

Habitat Effects on Organ Weights, Longevity and Reproduction in the Mountain Brushtail Possum, *Trichosurus caninus* (Ogilby)

J. L. Barnett^{AC}, R. A. How^{AD} and W. F. Humphreys^{ABD}

^ADepartment of Zoology, La Trobe University, Bundoora, Vic. 3083.

^BSchool of Biological Sciences, University of Bath, Claverton Down, Bath, BA2 7AY, England.

^CPresent address: Animal Research Institute, Department of Agriculture, Werribee, Vic. 3030.

^DPresent address: Western Australian Museum, Francis St., Perth, W.A. 6000.

Abstract

Fifty-seven mountain brushtail possums, *Trichosurus caninus* (Ogilby), were killed and examined from a population in north-eastern New South Wales; 34 were from preferred habitat and 23 from peripheral habitat. Maximum age attained was 17 y for females and 12 y for males. Body, kidney, spleen and male liver weights were greater ($P < 0.05$) in peripheral habitat, and female adrenal glands were heavier ($P < 0.05$) in preferred habitat. The mean number of corpora lutea per year of reproductive life was greater in peripheral-habitat females (1.56 ± 0.13 SE) than in preferred-habitat females (1.18 ± 0.11 ; $P < 0.05$). Adult sex ratio was parity in both habitats but the mean annual sex ratio of pouch young was 2.5 : 1 male : female in preferred habitat and 0.7 : 1 in peripheral habitat. The phenotypic distribution of transferrin differed between habitats. The data suggest that *T. caninus* in preferred and peripheral habitats were sufficiently distinctive in morphological, demographic, behavioural and genetic characters to be considered distinct subpopulations.

Introduction

Barnett *et al.* (1979a) compared a variety of blood parameters from the mountain brushtail possum, *Trichosurus caninus* (Ogilby), from peripheral and preferred habitats, and described differences in mean levels and seasonal variability in some values. The physiological response of *T. caninus* in peripheral habitats was closer to that of adjacent *T. vulpecula* (Kerr) populations than to that of adjacent *T. caninus* in preferred habitat. They suggested that these differences may result from either direct habitat effects or heredity, that is, that preferred- and peripheral-habitat *T. caninus* were distinct population demes.

This paper describes the age structure, organ weights and fertility of *T. caninus* in preferred and peripheral habitats in order to: (1) further characterize differences between these subpopulations; (2) try to discriminate between the environmental and hereditary components contributing to the observed differences.

Materials and Methods

The study site at Clouds Creek State Forest, north-eastern New South Wales, is characterized by areas of closed and tall open forests, large areas of pine plantation and a few areas of open forest and woodland. The distribution of these forest types, the study area (Barnett *et al.* 1976, 1977, 1979b), the criteria used to allocate animals to categories of preferred and peripheral habitat, and the rationale of this allocation have been described (Barnett *et al.* 1979a). Briefly, preferred habitat for *T. caninus* was closed and tall open forests; animals trapped even once in other forest types were assigned to the peripheral habitat. The distinction between habitats was based on previous trap history since 1968,

by means of How's (1972) fortnightly trapping data until 1972 and our subsequent data, and not on the site of final capture. This is more conservative than the method used in Barnett *et al.* (1979a) where distinction between habitats was based on history of previous captures since 1974.

T. caninus trapped in May and June 1977 were weighed, and their blood collected as described in Barnett *et al.* (1979b). They were then transported to a nearby building and exsanguinated under ether anaesthesia following an intraperitoneal pentobarbitone sodium (Nembutal) injection. The spleen, liver, kidneys, adrenals, heart, male gonads and prostatic urethra were removed from the carcasses, cleared of fat, blotted dry, weighed and fixed in 10% formol saline. The female reproductive tracts were removed, fixed in Bouin's fluid for 24 h and then transferred to 70% ethanol for subsequent examination of the corpora lutea. *T. caninus* is a monovular and polyoestrous species whose corpora lutea appear to persist throughout reproductive life (Smith and How 1973) and consequently represent the total number of oestrous cycles during an individual's lifetime.

Fifty-seven *T. caninus* were examined; of these five were less than 3 years old (juveniles and subadults according to Smith and How 1973), and not included in subsequent analyses of organ weights. Of 52 adults 27 had been marked as juveniles and were of known age (up to 10 y); the other *T. caninus* marked as adults were of known minimum age (up to 12+ y). These latter animals were aged by counting the tooth cementum annuli by the technique of Pekelharing (1970). The lower jaw was fixed in alcohol at the study site, subsequently cleared of tissue, and the third molar examined for cementum annuli. Some teeth (20%) did not stain adequately by this method; for these, the stain was removed with acid alcohol and the teeth etched with glacial acetic acid for 1 h, stained in 0.2% cresyl violet for 1–2 h, and differentiated when necessary in acid alcohol. A regression of known age (X from 2 to 10 y old) against age estimated from the cementum annuli (Y) showed a good fit ($Y = 0.96X + 0.51$, $n = 27$, $r^2 = 0.94$, $P < 0.001$) and it was assumed that the relationship held for the older animals.

Statistical Analysis

Contralateral organ weights did not differ significantly in weight, and the total paired organ weight has been used throughout. The raw data were subjected initially to linear regression analyses against both body weight and age, to eliminate weight and age as variables where necessary (see Barnett *et al.* 1974). None of the weight-corrected data were significantly regressed with age. Where one of the regressions between organ weight and body weight was significant, the following procedure was used to compare organ weights in animals from different habitats. Organ weights of animals with significant regression gradients were adjusted to organ weights of an animal with a mean body weight equal to that of the group that did not show a significant regression between organ and body weights. When both regression lines were significant (e.g. male heart weights) adjustment was made to the mean body weight of animals from both habitats combined. To compare body or organ weights from animals in different habitats where one or both of the regressions between weights and age were significant, weights of animals with significant regressions were adjusted to those of an animal 6 y old, the mean age of all adults examined. For example, in Table 1, kidney weights of males from peripheral habitats were not regressed significantly with body weight but those from preferred habitat were. Thus, to compare the effect of habitat on kidney weight in males, the weights of kidneys from preferred-habitat animals were adjusted to those of an animal with a body weight corresponding to the mean body weight of males from peripheral habitat. This allowed subsequent analysis independent of the effect of body weight. Similarly, body weights which showed significant regressions with age, in both habitats and sexes, were adjusted to those of an animal 6 y old; this allowed subsequent analysis of body weight independent of age effects.

The relationships between age distribution and both habitat and sex were tested by the Wilcoxon two-sample test corrected for tied values (Sokal and Rohlf 1969). Sample means were compared within sexes by Student's *t*-test or by the method of Least Significant Difference following an analysis of variance for sex or habitat effects (Sokal and Rohlf 1969).

Results

Presentation of Data

Parameters that regressed significantly with body weight are shown in Table 1. Overall regression equations (both habitats combined) were derived for male

body weights and epididymal weights against age, because equations for the separate habitats were not significantly different. The data with significant regression lines were corrected, by use of the gradients of the regression lines, as described in the section on statistical methods. The mean body weight to which an organ was corrected is shown in Table 2 in footnotes.

Table 1. Linear regression equations used to correct data for variations in body weight or age

Ages in years, from 3 to 12 y in males and from 3 to 17 y in females; body weights in grams, from 2350 to 3200 g in males and from 2250 to 3600 g in females; equation of the regression line is $Y = mX + c$ (m , gradient; c , intercept)

Parameter	Habitat	X	m	c	r	N
Males						
Heart	Preferred	Weight	0.0029 ± 0.00132	2.528 ± 3.7088	0.535	16
Heart	Peripheral	Weight	0.0082 ± 0.00200	-12.09 ± 6.071	0.820	10
Kidneys	Preferred	Weight	0.0025 ± 0.00092	5.497 ± 2.5755	0.595	16
Testes	Preferred	Weight	0.0030 ± 0.00069	-5.843 ± 1.9258	0.729	16
Epididymis	Combined	Age	0.1391 ± 0.02912	1.757 ± 0.1953	0.698	26
Body wt	Combined	Age	59.36 ± 16.021	2499.4 ± 107.47	0.603	26
Females						
Heart	Preferred	Weight	0.00329 ± 0.00112	-0.577 ± 3.2883	0.815	15
Liver	Preferred	Weight	0.0207 ± 0.0074	7.546 ± 22.025	0.570	14
Adrenals	Peripheral	Age	0.0092 ± 0.00326	0.143 ± 0.0277	0.682	9
Body wt	Preferred	Age	47.861 ± 13.511	2506.6 ± 132.60	0.684	16

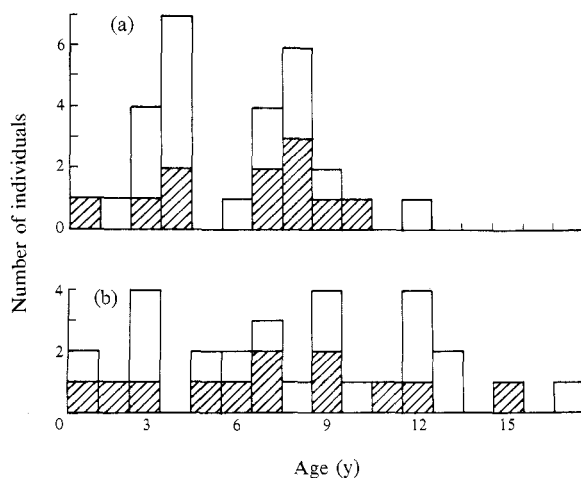


Fig. 1. Age distribution of *T. caninus* males (a) and females (b) from peripheral (hatched column) and preferred (open column) habitats.

Age Structure

The age distribution of the *T. caninus* sample is shown in Fig. 1. There were no differences between habitats in the age distributions of females, males, or of males and females combined. The combined data for both habitats showed that the age distribution differed between sexes ($0.05 > P > 0.025$); females were older than males. The sex ratio was 1.00 in both habitats.

Organ Weights

Of ten parameters, two differed between sexes and six between habitats in one or both sexes. Mean body, kidney, spleen and male liver weights were greater in animals from peripheral habitat, but female adrenal glands were heavier in animals from preferred habitat ($P < 0.05$, Table 2). The mean number of corpora lutea per year in females 2 or more years old was significantly greater from peripheral habitats ($P < 0.05$, Table 3) and there was no age-related trend in these data from either habitat ($P > 0.05$). These habitat effects occurred in both raw and

Table 2. Raw data and, data corrected for body weight or age, for age, body weight and organ weights in adult *T. caninus*

Values are means \pm standard errors, with sample sizes in parentheses. Data corrected to age of 6 y, except where indicated by footnote

Parameter	Preferred habitat		Peripheral habitat	
	Raw data	Corrected data	Raw data	Corrected data
Males				
Body wt (g)	2803 \pm 66.4 (16)	2811 \pm 56.2 (16)	2975 \pm 59.3 (10)	2928 \pm 40.4 (10)
Adrenals (g)	0.20 \pm 0.01 (16)		0.21 \pm 0.01 (10)	
Kidneys (g)	12.49 \pm 0.28 (16)	12.92 \pm 0.22 (16) ^A	13.54 \pm 0.57 (10)	
Liver (g)	65.62 \pm 1.87 (16)		72.00 \pm 2.23 (10)	
Spleen (g)	5.63 \pm 0.24 (16)		8.07 \pm 0.58 (10)	
Heart (g)	10.67 \pm 0.36 (16)	10.89 \pm 0.31 (16) ^B	12.44 \pm 0.60 (10)	11.55 \pm 0.35 (10) ^B
Testes (g)	7.87 \pm 0.27 (16)	8.39 \pm 0.19 (16) ^A	8.11 \pm 0.39 (10)	
Epididymis (g)	2.55 \pm 0.11 (16)	2.57 \pm 0.09 (16)	2.75 \pm 0.19 (10)	2.63 \pm 0.11 (10)
Prostatic urethra (g)	15.79 \pm 2.47 (16)	16.12 \pm 1.73 (16)	17.87 \pm 2.77 (10)	
Age (y)	5.9 \pm 1.88 (16)		6.8 \pm 0.74 (10)	
Females				
Body (g)	2934 \pm 73.3 (16)	2794 \pm 53.5 (16)	3075 \pm 94.1 (10)	
Adrenals (g)	0.24 \pm 0.01 (16)		0.21 \pm 0.01 (9)	0.20 \pm 0.01 (9)
Kidneys (g)	12.44 \pm 0.40 (16)		13.57 \pm 0.57 (10)	
Liver (g)	69.20 \pm 2.39 (14)	75.79 \pm 5.18 (14) ^C	76.29 \pm 3.92 (10)	
Spleen (g)	4.10 \pm 0.40 (16)		4.79 \pm 0.45 (10)	
Heart (g)	9.05 \pm 0.31 (15)	9.54 \pm 0.18 (15) ^C	9.62 \pm 0.32 (10)	
Age (y)	6.8 \pm 0.74 (16)		8.4 \pm 1.13 (10)	

^ACorrected for body weight to 2975 g, the mean body weight for males in peripheral habitat.

^BCorrected for body weight to 2869 g, the mean body weight for all males.

^CCorrected for body weight to 3075 g, the mean body weight for females in peripheral habitat.

corrected data, except for: (1) female adrenal gland weights where raw data showed no significant habitat effect; (2) female liver weights where body weight correction abolished the habitat effect. The measured components of the male genital tract showed no significant habitat effects (Table 2). The raw and corrected mean weights of heart and spleen in males were heavier ($P < 0.01$) than in females (Table 2).

Discussion

Despite the removal of *T. caninus* trapped in the pine plantation between 1963 and 1968 (How 1972), the age distribution in the two habitats was similar (Fig.

1), but the oldest animals of each sex were from preferred habitat and may reflect this removal. There was differential longevity between adults; females on average were 1.2 y older than males. The greatest age for males was 12 y, and for females 17 y; the oldest female was still reproductively active with a young in her pouch. There are few comparative data on longevity for wild Australian mammals: 20 y for *Macropus rufus* (Desmarest) (Newsome 1977), 2.5–3 y for *Isodon macrourus* (Gould) (Stodart 1977), 6 y for *Pseudocheirus peregrinus* (Boddaert) (How, unpublished), and about 13 y for *Trichosurus vulpecula* (Kerr) (Crawley 1973). Thus *T. caninus* is a long-lived marsupial, consistent with its slow development (How

Table 3. The age, number of corpora lutea and number of corpora lutea per year of reproductive life for *T. caninus* in preferred and peripheral habitats

Reproductive life begins at 2 y old

Age (y)	Preferred habitat		Peripheral habitat	
	Number of corpora lutea	Corpora lutea per year	Number of corpora lutea	Corpora lutea per year
< 1	0	—	—	—
1	—	—	0	—
2	—	—	1	1.00
3	1, 4	0.50, 2.00	5	2.50
4	—	—	—	—
5	8	2.00	7	1.75
6	4	0.80	9	1.80
7	8	1.50	7, 9	1.17, 1.50
8	7	1.00	—	—
9	8, 12	1.00, 1.50	11, 12	1.38, 1.50
10	10	1.11	—	—
11	—	—	17	1.70
12	12, 14, 15	1.09, 1.27, 1.36	12	1.09
13	8, 11	0.67, 0.92	—	—
14	—	—	—	—
15	—	—	25	1.79
16	—	—	—	—
17	16	1.00	—	—
Mean ± SE		1.18 ± 0.11		1.56 ± 0.13

1976), and this feature, as well as other aspects of its biology (Barnett *et al.* 1979a, 1979b; How 1981) is a correlate of a *K*-selected strategy (Pianka 1970).

Sexual dimorphism in organ weights is not unusual in animals (Bellamy *et al.* 1973; Barnett *et al.* 1974), although its absence in adrenal weight contrasts with the state in *T. vulpecula* (McDonald 1977). The adrenals of female *T. vulpecula* are nearly twice as large as those of males and enlarge further during lactation (Tyndale-Biscoe 1973). As all adult *T. caninus* females were lactating when killed, the absence of sexual dimorphism in adrenal weights is in marked contrast to *T. vulpecula*. The functional significance of sex differences in spleen and heart weights in the present study is unknown, although splenic weight is significantly correlated ($P < 0.01$) with white blood cell counts in females but not in males (our unpublished data).

No consistent trends in the variance of the data were found. Greater variance was found in corrected body weights ($F_{15,9} = 3.09$, $P < 0.05$) and age ($F_{15,9} = 10.33$, $P < 0.01$) for males in the preferred habitat, but it was greater for spleen ($F_{9,15} = 3.65$, $P < 0.05$) and uncorrected kidney weights ($F_{9,15} = 2.59$, $P < 0.05$) for males in peripheral habitat. A similar lack of trend in the variance was found in physiological measurements; plasma protein showed less variance and haematocrit and female erythrocyte count greater variance in preferred habitat (Barnett *et al.* 1979a).

In peripheral habitat *T. caninus* had more corpora lutea per year of reproductive life than those in preferred habitat, but there was no age-related trend in the data of either habitat ($r^2 = 0.002$ and 0.003 , respectively). Hence the effect on reproduction, be it of habitat or gene pool, remains consistent throughout the 16 years of data available.

Since *T. caninus* is monovular the number of corpora lutea represents the number of oestruses during the life of the individual. Females become reproductively active during their third year, i.e. after 2 y (Smith and How 1973), although not all 2-y-old females produce young (How 1976). Our data support these findings; mean values in preferred habitat are sometimes less than one, so some adult females failed to ovulate in each year (Table 3).

There are four possible explanations for the difference in mean numbers of corpora lutea, which are greater in peripheral-habitat females, although we present data which discount the first three. First, fewer females in peripheral habitat may become pregnant at first oestrus. However, there was no between-habitat difference in variance for the timing of first births each year ($F_{1,47} = 1.93$, $P > 0.1$) or in the actual time of first birth (Wilcoxon two-sample test: $t = 0.89$, $P > 0.4$). Second, females from peripheral habitats may have more young. Yet, between 1968 and 1971 the mean number of pouch young per year for females > 2 y old was 0.85 ($n = 34$) in peripheral and 0.80 ($n = 25$) in preferred habitats (from How 1972). Third, mortality among pouch young, followed by a return to oestrus (Smith and How, 1973), could be more common in peripheral-habitat females. However, between 1968 and 1971 mortality among the 23 pouch young of peripheral-habitat females was 43%, and that among 16 pouch young of preferred-habitat females was 56% (contingency $\chi^2 = 0.0003$, ns).

Fourth (the hypothesis we favour), the difference in ovulation rates between habitats could indicate different reproductive strategies. Preferred-habitat *T. caninus* are *K*-selected with a reduced ovulation rate, but peripheral habitat animals are more *r*-selected. Additional evidence for this change in reproductive strategy of peripheral-habitat *T. caninus* is provided by some data on pouch young. For the period 1968–77 the overall sex ratio of pouch young did not differ from unity ($\chi^2_5 = 6.59$, ns) but the yearly average (male : female) sex ratio was $2.47 : 1$ and $0.70 : 1$ in preferred and peripheral habitats respectively. As the adult sex ratio was unity in both habitats (from How 1972) and we can find no evidence of differential mortality among sexes in the two habitats, the consequence of a higher proportion of male pouch young in preferred habitat must be a difference in the dispersal pattern of the juveniles. The age that juveniles dispersed was not the same when sex and habitat were considered (Kruskall–Wallis test: $H_{adj} = 8.78$, $P < 0.05$). To identify where these differences occurred we conducted the conservative multiple-comparison test using experiment-wise error rate with $\alpha = 0.15$

(Daniel 1978, p. 212). The rules below include the groups that do not differ significantly:

Female preferred Female peripheral Male peripheral Male preferred

and their respective mean ages, at dispersal, were 87, 122, 137 and 148 weeks (mean for females, 104.5; for males 140.9; data from How 1972). When adjustment is made for the mean annual sex ratio of the juveniles in the preferred and peripheral habitats the mean age at dispersal for the two populations becomes 130.4 (preferred) and 119.4 (peripheral) weeks respectively, a difference of 11 weeks (0.21 y).

The association of females and previous young during a subsequent breeding season results in greater failure to breed, pouch young mortality, or both together (contingency $\chi^2 = 7.42$, $P < 0.001$; How 1981). This factor in conjunction with data on age at dispersal should result in greater pouch young mortality in the preferred habitat, where the mean duration of association between mother and offspring is greater. Although we could find no significant difference in pouch young mortality between habitats, there is a trend for the feedback between female reproductive failure and the presence of a previous offspring to act more strongly in the preferred habitat (Fisher's exact test, $P = 0.177$); only in preferred habitat were females known not to ovulate each year (Table 3). A possible explanation for this lower ovulation rate is that concentrations of free corticosteroid were higher in females from preferred habitat (Presidente *et al.* 1982), which suggests a stress

Table 4. The distribution of transferrin phenotypes amongst sex and habitat in *T. caninus*

Habitat	Sex	Phenotype			Σ
		F	FS	S	
Peripheral	M	2	3	4	9
Peripheral	F	6	3	1	10
Preferred	M	9	8	0	17
Preferred	F	9	7	1	17
Σ		26	21	6	53

response. Stress is known to affect several aspects of fertility in rats, mice and sheep (Arvay 1967; Howarth and Hawk 1968; Yang *et al.* 1969; Euker and Riegle 1973; Paris and Ramaley 1973, 1974). In the peripheral habitat, where the association between mother and offspring is shorter, the behavioural feedback is insufficient to suppress ovulation; however, we suggest it is sufficient to cause prenatal mortality and subsequent return to oestrus, resulting in an increased number of corpora lutea.

A further comparison made in two ways between *T. caninus* from the two habitats was genetic. First, plasma and erythrocytes collected earlier and stored frozen showed no electrophoretic variation at 25 loci, except for transferrin. However, the variation in electrophoretic mobility of transferrin could not be interpreted on a simple genetic basis (P. Baverstock, personal communication). Second, plasma

taken from the animals considered in this paper and stored in liquid nitrogen showed three transferrin phenotypes, in agreement with a Hardy-Weinberg codominant two-allele system ($\chi^2_2 = 0.31$, $P = 0.86$), which suggests a genetic basis (D. Cooper, personal communication). Further examination of these data (Table 4) showed that the distribution of transferrin phenotypes differed between habitats ($\chi^2_2 = 6.66$, $P = 0.036$) but not between sexes ($\chi^2_2 = 1.31$, $P = 0.52$).

Table 5. Summary of observed differences between *T. caninus* in preferred and peripheral habitats

Pf, greater in preferred habitat; Pp, greater in peripheral habitat. References: 1, Barnett *et al.* 1979b; 2, this paper; 3, Presidente *et al.* 1982; 4, data from How 1972

Class of observation	No. of differences	Differences	Reference
Gravimetric	5	Body; Pp	1
		Kidney; Pp	2
		Spleen; Pp	2
		Liver in male; Pp	2
		Adrenal in female; Pf	2
Demographic	2	Sex ratio of pouch young; Pf	2
		No. of corpora lutea per female per year; Pp	2
Genetic	1	Phenotypic distribution of transferrin	2
Behavioural	1	Age of dispersal of young; Pf	2
Endocrinological	1	Free corticosteroid in female; Pf	3
Haematological	5	Erythrocytes; Pp	1
		Haemoglobin concentration; Pp	1
		Haematocrit; Pp	1
		Plasma protein; Pp	1
		Plasma lipid; Pp	1
Parasite burden or prevalence	7	<i>Amplicacum robertsi</i> ; Pp	3
		<i>Adelonema trichosuri</i> ; Pp	3
		<i>Bertiella trichosuri</i> ; Pp	3
		<i>Ixodes</i> spp.; Pp	3
		<i>Trichosurolaelaps dioxia</i> ; Pp	3
		<i>T. crassipes</i> ; Pp	3
		<i>Paraustrostrongylus trichosuri</i> ; Pf	3
Seasonal variation	2	Haemoglobin; Pf	1
		Erythrocyte count; Pf	1
Total	24	Greater in preferred habitat, 7 Greater in peripheral habitat, 16 Genetic difference	

No difference observed in: plasma glucose (1); heart weight (2); testis weight (2); epididymis weight (2); prostatic urethra weight (2); age distribution (2); adult sex ratio (2); size of home range (4); number of pouch young per female per year (2); mortality of pouch young (2); timing of first birth (2).

Gene frequencies differed between habitats in males ($\chi^2_1 = 7.17$, $P = 0.007$) but not in females ($\chi^2_1 = 0.01$, $P = 0.91$).

The differences between habitats in the distribution of transferrin phenotypes is particularly relevant to the explanation proposed for the different numbers of corpora lutea per year in preferred and peripheral habitats. The transferrin locus affects some aspect of fertility in cattle (Ashton 1958, 1965; Ashton and Fallon

1962), pigs (Kristjansson 1964; Smith *et al.* 1968), poultry (Morton *et al.* 1965) and tuna (Fujino and Kang 1968) and a physiological basis for the effects has been proposed (cf. Ashton and Dennis 1971). In cattle the transferrin locus affects 'return to service', a phenomenon interpreted as reflecting embryonic or early foetal loss (Ashton and Fallon 1962), and in mice the locus influences, amongst other factors, the sex ratio of the young (Ashton and Dennis 1971).

These data show that populations of *T. caninus* in preferred and peripheral habitats differed in morphometric characters (organ weights), demographic parameters (fertility and sex ratio of the young), a genetic character (phenotypic variation in transferrin), and a behavioural characteristic (age of dispersal of juveniles). These populations also differ in the prevalence of burdens of parasites (Presidente *et al.* 1982) and in mean levels of various blood parameters (Barnett *et al.* 1979a). In addition, levels of some blood parameters changed seasonally; changes in peripheral-habitat *T. caninus* were more similar to those in adjacent and sympatric *T. vulpecula* than to those in adjacent preferred-habitat *T. caninus* (Barnett *et al.* 1979a). These data (summarized in Table 5) show that *T. caninus* in preferred and peripheral habitats are adopting different strategies, and suggest that the two groups of animals may be sufficiently different to be considered subpopulations.

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