Blood Parameters in Natural Populations of *Trichosurus* Species (Marsupiala : Phalangeridae) II*. Influence of Habitat and Population Strategies of *T. caninus* and *T. vulpecula*

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Abstract

Body weight and six blood parameters were determined in T. caninus and T. vulpecula from their preferred and peripheral habitats. Habitat had a large effect on T. caninus. Of the seven parameters measured, six (body weight, red blood cell count, haemoglobin concentration, haematocrit and plasma protein and lipid concentrations) were higher in the population from the peripheral habitat than in that from the preferred habitat. Only body weight was different in T. vulpecula, being higher in the peripheral than in the preferred habitat population. There were differences between T. caninus and T. vulpecula in four of the measured parameters (body weight, haematocrit, haemoglobin concentration and red blood cell count) irrespective of habitat, whereas plasma lipid concentration was the same in T. caninus from peripheral habitat and T. vulpecula, but differed in T. caninus between habitats. Four parameters showed significant seasonal variation in preferred-habitat T. caninus, three in peripheral-habitat T. caninus and one in T. vulpecula. However, the pattern of seasonal change in peripheral-habitat T. caninus was more similar to that in T. vulpecula than to that in preferred-habitat T. caninus, suggesting a physiological shift in peripheral-habitat T. caninus towards that of the more r-selected T. vulpecula. No differences were found between resident and dispersing T. caninus. T. caninus which had lost a pouch young and failed to maintain another in the same year had lower haematocrit and plasma lipid concentration than females in other reproductive states. It is suggested that the measurement of physiological responsiveness of populations may aid the understanding of adaptive strategies.

Introduction

Examination of body weight and six blood parameters in natural populations of the mountain possum *Trichosurus caninus* (Ogilby) and the brush-tailed possum *T. vulpecula* (Kerr) indicated different interspecific values in five parameters and different seasonal responses between the two species (Barnett *et al.* 1979). We suggested that there may be a relationship between these different physiological responses and the population strategies of the two species, with the more *r*-selected *T. vulpecula* showing less seasonal variation than the *K*-selected *T. caninus*.

This paper examines the inter- and intraspecific differences with respect to habitat, and the effect of status and reproductive condition of T. caninus, on the magnitude and seasonal variation in the parameters considered. T. caninus from peripheral and preferred habitats are compared to establish the effects of habitat on these parameters. T. caninus and T. vulpecula from peripheral and preferred habitats are compared to determine whether differences are species- or habitat-

* Part I, Aust. J. Zool., 1979, 27, 913-26.

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Values are means ± standard errors, except those for samples of two, which are ranges. Sample sizes in parentheses. Superscript letters indicate some pairs of

Species and habitat	Date						
habitat		Haemoolohin	Males	Glucose	Haemoslohin		Ghicose
		$(g dl^{-1})$	count l = 1	$(mg dl^{-1})$	$(g dl^{-1})$	$\frac{1}{1} = 1$	$(mg dl^{-1})$
T. caninus							
preferred	Feb. 1975	$^{A16.0\pm0.8}(7)$	Ι	90.2 ± 12.5 (6)	$^{A}14.6\pm0.7(9)$	I	$96 \cdot 1 \pm 11 \cdot 1$ (8)
	May 1975	$^{\Lambda}13 \cdot 8 \pm 0 \cdot 5 (9)$	I	87 · 2 ± 7 · 2 (8)	$^{\Lambda}12 \cdot 5 \pm 0 \cdot 4 (12)$	1	$109 \cdot 8 \pm 5 \cdot 5$ (11)
	Aug. 1975	14-4(1)	I	$126 \cdot 0(1)$	$12 \cdot 1 - 12 \cdot 4 (2)$	1	97 · 1 – 101 · 0 (2)
	Oct. 1975	$15 \cdot 4 \pm 0 \cdot 9$ (8)	$^{A4} \cdot 96 \pm 0 \cdot 38$ (8)	$^{A}107.8 \pm 12.4(6)$	$12 \cdot 5 \pm 0 \cdot 3 \ (20)$	$A4 \cdot 30 \pm 0 \cdot 25$ (16)	*95.4±6.5(19)
	Feb. 1976	$15.2\pm0.9(9)$	$^{A6} \cdot 32 \pm 0 \cdot 26$ (9)	$^{A77} \cdot 7 \pm 3 \cdot 9 \ (8)$	$14 \cdot 1 \pm 0 \cdot 4 (12)$	$^{A5} \cdot 30 \pm 0 \cdot 14$ (12)	$*82.9\pm5.9(11)$
	May 1976	$16.5\pm0.3(11)$	$6 \cdot 25 \pm 0 \cdot 17$ (11)	$84 \cdot 8 \pm 5 \cdot 0 \ (11)$	$14 \cdot 8 \pm 0 \cdot 6$ (13)	$5 \cdot 11 \pm 0 \cdot 19$ (13)	$84 \cdot 0 \pm 3 \cdot 1$ (13)
	Aug. 1976	$16 \cdot 3 \pm 0 \cdot 5$ (16)	$6 \cdot 05 \pm 0 \cdot 21$ (16)	$98 \cdot 1 \pm 4 \cdot 9 (16)$	$15 \cdot 1 \pm 0 \cdot 5$ (15)	$5 \cdot 13 \pm 0 \cdot 17$ (15)	$101 \cdot 4 \pm 5 \cdot 4$ (15)
Mean		$^{B}15 \cdot 6 \pm 0 \cdot 3 \ (61)$	$^{B}5 \cdot 96 \pm 0 \cdot 14 (44)$	$*91 \cdot 7 \pm 3 \cdot 0$ (56)	$^{B}13 \cdot 8 \pm 0 \cdot 2$ (83)	$^{B}4 \cdot 87 \pm 0 \cdot 13$ (56)	$+95 \cdot 1 \pm 2 \cdot 6$ (79)
T. caninus							
peripheral	Feb. 1975	$*14 \cdot 2 \pm 1 \cdot 3 (4)$	I	$106 \cdot 8 \pm 11 \cdot 5$ (4)	*14·1 (1)	Ι	117.1(1)
	May 1975	$*15 \cdot 3 \pm 0 \cdot 7$ (7)	l	$108 \cdot 9 \pm 9 \cdot 6$ (7)	*12 · 1 – 15 · 3 (2)	ł	92.9-103.4(2)
	Aug. 1975	$15 \cdot 0 \pm 0 \cdot 7$ (4)		106 - 2 - 147 - 8 (2)	15.6 ± 0.6 (3)	Ι	$112 \cdot 1 \pm 17 \cdot 1$ (3)
	Oct. 1975	$15 \cdot 2 \pm 1 \cdot 0$ (6)	$*6 \cdot 16 \pm 0 \cdot 19$ (6)	$^{B}104.0 \pm 15.8$ (4)	$13 \cdot 8 \pm 0 \cdot 9$ (4)	$5 \cdot 25 \pm 0 \cdot 39$ (3)	$96 \cdot 7 \pm 9 \cdot 8$ (4)
	Feb. 1976	$16 \cdot 9 \pm 0 \cdot 8$ (9)	$*6 \cdot 83 \pm 0 \cdot 43$ (9)	$B61 \cdot 9 \pm 10 \cdot 7$ (9)	I	1	I
	May 1976	$18 \cdot 4 \pm 0 \cdot 7$ (7)	$6 \cdot 61 \pm 0 \cdot 17$ (7)	$77 \cdot 5 \pm 6 \cdot 3$ (7)	$15 \cdot 1 \pm 1 \cdot 0$ (3)	$5 \cdot 53 \pm 0 \cdot 16$ (3)	$76 \cdot 1 \pm 3 \cdot 9$ (3)
	Aug. 1976	$17 \cdot 0 \pm 0 \cdot 5$ (7)	$6 \cdot 62 \pm 0 \cdot 12$ (7)	$96 \cdot 8 \pm 8 \cdot 0$ (7)	$15 \cdot 6 \pm 1 \cdot 0$ (5)	$5 \cdot 70 \pm 0 \cdot 04$ (5)	$95 \cdot 7 \pm 10 \cdot 9 (5)$
Mean		$^{B}16\cdot 3\pm 0\cdot 3$ (44)	$^{B}6 \cdot 60 \pm 0 \cdot 20 (29)$	$*90.9 \pm 4.9$ (40)	$^{B}14 \cdot 8 \pm 0 \cdot 4$ (18)	$^{B}5 \cdot 53 \pm 0 \cdot 12 \ (11)$	†96 · 8 ± 5 · 1 (18)
T. vulpecula							
combined	Feb. 1975	†12-3 (1)	1	115-0(1)	+10-9-15-9 (2)		93 · 3 – 141 · 9 (2)
	May 1975	$^{\dagger}12.4\pm0.6(4)$		123 · 2 ± 12 · 8 (4)	$+11 \cdot 4 \pm 0 \cdot 8 (4)$	ŀ	$91 \cdot 6 \pm 18 \cdot 2$ (4)
	Aug. 1975	18.4(1)	ŀ	93-3(1)	13 · 5 (1)	I	90.8(1)
	Oct. 1975	$13 \cdot 7 \pm 0 \cdot 5$ (5)	$^{+7} \cdot 02 \pm 0 \cdot 39 (5)$	$+85 \cdot 0 \pm 18 \cdot 2$ (4)	$13 \cdot 2 \pm 0 \cdot 6 (6)$	5.36 ± 0.29 (6)	$*94.6\pm 6.3$ (5)
	Feb. 1976	14.7-17.4(2)	+7 · 49 – 7 · 76 (2)	+84 · 8 - 107 · 5 (2)	11.8-15.0(2)	*5.57-6.18 (2)	*107.0-114.8 (2)
	May 1976	$16 \cdot 9 \pm 1 \cdot 0$ (4)	$9 \cdot 15 \pm 3 \cdot 07$ (4)	$96 \cdot 0 \pm 14 \cdot 8$ (4)	$15 \cdot 4 \pm 0 \cdot 6$ (4)	5.91 ± 0.30 (4)	70 · 6 ± 19 · 3 (4)
	Aug. 1976	15.9 ± 0.7 (3)	$6 \cdot 82 \pm 0 \cdot 26$ (3)	$119 \cdot 0 \pm 29 \cdot 1$ (3)	$13 \cdot 6 \pm 0 \cdot 5 (5)$	$6 \cdot 18 \pm 0 \cdot 58$ (5)	$124 \cdot 8 \pm 15 \cdot 2$ (5)
Mean		$14 \cdot 7 \pm 0 \cdot 5$ (20)	$7 \cdot 67 \pm 0 \cdot 85$ (14)	$103 \cdot 2 \pm 6 \cdot 9 (19)$	13 - 5 ± 0 - 4 (24)	$5 \cdot 78 \pm 0 \cdot 21$ (17)	$100 \cdot 2 \pm 6 \cdot 7 (23)$

specific. In addition, dispersing T. caninus are compared with residents and a comparison is made of T. caninus females in different reproductive states.

Materials and Methods

The study area and methods of collecting and analysing plasma proteins, glucose, lipid and haemoglobin concentrations, haematocrit and red blood cell counts have been described (Barnett *et al.* 1979).

T. vulpecula occurs in most tree communities in western and eastern Australia (Ride 1970), as well as in urban areas, but is replaced by T. caninus in the closed and tall open forests (nomenclature follows Specht 1970) of the south-east (Calaby 1966; How 1978). At Clouds Creek, in north-eastern New South Wales, T. caninus occurs mostly in closed and tall open forest (its preferred habitat) and T. vulpecula occupies mostly grazed woodland and open forest (Barnett et al. 1976). Both species were trapped in a pine plantation adjacent to all these habitats. We considered that individual T. caninus trapped exclusively in closed and tall open forest were in their preferred habitat, and those individuals trapped at any time in exotic pine plantations, grazed woodland or open forest were in their peripheral habitat. T. vulpecula captured exclusively in grazed woodland or open forest were, we considered, in their preferred habitat, and those caught at any time in pine plantations or open forest in sympatry with T. caninus were in their peripheral habitat. Although at Clouds Creek T. caninus does not live exclusively in habitats other than closed or tall open forest, T. vulpecula will occupy any tree community available but is probably excluded by T. caninus. Hence our division into preferred and peripheral habitats is strictly more correct for T. caninus than for T. vulpecula, in which the peripheral habitat may represent only a zone of increasing interaction with T. caninus. The population of T. vulpecula overlapping with T. caninus in open forest at Clouds Creek was less stable than the population in other areas, with individuals seldom in the trap record for more than 1 year (How 1972).

Blood samples were collected from each individual on its first capture in each trapping period; we trapped seven times over an 18-month period. The data were analysed by analysis of variance on the basis of sex, season and habitat, and the sample means were compared by the Least Significant Difference (Winer 1971). When no seasonal differences were found the data were reanalysed on the basis of sex and habitat. Only adult animals were used in the analyses. T. caninus and T. vulpecula were considered adult at \ge 3 years and \ge 2 years old respectively, on the basis of reproductive condition, body weight and head length (Smith and How 1973); most individuals were of known age. Twenty-two T. caninus were considered dispersing individuals. These were caught only once in the centre of the trapping area, moving through the area, or were lost from the trapping area after a period of residence greater than 1 year. Only two of these were adults (both females) and they were not included in the analysis; the remaining 20 possums were subadults < 3 years old, the age at which dispersal occurs (our unpublished data and How 1978). These 'dispersers' were compared with an equal number of resident individuals of the same age and sex and from equivalent seasons, to determine whether dispersing possums had different characteristics from residents. Season had to be eliminated as a variable because several of the parameters (glucose, protein, haemoglobin and red blood cell counts) vary seasonally (Barnett et al. 1979).

We recognize five reproductive states in adult female *T. caninus*: (1) non-lactating; (2) lactating with dependent pouch young ≤ 120 days old; (3) lactating with semi-dependent young ≥ 175 days old; (4) pouch young lost and not replaced that season; (5) pouch young lost but replaced in the same breeding season. Individuals from these categories were compared to assess the effect of female reproductive state on haematocrit, plasma lipid concentration and body weight. These variables were selected because they did not vary seasonally in the general population (Barnett *et al.* 1979), and they allowed assessment of the effect of reproductive condition independent of seasonal variation.

Results

Comparison of T. caninus from Preferred and Peripheral Habitats

Using the pooled data for *T. caninus* from peripheral and preferred habitats, we have previously shown significant seasonal changes in haemoglobin, plasma,

glucose and protein concentrations and red blood cell counts (Barnett *et al.* 1979). The seasonal changes observed in possums from the preferred habitat affect the same parameters and in a similar manner (Tables 1, 2; Barnett *et al.* 1979). In *T. caninus* from peripheral habitats only plasma, glucose and protein concentrations changed seasonally in this manner (Tables 1, 2; Barnett *et al.* 1979). Data from both sexes were pooled for the plasma protein analysis as this parameter was not sexually dimorphic (Table 2). The pattern of seasonal change in the remaining

Table 2.	Effects of habitat on plasma protein concentration in	n
	T. caninus with season, sexes combined	

Values are means \pm standard errors, in grams per decilitre. Values for combined habitats are from Barnett *et al.* (1979). Sample sizes in parentheses. Superscript letters indicate values in the same column which differ significantly

Time of year	Peripheral	Habitat Preferred	Combined
Feb. 1975	8.0 ± 0.3 (6)	8.3 ± 0.2 (15)	$8 \cdot 2 \pm 0 \cdot 1$ (21)
May 1975	$8 \cdot 1 \pm 0 \cdot 3$ (9)	7.9 ± 0.3 (21)	$8 \cdot 0 \pm 0 \cdot 2$ (30)
Aug. 1975	$7 \cdot 8 \pm 0 \cdot 2$ (7)	$7 \cdot 6 \pm 0 \cdot 1$ (3)	$7 \cdot 7 \pm 0 \cdot 1$ (10)
Oct. 1975	9.0 ± 0.4 (9)	$7 \cdot 6 \pm 0 \cdot 3$ (27)	7.9 ± 0.2 (36)
Feb. 1976	$^{A9.5 \pm 0.9}(9)$	$^{A8} \cdot 4 \pm 0 \cdot 3 (21)$	$^{A8} \cdot 7 \pm 0 \cdot 3 (30)$
May 1976	$^{A7.9} \pm 0.6$ (10)	$^{A7} \cdot 0 \pm 0 \cdot 1 (24)$	$A7 \cdot 2 \pm 0 \cdot 2$ (34)
Aug. 1976	$8 \cdot 0 \pm 0 \cdot 2$ (12)	$7 \cdot 5 \pm 0 \cdot 1$ (31)	$7 \cdot 6 \pm 0 \cdot 1$ (43)
Mean	$8 \cdot 3 \pm 0 \cdot 2$ (62)	$7 \cdot 7 \pm 0 \cdot 1$ (142)	

Table 3. Effect of habitat on body weight and blood parameters in adult *T. caninus* and *T. vulpecula*, seasons combined

Values are means \pm standard errors, with sample sizes in parentheses. Superscript letters indicate pairs of values in the same column which differ significantly

Species	Habitat	Body weight (g)	Lipids (mg dl ⁻¹)	Haematocrit (%)
T. caninus				
Male	Preferred	$^{A}2951 \cdot 6 \pm 34 \cdot 4$ (62)	$^{A}478 \cdot 8 \pm 15 \cdot 4 (57)$	$^{A}48 \cdot 4 \pm 0 \cdot 5 (61)$
	Peripheral	$^{A}3045 \cdot 5 \pm 34 \cdot 6 (44)$	$^{A}527 \cdot 2 \pm 19 \cdot 6 (37)$	$^{A}52 \cdot 1 \pm 0 \cdot 8 (43)$
Female	Preferred	$^{B}3001 \cdot 2 \pm 30 \cdot 9$ (84)	$^{B}497 \cdot 1 \pm 12 \cdot 9 (71)$	$^{B}42.0 \pm 0.5$ (84)
	Peripheral	$B3130.0 \pm 67.2$ (20)	$^{B}543 \cdot 8 \pm 29 \cdot 7 (17)$	$^{B}44.0 \pm 0.7(17)$
T. vulpecula				
Male	Combined	$2827 \cdot 5 \pm 57 \cdot 5$ (20)	$581 \cdot 1 \pm 27 \cdot 7$ (19)	$46 \cdot 4 \pm 1 \cdot 1$ (20)
Female	Combined	$2653 \cdot 9 \pm 47 \cdot 4$ (23)	$606 \cdot 9 \pm 33 \cdot 3 (23)$	40.8 ± 0.9 (24)

blood variables in possums from peripheral habitat was different from that in either those from preferred habitat or from both habitats combined. Haemoglobin concentration was greater in May 1976 than in May 1975 (as in the preferred habitat) but was not at a minimum value in winter 1975 (May-August), in contrast to the preferred habitat. Red blood cell counts were lower (P < 0.05) in October 1975 than during the rest of the year in the preferred habitat but not in the peripheral habitat (Table 1). Table 4. Effects of habitat on body weight and blood parameters of T. vulpecula with sex and season

Values are means ± standard errors, except those for samples of two, which are ranges. Sample sizes in parentheses. Superscript letters indicate pairs of values in the same column which are sionificantly different $^{*+}$ The third value is sionificantly different from the first two

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Date	Body weight (g)	Haematocrit (%)	Haemoglobin (g dl ⁻¹)	$10^{-12} \times red cell$ count l^{-1}	Proteins (g dl ⁻¹)	Glucose (mg dl ⁻¹)	Lipids (mg dl ⁻¹)
May 1975 Oct. 1975 May 1976	2500 · 0 (1) 2735 · 5 ± 143 · 4 (4) 2800 · 0 – 2900 · 0 (2)	$45 \cdot 0 (1) 44 \cdot 5 \pm 3 \cdot 12 (4) 43 \cdot 0 - 43 \cdot 0 (2)$	Male, prefi ^11.33 (1) 13.5±0.5 (4) ^15.0-19.8 (2)	erred habitat 5.4−8.5 (4)	$6 \cdot 9 (1)$ $6 \cdot 8 \pm 1 \cdot 05 (4)$ $7 \cdot 5 - 9 \cdot 8 (2)$	*91.0(1) *89.2±25.0(3) *51.9-113.7(2)	438 ⋅ 4 (1) 661 ⋅ 5 ± 49 ⋅ 8 (3) 526 ⋅ 1 − 722 ⋅ 9 (2)
Mean	A2735 · 7 ± 89 · 1 (7)	44 · 1 ± 2 · 6 (7)	$14 \cdot 3 \pm 1 \cdot 0$ (7)	$6.9\pm0.5(6)$	$7 \cdot 3 \pm 0 \cdot 7$ (7)	87 · 4 ± 13 · 8 (6)	612 · 0 ± 49 · 0 (6)
May 1975 Oct. 1975 May 1976	$\begin{array}{c} 2883 \cdot 3 \pm 101 \cdot 4 \ (3) \\ 3200 \cdot 0 \ (1) \\ 3000 \cdot 0 - 3200 \cdot 0 \ (2) \end{array}$	$50 \cdot 5 \pm 1 \cdot 3 (3)$ $44 \cdot 0 (1)$ $46 \cdot 0 - 47 \cdot 0 (2)$	Male, perip ^B 12·8±0·6 (3) 14·6 (1) ^B 16·2-16·6 (2)	oheral habitat $7 \cdot 7(1)$ $4 \cdot 7 - 18 \cdot 0(2)$	$8 \cdot 4 \pm 0 \cdot 4 (3)$ 7 \cdot 4 (1) 7 \cdot 0 - 8 \cdot 5 (2)	$\begin{array}{c} ^{\Lambda 134 \cdot 0 \pm 9 \cdot 8} (3) \\ 72 \cdot 4 (1) \\ ^{\Lambda 106 \cdot 7 - 111 \cdot 7} (2) \end{array}$	$523 \cdot 9 \pm 59 \cdot 3 (3)$ 662 \cdot 2 (1) 582 \cdot 3 - 863 \cdot 5 (2)
Меап	$^{\Lambda}3008 \cdot 3 \pm 77 \cdot 9$ (3)	$48 \cdot 1 \pm 1 \cdot 3 \ (6)$	$14 \cdot 3 \pm 0 \cdot 8 \ (6)$	$10 \cdot 1 \pm 4 \cdot 0$ (3)	$8 \cdot 0 \pm 0 \cdot 3 (6)$	$115 \cdot 5 \pm 10 \cdot 9$ (6)	$613 \cdot 3 \pm 60 \cdot 9$ (6)
May 1975 Oct. 1975 May 1976	$2250 \cdot 0 \pm 2700 \cdot 0 (2)$ $2383 \cdot 3 \pm 66 \cdot 7 (3)$ $2400 \cdot 0 - 2650 \cdot 0 (2)$	$43 \cdot 0 - 46 \cdot 0 (2)$ $41 \cdot 3 \pm 2 \cdot 90 (3)$ $37 \cdot 0 - 54 \cdot 0 (2)$	Female, pre ^c 10·6-12·2 (2) 13·1±1·1 (3) ^c 14·6-16·8 (2)	ferred habitat 5 $\cdot 5 \pm 0.6 (3)$ 5 $\cdot 7 - 6 \cdot 7 (2)$	$\begin{array}{c} 8 \cdot 0 - 9 \cdot 5 \ (2) \\ 8 \cdot 2 \pm 0 \cdot 3 \ (3) \\ 6 \cdot 9 - 7 \cdot 8 \ (2) \end{array}$	$\begin{array}{c} 46\cdot 6-85\cdot 2 \ (2)\\ B76\cdot 8-102\cdot 4 \ (2)\\ B31\cdot 4-69\cdot 8 \ (2) \end{array}$	$421 \cdot 1 - 486 \cdot 3 (2)$ $553 \cdot 1 \pm 47 \cdot 0 (3)$ $421 \cdot 7 - 634 \cdot 5 (2)$
Mean	$^{B}2450\cdot0\pm66\cdot4$ (7)	$43 \cdot 4 \pm 2 \cdot 3$ (7)	$13 \cdot 3 \pm 0 \cdot 9$ (7)	5·7±0·4 (5)	$8 \cdot 1 \pm 0 \cdot 3$ (7)	68 · 7±10 · 6 (6)	517·6±34·6(7)
May 1975 Oct. 1975 May 1976	$\begin{array}{c} 2500 \cdot 0 - 2700 \cdot 0 \left(2 \right) \\ 2550 \cdot 0 - 2600 \cdot 0 \left(2 \right) \\ 2800 \cdot 0 - 2850 \cdot 0 \left(2 \right) \end{array}$	$39 \cdot 0 - 47 \cdot 0 (2)$ $40 \cdot 7 \pm 1 \cdot 45 (3)$ $36 \cdot 0 - 37 \cdot 0 (2)$	Female, peri ^D 9.8-13.2 (2) 13.4±0.5 (3) ^D 14.3-15.9 (2)	pheral habitat $5 \cdot 3 \pm 0 \cdot 3$ (3) $5 \cdot 2 - 6 \cdot 1$ (2)	$7 \cdot 5 - 7 \cdot 6 (2)$ $7 \cdot 0 \pm 0 \cdot 7 (3)$ $5 \cdot 1 - 7 \cdot 8 (2)$	$^{+100\cdot 3-134\cdot 2}$ (2) $^{+98\cdot 0\pm 8\cdot 1}$ (3) $^{+57\cdot 9-123\cdot 3}$ (2)	$563 \cdot 8 - 591 \cdot 1 (2)$ 718 $\cdot 6 \pm 142 \cdot 4 (3)$ 562 $\cdot 2 - 755 \cdot 0 (2)$
Mean	$B2666 \cdot 7 \pm 57 \cdot 3$ (6)	$40 \cdot 1 \pm 1 \cdot 5$ (7)	$13 \cdot 3 \pm 0 \cdot 7$ (7)	$5 \cdot 4 \pm 0 \cdot 2$ (5)	$7 \cdot 0 \pm 0 \cdot 4$ (7)	$101 \cdot 4 \pm 9 \cdot 6 (7)$	$661 \cdot 1 \pm 62 \cdot 6$ (7)

Of the parameters which showed seasonal change, the overall mean values in the peripheral habitat were greater for haemoglobin concentration (P < 0.05), plasma proteins (P < 0.05) and red blood cell counts (P < 0.05); the overall mean value for plasma glucose concentration did not differ between habitats (Tables 1, 2).

Mean values of body weight, plasma lipid concentration and haematocrit, which did not show seasonal change, were greater (P < 0.05) in animals from peripheral than from preferred habitat (Table 3).

Comparison of T. vulpecula from Preferred and Peripheral Habitats

Marked seasonal variation in the trap-proneness of T. vulpecula (How 1972; our unpublished data) has precluded detailed analysis for seasonal variation in T. vulpecula. However, sufficient data are available for May 1975 and 1976 and October 1975 to analyse for the effects of habitat on T. vulpecula.

In both preferred and peripheral habitats the haemoglobin concentration was higher in May 1976 than in May 1975 (P < 0.05; Table 4) and followed the same pattern as the data from both habitats combined (Barnett *et al.* 1979). Only body weight showed a significant habitat-related difference; it was greater in the peripheral areas (P < 0.01; Table 4). There was sexual dimorphism in body weight (males > females) in both habitats (Table 4) similar to that found from the combined data (Barnett *et al.* 1979).

Comparison of T. vulpecula with T. caninus from both Preferred and Peripheral Habitats

As only body weight varied with habitat in *T. vulpecula* (cf. *T. caninus* where habitat influenced body weight, haematocrit, red cell blood count and haemoglobin, plasma protein and lipid concentrations) and the data were scarce for this species, the pooled habitat data from *T. vulpecula* are compared with the *T. caninus* data separated into the two habitats.

T. caninus differs from T. vulpecula in overall mean levels of body weight, haematocrit and haemoglobin concentration (higher in T. caninus) and in red cell counts and plasma lipid concentration (higher in T. vulpecula) (Barnett et al. 1979). These differences persist when the data from T. caninus are separated according to the original habitat (Tables 1, 3), except for mean plasma lipid concentration in T. caninus from peripheral habitat, which did not differ from the mean value in T. vulpecula (Table 3). However, the seasonal data showed some unexpected changes in that T. caninus from peripheral habitat showed a pattern of change in the parameters more similar to that in T. vulpecula than to that in T. caninus from the preferred habitats. Haemoglobin concentration in T. caninus from preferred habitat decreased significantly between February and May 1975 (P < 0.05) and the red cell count was lower in October 1975 (P < 0.01; Table 1). These changes did not occur in T. caninus from peripheral habitat or in T. vulpecula. An exception to this similarity in seasonal changes between T. caninus in peripheral habitat and T. vulpecula was in plasma glucose concentration, which decreased in peripheral T. caninus between 1975 and 1976 but not in T. vulpecula (Table 1).

Dispersing versus Resident T. caninus

No significant differences were found between resident and dispersing *T. caninus* (Table 5).

Table 5. Body weight and blood parameters in dispersing and resident subadult T. caninusValues are means \pm standard errors, except those for samples of two, which are ranges. Sample sizesin parentheses

Parameter	Dist	Dersers	Residents				
	Male	Female	Male	Female			
Body weight (g)	$2503 \cdot 1 \pm 69 \cdot 1$ (16)	$2275 \cdot 0 \pm 98 \cdot 8$ (4)	$2368 \cdot 7 \pm 79 \cdot 8$ (16)	$2500 \cdot 0 \pm 124 \cdot 2$ (4)			
Haematocrit (%)	$49 \cdot 9 \pm 1 \cdot 1$ (15)	$47 \cdot 9 \pm 2 \cdot 9$ (4)	$48 \cdot 5 \pm 1 \cdot 7$ (15)	$47 \cdot 3 \pm 1 \cdot 4$ (4)			
Haemoglobin (g dl ⁻¹)	16.5 ± 0.7 (15)	$15 \cdot 2 \pm 1 \cdot 2$ (4)	$\frac{15\cdot3\pm0\cdot5}{(15)}$	$13 \cdot 6 \pm 1 \cdot 0$ (4)			
Protein (g dl ⁻¹)	$7 \cdot 8 \pm 0 \cdot 2$ (15)	$7 \cdot 0 \pm 0 \cdot 3$	$8 \cdot 1 \pm 0 \cdot 4$ (15)	$6 \cdot 0 \pm 0 \cdot 7$ (4)			
Glucose (mg dl ⁻¹)	114.8 ± 7.5 (12)	$104 \cdot 2 \pm 9 \cdot 1$ (4)	$104 \cdot 9 \pm 7 \cdot 2$ (12)	$99 \cdot 5 \pm 12 \cdot 6$ (4)			
Lipid (mg dl ⁻¹)	570.4 ± 50.1 (8)	$565 \cdot 1 - 580 \cdot 9$	$466 \cdot 6 \pm 37 \cdot 7$ (8)	$523 \cdot 3 - 743 \cdot 0$			
10^{-12} × Red cell count l^{-1}	$6 \cdot 28 \pm 0 \cdot 22$ (11)	5.94 ± 0.08 (3)	6.05 ± 0.27 (11)	$6 \cdot 14 \pm 0 \cdot 39$ (3)			

Female Reproductive Status in T. caninus

Mean haematocrit was greater in lactating females with either dependent or semidependent young than in non-lactating females (P < 0.05). The mean haematocrit in females which lost their pouch young but did not replace it was lower than

Table 6.	Body	weight	and blood	parameters	of adult	female	T. caniņus	in different	reproducti	ve states
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Va	lues	are	means	±	standard	errors,	with	samp	le s	izes	in	parent	hese	S
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	Body weight (g)	Haematocrit (%)	Lipid (mg dl ⁻¹)
Non-lactating	$3002 \cdot 8 \pm 46 \cdot 2$ (18)	$40 \cdot 6 \pm 0 \cdot 8$ (18)	$\begin{array}{c} 429 \cdot 2 \pm 32 \cdot 1 \\ (12) \end{array}$
Lactating			
With pouch young ≤ 120 days	$3026 \cdot 2 \pm 51 \cdot 3$ (40)	$43 \cdot 0 \pm 0 \cdot 5$ (40)	$498 \cdot 0 \pm 13 \cdot 9$ (35)
With semi-dependent young ≥ 175	· · /	× ,	
days	$\begin{array}{rrr} 2987 \cdot 5 \pm & 48 \cdot 3 \\ (32) \end{array}$	$42 \cdot 4 \pm 0 \cdot 8$ (31)	$545 \cdot 8 \pm 21 \cdot 0$ (28)
First pouch young lost			
Without second young	$2766 \cdot 7 \pm 88 \cdot 2$	$35 \cdot 6 \pm 2 \cdot 9$	$472 \cdot 2 \pm 71 \cdot 4$
With second young	(3) 3190.0 ± 108.9 (5)	$45 \cdot 5 \pm 0 \cdot 9$ (4)	$470 \cdot 2 \pm 75 \cdot 0$ (5)

in all other groups (P < 0.05; Table 6). Plasma lipid concentration increased in adult female *T. caninus* during the development of the young. Lactating possums with older young had higher plasma lipid levels than those lactating with a small

young in the pouch (P < 0.05), and the latter had higher plasma lipid levels than non-lactating females (P < 0.05; Table 6).

Body weight did not change with reproductive status in female T. caninus (Table 6).

Discussion

Our data show that habitat considerably influences the overall mean values of the parameters we measured in *T. caninus*. Body weight, haematocrit, red blood cell count and haemoglobin, plasma protein and lipid concentrations were higher in possums from peripheral habitat than in those from their preferred habitat. The pattern of seasonal change in haemoglobin concentration and red blood cell count also differed between habitats.

The distinction between preferred and peripheral habitats is sometimes obscure; T. caninus assigned to the preferred habitat were always trapped in closed or tall open forests, whereas the home range of peripheral T. caninus included pine plantations but always some, often much, native forest (How 1972). We have thus been conservative in assigning individuals to the peripheral habitat. The limited penetration of T. caninus into pine plantations has been described by Barnett *et al.* (1977).

Comparison of the mean values of the parameters in T. caninus from peripheral habitat with T. vulpecula showed that mean body weight, haematocrit and haemoglobin concentration were greater in T. caninus and that red blood cell counts were greater in T. vulpecula. These differences are similar to those obtained by comparing the combined habitat data for T. caninus with T. vulpecula (Barnett et al. 1979).

Mean plasma lipid levels were lower in *T. caninus* (pooled data) than in *T. vulpecula* (pooled data) (Barnett *et al.* 1979). However, *T. caninus* from preferred habitat had lower plasma lipid levels than either *T. vulpecula*, or *T. caninus* from peripheral habitat. These results suggest that the increase in lipid level in *T. caninus* from peripheral habitat is a consequence of that habitat, whereas the difference in body weight and the other haematological parameters (haematocrit, haemoglobin and red blood cell counts) reflect the 'set point' species differences of *T. caninus* and *T. vulpecula*.

The cause of the between-habitat differences is unknown. However, differences associated with diet occur in haemoglobin concentration in mice (Francis and Strong 1938) and dogs (Weech *et al.* 1937), and dietary restrictions may lead to changes in serum proteins (Weech *et al.* 1935; Zeldis *et al.* 1945), plasma lipid concentrations (Zeldis *et al.* 1945) and red cell volume (Haxhe 1967) in dogs and to changes in plasma carbohydrate and cholesterol concentrations in horses (Fonnesbeck and Symons 1969).

Although there are species differences in most of the measured parameters irrespective of the habitat of T. caninus, the seasonal changes in T. caninus in peripheral habitats are more similar to those in T. vulpecula than to those in T. caninus in its preferred habitat. That is, in the original analysis of both habitats combined (Barnett et al. 1979) and in the present study of T. caninus in its preferred habitat, seasonal changes occurred in four (glucose, protein and haemoglobin concentrations and red blood cell count) of the seven variables considered, but in T. vulpecula only haemoglobin concentration changed. Three parameters (glucose, protein and haemoglobin concentration) changed in T. caninus in peripheral habi-

tat. The pattern of change in plasma glucose and protein concentrations differed from that in T. vulpecula, but the seasonal change in haemoglobin concentration was more similar to that in T. vulpecula than to that in T. caninus in preferred habitat. Hence T. caninus from the peripheral habitat exhibits a reduction in seasonal change of the blood parameters; thus either the population in peripheral habitat must be physiologically less responsive to seasonal changes in the environment, or the environment itself (probably the biotic factors) is less variable and requires less physiological adjustment.

Barnett *et al.* (1979) discuss the implications of physiological variability and population strategies for these two species and show reduced variability in blood parameters in the more *r*-selected species, *T. vulpecula*. The changed seasonal variability in the peripheral population of *T. caninus* suggests an *r*-selected adaptation relative to the greater variability in the same parameters of *T. caninus* in its preferred habitats. Temporary shifts from more *K*- to more *r*-selected population strategies have been predicted (MacArthur and Wilson 1967) and reported for natural populations (Reynoldson 1977), but are unlikely to occur on a short time scale in species with long generation time (May 1975).

We have no measure of the biotic factors operating at Clouds Creek, but the shift in physiological response of T. caninus in peripheral habitat towards that of a more *r*-selected species required us to consider whether the population biology of T. caninus differs between the two habitats. Persistent differences in age structure, density, sex ratio, survival, fertility or social organization between the two areas may define different demes and lead to the observed differences in T. caninus between the two habitats.

The history of the Clouds Creek study area could have led to different age structures in the two habitats. The establishment of a pine plantation since 1950 and clearing of agricultural land since 1972 have considerably modified the area and the possum populations (How 1972). Destruction of open forest has led to an 80% reduction in *T. vulpecula* populations since 1972 and a large area, of mainly *T. caninus* habitat, was lost to pine plantings. However, possums displaced by habitat destruction cannot re-establish themselves in adjacent areas that are already occupied by conspecifics (Tyndale-Biscoe and Smith 1969; How 1972). Between 1963 and 1968 possums caught in the pine plantation were removed to reduce damage to the pines. Subadults predominated in the removals during 1968 but there are no data for the preceding years. If subadults predominated in the removals throughout the period, then the peripheral population would be of less variable age, but age had little effect in mature animals on most of the parameters we considered (Barnett *et al.* 1979). Since 1968 all possums caught in the pines and elsewhere were released *in situ*.

The density and sex ratio of the *T. caninus* population in the preferred and peripheral areas are currently similar (our unpublished data). However, in the early 1970's the previous continuous removal of *T. caninus* from peripheral areas resulted in a density considerably less $(0.283 \text{ possums ha}^{-1})$ than in the adjacent preferred areas $(0.424 \text{ possums ha}^{-1})$; How 1972).

There are no overt differences in fertility and survival of T. caninus between preferred and peripheral areas (unpublished data). The only data on social organizations are for movements between recaptures of adults on successive nights from 1969 to 1971, and a comparison of resident and dispersing individuals. There

was no significant difference in movement between sexes or from individuals in different habitats [means \pm standard errors, in metres, peripheral: males $191 \cdot 9 \pm 22 \cdot 7$ (n = 4), females $261 \cdot 4 \pm 12 \cdot 5$ (n = 4); preferred: males $212 \cdot 9 \pm 29 \cdot 7$ (n = 7), females $184 \cdot 3 \pm 30 \cdot 8$ (n = 7)].

Intuitively one expects dispersing individuals to be at a disadvantage compared with resident animals, and a change in magnitude or in the variance of the measured parameters would be expected. None of the parameters we considered differed between resident and dispersing *T. caninus*. This may reflect the reproductive strategy of the species. Compared with *T. vulpecula*, *T. caninus* invests heavily in its offspring; young are associated with the mother for up to 3 years before dispersing, and after this stage have a high probability of continued survival (How 1972). Hence dispersal can occur when conditions are most favourable to subadult survival, in which case differences between residents and dispersers may not be expected.

The effect of reproduction on the parent may be examined by way of some of the blood parameters in female *T. caninus* in different reproductive states. Those females which lost a young and did not subsequently replace it had lower levels of haematocrit and plasma lipids than those in other reproductive states (Table 5). This may indicate that the successful raising of a young requires a certain level of fitness not possessed by these animals. Our data show an increase in plasma lipids in *T. caninus* as lactation proceeds; this may reflect an increase in milk lipids such as occurs in *T. vulpecula* (Gross and Bolliger 1959); lipid levels in maternal milk increase during the development of the young in both marsupials (Gross and Bolliger 1959; Griffiths *et al.* 1972) and eutherians (Larson and Smith 1974), and this increase may be reflected in circulating blood lipid levels (Davis and Sachan 1966).

It would be interesting to examine the effects of dispersal and reproductive status in T. vulpecula, as this species has lower parental investment in young and low survival of dispersing subadults (Dunnet 1964; How 1972). We have insufficient data to conduct these analyses.

Examination of the exact age structure and fertility of the populations from peripheral and preferred habitats will show whether the differences we have found in blood parameters are reflected in the population parameters. We are determining the age structure by counting the cementum annuli in the molars (Pekelharing 1970), and fertility from the persistent corpora lutea in the ovaries (Smith and How 1973).

In the last decade serious attempts have been made to integrate population genetics, population dynamics, productivity, bioenergetics, social behaviour and ecosystem interrelations to aid our understanding of adaptive strategies (see Kendeigh *et al.* 1977). A notable absence from this list of correlates of adaptive strategies is the within- and between-population and species variation in physiological responsiveness; these factors are important determinants of individual fitness. The data we have presented here and previously (Barnett *et al.* 1979) suggest that an extension of our approach may have considerable heuristic value in attempts to determine the proximal factors leading to inter-population differences in adaptive strategies.

Acknowledgments

This study was supported by grants from the Federal Department of the Environment and Conservation and the Zoology Department, La Trobe University. We wish to thank the New South Wales Forestry Commission both for their assistance for providing accommodation, and our colleagues Leigh Ahern, Jenny Barnett, Gill Humphreys and Dave Middleton for their assistance. We thank Darrell Kitchener for his comments on the draft of the manuscript.

References

Barnett, J. L., How, R. A., and Humphreys, W. F. (1976). Mammals of Clouds Creek, north-eastern New South Wales, and their distribution in pine and native forests. *Aust. Zool.* 19, 23-34.

Barnett, J. L., How, R. A., and Humphreys, W. F. (1977). Possum damage to pine plantations in northeastern New South Wales. Aust. For. Res. 7, 185–95.

Barnett, J. L., How, R. A., and Humphreys, W. F. (1979). Blood parameters in natural populations of *Trichosurus* species (Marsupialia : Phalangeridae). I. Age, sex and seasonal variation in *T. caninus* and *T. vulpecula. Aust. J. Zool.* 27, 913–26.

Calaby, J. H. (1966). Mammals of the Upper Richmond and Clarence rivers, New South Wales. CSIRO Div. Wildl. Res. Tech. Pap. No. 10.

Davis, C. L., and Sachan, D. S. (1966). Effect of feeding a milk fat depressing ration on fatty acid composition of blood lipids. J. Dairy Sci. 49, 1567-9.

Dunnet, G. M. (1964). A field study of local populations of the brush-tailed possum, *Trichosurus vulpecula*, in eastern Australia. Proc. Zool. Soc. Lond. 142, 665-95.

Fonnesbeck, P. V. and Symons, L. D. (1969). Effect of diet on concentration of protein, urea nitrogen, sugar and cholesterol of blood plasma in horses. J. Anim. Sci. 28, 216–19.

Francis, L. D. and Strong, L. C. (1938). Haemoglobin studies on the blood of female mice of the CBA strain: Effects of age, diet, strain, and reproduction. Am. J. Physiol. 124, 511-16.

Griffiths, M., McIntosh, D. L., and Leckie, R. M. C. (1972). The mammary glands of the red kangaroo, with observations on the fatty acid components of the milk triglycerides. J. Zool (Lond.) 166, 265-75. Gross, R., and Bolliger, A. (1959). Composition of milk of the marsupial Trichosurus vulpecula. Am. J. Dis. Child. 98, 768-75.

Haxhe, J. J. (1967). Experimental under-nutrition. II. The fate of transfused red blood cells. *Metab.* (Clin. Exp.) 16, 1092-5.

How, R. A. (1972). The ecology and management of *Trichosurus* species (Marsupialia) in N.S.W. Ph.D. Thesis, University of New England.

How, R. A. (1978). Population strategies in four species of Australian possums. In 'Ecology of Arboreal Folivores'. (Ed G. Montgomery.) (Smithsonian Press.)

Kendeigh, S. C., Wiens, J. A., and Pinowski, J. (1977). Epilogue. In 'Granivorous Birds in Ecosystem'. (Eds J. Pinowski and S. C. Kendeigh.) International Biological Program No. 12. (Cambridge University Press.)

Larson, B. L. and Smith, V. R. (eds.). (1974). 'Lactation, a Comprehensive Treatise. Vol. III. Nutrition and Biochemistry of Milk Maintenance.' (Academic Press Inc.: New York.)

May, R. M. (1975). Models for single populations. In 'Theoretical Ecology, Principles and Applications'. (Ed. R. M. May.) pp. 4-25. (Blackwell: Oxford.)

MacArthur, R. H., and Wilson, E. O. (1967). 'The Theory of Island Biogeography.' (Princeton University Press: Princeton, New Jersey.)

Pekelharing, C. H. (1970). Cementum deposition as an age indicator in the brush-tailed possum, *Trichosurus vulpecula* Kerr (Marsupialia). Aust. J. Zool. 18, 71-6.

Reynoldson, T. B. (1977). The population dynamics of *Dugesia polychroa* (Schmidt) (Turbellaria tricladida) in a recently constructed Anglesey pond. J. Anim. Ecol. **46**, 63-77.

Ride, W. D. L. (1970). 'A Guide to the Native Mammals of Australia.' (Oxford University Press: Melbourne.)

Smith, M. J., and How, R. A. (1973). Reproduction in the mountain possum, *Trichosurus caninus* (Ogilby), in captivity. Aust. J. Zool. 21, 321-9.

Specht, R. L. (1970). Vegetation. In 'The Australian Environment'. (Ed. G. W. Leeper.) 4th Ed. pp. 44-67. (CSIRO – Melbourne University Press.)

Tyndale-Biscoe, C. H., and Smith, R. F. C. (1969). Studies on the marsupial glider Schoinobates volans (Kerr). 3. Response to habitat destruction. J. Anim. Ecol. 38, 651-9.

Weech, A. A., Goettsch, M. D., and Reeves, E. B. (1935). Nutritional edema in the dog. 1. Development of hypoproteinemia on a diet deficient in protein. J. Exp. Med. 61, 299-317.

Weech, A. A., Wollstein, M., and Goettsch, E. (1937). Nutritional edema in the dog. V. Development of deficits in erythrocytes and haemoglobin on a diet deficient in protein. J. Clin. Invest. 16, 719–28. Winer, B. J. (1971). 'Statistical Principles in Experimental Design.' 2nd Ed. (McGraw-Hill Book Co.: New York.)

Zeldis, L. J., Alling, E. L., McCoord, A. B., and Kulka, J. P. (1945). Plasma protein metabolism – electrophoretic studies. Chronic depletion of circulating proteins during low protein feeding. J. Exp. Med. 82, 157–9.

Manuscript received 21 February 1979