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Pup retrieval in the African bush Karoo rat

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Maternal retrieval of 87 young representing 42 litters of the African bush Karoo rat *Otomys unisulcatus* F. Cuvier, 1829 was studied in the laboratory. All 17 females studied retrieved young by nipple-clinging, but ten females also mouth-carried the young in 45 out of 93 trials. Unlike nipple-clinging, mouth-carrying was poorly developed, as young were carried by various parts of the body in a non-stereotyped manner. Mouth-carrying in otomyine rodents is unusual; all other species previously studied use nipple-clinging exclusively. Mouth-carrying in *O. unisulcatus* can be interpreted in two ways: (1) Nipple-clinging probably evolved in the ancestral otomyines where it reduced the risk of predation on young in unprotected nests. *O. unisulcatus* occupies well-protected stick lodges where young are not very vulnerable to predation. Hence, the selective advantage of nipple-clinging in *O. unisulcatus* may be less than in the ancestral otomyines, and it is possible that mouth-carrying may replace nipple-clinging. (2) Alternatively, mouth-carrying may represent merely an experimentally induced response.

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Introduction

The bush Karoo rat *Otomys unisulcatus* F. Cuvier, 1829 (*Muridae*: *Otomyinae*) is endemic to the drier, sparsely vegetated western parts of southern Africa (De Graaff 1981, Skinner and Smithers 1990), and is one of eight otomyine species occurring in the subregion (Meester *et al.* 1986). Previous studies on the breeding biology and postnatal development of otomyine rodents indicate that nipple-clinging is characteristic of the taxon. Young Angoni vlei rats *O. angoniensis* (Kearney 1990), vlei rats *O. irroratus* (Davis and Meester 1981, Pillay 1990) and ice rats *O. sloggetti robertsi* (Willan 1990) rarely detach from the mother's nipples during the first few days of life. Removal of young for examination can be achieved only by blocking off their nostrils until they release their hold. Females of the above taxa retrieve and transport their offspring by nipple-clinging exclusively.

Otomyine young are well adapted for nipple-clinging, as indicated by the presence of appropriately notched incisors which are erupted at birth, facilitating attachment to the mother's nipples. In addition, females have only two pairs of inguinal nipples and litter sizes are small (range = 1-4); features common to the otomyines (Roberts 1951), suggesting that nipple-clinging may be present in all members of the subfamily (Willan 1990). Recent studies of the reproductive biology of O. unisulcatus (Wolhuter 1992, N. Pillay, unpubl.) showed that, whereas pup retrieval occurs mainly by nipple-clinging, some females mouth-carry individual young back to the nest box. In the present paper, we describe mouth-carrying in O. unisulcatus and provide possible explanations for its occurrence in this species.

Materials and methods

Animals used in this study were captive-born progeny of individuals trapped at Victoria West, Cape Province (31°24'S, 23°09'E).

Animals were held under partially controlled environmental conditions (15L:9D; $20-25^{\circ}C$; 60 -80% rH). Male/female pairs were individually caged in glass aquaria $90\times30\times40$ cm, each equipped with a single nest box $15\times15\times15$ cm. Food comprised *ad libitum* coarse grass, herbaceous plant material, cabbage, carrot and commercial rabbit pellets. Coarse wood shavings were provided as litter, and animals used uneaten plant material for nesting.

The method of retrieval of 87 young (42 litters) produced by 17 pairs was ascertained in 93 trials every second day from the day of birth (Day 0) for two weeks. Young were removed from the parent aquarium for approximately 10 minutes and, when returned, were placed 50 cm away from the entrance of the nest box. Thereafter, the method of retrieval of pups by the mother was noted (i.e. mouth-carrying or nipple-clinging). Observation periods lasted for up to 15 minutes, ceasing once all young in a litter had been retrieved by the mother or had returned to the nest box unaided (see below).

Results

During the first few days after birth, young *O. unisulcatus* clung continuously to the mother's nipples. In all or most trials, the 17 females used in the study retrieved their young by means of nipple-clinging. The female achieved this by positioning herself over one or more young, and using her fore-limbs to draw the young towards the nipples.

Table 1. Methods of maternal retrieval of young O. unisulcatus.

Parameters	n 17	Method of retrieval		
		Nipple-clinging only	Nipple-clinging and mouth-carrying	
Females		7	10	
Litters	42	18	24	
Pups	ps 87 3		50	
Trials	93	48	45	

Ten of the 17 females, in 45 out of 93 trials (48.4%), also retrieved their young by mouth-carrying (Table 1). Unlike nipple-clinging, retrieval by mouth-carrying was highly variable. The mother picked up individual young by different parts of its body (i.e. by the back, chest, flank, hind foot or nape of the neck). Females usually mouth-carried all members of a litter during any one trial. On five occasions, however, the mother month-carried only the first pup back to the nest box, allowing the remaining young to attach to her nipples when she returned from the nest box. In these instances, the first pup was left in the nest box by the mother before she returned for the others.

In all 10 females, retrieval by mouth-carrying had ceased when pups were six days old, and these females favoured nipple-clinging after this time. By day 8 – 10, young had their locomotor abilities sufficiently developed to return to the nest box unaided.

Discussion

With the exception of *O. unisulcatus*, none of the other otomyines referred to here have been observed to mouth-carry the young (Table 2), although Kearney (1990) reported that female *O. angoniensis* occasionally retrieved young which were left at the entrance of the nest box by pulling them up in the mouth. Close examination of Kearney's data suggests that the retrieval behaviour observed in *O. angoniensis* may have been misinterpreted, however, and it is more likely that females were pulling the young towards themselves without forsaking the nest box. Young *O. angoniensis* placed further away from the entrance of the nest box (i.e. beyond the reach of the mother) were retrieved by nipple-clinging (Kearney 1990), endorsing the above conclusion.

Mouth-carrying in *O. unisulcatus* apparently reflects the nesting habits of the species, as outlined below: *O. unisulcatus* is unique among the otomyines in that it constructs a twig lodge, which may have a volume in excess of 1 m³, within or beneath which the nest is constructed (Vermeulen and Nel 1988, Brown and Willan 1991, Kerley and Erasmus 1991).

Table 2. Number of litters mouth-carried and mean litter size in O. angoniensis, O. irroratus, O. s. robertsi and O. unisulcatus. Number of pups or number of pups mouth-carried are given in brackets.

Taxon	Litters examined	Litters mouth-carried	Litter size (\bar{x})	Source
O. angoniensis	12 (33)	0 (0)	2.75	Kearney 1990
O. irroratus	30 (70)	0 (0)	2.33	Davis and Meester 1981, Pillay 1990
O. s. robertsi	9 (13)	0 (0)	1.44	Willan 1990
O. unisulcatus	42 (87)	24 (50)	2.07	this study, Wolhuter 1992

Prototomys, the Pliocene ancestor of the modern *Otomyinae* (Pocock 1976) was probably mesically adapted (Taylor *et al.* 1989), occupying densely vegetated habitats and nesting on the surface (Willan 1990). Nipple-clinging would therefore have been selected for in *Prototomys* as an adaptation to reduce the risk of predation on the young (Willan 1990). This hypo-thesis is supported by consideration of *O. irroratus* and *O. angoniensis*, which appear ecologically analogous to *Prototomys* (i.e. occurring in comparatively densely vegetated habitats and normally nesting on the surface); both *O. irroratus* and *O. angoniensis* have exclusively nipple-clinging young (*inter alia* Davis and Meester 1981, Kearney 1990).

Viewed against the nesting habits of the other otomyines studied to date, O. s. robertsi and O. unisulcatus nest in well protected circumstances: O. s. robertsi in underground burrows (Willan 1990, Lynch 1992), and O. unisulcatus in the lodges described above. Hence, young O. s. robertsi and O. unisulcatus may be relatively safe from predation. On this basis, Willan (1990) maintained that nipple-clinging in these taxa is a plesiomorphic character, having little or no adaptive significance. It is therefore tempting to speculate that mouth-carrying behaviour evolved comparatively recently in O. unisulcatus, and may replace nipple-clinging behaviour.

The adaptive advantage of retrieval by mouth-carrying over that by nipple-clinging in *O. unisulcatus* is unknown. It is possible that mouth-carrying may allow more rapid translocation of young; pups retrieved by nipple-clinging must first be encouraged by the mother to attach to her nipples, presumably prolonging retrieval. In contrast to nipple-clinging, however, only a single pup may be transported in the mouth at any one time. Clearly, detailed observations of *O. unisulcatus* maternal behaviour are required to ascertain the adaptive significance of mouth-carrying behaviour.

On the other hand, several factors indicate that *O. unisulcatus* remains more suited for nipple-clinging, and that mouth-carrying in this species may represent an experimentally induced response. First, *O. unisulcatus* is adapted for nipple-clinging, possessing all the anatomical attributes required for this behaviour (above). Second, the literature on the growth and development of African rodents (see Neal 1990) shows that nipple-clinging is favoured by species having small litter sizes; *O. unisulcatus* has the second lowest known litter size of all otomyines (Table 2). Third, young *O. unisulcatus* are more or less permanently attached to the mother's nipples before weaning (Day 14), and are never mouth-carried by the mother except during retrieval. Hence, free-living neonates would not be expected to leave the nest before an age of 10 days, and retrieval by mouth-carrying would therefore not be expected to occur in nature. However, this conclusion requires testing by means of observations of free-living *O. unisulcatus*.

Fourth, *O. unisulcatus* appears to be adapted to carrying material back to the nest, and mouth-carrying of young may represent a modification of this behaviour. In nature, *O. unisulcatus* carry sticks and twigs which are used to construct their lodges (Vermeulen and Nel 1988, Kerley and Erasmus 1992). Similarly, food is

often carried back to the nest and consumed there (Brown and Willan 1991, Kerley and Erasmus 1992). In the laboratory, animals often fill the nest box with food (grass and vegetables), clearly reflecting the situation in nature. Mouth-carrying of pups appears to be comparatively poorly developed (i.e. young are picked up by various parts of the body), possibly supporting the present interpretation.

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