POPULATION ECOLOGY AND PHYSIOLOGY OF THE COMMON ROCK RAT, ZYZOMYS ARGURUS (RODENTIA: MURIDAE) IN TROPICAL NORTHWESTERN AUSTRALIA

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ABSTRACT.—The common rock rat, Zyzomys argurus, undergoes a marked seasonal change in abundance in rocky habitats of tropical Australia. Four local populations had highest numbers between the late-dry (September) and mid-wet (January) periods before undergoing a three- to four-fold decrease by the end of the wet season (April). Densities differed between these populations; one population disappeared in April. Immature individuals were more abundant in September when recruitment appeared maximal; the population decline is attributable to mortality in all age categories. Both sexes were reproductively active throughout the year, but pregnant females were most abundant in April. Litter size ranged from one to six and heavier females had more embryos. Gene frequencies of Z. argurus were significantly different between the wet (January and April) and dry (July and September) seasons and the ephemeral population had different gene frequencies from the others. Differences also occurred in concentration of plasma corticosterone, maximum corticosterone-binding capacity, and corticosteroid-binding globulin-bound corticosterone. In January, individuals in all local populations had normal body weight and albumin levels, and enlarged tail bases (a fat store). They also had elevated levels of free corticosterone, neutrophils, incidence of *Salmonella*, and total leucocyte count; lymphocyte to neutrophil ratios differed between populations. These data indicate that populations at differing densities and in average nutritional state had greater levels of physiological and pathological stress factors in the wet season suggesting that exogenous rather than endogenous factors control stress.

Most published information on small-mammal populations emanates from studies of species from higher latitudes in the northern (Krebs and Myers, 1974; Mihok et al., 1985), or southern hemisphere (Barnett et al., 1979; Bradley et al., 1980; Lee et al., 1977). Studies of tropical species are few and less comprehensive (Fleming, 1975). Criticisms have been made of many population studies in that experimental testing of hypotheses generally is ignored or that replicate populations of the species concerned or the treatment imposed are not studied (Hayne, 1978; Hurlbert, 1984; Snyder, 1978).

The objective of our study was to examine several populations of the same species in different tropical habitats over a period of time (Bradley et al., in press), to assess seasonal and spatial variation of population and physiological attributes studied.

Herein, we document the biology of the common rock rat (*Zyzomys argurus*), a saxicoline murid rodent that shows pronounced seasonal variation in numbers within the tropical northwest of Australia (Bradley et al., in press). The species is widely distributed in tropical Australia, occupying habitats in which larger rocks and boulders predominate (Begg, 1981; Watts and Aslin, 1981). Within the Mitchell Plateau region, Z. *argurus* is the most widely distributed species in the small-mammal assemblage and shows the greatest seasonal fluctuations in population size (Bradley et al., in press). In this respect it contrasts with the rodent, *Melomys* sp., restricted to closed forest, and the marsupial, *Wyulda squamicaudata*; both are arboreal and show little fluctuation in numbers (Humphreys et al., 1984; Kemper et al., 1987).

MATERIALS AND METHODS

Eight square trapping grids, each of 100 small aluminum traps spaced 15 m apart, were sited to sample as much of the topographical and vegetational heterogeneity as practicable. A trapline in a similar but disjunct habitat and between 300 and 500 m from each grid was operated to remove individuals for postmortem analyses.

All grids and removal sites were sampled during a 3–4-week period in September (and early October), 1981 and January, April, July, and September (and early October) 1982. Trapping periods lasted either five or six consecutive nights on each grid and a shorter trip was undertaken in November 1982 (Bradley et al., in press).

Unique toe clips were used to identify individuals. At first capture in any trapping period about 0.5 ml of blood was removed immediately from the suborbital sinus of all animals (Halpern and Pacaud, 1951; Riley, 1960). Measurements and observations on individuals follow those outlined for *Melomys* (Kemper et al., 1987); a cloacal swab generally was taken for later screening for *Salmonella* and *Arizona* (How et al., 1983).

Estimates of population size were made using the known-to-be-alive method; home-range size was calculated using the convex-polygon method for individuals captured more than three times near the center of a study grid.

Blood sampling and processing procedures have been detailed in Kemper et al. (1987). Plasma-albumin concentration was measured using the method of Rodkey (1965), scaled down to accommodate plasma samples of $10\mu l$. Bovine serum albumin (Sigma Chemical Co., USA) was used routinely as the standard and all values so determined were corrected for Z. *argurus* albumin-binding characteristics.

The plasma concentration of testosterone and corticosterone, and the glucocorticoid partitioning into free, albumin-bound and high-affinity-bound compartments were determined using methods described elsewhere (Bradley et al., 1976, 1980; McDonald et al., 1981). Corticosterone was assumed to be the major glucocorticoid in Z. *argurus*, a pattern common for rodents (La Plante et al., 1964; Pêron, 1960). The glucocorticoid assay was modified to use ^{3}H-corticosterone and corticosterone standards and the glucocorticoid measured in these assays will be referred to as corticosterone.

Animals from removal sites were killed with an overdose of Nembutal, measured, and their organs were removed for protein electrophoresis or histological studies. Uteri were examined to count the number of embryos or implantation scars that indicated state of maturity. Histological examination of male testes and assessment of the spermiogenic stage was used as an aid to assign males to mature or immature categories.

"Cellogel" electrophoresis of red-blood-cell extracts and plasma (Meera Khan et al., 1982) was used to investigate genetically determined protein variation. The proteins examined were: acid phosphatase, adenosine deaminanse, adenylate kinase, fructose-1,6-diphosphatase, glucose-6-phosphate dehydrogenase, hemoglobin, isocitrate dehydrogenase, lactate dehydrogenase, malate dehydrogenase, malic enzyme, 6-phosphogluconate dehydrogenase, and phosphoglucomutase. Globin was prepared by acid-acetone precipitation and separated by electrophores is in 8 M urea and 20 mM dithiothreitol (Hammerberg et al., 1974).

Multiple regressions were computed on all morphometric and physiological variables using GENSTAT (Rothamsted Experimental Station). Each effect was tested with all other effects of the same order and lower orders in the model. These analyses were used to indicate variables worthy of further investigation. Data were analyzed further by one-way analysis of variance followed by multiple-comparison tests if significant interaction was detected. Data sets with homogeneous variances, determined using Bartlett's test, were examined for significant effects using parametric analysis of variance and the GT2 multiple-comparison procedure (Sokal and Rohlf, 1981) at $\alpha = 0.05$. Data sets not homogeneous, even after transformation, were tested for significant effects using the Kruskall-Wallis one-way analysis of variance by ranks (Davies, 1971) and Dunn's multiple-comparison test (Daniel, 1978) at $\alpha = 0.05$.

To assess maturity status of the populations from capture-mark-recapture grids, discriminant-function analysis was performed on individuals of known reproductive status using the SPSS package. Variables tested as discriminators of sexual maturity for both sexes were head length and weight; additionally in females, condition of the vagina and teats and, in males, position of the testes and epididymal-sac condition were tested.

The Mitchell Plateau region of tropical northwestern Australia has one of the richest and least-altered assemblages of small terrestrial mammals on the continent (Kitchener et al., 1981), consisting of 19 species distributed across a marked topographical and vegetational gradient (Bradley et al., in press). The landforms and vegetation types of the Mitchell Plateau have been described previously (Bradley et al., in press; Hnatiuk and Kenneally, 1981). Of the eight capture-mark-recapture grids established, only four had populations of Z. *argurus*.

The Camp Creek Sandstone grid contained both low open woodland and hummock grass on the King Leopold Sandstone formation and Z. *argurus* was trapped over the entire 2.25-ha grid. Lone Dingo woodland grid was on a northern outlier of the main lateritic plateau and occupied a small valley and ridge adjacent to a deciduous vine thicket. The entire grid was burned 2 weeks before trapping in July. Z. *argurus* occupied only 1.3 ha of the grid; it avoided that portion with deep volcanic soils and no boulders. The Walsh Point mosaic grid had open woodland of *Eucalyptus* sp. over dense grasses; a rocky creek containing large boulders and deciduous vine thicket elements. Only 1.6 ha of the grid was occupied by Z. *argurus*; the remainder, a mangrove community flooded by tides, remained unoccupied. Walsh Point vine thicket was a deciduous-vine thicket of dense low forest between a beach and volcanic cliff and the entire 2.25-ha grid was occupied by Z. *argurus*.

RESULTS

Population Ecology

Population size, density, and composition.—The annual pattern of population numbers was similar on all grids (Table 1), being greatest in the late-dry or early-wet seasons (September–January) and least during the late-wet season (April). Breeding commenced in the late-wet season and the increase in numbers resulted from recruitment of the young of the year into the population.

Numbers on the inland Camp Creek grid declined markedly from a peak of 40 in January 1982 to 14 (with only two immature males present) in April 1982. The part of Walsh Point mosaic grid occupied by Z. *argurus* was waterlogged by a cyclone during trapping in January; the population was re-established by September when relatively high numbers were present. No males were captured on the Dingo Woodland grid in either April or July.

Densities of Z. *argurus* varied significantly between grids. The mean ($\pm SD$) of individuals per ha at Camp Creek (12.8 ± 4.5, $n = 5$) was significantly greater than on all other grids ($P < 0.01$) and Dingo Woodland grid (4.3 ± 1.4, $n = 5$) had a significantly ($P < 0.05$) denser population than Walsh Point vine thicket grid (2.3 ± 1.1, $n = 5$). There were no significant differences in density between either of these grids and the Walsh Point mosaic grid (3.5 ± 3.8, $n = 5$), where the population was transient and highly variable ($CV = 109\%$), probably because of seasonal flooding.

Capture rates for females (179 captures of 79 individuals) was not significantly greater than for males (175 captures of 95 individuals). The sex ratio was not significantly different from parity in the total sample or in any subsample, except for an excess of males on the Camp Creek grid during routine sampling in September 1982 ($\chi^2 = 6.43$, $d.f. = 1$, $P < 0.05$). Of 114 individuals collected from removal sites during the six trips, 51 were females and 63 males.

Survival.—The number of individuals surviving between trips was low on all grids (Table 1). There were intervals when populations at near-coastal sites (Walsh Point mosaic, Walsh Point vine-thicket, and Dingo Woodland grids) had either females, males, or both failing to survive. This indicates either periods of low susceptibility to capture or periods of higher dispersal or mortality.

The Camp Creek population had no significant differences between survival rates for any period. However, the high survival between April and July 1982 on this grid contrasts with the generally low survival in other areas.

Home range and movements.—There was no significant difference in mean ($\pm SD$) home-range areas of females ($1,168 \pm 1,154$ m^2, $n = 17$) and males (686 ± 500 m^2, $n = 13$). Within grids, there was no significant difference between females and males in the distances moved between successive captures. Females moved similar distances between recaptures on all grids although mean ($\pm SD$) distances moved by males on Walsh Pint mosaic grid (56.0 ± 23.6 m, $n = 11$) was greater ($P < 0.05$) than on the Camp Creek grid (28.0 ± 23.4 m, $n = 31$), but not on the Dingo Woodland (24.3 ± 21.1 m, $n = 11$) and Walsh Point vine-thicket (35.1 ± 19.0 m, $n = 6$) grids. No seasonal differences in patterns of individual movement within or between grids were apparent.

TABLE 1.—*Numbers of* Zyzomys argurus *of each sex captured on capture-mark-recapture grids during each sampling period and the percentage surviving to capture during the subsequent sampling period, Mitchell Plateau, northwestern Australia.*

	Grid							
	Camp Creek				Walsh Point (vine)			
	Females		Males		Females		Males	
Sampling period	n	%	n	%	n	%	n	%
September 1981	18	22.2	12	33.3	2	100.0	3	0
January 1982	20	30.0	18	22.2	4	75.0	4	25.0
April 1982	6	50.0	7	71.4	3	0	1	0
July 1982	9	11.1	12	25.0			2	50.0
September 1982	5	60.0	23	43.5	2	a	5	a
Totals	58	29.3	72	36.1	11	45.4	15	13.3

a Trapping not conducted after September 1982, hence number surviving unknown; number captured not included in total for September 1982 or grand total.

The population on the Walsh Point grid disappeared after a cyclone in January. No *Z. argurus* was caught there in April, and only a solitary juvenile male was caught in July, but by September the population was re-established and unmarked individuals of all categories were present. A single individual was captured on a nearby grid in July and on another nearby grid in July and September. These data suggest that dispersal within Z. *argurus* occurs from July to September and possibly later, although on established grids it was not possible to distinguish between recruits and immigrants. No differences in susceptibility to capture were detected between populations.

Reproduction, growth, and maturity.—During all collection periods some females and males showed histological evidence of reproductive activity (Fig. 1). Pregnant females were recorded during all sampling periods, but with a pronounced peak frequency during April. Litter size ranged from one to six with a mean ($\pm SD$) of 2.7 ± 1.2 ($n = 17$). The correlation between body mass and litter size was 0.520 ($n = 17$, $P < 0.05$). The smallest (24 g) reproductively active female was collected in April. Immature females were present throughout the year, but were represented by only a single specimen in April. Placental scars ranged from one to 11 with a mean ($\pm SD$) of 4.3 ± 2.8 ($n = 24$). No significant variation in number of embryos or scars was detected in different areas.

Variation in observer ability and difficulty in determining pregnancy by palpation made interpretation of pregnancy status in animals in the field uncertain. All females had a perforated vagina in April, indicating this was a peak period in reproductive activity.

Reproductively active males were present throughout the year (Fig. 1). Most immature males were recorded during the two late-dry sampling periods (September 1981 and 1982). The smallest reproductively active male weighed 24 g.

The rate of change in weight and head length did not differ significantly between females and males during the study; neither were differences observed in growth rates of individuals from different areas.

When only immatures were considered there was a significant difference ($t = 3.55$, $d.f. = 10$, $P < 0.01$) between mean ($\pm SD$) increments in weight (g/week) for females (0.55 ± 0.23, $n = 5$) and males (1.15 ± 0.36, $n = 7$), but not for mean length (mm/week) of the head (females, 0.19 ± 0.13, $n = 4$; males, 0.17 ± 0.05, $n = 7$).

Canonical discriminant-function analysis was performed on weight, head length, and the external reproductive criteria of individuals whose maturity was determined histologically. Discriminating functions correctly classified 93% of females and 91% of males in these samples and were used to assign live-caught individuals into maturity categories.

Teats of immature females invariably were barely visible; all had imperforate vaginae. However some mature females captured in January had teats that regressed to become indistinguish-

TABLE 1.—*Extended.*

Grid											
Walsh Point (mosaic)				Lone Dingo Woodland				Totals			
Females		Males		Females		Males		Females		Males	
n	%	n	%	n	%	n	%	n	%	n	%
3	0	3	66.7	4	25.0	3	66.7	27	25.9	21	38.1
1	0	5	0	2	50.0	2	0	27	37.0	29	17.2
				3	66.7			12	41.7	8	62.5
		1	100.0	4	75.0			13	23.1	15	33.3
6	16.7	8	37.5	4	a	3	a	11	36.4	31	41.9
10	10.0	17	35.3	17	41.2	8	25.0	90	32.2	104	34.6

able from nulliparous females. Body mass of immature females was <30 g except in January when heavier nulliparous females were present.

Immature males could not be distinguished on the criterion of the presence of abdominal testes as used by Begg (1981). Testes were found to move between scrotal and inguinal or abdominal positions within sampling periods and during handling. Both body mass and head length were external criteria used to discriminate immature and mature males; the former having a mean ($\pm SD$) body mass of 25.9 $\pm$ 7.4 g ($n = 9$) and a mean length of the head of 31.4 $\pm$ 2.0 mm ($n = 9$) and the former a mean body mass of 39.0 $\pm$ 5.6 g ($n = 45$) and a mean length of the head of 34.5 $\pm$ 1.5 ($n = 45$).

Morphometrics

The effects of four factors (maturity, sex, sampling period, and area) on 14 morphological, hematological, and physiological variables were tested using multiple regressions. All four main
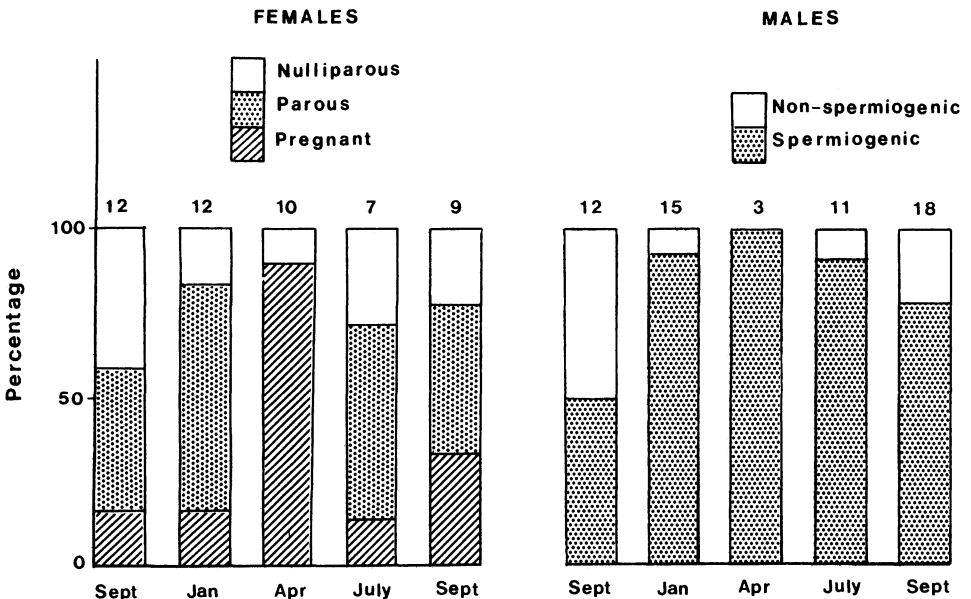

FIG. 1.—Reproductive condition of female and male *Z. argurus* from removal sites during the period of study. Pregnant females and those with placental scars, and males with spermiogenic testes are differentiated from immature individuals. Numbers of each sex examined are indicated.

TABLE 2.—*Mean (±SD) mass, head length, and tail diameter of adult* Zyzomys argurus *on different grids, Mitchell Plateau, northwestern Australia, 1981–1982.*

Character and grid	Females		Males		Totals	
	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n
Weight (g)						
Camp Creek	45.9 ± 7.1	43	40.6 ± 5.6	72	42.6 ± 6.7	115
Walsh Point (vine)	38.8 ± 3.6	9	42.2 ± 8.5	13	40.8 ± 7.0	22
Walsh Point (mosaic)	46.2 ± 5.5	6	40.2 ± 4.7	26	41.3 ± 5.3	32
Lone Dingo Woodland	40.2 ± 10.0	10	44.0 ± 5.6	6	40.5 ± 8.4	16
Head length (mm)						
Camp Creek	34.9 ± 1.6	45	34.5 ± 1.3	69	34.7 ± 1.4	114
Walsh Point (vine)	34.0 ± 1.6	9	34.8 ± 1.8	12	34.5 ± 1.7	21
Walsh Point (mosaic)	35.2 ± 1.3	4	34.4 ± 1.1	26	34.5 ± 1.1	30
Lone Dingo Woodland	33.8 ± 2.0	10	33.9 ± 2.2	6	33.8 ± 2.0	16
Tail diameter (mm)						
Camp Creek	6.7 ± 1.1	39	6.2 ± 0.9	69	6.3 ± 1.0	108
Walsh Point (vine)	6.2 ± 1.1	8	5.9 ± 0.7	11	6.0 ± 0.0	19
Walsh Point (mosaic)	6.7 ± 0.5	5	6.0 ± 0.7	25	6.1 ± 0.7	30
Lone Dingo Woodland	5.4 ± 0.9	9	5.3 ± 0.3	5	5.4 ± 0.7	14

effects and first- and second-order interactions were tested. In view of the large number of statistical comparisons made, only those with an *F*-value significant at the 1% level are discussed.

Weight.—Mean (±*SD*) weight of immatures (20.0 ± 7.7 g, *n* = 63) was significantly (*F* = 226.5, *d.f.* = 1, 196, *P* < 0.001) less than that of adults (42.0 ± 6.7 g, *n* = 185). There also was a significant (*F* = 4.68, *d.f.* = 3, 196, *P* < 0.01) sex-area interaction for weight. This interaction results from adult females being heavier than males at Camp Creek (*P* < 0.001) and Walsh Point mosaic grids (*P* < 0.05) but not on the other grids (Table 2). Adult females at Camp Creek (Table 2) were heavier than females at Walsh Point vine (*P* < 0.01) and Dingo Woodland grids (*P* < 0.01), and adult females at Walsh Point mosaic grid were heavier than those at Walsh Point vine grid (*P* < 0.05). Males did not differ significantly in body mass between grids.

Head length.—There were significant differences between maturity (*F* = 80.45, *d.f.* = 1, 186, *P* < 0.001), area (*F* = 6.40, *d.f.* = 3, 168, *P* < 0.01), and sampling periods (*F* = 3.78, *d.f.* = 5, 186, *P* < 0.01). Immatures had significantly shorter mean (±*SD*) length of the head (32.5 ± 2.1 mm, *n* = 59) than adults (34.5 ± 1.5 mm, *n* = 181). Adults on Dingo Woodland had shorter heads than those on Camp Creek, but the differences between all other areas were not significant.

The significant differences between sampling periods resulted from adults in July 1982 being smaller than at other times. Mean (±*SD*) head length of adults caught in July (33.8 ± 1.8 mm, *n* = 26) was significantly (*P* < 0.01) shorter than for those caught in January 1982 (34.9 ± 1.6 mm, *n* = 43) and September 1981 (34.9 ± 1.2 mm, *n* = 30), but not for those caught in April (34.6 ± 1.8 mm, *n* = 14), September (34.4 ± 1.2 mm, *n* = 29), and November 1982 (34.5 ± 1.2 mm, *n* = 29).

Tail diameter.—There was a significant interaction *F* = 3.26, *d.f.* = 5, 174, *P* < 0.01) between sex and sampling period in diameter of the tail base in addition to significant maturity (*F* = 52.13, *d.f.* = 1, 174, *P* < 0.001) and area (*F* = 12.34, *d.f.* = 3, 174, *P* < 0.001) effects. Immatures had significantly smaller mean (±*SD*) diameters of the tail base (5.1 ± 1.3 mm, *n* = 54) than adults (6.2 ± 1.0 mm, *n* = 171). Animals at Dingo Woodland had smaller diameter tails than those at Camp Creek (Table 2).

Adult males had significantly smaller tail diameters in January 1982 (*P* < 0.01) and November 1982 (*P* < 0.05) than females, but in all other sampling periods differences were not significant (Fig. 2). Tail diameters of males did not differ significantly through the year. Females had smaller diameter tails in September 1981 and 1982 than during January 1982 and November 1982 (both *P* < 0.001) and showed greater seasonal variation than males (Fig. 2).
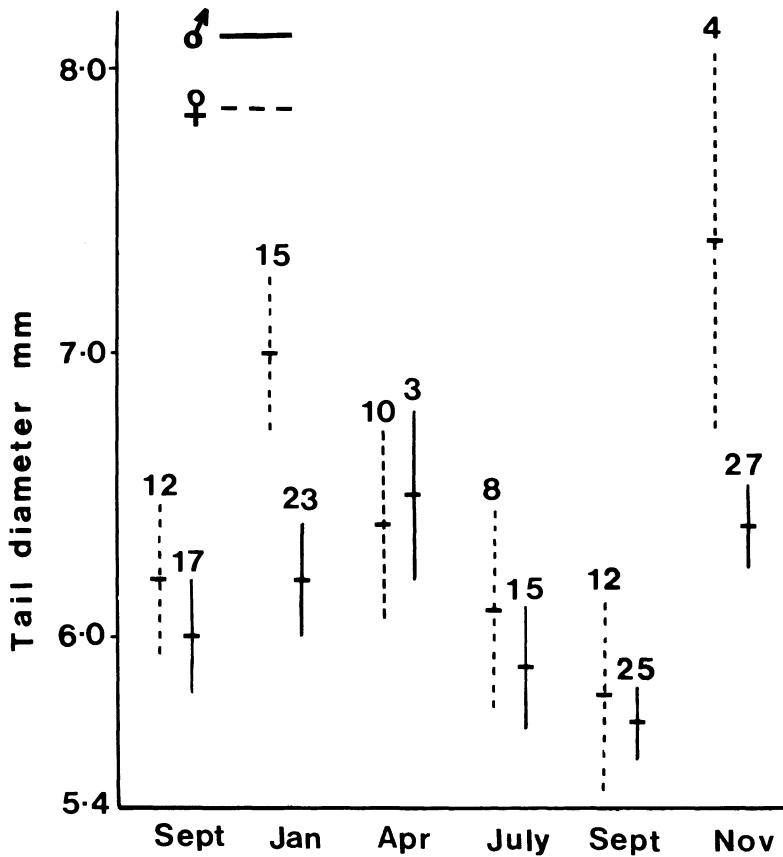
FIG. 2.—Temporal variation in the mean tail diameter (mm) of adult male and female *Z. argurus* at Mitchell Plateau, northwestern Australia, 1981-1982. Data are presented as $\bar{X} \pm SE$; sample sizes are indicated above each distribution.

Physiological

Hematocrit and hemoglobin.—No sex, maturity, sampling period, or area differences were significant for hematocrit, and only sampling period ($F = 4.83$, $d.f. = 4, 137$, $P < 0.01$) showed significant differences for hemoglobin. Hemoglobin levels were significantly lower in January and April 1982 than in July and September 1982. The two September sampling periods also differed significantly with that in 1981 lower ($P < 0.01$) than in 1982 (Table 3).

Leucocytes.—Total counts of leucocytes showed significant sampling-period effects ($F = 9.72$, $d.f. = 4, 197$, $P < 0.001$). Leucocyte counts were higher in January 1982 than in all other sampling periods except April (Table 3). There also was an area effect with animals at Dingo Woodland (4.07 ± 2.38 $10^3/mm^3$, $n = 20$) having significantly lower ($P < 0.05$) counts than those at Camp Creek (6.97 ± 4.61 $10^3/mm^3$, $n = 119$), but no differences between other grids were noted.

Examination of leucocyte differential counts showed a significant sample-period to area interaction ($F = 3.24$, $d.f. = 10, 129$, $P < 0.001$) in the lymphocyte to neutrophil ratio (Fig. 3). At Camp Creek, the ratio for January was significantly higher than for September than for September 1981 and 1982 ($P < 0.001$) and July 1982 ($P < 0.01$), whereas at Walsh Point mosaic grid it was significantly higher in January than September 1982 ($P < 0.001$) and September 1981 ($P < 0.05$). At Walsh Point vine grid, the lymphocyte-neutrophil ratio was higher in

TABLE 3.—*Mean (±SD) values for physiological characters that show significant seasonal variation for* Zyzomys argurus *at Mitchell Plateau, northwestern Australia.*

Character	September 1981		January 1982	
	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n
Hematocrit (%)	45.8 ± 4.3	47	45.9 ± 5.1	38
Hemoglobin (g/100 ml)	14.7 ± 1.6	44	14.2 ± 2.0	40
Free corticosterone (nM)	52.2 ± 30.6	37	128.3 ± 137.9	18
Albumin-bound corticosterone (nM)	66.3 ± 38.2	37	154.3 ± 144.7	18
Testosterone (nM)	17.2 ± 8.4	14	18.8 ± 5.2	8
Leucocytes (10³/mm³)	4.3 ± 2.0	44	9.2 ± 5.6	48
Neutrophils (%)	57.2 ± 13.2	34	49.0 ± 9.8	37
Lymphocytes (%)	39.9 ± 11.6	34	46.4 ± 8.6	37

September 1981 ($P < 0.01$) and January 1982 ($P < 0.05$) than in September 1982. At Dingo Woodland, the ratio in September 1981 and April 1982 was higher (both $P < 0.05$) than in September 1982 and July 1982. The significant differences between areas within sampling periods occurred in September 1981 when ratios on Walsh Point vine and Dingo Woodland grids were
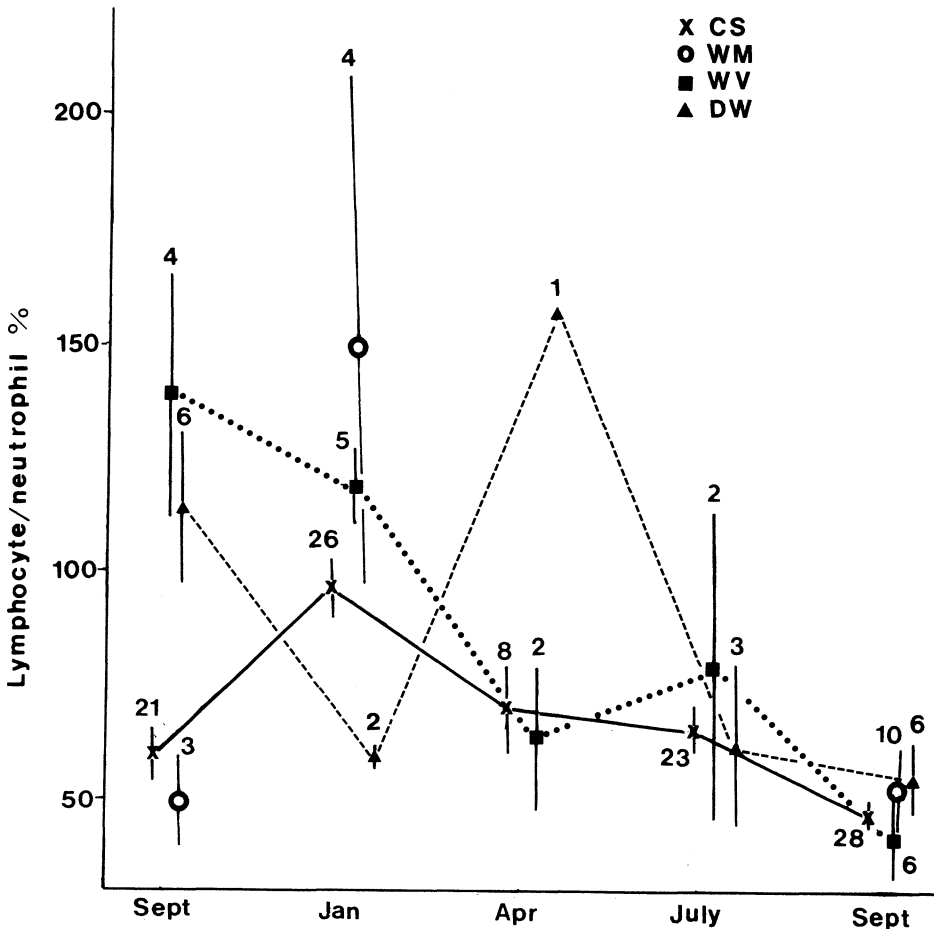

FIG. 3.—Temporal variation in the lymphocyte to neutrophil ratio in four populations of *Z. argurus*, Mitchell Plateau, northwestern Australia, 1981–1982. Data for the Camp Creek (CS), Walsh Point vine (WV), Walsh Point mosaic (WM) and Lone Dingo Woodland populations are presented as $\bar{X} \pm SE$; sample sizes are indicated above each point.

TABLE 3.—*Extended.*

April 1982		July 1982		September 1982	
$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n
48.0 ± 4.2	15	46.3 ± 7.6	29	44.8 ± 4.7	59
14.1 ± 3.3	14	15.6 ± 1.4	27	15.8 ± 2.4	57
48.8 ± 29.3	8	90.3 ± 92.2	11	50.1 ± 28.6	46
65.5 ± 36.6	8	110.9 ± 106.7	11	64.3 ± 37.6	46
31.2 ± 6.8	3	14.9 ± 9.2	13	19.1 ± 12.6	38
6.2 ± 3.8	16	6.2 ± 3.1	30	5.6 ± 3.2	49
56.9 ± 10.4	11	58.3 ± 10.3	28	67.0 ± 8.0	50
41.1 ± 10.1	11	36.3 ± 8.1	28	30.9 ± 7.7	50

significantly greater than on Camp Creek ($P < 0.001$) and Walsh Point mosaic ($P < 0.05$) grids, and in January 1982, when the ratio was greater on Walsh Point mosaic grid than on Camp Creek ($P < 0.01$) and Dingo Woodland ($P < 0.05$) grids.

Steroid Protein Interactions.—Equilibrium dialysis of *Z. argurus* plasma at 37°C using corticosterone yielded a high-affinity binding constant (3.70 ± 0.41; $n = 6$) 10^7 M^{-1} with no apparent sex difference in the binding. Using a 1% solution of *Z. argurus* albumin the low-affinity binding constant for the corticosterone-albumin binding was 0.25 ± 0.05 which represents five replicate determinations using albumin isolated from a plasma pool.

Corticosteroids and binding proteins.—Concentration of plasma corticosterone, maximum corticosterone-binding capacity, and corticosteroid-binding globulin-bound corticosterone showed significant ($P < 0.001$) differences with area ($F = 6.90$, $d.f.= 3$, $F = 183$; $= 7.99$, $d.f. = 3$, 82; and $F = 4.25$ $d.f. = 3$, 90 respectively), whereas free and albumin-bound corticosterone showed significant ($P < 0.001$) sampling-period differences ($F = 5.86$, $d.f. = 4$, 90 and $F = 6.43$, $d.f.$ $= 4$, 90, respectively). Plasma albumin was the only character to show a significant interaction; ($F = 3.70$, $d.f. = 4$, 137, $P < 0.01$) between sampling period and maturity.

Differences in plasma concentrations of free and albumin-bound corticosterone among sampling periods had identical patterns (Table 3). Values were significantly higher in January than during September 1981 and 1982, but differences between other sampling periods were not. There was no correlation between corticosteroid concentrations and the time of day of bleeding and, because bleeding procedures were kept rigorously constant, it was assumed these variations among sampling periods represented true seasonal patterns.

The significant differences in concentrations of plasma corticosterone, maximum corticosterone-binding capacity, and corticosteroid-binding globulin-bound corticosterone with area were essentially similar (Table 4). Values at Camp Creek and Walsh Point vine grids were similar but lower than those at Walsh Point mosaic and Dingo Woodland grids which also were similar.

TABLE 4.—*Mean (±SD) values for plasma-corticosterone partitioning in* Zyzomys argurus *that show significant differences among grids, Mitchell Plateau, northwestern Australia, 1981–1982.*

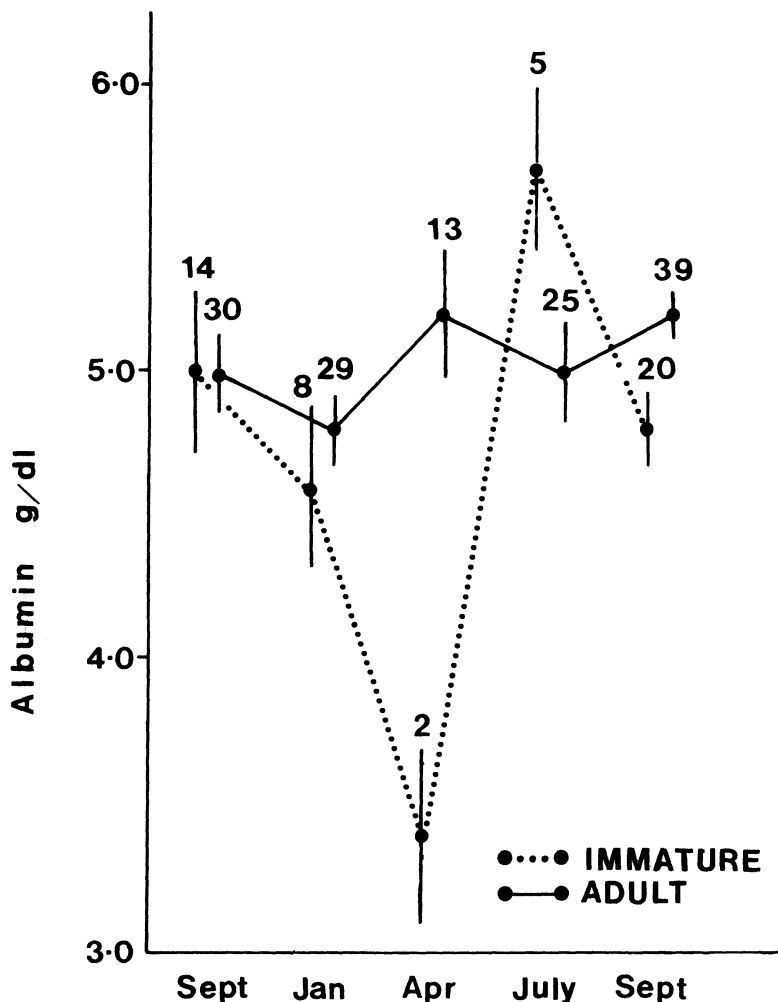| Grid	Concentration of plasma corticosterone (nM)		Maximum corticosterone-binding capacity (nM)		Concentration of cortisteroid-binding globulin-bound corticosterone (nM)	
	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n	$\bar{X} \pm SD$	n
Camp Creek	2,051.8 ± 1,116.0	121	2,922.2 ± 886.0	74	1,838.1 ± 961.7	74
Walsh Point (vine)	1,981.4 ± 846.7	22	2,833.3 ± 878.9	12	1,881.7 ± 934.9	12
Walsh Point (mosaic)	2,627.7 ± 1,088.1	26	3,656.8 ± 933.5	22	2,517.3 ± 1,004.8	21
Lone Dingo Woodland	2,975.8 ± 970.8	23	3,827.1 ± 790.5	13	2,568.2 ± 1,073.6	13
Overall $\bar{X}$ and total n	2,248.4 ± 1,132.8	193	3,144.2 ± 949.7	121	2,060.1 ± 1,034.7	121

Fig. 4.—Temporal variation in the mean albumin concentration (g/dl) for adult and immature Z. *argurus* at Mitchell Plateau, northwestern Australia, 1981–1982. Data are presented as $\bar{X} \pm SE$; samples sizes are indicated above each distribution.

The interaction between sampling period and maturity in albumin concentration (Fig. 4) resulted from immatures having significantly lower values in April and September 1982 than adults and also from major variation between sampling periods. Immatures had significantly lower values in April than at all other sampling periods except January and higher values in July than at all sampling periods except September 1981. Adults differed only between January and September 1982, being lower in the former.

Testosterone.—No significant differences were evident among males of different maturity, sampling periods, or areas. However, highest levels were recorded in April and these values were significant higher ($P < 0.05$) than those in July, but not other periods (Table 3). Body mass was not correlated with testosterone concentrations.

Pathogens

Routine rectal swabs from Z. *argurus* resulted in isolation of 14 *Salmonella* serotypes during the six sampling periods (How et al., 1983). The number of isolates and serotypes per swab were significantly higher in January 1982 than at other times of the year (How et al., 1983).

TABLE 5.—*Number of individual* Zyzomys argurus *of each hemaglobin phenotype captured on each grid, Mitchell Plateau, northwestern Australia, 1981–1982.*

Grid	Hb1-1	Hb2-1	Hb2-2	Hb3-2
Camp Creek	18	47	71	3
Walsh Point (vine)		17	7	
Walsh Point (mosaic)	5	16	17	2
Lone Dingo Woodland	1	8	11	2

Genetics

Using Cellogel electrophoresis, *Z. argurus* exhibited four hemoglobin phenotypes: Hb1-1, Hb2-1, Hb2-2 and Hb3-2. These were interpreted as the result of three allelic genes, designated *Hb¹*, *Hb²* and *Hb³*. Five offspring from two laboratory matings were in agreement with this mode of inheritance. No individuals with genotypes *Hb³/Hb¹* or *Hb³/Hb³* were observed. The Hb2 protein had the greatest anodal migration and Hb1 the slowest. The Hb3 protein was approximately midway between the other two. An attempt was made to determine the variant globin chain, but no chain separation was observed, although control human hemoglobin α and β chains separated as expected.

There was heterogeneity in gene frequencies among the grids ($\chi^2 = 10.9$, *d.f.* = 3, $P < 0.05$). The Walsh Point mosaic population had significantly higher frequency of *Hb¹* than that at either Camp Creek or Dingo Woodland (Table 5). All other pairwise differences were not statistically significant. At Walsh Point vine grid, there was an excess of heterozygotes ($P = 0.045$), but for all other grids, phenotype frequencies were not significantly different from Hardy-Weinberg expectations.

The phenotype frequencies of animals caught during one sampling period only were not different from those of animals caught during more than one sampling period ($\chi^2 = 2.6$, *d.f.* = 2, $P = 0.27$).

The *Hb¹* gene frequency at Camp Creek was 0.41 in January and 0.56 in April. At other times the frequencies averaged 0.26. These wet-season and dry-season gene frequencies were significantly different ($\chi^2 = 7.9$, *d.f.* = 1, $P = 0.005$). No variation was detected in any other protein examined electrophoretically.

DISCUSSION

Small-mammal population studies have been dominated by work on microtine rodents that generally show both multi-annual and seasonal variation in abundance in temperate and boreal regions of the northern hemisphere (Krebs and Myers, 1974). Studies on tropical species frequently are of short duration and generally have failed to show major fluctuations (Fleming, 1975; Kemper et al., 1987).

One of the most widespread and abundant murid rodents in the seasonally wet-dry tropics of Australia is the common rock rat (Begg, 1981). Both this study in northwestern Australia (Bradley et al., in press) and that in Arnhem Land of northern Australia (Begg, 1981) have shown similar marked seasonal fluctuations in abundance, although in neither study was the prospect of longer multi-annual changes in abundance examined. Populations reached peak densities late in the dry season (September) and maintained these numbers until the mid-wet season (January), before a three- to four-fold decrease occurred by the end of the wet season (April). Although virtually no seasonal variation occurs in *Melomys* (Begg et al., 1983; Kemper et al., 1987), irregular annual fluctuations in numbers were reported for the tropical murid, *Rattus colletti*, that correspond to sequences of abnormal seasons in the regular wet-dry tropics of Australia (Friend et al., in press; Redhead, 1979).

Despite the similarity of pattern in abundance on the four capture-mark-recapture grids in this study and the Arnhem Land Study (Begg, 1981), there were significant differences in population dynamics on our grids. The densest and most structurally stable population occurred

on the Camp Creek grid, a sandstone habitat. In the less dense populations, no females were captured during July 1982 at either grid at Walsh Point, whereas at Dingo Woodland, males were not captured during April and July. The entire population disappeared from Walsh Point mosaic grid after post-cyclonic flooding in January 1982 and only became re-established in September 1982.

Dispersal, a factor of major importance in small-mammal population ecology (Beacham, 1980; Gaines and McClenaghan, 1980; Lidicker, 1975), is difficult to assess from our data because of the short duration and relative infrequency of trapping periods. However, several immature animals were trapped in previously unoccupied areas during July and an immature male re-colonized Walsh Point mosaic grid at this time, suggesting that dispersal commences in most populations about July and extends to September, a timing similar to Begg's (1981) finding. Our genetic and physiological data on these few 'dispersing' individuals and other immatures showed no differences between them. The marked decrease in population numbers between January and April combined with fewer new animals captured during April suggested that this population decline resulted from mortality and not dispersal.

Breeding peaked in April (late-wet season) when population size was lowest (90% of females were pregnant) and continued at a reduced level throughout the dry season (July and September). Pregnant females were captured during all trips. These data, plus the observation that immature animals were recorded on all trips to Mitchell Plateau, show that breeding is similar in the Kimberley and Arnhem Land regions (Calaby and Taylor, 1983) and contrast with Begg's (1981) suggestion that breeding may extend for longer in the former region.

Tests of nulliparous females from removal sites invariably were barely visible and vaginae, were imperforate, characteristics similar to those recorded by Begg (1981), who also stated that immature females weighed <30 g. The smallest pregnant female in this study weighed 24 g, although females generally were considerably heavier when uterine scars or embryos were recorded. Calaby and Taylor (1983) also noted reproductive activity in females <30 g. Maturity occurs at about 5-6 months (Begg, 1981), but this may be dependent on time of year. Females weighing 24 g and 29 g were pregnant during April (the peak breeding season), whereas females weighing 36 g and 39 g were nulliparous in January (the period of lowest reproductive activity). Unlike the Arnhem Land (Begg, 1981) population, we found no pattern to the position of the testes with respect to scrotum during field examination. More than 83% of all immatures were captured on the grids in the late-dry season (September).

Adult females were heavier than adult males on both grids with denser populations (Camp Creek and Walsh Point mosaic grids) and the females on these grids generally were heavier than females on other grids. However, there were no temporal differences in adult body mass, suggesting that this measure of condition did not respond to seasonal variables.

The tail base of Z. argurus is a major site for fat storage (Begg, 1981) and as such is an indicator of the nutritional condition of individuals. Smaller tail diameters were recorded in the populations during the day (July) and late-dry (September) seasons, and males had smaller diameters than females in November and January, but not at other times. Begg (1981) concluded that in Arnhem Land the wet season was the time of greatest nutritional stress for Z. argurus; grass seeds, a key dietary component, only became available after seed set near the end of the wet season. If the phenology of seed set at Mitchell Plateau is similar, this increased seed availability may act as the catalyst for peak reproduction in April, but cannot explain the increased tail-fat reserves recorded earlier in the wet season in our study. Examination of the diet of Z. argurus (Watts, 1977) has shown that the species is not solely granivorous, but eats plant stems, leaves, and even small quantities of fungi and insects. It is possible that a dietary switch from seeds in the dry season to plant leaves and stems in the early wet season may explain the changed nutritional status of Z. argurus at Mitchell Plateau by the mid-wet season. A similar pattern was recorded in Microtus californicus in which grass leaves and stems are the main dietary items (88%) during the wet season, and grass heads and forb leaves the main items (88%) in the dry. Correlated with this dietary change was a decrease in reproductive, growth, and survival rates, and lower fat reserves (Batzli and Pitelka, 1971).

The individual physiological characters generally showed no variation with sex or maturity, but significant variations with area and sampling period. For concentration of plasma corticosterone, maximum corticosterone-binding capacity, and corticosteroid-binding globulin-bound corticosterone values were lower on Camp Creek and Walsh Point vine grids than on Walsh Point mosaic and Dingo Woodland grids.

The concentration of free corticosteroid in plasma has been shown to be an important indicator of physiological stress in both rodents and marsupials (Bradley et al., 1976, 1980; Bronson and Eleftheriou, 1964; Dantzer and Mormede, 1983; Eleftheriou, 1964; Lee et al., 1977; Lee and McDonald, 1985; McDonald et al., 1981). At Mitchell Plateau there was a bimodal peak in both free and albumin-bound corticosterone and levels were higher in January than at most other times of the year. Total leucocyte counts also peaked in January and there was a significant change in the lymphocyte to neutrophil ratio during this month, the middle of the wet season. An effect of glucocorticoids is to cause a mobilization of neutrophils from bone-marrow reserves (Athens et al., 1961; Dale et al., 1975) which results in a characteristic neutrophilia and contributes to the reduction in the lymphocyte to neutrophil ratio. Hematological responses to glucocorticoid, however, are not the same in all species. Glucocorticoid elevation in corticosteroid "resistant" species such as man and guinea pigs (*Cavia porcellus*) causes only a transient redistribution of circulating lymphocytes into alternative compartments of the lymphocyte pool (Fauci, 1975*a*, 1975*b*; Fauci and Dale, 1975*a*, 1975*b*). In marked contrast are the longer term hematological changes induced by administration of corticosteroid in glucocorticoid-sensitive species such as the laboratory mouse and rat (Claman, 1972).

An increased concentration of corticosterone in January was associated with elevated counts of neutrophils. However, an even greater increment in lymphocytes in the total leucocyte count (Table 3) resulted in an increased lymphocyte to neutrophil ratio and a lower percentage of neutrophils. January also was the period of major prevalence of *Salmonella*, an indicator of pathological stress in numerous mammalian populations (How et al., 1983).

Both pathogenic and physiological factors indicated January as a time of major population stress; it also was the period when reproductive activity was low and populations were at or close to their highest density. However, the relationship between increased density and stress indicators probably is not simply cause and effect, because elevated levels of factors related to stress occurred in all populations during January, irrespective of differences in the density of these populations at that time.

The coincidence of an elevated concentration of free corticosterone during January and the marked decrease in population numbers between January and April is of considerable interest in view of the findings of Bradley et al. (1976, 1980), Lee et al. (1977), and McDonald et al. (1981) of an association in small dasyurid marsupials between elevated concentrations of free cortisol and male mortality. *Z. argurus* individuals known to have survived in the populations after January had lower mean ($\pm SD$) levels of free corticosterone (58.1 $\pm$ 32.9 nM, $n = 6$) in January, than individuals (163.4 $\pm$ 157.7 nM, $n = 12$) that were not recaptured after January. They also had a higher lymphocyte to neutrophil percentage (107.0 as opposed to 92.9). Surviving individuals appeared, therefore, to be less stressed physiologically.

These data for the tropical murid *Z. argurus* can be contrasted with several of the hypotheses proposed to explain variation in numbers of temperate rodents. Interaction between herbivores and vegetation was one of the earliest hypotheses propounded to explain microtine-rodent cycles (Lack, 1954; Pitelka, 1957; Schultz, 1964) and more recently has been the focus of numerous correlative (Batzli and Pitelka, 1971; Evans, 1973) and experimental studies (Cole and Batzli, 1978, 1979; Desy and Thompson, 1983; Hestbeck, 1986). These investigators have shown that food availability, both quantitative and qualitative, influenced seasonal peaks in density, but failed to prevent severe population declines. Dietary selection, and the quantitative and qualitative aspects of *Z. argurus* food, were not examined in this study, but it appears from indices of condition (weight, tail diameter, and albumin levels) that individuals were not stressed nutritionally at peak densities.

Social behavior, operating through population attributes, physiology, or genotype, has been

hypothesised as a causative factor in the fluctuation of rodent numbers. The behavioral-genetic hypothesis (Chitty, 1967) primarily has been used to explain multi-annual cycles in rodent numbers (Myers and Krebs, 1971). Although we do not know if such cycles occur in Z. *argurus,* there were differences in gene frequencies for Z. *argurus* at Mitchell Plateau, with the Hb^1 gene being more frequent in the wet season (January and April). The 'ephemeral' population at Walsh Point mosaic grid had different gene frequencies from the other three.

The behavioral-multifactorial hypothesis (Lidicker, 1978; Wynne-Edwards, 1962) includes the proposal of changed densities affecting reproductive, survival, or dispersal regimes. The relevance of this hypothesis in explaining changes in Z. *argurus* numbers cannot be assessed because survival and dispersal regimes are poorly understood in this species. Reproduction in Z. *argurus* was much reduced at higher densities and dispersal was 'pre-saturation' (Lidicker, 1975), but the responses were similar in all populations irrespective of significant differences in peak densities.

The behavioral-stress phenomenon hypothesis (Christian and Davis, 1964) includes the suggestion that behavioral feedback at high population densities induces endocrine changes that in turn elevate glucocorticoid secretion. The consequence of this is the suppression of the immune response, alteration of white-cell count and other physiological changes (Christian, 1971), including a decline in, or a suppression of, reproductive activity (Andrews et al., 1975). Our study of the arboreal murid *Melomys* sp. cf. *burtoni* at Mitchell Plateau (Kemper et al., 1987) showed that at high densities *Melomys* had higher levels of free corticosteroid, slower growth, and delayed maturity. This suggested these were responses mediated by behavior feedback though the hypothalamus-pituitary-adrenal axis at high densities, the first such report in a tropical small-mammal species. However, Z. *argurus* populations at Mitchell Plateau all showed similar seasonal responses in concentrations of free corticosterone despite having different densities, suggesting these responses were not behaviorally induced by high densities.

At Mitchell Plateau, Z. *argurus* exhibited major spatial and temporal differences in populations responses. The four populations showed significant area (i.e., population) differences in density, and morphometric, physiological and genetic characters, whereas lymphocyte to neutrophil ratio varied with season and population. These data indicate that populations subjected to similar climates but occupying different habitats exhibit highly variable biological responses.

Indices of both physiological (free corticosterone and leucocytes) and pathological (*Salmonella*) stress had similar temporal patterns in the local populations of Z. *argurus* at Mitchell Plateau. They were elevated in January, the middle of the wet season. These patterns occurred irrespective of significant differences in local population densities, thus contrast with the density-related-stress indices recorded in *Melomys* populations at Mitchell Plateau (Kemper et al., 1987). It appears that stress in Z. *argurus* is environmentally induced. We suggest that a physiological-filter effect operates such that environmentally tolerant individuals (those with lower concentrations of free corticosterone in January) need to make fewer physiological adjustments in the wet season thus are more likely to survive to breed during subsequent seasons.

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