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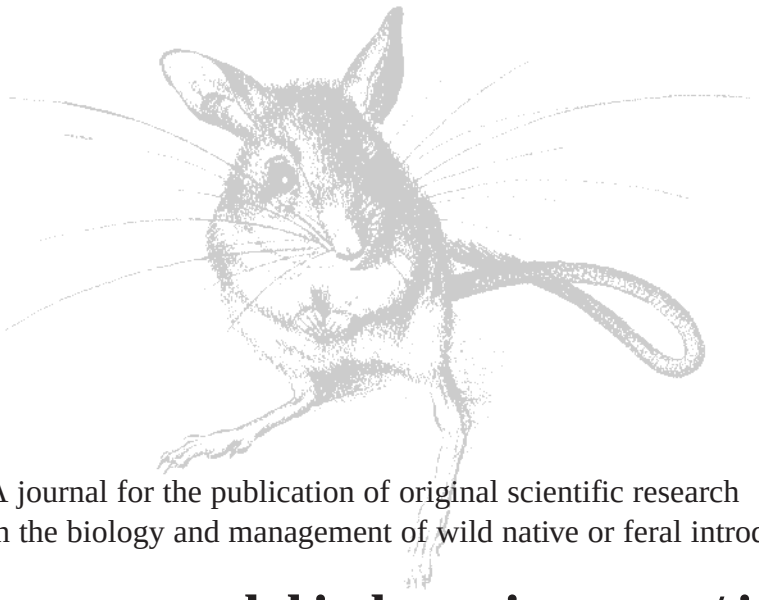

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Male Bias in Road-kills of Macropods

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Abstract

I determined the sex of a total of 251 road-kills of six macropod species in southern Australia over a 13-year period. There was a significant bias towards males in five species, ranging from 65 to 92% males, but there was no difference from parity in the red kangaroo, *Macropus rufus*. Male eastern grey kangaroos, *M. giganteus*, and male western grey kangaroos, *M. fuliginosus*, probably behave in ways that expose them to vehicles more than females. Male-biased road-kills of swamp wallabies, *Wallabia bicolor*, may reflect skewed population sex ratios. There are insufficient data on the behaviour and population structure of the red-necked wallaby, *M. rufogriseus*, and rufous-bellied pademelon, *Thylogale billardierii*, to determine which explanation is responsible for male-biased road mortality in these species.

Introduction

In a long-term survey of a section of highway in central Victoria, Coulson (1982, 1989) found that the majority of road-killed eastern grey kangaroos, *Macropus giganteus*, were male. Some road-killed swamp wallabies, *Wallabia bicolor*, were also recorded, but too few to discern any possible sex bias. However, it was noted that males predominated in incidental records of road-kills of both species elsewhere in Victoria and southern New South Wales (Coulson 1989). By contrast, Osawa (1989) found no difference from parity in a sample of 37 road-killed swamp wallabies on North Stradbroke Island, Queensland, in the only other published study of road-kills in macropods.

This paper extends these observations to other parts of the range of the eastern grey kangaroo and the swamp wallaby, and to other macropod species in southern Australia, with the aims of determining the prevalence of sex bias and seeking possible reasons for it.

Methods

I searched for road-killed macropods in the course of travel throughout southern Australia between September 1982 and April 1995. These trips covered Victoria, New South Wales, eastern South Australia and south-western Western Australia, as well as one visit to Flinders Island, Tasmania, over three days in June 1994.

I inspected all macropod road-kills and identified their species where possible. I determined their sex by examination of soft anatomy of moderately fresh carcasses, avoiding the bias towards large males inherent in determining the sex of carcasses by reference only to dimorphism in skeletal anatomy.

Results and Discussion

I recorded a total of 251 road-kills from six macropod species in which both species and sex could be determined (Table 1). Four of the red-necked wallabies belonged to the mainland subspecies, *M. rufogriseus banksianus*, while the majority were Bennett's wallabies, the nominate Tasmanian subspecies, *M. r. rufogriseus*, from Flinders Island. I compared the frequency of each sex with a sex ratio at parity using the *G*-test with William's correction for continuity (Sokal and Rohlf 1987). There was a significant bias towards males in five species, with ratios ranging from 65 to 92% males. There was no difference from parity in the red kangaroo, *M. rufus*.

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Table 1. Proportion of males, number of individuals sampled and significance of departure from parity in road-kills of six macropod species
n.s., not significant

Species	Males (%)	n	G_{adj}	P
Eastern grey kangaroo	65·3	98	9·285	<0·01
Western grey kangaroo	69·8	43	6·829	<0·01
Red kangaroo	42·3	26	0·606	n.s.
Red-necked wallaby	92·3	26	21·528	<0·001
Swamp wallaby	72·7	33	6·969	<0·01
Rufous-bellied pademelon	80·0	25	9·448	<0·01

Two hypotheses can be advanced to account for the male-biased patterns observed in this and previous studies. First, the sex ratio in populations of these species may be skewed, and vehicles merely sample members of each sex in proportion to their occurrence. Second, males may behave in ways that expose them to greater risk than females: males might have larger ranges that are more likely to encompass a road, or move within their ranges more rapidly and cross roads more often, or have a greater preference for habitats that are associated with roadsides, or be less alert or less likely to respond to vehicles. Although roadsides are known to provide habitat for macropods (e.g. Osawa 1989; Arnold *et al.* 1991*b*), and macropods are commonly surveyed from roads (e.g. Coulson 1990; Southwell and Fletcher 1990), no study exists of sex-based differences in either usage of roadside habitat or responses to vehicles on roads. However, there have been a number of studies of ranging behaviour in macropods, so the second hypothesis can be partially evaluated in terms of the movement patterns of each sex.

The two hypotheses are not mutually exclusive, but they generate quite different predictions. Neither hypothesis could be tested directly since there were no data available on demographics or behaviour of the populations from which the road-kills came. However, with the exception of the Flinders Island populations, road-kills were recorded over a wide geographic range, suggesting that the bias towards males was a general phenomenon. If so, evidence for the two hypotheses can be sought from studies throughout the range of these species.

Significant bias towards females, rather than males, has been reported in every published study of adult population structure in eastern grey kangaroos (Jarman and Southwell 1986; Johnson *et al.* 1987; Quin 1989; Jaremovic and Croft 1991) and western grey kangaroos, *M. fuliginosus* (Norbury *et al.* 1988; Arnold *et al.* 1991*a*, 1994). These data have been obtained from both shot samples and non-lethal surveys. The hypothesis that road-kills are a random sample of populations therefore is not supported in these two species. The second hypothesis, that the behaviour of males exposes them to greater risk, has some support. Although Jarman and Taylor (1983), Priddel *et al.* (1988*a*, 1988*b*) and Coulson (1993) were unable to detect any overall sex difference in home-range size of grey kangaroos, large adult males have been shown to have larger ranges than females in eastern (Jaremovic and Croft 1991) and western greys (Arnold *et al.* 1992), and large eastern grey males have been observed to make longer daily movements than female conspecifics (Clarke *et al.* 1989). Behavioural differences between age- and sex-classes thus offer the better explanation of male bias in road-kills of the two grey kangaroo species.

In the swamp wallaby, by comparison, there is no evidence of a sex difference in mobility. Although Edwards and Ealey (1975) stated that males had larger home ranges in this species, Troy and Coulson (1993) criticised this conclusion as being based on an inadequate sample size, and could not detect any sex difference in mobility in a subsequent study of a larger sample of wallabies at the same site, near Healesville, Victoria. T. Montague and D. McDonald (personal communication) also found no sex difference in home-range size of swamp wallabies radio-

tracked in Gippsland, Victoria. The only published analysis of population structure in the swamp wallaby reported a bias towards males at two sites in north-eastern New South Wales (Robertshaw and Harden 1986). If bias towards males is typical of swamp-wallaby populations, then the hypothesis that road-kills are a random sample is supported by the data obtained from widespread areas. The absence of bias reported by Osawa (1989) does not necessarily refute this hypothesis, since the sex structure of the Stradbroke Island population was unknown, and may have been at parity.

Trends in the composition of the sexes in the red-necked wallaby are possibly confounded by sampling bias. Johnson's (1986) finding of bias towards females in a live population of the mainland subspecies, obtained from a long-term observational study of known individuals, is least likely to be a sampling artefact. Shot samples of populations of Bennett's wallabies show a different trend: of the eight Tasmanian populations that were examined by Driessen (1992), seven did not differ from parity and one was male-biased. However, the primary sex ratios and sex-specific survivorship in these populations should have resulted in a predominance of females, leading Dreissen to conclude that the observed sex ratios were the result of active selection for larger individuals by recreational hunters, together with passive selection due to males being inherently easier to shoot. Similarly, in a New Zealand population sampled by shooting, Catt (1977) reported a sex ratio at parity in autumn and winter, but showing bias towards males in other seasons, when females apparently spent more time in cover and were harder to shoot. Overall, the sex-composition data provide little support for the hypothesis that road-kills are a random sample of the red-necked wallaby populations, particularly if the effects of shooting selection are taken into account. Instead, the only study of movements in this species supports the alternative hypothesis, since males had home ranges that were almost three times the area of females' ranges (Johnson 1987).

Driessen (1992) found bias towards males in shot samples of five of eight populations of the rufous-bellied pademelon, *Thylogale billardierii*, while the remainder did not differ from parity. If the Flinders Island population (not examined by Driessen) was similarly skewed in structure, there would be support for the hypothesis of road-kills as a random sample of the population. However, Driessen (1992) concluded that passive shooting selection was also operating in these samples, the greater activity of males making them more vulnerable to shooting. His conclusion, and the alternative hypothesis for sex bias in road-kills, cannot be evaluated because there is no information on the ranging behaviour of this species. Johnson's (1980) study of its congener, the red-necked pademelon, *T. thetis*, did not show a sex difference in home-range size ($t = 1{\cdot}123$, d.f. = 6, $P = 0{\cdot}305$).

Red kangaroos presented an anomalous pattern: the sex ratio in a small sample of road-kills had a trend towards female bias, but did not differ from parity. Studies of the population structure of red kangaroos, by a variety of sampling techniques, have all found that females predominate (Newsome 1977; Johnson and Bayliss 1981; Edwards *et al.* 1994; Pople and Cairns 1995), yet road-kills were not strongly biased towards females. Movement studies of red kangaroos have shown no overall difference between the sexes (Priddel *et al.* 1988*a*, 1988*b*; Croft 1991), although Norbury *et al.* (1994) found that subadult males had the largest ranges, and Edwards *et al.* (1994) found that subadult females and males up to 10 years old were more mobile. It is possible that both hypotheses apply in this species, so that greater mobility of males in at least some age-classes is counteracted by bias in sex ratio towards females in the population as a whole.

This study highlights the generality of male-biased road-kills in macropods, with the exception of the red kangaroo, and this preliminary evaluation of two hypotheses to account for this trend suggests that it may not be due to a single cause. A more definitive test of the hypotheses requires unbiased data on the structure of local populations, coupled with observations of the behaviour of individuals in relation to roads, and to moving vehicles, as have been conducted with North American deer, *Odocoileus* spp. (e.g. Waring *et al.* 1991; Romin and Dalton 1992).

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