J. Zool., Lond. (1987) **212,** 533-562

The demography and physiology of *Melomys* sp. (Rodentia: Muridae) in the Mitchell Plateau area, Kimberley, Western Australia

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(*Accepted 23 October 1986*)

(With 4 figures in the text)

Populations of a mosaic-tailed rat (*Melomys* sp.) were studied for one year in vine-thicket and mangrove habitats in the Mitchell Plateau area of the tropical Kimberley district of Western Australia. Demographic and physiological (haematological values, androgens, corticosteroids and their binding proteins) parameters were measured together with parasite prevalence and electrophoretic protein variation. Seasonal variation occurred in most parameters measured. Higher values were found in the vine-thicket for number of sympatric mammal species, growth rate of immatures and androgens. Higher values were found in the mangroves for population density, survival, size at sexual maturity, body weight, home range overlap, albumins, total and free-corticosteroids and parasite prevalence. The phenotypic frequencies of two protein polymorphisms (albumin and 6-phosphogluconate dehydrogenase) differed between sites, while a third (adenosine deaminase) showed no between-site differences; these suggest differential selection between the adjacent habitats which are separated by 10 km. The overall physiological response of *Melomys* was more entrained to seasonal variation in the vine-thicket than in the mangroves, which is in accord with the relative variation in the vegetation and temperature in the two areas. It is hypothesized that the greater population density in the mangroves results in behavioural feedback through the hypothalamo-pituitary-adrenal axis. This results in increased stress (higher free-corticosteroid levels) which slows the growth rate and the onset of sexual maturity. The study is the first to indicate that such a mechanism, commonly proposed for temperate small mammals, may operate in tropical areas.

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0022-5460/87/007533+30 $03·00

Introduction

Conspecific populations in closely adjacent areas can show marked temporal and spatial differences in many aspects of their biology, including gene frequency, behaviour, physiology, parasitology and demography (Barnett, 1977; Lee, Bradley & Braithwaite, 1977; Barnett, How & Humphreys, 1979*a*, *b*, 1982; Bradley, McDonald & Lee, 1980; Berry, 1981; Presidente, Barnett, How & Humphreys, 1982; review, Humphreys, Bradley, How & Barnett, 1984*b*). The demography and physiology of small mammals in temperate and boreal regions of the northern hemisphere have been studied extensively, particularly in the context of the regulation of population fluctuations potentially mediated by endocrine feedback from social interactions (Christian, 1950; Wynne-Edwards, 1962; Lidicker, 1965, 1976; Chitty, 1967; Krebs & Myers, 1974). These approaches have not been used to examine the characteristics of tropical small mammals.

The background to this study has been discussed (Bradley *et al.*, 1987). It was our purpose to examine aspects of the demography, physiology, parasitology and genetics of the tropical mosaic-tailed rat *Melomys* sp. cf. *burtoni* in different habitats throughout the year, and to compare our findings with those from temperate regions. The importance of an integrated, broad-based approach in studying natural populations has been stressed by Lidicker (1978) who stated 'one cannot ignore an organism's physiology and expect to fully understand its population dynamics'. We are preparing further papers which will present similar analyses on the murid rodent *Zyzomys argurus* and the marsupials *Dasyurus hallucatus* and *Isoodon macrourus* from the same study area.

The natural history of *Melomys* was reviewed by Watts & Aslin (1981) who considered that its biology was among the poorest known of any genera of Australian rodents. Several populations of *Melomys* have been studied (Wood, 1971; Begg, Walsh, Woerle & King, 1983; Kerle &

Burgman, 1984) and aspects of its taxonomy and evolution discussed (Lidicker, 1973; Baverstock *et al.*, 1977, 1978, 1980). The genus is characterized by a long gestation period (Watts & Aslin, 1981), small litter size (less than three: Gard, 1935; McDougall, 1946; Wood, 1971), rapid development and prolonged parental care. *Melomys* share with the other Old Endemics (*sensu* Watts & Aslin, 1981) their low reproductive potential, four teats in females and the habit of the young clinging to the mother's teats before being deposited in a nest.

After electrophoretic, karyotypic (P. Baverstock, pers. comm.) and morphological analysis, there remains some doubt as to the status of *Melomys* from the Mitchell Plateau area. As the taxonomy of *Melomys* is in need of review, we are not prepared at this stage to make taxonomic judgements and refer to the Mitchell Plateau form as *Melomys* sp. cf. *burtoni*.

Study area

The study was conducted on and adjacent to the Mitchell Plateau in the remote north-west of the Kimberley District of Western Australia (*c.*14° S, 125° E); throughout we use 'Mitchell Plateau' in reference to the geographical area rather than the geomorphological feature. The climate is typical of the wet-dry tropics with monsoonal rains in summer (November to March) and dry winters. Full descriptions of the climate, vegetation, community composition and general methods have been presented elsewhere (How *et al.*, 1983; Humphreys *et al.*, 1984*a*; Bradley *et al.*, 1987) and a résumé only is given here. *Melomys* were caught in appreciable numbers on only three of the eight grids that we trapped: a deciduous vine-thicket on the plateau at Lone Dingo (DV); a vegetation mosaic (WM) fringing Port Warrender where *Melomys* were trapped solely within the tidally inundated, evergreen mangrove section of the grid; and a deciduous vine-thicket between basalt cliffs and the beach near Walsh Point (WV). WM is situated 2 km south of WV and 10 km north-east of DV.

Six other species of mammal were trapped on the grids where *Melomys* occurred. These are *Isoodon macrourus* (Paramelidae), *Dasyurus hallucatus* (Dasyuridae), *Zyzomys argurus* and *Z. woodwardi* (Muridae) which were found on all the grids. The other three species were more restricted, namely *Mesembriomys macrurus* (Muridae: WM and DV), *Wyulda squamicaudata* (Phalangeridae: WV) and *Conilurus penicillatus* (Muridae: WM but only from the area outside the mangroves).

Methods

Field methods

We had 8 mark-release-recapture grids each containing 100 small mammal traps (Elliott Scientific Equipment, Upwey, Victoria) spaced 10 m apart (10 × 10). Each grid was matched as closely as possible by a site from which animals were removed for post-mortem examination; these sites were located outside the known range of movement by *Melomys*.

Each grid was trapped for 5 days on each of 6 roughly evenly-spaced trips between September 1981 and November 1982 (see Bradley *et al.*, 1987). WV was not trapped in November 1982 and DV, WM and WV were trapped for only 3 days in January 1982 due to a cyclone. The traps were checked each morning between 05:00 h and 11:00 h and the several field measurements made (weight, the lengths of the head, pes and tail). Reproductive status was assessed in females by condition of the vagina (perforate, imperforate, vaginal plug, blood), mammae (lactating, distended, regressed, barely visible) and rarely by palpating for

embryos. In males, reproductive condition was judged by position of the testes (scrotal, abdominal/inguinal) and condition of the epididymal sacs (not distended, distended, full). General condition and ectoparasite burdens were noted before release. On the first capture of an individual it was marked by toe-clipping.

On the first capture of an individual during any field trip it was bled from the orbital sinus (Riley, 1960) within 2 min of disturbing the animal in the trap. One micro-haematocrit tube of blood was retained for the determination of haematocrit and a blood smear was made and 10 μl of blood was added to 100 μl of Turk's fluid to enable white blood cell counting. The remaining blood was transported to the field laboratory in heparinized (potassium heparinate) 1·5 ml polypropylene centrifuge tubes.

In the field laboratory, haematocrit was read after centrifugation at 1200 rpm for 3 min in a microhaematocrit centrifuge (Clements Instrument Co., Victoria) and the haemoglobin concentration determined from a drop of the bulk blood using a haemoglobinometer (American Optical Co., USA). White blood cells were resuspended by repeated inversion and counted, together with microfilariae, in 5 fields of a counting chamber with a Neubauer ruling. The remainder of the blood was centrifuged using a Beckman B centrifuge (Beckman Instrument Co., USA) and the plasma removed. On the first 2 trips, the red blood cells were diluted with polyethylene glycol and kept at -20°C. After the second trip, the packed red blood cells were haemolysed with an equal quantity of water containing 10 mmol dithiothreitol and the haemolysate and plasma stored in liquid nitrogen.

Specimens were trapped at the removal sites using Elliott traps and returned to the field laboratory. There they were bled from the orbital sinus or by cardiac puncture and killed with an overdose of sodium pentobarbitone (Nembutal: Abbott Laboratories), usually on the day of capture. The animals were measured after death and reproductive condition assessed from gross dissection. Reproductive organs were removed, fixed in alcoholic Bouin's and stored in 70% alcohol. A portion of liver, one kidney, the heart, and sometimes muscle, were removed and stored in liquid nitrogen for later electrophoretic analysis.

Laboratory methods

After fixation, reproductive organs were weighed to the nearest milligram. Routine histological methods (paraffin embedding, 7 μm sections, haematoxylin/eosin staining) were used to prepare testes and male accessory glands for microscopic examination.

Plasma albumin and total, bound and free corticosteroid and androgen concentrations were determined after the methods described elsewhere (Bradley, McDonald & Lee, 1976, 1980; Lee *et al.*, 1977). Genetically determined protein variation in red blood cells and plasma was investigated using 'cellogel' electrophoresis (Meera Khan *et al.*, 1982). Proteins investigated were acid phosphatase, adenylate deaminase, adenylate kinase, albumin, alkaline phosphatase, esterase, fructose-1, 6 diphosphatase, glutamate-oxaloacetate transaminase, lactate dehydrogenase, malate dehydrogenase, phospholglucomutase and 6-phosphogluconate dehydrogenase. Electrophoresis of other tissues was used to examine the specific status of the populations.

Tooth wear

Cleaned skulls of animals taken from removal sites and accidental deaths from grids were allocated to 5 wear classes based on the amount of dentine exposed on the upper molar teeth (**Appendix 1**). Tooth impressions from animals captured on the grids were made in dental wax and compared with the tooth impression made from the skulls and scored appropriately.

Statistical

The data from *Melomys* were analysed to determine differences in parameters between the sexes, areas and through time. The parameters derived from blood samples were examined by regression analysis, after transformation of the data where necessary to normalize the distribution of the data, to determine their associations with time of bleeding and with body weight, as both may covary with physiological parameters

TABLE I

Regression statistics used to correct various parameters for covariance with body weight (g) of ***Melomys*** *sp. The units for testosterone and total plasma corticosteroid (TPCS) are nmol/l*

Sex	Regression equation	*P*	Corrected to mean body weight (g)
Male	log (TPCS) = 0·44 × log (wt.) + 2·302	0·013	80·9
Male	log (testosterone) = 1·059 × log (wt.) − 0·875	0·0004	83·0
Female	haematocrit (%) = 46·69 − 0·045 × wt.	0·0094	72·4

(Kirkpatrick *et al.*, 1976, 1977; Prothero, 1980). The time of day when blood samples were taken did not correlate with any of the blood constituents measured but some were correlated with body weight. In the latter case, individual data were corrected to mean body weight; other than those included in Table I, no variable showed significant association with body weight or with the time of day the blood sample was taken. The data were tested for homogeneity using Bartlett's test and transformed where necessary before applying a 2-way analysis of variance for unequal sample sizes with factors such as areas and field trip number. The Student-Newman-Keuls procedure for unplanned comparisons was used as the follow-up test to determine where significant differences occurred. Regression lines were compared using analysis of covariance and the a posteriori GT2 procedure was used as a follow-up test. One-way ANOVA by ranks and Friedman's non-parametric 2-way ANOVA were used in combination with the multiple comparison procedure of Dunn. All parametric procedures followed the algorithms in Sokal & Rohlf (1981) and non-parametric procedures those in Daniel (1978). Discriminant function analysis was based on Davies (1971) and the statistical tests based on Hotelling's *t*-squared (Sneath & Sokal, 1973).

Size at sexual maturity

The mean size of animals reaching sexual maturity is a primary character in the calculation of demographic statistics and for temporal comparison between areas and species. The entire sample cannot be used to estimate the size at which 50% of the population become sexually mature because the numbers in each age (size) class change with age (size) in a population with a stationary age distribution.

Criteria for sexual maturity

Data from both the removal and the mark-release-recapture grids were used to generate the database used to determine the mean size at sexual maturity, so that individuals of unknown status could be assigned objectively as mature or immature. Data from animals released in the field were included in the data set only if unequivocal observations were made on the parameters outlined in Table II. Animals from the

TABLE II

Criteria used to assign ***Melomys*** *to reproductive and non-reproductive classes using data from both the removal sites and the mark-release-recapture grids*

Category	Grid animals	'Removal' specimens
Mature female	Teats used, neonates present	Visible embryos, placental scars, teats used
Immature female	Teats not used	No visible embryos or scars, teats tiny
Mature male	Epididymal sac distended	Spermiogenic, accessories active
Immature male	Epididymal sac not distended	Aspermic, accessories inactive

removal sites were assigned to reproductive categories following dissection and histological examination of various tissues (Table II). The data derived from both internal and external observations were consistent.

Procedure

Using the criteria of sexual maturity described above, we ranked the individuals of each population in order of the parameter considered (head length or body weight) and distinguished them by their state of sexual maturity (mature or immature). Each population was analysed separately. A subset of these data was taken to include all individuals within the range in size of the overlap zone between mature and immature individuals, plus the 3 individuals above and below this range. Unlike the set, this subset was approximately normally distributed.

The numbers of immature (I) and mature (M) individuals were expressed as the cumulative probability of maturity (after angular transformation) yielding a straight line regression which accounted for most of the variance in the data. However, as the number of I and M individuals in the subset may not be equal, a weighted probability was applied to individuals in each of the I and M classes. This was derived so that each class accounted for 50% of the probability of the subset. Hence, if there are 25I and 16M individuals, the weighted probability (Pw) for each I is 0·5/25, and for each M is 0·5/16. The cumulative Pw is derived by summing the appropriate Pw in sequence through the ranked data and then applying the angular transformation; in practice it made only a marginal difference whether the weighted or unweighted probabilities were used.

Regressions for each sex and area were compared by analysis of variance on the slopes and intercepts. These data had non-parallel lines which invalidated the comparison of intercepts in which we were interested; the slope of the line is not of immediate interest, being a measure of the range in size at which the animals reach sexual maturity. All the regression lines gave a close fit to the data, so we calculated the adjusted Y values for the 45° level (50% probability of maturity) using the regression line for that set of data. The adjusted mean Y values were then compared using the GT2 unplanned multiple comparison test for unequal sample sizes (Sokal & Rohlf, 1981). This is essentially the same procedure used by Li (1964) for comparison of adjusted means of regressions with different regression coefficients.

Results

Numbers and density

On no grid did the number of individuals known to be alive (KTBA), or any subset, change significantly over the trapping programme (Table III). The mean numbers of individuals KTBA at WM and DV were not separable statistically but both sites had more individuals KTBA than

TABLE III

Known to be alive estimates of the population of **Melomys** *on three trapping grids at Mitchell Plateau from September 1981 to September 1982. m = male, f = female, i = immature, a = adult. No column shows, by* χ^2, *significant seasonal change in population known to be alive*

	WM					DV					WV				
Trapping time	ma	fa	mi	fi	$\sum$	ma	fa	mi	fi	$\sum$	ma	fa	mi	fi	$\sum$
September 1981	10	7	3	5	25	14	11	1	3	29	6	3	1	0	10
January 1982	9	6	2	4	21	11	10	2	4	27	6	1	0	1	8
April 1982	8	10	10	5	33	5	7	7	2	21	5	4	0	1	10
July 1982	12	10	7	5	34	18	6	0	3	27	7	5	1	2	15
September 1982	10	10	0	1	21	14	8	0	0	22	4	3	1	2	10

TABLE IV

Summary of demographic statistics for **Melomys** *on three trapping grids at Mitchell Plateau. The mean known to be alive (KTBA) population (±coefficient of variation) is given for the first five field trips. As* **Melomys** *occurred on the whole of DV and WV (2·25 ha) but only in the mangroves (0·68 ha) at WM, the density is given only for the mangrove part of WM*

Parameter	Grid					
	WM		DV		WV	
Mean population size:						
adult m	9·8	(15)	12·4	(39)	5·6	(20)
adult f	8·6	(22)	8·4	(25)	3·2	(46)
all adults	18·4	(15)	20·8	(25)	8·8	(23)
immature m	4·4	(92)	2·0	(146)	0·6	(91)
immature f	4·0	(43)	2·4	(63)	1·2	(70)
all immatures	8·4	(64)	4·4	(76)	1·8	(61)
mean population	26·8	(24)	25·2	(14)	10·6	(25)
Mean population density (ha^{-1})	39·7		11·2		4·8	
Mean survival between trips (% ±c.v.):						
adult m	62	(34)	43	(40)	61	(49)
adult f	73	(8)	41	(73)	49	(95)
immature m	59	(23)	45	(96)	50	(141)
immature f	47	(72)	25	(128)	17	(169)
Annual survival (%):						
m	23		3		14	
f	25		0		0	

WV (K-W test followed by Dunn's multiple comparison test using $\alpha = 0{\cdot}05$: $\chi^2_2 = 9{\cdot}533$, $P < 0{\cdot}009$). Analysing the sexes separately yielded the same result for adults (and for the total population) but no difference between sites in the numbers of immature individuals. As *Melomys* inhabited only the mangrove at WM (0·68 ha), but the whole (2·25 ha) of WV and DV, the effective population density at WM was greater than that at DV by a factor of 3·3. In calculating population density at WM, only that part of the grid inhabited by *Melomys* (i.e. the mangrove) was included. The population density (Table IV) differed between grids, from about 40 ha^{-1} in the mangroves at WM to about 5 ha^{-1} in the vine-thicket at WV, where *Melomys* made only patchy use of the habitat.

Breeding

Mature females, either pregnant or lactating, were found on the grids throughout the year (Fig. 1). Seasonality in breeding could be demonstrated statistically only after pooling the data from all three grids ($\chi^2_4 = 16{\cdot}06$, $P < 0{\cdot}01$) and was lowest in July (mid-winter). This pattern was confirmed by the data from dissected animals from the removal grids (Fig. 1). The proportion of nulliparous individuals in the populations did not change significantly over the year, averaging 26%.

Parous females examined post mortem showed a mean number of visible embryos of $2{\cdot}4 \pm 0{\cdot}05$ (range 2-3, $n = 25$) with $4{\cdot}3 \pm 2{\cdot}70$ (range 1-12, $n = 29$) placental scars. The mean number of embryos plus placental scars when both were present was $4{\cdot}65 \pm 2{\cdot}53$ (range 1-12, $n = 40$). Females thus have at least 1·9 litters on average. The real number will be greater as scars are difficult to see in late pregnancy and may be lost after parturition, and some individuals would probably have bred again if they had not been killed. No difference between sites could be detected in any of these measures ($P > 0{\cdot}1$; Kruskal-Wallis ANOVA).

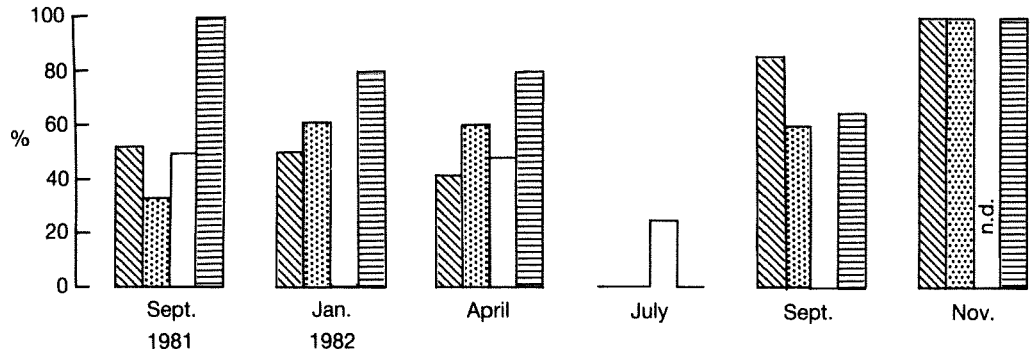

FIG. 1. Reproductive activity of female *Melomys* during the study at Mitchell Plateau. The bars in the histogram represent the number of *Melomys* that were pregnant and/or lactating as a percentage of the total number of individuals of reproductive age (i.e. those that were parous plus those pregnant and/or lactating). In each month, the first three bars represent data from field observations on the CMR grids: from left to right with the total sample size, DV ▩ (n = 46), WM ▨ (n = 47) and WV □ (n = 13). The right-hand bar in each month ▤ represents the combined data (n = 36) on dissected animals from the equivalent removal sites. n.d. = no data.

TABLE V

Statistics describing the regression of ***Melomys*** *head length or body weight (Y_s) on the cumulative weighted probability of sexual maturity (X; $Xi = \sin^{-1}\sqrt{\sum_{n=1}^{i} Pw}$; where Pw is the weighted probability for individual i)*

Grid	Sex	Slope	Intercept	r^2	n	P
			Y = weight (g)			
WV	m	0·488	27·22	0·80	6	0·016
WM	m	0·336	66·28	0·92	23	<0·001
DV	m	0·641	24·73	0·94	18	<0·001
WV	f	0·231	41·46	0·83	9	<0·001
WM	f	0·399	42·53	0·93	19	<0·001
DV	f	0·481	27·86	0·91	11	<0·001
			Y = head length (mm)			
WV	m	0·079	32·11	0·95	6	<0·001
WM	m	0·087	36·57	0·90	40	<0·001
DV	m	0·143	30·85	0·79	28	<0·001
WV	f	0·043	35·09	0·94	10	<0·001
WM	f	0·041	36·03	0·94	13	<0·001
DV	f	0·061	32·49	0·76	9	<0·003

Male reproductive status was related to size (age) of the animal. All males greater than 65 g and no males less than 39 g had spermiogenic testes and actively secreting accessory glands. Some dissected animals were in breeding condition in all sampling periods (33–100%). No significant seasonal changes were found in the weights of testes or of the seminal vesicle complex of animals examined post-mortem.

Sexual maturity

Regression equations of the cumulative probability of sexual maturity are shown in Table V for the three grids examined. The weight of *Melomys* from the three grids at which 50% of the

TABLE VI

Size at 50% sexual maturity of **Melomys** *on the trapping grids at Mitchell Plateau. The given values are adjusted to the 50% probability level using the slopes of the regressions (see Table III). Common letters in the columns denote values not differing significantly at the 1% probability level using the GT2 test*

Grid	Sex	Weight (g)	(S.E.)	*n*	Head length (mm)	(S.E.)	*n*
WV	m	a 49·2	(2·34)	6	a 35·7	(0·17)	6
WV	f	a 51·9	(0·78)	9	b 37·0	(0·08)	10
DV	m	a 53·6	(0·39)	18	b 37·5	(0·05)	28
DV	f	a 49·5	(0·63)	11	a 35·2	(0·26)	9
WM	m	81·4	(0·30)	23	40·5	(0·03)	40
WM	f	60·5	(0·37)	19	b 37·9	(0·11)	13

population was sexually mature is shown in Table VI, together with the multiple comparison tests. The tests did not discriminate fully between all categories but there is a general consistency between the two parameters used. The data from the mangroves at WM are unambiguous, with both the weight and head length at 50% maturity being markedly greater than in either of the two vine-thickets (WV and DV), and the males are much larger when they reach sexual maturity than are the females.

Body weight

Adult male *Melomys* were from 9-23% heavier than adult females, depending on the CMR grid considered ($P > 0{\cdot}0001$). Adults of each sex were significantly heavier in the high density population at WM (m, 100 g; f, 91 g) than the corresponding sex in the low density populations at DV (m, 91 g; f, 74 g) and WV (m, 87 g; f, 47 g), which did not differ from each other (two-way ANOVA with GT2 follow-up test; $F_{S1,216} = 32{\cdot}27$; $P < 0{\cdot}0001$). Among adults, seasonal changes in body weight were not statistically significant, except in females at DV which were heavier in the wet season (January) and lighter in the dry winter (July). Males showed a similar, but not significant, trend (Table VII). Immatures from both WM and DV showed similar seasonal changes in weight: in both areas the weight changes indicated growth from September 1981 through July 1982 but this was significant only at WM (Table VIII).

TABLE VII

Regression statistics describing the growth rate ($Yg{\cdot}d^{-1}$) on weight (W = log weight g) of **Melomys** *on the trapping grids at Mitchell Plateau*

Grid	Sex	Regression equation	*r*	*n*	t_s	*P*
WM	male	Y = 2·12 − 1·04W	0·795	32	7·18	<0·001
	female	Y = 1·50 − 0·71W	0·430	29	2·48	0·02
DV	male	Y = 2·16 − 1·04W	0·836	22	6·82	<0·001
	female	Y = 2·46 − 1·24W	0·536	12	2·01	0·072
WV	male	Y = 2·26 − 1·09W	0·802	9	3·55	0·009
	female	Y = 1·67 − 0·81W	0·506	5	1·02	0·385
Combined		Y = 1·94 − 0·94W	0·646	109	8·75	<0·001

TABLE VIII

Mean body weight (g) for adult male (m), adult female (f) and immature (i) ***Melomys*** *on different CMR grids at Mitchell Plateau during the study. The ANOVA tests for seasonal weight change; the annual percentage change in mean weight is shown*

Grid	Sex	Month					Annual change %	ANOVA		
		Sept.	Jan.	April	July	Oct.		*d.f.*	F_s	*P*
WM	m	98	105	104	100	96	109	4, 41	0·38	0·82
DV	m	95	95	96	86	92	112	4, 51	0·59	0·67
WM	f	85	91	91	92	92	108	4, 36	0·20	0·94
DV	f	79	82	79	61	71	134	4, 34	2·54	0·05
DV	i	26	33	44	45	—	173	3, 17	1·68	0·21
WM	i	35	38	46	63	—	180	3, 37	4·75	0·007

Growth rate

Regressions of growth rate ($g \cdot d^{-1}$) on body weight were calculated from recaptured animals covering all age classes (Table VII). We were unable to detect any differences in growth rate between either grids or sexes. Analysis of variance on the slopes and intercepts of regression lines pooled by sex or grid always indicated common slopes ($P > 0{\cdot}2$) and intercepts ($P > 0{\cdot}34$), even when the small sample sizes from WV were excluded (between sexes in DV and WM: ANOVA; slopes $F_{s1,91} = 1{\cdot}386$, $P = 0{\cdot}24$; intercepts $F_{s1,92} = 0{\cdot}444$, $P = > 0{\cdot}50$). Note the large variance in the growth rate data and the consistency in growth rates in males compared with females. Using the geometric mean regression, the growth rate is ($\log g \cdot d^{-1}$) $= 2{\cdot}013 - 0{\cdot}689$ log body weight ($r = 0{\cdot}65$, S.E.b $= 0{\cdot}107$). Overall growth rate is zero; that is growth ceases at a mean body weight of 103 g. Immature *Melomys* (those less than the weight at 50% sexual maturity) grew 48% faster at DV than in the high density population at WM, but there was no difference in growth rate between the sexes (Table IX: two-way ANOVA: interaction $F_{s1,34} = 0{\cdot}136$, $P = 0{\cdot}714$; Grid $F_{s1,35} = 5{\cdot}466$, $P = 0{\cdot}025$; Sex $F_{s1,35} = 0{\cdot}003$, $P = 0{\cdot}960$).

Tooth wear

Independent ranking with respect to wear class of tooth impressions made on live individuals and on the molars of their cleaned skulls were highly correlated (Spearman's $r = 0{\cdot}84$, $n = 26$, $P < 0{\cdot}0001$). Data from individuals caught repeatedly in the field showed a rate of tooth wear of 0·33 classes per month for each sex (95% intervals for sexes combined are 0·25–0·41;

TABLE IX

Statistics on the growth rate of immature ***Melomys****; those weighing less than the size at 50% sexual maturity (Table VI)*

Grid	Sex	Growth rate ($\log g \cdot d^{-1}$)		
		Mean	S.E.	*n*
WM	m	−0·61	0·060	15
WM	f	−0·59	0·064	10
DV	m	−0·41	0·081	8
DV	f	−0·45	0·085	5

Bartlett's test: $\chi^2_3 = 0{\cdot}361$, $P = 0{\cdot}946$

$n = 29$). Regression of wear class on weight (males from WM and DV but only females from WM due to lack of data) showed that both sexes at WM had a similar degree of wear for a given weight, but that the wear rates of both sexes were greater than at DV (ANCOVA with follow-up test: adjusted mean Y, DVm = 1·88, WMm = 2·24, WMf = 2·29; $F_{s2,131} = 6{\cdot}55$, $P < 0{\cdot}002$).

As growth rate was similar overall on both grids, and animals at WM were heavier, they thus lived longer; this means that teeth at WM not only wear faster than at DV, but that the wear continued for a longer period. Tooth wear rates are thus site-specific and hence cannot be used between areas for ageing individuals. The difference in wear rates may be due to dietary differences between grids but could result from variation in abrasive material ingested with the food (e.g. dust) or differences in tooth hardness.

Demography and movement

No grid showed a significantly biased adult sex ratio at any sampling time ($P > 0{\cdot}5$), but at both WM and DV the adult sex ratio favoured females only in April, the same month in which the immature sex ratio reached its greatest male dominance (Table III).

Survival was estimated from the grid recapture data as the number of individuals KTBA over the total number of individuals marked on the grid. Amongst adults, males showed higher absolute survival than females in both vine-thickets (DV and WV), but for females the reverse was the case at WM (Table IV). Amongst immatures, males showed higher survival than females at both WM and DV (Table IV). Statistical analysis of survival was conducted on the independent estimates of survival between sampling times of the four maturity and sex classes combined (Table IV); data from WV were excluded as their inclusion resulted in a significant Bartlett's test ($P = 0{\cdot}039$). Mean survival between sampling periods at WM (60·2%) was greater than at DV (38·5%; $F_{s1,30} = 5{\cdot}639$, $P = 0{\cdot}024$).

Movement by *Melomys* was assessed by calculating the average distance moved between recaptures within a trapping period using only data where three or more captures were made away from the periphery of the grid, or from the periphery of the mangroves at WM. Individuals moved the same mean distance at WM and DV (Table X), despite the large difference in density

TABLE X

Movement and home range of **Melomys** *on three grids at Mitchell Plateau. Home ranges were calculated from individuals where ⩾ 3 captures were made away from the periphery of the grid. The overlap index is a measure of how closely* **Melomys** *need to associate spatially with adjacent individuals and = estimated mean home range times the inverse of the estimated density of* **Melomys** *in the same area. Values greater than 1·0 indicate overlapping home ranges*

Parameter		WM		DV		WV	
		m	f	m	f	m	f
Distance between successive recaptures within trips (m)	mean	23·0	20·5	24·5	24·1	28·5	39·6
	S.E.	2·12	2·15	2·18	2·11	3·94	7·43
	n	76	83	50	49	19	8
Home range (m^2) where ⩾ 3 captures not on edge of grid	mean	1532	621	492	482	695	276
	S.E.	510·6	106·6	101·5	89·8	98·7	—
	n	5	7	11	11	4	1
Overlap index of: adults		2·2	0·79	0·27	0·18	0·17	0·04
adults of both sexes		2·7		0·45		0·24	
population		3·9		0·55		0·29	

between the grids, and both moved less distance than individuals at WV where *Melomys* made only patchy use of the grid (Kruskal-Wallis one-way ANOVA by ranks with Dunn's multiple comparison test: $\chi^2_2 = 8{\cdot}751$, $P < 0{\cdot}025$). However, the estimated home ranges differed in size ($F_{s5,33} = 4{\cdot}71$, $P = 0{\cdot}004$), with 33% of the variance occurring among groups. Follow-up tests showed that males from WM had larger home ranges than either sex from DV ($P < 0{\cdot}05$) but that the home range of no other group differed statistically in size.

The overlap index (Table X) shows that males in the mangroves at WM overlapped considerably in their home ranges. Our estimates of movement indicate that only on grid WM was any section of the *Melomys* population constrained into overlapping home ranges.

Haematological measures

Summary data and statistics for haematological indices and plasma constituents are presented in **Appendices 2** and **3.**

No individuals from the CMR grids died during handling and we recorded three cases of unilateral blindness; one of these, a large male from WV, was blind when first caught and was still present at the end of the study. The blood sampling caused one case and may have contributed to the second case of blindness. We are unable to provide a measure of the effect of repeated blood sampling on *Melomys*; all trapping areas were treated the same and whatever the effects of blood sampling they were insufficient to mask the many between sex, grid and seasonal differences in the measurements we made.

There was an inverse relationship between haematocrit and body weight in female *Melomys* (Table I). Haematocrit was not influenced by the grid or the time of year (Fig. 3) samples were taken; however, males had higher mean haematocrits (46%, S.D. = 4·8, $n = 137$) than females (43%, S.D. = 4·6, $n = 106$; $F_{s1,241} = 17{\cdot}2$, $P < 0{\cdot}0001$).

Mean haemoglobin concentration [Hb] was 13·6 g·dl^{-1} and did not differ between the sexes

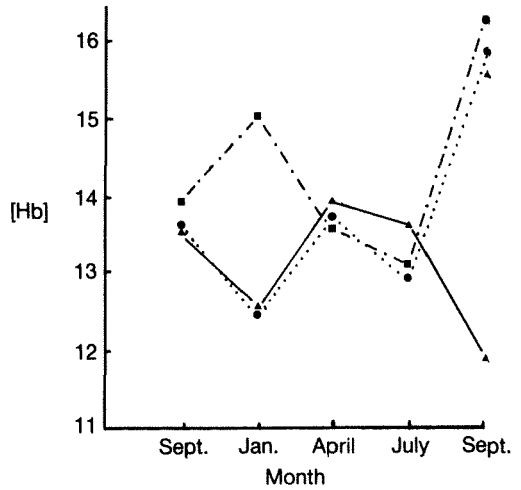

FIG. 2. Variation in the haemoglobin concentration from *Melomys* on the three CMR grids at Mitchell Plateau. Note that the changes are complex, unlike those for the other physiological parameters, including haematocrit, that were measured. ●·····● = WV; ▲————▲ = DV; ■—·—·—·—■ = WM.

($F_{s1,255} = 0{\cdot}63$, $P = 0{\cdot}43$). In analysis of variance, each sex showed significant interaction between the grid and time of year. Analysis of temporal changes in haemoglobin for the grids separately (by ANOVA after transformation of the data for WM and WV and by non-parametric Kruskal-Wallis test for DV due to heterogeneous data) showed significant temporal changes on all trapping sites but these were not in synchrony (Fig. 2, **Appendices 2** and **3**).

Total leucocyte counts were higher in females ($8{\cdot}94 \cdot 10^3$ mm^{-3}) than in males ($7{\cdot}27 \cdot 10^3$ mm^{-3}), and there were qualitative differences between the sexes. Females showed no between-grid differences in leucocyte count but they did show between-trip variation (ANOVA: interaction $F_{s4,80} = 0{\cdot}478$, $P = 0{\cdot}75$; time $F_{s4,84} = 3{\cdot}00$, $P = 0{\cdot}023$; grid $F_{s1,84} = 0{\cdot}388$, $P = 0{\cdot}535$). Males showed both between-grid and between-trip changes in leucocyte count (ANOVA: interaction $F_{s4,96} = 1{\cdot}029$, $P = 0{\cdot}397$; Time $F_{s4,100} = 2{\cdot}596$, $P = 0{\cdot}041$, Grid $F_{s1,100} = 8{\cdot}344$, $P = 0{\cdot}005$; the male leucocyte count was higher at DV ($8{\cdot}16 \cdot 10^3$ mm^{-3}) than at WM ($6{\cdot}38 \cdot 10^3$ mm^{-3}). In both sexes the leucocyte count was lowest in January.

Testosterone

Testosterone was detectable only in plasma from males: in the low density population at DV there was a strong direct relationship between testosterone concentration and body weight ($t_{s36} = 3{\cdot}88$, $P < 0{\cdot}0001$), but there was no such relationship in *Melomys* from the high density population at WM ($t_{s21} = -0{\cdot}2$, $P = 0{\cdot}85$). Two-way ANOVA on the weight-corrected data from WM and DV shows significant effects of grid and season (**Appendices 3** and **4**) on the concentration of testosterone (Fig. 3). Annual levels of testosterone at DV were 138% of those from the high density population at WM (**Appendix 2**), despite the higher mean weight of *Melomys* from WM. This result is the same even from the raw data (**Appendix 2**). Overall testosterone levels increased significantly between April and July and decreased significantly from September to November 1982 (Fig. 3 and **Appendix 4**).

Qualitative as well as quantitative differences existed between sites. Testosterone levels at WM dropped consistently from mid-dry season until April, while those at DV dropped sharply in April (Fig. 3); this is perhaps indicative of a more prolonged breeding season at DV and we are examining the male reproductive organs to ascertain their state of sexual activity.

Corticosteroids and their binding proteins

Albumin

In both sexes, albumin concentration was higher at WM than at other grids (**Appendices 2, 3** and **4**) and in both sexes overall plasma albumin levels were significantly higher in April and lower in November 1982 than during other sampling periods (Fig. 3 and **Appendix 4**).

Maximum corticosteroid binding capacity (MCBC)

No difference in MCBC was found between DV and WM in either sex (**Appendices 2, 3** and **4**). The raw statistics show considerable seasonal variation in MCBC (Fig. 3), with levels being low in the wet season (January) and increasing through the dry season (April-September). It proved impossible to eliminate the marked heterogeneity in the data, hence temporal comparison was made using the Kruskal-Wallis ANOVA which showed significant seasonal variation in MCBC (Fig. 3) in both males ($\chi^2_5 = 63{\cdot}9$, $P < 0{\cdot}0001$) and females ($\chi^2_5 = 61{\cdot}8$, $P < 0{\cdot}0001$).

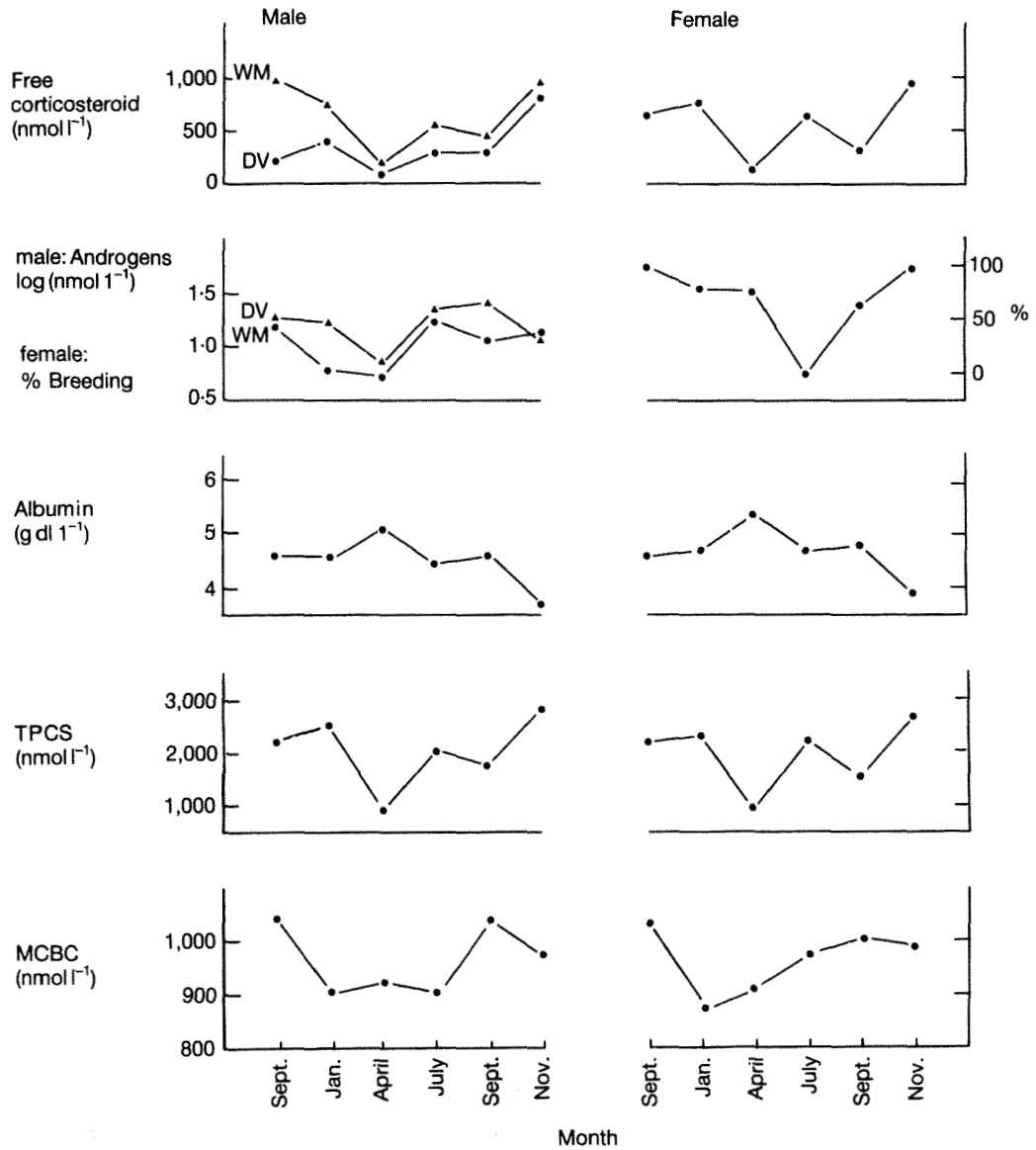

FIG. 3. Overall seasonal changes in the levels of plasma constituents of male and female *Melomys* at Mitchell Plateau. Note that in the second row testosterone concentration is plotted for males, while for females the data represent the proportion of mature females that were reproductively active (see caption to Fig. 1).

Total plasma corticosteroid concentration (TPCS)

TPCS was related to weight in males (Table I) but not in females. Male TPCS was scaled for the effect of body weight and the corrected data used in further analyses. TPCS was lower at DV than in *Melomys* from either of the coastal grids (WV and WM: Fig. 3, **Appendices 2, 3** and **4**). ANOVA showed significant interaction between month and site factors but this was lost if

TABLE XI

Statistics on the free corticosteroid levels of immature ***Melomys,*** *those weighing less than the size at 50% sexual maturity (Table VI)*

Grid	Sex	Free corticosteroids (log n mol l^{-1})		
		Mean	S.E.	*n*
WM	m	2·56	0·117	19
WM	f	2·42	0·202	9
DV	m	1·69	0·260	3
DV	f	2·20	0·144	7

Bartlett's test: $\chi^2_3 = 1{\cdot}463$, $P = 0{\cdot}691$

the small sample sizes from WV were excluded. Seasonal variation in TPCS was greater at the coastal grids than at DV. TCPS levels were lower in April than during any other sampling period (Fig. 3).

Free corticosteroids

Significant differences were found attributable to both the grid and seasonal factors which did not interact. Free corticosteroid concentrations were lower (*c.* 50%) in *Melomys* from DV than in those from WV or WM (**Appendices 2, 3** and **4**). A significant fall occurred in free corticosteroid levels between January and April 1982—however, the seasonal pattern is complex with troughs in April and September 1982 and peaks in January and July (Fig. 3). In immature *Melomys* (< weight at 50% sexual maturity), free corticosteroid concentrations were higher at WM than at DV but there was no difference between the sexes (Table XI: two-way ANOVA interaction $F_{s1,34} = 2{\cdot}504$, $P = 0{\cdot}123$; site $F_{s1,35} = 5{\cdot}322$, $P = 0{\cdot}027$; sex $F_{s1,35} = 0{\cdot}025$, $P = 0{\cdot}875$).

Multivariate analysis of the physiological data

Pairwise discriminant function analysis was conducted using body weight, TPCS, MCBC, [Hb], haematocrit, free corticosteroid and albumin on all combinations of both sex and grid (WM, DV). All comparisons showed significant differences ($P < 0{\cdot}02$ to $P < 0{\cdot}006$), except for the sexes at WM ($P = 0{\cdot}14$). This analysis was robust, giving the same outcome whether raw or range-scaled data were used and with the exclusion of body weight as a factor. Hence, physiologically, the sexes at WM respond similarly to, but differ from, those at DV, where the sexes respond physiologically in a different manner.

The centroids from a sampling period by site multiple discriminant analysis on the parameters used above are shown as a trajectory plot in Fig. 4. This clearly shows the closed centroid trajectories at DV and the open centroid trajectories at WM. Using data for both sexes, we compared the centroids for September 1981 with September 1982. This shows that the centroids at DV do not differ (Hotelling's $T^2 = 7{\cdot}56$, $P = 0{\cdot}37$), whereas at WM these centroids differ significantly (Hotelling's $T^2 = 53{\cdot}17$, $P < 0{\cdot}0001$).

Worm burdens

On post-mortem examination of *Melomys* from removal sites, six species of worm were found in 80 individuals, mostly at low prevalences (Table XII). The prevalence of *Physaloptera* was high (47%) but there was no significant association with season, site of collection or the sex of

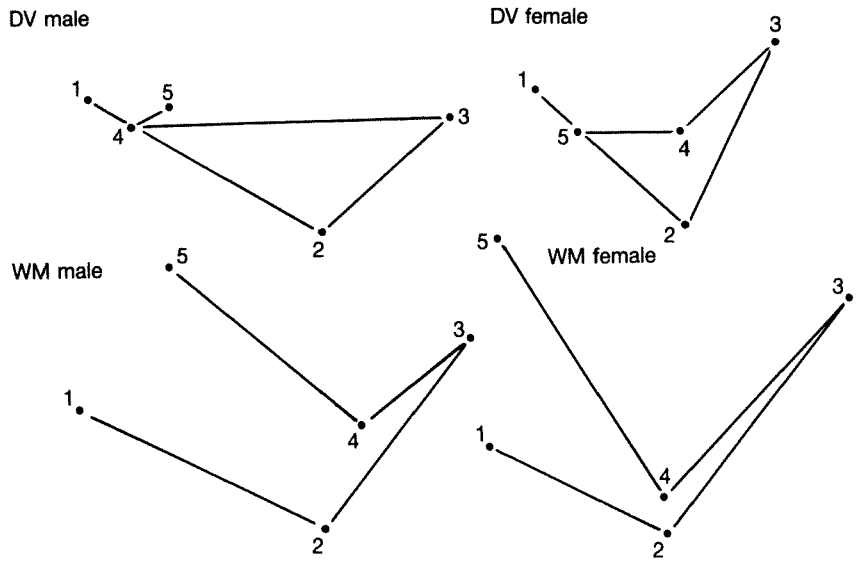

FIG. 4. Trajectory plot of the centroids derived from multiple discriminant analysis of the physiological data and body weight (see **Results**). The centroids from the analysis of data for both sexes from DV and WM are plotted in sequence of sampling time; 1 = September 1981, 2 = January 1982, 3 = April 1982, 4 = July 1982 and 5 = September 1982. The plots are to the same scale but off-set from each other to show the form of the individual trajectories. Note that the trajectories close at DV but at WM are widely separated in September of the two years sampled (see **Discussion**).

the host. There was strong heterogeneity in the prevalence of *Physaloptera* with host weight ($\chi^2_3 = 25{\cdot}1$, $P < 0{\cdot}001$). No *Melomys* < 57 g, and all those > 110 g, were infected with *Physaloptera*. The percentage prevalences in ascending 20 g weight classes were 0, 0, 11, 33, 35, 78, 100 and 100. Prevalence in coastal individuals was higher (38%) than that of plateau individuals (17%). In the two 40 g weight classes, between 40 and 119 g prevalences of *Physaloptera* were 235 and 217% greater on coastal than on plateau sites. The worm burdens closely fitted the negative binomial distribution, with a low k value indicating a high degree of aggregation in the samples ($\chi^2_3 = 10{\cdot}89$, $P > 0{\cdot}5$, $k = 0{\cdot}12$; fitted by the method of maximum likelihood). Mean

TABLE XII

Summary data on worms recovered post-mortem from **Melomys** *at Mitchell Plateau. The specific status of these parasites is uncertain at present*

Taxa	Genus	Location of worms in host	Location of host*	% prevalence ($n = 80$)
Nematoda	*Physaloptera*	stomach	cp	46·7
	Rictularia	intestine	p	3·8
	Metathelazania	lungs	p	3·8
	Breinlia	thoracic cavity	cp	8·8
Trematoda	*Brachylemis*	liver	p	1·3
Cestoda	*Raillietina*	small intestine	cp	6·3

* Coastal (c) and plateau (p) sites

worm burdens were similar irrespective of host location (*Physaloptera* per infected host—mean (range): coastal 10·3 (1–31), plateau 9·3 (1–42)).

Melomys become infected with *Physaloptera* irrespective of grid, sex or season. However, coastal *Melomys*, despite their larger size at maturity, become infected by *Physaloptera* more rapidly and the distribution of worms is highly aggregated in the *Melomys* population.

Protein polymorphisms

Three electrophoretically detected protein polymorphisms were found—adenosine deaminase (ADA), albumin (ALB) and 6-phosphogluconate dehydrogenase (6PGD). Phenotype and putative gene frequencies for all individuals captured on grids are shown in Table XIII. Independently determined phenotypes of individuals bled in more than one season were consistent and hence did not show the temporal variation found by McGovern & Tracy (1985).

For each polymorphism and for each grid, phenotype frequencies were homogeneous among trips. That is, there is no evidence of temporal variation in gene frequencies within the populations. The ADA gene frequencies were similar for all grids, and phenotype frequencies were in agreement with Hardy–Weinberg expectations. The ALB gene frequencies at DV were significantly different from both WM and WV (both $P < 0{\cdot}001$). WM and WV were homogeneous for ALB gene frequencies. All within population ALB phenotype frequencies were in general agreement with Hardy–Weinberg expectations.

TABLE XIII

Phenotype and gene frequencies for three protein polymorphisms of **Melomys** *from three grids at Mitchell Plateau*

	ADA				ALB						6PGD			
	1	2-1	2	f(1)	1	2-1	2	3-1	f(1)	f(2)	1	2-1	2	f(1)
WV	16	5	1	0·84	20	7	0	0	0·87	0·13	14	7	0	0·83
WM	35	17	0	0·84	35	14	3	4	0·79	0·18	27	19	3	0·74
DV	33	10	1	0·86	17	26	9	0	0·58	0·42	14	27	2	0·64

There was significant heterogeneity among grids in 6PGD gene frequencies. In pairwise tests, only WV and DV were statistically different ($P < 0{\cdot}05$), but the pooled combination of the adjacent coastal grids (WV and WM) was also different from DV ($P < 0{\cdot}05$). Furthermore, there was a significant excess of heterozygotes above Hardy–Weinberg expectation at DV ($P < 0{\cdot}05$). The deviation was significant when a correction for small sample size was used (Cannings & Edwards, 1969). Furthermore, the excess was apparent in April through November 1982, although it was not significant at any one collection, the maximum sample size being only 26 (July 1982). There were no indications of deviations from Hardy–Weinberg expectations on the other two grids sampled.

Multiple regression was used to test for associations between protein phenotypes and total and free corticosteroid levels, MCBC, haematocrit, haemoglobin and albumin concentrations and weight. Grid and sex were included in all models. One association was clearly significant, that between 6PGD and haemoglobin concentration, while the association between ALB and free corticosteroid approached statistical significance ($F_{s1,116} = 3{\cdot}50$, $P = 0{\cdot}064$): the ALB 2-1

and ALB 3-1 phenotypes had higher free steroid levels compared to ALB 1-1 and ALB 2-2 phenotypes (630 and 820 vs. 500 and 280 nmol l^{-1}, respectively).

Discussion

In the Mitchell Plateau area, *Melomys* were reproductively active throughout the year, although there was a marked decline in female reproductive activity in July (Fig. 1). No seasonality was detected in male indices of reproductive activity, but there was distinct seasonality in androgen levels. If androgen levels reflect breeding activity, the breeding period in males is shorter at WM than at DV (Fig. 3). That the breeding season is more restricted than indicated by the reproductive indices is supported by the increase in the weight of immatures during the year (Table VI); these indicate that the main period of recruitment of young is prior to September and that they gain weight through the following year.

Of the measurements on corticosteroids and their binding proteins, only total and free corticosteroids showed between grid differences, being higher at WM. Free corticosteroids are rarely measured in natural populations, and though they are an accepted index of stress (Dantzer & Mormede, 1983), the measurement may underestimate the true variation in stress due to the following factors. Mammals may be divided into two groups according to the predominant glucocorticoid hormone secreted: one produces mainly corticosterone, while the other produces mostly cortisol. It used to be thought that the ratio of these hormones was genetically fixed (Bush, 1953), but it has been shown recently that chronic ACTH stimulation of domestic rabbits could alter this ratio (Lland, Kolanowski, Ortega & Crabbe, 1982). Studies of snowshoe hares in Canada have shown that the *in vitro* pattern of adrenal glucocorticoid hormone secretion may change with population density, a more potent glucocorticoid being produced at higher population density (Fevold & Drummond, 1976). Similar changes *in vivo* have not been reported from natural populations, however, recent work (A. J. Bradley, unpubl.) on a marsupial, *Phascogale calura* (Dasyuridae), has shown that under conditions of stress in the field, associated with breeding, a significant alteration takes place in the pattern of glucocorticoid secretion. This alteration is pertinent because the altered secretion pattern favours the production of the more biologically active hormone cortisol (Kass, Kendrick & Finland, 1955). Hence, interpretation of the relative degree of stress indicated by the levels of free-corticosteroid in *Melomys* must await further analysis of the glucocorticoid secretion patterns and appropriate calculation of steroid partitioning in situations where several steroids compete for CBG sites (Dunn, Nisula & Rodbard, 1981).

The trajectory plots (Fig. 4) and their statistics suggest that the physiological response of *Melomys* was more entrained to seasonal variation at DV than at WM, an observation that is consistent with the more marked seasonality in the vegetation and temperature at DV than in the mangroves on the coast at WM.

Despite the rather prolonged breeding season of *Melomys* compared with temperate rodents, and typical of small mammals in the seasonal tropics (Fleming, 1975), there were marked seasonal changes in the plasma constituents. The wet season and its immediate aftermath (November to April) seem especially important, showing an elevation in stress levels (free corticosteroid; Fig. 3) and large increases in *Salmonella* prevalence and serotype diversity (How *et al.*, 1983). In contrast, androgen levels rose sharply in July and before the late dry-season increase in female breeding activity (Fig. 3).

The protein electrophoretic data can provide an indication of population structure at Mitchell Plateau. The possible determinants of phenotype frequencies are differential selection, random genetic drift (population size) and migration. Grids exchanging about one or more migrants per generation, in the absence of natural selection, will have similar gene frequencies. Since for 6PGD and ALB there are significant frequency differences between grids, natural selection must be operating if there is also reasonable gene flow. This indicates selectively important environmental differences among localities.

On the assumption of restricted or no gene flow between grids, there are two possible explanations for the phenotypic variation. First, that random genetic drift may be the sole determinant of gene frequencies, which has led to differences for 6PGD and ALB, but by chance alone ADA is the same in all areas. Secondly, natural selection may be responsible for the homogeneity in ADA frequencies. Of course, natural selection may be primarily responsible for all the frequencies, irrespective of migration, with similar selective pressures for ADA on all three grids and different pressures for ALB and 6PGD. Any entirely 'neutralist' explanation for the data would conclude that there is very little or no gene flow between localities.

Different evidence that natural selection is important comes from observations on an excess of 6PGD heterozygotes at DV. A trend towards an excess was present at each of the four sampling times which could be scored for 6PGD and was not an artefact of small sample sizes. Finally, it should be appreciated that, if natural selection is important, it may not necessarily be operating on the phenotypes investigated, but on phenotypes determined by genes closely linked to the protein encoding genes studied.

Intense selection also occurs in many rodent species in the temperate and boreal regions of the northern hemisphere associated with changes in population density (Krebs *et al.*, 1973), but numerous studies have failed to determine how the polymorphisms are maintained.

There is some evidence that *Melomys burtoni* in the Northern Territory may use rainforest as refugia in the dry season and disperse more widely after rain (Kerle & Burgman, 1984), although not all populations show such movement (Begg *et al.*, 1983). We have no evidence that *Melomys* sp. cf. *burtoni* populations at Mitchell Plateau have numerical cycles or that they disperse seasonally; in the first five sampling periods, during which all eight grids, and their equivalent removal sites, were trapped (Bradley *et al.*, 1987), only 14 of 370 *Melomys* captured at Mitchell Plateau were in habitats other than vine-thickets or mangroves. The three populations studied at Mitchell Plateau showed 1·4 to 1·9 fold numerical variation over the study period (Table III). This constancy of population numbers (typically 2–4 fold annual variation; Fleming, 1975), relative to temperate and boreal zone rodents (5–20 fold annual variation; Krebs & Myers, 1974), seems to be characteristic of tropical species in areas not disturbed by man (Fleming, 1975) and which, due to the small litter size characteristic of tropical small mammals (Myers & Master, 1983), is to be expected.

The three grids inhabited by *Melomys* at Mitchell Plateau differ in many respects. DV is exposed to much greater daily fluctuations in both temperature and relative humidity than are the coastal sites WM and WV (Bradley *et al.*, 1987). Litter-fall indicated primary productivity of the three trapping grids was similar, although the mangrove section of WM may be greater (Bradley *et al.*, 1987). While the mangroves at WM are evergreen, the vine-thickets at WV and DV are deciduous, with leaf fall being bimodal at DV and unimodal at WV (Bradley *et al.*, 1987). This implies that food variety and availability is more variable in the vine-thickets than in the almost monotypic mangrove stand at WM (they contained, respectively, about 30 and two species of angiosperm).

In addition to the lack of temporal and spatial variation in plant species, the tannins in the mangroves probably result in low species richness of arthropods feeding on them and could present nutritional problems for *Melomys*. Mangroves contain high tannin concentrations which restrict the availability of soluble plant proteins and polysaccharides, as well as the activity of digestive enzymes and symbiotic microorganisms in the herbivore's own gut (Swain, 1979). *Melomys* in vine-thickets are subject to greater contact with a wider range of predators and, due to the seasonal leaf fall, are more visually exposed than at WM. Further, potential interspecific competition from other small mammals does not occur at WM, while *Melomys* coexist with other species at DV and WV (Bradley *et al.*, 1987).

Towards an hypothesis

A principal aim of this study was to examine populations of *Melomys* in different habitats in order to evaluate the demographic and physiological flexibility of the species in a constrained geographical and hence climatic regime. This is in keeping with the statement of Snyder (1978) that 'we need simultaneous measurements on individuals within populations, and we need to observe different populations, and we need to observe different populations simultaneously. . . . Without a framework which incorporates all aspects of a population we are in danger of continuing to obtain partial answers which cannot be incorporated into common theory'.

This study shows a number of major differences between *Melomys* from different habitats at Mitchell Plateau (Table XIV); we will concentrate on grids WM and DV for which the data are most comprehensive and complete. There was no statistical disparity in the overall sex ratios, the breeding season (Fig. 1), embryo or litter rates of *Melomys* from the different grids. However, the nature of the data available for the latter two parameters does not permit fine discrimination. Overall growth rate did not differ between grids, but the growth rate of immatures was greater at DV than WM and the effective density of the populations was very different, being high in the mangroves which they shared with no other mammal populations, and low at DV where *Zyzomys argurus*, *Isoodon macrourus* and *Dasyurus hallucatus* were common and *Z. woodwardi* were present. The size at sexual maturity (Table VI) was much greater at WM than in the vine-thickets (WV and DV) and, because immatures at WM grew more slowly, the onset of sexual maturity must be delayed at WM compared with DV; this is coupled with greater annual survival (Table IV) and longevity at WM.

The most obvious difference in *Melomys* from different sampling areas is body size and the size at sexual maturity. Of any single attribute, size has the most profound general effects on species, influencing most aspects of their biology, including physiology and demography (Peters, 1983). For example, large females of *Peromyscus maniculatus* have more, bigger, and faster growing young and a shorter gestation period (Myers & Master, 1983). Increase in adult size has been observed during peaks in population density in *Microtus californicus* (Krebs, 1966).

Consideration of the physical factors, discussed above, suggests that DV is a less favourable environment than WM; the different demographic characteristics of *Melomys* on the two grids suggest that it is also perceived by *Melomys* as less favourable. DV *Melomys* were smaller, had lower population density, lower survival, greater growth rate as immatures and shorter life than at WM. Hence, DV *Melomys* were more *r*-selected (*sensu* MacArthur & Wilson, 1967) than those at WM. Despite these considerations, the levels of free corticosteroids show that *Melomys* at DV were less stressed than those at WM, while the parasite burdens and leucocyte counts suggest they were less immunosuppressed. The finding for *Melomys*, that animals in apparently less

optimal habitats, and which were more *r*-selected, showed less seasonal changes in physiological parameters, were less stressed and had lower parasite burdens is consistent with studies on the mountain possum, *Trichosurus caninus* (Barnett, How & Humphreys 1979*a*, *b*, 1982; Presidente *et al.*, 1982).

TABLE XIV

Summary of observations made on **Melomys** *inhabiting inland vine-thicket (DV) and coastal mangrove (WM) habitats at Mitchell Plateau. m = male, f = female*

Parameter	Overall similarity	Comments
Sympatric mammals	DV > WM	None in mangroves at WM, 4 at DV
Body weight	WM > DV	Seasonal variation at DV, not at WM
Growth rate: all	WM = DV	Measurement with low resolution
immature	DV > WM	
Size at maturity	WM > DV	
Breeding season	WM = DV	Androgens suggest a difference in males
Sex ratio	WM = DV = 1:1	Seasonal variation at DV, not at WM
Population density	WM > DV	
Survivorship	WM = DV	DV male > female; WM female > male
Movement	WM = DV	Despite density difference
Home range	WMm > DVmf	
Home range overlap	WM > DV	Overlap only at WM
Rate of tooth wear	WM > DV	
Haematocrit	WM = DV	Males > females
[Hb]	WM = DV	Males = females; complex time and site change
Leucocytes	WM < DV	Males but not females; both sexes minimal in Jan.
Albumin	WM > DV	High in Apr., low in Nov.
Testosterone	DV > WM	High in Apr. and July, low in Sept.–Nov.; strong weight dependence at DV; not at WM
MCBC	WM = DV	Low in Jan. (wet), high in dry season
TPCS	WM > DV	Low Jan.–Apr., high Apr.–July; DV > variable WM
Free corticosteroids	WM > DV	In adults and immatures
Genetics	WM ≠ DV	
Worm burdens	WM > DV	Infection rate WM > DV
Salmonella		
No. serotypes	WM > DV	18 and 12, respectively; significant change at WM; not at DV (How *et al.*, 1983)
Seasonality in serotypes/swab	WM > DV	WM shows marked peak in Jan., DV *c.* constant (How *et al.*, 1983)

We now examine the endogenous factors which may help to explain the demographic differences seen in *Melomys* from the different grids. Measures of individual condition have been used elsewhere to explore the factors underlying demographic changes, both in the northern hemisphere (review by Novak, 1978) and in Australia (Barnett, How & Humphreys, 1979*a*, *b*, 1982), and some of the problems of interpreting such data discussed (Humphreys *et al.*, 1984*b*). Three hypotheses have been proposed, all invoking social behaviour in which intrinsic mechanisms may control the numbers of rodents: I. The behavioural-genetic hypothesis (Chitty, 1958, 1960, 1967), which is mainly applicable to long-term cycling of populations. II. The behaviour hypothesis in which an increase in social interaction directly affects mortality, reproduction and

dispersal (Wynne-Edwards, 1962; Lidicker, 1965, 1976; DeLong, 1967; Healey, 1967; Tamarin, 1978). III. Stress hypothesis in which changing social interactions influence the neural and endocrine physiology and hence reproduction and mortality (Christian & Davis, 1964).

In the temperate and boreal zones of the northern hemisphere, field studies on rodents have concentrated on specific phases in the cycles of populations, mostly of microtine rodents; those concerned with the first hypothesis have examined the rising and falling phases of long-term population changes, while those concerned more with the second hypothesis have concentrated, more recently, on the spring decline in numbers as it is the most variable component in the annual population cycle (Flowerdew, 1972; Krebs & Myers, 1974; Krebs & Boonstra, 1978).

Are any of these hypotheses consistent with the *Melomys* data? The first hypothesis is inapplicable as *Melomys* had fairly constant populations and showed no evidence of seasonal dispersal or temporal changes in gene frequencies; there is no evidence of major population cycles in any *Melomys* species. The second hypothesis is not consistent with the *Melomys* data because, although the low density population (DV) grew faster as immatures and bred earlier than those from the high density population (WM), they showed lower survival. While there seems to be an endocrine component in the differences in response between the high and low density populations of *Melomys*, the data do not support the third hypothesis because the high density population is more highly stressed and yet has greater survival. We support a modification of the third hypothesis whereby only a large increase in stress causes greater mortality, whereas small increases in stress result in suppression of hormones involved in reproduction (cf. Massey, 1986) and of the rate of maturation and growth.

Of the physiological measures we made which show area-related differences, some were associated with potential behavioural feedback through the endocrine system. Despite seasonal fluctuation, TPCS, free corticosteroid, albumin and worm burdens were all greater at WM than at DV, while the converse was the case with androgen levels.

Our data suggest that there should be more frequent intraspecific contact at WM than at DV. Although we have no direct measure, the reasons for this are as follows. *Melomys*, unlike many temperate rodents (Ebling & Stoddart, 1978; Wakeley, 1982), do not make individual runways but use branches and vines for movement above the ground. The structure of mangroves provides fewer potential runways on the vegetation than are available in vine-thickets and the permanent runways need to be above the high tide level. As the mean distance between recaptures is similar at DV and WM but the population density is much greater at WM, where the home ranges broadly overlap, intraspecific contacts should be more frequent at WM. Such contacts are likely to be stressful as *Melomys burtoni* is particularly difficult to breed in captivity due to overt intraspecific aggression often resulting in injury (Watts & Aslin, 1981).

We are dealing with two factors which may contribute towards the observed differences in demography between DV and WM; these are the raised androgen levels at DV and the raised free-corticosteroid levels at WM. The development of aggressive behaviour depends on stimulation by androgens (or oestrogens) at appropriate times (Edwards & Rowe, 1975), while free-corticosteroid levels are an accepted index of stress.

If aggression in *Melomys* is related to androgen levels, as it is in microtine rodents (Gipps, 1983), then we may expect more aggressive males at DV compared with WM and perhaps higher juvenile losses, as found in voles (Gipps, Taitt, Krebs & Dundjerski, 1981). The only significant bias in the sex ratio, to males at DV in July, was associated with high androgen levels.

While it is clear that reproductive success in mice and voles is affected by stress (Bruce, 1967; Clarke, 1978), the mechanisms are unclear and the demographic consequences of the processes

are still largely conjectural, being based on indirect evidence (Clarke, 1978; Novak, 1978) and largely on species which undergo large changes in population numbers between years. Some of the consequences of hyperactivation of the pituitary-ACTH-adrenal axis are: a severe decline in reproductive potential; the inhibition of growth in young animals which delays the onset of sexual maturity and increases the interval between successive generations; the decline in reproductive vigour which is accompanied by a decrease in gonadotropin secretion and by increased susceptibility to disease, renal failure and cardiovascular damage; a decrease in birth rate and increase in age of maturity at higher densities (Novak, 1978). The associated inhibition of maturation may be a major factor stopping population growth in microtine rodents (Kalela, 1957; Koshkina, 1965), as at high density they matured more slowly and the interval between litters was greater. Many of these factors derived from studies of temperate and boreal zone rodents are also correlates of the high density population of *Melomys* (Table XIV) or may be inferred from the data.

Prior to sexual maturity, androgens of adrenal origin are present at very low levels. Secretion of adrenal androgens increases, even disproportionately, with increased adrenocortical stimulation, and these steroids can effectively inhibit reproductive function and maturation even in very low doses (Christian, Lloyd & Davis, 1965; Christian, 1971*a*, *b*). Immature *Melomys* in the high density population at WM had greater corticosteroid concentrations than those at DV, so increased adrenal androgens may be expected at WM; indeed of *Melomys* with detectable androgens, 11 (33%) from WM and none of 37 from DV were immatures ($\chi^2_1 = 10{\cdot}70$, $P = 0{\cdot}001$). It should be noted that much lower concentrations of androgens are required to inhibit maturation of young than to inhibit reproductive function in already mature animals (Varon & Christian, 1963; McCann & Ramirez, 1964). We suggest, therefore, that the lower growth rate of immature *Melomys* at WM could be due to elevated adrenal androgen levels resulting from the stimulation of the pituitary-adrenal axis, which also effects an increase in the level of free corticosteroids.

Density associated increases in stress levels, as indicated by free steroid levels, stress related delayed maturation and reduced fertility, immunosuppression, and mortality are well established in a range of rodents and dasyurid marsupials (Bradley, McDonald & Lee, 1976, 1980; Lee, Bradley & Braithwaite, 1977; Ebling & Stoddart, 1978; Snyder, 1978; Wakeley, 1982). These studies were conducted to investigate the causes of obvious demographic changes, marked population cycles in microtine rodents, or post-mating male die-off in small dasyurid marsupials. *Melomys* does not show such characteristics and yet physiologically has attributes consistent with the intrinsic regulatory mechanisms proposed for other small mammals.

We propose then that the greater population density at WM and associated elevation in intraspecific encounters led to elevated free-steroid levels at WM. This resulted in immunosuppression (more parasites and salmonella) and induced the production of adrenal androgens at WM, leading to a reduction in growth rate in immatures and delayed breeding in adults. The lower androgen levels in adults at WM suggest that, in this high density population, aggressive interactions should be reduced compared with DV. Whether the overtly different population strategies between DV and WM result from this mechanism or result from the genetical differences between the populations remains to be tested.

The general picture we have found for *Melomys* is similar to that found for the phalanger *Trichosurus caninus*, in both the physiological response of relatively *r*- and *K*-selected populations and in some details of the interpretation placed on the free corticosteroid response. In that species also, the more *K*-selected population had a higher free corticosteroid level which was

associated with reduced ovulation rate, and was hypothesized as resulting from the longer association of young with the mother, but with no change in survival (Barnett, How & Humphreys, 1982). It seems as though the common interpretation of a direct relationship between free corticosteroid induced stress levels and mortality is simplistic, and we consider that a better interpretation is likely to result when data are available from steroid partitioning after analysis of adrenal steroid secretory patterns and competition by multiple steroids for available binding sites on high affinity binding proteins, which, as discussed above, will better indicate the real levels of stress involved. Finally, *Melomys* would be a good experimental animal in the field because the regulatory mechanisms we have discussed can be examined by transplant experiments without having to await the unpredictable changes in population levels characteristic of microtine rodents.

This work was made possible by the co-operation of numerous people. For help with the field work we thank P. Baverstock, P. F. Berry, J. Dell, P. J. A. Presidente and L. Smith and especially the honorary assistance of M. Adams, J. L. Barnett, C. Blumer, R. Collyer, P. Griffin and D. King. P. J. A. Presidente identifed the helminth parasites which A. Smith and J. Bell helped to extract in an honorary capacity. Staff of the Mitchell Plateau Bauxite Company in Perth, Melbourne and on the Mitchell Plateau provided every assistance with logistics under frequently trying circumstances. Funding for the project came from the Mitchell Plateau Bauxite Company and the Western Australian Museum and some analyses were enabled by grants from the Australian Universities Research Grants Scheme to A. J. Bradley (grant number D18015574).

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Appendix 1

Criteria used to allocate tooth impressions to wear classes

Class	Criteria
I	Molars not all erupted
II	Narrow bands of dentine exposed between adjacent cusps but not joining other cusp groups
III	M1 and M2 cusp groups tending to join posterior groups but enamel not joined
IV	M1 and M2 cusp groups joined by enamel and/or dentine with ridge of enamel between them; M3 may be devoid of enamel mesially
V	M1–3 mostly devoid of enamel between cusp groups

Appendix 2

Summary statistics on uncorrected blood parameters from ***Melomys*** *sp.; when n = 2 (±standard error equals the range).*
Field trip number and month

			1 Sept./Oct. 1981			2 January 1982			3 April 1982			4 July 1982			5 September 1982			6 November 1982		
Parameter	Sex	Grid	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*	$\bar{x}$	S.E.	*n*
Free	♂	DV	263	(78)	14	423	(122)	6	107	(59)	9	333	(98)	17	321	(96)	6	853	(204)	7
corticosteroids		WM	960	(245)	9	749	(201)	6	182	(63)	15	577	(153)	13	424	(97)	6	932	(366)	6
		WV	1007	(281)	5	1469	(38)	2	54	(23)	2	1036	(247)	8	178	(79)	4		—	
(n mol l^{-1})	♀	DV	341	(84)	13	464	(179)	8	81	(36)	8	216	(96)	7	399	(109)	7	1274	(107)	3
		WM	960	(212)	8	842	(254)	5	163	(55)	13	848	(196)	12	273	(90)	6	901	(239)	8
		WV	1044	(324)	2	773	—	1	183	(36)	4	965	(460)	3	156	(45)	4		—	
Total	♂	DV	1375	(191)	15	1617	(262)	6	898	(181)	9	1471	(219)	17	1526	(142)	12	2392	(429)	7
corticosteroids		WM	2722	(283)	10	2668	(422)	7	944	(197)	16	2063	(399)	13	2053	(153)	10	2632	(742)	6
		WV	2847	(523)	5	3854	(101)	2	751	(174)	2	2775	(517)	8	1005	(250)	5		—	
(n mol l^{-1})	♀	DV	1601	(215)	13	1999	(421)	8	653	(178)	8	1307	(318)	7	1724	(253)	7	3387	(194)	3
		WM	2714	(437)	9	2502	(456)	6	1093	(192)	14	2745	(420)	12	1685	(145)	11	2512	(523)	8
		WV	3132	(679)	2	2627	—	1	1292	(118)	4	2295	(842)	4	1064	(164)	5		—	
Albumin	♂	DV	5·0	(0·27)	14	4·7	(0·27)	6	5·2	(0·23)	9	4·5	(0·08)	17	4·4	(0·06)	11	3·7	(0·08)	7
		WM	5·0	(0·30)	9	4·9	(0·45)	7	5·7	(0·14)	16	4·9	(0·09)	13	5·0	(0·05)	10	3·8	(0·16)	6
(g dl^{-1})		WV	3·8	(0·18)	5	4·5	—	2	5·1	(0·10)	2	4·4	(0·11)	8	5·0	(0·27)	5		—	
	♀	DV	4·7	(0·21)	13	4·7	(0·12)	8	5·1	(0·25)	9	4·8	(0·15)	7	4·5	(0·08)	7	4·2	(0·37)	3
		WM	4·9	(0·20)	8	5·0	(0·25)	6	5·9	(0·20)	14	4·8	(0·10)	12	5·0	(0·12)	11	4·1	(0·18)	8
		WV	4·4	(0·07)	2	5·3	—	1	5·3	(0·24)	5	4·8	(0·16)	4	4·9	(0·15)	5		—	
Maximum	♂	DV	1041	(7·6)	15	881	(41·4)	6	914	(23·6)	9	988	(40·7)	17	998	(24·2)	7	969	(15·2)	7
corticosteroid		WM	1035	(11·0)	10	885	(27·7)	6	922	(14·8)	15	986	(45·1)	12	1039	(7·5)	6	1020	(16·0)	6
binding capacity		WV	1055	(15·2)	5	924	(29·0)	2	924	(58·0)	2	902	(31·7)	8	1025	(18·5)	4		—	
	♀	DV	1050	(11·2)	13	928	(20·8)	8	927	(15·5)	9	887	(24·3)	7	1031	(36·6)	7	991	(34·5)	3
(n mol l^{-1})		WM	1038	(12·8)	10	878	(31·2)	5	926	(17·2)	13	922	(29·0)	13	1063	(18·8)	6	967	(18·8)	8
		WV	1067	(21·5)	2	953	—	1	993	(11·4)	5	885	(42·1)	3	1019	(27·2)	4		—	

Appendix 2 (*cont.*)

Haemoglobin concentration ($g\ dl^{-1}$)	♂	DV	14·2	(0·27)	14	12·9	(0·70)	8	14·1	(0·83)	7	13·7	(0·37)	16	12·5	(1·37)	11		—	
		WM	14·4	(0·64)	10	12·3	(0·82)	7	13·4	(0·75)	16	12·5	(0·71)	21	15·8	(0·34)	10		—	
		WV	14·5	(0·29)	6	14·2	(0·24)	3	12·9	(0·10)	2	13·8	(0·51)	8	17·1	(1·20)	4		—	
	♀	DV	12·7	(0·49)	10	12·2	(0·46)	10	13·8	(0·51)	7	14·0	(0·53)	6	11·1	(0·36)	7		—	
		WM	12·8	(0·45)	10	12·6	(0·49)	7	14·1	(0·30)	15	13·4	(0·53)	12	16·0	(0·43)	11		—	
		WV	13·3	(1·70)	2	16·2	—	1	14·3	(0·61)	5		—			—			—	
Haematocrit (%)	♂	DV	48	(0·7)	12	43	(3·1)	6	44	(1·2)	10	46	(1·5)	15	43	(1·1)	11		—	
		WM	50	(2·1)	11	48	(2·4)	7	45	(1·2)	12	46	(0·8)	20	46	(0·6)	10		—	
		WV	45	(1·0)	7	45	(2·0)	2	49	(6·0)	2	44	(1·4)	7	47	(2·3)	5		—	
	♀	DV	41	(0·8)	13	42	(1·6)	7	41	(0·6)	8	46	(1·5)	7	40	(1·9)	7		—	
		WM	44	(1·3)	10	48	(2·0)	4	43	(2·1)	13	44	(1·0)	11	44	(1·3)	11		—	
		WV	45	(1·0)	2	46	—	1	47	(1·1)	4	43	(1·1)	6	47	(1·8)	4		—	
Androgen ($n\ mol\ l^{-1}$)	♂	DV	6·6	(2·95)	13	18·9	—	1	7·7	(2·90)	8	26·3	(4·22)	16	29·3	(5·10)	9	11·5	(2·49)	6
		WM	11·8	(2·47)	8	9·5	(2·66)	4	4·7	(2·33)	6	17·4	(1·84)	11	16·9	(3·48)	7	12·8	(5·19)	6
		WV	5·3	(5·28)	5	0	—	2	12·4	(3·60)	2	26·8	(9·10)	8	8·0	(3·76)	5		—	
	♀	DV	0	—	13	0	—	1		—		0	—	2	0	—	3		—	
		WM	0	—	8		—			—			—			—			—	
		WV	0	—	2	0	—	1	0	—	5	0	—	5	0	—	5		—	
Body weight (g)	♂	DV	92	(4·6)	15	86	(9·2)	9	65	(9·0)	8	87	(5·0)	17	94	(4·8)	12		—	
		WM	84	(10·6)	11	96	(10·7)	9	79	(7·8)	16	86	(5·5)	21	98	(5·1)	10		—	
		WV	59	(11·7)	6	103	(8·7)	3	74	(12·0)	2	91	(8·9)	8	76	(11·9)	5		—	
	♀	DV	67	(6·9)	14	64	(9·8)	10	72	(10·6)	9	58	(5·4)	7	72	(5·4)	7		—	
		WM	65	(9·4)	10	64	(10·6)	8	76	(7·8)	15	86	(5·1)	12	92	(6·5)	11		—	
		WV	40	(18·0)	2	97	—	1	65	(8·9)	5	69	(7·9)	7	63	(10·7)	3		—	

Appendix 3

Analysis of variance on various measurements taken from the blood of ***Melomys***

			Overall			Interaction			Time			Site		
			d.f.	F_s	*P*	*d.f.*	F_s	*P*	*d.f.*	F_s	*P*	*d.f.*	F_s	*P*
Free corticosteroids	♂		14, 107	3·969	<0·0001	8, 107	1·484	0·171	4, 115	8·587	<0·0001	2, 115	4·154	0·018
	♀		14, 86	3·452	<0·0001	8, 86	1·053	0·403	4, 94	8·287	<0·0001	2, 94	6·236	0·0029
Androgens	♂		9, 59	5·543	<0·0001	4, 59	1·022	0·403	4, 63	9·568	<0·0001	1, 63	5·672	0·020
Albumins	♂		17, 129	6·282	<0·0001	10, 129	1·668	0·095	5, 139	13·471	<0·0001	2, 139	6·956	0·0013
	♀		17, 105	4·724	<0·0001	10, 105	0·931	0·508	5, 115	12·551	<0·0001	2, 115	5·051	0·0079
TPCs	♂		9, 102	4·845	<0·0001	4, 102	2·164	0·078	4, 106	7·619	<0·0001	1, 106	7·400	0·0076
	♀		11, 97	4·799	<0·0001	5, 97	2·11	0·071	5, 102	7·112	<0·0001	1, 102	5·937	0·017
Haematocrit	♂		14, 122	1·623	0·082		—			—			—	
	♀		14, 92	1·642	0·083		—			—			—	
Haemoglobin	♂		14, 128	2·058	0·018	8, 128	2·026	0·048	4, 131	2·149	0·078	2, 136	1·578	0·210
	♀		14, 98	6·525	<0·0001	8, 98	6·832	<0·0001	4, 106	3·325	0·013	2, 106	4·194	0·0177
MCBC	♂*		11, 115	3·662	0·0002	5, 104	0·249	0·939	5, 109	8·084	<0·0001	1, 109	0·474	0·493
	♀*		11, 90	8·058	<0·0001	5, 90	0·860	0·511	5, 95	16·803	<0·0001	1, 95	0·002	0·966
Haemoglobin		WM	9, 109	5·28	<0·0001	4, 109	1·39	0·24	4, 113	10·24	<0·0001	1, 113	0·04	0·84
		WV	9, 31	4·22	0·0012	4, 31	2·15	0·098	4, 35	5·69	0·0012	1, 35	2·37	0·13
		**DV	9, 86	2·00	0·049	4, 86	0·58	0·67	4, 90	3·07	0·020	1, 90	2·99	0·09

* Denotes significant Bartlett's test (heterogeneous variance) so the seasonal variation was tested using a non-parametric test (Kruskal–Wallis test) ♂ $\chi^2_5 = 63{\cdot}9$; $P < 0{\cdot}001$: $\chi^2_5 = 61{\cdot}8$; $P < 0{\cdot}001$

** DV showed considerable heterogeneity—a non-parametric test (Kruskal–Wallis) showed significant changes in haemoglobin concentration through time $\chi^2_4 = 21{\cdot}13$; $P = 0{\cdot}0003$

Appendix 4

Summary of a posteriori follow-up tests on those physiological variables which showed significant differences between months or grids. In each row (month and site separately) common letters denote columns which do not differ at $P = 0{\cdot}05$

	Month						Site		
Variable	1981 Sept.	1982 Jan.	April	July	Sept.	Nov.	DV	WM	WV
Free corticosteroid	a	ab		bc	c	a		a	a
Testosterone	ab	a	a	b	b	—			—
Albumin	a	a		a	a		a		a
TPCS	a	a		a	a	a		a	a
Haemoglobin	Complex: see text								
MCBC	Complex: see text								