Moore, Leslie Allan (2010) ***Niche differentiation, rarity, and commonness in the sympatric Australian white-tailed rats: Uromys caudimaculatus and Uromys hadrourus.*** **PhD thesis, James Cook University.**

CHAPTER 4. SMALL MAMMAL POPULATION DYNAMICS

Capture probabilities, population sizes, seasonal variations, reproductive cycles, and population demography of small mammals were explored using capture-mark-recapture analysis and population statistics. These findings have also been used in Chapter 7 to explore the influence of the coexisting small mammal assemblage on niche differentiation of *Uromys caudimaculatus* and *Uromys hadrourus*. The population dynamics of *U. caudimaculatus* and *U. hadrourus* are treated separately in Chapter 5. Of the other 13 mammal species captured in this study, only three species exceeded 50 individual captures: *Hypsyprymnodon moschatus*, *Melomys cervinipes*, and *Rattus fuscipes* (Table 3.2). Three species, *Rattus leucopus, Antechinus adustus,* and *Antechinus godmani*, comprised less than 50 individual captures each. Overall, seven species were caught too infrequently for capture-mark-recapture analysis (CMR) to be conducted: *Perameles nasuta*, *Isoodon macrourus*, *Antechinus flavipes*, *Mus domesticus*, *Pogonomys sp.*, *Cercartetus caudatus*, *and Melomys burtoni*. Apart from Wood (1971), Leung (1994), and Watts (1997), few mammal studies explored population dynamics in their studies of rainforest small mammals. Much of the data presented in this chapter, therefore, although undeniably basic population information, has not previously been examined and interpreted for the majority of rainforest small mammals.

4.1 NORTHERN BUSH RAT *RATTUS FUSCIPES CORACIUS*

4.1.1 Grid captures

Figure 4.1 shows the captures per 100 trapnights of *Rattus fuscipes.* A total of 1415 captures were made of 487 individuals, 272 males and 215 females. Grid 3 and Grid 5 generally caught more *R. fuscipes* but were surpassed by Grid 2 in the post-cyclone trapping session.

FIGURE 4.1

***Rattus fuscipes* grid captures by trapping session**

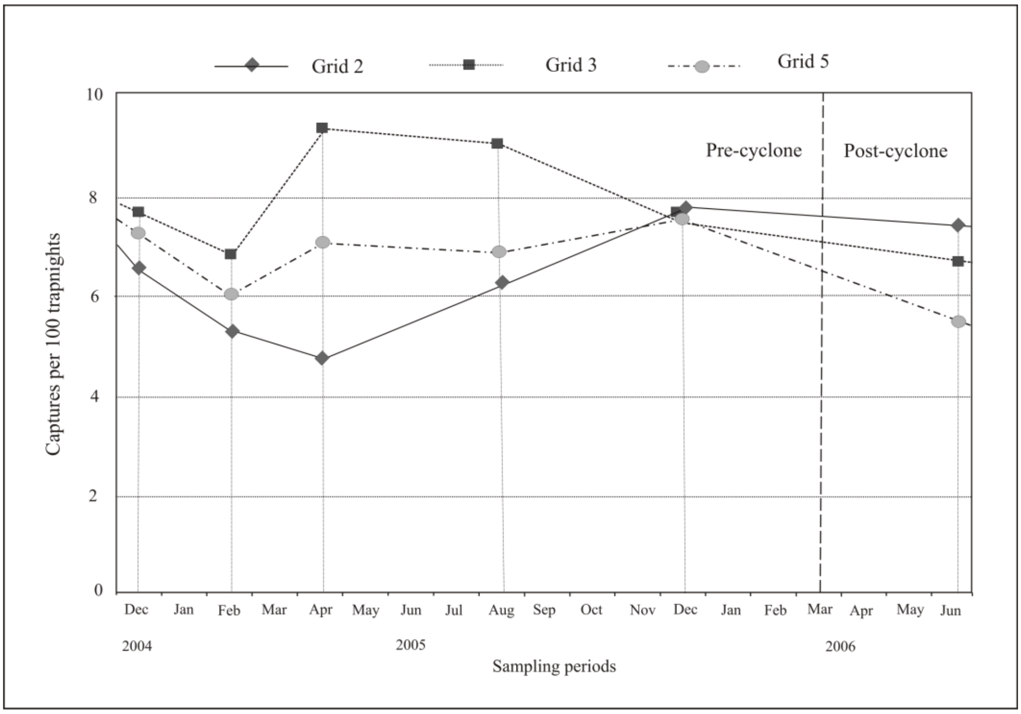
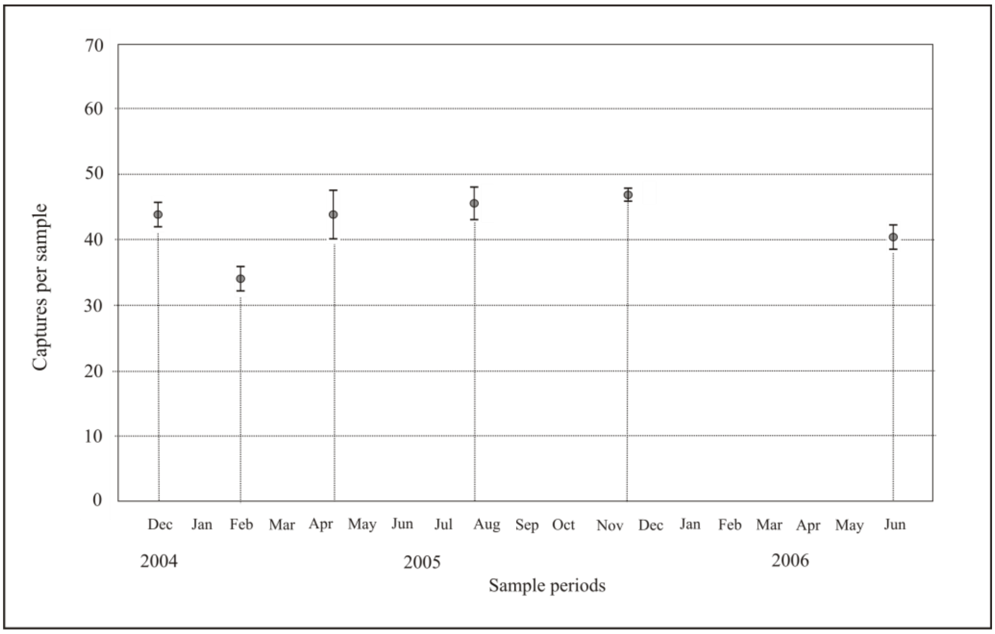


FIGURE 4.2

Mean trapping session captures ± s.e. of *Rattus fuscipes*



Grid 2 was the site most damaged by Cyclone Larry (severe vegetation damage). *Rattus fuscipes* captures from the three trapping grids were combined to calculate trapping session means (Figure 4.2). A Friedman ANOVA, a nonparametric alternative to one-way repeated ANOVA, indicated there was not a significant difference in the means of the six trapping sessions ($X^2_5 = 5.288$, $P=0.382$). In addition, an unpaired t-test comparing seasonal captures for the two trapping sessions April-May 2005 and May-June 2006 revealed that capture numbers did not change significantly post-cyclone ($t_4 = 0.336$, $P=0.754$).

4.1.2 Population density

The mean distance between trap locations for two successive captures of individual marked animals (trapping session captures or consecutive trapping sessions only) was calculated for *Rattus fuscipes*. The boundary strip ($\hat{W}$) for estimating species' density ($\hat{W}$ = d/2) was added to the grid area and densities calculated using mean trapping seassion captures. The mean movement distance ± SE for *R. fuscipes* was 38.84 metres and 6.44 metres respectively (d/2=19.42m). This distance was rounded to 20 metres altering the effective trap area from 2.6 hectares (trapping grid) to 3.36 hectares, an additional 0.76 hectares (approximately 23%). Population densities were calculated by using the total number of individuals caught each trapping session divided by the total area trapped (N/10.08ha). Rattus *fuscipes* density was stable throughout the year, ranging seasonally from 7.8 animals/ha in February (26 animals/grid), to 14 animals/ha in December (47 animals/grid), with a mean population density of 11.8 animals/ha (39.6 animals/grid).

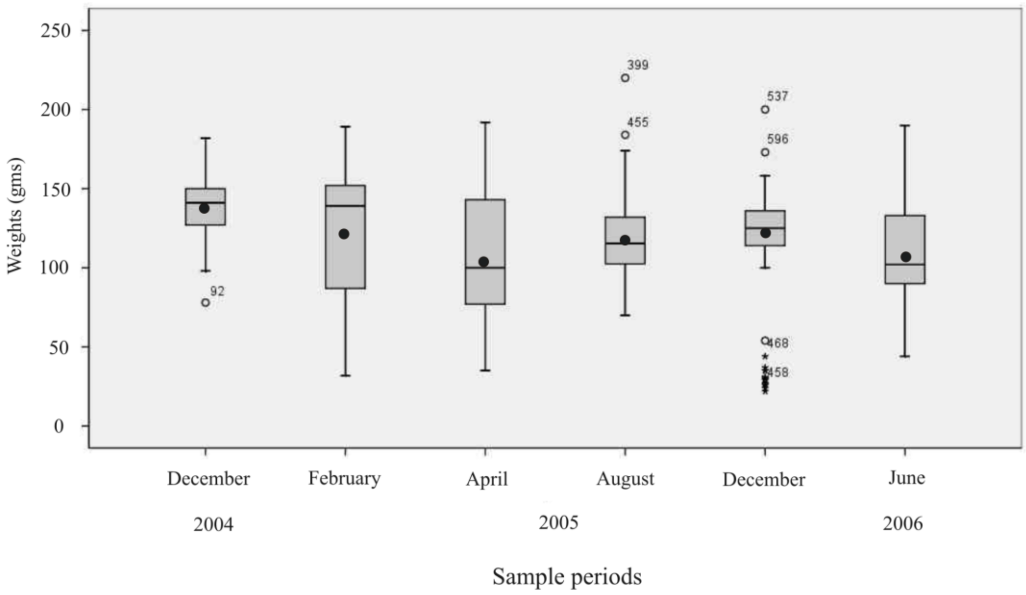
4.1.3 Adult body weights

Mean adult male *R. fuscipes* body weight ±SD was 136.0gms and 20.1gms respectively; mean adult female weight ±SD was 128.4gms and 18.5gms respectively (male N=386, female N=321). A paired t-test showed that adult male *R. fuscipes* were significantly heavier than adult females (t_{320}=3.197, P = 0.002). Figure 4.3 presents box-plots of the trapping session weights of *Rattus fuscipes*.

FIGURE 4.3

Rattus fuscipes **- mean and median trapping session weights**

The central box represents the middle half of the weight measurements (25th-75th percentiles) and the median (horizontal line); the black dot represents the mean; the vertical lines are the minimum and maximum data values; and outliers are shown as either circles or stars.



Repeated measures ANOVA showed significant weight differences between trapping sessions ($F_{1,5}$ =72.890, P=0.005). Numbers of larger animals (adults and large subadults) dominated in the months of December 2004 and February 2005 with an influx of smaller animals into the population (juveniles and small subadults) in the months of April and August 2004, and June 2006 (early-winter to early-spring).

4.1.4 Breeding

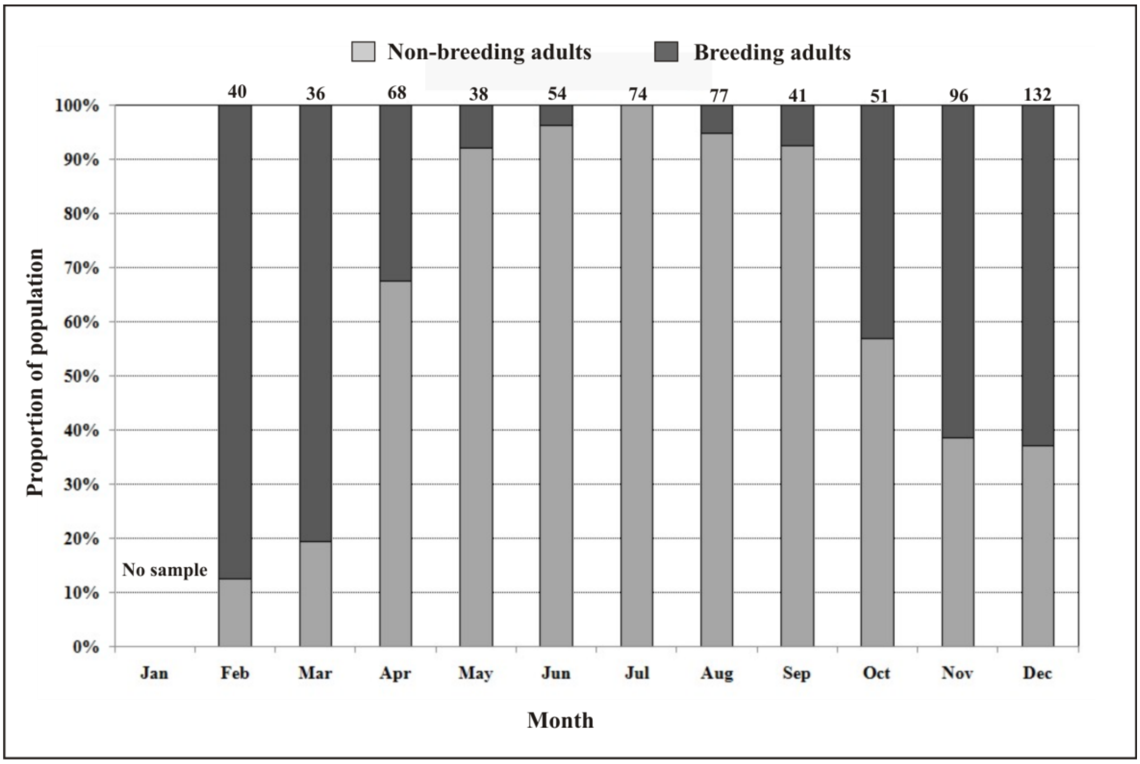
All individual captures of *R. fuscipes* were used in the following analyses (exploratory trapping 9 996 trapnights; experimental trapping 500 trapnights; and grid trapping 11

088 trapnights). Each adult *R. fuscipes* was assigned to one of two broad reproductive categories representing the distinct stages of the annual breeding cycle: reproductive codes 1-3 = non-breeding; reproductive codes 4 and 5 = breeding (refer to Chapter 2, Box 2.1).

FIGURE 4.4

Annual reproductive cycle of *Rattus fuscipes*

(Figure located at top of each bar = *N*)



Breeding animals dominated the population from October to February i.e., >50% of captured individuals were breeding (spring-late summer), with breeding decreasing from March onwards (Figure 4.4). Non-breeding animals dominated from March-September (late summer-early spring) with no captures of females in breeding condition in the winter months of June to August.

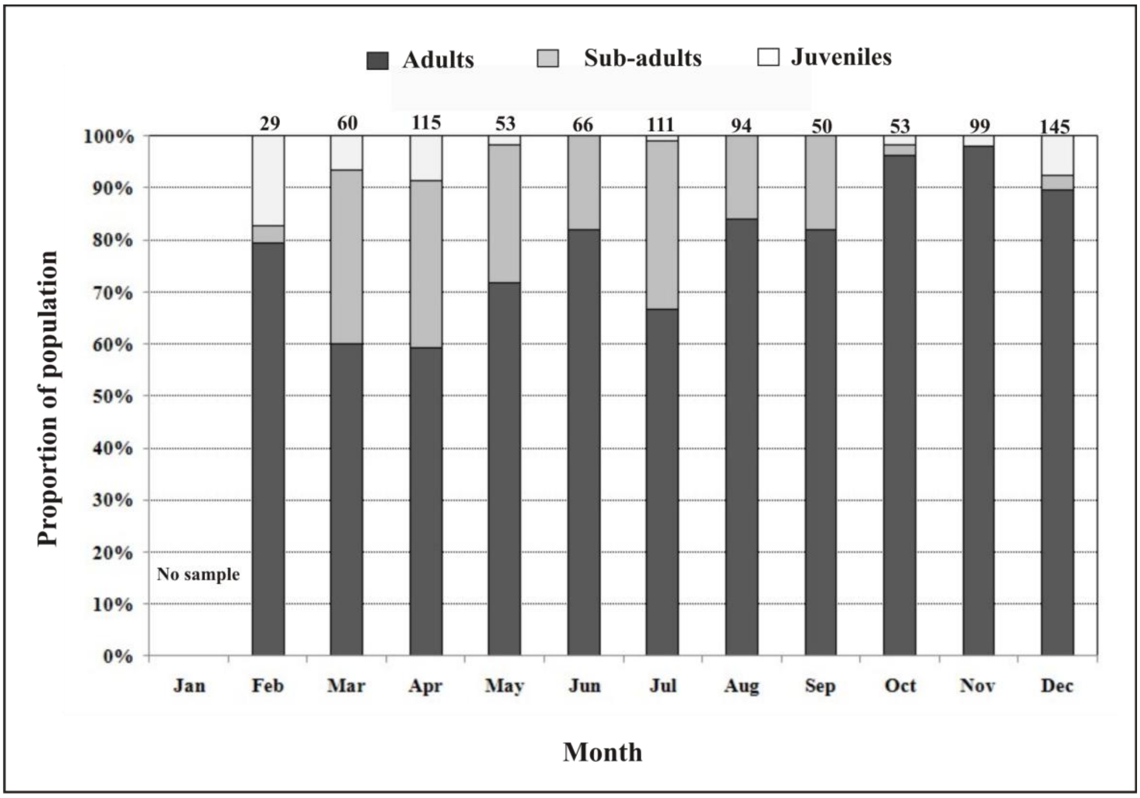
4.1.5 Annual Population Demography

Figure 4.5 presents the annual population demography of *R. fuscipes* observed in this study. Juveniles (<45gms) comprised 8-15% of the total population from December to April, with single juveniles captured in May and again in July. No juveniles were caught in August or September; juveniles began entering the population again in October.

FIGURE 4.5

Annual population demography of *Rattus fuscipes*

(Figure located at top of each bar = *N*)



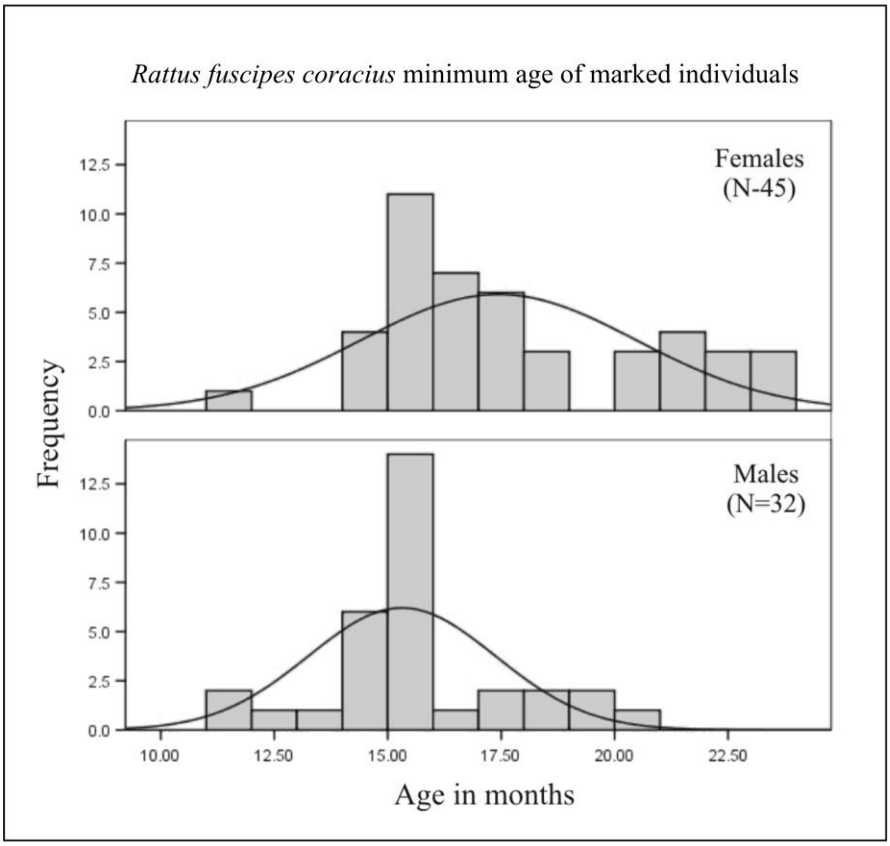
Subadults (46-99 gms) entered the population in March, reaching their maximum numbers in April and July, with captures declining from September onwards. Proportionally, adult numbers (>100 gms) were lowest in April i.e., ~60% of the total population. This decrease was caused by the heavy influx of juvenile and subadult animals post-breeding. The proportion of adults in the population was highest in October (96%) and December (90%).

4.1.6 Mean minimum age (longevity)

Mean minimum age of *R. fuscipes* was calculated from multiple capture records of marked animals based on the approximate age at the time of first capture (Watts and Aslin 1981, Crome *et al.* 1991). There were 209 multiple captures of 32 males and 45 females >12 months old used in the analysis i.e., individuals weighing ~100 gms when first caught (Figure 4.6).

FIGURE 4.6

***Rattus fuscipes* age distributions with fitted normal distribution curves**



The mean minimum age and standard deviation for marked males was 15.3 months ± 3.04. In contrast, the mean minimum age and standard deviation for marked females was 17.5 months ± 2.1. The oldest estimated male and female ages were 20 months and 24 months respectively. The majority of male ages peaked at 15 months (75%), with relatively few males surviving to 18 months old (<15%). Greater than 64% of females were estimated to be more than 18 months old; of these approximately 35.5% were >18 months old and 29% were 20 months or older. An un-paired t-test indicated that females were significantly longer-lived than males ($t_{1,75}$ = 3.667, P = <0.005).

4.1.7 Population estimation using capture-mark-recapture (CMR)

As for similar population estimation methods, this estimate does not represent the predicted population size of *R. fuscipes* existing on the grid itself but instead represents the population from which the sample is drawn. First captures and recaptures of *R. fuscipes* at each grid (Grids 2, 3, and 5) were analysed separately using a full Jolly-Seber analysis (Table 4.1). There was no constant seasonal pattern in population estimates: Grid 2 ranged from a high of 57 animals in February 2005 to an estimated low of 21 animals in April 2005; Grid 3 ranged from an estimated low of 38 animals in February 2005 to a high of 69 animals in April 2005; Grid 5 population estimates remained constant at 43-47 animals per trapping session. A repeated measures ANOVA showed that capture rates of *R. fuscipes* on each grid were similar ($F_{1,5}$ =3.075, P= 0.128). To obtain a total population estimate for all three grids, the first captures and recaptures of *Rattus fuscipes* were grouped and analysed using a full Jolly-Seber analysis (Table 4.2).

Table 4.1

Full Jolly-Seber analysis of estimated grid population size for *Rattus fuscipes*

Trapping session	Proportion of recaptures	Marked animals in population	Pop'n estimate	SE pop. est.	Survival estimate	SE survival	New animals	Probability of capture
Grid 2								
Dec 04	-	0	-	-	0.5742	0.2297	-	-
Feb 05	0.3125	17.8	**56.96**	28.98	0.3993	0.1169	-1.661	0.2809
Apr 05	0.5455	11.5	**21.08**	6.262	0.5455	0.0781	22.5	0.5217
Aug 05	0.2647	9	**34**	0	-	-	-	1
Dec 05	0.2292	-	-	-	-	-	-	-
Grid 3								
Dec 04	-	0	-	-	0.3529	0.02853	-	-
Feb 05	0.4706	18	**38.25**	3.865	0.5503	0.06801	47.7	0.8889
Apr 05	0.2881	19.81	**68.75**	9.603	0.4039	0.04083	37.41	0.8582
Aug 05	0.383	24.96	**65.18**	9	-	-	-	0.7211
Dec 05	0.4559	-	-	-	-	-	-	-
Grid 5								
Dec 04	-	0	-	-	0.4977	0.08016	-	-
Feb 05	0.4615	21.9	**47.45**	8.39	0.2564	0.01016	31.83	0.8219
Apr 05	0.25	11	**44**	0	0.5682	8.00E-06	18	1
Aug 05	0.5814	25	**43**	0	-	-	-	1
Dec 05	0.4043	-	**-**	-	-	-	-	-

Due to the extended interval between trapping sessions 5 and 6 (December 2005 and June 2006), trapping session 6 was not included in the analysis. Leslie's test for equal catchability was not significant at the 5% level (*P*=0.236), thus equal catchability was accepted. Population estimates varied from 132 animals in February to 233 animals in April, with a mean predicted population size of 188 animals per trapping session.

TABLE 4.2

***Rattus fuscipes* Jolly-Seber analysis population estimates for all three grids**

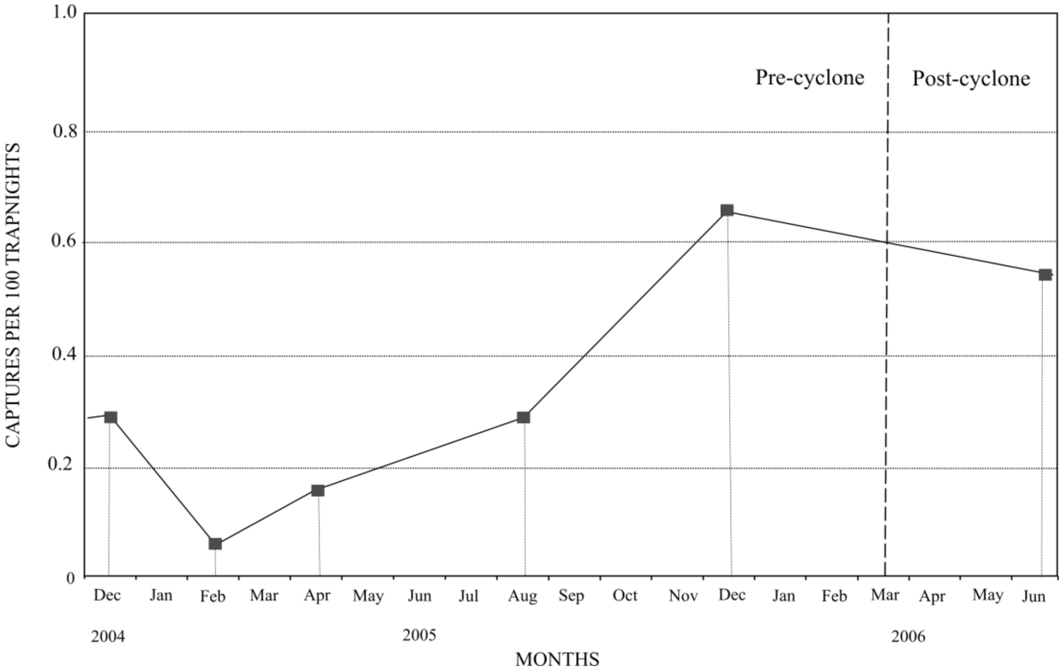
Trapping session	Proportion of recaptures	Marked animals in pop'n	Pop'n estimate	SE Pop'n est.	Surv. estimate	New animals	Prob. of capt.
Dec 04	-	0	-	-	0.603	-	-
Feb 05	0.412	54.35	**132.0**	24.74	0.874	118.2	0.386
Apr 05	0.316	73.79	**233.7**	48.89	0.506	81.23	0.325
Aug 05	0.319	63.58	**199.3**	27.58	-	-	0.581
Dec 05	0.312	-	**-**	-	-	-	-

4.2 CAPE YORK RAT *RATTUS LEUCOPUS COOKTOWNENSIS*

Figure 4.7 lists the grouped grid captures for all trapping sessions and shows *Rattus leucopus* was uncommon on the trapping grids during this study. A total of 27 individuals i.e., 10 males, 11 females, and six juveniles, were caught on 42 occasions. Grid 5 did not record *R. leucopus* until the fifth and sixth trapping sessions, with a single animal captured on each occasion. The data indicated the population peaked in December and dropped to its lowest numbers in February.

FIGURE 4.7

***Rattus leucopus* 1st captures per 100 trapnights**



4.2.1 Population Density

There were insufficient captures of *Rattus leucopus* to calculate mean distance between trap locations for two successive captures of individual marked animals. Although there is no certainty that their behaviour is identical, the boundary strip ($\hat{W}$) estimated for the morphologically-similar *R. fuscipes* (Moore and Leung 2008) was added to the grid area and densities of *R. leucopus* (3.36 ha). Population density was calculated using the total number of individuals caught each trapping session divided by the effective trap area of the grouped grids (N/10.08ha). The density of *R. leucopus* on the trapping grids was low throughout the year, ranging seasonally from 0.32 animals/ha in February, to 0.40 animals/ha in December. Previous studies in the same area of the Atherton Tablelands recorded densities of 0.43 animals/ha in continuous rainforest and 0.75 animals/ha in fragmented forest (Harrington *et al.* 2001).

4.2.2 Adult body weights

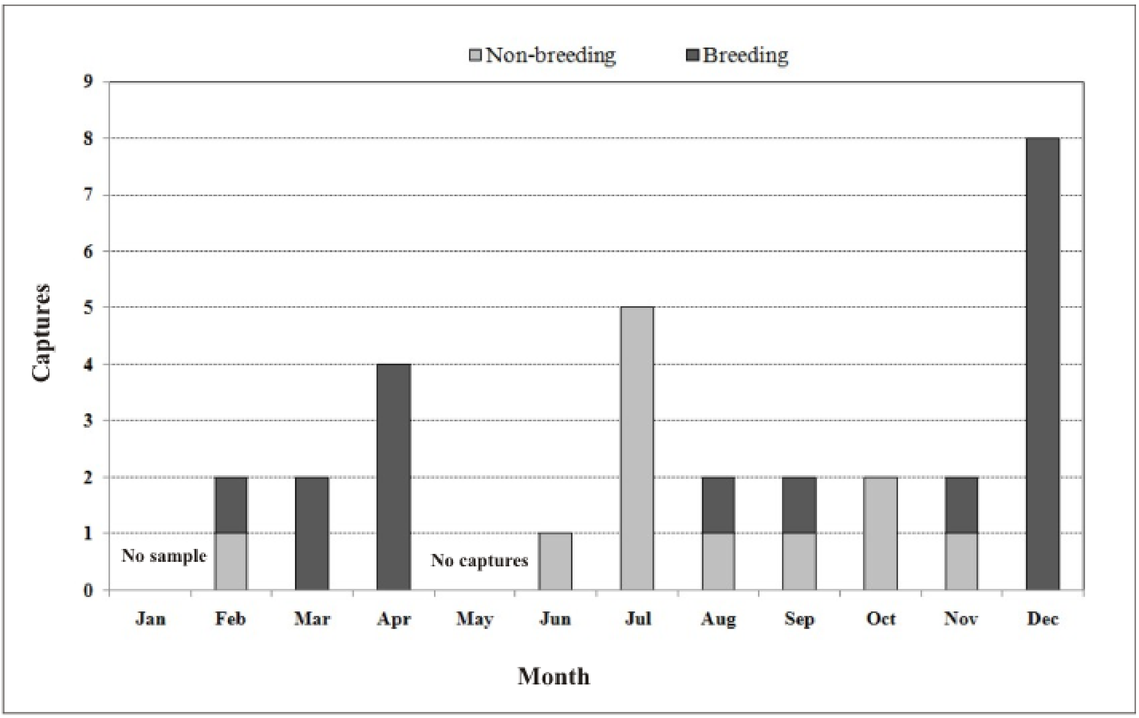
The mean body weight and SD of 11 adult male *Rattus leucopus cooktownensis* (>95gms) was 120.7 gms and 9.4 gms respectively; the mean body weight and SD of six adult female was 113.9 gms and 15.9 gms respectively. Although there was no significant difference in male and female body weights (t_{15}=0.956, P=0.354), the sample number is small and the result should be considered provisional.

4.2.3 Breeding

The reproductive status of each captured adult male and female *R. leucopus* was grouped into two broad categories representing the distinct stages of the annual breeding cycle: reproductive codes 1-3 = non-breeders, reproductive codes 4 and 5 = breeding (refer to Box 2.1).

FIGURE 4.8

Breeding observations of adult *Rattus leucopus* (both sexes combined)

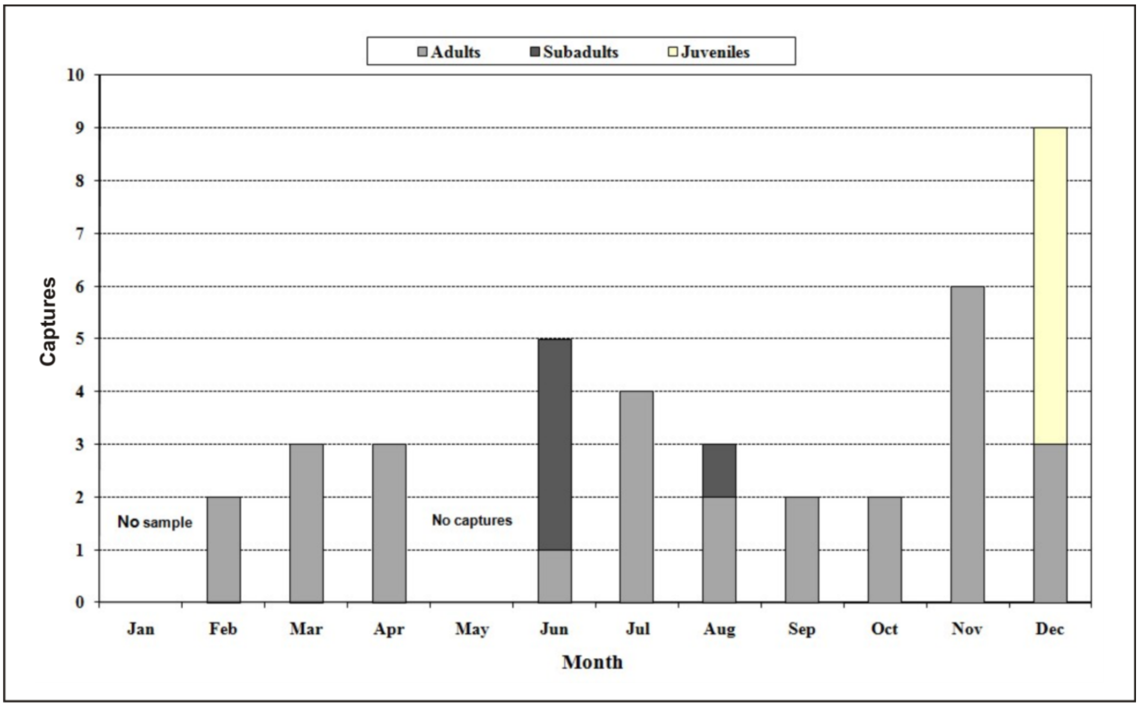


4.2.4 Annual population demography

The only subadults captured were recorded in July and August, with juveniles only observed in December (Figure 4.9).

FIGURE 4.9

***Rattus leucopus* annual population demography**



4.2.5 Mean minimum age (longevity)

Capture data were inadequate to estimate a minimum lifespan for this species.

4.2.6 Population estimation using capture-mark-recapture (CMR)

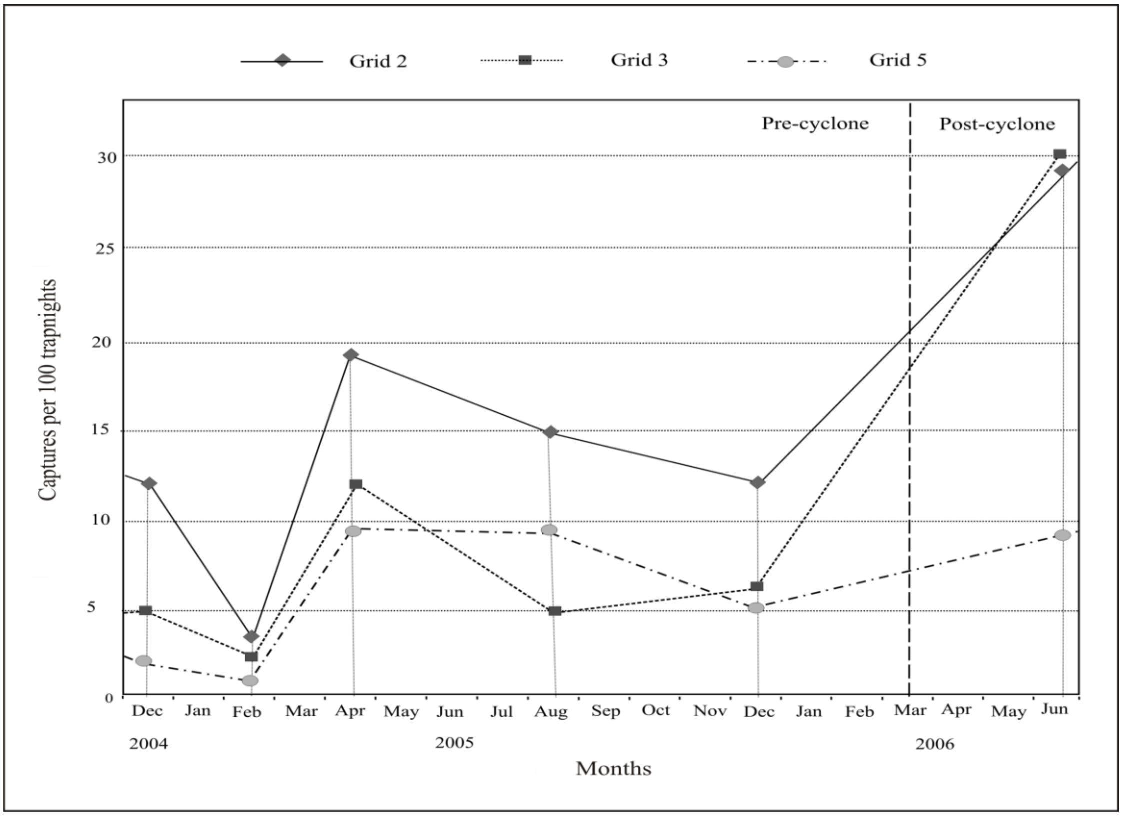
The recapture data were inadequate for these analyses.

4.3 FAWN-FOOTED MELOMYS *MELOMYS CERVINIPES*

A total of 335 grid captures were made of 159 individuals; these comprised 80 males and 79 females (Figure 4.10). There were many retraps i.e., repeated captures within the same trapping session (67%), but a low recapture rate i.e., captures of marked animals over successive trapping sessions (<14%). Figure 4.10 shows a significant increase in total capture numbers (all ages) post-cyclone at Grid 2 and Grid 3. Grid 5 suffered the least disturbance to vegetation from the cyclone while Grids 2 and 3 were extensively damaged.

FIGURE 4.10

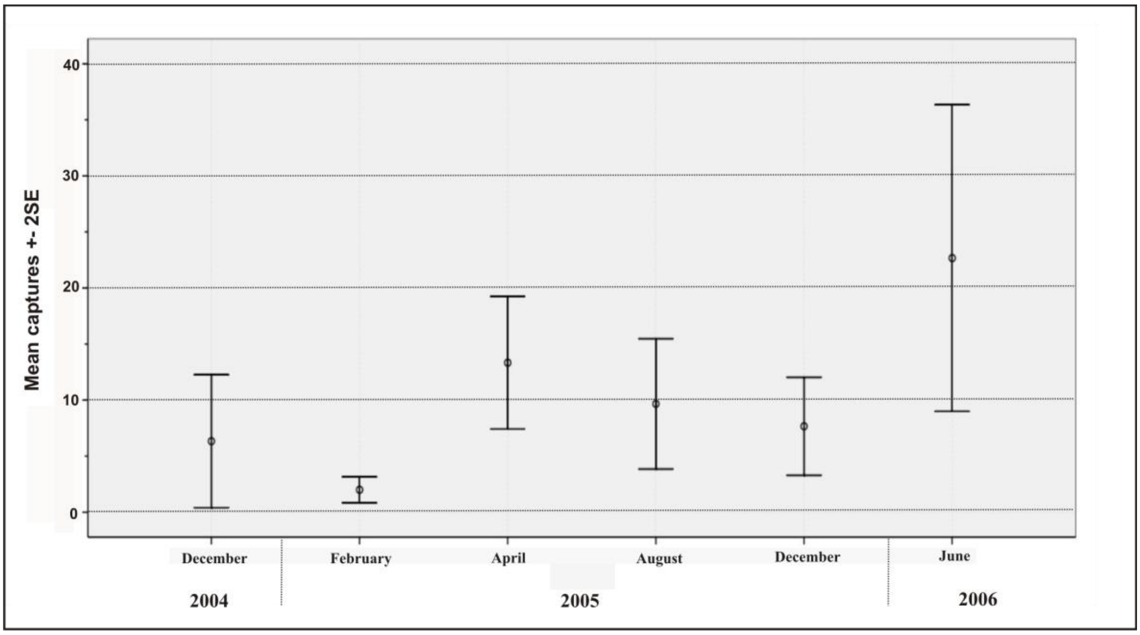
***Melomys cervinipes* – Individual grid captures per trapping session**



Capture data were transformed ($\log_e(x)$) as Levene's test for homogeneity of variances indicated that the variance of data in the groups was unequal. Repeated measures ANOVA revealed that Grid 2 caught significantly more *M. cervinipes* than the other two grids ($F_{1,5}$ =12.472, P=0.017). A Friedman ANOVA showed significant differences in capture rates between the trapping sessions ($X^2_{5,}$ =13.434, P=0.025) with the February 2005 trapping session significantly lower in captures, and April-May 2005 and June 2006 (post Cyclone Larry) significantly higher (Figure 4.11). However, an unpaired t-test comparing seasonal captures for the two trapping sessions April-May 2005 and May-June 2006 revealed that capture numbers did not change significantly post-cyclone (t_4 = -1.252, P=0.279).

FIGURE 4.11

***Melomys cervinipes* trapping session capture means and SE**



4.3.1 Population density

The mean distance between trap locations for two successive captures of individual marked animals (same captures or consecutive t only) was calculated for *M.*

cervinipes. The boundary strip ($\hat{W}$) for estimating species' density ($\hat{W}$ = d/2) was added to the grid area and densities calculated using mean trapping session captures. The mean movement distance for *M. cervinipes* was 54.17 metres ± SE of 5.11 metres (d/2=27.1m). This distance was rounded to 27 metres altering the effective trap area from 2.6 hectares (trapping grid) to 3.65 hectares, an additional 1.05 hectares (approximately 40%). Trapping densities were calculated using the total number of individuals caught each trapping session divided by the total area trapped (N/10.95ha). The density of *M. cervinipes* ranged seasonally from 0.55 animals/ha in December 2004 (2 animals/grid) to 3.7 animals/ha in April 2005 (13 animals/grid), and increased significantly post-Cyclone Larry in June 2006 to 6.2 animals/ha (23 animals/grid). The mean trapping session density was 2.83 animals per hectare (10.3 animals/grid).

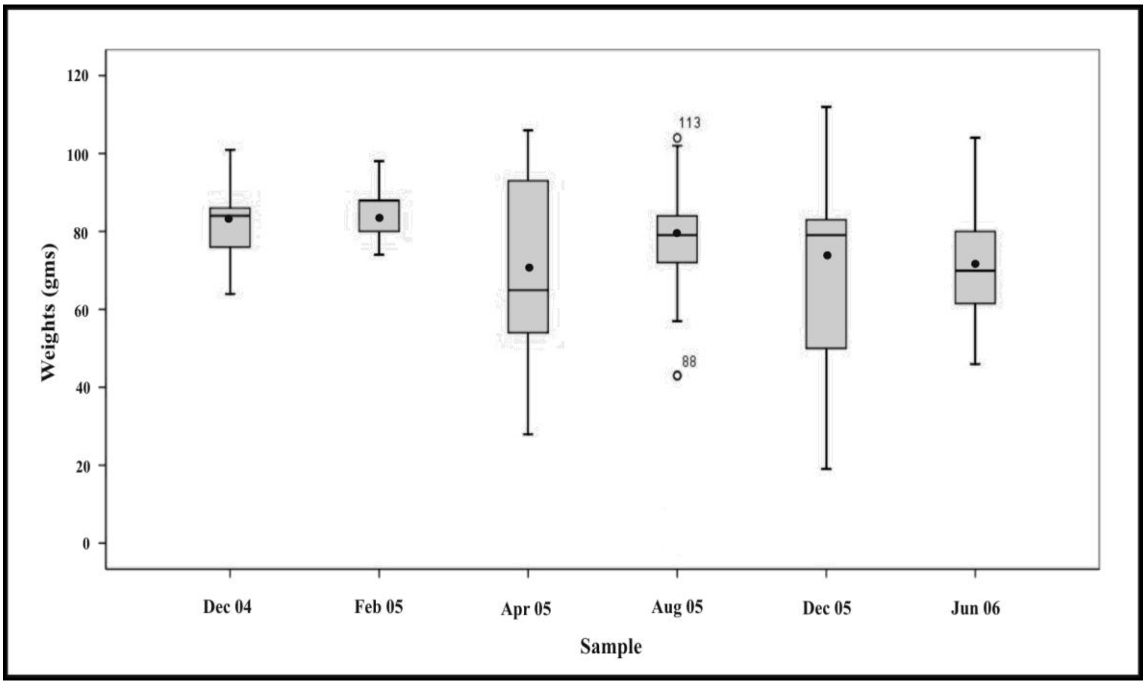
4.3.2 Adult body weights

The body weights of 1st capture adult *M. cervinipes* (>50gms) from the six trapping sessions were analysed for weight comparisons (251 animals). Adult male *M. cervinipes* mean body weight ± SD was 78.2 gms and 13.3 gms respectively; adult female mean body weight ± SD was 72.7 gms and 12.7 gms respectively (male N=142, female N=109). Adult males were significantly heavier than females (t_{249} = 3.327, P=0.001); the heaviest male and female weights were 108 gms and 103 gms respectively. A Friedman ANOVA highlighted significant differences in the means and standard deviations of body weights between trapping sessions (X^2_5 =23.171, P= >0.001). Population body weights (all age classes) were significantly higher in December 2004 and February 2005, significantly lower in April 2005 (Figure 4.12).

FIGURE 4.12

***Melomys cervinipes* - mean and median trapping session weights**

The central box represents the middle half of the weight measurements (25th-75th percentiles) and the median (horizontal line); the black dot represents the mean; the vertical lines are the minimum and maximum data values; and outliers are shown as either circles or stars.



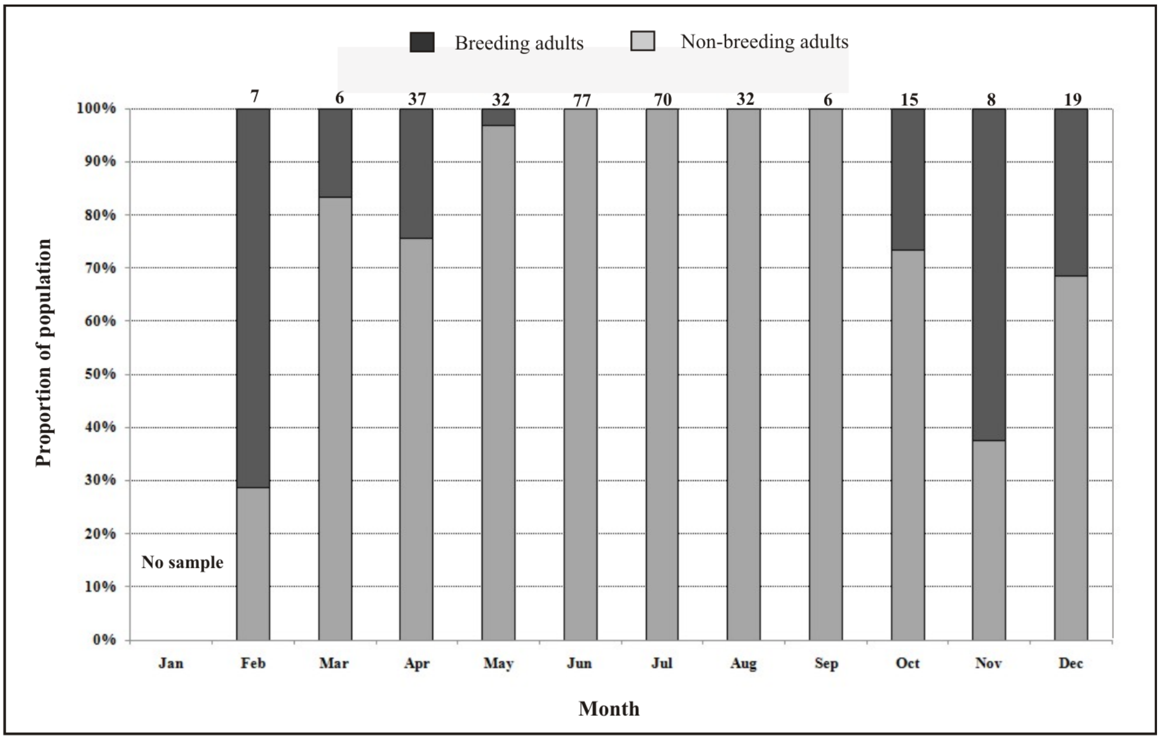
4.3.3 Breeding

All adult 1st captures and recaptures (marked animals caught on subsequent occasions) have been used in the following analyses i.e., exploratory trapping, experimental trapping, and grid trapping (*N*=347). The reproductive status of each adult male and female *M. cervinipes* was assigned to one of two broad categories representing the distinctive stages of the annual breeding cycle: reproductive codes 1-3 = non-breeding, reproductive codes 4 and 5 = breeding (refer to Chapter 1: Box 1). Figure 4.13 shows that animals were recorded as breeding from October to May.

FIGURE 4.13

Annual breeding cycle for adult *Melomys cervinipes*

(Figure located at top of each bar = *N*)



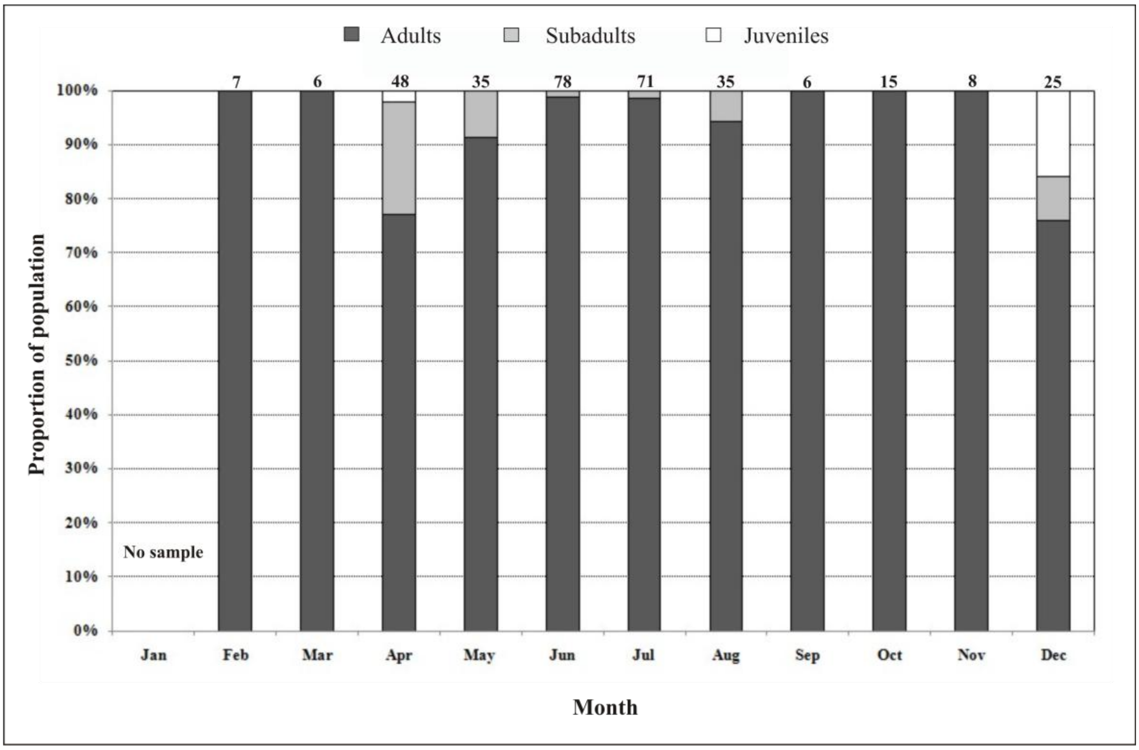
4.3.4 Annual population demography

Figure 4.14 presents the annual population demography observed for *M. cervinipes* in this study. Only a few juveniles (<30gms) were captured, possibly due to their weights being too low to set off traps. Individuals around 20gms (approximately 20 days old) were re-trapped without an adult parent on several occasions in December, and appeared to be independent at this weight. Juveniles were captured in December and again in April, suggesting that two breeding cycles had taken place. Adults dominate the population in all months, ranging from a low of 70% in April to 100% of all captures in the months of February-March and September-November.

FIGURE 4.14

Annual population demography for *Melomys cervinipes*

(Figure located at top of each bar = *N*)



4.3.5 Population estimation using capture-mark-recapture (CMR)

As for similar sampling procedures, this population estimate does not represent the predicted population size of *Melomys cervinipes* existing on the grid itself but instead represents the population from which the is drawn. Due to the extended interval between trapping sessions 5 and 6 (December 2005 and June 2006), trapping session 6 was not included in the analysis. First captures and recaptures of *M. cervinipes* at each grid (Grids 2, 3, and 5) were analysed separately using a full Jolly-Seber analysis (Table 4.3). Leslie's test for equal catchability was not significant at the 5% level (*P* = 0.800) and equal catchability was accepted.

TABLE 4.3

Full Jolly-Seber analysis for *Melomys cervinipes*

Trapping session	Marked animals in pop'n	Pop'n est.	SE pop. est.	Survival estimate	SE survival	New animals	Probability of capture	SE prob. of capture
Grid 2								
Dec 04				0.7024	0.1713		0.7064	0.16
Feb 05	1.124	**11.03**	3.093	0.7024	0.1713	19.55	0.7064	0.16
Apr 05	5.629	**25.45**	5.646	0.7024	0.1713	23.52	0.7064	0.16
Aug 05	1.134	**25.20**	6.391	0.7024	0.1713	14.91	0.7064	0.16
Dec 05	3.521	**19.09**	4.653	0.7024	0.1713	37.8	0.7064	0.16
Grid 3								
Dec 04				0.6464	0.1026		0.6287	0.1407
Feb 05	2.426	**5.61**	1.799	0.6464	0.1026	24.67	0.6287	0.1407
Apr 05	3.677	**29.13**	7.286	0.6464	0.1026	-4.682	0.6287	0.1407
Aug 05	14.11	**15.70**	3.006	0.6464	0.1026	4.38	0.6287	0.1407
Dec 05	7.953	**12.73**	3.985	0.6464	0.1026		0.6287	0.1407
Grid 5								
Dec 04				0.7099	0.07776		0.5954	0.1086
Feb 05	2.399	**9.12**	2.632	0.7099	0.07776	11.1	0.5954	0.1086
Apr 05	7.232	**20.67**	4.404	0.7099	0.07776	12.12	0.5954	0.1086
Aug 05	9.81	**26.61**	5.423	0.7099	0.07776	4.236	0.5954	0.1086
Dec 05	13.05	**23.13**	4.672	0.7099	0.07776	-3.505	0.5954	0.1086

6 (June 2006) was not included in the analysis due to the extended interval between the last two trapping sessions caused by the cyclone. Population estimates varied from 8.6 animals/grid in February 2005 to 25.1 animals/grid in April, with a mean estimated population of 18.6 animals per trapping session.

Estimated population size of Melomys cervinipes

Captures of *M. cervinipes* from Grids 2, 3, and 5, were combined to produce trapping session captures. The estimated population of *M. cervinipes* at Grid 2 was double that present at Grid 3 and Grid 5, and the predicted overall population sampled by the three trapping grids was 128 animals (Table 4.4).

TABLE 4.4

***Melomys cervinipes* Jolly-Seber population estimates**

Grid	Population estimate	SE Pop'n estimate	Upper 95% confidence interval	Lower 95% confidence interval
2	**64**	6.312	83	57
3	**31**	2.942	41	29
5	**33**	2.038	40	32

4.3.6 Mean minimum age (longevity)

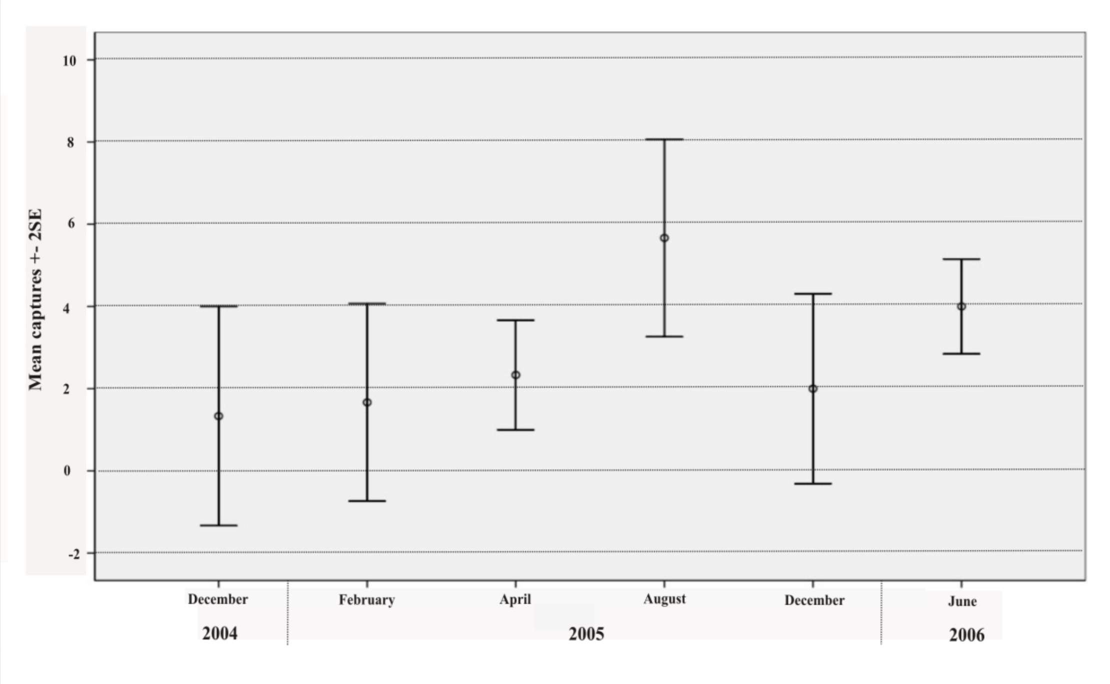
Capture data were inadequate to estimate a minimum lifespan for this species.

4.4 MUSKY RAT-KANGAROO *HYPSIPRYMNODON MOSCHATUS*

A total of 92 captures were made of 58 individual *Hypsiprymnodon moschatus* comprising 36 individual males and 22 females (N=58); there were 13 recaptures (multiple captures over successive trapping sessions), and 21 retraps (multiple captures within the same trapping session). The recapture rate of marked individuals was approximately 22% (13 recaptures/58 individuals). All grid captures were combined to produce trapping session captures (Figure 4.15). One-way repeated measures ANOVA revealed differences between trapping session captures ($F_{2,5}$ =24.272, P=0.039). Significantly more animals were caught in August 2005 and June 2006 and significantly fewer in December 2004. However, an un-paired t-test of seasonal captures for the two trapping sessions April-May 2005 and May-June 2006 indicated there was no significant difference in trapping session means before and after Cyclone Larry (t_4 =1.890, P= 0.132).

FIGURE 4.15

Mean and SE trapping session captures of *Hypsiprymnodon moschatus*



4.4.1 Population density

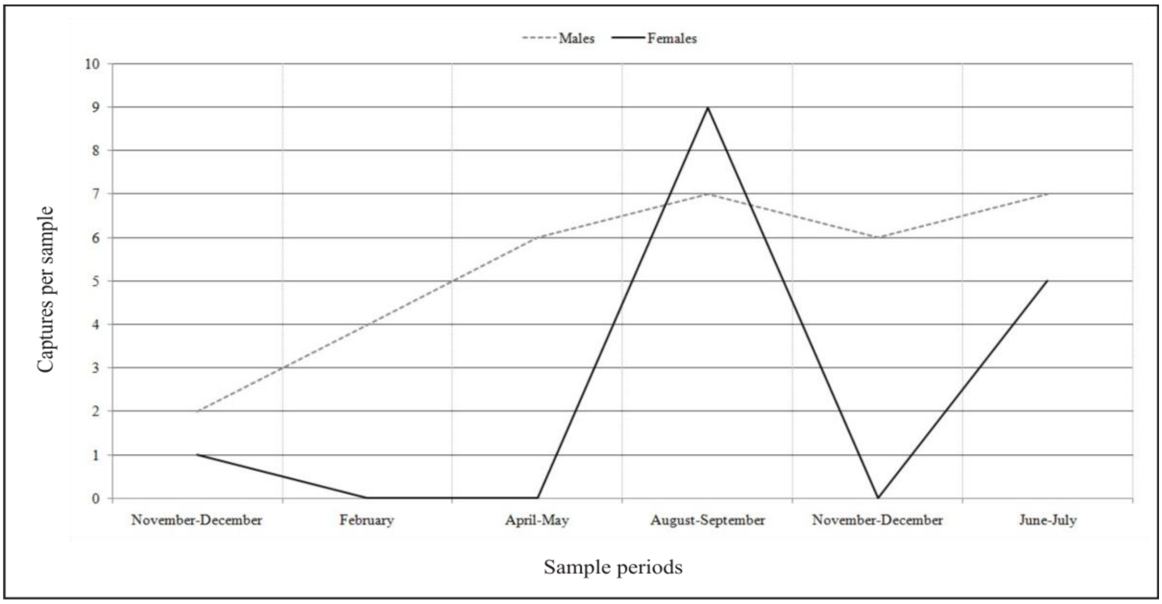
The mean distance between trap locations for two successive captures of individual marked animals (same trapping session or consecutive trapping sessions only) was calculated for *H. moschatus*. The boundary strip ($\hat{W}$) for estimating species' density ($\hat{W}$=d/2) was added to the grid area and densities calculated using mean trapping session captures. The mean movement distance ± SE for *H. moschatus* was 63 metres and 10.4 metres respectively (d/2=31.5m). This boundary strip distance altered the effective trap area from 2.6 hectares (trapping grid) to 3.83 hectares, an additional 1.23 hectares (approximately 47%). Population densities were calculated using the total number of individuals caught each trapping session divided by the total area trapped (N/11.5ha). The density of *H. moschatus* ranged seasonally from 0.26 animals/ha in December 2004 (1 animal/grid), to 0.61 animals/ha in April 2005, and 1.48 animals/ha in August 2005 (5.67 animals/grid). The mean population density per hectare was 0.73, 2.8 animals/grid. CMR estimates, however, resulted in population density ranging from 1.6 animals/ha (December) to 4.8 animals/ha (August), similar to that found by Dennis (1994) of 1.4 – 4.5/ha.

4.4.2 Adult body weights

More males (30) were captured than females (19). Adult (>400 gms) body weight and SD for male *H. moschatus* was 533.3 gms and 60.1 gms respectively; mean adult female weight and SD was 561.2 gms and 67.7 gms respectively. A Friedman ANOVA showed no separation in male and female body weights (X^2_{48} =2.273, P= 0.138). Although heavier animals were captured in February (all adult males), there were no significant interactions between weights and trapping session (X^2_5 =1.091, P =0.379). There was, however, a difference in capture rates between the sexes (Figure 4.16) with males caught on every trapping session and females only captured from June to December.

FIGURE 4.16

Trapping session captures of male and female *Hypsiprymnodon moschatus*



4.4.3 Breeding

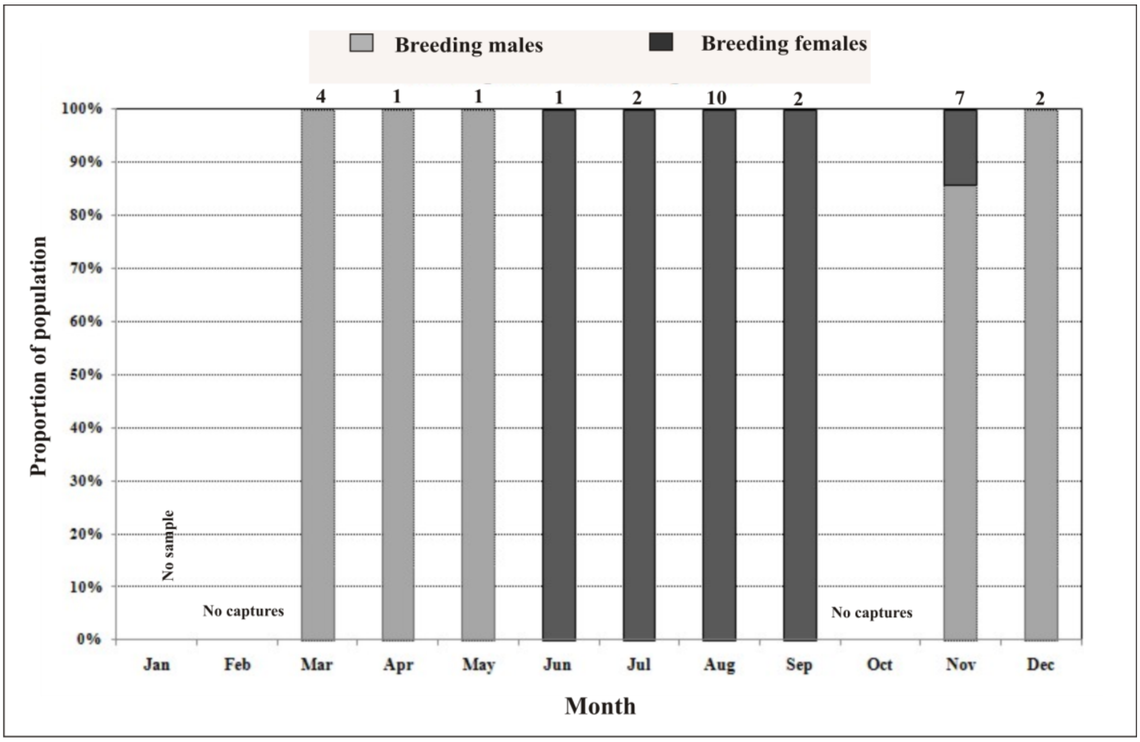
The minimum breeding weight recorded for males (testes large) and females (carrying young) was 520gms and 445gms respectively. The reproductive status of each adult male and female *H. moschatus* was placed into two broad categories representing the distinct stages of the annual breeding cycle: reproductive codes 6-7 = non-breeding; reproductive codes 8-10 = breeding (refer to Chapter 2, Box 2.1). Adult *H. moschatus* males were recorded in breeding condition from November to May, with enlarged testes and actively courting females (Figure 4.17). This is a similar male breeding season than that described by Dennis and Johnson (2008) who found males were sexually active from October to April. Breeding females with unfurred pouched young were first captured in early-June, with a single lactating female captured in late-

November signalling the end of the breeding season. There were no adult captures of either sex in the months of February and October.

FIGURE 4.17

Annual breeding cycle for adult *Hypsiprymnodon moschatus*[1,2]

(Figure located at top of each bar = *N*)



[1] Breeding males = enlarged testes and courting females – [2] Breeding females = pouched young/lactating

4.4.4 Annual population demography

There were no captures of juveniles (<200gms) over the entire study, although a number of subadult animals of both sexes (310gms – 395gms) were caught during the exploratory trapping. Adult female *H. moschatus* were trapped from June to September and all individuals in this period were carrying pouch young. A single lactating female was captured in late-November. Subadults were captured only in the months of June to August, and it is probable they represent offspring from the previous breeding season. Adult males were captured throughout the year.

4.4.5 Mean minimum age (longevity)

Capture data were inadequate to estimate a minimum lifespan for this species.

4.4.6 Population estimation using capture-mark-recapture (CMR)

As for similar sampling procedures, this estimate does not represent the predicted population size of *H. moschatus* existing on the grid itself and instead represents the population from which the sample is drawn. Although grid captures were combined capture numbers were often less than seven individuals, considerably fewer than the 20 animals required to satisfy the conditions that underlie capture-mark-recapture analysis. Jolly (1982) developed modifications that assume constant survival and capture rates in this circumstance to reduce the number of parameters to model and avoid an increase in the variability of parameter estimates (Cormack 1979; Begon 1983). This approach gives a more parsimonious model leading to more efficient estimators (Buckland 1980) and was used in this analysis (Table 4.5). Leslie's equal catchability distribution was not significant (X^2 =5.51, P = 0.064) and catchability was considered equal at the 5% level. The estimated *H. moschatus* population sampled by the three grids varied from approximately 18 animals in February (prior to the onset of breeding) to approximately 74 animals at the height of the breeding season in August. It is probable that the capture analysis was affected by the increased capture of females in August.

Table 4.5

Jolly-Seber analysis for *Hypsiprymnodon moschatus* (Constant Probability of Capture and Survival)

Trapping session	Marked animals in population	Population estimate	SE pop. est.	Survival estimate	Std. error survival	New animals	Probability of capture	SE prob. of capture
Dec 04				0.9661	0.1037		0.2869	0.07679
Feb 05	3.85	17.79	7.188	0.9661	0.1037	7.729	0.2869	0.07679
Apr 05	6.998	24.43	8.68	0.9661	0.1037	47.13	0.2869	0.07679
Aug 05	14.5	73.76	21.8	0.9661	0.1037	-27.28	0.2869	0.07679
Dec 05	24.77	38.71	10.43	0.9661	0.1037	7.729	0.2869	0.07679
Jun 06	34.86	52.29	15.91	0.9661	0.1037		0.2869	0.07679

4.5 OTHER SPECIES

The capture numbers of seven species were too low to undertake either mark-recapture analysis or detailed statistical treatment. These species, although rare, may comprise an important part of the resident small mammal community structure that influences the ecology and behaviour of *Uromys caudimaculatus* and *U. hadrourus*. Accordingly, analyses of the capture data for these species are presented here.

4.5.1 Rusty Antechinus *Antechinus adustus*

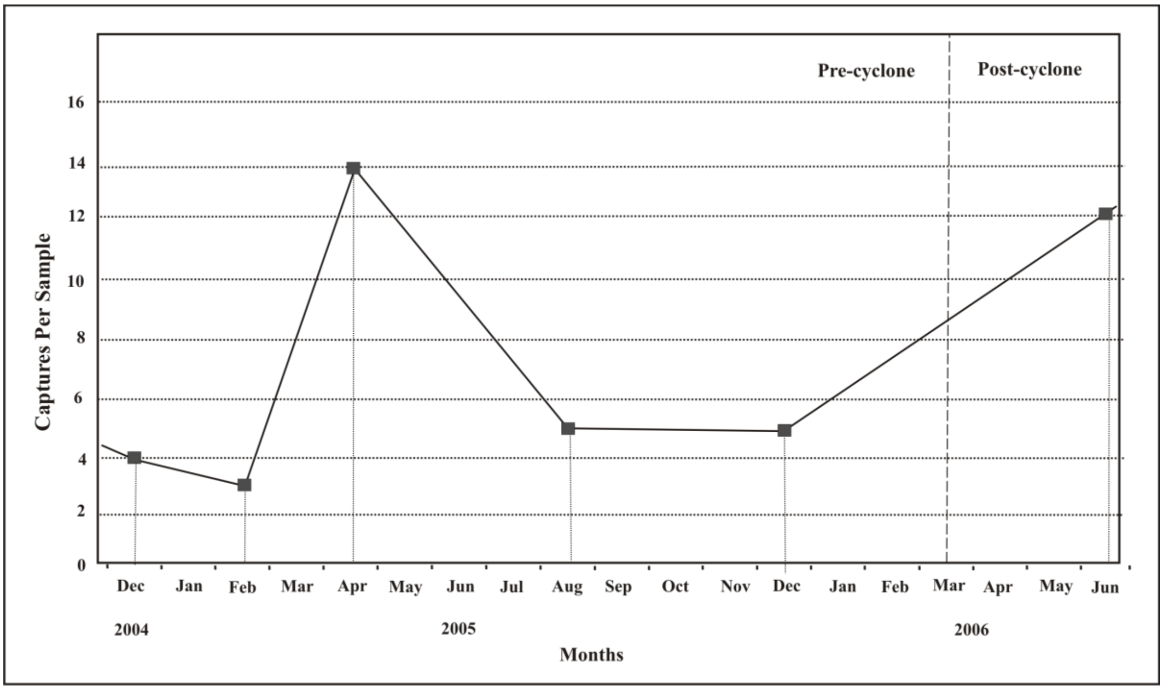
A total of 47 *Antechinus adustus* were captured in this study, 11 males and 36 females (Figure 4.18). Twenty-three individuals were caught during the six trapping sessions; the remainder (24) were captured in the exploratory trapping phase of the project.

Population Densities

It was not possible to calculate an effective trap area boundary strip due to the limited recaptures/retraps of *Antechinus adustus*. Consequently, the following trapping densities are based on the area of the trapping grid only and are therefore likely to be an overestimate of the true density. Population densities were calculated using the total number of individuals caught each trapping session divided by the total area trapped (N/7.8ha). Densities of *A. adustus* varied from 0.39 animals/ha in December 2004, to 1.29 animals/ha in April 2005; the mean population density was 0.92 animals/ha. These densities are considerably higher than that recorded by Watts (1997) at Koolomon Creek e.g., 0.05 to 0.97 individuals per hectare seasonally, with a mean density of 0.34/ha.

FIGURE 4.18

Trapping session captures of *Antechinus adustus*



Adult body weight

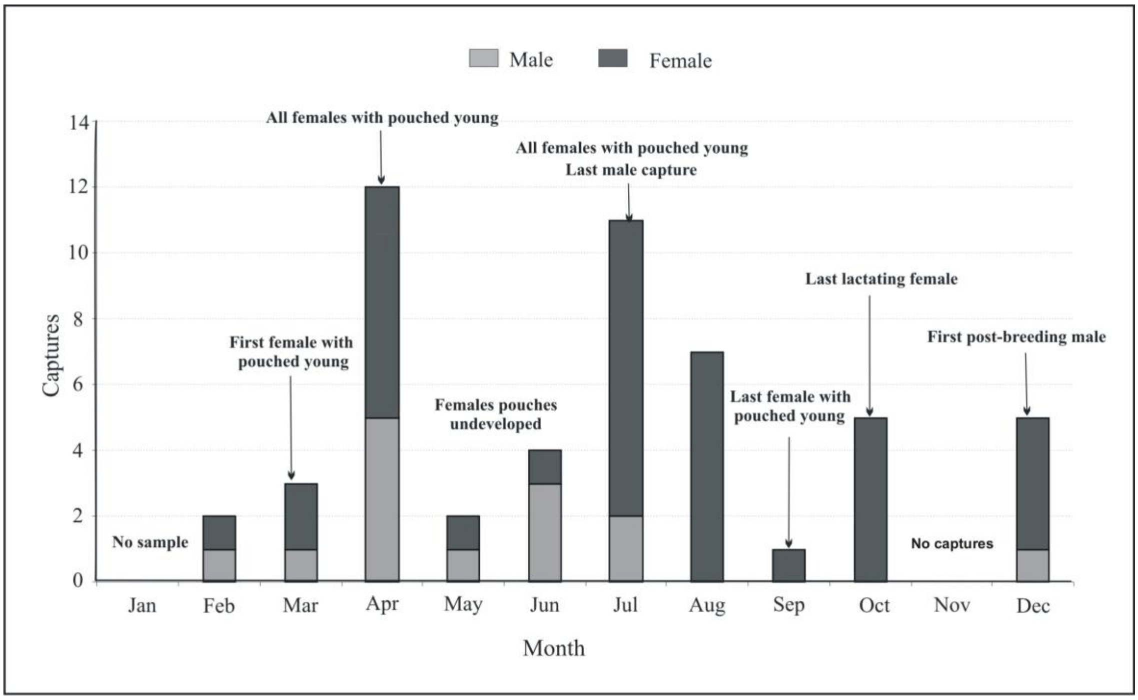
Male weights ranged from 21-44 gms and female weights ranged from 17-34 gms. Mean weight for male and females was 34.7 gms (SD=6.18 gms) and 26.6 gms (SD=3.59 gms) respectively (N=47). This is similar to that found by Watts (1997) of 33 gms (males) and 28 gms (females). An independent t-test showed that male weights were significantly heavier than those of females (t_{45}=4.174, *P* =0.001).

Breeding

Watts (1997) first recorded *A. adustus* females with pouch young from August onwards, indicating that mating had begun in late June to early July. She concluded that females produced one litter per breeding season, with the first pouch young recorded in early August and lactating females without young observed in late-September. My data suggest a different breeding pattern was in place from 2004–2006 on the Bartle Frere trapping grids. There appear to be two distinct breeding cycles represented on Figure 4.19, the first in March and April and the second from July to August. Scrotal males were recorded in February, March, and May, with the last male (non-breeding) caught on 5 July. No breeding males were captured in May or June. All breeding females were recorded carrying six young (N=17). The smallest female breeding weight recorded was 24gms, a female carrying six pouch young in July 2005.

FIGURE 4.19

***Antechinus adustus* annual breeding cycle using all captures**

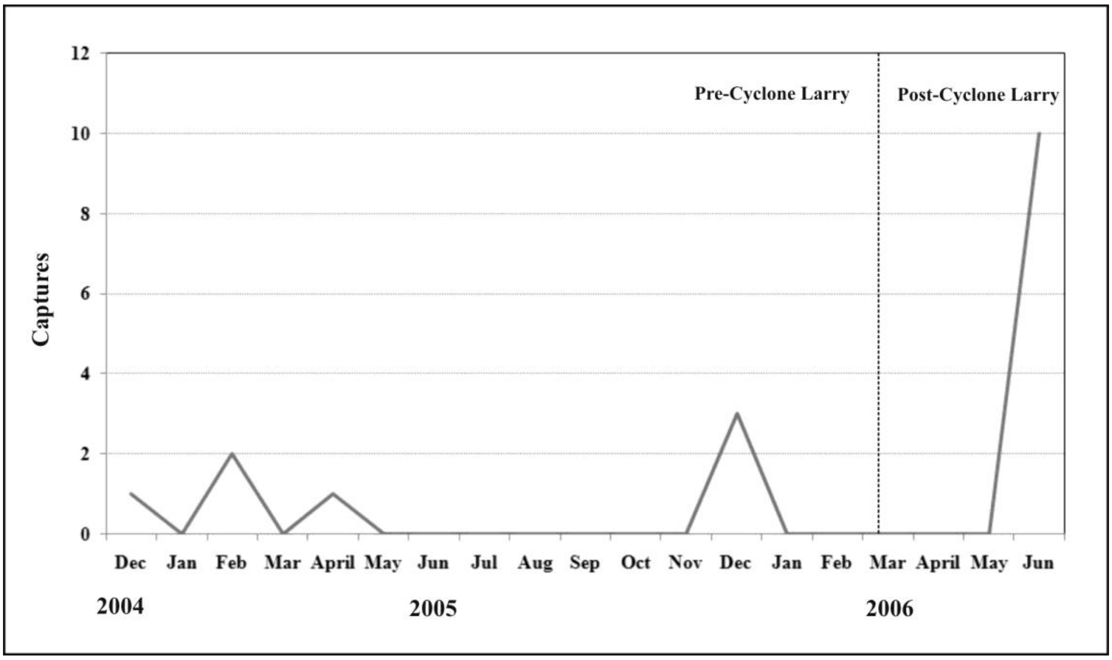


4.5.2 Atherton Antechinus *Antechinus godmani*

There 31 individual *Antechinus godmani* captured in this study, 16 males and 15 females. Of these 15 were captured during the exploratory and experimental trapping phases and 16 were caught by the six grid trapping sessions (10 males and 6 females) (Figure 4.20).

Figure 4.20

Trapping session captures of *Antechinus godmani*



Population density

It was not possible to calculate an effective trap area boundary due to limited recaptures and retraps of *A. godmani*. As such, the following population densities are based on the area of the trapping grid only and are therefore likely to be an overestimate of the true density. Densities were calculated using the total number of individuals caught each trapping session divided by the total area trapped (N/7.8ha). Densities of *A. godmani* varied from 0.13 animals/ha in December 2004 and March 2005 to 1.3 animals/ha in June 2006, three months after Cyclone Larry (3.4 animals/grid). The mean population density was 0.36 animals/ha.

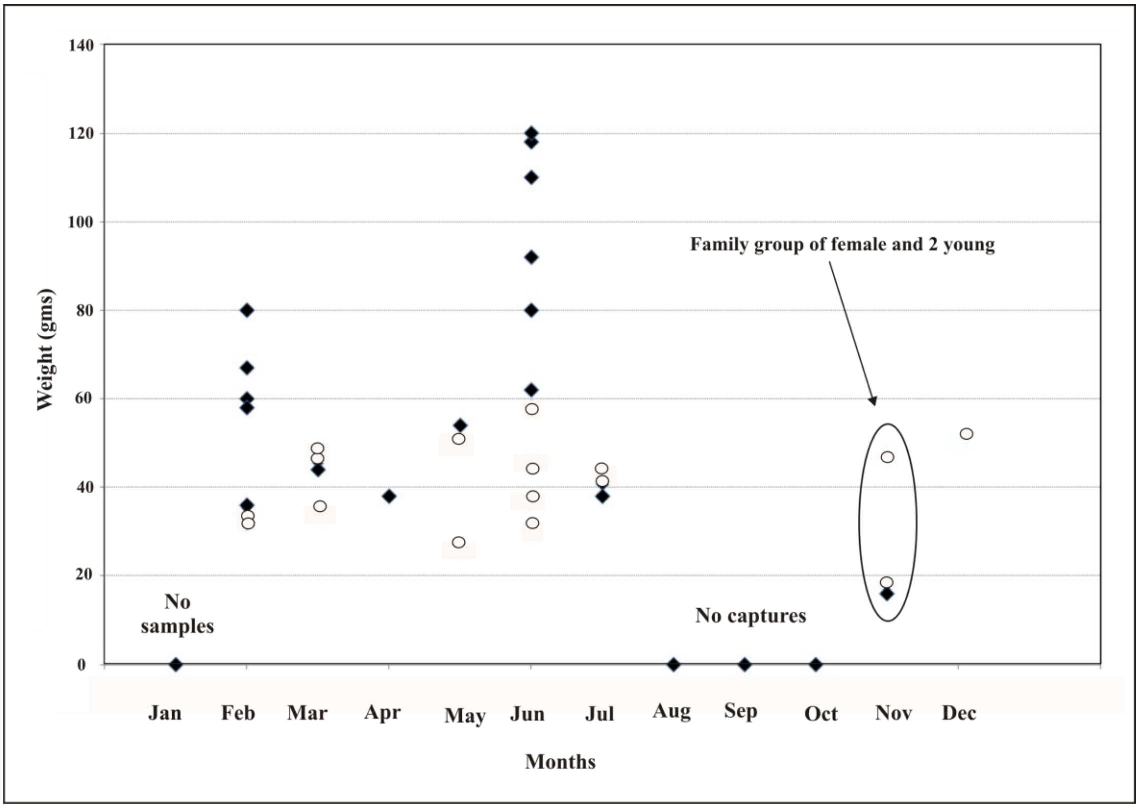
Adult body weight

The body weights of captured *A. godmani* varied considerably during the year with maximum male and female weights recorded in late May to early June (male=120gms; female=58gms).

Figure 4.21

Monthly variation in *Antechinus godmani* body weights

Open circles = females; Dark diamonds = males

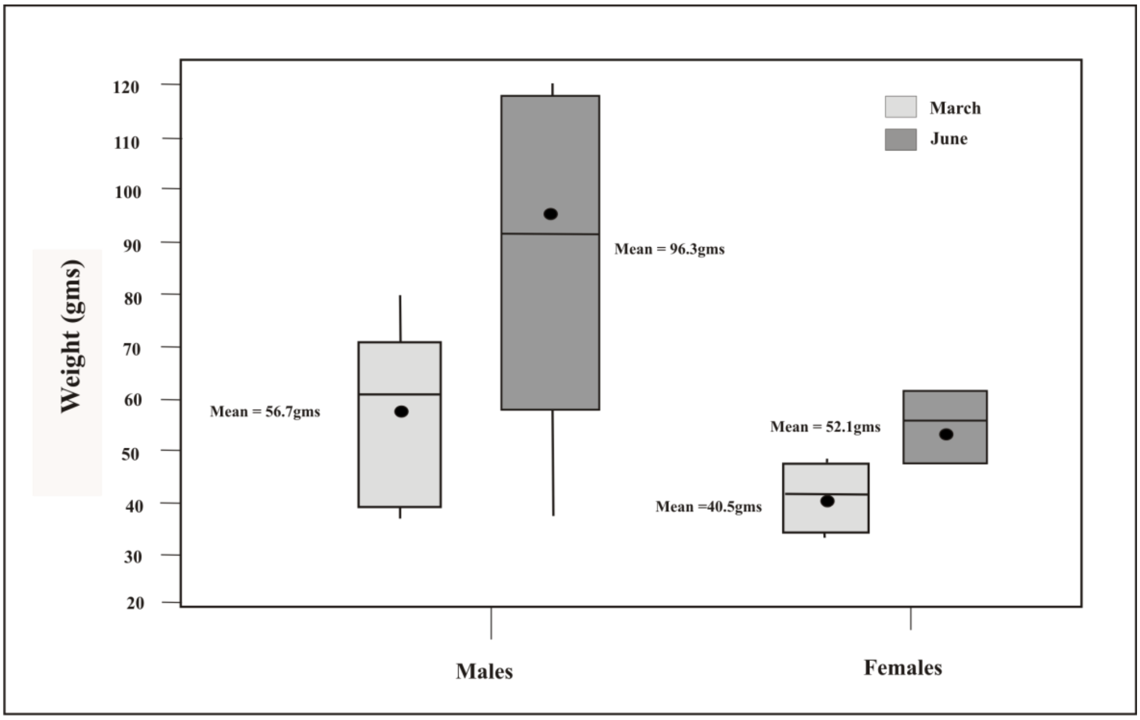


The weights for all *A. godmani* captures (exploratory, experimental, trapping sessions) are shown on Figure 4.21. Body weights were combined into two chronological groups: animals trapped from February to April (N=10) and animals trapped from June-July (N=12), and the results are shown on Figure 4.22. The central box represents the middle half of the measurements (25th-75th percentiles) and the median (horizontal line); the vertical lines are the minimum and maximum data values; means are shown as circles within the central box. Male mean weights increased by approximately 69% from March to June, while female mean weights rose by approximately 29%.

FIGURE 4.22

Antechinus godmani weight changes from March (non-breeding) to June (breeding)

The central box represents the middle half of the weight measurements (25th-75th percentiles) and the median (horizontal line); the black dot represents the mean; the vertical lines are the minimum and maximum data values.

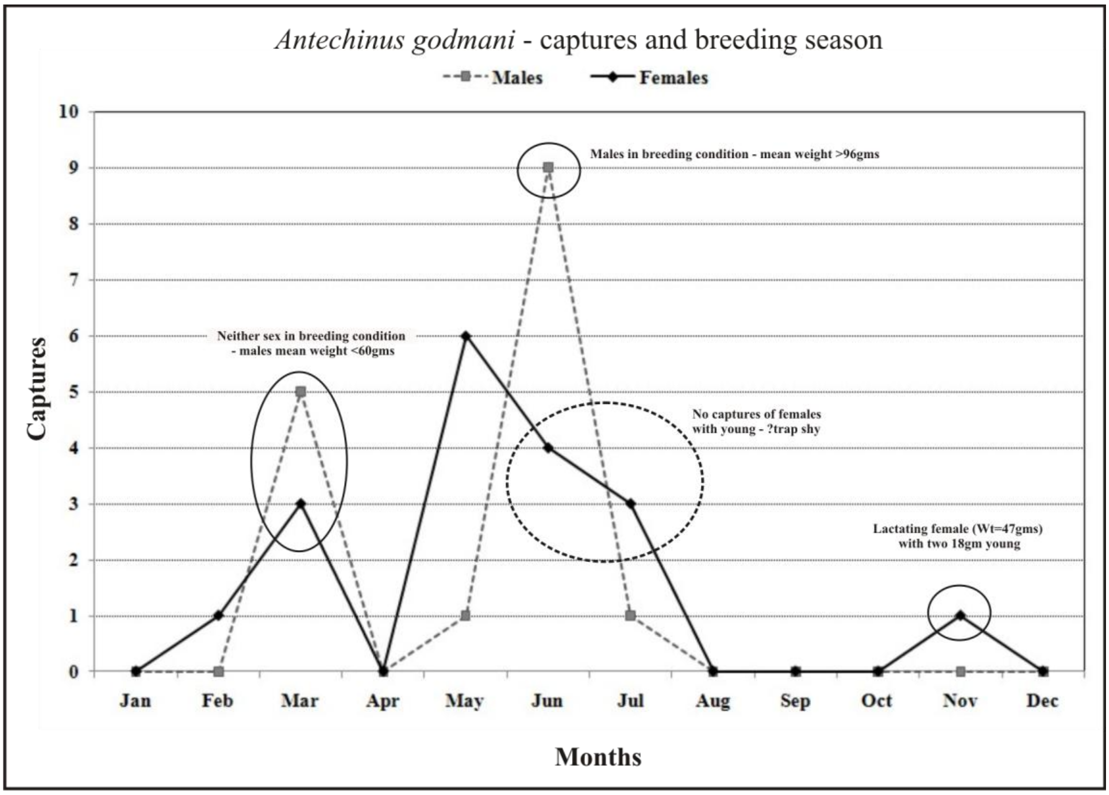


Breeding

Although female *A. godmani* carrying young were not captured in this study, a single lactating female weighing 47gms was caught on 28 November 2005 in the company of two 18gm juveniles. The capture of the family party suggests that the mean female body weight in June (52gms) probably represents the approximate breeding weight for females. A number of males trapped in June had damage to their fur and heads, presumably from fights with other breeding males. Apart from a single male captured in early July, no males were captured after June. An indicative annual breeding cycle for *A. godmani* is shown in Figure 4.23 based on the observed reproductive condition and weights of captured animals (N=31).

FIGURE 4.23

Annual breeding cycle of captured *Antechinus godmani*



4.5.3 Yellow-footed Antechinus *Antechinus flavipes rubeculus*

Only two male *Antechinus flavipes* were caught during this study, both at Grid 2. The first capture was of a subadult non-scrotal male (41gms) in February 2005 and the second was of a small-scrotal male (55gms) in mid-April 2005. The lack of *A. flavipes* on the trapping grids supports the hypothesis of Watts (1997) that this species and *A. godmani* rarely occur in the same localities.

4.5.4 Long-nosed Bandicoot *Perameles nasuta pallescens*

There were nine captures of *Perameles nasuta* comprising four adult males, four adult females, and one newly-independent juvenile (132gms). All trapped females were carrying pouch young; a female with two unfurred young in April, a female with two furred young in June, and two individuals each with two furred young in October. The single juvenile was captured in mid-April 2005 on four successive trapnights.

4.5.5 Northern Brown Bandicoot *Isoodon macrourus torosus*

Grid 3 was the only site that recorded this usually non-rainforest species. There were eight captures comprising six individual captures and two recaptures. The weights of the three males and three females trapped were 1090, 2000, 2100gms and 590, 620, and 650gms respectively. A female weighing 650gms was recorded with two pouch young in early September.

4.5.6 Long-tailed Pygmy-possum *Cercartetus caudatus*

A single female was captured in a ground-placed trap at Grid 5 in mid-December 2004. The animal weighed 33gms and had a developed pouch.

4.5.7 Tree mouse *Pogonomys sp.*

This species is arboreal and has never been caught in a terrestrial trap prior to this study. The non-breeding male was captured in late-April in dense understorey along a creek at Grid 5. Rainfall at the time of capture ranged from 40-90mm per day. The body measurements were as follows: weight: 68gms; head-body:123mm; tail-vent:165mm; pes:23.0mm. Previous captures have been made in the canopy between 12 and 33 metres, with a single capture in the understorey at 2.5 metres (Rader 2005).

4.5.8 Grassland Melomys *Melomys burtoni*

One non-breeding male *Melomys burtoni* weighing 58gms was captured at Grid 5 in June 2006, approximately 100 metres from the forest edge. Although a grassland specialist in north Queensland, this species has been recorded up to 200 metres within rainforest fragments previously (Harrington et al. 2001; Moore unpublished data).

4.5.9 House Mouse *Mus musculus*

Two non-breeding house mice were captured at Grid 2 approximately 250 metres from the forest edge along a disturbed section of creek.

4.6. HABITAT PREFERENCES OF SMALL MAMMAL ASSEMBLAGE

Trap location microhabitat for all mammal captures were classified into the following habitat types (refer to Chapter 2): 1) Ridge-open understorey; 2) Flat-open understorey; 3) Upper-mid slopes-open understorey; 4) Lower slopes–open understorey; 5) Lower slopes-dense understorey; 6) Gully–first order stream; 7) Riparian–second order stream. Chi-square tests for heterogeneity were conducted to identify habitat preferences and differences and the residuals are presented in Table 4.6. Shaded cells with bold font = significant positive association with microhabitat type; bold italicised font = significant negative association (greater than ± 6.0 has been used as the significance factor).

Table 4.6

Chi-square tests on species' trap location habitat types to identify habitat associations

Species		**Habitat 1**	**Habitat 2**	**Habitat 3**	**Habitat 4**	**Habitat 5**	**Habitat 6**	**Habitat 7**
Rattus fuscipes	*Observed N*	15	9	29	5	32	21	6
	Expected N	14.8.	14.8.	14.8.	14.8.	14.8.	14.8.	14.8.
	Residual	.3	-5.8	**14.3**	***-9.8***	**17.3**	**6.3**	***-8.8***
Melomys cervinipes	*Observed N*	18	3	19	5	23	16	7
	Expected N	11.5	11.5	11.5	11.5	11.5	11.5	11.5
	Residual	**6.5**	***-8.5***	**7.5**	***-6.5***	**11.5**	4.5	-4.5
Uromys caudimaculatus	*Observed N*	21	0	51	37	25	17	0
	Expected N	30.2	30.2	30.2	30.2	30.2	30.2	30.2
	Residual	***-9.2***	0	**20.8**	**6.8**	-5.2	***-13.2***	0
Antechinus adustus	*Observed N*	5	8	10	0	16	9	9
	Expected N	8.4	8.4	8.4	8.4	8.4	8.4	8.4
	Residual	-3.4	-.4	1.6	0	**7.6**	.6	.6
Hypsiprymnodon moschatus	*Observed N*	10	1	13	8	20	7	4
	Expected N	9.0	9.0	9.0	9.0	9.0	9.0	9.0
	Residual	1.0	***-8.0***	4	-1.0	**11.0**	-2.0	-5.0
Antechinus godmani	*Observed N*	0	7	3	0	20	2	6
	Expected N	7.3	7.3	7.3	7.3	7.3	7.3	7.3
	Residual	***0***	-.3	-4.3	***0***	**12.7**	-3.3	-1.3
Uromys hadrourus	*Observed N*	0	0	0	0	19	10	4
	Expected N	10	10	10	10	10	10	10
	Residual	***0***	***0***	***0***	***0***	**9.0**	**.0**	-6.0

Rattus fuscipes

There was significant bias in captures within habitat types for *R. fuscipes* (X^2_7=42.923, P=<0.001). Residuals showed that Habitat 3 (upper-mid slopes-open understory), and Habitat 5 (lower slopes-dense understorey) were positively selected by *R. fuscipes* (residuals 14.3, and 17.3 respectively). There were negative associations between trap locations for Habitat 2 (flat-open understory, Habitat 4 (lower slopes, open understorey), and Habitat 7 (riparian –second order stream) (residuals -5.8, -9.8, and -8.8 respectively). Overall, frequencies of captures showed that 49% of all *R. fuscipes* trap locations were in forest with an open understorey, and 51.4% were located in forest with a dense understorey and the riparian corridor.

Melomys cervinipes

Chi-square indicated that trap location habitat for *M. cervinipes* was not uniformly distributed (X^2_7=43.130, P=<0.001). Residuals showed that Habitat 3 (upper-mid slopes-open understory), and Habitat 5 (lower slopes-dense understorey) were positively selected by *M. cervinipes (*residuals 7.5 and 11.5 respectively). There were negative associations between trap locations for Habitat 2 (flat-open understory), Habitat 4 (lower slopes, open understorey), and Habitat 7 (riparian–second order stream). An unpaired t-test confirmed that *M. cervinipes* utilised similar microhabitats to *R. fuscipes* (t_{90}= -.759, P=0.450)

Hypsiprymnodon moschatus

Chi-square indicated that trap location habitat for *H. moschatus* was not uniformly distributed (X^2_7=25.778, P=<0.001). Residuals showed that Habitat 3 (upper-mid slopes-open understory) and Habitat 5 (lower slopes-dense understorey) were positively selected with approximately 21% and 32% of all captures occurring in

Habitats 3 and 5 respectively. Overall however, microhabitat use was not significantly different from *R. fuscipes* and *M. cervinipes* (t_{62} =.879, *P*=0.383)

Antechinus adustus

Although chi-square indicated there was a bias in trap location habitat for *A. adustus* (X^2_7=13.492, *P*=<0.036) the magnitudes of both the negative and positive associations were small. Residuals indicated positive associations between captures in open understorey on upper-mid slopes (Habitat 3) and dense understorey on the lower slopes (Habitat 5).

Antechinus godmani

There was a significant association between trap location habitat and *A. godmani*, captures with 46% of captures occurring in the densely-vegetated lower slopes (Habitat 5) (X^2_5=27.727, *P*=<0.001). Approximately 77% of all captures occurred in forest with dense understorey (Habitats 5-7).

4.6.1 Species-habitat inter-relationships

Using the results of the chi-square analysis, which showed habitat preferences of individual species, habitat inter-relationships between species was explored. A matrix of species captures by habitat type was developed and analysed using multiple linear regression while controlling for the variable *habitat.* Table 4.7 presents the Pearson product moment correlation coefficients produced by the regression and the two-tailed significance levels of the species' inter-relationships. *P*-values below 0.05 indicate statistically significant non-zero correlations at the 95.0% confidence level.

Table 4.7

Pearson product moment correlation

These correlation coefficients range between -1 and +1 and measure the strength of the linear relationship between the variables. Also shown in parentheses is the number of pairs of data values used to compute each coefficient. The third number in each location of the table is a P-value which tests the statistical significance of the estimated correlations.

Ag=*A. godmani*; **Aa**=*A. adustus*; **Rf**=*Rattus fuscipes*; **Uc**=*Uromys caudimaculatus*; **Uh**=*U. hadrourus*; **Hm**=*Hypsiprymnodon moschatus*; **Mc**=*Melomys cervinipes*;

		Ag	**Aa**	**Rf**	**Uc**	**Uh**	**Hm**	**Mc**
Ag	*Correlation*[1]		0.8952	0.5373	-0.1860	0.8583	0.5401	0.3843
	Size		(7)	(7)	(7)	(7)	(7)	(7)
	P-Value		**0.0064**	0.2136	0.6897	**0.0134**	0.2108	0.3947
Aa	*Correlation*	0.8952		0.4541	-0.4669	0.7281	0.3438	0.3960
	Size	(7)		(7)	(7)	(7)	(7)	(7)
	P-Value	**0.0064**		0.3061	0.2909	0.1011	0.4502	0.3792
Rf	*Correlation*	0.5373	0.4541		0.5026	0.6093	0.8187	0.9045
	Size	(7)	(7)		(7)	(7)	(7)	(7)
	P-Value	0.2136	0.3061		0.2503	0.1464	**0.0243**	**0.0051**
Uc	*Correlation*	-0.1860	-0.4669	0.5026		-0.0745	0.6194	0.4756
	Size	(7)	(7)	(7)		(7)	(7)	(7)
	P-Value	0.6897	0.2909	0.2503		0.8739	0.1380	0.2807
Uh	*Correlation*	0.8583	0.7281	0.6093	-0.0745		0.6309	0.5717
	Size	(7)	(7)	(7)	(7)		(7)	(7)
	P-Value	**0.0134**	0.1011	0.1464	0.8739		0.1287	0.1799
Hm	*Correlation*	0.5401	0.3438	0.8187	0.6194	0.6309		0.8567
	Size	(7)	(7)	(7)	(7)	(7)		(7)
	P-Value	0.2108	0.4502	**0.0243**	0.1380	0.1287		**0.0138**
Mc	*Correlation*	0.3843	0.3960	0.9045	0.4756	0.5717	0.8567	
	Size	(7)	(7)	(7)	(7)	(7)	(7)	
	P-Value	0.3947	0.3792	**0.0051**	0.2807	0.1799	**0.0138**	

1 = Correlation coefficient

There were strong positive microhabitat relationships between three sets of species:

1. *Rattus fuscipes* - *Melomys cervinipes* - *Hypsiprymnodon moschatus.*
2. *Antechinus godmani* - *Antechinus adustus*
3. *Antechinus godmani* - *Uromys hadrourus*;

Discussion

Pearson product moment correlation and X^2 revealed that although subtle differences in habitat use existed between the three species, *Rattus fuscipes*, *Melomys cervinipes, and Hypsiprymnodon moschatus* made use of a similar suite of open understorey and dense understorey rainforest microhabitats. Interestingly, all three species were negatively associated with forest on the lower slopes with an open understorey (Habitat 4). Forest with open understorey on the mid and lower slopes (Habitat 3 and Habitat 4) was strongly favoured (59% of captures) by *Uromys caudimaculatus* (Habitat 3 =34% and Habitat 4=25%) but it is not clear what form any competition would take given the significant differences in the diet and foraging behaviour of *U. caudimaculatus* (hard-shelled seeds and scansorial habit). While unknown, however, the influence of predation on species' habitat use may be significant (e.g., Volterra 1931; Lotka 1932; Monro 1967; Sih 1982; Werner and Gilliam 1984, Lima and Dill 1990, Houston *et al.* 1993; Werner and Anholt 1993 Gaston 1994; Bystrom *et al.* 2002; Chase and Leibold 2003). A second strong habitat-species relationship existed between *Antechinus godmani* and *A. adustus.* Although both species used forest with open and dense understorey, the X^2 residuals show that *A. adustus* were captured more often in open habitats e.g., 43% for *A. adustus* and 25% for *A. godmani*. The third habitat relationship was between *Antechinus godmani* and *Uromys hadrourus*: this pair of species favoured densely-vegetated habitat located on the lower slopes, in gullies, and along riparian corridors. *Uromys caudimaculatus* was the only species to have no significant relationship with any mammal species or habitat type i.e., its use of the available resources does not appear to be related to the structure of the coexisting small mammal assemblage. The habitat utilisation of *Uromys caudimaculatus* and *U. hadrourus* are explored further in Chapters 5-8.

4.7 ABUNDANCE VERSUS BIOMASS

The term biomass generally refers to the mass of living biological organisms in a given area or ecosystem (Williams *et al.* 2002). In this study, however, it is used to represent the ‘community’ mass of those small mammal species trapped on the study grids and is expressed as three totals: total mammal mass in the community per trapping session; the average species mass per trapping session; and mean species mass per unit area e.g., hectare. In trapping studies the total number of individuals caught can be a misleading variable when interpreting mammal density and the carrying capacity of the habitat in which they live. The problem is analogous to dietary studies where the numerical quantity of an extremely small food item e.g., clover seed, can potentially overshadow the significance of a smaller number of larger seeds which have a far greater food volume e.g., sorghum. Among the many physiological differences between large and small-bodied animals, larger vertebrate bodies require more food, reproduce more slowly, take longer to mature, and produce more waste than smaller bodies (Ernest 2004; Dunham and Vinyard 1997). In comparison, small animals tend to grow fast, breed early, and die younger (Savage *et al.* 2004). Thus, incorporating species’ body size (mass) as well as capture numbers provides a more accurate assessment of the underlying availability and exploitation of resources (Ernest 2004; Loeuille and Loreau 2006).

Maximum mammal biomass occurred in the April and June trapping sessions, presumably as the majority of independent young moved into the population following breeding earlier in the year. The mean trapping session biomass of the five mammal species which contained approximately 91% of all 1st captures are shown in Table 4.8 and Figure 4.24. These species comprise: *Rattus fuscipes* (632 captures); *Melomys cervinipes* (283 captures); *Uromys caudimaculatus* (223 captures); *Hypsiprymnodon moschatus* (66 captures); and *Uromys hadrourus* (19 captures). Although *Antechinus adustus*, *A. godmani*, and *Rattus leucopus* were more abundant, the latter species (*U. hadrourus*) has been included in this analysis to allow a comparison of its captures and biomass with that of *U. caudimaculatus*.

Table 4.8

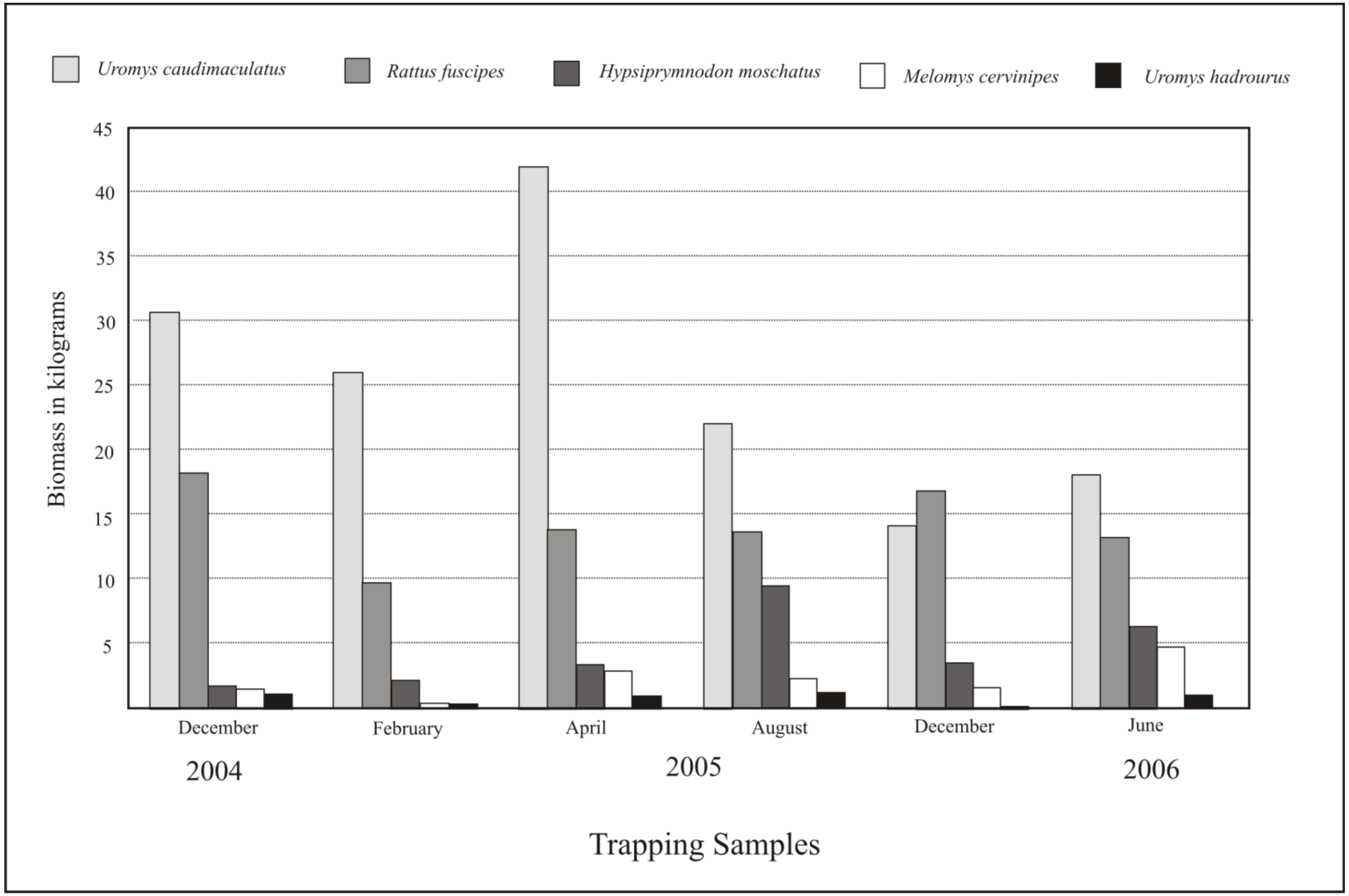
Species total capture numbers compared to mean biomass

Species	**Proportion of 1st captures (%)**	**Biomass per (kg)**	**Biomass per hectare (kg/ha)**
Rattus fuscipes	48.9	14.24	1.4
Melomys cervinipes	21	2.26	0.21
Uromys caudimaculatus	16.1	25.45	2.2
Hypsiprymnodon moschatus	4.9	4.47	0.39
Uromys hadrourus	1.4	0.81	0.07

Rattus fuscipes was the most abundant species recorded, with captures making up almost 49% of mean trapping session captures and a mean session biomass of >14 kg/. However, while captures of *U. caudimaculatus* comprised only 16.1% of total individual captures (one-third that of *R. fuscipes*) the species had the highest trapping session biomass of any mammal species (~25.5 kg/), almost twice that of the more abundant *R. fuscipes* and greater than 31 times that of its sister species *U. hadrourus* (0.07 kg/). It was potentially, therefore, the most significant consumer of available food resources on the grids.

Figure 4.24

Trapping session biomass of trapped mammal species (kilograms)



4.8 COMPARISON WITH OTHER STUDIES

Read (1984) found that in most published studies inconsistency in sampling configuration, intensity, and scope of small mammal studies meant that results were often not comparable. This conclusion also applies in part to this study. Previous north Queensland mammal studies have focussed on comparative differences between population of species or were directed at single question issues e.g., the effect of fragmentation on small mammals (Laurance 1994; Harrington *et al.* 2001) and the impacts of roads as barriers to movement (Goosem 2000, 2002). Another obstacle in comparing different studies on small mammals is that most studies have been undertaken in modified landscapes and/or have used a range of sampling methodologies e.g., Crome *et al.* 1991; Laurance 1994, Harrington *et al*. 2001; Goosem 2000, 2002). However, captures of rare species can be considered an indicator of both sampling effectiveness and species representativeness (Seaby and Henderson 2006). For that reason capture data for rare and uncommon species from two studies conducted nearby on the Atherton Tableland (Laurance, 1994; Harrington *et al.,* 2001) are compared with captures of rare species in this study (Table 4.9).

Laurance 1994

In this study captures of *Antechinus godmani* and *Hypsiprymnodon moschatus* were seven-fold greater than those of Laurance (1994), and *Antechinus adustus* captures were almost doubled. Four species, *Uromys hadrourus* (19), *Isoodon macrourus* (4), *Pogonomys sp.* (1), and *Melomys burtoni* (1) were not captured by Laurance. There are a number of possible explanations for this disparity between the two studies. Differences in species captures may be a result of the relative locations of the two study areas; Laurance’s research was centred on the township of Millaa Millaa, approximately 30km south of the Mt Bartle Frere sites.

TABLE 4.9

Comparison of rare species captures (Laurance 1994; Harrington *et al.* 2001; Moore 2009 - this study)

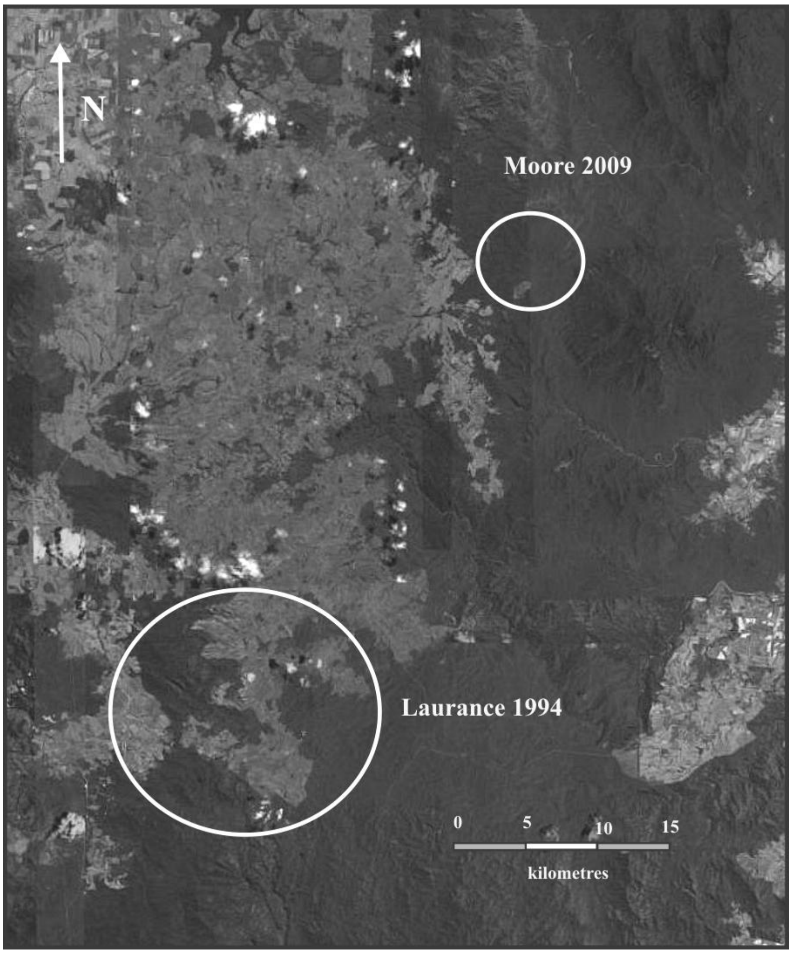
Species	**Continuous forest**		
	Laurance 1994	Harrington *et al.* 2001	This study
Pogonomys sp.	0	0	1
Antechinus adustus	16	0	28
Antechinus flavipes	1	0	1
Antechinus godmani	3	16	20
Hypsiprymnodon moschatus	7	6	46
Perameles nasuta	6	0	7
Isoodon macrourus	0	0	4
Uromys hadrourus	0	23	19
TOTALS	**34**	**45**	**126**
Trapnights	**19, 950**	**26, 800**	**11, 088**[1]
Captures/100 trapnights	**0.17**	**0.17**	**1.14**

[1] Trapping session data used only (total trapnights = 21, 584)

Another explanation may be the condition of the forest types which, although generally similar, are more disturbed and fragmented around Millaa Millaa than at Mt Bartle Frere (Figure 4.25). This greater level of disturbance may have resulted from edge effect impacts due to adjacent farming land being cleared for a longer period of time.

Figure 4.25

Locations of study sites for Laurance (1994) and Moore (2009)



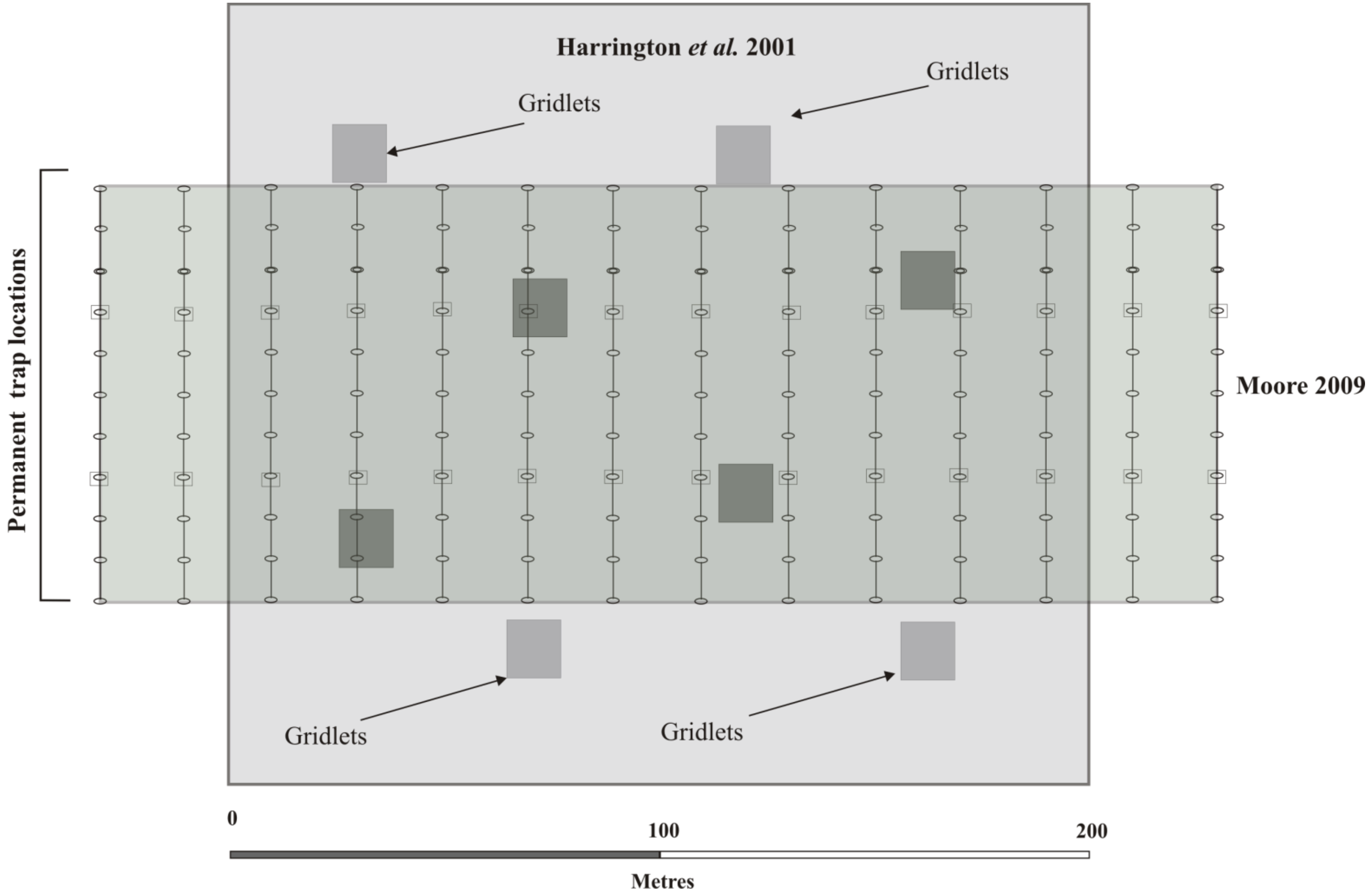
A third possible explanation for the difference in captures of rare species may be the different trapping grid formats used in each study. Laurance used a number of small independent 'gridlets' (30m x 30m trapping grids) with four grids at each site. The first gridlet was located adjacent to a permanent stream with subsequent gridlets following at 75 m intervals along a maximum elevational gradient (Laurance 1994). In contrast, three large independent grids (260m x 100m) were used in this study (refer to Chapter 2). Attempting to reconcile the significant difference in captures of rare species in these two studies emphasises the significant difficulties encountered when comparing between trapping studies, even when they are located in the same general area. A lack of detailed species' capture data precluded a calculation of Margelef's *D* index of biodiversity for Laurance's study.

Harrington *et al.* 2001

The field study reported in Harrington *et al.* (2001) was conducted in the same section of forest as this current PhD project. Consequently there is little doubt that the same mammal population was being sampled. Similarly to Laurance (1994) the trapping format comprised small grids (gridlets), but rather than being located independently in the landscape, the gridlets were set equidistantly within a surveyed four hectare site (200m x 200m). It is germane at this juncture to point out that the author of this PhD study designed the trapping format for the Harrington *et al.* (2001) study and conducted all the field trapping and identification of captured animals. Accordingly it can be said that the gridlets were not meant to be independent in that study and, as a result, the overall effective trapping area (*'W'*) is considerably larger than that of the individual gridlets themselves. The approximate area of *'W'* would have to be determined using species' inter-gridlet movements but it is possible that the overall effect approximates that of a larger single grid, similar to that used in this study (Figure 4.26). This was the intent at the time of the Harrington *et al.* study. It is also possible, therefore, that both the nearby study location (Mt Bartle Frere) and the closely-set gridlet format used by Harrington *et al.* explain the captures of *Uromys hadrourus*, a species not recorded in Laurance's Millaa Millaa study.

Figure 4.26

Comparison of 'gridlet' trapping (Harrington *et al.* 2001) and 'wide grid' trapping (Moore 2009)



Notwithstanding the presence of *U. hadrourus*, there are still significant differences between the two Mt Bartle Frere studies. In Chapter 3 (Table 3.7) it was revealed that that the species assemblage recorded in this study (Moore 2009) was significantly more diverse (Margelef's *D* index) than that recorded by Harrington *et al*. (2001) and Crome *et al.* (1991). Table 4.9 showed that while *U. hadrourus* and *A. godmani* captures were similar in the two studies *H. moschatus* captures were almost eight times greater (46) than that recorded by Harrington *et al.* (6). There were also six species caught in this study which were not captured by Harrington *et al*., *Antechinus adustus* (28), *Perameles nasuta* (7), *Isoodon macrourus* (4), *Antechinus flavipes* (1), and *Pogonomys* sp. (1).

Comparison with rainforest small mammal studies elsewhere in Queensland

A study by Wood (1971) addressed the ecology of *Rattus fuscipes assimilis* and *Melomys cervinipes* in south-east Queensland. Although that study was conducted in an isolated 65ha patch of *Agyrodendron*-dominated rainforest at Mt Glorious near Brisbane, the methodological approaches and statistical analyses used are similar to those in this thesis, and allow for comparison of the two studies. The size of the patch studied by Wood (1971) was 30 ha smaller than the largest of the four fragments (3, 8, 20, and 97 ha) studied by Harrington *et al.* (2001)

Rattus fuscipes

Although Wood observed significant population increases in *R. f. assimilis* in late summer to early autumn (March to May), this was not the case with *R. f. coracius*, whose population did not fluctuate significantly through the year. The peak breeding season occurred earlier and lasted longer in the northern race, early October to March, compared with November to January for the southern race *R. f. assimilis*. The onset and cessation of breeding was also more sharply delineated in the tropics, with no captures of adult females in breeding condition from June to September. In contrast, pregnant and lactating *R. f. assimilis* females were recorded in every month of the year. It is relevant to observe that *R. f. coracius* and *M. cervinipes* have been recorded breeding throughout the year in rainforest fragments on the Atherton Tablelands (Harrington *et al.* 2001; Moore unpublished data).

Wood found that non-adult *R. f. assimilis* dominated the population from February to September, suggesting that many adults either died following breeding or left the forest patch. In contrast, in this study adult *R. f. coracius* dominated the species' population in all months, ranging from a low of 56% (April) to a high of 97% (November) of all captures. The highest proportion of subadults and juveniles in the population occurred in April (44%). Juvenile *R. f. coracius* were present in the subadult population from December to April, earlier than the January to June observed for *R. f. assimilis*. Finally, the mean minimum age of *R. f. coracius* in this study suggests a higher longevity than that found in *R. f. assimilis*, probably due to a milder winter in the tropics. Wood found that only a few marked animals survived to a second breeding season at Mt Glorious, while in this study the oldest animals recorded (females) were 20 - 24 months of age, well into their second breeding season.

Melomys cervinipes

In this study on the Atherton Tablelands adult *Melomys cervinipes* dominated the population throughout the year and at no time did the proportion of non-adults exceed 25% of the total adult population. It is not clear what is meant when Wood (1971) states that "*the relatively long breeding season of M. cervinipes, commencing in September, 2 months earlier than R. fuscipes, and ending in February*…", as pregnant and lactating females were recorded at his study site in every month of the year and numbers peaked from October to June. These data would be better described as indicating an all-year breeding pattern with increased breeding in the optimum environmental conditions over the summer and autumn months. This continual breeding phenomenon was not observed in the continuous forest at Mt Bartle Frere but is known to occur in rainforest patches on the Atherton Tablelands (Harrington *et al.* 2001; Moore unpublished data). There were no observations of male or female *M. cervinipes* breeding on the trapping grids from June to October. Similar to that found at Mt Glorious however, the *M. cervinipes* population increased from April to June due to the influx of juveniles and subadults.

4.8.1 Summary

This study showed a significant increase in capture rates of rare or uncommon species compared to the two similar studies conducted in the same area of the Atherton Tablelands. In this study almost seven times the number of rare species were captured per trapnights (1.14 captures/100 trapnights) as was captured by Laurance (1994) and Harrington *et.al.* (2001). Interestingly, these two studies recorded the same ratio of rare-uncommon species captures i.e., 0.17 captures/100 trapnights. This correlation is despite a significant difference in total trapnights between the two studies, with Harrington *et. al.* undertaking 25% more trapnights (26, 800 TN) than Laurance (19, 950 TN). It is important to note that both these studies used small grid ('gridlets') trapping formats which, their data suggest, provides a high degree of correspondence in captures of rare species between different studies. However, the significant reduction in captures of rare and uncommon species when compared to this study indicates that sampling with small grids does not adequately sample either the diversity or relative abundance of rare species in an area. When specifically surveying for rare species, therefore, one large grid of traps appears to be more efficient in sampling the population than many small ones. Statistically, however, there are issues that need to be addressed in this sampling design and these are discussed further in Chapter 7 and Chapter 8.

The results of this study also show that the population dynamics of the southern species *Rattus fuscipes assimilis* and *Melomys cervinipes* observed by Wood (1971) differ from populations of their northern counterparts within continuous forest. They are, however, similar to that observed for these two species when they occur within rainforest fragments in north Queensland. It is possible this dissimilarity may be a result of latitudinal life history differences (e.g., Levinton 1983; Groeters and Shaw 1992, Kaufman 1995; Blackburn and Gaston 1996; Rohde 1992, 1998; Buzas *et al.* 2002; Cardillo 2002a, 2002b; Huitu 2003; Chapple 2005). The more probable explanation is the southern study (Wood 1971) was subject to the same influence of fragmentation and patch dynamics that has been documented in small mammal fragmentation studies on the Atherton Tablelands of north Queensland.

5. ECOLOGY AND POPULATION DYNAMICS OF THE GIANT WHITE TAILED RAT *UROMYS CAUDIMACULATUS CAUDIMACULATUS*

This chapter presents the detailed population ecology of the giant white-tailed rat *Uromys caudimaculatus.* Using the results of live-trapping conducted on three independent study grids, it examines abundance, population estimation using capture-mark-recapture statistics (CMR), breeding and recruitment, parental care, population demography, and general behaviour. Data were adequate for a full Jolly-Seber analysis when *Uromys caudimaculatus* captures were combined into trapping session captures. However, recapture data was not as robust when grids were treated separately, as recaptures of individual animals over more than two successive samples were rare and data was insufficient to conduct the analyses. To address this shortcoming, Jolly's modified model using constant probability of capture and survival (1982) was used in the CMR analyses.

5.1 TRAPPING RESULTS

Only captures resulting from grid trapping sessions are used in the following analyses. A total of 11048 trapnights resulted in 460 captures of 140 individual *U. caudimaculatus* (74 males and 66 females). Animals were caught both in cages and Elliot traps and trap success was 4.2 captures/100 trapnights. Table 5.1 presents a breakdown of capture types.

5.1.1 Grid Captures

There were no movements of individuals between trapping grids apart from one dispersing juvenile *U. caudimaculatus*, which was captured on Grid 3 on 22 April 2005 and recaptured on Grid 5 on 2 May 2005; a movement of approximately 1km in 10 days.

Table 5.1

Trapping session captures of *Uromys caudimaculatus*

1st captures[1]	Recaptures[2]	Retraps[3]	Total captures
140	121	199	460

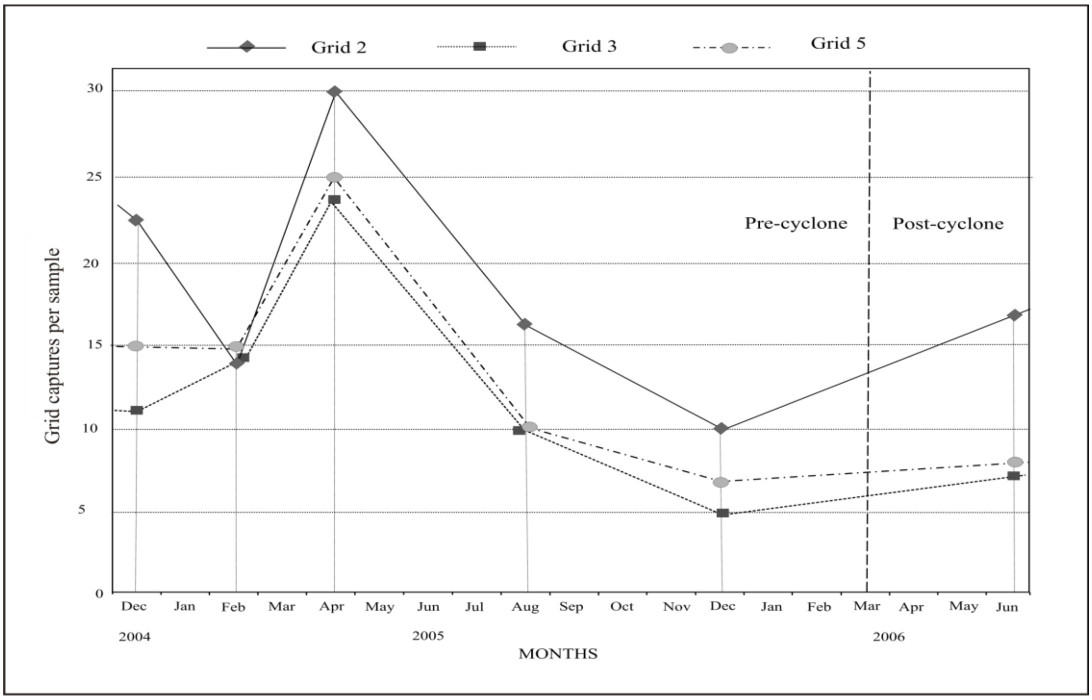
[1] Unmarked animal – first capture
[2] Captures of marked animals on successive samples
[3] Multiple captures of marked animals in same sample

Figure 5.1 presents the captures for all three study grids and shows that Grid 2 maintained a consistently higher capture rate for *U. caudimaculatus* over most trapping sessions. The approximate timing of Cyclone Larry (Category 4 storm) is indicated by the dotted vertical line. Mean grid captures of *U. caudimaculatus* for Grid 2, Grid 3, and Grid 5 were 18.33 ± 2.91 (range 10-30), 11.83 ± 2.75 (range 5-24), and 13.33 ± 2.72 (range 7-25) respectively. Numbers peaked in April at all three grids, probably due to the influx of freshly weaned juveniles into the population.

Trapping session captures were grouped by grid and repeated measures ANOVA revealed there were significant differences in capture rates of *U. caudimaculatus* between the three grids (F_2=2, P=0.002). More animals were caught on Grid 2 than Grid 3 and Grid 5; the latter two grids had similar capture rates. The trapping session capture mean and ±SD were 14.5 and 6.57 respectively. A Friedman ANOVA indicated that trapping session capture rates were also significantly different ($X^2{}_{,5}$ =12.596, P=0.027) with greater numbers of *U. caudimaculatus* caught in March-April 2005 than at any other time of the year. An unpaired t-test comparing seasonal captures for the two trapping sessions April-May 2005 and May-June 2006 revealed that capture numbers were significantly lower post-cyclone (t_4 =4.255, P=0.013).

FIGURE 5.1

Trapping session captures of *Uromys caudimaculatus* on the trapping grids



Mean sample capture totals (pooled data from the three grids) are provided in Table 5.2 and shown on Figure 5.2.

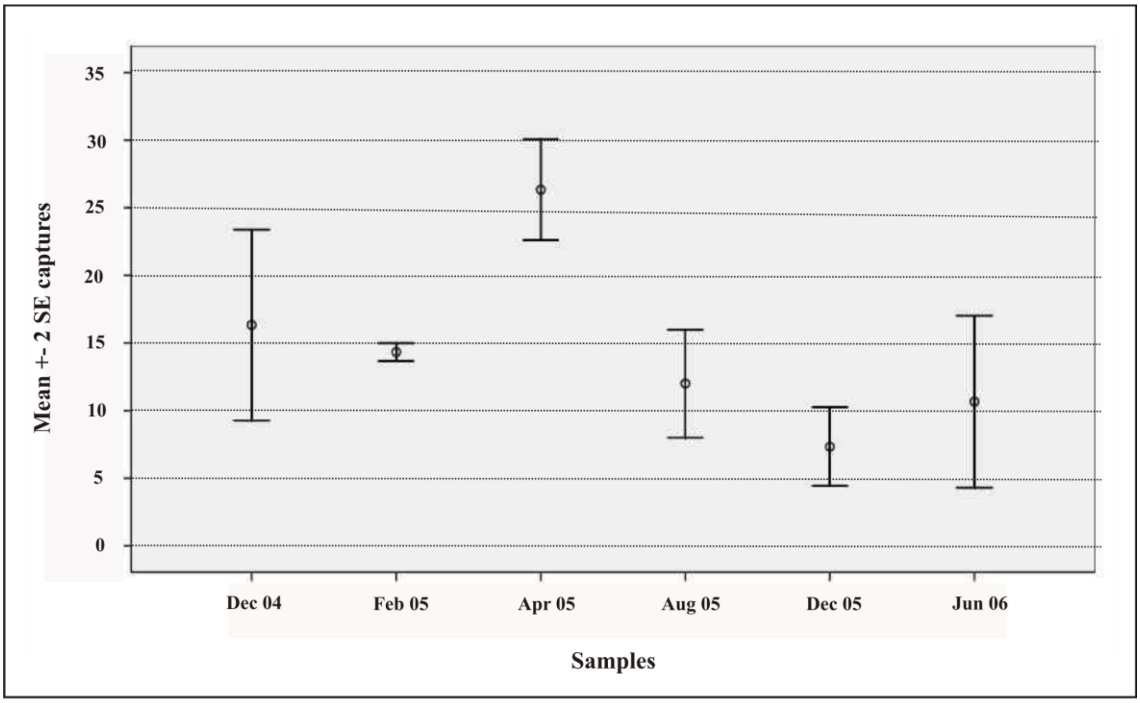
Table 5.2

Mean and SD of sample captures for *Uromys caudimaculatus*

Sample	Grids	Mean	SD
December 2004	3	16.33	6.110
February 2005	3	14.33	0.570
April 2005	3	26.33	3.214
August 2005	3	12	3.464
December 2005	3	7.33	2.516
June 2006	3	10.66	5.507
	18	Mean = 14.50	Mean = 7.031

FIGURE 5.2

Mean and 2 ± SE trapping session captures of *Uromys caudimaculatus*



5.1.2 Population density

The mean distance between trap locations for two successive captures of individual marked animals (trapping session captures or consecutive trapping sessions only) was calculated for *U. caudimaculatus*. The boundary strip ($\hat{W}$) for estimating species' density ($\hat{W}$ = d/2) was added to the grid area and densities calculated using mean sample captures. As overnight movements of 500 metres have been observed in some individuals (Moore 2008) this boundary strip may be an underestimate of $\hat{W}$ and result in a higher trapping density for the species. The mean grid movement distance ± SE for *U. caudimaculatus* was 67.6 metres and 4.3 metres respectively (d/2=33.8m). This distance was rounded to 34 metres altering the effective trap area from 2.6 hectares (trapping grid) to 3.94 hectares, an additional 1.34 hectares (approximately 52%). The total effective trapping area for the combined three grids was 11.82 hectares (three grids x 3.94ha). The 1st captures and recaptures for each grid were grouped to create totals and Table 5.3 presents the trapping session captures and animals/ha (*W'*= 11.82ha) for each trapping session. The mean trapping session population density of animals per hectare was 3.68 (SD = 1.67).

TABLE 5.3

Population density of *Uromys caudimaculatus* for each trapping session

Sample	**December 2004**	**February 2005**	**March 2005**	**August 2005**	**December 2005**	**June 2006**
Captures	49	43	79	36	22	32
Animals/ha (N/11.82ha)	4.15	3.64	6.68	3.05	1.86	2.71

5.1.3 Population estimation using capture-mark-recapture analysis (CMR)

As for similar population estimation models, these estimates do not represent the predicted population size of *U. caudimaculatus* existing on the grid itself and instead represent the predicted population from which the sample is drawn. Trapping session captures on individual grids were occasionally less than the 20 animals required to satisfy all the conditions that underlie capture-mark-recapture analysis. Consequently, Jolly's constant probability of capture and survival model was used to produce more efficient estimators (Table 5.4) (Refer Chapter 2). The estimated population sizes sampled by the three grids are shown in Table 5.5.

TABLE 5.4

Uromys caudimaculatus Jolly-Seber analysis (Constant Probability of Capture and Survival)

Trapping session	Marked animals in pop'n	Pop'n estimate	SE pop. est.	Survival estimate	SE survival	New animals	Probability of capture
GRID 2							
Feb 05	15.44	35.81	6.547	0.5277	0.05379	23.97	0.54
Apr 05	23.92	53.55	9.08	0.5277	0.05379	6.587	0.54
Aug 05	14.23	29.04	5.853	0.5277	0.05379	-0.41	0.54
Dec 05	13.41	17.11	3.792	0.5277	0.05379	26.75	0.54
GRID 3							
Feb 05	8.291	19.15	4.818	0.3075	0.05564	20.02	0.6446
Apr 05	12.44	34.16	8.158	0.3075	0.05564	7.46	0.6446
Aug 05	4.151	15.01	4.344	0.3075	0.05564	6.057	0.6446
Dec 05	1.399	9.155	3.028	0.3075	0.05564	6.543	0.6446
GRID 5							
Feb 05	7.429	19.7	3.973	0.3448	0.05459	20.28	0.7334
Apr 05	8.668	30.48	5.975	0.3448	0.05459	4.08	0.7334
Aug 05	7.435	14.25	3.024	0.3448	0.05459	0.508	0.7334
Dec 05	6.244	7.607	1.819	0.3448	0.05459	9.374	0.7334

Table 5.5

***Uromys caudimaculatus* Jolly-Seber population estimates**

Trapping session	Proportion of recaptures	Marked animals in pop'n	Pop'n estimate	SE pop. est.	Survival estimate	New animals	Probability of capture
Dec 04		0			0.6808		
Feb 05	0.3696	37.44	101.3	16.37	1.139	64.87	0.454
Apr 05	0.4198	75.66	180.2	27.85	0.6693	43.55	0.4494
Aug 05	0.5	82.09	164.2	31.98	1.403	-45.81	0.2558
Dec 05	0.7838	144.6	184.5	54.93			0.2005

5.1.4 Body size

Uromys caudimaculatus is one of the largest species in the genus *Uromys*. In this study, weight and reproductive condition were recorded from 159 adults (>500gms), comprising 88 adult males and 71 adult females. Mean adult male weight and ± standard deviation was 657.8gms and 72.5gms respectively; mean adult female weight and standard deviation was 624.1gms and 64.7gms respectively. An independent samples t-test showed that adult male weights were significantly larger than those of adult females (t_{157}=3.054, P=0.003). The largest adult male and female weights recorded were 820gms and 780gms respectively. Morphological measurements taken from specimens of adult *U. caudimaculatus* of Queensland origin housed at the Queensland Museum are given in Table 5.6. The measurements of both sexes were combined to generate the following ratios: the mean ratio of tail-vent to head-body was 1:1.16, the tail was approximately 16% longer than the head-body length (SE ± 2.65 mm); the mean and SE of the rear foot (pes) was 56.86 mm and 1.78 mm respectively.

TABLE 5.6

Adult *Uromys caudimaculatus* morphological measurements

Sex	Weight (g)	Head-Body (mm)	Tail-Vent (mm)	Pes (mm)
Male (10)	679.0 ± 59.2	283.5 ± 25.5.	335.5 ± 8.5	59.1 ± 7.0
Female (10)	613.4 ± 22.9	268.4 ± 12.2.	316 ± 6.8	56.0 ± 1.1

5.1.5 Young

A litter size of 1-3 has been recorded for *U. caudimaculatus* in captivity (Watts 1981), with young weighing approximately 20gms at birth. Two field observations have been made of females with litters of two young. Watts and Aslin (1981) recorded an adult female running up a tree with two young dangling from teats. One of the young dislodged and was found to weigh 40gms (3-4 days old), suggesting that small young may be carried by the female while foraging. The second observation was of a litter of two young born in a cage trap (Moore pers. obs.). The female was released without handling and entered a creek bank hollow with the young still firmly attached to the teats (Moore 1992 unpublished data).

Captive-born young weigh approximately 60gms at 7 days, 100gms at 14 days, and were eating solid food at about 30 days, when they weighed approximately 200gms (Watts and Aslin 1981). In this study, two captures were made of juvenile *U. caudimaculatus* while in the company of their female parent; their weights were 143gms and 160gms. A total of 16 juveniles (<300gms) were captured in this study. A linear regression of body weights for known-age juveniles (incorporating data from Watts 1981) was undertaken using the known age of laboratory animals (*RegAge*) and the known weight of these individuals (*RegWts*). The linear regression model used was Y = *a* + *b*X* with *RegWts* as the dependent variable. The equation of the fitted model adjusting for outliers was *RegWts = 17.3913 + 6.08696*RegAge.* Table 5.7 presents the results of the regression model. The field captures of juvenile *U. caudimaculatus* were fitted to this regression and the results are shown in Figure 5.3.

TABLE 5.7

Results of regression of body weight of juvenile *Uromys caudimaculatus* and known age in days (data from Watts and Aslin 1981)

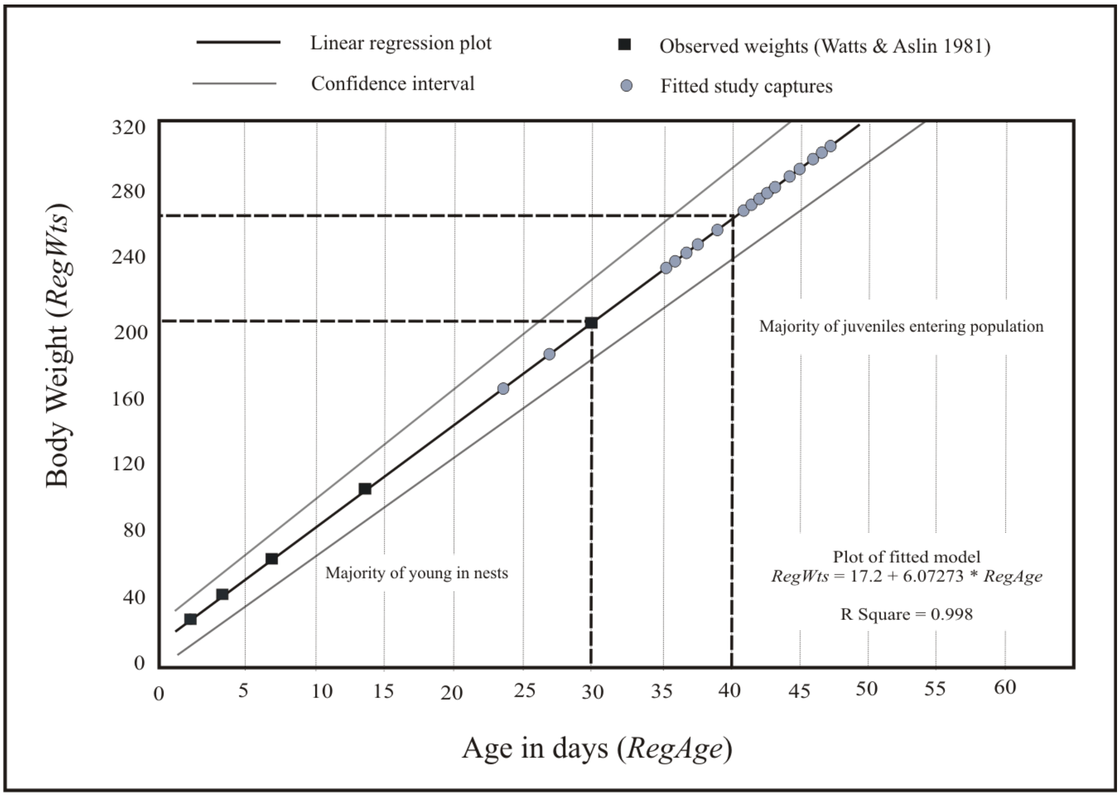
Model	R	R^2	Adjusted R^2	SE of Estimate	Change Statistics					Durbin-Watson statistic
					R^2 Change	F Change	df1	df2	Sig. F Change	
1	.999(a)	.998	.998	3.51620	.998	1640.529	1	3	.000	0.1230

a Predictors: (Constant), *WtsAge*
b Dependent Variable: *RegWts*

Since the *P*-value is less than 0.05, there is a statistically significant relationship between *RegWts* and *RegAge* at the 95.0% confidence level. The R-Squared statistic indicates that the model as fitted explains 99.8% of the variability in *RegWts*. The Durbin-Watson (*DW*) statistic tests the residuals to determine if there is any significant correlation based on the order in which they occur in the data file. Since the Durbin-Watson statistic is greater than 0.05 there is no indication of serial autocorrelation in the residuals at the 95.0% confidence level. It is probable that growth rates would reduce once young animals have to forage for themselves independent of the adult female and would become non-linear as a result. Although young *U. caudimaculatus* can begin foraging with their parent from approximately 24 days of age (~143gms) the majority of juvenile captures occurred between 230–300gms and suggests that weaning takes place at approximately 40 to 45 days (e.g., Watts 1981).

FIGURE 5.3

Linear regression of body weight-age for juvenile *Uromys caudimaculatus*



5.1.6 Breeding

Reproductive data of 331 adult *U. caudimaculatus* obtained from exploratory, experimental and grid trapping are used in the following analyses.

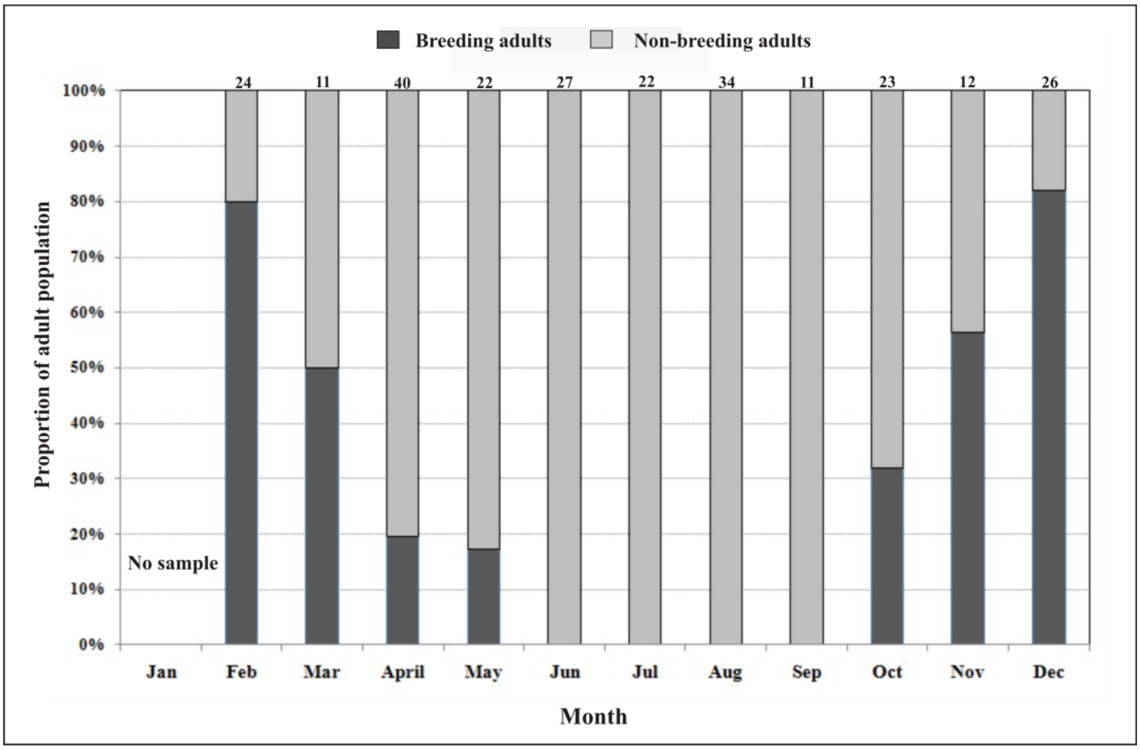
Female reproduction

The gestation period of *U. caudimaculatus* is approximately 41 days (Watts and Aslin 1981). A successful reproductive cycle would therefore take approximately 80 days to complete (gestation + weaning period) and it is unlikely that *U. caudimaculatus* would be capable of producing more than two litters per year. Lactating females were present between late November and early March (Figure 5.4). At that time their mean weight and SE was 662gms ± 11.2gms (range 585-770gms). Pregnant females were difficult to discern in the field but two individuals were recorded as pregnant in mid-December.

FIGURE 5.4

Uromys caudimaculatus **annual breeding cycle (adult males and females)**

(Figure located at top of each bar = *N*)



Male reproduction

Breeding males with distended epididymal sacs and large scrotal testes were recorded from October to March, with many males observed regressing in February and March. Occasional males were observed with enlarged testes at other times of the year i.e., April and May.

5.1.7 Division between juveniles, subadults, and adults

In a previous study of *U. caudimaculatus* (Wellesley-Whitehouse 1981) two age classes for captured animals were used: juveniles < 450 gms and adults > 450 gms.

Those categories were based on only 20 captures and the underlying rationale for the separation is uncertain. The same study recorded observations of one female lactating at 490gms and a '*breeding*' female at 420gms. In this study, mean weight and ±SE for scrotal males was 652.6gms and 6.41gms (range 550-800gms). Mean weight and ±SE for females with moderate teats (early breeding condition) was 639.6gms and 13.8gms (range 550-700gms). Thus, individuals of both sexes weighing more than 500gms were classified as adults. Juveniles were determined to be those individuals either still in the company of the female parent i.e., dependent, or freshly independent. Thus all individuals <300gms were classified as juveniles. Subadults were classified as those individuals weighing 301-499gms.

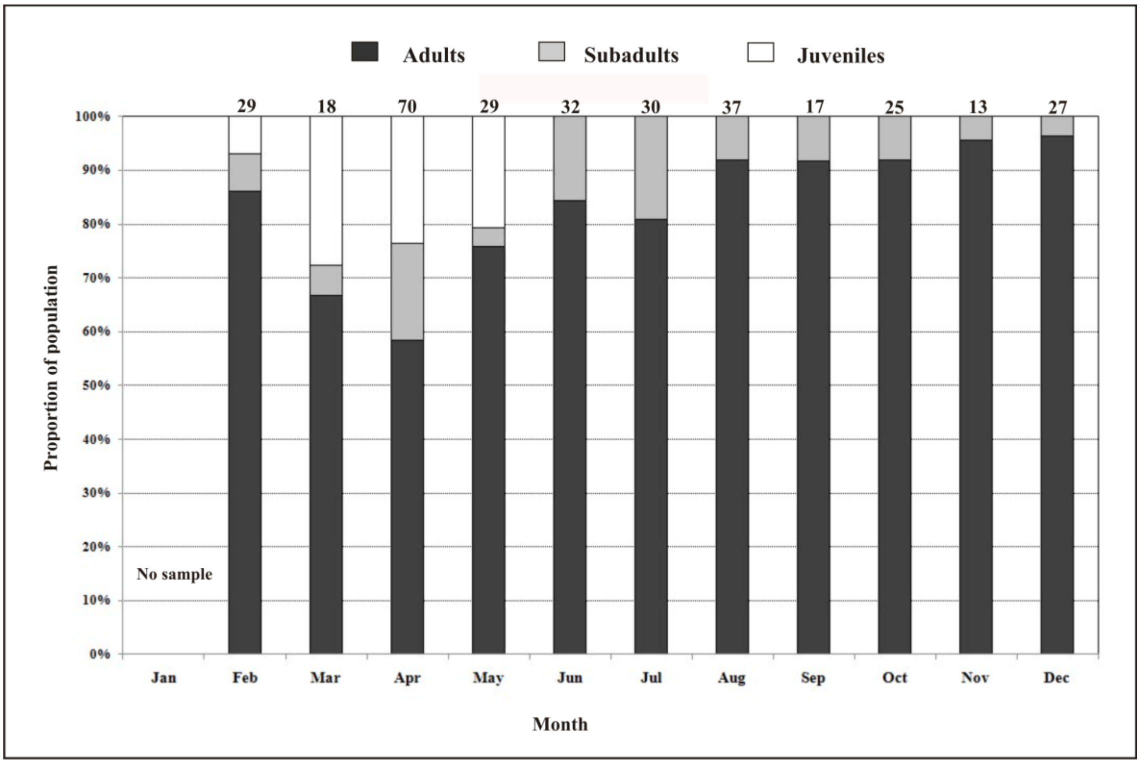
5.1.8 Annual Population Demography

Breeding data from 331 captures of adult *U. caudimaculatus* are used in the following analyses (exploratory, experimental, and grid trapping sessions). Figure 5.5 shows the proportion of *U. caudimaculatus* age classes recorded for each month of the annual population cycle. Juveniles and subadults are represented by the upper bars on the monthly columns. Subadults are represented in every month, comprising 4%–15% of the trapped population from August to March (spring-summer-autumn), rising to approximately 20% from April to July (winter). The double-peak of subadult captures (April and June-July) suggests two distinct breeding events in the population. Juveniles first appeared in small numbers in January, increasing to their greatest numbers from March to May. No juveniles were captured in the remaining seven months i.e., June to December.

FIGURE 5.5

Annual population demography of *Uromys caudimaculatus*

(Figure located at top of each bar = *N*)



5.1.9 Diet

The arrival of Cyclone Larry on 20 March 2006 (category 4 storm) disrupted the fruit collection experiments that had recently been set up on the trapping grids. The extensive damage to the forest sites meant that attempting to carry on the diet experiments was not possible. As a result, the following section comprises information gained from other field studies, searches of the literature, the collection and identification of predated fruit on the grids during trapping samples, and the identification of predated fruit found during the mapping of spooled animals (Table 5.6). The diet of *U. caudimaculatus* primarily comprises rainforest fruits and nuts but also includes fungi, insects, small reptiles, crustaceans, and birds eggs (Wessesley-Whitehouse 1981, Harrington *et. al.* 2001, Theimer 2001, 2003; Moore 2008). Field studies on the Atherton Tableland have shown that *Uromys caudimaculatus*'s consumption of the seed production of the hard-shelled, palatable tree seeds of Yellow Walnut, *Beilschmiedia bancroftii,* Cream Silky Oak, *Athertonia diversifolia* and Hairy Walnut, *Endiandra insignis*, is close to 100 per cent, leading to a very low recruitment rate of these trees compared to those with unpalatable seeds (Harrington *et al*. 1997, Dennis 1994, Theimer 2001). Seeds were eaten on the spot, removed to a buttress or fallen log where a midden of chewed seed cases was usually found, or buried in the earth up to 60 metres from the parent tree.

In this study insects formed an integral part of the diet of *U. caudimaculatus*. Spooling showed that rotting logs and branches were torn open in pursuit of large passalid beetles, a habit shared with the Pygmy White-tailed Rat, *Uromys hadrourus*, Striped Possum, *Dactylopsila trivirgata,* Musky Rat-kangaroo, *Hypsiprymnodon moschatus,* and Long-nosed Bandicoot, *Perameles nasuta.* Bark appeared to be a regular food item with signs of chewing being most noticeable on trees with buttresses (Figure 5.6). Most spooled animals used trees which had well-developed scars, indicating regular visitation. An alternative explanation for this bark-chewing behaviour may be its use as a 'territory-marker' by the species. However, many rodents are known to eat bark (Dodge, 1967, Green 1979; Hansson and Larsson 1978, Harder, 1979, Betancourt, *et al*., 1986; Hansson 1987, Roze, 1989, 2003, Predavec *et al.,* 2001). Table 5.3 lists those fruits recorded as being eaten by *U. caudimaculatus* pre-cyclone (March 2006). Fruits were identified using Cooper and Cooper (2004) and the Australian Tropical Forest Plants key (Hyland *et. al.* 2003).

FIGURE 5.6

Bark-chewing by a spooled *Uromys caudimaculatus*

TABLE 5.8

Identified diet items of *Uromys caudimaculatus*

Fruits and seeds		Insects
Agyrodendron sp.	*Ficus pleuracarpa*	Passalid beetles and larvae
Athertonia diversifolia	*Ficus racemosa*	Bracket fungi
Beilschmedia bancroftii	*Ficus watkinsiana*	Bark (cambium)
Beilschmedia oligandra (?)	*Mammea touriga*	
Cinnamomium laubatii	*Meliodinus australis*	
Corynocarpus cribbianus	*Piper sp.*	
Cryptocarya sp.	*Planchonella sp.*	
Cryptocarya oblata	*Prunus turneriana*	
Eleaocarpus angustifolius	*Syzigium alliligneum*	
Endiandra insignis	*Syzigium cormifloum*	
Syzigium gustavioides	*Syzigium johnsonii*	
Castanospora alphandii	*Syzigium kurandii*	
Calamus moti/australia	*Tourinia montana*	
Ficus congesta		

5.1.10 Habitat use

All captures of *U. caudimaculatus* (including retraps) were grouped into the following habitat types (refer to Chapter 2).

1. Ridge - open understorey
2. Flat - open understorey
3. Upper-mid slopes - open understorey
4. Lower slopes – open understorey
5. Lower slopes - dense understorey
6. Gully – first order stream
7. Riparian – second order stream
8. Dense wet forest–dominated by dwarf pandan sedge *Hypolytrum nemorum*

A chi-squared test (Table 5.9) showed significant bias in captures within habitat types (X^2_6 =193.654, P=<0.001).

Table 5.9

Chi-square frequencies for *U. caudimaculatus* trap location - habitat associations

Habitat type	Observed N	Expected N	Residual
1.00	26	38.9	-12.9
2.00	102	38.9	63.1
3.00	46	38.9	7.1
4.00	64	38.9	25.1
5.00	28	38.9	-10.9
6.00	3	38.9	-35.9
7.00	3	38.9	-35.9
Total	272		

Residuals showed that Habitat 2 (flat-open understory, Habitat 3 (upper-mid slopes with open understorey), and Habitat 4 (lower slopes, open understorey) were positively selected by *U. caudimaculatus* (residuals 63.1, 7.1, and 25.1 respectively). The negative correlation with Habitat 1 (ridge-open understorey) is probably an sampling artefact due to the small number of trap locations located within this habitat type. Habitats 5-7 (lower slopes/gullies/riparian with dense understorey) were strongly negatively correlated with trap locations. There were no captures of *U. caudimaculatus* in Habitat 8 (dense wet forest).The results indicate that the preferred habitat of *U. caudimaculatus* was those parts of the trapping grids which had an open understorey and were located on flat, upper and lower slopes of the rainforest. Although sometimes eclectic in its range of food items, it has been established that in rainforest the diet of *U. caudimaculatus* is primarily fruits and nuts (Watts 1977, Watts and Aslin 1981, Wellesley-Whitehouse 1981, Harrington *et. al.* 2001; Theimer 2001, 2003; Moore 2008). Consequently the species' infrequent use of streams may be influenced by fallen fruit being less detectable in this habitat due to loss by water movement and the difficulty of variable terrain. Its preference for flat and gently-sloping landscapes, which are generally less densely vegetated than lower slopes and streams, suggest fruit is more easily detected in these areas. Another possible explanation is that floristic or edaphic differences between the two habitats may negatively influence fruit type and abundance. It is of interest to note that a similar foraging strategy is adopted by Australia's other large terrestrial rainforest fruit exploiter, the cassowary, whose preferred feeding areas comprise flat or gently sloping terrain (Moore 2003, 2007).

5.1.11 Spooling analysis

Due to the effects of Cyclone Larry, only eight *U. caudimaculatus* were spooled and tracked. This resulted in only 1245 metres of spooling data, far less than for *U. hadrourus* (8142.5 metres). The proportion of on-ground travel by *U. caudimaculatus* (across the forest floor) was 92%; movement in trees accounted for only 5% of the total movement distance and appeared to be the result of individuals returning to nest hollows. Off-ground movement i.e., logs and sticks, appeared incidental and accounted for only 3% of total distance travelled.

5.1.12 Additional ecological data

Activity cycle

Although *U. caudimaculatus* is nocturnal in its habits, three observations were made of individuals leaving their burrows in the fading light of dusk. During the day animals usually took refuge in a ground burrow, large fallen log, or tree hollow. Claw marks on tree trunks often drew attention to the latter sites, which were generally located 10-30 metres from the ground (Figure 5.7).

FIGURE 5.7

Tree hollow used as a den by an adult female *Uromys caudimaculatus*

Spooling showed that adult female 0094 had her regular den hollow at the top of this large *Cryptocarya* sp., approximately 27 metres above the ground. On most occasions lianes were used by the female to climb the large trunk, although occasionally adjoining trees were also used to cross onto the nest tree at considerable heights above the ground.

Ground burrows were located under logs, fallen trees or other debris, and in the undercut banks of streams and dry gullies.

Sex ratio

Home range data is not available for *U. caudimaculatus* so it is not possible to postulate if any possible difference in home range sizes between the sexes might affect trapping bias. Mean female to male sex ratio was 1:1.2 (149 males/127 females). Although slightly biased against females, much of this difference may be explained by the lower capture rates for females at times of peak parturition. Streatfeild (2009) found that adult sex ratios were generally male-biased at two of his fragment sites but female-biased at a third fragment and in a continuous rainforest control site.

Mean minimum age (longevity)

In this study, the recapture rate of individuals over successive trapping sessions was low, with most individuals being caught on only two or three occasions. As such, there was insufficient data to estimate longevity. Recapture data from long-term trapping studies at Kirrama, north of Townsville indicate that *U. caudimaculatus* can reach an age of at least four years in the wild (Heinsohn and Heinsohn 1999; Moore 2008).

Predation

Known predators of *U. caudimaculatus* are the lesser sooty owl, *Tyto multipunctata,* which take individuals up to 300 grams in weight, the spotted-tailed quoll, *Dasyurus maculatus,* rufous owl *Ninox rufa* (seen roosting with a partly-eaten *Uromys caudimaculatus* in its claws), and pythons. It is likely that the dingo and feral cat also prey on this species (Moore 2008).

Home Range

It is difficult to determine the home range of *U. caudimaculatus*, which has to move widely to find food in what is generally an uncertain fruiting rainforest environment. Moore (2008) reported overnight movements of 500m and found that individuals made use of at least 4 hectares of forest over a four-day trapping study (Crome *et al.* 1991; Harrington *et al.* 2001; Moore unpublished data). In this study, spooling showed that individuals foraged intensively over the 2.6ha grids and extensively beyond.

Mean grid movement index (MGMI)

U. caudimaculatus exhibited considerable mobility around the trapping grids, with mean movement distance (N=126) between trap locations of 67.6m (SD=47.9) and a maximum movement of 230 metres (Figure 5.8). The close proximity of neighbouring cage traps (20m) may have encouraged some animals to stay within the area of initial capture, decreasing potential movement distances.

Figure 5.8

Distances moved between successive trap locations

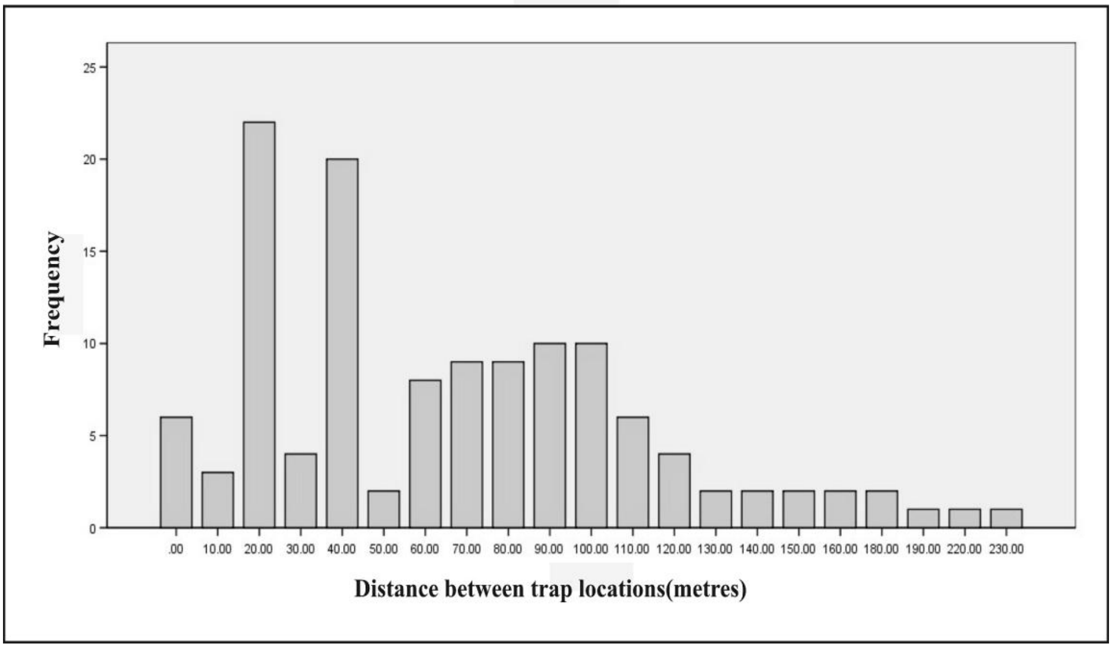


Table 5.10

Distance travelled between successive trap captures for *Uromys caudimaculatus*

Distance (m)	Frequency	Percent	Cumulative Percent
1-40	32	21.2	21.2
41-80	35	23.2	44.4
81-120	34	22.5	66.9
121-160	24	15.9	82.8
161-200	7	4.6	87.4
201-240	19	12.6	100.0
Total	151	100.0	

Although approximately 67% of successive grid movement distances were less than 120 metres (possibly due to trap format), a considerable number (12.6%) comprised movements greater than 200 metres (Table 5.10). There was no difference in grid movement distance between adult male and female *U. caudimaculatus* (t_{129}=0.476, *P*=0.635. This aspect of the species ecology is examined further and compared with the MGMI of *U. hadrourus* in Chapter 7.

5.1.13 Discussion

Uromys caudimaculatus comprised approximately 16% of the 1st captures on the study grids, approximately one-third that of the bush rat *Rattus fuscipes* (49%). In contrast, Streatfeild (2009) recorded a capture percentage for *U. caudimaculatus* of 30% of total species' captures in his fragment study sites. This higher figure is probably due to the use of only cage traps in Streatfeild's fragment study, causing a species-bias in captures due to smaller animals not being sampled as comprehensively as *U. caudimaculatus*. However, Streatfeild recorded a low density of *U. caudimaculatus* in his continuous forest control site, 1.32 animals/ha (SE=0.07), approximately one-third the mean density observed in this study. Trapping density of *U. caudimaculatus* in my study remained relatively stable throughout the year, ranging from a high of 6.68 animals/ha in March-April 2005 to a low of 1.86 animals/ha in December 2005. The mean density of animals per hectare over the 18 samples was 3.68 (SE=0.68). The cause of the lower density figure in Streatfeild's study is not known, but it is possible that the local population of *U. caudimaculatus* in his study may have been influenced by site-specific conditions prevailing at the control site.

Although comprising only 16% of the 1st captures, *U. caudimaculatus* made up the largest sample biomass (55% or 25.5 kg/sample), almost twice that of the more abundant *R. fuscipes* (29% or 14 kg/sample). As larger vertebrate bodies require more food and produce more waste than smaller bodies (refer to Chapter 4.7) *U. caudimaculatus* is therefore the principal mammalian exploiter of fruit and nut resources in the Australian tropical rainforest. The presence of *U. caudimaculatus* in the matrix of forest fragments and rural landscapes (Crome *et al.* 1994; Laurance 1994; Harrington *et al.* 2001; Moore 2008; Streatfeild 2009)) is probably due to the species' high dispersal ability (refer to Chapter 7 and Chapter 8) and its diverse diet, the latter enabling the species to exploit non-rainforest food items e.g., agricultural crops and fruits, maize, avocado macadamia, and peanuts (Moore 2008). It appears that landscape matrix populations of *U. caudimaculatus* are highly mobile and perhaps evanescent (Moore 2008). Streatfield (2009) found that fragment populations of *U. caudimaculatus* had lower population size and levels of allelic richness compared to un-fragmented continuous rainforest, suggesting restricted among-population gene flow. It was suggested that the effect of reduced genetic diversity, lower effective population size, and restricted gene flow would impact on the long-term viability of the small fragmented populations (Streatfeild 2009).

The limited spooling data suggests that although adapted to climb in trees foraging for fruit, *U. caudimaculatus* spent the majority of its time foraging on the ground. This behaviour is ecologically sound considering the biological effort required to clamber through branches obtaining single fruits in comparison to feeding on the more plentiful tree-fall on the forest floor below. In times of environmental stress, however, the species' ability to access scarce fruits while they are still on the tree gives it a considerable ecological advantage. Although no caching experiments were conducted during this study, the giant white-tailed rat is one of a number of known terrestrial seed dispersers in the Australian rainforest that cache seed. Theimer (2001, 2003) concluded that cache and seedling distributions indicated that most *Beilschmiedia bancroftii*, (Lauraceae) seedlings arose from rat-cached seeds.