

Inheritance of Tail Colour and White-spotting in *Conilurus penicillatus* (Muridae)

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Abstract

In the wild, *Conilurus penicillatus* has two tail colour morphs, one entirely black and the other with a white distal brush of variable length. These colour morphs have been used in the past for taxonomic purposes. A small proportion (4.6%) of laboratory-reared animals have a white interstitial section. Pedigree data were collected from a laboratory colony ($n = 173$) established using seven wild-caught animals from the north Kimberley region, Western Australia. The hypothesis tested was that black tail is inherited as a Mendelian character recessive to white tip. Matings between black-tailed individuals always gave black offspring. Crosses between other colour morphs also supported this hypothesis.

The reasons for the occurrence of the interstitial white tail form in the laboratory are unknown but could be related to temperature, diet, light regimes and/or inbreeding. Wild and laboratory (56%) populations have white-spots of fur on the forehead. No pathological conditions were noted to be related to either this character or tail colour.

Keywords: genetics, Australian rodent, Kimberley, *Conilurus*.

Introduction

Conilurus penicillatus, the Brush-tailed Tree Rat, occurs in open savannah woodland in monsoonal northern Australia and southern New Guinea. Its long tail has a moderately brushy tip which in wild-caught individuals is either black or white, the amount of white being variable. In the past, tail colour has been used, in combination with other characters, to describe species and subspecies in the genus *Conilurus* (e.g. *C. penicillatus hemileucurus*, *C. melibius* and *C. randi*) (Tate 1951). At present only one species, *C. penicillatus*, is recognised (Honacki *et al.* 1982).

White tail tips are found in many mammalian species, some having all individuals so marked and some with only a certain proportion of the population white-tipped. Examples of the latter are *Potorous tridactylus* (Marsupialia : Potoroidae) in which up to 80% of some populations are white-tipped and *Macropus parma* (Marsupialia : Macropodidae) in which about 50% of individuals are white-tipped (Strahan 1983). The heritability of tail colour has not been investigated in these species. Arboreal and semi-arboreal rodents often have white coloration on their long tails. Examples are *Mesembriomys gouldii* and *M. macrurus*, both northern Australian tree rats which are sometimes sympatric with *C. penicillatus*. In contrast to *C. penicillatus*, they always have white-tipped tails, and may be more arboreal than *Conilurus*.

In the course of studying the reproductive biology of captive *C. penicillatus*, pedigree data were obtained from a laboratory colony. We describe here the genetic analysis of tail colour and white-spotting in this colony.

Materials and Methods

A breeding stock of seven wild-caught *C. penicillatus* (one black-tailed and two white-tailed females; two black-tailed and two white-tailed males) was trapped at Mitchell Plateau (c. 14°30'S., 125°50'E.) in the north Kimberley region of Western Australia. These animals and their laboratory descendants totalled 173 individuals. The animals were housed under temperature and daylength regimes of Perth, Western Australia (1st year) and Adelaide, South Australia (2nd and 4th years). They were kept (as breeding pairs) in wire mesh cages measuring 0.5 m × 0.5 m × 0.5 m and provided with water and parrot seed mix *ad libitum*. The diet was supplemented with fruit, vegetables, green grass and germinating seeds. Neonates and juveniles were individually identified by combinations of tail colour and sex, and as adults by toe-clipping.

Results

As well as the typical tail colour morphs of white (W) and black (w), a small proportion (4.6%) of laboratory-reared *C. penicillatus* had one or two patches of white away from the tail tip (Fig. 1). These will be referred to as white/black and in the following genetic analyses were considered to be phenotypically white. In normal white-tailed forms the proportion of white varied from 16 to 68% (mean = 33%) of the total tail length.

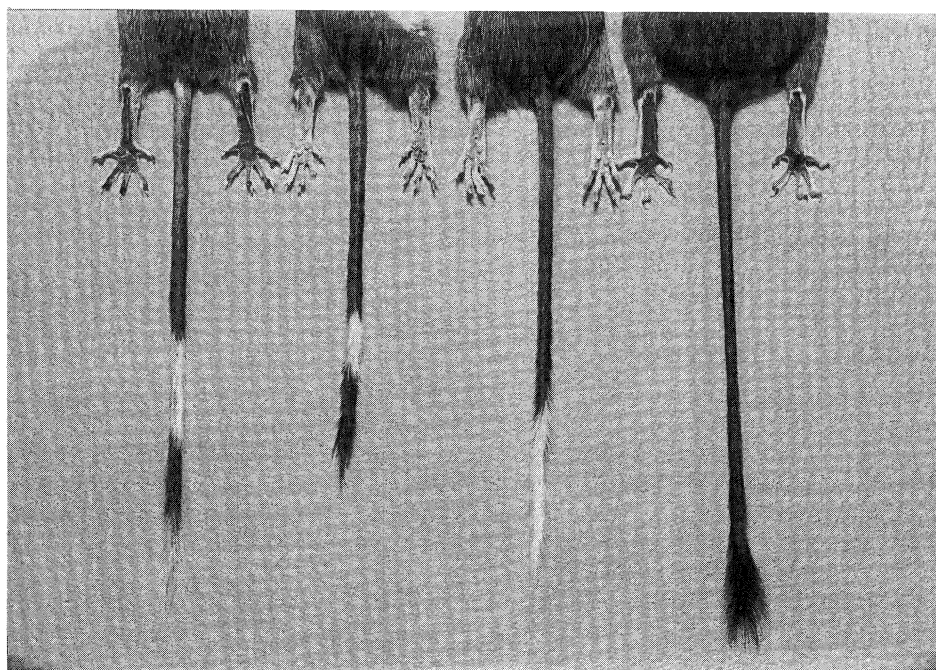


Fig. 1. Tail colours of *Conilurus penicillatus*. From left to right: SAM 14057, white/black; SAM 14058, white/black; SAM 14059, white; SAM 14056, black. SAM = South Australian Museum.

We tested the assumption that tail-tip colour is under the control of two alleles; *W* determining white and white/black, and *w* giving black tails. White cannot be recessive to black because matings between white individuals yielded some black offspring (Fig. 2, II.1 × II.2 and III.12 × III.13). Seven pairs of black-tailed animals yielded 31 black (13♀♀, 14♂♂, 4 unknown sex) but no white offspring.

We then considered matings between phenotypically white- and black-tailed individuals where there was *a priori* evidence that the white-tailed parent was heterozygous (*Ww*), one of its parents being black. The observed frequencies were not significantly different

($\chi^2_1 = 3.0$, $P > 0.05$, Table 1) from the expected ratios of 1 white to 1 black. Then we considered those white by black matings where the white parent was found to be Ww , *a posteriori* due to at least one black offspring. These litters were considered to be ascertained by truncate selection (since genetically similar matings which did not produce black offspring would not be ascertained) and tested by a fit to the truncated binomial distribution (Smith 1956). The expected numbers for the three matings were 13.2 black and 12.8 white and the observed values are shown in Table 1. The observed did not differ significantly from expected ($\chi^2_1 = 0.1$, $P > 0.5$).

Table 1. Results of matings between phenotypically white- (including white/black) and black-tailed *Conilurus penicillatus* where the white-tailed parent was a putative heterozygote
The expected ratio is 1 : 1

Evidence of heterozygosity	Parental pairs (n)	Offspring
<i>A priori</i>	white \times black (3)	white 26
	white/black \times black (2)	white/black 4
		black 18
<i>A posteriori</i>	white \times black (3)	white 12
		white/black 2
		black 12

Next we considered matings between phenotypically white-tailed individuals where there was *a priori* evidence that both parents were putative heterozygotes because of black grandparents. The frequency of white and black progeny agreed with the expected 3 to 1 ratio ($\chi^2_1 = 0.02$, $P > 0.5$, Table 2). Where the evidence suggested that both parents were heterozygous (Ww) because of black offspring, adjustment was made for ascertainment bias (truncate selection). The observed frequencies of tail colour in the offspring were not significantly different from the expected numbers of 23.2 white and 7.8 black ($\chi^2_1 = 1.3$, $P > 0.2$, Table 2).

Table 2. Results of matings between eight phenotypically white-tailed (including white/black) *Conilurus penicillatus* where all were putative heterozygotes
The expected ratio is 3 white : 1 black

Evidence of heterozygosity	Parental pairs (n)	Offspring
<i>A priori</i>	white \times white (2)	white 12
		white/black 1
		black 4
<i>A posteriori</i>	white \times white (1)	white 23
	white/black \times white (1)	white/black 3
		black 5

The above analyses show that the data are in agreement with the hypothesis that tail coloration in *C. penicillatus* is simply inherited, with white dominant to black. Other simple modes of inheritance are incompatible with the data, e.g. white/black cannot be considered black because this form crossed with black gives white offspring (Fig. 2, II.15 \times II.16);

the genes are not X-linked because black females have white sons (Fig. 3, II.16 × II.17) and white males have black daughters (Fig. 2, II.1 × II.2).

A sample of 68 *C. penicillatus* from a 5 km radius at the Mitchell Plateau, W.A., had 30 white- and 38 black-tailed individuals. Assuming Hardy-Weinberg equilibrium, genotype

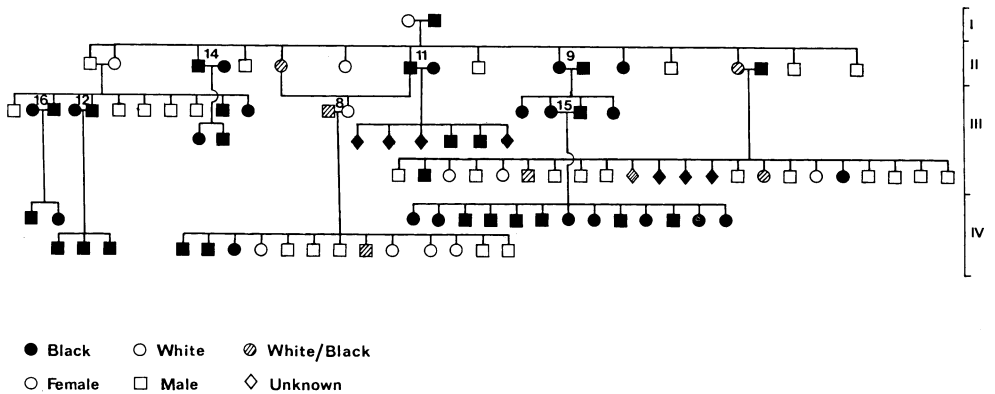


Fig. 2. Pedigree of one of the pairs of wild-caught *Conilurus penicillatus* showing sex and tail colour of the progeny. Roman numerals on right hand side are generation numbers. Numbers above mated pairs indicate same mating found in Fig. 3 or Fig. 4.

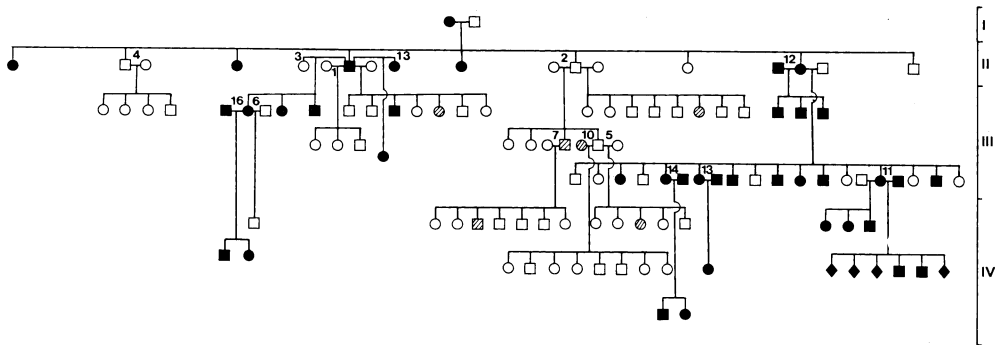


Fig. 3. Pedigree of a wild-caught, white-tailed male and a wild-caught, black-tailed female *Conilurus penicillatus*. Symbols and numbers explained in Fig. 2.

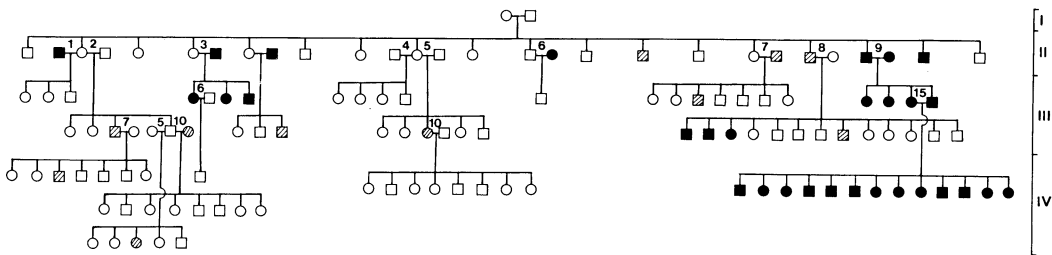


Fig. 4. Pedigree of a wild-caught, white-tailed male and a wild-caught, white-tailed female *Conilurus penicillatus*. Symbols and numbers explained in Fig. 2.

proportions can be estimated as 0.06 for *WW*, 0.38 for *Ww* and 0.56 for *ww*. Other populations of *C. penicillatus* are being studied for tail colour and preliminary results indicate that the proportion of white to black is quite variable, some populations being entirely black-tailed.

Approximately half (56%) of the laboratory population had a white spot of fur on the forehead. In some animals this blaze became less distinct or disappeared with age. The proportions of spotted to non-spotted *C. penicillatus* were not significantly different among the three tail colour forms ($\chi^2_2 = 4.41$, $P > 0.05$). However, the proportion of white-tailed animals with distinct, as opposed to faint, white spots was greater (67%) than that of black-tailed animals (43%) ($\chi^2_1 = 3.90$, $P < 0.05$).

Discussion

White-spotting is the most frequent coat colour effect associated with pathological conditions in mammals (Searle 1968), although its presence need not always be a pleiotropic effect (Hulbert and Doolittle 1973; Doolittle *et al.* 1975). Neither head-spotting nor white tail coloration was associated with any obvious pathological effects in our laboratory population and both the white head spot and white-tailed form are frequent in wild populations of this species.

The white/black tail form has not been observed in wild-caught *C. penicillatus* ($n = 130$) collected from many localities across the species' geographic distribution, yet it occurred in the laboratory colony. One possible explanation for this inconsistency is the different environmental conditions under which the laboratory colony was kept. Perth (32°S.) and Adelaide (35°S.) are temperate/mediterranean climates with long and short daylength cycles while the north Kimberley (14°S.) is tropical/monsoonal with far less annual variation in daylength. Temperature and light regimes are known to affect coat colour in some mammals (Searle 1968). The difference in diet for wild and captive individuals could also be a contributing factor.

Another possible explanation is that the white/black form was a result of homozygosity for a modifier gene which had a high frequency, perhaps due to founder effects, in the laboratory colony. The modifier gene may have been in high localised frequency in the wild parental population since all founders came from within a 1 km radius.

The brushy tail of *C. penicillatus* could be used in behavioural encounters. When released in the wild, animals bound off, tail held straight up and flicking rapidly from side to side. In the laboratory, alert animals hold their tails arched over their backs. A white tail tip, acting as a flag, may enhance the effect of these behaviours. It would be interesting to test whether predation pressure on *C. penicillatus* differs between white- and black-tailed individuals.

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