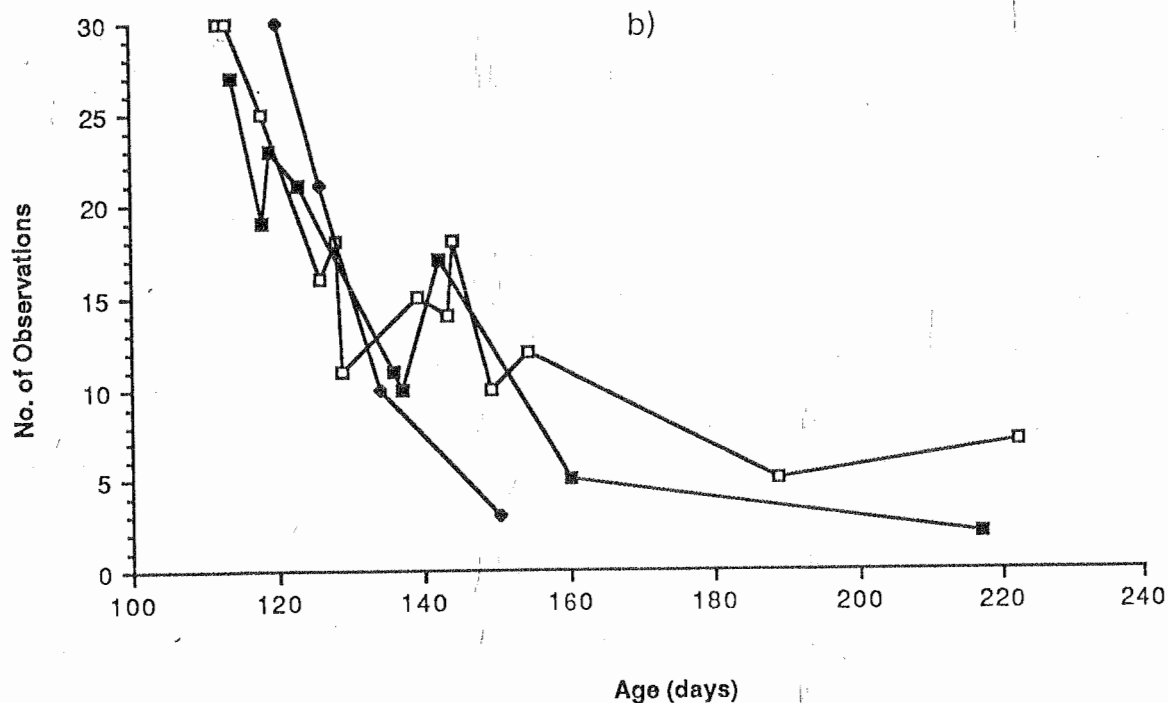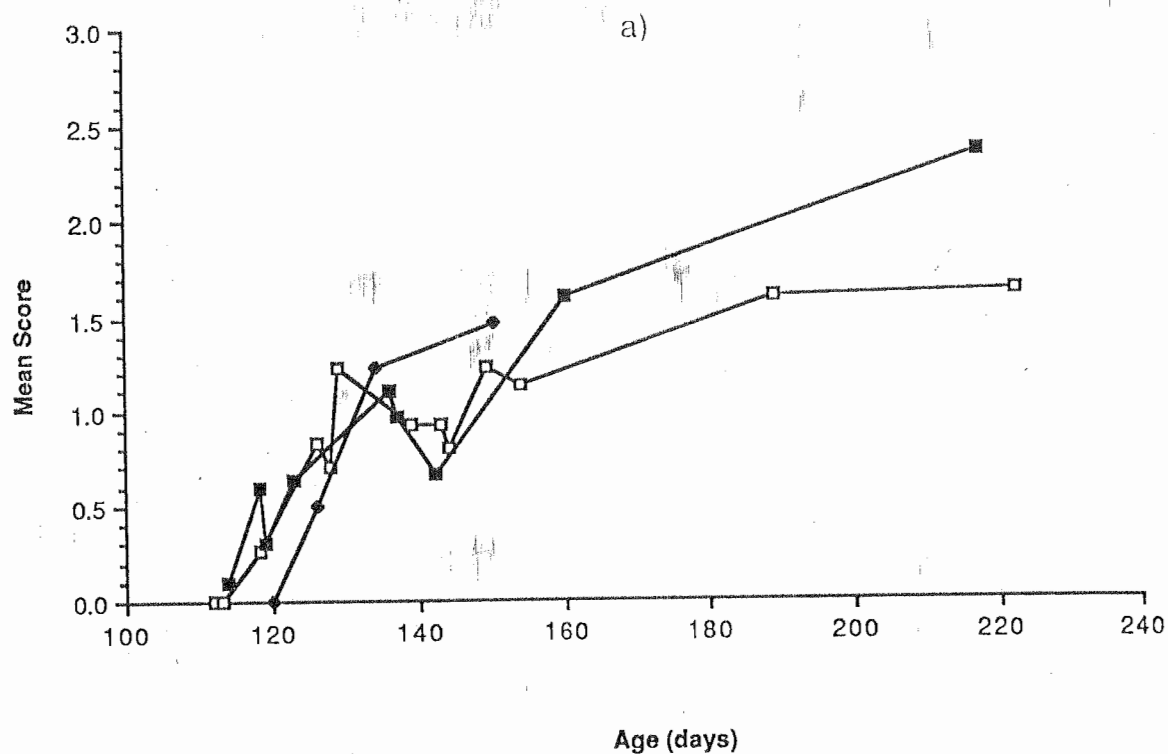
Figure 5.3.2   a) Individual scores (see text) of spatial proximity with increasing age of young and b) mean no. of observations (maximum=30) in which young were in physical contact with the mother. Subjects 1, 2 and 3 are represented by the solid square, open square and solid diamond, respectively.

movements; and S_y = number of occasions when the dyad was separated by the young's movements.

The resulting index (subsequently termed mother's responsibility for proximity - m.r.p.) can range from -1.0 (entirely the young's responsibility) to +1.0 (entirely the mother's responsibility). While this index provides little useful information if considered only for a single stage of the mother-young relationship, it is useful for comparative purposes (Martin and Bateson *op.cit.*); accordingly, the index was calculated for each week of the age of the pouch young observed. These results, presented in Figure 5.3.3, indicate that during the initial stages of vacation of the pouch by the young, the mother assumed responsibility for the maintenance of proximity. However, this pattern was observed to reverse by the 19th week of age. The latter trend was largely the result of the increased number of approaches of the young made toward the mother.
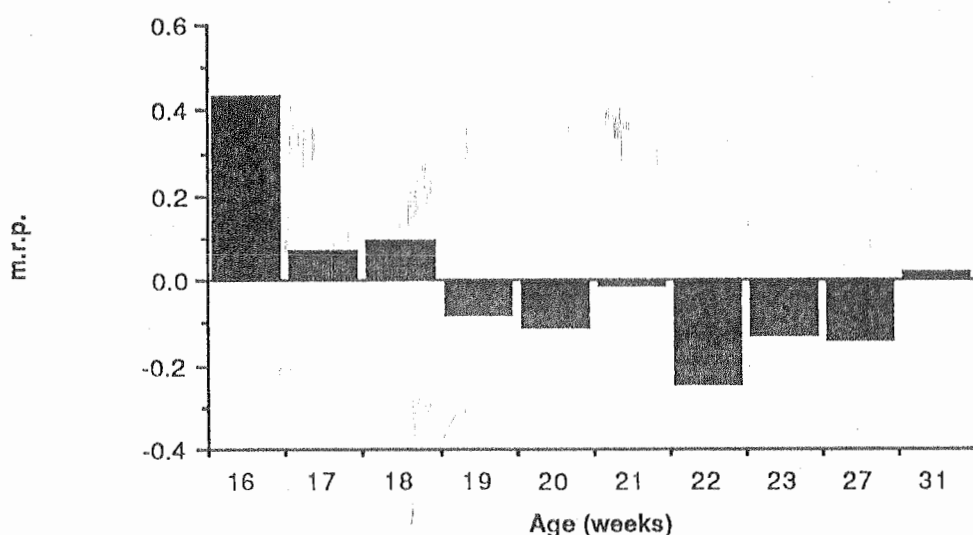
Figure 5.3.3   The value of the m.r.p. index (see text) with respect to the age of pouch-young (n=3).

5.3.4   Suckling

Suckling was characterised by two postures in the subjects observed in the present study.   The majority of episodes of suckling occurred while the female adopted a bipedal posture accompanied by contraction of the ventrum, giving a notably hunched appearance. The young assumed a quadrupedal posture in front of the mother with the head inserted into the pouch, occasionally raising the forelimbs to the pouch.   The second posture involved the adoption of a quadrupedal posture by the mother.   The abdomen was raised in order to allow the young access to the teat. The young similarly adopted a quadrupedal posture and forced its head beneath the abdomen of the mother. Although young were first observed out of the pouch at 112, 114 and 120 days, respectively, suckling from outside of the pouch was not observed until 118, 118 and 126 days of age; presumably suckling occurred within the pouch during the earlier periods. The mean total duration of suckling behaviour observed over the one hour observation period increased in all of the three subjects; however, at 20 weeks of age, the mean duration was lower than that recorded for the previous three weeks (Figure 5.3.4).   Young at foot continued to suckle until 136, 139 and 142 days of age, respectively, after which time all attempts to gain the teat (or pouch) were obstructed by the lack of cooperation of the mother (c.f. Figure 5.3.1c).
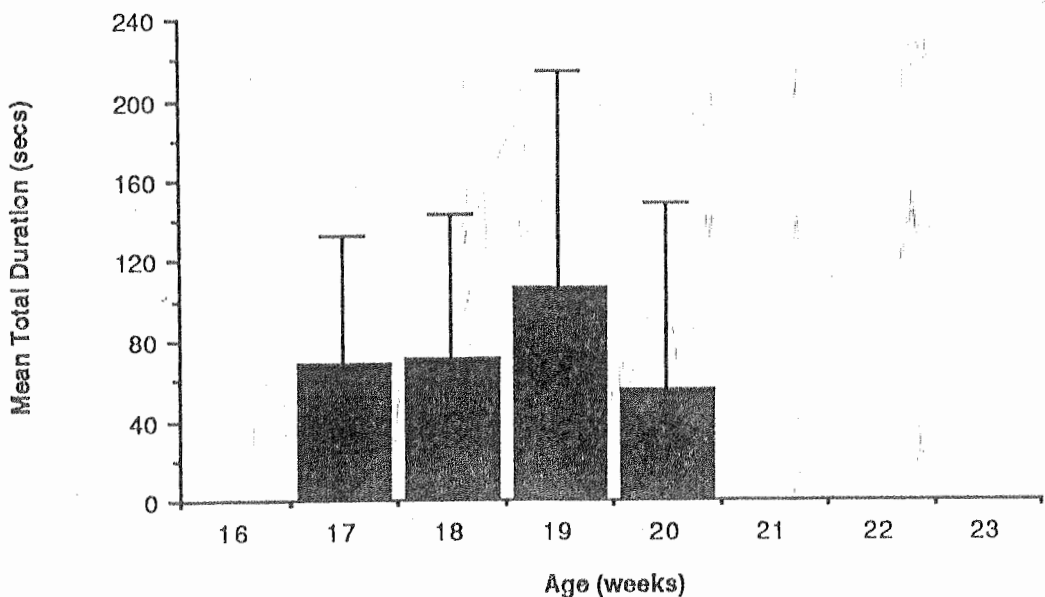
Figure 5.3.4   Mean (± one standard error) total duration of suckling behaviour of young (n=3) with respect to age.

5.3.5 Allogrooming

Allogrooming - the grooming of an individual other than oneself - was a conspicuous activity of mother-young dyads observed in the present study. The duration of each observed bout of allogrooming was recorded with a stopwatch and assessed with respect to which member of the dyad was performing the grooming actions

The great majority of allogrooming behaviour exihibited by both the mother and the young was directed towards the dorsal regions of the shoulders and head. The recipient (the groomee) generally adopted a quadrupedal posture, while the groomer assumed a bipedal posture facing perpendicularly to the individual being groomed. Both scratching with the forefeet and nibbling were used (Figure 5 3.5a).

Allogrooming was observed in 22 of the 26 observation periods, and in 65 of the 95 observed occurrences (68.4%), it was the mother which groomed the young The total durations of allogrooming were low during the early stages of vacation of the pouch, possibly because the young was groomed while within the pouch.   Adult females continued to groom their young until the latter were beyond 23 weeks of age; however, by 27 weeks the young were rarely observed to be groomed by their mothers (Figure 5.3.5b).

Figure 5.3.5a Allogrooming
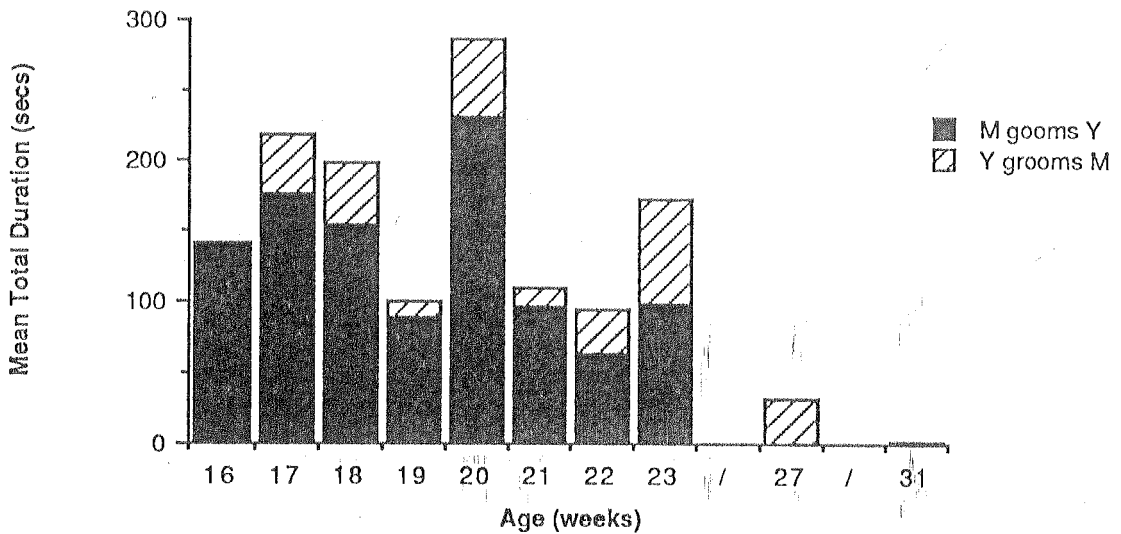
Figure 5.3.5b Changes in the mean total duration of allogrooming with age of young. M=mother; Y=young.

5.3.6 Agonistic Interactions

For the purposes of the present analysis, agonistic interactions were defined as events of three types:

a) displacement of one individual as the result of the approach of the other

b) pursuit of an individual

c) one individual cuffing the other.

In a), an agonistic encounter was scored only if the supplanting individual occupied the quadrant (as demarcated by the grid system) previously occupied by the supplanted individual.

In b), an agonistic encounter was scored only if the actions of the pursuer resulted in an escape reaction by the individual being pursued.

In c), an agonistic encounter was scored only if the aggressor made physical contact with the other individual.

Agonistic interactions were not a conspicuous element of the behaviour of mother-young pairs observed in the present study. In a total of 26 observed instances, 24 were directed by the mother toward the young. Of these, 13 (54%) involved displacement of the young, usually from a feeding site. In eight instances (33%), the mother pursued the young and on only three occasions (13%) was the mother observed to strike the young. The young was observed to displace the mother on only two occasions. Agonistic interactions were not observed in the two weeks following initial vacation of the pouch; however, their frequency increased after the young attained the age of 18 weeks (Figure 5.3.6).
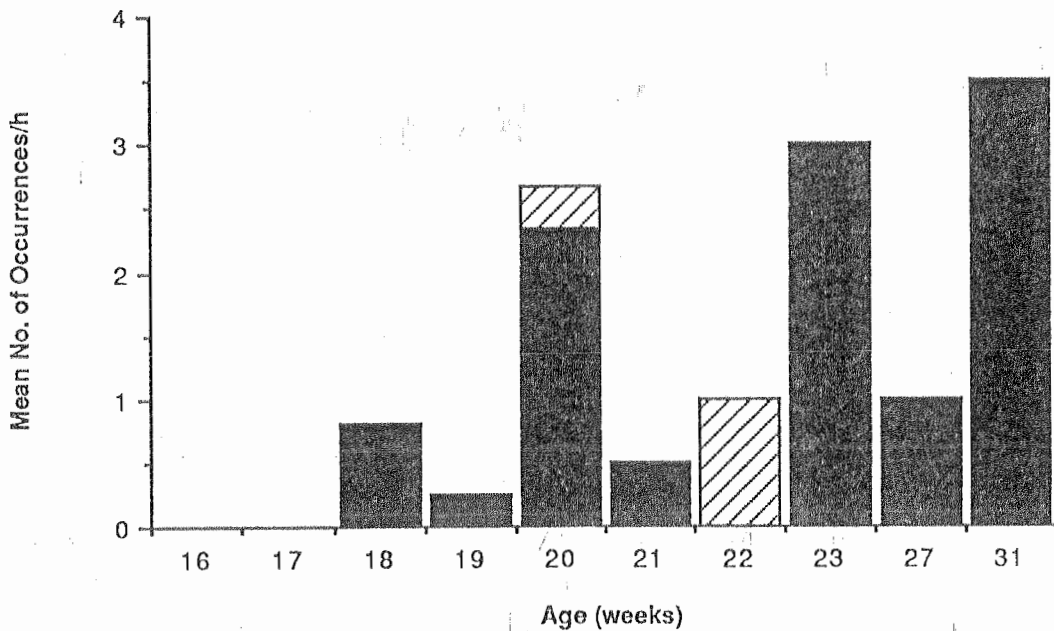
Figure 5.3.6   Changes in the mean no. of agonistic interactions with respect to the age of the young (n=3). Solid block denotes agonistic interactions directed by the mother toward the young; striated block denotes agonistic interactions directed by the young toward the mother.

5.3.7 Discussion

The observations made during the course of the present investigation of mother-young interactions in captive *P. tridactylus* indicate that this species exhibits a strategy of parental care similar to Russell's (1982) "pattern A", i.e., the young remain wholly within the pouch before exiting at a relatively advanced stage of development. A period of intermittent pouch occupancy ensues, although the frequency with which the young re-enter the pouch progressively decreases with age. Following final vacation of the pouch the young remain in association with the mother; in the case of the potoroo this period may extend beyond weaning.

As Russell (*op. cit.*) has suggested, the very nature of the marsupial pouch, when it is present, may be considered to exert considerable influence on the patterns of parental care exhibited by marsupials. The relatively long succourment of young within the well developed pouch of *P. tridactylus* and, indeed, other macropodoid marsupials, obviates the need for developing behaviour associated with the defense and retrieval of young, which occurs in several dasyurid species that leave the young in nests, e.g. *Antechinus stuartii* (Settle and Croft 1982), *Dasycercus cristicauda* (Ewer 1968a), *Sminthopsis crassicaudata* (Ewer *op. cit.*), *Dasyuroides byrnei* (Aslin 1974), as well as the didelphid *Marmosa cinerea* (Beach 1939).

The initial observed instances of vacation of the pouch in young *P. tridactylus* appeared in most cases to be a consequence of the deliberate actions of the young rather than fortuitous incident or active expulsion by the mother. This is in contrast to the observations of Russell (1973), who reported that young *Macropus rufus* and *M. eugenii* initially fall from the pouch during the course of pouch grooming by the mother, although toward the end of pouch life the young of these species leave the pouch by their own voluntary efforts.

The first excursions of the young were of brief duration and rarely resulted in the young moving more than 1m away from the mother. However, with increasing age, the duration of these excursions increased, as did the mean distance between the mother and her young. A similar initial reluctance to leave the security of the mother

has similarly been noted in *Macropus rufus* and *M. eugenii* (Russell 1973).

The low frequency with which young *P. tridactylus* left the presence of the mother and the mother's responsiveness to the occasional distress calls of the young were largely responsible for the high positive value of the m.r.p. index recorded during the 16th week of age of the young. However, with increasing age, the young departs the mother more frequently and the mother approaches the young less frequently, consequently, the roles of each individual in the maintenance of spatial proximity were reversed, as indicated by the negative values of the m.r.p. index after 18 weeks of age.

Several studies of both marsupial and eutherian species have indicated that the mother and young reverse their roles in the maintenance of spatial proximity. This trend has been observed in *M. rufus* (Russell 1973; Croft 1981a). *M. eugenii* (Russell *op.cit.*) and the dasyurid species *Antechinus stuartii* (Settle and Croft 1982) as well as in a number of eutherian species, including the domestic cat, *Felis domesticus* (Martin 1986).

The increasing reluctance of adult female potoroos to permit suckling (or entry to the pouch) by the young is consistent with observations made on *M. rufus* (Russell 1970). Among eutherian species, Martin (1986) has shown a similar response in domestic cats, with the mother increasingly adopting a "blocking" posture which denies the young access to the teat.

Although allogrooming is known to be effective in reinforcing social bonds in some eutherians, particularly primates (Sparks 1969), few studies have considered its role in species of marsupial. Russell (1984) has noted that allogrooming between adults occurs at considerably lower frequencies in marsupials than it does in eutherians, although it has been described in *M. eugenii* (Russell and Giles 1974) and has been noted to occur during agonistic interactions in *M. rufogriseus* (LaFollette 1971). Kitchener (1970, cited in Russell 1984) has suggested that allogrooming may be important in the maintenance of pair bonds in *Setonix brachyurus*. Davies (1979) has suggested a similar function of allogrooming in *Petrogale* spp., as has Ganslosser (1979,

cited in Russell 1984) for *Dendrolagus dorianus.*

Allogrooming appears to be a rare behavioural event between adult *P. tridactylus,* however Buchmann (in prep.) has recently described grooming between adults while they are within the nest. This form of "transfer grooming", however, is possibly not related to the formation or maintenance of social bonds, but rather, may be a response to the eliciting stimulus of the pelage of the adjacent individual.

Allogrooming was a conspicuous behavioural interaction between mother-young dyads observed in the present study. Russell (1973) reported that allogrooming was a prominent interaction between mother-young dyads in *M. rufus* and *M. eugenii,* and similar observations have been reported for *M. parryi* (Kaufmann 1974a), *Setonix brachyurus* (Kitchener 1970, cited in Russell 1984), *Aepyprymnus rufescens* and the dasyurids, *Antechinus stuartii* (Settle and Croft 1982) and *Dasyuroides byrnei* (Meissner and Ganslosser 1985). Unfortunately, the majority of behavioural studies on marsupials provide little, if any, information on the occurrence of allogrooming.

Allogrooming may be of importance in maintaining or reinforcing the mother-young relationship until the time of weaning. In the captive *P. tridactylus* observed in the present study, adult females devoted a considerable amount of time to grooming their young; however when the latter were beyond the age of 23 weeks, the frequency of this behaviour declined. This reduction may be a component of the general withdrawal of maternal care which initiates the weaning process. However, there are, to date, no detailed studies of quantitative variations in the levels of allogrooming by adult female macropods in relation to the age of young which might serve to substantiate this suggestion.

The young observed in the present study exhibited no signs of excessive soilage of the pelage or parasitic infestation, nor did they appear predisposed to perform "playful" behaviours which might result in soilage of the pelage. The majority of the mother's grooming actions were directed toward the head and shoulder regions of the young, as has similarly been noted in a number of macropodid species (Russell 1984). These observations may be interpreted to suggest that allogrooming is of functional

value in that it allows the mother to groom a region of the body of the young which is inaccessible to the young itself. However, as described in Section 6.2.12, potoroos appear to possess a full repertoire of effective grooming actions by the age of 17 weeks; furthermore they appear to be capable of performing effective grooming of the head and shoulder regions well before the stage at which allogrooming was observed to decrease in frequency.

Further investigation of the function of allogrooming in macropodoid species may indicate why this behaviour, which is largely lacking in adults, remains a conspicuous form of behavioural interaction of the mother-young relationship.

Although agonistic interactions were not a common feature of mother-young interactions in the subjects observed in the present study, the frequencies of agonistic encounters did show a clear tendency to increase as the young grew older. Almost invariably, these were directed by the mother toward the young. Although cuffing of the young was observed on only three occasions, it invariably followed the attempts of the latter to enter the pouch. Similar increases in the levels of aggression of the mother have been reported in *Macropus giganteus* (Kaufmann 1975) and *Thylogale billardierii* (Clancy 1982). Nelson and Goldstone (1986) have reported that a marked increase in the levels of agonistic acts directed toward the young of female *Peradorcas concinna*. Sampson (1971) has also reported similarly high levels of aggression directed toward the young by the parents in *Bettongia penicillata*.

An increase in the frequency of agonistic behaviour of females toward their young has been reported in a number of eutherian species, including reindeer, *Rangifer tarandus* (Espmark 1971) and moose, *Alces americana* (Altmann 1958). Martin (1986) has suggested that the level of maternal aggression in cats is increased when the mother is subject to a dietary regime of low nutritional value. Although no studies, to date, have considered the relationship of maternal nutrition and the levels of aggression in marsupial mother-young dyads, it is possible that the favourable conditions of captivity may result in a lower level of maternal aggression than that which might occur among free-living mother-young pairs.

The results of the present investigation suggest that the proccess of weaning in *P. tridactlyus* is mediated by a combination of behaviours of the adult female: denial of access to the teat, reduction of the mother's responsibility for maintenance of proximity, decreased levels of grooming the young and increased intolerance and levels of aggression toward the young. Although the attainment of independence may be in part "aided and abetted" by the increasing curiosity of the young, little evidence of the offsprings' own attempts to gain independence were observed. Indeed, repeated attempts to regain the teat (or pouch) by the young frequently resulted in overt conflict.

As Wilson (1980) noted, this conflict has commonly been considered to be a nonadaptive consequence of the rupture of the parent-young relationship. However, an alternative interpretation has been proposed by Trivers (1974) who argued that parent-offspring conflict is an expected result of selective processes operating in different directions on the two generations. Trivers (*op. cit.*) emphasised that the severance of the mother-young relationship during weaning is not solely the result of the mother reducing her investment in her offspring. The young, by attempting to remain dependent, may be considered to increase its own inclusive fitness while simultaneously the mother's fitness declines. The resulting conflict of interests undoutedly provides a basis for an increased level of maternal aggression during the course of weaning.

Weaning has been defined as the period during which parental investment decreases most sharply (Martin 1986). If, as Martin (*op.cit.*) suggests, lactation constitutes the major component of maternal investment, then the period of weaning in *P. tridactylus* observed in the present study may be considered to commence during the 20th week, as it is during this time that the total duration of suckling behaviour by the young was observed to decline. However, this estimate of the age of weaning should not be generalised to all young *P. tridactylus*, since the timing of weaning in several eutherian species has been shown to be influenced by a number of factors, including the nutritional state and experience of the mother and the sex and

developmental stage of the offspring (Martin *op.cit.*). Furthermore, weaning is a complex process, rather than a unitary event and is expressed by a range of behavioural reactions toward the young.

CHAPTER 6

THE ONTOGENETIC DEVELOPMENT OF *POTOROUS*

TRIDACTYLUS

6.1 Introduction

Ontogenetic processes have long been the subject of prolific debates within the disciplines of ethology and comparative psychology, however, many of these have centred around the dichotomous controversies of preformation versus epigenesis or, more recently, nature versus nurture, heredity versus environment and maturation versus experience (Hinde 1982; Oyama 1982; Oppenheim 1982). A considerable proportion of the vast literature pertaining to the complex of factors involved in development is based on studies of eutherian mammals to the almost total neglect of marsupial species.

As Tyndale-Biscoe and Janssens (1986) have noted, the relative immaturity of marsupial young affords an excellent opportunity for the study of ontogeny Considering this, and the unique nature of their post-natal development, surprisingly few detailed studies have examined ontogenetic processes in marsupials. The majority of investigations have restricted their attention to the development of morphological traits (discussed further in Section 6.4) and, to a lesser extent, of the development of physiological and neurological processes (Tyndale-Biscoe and Janssens *op.cit*). Such studies have provided little, if any, detailed information about the ontogeny of behaviour.

Behavioural development has been described in several dasyurid species, including *Antechinus stuartii* (Marlow 1961; Settle and Croft 1982a), *Dasyuorides byrnei* (Aslin 1974; Meissner and Ganslosser 1985), *Antechinomys laniger* (Happold 1972), *Planigale maculatus* (Aslin 1975) and *Sminthopsis crassicaudata* (Ewer 1968a). Unfortunately, few detailed studies have been made on representatives of other families, although some information is available on the didelphid *Didelphis virginiana* (Reynolds 1952; Hunsaker and Shupe 1977) and the peramelids, *Isoodon obesulus* and *Perameles gunnii* (Heinsohn 1966).

Among the Macropodidae, information on juvenile behaviour in *Macropus rufus* has been provided by Sharman and Calaby (1964) and Russell (1970). Russell (1973)

has made a detailed and quantitative investigation of the development of behaviour in this species and the tammar wallaby, *M. eugenii* and, to date, these are the most comprehensive studies available. Brief descriptions of juvenile behaviour have been given for *M. parryi* (Kaufmann 1974a), *M. giganteus* (Poole 1975), *Petrogale xanthopus, P. penicillata* (Hornsby 1978) and *Thylogale billardierii* (Rose and McCartney 1982; Clancy 1982).

The present investigation was undertaken in order to elucidate aspects of the behavioural ontogeny of *P. tridactylus*. It should, however, be recognised that behavioural development is intimately associated with the behavioural interactions which occur within the context of the mother-young relationship; consequently, the present study sought to focus largely upon the development of the normal maintenance activities of this species (Section 6.2). In addition, quantitative differences in the proportions and temporal patterning of adult and juvenile behaviour were examined (Section 6.3) and an account of the ontogeny of external morphology is given (Section 6.4).

6.2   The Ontogeny of Behaviour

6.2.1 Methods

In order to assess the first appearance of several behavioural elements in captive *P. tridactylus*, a series of daily examinations were made of the pouch young of adults maintained in small holding cages within a reversed daylight facility (Section 3.3). Except where otherwise stated, a total of five young were examined on a daily basis; however the death of two of these reduced the number to three during the later stages of the study. Additional relevant information was derived from subjects housed in large outdoor enclosures and those used in the investigation of mother-young interactions (Section 5.3).

Examination of the pouch young was performed while the mother was restrained in a hessian bag. During the period of permanent attachment to the teat, no attempt was

made to remove young from the pouch. However, notes were obtained on teat utilization and the effects of dislodgement from the teat (Section 6.2.2). Examinations following the period of permanent attachment were made on subjects which had been removed from the pouch and placed on a large table. In view of the undeveloped thermoregulatory ability of unfurred marsupial young (Tyndale-Biscoe 1973), early pouch young were kept out of the pouch for as short a time as was practical and all observations were made in a environment heated to ca. 25° C.

Age estimation of subjects for which the actual date of birth was not known was made based on the procedures outlined in Section 3.2; consequently, it should be emphasised that in some instances, the ages given are estimates with an error of ±4 days. Further, the age of the young at the first observed occurrence of a particular type of behaviour may not accurately reflect the actual age of initial occurrence. This is particularly true for behaviours of infrequent occurrence. In view of these considerations, all of the ages given must be taken as approximate rather than precise. The behaviours which were examined are described below in order of first appearance and are summarised in Figure 6.2.

6.2.2   Period of Permanent Attachment to the Teat

a) Teat selection

Hughes (1962) has suggested that in *Potorous tridactylus*, neonates entering the pouch of a multiparous female have no alternative but to attach to either of the teats situated on the side of the pouch opposite to that occupied by the previous young. In an attempt to test this suggestion, examinations were made on a total of 13 currently pouch-gravid females which revealed evidence of previous pouch occupancy, as indicated by the presence of a teat in various stages of regression. The animals used for this purpose comprised both captive subjects and animals observed during a concurrent program of capture-recapture trapping (Section 7). In three cases, observations were also made on successive young. The teats selected in these 16 observations are shown in relation to the teats previously used in Table 6.2.2a.

Table 6.2.2a   The number of young *P. tridactylus* selecting different teats in relation to the teats previously suckled by an earlier young.

a) Anterior teat previously used

	same side	opposite side	total
anterior	–	4	4
posterior	3	1	4
total	3	5	8

b) Posterior teat previously used

	same side	opposite side	total
anterior	1	3	4
posterior	–	4	4
total	1	7	8
total	4	12	16

Results of a chi-square analysis (with Yates' correction) revealed that young selected a teat on the opposite side of the pouch more frequently than the teat on the same side as the regressing mammary gland ($X^2 = 4.0$; p›0.05). There was no difference between selection of anterior and posterior teats on the opposite side ($X^2 = 1.8$).

b) Reattachment to teat following dislodgement

On several occasions during the course of examinations, several pouch young were inadvertently dislodged from the teat. Subsequent observations revealed that, in most cases, spontaneous reattachment to the same teat occurred (Table 6.2.2b). There was no clear relationship between age at dislodgement and subsequent survivorship, nor was there an apparent difference in the mortality of dislodged young (33%; n=6) and young which remained attached to the teat (42%; n=7).

Table 6.2.2b Age (days) and subsequent survivorship of young dislodged from the teat prior to the age of normal release of teat. (Note that three young were dislodged on more than one occasion)

Subject	Age/s at Dislodgement			Spontaneously Reattached?			Ultimate Fate
	1st	2nd	3rd	1st	2nd	3rd	
1	21	33	-	yes	no	-	died(34days)
2	46	51	54	yes	yes	-	survived
3	32	46	-	yes	yes	-	survived
4	24	-	-	no	-	-	died(26days)
5	16	-	-	yes	-	-	survived
6	43	-	-	yes	-	-	survived

Regular examination indicated that the period of permanent attachment to the teat lasted for 58 - 68 days (median=60) in subjects observed during the present study, even though the lateral fusion of the lips had disappeared at age 45-52 days (see Section 6.4).

6.2.3 Vocalisations

Perhaps surprisingly, young potoroos are capable of emitting repeated distress vocalisations, albeit of a low intensity, prior to the time when they first relinquish the teat. This was noted in three subjects which were inadvertently dislodged from the teat during examination. The earliest age at which a pouch young was observed to produce an audible vocalisation was 24 days. At this age the volume of the call was very low; however, the volume of the distress vocalisations increased with age.

Distress calls were most consistently observed when the young were removed from the pouch at the age of 70-100 days. The young continue to emit the distress call for a considerable time after complete weaning. Vocalisations of this type were noted in two juveniles at the estimated ages of 162 and 184 days, which is some 40-60 days after weaning. After this time the animal's vocal repertoire resembled the low-pitched, guttural growls characteristic of adults.

6.2.4   Investigative behaviour

The first indication of audible sniffing in the subjects observed in the present study was noted at 66-84 days of age (median=80). Sniffing increased in both frequency and intensity throughout pouch life and was a common behaviour in young during the later stages of intermittent pouch occupancy. However, in contrast to the findings of Buchmann (unpublished data), juveniles did not appear to engage in sniffing more frequently than adults and at the age of 30-32 weeks, juveniles were shown to spend similar amounts of time engaged in investigative behaviour (Section 6.3.2).

6.2.5 Righting and Quadrupedal Stance

The righting reflex in *Potorous tridactylus* attained maturity at the age of 72-81 days (median=76); however, at this age all attempts to retain a quadrupedal stance were unsuccessful. It was not until 77-90 days (median=84) that the young were capable of standing without falling.   Nevertheless, during this time the young were noticeably shaky on their feet and both the forelimbs and hindlimbs were splayed out from the body, apparently in order to retain the posture. Repeated distress calls were typically associated with this stage of development. No attempt at forward progression was made.

Shortly after the time when young were first observed to be capable of maintaining a quadrupedal posture, the ability to turn around was developed (79-90 days; median=85.5).   Initially, this was achieved by pivoting around on the hindlimbs assisted by the use of asynchronous lateral thrusts of the forelimbs.

6.2.6 Entry to the Pouch

Although potoroos were capable of regaining the pouch at 68-72 days (n=2) if the head was inserted by the investigator, it was not until 80-95 (median=88.5) days of age that the young were able to enter the pouch independently.   However, because the young were incapable of effective forward progression at this stage of development, entry to the pouch could only occur if the mother assumed responsibility for ensuring that herself and her young were in physical contact. On several occasions after the

completion of examinations, the young were replaced in an arena with the mother. In most of these observed reunions, the mother responded to the distress calls of the young by approaching it and adopting a posture which facilitated the entry of the young to the pouch (Section 5.3.1).

The ease with which the young regains the pouch improved with age. By the age of 96-112 days (median=101; n=4), young potoroos enter the pouch with impressive rapidity (<2s), as described in Section 5.3.1.

6.2.7 Bipedal Stance

Subjects observed during the present study were able to maintain a bipedal posture by the age of 94-103 days (median=99.5; n=4). Before this time, the animals were able to elevate their forequarters; however they appeared to experience difficulties in remaining upright for periods of time greater than 1-2s. Sniffing frequently accompanied the assumption of this posture.

6.2.8 Quadrupedal locomotion

The first observed instance of effective forward progression occurred in subjects of the ages 98-105 days (median=102.5; n=4). Before this time, subjects appeared to be reluctant to attempt any movement when placed on the examination table. These initial attempts at forward progression involved the asynchronous movements of all limbs, resulting in a slow and somewhat awkward movement, however, by 104-111 days, young potoroos exhibited the synchronous quadrupedal locomotion characteristic of the adult, as described in Section 4.5.3.

6.2.9 Cliff avoidance

When placed upon the edge of the examination table, subjects at an age of less than 105-110 days (median=109; n=5) consistently locomoted unhesitatingly over the edge. This occurred in both naive and experienced subjects. After this age, the animals approached the edge, lowered their forequarters and leaned over but appeared

reluctant to continue further   At 132 days, one male juvenile spontaneously jumped from a height of 0.4m but appeared reluctant to jump from a height greater than 0.6m. Adults were observed to jump without hesitation from cages at heights of over 1.5m above the ground; however their willingness to jump may have been prompted by their inclination to escape!

6.2.10 Period of Intermittent Pouch Occupancy

Young *Potorous tridactylus* were first observed out of the pouch at 106-120 days of age (median=112; n=6). The methods used in vacating the pouch have been described in Section 5.3.1. Durations of the period of intermittent pouch occupancy ranged from 15-20 days (median=17; n=6) before permanent vacation of the pouch at 125-134 days (median=128.5).

6.2.11 Bipedal Locomotion

Potoroos were capable of effective bipedal locomotion by the age of 115-118 days (median=117; n=3). Initial attempts at this were of brief duration and were interspersed with quadrupedal locomotion; however, after a further 2-3 days had elapsed, the animals were able to maintain this gait. Juvenile potoroos engaged in bipedal locomotion considerably more frequently than adults and continued to do so until well after weaning.

6.2.12 Autogrooming

Potoroos were capable of effectively grooming the entire surface of the body by 115-120 days (median=117; n=4). The patterns of grooming at this stage of development were similar to those of adults (described in Section 4.5). Most grooming actions involved cleansing of the muzzle with the synchronous strokes of the forelimbs, licking of the forelimbs and scratching of the posterior flanks with the hindlimb. These actions frequently occurred in isolation, however prolonged bouts were also commonly observed.

6.2.13 Ingestive Behaviour

The first instances of independent feeding were observed at 116-121 days (median=120; n=3), some 20 days before the young were weaned. Until this time, items of food were sniffed but not ingested. Initially, food was taken from the ground directly by the mouth without the use of the forelimbs; however, within a few days, all subjects were observed to utilize their forelimbs in the manipulation of food items with a dexterity comparable to those of adults. Young were never observed to exhibit copraphagia.

Drinking was observed in young at the ages of 124-156 days (median=149; n=4). However, for the reasons given in Section 6.2.1, these may be underestimates, as drinking appeared to be as infrequent in juveniles as it was in adults. Similarly to adults, young lapped up water with the tongue while gripping the water container with the forefeet (Section 4.5.1).

6.3   Quantitative Differences in the Behaviour of Adult and Juvenile *Potorous tridactylus*

6.3.1 Methods

Observations were made on subjects held in a 2.5 X 2.5 X 1.5m outdoor enclosure situated on the campus of the University of Tasmania. This enclosure was situated on level ground and was surrounded by three opaque walls; the fourth wall comprised a glass panel. The enclosure was roofed with a fly screen in order to reduce disturbance from domestic cats. The floor of the enclosure comprised a layer of wire mesh covered by 5cm of soil and topped with a complete covering of straw ca. 10cm thick. A triangular metal nest box was provided against one wall and food and water were provided at a single site in the centre of the enclosure. The enclosure was illuminated by 3 X 75W tungsten light bulbs covered with red filters.

Observations were made by the use of a "Canon" video camera positioned ca. 3.5m
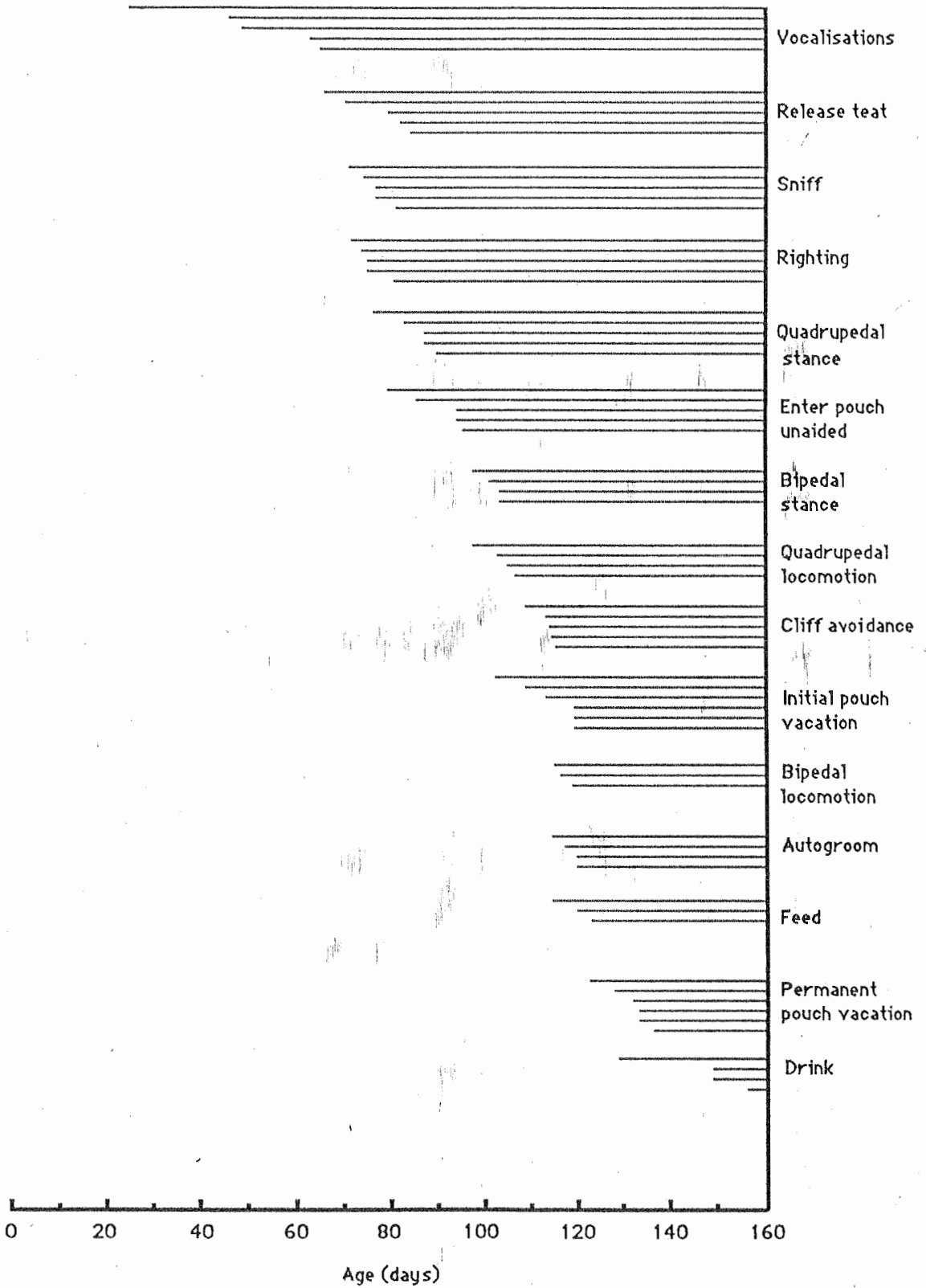
Figure 6.2 Summary of the ages at which behavioural elements were first observed in captive *P. tridactylus*

above and ca. 2.5m to the side of the enclosure. In this position, a focal length of 28mm ensured that the entire observation arena was in view. The video recorder was operated by means of an infra-red remote control unit connected to a timing mechanism. This permitted 10s of footage to be recorded at successive 2 min intervals; hence, this method of behavioural sampling was essentially equivalent to the instantaneous sampling method (Section 4.3.2). Recording commenced at 1800h and terminated at 0900h, resulting in a total of 450 observations per night for each subject.

The subjects used in the present investigation comprised six non-parous adult female potoroos and six fully weaned juveniles aged 30-32 weeks. This narrow range of age was selected in order to reduce the effects of differences resulting from the stage of ontogenetic development. Each mother-young dyad was placed in the enclosure for three days prior to the commencement of observations, in order to permit acclimation to the novel surroundings.

The inadequate resolution of the video camera prevented analysis of details of some behavioural elements; e.g. pouch grooming may have been confused with grooming of the genitals. To eliminate such ambiguities, only distinctly recognisable behaviours were considered:

1. Feeding

2. Drinking

3. Locomotion (both quadrupedal and bipedal forms)

4. Resting

5. Grooming (including allogrooming)

6. Investigation

Subsequent viewing of video taped records permitted the occurrences of these behaviours to be scored at the instant of the onset of each discrete 10s observation period.

6.3.2   Proportions of the Activity Period Devoted to Various Forms of Behaviour in
Adult and Juvenile *Potorous tridactylus*

The number of observed occurrences of each behaviour throughout the entire
activity period was recorded for each individual.   Comparisons of mean values
obtained for adult and juvenile subjects were made by the use of Student's t-tests, with p
< 0.05 as the selected level of significance.   The mean values ($\pm$ one standard error)
obtained for each behaviour are presented in Figure 6.3.2.

There was no significant difference between adults and juveniles with respect to
levels of feeding or drinking behaviour (Figures 6.3.2a and b, respectively).   Adults
engaged in locomotory activity significantly more frequently than juveniles (t = 3.851;
p < 0.005; Figure 6.3.2c) and juveniles spent a significantly greater proportion of the
activity periods engaged in resting behaviour (t = 2.931; p < 0.01; Figure 6.3.2d).   No
significant differences were found between adults and juveniles with respect to
grooming and investigative behaviour (Figures 6.2.3e and f, respectively).

6.3.3 Temporal Distribution of Adult and Juvenile Behaviour

The numbers of observed occurrences of each behaviour in each hour of the
activity period were scored for each subject.   In view of its infrequency, drinking
behaviour was not considered in the present analysis.   The mean values ($\pm$ one
standard error) for adults and juveniles were calculated and are presented in Figures
6.3.3a - e.

Both adult and juvenile potoroos observed in the present study exhibited substantial
similarities in the temporal distribution of their behaviour.   The times of emergence
from the nest-site were found to be similar in both adults and juveniles (mean = 2013h
and 2025h, respectively).   The times at which the subjects returned to the shelters
were variable and no significant difference between adult and juvenile subjects was
found (mean= 0709h and 0754h, respectively).   The durations of the activity periods of
adult and juvenile subjects were 11h 56min and 11h 29min, respectively.   However, it
should be noted that juveniles in particular spent a considerable proportion of this
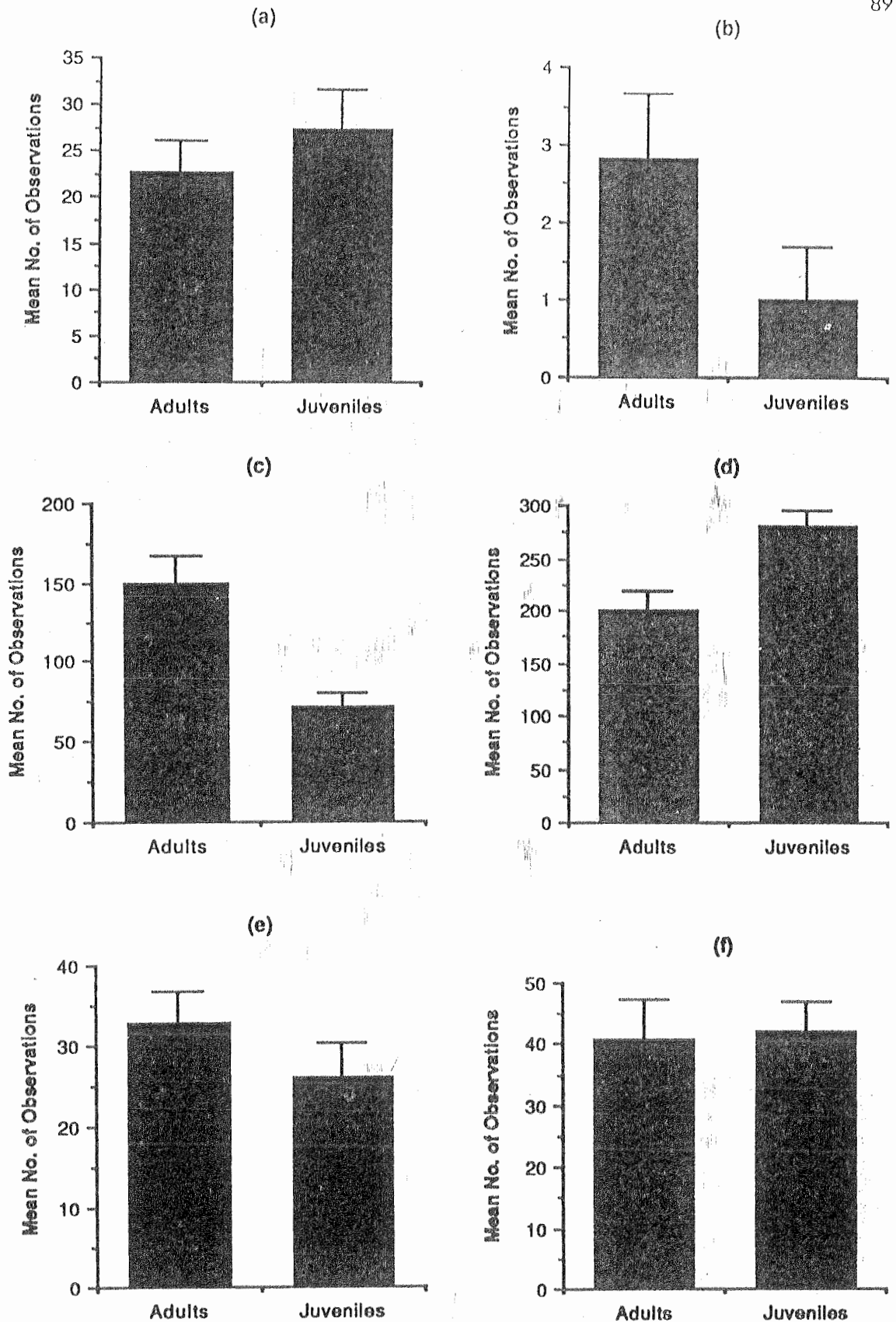
Figure 6.3.2 Mean (± one standard error) no. of observations of: a) feeding;
b) drinking; c) locomotion; d) resting; e) grooming and f)
investigative behaviour for adult (n=6) and juvenile (n=6) subjects

time engaged in resting.

Feeding showed a conspicuous peak during the initial stages of the activity period in both adults and young (Figure 6.3.3a) and a similar pattern was observed with respect to investigative behaviour (Figure 6.3.3b). Adults exhibited locomotory behaviour at a relatively constant level throughout the course of the activity period. Juveniles showed a similar pattern, albeit at a lower level, with the exception of a peak prior to returning to the nest box (Figure 6.3.3c). Juveniles were observed to rest more frequently than adults, particularly during the later stages of the activity period. The high levels of resting observed in both adults and juveniles at the onset and end of the activity period reflect the use of the nest box before and following periods of activity (Figure 6.3.3d). Juveniles exhibited an apparent peak in the levels of grooming during the early stages of the activity period, however this may have been the result of the unusually high levels exhibited by a single individual, as indicated by the high value of the standard error (Figure 6.3.3e). A similar peak in the grooming activity of juveniles was noted toward the end of the activity period. There was no clear pattern with respect to adult subjects.

6.4   Ontogeny of Morphological Traits

The development of external features has been documented in a number of macropodid marsupials (Dunnet 1962; Ealey 1967; Maynes 1972, 1976; Sharman *et al* 1964; Johnson 1978; Shield and Wolley 1960; Tyndale-Biscoe 1968; Poole *et al* 1982; Rose and McCartney 1982) and has served to provide a considerable amount of information valuable for the age-estimation of pouch young and juveniles. However, as Maynes (1976) has suggested, many of these studies are of limited value for comparative purposes, as no information is given for growth until the time when the animal attains its ultimate adult size. This situation is, to date, applicable to *Potorous tridactylus* and the need for extended examination of growth in this species is acknowledged.
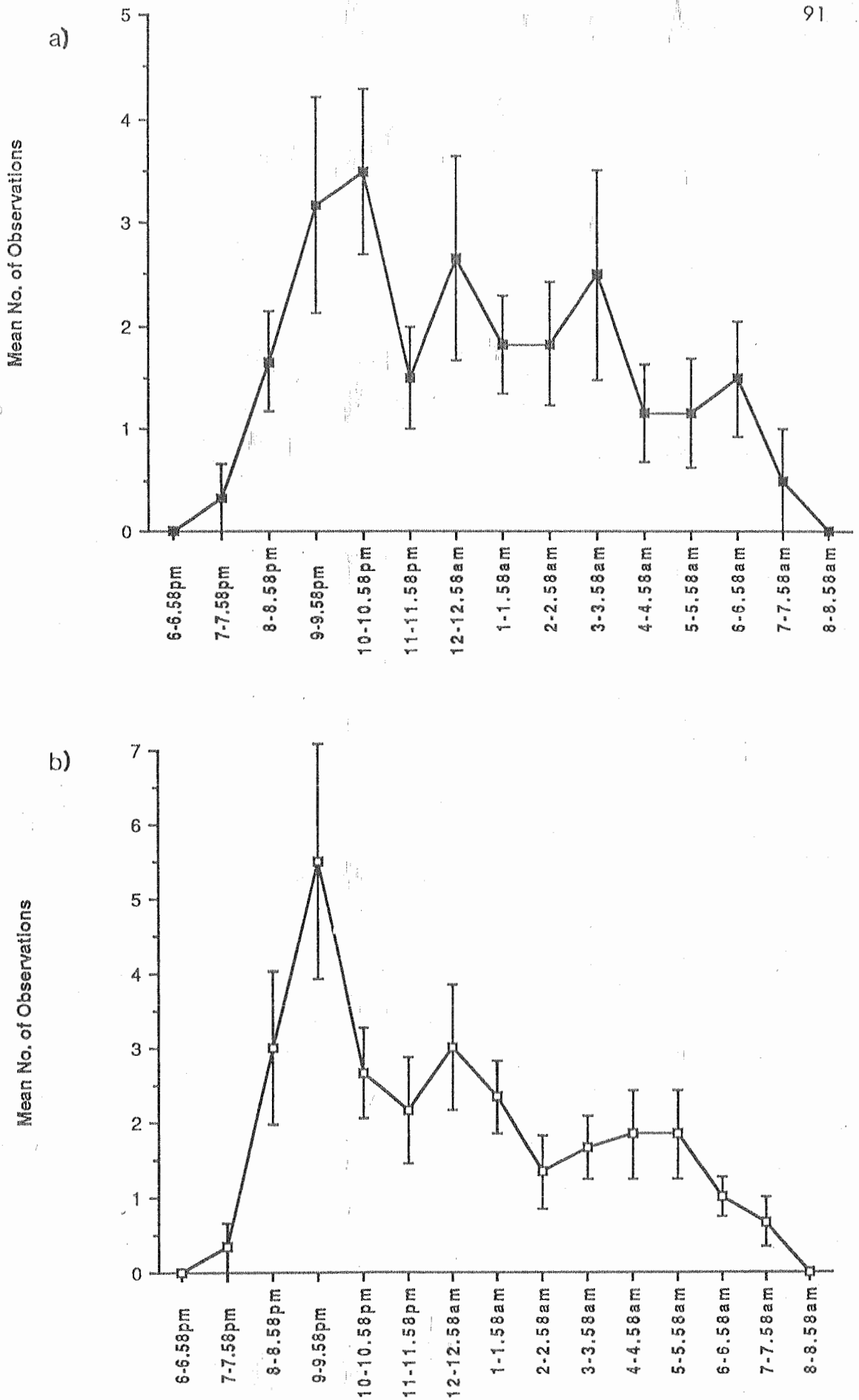
Figure 6.3.3a   Mean (± one standard error) no. of hourly observations(max=30) of feeding behaviour in: a) adult (n=6) and b) juvenile (n=6) subjects
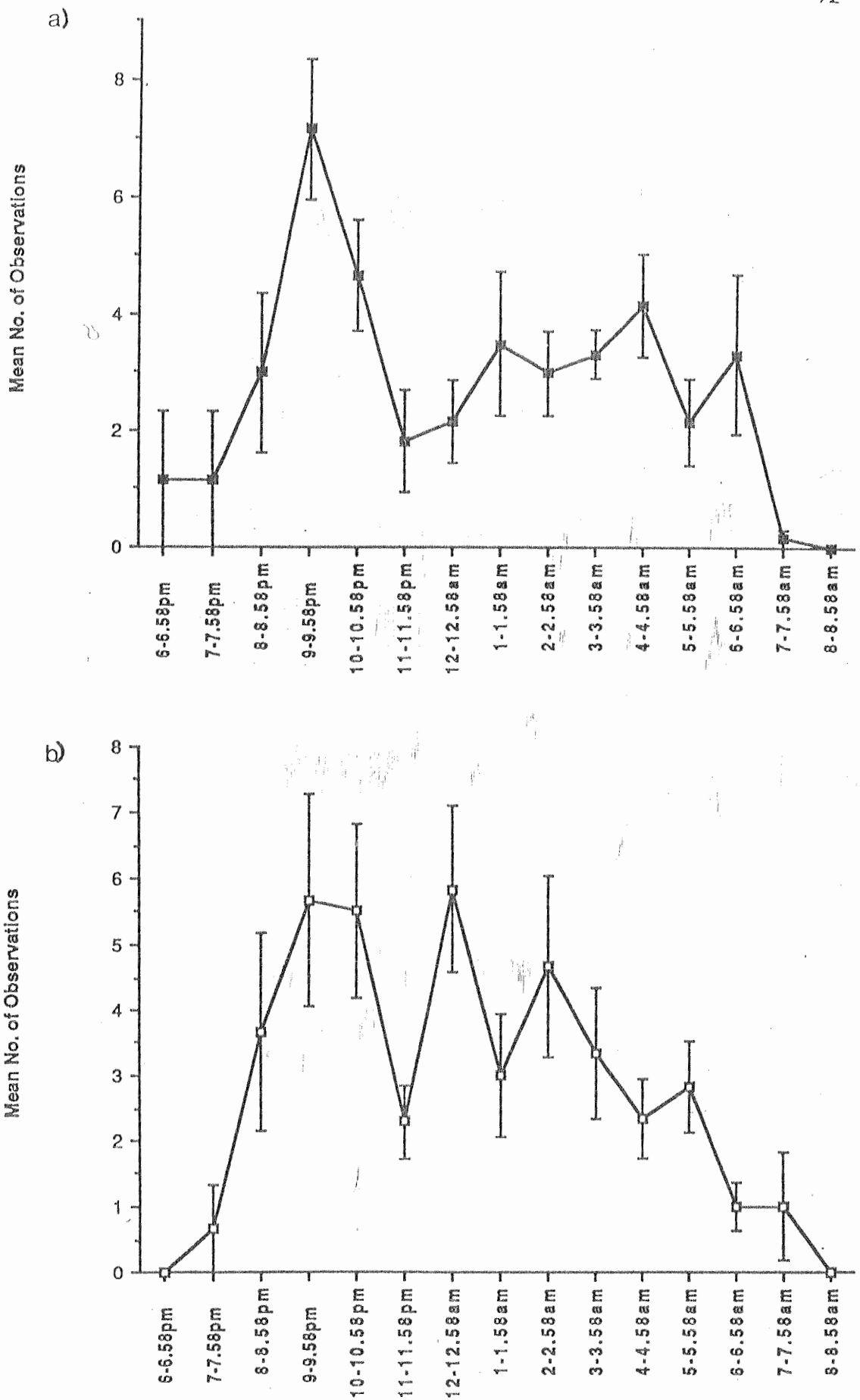
Figure 6.3.3b Mean (± one standard error) no. of hourly observations(max=30) of investigative behaviour in: a)adult (n=6) and b)juvenile (n=6) subjects
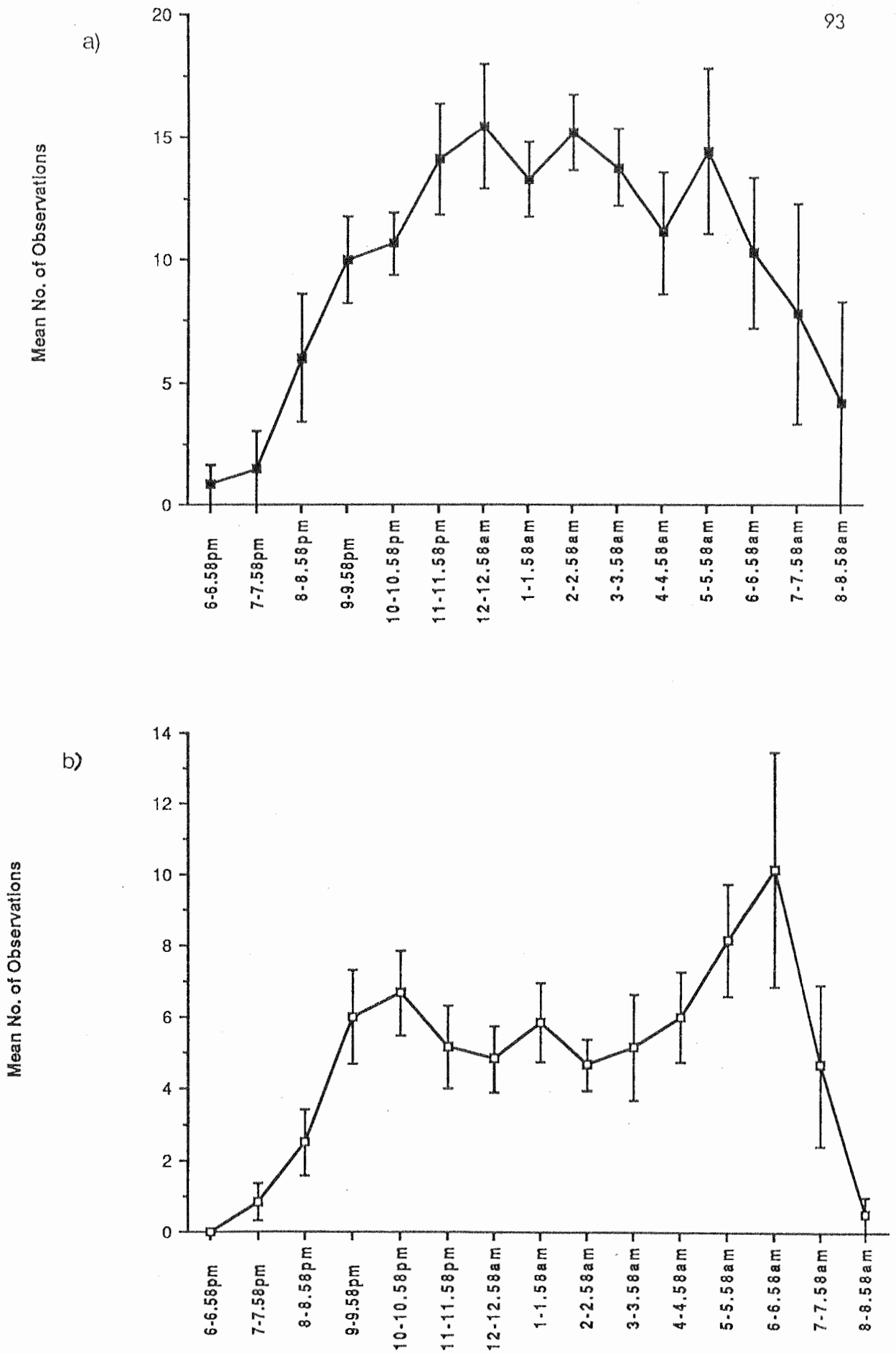
Figure 6.3.3c Mean (± one standard error) no. of hourly observations(max=30) of locomotory activity in: a) adult (n=6) and b) juvenile (n=6) subjects

Figure 6.3.3d   Mean (± one standard error) no. of hourly observations(max=30) of resting behaviour in: a) adult (n=6) and b) juvenile (n=6) subjects

a)

b)

Figure 6.3.3e   Mean (± one standard error) no. of hourly observations(max=30) of grooming behaviour in: a) adult (n=6) and b) juvenile (n=6) subjects

During the course of daily examinations of behavioural ontogeny, incidental observations of the development of a number of external features were made. All examinations were made with the aid of a 10x hand lens. In addition, measurements of head and pes lenths were obtained for subjects at regular intervals during the course of development. These provided a useful basis for comparison with the results obtained by previous investigators (Guiler 1960a; Hughes 1962; Heinsohn 1968).

6.4.1 Results

In agreement with Hughes (1962), several morphological features were noted at an earlier age than reported by Guiler (1960a). This was true of the eruption of hair over the general body surface and the eruption of the vibrissae, as well as the age at which the pinnae separated from the head. Other features, however, were noted at ages similar to those documented by Guiler (1960a), Hughes (1962) and Heinsohn (1968). These observations are summarised in Figure 6.4a. The length of the head increased linearly with the age of the pouch young and the length of the pes increased in a sigmoidal fashion, as has been previously described in this species by Bryant (1982). A similar pattern has been observed in other potoroid species (Seebeck and Rose, in prep.). The growth of the head and pes in young *P. tridactylus* is given in Figure 6.4b.

6.5 Discussion

The relatively advanced state of development of the forelimbs and head is one of the striking features of neonate *Potorous tridactylus*. The large size of these structures, relative to the hindlimbs, tail and ear, and, in addition, the presence of claws on the manus, serve to illustrate the precocial nature of those morphological features that are of functional significance in the journey from the urogenital opening to the pouch.

Following arrival to the pouch, the neonatal potoroo is able to attach to one of four teats. However, in the case of multiparous females, teat selection appeared be influenced by obstruction due to active or regressing mammary glands which
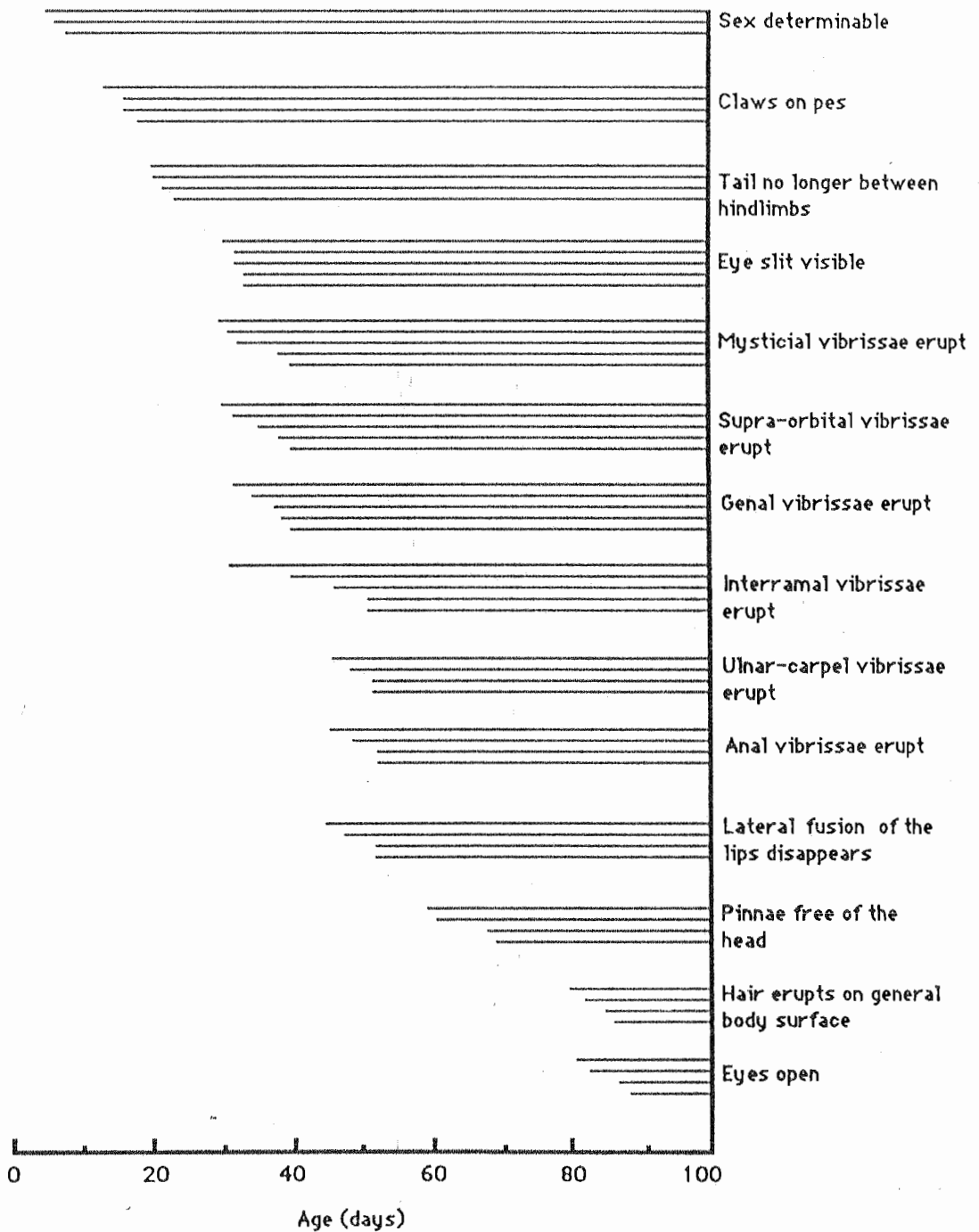
Figure 6.4a Summary of the ages at which morphologial features were first observed in captive *P. tridactylus*

Figure 6.4b Growth of the pes and head in captive *P. tridactylus*
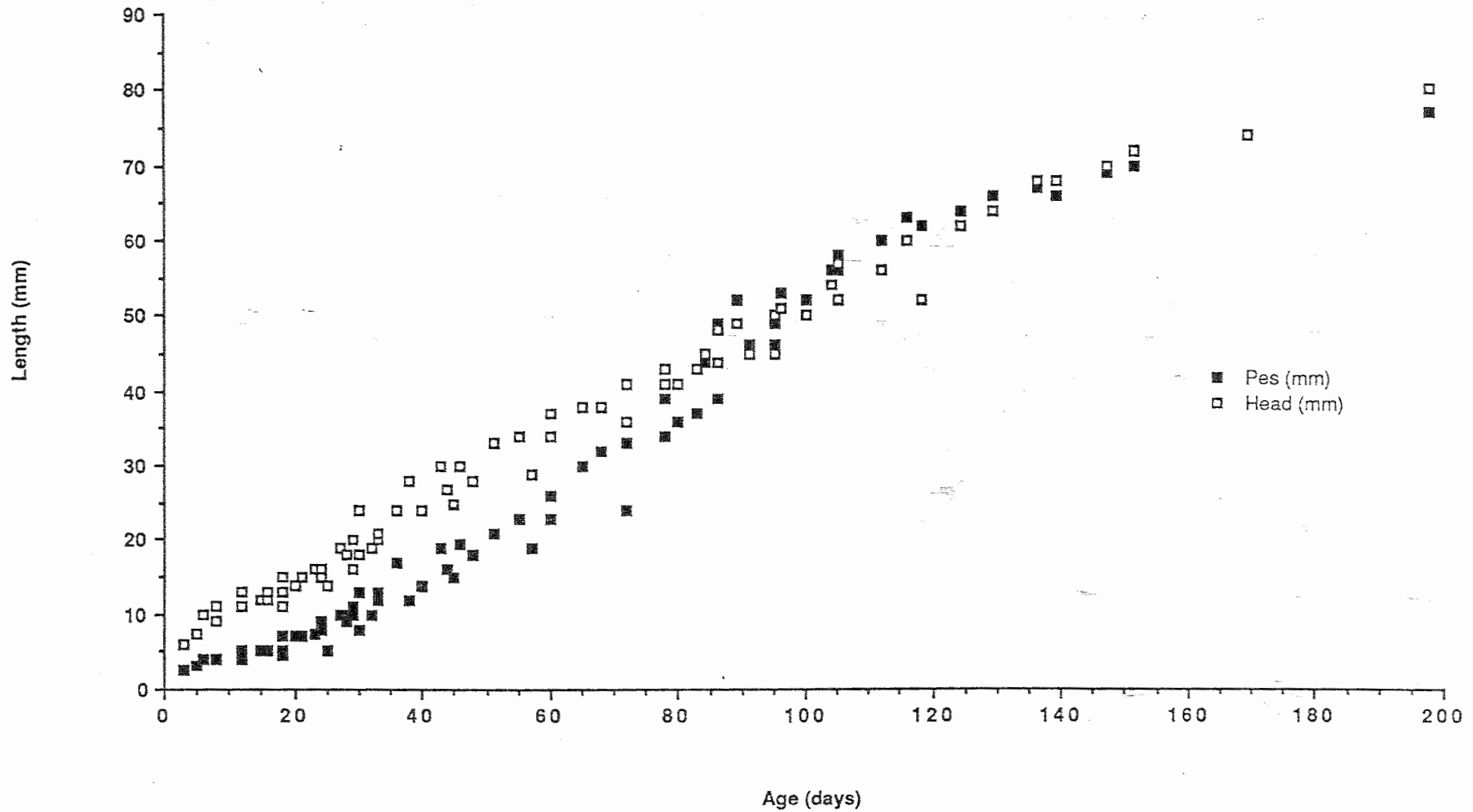
effectively limited the choice available. These observations are in agreement with the suggestion of Hughes (1962). Crowley (1984) noted a similar pattern of teat selection in *P. tridactylus*, however the number of observations she made was small. In studies of reproduction in *Macropus giganteus* and *M. fuliginosus*, Poole (1973, 1975) similarly found that obstruction by an active mammary gland precluded attachment to the other teat on the same side of the pouch. It would be of interest to determine the pattern of teat selection in *Hypsiprymnodon moschatus*, the sole macropodoid marsupial known to give birth to two young regularly.

Neonatal marsupials are equipped with several morphological features that enable them to secure the teat (Lillegraven 1975; Tyndale-Biscoe 1973). Hughes (1962) has described some of these in *P. tridactylus* and has suggested that the period of permanent attachment is an involuntary consequence of changes in the dimensions of the mouth, tongue and teat. Presumably in the potoroo, as in most marsupials, permanent attachment to the teat is largely the result of the expansion of the distal portion of the teat inside the mouth and an accompanying lateral fusion of the lips (Merchant and Sharman 1965; Tyndale-Biscoe 1973). It is not until the membrane that fuses the lips disappears that young are able to release the teat (Russell 1982).

The observation that the young potoroo is able to reattach spontaneously to the teat following dislodgement is in contrast to the reports of previous investigators (Wood-Jones 1923; Troughton 1943; Gasking 1965) who perpetuated the fallacy that removal of marsupial young from the teat results in damage to the fused lips and prevents reattachment. Ashman *et al.* (1975) addressed the issue in *Setonix brachyurus* and reported that dislodgement of young from the teat did not prejudice reattachment and subsequent survival. Similar observations have been reported in *M. rufus* (Sharman and Calaby 1964, Merchant and Sharman 1966), *M. parryi, Lagorchestes conspicillatus, Onychogalea fraenata* and *Wallabia bicolor* (Johnson 1981) during the course of cross-fostering experiments.

Hughes (1962) recorded the period of permanent attachment in *P. tridactylus* as extending over 64 days in one instance and 46 in another; however he considered the

latter to be an underestimate as the offspring subsequently died. The results of the present study revealed a period of permanent attachment of 60 days, which is comparable with the estimate given by Bryant (1982).

In agreement with the observations of Heinsohn (1968), audible sniffing was first observed in pouch young following the age of release of the teat. However, it is possible that the olfactory capabilities of the potoroo are developed well before this age, as has been demonstrated in *Dasyurus viverrinus* (Hill and Hill 1955) and *Didelphis virginiana* (McGrady, cited in Russell 1982). Furthermore, the olfactory nerve in neonate marsupials connects with the olfactory lobe and the nasal epithelium is endowed with sensory cells (Tyndale-Biscoe 1973). Several authors have suggested that olfactory stimuli assist in the navigation of the neonate marsupial toward the pouch (Frith and Calaby 1969; Tyndale-Biscoe *op.cit.*); nevertheless, the mechanism involved remains obscure (Russell 1982).

Although the potoroo is capable of regaining the pouch at 80-95 days of age, its inability to engage in effective locomotion prevents it from doing so unless the mother assumes reponsibility for closing the distance between herself and her young. Consequently, it is not suprising that the distress call is most consistently heard during the period of 70-100 days of age, when the young is incapable of effective forward progression and therefore must rely on the mother to close the distance between the two when the young is jettisoned from the pouch.

Rose and McCartney (1982) observed that the pouch young of *Thylogale billardierii* do not emit squeaking sounds until after they release of the teat. However, in the subjects observed in the present study, distress calls were noted in pouch young before the time of the initial release of the teat, as has also been reported in this species by Hughes (1962) and in *Macropus rufus* by Sharman and Calaby (1964). However, the call appears to be of little functional value until the young is at least 80 days old, as before this age the young is incapable of independently entering the pouch; furthermore, the mother appears to be incapable of rendering it aid to do so. It may be expected that during early pouch life the young is prevented from falling out by its

secure attachment to the teat; however, following the release of the teat there is a period of ca. 20 days during which time the young is likely to perish if ejected from the pouch. This was clearly demonstrated during the course of incidental observations made during the day. After the investigator had entered the observation enclosure during the course of routine feeding, one particular pouch-gravid subject was noted to exhibit signs of distress, such as displacement feeding, trembling and markedly increased levels of locomotory activity. During its attempts to escape the observer, its 73 day old offspring was jettisoned from the pouch. The investigator subsequently left the enclosure and entered a hide in order to observe the reaction of the mother to the distress calls of the young. Although the mother responded to these calls by approaching the young and adopting the upright bipedal posture which facilitates the entry of the young to the pouch, the young was insufficiently coordinated at this age to be able to effect re-entry. Furthermore, the mother made no attempt to assist the young back into the pouch. This situation continued for 20 min before the investigator considered it expedient to intervene. It is surprising that, despite their considerable manual dexterity, the adult potoroo, and indeed other macropodoids, do not exhibit an ability (or inclination) to be able to render the young assistance.

With the exception of the single initial journey from the urogenital opening to the pouch, the first encounter of a young macropodid with the external environment takes place when the head first protrudes from the pouch. Protrusion of the head from the pouch has been noted in several species, including *Macropus rufus* and *M. eugenii* (Russell 1973), *M. robustus* (Croft 1981b), *Thylogale billardierii* (Clancy 1982; Rose and McCartney 1982) and *Aepyprymnus rufescens* (Johnson 1980b), but was not a conspicuous behaviour of young *P. tridactylus* observed during the present study.

Protrusion was observed on only one occasion during the course of observations on adult females with advanced pouch young; in this instance, the young protruded its head slightly more than halfway from the pouch while the mother was resting in a bipedal posture. However, the young were frequently noted to protrude the nose and forelimbs (Section 5.3). As Hughes (1962) has suggested, this behaviour may facilitate

the circulation of air through the pouch. These observations are in disagreement with Kershaw's (1971) photographic representation of an apparently stuffed specimen of *P. tridactylus* with a young protruding its head ostentatiously from the pouch!

A number of authors have suggested that macropodid young develop food preferences during the period of protrusion of the head (Russell 1974, Poole 1975); however, no evidence of feeding by the young while the latter were within the pouch was noted in the present study. It is possible that the digging habits of *P. tridactylus* may result in soilage or injury to the young if it protruded its head while the mother was feeding. Further, the low suspension of the body and frequent use of quadrupedal locomotion in this species may prevent the young from protruding its head. It should be noted that the related species, *Bettongia gaimardi*, frequently exhibits bipedal locomotion; hence, it is perhaps not suprising that the young of this species often protrudes the head from the pouch (pers. observation). It is possible that the young potoroo develops food preferences through olfactory imprinting while within the pouch; however, there appears to be no information available on the olfactory biology of this species which might serve to substantiate this suggestion.

Maynes (1976) has suggested that there is considerable uniformity in the proportion of the adult body weight gained by macropodoid young at the time of permanent vacation of the pouch. The weight at the time of permanent vacation of the pouch in the young observed in the present study ranged from 17-21% of the maternal body weight. These are within the ranges quoted by Maynes (*op.cit.*) for other species. It is possible that at this stage of the development of the young the advantages accruing to it by longer periods of pouch occupancy are outweighed by the burden imposed upon the mother.

The low levels of locomotion exhibited by young *P. tridactylus* are perhaps suprising when compared with the high levels of locomotory activity described in numerous eutherian species. However, it is possible that this difference is related to the almost complete absence of "play" behaviour in the subjects observed in the present study. In contrast to adults, juvenile subjects frequently engaged in bipedal

locomotion. Although no quantitative record of the velocity of locomotion was obtained, it was apparent that juveniles moved with considerably greater speed than adults. This may have assisted the young in maintaining spatial proximity between itself and the mother. Further, in view of Dawson and Taylor's (1973) suggestion that the bipedal gait is an energetically-conservative form of locomotion, relative to the quadrupedal form, it may be considered that the extensive use of the bipedal hop by young potoroos is an adaptive behaviour which serves to reduce their energy expenditure.

Juvenile *P. tridactylus* were shown to spend a significantly greater proportion of the activity period engaged in resting behaviour, relative to adults. A similar observation has been reported in the same species by Buchmann (pers. comm.). It is possible that the high levels of resting behaviour in the juvenile are of adaptive value in reducing the risk of predation.

The temporal distribution of the behaviour of adult *P. tridactylus* over the activity period is consistent with the observations of Buchmann (in prep.). Interestingly, adults and juveniles exhibited considerable similarities in the temporal patterning of their behaviour. These observations suggest that there is a degree of synchrony in the behaviour of the mother and her offspring which might serve to maintain the mother-young relationship, at least until the young are of the age of 30-32 weeks. The temporal distribution of feeding behaviour was particularly similar in adult and juvenile subjects. The similar trend observed for investigative behaviour is possibly a result of the close temporal association between feeding and investigative activities.

CHAPTER 7

HOME RANGE AND HABITAT UTILIZATION

7.1 Introduction

The concept of "home range", as an aspect of the population biology of mammalian species, has been subject to a number of interpretations (Jorgensen 1968). Hayne (1949) has noted that certain areas within a home range may be more intensively used than others and, accordingly, has described a method for the delineation of such "centres of activity". In addition, several authors have drawn a distinction between home range and territory; the latter being defined as that area into which entry by conspecifics is excluded. The territory may comprise part or all of the home range and exclusion may be achieved through overt aggression, ritualized display or vacillation in approach-avoidance responses at varying distances from the geographical centre of the territory (Lorenz 1963; Hinde 1970).

There are a number of other usages of the term home range (Jorgensen 1968; Anderson 1982), however, the definition adopted in the present study is essentially equivalent to that proposed by several previous authors (e.g. Burt 1943; Stickel 1954), namely, a home range is "that area over which an animal normally travels in the pursuit of its routine activities" (Jewell 1966, cited in Russell 1974).

The size, shape and distribution of home ranges can be influenced by a large number of abiotic and biotic environmental factors, including temporal variations in population density, the recruitment and mortality of individuals (Blair 1940; Stickel 1954), seasonal variations in the availabilty of food supply and cover (Layne 1954) and the body size of individuals (McNab 1963; Lindstedt *et al.* 1986) and their metabolic requirements (McNab *op. cit.*; Mace and Harvey 1983).

Such factors undoubtedly militate against attempts to obtain an accurate estimate of the size of a home range. Additionally, the assumptions inherent in the methods employed to determine home range size have, in themselves, considerable effect on the obtained estimate (Section 7.2). As Stickel (1954) has noted, one might question the value of attempting "to measure anything as indefinite and variable as a home range" (p.1). Nevertheless, provided that caution is exercised in the extrapolation of results to

different areas at different times, an estimate of home range size provides useful information about the spatial relationship of animals with their environment and an indication of their interactions with other individuals.

As Russell (1974a,b) has emphasised, little is known of the home range and movements of macropodoid marsupials, particularly the smaller representatives of the superfamily. With respect to the larger species, information has been obtained for *Macropus rufus* (Frith 1964; Frith and Calaby 1969; Bailey 1971), *M. giganteus* (Kirkpatrick 1967; Grant 1973; Bell 1973; Kaufmann 1975), *M. robustus* (Ealey 1967; Russell and Richardson 1971), *M. parryi* (Kaufmann 1974a) and *M. antilopinus* (Russell and Richardson 1971; Croft 1982). Brief accounts are available for *Wallabia bicolor* (Edwards and Ealey 1975), *Petrogale inornata* (Dwyer 1972) and *Thylogale thetis* (Johnson 1980). *Setonix brachyurus* is one of the few small macropodid marsupials that has been investigated in detail (Dunnett 1962; Holsworth 1967; Nicholls 1971; Kitchener 1972, 1973). Among the Potoroidae, Sampson (1971) has studied the home range of *Bettongia penicillata* and Taylor (in prep.) has examined the spatial use of the environment of *B. gaimardi*.

The home range and habitat preferences of *Potorous tridactylus* have been described by Guiler (1958), Heinsohn (1968), Kitchener (1972) and Seebeck (1981) and these provide a useful basis for comparison with the results of the present study. The latter was undertaken with the initial aim of examining the relationship between the reproductive status of female *P. tridactylus* and the spatial use of environment, as well as patterns of juvenile dispersal. Unfortunately, insufficient data was obtained for female and juvenile individuals and consequently only brief and fragmentary comparisons were possible. Nevertheless, a considerable amount of information relevant to the examination of home range parameters and habitat utilization was obtained.

7.2 Description of the Study Site

A live-trapping program utilizing the capture-recapture method was conducted at Porter's Hill, Mt. Nelson (E.147° 23' S.42° 54') extending over a period of 8 months from August 1986 to March 1987. The area was approximately 62ha and comprised a number of plant-assocations typical of dry sclerophyll forest in the later stages of regeneration following fire (A. Duncan, pers. comm.). Porter's Hill has suffered from three major fires within the past 20 years, the most recent having occurred in 1979 and resulting in a reduction of the density of the canopy of the dominant *Eucalyptus* spp. In addition, the 1974 - 83 drought has been indirectly responsible for proliferation of drought-resistant species, particularly *Casuarina* spp.

The dominant plant associations comprised largely *Eucalyptus* and *Casuarina* spp. The southerly aspect was dominated by *E. globulus* with an understorey of *Casuarina stricta* and *Leptospermum scoparium* tending to be replaced by *E. viminalis* and *E. pulchella* with an understorey of *Bedfordia linearis* and *Salicina tasmanica* in the drier regions. The dry eastern and south-eastern slopes supported an open association of *E. linearis* and *E. viminalis* with an understorey of *Exocarpus cupressiformis*, *Bursaria spinosa* and *C. stricta*. The dry and rocky northern slopes were dominated by dense strands of *C. stricta*, interspersed with open areas of *Acacia dealbata* and *A. mollisima*.

Several areas of open grassland, comprised largely of *Poa* spp., *Lepidosperma* spp. and *Lomandra longifolia*, occurred within the study site. A number of species of shrub were widespread, including *Dodonaea viscosa*, *Astraloma humifusum*, *Eparcris impressa* and *Correa speciosa*. Kitchener (1973) has reported that the area supports several species of fungi of the order Agaricales.

The study area was characterised by shallow, impervious soils based on a dolerite bed-rock. A number of temporary ponds and a narrow temporary creek provided the only free-standing bodies of water; the latter, however, was outside the area that was used for trapping. Several fire-breaks transected the northern sector and an

unimproved road extended along the north-western slopes toward a private residence situated at the summit of the hill

The north-eastern extremity of the study site was demarcated by an area of cleared pasture. The eastern to south-eastern boundaries were adjacent to cleared land and suburban development. The western border of the study site was comprised of a dense strand of *E. globulus* which dominated the ridge leading to Mount Nelson. This region constituted the only virgin tract of land which bordered the study-site.

7.3 Home Range

7.3.1 Methods of Trapping and Determination of Home Ranges

The traps used in the present study were identical to those described in Section 3.1. They were positioned at 15-35 m. intervals along approximately straight-line tracks, each comprising either 10 or 20 traps. Individual lines were trapped for between six and eight nights, yielding a total of 120-160 trap nights per line. The traps were then relocated along adjacent lines. The distance between each line ranged from 45 -100m.

The repeated relocation of traps resulted in a total of 306 trap stations being distributed across an area of 35 ha. The position of each trap station is shown in relation to altitude and slope in Figure 7.3.1.

The practice of relocating traps across the study area was necessitated by considerations of availability and the need for adequate coverage of the area. Unlike studies which employ a grid system with permanently positioned traps, the present design was not suitable for the valid assessment of a number of population parameters, such as temporal variations in range lengths. However, the present design may be expected to compensate for problems such as differential trap-responses. Guiler (1958) has suggested that *P. tridactylus* does exhibit negative responses to traps over successive captures and has recommended the use of short-term trapping programs as a means of alleviating such potential sources of bias.

Captured potoroos were restrained in hessian bags and marked on the right ear

Figure 7.3.1   Aerial orthophotographic map of the Porter's Hill study site, showing the spatial distribution of trap stations. Numbered stations refer to the position of each trap with respect to the trap line. Contour interval on the overlay is 10m. Scale: 1:5000

with both a numbered tattoo and a numbered fingerling tag (Section 3.2). The combined use of these two methods proved effective in the identification of all individuals at subsequent recaptures and did not appear to result in mortality or other deleterious consequences. Measurements of head, pes and ear length were taken, using the methods described in Section 3.2. General notes were made on the presence of ectoparasites, apparent injury or loss of fur and, in the case of females, the condition of the pouch and the presence or absence of pouch young. The latter were measured and aged by the methods described in Section 3.2. In order to minimize the risk of pouch-gravid females ejecting their young, the latter were returned to the pouch following examination and gentle pressure applied to the sphincter muscle of the pouch opening, as recommended by Buchmann (pers. comm.). In addition, pouch-gravid females were left within the hessian bag and allowed to emerge spontaneously. All individuals were released at the sites of their capture.

During the initial stages of trapping, a record was maintained of the direction in which individuals moved following release. However, one released individual was observed to travel along a wide and circuitous route which resulted in the animal travelling in the opposite direction to that originally observed. In areas of dense vegetation such changes in direction would generally go unnoticed. It was considered that the animals would be disorientated following their release from the restraining bag. Moloney (1982) reported that the direction followed after release was highly variable and lacked any clear trend. For these reasons, it was considered that the direction in which an individual moves following its release is of little value in determining trends relating to movement toward the geographical centre of the home range or the nest site.

Several techniques are available for demarcating the boundaries of a home range (e.g. Stickel 1954; Hayne 1949; Anderson 1982). Stickel (*op. cit.*) has suggested that the "exclusive boundary strip" method provides the most accurate estimate of the size of a home range. However, due to the irregular positioning of traps and the fact that a number of the observed home ranges extended beyond the limits of the study area, this

method was not employed. Instead, all estimates of home range made in the present study were based on the minimum area method (Stickel *op. cit.*), which involves connecting the outer most points of capture to form a convex polygon. While this method provides a conservative estimate of the size of a home range, it does conform with the limitations of the present design and does permit several valid conclusions to be drawn. In addition, the mean range length for each individual was calculated, based on the average of the distances between successive captures.

Regardless of the method adopted for demarcating the home range, there remain several factors which need to be considered when interpreting estimates obtained from capture-recapture studies. Many authors disregard occasional sallies which take the animal well beyond the "borders" of the home range (Burt 1943; Stickel 1954), while other authors incorporate such forays within the "total range" of the animal (Hayne 1949; Johnson 1980). As Stickel (*op. cit.*) has noted, extended movements may result in the invasion of depopulated areas and therefore the extension of the range of a species. Following the recommendation of Burt (1943), extensive forays were not included in the determination of the home range of *Potorous tridactylus*.

By definition, a home range can only be determined for individuals which are resident within a study area. Many studies employ the criterion of repeated capture over a relatively long period of time as a necessary prerequisite for the accurate determination of home range (e.g. Sampson 1971). For the purposes of the present study, an individual was deemed to be a resident if it was captured on at least five occasions. In addition, the interval between the initial and final capture of an individual was required to exceed one month before residency was assumed. While these criteria may appear to satisfy the requirements described above only minimally, they were considered to be adequate on the basis of the following rationale: because only a small sector of the entire study area was trapped at any one time, it is reasonable to assume that if an individual was captured within that, or adjacent sectors on at least five occasions, then that individual was unlikely to be exhibiting the nomadic tendencies of a transient individual. Furthermore, individuals which were deemed to

he residents exhibited no apparent signs of poor condition ectoparasitic infestation or physical injuries. A single exception was a large (1650g) male which was noted to possess considerable damage to the pinnae of the ears and relatively high numbers of ectoparasites. However, this individual was captured on 14 occasions over a period of five months. The criteria for residency or transcience were selectively applied in order to permit an estimate to be made for one of the few females trapped in the area. The home range for this individual was calculated on the basis of only four captures; however it was captured in the same area over a period of five months.

The validity of the estimate of a home range is affected by the spacing of traps (Stickel 1954) and the response of the species (or individuals) in question (Balph 1968). Furthermore, several assumptions are inherent in the use of the capture-recapture method to estimate home range, *viz* the probability of capture on encountering a trap is high and constant throughout the home range; the trapped area is as large or larger than the home range, the frequency of capture at a particular trap site reflects the frequency of visits to it by the animals and each animal has an equal chance of being captured upon encountering a trap (Lehner 1979) The extent to which these assumptions were considered to be valid is discussed below.

7.3.2 Results

A total of 123 captures of *P. tridactylus* were obtained in the course of 3116 trap nights, yielding a success rate of 3.95%. There was an increase in the number of captures during the summer months (X^2 =38.1; d.f.=7; p <0.01), as shown in Figure 7.3.2a. The ratio of males:females was 3.4.

A total of 17 male potoroos were captured over the period of trapping. The number of recaptures of each of these ranged from 0-15 (mean=5.35±1.08). On the basis of the criteria outlined in Section 7.3.1, ten male potoroos were deemed to be residents and home ranges for each of these were estimated by the minimum area method previously described. These resident males were recaptured on average, 8.3 times. The mean area of the home range of male *P. tridactylus* was estimated to be 4.36±0.95 ha (range =

1.03 - 9.79 ha) and, not unexpectedly, the areas of the home ranges were highly correlated (Pearson's r = 0.951; d.f.=18; p<0.0001) with their circumference (mean=909±105m; range=479-1431m). There was a considerable overlap between the home ranges of males (mean=62.2±7.7%; range= 26.8-100%). There was no significant correlation between the weight of resident males and the area of their home ranges, nor the degree of overlap between their home ranges.
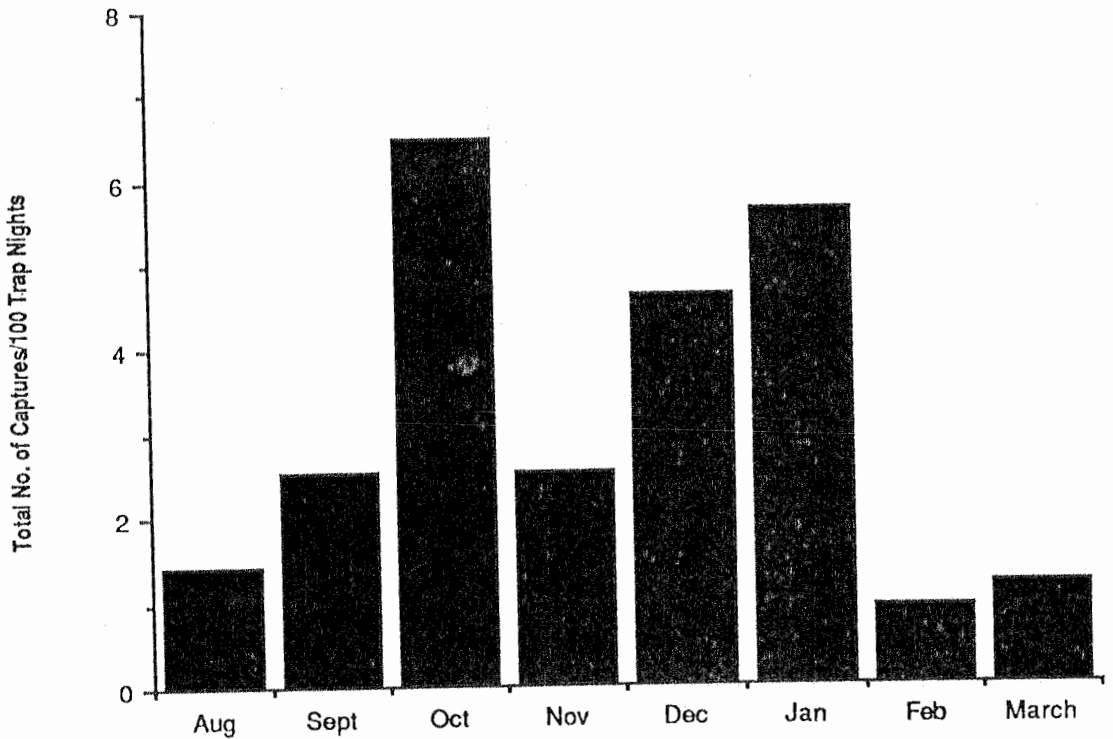
Figure 7.3.2a   Total number of captures obtained per 100 trap nights in each month of the trapping program

The mean range length of the resident males was 130±11m (range 0-593; n=80), whereas that of the transient males was 157±37 (range 31-313; n=8). Although one might expect the range lengths of transients to be considerably greater than those of resident individuals, the use of unpaired Student's t-tests indicated no significant differences. However this may have been due to the small number of range lengths estimated for the transient group.

As previously mentioned, only one female was captured on a sufficient number of occasions to permit an estimate of the size of home range to be made. The area and circumference of the home range of this individual were 0.93ha and 496m, respectively, considerably smaller than those obtained for males. However, it should be noted that this estimate was based on only four captures and is therefore likely to be an underestimate. The overlap between the home range of this animal and those of adjacent males was 74%. The mean range length of this female was 152±30m (range 117-212, n=3). Only four other females were captured during the period of trapping, but none of these were captured more than twice. The mean range length of these transient females was 267±160m (range107-428; n=2). Unfortunately, insufficient data precluded the possibility of determining variations in the range length of pouch-gravid females in relation to the age of their young

At the time of their capture, all females carried pouch young which varied in age from 42 to 85 days. On one occasion, a female was trapped with her recently weaned young. The estimated age of the latter was 140 days, suggesting that the young may remain in close association with the mother, at least until this age. Another individual was observed to be carrying twins of 38 and 86 days of age. The occurrence of twins among macropodoid marsupials is not a common phenomenon and, to the best of the knowledge of the author, has not been previously reported in free-living *P. tridactylus* (see Appendix B).

The estimated population density, based on the number of male and female individuals captured within the area delineated by the traps, was 0.31/ha in resident individuals and 0.63/ha in all individuals combined. The population parameters estimated for *P. tridactylus* during the course of the present study are given in Table 7.3.2, in relation to estimates obtained by previous investigators. The spatial distribution of the home ranges of all resident individuals is shown in Figure 7.3.2b.
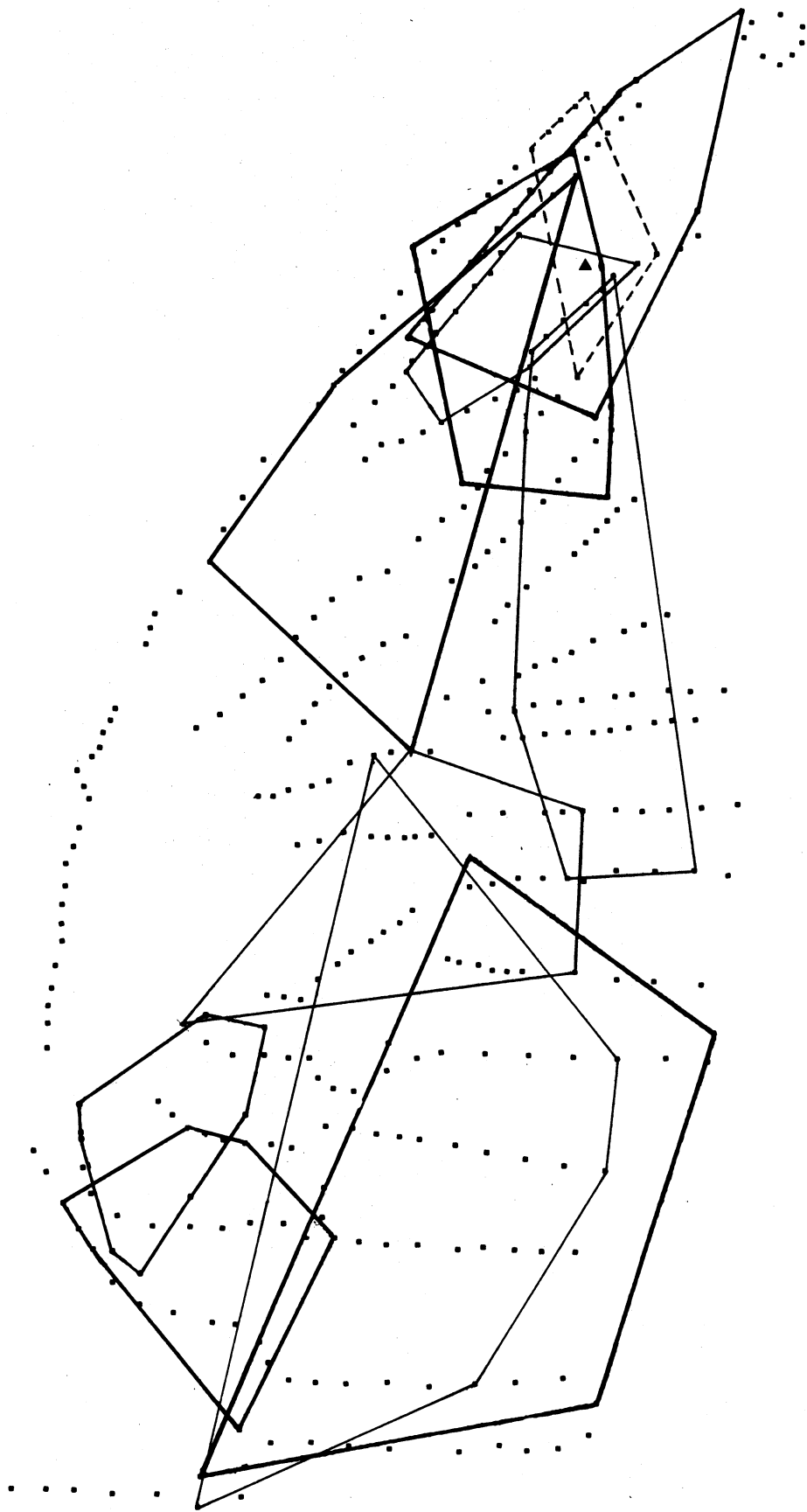
Figure 7.3.2b   The spatial distribution of estimated home ranges in males

(solid lines) and in a female (broken line) .   Symbol (▲)

refers to location of a nest site
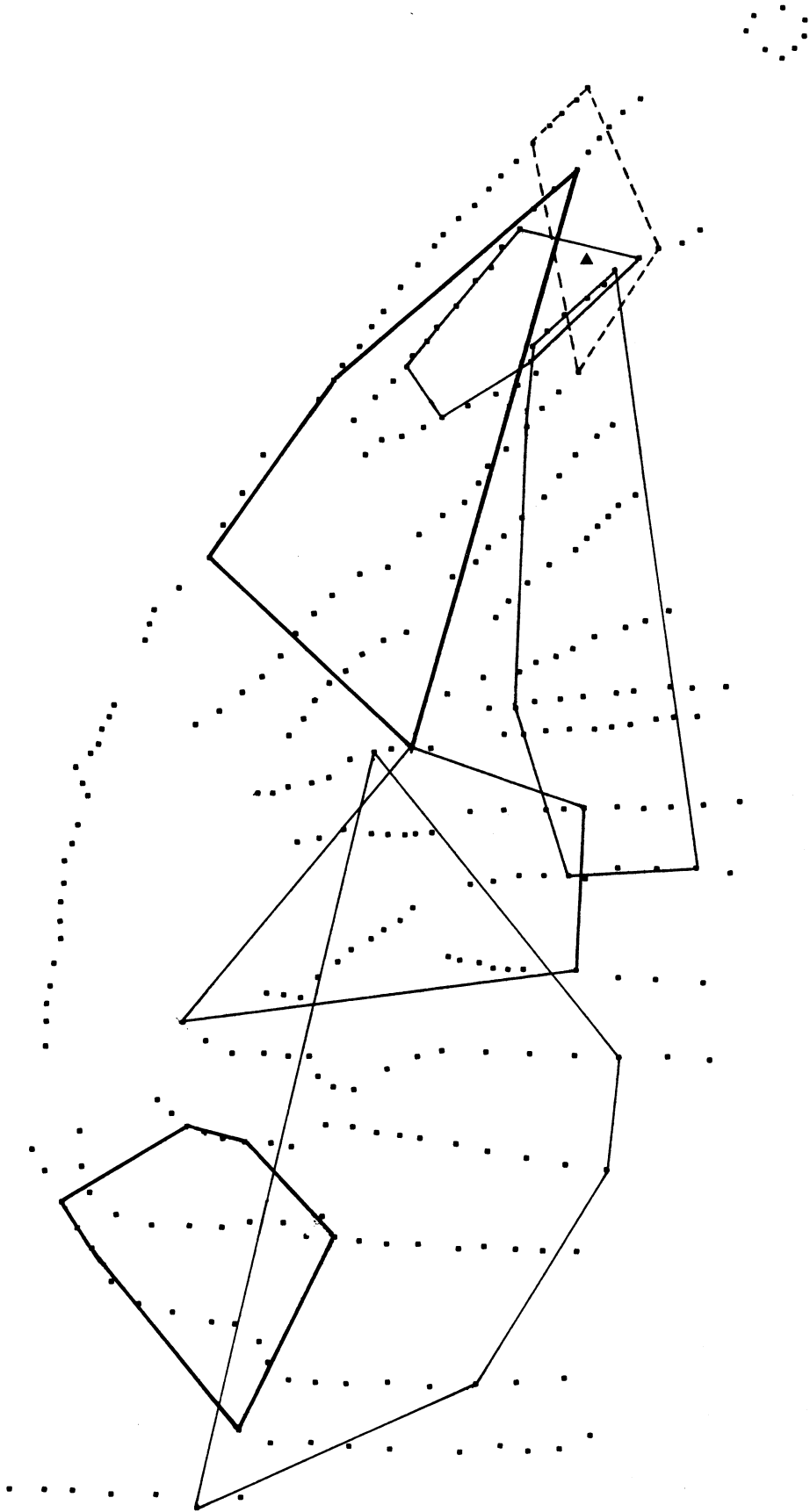
Figure 7.3.2b   The spatial distribution of estimated home ranges in males
(solid lines) and in a female (broken line)   Symbol (▲)
refers to location of a nest site

Table 7.3.2 Summary of the population parameters of *P. tridactylus* observed on Porter's Hill in relation to the estimates of previous investigators who have also used this site. Values given for the present study refer to mean ± one standard error and range (in brackets) (M=male; F=female).

Source		No. of resident individuals captured	Mean area of home range (ha)	Mean circumference of home range (m)	* Mean range length (m)	Density (Individuals /ha)	% overlap of home ranges
Present study	M	10	4.36±0.94 (1.02-9.79)	909±105 (479-1431)	130±11 (0-593)		62.6±7.7
						} 0.31	
	F	1	0.94	469	152±29 (117-212)		74
Guiler (1958)	M	25	-	-	-		-
						} 2.5	
	F	18	-	-	-		-
Kitchener (1973)	M	5	19.4 (12.0-34.4)	-	-		
						} 0.19	"considerable"
	F	5	(2.0-11.5)	-	-		

*including transient individuals

With the exception of the ubiquitous brush-tail possum, *Trichosurus vulpecula* which was captured on 100 occasions (excluding recaptures), the only other small marsupial common in the area was the brown bandicoot, *Isoodon obesulus*, which was captured on 144 occasions (excluding recaptures). This latter species had a density of 0.55 resident individuals/ha over the entire study area. This is considerably higher than the estimate obtained for *P. tridactylus* and presumably reflects the smaller home-range of *I. obesulus* (mean= 2.5 ha and 1.3 ha for male and female individuals, respectively: P. Clunie, pers. comm.).

Barred bandicoots, *Perameles gunnii*, were captured on only four occasions and the

ringtail possum, *Pseudochirus peregrinus*, was captured on a single occasion; presumably the strict aboreal habits of the latter species were not conducive to its capture in traps set at ground level. The most frequently captured eutherian species were rodents, particularly the black rat, *Rattus rattus*. Rabbits, *Oryctolagus cuniculus*, although abundant in the area, were captured on only three occasions. The native cat, *Dasyurus viverrinus*, was not captured but was known to occur in the area (Dorney, pers. comm.). Domestic dogs and feral cats were known to frequent the study site and were presumed to be responsible for the disturbance of traps on a large number of occassions. Several species of bird and reptiles, including the tiger snake, *Notechis ater*, were infrequently captured. A comprehensive summary of all of the captures sustained is presented in Appendix A.

As previously suggested, the calculated estimate of home range may be influenced by a number of considerations. The areas of the home ranges estimated for both male and female individuals in all cases were considerably larger than the spacing between trap stations thereby satisfying one of the criteria proposed by Stickel (1954) for the accurate determination of the size of home ranges. However, a significant proportion of the borders of the home ranges of four animals coincided with the borders of the area trapped; thus the estimates obtained for these individuals may be expected to be a conservative measure. With the exception of one individual, it was not considered that the home range of these animals would extend very much further, as the area 30-140m beyond the boundary of these home ranges comprised either open pasture or urban development. Nevertheless, the limited number of captures obtained for several resident individuals, in addition to the use of the minimum area method for the demarcation of home ranges, would presumably result in conservative estimates of the area of home ranges.

As was observed by Guiler (1958), *P. tridactylus* appeared to exhibit a negative trap response. There was a noticeable decline ($X^2 = 16.953$; d.f. $= 7$; $0.01 < p < 0.02$) in the number of captures obtained following the first night of trapping in each new line, as indicated in Figure 7.3.2c.
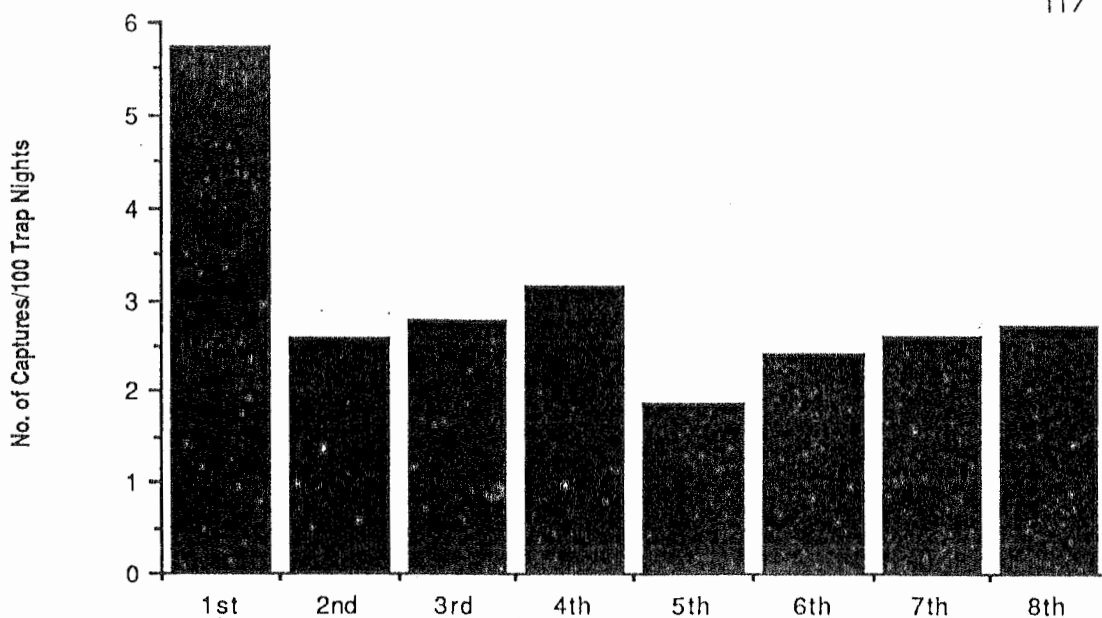
Figure 7.3.2c Numbers of captures obtained per 100 trap nights during successive nights (1-8) of trapping along each trap line

7.4 Habitat Utilization

7.4.1 Methods

The habitat utilization of *Potorous tridactylus* was examined by calculation of the number of captures per 100 trap nights with respect to three vegetational dimensions.

The vegetational parameters considered were:

1. Density of Canopy

This was determined by allocating the percentage cover of the canopy of dominant species into three arbitary categories: open, moderate and dense. No attempt was made to distinguish between dominant species, however these were almost invariably either *Eucalyptus* spp. or *Casuarina stricta*, as described in Section 7.2.

2. Percentage Ground Cover

An index of percentage ground cover was created by determining the amount of dead and living plant material of less than ca. 0.5m in height which covered the substrate. In most areas, the ground cover comprised *Poa australis* and *Lepidosperma* spp., although dense layers of leaf litter, fallen branches, bark and logs were also used.

The amount of this material that was present within a 2m radius of each trap station was allocated to one of four categories -: 0-25%, 25-50%, 50-75% and 75-100%.

   3. Structural Density

This parameter provided an indication of the density of the undergrowth. It was calculated on the basis of the number of vertical structures of greater than 1m in height within a 2m radius of the trap station. These structures included the trunks of the dominant *Eucalyptus* and *Casuarina* species, as well as all shrubs, as described in Section 7.2. The obtained values were allocated to one of five arbitary categories:

        1 - 0-4 vertical structures

        2 - 5-8 vertical structures

        3 - 9-12 vertical structures

        4 - 13-16 vertical structures

        5 - > 16 vertical structures

7.4.2 Results

The results for each vegetational parameter are presented in Figure 7.4. There was no clear relationship between the number of captures obtained and the density of the canopy. With respect to the percentage ground cover, larger numbers of captures were made in areas comprising less dense cover; however, the differences were not significant. Significantly higher numbers of captures were obtained in areas of high structural density than in areas of low structural density (X^2 = 10.265; d.f. = 4; $0.02 < p < 0.05$). Few captures of *P. tridactylus* were obtained in an area of open woodland which extended between the trap stations of line 901-910 and 1011-1020 (c.f. Figure 7.2). It should be noted that the two largest home ranges observed in the present study were included in this area. In addition, one individual was captured once during a total 56 trap nights in an area which had recently been burnt.
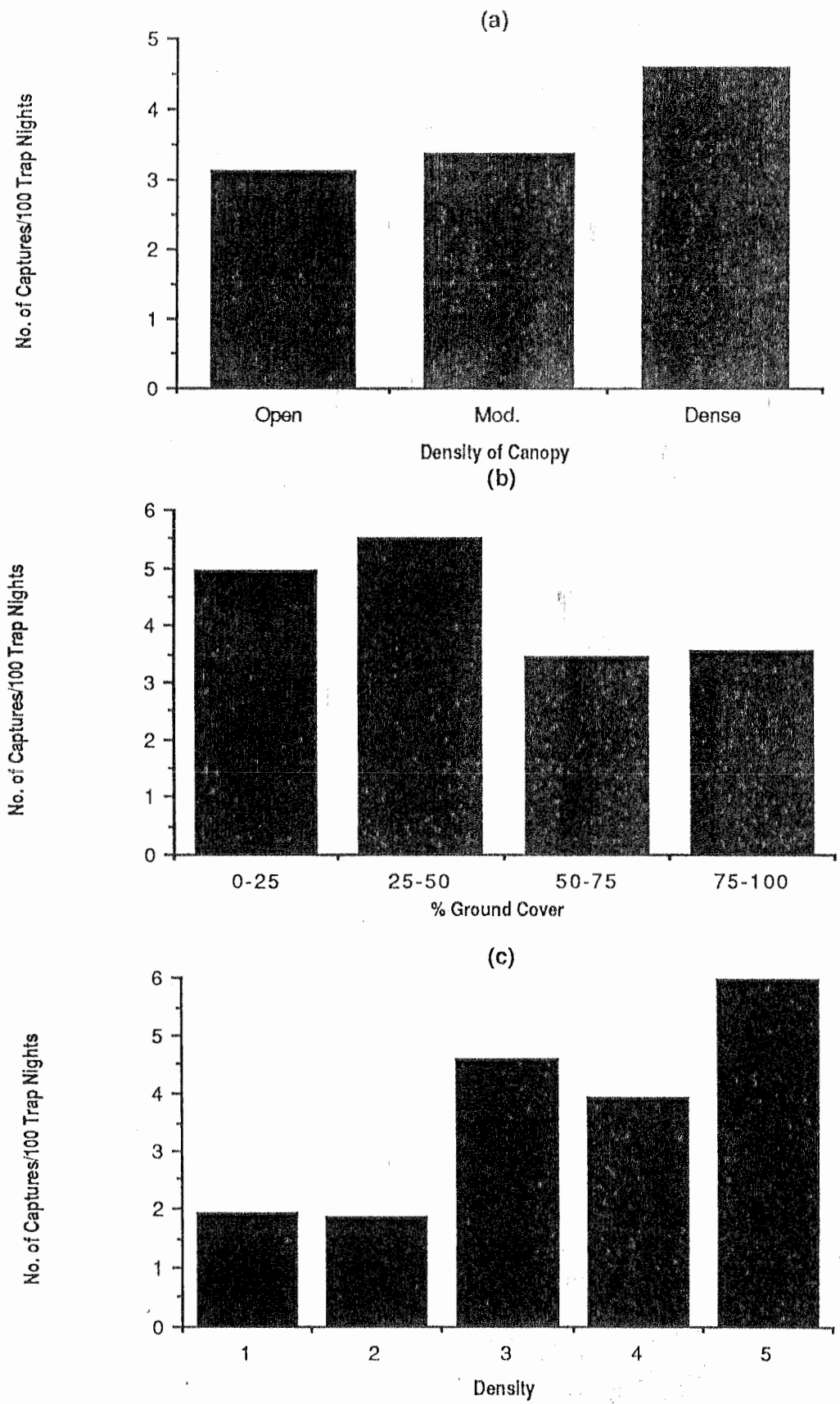
Figure 7.4   Numbers of captures of *P. tridactylus* obtained per 100 trap
nights with respect to a) density of canopy; b) percentage
ground cover; c) structural density. See text for definition of
each vegetational parameter

7.5 Discussion

Home range has been defined as that area which an animal becomes familiar with during the course of its routine activities and, as such, may be considered to confer considerable adaptive advantage to that animal. The value of familiarity with an area in the ability of an animal to escape predation has been elegantly demonstrated by Metzgar (1967) who has shown that mice (*Peromyscus leucopus*) which are familiar with an environment are more successful in escaping predation by screech owls than are mice without any such experience in the same habitat. If, as Heinsohn (1968) has suggested, *Potorous tridactylus* is susceptible to predation from a variety of raptorial birds, then one can envisage the importance of the home range of this species. Further, familiarity with an area provides distinct advantages to the animal's ability to locate potential food sources and nest sites (Ewer 1968b).

The area of the home range may be considered to reflect the food requirements of a species. As McNab (1963) has suggested, the size of the home range is influenced by the energy requirements of animals, which in turn is related to their size. However, the area over which the animals forage is limited by the metabolic demands of locomotion.

As indicated in Table 7.3.2, the size of the home ranges of both male and female *P. tridactylus* were considerably smaller than those that had been previously described for the same species in the same area by Kitchener (1973). It is possible that these differences reflect the conservative estimate obtained in the present study. However, the discrepency may also be attributable to the higher population density calculated for the animals observed in the present study. Kitchener (*op cit*) gave an estimate of population density as 0.19 animals/ha for resident individuals, which is somewhat lower than the estimate obtained in the present study (0.31 resident individuals/ha). In addition, Guiler (1958) has reported a population density of 2.5 individuals/ha on Porter's Hill and a density of 12 individuals/ha at Stewart's Bay, Tasman Peninsula. However, he did not state whether these estimates were obtained for resident

individuals only or for transients and residents combined. If his estimates do apply to both resident and transient individuals, they are still considerably higher than the comparable values presented by Kitchener (*op. cit*) (1.02 individuals/ha) and the present study (0.62 individuals/ha). In a study of a population of *P. tridactylus* in Victoria, Seebeck (1981) reported a population density "nearly ten times as high" as that given by Kitchener (*op.cit*), however, the former author did not state whether the estimates were based on resident individuals only. Although Seebeck's (*op.cit*) estimates can not be considered to be comparable with those obtained by Guiler (*op. cit.*), Kitchener (*op. cit*) and the present study, it is nevertheless clear that density estimates of *P. tridactylus* have been highly variable.

The variations in the estimates of the population density of *P. tridactylus* on Porter's Hill which have been observed in each of the three studies mentioned above may be a reflection of the various changes which have occurred in the area. The region has experienced a considerable expansion in the degree of urban development in the 30 years which have elapsed since Guiler's (1958) survey. The reduction in the area of adjacent natural bushland has presumably limited the number of routes by which animals can enter or leave the area. In addition, the increase in the population of domestic dogs and cats which invariably accompanies increased urbanisation has undoubtedly resulted in increased predation pressure on the local native fauna. Furthermore, Porter's Hill suffered from the effects of major fires in 1967, 1972 and 1979. These, and a severe drought which lasted from 1974-1983, have been responsible for a number of deleterious effects on the vegetation which, in turn, may have influenced the local fauna. It is possible that the relatively higher population densities recorded by Guiler (1958) at Porter's Hill and by Seebeck (1981) in Victoria are representative of less disturbed areas.

It is difficult to account for the small number of females which were captured during the course of the trapping program. It is possible that there is a sex difference in trap response, as previous investigators (Guiler 1958; Heinsohn 1968) have reported disparities in the numbers of males and females captured. As previously mentioned,

the present trapping program yielded 17 males and five females which were recaptured 91 and 32 times, respectively. If females do show a negative trap response to a greater degree than males, then one might expect this to be reflected in a lower number of recaptures obtained for females relative to the number of individuals of each sex. However, this was not the case. It is, of course, possible that there were fewer females in the area. Alternatively, it may be suggested that the observed disparity may reflect the limited movements of the females relative to the more wide-ranging behaviour of males.

The small size of the home range of the resident female, relative to that of the males, is in agreement with the results obtained by Kitchener (1973) and Buchmann (unpublished data). This sex-related difference cannot be solely attributed to differences in body weight, as sexual dimorphism is not pronounced in this species. Nevertheless, several other factors may account for the difference, including the wide ranging behaviour of males in their attempts to locate potential mates. Conversely, it is possible that the metabolic demands of lactation act to reduce the range of females. If both, or either, of these factors do influence the size of the home range, then one would not expect the dimorphism of home range size to vary seasonally, since *P. tridactylus* breeds continuously throughout the year. However, the size of the home ranges of females may show variations during the reproductive cycle.

Guiler (1958) has suggested that the distribution of individuals is not homogenous and that certain areas have high densities. A comparable phenomenon was noted on the northern slopes of the present study site and may be attributable to variations in the distribution of food sources. Interestingly, the home range of the only resident female also occurred in this area and was overlapped by the ranges of five males (Figure 7.3.2b).

In a study of the home range of *P. tridactylus* in an area of heath in north-western Tasmania, Heinsohn (1968) has observed that the home ranges of females overlap substantially with those of males. Similarly, Kitchener (*op.cit.*) has reported considerable overlap in the home ranges of adult *P. tridactylus* but did not indicate if

there was a sex difference with respect to degrees of overlap. A considerable overlap of the home ranges of both males and females (62.6% and 74%, respectively) was similarly recorded in the present study. Unfortunately, the insufficient data obtained for females precluded the statistical evaluation of sex differences in the degree of overlap in home ranges.

The degree to which the home range of an individual overlaps with that of another has generally been considered to be indicative of the relative levels of interaction between those two individuals (Jorgensen 1968; Sampson 1971). The considerable overlap reported by Kitchener (*op. cit.*) and in the present study suggests that *P. tridactylus* does not defend territories encompassing their entire home range, although it is possible that an exclusive "core area" is maintained. As several authors have noted, captive *P. tridactylus* frequently engage in agonistic behaviour, particularly between males which are housed with a female in oestrus (Hughes 1962; Buchmann, in prep.); however, little evidence of agonistic interactions between captive females was noted in the present study, as was similarly noted by Hughes (*op.cit.*). It should be recognized that the conditions of captivity inhibit a response of passive avoidance and therefore cannot be considered an accurate indication of the potential interactions which may serve to maintain the integrity of the home ranges of free-living individuals.

Only a single occupied nest was found on the study site during the course of the present program of trapping (Figure 7.3.2b). This was concealed within an area of *Poa australis* located along the upper margins of the northern slopes and occurred within an area of overlap between the home ranges of two male individuals and the female. Two individuals were flushed from within this nest during the day, but it was not possible to determine their sexes. This observation suggests that *P. tridactylus* nest together in their natural environment, as has been observed by Buchmann (pers. comm.) and as has been shown in captive individuals (Section 4.5.4). This is in contrast to the observations made by Kitchener (1972) on the quokka, *Setonix brachyurus* on Rottnest Island, who found that *S. brachyurus* defends daytime shelters. It is possible

that the difference between the two species is a result of differences in the availability of areas of vegetation suitable for nesting. In contrast to Rottnest Island, a considerable proportion of the area of Porter's Hill was characterised by an abundance of vegetation, including *Poa australis*, *Lomandra longifolia* and *Lepidosperma* spp., which may be utilized by the potoroo as nest sites; hence it is unlikely that vegetation suitable for nest sites would be a limiting resource in this area. A further consideration is the different temperature regimes in these two regions. As Kitchener (1972) has suggested, the utilization of shelters in *S. brachyurus* may be an important aspect of the ability of this species to avoid the high temperatures which are experienced on Rottnest Island. Although the nest of *P. tridactylus* may be important in the reduction of evapotranspiration during excessive periods of heat, as has been suggested for *S. brachyurus* (Kitchener *op. cit.*) and *Bettongia penicillata* (Sampson 1971; Christensen and Leftwich 1980), it is more likely that nests are of value in conserving body temperature during the winter months. If this is the case, then communal nesting would be expected to be of adaptive value.

The utilization of the habitat of *P. tridactylus* suggests that this species shows a preference for areas characterised by dense vegetation near ground level. However, it should be noted that the vegetation-type in which captures are sustained cannot be considered to be entirely representative of the habitat preference of this species, as competitive interactions between conspecifics may restrict subordinate individuals to suboptimal habitats. Several investigators have recorded a similar pattern of habitat utilization in the potoroo (Guiler 1958; Heinsohn 1968; Kitchener 1973; Seebeck 1981). The closely related *P. longipes* is similarly found in areas of dense vegetation (Seebeck 1983), as are some other macropodid species, for example *Setonix brachyurus* and *Macropus eugenii* (Russell 1974b). The utilization of dense areas of vegetation presumably serves to reduce the risk of predation imposed upon *P. tridactylus*, as suggested by Heinsohn (*op. cit.*). However, Taylor *et al.* (1985) have reported *P. tridactylus* from an area of rainforest where the density of cover is low. Whether the potoroo is common in such a habitat is, to date, unknown, as studies of this species have

been generally conducted within regions of dry sclerophyll forest.

Although the percentage ground cover was not shown to have a significant effect on the number of individuals captured, the relatively high incidence of capture in areas with a low percentage ground cover tends to suggest that potoroos frequently exploit areas which serve to facilitate their ability to penetrate the substrate while digging for food items.

Guiler (1971a) has suggested that *P. tridactylus* is able to survive within a region which is subject to fire by virtue of its ability to exploit subterranean food items. Seebeck (1981) has similarly observed this species in recently burnt areas and suggests that their ability to survive may be due to their use of the burrows of other species in order to escape the fire. The observation of an individual within an area of the study site which had recently been burnt further indicates that the potoroo does enter such habitats, however the size of this area was small and it was surrounded by dense vegetation.

CHAPTER 8

GENERAL DISCUSSION

The present study endeavoured to emphasise that the paucity of information available about the behaviour of marsupials has hindered attempts to develop a holistic understanding of their biology. Although the traditional disciplines of physiology and taxonomy have contributed greatly to our present knowledge, appreciable difficulty is experienced when attempts are made to integrate information from these subjects with what little is known about the behaviour of marsupials and their relationships with their external environment.

It should be recognised that the behaviours exhibited by captive individuals may not be strictly comparable to the behaviour of their free-living conspecifics. The effects of restraint may contribute to the expression of patterns of behaviour which are not readily observed in free-living individuals. For example, the high levels of aggression reported in captive *P. tridactylus* by Hughes (1962) and Buchmann (in prep.) may be, in part, a consequence of the inability of an individual to escape the aggressive tendencies of dominant conspecifics. It is clear that the results of observations made on captive individuals require further support from studies of free-living individuals.

In addition to the constraints of captivity, the behaviour of animals may be influenced by a large number of factors. Although attempts to minimize the influence of these are desirable, some influences that cannot be controlled may always remain. The observation that rainfall considerably reduces the levels of activity exhibited by captive *P. tridactylus* is one example of the factors which can have profound effects on the behaviour of an animal. Further climatic and astronomical variables, such as wind, humidity and lunar cycle may similarly influence behaviour, as has been shown in the quokka, *Setonix brachyurus* by Packer (1965).

A further, and possibly dramatic, influence is the investigator's own interpretation of what constitutes a certain behaviour. It is imperative that the investigator defines the principle criteria of the behaviour he is describing. Unfortunately, many studies which provide accounts of poorly defined behaviours often fail to disclose what it is that the animal actually has to do to be considered as exhibiting those behaviours.

The present study was mainly aimed at investigating several aspects of the maternal

behaviour in *P. tridactylus*. It should be recognized that this area has been the subject of neglect and, to date, still remains one of the most poorly documented areas of their biology.

The results of the present investigation of maternal behaviour disclosed a number of quantitative differences in the behaviour of adult female *P. tridactylus* in relation to the presence or absence of young in the pouch. Recapitulating, it was shown that pouch-gravid *P. tridactylus* show an increase in food consumption and levels of resting behaviour and a decrease in locomotory activity, relative to non-parous females. Each of these quantitative behavioural changes would serve to reduce the metabolic demands placed upon the mother during the energetically expensive period of lactation. It was suggested that potoroos may adopt strategies of feeding that involve relatively low levels of locomotion.

Unfortunately, little comparative infomation which might serve to substantiate this hypothesis is available for other marsupial species. However, some details are available for eutherians. A decrease in the size of the home range during the period of lactation has been demonstrated in several species of rodents. For example, Brooks and Banks (1971, cited in Behrends *et al.* 1986) have found that the size of the home range of collared lemmings (*Dicrostonyx groenlandicus*) decreased eight-fold during the period extending from late gestation to weaning. Similarly, Madison (1978) has suggested that the reduced ranges observed in lactating meadow voles (*Microtus pennsylvanicus*) may be combined with an increased reliance upon local food resources to result in a substantial reduction in energy expenditure. Conversely, an increase in the sizes of the home ranges of lactating female kangaroo rats (*Dipodomys merriami*) has been reported by Behrends *et al.* (1986). These authors suggest that this observed increase is the result of greater food requirements and, hence the need to forage more widely.

Which of these alternative strategies is adopted may be dependent upon the availability of food resources. In the case of the potoroo, which breeds throughout the year (Guiler 1960b), the range lengths may be expected to vary with seasonal

fluctuations in the availability of resources. The observations of Buchmann (in prep.) suggest that *P. tridactylus* is an opportunistic feeder; consequently it may be supposed that increased levels of food consumption do not neccessarily demand a concurrent increase in the movements of this species.

This suggestion has some implications to the strategy of foraging which may be adopted by free-living, pouch-gravid *P. tridactylus*. It might be supposed that the size of the home range decreases during the period of lactation. Female potoroos have been shown to have smaller home ranges than males (Kitchener 1972; Buchmann unpublished data; present study, Section 7), despite the fact that sexual dimorphism in this species is negligible. However, it would be premature to suggest that this observed difference is due to a reduction in the movements of lactating females, as it can conversely be considered to represent a more wide ranging behaviour by males which would serve to increase their probability of breeding. The use of radio-tracking to determine variations in the range lengths of females during the course of their reproductive cycle would provide useful information on this subject.

In the course of investigation of mother-young interactions in *P. tridactylus*, it became apparent that as a result of the succourment of the young within the pouch, few direct interactions occur between the mother and her young during the period of permanent pouch occupancy, although some interaction may occur during pouch grooming by the mother. It was shown that in the two weeks following the initial vacation of the pouch, the mother played a major role in the maintenance of the mother-young bond. However, by the time the young attained the age of 20 weeks, the role of the mother in the maintenance of the mother-young relationship was reduced. It is possible that this reduction in maternal care is associated with the increasing selective disadvantage imposed upon the mother by dependent young. Conversely, it may be considered that continued maternal care is of value from the point of view of the young. The incompatible requirements of the two individuals may be responsible for what Trivers (1974) has termed the parent-offspring conflict, however further investigation of this aspect of the mother-young relationship of marsupial species is

required before Trivers' theoretical model can be extended to embrace all mammals. The weaning of young *P. tridactylus* is not achieved solely through increased levels of aggression, as agonistic interactions between the mother and her young were not a conspicuous feature of the mother-young relationship. It is possible that the observed decrease in the levels of allogrooming may play a passive, but important role in the termination of the mother-young relationship. However, the motivational bases of allogrooming, and indeed of grooming in general, are obscure and require further investigation.

In a comprehensive review of the behaviour of the macropodoid marsupials, Russell (1974) has delineated five stages in the development of the young. However, her proposals were based exclusively on information obtained from studies of the red kangaroo, *Macropus rufus*, and in view of the results obtained in the present study they cannot be considered to be representative of the patterns of development found in all macropodoid marsupials. In contrast to Russell's (*op.cit*) account, the potoroo appears to lack a stage when the head is regularly protruded from the pouch. It is nessessary to obtain further information on the development of other macropodoid marsupials before clear similarities and differences can be determined.

It was suggested that observed similarities in the temporal distribution of the behaviour of adult and juvenile *P. tridactylus* over the activity period indicate some degree of synchrony within the mother-young dyads. It is possible that this close association may facilitate the development of habitat preferences and expand the food preferences of the juvenile through a process of preceptual learning. Unfortunately, the role of learning in the development of behaviour in marsupial species in an almost totally neglected area of their biology. The few studies which have addressed this aspect of marsupial behaviour have generally concentrated on the traditional paradigms of discrimination and operant learning; furthermore, they were often based on experimental designs or procedures of dubious validity (Kirkby 1977). It is clear that further work on the role of learning in the development of behaviour of marsupial species is required.

The considerable overlap observed in the home ranges of free living male *P. tridactylus* during the current program of capture-recapture trapping provides little evidence of strict defense of territory in this species. The observation that the home ranges of free living male *P. tridactylus* overlapped considerably with that of the sole resident female implies that the resource of a potential mate is an important factor influencing the spatial distribution of the home range of male individuals. Kaufmann(1974) has suggested that the level of social organisation obtained by various macropodoid species is influenced by the considerations of body size, habitat preference, food habits and activity cycles. With respect to these factors, *P. tridactylus* may be expected to exhibit low levels of sociability. However, the observation made in the present study, and by Buchmann (in prep.) that free living and captive individuals use communal nest sites suggests that the potoroo is not strictly a solitary animal. Unfortunately, the paucity of information available for the small nocturnal representatives of the family Potoroidae impedes full consideration of the environmental factors which influence social organisation. Clearly, further investigations of the behaviour of these species in social contexts are required in order to elucidate the levels of sociability exhibited by free-living populations.

The brown bandicoot, *Isoodon obesulus* was the only other strictly ground-dwelling terrestrial marsupial common in the study site during the course of capture-recapture trapping and was evidently sympatric with the potoroo. In common with the potoroo, *I. obesulus* is semi-fossorial, nocturnal and inhabits areas of dense vegetation (Heinsohn 1966; Moloney 1982). However, direct competition between the two species is probably reduced by trophic niche separation. Several investigators have examined the diet of *I. obesulus* and shown this species to be primarily an insectivore/omnivore (Heinsohn 1966; Moloney 1982; Quin 1985). Although *P. tridactylus* similarly includes a variety of arthropods in its diet, Guiler (1971a) has suggested that unlike *I. obesulus*, a substantial component of the diet comprises hypogean fungi. Furthermore, both species appear to be opportunistic feeders (Stoddart and Braithwaite 1979; Moloney 1982; Buchmann, in prep.). Nevertheless, further study of the diet of the two

species, particularly *P. tridactylus*, is required before it can be unequivocally stated that there is no significant degree of competition between these species. It should be additionally noted that a further source of niche separation might include species-specific differences in the temporal patterning of the activity period, as *I. obesulus*, unlike the potoroo, appears to spend a substantial proportion of its nocturnal activity period within nests (P. Clunie, pers. comm.).

The occupation of relatively large home ranges within areas of low, dense vegetation suggests that the continued conservation of *P. tridactylus* is dependent to a large extent upon the nature of land management practices. Seebeck (1981) has suggested that the maintenance of viable populations requires that suitable areas be protected from grazing and that habitat suitability should be maintained by selective clearing or low intensity burning. It should be recognized that, although *P. tridactylus* remains common in Tasmania, many mainland populations are endangered (Seebeck 1981). This predicament is even more pronounced in potoroids with a restricted distribution, such as *P. longipes* and *Bettongia lesueur* and *B. penicillata*. For several representatives of the Potoroidae, conservation measures come too late.

Aside from their own intrinsic interest, study of these species is required in order to ensure that the representatives of this family do not suffer the fate that has already befallen a large number of the marsupial species.

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. *Behaviour,* **49**, 227-67.

Altmann, M. (1958). Social integration of the moose calf. *Anim. Behav.,* **6**, 155-59.

Amos, P. J. (1982). The potoroo in Queensland. *Qld. Agric. J,* **108**, 5-6.

Anderson, D. J. (1982). The home range: a new nonparametric estimation technique. *Ecology,* **63**, 103-12.

Andrew, D. L. and Settle, G. A. (1982). Observations on the behaviour of species of Planigale (Dasyuridae, Marsupialia) with particular reference to the narrow-nosed planigale (*Planigale tenuirostris*) in *Carnivorous Marsupials* (M. Archer, ed.) pp. 311-24. Royal Zoological Society of N.S.W., Sydney.

Andrewartha, H. G. and Barker, S. (1969). Introduction to a study of the ecology of the Kangaroo Island wallaby, *Protemnodon eugenii* (Desmarest) within Flinders Chase, Kangaroo Island, South Australia. *Trans. Roy. Soc. S.Aust.,* **93**, 127-133.

Archer, M. (1974). Some aspects of reproductive behaviour and the male erectile organs of *Dasyurus geoffrai* and *D. hallucatus* (Dasyuridae: Marsupialia). *Memoirs Qld. Mus.,* **17**, 63-67.

Ashman, R., Shield, J. and Waring, H. (1975). Nipple reattachment by dislodged pouch young of the quokka, *Setonix brachyurus. J. Reprod. Fert,* **42**, 179-81.

Aslin, H. J. (1974). The behaviour of *Dasyuroides byrnei*(Marsupialia) in captivity. *Z. Tierpsychol.,* **35**, 187-208.

Astic, L., Royet, J. P. and Saucier, D. (1976). Ontogenèse du Rythme Nycthéméral des Etats de Vigilance Chez le Rat-Kangourou (*Potorous apicalis*). *Physiol. Behav.,* **17**, 39-42.

Astic, L. and Saucier, P. (1978). Sommeil in Marsupio Chez le Rat-Kangourou (*Potorous apicalis*). *Physiol. Behav.,* **20**, 363-68.

Badoux, D. M. (1965). Some notes on the functional anatomy of *Macropus giganteus* Zimm. with general remarks on the mechanics of bipedal leaping. *Acta. anat,* **62**, 418-33.

Baenninger, L. P. (1967). Comparison of behavioural development in socially isolated and grouped rats. *Anim. Behav.,* **15**, 312-23.

Bailey, P. T. (1971). The red kangaroo, *Megaleia rufa* (Desmarest), in north-western New South Wales. I. Movements. *C.S.I.R.O. Wildl. Res,* **16**, 11-28.

Balph, D. F. (1968). Behavioural responses of unconfined vinta ground squirrels to trapping. *J. Wildl. Manage.,* **32**, 778-94.

Barbour, R. A. (1977). Anatomy of marsupials. *In The Biology of Marsupials* (B. Stonhouse and D. Gilmore, eds.). pp. 237-72. Macmillan, London.

Barker, S., Brown, G. D. and Calaby, J. H. (1963). Food regurgitation in the Macropodidae. *Aust. J. Sci.,* **25**, 430-32.

Barnes, R. D. and Barthold, S. W. (1969). Reproduction and breeding behaviour in an experimental colony of *Marmosa mitis* Bangs (Didelphidae). *J. Reprod. Fert. Suppl.*, **6**, 477-82

Barnett, S. A. (1958). Experiments on "neophobia" in wild and laboratory rats. *Brit. J. Psychol.*, **49**, 195-201.

Bates, P. C., Bigger, T. R. L., Hulse, E. V. and Palmer, A. (1972). The management of a small colony of the marsupial *Potorous tridactylus* and a record of its breeding in captivity. *Lab. Anim.*, **6**, 301-13.

Beach, F. (1939). Maternal behaviour of the pouchless marsupial *Marmosa cinerea*. *J. Mammal.*, **20**, 315-22.

Behrends, P., Daly, M. and Wilson, M. I. (1986). Aboveground activity of Merriam's Kangaroo rats (*Dipodomys merriami*) in relation to sex and reproduction. *Behaviour*, **96**, 210-226.

Bell, H. M. (1973). The ecology of three macropod marsupial species in an area of open forest and savannah woodland in North Queensland. *Aust. Mammal.*, **37**, 527-44.

Biggins, J. C. (1984). Communication in possums: a review. In *Possums and Gliders* (A.P. Smith and I.D. Hume, eds.). pp. 35-57. Australian Mammal Society, Sydney.

Biggins, J. C. and Overstreet, D. H. (1978). Aggressive and non-aggressive interactions among captive populations of the brush-tailed possum, *Trichosurus vulpecula* (Marsupialia: Phalangeridae). *J. Mammal.*, **59**, 149-59.

Blackhall, S. V. (1980). Diet of the eastern native-cat, *Dasyurus viverrinus* (Shaw), in southern Tasmania. Aust. Wildl. Res., **7**, 191-97.

Blair, W. F. (1940). Home ranges and populations of the meadow vole in southern Michigan. *J. Wildl. Managmt*, **4**, 149-61.

Bolton, B. L. and Latz, P. K. (1978). The western hare-wallaby *Lagorchestes hirsutus* (Gould) (Macropodidae) in the Tanami Desert. *Aust. Wildl. Res.*, **5**, 285-93.

Bombardieri, R. A. and Johnson, J. I. (1969). Daily activity schedule of captive opossums. *Psychon. Sci.*, **17**, 135-36.

Braithwaite, R. W. (1974). Behavioural changes associated with population cycles of *Antechinus stuartii*. *Aust. J. Zool.*, **22**, 45-62.

Brereton, J. LeG. (1966). The evolution and adaptive significance of social behaviour. *Proc. Ecol. Soc. Aust.*, **1**, 14-30.

Brockway, J. M., McDonald, J. D. and Pullar, J. D. (1963). The energy cost of reproduction in sheep. *J. Physiol.*, **167**, 318-27.

Bryant, S. L. (1982). *Physiological Aspects of Reproduction in Male and Female* Potorous tridactylus. Hons. thesis, University of Tasmania.

Bucher, J. E. and Fritz, H. E. (1977). Behaviour and maintenance of the woolly opossum (*Caluromys*) in captivity. *Animal. Sci.*, **27**, 1007-1012.

Buchmann, O. L. K. and Grecian, E. A. (1974). Discrimination-reversal learning in the marsupial I*soodon obesulus* (Marsupialia: Peramelidae). *Anim. Behav.*, **22**, 975-81.

Buchmann, O. L. K. and Guiler, E. R. (1974). Locomotion in the potoroo. *J. Mammal.*, **55**, 203-5.

Buchmann, O. L. K. and Guiler, E. R. (1977). Behaviour and ecology of the Tasmanian devil, *Sarcophilus harrisii*. In *The Biology of Marsupials* (B. Stonehouse and D. Gilmore, eds.). Macmillan Press, London.

Burbidge, A. A. and Jenkins, R. W. G. (eds) (1984). *Endangered Vertebrates of Australia and its Island Territories*. Report of the Working Group on Endangered Fauna of the Standing Committee of the Council of Nature Conservation Ministers. Australian National Parks and Wildlife Service, Canberra.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *J. Mammal.*, **24**, 346-52.

Calaby, J. W. (1960). Observations on the banded ant eater *Myrmecobius fasciatus* Waterhouse (Marsupialia), with particular reference to its food habits. *Proc. Zool. Soc. Lond.*, **135**, 183-207.

Calaby, J. H. (1966). Mammals of the upper Richmond and Clarence Rivers, New South Wales. *C.S.I.R.O. Div. Wildl. Res. Tech. Pap.*, **10**, 1-55.

Calaby, J. H. (1971). The curent status of Australian Marcopodidae. *Aust. Zool.*, **16**, 17-31.

Caughley, G. (1964). Social organisation and daily activity of the red kangaroo and grey kangaroo. *J. Mammal.*, **45**, 429-436.

Christensen, P. (1975). The breeding burrow of the banded anteater or numbat. *Western Aust. Nat.*, **13**, 32-34.

Christensen, P., Maisey, K. and Perry, D. H. (1984). Radio tracking the numbat, *Myrmecobius fasciatus*, in the Perup Forest of Western Australia. *Aust. Wildl. Res.*, **11**, 275-88.

Christensen, P. and Leftwich, T. (1980). Observations on the nest-building habits of the brush-tailed rat-kangaroo or woylie (*Bettonia penicillata*). *J. Roy. Soc. W. Aust.*, **63**, 33-38.

Cicala, G. A., Albert, I. B. and Ulmer, F. A. (1970). Sleep and other behaviours of the red kangaroo (*Megaleia rufa*). *Anim. Behav.*, **18**, 789-90.

Cisar, C. F. (1969). The rat-kangaroo (*Potorous tridactylus*). Handling and husbandry practices in a research facility. *Lab. Anim. Care.*, **19**, 55-59.

Clancy, T. F. (1982). *Aspects of the behaviour of the Red-bellied Pademelon* Thylogale billardieri *(Desmarest 1882) in captivity*. Unpublished Hons. thesis, University of Tasmania.

Collins, L. R. (1973). *Monotremes and Marsupials. A reference for zoological institutions*. Smithsonian Institution Press, Washington.

Croft, D. B. (1981a). Behaviour of red kangaroos, *Macropus rufus* (Desmarest 1822) in north western New South Wales, Australia. *Aust. Mammal.*, **4**, 5-58.

Croft, D. B. (1981b). Social behaviour of the euro, *Macropus robustus* (Gould), in the Australian arid zone. *Aust. Wildl. Res.*, **8**, 13-49.

Croft, D. B. (1982). Some observations on th behaviour of the antilopine wallaroo, *Macropus antilopinus*(Marsupialia: Macropodidae). *Aust. Mammal.*, 5, 5-13.

Croft, D. B. (1985). Inter- and intraspecific conflict between arid-zone kangaroos at watering points. *Aust. Wild. Res.*, 12, 337-48.

Crowcroft, P. and Godfrey, G. K. (1968). The daily cycle of activity in two species of *Sminthopsis*(Marsupialia: Dasyuridae). *J. Anim. Ecol.*, 37, 63-73.

Crowley, H. M. (1984). *Aspects of Lactation in* Potorous tridactylus *Kerr.* Unpublished Hons. thesis, University of Tasmania.

Cuttle, P. (1982). A preliminary report on aspects of the behaviour of the dasyurid maruspial *Phascogale tapoatafa*. In *Carnivorous Marsupials* (M. Archer, ed.). pp. 325-32. Royal Zoological Society of N.S.W., Sydney.

Coulson, G. M. (1977). Social behaviour of eastern grey kangaroos *Macropus giganteus* and western grey kangaroos, *Macropus fuliginosus*. *Aust. Mammal. Soc. Bull.*, 3, 10.

Davies, W. G. (1979). Social organisation of the rock-wallaby (*Petrogale puella)* in north Queensland. *Aust. Mammal. Soc. Bull.*, 6, 18-19.

Davis, J. A. Jnr. (1961). Exhibition of nocturnal mammals by red light. *Int. Zoo. Yr. Bk.*, 3, 9-11.

Dawson, T. J., Denny, M. J. S., Russell, E. M. and Ellis, B. (1975). Water usage and diet preferences of free-ranging kangaroos, sheep and feral goats in the Australian arid zone during summer. *J. Zool. Lond.*, 177, 1-23.

Dawson, T. J., Robertshaw, D. and Talyor, C. R. (1974). Sweating in the red kangaroo: an evaporative cooling mechanism during exercise, but not in the heat. *Am. J. Physiol.*, 227, 494-98.

Dawson, T. J. and Talyor, C. R. (1973). Energetic cost of locomotion in kangaroos. *Nature*, 246, 313-14.

Delroy, I. B., Earl, J., Radbone, I., Robinson A.C. and Hewett, M. (1986). The breeding and re-establishment of the brush-tailed bettong. *Bettongia penicillata*, in South Australia. *Aust. Wildl. Res.*, 13, 387-96.

Dickman, C. R. (1982). Some observations of the behaviour and net utilisation of free living *Antechinus stuartii* (Marsupialia: Dasyuridae). *Aust. Mammal.*, 5, 75-77

Dimpel, H. and Calaby, J. H. (1972). Further observations on the mountain pygmy possum, (*Burramys parvus*). *Vict. Nat.*, 89, 101-106.

Dixon, J. M. (1971). *Burramys parvus* Broom (Marsupialia) from Falls Creek area, Bogong High Plains, Victoria. *Vic. Nat*, 88, 133-38.

Dunbar, R.I.M. (1976). Some aspects of research design and thier implications in the observational study of behaviour. *Behav.*, 58, 78-98.

Dunnet, G. M. (1962). A population study of the quokka, *Setonix brachyurus* (Quoy and Gaimard) (Marsupialia). II. Habitat, movements, breeding and growth. *C.S.I.R.O. Wildl. Res.*, 7, 13-32.

Dwyer, P. D. (1972). Social organisation of a population of rock-wallabies, *Petrogale inornata*. *Aust. Mammal.*, 1, 72.

Ealey, E. H. M. (1967). Ecology of the euro, *Macropus robustus* (Gould) in north-western Australia. II. Behaviour, movements and drinking patterns. *C.S.I.R.O. Wildl. Res.*, 12, 9-80.

Ealey, E. H. M. and Main, A. R. (1967). Ecology of the euro, *Macropus robustus* (Gould), in north-western Australia. III. Seasonal changes in nutrition. *C.S.I.R.O. Wildl. Res.*, 12, 53-65.

Eberhard, I. H. (1978). Ecology of the koala, *Phascolarctos cinereus* (Goldfuss) Marsupialia: Phascolarctidae, in Australia. In *The Ecology of Aboreal Folivores* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington.

Edwards, G. P. and Ealey, E. H. M. (1975). Aspects of the ecology of the swamp wallaby *Wallabia bicolor* (Marsupialia: Macropodidae). *Aust. Mammal.*, 1, 307-17.

Eibl-Eibesfeldt, I. (1975). *Ethology. The Biology of Behaviour.* 2nd. ed. Holt, Rinehart and Winston, New York.

Eisenberg, J. F. (1981). *The Mammalian Radiations.* University of Chicago Press, Chicago.

Eisenberg, J. F. and Leyhausen, P. (1972). The phylogenesis of predatory behaviour in mammals. *Z. Tierpsychol.*, 30, 59-93.

Eisenberg, J. F., Collins. L. R. and Wemmer, C. (1975). Communication in the Tasmanian devil *(Sarcophilus harrisii)* and a survey of auditory communication in the Marsupialia. *Z. Tierpsychol.*, 37, 379-99.

Ellis, B. A., Russell, E. M., Dawson, T. J. and Harrop, C. J. F. (1977). Seasonal changes in diet preferences of free-ranging red kangaroos, euros, and sheep in western New South Wales, Australia. *Aust. Wildl. Res.*, 4, 127-44.

Espmark, Y. (1971). Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L.). *Z. Tierpsychol.*, 29, 42-81.

Ewer, R. F. (1968a). A preliminary survey of the behaviour in captivity of the dasyurid marsupial, *Sminthopsis crassicaudata* (Gould). *Z. Tierpsychol.*, 25, 319-465.

Ewer, R. F. (1968b). *Ethology of Mammals.* New York, Plenum Press.

Ewer, R. F. (1969). Some observations on the killing and eating of prey by two dasyurid marsupials: The mulgara, Dasycercus *cristicaudata* and the Tasmanian devil, *Sacrophilus harrisii*. *Z. Tierpsychol.*, 26, 23-38.

Fanning, F. D. (1982). Reproduction, growth and development in *Ningaue* sp. (Marsupialia: Dasyuridae) from the Northern Territory. In *Carnivorous Marsupials* (M. Archer, ed.) pp. 23-37. Australian National University Press, Canberra.

Fleay, D. (1932). Swainson's phascogale (the "bush mouse"). *Vict. Nat.*, 49, 132-34.

Fleming, M. M., Harder, J. D. and Wukie, J. J. (1981). Reproductive energetics of the virginia opossum compared with some eutherians. *Comp. Biochem. Physiol.*, **70B**, 645-48

Flynn, T. T. (1922). Parturition in *Potorous. Proc. Linn. Soc. N.S.W.*, **47**, 28.

Franq, E. N. (1969). Behavioural aspects of feigned death in the opossum *Didelphis marsupialis. Am. Midl. Nat.*, **81**, 556-68.

Frappell, P. B. and Rose, R. W. (1986). A radiographic study of the gastrointestinal tract of *Potorous tridactylus*, with a suggestion as to the role of the foregut and hindgut in potoroine marsupials. *Aust. J. Zool.*, **34**, 463-71.

Frauca, H. (1969). A northern extension of the range of the potoroo, *Potorous tridactylus* Kerr, in Queensland. *Aust. Zool.*, **15**, 124-26.

Frey, H. and Fleming, M. R. (1984). Thermoregulatory behaviour of free-ranging feathertail gliders *Acrobats pygmaeus* (Marsupialia: Burramyidae) in Victoria. In *Possums and Gliders* (A. P. Smith and I. D. Hume, eds.) pp. 393-401. Australian Mammal Society, Sydney, 1984.

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.W. Cheshire, Melbourne.

Ganslosser, U. (1977). Beobachtungen an Doria-Baumkanguruhs (*Dendrolagus dorianus*) und Graven Baumkanguruhs (*Dendrolagus inustus*) in Zoologischen Gärten. *Zool. Anz.*, **198**, 393-412.

Ganslosser, U. (1980).Vergleicherde Untersuchungen zur Kletterfahigkeit einiger Baumkanguruh-Arten (*Dendrolagus*, Marsupialia). *Zool. Anz.*, **205**, 43-66.

Ganslosser, U. (1983). Quantitative Untersuchungen zum Sozialverhalten des Doria-Baumkanguruhs (*Dendrolagus dorianus*, Ramsay, 1883) in Gefangenschaft. *Zool. Anz.*, **211**, 1-29.

Ganslosser, U. and Welhelm, P. (1986). Sex- and age- dependant differences in frequencies of social interactions between captive red kangaroos, *Macropus rufus* (Desmarest, 1822). *Zool. Anz.*, **216**, 58-71.

Ganslosser, U. and Werner, I. (1984). Zur Haufigkeit freundlicher und agonistischer verhaltens-muster in einer Gruppe von Rotbauchfilandern (*Thylogale billardieri* Desmarest) (Marsupialia, Macropodidae). *Zool. Anz.*, **213**, 51-67.

Gasking, W. R. (1965). Breeding kangaroos and wallabies in captivity. *Int. Zoo. Yr. Bk.*, **5**, 106-9.

Giles, D. C. and Russell, E. M. (1975). Allogrooming in *Macropus eugenii. Aust. Mammal.*, **1**, 387.

Glickman, S. E. and Sroges, R. W. (1966). Curiosity in zoo animals. *Behav.*, **26**, 151-88.

Goldingay, R. L. (1984). Photoperiodic control of diet activity in the sugar glidr (*Petaurus breviceps*). In *Possums and Gliders*. (A. P. Smith and I. D. Hume, eds.) pp. 385-91. Australian Mammal Society, Sydney, 1984.

Goldstone, A. D. and Nelson, J. E. (1986). Aggressive behaviour in two female *Peradorcas concinna*(Macropodidae) and its relation to oestrus. *Aust. Wildl. Res.*, **13**, 375-85.

Gordon, G. (1974). Movements and activity of the short-nosed bandicoot, *Isoodon macrourus*Gould (Marsupialia). *Mammalia*, **38**, 405-31.

Grant, T. R. (1973). Dominance and association among members of a captive and a free-ranging group of grey kangaroos (*Macropus giganteus*). *Anim. Behav.*, **21**, 449-56.

Grant, T. R. (1974). Observations of enclosed and free-ranging grey kangaroos *Macropus giganteus*. *Z. Saugetierk.*, **39**, 65-78.

Green, R. H. (1967). Notes on the devil (*Sarcophilus harrisii*) and the quoll (*Dasyurus viverrinus*) in north-eastern Tasmania. *Rec. Queen Vict. Mus.*, **27**, 1-13.

Griffiths, M. and Barker, R. (1966). The plants eaten by sheep and by kangaroos grazing together in a paddock in south-western Queensland. *C.S.I.R.O. Wild. Res.*, **1**, 145-67.

Guiler, E. R. (1958). Observations on a population of small marsupials in Tasmania. *J. Mammal.*, **39**, 44-58.

Guiler, E. R. (1960a). The pouch young of the potoroo. *J. Mammal.*, **41**, 441-51.

Guiler, E. R. (1960b). The breeding season of *Potorous*. *Aust. J. Sci.*, **23**, 126-27.

Guiler, E. R. (1961). Notes on the externals of the potoroo, *Potorous tridactylus* (Kerr). *Pap. proc. Roy. Soc. Tas.*, **95**, 41-8.

Guiler, E. R. (1970a). Observations on the Tasmanian devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae). I. Numbers, home range, movements and food in two populations. *Aust. J. Zool.*, **18**, 49-62.

Guiler, E. R. (1970b). Observations on the Tasmanian devil, *Sarcophilus harisii* (Marsupialia: Dasyuridae). II. Reproduction, breeding and growth of young. *Aust. J. Zool.*, **18**, 63-70.

Guiler, E. R. (1971a). Food of the potoroo (Marsupialia: Macropodidae). *J. Mammal.*, **52**, 232-4.

Guiler, E. R. (1971b). The husbandry of the potoroo. *Int. Zoo. Yr. Bk.*, **11**, 21-2.

Happold, M. (1972). Maternal and juvenile behaviour in the marsupial Jerboa *Antechinomys spenceri*(Dasyuridae). *Aust. Mammal.*, **1**, 27-37.

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*. Unpublished Hons. thesis, University of Tasmania.

Hayssen, V. (1980). Observations of the behaviour of the Brazilian short bare-tailed opossum (*Monodelphis domestica*Wagner) in captivity. *Bull. Aust. Mamm. Soc.*, **6**, 37.

Heinsohn, G. E. (1966). Ecology and reproduction of the two species of Tasmanian bandicoots, *Perameles gunnii* and *Isoodon obesulus*. *Calif. Publ. Zool.* **80**, 1-107.

Heinsohn, G. E. (1968). Habitat requirements and reproductive potential of the macropod marsupial *Potorous tridactylus* in Tasmania. *Mammalia*, **32**, 30-43.

Henry, S. R. (1984). Social organisation of the greater glider (*Petauroides volans*) in Victoria. In *Possums and Gliders* (A. P. Smith and I. D. Hume, eds.). pp. 221-28. Australian Mammal Society, Sydney.

Henry, S. R. and Craig, S. A. (1984). Diet ranging behaviour and social organisation of the Yellow-bellied glider (*Petaurus australis* Shaw) in Victoria. In *Possums and Gliders* (A. P. Smith and I. D. Hume, eds.). pp. 331-41. Australian Mammal Society, Sydney.

Hickman, V. V. and Hickman, J. L. (1960). Notes on the habits of the Tasmanian dormouse phalangers *Cercatetus nanus*(Desmarest) and *Eudromicia lepida* (Thomas). *Proc. Zool. Soc. Lond.*, **135**, 365-74.

Hill, J. P. and Hill, W. C. O. (1955). The growth stages of the native cat (*Dasyurus viverrinus*) together with observations on the anatomy of the newborn young. *Trans. Zool. Soc. Lond.*, **28**, 349-452.

Hinde, R. A. (1970). *Animal Behaviour: a Synthesis of Ethology and Comparative Psycholgoy.* 2nd ed. McGraw-Hill, New York.

Hinde, R. A. (1982). *Ethology. Its nature and relations with other sciences.* Fontana Paperbacks. Glasgow.

Hocking, G. (1978). Mammals. In *The South West Book. A Tasmanian Wilderness* (Gee, H. and Fenton, J. eds.). Australian Conservation Foundation.

Holsworth, W. N. (1967). Population dynamics of the quokka, *Setonix brachyurus*, on the west end of Rottnest I., Western Australia. I. Habitat and distribution of the quokka. *Aust. J. Zool.*, **15**, 29-46.

Hope, J. H. (1969). *Biogeography of the mammals of the Islands of Bass Strait with an Account of Variation in the genus* Potorous. Unpublished Ph.D. thesis, Monash University.

Hopkins, D. (1977). Nest building behaviour in the immature Virginia opossum (*Didelphis virginiana*). *Mammalia*, **41**, 361-62.

Hornsby, P. (1978). A note on the pouch life of rock wallabies. *Vict. Nat.* **95**, 108-11.

Howe, D. (1975). Observations on a captive marsupial mole, *Notoryctes typhlops*. *Aust. Mammal.*, **1**, 361-65.

How, R. A. (1981). Population parameters in two congeneric possums, *Trichosurus* spp. in north-eastern New South Wales. *Aust. J. Zool.*, **29**, 205-15.

Hudson, J. W. and Dawson, T. J. (1975). Role of sweating from the tail in the thermal balance of the rat-kangaroo *Potorous tridactylus*. *Aust. J. Zool.*, **23**, 453-61.

Hughes, R. D. (1965). On the age composition of a small sample of individuals from a population of the banded hare wallaby *Lagostrophus fasciatus* (Peron and Lesueur). *Aust. J. Zool.* **13**, 75-95.

Hughes, R. L. (1962). Reproduction in the macropod marsupial *Potorous tridactylus* (Kerr). *Aust. J. Zool.*, **10**, 193-224.

Hume, I. D. (1982). *Digestive Physiology and Nutrition of Marsupials.* Cambridge University Press, Cambridge.

Hunsaker, D. and Shupe, D. (1977). Behaviour of New World Marsupials. In *The Biology of Marsupials* (D. Hunsaker, ed.) pp. 279-347. Academic Press, New York.

Hutson, G. D. (1975). Sequences of prey-catching behaviour in the brush-tailed marsupial rat *(Dasyuroides burnei)*. *Z. Tierpsychol.*, **39**, 39-60.

Hutson, G. D. (1976). Grooming behaviour and birth in the dasyurid maruspial, *Dasyuroides byrnei. Aust. J. Zool.*, **24**, 277-82.

Hutson, G. D. (1982). An analysis of offensive and defensive threat displays in *Dasyuroides byrnei*(Dasyuridae, Marsupialia). In *Carnivorous Marsupials* (M. Archer, ed.) pp. 345-63. Sydney Royal Zoological Society of N.S.W., Sydney.

Jewell, P. A. (1966). The concept of home range in mammals. *Symp. Zool. Soc. Lond.*, **18**, 85-109.

Joblin, K. (1981). Social organisation and spatial distribution in the brush-tailed rock-wallaby, *Petrogale penicillata. Aust. Mammal. Soc. Bull.*, **7**, 43-44.

Johnson, C. N. and Johnson, K. A. (1983). Behaviour of the bilby, *Macrotis lagotis* (Reid), (Marsupialia, Thylacomyidae) in captivity. *Aust. Wildl. Res.*, **10**, 77-87.

Johnson, K. A. (1978). Methods for the census of wallaby and possum in Tasmania. *Wildl. Division Tech. Report.* **78/1**, Tasmanian N.P.W.S., Hobart.

Johnson, K. A. (1980). Spatial and temporal use of habitat by the red-necked pademelon, *Thylogale thetis* (Marsupialia: Macropodidae). *Aust. Wildl. Res.*, **7**, 157-66.

Johnson, K. A. and Rose, R. (1983). Tasmanian Bettong. In *The Australian Museum Complete Book of Australian Mammals.* (R. Strahan, ed.) p. 186. Angus and Robertson, Sydney.

Johnson, P. M. (1980a). Field observations on group compositions in the agile wallaby, *Macropus agilis* (Gould) (Marsupialia: Macropodidae). *Aust. Wildl. Res.*, **7**, 327-31.

Johnson, P. M. (1980b). Observations of the behaviour of the rufous rat-kangaroo *Aepyprymnus rufescens* (Gray) in captivity. *Aust. Wildl. Res.*, **7**, 347-57.

Johnson, P. M. (1983). Rufous Bettong. In *The Australian Museum Complete Book of Australian Mammals* (R. Strahan, ed.) p. 190. Angus and Robertson, Sydney.

Johnson, P. M. and Strahan, R. (1982). A further description of the musky rat-kangaroo, *Hypsiprymnodon moschatus*Ramsay, 1876 (Marsupialia: Potoroidae), with notes on its biology. *Aust. Zool.*, **21**, 27-46.

Johnson, P. G., Davey, R. J. and Seebeck, J. H. (1984). Chromosome homologies in *Potorous tridactylus* and *P. longipes* (Marsupialia: Macropodidae). Based on G-banding patterns. *Aust. J. Zool.*, **32**, 319-24.

Johnston, P. G. and Sharman, G. B. (1976). Studies on populations of *Potorous* Desmarest (Marsupialia). I. Morphological variation. *Aust. J. Zool.*, **24**, 573-88.

Johnston, P. G. and Sharman, G. B. (1977). Studies on populations of *Potorous* Desmarest (Marsupialia). II. Electrophoretic, Chromosomal and breeding studies. *Aust. J. Zool.*, **25**, 733-47.

Jorgensen, C. D. (1968). Home range as a measure of probable interactions among populations of smal mammals. *J. Mammal.*, **49**, 104-12.

Kaufmann, J. H. (1962). Ecology and social behaviour of the coati, *Nasuta narica*, on Barro Colorao Island, Panama. *Uni. Calif. Publ. Zool.*, **60**, 95-222.

Kaufmann, J. H. (1974a). Social ethology of the whiptail wallaby, *Macropus parryi* in north eastern New South Wales. *Anim. Behav.*, **22**, 281-396.

Kaufmann, J. H. (1974b). The ecology and evolution of social organisation in the kangaroo family (Macropodidae). *Am. Zool.*, **14**, 51-62.

Kaufmann, J. H. (1974c). Habitat use and social organisation of nine sympatric species of macropodid marsupials. *J. Mammal.*, **55**, 66-80.

Kaufmann, J. H. (1975). Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus. Anim. Behav.*, **23**, 214-21.

Kavanagh, R. P. and Rohan-Jones, W. G. (1982). Calling behaviour of the Yellow-bellied glider *Petaurus australis* Shaw (Marsupialia: Petauridae). *Aust. Mamm.*, **5**, 95-111.

Kean, R. I. (1967). Behaviour and territorialism in *Trichosurus vulpecula* (Marsupialia). *Proc. N.Z. Ecol. Soc.*, **18**, 42,47.

Kerle, J. C. and Borsboom, A. (1984). Home range, den tree use and activity patterns in the greater glider, *Petauroides volans.* In *Possums and Gliders* (A. P. Smith and I. D. Hume, eds.) pp. 229-36. Australian Mammal Society, Sydney, 1984.

Kershaw, R. C. (1971). Notes on Tasmanian rat kangaroos. *Vict. Nat*, **88**, 4-10.

Kirkby, R. J. (1977). Learning and problem-solving behaviour in marsupials. In *The Biology of Marsupials* (B. Stonehouse and D. Gilmore, eds.). Macmillan Press, London.

Kirkpatrick, T. H. (1966). Studies of the Macropodidae in Queensland. 4. Social organisation of the grey kangaroo (*Macropus giganteus*). *Queensl. J. Agr. Anim. Sc.*, **23**, 317-22.

Kirkpatrick, T. H. (1967). The grey kangaroo in Queensland. *Queensland Ag. J.*, **93**, 550-52.

Kirsch, J. A. W. and Calaby, J. H. (1977). The species of living marsupials: an annotated list. In *The Biology of Marsupials* (B. Stonehouse and D. Gilmore, eds.). Macmillan Press, London.

Kirsch, J. A. and Waller, P. F. (1979). Notes on the trapping and behaviour of the Caenolestidae (Marsupialia). *J. Mammal.* **60**, 390-95

Kitchener, D. J. (1972). The importance of shelter to the quokka, *Setonix brachyurus* (Marsupialia) on Rottnest Island. *Aust. J. Zool.*, **20**, 281-99.

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**, 231-40.

Klopfer, P. H. and Klopfer, M. S. (1970). Patterns of maternal care in lemurs: I. Normative description. *Z. Tierpsychol.*, **27**, 984-96.

Koeppl, J. W., Slade, N. A. and Hoffman, R. S. (1975). A bivariate home range model with possible application to ethological data analysis. *J. Mammal.*, **56**, 81-90.

Lafollette, R. M. (1971). Agonistic behaviour and dominance in confined wallabies, *Wallabia rufogrisea frutica*. *Anim. Behav.*, **19**, 93-101.

Lavery, H. J. (1985). *The Kangaroo Keepers.* University of Queensland Press, St. Lucia, Qld.

Layne, J. N. (1954). The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. *Ecol. Mono.*, **24**, 227-67.

Lee, A. K. and Cockburn, A. (1985). *Evolutionary Ecology of Marsupials.* Cambridge University Press, Cambridge.

Lehner, P. N. (1979). *Handbook of Ethological Methods.* Garland STPM Press, New York.

Le Souef, A. S. and Burrell, H. (1926). *The Wild Animals of Australasia.* Harrop, London.

Lilligraven, J. A. (1975). Biological Considerations of the Marsupial. Placental dichotomy. *Evolution*, **29**, 707-22.

Lindstedt, S. L., Miller, B. J. and Buskirk, S. W. (1986). Home range, time, and body size in mammals. *Ecology*, **67**, 413-18.

Lisk, R. D., Prettow, R. A. and Friedman, S. M. (1969). Hormonal stimulation necessary for elicitation of maternal nest-building in the mouse (*Mus musculus*). *Anim. Behav.*, **17**, 730-37.

Lochmiller, R. L., Whelan, J. B. and Kirkpatrick, R. L. (1982). Energetic cost of lactation in Microtus pinetorum. *J. Mammal.*, **63**, 475-81.

Lorenz, K. (1963). *On Aggression.* Harvest, New York.

Low, B. S. (1978). Environmental uncertainty and the parental strategies of marsupials and placentals. *Am. Nat.*, **112**, 197-213.

Lyne, A. G. (1964). Observations on the breeding and growth of the marsupial *Perameles nasuta* Geoffrey, with notes on other bandicoots. *Aust. J. Zool.*, **12**, 322-39.

Lyne, A. G. (1974). Gestation period and birth in the marsupial *Isoodon macrourus.* *Aust. J. Zool.,* **22**, 303-9.

Lyne, A. G. (1981). Activity rhythms in the marsupials *Isoodon macrourus* and *Perameles nasuta* in captivity. *Aust. J. Zool.,* **29**, 821-38.

McCartney, D. J. (1978). *Reproductive Biology of the Tasmanian Pademelon,* Thylogale billardieri. Unpublished Hons. thesis, University of Tasmania.

Mace, G. M. and Harvey, P. H. (1983). Energetic contrainst on home-range size. *Am. Nat.,* **121**, 120-32.

McKenna, J. J. (1982). The evolution of primate societies, reproduction and parenting. In *Primate Behaviour* (J. L. Fobes and J. E. King, eds.). Academic Press, New York.

Mackerras, M. J. and Smith, R. H. (1960). Breeding of the short-nosed marsupial bandicoot, *Isoodon macrourus* (Gould) in captivity. *Aust. J. Zool.,* **8**, 371-82.

MacLennan, D. G. (1984). The feeding behaviour and activity patterns of the brushtail possum, *Trichosurus vulpecula,* in an open eucalypt woodland in southeast Queensland. In *Possums and Gliders* (A. P. Smith and I. D. Hume, eds.) pp. 155-61. Australian Mammal Society, Sydney.

McManus, J. J. (1967). Observations on the sexual behaviour of the opossum, *Didelphis marsupialis. J. Mammal.,* **48**, 486-87.

McManus, J. J. (1970). Behaviour of the opossums *Didelphis marsupialis virginiana. Amer. Midl. Nat.,* **84**, 144-69.

McManus, J. J. (1971). Activity of captive *Didelphis marsupialis. J. Mammal.,* **52**, 846-48.

Mcnab, B. K. (1963). Bioenergetics and the determination of home range size. *Am. Nat.,* **97**, 133-40.

McNab, B. K. (1978). The comparative energetics of neotropical marsupials. *J. Comp. Physiol.,* **125**, 115-28.

Madison, D. M. (1978). Movement indicators of reproductive events among female meadow voles as revealed by radiotelemetry. *J. Mammal.,* **59**, 835-43.

Marlow, B. J. (1958). A survey of the marsupials of New South Wales. *C.S.I.R.O. Wildl. Res.,* **3**, 71-114.

Marlow, B. J. (1961). Reproductive behaviour of the marsupial mouse, *Antechinus flavipes* (Waterhouse) (Marsupialia) and the development of the pouch young. *Aust. J. Zool.,* **19**, 203-18.

Marlow, B. J. (1969). A comparison of the locomotion of two desert-living Australian mammals, *Antecinomys spenceri* (Marsupialia: Dasyuridae) and *Notomys cervinus* (Rodentia: Muridae). *J. Zool., Lond,* **157**, 159-67.

Martin, P. (1986). An experimental study of weaning in the domestic cat. *Behaviour,* **96**, 221-49.

Martin, P. and Bateson, P. (1985). *Measuring behaviour. An introductory guide.* Cambridge University Press, Cambridge.

Mattingly, D. K. and McClure. P. A. (1982). Energetics of reproduction in large-littered cotton rats (*Signodon hispidus*). *Ecology*. **63**, 183-95.

Maynes, G. M. (1973). Reproduction in the parma wallaby, *Macropus parma* Waterhouse. *Aust. J. Zool*. **21**, 331-51.

Maynes, G. M. (1976). Growth of the parma wallaby, Macropus parma Waterhouse. *Aust. J. Zool.*, **24**, 217-36.

Maynes, G. M. (1977). Distribution and aspects of the biology of the parma wallaby, *Macropus parma*, in New South Wales. *Aust. Wildl. Res.*, **4**, 109-25.

Meissner, K. and Ganslösser, U. (1985). Ontogeny of social behaviour of the kowari, *Dasyuroides byrnei* Spencer, 1896 (Marsupialia: Dasyuridae) I. A comparison of the behavioural repertoire of juvenile and adult kowaries. *Zool. Anz*, **214**, 291-308.

Menzel, E. W. Jr. (1962). The effects of stimulus size and proximity upon avoidance of complex objects in rhesus monkeys. *J. Comp. Physiol. Psychol.*, **55**, 1044-46.

Menzies, J. I. and Pernetta, J. C. (1986). A taxonomic revision of cuscuses allied to *Phalanger orientalis*(Marsupialia: Phalangeridae). *J. Zool., Lond*, **1**, 551-618.

Merchant, J. C. and Sharman, G.B. (1966). Observations on the attachment of marsupial pouch young to the teats and on the rearing of pouch young by foster-mothers of the same or different species. *Aust. J. Zool*, **14**, 593-609.

Metzgar, L. M. (1967). An experimental comparison of screech own predation on resident and transient white-footed mice (*Peromyscus leucopus*). *J. Mammal.*, **48**, 387-91.

Millar, J. S. (1975). Tactics of energy partitioning in breeding *Peromyscus. Can. J. Zool.*, **53**, 967-76.

Millar, J. S. (1977). Adaptive features of mammalian reproduction. *Evolution*, **31**, 370-86.

Millar, J.S. (1979). Energetics of lactation in *Peromyscus maniculatus. Can. J. Zool.*, **57**, 1015-19.

Mollison, B. C. (1960). Food regurgitation in Bennett's wallaby, *Protemnodon rufogrisea*(Desmarest), and the scrub wallaby, *Thylogale billardieri*(Desmarest). *C.S.I.R.O. Wildl. Res.*, **5**, 87-88.

Molnar, R. E. and Goldfinch, A. J. (1981). Gait transition in the brush-tailed possum (*Trichosurus vulpecula*). *Aust. Mammal.*, **4**, 59-60.

Moloney, D. J. (1982). *A comparison of the Behaviour and Ecology of the Tasmanian bandicoots*, Perameles gunnii *(Gray 1838) and* Isoodon obesulus *(Shaw and Noddier 1797).* Unpublished Hons. thesis, University of Tasmania.

Mooney, N. J. and Johnson, K. A. (1979). Methods for the census of wallaby and possum in Tasmania. *Wildl. Division Tech. Report*. Tasmanian N.P.W.S., Hobart.

Morton, S. R. (1978). An ecological study of *Sminthopsis crassicaudata*(Marsupialia: Dasyuridae) II. Behaviour and social organisation. *Aust. Wildl. Res*, **5**, 163-82.

Morton, S. R. and Burton, T. C. (1973). Observations on the behaviour of *Thylogale billardieri*(Desmarest) in captivity. *Aust. Zool.*, **18**, 1-14.

Moss, V. N. (1978). *Studies on the maintenance activities of the Eastern Native Cat* Dasyurus viverrinus *(Shaw, 1800)*. Unpublished Hons. thesis, University of Tasmania.

Myers, K. (1967). Ecology and behaviour - a review of the ways in which Australian ecologists use behaviour in their studies. *Proc. Ecol. Soc. Aust.*, **2**, 79-106.

Nelson, J. E. and Goldstone, A. (1986). Reproduction in *Peradorcas conicinna* (Marsupiaia: Macropodidae). *Aust. Wildl. Res.*, **13**, 501-5.

Nelson, M. M. and Evans, H. M. (1961). Dietary requirements for lactation in the rat and other laboratory animals. In *Milk: the Mammary Gland and its Secretion* Vol. 2. (S. K. Kon and A. T. Cowie, eds). Academic Press, New York.

Newsome, A. E. (1980). Differences in the diets of male and female red kangaroos in Central Australia. *Afr. J. Ecol.*, **18**, 27-31.

Nicholls, D. G. (1971). Daily and seasonal movements of the quokka, *Setonix brachyurus*(Marsupialia) on Rottnest Island. *Aust. J. Zool.*, **19**, 215-26.

Nicol, S. C. (1977). Thyroid function of the potoroo, *Potorous tridactylus*(Kerr). *Aust. J. Zool.*, **25**, 419-21.

O'Callaghan, B. W. (1974). *Studies on the behaviour of* Isoodon obesulus *(Shaw and Nodder 1797)*. Unpublished Hons. thesis, University of Tasmania.

Oppenheim, R. W. (1982). Preformation and epigenesis in the origins of the nervous system and behaviour: issues, concepts and their history. In *Perspectives in Ethology Vol. 5. Ontogeny* (P. P. G. Bateson and P. H. Klopfer, eds). Plenum Press, New York.

Oyama, S. (1982). A reformulation of the idea of maturation. *In Perspectives in Ethology Vol. 5. Ontogeny* (P. P. G. Bateson and P. H. Klopfer, eds). Plenum Press, New York.

Packer, W. L. (1963). Homing behaviour in the quokka, *Setonix brachyurus* (Quoy and Gaimard) (Marsupialia). *J. Roy. Soc. W. Aust.*, **46**, 28-32.

Packer, W. L. (1965). Environmental influences on daily and seasonal activity in *Setonix brachyurus* (Quoy and Gaimard) (Marsupialia). *Anim. Behav.*, **13**, 270-83.

Packer, W. L. (1969). Observations on the behaviour of the marsupial *Setonix brachyurus*(Quoy and Gaimard) in an enclosure. *J. Mammal.*, **50**, 8-20.

Parker, P. (1977). An ecological comparison of marsupial and placental patterns of reproduction. In *The Biology of Marsupials* (B. Stonehouse and D. Gilmore, eds.), Macmillan press, London.

Poole, W. E. (1975). Reproduction in the two species of grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest). II. Gestation, parturition and pouch life. *Aust. J. Zool.*, **23**, 333-54.

Poole, W. E. and Pilton, P. E. (1964). Reproduction in the grey kangaroo, *Macropus canguru*, in captivity. *C.S.I.R.O. Wildl. Res.*, **9**, 218-34.

Priddel, D. (1986). The diurnal and seasonal patterns of grazing of the red kangaroo, *Macropus rufus* and the western grey kangaroo *M. fuliginosus*. *Aust. Wildl. Res.*, **13**, 113-20.

Quin, D. G. (1985). *Aspects of the Feeding ecology of the bandicoots,* Perameles gunnii (*Gray 1838*) *and* Isoodon obesulus (*Shaw and Nodder 1797*) (*Marsupialia: Peramelidae*) *in Southern Tasmania.* Unpublished Hons. thesis, University of Tasmania.

Randolph, P. A., Randolph, J. C., Mattingly, K. and Foster, M. M. (1977). Energy costs of reproduction in the cotton rat, *Sigmodon hispidus*. *Ecology,* **58**, 31-45.

Reynolds, H. C. (1952). Studies on reproduction in the opossum (*Didelphis virginiana virginana*). *Univ. Calif. Publ. Zool.*, **52**, 223-84.

Rigby, R. G. (1972). A study of the behaviour of caged *Antechinus stuartii*. *Z. Tierpsychol.*, **31**, 15-25.

Robbins, M. and Russell, E. (1978). Observations on movements and feeding activity of the koala in a semi-natural situation. In *The Koala: Proceedings of the Taronga Symposium on Koala Biology, Management and Medicine, Sydney, 11th and 12th March 1976.* (Bergin, T. J. ed.). Zoological Parks Board of N.S.W.

Rose, R. W. (1986a). The habitat, distribution and conservation status of the Tasmanian bettong, *Bettongia gaimardi* (Desmarest). *Aust. Wildl. Res.*, **13**, 1-6.

Rose, R. W. (1986b). The control of pouch vacation in the Tasmanian Bettong, *Bettongia gaimardi. Aust. J. Zool.*, **34**, 485-91.

Rose, R. W. and McCartney, D. J. (1982). Growth of the red-bellied pademelon, *Thylogale billardierii* and age estimation of pouch young. *Aust. Wildl. Res.*, **9**, 33-38.

Rosenblatt, J. S. and Lehrman, D. S. (1963). Maternal behaviour of the laboratory rat. In *Maternal Behaviour in Mammals* (H. L. Rheingold, ed.). John Wiley and Son.

Rosenblatt, J. S., Siegel, H. I. and Mayer, A. D. (1979). Progress in the study of maternal behaviour in the rat: hormonal, non-hormonal, sensory, and developmental aspects. In *Advances in the study of Behaviour* (J. S. Rosenblatt, R. A. Hinde, C. Beer, M. Busnel, eds.). Vol. 10, pp 226-311. Academic Press, New York.

Ross, S., Swain, P. B., Zarrow, M. X. and Denenberg, V. H. (1963). Maternal behaviour in the rabbit. In *Maternal Behaviour in Mammals* (H. L. Rheingold, ed.). John Wiley and Son.

Russell, E. M. (1969). Summer and winter observations of the behaviour of the euro *Macropus robustus* (Gould). *Aust. J. Zool.*, **17**, 655-65.

Russell, E. M. (1970a). Agonistic interactions in the red kangaroo *(Megaleia rufa). J. Mammal.*, **51**, 80-88.

Russell, E. M. (1970b). Observations on the behaviour of the red kangaroo (*Megaleia rufa*) in captivity. *Z. Tierpsychol.*, **29**, 385-404.

Russell, E. M. (1971). Changes in behaviour with temperature in the red kangaroo, *Megaleia rufa. Aust. J. Zool.*, **19**, 207-13.

Russell, E. M. (1973). Mother-young relations and early behavioural development in the marsupials *Macropus eugenii* and *Megaleia rufa*. *Z. Tierpsychol.*, **33**, 163-203.

Russell, E. M. (1974a). The biology of kangaroos (Marsupialia. Macropodidae). *Mammal Rev.*, **4**, 1-59.

Russell, E. M. (1974b). Recent ecological studies on Australian marsupials. *Aust. Mammal*, **1**, 189-211.

Russell, E. M. (1979). The size and composition of groups in the red kangaroo *Megaleia rufa*. *Aust. Wildl. Res.*, **6**, 237-44.

Russell, E. M. (1982). Patterns of parental care and parental investment in marsupials. *Biol. Rev.*, **57**, 423-86.

Russell, E. M. (1984). Social behaviour and social organisation of marsupials. *Mammal Rev.*, **14**, 101-54.

Russell, E. M. (1986). Observations on the behaviour of the honey-possum, *Tarsipes rostratus* (Marsupialia: Tarsipedidae) in captivity. *Aust. J. Zool. Suppl.*, **121**, 1-63.

Russell, E. M. and Giles, D. C. (1974). The effects of young in the pouch on pouch cleaning in the tammar wallaby, *Macropus eugenii* Desmarest (Marsupialia). *Behaviour*, **51**, 19-37.

Russell, E. M. and Harrop, C. J. F. (1976). The behaviour of red kangaroos (*Megaleia rufa*) on hot summer days. *Z. Tierpsychol.*, **40**, 396-426.

Russell, E. M. and Nicholls, D. G. (1972). Drinking behaviour in the red kangaroo (*Megaleia rufa*) and the euro (*Macropus robustus*). *Z. Saugetierk.*, **37**, 311-15.

Russell, E. M. and Nicholls, D. G. (1974). Distress vocalisations of young of the red kangaroo, *Megaleia rufa* (Marsupialia: Macropodidae). *Aust. Mammal.*, **1**, 251-4.

Russell, E. M. and Pearce, G. A. (1971). Exploration of novel objects by marsupials. *Behaviour*, **41**, 312-32.

Russell, E. M. and Richardson, B. J. (1971). Some observations on the breeding, age, structure, dispersion and habitat of populations of *Macropus robustus* and *Macropus antilopinus*. *J. Zool., Lond.*, **165**, 131-42.

Russell, R. (1984). Social behaviour of the yellow-bellied glider, *Petaurus australis* in north Queensland. In *Possums and Gliders* (A. P. Smith and I. D. Hume, eds.) pp. 343-53. Australian Mammal Society, Sydney, 1984.

Ryan, A. T., Hale, B., Megirian, D. and Sherrey, J. H. (1983). The effects of hypoxia and CO_2 on the sleep-waking pattern of the potoroo (*Potorous tridactylus apicalis*). *Physiol. Behav.*, **30**, 237-42.

Sampson, J. C. (1971). *The biology of* Bettongia penicillata *Gray 1837*. Unpubl. Ph.D. thesis, University of Western Australia.

Schmidt, G. H. (1971). *Biology of Lactation*. W. H. Freeman and Company, San Francisco.

Schultze-Westrum, T. (1965). Innenartliche Verstandigung durch Dufte beim Gleitbeutler *Petaurus breviceps papvanus*Thomas (Marsupialia: Phalangeridea). *Z. Vergl. Physiol.*, **50**, 151-220.

Seebeck, J. H. (1981). *Potorous tridactylus*(Kerr) (Marsupialia: Macropodidae): its distribution, status and habitat preferences in Victoria. *Aust. Wildl. Res*, **8**, 285-306.

Seebeck, J. H. (1982). Long-nosed potoroo *Potorous tridactylus*: husbandry and management of a captive colony. In *Proceedings of the Scientific Meeting of the Australian Mammal Society, Healesville, Victoria, Feb. 1979* (D. D. Evans, ed.). Zoological Board of Victoria, Melbourne.

Seebeck, J. H. (1983). Long-footed potoroo. In *The Australian Museum Complete Book of Australian Mammals* (R. Strahan, ed.) p. 183. Angus and Robertson, Sydney.

Seebeck, J. H. and Johnston, P. G. (1980). *Potorous longipes*(Marsupialia: Macropodidae); a new species from eastern Victoria. *Aust. J. Zool.*, **28**, 119-34.

Settle, G. A. and Croft, D. B. (1982a). The development of exploratory behaviour in *Antechinus stuartii*(Dasyuridae: Marsupialia) young in captivity. In *Carnivorous Marsupials*(M. Archer, ed.) pp. 383-96. Royal Zoological Society of N.S.W., Sydney.

Settle, G. A. and Croft, D. B. (1982b). Maternal behaviour of *Antechinus stuartii* (Dasyuridae: Marsupialia) in captivity. In *Carnivorous Marsupials*(M. Archer, ed.) pp. 365-81. Royal Zoological Society of N.S.W. Sydney.

Sharman, G. B. and Barber, H. N. (1952). Multiple sex-chromosomes in the marsupial, *Potorous*. *Heredity*, **6**, 345-55.

Sharman, G. B. and Calaby, J. H. (1964). Reproductive behaviour in the red kangaroo, *Megaleia rufa*, in captivity. *C.S.I.R.O. Wildl. Res*, **9**, 58-85.

Shaw, G. and Renfree, M. B. (1984). Concentrations of oestradio-17B in plasma and corpora lutea throughout pregnancy in the tammar, *Macropus eugenii*. *J. Reprod. Fertil.*, **72**, 29-37.

Shaw, G. and Rose, R. W. (1979). Delayed gestation in the potoroo *Potorous tridactylus* (Kerr). *Aust. J. Zool.*, **27**, 901-12.

Shield, J. (1968). Reproduction in the quokka, *Setonix brachyurus*, in captivity. *J. Zool., Lond.*, **155**, 427-44.

Sheild, J. W. and Woolley, P. (1961). Age estimation by measurement of pouch young of the quokka (*Setonix brachyurus*). *Aust. J. Zool.*, **9**, 14-23.

Shillito, E.E. (1963). Exploratory behaviour in the short-tail vole, *Microtus agrestis*. *Behaviour*, **21**, 145-54.

Slater, P. J. B. (1978). Data collection. In *Quantitative Ethology*. (P. W. Colgan, ed.). John Wiley and Sons, New York.

Smith, A. P. (1984). Demographic consequences of reproduction, dispersal and social interaction in a population of Leadbeaters Possum (*Gymnobelideus leadbeateri*). In *Possums and Gliders* (A.P. Smith and I.D. Hume, eds.) pp. 359-73. Australian Mammal Society, Sydney.

Smith, M. (1979a). Behaviour of the koala, *Phascolarctos cinereus*(Goldfuss), in captivity. I. Non-social behaviour. *Aust. Wildl. Res.*, **6**, 117-28.

Smith, M. (1979b). Behaviour of the koala, *Phascolarctos cinereus*(Goldfuss), in captivity. II. Parental and infantile behaviour. *Aust. Wildl. Res.*, **6**, 129-40.

Smith, M. (1980a). Behaviour of the koala, *Phascolarctos cinereus*(Goldfuss), in captivity. III. Vocalisations. *Aust. Wildl. Res.*, **7**, 13-34.

Smith, M. (1980b). Behaviour of the koala, *Phascolarctos cinereus*(Goldfuss), in captivity. IV. Scent marking. *Aust. Wildl. Res.*, **7**, 35-40.

Smith, M. (1980c). Behaviour of the koala, *Phacolarctos cinereus*(Goldfuss), in captivity. V. Sexual behaviour. *Aust. Wildl. Res.*, **7**, 41-52.

Smith, M. (1980d). Behaviour of the koala, *Phascolarctos cinereus*(Goldfuss), in captivity. VI. Aggression. *Aust. Wildl. Res.*, **7**, 177-90.

Smith, M. J. (1983). Desert rat-kangaroo. In *The Australian Museum Complete Book of Australian Mammals* (R. Strahan, ed.). Angus and Robertson, Sydney.

Smolenski, A. (1986). *Comparative Aspects of lactation in* Potorous tridactylus *and* Bettongia Gaimardi. Unpublished Hons. thesis, University of Tasmania.

Sorenson, M. W. (1970). Observations on the behaviour of *Dasycercus cristicauda* and *Dasyuroides byrnei* in captivity. *J. Mammal.*, **51**, 123-30.

Southern, H. N. ed. (1965). *The Hand-book of British Mammals*. Blackwell, Oxford.

Sparks, J. H. (1969). Allogrooming in primates: a review. In *Primate Ethology: essays on the Sociosexual Behaviour of Apes and Monkeys.* (D. Morris, ed). Aldine Publishing Co., Chicago.

Stewart, E. C. F. and Setchell, P. J. (1974). Seismic recording of kangaroo activity. *Search*, **5**, 107-8.

Stickel, L. F. (1954). A comparison of certain methods of measuring ranges of small mammals. *J. Mammal.*, **35**, 1-15.

Stodart, E. (1966a). Management and behaviour of breeding groups of the marsupial *Perameles nasuta* (Geoffrey) in captivity. *Aust. J. Zool.*, **14**, 611-23.

Stodart, E. (1966b). Observations on the behaviour of the marsupial *Bettongia lesueur* (Quoy and Gaimard) in an enclosure. *C.S.I.R.O. Wildl. Res.*, **11**, 91-101.

Stodart, E. (1977). Breeding and behaviour of Australian bandicoots. In *The Biology of Marsupials* (B. Stonehouse and D. P. Gilmore, eds.) pp. 179-92. Macmillan, London.

Stoddart, D. M. and Braithwaite, R. W. (1979). A strategy for utilization of regenerating heathland habitat by the brown bandicoot (*Isoodon obesulus*; Marsupialia, Peramelidae). *J. Anim. Ecol.*, **48**, 165-79.

Strahan, R. (1981). *A Dictionary of Australian Mammal Names*. Angus and Robertson, Sydney.

Strahan, R. ed. (1983). *The Australian Museum Complete Book of Australian Mammals*. Angus and Robertson, Sydney.

Suckling, G. C. (1984). Population ecology of the sugar glider, *Petaurus breviceps*, in a system of fragmented habitats. *Aust. Wildl. Res.*, **11**, 49-75.

Taylor, R. J. (1980). Distribution of feeding activity of the eastern grey kangaroo, *Macropus giganteus* in coastal lowland of south-east Queensland. *Aust. Wildl. Res.*, **7**, 317-25.

Taylor, R. J. (1983a). The diet of the eastern grey kangaroo and wallaroo in areas of improved and native pasture in the New England Tablelands. *Aust. Wildl. Res.*, **10**, 203-11.

Taylor, R. J. (1983b). Association of social classes of the wallaroo, *Macropus robustus* (Marsupialia: Macropodidae). *Aust. Wildl. Res.*, **10**, 39-46.

Taylor, R. J., Bryant, S. L., Pemberton, D. and Norton, T. W. (1985). Mammals of the Upper Henty River Region, Western Tasmania. *Pap. Proc. R. Soc. Tasm.*, **119**, 7-14.

Thomson, J. A. and Owen, W. A. (1964). A field study of the Australian ringtail possum, *Pseudocheirus peregrinus* (Marsupialia: Phalangeridae). *Ecol. Monogr.*, **34**, 27-52.

Triggs, B. (1985). *Mammal Tracks and Signs. A field guide for south-eastern Australia.* Oxford University Press, Melbourne.

Trivers, R. L. (1974). Parent-offspring conflict. *Am. Zool.*, **14**, 249-264.

Troughton, E. (1943). *Furred Animals of Australia.* 2nd ed. Angus and Robertson, Sydney.

Trupin, G. L. and Fadem, B. H. (1982). Sexual behaviour of the grey short-tailed opossum (*Monodelphis domestica*). *J. Mammal.*, **63**, 409-14.

Turner, V. (1984). *Eucalyptus* pollen in the diet of the feather-tailed glider, *Acrobates pygmaeus* (Marsupialia: Burramyidae). *Aust. Wildl. Res.*, **11**, 77-81.

Tyndale-Biscoe, C. H. (1968). Reproduction and post-natal development in the marsupial *Bettongia lesueur* (Quoy and Gaimard). *Aust. J. Zool.*, **16**, 577-602.

Tyndale-Biscoe, C. H. (1973). *The Life of Marsupials.* Edward Arnold, London.

Tyndale-Biscoe, C. H. (1974). Reproduction in marsupials. *Aust. Mammal.*, **1**, 175-80.

Tyndale-Biscoe, C. H. and Janssens, P. A. (1986). Biomedical research: a new role for marsupials. *Search*, **17**, 267-69.

Van Dyck, S. (1979). Behaviour in captive individuals of the dasyurid marsupial *Planigale maculata* (Gould 1851). *Mem. Qld. Mus.*, **19**, 413-31.

Vestal, B. M., Lee, A. K. and Saxon, M. J. (1986). Interactions between adult female and juvenile *Antechinus stuartii* (Marsupialia: Dasyuridae) at the time of juvenile dispersal. *Aust. Mammal.*, **9**, 27-33.

Vase, H. M. (1972). Some observations on a honey possum (*Tarsipes spenserae*) in captivity. *West. Aust. Nat.*, **12**, 61-67.

Vase, H. M. (1973). Feeding habits of the Western Australian honey-possum, *Tarsipes spenserae.* *J. Mammal.*, **54**, 245-47.

Walen, K. H. and Brown, S. W. (1962). Chromosomes in a marsupial (*Potorous tridactylus*) tissue culture. *Nature*, **194**, 406.

Wakefield, N. A. (1970). Notes on the Australian pigmy-possums *(Cercatetus,* Marsupialia) Phalangeridae. *Vict. Nat.,* **87**, 11-18.

Watts, C. H. S. (1969). Distribution and habits of the rabbit bandicoot. *Trans. Roy. S. Aust.,* **93**, 135-41.

Wellington Moore, Jr., D. V. M., Ph.D. and Gillespie, L. J. (1968). Hemogram of the rat-kangaroo, *Potorous tridactylus. Am. J. Vet. Res.,* **29**, 1073-76.

Wells, R. T. (1978a). Thermoregulation and activity rhythms in the hairy-nosed wombat, *Lasierhinus latifrons*(Owens) (Vombatidae). *Aust. J. Zool.,* **26**, 639-51.

Wells, R. T. (1978b). Field observations of the hairy-nosed wombat, *Lasierhinus latifrons*(Owens). *Aust. Wildl. Res.,* **5**, 299-303.

Wemmer, C. and Collins, 1. (1978). Communication patterns in two phalangerid marsupials, the gray cuscus (*Phalanger gymnotis*) and the brush-possum (*Trichosurus vulpecula*). *Saugetierkundl. Mitt.,* **26**, 161-72.

White, G. (1985). *Birds and Other Vertebrates of South West Tasmania (with emphasis on coastal environments*). Published by the author, Sydney.

Wilson, E. O. (1980). *Sociobiology. The Abridged Edition.* The Belknap Press of Harvard University Press.

Wilson, G. R. (1974). How kangaroos swim. *Search,* **5**, 598-600.

Windsor, D. E. and Dagg, A. I. (1971). The gaits of the Macropodidae (Marsupialia). *J. Zool., Lond.,* **103**, 165-75.

Winter, J. and Atherton, R. C. (1984). Social group size in north Queensland ringtail possums of the general *Pseudocheirus*and *Hemibelideus.* In *Possums and Gliders* (A. P. Smith and I. D. Hume, eds.) pp. 311-19. Australian Mammal Society, Sydney, 1984.

Wood-Jones, F. (1923). *The Mammals of South Australia Part I.* Government Printer, Adelaide.

Wood-Jones, F. (1924). *The Mammals of South Australia Part II.* Government Printer, Adelaide.

Woods, J. T. (1960). The genera *Propleopus* and *Hypsiprymnodon* and their position in the Macropodidae. *Mem. Qld. Mus.,* **13**, 199-221.

Wunschmann, A.(1966). Einige Gefangenschafts Beobachtungen an Breitstirn-wombats (*Lasiorhinus latifrons*) Owen, 1845. *Z. Tierpsychol.,* **23**, 56-71.

Young, J. Z. (1950). *The Life of Vertebrates.* Oxford University Press, London.

APPENDICES

Appendix A

Summary of Removal Trapping and an Analysis of
Trap Efficiency in Relation to Trap Design

A.1   Summary of Removal Trapping

Removal trapping was carried out at ten different sites, all within a 40km radius of Hobart. With the exception of three areas, all sites were characterised by *Eucalyptus* spp. and *Casuarina* spp. typical of dry sclerophyll forest. The Leslie Vale trapping site consisted of a mixed association of wet and dry sclerophyll species. The trapping site at Granton was characterised by widespread clearing for the purposes of sheep grazing; consequently it is not surprising that captures of *P. tridactylus* were not made in this area. The trapping site at Kingston was in the initial stages of recovery following an extensive fire and comprised dense thickets of bracken (*Pteridium esculentum*) in association with a sparse covering of *E. viminalis*. The location of all areas trapped are given in Table A.1.

Removal trapping was conducted in accordance with the methods previously described (Section 3.1). The overall total success rate, based on the total number of all species caught over a total of 1221 trap nights, was 21.13%. The success rate for *Potorous tridactylus* was 5.08%. Other marsupials which were frequently captured included:

Trichosurus vulpecula	8.19%
Isoodon obesulus	2.46%
Perameles gunnii	0.57%
Dasyurus viverrinus	3.03%

In addition, three species of rodents were occasionally captured:

Rattus rattus	0.65%
Rattus lutreolus	0.24%
Pseudomys higginsi	0.16%

Several other species were infrequently trapped. A comprehensive summary of all species captured is presented in Table A.1.

A.2 Trap Effeciency in Relation to Trap Design

In a study of the population parameters of the brown bandicoot, *Isoodon obesulus*, Moloney (1982) recorded a considerable disparity between the efficiency of hook and treadle trap designs. He estimated the latter to be 50% less effective in the capture of *I. obesulus*. Similarly, Sampson (1971) has estimated that traps employing a hook mechanism were significantly more efficient in the capture of *Bettongia penicillata*, but found no difference between hook and treadle designs in the success rate for the capture of *I. obesulus* and *Trichosurus vulpecula*.

Such differential trap efficiency has important implications for live-trapping programs that utilize the capture-recapture method for the determination of various population parameters as it violates the assumption that each individual has an equal probability of capture when encountering a trap.

In order to determine the relative efficiency of each type of trap design in the capture of species for which they are frequently employed, the total number of captures accrued throughout both removal and capture-recapture trapping (a total of 4337 trap nights) was examined in relation to trap design. The data was analysed by use of chi-square with Yates' correction and $p < 0.05$ as the selected level of significance.

With respect to *P. tridactylus*, there was no significant difference between the efficiency of hook or treadle designs. However, hook designs were found to be significantly less effective in the capture of *Isoodon obesulus* ($X^2 = 11.358$; d.f.=1; $p < 0.001$) and *T. vulpecula* ($X^2 = 15.858$; d.f.=1; $p < 0.001$).

A considerably high proportion (26.17%) of the traps used in both removal and capture-recapture trapping programs revealed signs of the presence of animals, yet sustained no captures. Chi-square analysis revealed that traps employing a hook mechanism were disturbed significantly more frequently than traps which were operated by a treadle mechanism ($X^2 = 7.475$; d.f.=1; $0.001 < p < 0.01$).

Locality		Undisturbed	Disturbed (No capture)	Potoroo (Potorous tridactylus)	Bettong (Bettongia gaimardi)	Brown bandicoot (Isodon obesulus)	Barred bandicoot (Perameles gunnii)	Native cat (Dasyurus viverrinus)	Brushtail possum (Trichosurus vulpecula)	Ringtail possum (Pseudocheirus peregrinus)	Black rat (Rattus rattus)	Swamp rat (Rattus lutreolus)	Long-tailed mouse (Psuedomys higginsi)	Rabbit (Oryctolagus cuniculus)	Blackbird (Turdus merula)	Starling (Sturnus vulgaris)	Blue wren (Malurus cyaneus)	Grey shrike-thrush (Colluricincla harmonica)	Currawong (Strepera fuliginosa)	Bluetongue lizard (Tiliqua nigrolutea)	Tiger snake (Notechis ater)	Total No. Of Trap Nights
Woodward Prpty	H	80	25	6	0	3	0	2	11	0	0	0	0	0	0	0	0	0	0	0	0	127
	T	81	13	11	0	5	0	0	30	0	0	1	0	0	0	0	0	0	0	0	0	141
Mt. Nelson	H	71	5	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	79
	T	40	1	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	45
Leslie Vale	H	7	17	3	0	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0	33
	T	40	52	17	0	2	0	0	17	0	3	0	2	0	1	0	0	0	0	0	0	134
Hounville	H	56	27	0	0	3	0	6	8	0	0	0	0	0	0	0	0	0	0	0	0	100
	T	60	23	0	0	3	1	5	7	0	2	0	0	0	0	1	1	0	0	0	0	103
Taroona	H	17	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	19
	T	9	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
Ferntree	H	82	36	2	0	2	1	0	12	0	0	0	0	0	0	0	0	0	1	0	0	136
	T	18	9	0	0	1	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	36
Kingston	H	16	14	4	0	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	45
	T	28	15	0	0	3	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	72
Lea	H	10	4	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	17
	T	20	2	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	26
Granton	H	15	7	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	25
	T	15	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
Tinderbox	H	18	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26
	T	17	3	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	26
Porter's Hill	H	1180	622	88	0	131	0	0	36	0	9	0	0	3	12	0	0	2	0	6	0	2135
	T	431	250	35	0	113	4	0	64	1	56	3	0	0	9	0	0	5	0	22	1	981
Grand Total	H	1552	762	108	0	143	3	18	118	1	12	0	0	3	14	0	0	2	1	6	0	2742
	T	759	373	77	1	131	8	19	115	0	61	6	2	0	10	1	1	5	0	24	1	1595
	H+T	2311	1153	185	1	274	11	37	233	1	73	6	2	3	24	1	1	7	1	30	1	4337

Table A.1 Summary of captures sustained during the course of removal trapping (10 localities) and capture-recapture trapping (Porter's Hill) in relation to trap design. (H=hook; T=treadle)

Removal of the bait without activation of the release mechanism accounted for 49.78% of all disturbances. In 26.96% of cases, the bait was not taken, but the release mechanism had been activated. In 14.62% of instances, the bait had been removed and the release mechanism activated but no capture was obtained. Finally, 8.63% of the disturbed traps had been displaced from the site where they were originally set, and in some cases had been moved up to ca. 5m away. In several instances, an animal was found dead nearby. The condition of the carcases of these animals implicated attacks by domestic dogs or domestic or feral cats.

Appendix B

An Observation of Twins in Free-Living *Potorous*

tridactylus

With the exception of the musky-rat kangaroo, *Hypsiprymnodon moschatus*, all macropodoid marsupials typically give birth to a single young. Although the presence of twins has been recorded in a number of species, it is not a common phenomenon. Rates of incidence of twins have been reported as four out of 1990 births (Frith and Sharman 1964) and seven out of 999 births (Newsome 1965) in the red kangaroo, *Macropus rufus*; two out of 328 births in the eastern grey kangaroo, *M. giganteus* (Poole 1975); an estimated one out of 500 births in the euro, *M. robustus* (Ealey 1967) and two out of 262 births in the tammar wallaby, *M. eugenii* (Innes 1980). In many of the observed instances of twins, the young are not monozygotic but, rather, are seperated in age by an interval comparable to the duration of the gestation period.

Several other authors have reported the occurrence of twins in these species (e.g. Sharman and Pilton 1964; Poole and Catling 1974) and other macropodids, including *Setonix brachyurus* (Tyndale-Biscoe, cited in Innes 1980). However, few records of the birth of twins have been documented in members of the family Potoroidae; presumably this is, in part, a reflection of the little research that has been conducted on these species.

The present investigation provides a description of twins in the potoroo *P. tridactylus*. Although twins have previously been reported in captive individuals of this species (e.g. Collins 1973), there appears to have been, to date, no previous descriptions of twins in a free-living individual.

Two young were found to simultaneously occupy the pouch of an adult trapped during the previously described program of capture-recapture trapping. The two young were of the ages 38 and 86 days. The difference in the ages of the two young (48 days) is ten days longer than the gestation period of this species (38 days; Hughes 1962). These observations suggest that the mechanism which normally retains the blastocyst in a

dormant state had failed.

The younger twin was noted to be in poor condition at the time of capture (see Plates 1 and 2), and weighed 85% of the normal weight of a 38 day old pouch young, as given by Guiler (1960a). Further, at the time of initial observation, the young was noted to be off the teat. Since the period of permanent attachment to the teat in this species normally occupies 60 days, it is possible that the presence of the older individual was responsible for the premature dislodgement of the younger individual from the teat. This younger individual died the day following the initial capture.

The pattern of teat selection in the two young was consistent with Hughes' (1962) suggestion that successive young occupy alternate sides of the pouch. The older individual was suckling from the left anterior teat whereas the younger individual was suckling from the right anterior teat. The length of the teats were 22mm and 14mm, respectively, and were considerably longer than the two posterior teats.

B.1 Quantitative Analysis of Milk Composition

Methods

Sufficient quantities of milk from both of the teats utilized by the two young were obtained in order to allow a quantitative assay of carbohydrate, lipid and protein composition to be made. Unfortunately, the death of the younger individual prevented further samples from being taken.

The methods and tehniques employed to obtain milk samples were identical to those employed by Smolenski (1986); consequently they will not be reiterated here. The subsequent analyses of these samples were made following the methods outlined by Smolenski (*op. cit*). The obtained values for the above components of the milk were compared with the values obtained in previous investigations of the same species; i.e. Crowley (1984) and Smolenski (1986). These results are presented in Table B.1.

Scale = 1: 1.65

Plates 1 and 2 Photographs of twin *Potorous tridactylus*. Note the
deteriorated condition of the smaller individual

Results

Table B.1   Summary of the carbohydrate, lipid and protein content (g/100mls) in the milk of the teats suckled by twin pouch young of disparate age, in relation to previously obtained values for single young at the same age.

	Present study twins	* Crowley (1984) single young	*Smolenski (1986) single young
Protein			
38 days	6.5	5	3-4
86 days	7.2	6.5	8
Lipid			
38 days	5.6	1	2
86 days	6.8	1	4
Carbohydrate			
38 days	9.9	7	10-11
86 days	10.3	10	10-11

*values are approximate only

Discussion

It should be noted that the values obtained for the twin pouch young are based on the analysis of a single sample of milk and hence are of limited value for comparative purposes. Nevertheless, the results outlined in Table B.1 suggest that the milk secreted by the two mammary glands utilized by the twin potoroos do differ with respect to protein and fat concentration. As Smolenski (1986) and Crowley (1984) have shown, the levels of both of these substances increase during the pouch life of young. Interestingly, the levels of these components in the milk from the teat suckled by the younger twin were considerably higher than that which would be expected for a single pouch occupant of the same age.

Normally, when older young commence their vacation of the pouch at 112 days, the decrease in the frequency of suckling initiates the resumption of the development of the

previously dormant blastocyst. By the time the older young has permanently vacated the pouch the next young is born. At this point the mother is producing milk of two very different compositions to suit the requirements of both the new pouch young and the young at foot. This situation is short lived since the older individual is weaned soon after. The case of the twin-bearing female is unusual in that milk of two different compositions were being produced in the middle of the cycle of lactation rather than at the point of birth of the new young and weaning of the older young.