



# Biparental care and obligate monogamy in the rock-haunting possum, *Petropseudes dahli*, from tropical Australia

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Monogamy is rare among mammals, including marsupials. I studied the social organization of the little-known rock-haunting possum in Kakadu National Park in Northern Australia. Preliminary field observations revealed that the majority of possums live in cohesive groups consisting of a female–male pair and young, suggesting a monogamous mating system. I used radiotracking to determine home range patterns, and observations to measure the degree of symmetry between the sexes in maintaining the pair bond and initiating changes in group activity. I also measured the extent of maternal and paternal indirect and direct care. Nocturnal observations and radiotelemetric data from 3 years showed that six possum groups maintained nonoverlapping home ranges with long-term consorts and young sharing dens. Males contributed more than females to maintaining the pair bond but they contributed equally to parental care. For the first time, the parental behaviours of bridge formation, embracing, marshalling of young, sentinel behaviour and tail beating are reported in a marsupial. Males participated to a high degree in maintaining relationships with one mate and their offspring. Collectively, these results suggest that the mating system of this wild population of rock-haunting possums is obligate social monogamy.

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Monogamy is common in birds, but rare among mammals. This may be due to much of the young mammal's development occurring internally rather than externally and the production of milk by mothers for food. This leaves little for the male to contribute to the rearing of young (Orians 1969). Why males should remain faithful to one partner in mammalian species is unclear, and several hypotheses have been proposed to explain the evolution of monogamy (Clutton-Brock 1989). The majority of these seek to explain two main types of monogamy, facultative and obligate (Kleiman 1977). Facultative monogamy describes systems where males will usually mate with other females if given the opportunity and provide only limited paternal care (Kleiman 1977). It is thought to evolve when males are unable to monopolize more than one female, either because females are highly dispersed (Kleiman 1981) or because males are unable to defend home ranges large enough to accommodate more than one female (Gosling 1986). In contrast, obligate monogamy is usually associated with extensive male care (Clutton-Brock & Harvey 1976; Kleiman & Malcolm 1981), and is thought to evolve because male care is required for the successful rearing of offspring (Clutton-Brock 1989; but see Komers 1996).

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The need for male care is widely accepted as an explanation for the evolution of obligate monogamy in mammals (Kleiman & Malcolm 1981; Clutton-Brock 1989). Direct male care includes socialization, allogrooming, contact with and huddling with young, retrieving and transporting young, active defence, babysitting and providing food to young (Kleiman & Malcolm 1981). Behaviours representing indirect 'male parental investment' include antipredatory behaviours, territorial maintenance and investment in the pair bond ('provisioning the female': Kleiman & Malcolm 1981). Other characteristics of obligate monogamy include cohesive and persistent pair bonds between adults, with mutual or asymmetrical attraction (Eisenberg et al. 1972; Kleiman 1981) and strong bonds between paired adults and their slowly developing young (Kleiman & Eisenberg 1973). In contrast, facultative monogamy is characterized by weak social relationships between adult females and males and their young (Palombit 1996).

To date, most work on monogamy has focused on eutherian mammals, while marsupials have received less attention. The dominant role of the female is exemplified in the marsupial radiation, where pouches offer a mode of protection and transport of young that males cannot provide. None the less, arboreal marsupials have a wide range of mating systems including monogamy. For example, yellow-bellied gliders, *Petaurus australis*, live in

groups ranging from an adult pair and one or two offspring (Henry & Craig 1984; Craig 1985; Goldingay & Kavanagh 1990) to polygynous groups of up to five adults (Russell 1984). These gliders may even alternate between mating strategies in some populations (Russell 1984; Goldingay 1992). Other marsupials thought to be socially monogamous include the long-footed potoroo, *Potorous longipes* (Scotts & Seebeck 1989; Green et al. 1998), the allied rock wallaby, *Petrogale assimilis* (Horsup 1986; Barker 1990), and two possums in the family Pseudocheiridae, *Hemibelideus lemuroides*, and *Pseudocheirus peregrinus* (Winter 1996).

Although direct male care has been reported for ca. 2% of marsupials, no research has been done to determine whether marsupials display facultative or obligate monogamy. If male care is necessary for successful rearing of the young, then we should expect to see such behaviour in monogamous marsupials. Paternal care has been recorded in extended family groups of the polygynous sugar glider, *Petaurus breviceps* (Schultze-Westrum 1965; Suckling 1980; Klettenheimer et al. 1997) and Tasmanian devil, *Sarcophilus harrisii* (Turner 1970), but these studies involved captive animals and were not supported by data from wild populations. Thus, there is still no strong evidence that males provide direct care in wild populations of marsupials. My aim in this study was to assess where the little-known *Petroseudes dahli* (family Pseudocheiridae) fits on the monogamy–polygyny continuum.

My preliminary field observations revealed that these possums live in family groups consisting of an adult female and male with up to two offspring from different seasons. Both adults remain close to one another and their young throughout nocturnal foraging excursions. Like other possums, the young spend their early life in the mother's pouch and ride on her back as they grow older. Before dispersing, they travel independently but remain with the family group. Collectively, these observations suggested that these possums have a monogamous mating system. For monogamy to be obligate rather than facultative, I would expect evidence of both females and males investing in their pair bond and in the young. To determine the degree of social monogamy in this species I asked four questions. (1) Is there symmetry or an asymmetry between the sexes in maintaining the pair bond? (2) Which sex dominates the decision-making process in terms of changes in group activity? (3) To what extent is there paternal care? (4) Do home ranges overlap and are territories exclusive?

## METHODS

### Study Animals

*Petroseudes dahli* is a large, rock-living possum (2 kg) with a wide distribution across tropical northern Australia, from Western Australia to Queensland (Kerle & Winter 1991). Very little is known about its biology. My studies revealed possums used rock crevices as dens and, at night, moved from the rocks to feed in nearby trees where they ate leaves, fruits and flowers.

### Study Site

The study site was located in Kakadu National Park, northern Australia, on the edge of the Arnhem Land Plateau. The site (2.2 km<sup>2</sup>) is bordered by the East Alligator River to the east, the Magella floodplain to the north, the Arnhem Land Plateau to the west and a tributary of the East Alligator River to the south. Erosion of the Arnhem Land Plateau during the Tertiary period left numerous sandstone outliers on the flat lowlands within the site. These isolated rock outcrops are 5–100 m high and deeply fissured. Dry rainforest trees surround the rock outliers, but further from the rocks tall woodland species such as *Eucalyptus miniata* and *E. tetradonta* dominate. Each year park rangers burn the region early in the dry season to prevent 'hot' destructive fires. There are two distinct seasons: a dry season from May to September and a wet season from November to March, with an annual rainfall of 1400 mm. Potential predators of possums in the area include owls, dingoes, *Canis familiaris*, feral cats, *Felis catus*, northern quolls, *Dasyurus hallucatus*, saltwater crocodiles, *Crocodylus porosus*, and Oenpelli pythons, *Morelia oenpelliensis*.

### Identification of Individuals

I caught four adult possums by hand and fitted each of them with a radiocollar consisting of a soft leather collar with a two-stage radiotransmitter (Sirtack, Havelock North, New Zealand, 24-g transmitter, <1% possum body mass). I cut each leather collar to create a weak point so that it would fall off the animals if they were not recaptured. A short (5 cm), flexible antenna attached to the transmitter canister was directed over the back of each animal. I attached various colour combinations of road-sign reflective tape to each collar, transmitter canister and antenna to facilitate nocturnal identification of individuals at a distance. This tape was visible only when strong light was directed towards it and was unlikely to affect predation. I partially covered the first possum I captured (adult female) with a cloth bag while I fitted the radiocollar. Although this possum remained calm, I decided to anaesthetize subsequent animals to allow me to take blood samples (0.5–1.5 ml was taken from the brachial artery for future genetic work), and to minimize disturbance to the possums. I anaesthetized the remaining three possums (two females, one male) by intramuscular injection of Zoletil (Tiletamine/Zolazepam, dosage 5 mg/kg). Recovery time for anaesthetized animals was variable (15–45 min). I waited until they were fully recovered (90–330 min after initial recovery) before releasing them at their site of capture. I am confident that the handling process, radiocollars and field tracking did not visibly influence possum behaviour or encourage predation.

The study was approved by the Northern Territory University Animal Experimentation Ethics Committee and was carried out under Regulation 27 of the National Parks and Wildlife Regulations.

The four radiocollared individuals allowed me to identify seven adult individuals from three possum groups. Members of one group included two radiocollared adult

**Table 1.** Behavioural classes involving behavioural interactions between possums

Initiation of pair bond maintenance	Initiation of group activity changes	Parental care
Move to within 1 m	Sit	Allogroom
Follow	Move along rocks	Sit on
Sit in contact	Move from rocks to trees	Sit in contact
Climb over	Move in tree	Embrace
Sit on	Move between trees	Bridge formation
Allogroom	Move to rocks from tree	Babysit
Vocalize towards		Naso-naso
Naso-naso		Naso-buccal
Naso-buccal		Naso-rump
Naso-rump		Naso-frontal
Naso-frontal		Climb over
		Tail beat
		Move to within 1 m
		Follow
		Sentinel

Parental care behaviours were interpreted as direct care apart from climb over, tail beat, move to within 1 m, follow and sentinel which were interpreted as indirect care.

females, an adult male and young. Two other possum groups both included one radiocollared adult, another adult of the opposite sex and young. I used a combination of factors such as location, group size and age of young to identify three additional possum groups. Breeding is asynchronous with a maximum of two young born in a year; thus, each group had young of different sizes (and number) at any one time. Within these three groups, I distinguished between the adult sexes by the presence of testes or a pouch.

### Behavioural Observations

Binoculars (10 × 50, wide angle 7°) and a 6-V miners' headlamp aided nocturnal observations. I covered the torch beam with red cellophane to reduce disturbance to the possums. To ensure minimal observer effect, I observed possums from a distance of 10–30 m and commenced observation sessions only after one adult possum of the group began to feed, groom, or move towards the trees growing away from the rock. I stopped sessions when possums moved out of view and recommenced observations only if I was able to follow the group without disturbing them. During the study I identified 16 different possum groups, and collected home range data for six of these groups. I obtained 2132 fixes of 13 adult possums over 160 nights. The number of individual fixes ranged from 8 to 50 ( $\bar{X} \pm SD = 29 \pm 14$ ) and were recorded over 3–36 months ( $\bar{X} \pm SD = 23 \pm 11.5$ ). Home range sizes were estimated by the minimum convex polygon method.

### Cohesiveness

I used scan sampling (Altmann 1974) to measure cohesiveness within possum groups. I recorded the distance to the nearest possum every 5 min for an average of 82 min per session. Possums were observed between 2200

and 0200 hours during September 1996, October 1996 and March 1997. I made nine observations of six possum groups (one or two observations per group, 18 individual possums) with 16–150 nights between replicate observations of the same group. A total of 12.25 h of data were collected.

### Pair Bond Maintenance and Parental Care

I used focal (sub) group sampling (Altmann 1974) to measure the overall level of symmetry in pair bond maintenance within each group. Possums were observed between 2200 and 0200 hours during May, July, October and November 1997 and April, May and August 1998. I made 35 observations of six possum groups (three to nine observations per group, 18 individual possums) with 1–180 nights between replicate observations of the same group. A total of 45.20 h of data were collected.

Behaviours of possums were categorized into three classes: (1) pair bond maintenance; (2) initiation of changes in group activity; and (3) parental care (Table 1). Pair bond maintenance and initiation of changes in group activity involved interactions between adult males and females. I classified parental care behaviours as direct and indirect care of the young. Direct care involved interactions between adults and young possums, and included 'allogrooming', 'bridge formation' and 'baby-sitting'. Similarly, the behaviours 'embracing', 'sitting on' and 'in contact' with young were interpreted as direct care behaviours because they are associated with resting with young (Kleiman & Malcolm 1981). Direct care behaviours that assist with the social development of young include nasal sniffing and greetings (after Kleiman & Malcolm 1981) such as 'naso-buccal', 'naso-rump', 'naso-frontal' and 'naso-naso'. Indirect care behaviours involve antipredatory and territorial activities.

Three behaviours that require definition are the embrace, bridge formation and tail beat. Embraces

involved possums placing both forearms around the body of a young possum while the young sat in close contact with the adult's chest. Bridge formation is the method adults used to provide access for juveniles, no longer at back young stage, to tree branches out of reach. The adult stretched its body between the two branches and froze until the young ran over their back and on to the new branch. Tail beating is the act of rhythmically beating the bare underside of the tail against a branch or rock resulting in a 'slapping' noise, or in more vigorous situations, violent shaking of the tree. It may warn young of the presence of predators.

### Data Analysis

Owing to limited data for two groups, I restricted my analysis to the four groups for which I had large sample sizes. I summed the total frequency of behaviours observed within each of the three behavioural classes (Table 1) to obtain a raw score for each individual on each night. Because observation times varied, I standardized these scores according to the average duration of observation sessions (85 min). That is, for each night's observation, I divided the raw frequency score for an individual by the duration of that observation session (min) and then multiplied by 85 (min). The data were analysed using a repeated measures ANOVA with group (four groups, random repeated measures factor) and gender as factors, and with sample night as the repeated measure (5 nights, random repeated measures factor nested in group and gender).

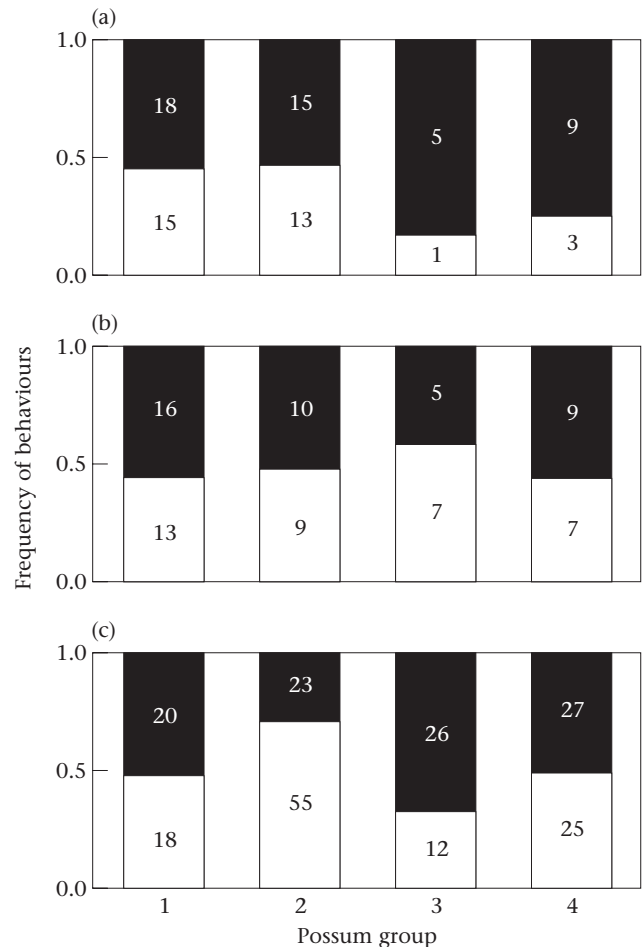
### Sentinel Behaviour

Sentinel watch is an antipredator behaviour that is a form of indirect parental care (Kleiman & Malcolm 1981). Typically, possums on sentinel watch sat on low branches or on exposed rock ledges and faced outwards with their eyes wide open. I recorded sentinel behaviour from five groups during eight observation sessions (one to three sessions per group, 12 h total). I used scan sampling every 30 s and collected data between 2200 and 0200 hours.

## RESULTS

### Group Structure and Cohesiveness

Of the 16 possum groups, 15 consisted of an adult female and an adult male, often with young from one or two generations. Young possums ranged in maturity and size from pouch young (15% of adult size) to large independently mobile young 80% of adult size. Only one group differed from this type of family unit: this was a stable adult group of two females and one male, with young. Regardless of group size and structure, all possums moved and foraged in a coordinated manner. During the study all the possums I observed kept close to other members of their family groups, and seldom ventured 1 m from another individual (mean distance between individuals  $\pm$  SD =  $0.7 \pm 0.76$  m, range 0–4 m).



**Figure 1.** Relative frequency of behaviours that: (a) contributed to the maintenance of pair bonds; (b) can be interpreted as behaviours involved in changing group activity; and (c) involved direct and indirect care in four possum groups. Sentinel behaviours are not included in (c). □: Females; ■: males. Numbers on bars indicate total number of observations for each individual possum from each group.

### Pair Bond Maintenance

Males were more likely to initiate behaviours that could contribute to maintaining the pair bond (Fig. 1a). There was no significant difference between groups (ANOVA:  $F_{3,16}=1.58$ , NS) or interaction between sex and group ( $F_{3,16}=0.07$ , NS) but there was a significant difference between the sexes ( $F_{1,3}=85.04$ ,  $P<0.05$ ). The most common behaviour observed in this class was 'maintaining close proximity to each other', whereby possums followed the leading possum when travelling across the rocks or between trees, moved to within 1 m of, or sat in contact with their mate. Both sexes were leaders, with females (six individuals, 27 observations) leading at similar rates as males (six individuals, 22 observations;  $\chi^2_1=0.5$ , NS). Males climbed over females (three observations) but females did not climb over males. Male pair bond maintenance occurred year round and included times when the female was not in oestrus. Family group members always shared dens (three groups, mean den

number 1.3, range 1–2) within rock torrs, further facilitating the reinforcement of bonds.

### Initiation of Group Activity Change

The results showed close synchrony of all activities by the adult male and the adult female (Fig. 1b). There was close coordination between pairs and sharing of roles. Neither sex initiated a change in group activity more than the other. There was no significant difference between the sexes (ANOVA:  $F_{1,3}=1.89$ , NS) or groups ( $F_{3,16}=0.5$ , NS) with no interaction between sex and group ( $F_{3,16}=0.57$ , NS).

### Direct Care

There was no significant difference between groups in the symmetry of parental care (Fig. 1c). There was no significant difference between the sexes (ANOVA:  $F_{1,3}=0.21$ , NS) or groups ( $F_{3,16}=0.17$ , NS) and there was no interaction between sex and group ( $F_{3,16}=1.08$ , NS). I observed behaviours associated with direct care of the young in both males (four individuals, 26 observations) and females (five individuals, 22 observations). Resting in contact with young and mutually greeting them made up the highest frequencies of direct care behaviours. Four of six groups had a female or a male crouch and sit in contact with young. Two groups had both. Males crouched and sat in contact with young (four individuals, seven observations) at triple the rate of that of mothers (two individuals, two observations).

### Indirect Care

Indirect care behaviours did not differ between the sexes (ANOVA:  $F_{1,3}=0.002$ , NS) or groups ( $F_{3,16}=0.34$ , NS), with no interaction between sex and group ( $F_{3,16}=0.62$ , NS). Males moved to within 1 m of the young more often (four individuals, seven observations) than females (one female, two observations).

### Antipredator Behaviour

Both sexes showed antipredator behaviours such as sentinel watch, tail beating, vocalizations and marshalling of the young. Tail beating occurred at equal frequencies in males and females, and was observed only in response to the presence of dingoes or myself. Another parental care behaviour shared by both sexes was the marshalling of young. When family groups moved between trees or over rocks, they always travelled in a line with the young positioned between the adults. Males took the lead on 22 occasions (four different males, four groups) and females on 25 occasions (six different females, six groups;  $\chi^2_1=0.19$ , NS). Females vocalized more often (three individuals, three observations) than males (no observations).

### Home Ranges

The home ranges of six possum groups were discrete and nonoverlapping (Fig. 2) and ranged in size between

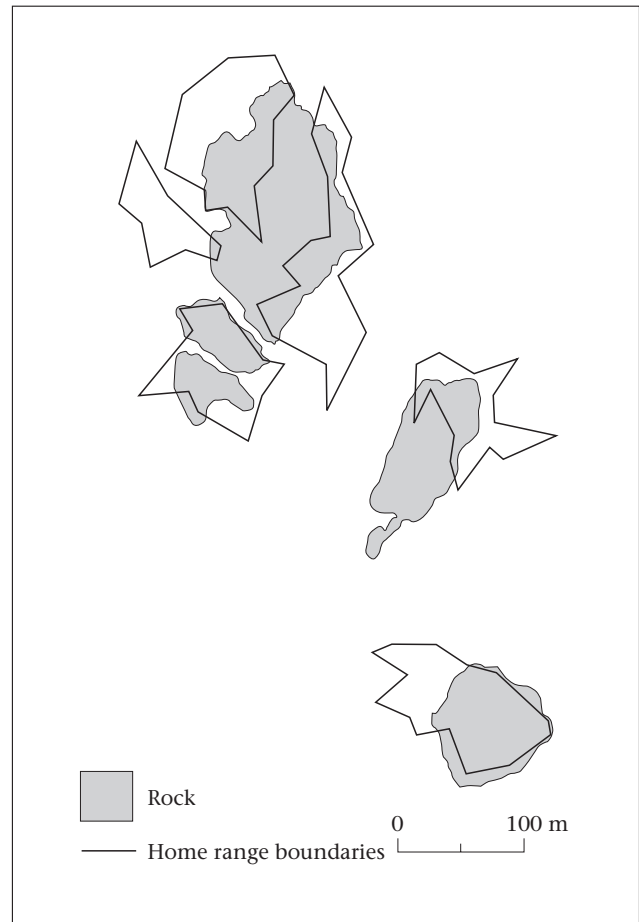


Figure 2. Home ranges of six possum groups studied over 3 years.

0.5 and 1.2 ha (mean 0.9 ha). Females and their mates had exactly the same home ranges. Density was calculated to be 0.4 adult possums/ha. I observed both sexes engaging in scent marking within their home ranges. To scent-mark, possums rubbed or pressed their cloacal-caudal region or chest against the rock surface or tree branch. Scent marking was most vigorous around den sites, but possums also marked rock ledges and trees within their home ranges. Scent marking was observed within all group home ranges. The sexes scent-marked equally often (females: 11 observations; males: 12 observations). No overt agonistic behaviour was observed between possum groups. However, I observed two possums of unknown gender from different groups adopt a stiff upright posture with widely opened eyes, which they directed towards possums from neighbouring groups 20 m away.

### Maternal Aggression

I observed one adult female defending very small pouch young on two occasions. This female directed an open paw and forearm swing at her mate who moved past the young while it was seated on a narrow horizontal branch. A short growl accompanied this gesture and afterwards the mother immediately scooped the young

on to her back. This mother directed a similar behaviour towards her subadult offspring who sat on her briefly while descending a vertical tree trunk, possibly jeopardizing her grip.

### Polygynous Group

Compared with the other groups, members of group 6 showed a similar frequency of behaviours in only the 'pair bond maintenance' class of behaviours. The male initiated very few changes in group activity and contributed to only one direct parental care behaviour (babysitting). He sat on a low branch within 1 m of a stationary juvenile possum while the other group members fed.

## DISCUSSION

My results show that female *P. dahli* shared small home ranges with one male (Fig. 2) who assisted with care and protection of the young (Fig. 1c). Individual possum groups maintained discrete nonoverlapping home ranges, and their maintenance was carried out by both sexes in the form of extensive scent marking. Dens and foraging areas were the most heavily marked areas within group home ranges, which suggests a high degree of resource defence. These results, together with my detailed behavioural observations, strongly suggest that *P. dahli* shows obligate monogamy. For example, one consistent feature of obligate monogamy is the existence of cohesive and persistent pair bonds with mutual or asymmetrical attraction between adults (Eisenberg et al. 1972; Kleiman 1981). I found that both sexes of *P. dahli* maintained strong pair bonds, as shown by the diverse array of maintenance behaviours, which is a measure of bond 'strength' (Hinde 1983). Males maintained the pair bond at a higher rate than females (Fig. 1a) and participated in extensive paternal care, including direct care (Fig. 1c). Both sexes shared the decision-making process in terms of changing group activity (Fig. 1b).

A second attribute of obligate monogamy is the presence of long-lasting bonds between parents and young (Kleiman & Eisenberg 1973). Such bonds occur in a range of obligate monogamists including gibbons, canids (Kleiman & Eisenberg 1973) and dwarf mongoose, *Helogale undulata rufula* (Rasa 1987). In marsupials, another possum in the family Pseudocheiridae, *Pseudocheirus peregrinus*, may have postweaning relationships between mother and daughter. However, a study from one population suggests that pair bonds are not maintained year round (Thomson & Owen 1964). In my study, both sexes of *P. dahli* showed substantial long-term care of offspring. The most unusual interactions I observed between parents and young were the embrace by adult males and the bridge formation. I observed both sexes embracing young, whereas only females engaged in bridge formation. These behaviours have not been reported in marsupials, but a similar form of embrace has been observed in primates. Embraces among primates are thought to inform adults of the stage of maturation in

offspring (Carpenter 1940) or are a way subordinates are reassured by dominant group members (Ellefson 1974). In siamang, *Hylobates syndactylus*, embraces are thought to play a role in maintaining pair bond affinity (Palombit 1996). In *P. dahli*, adults only embraced young, and males embraced young for long periods, yet they cannot provide milk nor did they offer transport. Thermoregulation is of low priority in the tropics, and males are not dominant group members. Rather, the young actively snuggled under the male's body, suggesting that reassurance is required.

A third feature of obligate monogamy is the rearing of younger siblings by juveniles (Kleiman 1977). In other pair-forming possums, (e.g. *Ailuros ursinus*, *Trichosurus caninus*, *H. lemuroides*, *P. peregrinus*), there is no overlap of young (Winter 1996). In contrast, *P. dahli* have overlapping generations of young, and I observed young interacting with each other on several occasions. Large groups of possums have been reported in other populations of *P. dahli*, suggesting that in some cases juveniles may help to rear siblings (Kerle & Winter 1991). In my study one possum group consisted of two adult females and an adult male, which suggests that juveniles may stay with the group. Clearly, further work is required to establish the frequency of this group structure within a predominantly monogamous system.

What factors have led to the evolution of monogamy in rock-haunting possums? The most widely accepted view is that monogamy evolved because of the need for biparental care, such as provision of food for young (Orians 1969; Kleiman 1977; Kleiman & Malcolm 1981). Clearly, opportunities for herbivores to provide food to their young are limited. None the less, male *P. dahli* may provide young with a greater potential for learning to recognize and consume a wider range of food types than if the young were exposed only to their mother. These possums forage all year round in a close-knit group, with both sexes initiating and taking turns at leading the group to food trees. Food choice is thus made by two adults, not just one, which may enable young possums to experience a broad range of plant materials.

Several authors have suggested that mammalian monogamy may have evolved in response to predators (Kleiman & Malcolm 1981; Clutton-Brock 1991). Thus, *P. dahli* may have evolved obligate monogamy and biparental care in response to a range of past predators such as the smaller thylacinids and the dasyuroids of the Miocene, as well as more recent predators such as dingoes. Significantly, *P. dahli* is the only marsupial known to show sentinel behaviour and they have a wide range of antipredator behaviours including a well-coordinated sentinel system that involves both sexes. Furthermore, both males and females tail-beat in response to the presence of predators (dingoes and humans). Tail beating can be likened to the footdrum of kangaroos and has been interpreted as parental care in kangaroo rats, *Dipodomys spectabilis*, with mothers informing their young of the presence of predators (Randall & Matocq 1997). In *P. dahli*, groups of two adults and one or two offspring may be the optimum size for living cryptically and evading predators. Males can provide antipredator protection

and are likely to assist with reinforcing antipredator behaviours in young.

Although the biparental care hypothesis has received most attention (Clutton-Brock 1989), the most recent phylogenetic analysis of the evolution of monogamy in mammals suggests that solitary females that occupy small and exclusive ranges promote monogamy more than any other feature (Komers & Brotherton 1997). These spatial attributes of females allow males to monopolize single females. In my study, female *P. dahli* had home ranges that were both small and exclusive (Fig. 2). Pairs maintained long-term home ranges on isolated rock outcrops and actively scent-marked within them. The mean home range size of *P. dahli* (0.6 ha) is much smaller than that predicted (6.0 ha) for plant-eating mammals of similar body size (Peters 1986), which supports the female space use hypothesis (Komers & Brotherton 1997). The home ranges of *P. dahli* may be smaller than expected because plant productivity and species richness increase with proximity to rock outcrops in the wet-dry tropics (Freeland et al. 1988).

Why do male *P. dahli* remain with the same female, rather than attempting to monopolize multiple females? The fact that males remain in close contact with the same female throughout the night, and share the same den by day, suggests that males guard one female permanently. Oestrus is asynchronous, so if mate guarding was important only during female oestrus, then I would expect males to mate with other females. Theoretically, a male could guard each oestrous female at a time. However, because female home ranges are exclusive, the risks of predation for a male moving between rocky shelter sites to guard more than one female would be high. Moving between females would also leave unguarded females exposed to unpaired males. Thus, to monopolize a single female, male *P. dahli* may be forced to guard females permanently, as occurs in other monogamous mammals (e.g. Kirk's dikdik, *Madoqua kirki*, see Komers 1996). My results support the notion that monogamy may have evolved as a result of male mate guarding (Brotherton & Manser 1997).

An alternative hypothesis for the evolution of monogamy is that males are not able to defend resources required by multiple females (Murray 1984; Gosling 1986). However, several authors have pointed out that there is little evidence to support this hypothesis in mammals (Clutton-Brock 1989; Anzenberger 1992). In my study, one of 16 possum groups consisted of an adult male with two adult females. This suggests that males can defend enough resources for more than one female. However, it is unclear whether the two females in this group were related.

In conclusion, my behavioural studies have revealed extensive biparental care *P. dahli*. Several factors that may have contributed to the evolution of monogamy in this species include the need for biparental care, predator protection, mate guarding and the occupation of small discrete home ranges by solitary females. For the first time, the parental behaviours of bridge formation, embracing, marshalling of young, sentinel behaviour and tail beating are reported in a marsupial. In *P. dahli*, both

sexes maintained the pair bond and initiated group activity changes, there was a high degree of paternal care, and pairs maintained small and exclusive home ranges. Collectively, these results suggest that this marsupial shows social obligate monogamy.

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