

The Mardo: an examination of geographic variation in morphology and reproductive potential in *Antechinus flavipes* in southwestern Australia

R.A. How¹, N.K. Cooper¹, L. Girardi² and B.G. Bow³

¹Western Australian Museum, Francis Street, Perth, Western Australia, 6000 Australia;

²Department of Agriculture, Manjimup, Western Australia 6258, Australia;

³Environmental Biology, Curtin University of Technology,
GPO Box U1987, Perth, Western Australia 6000, Australia

Abstract – The locality of Western Australian Museum specimens of *Antechinus flavipes* from southwestern Australia exhibits a marked disjunction in the species distribution. The northern distribution is characterised by females that have 10 nipples, while the southern distribution has females with 8 nipples; the two distributions come into close proximity east of Albany. Strong sexual dimorphism exists in both external and cranial variables within the two distributions. Although the cranial and external variables of each sex do not differ significantly between populations, multivariate analyses indicate that females of the two distributions show a strong separation in cranial variables on the first canonical variate. Variation in reproductive potential, as evidenced by differing nipple number, and molecular genetic studies of congeners in eastern Australia indicate the presence of cryptic species in *Antechinus*, suggesting a molecular examination of the two distributional groups in Western Australia is warranted.

INTRODUCTION

The dasyurid marsupial genus *Antechinus* is represented in Australia by ten species (van Dyck and Crowther, 2000), only one of which, *A. flavipes*, occurs in Western Australia. The genus is the best researched of Australia's carnivorous marsupials with many significant features of their biology summarised by Lee and Cockburn (1985). All members of the genus are monoestrus and polyovular, with males exhibiting mass mortality after the short breeding season (Woolley, 1966). *A. flavipes* is commonly known as the Yellow-footed Antechinus in eastern Australia (van Dyck, 1998), but in Western Australia, where it does not have yellow feet, it is called the Mardo; some biologists recognising it as a distinct subspecies, *A. f. leucogaster* (Wakefield and Warneke, 1967).

The detailed examination of geographic variation in nipple number of females within *Antechinus* (Cockburn *et al.*, 1983) brought to prominence the reproductive and possible taxonomic variation in the genus in the diverse habitats of eastern Australia. Recent re-examination of *Antechinus* in eastern Australia (Dickman *et al.*, 1998; Sumner and Dickman, 1998) has highlighted the complex nature of the systematics within part of the genus and the confusion over the identity and distribution of some species.

In Western Australia *A. flavipes* occurs in a relatively wide array of habitats in the more mesic

southwestern parts of the state. A detailed examination of the distribution of all mammals in the south west forests and adjacent regions for the Regional Forest Agreement process highlighted a major disjunction in the distribution of specimens of *A. flavipes* held in the collections of the Western Australian Museum. This disjunction occurred between the northern and southern forest blocks where no specimens were available from a broad expanse of forest in the region south of Collie. It was also known that nipple number varied across the range of *A. flavipes* distribution in Western Australia (Dell, personal communication).

This paper documents the variation in both reproductive potential, as reflected by nipple number, and morphology of the populations that represent the northern and southern sections of the distribution of *A. flavipes*.

MATERIALS AND METHODS

All specimens used in this study were from the Western Australian Museum's mammal collection.

An examination of 101 female *A. flavipes* was undertaken to determine nipple number and external characteristics, while a total of 52 (29 male, 23 female) individuals from across the range of *A. flavipes* in Western Australia were measured for cranial variables (Table 1).

For females, nipples were counted and examined

Table 1 Specimens examined for morphological variables. The sexes from northern and southern distributions are separated and identified by their Western Australian Museum registration number (M), their locality and the latitude (expressed as decimal degrees south) and longitude (expressed as decimal degrees east).

North Females; M5560, Byford, 32.2944, 116.0722; M7113, Mundaring, 31.9167, 116.1667; M7784, Byford, 32.25, 116.0833; M8071, Mundaring, 31.95, 116.1333; M8072, Byford, 32.2667, 116.0833; M8852, Waroona, 32.8333, 115.9833; M16020, Gracefield, 34.0833, 117.3333; M24349, Jarrahdale, 32.35, 116.1333; M26118, Canning River, 32.15, 116.1333; M27911, Nth Danadalu, 32.5167, 115.9667; M36552, Collie, 33.3667, 116.2; M43339, Porongurup, 34.6833, 117.9; M47795, Collie, 33.3667, 116.15.
North Males; M279, Gracefield, 34.0833, 117.3333; M1411, Wokalup, 33.1, 115.8833; M5276, Perth, 32.0833, 116.1167; M5559, Byford, 32.2944, 116.0722; M5561, Byford, 32.2944, 116.0722; M5726, Byford, 32.2944, 116.0722; M5727, Byford, 32.2944, 116.0722; M6018, Glen Forrest St, 31.9736, 116.1306; M7103, Mooterdine, 32.75, 116.7833; M7104, Mooterdine, 32.75, 116.7833; M7941, Byford, 32.25, 116.0833; M8073, Byford, 32.2667, 116.0833; M15365, Hood Point, 34.375, 119.6125; M19891, Waroona, 32.85, 115.9167; M23848, Stirling Range, 34.4, 117.95; M27887, Porongurup, 34.6833, 117.9.
South Females; M7112, Waychinicup, 34.9167, 118.3333; M10990, Mt Lindesay, 34.85, 117.3167; M15203, Nannup, 34.1667, 115.6667; M15204, Nannup, 34.1667, 115.6667; M15205, Pemberton, 34.4, 115.9833; M19258, Two People Bay, 34.9653, 118.1375; M19262, Two People Bay, 34.975, 118.2; M19263, Two People Bay, 34.9936, 118.2167; M34575, Pemberton, 34.45, 116.0333; M34579, Pemberton, 34.45, 116.0333.
South Males; M1334, Kulikup, 33.8333, 116.6667; M1401, Chorkerup, 34.8333, 117.6833; M1822, Chorkerup, 34.8333, 117.6833; M2037, Rosa Brook, 33.95, 115.1833; M7101, King Creek, 34.9167, 118.1667; M7105, King Creek, 34.8333, 118.1667; M7111, Waychinicup, 34.9167, 118.3333; M7640, Waychinicup, 34.9, 118.35; M19121, Mt Lindesay, 34.8333, 117.3; M20954, West Cape Howe, 35.15, 117.6167; M23626, Margaret River, 33.9167, 115.2; M24993, Northcliffe, 34.6333, 116.1167; M34566, Pemberton, 34.45, 116.0333.

for size and condition (distended or undeveloped). Attached pouch young were noted.

Tooth numbering follows Luckett (1993). Skull measurements were taken for the following variables: – GSL, Greatest Skull Length; ZW, Zygomatic Width; OB, Least Interorbital Width; I¹I⁴, Upper Incisor Row; C¹M⁴, Upper Canine to end of Upper Molar 4; M¹M⁴, Length of Upper Molar Row; M¹M³, Length of Upper Molar 1 to Upper Molar 3; LM³RM³, Width across outside of Upper Left and Right Molar 3; M₁M₄D, Length of Lower Molar 1 to

Lower Molar 4; M₁M₃D, Length of Lower Molar 1 to Lower Molar 3; CONRAM, Condyle to Ramus; ANGCON, Angular Process to Condyle; WIB, Width between Bullae; WOB, Width outside Bullae; BUL, Bulla Length; MLPV, Maxillary Vacuity Length; IPVD, Premaxillary Vacuity to Maxillary Vacuity; PALAT, Palatal Length; NASW, Nasal Width; NASL, Length of Nasal; BD, Braincase Depth; I₁M₄D, Length of First Lower Incisor to Lower Molar 4; DL, Dentary Length. Head-vent Length, Tail-vent Length, and Hind-foot Length (minus claw) were also measured.

Skulls were categorised into two age groups, mature and adult, according to the extent of toothwear and fusion of cranial sutures. Age was confirmed by examination of external reproductive status of the animal. Sex was determined for all specimens.

All measurements were recorded with digital callipers and statistical analysis was carried out using Genstat 5 (Genstat 5 Committee, NAG, 1993) and STATISTICA for Windows (Volume III), StatSoft, Inc. 1984–1995.

Canonical Variate Analysis (CVA)

Multiple regression was used to investigate variation due to sex, age and possible group differences for each of the 23 cranial and 3 external characters. These analyses checked for normality by plotting residual v fitted values and statistical outliers were then examined for measurement accuracy. Each variable was regressed on sex, age and group and the extent of interaction between these factors was investigated for evidence of interdependence. Three variables which showed significant interactions between sex and age [MLPV, $P=0.019$; M₁M₄D, $P=0.046$; I₁M₄D, $P=0.032$] were not used in further analyses.

Canonical Variate Analysis (Discriminant Analysis) was used to examine the multivariate relationships between groups. Where a subset of characters was required, they were selected by sequential multivariate analysis of variance, using backward elimination to reduce Wilks' Lambda as the selection criteria.

RESULTS

Biogeographic Separation

The distribution of Museum specimens of *A. flavipes* in southwestern Australia is presented in Figure 1. The species is generally confined to the forested and woodland areas of the southwest and there are no recent specimens from the Swan Coastal Plain and in the Jarrahdale forest block south of Collie (33°22'S) and north of Manjimup (34°15'S). The latter feature of the distribution gives rise to the disjunct distribution evident in Figure 1.

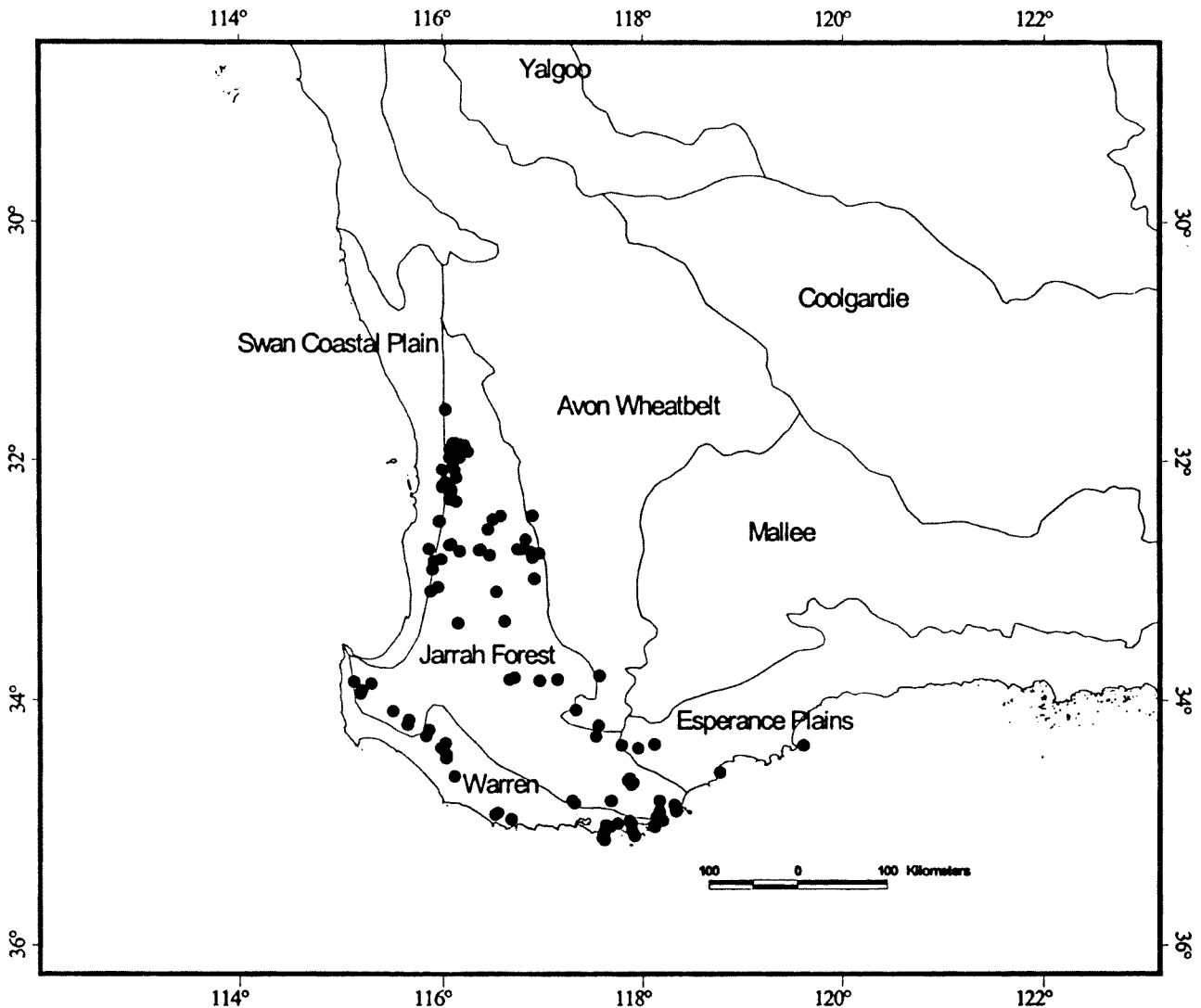


Figure 1 Distribution of specimens of *A. flavipes* in the collections of the Western Australian Museum and the biogeographic regions of southwestern Western Australia.

Reproductive Potential

Detailed examination of pouches and counts of nipple numbers were made on all female *A. flavipes* held in the collection. The distribution of females with either eight or ten nipples is presented in Figure 2. Two individuals had 9 nipples; these are also indicated in Figure 2.

All females with 8 nipples are confined to the southern moister region of WA, particularly the Warren biogeographic region, and extend as far east as Two Peoples Bay. Just north of this location the 10 nipple females reach their most southeastern limit, such that the 10 and 8 nipple distributions are in close proximity (Figure 2). The areas of the Porongurup (34°43'S) and Stirling Ranges (34°25'S) and the woodlands and forests to the northwest are the domain of the 10 nipple females.

The marked similarity between Figures 1 and 2 indicate that the disjunct distributions noted in Figure 1 correlate closely with the two different nipple forms of the species.

Morphological Variation

The analysis of both external and cranial morphology of *A. flavipes* was undertaken on the two disjunct distributions of both a northern 10-nipple population and a southern 8-nipple population. The individuals with 9 nipples were grouped geographically with the northern population.

The external and cranial morphology of *A. flavipes* shows clearly that the species is sexually dimorphic (Table 2). Nineteen and 22 of the variables in northern and southern populations, respectively, showed males significantly ($P < 0.05$) larger than females. Consequently, males and females have been treated separately in all statistical analyses.

Univariate

There was strong sexual dimorphism in external morphological features measured in *A. flavipes* with males in both distributional groups being larger than females (Table 2).

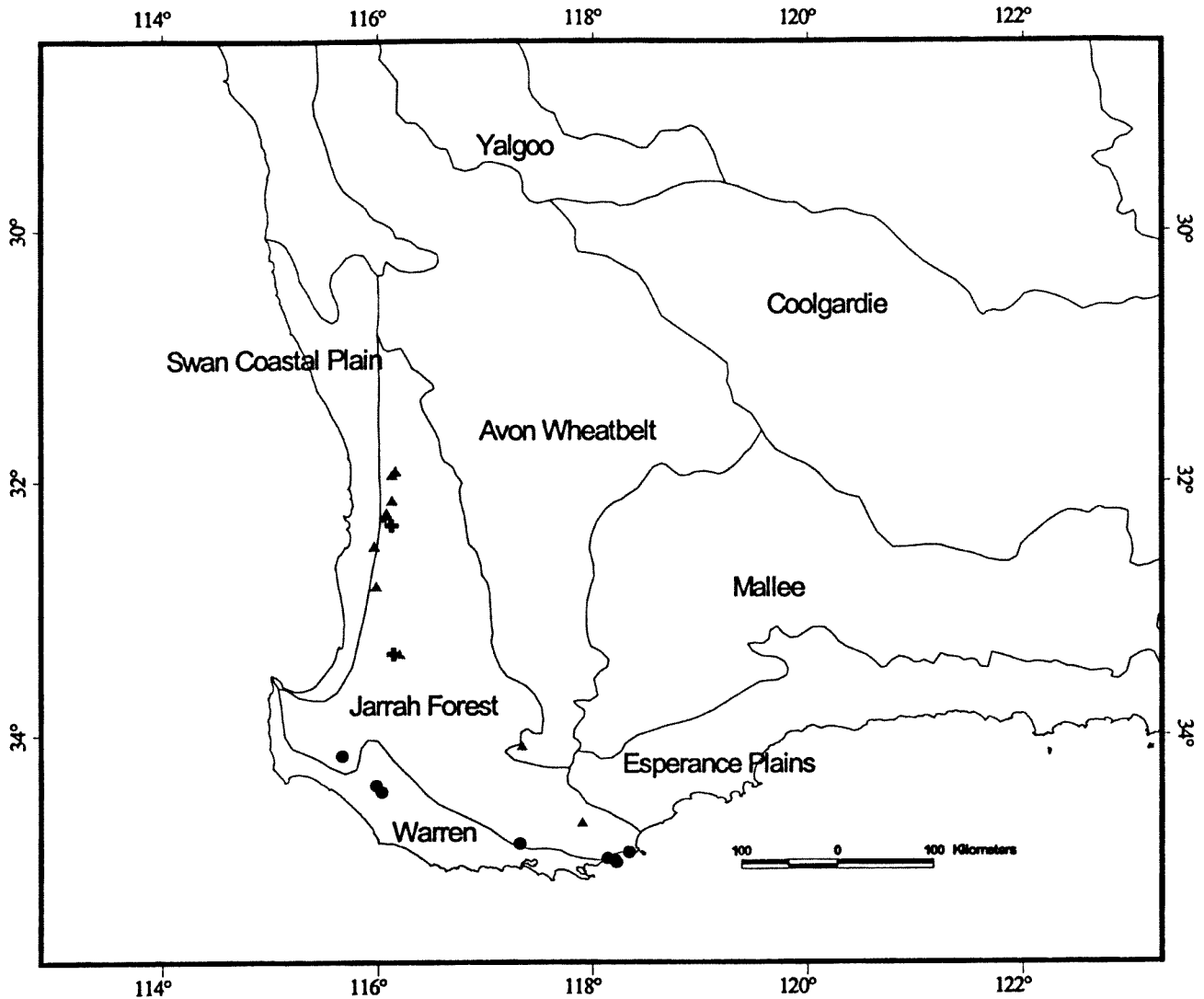


Figure 2 Distribution of female specimens of *A. flavipes* and their nipple numbers in southwestern Western Australia. Triangles- ten nipple, crosses- nine nipple and circles- eight nipple individuals.

For cranial variables, females were significantly smaller than males in both distributional groups of *A. flavipes* in southwestern Australia; only I^1I^4 , WIB, MLPV and IPVD showed no statistically significant sexual dimorphism in either distribution (Table 2).

No significant differences were detected between males or females from the two distributions except for interorbital width [OB] where males ($P < 0.05$) and females ($P < 0.01$) in the southern distribution were significantly larger than their northern counterparts.

Multivariate

Males

A CVA using cranial variables and *a priori* grouping by distribution showed an overlap of the CVA scores between the northern and southern groups (Figure 3A) This analysis was based on three characters [OB, NASL, M^1M^4] selected by backward elimination (Table 3), but essentially the

same results were obtained using the full set of 20 cranial measures. The pattern of correlation between the three selected characters and the first canonical function show that this is largely a size discriminator. There is overlap of the CV1 scores both with longitude and latitude. The Mahalanobis (D-squared) distance between the groups was 1.2346.

Females

A CVA using cranial variables and *a priori* grouping by distribution showed almost complete separation (only 3 individuals from each group overlapped) of the CVA scores between the northern and southern groups (Figure 3B). This analysis was based on three characters [OB, NASW, I^1I^4] selected by backward elimination (Table 3), but essentially the same results were obtained using the full set of 20 cranial measures, with no overlap of the CV scores. The pattern of correlation between

Table 2 Mean, standard deviation and sample size of all external and cranial measures for male and female *Antechinus flavipes* in northern and southern distributions in southwestern Australia. Significance levels for sexually dimorphic characters in each distribution are indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	North		South	
	Males	Females	Males	Females
Head-Vent	112.67±8.26(9)**	93.78±7.94(12)	113.38±10.17(8)***	96.30±8.96(10)
Tail-Vent	86.85±6.19(8)**	76.61±5.13(12)	85.75±7.91(8)***	73.13±5.05(9)
Hind Foot	18.80±1.18(9)**	16.77±1.23(12)	20.05±3.51(8)**	16.50±1.30(10)
GSL	30.01±0.91(16)***	28.57±0.54(12)	30.16±1.35(13)***	28.15±0.99(10)
ZW	17.30±0.8**1(15)	16.34±0.60(13)	17.56±1.32(11)**	16.05±0.67(10)
OB	6.31±0.20**(16)	6.10±0.19(13)	6.54±0.33(13)*	6.31±0.13(10)
II ⁴	2.79±0.17(14)	2.74±0.08(12)	2.79±0.19(13)	2.65±0.16(10)
C'M ⁴	10.92±0.29(16)***	10.37±0.25(13)	10.91±0.41(13)**	10.29±0.39(10)
M ¹ M ⁴	6.29±0.14(16)*	6.16±0.12(13)	6.36±0.21(13)*	6.19±0.19(10)
M ¹ M ³	5.47±0.16(15)	5.38±0.12(13)	5.51±0.17(13)*	5.34±0.19(10)
LM ³ RM ³	9.49±0.34(15)	9.42±0.23(13)	9.72±0.43(12)*	9.27±0.43(10)
M ₁ M ₄ D	6.92±0.17(16)***	6.67±0.14(13)	6.92±0.23(12)*	6.68±0.23(10)
M ₁ M ₃ D	5.22±0.19(16)*	5.09±0.11(13)	5.25±0.14(12)***	5.00±0.15(10)
CONRAM	5.11±0.25(16)***	4.72±0.20(13)	5.28±0.54(13)*	4.72±0.36(10)
ANGCON	5.75±0.36(16)**	5.40±0.29(13)	5.92±0.51(13)	5.58±0.31(10)
WIB	3.96±0.20(15)	3.85±0.18(13)	4.05±0.20(11)	3.96±0.10(10)
WOB	11.46±0.41(13)**	11.0±10.25(12)	11.63±0.60(12)**	10.95±0.49(10)
BUL	5.84±0.29(13)	5.62±0.25(13)	5.79±0.20(13)**	5.44±0.26(10)
MLPV	4.33±0.34(16)	4.26±0.46(12)	4.28±0.43(12)	4.48±0.26(8)
IPVD	4.95±0.29(15)	4.82±0.52(11)	4.92±0.36(12)*	4.56±0.30(7)
PALAT	14.65±0.44(14)***	13.82±0.34(13)	14.64±0.73(13)**	13.61±0.52(10)
NASW	4.03±0.34(16)*	3.77±0.25(13)	1.11±0.48(13)*	3.71±0.17(10)
NASL	12.90±0.52(14)***	12.01±0.48(13)	12.99±0.84(13)*	12.10±0.65(10)
BD	7.87±0.23(16)***	7.34±0.26(13)	8.00±0.43(12)**	7.55±0.20(10)
I ₁ M ₄ D	12.85±0.38(15)***	12.26±0.29(13)	12.95±0.49(12)**	12.15±0.48(10)
DL	21.94±0.79(15)***	20.72±0.44(13)	12.02±1.08(13)**	20.41±0.99(10)

Table 3 CVA scores for males and then females; grouped by locality 'N' and 'S'. Correlation between original data and functions.

Variable	Males CVA 1	Females CVA1
OB	-0.7931	0.5425
NASL	-0.1178	
NASW		-0.0872
II ⁴		-0.3103
M ¹ M ⁴	-0.5119	

the three selected characters and the first canonical function show that this is largely a shape discriminator. The limited overlap of CV1 scores with longitude (Figure 3) indicates that the differences between females in the two distributions persist over a large longitudinal range. The Mahalanobis (D-squared) distance between the group centroids was 5.363.

The difference in the variables selected for multivariate examination of males and females suggests there is a shape difference in the anterior portion of the skulls in the two sexes.

DISCUSSION

The geographic variation in the litter size of

Antechinus species was first evaluated in detail by Cockburn *et al.* (1983) with an examination of *A. swainsonii*, *A. stuartii* and *A. flavipes* in eastern Australia. They showed that major geographic variation existed in the nipple number of *Antechinus* populations. In *Antechinus* species the number of young born may be in excess of the number of nipples (Woolley, 1966), however, the maximum number of young weaned into the population is the same as the number of nipples and, consequently, nipple number is an indicator of the reproductive potential of the species or population. Subsequent research on *Antechinus* has indicated that some of this variation in nipple number may be associated with specific taxonomic differences in the populations as well (Lee and Cockburn, 1985).

Our study has shown the existence of discrete northern and southern distributional groups of *A. flavipes* in southwestern Western Australia. These two groups come into close proximity in the Two Peoples Bay area east of Albany. We have also shown that the two distributions have different reproductive potential with northern and southern females having 10 and 8 nipples, respectively. This disjunction in both the species distribution and the variation in nipple number of females in the two areas indicated the need for a re-examination of the morphology of *A. flavipes* in southwestern Australia,

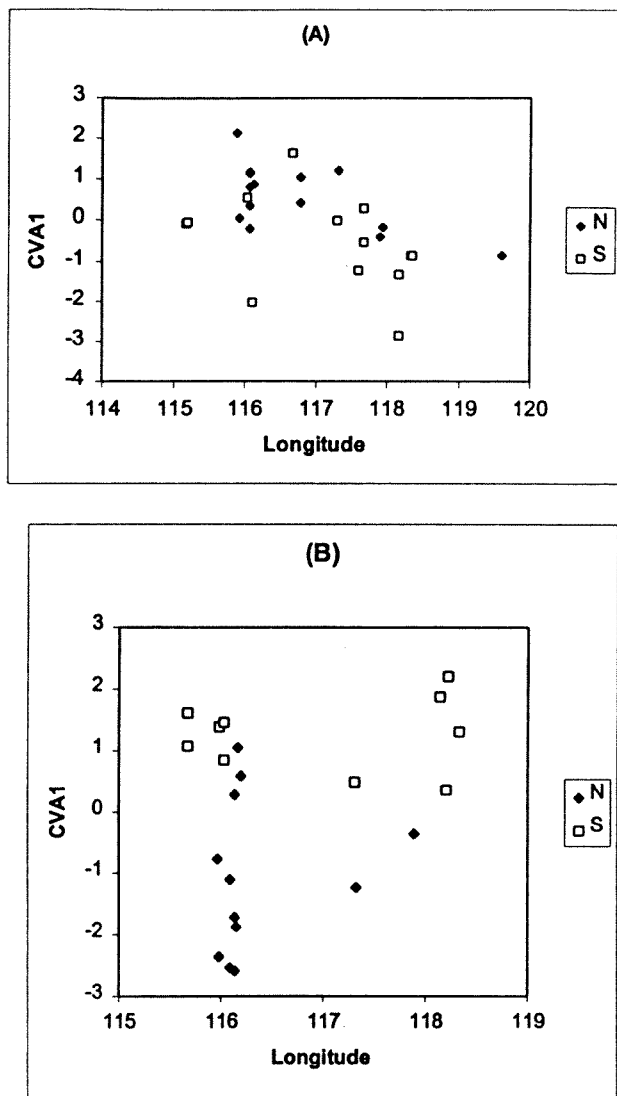


Figure 3 Plot of Canonical Variate 1 against longitude for (A) male and (B) female *A. flavipes* in southwestern Australia.

particularly given that Dickman *et al.* (1998) indicated that species complexes existed in *A. stuartii* and, probably, in *A. flavipes* in eastern Australia.

Cockburn *et al.* (1983) did not include populations of *A. flavipes* from Western Australia, but they did show that in eastern Australia this species was allopatric or broadly parapatric with the widespread and common Brown Antechinus, *A. stuartii*, and occurred mainly inland of the Great Dividing Range. Across the broad distribution of *A. flavipes* in eastern Australia, Cockburn *et al.* (1983) were able to identify populations with nipple numbers varying from 8 to 13 and concluded that – “Nipple number is highest at high elevations in southeastern Australia, and lowest at low latitudes and on the exposed capes and promontories in southeastern Australia.”

In Western Australia the lower nipple number

distribution occurs at higher latitudes along the southwestern fringes of the state. This correlates closely with the prediction that nipple number is lower in environments where rainfall is more predictable, and higher in more strongly seasonal environments with less predictable rainfall and resources (Cockburn *et al.*, 1983; Watt, 1997). The southern distribution of *A. flavipes* is closely correlated with the Warren bioregion, a region that is characterised by the high rainfall that encompasses the tall Karri forests of southern Western Australia (Thackway and Cresswell, 1995). The drier forests and more seasonal rainfall of the Jarrah Forest bioregion subscribe the northern distribution group. This marked difference in the distributions of the two groups and their different reproductive potential indicates that *A. flavipes* has evolved different life history strategies in different environments within the forests of southwestern Australia.

Sexual dimorphism exists in both distributional groups of *A. flavipes* in Western Australia with males being larger than females in both external and cranial variables. However, males and females do not show a significant difference in morphology between the two groups. Detailed multivariate analysis of cranial morphology in females indicates that there is a shape separation in CV1 between the two distributions and that this persists over a large longitudinal range. Whatever environmental factor(s) are driving this separation appear to be acting more intensively at greater longitudes (easterly), as overlap in multivariate space occurs only between western specimens where the distributions are most widely separated latitudinally (see Figure 2).

In a detailed examination of genetic variation in *A. flavipes* across its range, Baverstock *et al.* (1982) found no variation in electrophoretically determined loci in populations from Mt Spec in north Queensland through New South Wales, Victoria and south to Adelaide, however, no Western Australian specimens were examined. This electrophoretic examination covered populations representing the two recognised but disjunct subspecies in *A. flavipes* in eastern Australia, *A. f. rubeculus* from north Queensland and *A. f. flavipes* from southeastern Australia (van Dyck, 1998). However, Sumner and Dickman (1998) found variation in two allozymes from populations from within *A. flavipes* in southeastern Australia.

Despite similarities in both external and cranial morphology in the two distributions, the separation of females in multivariate space suggests that the taxonomic status of *A. flavipes* in Western Australia is in need of re-examination at a molecular level. This would help resolve the taxonomic status of *A. flavipes* in Western Australia compared to currently recognised congeners in eastern Australia and also

as to whether a cryptic species exists in *A. flavipes* within Western Australia, as has been determined within *A. stuartii* in eastern Australia (Dickman *et al.* 1998).

Bow (unpubl.) has shown that the variation in nipple number in the Grey-bellied Dunnart, *Sminthopsis griseoventer*, also correlated with different bioregions. In *S. griseoventer*, females with eight, seven and six nipples were recorded, but all the six and seven nipple females were confined to the Warren bioregion while other populations in the Jarrah Forest, the Swan Coastal Plain and Boullanger Island had 8 nipples. A recent re-examination of *S. griseoventer* by Crowther *et al.* (1999), including the description of a new subspecies from Boullanger Island, indicated considerable morphological variation in this species throughout its range in southwestern Australia, however, no evaluation between forms with different nipple numbers was undertaken.

The habitats in the Warren bioregion on the southern fringe of Western Australia have influenced the life history strategies of at least two small dasyurid marsupials, indicating that resources in that area are significantly different to those of the adjacent Jarrah bioregion. A separation of females in multivariate space suggests that different selection pressures are operating on this sex in the two distributions. It remains to be determined whether these differences transfer into taxonomic differences within the respective distributional groups.

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