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Melomys cervinipes (Rodentia: Muridae)*

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Abstract: *Melomys cervinipes* (Gould, 1852) is a murid rodent commonly called the fawn-footed mosaic-tailed rat. A small, russet brown rodent with light fawn-colored feet, it is 1 of 21 currently recognized species in the genus *Melomys*. The species is endemic to Australia, occurring in the rainforests and forests along the eastern coast. *M. cervinipes* is listed as "Least Concern" by the International Union for the Conservation of Nature and Natural Resources.

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Key words: Australia, fawn-footed melomys, murid, scansorial, rainforest, Wet Tropics

Synonymy completed 22 August 2017

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Melomys Thomas, 1922

Mus: Linnaeus, 1758: 59. Type species *Mus musculus* Linnaeus, 1758 by Linnaean tautonymy. See Thomas (1911: 146) and ICZN (1958: 41).

Rattus: Fischer, 1803: 128. Type species *Mus decumanus* Pallas, 1779: 91. [= *Rattus norvegicus* Berkenhout, 1769: 5] by monotypy. See Hollister (1916: 206).

Uromys: Peters, 1867: 343. Type species *Mus macropus* Gray, 1866 [= *Uromys caudimaculatus* Krefft, 1867: 316) by monotypy.

Melomys Thomas, 1922: 261. Type species *Uromys rufescens* Alston, 1877: 124 [= *Melomys rufescens* Alston, 1877: 124] by original designation.

Melomys cervinipes (Gould, 1852)

Fawn-footed Melomys

Mus cervinipes Gould, 1852: [1845–1863]. Type locality “Stradbrook Island”, Moreton Bay, Queensland, Australia.

Rattus leucosternum cervinipes: Fitzinger, 1867:12. Name combination.

Uromys cervinipes: Thomas, 1888:237. Name combination.

Uromys banfieldi De Vis, 1907:8. Type locality "Dunk Island, an island lying a little to the north of Cardwell, in lat. 15, long. 145", South Mission, Queensland, Australia.

Melomys cervinipes: Thomas, 1922:261. First use of current name combination.

Melomys cervinipes eboreus: Thomas, 1924:297. Type locality "Dinner Creek, Ravenshoe. 2900'", Mount Hypipamee National Park, Queensland, Australia.

Melomys cervinipes pallidus Troughton and Le Souef, 1929:98. Type locality "Hinchinbrook Island, near Cardwell, Queensland", Australia.

Melomys cervinipes cervinipes: Iredale and Troughton, 1934:86. Name combination.

Melomys banfieldi: Iredale and Troughton, 1934:86. Name combination.

Melomys limicauda Troughton, 1935:255. Type locality "Hayman Island in the Whitsunday Group, on the north Queensland coast between Bowen and Mackay", Australia.

Melomys cervinipes banfieldi: Rümmler, 1936:252. Name combination.

Melomys cervinipes limicauda: Tate, 1951:292. Name combination.

Melomys cervinipes bunya Tate, 1951:293. Type locality "Bunya Mountains, 3500 feet", Queensland, Australia.

CONTEXT AND CONTENT. Order Rodentia, family Muridae, subfamily Murinae, tribe Uromyini. The genus *Melomys* contains 21 species, of which 18 are native to New Guinea, Indonesia and the Solomon Islands (Menzies 1996; Wilson and Reader 2005) and 3 are native to Australia: grassland melomys *Melomys burtoni*, Cape York melomys *Melomys capensis* and *M. cervinipes* (van Dyck and Strahan 2008; Jackson and Groves 2015). No subspecies are recognized within *M. cervinipes*. A 4th Australian species, Bramble Cay melomys *Melomys rubicola*, was declared extinct in June 2014 (Woinarski et al. 2014).

NOMENCLATURAL NOTES. The original female specimen collected by Gould (1852) is the designated lectotype BM 52.12.15.1 (Thomas 1921). Thomas (1888, 1902) and Thomson (1889) first mention *Uromys cervinipes* in their publications, however, the designation of the species *cervinipes* to the genus *Uromys* was only formally described by Ogilby (1892). Tate (1951) identified 9 subspecies (races) within *Melomys cervinipes*, 2 of which were elevated to full species rank (*M. capensis* and *M. rubicola*) and *Melomys cervinipes albiventer* was synonymized within the sister taxon *M. burtoni*. All other races were synonymized within *cervinipes* by Watts and Aslin (1981) and Mahoney and Richardson (1988).

The generic name, *Melomys* is derived from the English *Melanesia*, indicating the wide distribution of species from this genus (Thomas 1922), and the Greek *mys* for mouse (Borror 1960). The species name *cervinipes* is from the Latin *cerv* for deer or fawn and *pes* for foot (Borror 1960), referring to the light coloring (fawn) of the feet. Other vernacular names include buff-footed rat (Gould 1852), (fawn-footed) mosaic-tailed rat (Taylor and Horner 1970), (fawn-footed) naked-tailed rat (McKenzie et al. 1976), large khaki rat (Redhead 1983), fawn-footed scale-tailed rat (Redhead 1983), tawny-foot Melanesian-mouse (Moore and Burnett 2008), fawn-footed melomys (Roberts 1963) and looloong (Aboriginal name; Braithwaite et al. 1995).

DIAGNOSIS

Melomys cervinipes (Fig. 1) is a small murid rodent so morphologically similar to its congener *M. burtoni* that field identification is often difficult. Although the 2 species occupy different habitats, there appears to be some overlap (van Dyck and Strahan 2008), making accurate field identification essential. Dyer (2007) found that absolute tail length and body mass, based on age class, could be simple field measures. However, how the age classes of animals were identified in the field was not given, and the tail ranges were very small considering the high sample numbers (e.g., length ranging just ± 0.5 mm from the species mean for mature male *M. burtoni*). This is questionable, considering that tail length and body mass have been found to show considerable overlap in prior studies (Keith 1970; Watts and Aslin 1981; Moore and Burnett 2008), thus it is suggested that these are unlikely to be useful field identification measures. Keith (1970) found that tail length, as expressed as a percentage of head and body length, was longer for *M. cervinipes* by approximately 7%. However, this requires further validation, as the sample size for *M. burtoni* was quite small ($n = 7$). The number of tail scale rows differs between species, with *M. cervinipes* having 13 and *M. burtoni* having 14–15 (Keith 1970). Frost (2008) and van Dyck et al. (2013) have developed a method of field identification using the length of the 1st and 5th interdigital pads, whereby individuals with a 1st interdigital pad greater than 2.3 mm and a 5th interdigital pad greater than 1.7 mm can be classified as *M. cervinipes*. The 2 species can also be distinguished by their dentition (Keith 1970; Knox 1978), although this is not useful for identification in the field. The tooth rows of *M. cervinipes* show a greater angle of divergence, and the length of the tooth row is longer relative to the difference in the distance across the mouth between M^{1-1} and/or M^{3-3} (Keith 1970). The upper molar alveolar patterns are also distinct, with *M. cervinipes* showing 4 roots on the 1st and 2nd upper molars, whereas *M. burtoni* have 5 (Knox 1978). M1 alveolar length is also a distinctive character (93.5% effectiveness of species determination), with a value greater than 3.1 mm characteristic of *M. cervinipes* (Knox 1978). *M. cervinipes* shows a broader interorbital region than *M. capensis*, which is posteriorly undercut at the sides of the orbits, and with more pronounced ridges on the upper surface (Watts and Aslin 1981). In addition, the anterior palatal foramina broadens posteriorly and the molars are larger (Watts and Aslin 1981).

Melomys cervinipes can also be differentiated from *M. capensis* and *M. rubicola* based on geographic range. *M. capensis* is found on the Cape York Peninsula and *M. rubicola* is found on Bramble Cay Island (van Dyck and Strahan 2008).

GENERAL CHARACTERS

Melomys cervinipes is a small, light gray-brown to russet brown (color is highly variable and can change with age; Watts and Aslin 1981) murid rodent with a white to cream ventral surface, a brown to black tail and light fawn-colored feet (Moore and Burnett 2008). Young animals are often a uniform light gray (Watts and Aslin 1981). The fur is soft, fine and long, and dark whiskers are conspicuous on the muzzle (Watts and Aslin 1981). There is no apparent sexual dimorphism in color. The ears are short, rounded and dark gray to black in color, and the eyes bulge conspicuously (Watts and Aslin 1981). As for all members of the tribe Uromyini, the tail is naked, with the scales arranged in a mosaic-like pattern (interlocking with little overlap, Watts and Aslin 1981), with short hairs (Harrison 1962; Breed and Ford 2007), and is approximately equal to the head-body length (Watts and Aslin 1981). The tail is partially prehensile, with the tip capable of curving round objects to potentially provide support (Harrison 1962). The hind feet are long and wide. Mean measurements (value ± *SD*; with parenthetical ranges when appropriate – compiled from Harrison 1962; Keith 1970; Taylor and Horner 1970; Wood 1971; Watts and Aslin 1981; Leung 1999; Moore and Burnett 2008) of *M. cervinipes* (both sexes) were: body mass 72.9 ± 12 g (37–120 g); head–body length 133.5 ± 12.7 mm (100–197 mm); tail length

142.6 ± 10.9 mm (105–180 mm); Hind foot length 27.5 ± 0.8 mm (25–29.2 mm); ear length 18.3 ± 1.6 mm (14–20.9 mm).

The head is broad (Watts and Aslin 1981) and the skull delicate (Fig. 2). The skull is difficult to distinguish from that of *M. burtoni*, although there is a tendency towards larger size, with divergence in the posterior molar rows, compared to the more parallel rows of *M. burtoni* (Keith 1970). Mean ± *SD* craniodental measurements (mm; with parenthetical range – compiled from Harrison 1962; Keith 1970; Watts and Aslin 1981; Bryant 2013; T.R. pers. obs.) of adult *M. cervinipes* (both sexes) were: greatest skull length 33 ± 1.7 (26.4–39.5); condylobasal length 31.2 ± 1.6 (28.9–33.4); basal length 28.8 ± 1.7 (26.5–31.1); zygomatic breadth 17.4 ± 0.9 (13.7–20.7); interorbital width 5.3 ± 0.1 (3.8–6.6); interparietal length 9.9 ± 0.2 (9.5–10.1); interparietal width 4.6 ± 0.2 (4.3–4.8); braincase width 15.3 ± 0.2 (15–15.6); rostrum length 10.9 ± 0.7 (7.1–11.6); rostrum width 3.6 ± 0.2 (3.3–3.9); maximum rostrum width 6.4 ± 0.1 (4.8–7.6); palatal length 17.2 ± 0.8 (16.2–18.3); length of the anterior palatal foramina 5.8 ± 0.4 (4.9–7.9); Anterior palatal foramina width 2.3 ± 0.1 (1.6–3); inside^{M1-1} width 2.8 ± 0.2 (2.2–4.1); outside^{M1-1} width 6.9 ± 0.2 (6.6–7.2); inside^{M3-3} width 4.1 ± 0.1 (2.9–5.3); crowns^{M1-2} length 5.4 ± 0.2 (5.2–5.6); crowns^{M1-3} length 6.5 ± 0.2 (6.3–6.7); upper molar alveolus 6.8 ± 0.3 (5.9–8.7); length of incisive foramen 13.5 ± 0.1 (10.3–17.2); bulla length 5.1 ± 0.2 (4.4–6.7).

DISTRIBUTION

Melomys cervinipes is endemic to Australia, occurring along the eastern coast and subcoastal areas of Queensland and New South Wales (Fig. 3). They are found from sea level (0 m) up to between 1221 m (Mt. Elliot; Williams et al. 1993a) and 1600 m (DEHP, 2017) above sea level, ranging from tropical Northern Queensland, south of the Cape York peninsula

(10°45'0" S; 142°34'60"E) down to central New South Wales, approximately 50 km north of Sydney (33°25'48.15" S; 151°15'50.13"; Bryant and Fuller 2014; Fig. 3).

FOSSIL RECORD

Rodent fossils appear in Australia's rock strata dating 5–4.5 million years ago (Ma, Long et al. 2002; Rowe et al. 2008; Nilsson et al. 2010) and fossil evidence shows 3 waves of rodent migration into Australia: the first wave (± 4.5 Ma) bringing the Conilurini; the second wave (± 2 Ma) bringing the Hydromyini and Uromyini; and the third wave (± 1.28–0.85 Ma) bringing the genus *Rattus* (Nilsson et al. 2010; Rowe et al. 2011). The mosaic-tailed rats were part of the second wave occurring during the mid-Pleistocene, approximately 1.8 Ma (Breed and Ford 2007; Nilsson et al. 2010).

Fossil records of Uromyine rodents in Australia are limited. *Uromys* sp. were recorded in a limestone quarry on the northeast face of Mount Etna (23°9'23.35"S; 150°28'49.90"E, approximately 25 km north of Rockhampton, Queensland; Hocknull et al. 2007), dated approximately 500,000 years old; however, the only definitive fossil record of *Melomys* is in late Pleistocene fossils from Pyramids cave (~ 6.5 km north east of Buchan, Victoria; 37°26'59"S; 148°12'59"E; Mahoney 1965), dated approximately 33,000–15,450 years old (Wakefield 1972).

FORM AND FUNCTION

The dental formula of *Melomys cervinipes* is i 1/1, c 0/0, p 0/0, m 3/3, with a total of 16 teeth (Breed and Ford 2007). The upper molar alveolar pattern and alveolar length of M1 distinguish the species from *M. burtoni* (Knox 1978). *M. cervinipes* show 4 distinctive roots on M1 and M2, and 3 roots on M3, while *M. burtoni* show a pattern of 5 roots on M1 and M2 and 3 roots on M3, Knox 1978). M1 alveolar length of *M. cervinipes* ranges between 3.1–3.7 mm compared to the smaller range of *M. burtoni* (2.4–3.1mm; Knox 1978). Upper incisors are opisthodont and the anterior palantine foramina is long, ending in line with the anterior face of the 1st molar (Menzies 1996).

As is typical of most rodents, there are 2 clearly demarcated regions to the stomach: the forestomach (corpus) and the hindgut (antrum), with the corpus being considerably larger, with an extended fundic diverticulum for the potential storage of non-fibrous plant material (Breed and Ford 2007). The small intestine is approximately 50% of the total length of the intestinal tract (Breed and Ford 2007).

Brain weight for *M. cervinipes* is estimated at 1.9 g, accounting for approximately 2.7% of overall body mass (Mace et al. 1981). According to Menzies (1996), the supraorbital crest extends as a weak ridge across the posterior surface of the cranium, fading as it reaches the posterior parietal margin. The parietal-squamosal suture turns away from the post-orbital ridge, dipping downwards to form 90° (Menzies 1996).

The gonads of *Melomys* resemble those of *Rattus norvegicus* in their general morphology and histology (Taylor and Horner 1970). Adult females have 2 pairs of inguinal teats (Harrison 1962; Calaby and Wimbush 1964; Barnett et al. 1977; Watts and Aslin 1981). Although considered rare, sexual quiescence in adult females is characterized by closing of the vagina and ovarian inactivity, with absence of mature follicles and large corpora lutea, presence of only small and medium-sized (350–450 pm) follicles (with extensive atresia), and advanced luteal degeneration (Taylor and Horner 1970). The adult female bears 2 uterine horns, typical of murids. The ovary of non-pregnant females is also typical of most murids, with atresia of follicles at different stages of development and healthy maturity follicles of various sizes (Taylor and Horner 1970). Ripe follicles are considerably smaller than newly formed corpora lutea, measuring only 750–800 pm in diameter, compared to 1000 pm, respectively (Taylor and Horner

1970). The average ovulation rate is 3.25 per estrus (range 2–4) and ovulatory activity and corpora luteal formation is evenly distributed between the 2 ovaries (Taylor and Horner 1970). Pregnant females bear considerably larger corpora lutea (~ 1700 pm) than non-pregnant females during the early stages of pregnancy, when average embryo crown-rump length is 37.5 mm (Taylor and Horner 1970). The corpus luteum decreases in size as the embryo increases in size, indicating a decrease in the function of the corpus luteum at this time (Taylor and Horner 1970). Larger follicles are atretic (Taylor and Horner 1970).The ovaries of juvenile females are characterized by naked peripheral ova, numerous small and medium-sized follicles (approximately 475 pm) and extensive atresia (Taylor and Horner 1970).

Adult breeding males have scrotal or inguinal testes (mean = 2.78 g, Breed and Taylor 2000), which are relatively large in relation to body size for a murid (Breed and Taylor 2000), being 2% of the body mass (Breed 1997a). Non-breeding males show some regression of the testes and accessory sex glands (Taylor and Horner 1970). The glans penis is morphologically similar to other murids (Breed 1986). It is relatively long (mean length = 7.2 mm), being 0.7–4.7 mm longer than 19 other species of Australian rodent, while the mean maximum width is 0.1–2.1 mm wider than 20 other Australian murids (mean = 3.2 mm; Morrissey and Breed 1982). However, while the length and maximum width of the glans penis is greater in *M. cervinipes* than *M. burtoni*, the width near the outer rim is 0.3 mm narrower (mean = 2.1 mm; Morrissey and Breed 1982). Small spines are absent from the base of the glans penis, but are visible near the tip, and epidermal folding is evident (Morrissey and Breed 1982). The proximal baculum is short and wide (mean ± *SD*: length = 4.3 ± 0.3 mm; width = 2.6 ± 0.2 mm; L:B ratio = 1.6; Breed 1986). The large (mean: 13.1 mm, range: 9.3–19.1 mm, Taylor and Horner 1970), well-developed saccular seminal vesicles have coagulating glands lying on the inner curves (Breed

1986) and the seminal vesicles are bound to the prostate at the base. Active spermatogenic seminiferous tubules have an average diameter of 136 µm (114–152 µm), while the lumina of the epididymal tubules, which are lined with pseudostratified ciliated columnar epithelium, averages 137 µm (100–180 µm, Taylor and Horner 1970). In contrast, inactive seminiferous tubules and the lumina of the epididymal tubules average 75µm (58–96 µm) and 20 µm (10–30 µm), respectively, with no active spermatogenesis (Taylor and Horner 1970). Male accessory glands include the following: 1 pair of small medial ventral prostates (Breed 1986); 1 small pair of dorso-lateral prostates, with ducts entering the urethra on the ventrolateral surface (Breed 1986); 1 typical pair of dorsal prostates (Breed 1986), with numerous acini (Taylor and Horner 1970); 1 pair of Cowper's glands (mean diameter = 2.7 mm, range = 1.8–3.6 mm, Taylor and Horner 1970); a compact collection of ampullary gland tubules lying towards the distal end of the vas deferens (Breed 1986); 1 pair of bulbourethrals (Breed 1986); preputial glands are absent (Taylor and Horner 1970; Breed 1986), which is common to the Uromyini (Breed 1986). Sperm length averages 107 µm (Breed and Taylor 2000) and the falciform sperm head is more complex than that of Australasian *Rattus*, with 2 additional, elaborate F-actin containing processes (ventral) extending from the upper concave surface (Breed and Sarafis 1978; Breed 1984; Breed and Aplin 1994; Breed 1997b), joining at the base (Breed 1997b). While the apical hook ultrastructural organization resembles the falciform spermatozoa of *Rattus*, there are 2 ridges of subacrosomal material along the upper convex margin of the nucleus (Breed 1984; Breed and Leigh 1991; Breed 1997b). Juvenile males have smaller testes than adult males, which are situated in the lower abdominal position, and spermatogenesis, if present, does not progress beyond the primary spermatocyte stage (Taylor and Horner 1970). The average diameters of the seminiferous tubules (mean = 58 µm; range = 48–80 µm) and the tubular lumina (mean = 21 µm;

range = 10–50 μm) are small, as are the accessory sex glands (Taylor and Horner 1970). The seminal vesicles are small (mean = 2.8 mm) and are generally non-secretory in nature, while the luminar area is enclosed in an extensive bed of connective tissue, which is minimal in adults (Taylor and Horner 1970). The juvenile prostate has distinct, but small and simple, acini lined with pseudo-stratified low columnar epithelium and the Cowper's glands are considerably smaller than adults, averaging 0.75 mm in diameter (Taylor and Horner 1970).

Mean ± *SE* blood chemistry values were: glucose (*n* = 31; 4.23 ± 0.19 mmol/l), corticosterone (*n* = 38; 655 ± 75.96 ng/ml) and testosterone (*n* = 33; 0.1 ± 0.01 ng/ml; Turner 2015). The mean ± *SE* percentages (%) of 4 metabolites obtained from *M. cervinipes* (*n* = 4) injected with 3 doses (5, 25 and 100 mg/kg, respectively) of [^{14}C] phenol were: Quinol glucuronide (10.7 ± 2.8, 11.3 ± 4.0, 23.1 ± 1.1), phenyl glucuronide (66.7 ± 4.1, 55.3 ± 4.3, 55.4 ± 2.5), quinol sulfate (1.3 ± 0.1, 1.1 ± 0.1, 3.5 ± 0.7) and phenyl sulfate (16.4 ± 4.4, 14.2 ± 6.8, 7.8 ± 2.9; Baudinette et al. 1980).

ONTOGENY AND REPRODUCTION

Sexual maturity in *Melomys cervinipes* generally occurs at approximately 45–60 g body weight (Taylor and Horner 1970; Barnett et al. 1977) and can be estimated when combined head and body length (excluding the tail) reaches 95 – 120 mm (Taylor and Horner 1970). The adult pelage is nearly completely attained by the time of sexual maturity (Taylor and Horner 1970). Sexual maturity in males is clearly observed when the testes are descended (Barnett et al. 1977) and testis length distinguishes spermatogenic individuals from sexually inactive individuals due either to immaturity or to regression (Taylor and Horner 1970). Testes measuring 12–14 mm signify sexual maturity (Taylor and Horner 1970).

Sexual maturity is observed in females by the presence of prominent nipples (Barnett et al. 1977) and a perforate vagina (Taylor and Horner 1970), which occurs at approximately 80 days (75–85; Breed 1979). In addition, milk can be expressed easily from lactating females (Wood 1971), also providing an indicator of breeding condition. Females are polyestrous (Taylor and Horner 1970) and Breed (1978a) noted a considerably long cycle of 10–24 days (average 17), which could be associated with higher peripheral levels of progesterone (Breed 1978b; Watts and Kemper 1989). Breed (1978b) suggested 1 day of pro-estrus, 1–3 days of estrus and between 6 and 19 (mean 14.3 ± 0.6) days of diestrus. Females shows spontaneous ovulation, suggesting that there is no distinct breeding season (Taylor and Horner 1970; Kemper 1980).

Breeding tends to increase during the wet season (Breed and Ford 2007). However, this is highly variable from year to year (Wood 1971), as for other *Melomys* species. (e.g. *M. burtoni*, Taylor and Horner 1970). Breeding generally commences in late spring and summer (September–February) in the more southern areas of Queensland (Stradbroke to Mackay; McDougall 1946; Taylor and Horner 1970; Wood 1971), and extends into autumn and winter (March – August) in the northern regions of Queensland (Mossman to Cooktown; Lönnberg and Mjöberg 1916; Taylor and Horner 1970). Wood (1971) suggest that males and females form stable breeding pairs.

Gestation lasts approximately 27–40 days (Crichton 1969; Breed 1979; Sutherland and Dickman 1999; Watts and Aslin 1981), one of the longest among native Australian rodents (Breed 1978a). Age at first reproduction is approximately 7 months (Nowak and Paradiso 1983; Strahan 1983). Mass is not necessarily a good predictor of age at first reproduction as there is high individual variation in body mass both within and between populations (TR, pers. obs.). In the southern regions, young have been observed in summer (early November–early January in south-eastern regions of Queensland, Taylor and Horner 1970; October and February in north-eastern New South Wales, Barnett et al. 1977), although birthing can occur later (late Feb–April in Mackay; Taylor and Horner 1970). While breeding can take place within the same season of birth (Wood 1971), generally breeding does not commence until the following year (Freeland 1972; Watts and Kemper 1989). Taylor and Horner (1970) suggest that *M. cervinipes* may show post-partum estrous, although this requires further investigation.

Litter size ranges from 2–4 (Lönnberg and Mjöberg 1916; McDougall 1946; Davies 1960; Keith 1968; Taylor and Horner 1970; Wood 1971; Breed 1979; Watts and Kemper 1989), with an average of 1.8 (Wood 1971), and generally the sex ratio of young born into a population is 50:50 (Wood 1971). Young are precocious and relatively large at birth (± 5 g and 50 mm; Watts and Aslin 1981), with fine, dorsally pigmented hair. Incisor teeth are developed (Calaby and Wimbush 1964), with early terminal modification as grasping rather than gnawing structures (Lawrence 1941; Hamilton 1953; Calaby and Wimbush 1964; Taylor and Horner 1970) to facilitate nipple clinging (Lönnberg and Mjöberg 1916; Gard 1935; McDougall 1944; Davies 1960; Taylor and Horner 1970). Nipple clinging likely arose early in the evolution of the mosaic-tailed rats (Calaby and Wimbush 1964) and, given the high occurrence of nipple clinging behavior in the Muridae in general, this trait is likely ancestral to the family (Gilbert 1995). Numerous hypotheses have been proposed to explain the evolution of nipple clinging in the murids, specifically *M. cervinipes,* such as predator avoidance (Vestal 1938; Egoscue 1962; Taylor and Horner 1970) and sibling competition (Gilbert 1995). Young are fully furred with eyes open by 10 days and can be weaned at 20 days, indicating relatively rapid development (Watts and Aslin 1981). Mothers actively retrieve young back into the nest (Watts and Aslin 1981) and young will nipple cling beyond weaning if possible (TR, pers. obs.). This mode of reproduction suggests a prolonged prenatal contribution of care, with a relatively standard contribution to postnatal care (Taylor and Horner 1970).

ECOLOGY

Population characteristics. **—**Average population density for *Melomys cervinipes* has been estimated between 0.08 and 0.40 individuals/ha in various sized areas and forest fragments on the Atherton Tablelands of Queensland (Leung et al. 1993) and between 0.88 and 1.27 individuals/ha in sclerophyll forests of South East Queensland (Burnett 2010). Abundance increases in forests with large trees, vines and leaf litter (Wood 1971; Barnett et al. 1978), and also increases as the quantity of climbing plants, sub-canopy and ground cover increases, providing valuable food resources (Laurance 1994; Williams & Marsh 1998; Williams et al. 2002). Abundance can be limited by the diversity of canopy tree species (Rader and Krockenberger 2006). Interestingly, while Leung et al. (1993) found that relative density is proportional to forest area, suggesting that population density is relatively consistent between areas, other studies have found that fragmentation increases population size (Cox et al. 2003; Laurance 1994). Subsequently, *M. cervinipes* are more abundant in patches and forest edges than in continuous vine forest (Goosem 2000), most likely due to increased abundances of vines and other climbing plants that assist foraging and climbing behavior (Wood 1971; Laurance 1994; Cox et al. 2003; Moore and Burnett 2008). Indeed, Barnett et al. (1978) and Wood (1971) noticed increased abundance with increasing liana density. However, fragmentation limits dispersal between forest patches by opening up space with little overhead cover (Bentley 2008; Elmouttie 2009), potentially exposing individuals to greater predation risk.

Space use. **—**Typically, in the northern-most parts of its range, *Melomys cervinipes* occurs predominantly in dark, cool and damp conditions characteristic of closed continuous forest (Wood 1971; Barnett et al. 1978; Watts and Aslin 1981; Leung et al. 1993; Rader and Krockenberger 2006) but also occurs in rainforest fragments (Laurance 1992, 1994; Goosem 2000) and deciduous vine thickets (Williams et al. 1993b). Progressing south, *M. cervinipes* becomes less restricted in habitat preferences and is found in wetter, open forests (Watts and Aslin 1981; Peeters et al. 2014), wet sclerophyll to subtropical rainforest (Barnett et al. 1978), warm-temperate rainforests (including fragments, Cox et al. 2003), grassy open forest adjacent to rainforest (Dwyer et al. 1979; Woodall 1989), open shrubland (Woodall 1989), woodlands (Harrison 1962), often dominated by dry, tall Eucalypts on sandy soil (Taylor and Horner 1970; Peeters et al. 2014), closed palm forest (Martin 1975), tropical and sub-topical closed-forest (Watts and Aslin 1981), coastal mangrove forests (Lavery and Johnson 1974) and even cane fields adjacent to forested areas (up to 200m, McDougall 1944). Woodall (1989) recorded captures of *M. cervinipes* on Carlisle Island (20°47' S, 149°17'E, 35 km northeast of Mackay, Queensland) in closed forest dominated by *Bosistoa medicinalis*, open forests dominated by *Eucalyptus alba*, *E. polycarpa*, *E. tesselaris*, *Acacia solandri* and *Casuarina equisetifolia*, and open shrubland dominated by *Aglaia*, *Crinum*, *Macaranga, Scaevola*, *Sophora*, *Celtis*, *Olea* and *Cycas*. Hockings (1981) did not capture *M. cervinipes* in any habitat at Beerwah (26° 51' 26.28" S, 1152° 57' 18.72" E) or in scribbly gum-*Banksia aemula* habitat in the Cooloola State Forest (26° 3' 27.5112" S, 153° 2' 33.5256" E), suggesting landscape variation in distribution. The canopy floor and different vertical forest layers (at least up to 16m; Rader and Krockenberger 2006) are used. *M. cervinipes* spends between 30–90% of the time travelling in the canopy, with large amounts of individual variation (Rader and Krockenberger 2006).

Within a habitat, individuals only travel short distances (Elmouttie 2009). While long distance movements of between 350 m and 1500 m have been recorded, range lengths tend to be an order of magnitude smaller, ranging up to about 83 m for males and 81 m for females in New South Wales (Barnett et al. 1978) and 70.7 m for adults in Queensland (Bentley 2008). Range length is generally shorter in summer (11.9 ± 1.4 m) compared to winter (17.2 ± 3.9 m, Bentley 2008), perhaps due to increased resource abundance in the summer months, reducing the need to travel to find food. The home range is relatively small, averaging 0.42 ha (males = 0.31–0.67 ha; females = 0.21–0.5 ha; Rader and Krockenberger 2006), with no significant difference between the sexes (Wood 1971; Rader and Krockenberger 2006; Bino et al. 2014; but see Smith 1985). The core area of activity is smaller, averaging approximately 0.091 ha (Rader and Krockenberger 2006). Home ranges of individuals, both within and between sexes, overlap (Smith 1985) and there is little evidence of territorial exclusion, including a lack of correlation between body size and territory size (Rader and Krockenberger 2006). Body mass is negatively correlated with tree species diversity, suggesting that larger individuals occupy areas with lower canopy tree diversity (Rader and Krockenberger 2006). Rader and Krockenberger (2006) suggest that these areas often contain denser layers of sub-canopy, understorey and/or vine species, potentially providing greater cover from predation.

In captivity, life span is approximately 2 years (Hayes et al. 2006). In the wild, individuals are known to survive to a second breeding season (Wood 1971), thus longevity is estimated to be between 1 and 2 years (Laurance 1991). Adult population sex ratios average 50:50 (Taylor and Horner 1970; Wood 1971; Smith 1985; Horskins 2005).

***Diet.* —**The diet of *Melomys cervinipes* is characteristic of a generalist, consisting primarily of foliage and vegetation (Harrison 1962), and has also been reported to feed on fruits and seeds, as well as fungi, insects and flowers (Wood 1971; Rader and Krockenberger 2006; Elmouttie 2009; Elmouttie and Mather 2012), as well as human food products (S. Burnett, pers. comm.). This is supported by the morphology of the fore-stomach (Breed and Ford 2007). *M. cervinipes* climbs to access fruits, flower and nuts in the forest canopy (Rader and Krockenberger 2006). Due to the wide habitat and geographical distribution of *M. cervinipes*, there is evidence of regional and habitat differences in diet. For example, Vernes and Dunn (2009) found that fungi comprised 67% of the diet of *M. cervinipes* in heath-wet sclerophyll, whereas fungi comprised only 10% of the diet of individuals occurring in rainforests. It has also been suggested that animals living in edges have a higher proportion of fruits, leaves and flowers in their diet due to the high abundance of these resources in these types of areas (Laurance 1994).

Diseases and parasites. ***—****Melomys cervinipes* carries several internal and external disease-causing agents. Leptospirosis is a zoonotic emerging infectious disease (Brandling-Bennett and Pinheiro 1996; Levett 1999) caused by pathogenic leptospire bacteria (World Health Organization 2003). Internally, *M. cervinipes* is a known urinary carrier of 3 leptospirosis *Leptospira* serovars, namely *celledoni* in the Celledoni serogroup (Emanuel et al. 1964), *zanoni* in the Pyrogenes serogroup (Biosecurity Australia 2000) and is considered to be a maintaining host of the *bindjei* serovar in the Canicola serogroup (along with *M. burtoni*, Battey et al. 1964). In addition, antibodies to serotype *L. pomona* have been found in the sera of *M. cervinipes*, although the strain itself was not isolated and *M. cervinipes* are not identified as urinary carriers (Battey et al. 1964). Six other bacteria found in *M. cervinipes* are *Mycoplasma haemomuris* (Mackerras 1958), *Spirillum minus* (Cook et al. 1967), *Eperythrozoon coccoides* (Cook et al. 1967), *Brucella suis* type 3 (Cook et al. 1966, 1967), *Coxiella burnetii* (Cook et al. 1967) and the

TVS1 and TVS2 strains of *Orientia tsutsugamushi*, of which the TSV2 strain is highly virulent (Cook et al. 1967; Campbell and Domrow 1974; Glazebrook et al. 1978).

Melomys cervinipes is also parasitized by at least 35 species of internal parasite from 7 Orders. These include (complied from Johnston and Mawson 1941; Mackerras 1958; Sprent and Mines 1960; Mawson 1961; Sprent 1963; Sprent and McKeown 1967; Bhaibulaya 1968, 1979; Freeland 1983; Beveridge 1985; Hugot and Quentin 1985; Spratt and Singleton 1986, 2001; Singleton et al. 1991; Gibbons and Spratt 1995; Smales 1997, 2009; Smales et al. 2004; Spratt 2008): Order Cyclophyllidea (2 species: *Bertiella* sp. and *Raillientina celebensis*), Order Panagrolaimida (1 species: *Strongyloides* sp.), Order Plagiorchiida (1 species: *Platynosomum australiense*), Order Porcephalida (1 species: *Linguatula serrata*), Order Rhabditida (16 species: *Angiostrongylus mackerrasae, Chisholmia bainae, C. mawsonae, Equilophos polyrhabdote, Hepatojarakus fasciatus, H. pycnofasciatus, Mammanidula melomyos, Nippostrongylus magnus, N. typicus, Odilia brachybursa, O. emanuelae, O. mackerrasae, O. melomyos, Parasabanema praeputiale, Peramelistrongylus* sp. and *P. skedasto*), Order Spirurida (10 species: *Allodapa* sp., *Cercopithfilaria johnstoni, Heterakis spumosa, Mastophorus muris, Monanema australis, Ophidascaris robertsi, Physaloptera banfieldi, Polydelphis anoura, Syphacia darwini* and *Toxocara mackerrasae*), Order Trichocephalida (3 species: *Calodium hepatica, Capillaria* sp. 1 and *Trichurus muris*) and unidentified microfilaria (Mackerras 1962). Freeland (1983) suggested that *Ophidascaris robertsi* does not readily infect *M. cervinipes* in the natural environment, although *M. cervinipes* does demonstrate susceptibility in a laboratory environment.

Externally, as with other rodents, *M. cervinipes* is subject to mite, tick, flea and louse infestation. 48 species of external parasite have been recorded on *M. cervinipes* from 5 Orders. These include (complied from Radford 1943, 1954; Domrow and Smith 1955; Roberts 1960, 1970; Domrow 1960, 1961, 1962, 1967, 1971, 1978, 1987, 1991; Kuhn and Ludwig 1966; McKenzie et al. 1976; Doube 1979; Fain and Lukoschus 1981; Domrow and Lester 1985): Order Ixodida (3 species: *Haemaphysalis humerosa, Ixodes holocyclus* and *I. tasmani*), Order Mesostigmata (12 species: *Domrownyssus dentatus*, *Haemolaelaps domrowi*, *Laelaps assimilis*, *L. echidinus, L. mackerrasi, L. nuttalli, L. rothschildi, L. southcotti, Mesolaelaps anomalus, M. bandicoota*, *Paramelaelaps bandicoota* and *Trichonyssus praedo*), Order Psocodea (1 species: *Hoplopleura* sp.), Order Sarcoptiformes (3 species: *Notoedres muris, Murichirus enoplus* and *M. lobatitarsis*) and Order Trombidiformes (33 species: *Ascoschoengastia indica, A. rattus, Eutrombicula hirsti, Guntheria andromeda, G. bamaga, G. cassiope, G. coorongensis, G. derrick, G. dumosa, G. heaslipi, G. innisfailensis, G. kallipygos, G. lappacea, G. mackerrasae. G. petulans, G. pseudomys, G. scaevola, G. shieldsi, G. smithi, G. wongabelensis, Helenicula kohlsi, Leptotrombidium delicense, Neotrombicula antechinus, Odontocarus sp., Paraspeleognathopsis sp., Schoutedenichia emphyla, Walchia sp., W. fuller* and *W. morobensis*). Domrow (1967) reported *G. antipdoianumi, G. queenslandica*, *P. bakeri* and *Radfordia fanningi* from *M. cervinipes* originating in grassland. Given the generally sharply defined habitat contrast between *M. cervinipes* and *M. burtoni*, it is likely that the host species was misidentified.

M. cervinipes are also known to carry at least 5 different species of keratinophilic fungi, namely *Arthroderma curreyi*, *A. cuniculi*, *A. cajetani*, *Chrysosporium* sp. (Rees 1967) and *A. tuberculatum* (Hubalek 2000).

Interspecific interactions. **—***Melomys cervinipes* is sympatric over parts of its range with 2, almost morphologically indistinguishable species, namely *M. burtoni* (Taylor and Horner 1970; Watts and Aslin 1981; Frost 2008) and a currently undescribed mosaic-tailed cryptic taxon, *species nova* (Bryant et al. 2011). This taxon is not monophyletic with any *Melomys* (Australian or New Guinean) and is considered a sister taxon to *Melomys* and *Solomys* (Bryant et al. 2011). While *M. cervinipes* and *M. burtoni* are generally sharply segregated in space (Smith 1985), utilizing different habitats (rainforest vs. grassland). *M. cervinipes* currently possesses an allopatric distribution to *M. capensis*, with *M. capensis* being restricted to the Cape York Peninsula and *M. cervinipes* occurring south of this region (Bryant and Fuller 2014).

Melomys cervinipes commonly occurs with the Cape York rat *Rattus leucopus* in the same habitat, suggesting limited competition (Laurance 1994). Co-occurrence is likely possible because Cape York rats rarely leave the forest floor, whereas *M. cervinipes* is scansorial (Wood 1971). In contrast, *M. cervinipes* abundance is lower in habitats occupied by bush rats *Rattus fuscipes* and giant white-tailed rats *Uromys caudimaculatus*, suggesting competitive exclusion as a consequence of diet (both consume seeds, nuts, stems and leaves, Watts 1977) or space use (both species are scansorial; Laurance 1992) by these larger bodied species. *M. cervinipes* also co-occurs with several other mammal species: feathertail gliders *Acrobates pygmaeus* (Vernes et al. 2006), rufous bettongs *Aepyprymnus rufescens* (Vernes et al. 2006), rusty antechinus *Antechinus adustus* (Smith et al. 2017), yellow-footed antechinus *A. flavipes* (Goosem 2000), Atherton antechinus *A. godmani* (Harrison 1962; Harrington et al. 2001), and brown antechinus *A. stuartii* (Vernes et al. 2006), northern bettong *Bettongia tropica* (Williams et al. 1996), long-tailed pygmy possums *Cercartetus caudatus* (Rader and Krockenberger 2006) and eastern pygmy possums *C. nanus* (Vernes et al. 2006), striped possums *Dactylopsila trivirgata* (Williams et al. 1996). Bennett’s tree-kangaroos *Dendrolagus bennettianus* and Lumholtz’s tree-kangaroo *D. lumholtzi* (Williams et al. 1996), lemuroid ringtail possums *Hemibelideus lemuroides* (Williams et al. 1996), water rats *Hydromys chrysogaster* (Williams et al. 2006), musky rat-kangaroos *Hypsiprymnodon moschatus* (Harrison 1962; Rader and Krockenberger

2006), northern brown bandicoots *Isoodon macrourus* (Williams et al. 1993a; Harrington et al. 2001; Rader and Krockenberger 2006) and long-nosed bandicoots *Perameles nasuta* (Harrison 1962; Harrington et al. 2001; Vernes et al. 2006), spectacled hare-wallabies *Lagochestes conspicillatus* (Williams et al.1996), brown hares *Lepus capensis* (Williams et al. 1996), agile wallabies *Macropus agilis*, antilopine kangaroos *M. antilopinus*, eastern grey kangaroos *M. giganteus* (Williams et al. 1996), parma wallabies *M. parma* (Vernes et al. 2006), whip-tail wallabies *M. parryi*, wallaroos *M. robustus* (Williams et al. 1996) and red-necked wallabies *M. rufogriseus* (Vernes et al. 2006), black-footed tree-rat *Mesembriomys gouldii* (Williams et al. 1996), house mice *M. musculus* (Williams et al. 1996), platypus *Ornithorhynchus anatinus* (Harrison 1962; Vernes et al. 2006), rabbits *Oryctolagus cuniculus* (Williams et al. 1996), yellow-bellied gliders *Petarus. australis* (Vernes et al. 2006), mahogany gliders *P. gracilis*, sugar gliders *P. breviceps* (Jackson 2001), squirrel gliders *P. norfolcensis* (Williams et al. 1996) and greater gliders *Petauroides volans* (Vernes et al. 2006), allied rock-wallabies *Petrogale assimilis* (Williams et al. 1996), unadorned rock-wallabies *P. inornata* (Williams et al. 1993a), Godman's rock-wallabies *P. godmani*, Mareeba rock-wallabies *P. mareeba* and Sharman's rock-wallabies *P. sharmani* (Williams et al. 1996), brush-tailed phascogales *Phascogale tapoatafa* (Williams et al. 1996), koalas *Phascolarctos cinereus* (Vernes et al. 2006), long-tailed planigales *Planigale ingrami* (Williams et al. 1996) and common planigales *P. maculata* (Rowland 2015), prehensile-tailed rat *Pogonomys mollipilosus* (Rader and Krockenberger 2006), long-nosed potoroos *Potorous tridactylus* (Vernes et al. 2006), common ringtail possums *Pseudocheirus peregrinus* (Vernes et al. 2006), green ringtail possums *Pseudocheirops archeri* (Harrison 1962), Daintree River ringtail possums *Pseudochirulus cinereus* and Herbert River ringtail possums *P. herbertensis* (Williams et al. 1996), delicate mice *Pseudomys delicatulus* and eastern chestnut mice *P. gracilicaudatus* (Williams et al. 1996), swamp rats *Rattus lutreolus* (Vernes et al. 2006), brown rats *R. norvegicus*, black rats *R. rattus*, canefield rats *R. sordidus* and pale field rats *R. tunneyi* (Williams et al. 1996), white-footed dunnarts *Sminthopsis leucopus*, stripe-faced dunnarts *S. macroura,* common dunnarts *S. murina* and red-cheeked dunnarts *S. virginiae* (Williams et al. 1996), feral pigs *Sus scrofa* (Harrison 1962; Rader and Krockenberger 2006), short-beaked echidnas *Tachyglossus aculeatus* (Harrison 1962; Vernes et al. 2006), red-legged pademelons *Thylogale stigmatica* (Harrison 1962; Vernes et al. 2006) and red-necked pademelons *T. thetis* (Vernes et al. 2006), mountain brushtail possums *Trichosurus caninus* (Vernes et al. 2006), coppery brushtail possums *T. johnstonii* (Williams et al. 1996) and common brushtail possums *T. vulpecula* (Harrington et al. 2001), masked white-tailed rats *Uromys hadrourus* (Harrington et al. 2001), swamp wallabies *Wallabia bicolor* (Vernes et al. 2006) and common rock rats *Zyzomys argurus* (Williams et al. 1996). *M. cervinipes* also has numerous natural predators, including dingoes *Canis lupus dingo* (Vernes et al. 2001; Hayes et al. 2006), spotted tail quolls *Dasyurus maculatus* (Hayes et al. 2006; Moore and Burnett 2008) and northern quolls *D. hallucatus* (Moore and Burnett 2008), sooty owls *Tyto tenebricosa* (Holmes 1994; Moore and Burnett 2008) and lesser sooty owls *T. multipunctata* (Moore and Burnett 2008; McDonald et al. 2013), southern boobooks *Ninox boobook* (Moore and Burnett 2008), Amethystine pythons *Morelia amethistina* (Moore and Burnett 2008), carpet pythons *M. spilota variegata* (Hayes et al. 2006; Moore and Burnett 2008), spotted pythons *Antaresia maculosa* (Moore and Burnett 2008) and red-bellied black snakes *Pseudechis porphyriacus* (Hayes et al. 2006). Feral cats *Felis catus* are also predators of *M. cervinipes* (Moore and Burnett 2008).

Melomys cervinipes is important for increasing germination of rainforest fruits (by a factor of 3.5) due to their removal of the pericarp, suggesting they are mutualistic frugivores with fruiting rainforest tree species (Elmouttie and Mather 2012). Out of 19 rainforest fruit species presented to both *M. cervinipes* and bush rats, 16 (84% of species) showed increased germination rates, whereas the germination rates of *Neisosperma poweri, Beilschmiedia recurva* and *Endiandra monothyra sub monthyra* were not affected (Elmouttie and Mather 2012). Interestingly, as bush rats does not feed on either *Syzgium gustavioides* or *Beilschiedia bancrofti* (Elmouttie and Mather 2012), *M. cervinipes* could be particularly important for these species. Although *M. cervinipes* has been reported to occur in sugarcane *Saccharum* sp., it is rarely captured in this habitat type, and is thus unlikely to be a major crop pest, unlike *M. burtoni* (Dyer et al. 2011). Live-trapping with a bait mixture of peanut butter, honey, vanilla essence and rolled oats (Rowland 2015) is suitable for *M. cervinipes*, although they will still enter traps baited only with rolled oats and vanilla essence (Laurance 1992), peanut butter and rolled oats (Barnett et al. 1978) or even linseed oil soaked cardboard (Horskins 2005). Trapping success is approximately 2.23 times higher in arboreal traps than terrestrial traps (Laurance 1992).

BEHAVIOR

Melomys cervinipes is nocturnal (Taylor and Horner 1970; Wood 1971), with variations in activity depending on time of year and moonlight (Wood 1971). Most activity takes place soon after sunset, between 5–11 pm, and again before sunset, between 2–5 am (Wood 1971). However, *M. cervinipes* have been captured at all hours throughout the night (T. Stewart, unpubl. data). There is no discernable change in activity between seasons (Wood 1971).

Melomys cervinipes is scansorial (Taylor and Horner 1970; Watts and Aslin 1981), favoring trees with epiphytic or attached vegetation growing on them (e.g. vines, creepers, Wood 1971). *M. cervinipes* makes extensive use of the arboreal environment for foraging (Rader and

Krockenberger 2006) and nesting (Wood 1971). Nests are located in the center of the home range, both on, and above, the ground (between 0.8 and 16 m), with both sexes using multiple nests (up to 2) simultaneously (Rader and Krockenberger 2006). Ground nest are usually located in burrows and hollows. Arboreal nests may be constructed of leaves, such as *Calamus* sp. and *Pandanus* sp. (Moore and Burnett 2008). *M. cervinipes* also utilizes grass trees *Xanthorrhoea* for food and nesting (Williams et al. 1993a). Nests have also been associated with human materials (e.g. beneath sheets of corrugated iron, inside furniture etc., S. Burnett, pers. comm.).

Olfactory recognition of mammalian predators is observed during the late wet season (May; Hayes et al. 2006). Interestingly, *M. cervinipes* avoids both familiar (quoll, dingo) and unfamiliar predators (Tasmanian devil *Sarcophilus harrisii*, red fox *Vulpes vulpes*) during this time (Hayes et al. 2006). No avoidance of predator cues, apart from quoll cues, is observed in the late dry season (October–November) and *M. cervinipes* do not appear to avoid reptilian predator cues (carpet python, Hayes et al. 2006). Hayes et al. (2006) suggested that this recognition and avoidance pattern occurs during the late wet season because there are more juveniles, which could be beneficial for minimizing predation risk and maximizing survival. *M. cervinipes* may utter loud distress calls upon handling (Meek and Peak 2008; T. Rymer, pers. obs.).

Melomys cervinipes display behavioral syndromes (i.e. personality), with some individuals being consistently bolder than others (Turner 2015). Activity in the open field was found to be repeatable over a 24-hour period, and activity in the open field was correlated with activity in both novel object and predator avoidance tests (Turner 2015). Interestingly, when exposed to a handling stress, bolder animals show increased testosterone production, rather than inhibition, as should occur with increased glucocorticoid synthesis (Retana-Márquez et al. 2003; Hardy et al. 2005), compared to more shy individuals (Turner 2015). However, testosterone is energetically expensive to produce, and these bolder animals consequently show decreased glucose concentrations under stressful situations (Turner 2015). Anxiety behavior, as measured by the time spent active in the open arms of a plus maze, was not correlated with corticosterone (a stress glucocorticoid, Charmandari et al. 2005) production, suggesting decoupling of personality traits (Turner 2015). This is predicted in complex environments, such as tropical rainforests, where habitat complexity may select for both behavioral flexibility (associated with reactive coping styles) and boldness (associated with proactive coping styles, Delarue et al. 2015).

GENETICS

The genus *Melomys* in Australia and New Guinea are monophyletic, excluding *Paramelomys* (Bryant et al. 2011), and is paraphyletic with *Solomys* (Watts and Baverstock 1995; Rowe et al. 2008; Bryant et al. 2011). Indeed, Menzies (1996) suggested that *Paramelomys* is a plesiomorphic sister group to *Melomys*. Genetic studies suggest that *Melomys* and *Solomys* diverged approximately 2.3 Ma (Bryant 2013). This close relationship between *Melomys* and *Solomys* is also evidenced in the region encoded by exon 6 of Zp3 (zona pellucida glycoprotein 3), where both groups share a histidine in position 298 (Swann et al. 2007). The 3 extant Australian *Melomys* species, and the extinct *M. rubicola*, shared a common ancestor approximately 1.3–1.5 Ma, after which *M. burtoni* diverged from *M. cervinipes*, *M. rubicola* and *M. capensis* (Bryant 2013; Bryant and Fuller 2014).

Melomys cervinipes has the karyotypic form 2n = 48 chromosomes (2N; Baverstock et al. 1980), although the modal number of chromosomes can differ between cell to cell, and up to 12 additional B-chromosomes may be present (Baverstock et al. 1977). The 1st pair of chromosomes is subacrocentric (Baverstock et al. 1980).

Melomys cervinipes is split into 3 divergent genetic clades (northern, central and southern; Bryant and Fuller 2014), and the phylogeography reflects multiple instances of allopatric divergence. One product of these successive divergence events is that northern and southern lineages have fixed differences across 10% of loci (Baverstock et al. 1980). The northern clade is distributed between the Burdekin gap and Laura Basin in north Queensland, and is closely related to *M. rubicola/M. capensis* in the northern regions, having diverged approximately 1.2–0.77 Ma (Bryant et al. 2011; Bryant and Fuller 2014), possibly due to isolation across the Normanby gap in far north Queensland (Bryant et al. 2011). Roughly, the northern lineage corresponds to populations north of Townsville in the Wet Tropics of far north Queensland (Campbell 1996). Although *M. cervinipes* is phylogenetically close to *M. capensis*, it is electrophoretically distant, demonstrating rapid protein evolution in comparison to *M. capensis* and *M. burtoni* (Wilson and Reeder 2005). Secondary contact has been documented between the northern and central lineages on the northern side of the Burdekin gap, where both occur in sympatry (Bryant and Fuller 2014). The central and southern lineages diverged across the Brisbane Valley Barrier (which continues to limit their distribution) approximately 0.94–0.49 Ma (Bryant et al. 2011; Bryant 2013; Bryant and Fuller 2014). The central lineage ranges from the northern side of the Burdekin gap to the Brisbane Valley Barrier, below which the southern lineage occurs (Bryant 2013; Bryant and Fuller 2014).

A currently undescribed taxon designated *species nova* occurs in sympatry with *M. cervinipes*, having been recorded in the Tully region, Wooroonooran National Park (Bryant et al. 2011) and Mount Lewis in North Queensland (Bryant 2013). The species shares a most recent common ancestor with all Australian and New Guinean *Melomys* and *Solomys*, although is morphologically indistinguishable for *M. cervinipes* and is not monophyletic with *Melomys* from either Australia or New Guinea (Bryant et al. 2011). *Species nova* is highly genetically distinctive from members of the *Melomys* genus (0.7–5% divergent with a 1 base pair indel in the AP5 intron) and is also divergent from sympatric *M. cervinipes* (0.3–3.7% divergent; Bryant et al. 2011). It is suggested that *species nova* diverged from the *Melomys/Solomys* clade approximately 2.5 Ma (Bryant et al. 2011). The presence of 7 fixed genetic substitutions and 2 fixed indels (in the nuclear loci) suggests reproductive isolation is occurring between *M. cervinipes* and *species nova* (Bryant et al. 2011).

CONSERVATION

Melomys cervinipes is listed as "Least Concern" by the International Union for the Conservation of Nature and Natural Resources Red List (IUCN 2015) due to its wide distribution, apparent large population size and lack of major threats (Burnett and Winter 2008). *M. cervinipes* utilizes closed forest environments, or forest fragments greater than 1 hectare in area (Cox et al. 2003), although it does occur in more open forests areas (S. Burnett, pers. comm.), disturbed forests and edges, often appearing at greater population densities in habitat fragments than unfragmented rainforest (Laurance 1994). However, while *M. cervinipes* is capable of using habitat corridors for movement and gene flow, resulting in little genetic variation between fragmented populations (Leung et al. 1993), it is inhibited from travelling between fragments by human-formed barriers, such as cleared areas, roads and power line corridors (Barnett et al. 1978; Goosem and Marsh 1997). Consequently, consideration on remaining patch size and connectivity is advisable when clearing forest inhabited by *M. cervinipes*.

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FIGURES and LEGENDS

Fig. 1. —Adult female fawn-footed melomys *Melomys cervinipes* from Cairns, Queensland, Australia. Photograph by T. Rymer.

Fig. 2. —Dorsal, ventral and lateral view of skull and lateral view of the mandible of an adult female fawn-footed melomys *Melomys cervinipes* (James Cook University Cairns Museum Collection, #45). Greatest length of skull is 29.06 mm. The specimen was collected in Kirrima, Queensland, Australia (specific date and location unknown). Photograph by D. Wilson, used by permission.

Fig. 3. —Geographic distribution of fawn-footed melomys *Melomys cervinipes* in Australia. Map redrawn from Atlas of Living Australia (ALA: http://bie.ala.org.au/species/Melomys+cervinipes; retrieved 25 November 2016). The box with asterisk indicates historical records listed as *M. cervinipes*, however, these are likely to be *M. capensis* based on current biological knowledge of the two species.