Morphological Variation among Populations of the Mountain Brushtail Possum, *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia)

D. B. Lindenmayer^A, K. L. Viggers^B, R. B. Cunningham^C and C. F. Donnelly^D

^ACentre for Resource and Environmental Studies, The Australian National University, Canberra, ACT 0200, Australia.

^BDivision of Biochemistry and Molecular Biology, The Australian National University, Canberra, ACT 0200, Australia.

^CStatistical Consulting Unit of the Graduate School, The Australian National University, Canberra, ACT 0200, Australia.

Abstract

The results are described of a study of morphometric variation among populations of the mountain brushtail possum, *Trichosurus caninus* Ogilby. Trapping surveys were completed at seven sites from southern Victoria to central Queensland. The variables measured from each of the 102 animals captured included head length, skull width, total body length, tail length, pes length, length of the ear conch, body girth, belly girth and the pelage colour.

Canonical variate analysis highlighted the existence of a marked separation between populations in Victoria and those in New South Wales and Queensland. The first canonical variate accounted for 89% of the variation between the populations and was dominated by the length of the ear conch, tail length and pes length. There also were differences between the populations for several other morphometric measures including the head and body length.

We recorded considerable variation in the fur colour of *T. caninus* both within and between the populations surveyed. However, no consistent pattern in the geographic variation of fur coloration was evident. We do not know the ecological or evolutionary causes underlying the observed differences in morphological characteristics amongst the populations of *T. caninus*. Further work is planned to examine the genetic variability of the populations and to assess the taxonomic significance of our findings.

Introduction

Many Australian mammals, from a wide range of taxonomic groups, exhibit variation in external morphology throughout their geographic distributions. Some of these taxa include the koala (Phascolarctos cinereus; Martin and Lee 1984); the fat-tailed dunnart (Sminthopsis crassicaudata; Morton and Alexander 1982); the water rat (Hydromys chrysogaster; Watts and Aslin 1981); and the long-nosed potoroo (Potorous tridactylus; Johnston and Sharman 1976). Another notable example is the common brushtail possum (Trichosurus vulpecula), a species characterised by marked changes in coat colour and body size throughout its distribution in Tasmania and mainland Australia (Kerle 1984; Kerle et al. 1991) as well as in New Zealand (Cowan 1990). Few studies of variation in the external morphology in the closely related mountain brushtail possum (Trichosurus caninus) have been undertaken, although several authors have noted the existence of variations in the pelage colour including grey and melanic colour forms (e.g. Calaby 1966; Kerle 1984). T. caninus typically occurs in tall, wet forests, including rainforest, throughout eastern Australia but not Tasmania (How 1972; Green 1974; Lindenmayer et al. 1990). The distribution of T. caninus ranges from southern Victoria (Victorian Mammal Database 1994) to west of Gladstone in central Queensland (Queensland Museum Mammal Database 1994). Here, we report the results of a study of the external morphology of T. caninus from throughout its known geographic range.

Methods

Study Sites

Trichosurus caninus was trapped at seven sites between October and November 1993. The survey sites (Fig. 1) were Cambarville in central Victoria (37°33′S, 145°53′E, 800 m above sea level); Bellbird in north-eastern Victoria (37°37′S, 148°48′E, 300 m above sea level); Allyn River Forest Park in central New South Wales (32°07′S, 151°28′E, 300 m above sea level); Whian Whian State Forest in north-eastern New South Wales (28°37′S, 153°20′E, 400 m above sea level); Byrangery Reserve in north-eastern New South Wales (28°37′S, 153°25′E, 200 above sea level); the Conondale Ranges in south-eastern Queensland (26°26′S, 152°35′E, 400 m above sea level); and Bulburin State Forest in central Queensland (24°33′S, 151°28′E, 600 m above sea level). The survey sites supported different types of vegetation ranging from wet sclerophyll eucalypt forest at Cambarville and Bellbird (see Seebeck et al. 1984; Scotts and Seebeck 1989) to subtropical rainforest at the other study areas (Queensland Department of Forestry 1984; Queensland Department of Primary Industries 1994; A. M. Gilmore, unpublished data).

Field Trapping Procedure

Trichosurus caninus was trapped in large wire cage traps baited with apple. A total of 50 traps was used at each site. The number of trap-nights at each location ranged from a minimum of 150 (Allyn River Forest Park) to 400 (Conondale Ranges). All animals captured were sedated with 'Zoletil' (tiletamine hydrochloride and zolezepam hydrochloride) (Virbac, Sydney, Australia) to facilitate the collection of a range of morphometric measurements (Viggers and Lindenmayer 1995). Animals were released at the point of capture when recovery was complete. Recaptured animals were identified readily by the area of skin on the neck that was shaved to facilitate the collection of blood samples. This ensured that they were not measured twice.

Collection of Body Measurements and Other Parameters

The body measurements that were recorded are defined in Table 1. Mean values and the associated standard errors for each measure are presented in the Appendix. Information was also collected on the body weight, sex and reproductive status of animals. In addition, we used a tooth-wear classification system to assign to animals to different age-classes. This procedure was developed for studies of *T. vulpecula* (see Winter 1980). An assessment was made of the pelage colour on the dorsum of each animal by matching the fur colour with shadings in a Munsell soil colour chart (Kallomorgen Corporation, Baltimore, USA). The same workers (D.B.L. and K.L.V.) collected all measurements for all of the individuals sampled in the study to reduce the potential differences between data recorders.

Table 1. A definition of the various morphometric measurements collected during studies of the mountain brushtail possum, *T. caninus*

Measurement	Description				
Head length	The distance from the tip of the nose to the external occipital protuberance				
Skull width	The distance across the widest part of the head (immediately in front of the ears)				
Total body length	The length of the body measured from the tip of the nose along the head and spine to the tip of the uncurled tail				
Tail length	The distance from the base of the tail to the tip of the tail				
Pes length	The distance from the heel to the tip of the largest toe (excluding the claw)				
Length of the ear conch	The distance from the notch at the base of the pinna to the highest point of the pinna				
Eye size	The distance between the medial canthus and lateral canthus of the right eye				
Chest girth	The body girth measured immediately behind the forelimbs				
Belly girth	The body girth measured immediately behind the caudal rib				

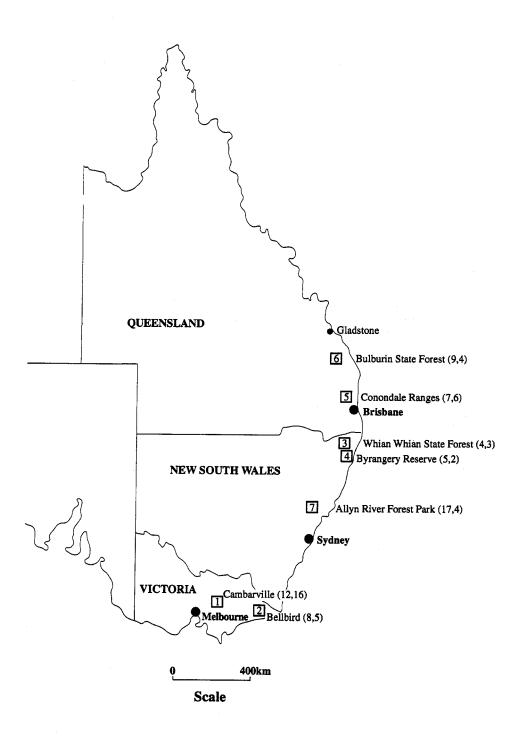


Fig. 1. The geographic distribution of sites surveyed for the mountain brushtail possum, *Trichosurus caninus*. The number assigned to each site corresponds to the chronological order in which they were sampled. The values in parentheses are the numbers of animals sampled at each site (males, females).

Statistical Analysis

Canonical variate analysis (Blackith and Reyment 1971) was used to formally examine the morphological differences between the various populations sampled as well as the morphological differences between adult male and adult female *T. caninus*. Other applications of these multivariate statistical procedures are provided by Phillips *et al.* (1973) and Campbell and Kitchener (1980). An alternative method to canonical variate analysis for multivariate morphometric analysis is discriminate analysis, essentially a pairwise statistical procedure, which was not used in this study.

Canonical variate analysis was used to identify linear combinations of morphological variables that best discriminated between populations of animals. Hence, combinations of values were sought that maximised the variation between populations relative to the variation within populations. An important assumption that underpins the use of significance tests in canonical variate analysis is the homogeneity of covariance matrices. Notably, the use of various diagnostic methods (see Phillips *et al.* 1973) indicated that this assumption was not violated in our analyses.

Only data from those individuals categorised as Age-class 3 or older were used in canonical variate analyses of morphometric variation in *T. caninus*. We excluded juvenile and subadult animals in an attempt to minimise any confounding of age and body shape.

Results

A total of 102 animals (62 males and 40 females) was captured at the seven survey sites (Fig. 1). As a result of male-biased trapping success at a number of survey sites, there was potential confounding between population and sex differences. A close examination of our data from Cambarville and Conondale revealed no significant differences in external morphology between males and females (Wilkes' lambda = 12.6, P = 0.82; Wilkes' lambda = 12.5, P = 0.81; respectively). In addition, canonical variate analyses completed first for males, and then for females, gave similar results. Given these findings, morphological data gathered from both sexes were combined and used in subsequent multivariate statistical analyses.

Although we recorded information on the body weight of all of the animals captured, we have not presented a formal analysis of these data because this measure may be highly sensitive to a range of factors such as differences in diet, reproductive status and physical condition. The mean values for body weight showed no consistent pattern. The heaviest mean body weights were recorded at Byrangery Reserve and Whian Whian State Forest (3.5 and 3.1 kg respectively) and the lightest were from Allyn River, Bulburin State Forest and Bellbird (2.3, 2.5 and 2.6 kg). The mean values for the body weights of animals at the other two sites were 3.0 kg (Cambarville) and 2.8 kg (Conondale).

Multivariate Statistical Analyses

An examination of the bivariate distributions of morphometric measures revealed that (1) there were distinct clusters of values for some pairs of attributes (see Fig. 2), and (2) an analysis on the linear scale was appropriate.

A global test of differences between multivariate means showed a significant difference between populations of T. caninus (Wilkes' lambda = 364, d.f. = 54, P < 0.001). The results of canonical variate analysis indicated that the first canonical variate accounted for 89% of the variation in external morphology between the populations of T. caninus. A total of 6% of the variation was explained by the second canonical variate. The other two dimensions accounted for only 5% of the variation and were not significant. Thus, they did not warrant further examination. The coefficients of the first canonical variate and the associated coefficients scaled by the within-group standard deviations of the corresponding variables given in Table 2 show that the weighted-average estimates for the first canonical variate are dominated by positive values for the length of the ear conch and pes length, and a negative value for the tail length. The second canonical variate is dominated by only one attribute: total body length (Table 2).

Inspection of Fig. 3 highlighted a complete separation along the first canonical variate between the two populations in Victoria (Cambarville and Bellbird) and those surveyed in New South Wales and Queensland. As the first canonical variate is dominated by the length of the

Fig. 2. A scatter plot matrix showing data in the form of bivariate plots.

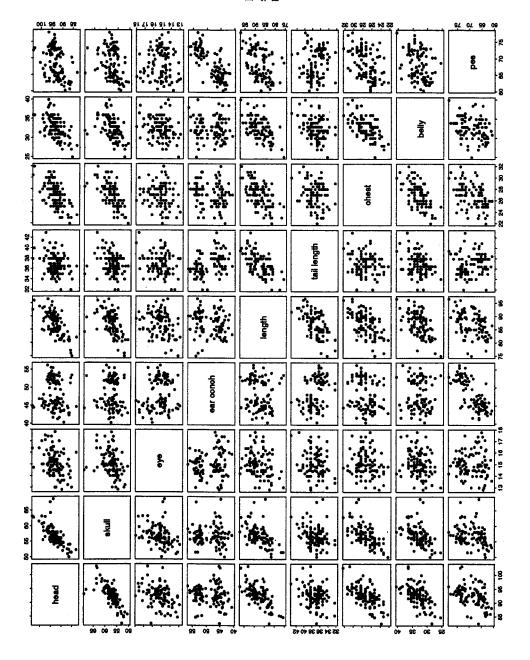


Table 2. Coefficients for the first and second canonical variate from analyses of the morphology of *T. caninus*

The values given in parentheses are the coefficients scaled by the within-group standard deviations. Asterisks denote those measures with the largest coefficients and which best discriminate between the populations of *T. caninus*

Variable	First canonical variate coefficients	Second canonical variate coefficients		
Head length	0.151 (0.438)	-0.058 (-0.170)		
Skull width	0.027 (0.070)	-0.040 (-0.105)		
Eye size	0.056 (0.054)	-0.059 (-0.087)		
Length of the ear conch	-0.586 (-0.819)*	0.044 (0.061)		
Total body length	-0.107 (-0.346)	-0.279 (-0.903)*		
Tail length	0.451 (0.721)*	0.090 (0.143)		
Chest girth	-0.091 (-0.158)	-0.104 (0.182)		
Pes length	-0·302 (-0·696)*	0.036 (0.083)		

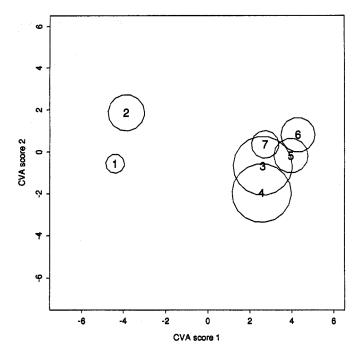


Fig. 3. The mean and the associated 95% confidence intervals for the first and second canonical variate scores. The numbers represent different populations of *T. caninus* that were sampled: 1, Cambarville; 2, Bellbird; 3, Whian Whian State Forest; 4, Byrangery Reserve; 5, Conondale Ranges; 6, Bulburin State Forest; 7, Allyn River Forest Park.

ear conch, the pes and the tail (Table 2), these attributes provide the best discriminators between the populations of T. caninus. An examination of the bivariate scatter plots for the length of the ear conch, the pes and the tail (Fig. 2) shows that there was only limited overlap in the values of these measures between the two Victorian populations and those from elsewhere. T. caninus from Victoria were characterised by a longer ear conch (P < 0.001) and longer pes (P < 0.001) than animals measured at the other locations. In addition, the tail length was shorter and the head length was longer in the Victorian animals. Body length was also a useful measure for discriminating between populations of T. caninus. Our data indicated that the total body length of T. caninus at Cambarville was longer than that of animals at Bellbird (P < 0.001) but not those of the other populations. There was also a separation for this measure between populations in northern New South Wales and those in Queensland.

Analyses of Colour Variation

We recorded more than 16 different pelage colours in T. caninus, which was reduced to six classes by assigning the values for fur colour to broad groupings (Table 3). Since almost 70% of the animals captured had olive-grey fur and belonged to just one fur colour category (Table 3), we reduced this further to just two categories: one for animals with olive-grey fur and the other that included all the other coat colours. Statistical analyses revealed significant differences between the populations in the proportion of animals with olive-grey fur ($\chi^2 = 26 \cdot 6$, d.f. = 6). Notably, the proportion of olive-grey animals in the two Victorian populations was not significantly different from that in the other populations sampled ($\chi^2 = 3 \cdot 6$, d.f. = 1). Therefore, unlike some morphometric measures such as length of the pes and the ear conch, no consistent patterns were apparent in the geographic variation of body fur colour in T. caninus. Indeed, the highest proportion of animals with grey fur was recorded at Cambarville and Conondale (Table 3). The population at Whian Whian State Forest had the lowest proportion of olive-grey-furred animals (zero from seven individuals, with all being black or dark brown) (Table 3).

Table 3. The number of animals in broad colour classes from each of the seven field survey sites. The definition of each of the broad colour categories is based on colours in the Munsell Soil Colour Chart. The Munsell Soil Chart colour/s that comprise (1) the black colour category are 2.5 YR 3/0, 2.5 YR 2.5/0, 7.5 YR 2/0, and 2.5 Y 2/0; (2) the dark brown colour category are 10YR 2/1 and 5YR 2.5/1; (3) the coffee brown colour category is 10YR 3/3; (4) the steel grey colour category are 7.5 YR 3/0, and 2.5 Y 3/0; (5) the olive grey colour category are 5Y 2.5/2, 5Y 2.5/1, 5Y 3/1, and 5Y 3/2; (6) the light grey colour category are 5Y 4/2, 2.5 YR 4/0, 5Y 4/1

Site	Number of animals in colour categories							
	Black	Dark brown	Coffee brown	Steel grey	Olive grey	Light grey		
Cambarville	1	2	0	2	23	0		
Bellbird	0	0	0	7	6	0		
Whian Whian	3	4	0	0	0	0		
Byrangery	2	0	0	1	3	1		
Conondale	0	0	0	2	11	0		
Allyn River	0	0	0	7	14	0		
Bulburin	0	0	1	3	9	0		
Totals	6	6	1	22	66	1		

Discussion

Our analyses revealed significant differences in external morphology between populations of *T. caninus*. In comparison with populations from Queensland and New South Wales, those from Victoria were characterised by longer ears, a longer pes and a shorter tail. These findings (except for the tail) were contrary to the expected thermoregulatory response of decreasing

length of appendages in homeotherms associated with increasing latitude, as predicted by Allen's rule (Allaby 1985). Hence, our results suggest that factors other than climate have influenced the morphology of *T. caninus*. Other differences were also recorded between the various populations such as the length of the head and body. However, no consistent pattern in geographic variation of these measures was apparent and we are unable to suggest which factors may have contributed to the morphological differences that were observed. Notably, it is clear from the data on elevation for the survey sites given above, together with an inspection of Fig. 3, that, unlike the strong relationship between latitude and morphometric variation in *T. caninus*, no such relationships with elevation are apparent.

While our data highlight the existence of considerable geographic variation in some measures of the external morphology of *T. caninus*, there does not appear to be a cline in the species, but rather a separation between the southern (Victorian) and northern (New South Wales and Queensland) populations. Given these results, additional surveys for *T. caninus* in the forests between Bellbird and Allyn River (see Fig. 1) would be useful to determine if the external morphology of these animals was similar to equivalent measures from populations in Victoria or those further north. It might then be possible to determine whether there are two distinct populations, and where the separation occurs.

While our analyses most clearly demonstrate the existence of significant differences between some populations of *T. caninus* for a subset of measured variables, we consider that it is premature to speculate about the taxonomic significance of our findings. Blood and tissue samples have been collected from *T. caninus* as part of the field protocol for this investigation (Viggers and Lindenmayer 1995). Subsequent analyses, using an array of metrics of genetic divergence, will be completed to further investigate the differences between the populations that were surveyed. These studies will attempt to establish whether the highly significant differences between populations recorded for some morphometric measures are mirrored by variations in gene frequencies.

Analyses of Colour Variation

We recorded considerable inter- and intra-population variation in the pelage colour of *T. caninus* and animals from two or more broad colour groupings were recorded from all of the sites surveyed (Table 3). Furthermore, gold and red coloured *T. caninus* have been sighted in the north coast region of New South Wales (D. Milledge, personal communication), but animals with fur of these colours were not captured in this study (Table 3). The basis for variations in the pelage of *T. caninus* is poorly understood. For example, we trapped several adult female *T. caninus* that were olive-grey but had back-young with black fur. This range of observations suggests that there is no consistent geographic pattern of variation in fur coloration of *T. caninus*. Other factors may have an important influence on the pelage colour in the species. Given this, we have recently commenced a study to examine the possible existence of a genetic basis for the variation in fur colour.

Acknowledgments

We thank the many very helpful friends and colleagues who assisted with this study, particularly Mr A. Gilmore and Dr A. Watt. We are most grateful to those people who discussed the biology and distribution of *T. caninus* and/or assisted in locating survey sites, including Mr A. Gilmore, Dr A. Watt, Dr. J. Dubach, Dr. R. Lacy, Mr D. Scotts, Dr J. Winter, Dr R. Kavanagh, Professor H. Nix, Dr D. Spratt, Mr G. Smith, Ms R. Lott, Mr A. Murray, Dr S. Henry, Mr P. Haycock, Mr D. Milledge, Dr J. Kehl, Dr A. Claridge, Mr H. Heinz, Mr D. Rolfe, Mr S. Van Dyck, Mr D. Rolfe and Ms P. Maidens. Mr A. Gilmore provided information on vegetation surveys that had been completed in the areas where trapping was undertaken.

The trapping of animals was completed under the following permits: Australian National University Ethics Committee (M.CRE.2.93; CRE.3.94); Victorian Department of Conservation

and Natural Resources (RP-92-116; RP-93-047; RP-93-146); State Forest of New South Wales (04716); New South Wales National Parks and Wildlife Service (Authority No. 1298); Queensland National Parks and Wildlife Service (1755) and Queensland Department of Primary Industries [Forest Service] (577; 1035/93; 31).

Part of the funding for this study was provided by the Potter Foundation and the Ingram Trust. We most gratefully acknowledge the support of these organisations. We thank CSIRO Division of Wildlife and Ecology for logistic and financial assistance that allowed this project to proceed. D. B. L. was supported by an Australian Research Council Post-doctoral Fellowship. K. L. V. was funded by an Australian National University Post-graduate Scholarship.

References

- Allaby, M. (1985). 'The Oxford Dictionary of Natural History.' (Oxford University Press: Oxford.)
- Blackith, R. E., and Reyment, R. A. (1971). 'Multivariate Morphometrics.' (Academic Press: New York.)
- Calaby, J. H. (1966). Mammals of the Upper Richmond and Clarence Rivers, New South Wales. Division of Wildlife Research Technical Paper No. 10. (CSIRO: Melbourne.)
- Campbell, N. A., and Kitchener, D. J. (1980). Morphological divergence in the genus *Eptesicus* (Microchiroptera: Verpertillionidae) in Western Australia: a multivariate approach. *Australian Journal of Zoology* 28, 457-74.
- Cowan, P. (1990). Family Phalangeridae. In 'The Handbook of New Zealand Mammals'. (Ed. C. M. King.) pp. 67–98. (Oxford University Press: Auckland.)
- Green, R. H. (1974). Mammals. In 'Biogeography and Ecology in Tasmania'. (Ed. W. D. Williams.) pp. 367–96. (Junk: The Hague.)
- How, R. A. (1972). The ecology and management of *Trichosurus* spp. (Marsupialia) in N.S.W. Ph. D. Thesis, University of New England, Armidale.
- Johnston, P. G., and Sharman, G. B. (1976). Studies of *Potorous* Demarest (Marsupialia). I. Morphological variation. *Australian Journal of Zoology* **24**, 573-88.
- Kerle, J. A. (1984). Variation in the ecology of *Trichosurus*: its adaptive significance. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 115–28. (Surrey Beatty and Sons: Sydney.)
- Kerle, J. A., McKay, G. M., and Sharman, G. B. (1991). A systematic analysis of the brushtail possum, Trichosurus vulpecula (Kerr 1792) (Marsupialia:Phalangeridae). Australian Journal of Zoology 39, 313-31.
- Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P., and Nix, H. A. (1990). The habitat requirements of the mountain brushtail possum and the greater glider in the montane ash-type eucalypt forests of the central highlands of Victoria. *Australian Wildlife Research* 17, 467–78.
- Martin, R., and Lee, A. K. (1984). The koala, *Phascolarctos cinereus*, the largest marsupial folivore. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 463-7. (Surrey Beatty and Sons: Sydney.)
- Morton, S. R., and Alexander, F. (1982). Geographic variation in the external morphology of *Sminthopsis* crassicaudata (Dasyuridae, Marsupialia). In 'Carnivorous Marsupials'. (Ed. M. A. Archer.) pp. 695–8. (Royal Zoological Society of New South Wales: Sydney.)
- Phillips, B. F., Campbell, N. A., and Wilson, B. R. (1973). A multivariate study of geographic variation in the whelk *Dicathais*. *Journal of Experimental Marine Biology and Ecology* 11, 27-69.
- Queensland Department of Forestry (1984). Conondale Range Management Plan. (Department of Forestry: Brisbane.)
- Queensland Department of Primary Industries (1994). Management Plan. Granite Creek (State Forest 391). (Queensland Department of Primary Industries Service: Monto.)
- Queensland Museum Database (1994). 'Queensland Museum Database.' (Queensland Museum: Brisbane.) Scotts, D. J., and Seebeck, J. H. (1989). Ecology of *Potorous longipes* (Marsupialia: Potoridae); and
- preliminary recommendations for management of its habitat in Victoria. Arthur Rylah Institute for Environmental Research Technical Report Series No. 62. (Department of Conservation, Forests and Lands: Melbourne.)
- Seebeck, J. H., Warneke, R. M., and Baxter, B. J. (1984). Diet of the bobuck, *Trichosurus caninus* (Ogilby) (Marsupialia: Phalangeridae) in a mountain forest in Victoria. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 145-54. (Surrey Beatty and Sons: Sydney.)
- Victorian Mammal Database. (1994). 'Atlas of Victorian Mammals.' (Department of Conservation and Natural Resources: Melbourne.)

Viggers, K. L., and Lindenmayer, D. B. (1995). The use of Zoletil (tiletamine hydrochloride and zolezepam hydrochloride) for sedation of the mountain brushtail possum, *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia). *Australian Veterinary Journal* 72, 215–16.

Watts, C. H., and Aslin, H. (1981). 'The Rodents of Australia.' (Angus and Robertson: Sydney.)

Winter, J. W. (1980). Tooth wear as an age index in a population of the brush-tailed possum *Trichosurus* vulpecula (Kerr). Australian Wildlife Research 7, 359-63.

Appendix. Means of the various morphometric measures collected from *T. caninus* trapped at each survey site

Values for standard errors are given in parentheses below each mean value. The various morphometric measures are (1) head length, (2) skull width, (3) eye size, (4) length of the ear conch, (5) total body length, (6) tail length, (7) chest girth, (8) belly girth and (9) pes length

Site	Morphometric measures								
	1	2	3	4	5	6	7	8	9
Cambarville	93·7	57·2	15·0	52·6	89·7	36·4	27·9	33·3	73·0
	(0·26)	(0·44)	(0·10)	(0·24)	(0·52)	(0·28)	(0·33)	(0·42)	(0·37)
Bellbird	89·7	55·3	14·5	51·2	81·8	34·8	26·4	31·2	70·8
	(0·86)	(0·61)	(0·29)	(1·02)	(1·08)	(0·41)	(0·45)	(0·90)	(0·89)
Whian Whian	94·6	58·9	16·1	45·3	88·1	37·2	27·6	34·9	66·6
	(1·18)	(1·06)	(0·36)	(0·42)	(1·27)	(0·71)	(0·58)	(0·78)	(0·65)
Byrangery	97·6	61·7	15·5	45·8	92·2	39·7	29·6	34·6	68·9
	(1·66)	(0·88)	(0·48)	(0·36)	(0·94)	(0·68)	(0·80)	(1·20)	(1·38)
Conondale	92·2	56·2	15·4	43·9	86·9	37·7	26·7	32·0	64·7
	(1·17)	(0·55)	(0·36)	(0·42)	(0·83)	(0·35)	(0·40)	(0·81)	(0·46)
Bulburin	89·2	54·2	15·3	44·9	84·5	37·7	25·3	31·5	63·0
	(0·76)	(0·67)	(0·39)	(0·38)	(1·01)	(0·46)	(0·44)	(0·69)	(0·52)
Allyn River	92·6	57·2	14·5	45·9	86·7	37·7	26·1	31·9	65·7
	(0·70)	(0·83)	(0·18)	(0·32)	(0·73)	(0·39)	(0·42)	(0·52)	(0·54)

Manuscript received 19 September 1994; revised 19 January 1995; revised and accepted 11 July 1995