

**Ecology and physiology of the northern quoll, *Dasyurus hallucatus*
(Marsupialia, Dasyuridae), at Mitchell Plateau,
Kimberley, Western Australia**

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(With 1 plate and 4 figures in the text)

Breeding, population dynamics and seasonal changes in physical and physiological parameters were examined in the northern quoll (*Dasyurus hallucatus*) at Mitchell Plateau, Western Australia, between September 1981 and November 1982. Females gave birth to a single litter of young in July or August. Births were earlier on near-coastal sites than on inland sites. Litter size was greater on inland sites and litter size differed between years. By September all females were either carrying pouch young or were lactating. Lactation ceased by April. Testosterone levels in males peaked in July. There were significantly more male than female pouch young. However, in only one grid was the adult sex ratio different from parity, with an excess of females in September 1981 and 1982. Embryonic mortality was > 53% but loss of pouch young was small. Although males and females moved similar distances between successive recaptures, the extent of movement varied seasonally, being greatest in September. Males were generally larger and heavier than females. Seasonal variations were recorded for most physical and physiological parameters. The most pronounced changes occurred towards the end of the dry season (July to September) for both males and females. Over this period there was a significant decline in weight (males), haematocrit (males), plasma albumin (males) and leucocytes (both males and females) and significant elevations in values of haemoglobin and both free and protein-bound cortisol in both males and females. Few males survived the post-mating period from July to September. They appeared to decline in condition over this period more markedly than females: they lost more weight, their haematocrit and plasma albumin values declined to a greater extent, and they were more heavily infected with lice (*Boopis uncinata*). Males with lower testosterone and higher free and protein-bound cortisol had increased prospects of surviving the breeding season, which suggests that it is the dominant males that are less likely to survive the breeding season. Individuals in the three major populations at Mitchell Plateau differed greatly in their physiological values. The high-density population in a sandstone area had intermediate levels of free cortisol and higher haematocrit values than both the other populations, and higher levels of haemoglobin than the population on laterite substratum.

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Introduction

Post-reproductive mortality of all males of certain species of dasyurid marsupials (*Antechinus* spp. and *Phascogale* spp.) has aroused much recent interest in this family of marsupials and has led to the characterization of several different life history strategies (Lee, Woolley & Braithwaite, 1982).

The northern quoll, *Dasyurus hallucatus* (Plate I), is the largest and most widespread dasyurid in tropical Australia (Kitchener, Keller, Chapman, McKenzie, Start & Kenneally, 1981) and at Mitchell Plateau it is an abundant species in a wide variety of habitats (Bradley, Kemper, Kitchener, Humphreys & How, 1987). The species has a life history strategy characterized by monoestry with pronounced reproductive seasonality and by both sexes surviving to reproduce in subsequent breeding seasons; however, there is some evidence that males have a higher turnover with some individuals dying after mating (Begg, 1981*a*). These life history parameters are characteristic of Strategy II species and contrast with those of Strategy I species where mortality of all males occurs at the conclusion of a short breeding season (Lee *et al.*, 1982).

Previous studies (Barnett, 1973; Lee, Bradley & Braithwaite, 1977; Cuttle, 1982; Bradley, 1987) have examined the ecology and physiology of dasyurids that show total post-reproductive mortality of all males. Death of dasyurid males at the end of the first breeding season is considered to result from stress mediated through an increase in plasma glucocorticoid concentration (Barnett, 1973; Lee *et al.*, 1977; Bradley, 1987), and to be exacerbated by a reduction in plasma corticosteroid binding globulin (CBG) concentration associated with a progressive rise in plasma androgen (Bradley, McDonald & Lee, 1980; Bradley, 1987). As glucocorticoids are known to inhibit most stages of the inflammatory and immune responses of animals (Fauci, 1979), it is not surprising to find that the debilitating effects of increased glucocorticoids in these males are manifest by anaemia (Cheal, Lee & Barnett, 1976), lymphocytopenia and neutrophilia (Cheal *et al.*, 1976; Bradley, 1987), splenic hypertrophy (Barker, Beveridge, Bradley & Lee, 1978), gastrointestinal haemorrhage and disease (Bradley *et al.*, 1980; Bradley, 1987), immune suppression and disease (see review by Lee & McDonald, 1985), unspecified degeneration of major organs (Williams & Williams, 1982) and by negative nitrogen balance (Bradley, 1987).

The pattern of clinical health of those dasyurids that do not show post-mating mortality of all males has not been seriously investigated in the field. Such studies are considered of importance to our understanding of the mechanisms underlying life history strategies of dasyurids and perhaps

to the evaluation of the significance of stress and its debilitating effects on male dasyurids following mating.

This study was principally designed to investigate the ecophysiology of *D. hallucatus* in different habitats and is part of a larger study of the ecophysiology of tropical small mammals (Humphreys, How, Bradley, Kemper & Kitchener, 1984; Kemper, Kitchener, Humphreys, How, Bradley & Schmitt, 1987; Kemper, Kitchener, Humphreys, How, Schmitt & Bradley, In prep.; Bradley, Kemper, Kitchener, Humphreys & How, 1987; Bradley, Kemper, Kitchener, Humphreys, How & Schmitt, 1988). Additionally, the physiological changes of post-mating males of this species were compared to those in other dasyurids that show either a complete or incomplete post-mating male mortality.

Materials and methods

Trapping and measurements

Eight capture-mark-release (CMR) trapping grids, each of 100 traps, were sited and operated as detailed in Bradley, Kemper, Kitchener, Humphreys & How (1987). The term 'trip' has been used throughout to define the 6 discrete trapping periods in September–October 1981, January 1982, April 1982, July 1982, September–October 1982 and November 1982. Removal sites, from which animals were removed for post-mortem examination, were established in vegetation similar to that occurring on each CMR grid.

Individuals were identified by unique ear markings. At the first capture of an animal at any trapping period, about 0.5 ml of blood was immediately removed from the orbital sinus (Halpern & Pacaud, 1951; Riley, 1960). Individuals were sexed, then weighed and measured for head length, scrotal length and width and diameter of the tail base (tail diameter). Reproductive condition was assessed. In females, the condition of the teats (barely visible, lactating, distended, regressed), appearance of the pouch and presence of pouch young, and the crown-to-rump, pes and tail lengths and extent of furring of pouch young were recorded. In males, scrotal size and epididymal sac condition (full, distended, undistended) were recorded. A scrotal index was calculated using the product of scrotal length and width. At subsequent recaptures within a trapping period only trap position, weight and reproductive condition were noted. A cloacal swab was generally taken for later screening for *Salmonella* and *Arizona* (How, Bradley, Iveson, Kemper, Kitchener & Humphreys, 1983).

Estimates of population size were made using the known-to-be-alive (KTBA) method, while home range size was calculated, using the method of Mohr (1947), from individuals captured more than 3 times.

Blood sampling and analyses

These procedures have been detailed in Kemper, Kitchener, Humphreys, How, Bradley & Schmitt (1987).

The plasma concentration of testosterone and cortisol and the glucocorticoid partitioning into free, albumin-bound and high-affinity bound compartments were determined using methods described elsewhere (Bradley, McDonald & Lee, 1976, 1980; McDonald, Lee, Bradley & Than, 1981). Cortisol was assumed to be the major glucocorticoid in *D. hallucatus* as is usual for marsupials (Oddie, Blaine, Bradshaw, Coghlan, Denton, Nelson & Scoggins, 1976). The glucocorticoid assay was modified to use ³H-cortisol and cortisol standards.

Animals from removal sites were transported in calico bags to the field laboratory, where their blood was sampled and treated as above. They were killed with an overdose of Nembutal, weighed and measured and their external reproductive condition was assessed. Liver, heart and kidney were dissected from all killed animals and frozen in liquid nitrogen for protein electrophoresis (14 proteins were studied but no genetic variation was detected). The reproductive tracts were removed and fixed in Bouin's solution for later histological examination. Macroscopic examination was made of female uteri to count the number of

embryos. Histological examination of male testes and assessment of the spermatogenic stage was used as an aid to assign males to juvenile or adult categories.

Statistics

Multiple regressions were computed using GENSTAT (Rothamsted Experimental Station). Each effect was tested with all other effects of the same order and lower orders in the model. Because of the large number of tests only those with $P < 0.01$ were used to indicate which variables were worthy of further investigation. These were tested for homogeneity of variance (Bartlett's test; Sokal & Rohlf, 1981) and log transformed where necessary before follow-up tests for differences between age, sex, trip and area groups. When a single comparison was investigated *t*-tests were applied, using the pooled variance (Snedecor & Cochran, 1969). The Behrens Fisher test (conservative for type 1 errors) was used for multiple comparisons at $\alpha < 0.05$. Comparison between seasonal movement of adults was examined using Dunn's Multiple Comparison test (Daniel, 1978) following Kruskal-Wallis one-way analysis of variance (Davies, 1971). All data in text and tables are presented as mean, standard deviation and sample size, e.g. 3.2 ± 0.76 (27).

Study areas

The landforms and vegetation types of the Mitchell Plateau have been described previously (Hnatiuk & Kenneally, 1981; Bradley, Kemper, Kitchener, Humphreys & How, 1987). Of the 8 CMR grids established, 5 had populations of *D. hallucatus*. Brief details of these grids follow.

The Camp Creek Sandstone (CS) grid contained both Low Open Woodland and Hummock Grass *Plechtrachne* sp., on the King Leopold Sandstone formation. *Dasyurus hallucatus* were trapped over the entire 2.25 ha grid and on 2 additional traplines sited 100 and 200 m distant from the grid in deeper gullies.

Lone Dingo Woodland (DW) grid occurred on a northern outlier of the main lateritic plateau and occupied a small valley and ridge contiguous to the deciduous Lone Dingo Vine Thicket (DV) grid. The entire DW grid was burnt during June 1982. *Dasyurus hallucatus* occupied the entire 2.25 ha of each grid, and individuals regularly moved between both areas. For the purposes of this study, the areas DW and DV were treated as one population (DW/V).

The Walsh Point Mosaic (WM) grid had Open Woodland of *Eucalyptus* spp. over dense grasses and a rocky creek containing large boulders and deciduous thicket elements. This 1.6 ha of the grid was occupied by *D. hallucatus*, while a sharply defined area of Low Closed Forest (Mangrove) that was flooded tidally remained unoccupied.

Walsh Point Vine Thicket (WV) was a deciduous vine thicket of dense Low Forest between a beach and volcanic cliff c. 2 km from WM. The seaward aspect of the forest was more deciduous and provided little cover between July and September. The entire 2.25 ha grid was occupied by *D. hallucatus*.

The DW/V grids and the WM/V grids and removal sites were adjacent to, or within 2 km of, the coast, while CS was located over 15 km inland. For the purposes of general discussion DW/V and WM/V grids and removal sites are referred to as coastal localities and CS grid and removal sites as inland localities.

Results

Demography

Trappability

Female *D. hallucatus* were shown to be caught more frequently than males when data from all trips and grids were combined. Fifty-one females were caught 268 times, while 46 males were caught 132 times ($\chi^2_1 = 33.4$, $P < 0.001$). The sex ratio was constant for each trip, although capture rates were greatest in September and least in January.



PLATE I. Adult northern quoll, *Dasyurus hallucatus*, from Dolphin Island, Dampier Archipelago, Western Australia. Photo: Sue Wilkins, Agriculture Protection Board, Western Australia.

Reproduction

Females with recent pouch young or with moist developing pouches were first recorded in July. By September all females were either lactating or carried pouch young; one animal at WM had a moist pouch suggesting pregnancy. Lactation continued through November and into January in both localities (Fig. 1).

The timing of reproduction (Fig. 1) was significantly earlier at near-coastal localities than at inland localities (combined data $P=0.0039$, Fisher's Exact Test). Of the eight females caught in July on near-coastal grids, two had small pouch young and two had moist and developing pouches indicative of pregnancy. All four females from near-coastal removal sites had developing uterine blastocysts and moist pouches. None of the 15 inland females caught on grids in July had pouch young or moist pouches and neither of the two females from removal sites showed any sign of reproductive activity. Earlier reproduction on near-coastal sites was also indicated by the head lengths of litters at the two types of sites. In September 1981, mean head length of pouched young was 13.8 ± 2.8 (6) mm from inland and 21.1 (1) mm from coastal localities, while for September 1982 it was 12.2 ± 2.4 (11) mm and 22.9 ± 2.1 (4) mm, respectively ($F_{1,13} = 61.6$, $P < 0.001$).

All females examined had eight nipples. Litter size did not differ significantly between inland and coastal regions in September 1981: 6.1 ± 2.2 (9) and 8.0 (1); but it was significantly different in

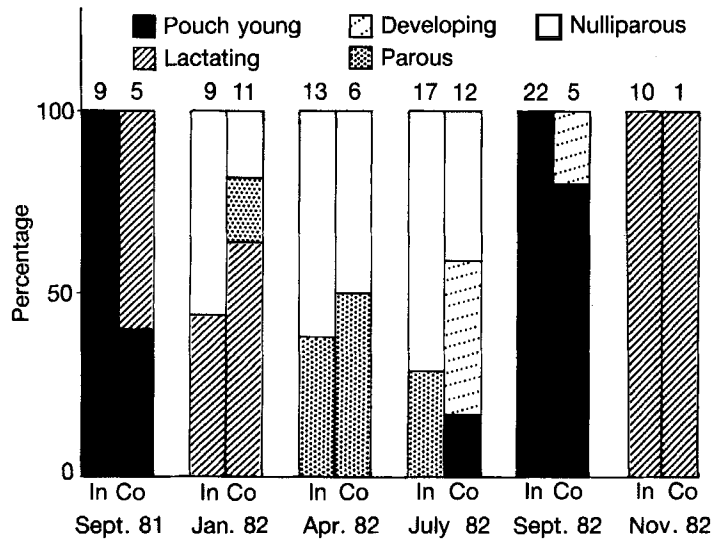


FIG. 1. Reproductive status of female *Dasyurus hallucatus* captured in inland (In) and coastal and near-coastal (Co) sites at Mitchell Plateau between September 1981 and November 1982. Numbers above each bar are sample size.

TABLE I

The number of individuals of each sex recorded on the CS grid and adjacent traplines and all grids combined during the study period. The percentage survival to the subsequent trip is presented in brackets

	Number of individuals recorded (% surviving to next trip)					
	Sept. 1981	Jan. 1982	Apr. 1982	July 1982	Sept. 1982	Mean % survival All trips
CS grid						
♀♀	6 (50)	6 (66.7)	13 (92.3)	16 (75)	22	(75.6)
♂♂	2 (0)	5 (20)	10 (80)	19 (5.3)	5	(27.8)
All grids						
♀♀	11 (64)	12 (66.7)	19 (89.5)	27 (59.3)	27	(70)
♂♂	4 (25)	7 (28.6)	17 (58.8)	26 (11.5)	8	(29.6)

September 1982: respectively, 7.8 ± 0.4 (22) and 6.3 ± 2.2 (4) ($t=3.3$, $P<0.01$). Litter size was greater in 1982 than 1981 on inland sites ($t=3.6$, $P<0.01$) and for all sites combined. There were significantly more males than females among the pouch young: 4.1 ± 1.8 (35), 3.0 ± 1.6 (35) ($\chi^2=7.81$, $P=0.005$).

Four females were recorded with 17.0 ± 5.4 developing blastocysts. This indicated that a considerable loss of embryos occurred in *D. hallucatus*.

TABLE II

Significant effects from multiple regressions of morphometric and physiological parameters and sex, age, trip and area for *Dasyurus hallucatus* at Mitchell Plateau. Significant *F* values and degrees of freedom are presented (** = $P < 0.01$, *** = $P < 0.001$)

Dependent variable	Independent variable									
	Sex × trip × area	Sex × trip	Sex × area	Age × trip	Age × area	Trip × area	Sex	Age	Trip	Area
Weight		7.56 5,131 ***			4.93 2,131 **		267.9 1,131 ***	65.5 1,131 ***	27.1 5,131 ***	
Head length				62.9 2,147 ***			76.7 1,147 ***	25.4 1,147 ***	14.0 5,147 ***	
Tail diameter							18.5 1,70 ***	22.6 1,70 ***	11.1 5,70 ***	
Scrotal index						5.24 3.43 **			6.87 5.43 ***	
Testosterone									11.5 5.43 ***	
Haematocrit	4.81 2,111 **									9.92 2,111 ***
Haemoglobin									3.56 4,113 **	8.62 2,113 ***
Leucocytes									8.50 4,113 ***	10.9 2,113 ***
TPCS	8.96 2,116 ***	3.88 5,116 **	5.04 2,116 **					6.94 5,116 ***	7.24 2,116 ***	
MCBC		4.26 5,117 **					15.3 1,117 ***	12.8 5,117 ***	6.78 2,117 ***	
Free cortisol	6.23 2,116 ***							8.69 5,116 ***		
CBG Bd cortisol	11.2 2,116 ***	4.03 5,116 **	4.93 2,116 **				7.41 1,116 **	7.92 5,116 ***	7.55 2,116 ***	
Albumin Bd cortisol								5.90 5,116 ***	5.63 2,113 **	
Total plasma albumin						3.03 9.124 **	14.1 1,124 ***		18.2 5,124 ***	

TABLE III

Morphological and physiological factors showing significant trip or sex differences for *Dasyurus hallucatus* at Mitchell Plateau

Variable	Trips						
	September 1981	January 1982	April 1982	July 1982	September 1982	November 1982	
Weight (g)	♀	412.5 ± 74.8 (11)	326.8 ± 118.4 (12)	378.4 ± 88.6 (17)	383.0 ± 60.6 (24)	340.0 ± 52.7 (8)	381.8 ± 42.8 (3)
	♂	498.8 ± 104.5 (11)	240.6 ± 67.4 (12)	563.6 ± 118.8 (19)	638.3 ± 127.0 (28)	498.1 ± 120.9 (26)	666.7 ± 14.4 (11)
Head length (mm)	♀	72.1 ± 3.9 (4)	67.9 ± 5.9 (6)	69.5 ± 3.1 (17)	68.5 ± 2.4 (26)	68.3 ± 4.1 (6)	73.3 ± 2.7 (3)
	♂	76.0 ± 4.8 (2)	64.0 ± 4.6 (5)	75.3 ± 4.3 (12)	74.5 ± 3.6 (13)	73.4 ± 5.5 (10)	83.1 ± 6.2 (10)
Tail diameter (mm)	♀	13.6 ± 1.1 (3)	12.9 ± 3.1 (2)	15.5 ± 2.2 (17)	14.6 ± 1.9 (26)	12.6 ± 1.7 (7)	12.7 ± 2.2 (3)
	♂	—	11.0 ± 1.8 (2)	15.7 ± 1.4 (17)	17.0 ± 2.0 (26)	14.4 ± 2.6 (7)	14.9 ± 2.3 (3)
Scrotal index (mm ²)	♂	330.6 ± 23.6 (4)	171.1 ± 84.7 (2)	415.1 ± 64.9 (14)	394.6 ± 60.7 (25)	363.1 ± 67.4 (7)	315.7 ± 10.2 (3)
Testosterone (nM)	♂	36.5 ± 5.7 (10)	25.5 ± 10.6 (12)	54.6 ± 14.0 (18)	87.3 ± 21.0 (25)	34.9 ± 15.1 (24)	27.0 ± 15.7 (3)
Haematocrit (%)	♀	46.4 ± 3.2 (4)	45.6 ± 7.5 (6)	44.8 ± 3.9 (15)	44.4 ± 5.6 (26)	44.9 ± 3.3 (7)	—
	♂	45.3 ± 5.0 (13)	44.8 ± 6.1 (16)	46.9 ± 4.2 (32)	48.0 ± 6.5 (52)	43.9 ± 2.2 (33)	—
Haemoglobin (g%)	♀ & ♂	15.8 ± 1.8 (14)	15.3 ± 2.8 (14)	15.9 ± 1.3 (32)	15.1 ± 1.9 (48)	16.4 ± 2.0 (31)	—
Leucocytes (10 ³ /mm ³)	♀ & ♂	8.18 ± 3.38 (9)	9.79 ± 6.10 (9)	9.21 ± 3.22 (17)	15.31 ± 8.16 (23)	10.97 ± 4.97 (26)	— (9)
TPCS (nM)	♀	111.1 ± 40.4 (4)	157.9 ± 84.4 (4)	204.6 ± 50.0 (16)	136.4 ± 49.7 (24)	185.5 ± 55.9 (8)	224.6 ± 85.8 (3)
	♂	176.8 ± 80.3 (9)	166.3 ± 133.8 (9)	145.1 ± 50.6 (17)	106.1 ± 47.1 (23)	161.1 ± 67.7 (26)	152.7 ± 55.6 (9)
MCBC (nM)	♀	247.2 ± 30.3 (4)	271.4 ± 69.0 (4)	294.9 ± 35.0 (16)	220.7 ± 24.3 (24)	227.5 ± 46.7 (8)	226.2 ± 20.5 (3)
	♂	252.8 ± 44.9 (9)	254.8 ± 54.8 (9)	223.1 ± 22.2 (17)	200.3 ± 33.0 (23)	215.4 ± 15.5 (26)	168.0 ± 28.6 (9)
Free cortisol (nM)	♀	9.3 ± 4.2 (4)	16.6 ± 13.5 (4)	19.8 ± 7.2 (16)	14.1 ± 6.5 (24)	22.3 ± 8.7 (8)	32.9 ± 18.6 (3)
	♂	19.6 ± 14.4 (9)	19.8 ± 19.5 (9)	16.0 ± 7.8 (17)	10.3 ± 5.2 (23)	19.4 ± 10.7 (26)	22.6 ± 9.1 (9)
CBG Bd cortisol (nM)	♀	86.2 ± 28.8 (4)	116.6 ± 54.6 (4)	154.2 ± 39.1 (16)	97.8 ± 32.0 (24)	127.2 ± 38.9 (8)	143.5 ± 41.3 (3)
	♂	123.6 ± 47.6 (13)	118.4 ± 89.1 (13)	103.4 ± 31.7 (33)	73.8 ± 29.8 (47)	109.1 ± 38.4 (34)	96.4 ± 33.8 (12)
Albumin Bd cortisol (nM)	♀ & ♂	21.0 ± 16.6 (9)	25.4 ± 21.2 (9)	28.2 ± 12.1 (17)	21.8 ± 11.2 (23)	35.2 ± 14.8 (26)	44.8 ± 24.7 (9)
Plasma albumin (g/dl)	♀	4.4 ± 0.3 (4)	4.0 ± 0.4 (4)	4.2 ± 0.3 (16)	4.6 ± 0.5 (24)	4.4 ± 0.4 (8)	4.0 ± 0.4 (3)
	♂	4.7 ± 0.1	3.7 ± 0.1	4.3 ± 0.2	5.0 ± 0.5	4.5 ± 0.3	4.1 ± 0.2

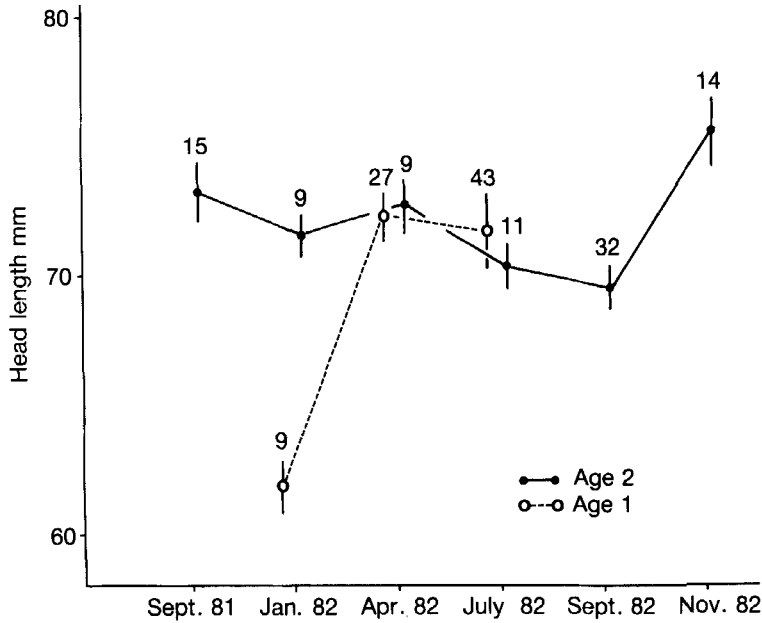


FIG. 2. Head length of *Dasyurus hallucatus* at Mitchell Plateau between September 1981 and November 1982. One-year-old (O) and two-year-old (●) individuals. Mean, standard error of the mean and sample size indicated.

TABLE IV
Physiological factors showing significant area differences for Dasyurus hallucatus at Mitchell Plateau

Variable	Grid		
	CS	DW/V	WM/V
Leucocytes ($10^3/\text{mm}^3$)	10.4 ± 4.7 (89)	16.2 ± 7.5 (17)	12.6 ± 8.8 (33)
Haematocrit (%)	46.7 ± 4.6 (100)	43.0 ± 5.2 (17)	43.7 ± 5.7 (30)
Haemoglobin (g%)	16.0 ± 1.6 (95)	14.2 ± 1.8 (18)	15.4 ± 2.5 (33)
TPCS (nM)	156.7 ± 67.5 (111)	109.3 ± 45.5 (16)	190.3 ± 70.0 (26)
MCBC (nM)	230.9 ± 43.9 (111)	203.6 ± 30.5 (16)	257.2 ± 50.2 (26)
Free cortisol (nM)	17.6 ± 11.1 (111)	11.5 ± 5.9 (16)	21.2 ± 10.9 (26)
CBG Bd cortisol (nM)	110.3 ± 43.0 (111)	79.4 ± 31.0 (16)	133.9 ± 47.3 (26)
Albumin Bd cortisol (nM)	28.3 ± 16.7 (111)	18.4 ± 9.3 (16)	34.8 ± 16.7 (26)
Albumin (g/dl)	4.4 ± 0.5 (111)	4.4 ± 0.4 (16)	4.5 ± 0.6 (26)
Scrotal index (mm^2)	378.5 ± 73.7 (39)	375.5 ± 86.1 (13)	416.2 ± 73.6 (6)

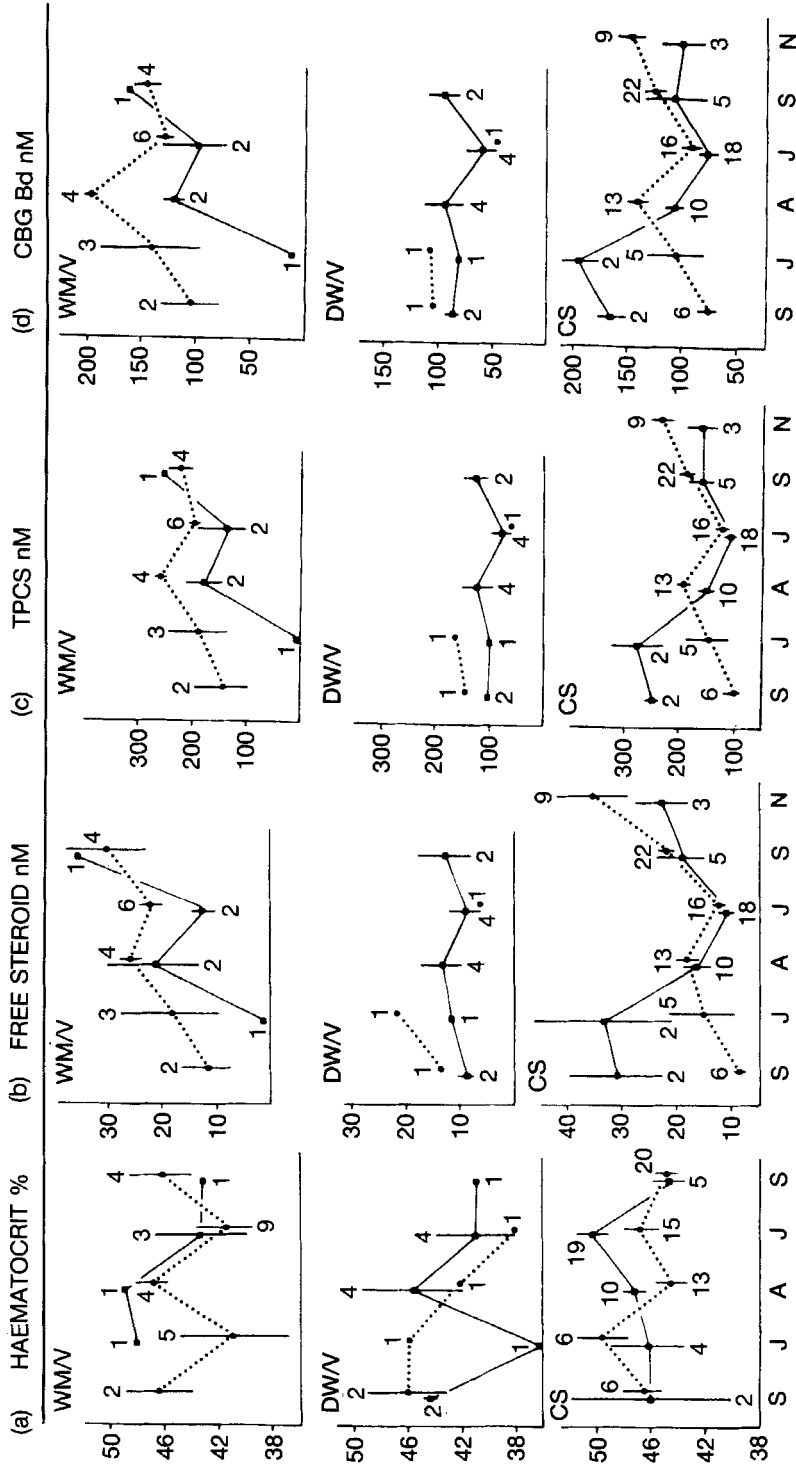


FIG. 3. Changes in haematocrit and steroid levels of *Dasyurus hallucatus* on grids WM/V, DW/V, CS (see text) at Mitchell Plateau between September 1981 and November 1982. (a) Haematocrit, (b) free cortisol, (c) total plasma cortisol and (d) globulin-bound cortisol. Mean, standard error of the mean and sample size indicated for males (solid lines) and females (broken lines).

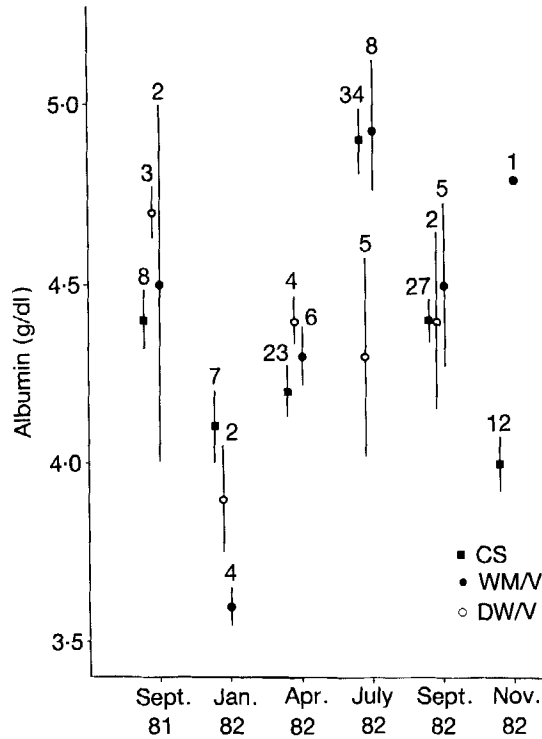


FIG. 4. Changes in total plasma albumin levels of *Dasyurus hallucatus* at Mitchell Plateau between September 1981 and November 1982 on the following grids: CS (■); DW/V (○); WM/V (●). Mean, standard error of the mean and sample size indicated.

Population composition and size

The largest population of *D. hallucatus* occurred on the inland sandstone grid (CS). Comparison of mean (five trips) population size on the five CMR grids occupied by *D. hallucatus* showed that CS (13.2 ± 3.3) had higher numbers ($P < 0.01$) than WV (4.4 ± 3.4), DV (2.4 ± 1.1), DW (2.2 ± 1.5) and WM (1.8 ± 0.8) (data from Bradley, Kemper, Kitchener, Humphreys & How, 1987); population sizes on WV, DV, DW and WM grids did not differ significantly.

The CS population was greatest in July and least in January before most of the weaned young entered the trappable population (Table I). The difference in numbers recorded between September 1981 and September 1982 was due to an increase in the area trapped from January 1982, when two approximately parallel traplines were established to the west of the grid to monitor the movements and home range of both the larger marsupials *Wyluda squamicaudata* and *Dasyurus hallucatus*.

Only on CS in September 1981 and 1982 was the sex ratio significantly different from parity ($\chi^2_1 = 10.7$, $P < 0.01$), with an excess of females (Table I).

Movement

Individual *D. hallucatus* were frequently observed to move beyond the boundaries of the grids after release, indicating that home ranges extended outside the trapping grids. On CS, where

additional traplines were placed, the home ranges of seven females (2.3 ± 1.2 ha) were not significantly greater than those of two males (1.8 ± 1.6 ha). The movements of females between successive captures (73.2 ± 84.9 (92) m) were also similar to those of males (85.7 ± 82.1 (49) m) on this extended trapping area. Individuals moved further ($P < 0.05$) between successive captures on CS in September (103.6 ± 99.2 (53) m) than in July (61.3 ± 82.2 (50) m) and April (61.3 ± 51.2 (27) m) but not January (70.1 ± 39.3 (8) m); the differences between July, April and January were not significant. One long-range movement was recorded within a day, a male moving 2.5 km between the WM and WV grids in July.

Survival

Survival of individuals in the population between successive trapping trips is presented in Table I for both the CS population and all populations combined. Males have a lower mean survival (28%) than females (76%) over all trips, although this is only statistically significant between July and September 1982 ($P < 0.001$, Fisher's Exact Test). The seasonal variation in survival for both sexes is similar, being lower during the breeding period, July–September.

Of the 10 parous females caught on grids in September 1981, three survived, all producing pouch young in the following July–September. An adult male from DW/V survived the 1981 mating period; on CS only one adult male, first caught in April 1982, appeared to survive to breed in July 1982.

Morphology

In a preliminary examination of morphological and physiological variables, the four populations (CS, DW/V, WM and WV) were analysed separately. No significant differences were observed between WM and WV and consequently data for these two populations (WM/V) were combined. Parous females caught during January, April and July 1983 were considered to be in their second year. Significant associations between morphological and physiological variables, and the independent variables of sex, age, trip and area are presented in Table II. These are discussed below.

Weight

There were significant sex-trip and age-area interactions for body weight. Males were significantly heavier than females during all trips except January 1982 (Table III). Both sexes lost weight between July and September, although only male weight loss was statistically significant. The significant reduction in mean body weight between September 1981 and January 1982 in both sexes is accounted for by the recruitment of young of the previous breeding season into the trappable population by January.

The age-area interaction results from first-year animals being significantly heavier on DW/V (565 ± 36 (8) g) than on WM/V (414 ± 40 (17) g) and CS (454 ± 25 (52) g). First-year individuals were also heavier than second-year individuals on DW/V (463 ± 28 (10) g), WM/V (385 ± 13 (16) g) and CS (425 ± 16 (4) g).

Head length

The age-trip interaction for this parameter is a result of young (first-year) individuals being significantly smaller than older (second-year) individuals in January but not at other seasons (Fig. 2). Males (74.1 ± 5.6 (62) mm) had significantly longer heads than females (69.4 ± 4.0 (107) mm).

Tail diameter

First-year individuals had a significantly larger tail diameter (14.7 ± 2.6 (38) mm) than second-year individuals (13.9 ± 2.4 (42) mm) and males (15.2 ± 2.6 (28) mm) had a significantly larger tail diameter than females (13.8 ± 2.4 (52) mm). Tail diameters were significantly larger in April and July in both sexes than in any other trip (Table III).

Scrotal index

Males from different areas showed no significant differences in scrotal index during the same trip. However, the change in males on DW/V from having the largest scrotal index in April to the smallest in July probably accounts for the significant interaction between trip and area in this parameter. The scrotal index was significantly ($P < 0.001$) smaller in January than in any other trip (Table III).

Physiology

Testosterone

Testosterone concentration was significantly higher in July than on all other trips and significantly higher in April than in September 1981, September 1982 and January 1982 (Table III).

Haematocrit

The significant sex-trip-area interaction (Table II) in haematocrit values is shown graphically in Fig. 3a. Individuals on CS (46.7 ± 4.6 (100)%) had higher ($P < 0.01$) haematocrits than both DW/V and WM/V (Table IV). Males in September 1982 (Table III) had significantly lower values than in July ($P < 0.001$) and April ($P < 0.05$), but differences between other trip comparisons were not significant; females showed no significant trip differences.

Haemoglobin

Haemoglobin concentration showed significant effects with both trip and area (Table II), but differences between individual trips (Table III) could not be detected using the Behrens Fisher test. The DW/V population had lower ($P < 0.01$) values than CS but there were no other significant area differences (Table IV).

Leucocytes

Total leucocyte counts (WBC) varied with both area and trip (Table II). Values were higher on DW/V ($P < 0.05$) than on either WM/V or CS; the latter two did not differ significantly (Table IV). Counts were higher ($P < 0.05$) in July than for other trips (Table III). Counts for September 1982 were higher than for September 1981 (Table III).

Steroids and proteins

Equilibrium dialysis at 36 °C using cortisol and 1:5 diluted plasma yielded a high-affinity binding constant (K_T) of $6.10 (\pm 0.32) 0.10^7 \text{ M}^{-1}$. This constant represents the mean \pm S.D. for a combined group of three females and three males. There was no apparent sex difference in this binding constant. No high-affinity binding was detected for either testosterone or 5 α -dihydrotestosterone.

Maximum cortisol binding capacity (MCBC) had a significant sex-trip interaction and significant area differences. Females had significantly ($P < 0.05$) higher MCBC values than males in January, April, July, September and November of 1982, but significantly lower values in September 1981 (Table III). Values were higher ($P < 0.05$) on WM than on the other grids while CS had higher ($P < 0.05$) values than DW (Table IV).

There was a significant interaction between sex, trip and area for each of free cortisol, total plasma cortisol (TPCS) and cortisol bound to cortisol-binding globulin (CBG Bd). The nature of this three-way interaction is illustrated for the three parameters (Fig. 3b, c, d, respectively).

Females generally had more free cortisol than males did (except in November). Cortisol values generally increased among females for all trip comparisons over the study except in July. For males, cortisol was lower in July than at all other seasons (Fig. 3b). Free cortisol levels were higher on WM than on CS, where in turn they were higher than on DW (Table IV). An examination of these interactions shows the pattern is similar in TPCS (Fig. 3c) and CBG Bd (Fig. 3d). In the densest population (CS), males had higher levels of free cortisol than females in both September 1981 and January 1982, but significantly lower levels in November 1982.

Levels of free steroids were not correlated with weight in any month, nor were the pooled data. Testosterone levels (Y) were directly related to individual weight (X) ($\log Y = 0.0005X + 1.416$, $t = 2.33$, $N = 52$, $P < 0.05$). For the pooled data the weight-corrected testosterone levels (Y) to the mean body weight (577 g) were inversely related to free steroid levels (X) ($\log Y = 1.935 - 0.013X$, $t = -4.673$, $N = 52$, $P < 0.0001$).

Albumin-bound cortisol values were highest on WM, lower on CS and lowest on DW (Table IV). Values for all trips were different, significantly so ($P < 0.05$) except in comparison of September 1981 with July 1982, and January 1982 with April 1982 (Table III).

Total plasma albumin concentrations differed between trips and areas, and were dependent upon the sex of the animals (Table II). Concentrations were higher in July than all other months on CS and WM, but not on DW. Values declined on all grids between September 1981 and January 1982 and, on CS, declined significantly between September 1982 and November 1982 (Fig. 4). Males (4.61 ± 0.55 (59) gdl^{-1}) had higher ($P < 0.01$) values than females (4.33 ± 0.45 (94) gdl^{-1}).

Pathogens

Thirty *Salmonella* serotypes were isolated from *D. hallucatus* at Mitchell Plateau. This represents the greatest number of serotypes isolated from any of the 18 mammal species examined from this region (How *et al.*, 1983).

Salmonella prevalence in *D. hallucatus* varied between sampling periods, with the greatest number of serotypes per swab and isolates per swab in April. There were no significant differences between inland and coastal sites in *Salmonella* prevalence (How *et al.*, 1983).

Discussion

This study of *Dasyurus hallucatus* at Mitchell Plateau was based on a 14-month study of three mark-recapture populations and individuals from several removal sites. Life history events and their timing were generally similar to those described for populations in the Northern Territory (Johnson, 1964; Calaby & Keith, 1974; Begg, 1981a). Young were born between late July and September (dry season) and all females, except one, were lactating or had pouch young in September; the one exception was a female in September which had a moist and developed pouch indicative of pregnancy.

The sex ratio of *Dasyurus hallucatus* at Mitchell Plateau changed significantly on grids during the progress of a cohort. Among pouch young there was a significant excess of males, but by weaning (January) the sex ratio was near parity. After the breeding season in July–August the survival rate of independent adults was lower for males than for females, so that the sex ratio was strongly biased towards females by September in each year. Overall sex ratios of *D. hallucatus* and the relative frequency with which either sex was caught was similar at Mitchell Plateau and Arnhem Land, Northern Territory, with females trapped significantly more often than males. Although only one male survived to a second reproductive season at Mitchell Plateau, six females (37%) bred in consecutive seasons. Begg (1981a) recorded 21% females breeding in two successive years and 6% that bred in three successive years in his Northern Territory population.

No accurate measure of survival of pouch young was possible in this study, but evidence from those females with either lactating or distended teats in November and January suggests that survival to weaning was high. In the Northern Territory, there was a 4.8% loss of pouch young between July and August, and a 27.6% loss between August and September (Begg, 1981a). Maturity occurred at about 11 months in both sexes.

Males were generally larger and heavier than females. Begg (1981a) noted that differences between the weight of the sexes was first observed at about 5 months of age. Unlike the situation in *Antechinus stuartii* males, which show a great deal of movement during the mating period (Lee *et al.*, 1977), there was no observable difference in the pattern or extent of movement between female and male *D. hallucatus*. Seasonal changes in the diameter of the tail base of *D. hallucatus* were similar in pattern to weight changes and suggest that this parameter may be an indicator of nutritional condition of individuals as has been shown for the murid rodent *Zyromys argurus* in the tropics (Begg, 1981b; Bradley, Kemper, Kitchener, Humphreys, How & Schmitt, 1988).

Following the peak breeding activity in *D. hallucatus* in July, testosterone levels of males declined sharply and there was a coincident decline in condition compared to females. This is reflected in their greater loss of weight and fall in haematocrit and plasma albumin values over the period July 1982 to September 1982 (other blood parameters show no inter-sex differences over that period). Maximal testosterone levels coincided with a June peak in breeding in male eastern quoll (*D. viverrinus*) in Tasmania (Bryant, 1986).

Post-mortem examination by P. Presidente (pers. comm.) of four male and six female *D. hallucatus* captured and killed from the study population in July showed no strong indication of any pathological condition (such as ulceration of the intestinal tract or infections—pathologies

TABLE V

Blood plasma parameters, weight and head length from males in July 1982 that were known to have survived to September 1982 and those not caught after July. Statistics are based on the Kruskal-Wallis non-parametric ANOVA

Variable	Surviving ♂♂	Unknown status	Significance levels
TPCS (nM)	156.67 ± 25.03 (3)	98.91 ± 45.24 (21)	0.045
MCBC (nM)	232.3 ± 52.3 (3)	189.86 ± 43.53 (21)	ns
Total plasma			
Albumin (g/dl)	5.27 ± 0.60 (3)	4.99 ± 0.53 (21)	ns
Free cortisol (nM)	15.30 ± 1.08 (3)	9.61 ± 5.16 (21)	0.032
CBG Bd (nM)	111.70 ± 22.81 (3)	68.38 ± 26.92 (21)	0.021
ALB Bd (nM)	29.67 ± 3.10 (3)	17.93 ± 10.9 (21)	0.049
Testosterone (nM)	53.00 ± 24.06 (3)	91.10 ± 15.83 (21)	0.018
Hb (g%)	14.53 ± 3.13 (3)	15.63 ± 1.53 (21)	ns
Hct (%)	44.7 ± 11.7 (3)	48.4 ± 5.9 (22)	ns
Leucocytes (10 ³ /mm ³)	15.9 ± 10.5 (3)	14.9 ± 5.9 (21)	ns
Wt (g)	600.00 ± 10.00 (3)	643.81 ± 135.18 (21)	ns
Head length (mm)	74.43 ± 2.40 (3)	74.12 ± 3.66 (22)	ns

ns, not significant

that are associated with stress-related mortality in many small dasyurids (McDonald *et al.*, 1981). An infestation with intestinal fluke (*Fibricola* sp.) in one male, and nematode larvae (*Abbreviata* sp.) in the peritoneal cavity and viscera of one female, may have been of pathological significance. Only males had bite wounds and scars and males were more heavily infested with lice (*Boopis uncinata*) than were females (P. Presidente, pers. comm.).

There is no complete post-breeding mortality in male *D. hallucatus* as occurs in some other dasyurids (Lee *et al.*, 1977; Bradley, 1987). Males did, however, undergo a major decline in numbers after the peak of breeding in July and August, such that by December–January there were very few adult males alive; a far higher proportion of the adult females had survived. At other times of the year male and female survival was similar.

The changes in blood values of *D. hallucatus* were the most complex yet recorded in our study of small mammals (see Barnett, How & Humphreys, 1979a, b, 1982; Bradley, Kemper, Kitchener, Humphreys, How & Schmitt, 1988; Humphreys *et al.*, 1984; Kemper, Kitchener, Humphreys, How, Bradley & Schmitt, 1987; Kemper, Kitchener, Humphreys, How, Schmitt & Bradley, in prep. Most blood parameters suggest that major changes occurred between July and September 1982 for both males and females, with significant elevations in the values of haemoglobin and total, CBG-bound, free and albumin-bound steroids and significant declines in the values of leucocytes and haematocrit (males only) and plasma albumin (males only). This period corresponded to a decreased survival in the populations, particularly amongst males (Table I).

However, this increased mortality of male *D. hallucatus* may be mediated by factors that are fundamentally different from those causing post-mating mortality in *Antechinus* and *Phascogale*. Males had lower levels of free and protein-bound cortisol, hence there was no indication that males were suffering greater general stress than females from April 1982 to November 1982.

The decrease in body weight of both sexes between July 1982 and September 1982 is coincident with an increase in free cortisol levels (Table III). This is consistent with the proposition that an

increase in free cortisol levels elevates protein catabolism, resulting in a negative nitrogen balance and loss of weight. Conversely, free cortisol levels decreased between April and July, which corresponded to an increase in body weight.

In *Dasyurus hallucatus* males during July, there was no significant correlation between MCBC and testosterone ($r^2 = 0.0029$). This contrasts with the strong inverse relationship between these two parameters in small dasyurids that show total post-mating mortality (*Antechinus stuartii*: Bradley *et al.*, 1980; *A. flavipes*: McDonald *et al.*, 1981; and *Phascogale calura*: Bradley, 1987), but is similar to the lack of correlation observed in *Sminthopsis crassicaudata* (McDonald *et al.*, 1981) which also has only a partial male mortality at breeding. In dasyurids with a complete post-mating mortality of males, the increase in testosterone that occurs during the breeding season is also associated with an increase in free cortisol levels (Bradley *et al.*, 1980; McDonald *et al.*, 1981; Bradley, 1987) as a result of more frequent aggressive encounters among males (Braithwaite, 1974). This event is thought to be mediated via direct effects of testosterone in suppressing CBG and a consequent increase in free corticosteroids (Bradley *et al.*, 1980).

An examination of the values for the plasma constituents of males in July 1982 showed that those known to survive to September 1982 had significantly higher levels of free and protein-bound cortisol, but lower levels of testosterone, than those males which were not caught after July 1982 (Table V).

In many species, dominant males have much higher levels of testosterone than do subordinates (Moberg, 1985). In captive *D. viverrinus* one or two dominant males mate with females, allowing no access by subordinate males to the females. Dominant males lose weight after reproducing and appear in poor condition, while subordinate males retain body weight and condition (J. Merchant, pers. comm.).

It is probable that the male *D. hallucatus* with high free cortisol and low testosterone levels are socially subordinate and are more likely to survive through to September, while the males with low free cortisol and high testosterone levels may be dominant but have poorer prospects of survival. Whether the high corticosteroid levels suppress testosterone levels is unclear, because brief stress can increase circulating testosterone while the long-term effect of glucocorticoid is to suppress testosterone secretion (Moberg, 1985).

Earlier studies have shown that post-mating mortality in some male dasyurids results from a broad syndrome of behavioural, physical and physiological changes. These changes are thought to be stress-related and mediated through increased plasma glucocorticoids. This present study indicates that high free corticosteroids do not necessarily produce the broad syndrome of changes leading to death found in some other dasyurids.

There were some differences in population biology between coastal and inland habitats. Birth of young, and presumably mating, was 3–4 weeks earlier in coastal than in inland populations and population density was far greater on the inland grid (Bradley, Kemper, Kitchener, Humphreys & How, 1987). This inland habitat of rocky valleys and sandstone platforms seems able to support dense populations of *D. hallucatus* (Kitchener *et al.*, 1981; Begg, 1981a).

Individuals in the dense population on CS had intermediate levels of free cortisol, a prime indicator of stress in dasyurids (Bradley, 1987), and were in good condition with high levels of haematocrit and haemoglobin and low counts of leucocytes (Table IV). The lower-density populations on DW/V and WM/V had lower haematocrit values than were found on CS, and the populations on DW/V also had lower haemoglobin levels than that on CS. DW/DV and WV/WM populations, however, had, respectively, higher and lower levels of free cortisol than the one on CS. Hence, in contrast to *Melomys* (Kemper, Kitchener, Humphreys, How, Bradley & Schmitt,

1987), there was no association between population density and stress (free cortisol) in *D. hallucatus*, and there is a suggestion that the higher-density population is also in the best clinical condition.

These population differences occur despite the extensive and seemingly continuous distribution of this species in the region (Bradley, Kemper, Kitchener, Humphreys & How, 1987). This study, and those on two murid rodents from Mitchell Plateau (Kemper, Kitchener, Humphreys, How, Bradley & Schmitt, 1987; Bradley, Kemper, Kitchener, Humphreys, How & Schmitt, 1988), indicate the extent of the physiological and ecological variability that can occur between adjacent local populations of a species within and between years. These findings are of wider importance in that they indicate the need for caution in adopting life history theories or management strategies for a species based on short-term studies on a single local population.

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