Original Investigation

Reproduction and ontogeny of *Mastacomys fuscus* (Rodentia: Muridae) in the Australian Alps and comparisons with other small mammals living in alpine communities

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ABSTRACT

Two species of small rodents, *Mastacomys fuscus* and *Rattus fuscipes*, and one small dasyurid marsupial *Antechinus swainsonii* live sympatrically in the subalpine habitat of SE Australia. This paper describes the reproductive characteristics and ontogeny of *M. fuscus*, and shows that the three species have different reproductive strategies that, in part, are a reflection of their different phylogenies. Cold and snow in winter, and a short summer season, limit the length of time available for reproduction and development. The rodent species exhibit similar reproductive characteristics to those in alpine regions of Europe, North America and South Africa.

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Introduction

Reproduction of small mammals living in alpine habitats is restricted to a short period of the year when environmental conditions are least unfavourable. Studies on individual species in the Northern Hemisphere have shown that the duration of the reproductive season (births) is shorter, and females on average have fewer litters per year, at higher altitudes than at lower altitudes and that young never (or rarely) breed in the year of their birth (Millar 1984; Millar and Innes 1985; Le Louarn and Janeau 1975; Janeau and Aulagnier 1997). None of these studies has considered whether there is a range of different reproductive strategies within a community of sympatric small mammals in alpine habitats. Even less is known about reproduction of alpine small mammals in the Southern Hemisphere.

The Australian Alps of mainland Australia support a community of four species of endemic terrestrial small mammals: two are rodents (*Mastacomys fuscus* Thomas, 1882 and *Rattus fuscipes* (Waterhouse, 1839)), and two are marsupials (*Antechinus swainsonii* (Waterhouse, 1840) and *Burramys parvus* Broom, 1896). In Kosciuszko National Park (KNP), the first three species co-exist throughout most of the alpine and subalpine habitats, the fourth occurs only in rocky habitats at higher altitudes (where it co-exists with the other three species). The principal species of this study is *Mastacomys fuscus*, a species found only above c 1000 m in KNP (K. Green, pers. comm.). Although described in 1882, very little was

known about its distribution and ecology until the 1960s (Calaby and Wimbush 1964). More recent studies have embraced a wider range of investigation including home range (Bubela et al. 1991), diet (Carron et al. 1990), habitat selection (Carron 1985), social organisation (Bubela and Happold 1993) and distribution (Green and Osborne 2003); further information on *M. fuscus* is given by Happold (1983, 1989, 1998).

The aims of this study were (a) to describe the reproduction and ontogeny of *M. fuscus* in captivity, and hence to provide a means of aging young individuals in their natural habitat, and (b) to compare the reproductive strategies of *M. fuscus* with the three sympatric species and with similar alpine small mammals in other parts of the world. A future paper will describe the demography of *M. fuscus*, *R. fuscipes* and *A. swainsonii* over a period of nine years.

Materials and Methods

The data presented in this paper have been derived from studies in the field and in captivity. The field study site was in a valley close to Smiggin Holes (36°24'S, 148°26'E, ca. 1650 m a.s.l.) in Kosciuszko National Park, New South Wales, Australia. The habitat is characterised by extensive heathlands (primarily *Prostanthera*, *Phebalium*, *Callistemon*, *Leptospermum*, *Hovea*, and *Kunzea*) with *Poa* grass tussocks forming an understorey. Bogs and subalpine woodlands (mainly composed of snow gums *Eucalyptus pauciflora* ssp. *niphophila*) interdigitate with the heathlands and grasslands (Costin et al. 1979). A small stream runs through the centre of the study area. The climate is similar to that in other subalpine regions of the world: summer is temperate with a considerable daily range in temperature, and winter is cold with below freezing temper-

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atures at night, and with snow (90–350 cm in depth) for 18–25 weeks of the year (Happold 1998). General descriptions of the Australian Alps, and its flora and fauna, are given by Costin et al. (1979), Good (1989), and Green and Osborne (1994).

Captive colonies were established from individuals captured at several localities (1400–1700 m) close to Smiggin Holes. The only way was to establish breeding pairs was to house them in large outdoor semi-natural enclosures; individuals placed in indoor cages did not form male–female bonds (often the male was killed) and they did not breed. Six enclosures were constructed in the grounds of the Australian National University in Canberra (35°18S, 149°08E, ca. 600 m). Each enclosure was made from the galvanised metal of an above-ground swimming pool (4 m diameter, 90 cm tall); it was placed on chicken netting (2.5 cm mesh) which formed a “mouse-proof” seal. Soil was placed on top of the netting and was sowed with mixed grass seed; logs were placed randomly on the soil surface. The top of the enclosure was covered with similar sized netting to exclude predators. A water sprinkler was placed in the centre of each enclosure (above the upper netting) and the times of sprinkling were controlled by a computer clock. Three or four nestboxes (15 cm by 15 cm by 20 cm tall) made of wood and with a hinged lid and circular entrance hole were placed close to the logs. When fully established, each enclosure was a ‘semi-natural’ moist environment covered with long grass and herbs and with many places for shelter. The enclosures were subject to the natural temperate climate (including frosts in winter), although during the hot summer months they were covered with 80% shade cloth. Part of the upper netting could be opened allowing access into each enclosure for examination of the animals and the nestboxes. Each enclosure contained one or more females and at least one male at all times. Some pregnant females (field caught or from the enclosures) were placed in large glass-fronted observation cages so that detailed observations could be made on the ontogeny of young.

Individuals in the enclosures were fed on the naturally growing grasses and herbs, supplemented at times with freshly picked grasses collected nearby, carrots and wheat. In the observation cages, individuals were fed on freshly cut stems and leaves of grass, supplemented by carrot, wheat and standard small mammal trapping bait (oats mixed with peanut butter and honey). Grass and fresh natural foods were essential for survival and reproduction because animals would not eat commercial rodent pellets. Water was provided *ad libitum*.

Observations and measurements on young animals were made daily (up to c 40 days of age) and every 2–3 days thereafter until about 140 days of age. Linear measurements were made with calipers (to the nearest mm) and mass was recorded with Pesola spring balances (to nearest 0.1 g from birth to 10 g, and to nearest 1 g thereafter). Young animals born in captivity were marked individually by clipping of the fur on selected parts of the pelage and/or by colour marking of the fur. Animals caught in the field (whether released for the capture-mark-release studies [D.C.D. Happold in prep.] or kept in the enclosures for studies on reproduction) were marked using a combination of punched ear holes and toe clips. Visual observations of the behaviour of young animals were made in a small neutral arena.

The times when various stages of reproduction occurred were recorded using a modified Julian Calendar. However, to take into account that the seasons in the Southern Hemisphere are six months out of phase with those in the Northern Hemisphere, Day 1 was 1 July (rather than 1 January) and Week 1 was the 1–7 July (rather than 1–7 January). Hence the period when reproduction occurred in spring and summer (October–March) was part of a continuous sequential numbering system, rather than being the end of one calendar year and the beginning of the next year.

The age of young animals captured at Smiggin Holes was determined by the growth curves of body measurements and mass of

young born in captivity. Because these captive young were reared in semi-natural conditions, and reared on a diet similar to that in the wild, it is assumed that the growth rates (and hence age) of wild and captive young are very similar. Only wild-living young of less than about 80 g can be aged with confidence; above this mass and below the pre-winter subadult mass (i.e., 110 g – Table 1), the variation in assessed age is large and hence estimation of the date of birth is unreliable.

Mastacomys fuscus is classified as “Vulnerable” by the New South Wales Species Conservation Act of 1995. Because of the rarity of the species, studies on reproduction and development that would have involved autopsies were not possible. Only 1–3 individuals were removed from a few selected populations in KNP to establish the captive colonies. There was no evidence that the careful removal of a few individuals had adverse effects on these populations.

The field study at Smiggin Holes, and the associated study on reproduction and ontogeny, were conducted between 1981 and 1994 under the following permissions: Animal Ethics Committee of the Australian National University (No: F.BTZ.56.95 and F.BTZ.65.97); New South Wales National Parks and Wildlife Service (Permits A125 and C275); and ACT Parks and Conservation Service (Permit K1107).

Results

Nesting behaviour of females

In the mountains, females build dense spherical nests from the stems of *Poa* grasses. Each nest has a single entrance and a single internal cavity, and can be up to c 30 cm in diameter. Nests are built under boulders, and under the matted stems of dense shrubs and fallen trunks of trees. The nest is very similar in structure to nests constructed before winter, and many nests may serve both as a refuge under the snow during the winter and for rearing the young in summer. The size and insulating characteristics of the nest are likely to be of importance, especially to the first litters born in Weeks 17–22 (21 October–1 December) when temperature at night is near or below freezing and snow is still lying on the ground. In captive colonies, nests of similar construction were built either in nestboxes or under logs. The female cuts grass stems with a sideways cut of her incisor teeth, and carries the grass stems in her mouth. She continues to carry grasses to the nest throughout the time that she is suckling the young in the nest. There is no digging with the limbs during nest building (D.C.D. Happold, unpubl.).

Gestation

The length of gestation was determined by the minimum interval between litters of captive females in the enclosures. The number of days between litters (during a single reproductive season) ranged from 33 to 101 ($n = 15$) and the five minimum intervals were 33, 35, 37, 38 and 41 days (mean = 36.8). The data suggest there is a postpartum oestrus, but also that some females did not conceive at the postpartum oestrus.

Litter size

Twenty-seven litters were born to 12 females in captivity. Mean litter size was 2.3 (range 1–4, mode 2, $n = 27$; 1 young/litter = 2, 2 young/litter = 16, 3 young/litter = 8, 4 young/litter = 1).

Annual reproductive cycle of females

At Smiggin Holes, during the nine years of this study, there was a single reproductive season (i.e., the period of the year when young were born) that lasted for about 21 weeks from Week 17

Table 1

Growth rates of young *Mastacomys fuscus* reared in semi-natural conditions during the first 110 days of life. Rates are given as the mean value at 10-day intervals ($n=4-10$ individuals): (a) percentage of pre-winter subadult value, (b) growth rate/day. Pre-winter subadult values are head and body 145 mm, tail 105 mm, hindfoot 32 mm, ear 20 mm, and mass 110 g. Weaning occurs on Day 33.

Age (days)	Head and body length	Tail length	Hindfoot length	Ear length	Mass
10	47%, 1.8 mm/day	31%, 1.4 mm/day	53%, 0.8 mm/day	30%, 0.3 mm/day	12%, 0.6 g/day
20	56%, 1.3 mm/day	46%, 1.2 mm/day	72%, 0.5 mm/day	70%, 0.7 mm/day	16%, 0.5 g/day
30	65%, 1.2 mm/day	59%, 1.3 mm/day	81%, 0.3 mm/day	85%, 0.3 mm/day	25%, 0.8 g/day
40	74%, 1.1 mm/day	71%, 1.2 mm/day	87%, 0.2 mm/day	90%, 0.1 mm/day	40%, 1.7 g/day
50	81%, 0.6 mm/day	82%, 0.8 mm/day	94%, 0.1 mm/day	95%, 0.1 mm/day	52%, 1.3 g/day
60	87%, 0.6 mm/day	87%, 0.3 mm/day	97%, 0.1 mm/day	100%, 0	63%, 1.3 g/day
70	91%, 0.3 mm/day	92%, 0.4 mm/day	97%, 0.1 mm/day	100%, 0	67%, 0.5 g/day
80	95%, 0.1 mm/day	100%, 0	100%, 0	100%, 0	72%, 0.2 g/day
90	95%, 0	99%, 0	100%, 0	100%, 0	74%, 0.1 g/day
100	99%, 0.1 mm/day	99%, 0	100%, 0	100%, 0	79%, 0.2 g/day

(21–27 October) to Week 37 (10–16 March) (Fig. 1a, $n=124$ young). However, most births occurred over a much shorter period of time: 52% during the four-week period from Week 25 to Week 28 (16 December–12 January), and 77% during Weeks 22 to 30 (25 November–26 January). Births during Weeks 17 to 21 (i.e., before the majority of births occurred) were restricted to only four of the reproductive seasons (1982–83, 1983–84, 1987–88, 1990–91); in these four years the snow pack melted earlier than normal (see Table 3 in Hapold 1998). In season 1982–83, when snowmelt occurred during Week 14 (30 September–6 October), the first young were born in Weeks 17, 18 and 19 – much earlier than in any other year during this study. In theory, a female that gave birth to young early in the season (e.g., between Weeks 17 and 21) could give birth to a second litter, after a postpartum oestrus and a gestation of about five weeks, in about Week 25 or Week 26, and a third litter in between Weeks 31 to 33. However, the distribution of births (Fig. 1a) suggests that, in most years, births during Weeks 19 to 26–27 were first litters, and litters during the later part of the

reproductive season were second litters. In the field, second pregnancies (assessed by palpation) were recorded for a limited number of females.

In contrast, in captive conditions (600 m), the duration of births was about 30 weeks from Week 14 (early October) to Week 40 (early April).

Ontogeny of young *Mastacomys fuscus*

Morphological development

Young are altricial and relatively large at birth (mean values on Day 1: head and body 50 mm, tail 18 mm, hindfoot 9 mm, ear 3.4 mm, mass 9 g). The skin on the back is darkly pigmented and covered by very short fine medium-brown fur, the sides are paler, the ventral surface is pink and naked, and the limbs are darkly pigmented dorsally. Upper and lower incisors are barely visible, and eyes and auditory meatus are closed. By Day 3, long white guard hairs have grown on the rump and thighs, and the ventral surface has a slight covering of white fur. By Day 5, the young have an overall “fluffy” appearance, nasal vibrissae are 6 mm long, and the ventral surface has turned greyish. By Days 7 and 8, the remains of the umbilical cord have regressed, the back and flanks are well-furred and the hairs are clearly bicoloured – grey at base and dark brown at tip. Eye slits are distinct and the eyelids are covered with fur. The upper and lower incisors are clearly visible. By Days 9 and 10, the pelage on the back is 2–3 mm long, with guard hairs of 4 mm, the nasal vibrissae are 10 mm, and the limbs are covered with fine down except for the toes which are still pink and naked. Eyes and auditory meatus are still closed. The auditory meatus opens on Days 11 or 12, and eyes open on Days 13–14. By Day 15, the young look like miniature fluffy adults.

The length of head and body, tail, hindfoot, ear and mass in relation to age are shown in Fig. 2. The ear and hindfoot attain pre-winter subadult size on about Day 50, the tail on about Day 75, and head and body on about Day 90 (Fig. 2a, Table 1). Mass increases slowly (Fig. 2b), attaining about 79% of pre-winter subadult on Day 100 and pre-winter subadult mass by Day 120. Growth rates, as shown by young born in captivity, also vary greatly. During the first 70 days of life, when growth is at its most rapid rate, the average rate of growth for head and body, tail, hindfoot, and ear is 1.17, 1.11, 0.3 and 0.24 mm/day, respectively. However, rates vary with age (Table 1); the maximum growth rate for linear measurements is during the first 10 and 20 days of life, followed by declining rates thereafter. For mass, growth rate is 0.6 g/day for the first 10 days, increases to 1.3 to 1.7 g/day during Days 30 to 60, and then declines thereafter; the time of greatest mass increase is during the last days of lactation and the first days of eating solid food. In the field, by autumn, the young of the year (now subadults) are not reproductively active and weigh not more than about 110 g. Full adult mass (120–130 g) and reproductive maturity are attained after the first

Fig. 1. The number of births each week during the reproductive season at Smiggin Holes, Kosciuszko National Park (1982–83 to 1990–1991). (a) *Mastacomys fuscus* ($n=121$ young), (b) *Rattus fuscipes* ($n=248$ young). Week of birth was assessed from the mass and head/body length of a young animal when first captured (see text). Week 16 = 14–20 October, Week 37 = 10–16 March. Black bars indicate the earliest births in the 1982–83 reproductive season. Arrow indicates the week containing the summer solstice. *: no births recorded.

Fig. 2. Growth rates of young *Mastacomys fuscus* reared in semi-captivity. (a) Head and body, tail, hindfoot, and ear. (b) Mass. Sample size: $n = 10$ young in four litters; n (each data point) = 5–10. Symbols indicate mean values; vertical bars indicate range of values. Arrows indicate the age when approximately 95% of pre-winter subadult size is attained (Table 1).

winter when about 10 months of age (if born in a first litter) or 8 months (if born in a second/third litter).

Development of locomotion

At birth, neonates exhibited very little locomotion: when lying on the back they showed “digging” movements with the forelimbs and were able to twist and roll over to the crouch position, and they were able to perform circus movements (circular movement within a diameter of about the body length using only the forelimbs). When in a group, neonates nudged each other and “pushed under” the other siblings. These limited movements continued until by Day 4 at which time the righting reflex was well developed, and neonates were able to crawl in a straight line with coordinated limb movements; all individuals still exhibited circus movements, nudging, pushing under and crawling over. By Day 7, shuffling walk with good hindlimb coordination was possible, and circus movements were rarely seen. At the time that the eyes were beginning to opening (Day 13), young were able to walk (unsteadily) with diagonal limb coordination, and were just able to hop/jump on all four limbs. On Day 14 (eyes open), diagonal limb coordination was perfected, quad-hopping for 2–5 hops was possible, and young were able to sit upright with the body resting on the hindfeet and the forelimbs raised above the ground. Walking (with ventral surface held above the ground) and trotting was first observed on Day 16, as was the rapid escape reaction. The slow quad-hop, as seen in adults, was evident on Day 18 or 19. Thereafter, locomotion was essentially adult-like.

Development of sense organs and sensory perception

During Days 1 to 4, there is no response to sound (a handclap) or light (flashlight); eyes are closed and eyelids are barely visible. The auditory meatus is closed and the ear pinnae are free. By Day 4, brushing the vibrissae on the snout causes a head movement away from the stimulus. On Days 5 and 6, low squeals are produced when the skin of the back and sides is prodded gently and when the young are disturbed in the nest. The head can be raised to sniff the air, and the head is moved rapidly when the vibrissae are brushed, suggesting that the sense of smell and tactile perception are developing. There is an active wriggling reaction when air is blown over the body and when a light is flashed over the head (even though the eyes are still closed), but no response to hand claps. During Days 7–11, the ear pinna grows but the auditory meatus remains closed and the eyelids become more defined. On Day 13, in most young, the eyes begin to open and there is a strong reaction to a flash, and the auditory meatus begins to open and there is a rapid response to hand claps. By Day 13 or 14, all the major sense organs (sight, sound, smell and tactile) are fully functional.

Development of feeding behaviour

Young suck milk from their mother until Days 30–33 although a few young were observed to suck until Day 44. On Day 14 (just when the eyes were open), some young took grass stems into the mouth but were unable to chew them or to bite pieces off sideways (as adults do). This behaviour continued sporadically until Day 22 when grass stems were shredded in the mouth but not eaten. On Day 29, grasses were held in the forefeet and small pieces were bitten off sideways and eaten. By Day 33, holding and eating grass was completely adult-like. Young continued to suck during the first few days of eating grass, and most were completely weaned by Day 33 (see also parental behaviour below).

Development of grooming behaviour

The mother grooms the young from soon after they are born until they are weaned (about Day 33). The young begin to groom themselves on Day 6 by brushing nose and mouth with the forefeet. On Day 9, the face is groomed and on Day 13 the forelimbs are licked. Attempts to groom the hindlimbs and ventral surface begin on about Day 14 (rather unsuccessfully), and are perfected by Days 19–20. Grooming of tail and rump was not observed until after Days 35.

Development of vocal sounds

Neonates emit soft piping, squeaking and grating noises from Day 1 until Days 10–15. On Day 5, squeals (when hurt) were recorded for the first time, and from Day 7 onwards a frequently heard noise was a soft sucking click. This clicking sound was emitted until about Day 25, close to the time of weaning. A very characteristic sound of adults, ‘tooth chattering’, emitted when nervous or distressed, was first heard on Day 14, and on Day 18 squeals and loud squeaks were heard when young were grooming each other or sparring. Typical adult vocalisations (tooth chattering, squeaks, squeals) were fully developed by Days 20–25.

Development of social behaviour

Most individuals are born in litters of more than one young and therefore experience social contact with siblings and their mother. During the first week of life, young huddle in the nest when they are not sucking and nipple-clinging. From about Day 5 onwards, young

showed the first signs of social behaviour. The principal forms of amicable behaviour recorded were:

- (1) Contact for investigation, such as nose-to-nose sniffing and nose-anus sniffing.
- (2) Huddling, when two or individuals crouch together and stay in physical contact for 5 or more seconds.
- (3) Nudging, when an individual pushes its nose or head against the side of another individual.
- (4) Climbing over, when an individual scrambles over another individual (and may then rest upon that individual).
- (5) Pushing under when an individual pushes underneath another.
- (6) Following, when an individual walks or runs in close proximity behind another without the intent to attack.
- (7) Social grooming when an individual licks and scratches the pelage of another.

From about Day 5 onwards, when locomotor abilities are still very limited, young huddle together and indulge in nudging (nose-to-nose sniffing, nose-anus sniffing), contacts for investigation, and pushing under. On Day 6, as locomotor abilities improve, climbing over becomes possible. On Day 11 or 12, just before the eyes open, young start to show social grooming. Following is not observed until young can walk at about Day 13 or 14. Each of these behavioural characteristics is preceded by a similar-looking precursor. Once the eyes are open, and walking and running are possible, each of these elements of social behaviour become more defined and more frequent. As the young grow older, siblings often huddle in two or threes when outside the nest, and indulge in social grooming. Social cohesion between mother and young remains for many weeks, and they will nest together even when alternative nesting places are available. In the field, a mother and her young have been caught in the same trap when the young were 30–60 days of age.

Parental behaviour

Only the mother rears the young. Males take no part in rearing and looking after the young; rather, females show agonistic behaviour towards males, chasing and attacking any male that comes near to the nest. After parturition, the mother adopts a “broody hen” stance within the nest with her body curled over and resting on her rump and her head pulled into towards her chest, so the young are completely invisible. During the first few days of life, the mother usually leaves her young in the nest when she forages, and covers them with cut grass stems. The young nipple-cling tenaciously to their mother until Days 20–25 (mass c 25 g), and are beginning to be independent. The mother suckles her young almost continuously until about Day 20, and spasmodically after the young begin to eat grass. If one of the young becomes separated from its mother outside the nest, the mother retrieves it by holding it loosely with her incisor teeth.

After weaning, the young usually nest with their mother. The young began to exit the nest independently in the semi-natural enclosures about Day 20, although the youngest individuals caught in the field were about 30–35 days of age (30–40 g).

Discussion

Litter size

Only two previous studies provide information on litter size: Calaby and Wimbush (1964) recorded that two autopsied females contained two and three foetuses, respectively, and a female in captivity produced litters of three, two, and one young; and Happold (1989), using a smaller data set than in the present study, recorded

mean litter size as 1.9 (range 1–4, $n=4$). This study confirms the small mean litter size (by rodent standards) and range of litter size recorded previously, but the larger sample provides a greater degree of accuracy. Small litter sizes have been recorded for two other species of specialised alpine small rodents in other parts of the world (Table 4).

Ontogeny

The growth curves for *M. fuscus* are not dissimilar to those of other small rodents. At birth, head and body, tail, hindfoot, ear, and mass are 34, 17, 28, 17 and 8%, respectively of pre-winter subadult values. The sequence at which these measurements attain adult, or near-adult, values is also similar to that of other small rodents; firstly hindfoot and ear, followed by tail, head and body, and mass (Fig. 2, Table 1). The growth patterns of *R. fuscipes* show similar values and trends although birth mass is only 5% of the subadult value (D.C.D. Happold, unpubl.). South African rodents of similar size to *M. fuscus*, *Otomys sloggetti robertsi* (Willan 1990) and *Dasymys incomtus* (Pillay 2003), exhibit the same characteristics of growth. However, the time taken to reach sexual maturity in *M. fuscus* and *R. fuscipes* (8–10 months), is considerably longer than for *Otomys sloggetti robertsi* (112–126 days) and *Dasymys incomtus* (females 120–130 days) and for many smaller-sized temperate and tropical species (see Happold 1978). The development of behavioural characteristics follows a predictable sequence, and the closeness and longevity of the mother-young bond appears to be an adaptation to the harshness of the alpine environment. It is noteworthy that agonistic behaviour does not develop until sexual maturity at 8–10 months of age.

Determinants of reproductive characteristics

Millar and Innes (1985) showed that the reproductive characteristics of individuals of *Peromyscus maniculatus borealis* living at higher altitudes in western Canada differed from those at lower altitudes in a number of ways: timing of births is later, duration of the reproductive season (births) is shorter, young never (or rarely) breed in the year of their birth, and females on average have fewer litters per year. Similar characteristics are exhibited in *M. fuscus*: the duration of reproduction in the study area (1650 m) was 21 weeks, from Week 17 to Week 37 (Fig. 1a) although the majority of births (77%) was recorded during only nine weeks (Weeks 22 to 30). In captive conditions (Canberra, 600 m, where the climate is milder than in KNP), reproductive release enables the duration of births to be extended to about 30 weeks (Week 14 [early October] to Week 40 [early April]). Young individuals do not breed in the year of their birth, and females on average have two litters per year.

Rattus fuscipes, in contrast, has a much wider biogeographic distribution than *M. fuscus*. In the study area, the duration of reproduction was 18 weeks, from Week 20 to Week 37 (Fig. 1b) with the majority of births during 12 weeks (Weeks 22 to 33) (D.C.D. Happold, unpubl.). Likewise, young do not breed in the season of their birth, and females on average have two or three litters per year. In other parts of its range, *R. fuscipes* has a much more extensive reproductive season: in the Loch Valley, southern Victoria (37°48'S, 147°00'E, 330–580 m) where the winters are cool and where there may be 1–2 days of snow each month in the winter, reproduction lasts for c 40 weeks each year (Warneke 1971), and in south-east Queensland (27°20 S, 152°46E), reproduction lasts for c 40 weeks (Wood 1971). In both locations, the proportion of pregnant females is greatest from spring to autumn (October–May). In the laboratory, *R. fuscipes* breeds throughout the year (Taylor 1961; Taylor and Horner 1973).

The third species, *Antechinus swainsonii*, has a different set of reproductive characteristics: it is semelparous, mating is highly

synchronized, all males die shortly after mating, and births are highly synchronized and predictable within any population (Cockburn 1985). The timing of mating (and hence birth of young) is later at higher altitudes than at lower altitudes (Dickman et al. 1983), and a female typically has ten nipples and ten young, more than conspecifics at lower altitudes which have 6–8 young. Hence females in KNP produce only one litter per year, mating occurs during Weeks 9 to 11 (26 August–14 September), and all births occur during Weeks 14–16 (1–20 October; Table 2). Young never breed during the year of their birth, and both males and females become reproductively active when 11 months of age.

Comparison of the small mammals in Kosciuszko National Park

The three species in the study area, and *Burramys parvus* which lives at higher altitudes in KNP, differ considerably in their reproductive characteristics (Table 2) and in the developmental characteristics of the young (Table 3). The two species of rodents show some similarity in that they have a similar adult mass and produce 1–2 (perhaps occasionally 3) litters/year; however, they differ in length of gestation and mean litter size, and hence the reproductive capacity (=young/female/year) and lifetime production of young in *R. fuscipes* is double that of *M. fuscus*. The two species of small marsupials differ from the rodents in most respects; both species have a single litter each year. Of the two marsupials, *A. swainsonii* is larger, has a longer gestation, more young/litter, and breeds only once in a lifetime; very occasionally a female survives to breed during a second season. *Burramys parvus* has a much smaller litter size and produces fewer young/year than *A. swainsonii*, but if a female breeds each year for four years, she may have almost the same lifetime production as a female *A. swainsonii*. The differences in reproductive effort (R_e) (Millar 1977) highlight the differences between the species (Table 2). *Mastacomys fuscus* has the lowest R_e , a fact probably related to its diet of *Poa* grass, small litter size and few litters/year. *Rattus fuscipes* has a R_e double that of *M. fuscus* due to its shorter gestation, larger litter size, and a more varied omnivorous diet. *Antechinus swainsonii* has a R_e which is 4.5 times that of *M. fuscus* and double that of *R. fuscipes*. This is achieved by the large litter size (even though there is only one litter per year), the long period of lactation, and the large size of the young in relation to adult mass at weaning (Tables 2 and 3). Such a high R_e is probably only possible because *A. swainsonii* is entirely insectivorous and the time when the young are sucking coincides with a high abundance of insect prey soon after snowmelt. *Burramys parvus* shows similar marsupial reproductive characteristics to *A. swainsonii*, but differs in its shorter gestation, fewer young/litter, shorter time period to weaning, and hence lower R_e , and because a female in the wild can live for at least four years. The overall effect of these differing reproductive characteristics of the four species is considerable variation in reproductive capacity, lifetime production and R_e , and has important implications for seasonal changes in population numbers and composition. For species which occur naturally at lower altitudes (*R. fuscipes* and *A. swainsonii*) or have been bred in semi-captive conditions at lower altitudes (*M. fuscus*), the alpine environment constricts the duration of reproduction and delays the onset of reproduction after winter; for rodents, it limits the number of litters that can be born during the reproductive season. Similar conclusions have been documented for some species of small mammals in the northern hemisphere (e.g., Millar and Innes 1985; Le Louarn and Janeau 1975), but are previously unreported in Southern Hemisphere small mammals. The major difference in these Australian species is determined by two of the species being rodents and two being small marsupials. The most obvious difference is that the marsupials have a short gestation, very low mass of neonates, slow growth rate, and a longer time between birth and weaning compared to the rodents (Tables 2 and 3). When the length

Table 2
Reproductive characteristics of four alpine and subalpine species of small mammals in Kosciuszko National Park, Australia. The data are taken exclusively from individuals in Kosciuszko National Park, Australia and hence vary from similar data elsewhere.

Species	Subfamily/ Family/ Order	Adult female weight (g)	Gestation (days)	Weeks in which births recorded	Litters/year	Mean litter size (range)	Weight of single young at weaning (g)	Reproductive capacity (Young born/ female/year)	Longevity of females in the wild (years)	Lifetime Production of young	Reproductive effort (R_e)
<i>Mastacomys fuscus</i> (1, 5)	Murinae, Muridae, Rodentia	130–150	35	17–37	1–2	2.3 (1–4)	35–41	2–5	Up to 2	4–10	0.82
<i>Rattus fuscipes</i> (2)	Murinae, Muridae, Rodentia	125–150	23	20–37	1–2	5.4 (4–6)	c. 30	5–10	Up to 2	10–20	1.70
<i>Antechinus swainsonii</i> (3)	Phascogalinae, Dasyuri- dae, Dasyuro- morpha, Burramyidae, Diprododonti-	60–70	28–35	14–16	1	9 (8–10)	20–25	9	1 (very rarely 2)	9	3.73
<i>Burramys parvus</i> (4)		30–50	13–16	20–24	1	2.26 (1–4)	18	2–3	4	8–12	1.24

$R_e = N \times W_w^{0.75} / m^{0.75}$ where N : mean litter size, W_w : weight of single young at weaning, and m : adult female weight (Millar 1977). (1) This study, Happold (1983, 1989). (2) This study, Taylor (1961). Taylor and Calaby (1988). (3) This study, Williams and Williams (1982). (4) Kerle (1984); additional data from Mansergh and Scotts (1990) and Broome (1995). (5) Formerly placed in the subfamily Conilurinae ("Australian Old Endemics"); this subfamily is now in synonymy, and the species is placed in the "Pseudomys Group" of the Murinae (Musser and Carleton (2005), Aplin (2005), Breed and Ford (2007). Some authorities place *fuscus* in the genus *Pseudomys* (Aplin 2005; see also Musser and Carleton 2005).

Table 3
Characteristics of development of young of four species of alpine and subalpine small mammals in Kosciuszko National Park, Australia.

Species	Weight of single young at birth (g)	Relative weight of single young at birth (as % of adult weight)	Relative weight of litter at birth (as % of adult weight)	Weight of single young at weaning (g)	Age at weaning (days)	Relative weight of single young at weaning (as % of adult weight)	Relative weight of litter at weaning (as % of adult weight)	Growth rate of young/day from birth to weaning (g/day)
<i>Mastacomys fuscus</i>	9	6%	15%	35–41	35–40	25–29%	57–67%	0.74
<i>Rattus fuscipes</i>	5.5	4%	21%	c. 30	c. 28	21%	115%	0.87
<i>Antechinus swainsonii</i>	0.016 ^a	0.025%	0.22%	20	98	30%	270%	0.20
<i>Burrhamys parvus</i>	0.023 ^b	0.057%	0.16%	18	60	45%	101%	0.32

^a Chris R. Dickman (pers. comm.).

^b Linda S. Broome (pers. comm.).

of time for gestation and lactation (=time to weaning) are added together, *R. fuscipes* takes the shortest time to produce weaned young, and *A. swainsonii* takes the longest time.

Comparisons with some rodents from other alpine regions

Three species of rodents from alpine regions of other continents were chosen to compare with the Australian species discussed here (Table 4). They represent different subfamilies (Arvicolinae, Otomyinae, Neotominae) to the Australian subfamily (Murinae), and differ widely in their reproductive characteristics. The two smaller species, *Chionomys nivalis* and *Peromyscus maniculatus borealis* have a short gestation and only two litters per year, but *C. nivalis* has a smaller mean litter size (3.0) than *P. maniculatus* (5.25) which results in a smaller reproductive capacity (Le Louarn and Janeau 1975; Millar and Innes 1985). As with the Australian species, none is known to breed in the season of birth. *Peromyscus maniculatus borealis* has a high R_e , similar to that of *A. swainsonii*, due to its large litter size. The third species, *Otomys sloggetti robertsi*, is the largest species, with the longest gestation, least number of young, and lowest R_e (N. Pillay, pers. comm.). All three species of rodents from other alpine regions show that different strategies in alpine and subalpine regions are possible; however, there is no long-term information on inter-annual variation in production, nor on inter-annual changes in demography. Of these three species, *O. sloggetti robertsi* shows remarkable similarity to *M. fuscus* in many aspects of its biology, including size, diet, morphology, reproductive characteristics, and R_e (Hinze 2005; Schwaibold and Pillay 2006; Willan 1990). However, unlike *M. fuscus*, it appears to be capable of 3–4 litters/year. Also, unlike *M. fuscus*, *O. sloggetti robertsi* has a communal social behaviour (Hinze 2005; Schwaibold and Pillay 2006), a characteristic that may contribute to its higher reproductive capacity. However, compared with this study, none of these studies on other continents consider the inter-specific differences within communities.

Life histories and reproductive strategies of Australian alpine small mammals

It has long been acknowledged that life histories and reproductive characteristics are adaptive and correlated with environmental variables (Millar 1977), and that there are complex relationships between body size and reproduction (Eisenberg 1981; Read and Harvey 1989). The life histories of small mammals (compared with large mammals) are determined by small body size, short time to maturity, short lifespan, relatively large litter size, and short time to weaning (Millar 1977; Tuomi 1980). The species considered in this paper are all “small” but they differ in detail (see Tables 2 and 3) and hence each has a different life history and reproductive strategy. Certain characteristics are common to the two species of rodents and *A. swainsonii*: none breed in the winter, none breed in the season of birth, gestation and lactation are limited to no more than ca. 20 weeks of the year, and females live for only 1–2 reproductive seasons. The number of weeks required for gestation and lactation of a single litter is 10 weeks in *M. fuscus*, 7 weeks in *R. fuscipes*, and 20 weeks in *A. swainsonii*. The two species of rodents may have a second (or even a third) litter in the same reproductive season, but *A. swainsonii* does not have that option because all the males have died.

In alpine regions, for rodents, the date of snowmelt in spring and the date when cold weather and snowfall begins in the following autumn determine the length of the reproductive season. In KNP, when snowmelt was early (Week 14) the earliest births of young *M. fuscus* were in Weeks 17–18, whereas when snowmelt was in Week 20, first births were in Week 23 (Fig. 3). Only when first births were in Weeks 17–18 (as occurred only once – 1982–1983 – dur-

Table 4
Reproductive characteristics of three species of alpine and subalpine small mammals in France, South Africa and Canada.

Species (location)	Subfamily/ Family/ Order	Adult female weight (g)	Gestation (days)	Litters/year	Mean litter size (range)	Weight of single young at weaning (g)	Reproductive capacity (Young born/ female/year)	Longevity of females in the wild (months) ^a	Lifetime Production of young	Timing and duration of reproductive season	Reproductive effort (R_e)
<i>Chionomys nivalis</i> (Hautes-Alpes, France) (1)	Arvicolinae, Cricetidae, Rodentia	35–40	20–22	2	3.0 (2–4)	15	6 (4–8)	15–20	6 (4–8)	1500 m: May–Sep, 17 weeks. 1600 m: Jun–Sep, 13 weeks. 1800–2600 m: Jun–Aug, 10 weeks 2000 m: Aug – Mar, 32 weeks	1.58
<i>Otomys sloggetti robertsi</i> (Lesotho) (2)	Otominae, Muridae, Rodentia	111	38	3–4 ^b	2.44 (1–3)	29	7–10	13–36	c. 14–28 ^b	1600 m: May–Aug, 12 weeks. >1900 m: mid Jun – early Aug, 7 weeks	0.89
<i>Peromyscus maniculatus borealis</i> (W. Canada) (3)	Neotominae, Cricetidae, Rodentia	19–20	25	2	5.25 (3–7)	c. 11	c. 10	10–15	c. 10		3.35

See Table 2 for definition of R_e . (1) Le Louarn and Janeau (1975), Janeau and Aulagnier (1997). (2) Willan (1990), A. Hinze and N. Pillay unpublished. (3) Millar and Innes (1985), Millar (1994), Millar et al. (1986).

^a For the majority of females; a few may survive to breed in the following season.

^b Estimate.

Fig. 3. The dates of the first three births of *Mastacomys fuscus* each year at Smiggin Holes, Kosciuszko National Park, in relation to date of snowmelt (1982–1990). Week 14 = 30 September–6 October; Week 20 = 11–17 November. Correlation: $F_{1-25} = 22.828$, $r^2 = 0.456$, $p < 0.0001$. Snowmelt data from Spencer's Creek (36° 26' S, 148° 17' E, 1830 m) (see Happold 1998).

ing the nine-year study), would there have been adequate time for a female to have three litters during the year. For *R. fuscipes*, the date of snowmelt does not seem to have such an important influence; the first births in any year were during Weeks 20–22; none were recorded during weeks 16–19, even in 1982–83 when the snowmelt was in Week 14 (cf. *M. fuscus*, Fig. 1a).

The two species of rodents show variation that may be attributed to their evolutionary history. *Mastacomys fuscus* is an “Australian Old Endemic”, i.e., its ancestors and those of the other species in the Conilurinae (Table 2) are considered to have entered Australia 5–10 million years ago, whereas *Rattus fuscipes* is considered a “new invader” and its ancestors invaded Australia during the Pleistocene (Watts and Aslin 1981; Breed and Ford 2007). Yom-Tov (1985) showed that the “old invaders” produce smaller litters, have a longer gestation, a longer weaning period, and take longer to reach maturity compared with the “new invaders”. *Mastacomys fuscus* shows all of these characteristics (Tables 2 and 3). In addition, and not considered by Yom-Tov (1985), *M. fuscus* has a lower reproductive fecundity, lower lifetime production of young, and a lower R_e .

Antechinus swainsonii shows a completely different set of characteristics to the rodents. Russell (1982) showed that, in marsupials, parental care and parental investment is influenced by the type of pouch. The open pouch of small dasyurids necessitates that the young are left in a nest until they become endothermic, have fur, and the eyes are open (Russell's Pattern A); such dasyurids have large litters which, at weaning, have a mass greater than that of the mother (270% for *A. swainsonii*). *Antechinus swainsonii* when compared with the two rodents invests much more energy (higher R_e) and time into reproduction, has a greater reproductive capacity, and fewer litters per year.

The theory of r- and K-selection has been applied to many communities of small mammals living at low altitudes in tropical and temperate ecosystems (see Perrin 1980 for review and references), but not to communities in alpine regions where cold and snow are significant environmental characteristics. *Mastacomys fuscus* shows the classic characteristics of a K-selected species as applied to small rodents (iteroparity, long generation time, precocial young, high survival rate, low fecundity, high investment in defence, and

a population density which does not exhibit large intra- and inter-annual fluctuations). *Rattus fuscipes* is not so K-selected and fits more easily mid-way on the r-K selection spectrum. It is much more difficult to assess *A. swainsonii* in this respect. It is clearly r-selected in some characters (semelparity, altricial young, high fecundity, and a population density which fluctuates greatly, but predictably, during the year) but is more K-selected in others (long generation time) primarily as a result of its marsupial life-history. These three reproductive strategies occur under exactly the same environmental influences and all are clearly well adapted to the alpine habitat; however, these differences result in very different demographics and strategies.

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