

The life history of *Pseudocheirus occidentalis* (Pseudocheiridae) in the jarrah forest of south-western Australia

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Abstract. Life-history attributes are described for the threatened ngwayir or western ringtail possum (*Pseudocheirus occidentalis*) in inland jarrah (*Eucalyptus marginata*) forest east of Manjimup, south-western Australia. Data on 81 individuals were collected over 18 months. There was no sexual dimorphism and body size was similar to that found in other *P. occidentalis* populations, but larger than the closely related *P. peregrinus* in eastern Australia. Breeding at Chariup was more strongly seasonal than that of coastal populations, with 77% of births in May–June and the remainder in October–November. All neonates were singletons except for one instance of non-viable twins. No females bred twice in the same year. The growth rate of the head length of pouch young (<5 months of age) was 0.245–0.362 mm day⁻¹ and curvilinear toward an asymptote thereafter. Temporal variations in body condition, coat condition and ectoparasites were significant. Mortality was highly seasonal (84% of deaths were April–September) and predominantly caused by predation, mainly by fox (*Vulpes vulpes*) and cat (*Felis catus*). More effective and strategic control of introduced predators prior to and during autumn/winter, could therefore improve the viability of jarrah forest populations. Nutrition appears to influence many of the life-history traits of *P. occidentalis*. Nutrition also may partly explain the differences in size, life history and conservation status between *P. occidentalis* and *P. peregrinus*.

Introduction

A scientific understanding of biodiversity and of ecosystem processes is fundamental to their effective conservation and management. Knowledge of the biology and life history of a species is particularly important (Lindenmayer and Burgman 2005). Critical knowledge gaps in this understanding hamper the effective conservation management of ecosystems such as the jarrah forest (CALM 2004; Wardell-Johnson *et al.* 2004).

Pseudocheirus occidentalis (Thomas, 1888; Pseudocheiridae) (ngwayir or western ringtail possum) is endemic to south-western Australia and is a specialised arboreal folivore that feeds predominantly on the leaves of a few select species (Jones *et al.* 1994a, 1994b; Jones 1995; Jones and Hillcox 1995; Kerle 2001). Since the European settlement of south-western Australia in the 1820s, the distribution of *P. occidentalis* has been reduced by ~80–90% and the species is now absent from most of its former northern and inland range (Fig. 1) (Jones 2004; P. de Tores, unpublished data). *P. occidentalis* is consequently classified as Vulnerable under the IUCN (1994) criteria and as 'fauna which is rare or likely to become extinct' under the Western Australian *Wildlife Conservation Act 1950*. Only three large populations remain (Jones 2004; P. de Tores, unpublished data). The densest

population, located around Bunbury and Busselton, is in the southern extremity of the Swan Coastal Plain where the dominant peppermint tree (*Agonis flexuosa*) constitutes 90–95% of the species' diet (Jones *et al.* 1994b). Similarly, the smaller south coast population around Albany is to be found mainly in near-coastal habitat where peppermint is common or dominant. The most extensive remnant population survives inland in the Upper Warren (in the IBRA Jarrah Forest Bioregion: Thackway and Cresswell 1995), east of Manjimup. Here, the peppermint tree is effectively (naturally) absent and jarrah foliage constitutes the species' staple diet (Jones *et al.* 1994b). Another conspicuous difference between the populations in coastal peppermint woodlands and in inland jarrah forest is the generally rare use of dreys (self-constructed nests) in inland areas, where tree hollows and balga (*Xanthorrhoea preissii*) constitute the main form of diurnal shelter (Inions *et al.* 1989; Jones *et al.* 1994b; Wayne 2005).

The current understanding of the biology and ecology of *P. occidentalis* is largely derived from studies within the coastal peppermint woodlands and in the near-coastal tuart (*Eucalyptus gomphocephala*) and peppermint forest at Ludlow (both sites are near Busselton) (Ellis and Jones 1992; Jones *et al.* 1994a, 1994b; Jones and Hillcox 1995). In

contrast, detailed published knowledge of *P. occidentalis* in the jarrah forest is relatively limited (i.e. Inions *et al.* 1989; Jones *et al.* 1994b). More recently, the survivorship of *P. occidentalis* was found to be substantially reduced during logging operations in the jarrah forest (A. Wayne, unpublished data). In response to these findings, more extensive research has sought to improve the detection efficiency of survey methods for this cryptic species (Wayne *et al.* 2005a, 2005b). The findings of these studies facilitated investigations into the selection of diurnal refuges (Wayne 2005) and the anthropogenic factors related to the distribution and abundance of *P. occidentalis* at local and landscape scales within the Upper Warren (Wayne *et al.* 2005c). The purpose of these studies was to improve the biological and ecological understanding of the ngwayir within the jarrah forest as a means of improving its conservation and habitat management.

As part of the research program, this study investigated aspects of the life history of *P. occidentalis* in an inland jarrah forest. We present data collected in 2002 and 2003 from individuals trapped, hand-captured and radio-collared

in a 25-ha portion of extensive jarrah forest in Chariup (part of Perup), in the Upper Warren. In particular, the morphology, reproduction, growth, temporal changes in condition and mortality of *P. occidentalis* individuals were investigated. A comparison of these results with data for other *P. occidentalis* populations and those of the closely related *P. peregrinus* is also presented.

Methods

Study area

The study area in Chariup forest block was within the southern portion of Perup Nature Reserve, 270 km south-south-east of Perth, 40 km east of Manjimup, south-western Australia (34°16'S, 116°37'E) (Fig. 1). Perup comprises 52 000 ha of dry sclerophyll forest with an overstorey dominated by jarrah and marri (*Corymbia calophylla*), and has been managed as a nature reserve since 1972 (CALM 1998). Prior to this the area was vested as State forest and commercially logged for timber. The region experiences a Mediterranean-type climate with warm dry summers and cool wet winters. The local average annual rainfall is ~700 mm, and the monthly mean minimum and maximum temperature range is ~5–28°C (ANUCLIM 2001 data: Hutchinson *et al.* 1999). The topography is characterised by gently undulating plateau tops, low lateritic ridges and broad valleys, 220–280 m above sea level. In recognition of the value of the remnant native fauna and the predation threat from the introduced red fox (*Vulpes vulpes*), irregular baiting using 1080 toxin began in some areas as early as 1977. Regular broad-scale aerial fox-baiting commenced in 1996 (CALM 2000). The Chariup study site had not been burnt for 18 years. More detailed management history and habitat attributes of the study area are described by McArthur and Clifton (1975), Wilde and Walker (1984), Strelein (1988), CALM (1998), and Burrows and Christensen (2002). The same study site was used for several other studies of *P. occidentalis* (Wayne 2005; Wayne *et al.* 2005b) and the life history of *Trichosurus vulpecula hypoleucus* (koomal or common brushtail possum) (Wayne *et al.* 2005d).

Trapping and capture

Arboreal traps were shown in a previous study to capture more than nine times as many *P. occidentalis* as the same traps placed on the ground (Wayne *et al.* 2005b). Hence, a 500 m × 500 m grid of 121 arboreal trapping points spaced 50 m apart (i.e. 11 parallel transects with 11 points each) was used in this study. The arboreal platforms were constructed from a metal frame with a reinforced plywood decking (1200 mm × 200 mm × 10 mm) and were attached to trees ~1.8 m above ground. Sheffield wire mesh cages (220 mm × 220 mm × 590 mm) were secured to the platform using elastic hooks. A small straight bush stick was placed under the entrance of all traps to avoid tail injury to captured possums (i.e. to stop the tail potentially becoming wedged between the trap door and the platform decking). A thick hessian bag covered the traps to provide protection from the weather and exposure. Traps were baited with flour and vegetable oil dough scented with rose essence (12 mL rose fragrance per kilogram of flour: Wayne *et al.* 2005b). Ten trapping sessions were conducted between June 2002 and November 2003, each for 3 or 4 consecutive days, and generally 8 weeks apart (Table 1). Trapping was periodically supplemented with captures made either by hand (generally 0–4 m above ground), by a catch-pole (range = 2–8 m above ground), or by tranquilliser dart gun (range = 6–12 m above ground). The specially designed (by B. Terrel) air gun was used to deliver custom-made darts (developed by P. de Tores) that contained Zoletil™ sedative. Two trapping sessions were conducted in June 2002, at the commencement of the study, and hand-capture methods were responsible for all captures made in November 2002, March 2003 and August 2003. Greater hand-capture effort was directed towards females.

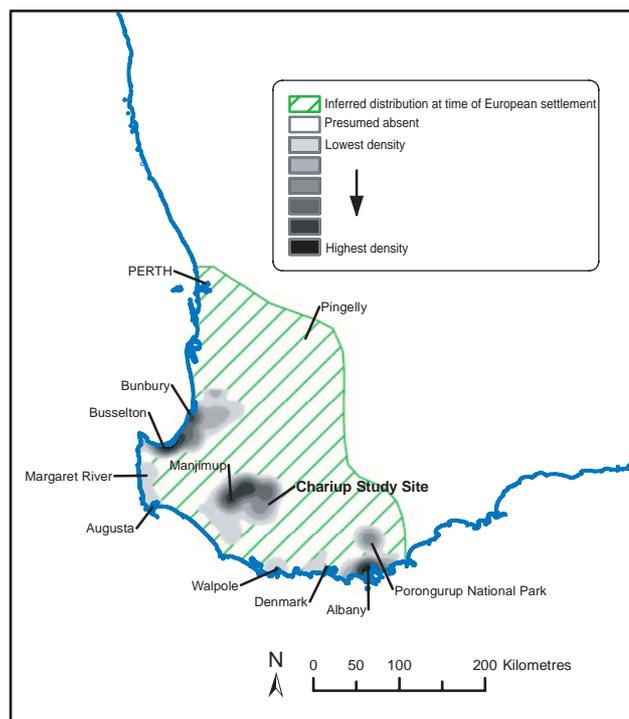


Fig. 1. Historic and current distribution of *Pseudocheirus occidentalis* (exclusive of subfossil records) and the location of the Chariup study site. Source: P. de Tores. Note: the density of location records reflects, in part, surveying effort, increased public awareness and proximity to major towns. It does not necessarily reflect the density of *P. occidentalis*. Prior to the commencement of European settlement of south-west Western Australia in the 1820s, and based on subfossil evidence, *P. occidentalis* occurred between Geraldton on the mid-west coast and Eucla on the southern edge of the Nullarbor Plain, and up to 150 km inland at Tutanning Nature Reserve, near Pingelly (P. de Tores, unpublished data).

Animal handling and data collection

During the initial phase of the study (June and July 2002), all adult possums captured for the first time were sedated using an intramuscular (quadri-cep) injection of Ketamine (20 mg kg⁻¹) and Xylazine (7 mg kg⁻¹), or Zoletil (10 mg kg⁻¹) to minimise handling stress and to facilitate the examination of tooth wear and pouch young and, for some, the fitting of radio-collars. Sedation for examination was not used after July 2002 owing to the quiet nature of these animals and the ease with which they can be handled (except the examination of tooth wear).

Individuals were considered to be pouch young when suckling within the pouch, and juveniles when they had emerged from the pouch but were dependent on their mothers (i.e. back young). Subadults were at least semi-independent but were sexually immature. Adults were considered mature on the basis of testes size (>10 mm wide, >15 mm long) or the presence of a well-developed pouch.

The main morphological measurements collected from captured individuals are summarised in Appendix 1. A relative and approximate measure of age was determined using an arbitrary nine-class system based on tooth wear and the extent of exposed dentine (Thomson and Owen 1964). Coat condition was subjectively assessed on the extent of hair loss and matting, density, uniformity, and general appearance. Ectoparasites (Arachnida; Acarina) were counted on each animal's head.

Mortality events

Mortality-sensitive radio-transmitting collars (Biotrack, UK) were fitted to a subset of the adult population (21 males, 22 females) as part of a complementary study of habitat selection (Wayne 2005). Radio-collared individuals were scanned weekly to check whether they were still alive. When mortality radio-signals were detected, the collars were located and any possum remains examined. Where possible, necropsies and biopsies were conducted to assist with identifying factors contributing to the cause of death.

Condition index

Indices of 'body condition' attempt to quantify the general health and fitness of individuals (Humphreys *et al.* 1984; Viggers *et al.* 1998). An appropriate and meaningful condition index based on adult body mass and body size (head length or pes length) was not possible because of a lack of relationship between these factors. A condition index (CI) was therefore derived from the residuals of body mass from a linear mixed model, in which possum identity was fitted as a random effect. This produced a condition index that accounted for individual differences in body mass and was specific to each individual (see Wayne *et al.* 2005d for further details).

Data analysis

Morphometric measurements were tested for differences between the sexes using linear mixed models that accounted for multiple measurements of the same individual over time by including possum identity as a random effect. Analysis of variance (ANOVA) was used to identify differences between time classes (months or seasons) with respect to CI, coat condition and ectoparasites (log-transformed).

The growth rate of small pouch young was determined for two individuals for which there were multiple measurements. Based on these two growth rates and assuming a head length at birth of 7 mm (Jones *et al.* 1994b) and linear growth within the pouch, the date of birth (month) was estimated for each pouch young. The head length of pouch young through to adulthood was characterised using multiple measurements of seven (4M:3F) young animals (two to three measurements each). A linear mixed model of age was used to characterise the growth of individuals from ~5 months of age. Possum identity was fitted as a random effect in this model to account for within-possum variability.

Results

Capture data

There were 96 trap captures of *P. occidentalis* from 3308 trap-nights, and an additional 50 hand-captures during the 18-month study (Table 1). Of the 81 individuals (31M:50F) involved in this study, the 34 (15M:19F) that were captured more than once were captured, on average, 2.9 times each (maximum seven captures each).

Morphometric data

The mean body mass and other morphological measurements (head length, pes or tail length) did not differ significantly between adult males and females (Table 2). Subadults of both sexes ranged between 600 and 800 g. The body masses of mature males and females were greater than 800 g. The mean adult weight was 1080 g and individuals weighed up to 1330 g. All individuals were similar in colour, with a very dark brown dorsal and lateral coat and were creamy white ventrally and immediately behind the ears. An albino was observed on site on several occasions 18 months before the commencement of this study but was not re-encountered during the study.

Table 1. The number of *P. occidentalis* individuals captured per month by trapping or hand-capture at Chariup

Month	Total no. individuals	Males			Females		
		Juveniles	Subadults	Adults	Juveniles	Subadults	Adults
Jun. 2002	16			7		1	8
Jul. 2002	8		1	3			4
Aug. 2002	16			5		1	10
Oct. 2002	18			8	1		9
Nov. 2002	11	1		3			7
Dec. 2002	17	1	1	6	1	1	7
Feb. 2003	5			1		1	3
Mar. 2003	9			1			8
Apr. 2003	13	1		3		1	8
Jun. 2003	7			4		1	2
Aug. 2003	2			1			1
Nov. 2003	13			4	1	1	7

Reproductive data

Breeding season and fecundity

Twenty-five female *P. occidentalis* were observed breeding during 2002. A further four adult females were caught during 2002 but exhibited no signs of breeding; however, their capture history was insufficient to be able to assess with certainty whether or not they bred in that year (i.e. they were captured one to two times each).

On the basis of the head length of 18 pouch young and observed growth rates (see below), it was estimated that 77% were born in May and June 2002 (44% and 33% respectively), and the remainder were born in October and November 2002 (17% and 6% respectively). In 2003, only three autumn–winter births, and one November birth were recorded on account of sampling limitations. Only two females were observed throughout both the 2002 and 2003 breeding seasons and both individuals bred in both years. No females were observed to breed more than once per year.

In all but one case, females had single pouch young. Twins less than 1 week old were observed on one occasion but when the mother was recaptured 2 months later, only one pouch young remained. The sex ratio of the 14 pouch young for which sex was identified was 1:1.

Offspring growth rates and development

Repeat measurements of the head length of pouch young were achieved in two cases; the head length of a male grew from 9.9 mm to 32.0 mm in 61 days (0.362 mm per day) and that of a female grew from 19.1 mm to 24.0 mm in 20 days

(0.245 mm per day). For the growth rates of individuals estimated to be more than 5 months old, the relationship between head length and age (months) was made linear by transforming age to the negative reciprocal of age. A linear mixed model of this relationship was:

$$\text{Head length (mm)} = 77.98 + 109.04 \times (-1/\text{age}) \quad (P < 0.0001)$$

Because of the data limitations (i.e. the numbers of individuals and of repeat measurements) and the estimations of age in months, this growth model provides only a rough approximation (Fig. 2). Nonetheless, *P. occidentalis* appears to mature at, and is capable of reproducing from, ~12 months of age. Body mass at the commencement of adulthood was more than 900 g and head length was more than ~69 mm. The body mass of older adults would range between 800 g and 1330 g, depending on the individual and over time.

Temporal changes in condition

To examine whether the condition of adult possums differed significantly over time, an ANOVA was modelled with month, sex and their two-way interaction as the factors, and the condition index (CI) as the response variable. The model found no significant difference in CI according to sex or the interaction between month and sex, but the CI did significantly vary between months ($F_{11,107} = 3.0554$, $P = 0.0014$). The CI was poorest in autumn and winter (June and July 2002, March and June 2003) and greatest in late spring and summer (November and December 2002 and November 2003) (Fig. 3). There was insufficient data to test whether the cyclical patterns of the CI differed between females that bred

Table 2. Morphometric measures of *P. occidentalis* at Chariup summarised according to sex and age

There were no significant differences (at the 5% significance level) in the body mass, head length, pes length and tail length between adult male and adult female samples. Numbers in parentheses indicate the number of measurements in each category

Measure	Female			Male		
	Juveniles (3)	Subadults (7)	Adults (77)	Juveniles (3)	Subadults (2)	Adults (46)
Body mass (g)						
Mean	415.5	733.4	1086.1	421.7	728.0	1061.8
s.e.	104.1	46.0	16.8	114.0	72.0	19.1
Head length (mm)						
Mean	60.4	67.3	73.8	57.8	69.8	73.5
s.e.	3.0	2.1	0.5	1.3	2.0	0.6
Long pes length (mm)						
Mean	42.1	47.3	50.5	40.5	46.6	50.1
s.e.	2.9	1.0	0.3	1.7	0.9	0.4
Tail length (cm)						
Mean	28.0	34.9	37.3	28.9	31.3	36.9
s.e.	2.6	1.0	0.3	2.9	0.8	0.5
Left testis length (mm)						
Mean					10.5	23.2
s.e.					0.5	0.4
Left testis width (mm)						
Mean					5.8	16.5
s.e.					0.2	0.3

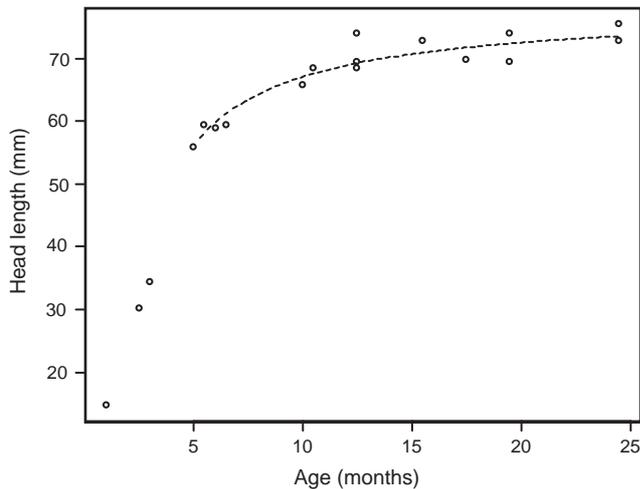


Fig. 2. The relationship between head length and age of *P. occidentalis* pouch young at Chariup.

in autumn, and those that bred in spring – the demands of lactation might affect condition.

Coat condition was highly variable between individuals and over time, including several cases of almost complete fur loss and superficial skin conditions (inconclusive results from skin biopsies) on the back and rump of some animals. Coat condition changed significantly with the seasons ($F_{3,111} = 3.4961$, $P = 0.0180$) and was better in autumn and winter than in spring and summer (Fig. 4). Coat condition also was significantly and negatively related to the condition index

($F_{1,113} = 10.794$, $P = 0.0013$). Ectoparasites on *P. occidentalis* (mostly ticks) varied significantly with the seasons ($F_{3,111} = 5.5744$, $P = 0.0013$), and were more abundant in winter and spring and least abundant in autumn (Fig. 5).

Longevity estimates

Four of the *P. occidentalis* involved in this study were known as adults from a previous study conducted between November 2001 and March 2002 (Wayne *et al.* 2005b). Two of these individuals were radio-collared and were estimated to be at least 2.5 years of age when they died. The remaining two individuals were caught in this study only once or twice, at which time they were at least 2 years of age. Tooth wear was classified for 13 adult males and 15 adult females. The average tooth wear score was 6 for both sexes (i.e. approximately equivalent to a 2–3-year-old *P. peregrinus* at Warramate Hills, Victoria: Thomson and Owen 1964). The highest scores were 8 and 9 for females and males respectively (i.e. approximately equivalent to a ≥ 4 -year-old *P. peregrinus* at Warramate Hills, Victoria: Thomson and Owen 1964).

Mortality

In total, 32 of 46 radio-collared individuals died during the 18-month study (i.e. a 46% annual adult mortality rate); 27 deaths (84%) were between April and September. Predation was the cause of 26 (81%) deaths, many of which occurred in ‘pulses’ where multiple mortalities were observed within periods of 1 or 2 weeks. On the basis of the animal signs associated with the possum remains, up to four

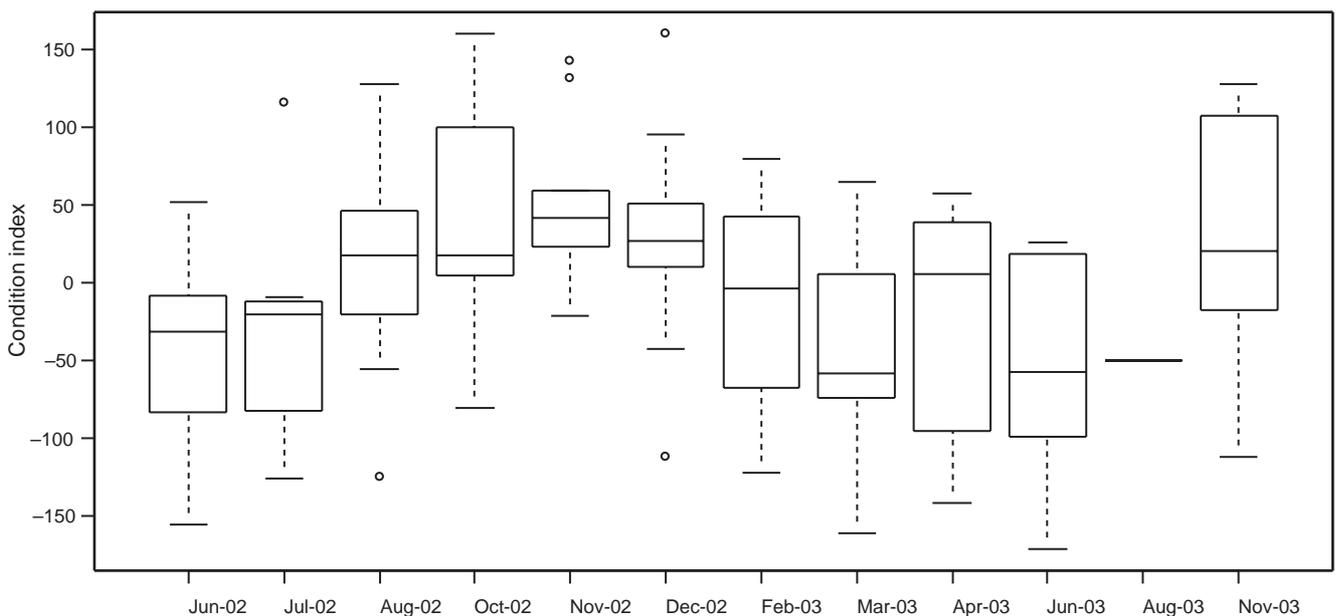


Fig. 3. Box plots by survey month showing temporal variation in the condition index of adult *P. occidentalis* at Chariup. Sample sizes for the 12 sample months were 15, 7, 14, 17, 10, 14, 4, 9, 12, 6, 1 and 10 respectively. The horizontal line in each box indicates the sample median, the lower and upper extents of the box (i.e. ‘hinges’) indicate the 25th and 75th percentiles, the T-bar ‘whiskers’ indicate the maximum and minimum values, with the exception of sample outliers (symbolised by ‘O’).

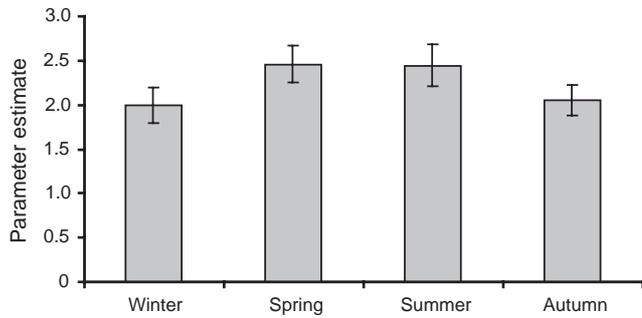


Fig. 4. Seasonal variation in coat condition of *P. occidentalis* at Chariup, based on the mean and standard error of a subjectively derived score (1–5), where 1 = very good and 5 = very poor (i.e. the coat condition score decreases as coat condition improves).

of the predation events may have been by a raptor (probably wedgetail eagle, *Aquila audax*) and up to six may have been by chuditch (*Dasyurus geoffroii*). It is likely that at least 16 animals were killed by either fox or cat (*Felis catus*). Evidence of red foxes, feral cats, chuditch and wedge-tailed eagles was found at the study site.

Discussion

Morphology

The lack of sexual dimorphism in adult *P. occidentalis* in the jarrah forest at Chariup was similar to that in the near-coastal populations in peppermint habitats around Busselton, Augusta and Albany (Ellis and Jones 1992; Jones *et al.* 1994b). Although this species is similar in size to *P. peregrinus viverinus* on Flinders Island (which also is not sexually dimorphic; Munks 1995), *P. occidentalis* is slightly larger and darker than other populations of *P. peregrinus* (e.g. Hughes *et al.* 1965; How *et al.* 1984; Pahl and Lee 1988).

Reproduction

Breeding season

The seasonality of breeding at Chariup was more acute than in the near-coastal populations of *P. occidentalis*, where

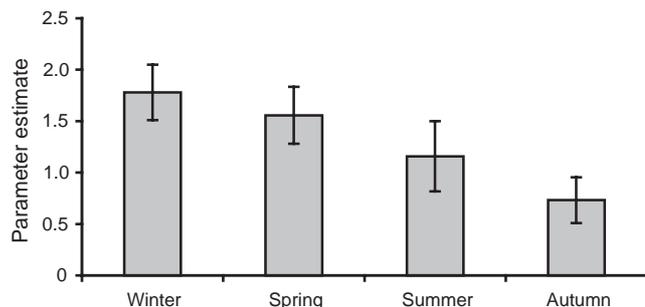


Fig. 5. Seasonal variation in the abundance of ectoparasites found on *P. occidentalis* at Chariup, based on the mean and standard error of the log-transformed number of ticks and mites found on an individual's head.

breeding occurs throughout most of the year (with peaks in April–June and October–December: Jones *et al.* 1994b). At Chariup, 77% of births occurred in May–June, and the remainder in October–November. As with other mammal species, seasonality of breeding is often a fundamental response to food availability (Bronson and Heideman 1994). Therefore, the difference in breeding seasonality between *P. occidentalis* populations probably reflects phenological and nutritional differences in the principal food species. For several arboreal marsupial species, including *P. peregrinus*, it has been suggested that predominantly autumn breeding ensures that the late stages of lactation and weaning of offspring (i.e. the period of highest nutritional demand for mothers: Munks and Green 1995) occur during late spring and early summer, when young foliage is most abundant (Pahl and Lee 1988; Munks 1995).

At Chariup, the period of late lactation by mothers and weaning of offspring (i.e. 5–6 months of age) born in autumn coincides with the emergence of young jarrah leaves (the preferred diet of *P. occidentalis*: Jones *et al.* 1994b) between August and November. The young jarrah leaves mature between December and February (Abbott and Loneragan 1986; Abbott *et al.* 1989). In keeping with a bimodal seasonal pattern of plant productivity that occurs in southwestern Australia, jarrah also may have a secondary leaf growth flush in autumn (Abbott and Loneragan 1986; Abbott *et al.* 1989). The secondary peak in *P. occidentalis* births in October–November results in the weaning of offspring coinciding with this secondary growth flush in jarrah.

In the peppermint woodlands near Busselton, young peppermint leaves are the preferred diet (Ellis and Jones 1992; Jones *et al.* 1994b). The winter and early spring leaf growth of peppermint trees would support the mothers and weaning offspring born in summer–early autumn. The mid-to-late-autumn peak of births (Jones *et al.* 1994b) results in the timing of weaning coinciding with the annual peak in nitrogen levels in peppermint leaves (i.e. October: Jones *et al.* 1994a). Furthermore, no or very few offspring are born in August–September that would subsequently be weaned when foliar nitrogen levels in peppermint trees are at their lowest (i.e. February: Jones *et al.* 1994a). Additional evidence for the influence of nutrition on the timing of *P. occidentalis* births is the aseasonality of breeding in a captive population where daily vitamin and mineral supplements were provided (Ellis and Jones 1992).

Fecundity and nutrition

Although no twins were successfully reared to pouch emergence at Chariup, the incidence of twins in coastal populations is not uncommon (17% of breeding mothers: Jones *et al.* 1994b). Double breeding was not observed for wild *P. occidentalis* either at Chariup or elsewhere (Jones *et al.* 1994b). However, a captive female *P. occidentalis* raised four single young in rapid succession within the first

2 years of maturity (Ellis and Jones 1992). The fecundity of *P. occidentalis* at Chariup of one young per adult female per year is, therefore, less than either its full potential or that of near-coastal conspecifics. Reproductive output at Chariup appears to be limited by environmental constraints. More longitudinal data from multiple sites are required to verify whether the observations at Chariup are representative of other jarrah forest populations.

Nonetheless, nutrition is a plausible key factor influencing fecundity (e.g. Norton 1987; Bronson and Heideman 1994). Preliminary measures of nitrogen (N), phosphorus (P), and potassium (K) levels in jarrah leaves at Chariup (mean = 0.86%, 0.01%, and 0.37% dry weight, respectively) appear approximately comparable to (P), or less than (N, K), the nutrient levels in peppermint tree leaves near Busselton (Jones *et al.* 1994a). However, nutrient levels within the same tree species do vary between individual trees and geographically. For individual trees nutrient levels vary seasonally with tree maturity, leaf maturity, and leaf position within the tree canopy (e.g. Hingston *et al.* 1980; Jones *et al.* 1994a). Furthermore, an animal's ability to access foliar nutrients is dependent on its physiology (e.g. Chilcott 1984; Chilcott and Hume 1984a, 1984b; Hume *et al.* 1984; Pahl 1987a; Foley 1992) and the types and concentrations of secondary metabolites, such as formylated phloroglucinol compounds, to which *Pseudocheirus* spp. are sensitive (e.g. Hume *et al.* 1996; Marsh *et al.* 2003a, 2003b). Therefore, determining the nutritional differences of tree species and the influences that these may have on reproduction of *P. occidentalis* is complex and requires specific investigation.

Additional evidence for nutrient limitation in the jarrah forest is found in the larger home ranges and lower densities of *P. occidentalis* in this type of habitat (A. Wayne, unpublished data) than in the near-coastal populations around Busselton (Jones *et al.* 1994a, 1994b). Furthermore, when compared with peppermint woodland around Busselton that was unoccupied by *P. occidentalis*, occupied peppermint woodland tended to have higher nutrient levels (particularly nitrogen) in late summer, when nitrogen and phosphorus levels were at an annual low (Jones *et al.* 1994a; see also Braithwaite *et al.* 1983, 1984 for nutritional influences on arboreal marsupial densities).

When compared with *P. peregrinus* in eastern Australia, the reproduction and life history of *P. occidentalis* appear to be more constrained. For example, the average litter sizes of *P. peregrinus* range from 1.8 to 2.0 (e.g. Hughes *et al.* 1965; How 1978; How *et al.* 1984; Munks 1995; Smith *et al.* 2003) and litters of up to four young have been observed (e.g. Pahl and Lee 1988). Furthermore, up to 50% of female *P. peregrinus* may breed twice in the same year (e.g. Hughes *et al.* 1965; Pahl and Lee 1988). Fecundity at Chariup is, therefore, little more than half that of wild populations of *P. peregrinus*, which have 1.8–2.4 young per adult female per year (Hughes *et al.* 1965; How 1978; Pahl and Lee 1988; Munks 1995). The

more solitary nature of *P. occidentalis*, and its relatively larger body size also may reflect evolutionary responses to the poorer nutritional quality of its diet (Smith and Lee 1984; Ellis and Jones 1992; Jones *et al.* 2004). The lower fecundity of *P. peregrinus* on Flinders Island in comparison with other populations in eastern Australia also has been speculated to relate to the nutrient status and age of the forest habitat (Munks 1995). The soil fertility in south-western Australian forests and the nutrient concentrations in the dominant tree species of the region are recognised as some of the most impoverished in the world (Hingston *et al.* 1980, 1989; Dell and Havel 1989). Therefore, given that captive *P. occidentalis* are capable of reproductive outputs similar to that of *P. peregrinus*, it is plausible that the lower fecundity observed in wild *P. occidentalis* may be partly explained by nutritional constraints (e.g. Norton 1987; Bronson and Heideman 1994).

Offspring and adult sex ratios

The sex ratio of pouch young at Chariup (7M:7F) was similar to that of *P. occidentalis* at Abba River, near Busselton (4M:3F; Jones *et al.* 1994b), in captivity (5M:6F; Ellis and Jones 1992), and for *P. peregrinus* elsewhere in Australia (e.g. Hughes *et al.* 1965; Munks 1995). *P. occidentalis* at Locke Estate near Busselton, on the other hand, had a significant female bias among the pouch young (6M:14F) and adult (20M:43F; Jones *et al.* 1994b) populations. Although there was an adult female bias in the animals captured at Chariup (31M:50F), this is not an accurate measure of the population because there was a greater hand-capture effort towards females. It has been speculated that equal sex ratios for *P. occidentalis* are indicative of stable populations, that female bias is indicative of an expanding population in a high-quality habitat, and that a male bias is indicative of marginal or declining habitat conditions (Jones 2004; Jones *et al.* 2004). This remains to be verified. Nonetheless, relationships between population dynamics and sex ratios also have been suggested for *T. vulpecula* (e.g. Green 1984; Kerle 1984), including a tendency for mothers to produce more male offspring when competition for resources becomes intense (Johnson *et al.* 2001).

Offspring growth rates

The growth rates of head length of pouch young at Chariup (0.245–0.362 mm per day) were slower than those observed by Jones *et al.* (1994b) in coastal woodlands near Busselton (0.417 mm per day), but comparable to those observed for *P. peregrinus* in Victoria (0.229–0.307 mm per day; How *et al.* 1984), for captive *P. peregrinus* in Tasmania (~0.302 mm per day; Munks and Green 1997), and for *P. herbertensis* in Queensland (0.329 mm per day; Haffenden 1984). The influence of maternal body mass and the nutritional quality of the maternal diet on the milk properties may explain differences in growth rates between populations

(Munks *et al.* 1991; Munks 1995; Munks and Green 1997). Interestingly, the same tendency for slower increases of head length at Chariup compared with those observed in the woodlands near Busselton was found for *Trichosurus vulpecula hypoleucus* (Wayne *et al.* 2005d).

A growth curve using the body mass of young *P. occidentalis* in captivity was developed by Ellis and Jones (1992). Caution is required when using either head length or body mass as an estimator of age because differences between populations and sexes have been observed for immature *P. peregrinus* (Pahl 1987b; Munks and Green 1997). Despite this, the use of head length when estimating age is considered more reliable than using body mass given the linear growth of head length until weaning (Munks and Green 1997), and the highly variable nature of body mass (e.g. Pahl 1987b). More comprehensive data for *P. occidentalis* would be required to provide a more reliable age estimator based on head length that accounted for potential differences between populations, sexes and seasons. Nonetheless, the results from this study indicate that after approximately the first 5–6 months, when weaning may commence (How 1978; Pahl and Lee 1988), head length growth is curvilinear towards an asymptote.

Known-age females at Chariup were first observed breeding at ~12 months. This is similar to the age observed for captive *P. occidentalis* (Ellis and Jones 1992), and wild *P. peregrinus* (Thomson and Owen 1964; How *et al.* 1984; Pahl and Lee 1988; Munks and Green 1995). The timing of breeding, litter size and the incidence of double breeding of *P. peregrinus* have been related to the age and body mass of females, with heavier, multiparous females likely to be more fecund than primiparous adults (Pahl and Lee 1988; Munks 1995). Female *P. peregrinus* that breed twice in the same year also wean their offspring sooner (5–6 months compared with 7–8 months: Pahl and Lee 1988; Munks 1995). Whether similar trends occur in *P. occidentalis* remains to be determined, but the accessibility and quality of nutrients are likely to be ultimate key factors (as has been observed for *T. vulpecula*: Kerle 1984) and should, therefore, be incorporated into any such investigation.

Temporal changes in condition

The seasonal variations in the condition index of *P. occidentalis* at Chariup were similar for males and females, with condition being poorest in autumn and winter and best in late spring and early summer (Fig. 3). Similar seasonal variations in body mass also have been observed for *P. peregrinus*. However, in these cases, the peaks and troughs were generally slightly out of phase between males and females (How *et al.* 1984; Pahl 1987b; Munks 1995). The pronounced environmental seasonality (including jarrah phenology) experienced at Chariup may account for the synchrony in the condition index between the sexes observed there. Ectoparasite (ticks and mites) loads on *P. occidentalis* at

Chariup also were most abundant in the wetter seasons of winter and spring, when body condition was generally poor, but also may coincide with the life cycle of the parasites. Whether ticks and mites significantly affect condition remains to be determined, but it has been suggested that relative ectoparasite loads may be an indicator of stress (e.g. Humphreys *et al.* 1984).

Coat condition at Chariup also varied seasonally, but inversely, with the condition index. Having a good coat during winter, when the weather is wettest and coolest, may provide greater protection from climatic conditions. Good coat condition also coincided with the main breeding season.

Longevity and mortality patterns

The oldest observed age of *P. occidentalis* at Chariup of 2.5 years is an underestimate of longevity, given the limited duration of this study. The oldest observed age of *P. occidentalis* in the jarrah forest is 4 years (A. Wayne, unpublished data). Tooth wear may be another useful non-destructive means of estimating age. However, considerable care is required to ensure that variations according to sex, location and diet are appropriately accounted for (e.g. Pahl 1987b). On the basis of the available tooth wear data and adult survival rates, it is generally assumed that the average adult age of wild *P. occidentalis* in the jarrah forest is around 3 years and rarely exceeds 4 or 5 years. More extensive data on longevity are required to verify this. *P. peregrinus* have similar life expectancies (How 1978), but may live up to 6 years according to estimations from tooth wear (Pahl 1987b) or 8 years in captivity (Thomson and Owen 1964).

As well as longevity, the viability of a population depends on the successful rearing of the next generation through to sexual maturity. With insufficient data for the survival of young *P. occidentalis* (Jones *et al.* 1994b), observations of *P. peregrinus* may give some indication. The average survivorship of young through to maturity is 30% across many of the *P. peregrinus* populations that have been studied, but may be as low as 2% during drought years – predation generally being the major cause of death (see Pahl 1987b). The population viability implications of anything significantly less than 100% survival of *P. occidentalis* young through to maturity in the jarrah forest may be profound, given an annual fecundity rate of one young per mature female and a relatively short life span. To maintain population size a female needs a minimum of two successful reproductive seasons (i.e. three years of age) and 100% offspring survival to maturity. Therefore, anything that reduces either offspring survival or the average life expectancy of a female to three years or less may threaten the viability of the population. Differences in the fecundity, offspring survivorship and longevity between *P. occidentalis* and *P. peregrinus* will result in differences in the ability of populations to withstand and recover from negative population pressures, and may

partly explain the differences in the conservation status between these species.

The deaths of adult *P. occidentalis* at Chariup were associated with the cooler, wetter months of the year (84% of deaths occurred between April and September), when body condition was poor. A similar mortality pattern was observed at Kingston (26 km to the north-east of Chariup) where 89% ($n = 9$) and 93% ($n = 14$) of the deaths of radio-collared animals occurred between April and September in unlogged and logged jarrah forest, respectively (A. Wayne, unpublished data).

The seasonal patterns of mortality and body condition of *P. occidentalis* at Chariup are associated with temporal cycles in food quality and quantity (see above). For example, the increase in body condition coincides with the emergence of young jarrah leaves (August–November). Seasonal periods of poor condition and high mortality coincide with periods of little or no new leaf growth on jarrah (i.e. winter). Higher rates of mortality in winter also have been observed for *T. vulpecula* (particularly males) in New Zealand, following the loss of fat reserves during autumn (e.g. Efford 2000).

The seasonal commencement of the decline in condition of *P. occidentalis* at Chariup also coincides with the hottest and driest months of the year (December–March). Sensitivity to heat and drought-induced stress has been observed in *P. occidentalis* around Busselton (Jones *et al.* 1994b). Furthermore, weight loss and deaths of *P. peregrinus* in Victoria in late summer were associated with excessive heat and drought (Thomson and Owen 1964; Pahl 1987b). However, there were only two out of 32 deaths (both apparently due to predation) at Chariup between December 2002 and March 2003, in similar temperatures to those experienced by the population studied by Pahl (1987b). Manjimup, which has a milder climate than Chariup, had 33 days with maximum temperatures of 30–34°C, and 10 days with maxima of 35–39°C (CALM weather records). Therefore, although the hot summer drought may be contributing to the stress and poorer condition of *P. occidentalis* at Chariup, it does not account for the high mortality rates in the cooler and wetter months between April and September.

It is possible that protection from the weather by diurnal refuges may help to reduce summer mortality of *P. occidentalis* in jarrah forest. The preference for deeper hollows by *P. occidentalis* and *T. v. hypoleucus* in the jarrah forest (Inions *et al.* 1989) led to speculation that the use of dreys was rare in these forests because of the need for added insulation in inland regions where the seasonal and diurnal variations in temperature, and the severity of summer drought, are greater (Jones *et al.* 1994a, 1994b); Kerle (2004) speculated similarly about *P. peregrinus* in eastern Australia. However, dreys are used in some dense habitats within the jarrah forest, which are capable of supporting dense populations (Wayne 2005). It therefore seems more likely that the differences in types of diurnal refuge between coastal and inland populations are mainly a response to habitat structure,

rather than habitat selection being determined simply by physiological limitations (Wayne 2005). Specific physiological studies would more precisely quantify when, and to what extent, *P. occidentalis* may be physiologically stressed, and hence to what extent they may be susceptible to heat and drought stress in summer and/or malnutrition in winter.

Predation was the cause of most deaths at Chariup, and is expected to be a major determinant of the demographic characteristics and viability of jarrah forest populations. The apparent predation pulses observed at Chariup also are indicative of so-called 'rogue predators' (Dickman 1996), whereby the impact of individuals with hunting skills developed for particular prey may have a major impact on populations.

Foxes or cats appeared to be responsible for most predation events at Chariup. These also are major predators of other *Pseudocheirus* populations (Thomson and Owen 1964; Jones *et al.* 1994b, 2004; Dickman 1996; Russell *et al.* 2003). At Chariup, most deaths occurred (i.e. April–September) when other prey, such as reptiles and invertebrates, were scarce (see also Molsher 1999; Molsher *et al.* 1999, 2000). Winter is the breeding season for foxes (e.g. Saunders *et al.* 1995) and is the period when adult fox densities and mobility are potentially at their greatest. The capture rates and lethal baiting of feral cats also are higher in late autumn and winter, which is thought to be due to the scarcity of food, increased energy needs and/or increased dispersal of young adult cats (e.g. Molsher 2001; Burrows *et al.* 2003).

The abundance of ngwayir (which are particularly predator-naïve: A. Wayne, personal observation) in the Upper Warren was positively associated with sustained and intensive fox-baiting (Wayne *et al.* 2005c) over and above the four standard fox-baiting sessions per year (CALM 2000) in operation in the Chariup site and in most publicly managed jarrah forests. Although the standard level of fox-baiting is sufficient to allow population recovery of other native jarrah forest fauna species (CALM 2000; Orell 2004), the results from this study suggest that predation may still be a problem for the long-term viability of *P. occidentalis* populations in jarrah forest. On the basis of the seasonal pattern of mortality of *P. occidentalis* and of fox and cat activity, it is highly likely that strategically timed and increased control of introduced predators before and during autumn/winter could be particularly effective in reducing the rate of deaths during this period. The extent to which predators cause the premature death of potentially physiologically stressed *P. occidentalis* in autumn/winter remains to be determined. Such knowledge could help determine the effectiveness of more intensive baiting at this time.

Conclusions

This study has substantially increased the knowledge of the life history of *P. occidentalis* in the jarrah forest, about which

very little was known. In comparison with the near-coastal populations in peppermint habitat, the population at Chariup exhibited lower fecundity with smaller litter sizes, slower growth rates of offspring, larger home ranges, and lower densities. The higher fecundity of *P. occidentalis* in captivity further demonstrates the extent of the environmentally limited reproductive potential of the Chariup population. Furthermore, differences in the seasonality of breeding appear to be associated with the seasonal variations in foliar nutrients and in the phenology of the trees that constitute the staple diet of the Busselton and Chariup populations (peppermint and jarrah respectively). Seasonal variations in the body condition of adults also were associated with food quantity and quality (i.e. availability of young jarrah leaves). The high incidence of mortality (principally by predation) between April and September corresponds with periods when body condition is poor. A strategic approach to reducing the numbers of predators immediately before and during this period would probably be particularly beneficial to conservation efforts for *P. occidentalis*. In summary, several of the demographic and reproductive patterns of the *P. occidentalis* population in the jarrah forest at Chariup appear to be influenced by nutrition.

At a species level, *P. occidentalis* has a lower reproductive potential than that of *P. peregrinus* in eastern Australia. Other evidence suggesting that *P. occidentalis* may be nutritionally constrained includes its more solitary nature, larger body size, and the fact that the soils and dominant tree species in south-western Australia are among the most nutrient-impooverished in the world. Differences in life history and conservation status between *P. occidentalis* and *P. peregrinus* may thus be partly explained by nutrition.

These findings together provide some clear directions for future research such as: (1) investigating the role and importance of nutrients; (2) developing a deeper understanding of the processes behind biological patterns (e.g. seasonal differences in breeding, causes of mortality, and physiology of heat stress); (3) population viability modelling based on our improved understanding; and (4) determining what implications these findings may have for the conservation and management of *P. occidentalis* and its habitat.

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Appendix 1. Morphometric and life-history data collected for *P. occidentalis* individuals at Chariup

Attribute	Description
Dorsal, lateral and tail fur colour	Munsell Soil Colour Charts (Munsell 1954)
White tail length	Length of white tail tip (cm)
Body mass	Body mass (g), accuracy 10–20 g
Tooth wear	Scale 1–9 (Thomson and Owen 1964)
Head length	Occipital protuberance to nose tip (mm)
Pes length	Hind foot length, from the heel to the tip of the longest toe, excluding the claw (mm)
Tail length	Ventral tail base to tail tip (mm)
Age	A = adult (sexually mature); SA = subadult (semi-independent, immature); J = juvenile (dependant); PY = infant, pouch young.
Ectoparasites	Approximate count (to the nearest 10) of visible ticks and mites around the ears and head
Coat condition	Subjective score: 1 = very good; 2 = good; 3 = fair; 4 = poor; 5 = very poor
Testis length	Left testis length (mm)
Testis width	Left testis width (mm)
Pouch condition	U = undeveloped; P = parous but not active; A = active (moist, clean), no pouch young; S = suckling young; L = lactating but no pouch young
Lactating teat position	L = left, R = right
Pouch young head length	Pouch young head length (mm)
Pouch young sex	Pouch young: M = male; F = female