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The Biology of the Northern Brown Bandicoot, *Isoodon macrourus* (Marsupialia : Peramelidae) at Mitchell Plateau, Western Australia

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Abstract

Breeding, population dynamics and seasonal changes in physical and physiological parameters were examined in *Isoodon macrourus* at the Mitchell Plateau between September 1981 and November 1982.

Females gave birth to litters of $2{\cdot}5 \pm 1{\cdot}0$ (16) young between September and April. They produced up to three litters in a breeding season with an average interval between successive litters of 89·5 (51–108) days. Adult testosterone levels and scrotal size began to increase in July and peaked in September 1982. The overall ratio of adult males to adult females was 1 : 0·54; it was 1 : 0·80 for pouch young.

Females were more frequently trapped on sequential trips than were males. Density on the grids increased towards the end of the dry season (July and September 1982)—mostly as a result of increased numbers of females. Adult males and females moving onto the grids during the dry season tended to select different habitats. Adult males moved significantly more in the wet season (September 1981, January and April) than they did in the dry season (July and September 1982); they also moved significantly more than adult females in the wet season.

Seasonal variations were recorded for most physical and physiological parameters. During the wet period from September 1981 to January 1982, body weight, haemoglobin, haematocrit and total plasma albumin declined, while total white blood cells and proportion of lymphocytes to granular leucocytes rose. This indicated that this period was one of change in condition for this species. Compared to adult females, adult males were larger and heavier, had higher values of haematocrit and lymphocytes, and lower values of granular leucocytes, free steroids, CBGBd and albumin bound corticosteroid. There was considerable between-year variability in condition of individuals and both sexes differed significantly in September 1981 and 1982 in their weight, haematocrit, total white blood cells, granular leucocytes, MCBC and testosterone. Individuals at disparate localities at the Mitchell Plateau showed similar seasonal physiological and physical responses, except for one grid where they were heavier.

Introduction

The northern brown bandicoot, *Isoodon macrourus*, has been studied in high rainfall areas from New South Wales to the Northern Territory (Friend 1989). The various studies indicate that the period of births can range from strongly seasonal to aseasonal (Gordon 1974; Gemmell 1982; Hall 1983; Friend 1989). Breeding may be influenced by the light regime (Gemmell 1982) or by food availability which is itself influenced by rainfall (Friend 1989).

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In the wild, females reach sexual maturity at about three months (Friend 1989), and have a very short gestation period of 12·5 days (Lyne 1974). They can produce up to four litters a year of mean size 2·6 to 3·4 individuals at 54–60 days intervals (Gordon 1971, 1974; Gemmell 1982; Hall 1983; Friend 1989). This high reproductive potential permits *I. macrourus* to rapidly build up in numbers when conditions are favourable (Friend 1989). Males are capable of reproduction at the same age as females but in captivity sire their first litter at about 12·5 months (Gemmell 1987).

This paper examines the changing physiological status of *I. macrourus* individuals in populations from different habitats and potentially different demography. It is one of a series of papers resulting from a simultaneous study of a number of species of small mammals in various communities at the Mitchell Plateau in the north-western Kimberley District of Western Australia (How *et al.* 1983; Humphreys *et al.* 1984; Bradley *et al.* 1987; Kemper *et al.* 1987; Bradley *et al.* 1988 and Schmitt *et al.* 1989).

Materials and Methods

Trapping and Measurements

Eight capture-mark-release (CMR) sites were established as a 10×10 grid using a 15 m trap-spacing, as detailed in Bradley *et al.* (1987). A trapline in a similar but disjunct habitat was established for each CMR grid from which individuals were removed for post-mortem examination.

We identified individuals by the application of unique ear marks. When an individual was first caught in any trapping period we removed a blood sample from the orbital sinus (Halpern and Pacaud 1951; Riley 1960). Linear and weight measurements were taken and reproductive conditions assessed: in females from the appearance of the teats (barely visible, lactating, distended, or regressed) and of the pouch and the presence of pouch young (the crown to rump, pes and tail lengths and the extent of furring of pouch young were recorded); and in males from the scrotal length, width and the condition of the epididymal sac (full, distended, undistended). A cloacal swab was taken to screen for *Salmonella* and *Arizona* (How *et al.* 1983). On subsequent recaptures within a trapping period the trap position, weight and reproductive conditions were noted.

Population size was estimated using the known-to-be-alive (KTBA) method, and area of the grids utilised (GAU) was calculated following Mohr (1947) for those individuals captured more than three times.

Blood Sampling and Analyses

These procedures have been detailed in Kemper *et al.* (1987).

We measured the plasma concentration of testosterone and corticosterone and the glucocorticoid was partitioned into free, albumin bound and high affinity bound compartments. Cortisol was assumed to be the major glucocorticoid in *I. macrourus*. The glucocorticoid assay was modified to use 3H-corticosterone and corticosterone standards.

Steroid protein interactions were measured from equilibrium dialysis at 37°C, using 3H-corticosterone. This yielded a high affinity binding constant of $5 \cdot 84 \pm 0 \cdot 46$ M^{-1} (5) with no apparent sex difference in the binding. We used five replicates of a 5% solution of *I. macrourus* albumin, isolated from a plasma pool, to determine a low affinity binding constant (KA [PA] for the albumin-corticosterone binding) of $2 \cdot 0 \pm 0 \cdot 06$.

Animals from removal sites were transported to the field laboratory and killed with an overdose of Nembutal. Linear and weight measurements were taken and the external reproductive conditions assessed. Liver, heart and kidney were dissected out and stored in liquid nitrogen for protein electrophoresis (fourteen proteins were studied but no genetic variation was detected). The reproductive tract was removed and fixed in Bouin's solution and later examined histologically. We counted the number of embryos and implantation scars as an indication of sexual maturity.

To help in the delineation of reproductive maturity we assessed the spermiogenic stage of testes from histological preparations.

Statistics

To identify variables worthy of further investigation we ran multiple regression analyses (using GENSTAT; Rothamsted Experimental Station, on a DEC-10 at the Western Australian Regional Computing Centre) to test each effect with all other effects of the same or lower orders in the model. Because of the large number of tests only those with $P < 0 \cdot 01$ were used to indicate which variables were worthy of further investigation. When a single comparison was investigated, t tests were applied using the pooled variance (Snedecor and Cochran 1969). When more than one comparison was made

we used the Behrens Fisher test (conservative for type 1 errors) or, where stated, the GT2 test (Sokal and Rohlf 1981) at $P<0{\cdot}05$.

Some variables were log transformed where appropriate and homogeneity of variance was tested using Bartlett's test (Sokal and Rohlf 1981) before the follow up tests were performed. The seasonal movement of adults was examined using Kruskall–Wallis one-way analysis of variance (Davies 1971) followed by Dunn's Multiple Comparison test (Daniel 1978).

Throughout the paper significant levels are denoted by $*=P<0{\cdot}05$, $**=P<0{\cdot}01$ and $***=P<0{\cdot}0001$. Error bounds are standard deviations unless otherwise specified.

Study Areas

The study was conducted on, and adjacent to, the Mitchell Plateau in the remote northwest of the Kimberley district of Western Australia (*c.* 14°S.,125°E.); the climate is typical of the wet-dry tropics, having monsoonal rains in summer (usually November to March) and dry winters. Full descriptions of the climate, vegetation, community composition and general methods, including descriptions of the trapping grids, have been presented elsewhere (Hnatiuk and Kenneally 1981; How *et al.* 1983; Humphreys *et al.* 1984; Bradley *et al.* 1987). Hence in this paper we present only sufficient methodological detail required to follow the paper and where the methods differ from those published.

I. macrourus was captured on five out of eight trapping grids: deciduous vine thicket (DV) and a contiguous eucalypt woodland (DW) at Lone Dingo; a vegetation mosaic (WM); a deciduous vine thicket (DV) at Port Warrender and a riparian site along Camp Creek (CP).

We trapped *I. macrourus* in the same habitat as *Dasyurus hallucatus* (Marsupialia : Dasyuridae) and the murid rodents *Melomys* sp. cf. *burtoni*, *Zyzomys argurus* and *Z. woodwardi* (Bradley *et al.* 1987). *I. macrourus* is widespread in the area and is found from coastal to inland habitats, being absent only from the sandstone complex. It is most abundant on the plateau itself in both vine thickets and open woodland (Bradley *et al.* 1987).

Results

Trappability

This is calculated only for individuals from DV and DW, due to inadequate sample size in the remaining grids.

Individuals were captured on average, 3·5 times during the course of the study. There was no significant difference ($\chi^2_2=0{\cdot}91$) in the trappability of adult males (23/77 individuals/captures), adult females (12/52) and juveniles (8/23). Nor was there any significant difference in their trappability within trips.

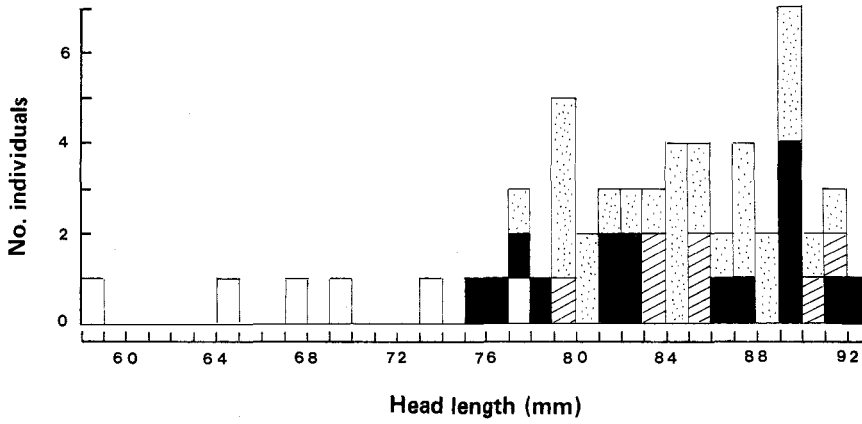

Fig. 1. Frequency histogram of the head lengths of female *Isoodon macrourus* at the Mitchell Plateau that: (1) had pouch young (black area); (2) were lactating or had distended teats, but had no pouch young (cross-hatched area); (3) adults but with regressed teats (stippled area); (4) juveniles with small teats and little or no pouch development (white area).

Reproductive Maturity

Females were judged to be adult when their head length exceeded 75 mm. Above this length females variously had pouch young, distended teats indicative of lactation or recent

weaning, or darkly pigmented teats indicating they were parous (Fig. 1). One exception was noted; it had a head length of 77 mm but had teats and a pouch of a juvenile appearance. The smallest pregnant female weighed 477 g.

Males were judged to be adult when the head length exceeded 78 mm or the scrotal index (max. length × max. width) exceeded 400 mm^2. Males with elevated levels of testosterone always had a head length >78 mm (Fig. 2). Elevated levels of testosterone were always associated with a scrotal index greater than 400 mm^2. Histological examination of 12 males showed that 11 had mature sperm in testes and epididymides. Those with mature sperm had a scrotal index which averaged 683 (range 491–875). The other male, which had a scrotal index of 385, was juvenile; its testicular tubules had both small diameters and lumen, and sperm were absent from the tubules and epididymides.

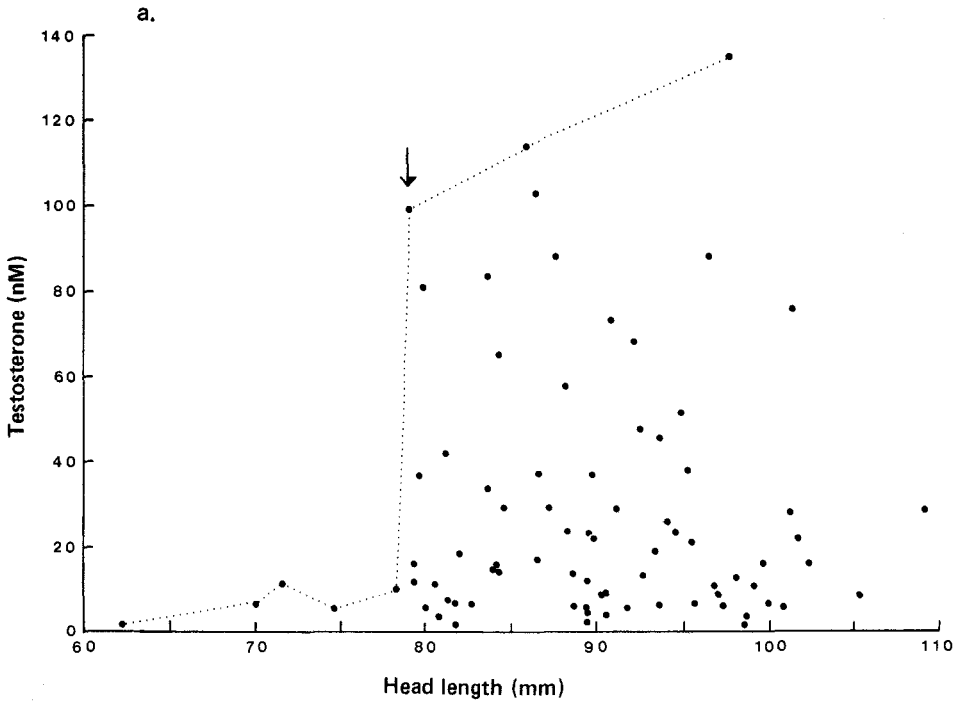

Fig. 2. Relationship between levels of testosterone and head length in male *Isoodon macrourus* at the Mitchell Plateau.

Table 1. Mean distance (m) travelled by adult male and adult female *Isoodon macrourus* between successive captures on DV/DW grids for each trip and for all trips combined

	♂♂			♀♀		
	Mean	SD	N	Mean	SD	N
			Wet			
September 1981	100·4	61·28	5	47·0	18·39	2
January 1982	103·0	51·90	4	55·8	23·23	3
April 1982	61·8	34·29	4	44·5	40·54	6
Total wet season trips	89·3	50·85	13	48·1	31·46	11
			Dry			
July 1982	60·8	12·64	9	92·7	92·08	6
September 1982	38·9	35·98	15	67·1	25·45	8
Total dry season trips	47·1	31·00	24	70·1	61·49	14

Movement

Movement was assessed only for individuals from DV and DW (Table 1). In September 1981 we trapped after the start of the wet season, while in September 1982 we trapped before the start of the wet season.

Adult males moved significantly more ($t_{35}=2{\cdot}73^{**}$) in the wet season (September 1981 to April 1982) than they did in the dry season (July 1982 to September 1982; Table 1). Additionally, during the wet season adult males moved significantly ($t_{22}=2{\cdot}43^{*}$) further than adult females.

The grid size was inadequate to examine home range, however it was adequate to indicate whether dispersion patterns within the grids varied over time. The grid area utilised (GAU) by individuals increased with the number of captures (Fig. 3) and there was no indication that adults of either sex differed in GAU. There was a strong indication, however, that individuals restricted their utilisation to only a part of the grids; this is supported by the plateaux seen in Fig. 3 at an area at less than one third of the grid. After five captures (see Fig. 3) the GAU of adults which utilised both grids was 7063 ± 3495 (7) m^2.

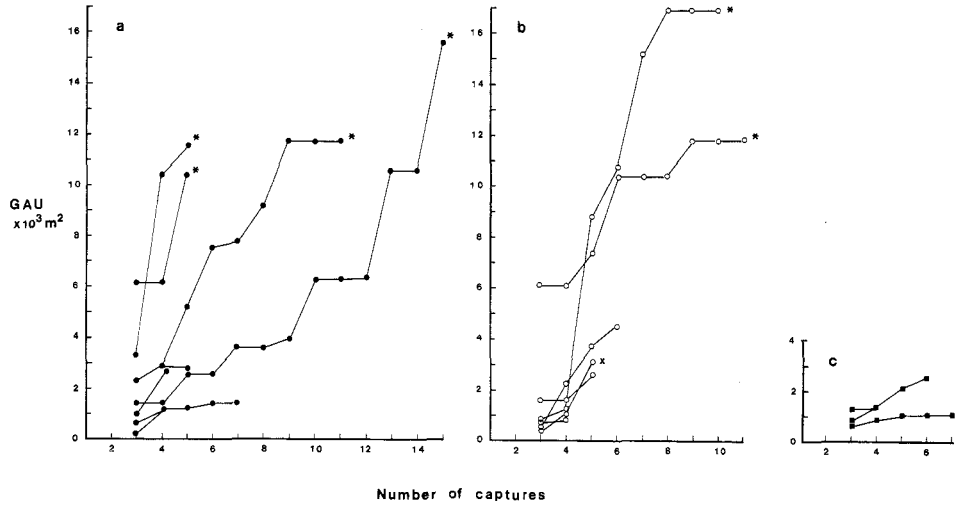

Fig. 3. Increase in the area of the trapping grid utilised (GAU) (1000 m^2) with successive captures for individual *Isoodon macrourus* in the DV and DW grids at the Mitchell Plateau; (a) adult males; (b) adult females; (c) juveniles. * individuals captured on both grids.

Population Size

Almost twice as many individual adult males (23) as adult females (12) were recorded from DV/DW over the study period. From the number of individuals known to be alive (KTBA) in the combined DV and DW grids, adult males were preponderant over adult females from September 1981 to April, but were similar to females in number in July and September 1982. Most juveniles (5) were recorded in April.

In the woodland (DW), there was a steady increase in the proportion of females among adults resulting from both an actual increase in adult females and a decrease in adult males (Fig. 4*a*). In the deciduous vine thicket (DV), there was a preponderance of adult males over adult females during each trip, although the numbers of adults of both sexes in the vine thickets increased markedly during the hot dry months of July and September 1982 (Fig. 4*b*). In the dry period (July and September 1982) adult males were more sedentary and had a preference for the deciduous vine thicket.

Captures on the DV/DW Grids

The proportion of individuals recaptured on sequential trips was; female adults, $91 \pm 11\%$ (4), male adults, $53 \pm 15\%$ (4) and juveniles, $80 \pm 35\%$ (3). Adult females were always

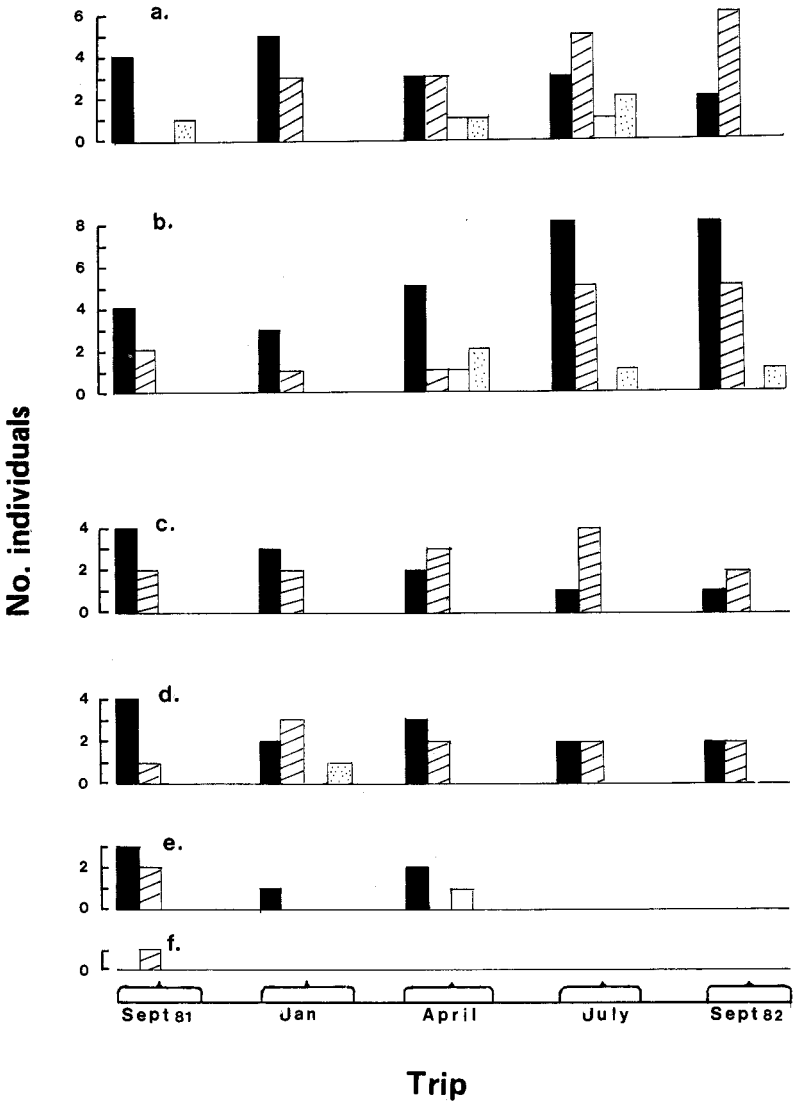

Fig. 4. Histogram of frequency of adult males (black area), adult females (cross-hatched area), juvenile males (white area), and juvenile females (stippled area) captured at the Mitchell Plateau during each trip: (a) DW grid; (b) DV grid; (c) individuals from (a) and (b) that occurred one or more times on both grids; (d) WM grid; (e) CP grid; (f) WV grid.

captured more frequently on sequential trips ($t_3 = 3{\cdot}56$*) than were adult males; juveniles were not significantly different from adults of either sex.

Breeding

The timing of births was estimated using the growth curve for *I. macrourus* from Mackerras and Smith (1960). Young were born between September and April (Fig. 5). Young born in September began to enter the trappable population by January. The greatest number of juveniles were captured in April which indicates that January was the peak period of births.

Breeding was seasonal with all adult females having pouch young in January (7) and none with pouch young in July (20), (Fisher's exact test ***). The proportion of females with pouch young in other trips was: April 44% (9); September 1981 29% (7); September 1982 6% (18) and November 75% (4).

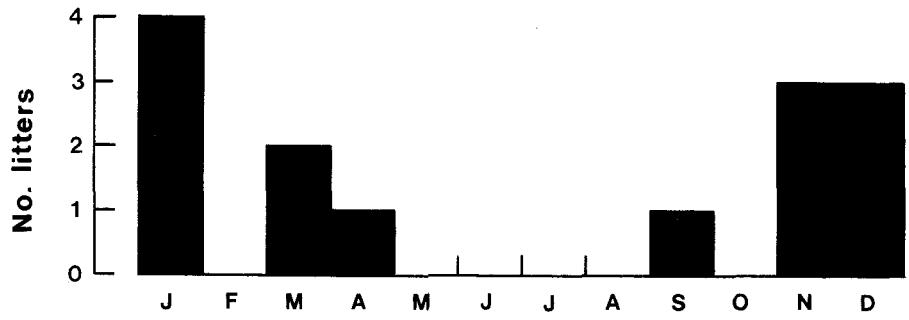

Fig. 5. Frequency of births (dates estimated, see text) in each month in 1982.

During the study 16 litters were known to have been produced by 12 females. Two females had two litters and one female had three litters within the same breeding season (September 1981–April 1982) at an estimated interval of 90 (range 51–108) days. One had a third litter in the next breeding season 162 days after the previous litter. However, as no female was captured on every trip we probably missed some litters; this would result in our underestimating both the litter frequency and the interval between litters.

The sex ratio (♂ : ♀) among neonates was 1 : 0·8 (13) with the litter size being 2·5 ± 1·03 (16). Three females had sequential litters sizes of 4 : 3, 2 : 4 : 1, 2 : 2 : 3.

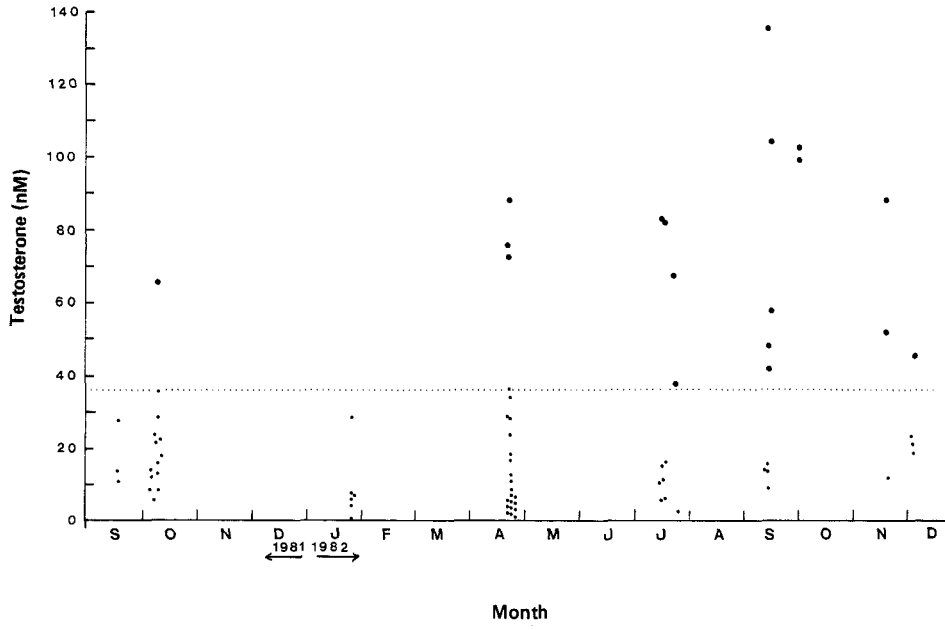

Fig. 6. Levels of testosterone in males at the Mitchell Plateau during each trip. The horizontal broken line is the level of testosterone in juveniles.

We took the maximum level of testosterone recorded in juveniles (36 nM) as an indication of the base level. Testosterone levels in adult males were extremely variable. The proportion of individuals with testosterone levels elevated above the basal level increased through most of 1982 (January 0%, April 17%, July 36%, rising to a peak in September at 64% and falling in November to 43%) (Fig. 6). The proportion in September 1981 was lower (6%) than in September 1982 and could indicate between-year variation in the timing of male sexual behaviour.

Table 2. Significant effects from multiple regressions of physical and blood parameters on area, sex and age for *Isoodon macrourus*

The areas were Lone Dingo area (DV + DW + associated removal sites), Walsh Point (WM + associated removal sites and CP). F values (bold) and degrees of freedom are given when $P<0{\cdot}01$ (**) and $P<0{\cdot}001$ (***)

	Sex/area	Trip/area	Sex	Age	Trip	Area
Weight			***	***	**	**
			52·75	**46·82**	**3·39**	**15·04**
			1,127	1,127	5,127	2,127
Head length			***	***	**	
			36·63	**101·51**	**3·88**	
			1,129	1,129	5,129	
Tail length			***	***	**	
			26·95	**42·66**	**3·52**	
			1,68	1,66	4,66	
Haemogloblin					**	
					3·46	
					5,106	
Haematocrit			***		***	
			12·18		**6·40**	
			1,103		4,103	
Total white blood cells	**				**	
	8·25				**3·49**	
	1,97				4,97	
Granular leucocytes			***		**	
			13·75		**4·09**	
			1,97		4,97	
Lymphocytes			***		**	
			14·37		**4·52**	
			1,97		4,97	
Monocytes						
Total plasma albumin					**	
					4·28	
					5,111	
MCBC					**	
					4·37	
					5,114	
Total free steroids			***			
			26·92			
			1,107			
CBGBd			***			
			19·33			
			1,111			
Albumin bound corticosteroid		**	***			
		2·98	**23·38**			
		7,107	1,107			
Testosterone					**	
					3·69	
					5,62	
Scrotal index				***	***	
				22·48	**5·84**	
				1,77	5,77	
Salmonella prevalence						

Physical and Physiological Parameters

Individuals moved between the adjacent grids DV and DW, confusing the area distinction between populations in these two different habitats. So we initially checked to determine whether the physiological responses on these two grids were similar. Individuals were placed in three groups: those collected on one or more occasions on both DV and DW, and individuals found only on DV or DW. The variables listed in Table 2 were then regressed against the independent variables: sex, age, trip and group. This included all 3-way and lower order interactions. The only significant effect with the groups was the percentage of granular leucocytes. The mean for individuals restricted to DV [41·6±9·65% (22)] was lower than the mean for individuals restricted to DW [53·6±8·70% (19); $t_{46}=4·024$***], or that of individuals which used both DV and DW [52·3±14·20% (18); $t_{46}=3·534$***]. As this was the only difference between DW and DV, the data from these contiguous sites at Lone Dingo have been grouped together for comparison with populations at WM and CP. The WV grid was omitted from the following analysis because only one *I. macrourus* was collected there.

We also examined the appropriateness of pooling all adult females for later analysis by testing for differences between three reproductive groups: females with pouch young, adult females with distended teats but no pouch young, adult females with small teats and no sign of recent reproductive activity. All recorded physical and physiological parameters were regressed on these three female groups and trip. There were no significant associations ($P<0·01$) for the three reproductive groups alone nor were there significant interactions between female group and trip. As a result of this analysis all adult females were grouped together in the following analyses.

All CMR Grids and Removal Sites

For the purpose of the physiological and physical examination, individuals bled and released in the field at removal sites adjacent to CMR grids were incorporated with those from the grids.

There were a number of significant associations between area, sex, age and trip and the physical and physiological parameters recorded in the three populations (Table 2). Only percentage of monocytes and number of *Salmonella* serotypes were not significantly associated with any of the independent variables. The significant associations of all the other parameters are discussed below. Mean values and standard deviations for significant association by trip are given in Appendix I. Weight was the only significant association with area. There was a sex-area interaction for total leucocytes and a trip-area interaction for albumin bound corticosteroid.

Weight (g) (Appendix I)

Adult males [1032±321 (82)] were heavier than adult females [704±143 (56); ($t_{127}=8·84$***)] throughout the year. Juveniles weighed 397±162 (15). Adults were heaviest in September 1981, April and November and lightest in September 1982, January and July.

Head Length (mm) (Appendix I)

Adult males had longer heads [91±7 (83)] than adult females (84±5 (56); $t_{129}=6·873$***]. Mean head length of adults varied significantly with sampling period. Males had shorter heads in January and July than September 1981, April and November, while females had shorter heads in January, July and September 1982 than in September 1981 and November.

Tail Length (mm) (Appendix I)

Adult males had longer tails [171±17 (56)] than adult females [151±16 (23); $t_{66}=5·593$***]. Mean tail lengths of adults varied significantly with sampling period; they were shorter in July and September 1982.

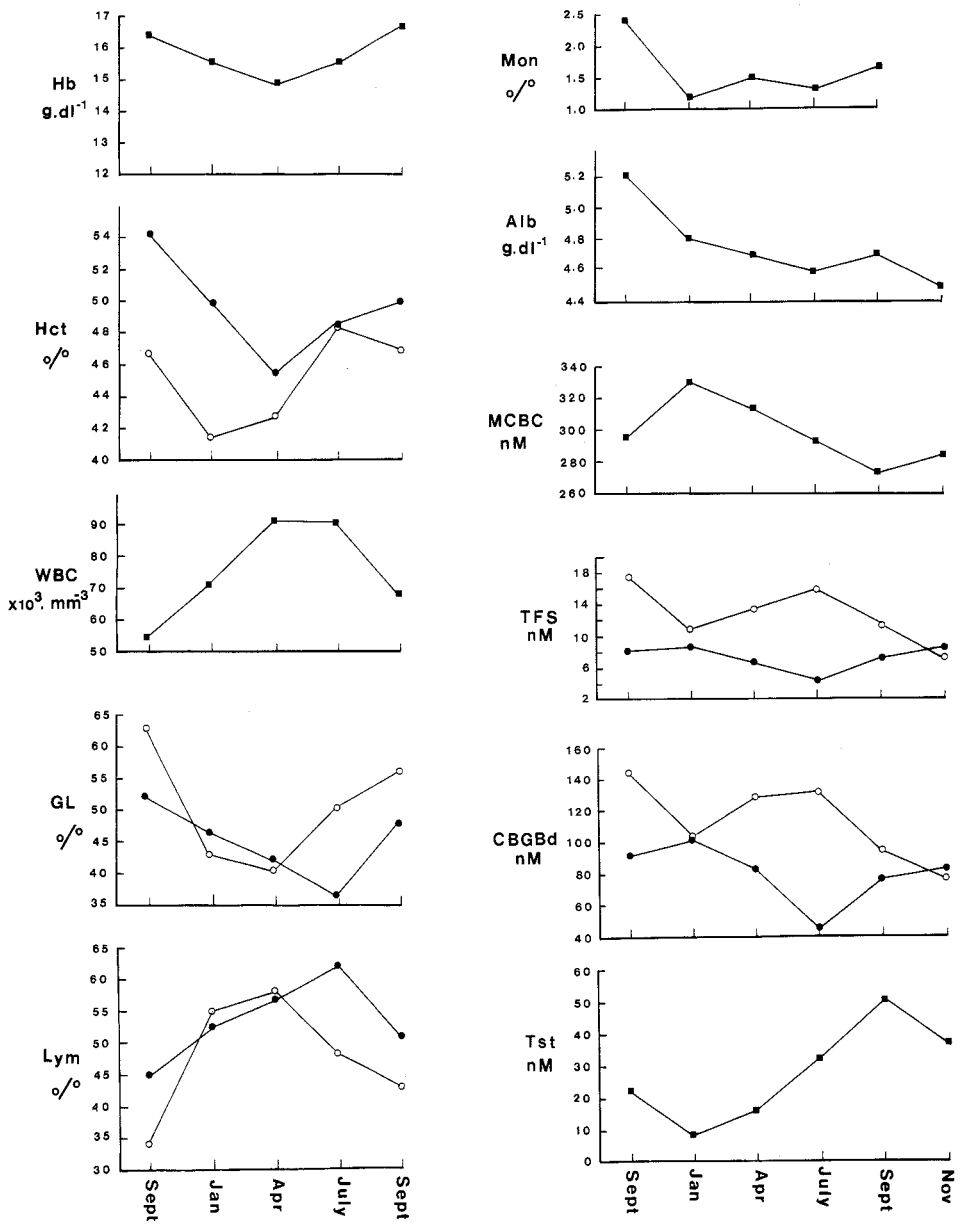

Fig. 7. Seasonal changes in levels of plasma constituents of *Isoodon macrourus* at the Mitchell Plateau. Males and females plotted separately if values for sexes differed significantly. ■, both males and females; ●, males; ○, females.

Haemoglobin Concentration (Hb. g.dl^{-1}) (Fig. 7 and Appendix I)

Haemoglobin varied between trips in both adults and juveniles, but follow-up tests were unable to distinguish between specific trips. Mean Hb was highest during both September trips and lowest in April and July.

Haematocrit (Hct. %) (Fig. 7 and Appendix I)

Haematocrit was higher in males ($t_{103} = 4{\cdot}39$***) than in females, and in both sexes varied significantly throughout the year. Hct was highest in September 1981 and fell

significantly in January and again increased significantly between April and July. Hct was higher in September 1981 than in September 1982.

Total White Blood Cells (WBC. 10^3 mm^{-3}) (Fig. 7 and Appendix I)

The significant sex and area interaction is due to males having lower WBC [7·2 ± 3·65 (45)] than females [8·1 ± 4·36 (38)] at Lone Dingo, but males having higher values [9·8 ± 5·10 (21)] than females (7·5 ± 4·87 (13)] at Walsh Point. Despite this, mean WBC levels for each sex did not differ significantly between areas. WBC increased significantly from September 1981 through April, and declined significantly between July and September 1982, with the latter being significantly higher than in September 1981.

Granular Leucocytes (GL. %) (Fig. 7 and Appendix I)

Females [51 ± 14 (47)] had higher GL than males [44 ± 12 (59), $t_{97} = 3 \cdot 34^{**}$]. GL differed significantly between all combinations of trips except between January and July and between April and July. GL was highest in both Septembers and lowest in April.

Lymphocytes (Lym. %) (Fig. 7 and Appendix I)

GL and Lym sum to approximately 100% when monocyte counts are low, as was the case in this study. Consequently, the pattern for Lym is the reverse of that for GL. Female values [47·4 ± 13·44 (47)] were lower than males [54·7 ± 12·78 (59); $t_{97} = 3 \cdot 323^{**}$]. The mean values for males and females for each trip is also the converse of the pattern presented for granular leucocytes.

Monocytes (Mon. %) (Fig. 7 and Appendix I)

Mon was not significantly associated with any of the independent variables. The overall value was 1·6 ± 1·36 (106).

Total Plasma Albumin (ALB. $g.dl^{-1}$) (Fig. 7 and Appendix I)

ALB varied between trips in both adults and juveniles but follow up tests were unable to distinguish between specific trips. Mean ALB was highest during both September trips and lowest in April. ALB was higher in September 1981 than in July (GT2 test).

Steroid-Protein Interactions

Equilibrium dialysis at 37°C, using H^3 corticosterone, yielded a high affinity binding constant of 5·84 ± 0·46 M^{-1} (5) with no apparent sex difference in the binding. Using a 5% solution of *I. macrourus* albumin, a low affinity binding constant $K_A[P_A]$ for the albumin, corticosterone binding was 2·0 ± 0·06, which represents five replicate determinations using albumin isolated from a plasma pool.

Maximum Corticosteroid Binding Capacity (MCBC. nM) (Fig. 7 and Appendix I)

Mean MCBC values between all combinations of trips were significantly different from each other. They rose from moderate levels in September 1981 to a peak in January and fell steadily thereafter to November.

Total Free Steroids (TFS. nM) (Fig. 7 and Appendix I)

TFS were higher in females [13·1 ± 10·52 (61)] than in males [6·8 ± 5·25 (80); $t_{107} = 4 \cdot 95^{***}$], but there were no area or seasonal changes.

Corticosteroid Binding Capacity (CBGBd. nM) (Fig. 7 and Appendix I)

CBGBd was higher in females [116·0 ± 66·09 (61)] than in males [76·0 ± 52·97 (80); $t_{111} = 4 \cdot 181^{***}$], but there were no area or seasonal changes.

Albumin Bound Corticosteroid (ABC. nM) (Fig. 8 and Appendix I)

ABC showed significant interaction between trip and area. It was higher from animals at Lone Dingo than from those at Walsh Point in all trips except in April and September.

Overall, ABC was higher in females [22·6 ± 18·5 (61)] than in males [12·3 ± 9·9 (80); $t_{107} = 4{\cdot}53^{***}$].

Testosterone (Tst. nM) (Fig. 7 and Appendix I)

Tst varied significantly between trips; follow up tests showed that Tst was higher in September 1982 than in January or April (GT2 test).

Scrotal Index (mm^2) (Appendix I)

The adult scrotal index varied significantly between all trips. It was highest in September 1981 and fell steadily to a low in July, and increased again in September 1982 and November, but did not reach the peak mean values of September 1981.

Salmonella

Number of *Salmonella* serotypes per swab were not significantly associated with any of the independent variables. Their overall value was 0·9 ± 0·27 (142) serotypes per swab.

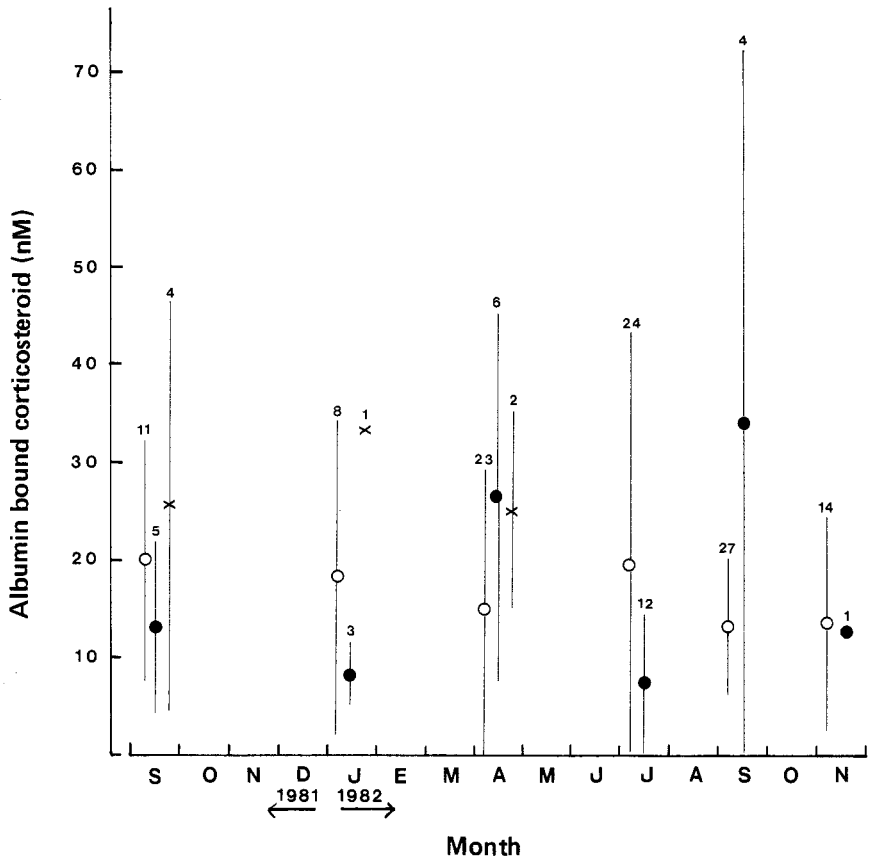

Fig. 8. Mean ± SD of albumin bound corticosteroid (nM) for *Isoodon macrourus* at the Lone Dingo (●), Walsh Point; (○) and the CP (×) sites for the six trips. Sample size indicated.

Discussion

Breeding and Sexual Maturity

We built up a picture of sexual maturity from a combination of the condition of the pouch, teats and reproductive tract; and from scrotal size, evidence of spermiogenesis and testosterone levels. In both males and females this permitted allocation of individuals to

classes of sexual maturity. In this we are supported by Gemmell (1987) who concluded that age and weight were poor predictors of sexual maturity in both sexes of *I. macrourus*, but that in females an increase in teat size and a clean pouch are good indicators of ovulation (and correlate with a rise in the concentration of plasma progesterone).

Our field studies indicated that males were sexually mature when testosterone concentration was greater than 6·0 nM (Fig. 2). This agrees closely with Gemmell's (1987) finding from captive populations of *I. macrourus*, that scrotal skin pigmentation occurred at an age of *c.* 180 days after the initial rise in plasma testosterone above 6·9 nM (2 ng Ml^{-1}). However, Gemmell did not find sperm in the male reproductive tract for a further 20 days, when he found that they were only functional (i.e. sired their first litter) at about 12·5 months. Hence, while our criteria for sexual maturity is probably accurate for females; for males it may include some immature individuals.

Female *I. macrourus* at the Mitchell Plateau gave birth to young between September and April, which is similar to the seasonal pattern for this species at Kapalga, N.T. (Friend 1989).

The seasonal change in habitat use by adult *I. macrourus* at the Mitchell Plateau, indicated by the reduced proportion of males at DW during the dry season, does not seem to have resulted from, or to be caused by, any change in the condition of individuals. This is supported by the lack of statistical interaction between sex and trip, and sex and area, for the physiological and physical variables measured. Thus, reduction in number of males caught is more likely a function of their behaviour than of mortality, because we could find no physiological or morphological evidence that males were more stressed or were in poorer clinical condition than females. If anything, the contrary was the case. For example, males had lower levels of free corticosteroids and granular leucocytes, both of which have been used as indicators of reduced stress (see Dantzer and Mormede 1983; Bradley *et al.* 1980; Kitchener *et al.* 1987—but also see Kemper *et al.* 1987). In addition, males also had higher haematocrits and similar levels of haemoglobin, total white blood cells and total plasma protein. We consider the reduction in males at DW during the dry season reflects their decreased mobility at that time (Table 1), since there is a decrease in males using both grids (Fig. 4*c*), given that they are equally as trappable as females. Changes in movement have been recorded elsewhere for *I. macrourus*, especially in females during the breeding season (Stoddart and Braithwaite 1979; Friend 1989).

The mean litter size (2·5) of *I. macrourus* at the Mitchell Plateau was lower than those reported for other populations (2·6 to 3·4: Gordon 1971, 1974; Hall 1983; Friend 1989; Gemmell 1982). Litter size can be influenced by many factors such as the nutritional status of mothers, environmental conditions (Sadlier 1968) and genetic factors. We have no indication of nutritional or physiological stress in females, and the weight of females was comparable to that found in those studies with greater litter size. We could find no evidence that females with pouch young, or females that had recently bred, were in poorer condition than those which had not recently bred, as may be expected under conditions of nutritional stress. Nor was there evidence of a reduction in litter size during the breeding season as was noticed by Friend (1989).

Nonetheless, the population as a whole showed a pronounced change in body condition over the wet season (September 1981 to April), as evidenced by a decline in weight and haematocrit and a concomitant increase in WBC. We did find, however, indications that the season in 1982 may have been less favourable than in the previous year when the wet season started earlier. A number of physiological variables differed substantially between the two Septembers (weight, Hct, WBC, GL, MCBC and Tst). The short wet season at the start of the study and the lack of early rain in October 1982 (Bradley *et al.* 1987) could have contributed to the apparent lowering of condition of the animals towards the end of the study.

The significant association between the physical parameters and trip is due to seasonal breeding, when data from juveniles and recently matured adults collected only on certain trips is included.

Differential lymphocytes and neutrophil counts are widely used as indicators of clinical condition and may reflect stress and immunological challenge from infections (Ham and

Cormack 1979). However, they have been shown also to be associated with reproductive conditon (Dobrowolska and Gromadzka 1978), ontogenesis (Rogatko 1970), season, year and sexual activity (Kostelecka-Myrcha 1967; Rogatko 1970) and population density (Dieterich and Feist 1980). The fall in the ratio of lymphocytes to granular leucocytes in *I. macrourus* over the wet season is indicative also of changing condition in the animals. In *I. macrourus* both free cortisol and the sex hormones may act synergistically to cause a lymphopenia and neutrophilia. Another effect of glucocorticoids is to cause a mobilisation of neutrophils from bone marrow reserves (Athens *et al.* 1961; Dale *et al.* 1975) which results in a characteristic neutrophilia and thus contributes to the reduction in the L : N ratio.

Some of the haematological changes observed in this study may be largely explained in terms of pituitary-adrenal and pituitary-gonadal activation. For example, in males there was a marked reduction in lymphocyte number in the months prior to the onset of breeding. During that period there was an increase in the scrotal index and plasma testosterone concentation, reflecting preparation of the reproductive organs for breeding. Between September 1981 and April, when a significant decline in both plasma testosterone concentration and scrotal index occurred, the lymphocyte number increased.

Females had higher plasma free corticosterone concentrations than males through the year and this may have caused the higher lymphocyte counts in males, as glucocorticoid hormones are immunosuppressive (Dougherty and White 1944; Dougherty 1952; Cohen 1971; Claman 1972); however, under some circumstances sex steroid hormones such as oestradiol and testosterone may also be immunosuppressive (Wyle and Kent 1977).

The high haemoglobin and haematocrit values found in both male and female *I. macrourus* during September at the commencement of the breeding season, probably reflects an improvement in the nutritional status of individuals in the preceding months. Decline in haemoglobin concentration and haematocrit has been linked to the development of an iron deficiency anaemia in Caribou during lactation (McEwan 1968). However, such an anaemia is unlikely to explain the decline of these blood parameters in *I. macrourus* after September, because no difference was detected between lactating and non-lactating females.

I. macrourus, like the other species so far reported in detail from our Mitchell Plateau study, [*Melomys* sp. cf. *burtoni* (Kemper *et al.* 1987), *Z. argurus* (Bradley *et al.* 1988) and *D. hallucatus* (Schmitt *et al.* 1989)], showed marked seasonal changes in body condition, as indicated by changes in measured physical and physiological parameters. However, *I. macrourus* is different from these other species at the Mitchell Plateau by not showing a concomitant increase in level of stress during the period of loss of body condition. Stress was clearly indicated in the other species by increased levels of free steroids, or increase in *Salmonella* infestations or ectoparasite burdens. *I. macrourus* also differed from other species by not showing marked differences between sites in physiological parameters.

These data are consistent with the view that *I. macrourus* appears less affected by the strong climatic seasonality or environmental patchiness than the other species so far reported on from the Michell Plateau. This may be related to the wider range of habitat utilised by *I. macrourus* (also reflected by their greater movement, or transience) when compared to *Melomys* sp. cf. *burtoni* and *Z. argurus*. Also, of this group of mammals, it is the only true omnivore (Gordon 1983). Its ability to be more opportunistic in selection of habitat and food can be expected to advantage it in ameliorating the effects of seasonal and site differences in habitat (over the rodents) and food (over the rodents and the marsupial carnivore *D. hallucatus*). Further, *I. macrourus* showed none of the breeding related stress that affects *D. hallucatus* and some other dasyurid marsupials (see Schmitt *et al.* 1989).

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Appendix I. Mean ± SD and sample size (in brackets) of the physical and physiological parameters that were significantly ($P<0.01$) associated with trip (see Table 2)

Where sex or age were also associated, the values are separated

Parameter	Sex/ age	September 1981	January	April	July	September 1982	November
Body weight (g)	A ♀	(5) 877·0 ± 165·5	(7) 675·0 ± 109·2	(8) 798·1 ± 78·7	(15) 642·7 ± 125·9	(17) 651·8 ± 109·7	(4) 801·3 ± 194·1
	A ♂	(15) 1209·7 ± 381·1	(11) 918·6 ± 326·9	(14) 1063·6 ± 319·9	(19) 969·5 ± 321·0	(14) 911·4 ± 215·5	(9) 1148·9 ± 229·3
	J %	(1) 635·0	(1) 92·0	(8) 358·8 ± 136·0	(4) 487·5 ± 119·3	(1) 400·0	NA
Head length (mm)	A ♀	(5) 86·0 ± 3·9	(7) 80·8 ± 4·6	(8) 86·7 ± 3·9	(15) 81·9 ± 5·2	(17) 84·3 ± 4·1	(4) 87·3 ± 7·2
	A ♂	(14) 95·0 ± 7·8	(10) 87·8 ± 8·8	(15) 91·4 ± 6·6	(20) 88·7 ± 6·7	(15) 89·4 ± 5·8	(9) 93·1 ± 6·8
	J %	(1) 79·1	(1) 49·2	(9) 69·2 ± 6·8	(4) 71·8 ± 3·2	(1) 73·4	NA
Tail-vent length (mm)	A ♀	(2) 160·5 ± 27·6	(2) 141·5 ± 23·3	(4) 164·0 ± 12·4	(5) 142·8 ± 14·0	(10) 150·7 ± 14·1	NA
	A ♂	(11) 184·4 ± 13·2	(8) 160·0 ± 14·9	(12) 175·1 ± 15·5	(14) 166·4 ± 17·9	(11) 168·3 ± 17·7	NA
	J	NA	(1) 93·0	(7) 124·0 ± 13·3	(1) 125·0	(1) 130·0	NA
Haemoglobin ($g.dl^{-1}$)	All	(21) 16·5 ± 2·2	(17) 15·6 ± 2·1	(27) 14·9 ± 1·8	(39) 15·5 ± 1·5	(26) 16·6 ± 2·4	(1) 12·6
Haematocrit (%)	A & J ♀	(5) 46·8 ± 5·0	(7) 41·3 ± 4·0	(12) 42·8 ± 5·6	(14) 48·4 ± 4·4	(15) 46·9 ± 3·2	NA
	A & J ♂	(13) 54·2 ± 4·3	(8) 49·8 ± 6·0	(16) 45·4 ± 5·3	(20) 48·4 ± 5·4	(14) 49·9 ± 4·6	NA
WBC ($10^3/mm^3$)	All	(19) 54·5 ± 31·5	(16) 70·6 ± 42·2	(30) 90·4 ± 43·7	(39) 90·6 ± 45·1	(19) 67·4 ± 35·5	NA

		(6)	(3)	(9)	(15)	(14)	
Granular leucocytes (%)	A & J ♀	63·8 ± 17·9	43·0 ± 4·4	40·4 ± 11·8	50·3 ± 8·5	55·5 ± 13·4	NA
		(14)	(3)	(15)	(19)	(8)	
	A & J ♂	52·3 ± 9·9	46·3 ± 4·0	42·0 ± 9·5	36·8 ± 13·5	48·0 ± 12·2	NA
		(6)	(3)	(9)	(15)	(14)	
Lymphocytes (%)	A & J ♀	34·2 ± 16·9	55·7 ± 4·0	57·9 ± 11·6	48·3 ± 8·0	43·4 ± 13·6	NA
		(14)	(3)	(15)	(19)	(8)	
	A & J ♂	45·4 ± 10·0	52·7 ± 4·0	56·7 ± 9·4	61·9 ± 13·7	50·8 ± 12·6	NA
		(20)	(6)	(24)	(34)	(22)	
Monocytes (%)	All	2·4 ± 1·6	1·2 ± 0·4	1·5 ± 1·3	1·3 ± 0·9	1·6 ± 1·7	NA
		(20)	(12)	(31)	(36)	(31)	(11)
Total plasma albumins ($g.dl^{-1}$)	All	5·2 ± 0·8	4·8 ± 0·9	4·7 ± 0·5	4·6 ± 0·5	4·7 ± 0·5	4·5 ± 0·5
		(20)	(12)	(31)	(36)	(31)	(11)
MCBC (nM)	All	296·8 ± 70·9	330·7 ± 61·3	313·7 ± 48·0	292·5 ± 35·2	272·1 ± 21·3	283·8 ± 33·6
		(6)	(6)	(13)	(15)	(17)	(4)
Total free steroids (nM)	A & J ♀	17·3 ± 9·5	10·9 ± 10·5	13·4 ± 9·9	15·6 ± 11·6	11·3 ± 11·3	7·3 ± 6·8
		(14)	(6)	(18)	(21)	(14)	(7)
	A & J ♂	8·0 ± 4·8	8·7 ± 7·1	7·3 ± 5·8	4·1 ± 5·0	7·2 ± 3·6	8·4 ± 5·4
		(6)	(6)	(13)	(15)	(17)	(4)
CBGBd (nM)	A & J ♀	144·4 ± 62·9	105·5 ± 69·5	129·0 ± 76·6	132·3 ± 72·2	94·4 ± 49·0	78·0 ± 60·7
		(14)	(6)	(18)	(21)	(14)	(7)
	A & J ♂	92·4 ± 67·4	103·6 ± 65·8	84·5 ± 56·6	46·5 ± 41·7	78·1 ± 34·0	82·9 ± 37·4
		(6)	(6)	(13)	(15)	(17)	(4)
Albumin bound corticosteroids (nM)	A & J ♀	30·2 ± 16·6	17·4 ± 16·3	23·9 ± 18·2	27·1 ± 20·5	19·3 ± 19·7	11·7 ± 10·3
		(14)	(6)	(18)	(21)	(14)	(7)
	A & J ♂	15·0 ± 9·2	16·8 ± 14·1	13·1 ± 10·6	7·1 ± 9·5	13·0 ± 6·6	14·6 ± 9·8
		(13)	(6)	(18)	(20)	(14)	(7)
Testosterone (nM)	All	22·2 ± 15·5	8·8 ± 10·3	15·5 ± 18·5	32·5 ± 29·7	50·5 ± 44·3	37·5 ± 26·8
		(15)	(10)	(15)	(20)	(15)	(9)
Scrotal index (mm^2)	A ♂	728·8 ± 110·0	657·7 ± 121·5	557·7 ± 171·8	518·6 ± 122·6	647·9 ± 8·5	673·3 ± 69·9
	J ♂	NA	NA	(3)	(1)		(4)
				169·7 ± 90·9	520·0	NA	257·3 ± 190·3

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