6.1 Macropod prey selection

In the S.R.S.F. both the proportion of the three larger macropod species in the scats and the proportion of their observed numbers was similar between years (see Table 6.1). At Diamond Flat the proportion of these species in the scats varied significantly while the proportion observed did not. This latter finding indicated that the relative proportion of macropod species in the diet could change without any change in the relative proportion of these observed species.

While the two sites differed significantly in the relative proportions of the species found in the scats and those observed, in 1979 they were not significantly different in 1980. Although this indicated a similarity in the relative proportion of macropod species in the diet from the two sites in 1980, it obscures the finding that macropods as a group were significantly more important at Diamond Flat that year, (see Table 3.3).

Despite the inconsistencies between years the comparison showed that the two proportions for all sites by year were significantly different, (see Table 6.1). In all cases these differences occurred as a result of a greater proportion of *W. bicolor* in the scats than was observed and a lower proportion of *H. giganteus* in the scats than was observed. *H. rufogriseus* was found in a similar proportion in both the scats and observed numbers.
### TABLE 6.1

**A COMPARISON OF THE PROPORTION OF THE THREE LARGE MACROPOD SPECIES FOUND IN THE SCATS WITH THEIR RESPECTIVE PROPORTIONS OBSERVED ON TRANSECTS**

<table>
<thead>
<tr>
<th>SITE</th>
<th>SPECIES</th>
<th>Percentage of each species in the scats</th>
<th>Percentage of each species observed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>% freq % freq</td>
<td>% freq % freq</td>
</tr>
<tr>
<td>S.R.S.F.</td>
<td><em>W. bicolor</em></td>
<td>70( 81) 69( 53)</td>
<td>52(332) 53(215)</td>
</tr>
<tr>
<td></td>
<td><em>H. rufogriseus</em></td>
<td>24(28) 26(20)</td>
<td>28(181) 23(96)</td>
</tr>
<tr>
<td></td>
<td><em>H. giganteus</em></td>
<td>6( 7) 5( 4)</td>
<td>20(124) 24(98)</td>
</tr>
<tr>
<td>Comparison between years</td>
<td>$\chi^2 = 0.13, \text{ ns}$</td>
<td>$\chi^2 = 4.68, P&lt;0.10$</td>
<td></td>
</tr>
<tr>
<td>Diamond Flat</td>
<td><em>W. bicolor</em></td>
<td>79(101) 60( 85)</td>
<td>43(91) 47(47)</td>
</tr>
<tr>
<td></td>
<td><em>H. rufogriseus</em></td>
<td>19(24) 23(33)</td>
<td>25(54) 25(25)</td>
</tr>
<tr>
<td></td>
<td><em>H. giganteus</em></td>
<td>1( 1) 16(23)</td>
<td>32(69) 29(29)</td>
</tr>
<tr>
<td>Comparison between years</td>
<td>$\chi^2 = 22.19, P&lt;0.001$</td>
<td>$\chi^2 = 0.05, \text{ ns}$</td>
<td></td>
</tr>
<tr>
<td>Comparison between sites</td>
<td>Proportion in scats</td>
<td>Proportion observed</td>
<td></td>
</tr>
<tr>
<td>for each year</td>
<td>1979 1980</td>
<td>1979 1980</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\chi^2 =$</td>
<td>6.60 5.68</td>
<td>15.08 1.36</td>
</tr>
<tr>
<td></td>
<td>P&lt;0.05 P&lt;0.10</td>
<td>P&lt;0.001 ns</td>
<td></td>
</tr>
<tr>
<td>Comparison of proportions</td>
<td>S.R.S.F.</td>
<td>Diamond Flat</td>
<td></td>
</tr>
<tr>
<td>for each year</td>
<td>1979 1980</td>
<td>1979 1980</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\chi^2 =$</td>
<td>16.43 14.15</td>
<td>59.31 6.30</td>
</tr>
<tr>
<td></td>
<td>P&lt;0.001 P&lt;0.001</td>
<td>P&lt;0.001 P&lt;0.05</td>
<td></td>
</tr>
</tbody>
</table>

N.B. All chi-squared values have 2 degrees of freedom.

### 6.2 Multi-specied scats

In 94% of the scats, only one species occurred in each scat. This percentage varied between sites with fewer multi-species occurrences at Petroi (5.5%) and Diamond Flat (6.0%) than in the S.R.S.F. (9.0%). The composition of these species also varied between sites. Macropod species were found in approximately 50% of the multi-specied scats from Petroi and S.R.S.F. while all but one multi-specied scat (95%) from Diamond Flat contained macropod hair.
6.3 Relative potential predation pressure

As was shown in earlier sections (3.2 and 4.4) both the relative number of the three main macropod species and the relative number of the dingoes varied between sites. The relative proportions of *H. bicolar* in the S.R.S.F., Diamond Flat and Petroi were respectively 3.6 : 2.7 : 1.0 and for all three macropod species 5.4 : 4.4 : 1.0.

The relative numbers of dingoes for the three sites, S.R.S.F., Diamond Flat and Petroi were respectively 1 : 3.4 : 2.6. Thus the relative number of dingoes per swamp wallaby was 1.0 : 4.5 : 9.0 and the relative number of dingoes per the 3 larger macropod species was 1.0 : 4.2 : 14.0.

These latter two ratios indicate the relative potential predation pressure between the three sites for the respective species. There was 4.5 times as many dingoes per swamp wallaby at Diamond Flat than there was in the S.R.S.F. site and 4.2 times as many dingoes per one of the 3 larger macropod species. The relative potential predation pressure for macropods was twice as high at Petroi than at Diamond Flat.

6.4 Dietary shift

The shot density (section 4.3) varied between sites. The impact of shooting such a relatively high percentage of the *H. bicolar* (0.11 animals/hectare) at Diamond Flat, and thus further changing the relative prey availability, may have contributed to the concurrent increase (20%) in the percentage occurrence of the non-swamp wallaby macropod component of the dingoes’ diet. At the S.R.S.F. site where the shooting density was 0.03 a/h the increase in the percentage occurrence of the non-swamp wallaby macropod component of the dingoes diet was only 5 percent. At Petroi where there was no shooting the increase was 7 percent.
CHAPTER 7

DISCUSSION AND CONCLUSION

7.1 Macropod numbers

7.1.1 Declining numbers

Of much advantage to this study was the availability of information from previous studies which had collected macropod density data from the various sites used in this study. Bradley (1977) worked in the S.R.S.F. while Southwell (1976 and 1981) and Harden and Statham (pers. comm.) estimated macropod abundance at Diamond Flat and Petroi respectively. Although differing techniques and observers do not allow a direct comparison between these studies certain generalisations can be made which aid in presenting a background to the results obtained in this study.

Bradley (1977) estimated a density of 0.85 animals per hectare (a/ha) for the three large species at the S.R.S.F. site. This was approximately twice the estimate of this study (0.44 a/ha) even though part of the transect routes were common to both studies and the techniques similar. This discrepancy may have resulted from the dispersal of these species away from the transect route during this study as an outcome of the drought, differing observer bias, an actual decline in the numbers of these species, or a combination of all three. At Petroi (1974-1976), Harden and Statham determined the density of *H. bicolor* by vehicle-driven transects and calculation by the same formulae as used in this study to be 0.19 a/ha. This was again twice that calculated for that site in this study (0.08 a/ha). In this latter comparison the density derived by driven transects may be significantly different from that of walked transects since Bradley (1977) found the two methods were significantly different in his study. He found the density estimate derived from walked transects was twice that of the estimate obtained from the driven transects. Thus in this latter comparison the real
difference was likely to be greater than the two density estimates indicate.

The work by Southwell (1976 and 1981) at Diamond Flat was restricted by design to the more open forest and woodland and as such his transect data is atypical of the larger area in this study called Diamond Flat. This open habitat was utilised to a greater extent by *H. rufogriseus* and *H. giganteus* (Southwell, 1976) and hence his density estimates were higher than in the present study for those species and lower for *H. bicolor*.

The implication of these findings is that the decline in numbers of the three large macropod species may have been in operation prior to this study in all sites. Initially it was thought that such a decline was confined to Petroi since it was noticeable to the author and co-workers at that site.

7.1.2 Group size

Group sizes observed by Southwell (1976 and 1981) and those in this study at Diamond Flat were comparable. The majority of *H. bicolor* sightings were of single individuals (94% - Southwell, 1976; and 99% in this study) and similar to reports by Calaby (1966), Kirkpatrick (1970), Frith (1973), and Edwards and Ealey (1975). The frequency of group size for *H. rufogriseus* and *H. giganteus* was also similar between the studies with twice as many sightings of *H. rufogriseus* in groups of 1 than of groups of 2, and a mean group size of approximately 3 for *H. giganteus*.

However, group size of *H. giganteus* in this study varied significantly between sites with a greater number of solitary individuals being present in the site with the relatively lower dingo predation pressure. A number of socio-ecologists (Crook and Gartlan, 1966; Alexander, 1974; Jarman, 1974; Johnson, 1979) have suggested that predation pressure was a factor involved in group formation and these data support such an hypothesis especially since the densities (another group formation variable - Southwell, 1981) were similar between sites.
7.2 Swamp wallaby biology

7.2.1 Age structure

While there may have been inherent biases in the shot sample, the age structures of both sites were similar even though the shooting intensities differed markedly between sites. With the high proportion of the swamp wallabies shot adjacent to the transect route at Diamond Flat it seems likely that all age classes of the swamp wallaby age structure would have been represented in the sample. Thus the presence of fewer young animals than would have been expected if the sample was taken at random from a stable population, may mean that there was a high and unsustainable mortality of young reducing the recruitment rate. Caughley (1974) cautions against interpreting age ratios without a knowledge of the rate of increase. In the present study these conclusions were indirectly supported by the evidence for a decline (a negative rate of increase) in the number of *L. bicolor* over the past 4 years. Caughley (1974) further states the magnitude of the mortality rate cannot be assessed from age ratios especially if the mortality factor/s affect all age classes equally. Thus the age structures from each site in the present study may be similar, yet result from a different mortality rate.

7.2.2 Morphology

The mean weights of both the sexes in this study were lighter than those reported in the published literature. Males were 4 to 7kg lighter while females (except for the finding of Kirkpatrick, 1970) were 2 to 6kg lighter. Merchant (1983) presented a range for each sex (12.3-20.5kg for males and 10.3-15.4kg for females) and for each the mean for the present study was at the lower end of these ranges (13 and 11kg respectively). The sample size was not included for each of these published weights and this difference may possibly have arisen from small sample sizes. In this study the 148 males and 91 females were considered adequate to estimate the mean weight of each sex in the study area. One other factor that may have compounded this difference was geographical variation. However, there was no apparent latitudinal or longitudinal gradient to these published weights.
In the field positive identification of the sexes was not possible unless the subject was a relatively large individual, as such individuals were then usually males. However, the comparison of the morphometric measurements for each sex revealed a statistically significant sexual dimorphism and this may have been biologically meaningful.

Morphometric measurements were taken to examine the hypothesis that canine predators in general were selecting certain types of individuals from the prey population (Mech, 1970). If the dingoes were selecting wallabies possessing certain attributes, these attributes may vary in the two swamp wallaby populations differing in the level of predation. The comparison of females between sites revealed that the measured morphometric parameters from this sex were not significantly different but, the comparison for males indicated that these parameters varied significantly at the 10% level between sites. There was a trend for Diamond Flat males to be heavier and bigger in the upper torso than males from the S.R.S.F. site. However, such a finding does not validate the hypothesis. The trend may not have been a direct outcome of predation, i.e. due to the selection of smaller males by dingoes, it may have indirectly arisen from the differing levels of predation and it is suggested that this difference in morphology between the two male populations was related to the elevated reproductive requirements of Diamond Flat males. In other macropod species (for example *Thylacoleo thetis*, Johnson, 1977; *Macropus parma*, Maynes, 1977) male aggression, associated with reproductive drive, has been correlated with the development of larger biceps and chest in the dominant males. Such a change at the individual level indicates the possibility that populations may also vary in the size of the upper torso as a result of increased male aggression.

7.2.4 Sex ratio

The similarity in the sex ratio derived from the shot sample for each site indicated that the higher predation pressure was not associated with an increased selection of one sex in preference to the other. Further, the similarity of the sex ratio of the shot sample and that of the pouch young indicate that the dingo selected the different sexes at random. Johnson (1977) stated that sex specific mortality could be
examined by comparing the mean age of each sex. In his study he interprets the lower mean age of male *T. thetis* to indicate a proportionally higher mortality of males. In this study the mean molar indices, a measure of relative age, were not significantly different between sexes. While this infers that there was no sex specific mortality it is possible that the molar index may be sexually dimorphic. However, not all macropod species exhibit the age and sex variation in dental morphology that is found in *M. rufus* (Desmarest) (Sharman *et al.*, 1964) and *M. agilis* (Gould) (Newsome *et al.*, 1977). Kirkpatrick (1964) and Wood *et al.* (1983) found no sex related difference in the molar index for *M. giganteus*. This section remains speculative especially as the dental morphology of *Wallabia bicolor* is different to three latter species in that *W. bicolor* has no molar progression (Sanson, 1980).

7.2.5 Reproductive biology

If the molar indices were directly comparable between sexes, the males reached sexual maturity earlier than the females. With the small sample of immatures, 5 males and 11 females, the difference in the onset of sexual maturity (males M.I. = 1.7 and females M.I. = 1.9) may not have been significant. Kirkpatrick (1970) reported sexual maturity in both sexes at 15 months. This finding contrasts with the onset of maturity in most other macropod species where the females reach sexual maturity before the males. [For example *M. rufus*, (Sharman and Pilton, 1964; Newsome, 1965), *M. giganteus*, (Kirkpatrick, 1965), *M. parma*, (Maynes, 1977), *M. parryi*, (Maynes, 1973), *T. thetis*, (Johnson, 1977), *M. agilis*, (Merchant, 1976), *M. rufogriseus*, (Merchant and Calaby, 1981), and *M. eugenii*, (Smith, 1983)].

All sexually mature females were either pregnant and/or suckling a pouch young. Only 4% of the sexually mature females were not pregnant even though the area was declared drought-stricken during this study. In arid Australia the occurrence of drought often caused a large proportion of female *M. rufus* (Newsome, 1964 and 1965) and *M. robustus* (Gould) (Ealey, 1967) to enter anoestrus. However, the drought was not severe in the study area. Pasture, although poor, was not critical for *W. bicolor* since it is predominantly a browser (Harrington, 1976; Sanson, 1980). Furthermore, none of the shot sample were found in poor condition and in
fact many contained large fat reserves.

There was no evidence of the preparturition fertilisation reported by Sharman et al. (1966) and Merchant (Calaby and Poole, 1971). However, the chance of sampling this state within a wild population was considered low. From the 91 retrieved females only 3 possessed a swollen uterus and none of these contained a blastocyst in the other uterus.

Pouch young were present in all monthly samples but the estimated months of birth for these pouch young were significantly different between sites. (This difference between the two sites will be discussed in section 7.3.9). The 68 pouch young found attached to a teat showed no preference to a particular side nor anterior/posterior positions. In *H. giganteus* (Poole, 1973) there was a preference for both anterior teats. *H. rufus* (Sharman and Calaby, 1964) showed a preference for the right posterior teat while *H. rufogriseus* (Merchant and Calaby, 1981) showed a preference for the left anterior teat. When one teat was previously suckled and still elongated the newly born pouch young selected the opposite side, and the anterior and posterior teat equally in this study, as did *H. giganteus* and *H. rufus*. *H. rufogriseus* did not show a tendency for selection of a teat from the opposite side.

7.3 Dingo diet

7.3.1 General

The type of prey species taken in this study did not alter the notion, as previously mentioned (see section 1.2.5), that the dingo is a hunter of predominantly native mammalian prey species preferring the larger species, especially the macropods. The large array of species found in this study was similar to the other diet studies in eastern Australia (Coman, 1972; Newsome et al., 1973; Newsome et al. 1983; Robertshaw and Harden, 1984).

The highest percentage occurrence of a single prey species was recorded in this study. Overall *H. bicolor* had a percentage occurrence of 44% but reached a maximum of 58% at Diamond Flat in 1979. Prior to this study the previous highest occurrence was recorded by Whitehouse
(1977) in Western Australia. He found that *Macropus rufus* comprised 40% of the diet. These results emphasise the preference for macropod prey by the dingo in these respective studies.

7.3.2 *Seasonal variation in the diet*

A seasonal variation in the diet, as illustrated by the increase in the equitability of prey in the diet from March to October, was found in both sites in this study and that of Robertshaw and Harden (1984). No results were found that were contrary to their hypothesis that this change reflected a change in hunting strategy imposed on adults with young, and on the young by a physical inability to capture large prey, both resulting in a relative increase in the number of small prey taken. Of interest, in this study, is the correlation between this period and that of an increased number of dingo scats on the fire trails for both Petroi and Diamond Flat. Conversely, there was an absence of this peak in scats in the S.R.S.F. site (see Figure 3.2) even though there was a seasonal change in the diet at that site. This indicates that the equitability of prey species in the diet was not related to the increased number of scats *per se*. Furthermore, as the study area of these two projects overlapped but were separated in time by 5 years, the similarity of this finding may indicate that the above hypothesis was more viable than the alternative one of relating the increased equitability to the availability of prey, since the composition of the prey species in the diets from the two studies have changed.

7.3.3 *Increased specialisation*

Robertshaw and Harden (1984) showed that the diet of two adjacent but distinct dingo populations became more specialised in consecutive years of increasing dingo numbers by comparing the annual equitability of the prey species consumed. In this study two sites were compared where the respective dingo populations differed in their relative numbers. The findings of the two studies were comparable since both showed that the diet from the site or year with a relatively high number of dingoes had a low equitability of prey species reflecting a marked selection for macropods and especially *W. bicolor* in that site or year.
Robertshaw and Harden (1984) hypothesised that the increase in dingo numbers reduced the effective prey availability between years even though they had no data to support their assumption that prey numbers remained constant. In this study, not only were the relative numbers of dingoes examined but also the relative numbers of the three larger macropod species, so as to crudely assess the relative prey availability of the major dietary items between sites. With approximately 4 times as many dingoes per common macropod in the site with more dingoes, the effective prey availability for at least the major dietary items were significantly different between sites. Thus in this study there was support for the notion that dingoes with reduced prey availability concentrated more on the larger native game (macropods and especially *H. bicolor* in this study).

This increased specialisation on so few species as a result of reduced prey availability is contrary to the Optimal Foraging Theory. One prediction of this theory is that the lower the abundance [or more correctly the availability] of food the greater the range of food items in the diet (Schoener, 1971). Without contradicting Optimal Foraging Theory there are two possible explanations for this difference. Firstly, the dingoes may not have been foraging optimally. There is a possibility that dingoes, like wolves, self-regulate their numbers to some extent (Harden, pers. comm.). This ability may hold dingo numbers below the "carrying capacity" of the prey populations allowing the selection of prey in a system with reduced pressure for, or devoid of pressure towards, optimal foraging. Furthermore, it may be possible that the dingo and prey numbers cycle as has been observed in other predator-prey situations (Pearson, 1966; Clark, 1972). A time-lagged response by a predator to an increase in prey abundance would imply a temporary over-abundance of prey to which the predator would not have to respond to optimally. Optimal Foraging Theory should integrate the relative number of predators and prey rather than assume that the predator is at or near the carrying capacity for the prey available. In this study it was unlikely that the major prey species were over-abundant as a result of either of the above two conditions as their abundances had declined prior to and during the study. Secondly, Robertshaw and Harden (1984) postulated that the change in the diet was associated with a change in the sociality of the dingo and as such what may have been optimal for
solitary hunting may not have been optimal for hunting in/or for groups of 2 or more. Bowen (1981) found that, although both group-living and solitary or paired coyotes living in the same area were in good nutritional condition, group-living coyotes spent less time hunting and more time resting than solitary or paired coyotes. This may indicate the conditions for optimal foraging vary with group size in coyotes and possibly explain the increased specialisation in the diet of dingoes when their effective prey availability decreased.

7.3.4 Selection of prey species

The dingo is often referred to as an opportunistic predator (Newsome, 1983) and it has acquired this label as a result of the wide variety of prey species found in its diet. This wide variety was again illustrated by this study but it should be noted that the majority of the diet consisted of only half a dozen main species (as was the case with the other diet studies) with most food items appearing at <1%.

Opportunistic hunting implies the taking of the prey item or species when available individuals are encountered (Van Vurer and Thompson, 1982). While it is difficult to estimate what proportion of a prey species population is available to the predator at any one time it seems unlikely that the less frequently taken species are taken in proportion to their availability, for example the cattle in this study and sheep in the study by Whitehouse (1977). The infrequently occurring items in the diet are probably taken only if the dingo was hungry at the time of the encounter.

The selection of the main prey items, *W. bicolor* in this study, may also be disproportionate to their availability. But in this case a greater proportion of these species may be taken relative to their availability. While there still remains the problem of equating availability to abundance, proportionally more *W. bicolor* were found in the scats than were observed at either site relative to the other observed macropods. This finding is further supported by the greater proportion of *W. bicolor* in the diet from the site having the relatively lower macropod availability. If dingoes took *W. bicolor* in proportion to their availability fewer occurrences would be expected from this site rather
than the observed increase in occurrence. Thus the dingo is a selective hunter of the larger native species as illustrated by the selection of *H. bicolor* in this study.

### 7.3.5 Dietary shift

In most predator-prey studies, where the interaction was manipulated by man, the population dynamics of the prey species was observed following the eradication or marked lowering of predator numbers in the local area. In this study the diet of the predator was observed following the marked reduction of the major prey species numbers (by predation and by the high shooting intensity) at Diamond Flat. This further reduction in macropod availability as a outcome of the shooting resulted in an increase in the equitability index as predicted by Optimal Foraging Theory. However, while there was an increase in the number of mammalian species consumed (13 to 17 species) and a greater evenness of distribution of these species in the diet, there tended to be more macropod in the diet even though the composition of this component was significantly different between years at Diamond Flat. The major effect of reducing *H. bicolor* numbers was the concurrent increase in *H. giganteus* in the diet which significantly altered the proportion of macropods in the diet. While this change was significant it was not great enough to alter the disproportionate selection for *H. bicolor* and the disproportionate selection against *H. giganteus* in relation to their observed numbers. This indicated a high level of inertia in the selection of *H. bicolor* by dingoes at this site. For switching to have occurred (as defined by Murdoch, 1969) a reduction in excess of the 50-75% from this site would apparently be required.

### 7.3.6 Age of macropod prey

Robertshaw and Harden (1984) advanced the hypothesis "that this concentration on the larger prey at higher dingo densities was related to a change in social organisation and hunting strategy, the result of which was that more dingoes fed from individual macropod kills". This they (manuscript) stated assumed that dingoes did not switch to prey upon the smaller individuals of these species as was found by Shepherd (1981). Their examination of the age of macropod prey consumed (manuscript)
showed that, as dingo numbers increased, the relative importance of the independent macropods in the diet of the dingoes increased. While it was not the intention of this study to verify these findings a similar trend was apparent. In this study the ratio of dependent to independent macropods was similar to that found by Robertshaw and Harden (manuscript). The ratio from the years with low dingo numbers in Robertshaw and Harden (manuscript) corresponded to the ratio from the site with the relatively higher macropod availability and the ratio from the year with high dingo numbers corresponding to the ratio from the site with the relatively lower macropod availability. (While these findings indicate a similarity between the two studies, the different proportion of scats containing bone material in each study warrants a reappraisal but to do so is beyond the aim of this section).

Less than 2% of the scats containing bone fragments also contained bone remains from both independent and dependent macropods. This suggested that the two age classes were not eaten at the same time. Females with large pouch young must then either eject the young before being killed or the pouch young were not consumed together with the female.

Of those scats whose bone material was allocated to an age class in this study, twice as much independent material was taken in the site with reduced macropod availability. However the proportion of scats aged from bone fragments to the total number of scats collected was not significantly high enough to assume that this was the relative importance of these age classes to the dingo. The unaged component of the macropod intake consisted of those scats containing no bone. It would be unlikely that dependents could be consumed without the ingestion of identifiable bone material so this latter component probably represents material ingested from independent macropods. The addition of this component to the independent age class would negate the difference between sites in the proportion of the two age classes consumed. (The percentage of independent macropod would then be 78%, 76% and 77% for the S.R.S.F., Diamond Flat and Petroi sites respectively).

While the proportion of dependents in the diet may be similar between sites, the seasonality of this age class in the scats varied
between sites. In the S.R.S.F. site there was a marked seasonal intake of dependents from August to March while at Diamond Flat this trend, although present in 1979, was reduced (see Figures 3.8 and 3.10). However, these graphical representations of the importance of the respective age classes only refer to the aged bone material and do not represent the relative proportion found in the diet because of the large unaged component. The inclusion of the scats containing no bone material as indicating independent material consumed by dingoes revealed that the only site with a significant difference in the proportion of each age class consumed within the year was the S.R.S.F. site.

7.3.7 Utilisation of macropod carcases

A similar percentage occurrence of a food item only indicates a similar importance of that food item to the diet but the occurrence may consist of many items under utilised or fewer individual items more fully utilised. The independent macropods have sufficient biomass to provide several times the daily intake requirements of a dingo (as determined by Robertshaw, 1976; and Green, 1978). This biomass may then be exploited by either one dingo utilising the carcase over several days or by a number of dingoes utilising the carcase. Robertshaw and Harden (1984) stated that as decomposition and scavengers limit the usefulness of macropod carcases as a food source, the increase in utilisation they observed in their study was likely caused by an increase in the number of dingoes eating a kill together. While they initially based their finding of increased utilisation on the field observation of a limited number of macropod kills they later (manuscript) examined the weight and type of bone fragments consumed to show that the increased dingo numbers were correlated with a greater utilisation of the carcase.

Their findings and those of this study were again comparable. The mean weight of bone fragments per scat containing independent bone material was found to be greatest in the year with the highest dingo numbers (Robertshaw and Harden, manuscript) and significantly higher for those sites with the relatively lower macropod availability in this study. The mean number of skeletal zones per scat containing independent bone material was highest in the year with the highest dingo numbers (Robertshaw and Harden, manuscript) and significantly higher in the sites.
with the lower macropod availability. These findings indicate that dingoes consumed more bone material and a wider selection of skeletal zones when the effective macropod availability was reduced.

Field observations in this study support this finding. Carcases and kills at Diamond Flat were quickly and fully utilised while in the S.R.S.F. site (the site with the relatively higher macropod availability) carcases and kills were not fully utilised by the dingoes and were quickly consumed by maggots and other scavengers.

There was one major difference between the two studies. The proportion of scats containing bone varied significantly between sites in this study while there was no significant variation in the proportion of bone material between years in Robertshaw and Harden (manuscript). The site with the higher macropod availability per dingo had significantly more scats without bone material than the corresponding years of relatively low dingo numbers. While the mean weights of bone material and the mean number of skeletal zones per scat corresponded, the higher proportion of scats without bone is interpreted to indicate that their relative utilisation rates were not similar. Likewise between sites in this study, the higher proportion of scats without bone could only result from a further reduction in utilisation of the macropod kills from the relative utilisation rates assessed from the bone fragment analysis. Thus the dingoes in the site with the effectively lower macropod availability, not only concentrated more on the larger macropods, but also more fully utilised those individuals they killed.

These changes buffer the dingo population against decreases in the availability of the major dietary items which may arise from increases in its own numbers (Robertshaw and Harden, 1984) or a decrease in the number of wallabies per dingo.

7.3.8 The number of individual macropods consumed

The determination of the relative utilisation rates for the two age classes is important in equating the relative importance of these classes to the dingo, as indicated by their respective frequency of occurrence in the diet, to an estimate of the number of these individuals
consumed. The number of independents, which are approximately 4-7 times heavier than dependents, are overestimated by the relative percentage occurrence and the relative number of dependents are underestimated. While dependents were probably fully utilised because of their small size, independents were utilised at different rates between the sites. Thus while it was not possible to assess the absolute utilisation rate of independents at any particular site and thus obtain the absolute number of individuals consumed, the effect of dingo predation on the two age classes can be inferred from these findings. If independents were fully utilised the ratio of 1 dependent to every 4 independents in the scats may represent an equal number of individuals consumed from each age class. Thus as carcasses were observed to be approaching complete utilisation at Diamond Flat the ratio of 1 scat containing the remains of a dependent macropod to every 5 containing the remains of independent macropods (1:5) indicates an approximate parity in the number of each age class consumed. However, this parity represents a high selection for the younger animals. At the S.R.S.F. site the ratio of 1:2 for the spring-summer period also indicates a high selection of young animals but because the utilisation of independent carcasses was lower in this site this lower ratio does not indicate that the selection of young was higher than at Diamond Flat. The ratio of 1:11 for the winter period in the S.R.S.F. site probably reflects the seasonality of available young.

7.3.9 Disruption of *H. bicolor* breeding season

While Kirkpatrick (1970) and Poole (1981) state that *H. bicolor* breed continuously throughout the year, evidence from Harrington (1976) and Jones (pers. comm.) indicate a summer peak of births. These latter findings are particularly relevant to this study since Harrington (1976) worked at Diamond Flat and Jones (in 1977) worked in the north-eastern end of the S.R.S.F. site. In this study *H. bicolor* were found to have bred with a spring-summer peak of births in the S.R.S.F. but continuously throughout the year at Diamond Flat. At Diamond Flat dingo numbers had been increasing before the study by Harrington (1976); (Robertshaw and Harden, 1984) and have probably continued to increase and peak in 1980 (pers. obs.). Thus results from these prior studies and this study, suggest that *H. bicolor* may breed seasonally where the predation pressure is low but under greater predation pressure reduced macropod availabil-
ity per dingo) breeding becomes continuous throughout the year. The evidence of seasonality in the estimated month of births is supported by the seasonal occurrence of dependent macropods in the scats from the S.R.S.F. site.

While it is not known why the S.R.S.F. population breed in this synchronised fashion, the breakdown of this synchronisation could result from a high mortality of pouch young. With most females already pregnant the birth of the next young would occur within the next month. Repeated loss of pouch young for a significant proportion of the breeding females would produce the continual breeding pattern observed at Diamond Flat in this study.

Of the three factors, reported by Russell (1974), to result in the high mortality of older pouch young, only two were relevant to this study. The major cause of mortality in most macropod species, according to Russell (1974), was inadequate nutrition of the large pouch young during drought conditions. However this was not considered significant for *W. bicolor* in this study area. The other more relevant factors were the mechanical loss of large pouch young from the pouch of a disturbed female at flight, and the separation of older pouch young which are spending short periods out of the pouch, and young-at-foot from the mother leaving the young subject to starvation and predation. The former reaction was elicited by the author on three occasions to verify that *W. bicolor* would react in such a fashion.

Initially it was thought that the effect of the increased dingo predation on the sexually mature females could be assessed by counting the number of corpora albicantia in the ovaries. The number of scars so counted was to have been related to the number of pregnancies per year for the females for each site. This could not be achieved as such scar tissues are only transient structures in this species. However, this histological work revealed that there were more active corpora lutea in the females from Diamond Flat. This indicated not only a greater number of ovulations per female but a greater turnover of pregnancies per female at this site suggesting a higher mortality rate of pouch young than in the S.R.S.F. site.
One further illustration of the extent of this disruption to the breeding biology of _H. bicolor_ was the significant difference in the testicular and epididymal weights and testicular volumes between the sites. While all sexually mature males remained fertile throughout the year in both sites there was a significant seasonal difference in the reproductive demand placed on the males from the S.R.S.F. as was indicated by the change in testicular weight throughout the year. The period of greatest testicular weight was similar to the period in which the pouch young were estimated to have been born. At Diamond Flat testicular weight was elevated throughout the year and may have been correlated to the continuous output of young at that site.

The extent to which this disruption has to occur before breeding of the whole _H. bicolor_ population is affected is not known. Both _H. bicolor_ populations in this study were probably on the decline as a result of a reduced recruitment rate. Hence the level of disruption needed would have to be higher than the mortality level required to reduce the respective recruitment rate since only one site was observed to have been breeding continuously.

7.4 Conclusion

The findings of this study support the notion that the dingo has a highly adaptable social organisation whereby the dingoes' hunting strategy adapts to changes in the size of the major prey. These changes may occur within a prey species as the ratio of younger to older individuals changes (Robertshaw and Harden, 1984 and manuscript) or between areas where the size of the major prey species differ (Newsome et al., 1973; and Newsome, 1983). In either case when small game is the major dietary component the dingo may be a solitary hunter but when large prey are available dingoes may hunt co-operatively. While the larger hunting group is probably not necessary to kill the larger wallabies in this study area these larger groups are advantageous when macropod availability per dingo declines so as to efficiently exploit the prey base by greater utilisation of the carcass.

With the exception of Robertshaw and Harden (1984), most studies on the food habits of dingoes have only documented the basic array and
frequency of the prey species consumed. This only answers the simplest of management questions - what do dingoes eat? How they select what they eat and what effect they have on their prey populations are more crucial problems for wildlife managers.

In this thesis an attempt has been made to answer these more crucial problems. Although prey selection and its consequences in this thesis was confined to the major prey species, the effect of dingo predation on the less frequent prey items in the diet would be minimal to such prey populations because they are of such low importance to the dingo. However this still warrants further examination as species which occur at low densities (including rare fauna) may be limited in a localised area by the occasional predation by dingoes.

The lack of both prey availability and dingo abundance data were the major shortcomings of the work by Robertshaw and Harden (1984). In this study an attempt was made to solve these problems by estimating the relative abundance of dingoes and the three larger macropod species in the diet. The study was successful in establishing that the two sites differed in the relative number of wallabies per dingo. However it could not be discerned how the relative number of wallabies per dingo was related to the availability of these wallabies to the dingoes. But as the difference in the relative number of wallabies per dingo was large it was assumed that it reflected a real difference in availability between sites.

The examination of the effects of dingoes on their prey populations revealed the following :-

1) that dingo predation on macropods could disrupt their breeding patterns. The subsequent replacement after the loss of dependent young, if a frequent occurrence in the wallaby population, would disrupt a synchronised breeding pattern. It is suggested that this may occur through harassment of females with large pouch young causing them to be separated from their young; through
the ejection of large young from the pouch or the separation of these young from their mothers when spending short periods out of the pouch.

2) that the decline in the recruitment rate observed in this study may have resulted from the high selection of dependent young.

This suggested that the prime impact of dingo predation on the *W. bicolor* population was on recruitment into the adult population. While it is likely that dingoes have affected the recruitment rate of *W. bicolor* it can not be concluded, from this study, that dingo predation could control *W. bicolor* numbers. But the likelihood of dingoes exerting some control on wallaby numbers is possible for two other reasons. Firstly, with *W. bicolor* being monotocous and requiring in excess of 250 days to rear its sole young, it is unlikely that *W. bicolor* has the potential to increase production at a rate that would greatly outproduce the dingo. Such a disparity in the breeding potential between predator and prey prevents the dingo from controlling rabbits and feral goats and pigs. Secondly, the dingo has the potential to switch to another (one or more) prey species if the reduction in the number of individuals of a major prey species was to affect its own numbers. The ability to change the diet, breaking the negative feedback of prey numbers on predator numbers, is necessary for any predator to control the number of its prey. The examination of the ability of dingoes to control wallaby numbers is one avenue for future research to extend the findings of this study. Such a study would have to demonstrate that fluctuations in wallaby numbers were caused by variations in the extent to which these species are selected and that dingo predation could stop the wallaby numbers from increasing in the advent of the lack of any self-limiting control by the wallaby population.

The examination of how dingoes selected their major prey items revealed the following:

1) that dingoes are predators of the larger native game which in this study were the macropods.
2) the selection of the three larger macropod species was disproportionate to the observed numbers of these species and showed a strong preference for *H. bicolor*.

3) within *H. bicolor* the selection of individuals was:
a) not disproportionately biased towards a particular sex, but was
b) greater for the dependent age class

4) that the utilisation of the larger individuals of the larger prey species may vary so that in years or areas when dingoes were less frequent the number of individual prey taken would be higher per dingo than in years or areas when dingoes were more frequent and carcases more fully consumed.

This demonstration of prey selection in eastern New South Wales needs to be repeated in drier, more arid Australia. In that area the dingo may have different pressures directing prey selection, for example the different composition and size of potential prey species and the variable climatic conditions. Thus before any generalisation can be made concerning prey selection by dingoes, these arid areas will have to be similarly examined to obtain more information than the simple diet observations that have been published to date. Furthermore as both the dingo and the macropod species may live for several years, the relatively short term nature of this study may lead to false impressions of this dynamic system. For example, within two years, both the composition of the prey populations and the prey species in the diet have changed (pers. obs.). This emphasises the necessity for caution in generalising these findings and illustrates the complexity in a predator-prey interaction.