Early warning signs of population irruptions in Eastern Grey Kangaroos (*Macropus giganteus*)

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Title

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Summary

Left unchecked, macropods (kangaroos and wallabies) can exhibit irruptive population dynamics, rising rapidly to a peak, then crashing when overwhelmed by inadequate resources. This predictable population trajectory frequently leads to overabundance issues, particularly in peri-urban parks and nature reserves. Management decisions are usually guided by estimates of population density, which can be difficult to obtain, sometimes inaccurate, and often inadequate because long-term data are needed to estimate population growth. Alternatively, density-dependent vital rates could be used to predict the growth trajectory of a population before management issues become evident. We applied a framework of sequential changes in vital rates to examine potential indicators of population growth trajectory. We sampled 16 populations of Eastern Grey Kangaroo (*Macropus giganteus*) in south-eastern Australia. Using a range of methods, we measured one vital rate (female reproductive rate) and one surrogate rate (adult sex ratio). As population density increased before irruptive peaks, female reproductive rate (90% breeding) was higher than during post-peak declines (66% breeding). Similarly, sex ratios in increasing populations were at parity, then became more female-biased (65%

females) after peaks. These variables are readily measured in small parks and reserves, and therefore offer promising indicators of population growth trajectory, which can be used to forecast management issues and initiate timely management actions.

Key words

Population dynamics, wildlife management, macropod, kangaroo, population trajectory, irruption, density-dependence, vital rates

Implications for Managers

- Unmanaged macropod populations are likely to undergo a classic irruption, rising quickly to a peak then crashing to a much lower level than before.
- Population peaks and crashes can have severe impacts on animal welfare, human safety, habitat condition and ecological function.
- Regular population surveys can reveal classic irruption patterns, but managers often do not have access to appropriate long-term data sets.
- Two simple measures, female reproductive rate and adult sex ratio, offer a convenient alternative to predict irruptions for timely management interventions.

Introduction

In the absence of predation, populations of large herbivores often exhibit irruptive dynamics (Young 1994; McCullough 1997). Starting at low densities under favourable conditions, populations can increase rapidly to a peak, then crash in response to an overwhelming decline in the availability of food per head, eventually settling around a carrying capacity much lower than the peak (Caughley 1970; Forsyth & Caley 2006; White *et al.* 2007). Problems of overabundance often become evident during the peak and crash phases. Caughley (1981) identified four symptoms of overabundance: threats to human life or livelihood, disruption of ecosystem function, loss of habitat for other species, and poor animal welfare. Management of overabundance usually involves reducing population density by immediate removal of animals, generally by lethal methods, but other options such as fertility control may be appropriate if management is undertaken in a timely manner (Wimpenny *et al.* this volume).

Effective management intervention requires sufficient data to predict population change, which is usually based on long-term monitoring of population density (Mayle *et al.* 1999; Pople 2004; Morellet *et al.* 2007). However, long-term data are often not available and density estimates can lack precision and accuracy (Gaillard *et al.* 2003). In the absence of adequate data on population density, density-dependent vital rates can be used to predict the growth trajectory of a population and inform management decisions. Eberhardt (2002) suggested that vital rates of long-lived vertebrates, mostly ungulates and marine mammals, responded to density changes in a predictable sequence. As population density increases, juvenile survival is first to decrease, followed by a delay in age at first reproduction, then a decrease in adult female reproductive rate, and finally in adult survival as the population approaches carrying capacity. In a review of empirical studies on large herbivore density-dependence, Bonenfant *et al.* (2009) found that changes occurred in the predicted sequence as population density increased in the four species that showed density-dependence in all of these vital rates. Managers of Roe Deer (*Capreolus capreolus*) in France have put this concept into practice by using ecological indicators, including reproductive rate, to inform management decisions (Morellet *et al.* 2007).

The practicality of measuring vital rates in a population survey depends on the species, the monitoring techniques and the environmental conditions at the site. Assessing juvenile survival is often impractical because carcasses are difficult to detect (Hurley *et al.* 2017), unless costly telemetry methods are applied to large samples (e.g. Smith & Anderson 1998; Sarno *et al.* 2002). Likewise, assessing changes in age of primiparity requires longitudinal data on individuals of known age (Festa-Bianchet *et al.* 1995). In contrast, female reproductive rate is one vital rate that is often easier to measure because live young are more readily observed. It can be quantified in terms of the number of adult females detected, which is typically expressed as a cow:calf or doe:fawn ratio in ungulates (e.g. Eberhardt *et al.* 1996; Hoffman *et al.* 2010). Female reproductive rate therefore offers promise as a convenient indicator of irruption phase.

As with juvenile survival, adult survival is difficult to measure. However, adult sex ratio may be density-dependent in sexually dimorphic species (Clutton-Brock *et al.* 2002), because males have lower survival rates than females at high population density when food is limited (e.g. Clutton-Brock & Guinness 1985). Sex-biased dispersal can also affect adult sex ratio if there is an increase in emigration of males, the dispersing sex in most mammals (Greenwood 1980; Dobson & Jones 1985), at high density (Clutton-Brock *et al.* 2002). Thus, density effects on sex-dependent survival and sex-biased dispersal often work in the same direction: as density increases, the population becomes increasingly female biased. As a surrogate for adult mortality, adult sex ratio is therefore a second potential indicator of irruption phase, and is readily measured in a management context

The Eastern Grey Kangaroo (*Macropus giganteus,* EGK) is a large marsupial herbivore. This species can reach high densities to the point where populations display one or more of Caughley's (1981) symptoms of overabundance (Coulson 2001, 2007; Adderton Herbert 2004), but data on population density and growth trends are often inadequate to guide effective management of this species (Coulson 2007). Characteristic irruption profiles have been reported in this species at some sites (ACT Government 2010) and there has been anecdotal evidence of irruptions at other sites (e.g. Coulson *et al.* 1999a; Ingram 2018). As a long-lived vertebrate, the EGK would be expected to conform to Eberhardt's (2002) paradigm for ungulates and exhibit equivalent density-dependent changes in vital rates while undergoing an irruption.

The applicability of Eberhardt's (2002) paradigm to the EGK is unknown. As marsupials, EGK have a markedly different life history to their eutherian counterparts. Gestation is only 37 days in EGK; the highly altricial young are suckled in the pouch for 280-320 days, then for another six months after pouch exit (Poole 1975). Thus gestation and birth are energetically inexpensive; the greatest costs of reproduction arise from large young in the pouch, when their lactation demands are highest (Cripps *et al.* 2011: Gélin et al. 2013). An inexpensive gestation relative to ungulates may result in reproductive rate being less sensitive to population density than in eutherian species, and therefore a poorer indicator of population trajectory. In contrast, adult sex ratio is potentially more sensitive to population density. EGK show extreme sexual size dimorphism (Jarman 1989), which is second only to the dimorphism in otariid seals (Weckerly 1998). Studies of other kangaroo species have shown heavily male-biased mortality during drought, when forage was extremely limited (Norbury *et al.* 1986; Robertson 1986). If this effect also applies to density-dependent food limitation, adult sex ratio may be particularly responsive to density in EGK, and hence provide a powerful indicator of population trajectory.

Our study had two aims. First, we sought evidence of irruptions in a large set of EGK populations in south-eastern Australia. Second, we used Eberhardt's (2002) paradigm as a framework to examine potential indicators of the population trajectory displayed by these populations. We tested two likely density-dependent variables for evidence of change *before* and *after* an irruption: female reproductive rate and adult sex ratio as a surrogate for adult survival. We predicted that reproductive rate would be higher and adult sex ratio would be less female-biased *before* an irruptive peak than *after* a peak.

Methods

We examined populations of EGK at 16 sites in south-eastern Australia: 12 in Victoria and two each in Tasmania and the Australian Capital Territory (ACT) (Table 1). The sites were managed by a number of agencies for a range of purposes, and each site came to our attention because managers were concerned about issues of overabundance, particularly negative impacts on human safety, animal welfare, biodiversity values and ecosystem processes (Caughley 1981; Coulson 2007). We have withheld the details of four sites, identifying them only by letter codes (D, F, L & M) in Table 1, because population data for these sites were provided to us confidentially and we conducted sampling on a private, contractual basis for the management agency at these sites.

The sites ranged from 50 ha to 44,000 ha in area and included a variety of habitats (Table 1). Ten of the sites were peri-urban, while the remainder were in rural settings. EGK were the dominant herbivore at all sites. There were also populations of Bennett's Wallaby (*Notamacropus rufogriseus*), Tasmanian Pademelon (*Thylogale billardierii*) and Common Wombat (*Vombatus ursinus*) at Darlington and Point Lesueur on Maria Island, Tasmania. EGK were deliberately introduced to six of the sites, including Government House, ACT, and Darlington and Point Lesueur. EGK occurred naturally at the other sites, although abundance was initially very low at some of these. For example, only one EGK was detected in surveys prior to the establishment of a park at Portland Aluminium (Coulson *et al.* 1999b).

The occurrence of predators varied among the sites (Table 1). Predators were naturally absent from the two Maria Island sites, and were excluded from two Victorian sites (Site F and Woodlands Historic Park) by purpose-built fencing. All other sites had Red Foxe (*Vulpes vulpes*), which are effective predators of juvenile kangaroos (Banks *et al.* 2000). A number of sites (e.g. Plenty Gorge Parklands and Yan Yean Reservoir Catchment) were exposed to incursions by domestic Dog (*Canis lupus*) from neighbouring farms and suburbs at times, but only Tidbinbilla Nature Reserve had a resident population of Dingo (*C. l. dingo*), which are capable of killing adult kangaroos (e.g. Purcell 2010).

The sites also varied in the opportunity for immigration and emigration (Table 1). Populations at half of the sites were closed to movement: one site was completely isolated and seven, including Gresswell Forest Nature Conservation Reserve and Puckapunyal Military Area, were enclosed by kangaroo-proof fencing. Another four sites, including Plenty Gorge Parklands and Serendip Sanctuary, were bounded by fences that did not constrain kangaroo movement; these and the two sites on Maria Island were surrounded by physical barriers or mostly inhospitable habitat, so were essentially closed, but some movement undoubtedly occurred across their boundaries. Only Anglesea Golf Course and Tidbinbilla Nature Reserve could be considered fully open to movement, because they were embedded in continuous EGK habitat.

We compiled available information on EGK abundance at each site over time to determine the population profile prior to and during the time of sampling (Appendix 1). We drew on published papers, unpublished reports and management plans, including some confidential material. Only three sites (Puckapunyal Military Area, Serendip Sanctuary and Woodlands Historic Park) had a time series of abundance data, based on fairly regular, mostly annual surveys (Fig. 1). Others were even more patchy. Yan Yean Reservoir Catchment, for example, had reports of kangaroo overabundance as early as the 1950s, followed by a few orthodox surveys using a variety of techniques over subsequent decades (Coulson *et al.* 1999a, 2000). Sites such as Plenty Gorge Parklands, Point Lesueur and Portland Aluminium were poorly documented, so we drew on occasional surveys and anecdotal accounts from park staff and other sources. As a result, we could not conduct formal analyses of irruptive dynamics, as proposed by Forsyth and Caley (2006) or include years before or after the peak as a co-variate in the analysis. Instead, we classified our sampling events as representative of the phase of increasing abundance *before* an irruptive peak, or as the phase *after* a peak, based on the population profile at each site. We sampled only two populations while a crash was underway, so we pooled those with samples taken during later periods of fluctuating, lower density to represent the *after* phase.

We collected demographic samples from each of these sites (Appendix 1). We sampled 13 sites once, two sites (Woodlands Historic Park, Portland Aluminium) twice over ten years, and one (Serendip Sanctuary) three times over six years. We recorded data on female reproductive rate for every site, but could not obtain data on adult sex ratio at four sites due to sampling biases. For example, we sampled the Yan Yean Reservoir Catchment population in the course of a project on habitat use by adult females (Moore *et al.* 2002), so males were inherently under-represented.

We measured female reproductive rate and adult sex ratio in these populations in a number of ways. Culling was conducted by the management agency at ten sites (Table 1). At these sites, we examined a sample of kangaroos taken by professional shooters, who were instructed to shoot without bias for sex or age. The shooters euthanased pouch young in the field, then returned them to the mother's pouch before delivering all carcasses to us at a central processing area. We recorded the sex of each kangaroo and classified it as adult, if a female with everted teats or a male with scrotal width > 30 mm (Poole & Catling 1974), or as sub-adult otherwise. For adult females, we also determined reproductive status, classifying them as breeding if there was a pouch young and/or an elongated, lactating teat indicative of an unweaned young-at-foot (Poole 1975).

At a second set of seven sites, we used several different techniques to capture EGK, primarily for research purposes (Table 1). Once each kangaroo was immobilised, we examined it and recorded sex, age class and female reproductive status as for culled samples. We sampled two sites (Portland Aluminium and Serendip Sanctuary) by both culling and capture at different times (Table 1).

At a third set of sites (Sites D and L), we sampled the population by observing EGK feeding at twilight by checking all areas of open, grassy habitats (Caughley 1964; Southwell 1987). We examined all individuals in a group, when possible, using a telescope and/or binoculars to aid observation. We determined the sex-age class of each individual using simple morphological criteria (Jaremovic & Croft 1991), and classified adult females as breeding if they had a distended pouch wall indicative of a young.

We used independent sample t-tests to compare reproductive rate and adult sex ratio *before* and *after* irruptive peaks. We used the Shapiro-Wilk test to evaluate the assumption that data were normally distributed: the data for each group met this assumption.

Results

There was evidence of irruptive dynamics occurring at all 16 study sites. Irruptions were well documented for 11 of these sites and could be confidently inferred from other sources for the remaining five sites (Appendix 1). One of the clearest examples was Serendip Sanctuary, which was surveyed nine times between 1995 and 2009 (Fig. 1). Abundance at this site increased steadily over 11 years until it reached a peak of 698 kangaroos (4.5/ha) in 2006, then fell by 294 in six months. Parks Victoria subsequently culled a further 114 kangaroos on animal welfare grounds. Irruptions followed this sequence at most sites, rising rapidly to a peak then crashing to a low density, often followed by a phase of post-irruptive fluctuations. At four sites, abundance had been increasing rapidly, but did not reach a natural peak, because managers intervened by culling to reduce abundance to low levels.

The two density-dependent demographic variables differed *before* and *after* irruptions (Fig. 2). The proportion of adult females with pouch young was higher (mean = 90%, range 77–96%) *before* than *after* (mean = 66%, range 18–92%) irruptive peaks (t_{18} = 2.52, $P <=$ 0.011). The adult sex ratio was close to parity (mean = 47% females, range 32–61%) *before* irruptive peaks, whereas adult females predominated (mean = 65%, range 51–79%) *after* peaks (t_{13} = 3.19, P = 0.003).

Discussion

Most EGK populations that we examined followed the classic irruption sequence that has been reported in other large herbivores (e.g. Leader-Williams 1980; Kaji *et al.* 2004). These EGK populations typically began at a low density, founded either by a few resident individuals or deliberate introductions. The founders encountered sites that provided a range of suitable habitats, some with connectivity to surrounding habitat, but most sites were confined to some extent, and also protected by, boundary fencing. Within these boundaries, EGK encountered little interspecific competition for resources (except on Maria Island) and had few if any predators. Under such agreeable conditions, each EGK population followed a trajectory of increasing abundance.

This irruption sequence proceeded at most sites. Some experienced dramatic population crashes, causing both physiological and ecological impacts. Serendip Sanctuary was a particularly clear example, with population surveys showing a steady rise in abundance to a peak of 4.5 kangaroos/ha, followed by crash to 58% of the peak (Fig 1). By that time, yearly rainfall was only 59% of the average, pasture biomass was extremely low, body condition was poor, prevalence of 'lumpy jaw' disease (54%) was unprecedented for a wild population, and rates of natural mortality and road-kill were high (Borland *et al.* 2011). Parks Victoria has since maintained the population at a lower density through a combination of culling and fertility control (Wimpenny *et al.* this volume). Maria Island National Park provided another example. The EGK population rose from its introduction in the 1970s and fell in the early 1990s (Coulson 2001). As the population crashed, animal health and welfare was poor, mortality of young at foot was high, and intense grazing pressure led to localised soil erosion, all exacerbated by a prolonged period of low rainfall (Ingram 2018). In response, the Tasmanian Parks and Wildlife Service began an annual culling program in 1994, when we sampled the population, shooting 3503 EGK over 20 years (Ingram 2018). Puckapunyal Military Area illustrated the sheer scale of an irruption at a large site. The abundance of EGK increased during the 1980s and 1990s (Anderson *et al.* 2007); by 2001 'up to 100,000 kangaroos at Puckapunyal were in various stages of starvation, illness and misery' (Clarke & Ng 2006). At least 20,000 EGK died from lack of food, amid public outcry, followed by a cull of 15,000 kangaroos in 2003 (Clarke & Ng 2006).

Managers of only a few sites have anticipated these unsustainable increases by initiating control programs earlier. Extremely rapid population growth of EGK at Government House was curtailed by a combination of culling, translocation and fertility control (Coulson 2001). Similarly, the EGK population that had been introduced to a predator-exclusion zone of Woodlands Historic Park increased rapidly through the 1990s, then was reduced by a culling program specifically to restore habitat for the endangered Eastern Barred Bandicoot (*Perameles gunnii*) (Coulson 2001; Winnard & Coulson 2008). Managers at two other sites, which we have not identified due to likely public opposition, also acted promptly to avoid the negative effects of irruptive peaks. If managers of the other 12 sites had clear warning signs of impending irruptions, they could have assessed the risks involved and implement timely control measures as needed. However, managers often do not have adequate data on the population trajectory at a site.

Eberhardt's (2002) paradigm provides a theoretical basis for predicting trends in population growth of EGK. This paradigm describes sequential changes in vital rates as density-dependent pressures intensify as a population approaches an irruptive peak. We adapted this paradigm to assess two density-dependent variables for evidence of change *before* and *after* an irruption: female reproductive rate, and adult sex ratio as a surrogate for adult survival. As predicted, reproductive rate was higher *before* an irruptive peak than *after* a peak, despite the relatively low energetic costs of gestation and early lactation in this marsupial herbivore. Also as predicted, adult sex ratio was at parity *before* an irruptive peak, but female biased *after* a peak, reflecting likely male-biased mortality and/or dispersal as food availability per head deteriorated in this highly dimorphic species. We were unable to determine which of these two variables may have been the more sensitive to density-dependence, because we could not sample irrupting populations on a continuous time scale. The exact year/s of the peaks were not known at a number of the sites where we relied on anecdotal records, and expected peaks were forestalled by management interventions at other sites (Appendix 1). Nonetheless, these two variables are promising indicators of population trajectory, with strong potential for guiding management decisions for EGK populations. Importantly, both variables can be measured without capturing or killing individuals, using inexpensive, readily-available equipment, and do not require a high level of skill.

Reproductive rate differed markedly between phases. On average, 90% of females were breeding *before* a peak, compared with only 66% *after*. We recorded the lowest rate (18%) at Serendip Sanctuary immediately after its irruptive peak, consistent with Quin's (1989) report of extremely low fecundity (8%) in a small sample of adult females soon after the population crash at Yan Yean Reservoir Catchment. The reproductive rate of a population can be assessed at a distance when kangaroos congregate in open grassland to feed at dusk and dawn (Caughley 1964; Southwell 1987). Births of EGK are concentrated in summer in south-eastern Australia (Poole 1983) and young remain in the pouch for about 10 months (Poole 1975), so surveys of reproductive rate should be conducted in winter or spring to enhance detection of pouch young, which are evident from distention of the pouch. Female reproductive rate in EGK can be influenced by a number of other factors, such as foraging rate, body size and age (Gélin *et al.* 2015; Quesnel *et al.* 2018; Toni *et al.* 2020), so this measure will be subject to some variation. Nonetheless, our results confirm that irruption phases can be distinguished using reproductive rate.

Adult sex ratio also differed between phases. On average, females comprised 47% of the adult population *before* a peak, compared with 65% *after.* As for reproductive rate, we recorded the most extreme adult sex bias (79%) immediately after the irruptive peak at Serendip Sanctuary. Again, this was consistent with Quin's (1989) report of adult female bias (58%) soon after the population crash at Yan Yean Reservoir Catchment. Like reproductive rate, the adult sex ratio of a population can be assessed at a distance because kangaroos are highly sexually dimorphic (Jarman 1983). However, care must be taken to distinguish younger, smaller males from adult females.

Conclusion

Two simple variables, reproductive rate and adult sex ratio, can distinguish between the increasing and decreasing phases of a population irruption in EGK. Both variables can be measured inexpensively, using straightforward methods, and without harming animals. Monitoring these population indicators therefore offers a convenient technique for forecasting management issues arising in irruptive populations, allowing time to develop appropriate management responses. However, managers should also consider the climate outlook: a run of good seasons is likely to sustain an increase phase for longer and allow a higher peak in abundance to be reached, whereas poor conditions are likely to suppress a peak and hasten the onset of decline.

We propose a rule-of-thumb for managers of EGK populations: if surveys show the adult sex ratio ≤ 50% females) with ≥ 80% of females breeding, the population is likely to be growing strongly. A population with this profile is effectively unconstrained by density-dependent effects so is on a clear pathway towards a peak. This rule-of-thumb provides a trigger for implementing a range of management actions as appropriate: population surveys, impact monitoring, asset protection and population reduction by fertility control and/or culling. On the other hand, if the adult sex ratio becomes female biased (> 50% female) and < 80% of females are breeding, the population has probably passed a peak and a range of management issues will be evident. Management at this stage tends to focus on damage mitigation and belated population control.

Our proposed rule-of-thumb meets most of the criteria for an effective ecological indicator: easily measured, sensitive to system stresses, anticipatory, integrative and able to predict change that can be averted by management actions (Dale & Beyeler 2001). However, our rule-of-thumb will benefit from further validation and refinement. For example, an effective indicator should also have low variability in response to change (Dale & Beyeler 2001), but it is unclear how the two density-dependent variables will perform over a range of growth trajectories. We encourage managers of EGK populations to evaluate these two variables against independent measures of growth trajectory. In the absence of supporting survey data, we recommend that managers apply our rule-of-thumb to give early warning of an irruption peak and guide future management actions.

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Table 1: Characteristics of the study sites in south-eastern Australia.

Site	Management agency	Site description	Area (ha)	Boundary	Source	Predators	Kangaroo impact	Sampling method	Sample size
Anglesea Golf Course	Anglesea Golf Club	Peri-urban: golf course	73	Open	Resident	Fox	1,4	Capture	96
Darlington	Parks and Wildlife Service, Tasmania	Rural: retired pasture, woodland	240	Open	Introduced	None	2,3,4	Shoot	150
Government House	Commonwealth of Australia	Peri-urban: grassy woodland	53	Fence	Introduced	Fox	1,3,4	Capture	124
D	Withheld	Peri-urban: wetland, grassy woodland	160	Fence*	Resident	Fox	1	Observe	101
Gresswell Forest Nature Conservation Reserve	Parks Victoria	Suburban: woodland	53	Fence	Resident	Fox	2,3,4	Capture	35
F	Withheld	Rural: grassy woodland	400	Fence	Resident	None	3	Shoot	83

Plenty Gorge Parklands	Parks Victoria	Peri-urban: retired pasture, wetland, woodland	1355	Fence*	Resident	Fox	1,2,3,4	Capture	28
Point Lesueur	Parks and Wildlife Service, Tasmania	Rural: retired pasture, woodland	Δ	Open	Introduced	None	2,3,4	Shoot	432
Portland Aluminium	Alcoa Australia	Peri-urban: farmland, plantation, wetland, shrubland	450	Open	Resident	Fox	1,4	Shoot	88,77^
Puckapunyal Military Area	Department of Defence	Rural: retired pasture, woodland	44000	Fence	Resident	Fox	1,2,3,4	Withheld	75
Serendip Sanctuary	Parks Victoria	Peri-urban, retired pasture, wetland, woodland	250	Fence*	Introduced	Fox	1,4	Shoot	114,125 ,296^
L	Withheld	Suburban: grassland, woodland	130	Fence	Resident	Fox	1,4	Observe	24
M	Withheld	Rural: golf course, wetland, woodland	340	Withheld	Introduced	Fox	1,2,3	Shoot	48

Tidbinbilla Nature Reserve	Parks and Conservation Service, ACT	Rural: retired pasture, woodland	5450	Open	Resident	Fox & Dingo	2,3,4	Shoot	333
Woodlands Historic Park	Parks Victoria	Peri-urban: grassy woodland	400	Fence	Introduced	None	3,4	Shoot	359,48^
Yan Yean Reservoir Catchment	Melbourne Water	Peri-urban: retired pasture, plantation, wetland, woodland	2250	Fence*	Resident	Fox	1,3,4	Capture	78

Footnote: Δ Exact study area could not be defined. * Fence not kangaroo-proof. ^ Multiple samples collected. Kangaroo impact: 1) threaten human life or livelihood, 2) disrupt ecosystem function, 3) degrade habitat for other species, 4) suffer poor animal welfare.

Figure legends

Figure 1. Abundance of Eastern Grey Kangaroo (Macropus giganteus) at Serendip Sanctuary, Victoria, recorded in surveys by Parks Victoria. Each point represents a single population count, without any measure of associated error. Parks Victoria conducted a cull of 114 kangaroos in 2007.

Figure 2. Percentages of adult female Eastern Grey Kangaroo (Macropus giganteus) breeding, and of females in the adult age class, at sites in south-eastern Australia before and after an irruptive peak. n values and standard error of the means are given above the bars.

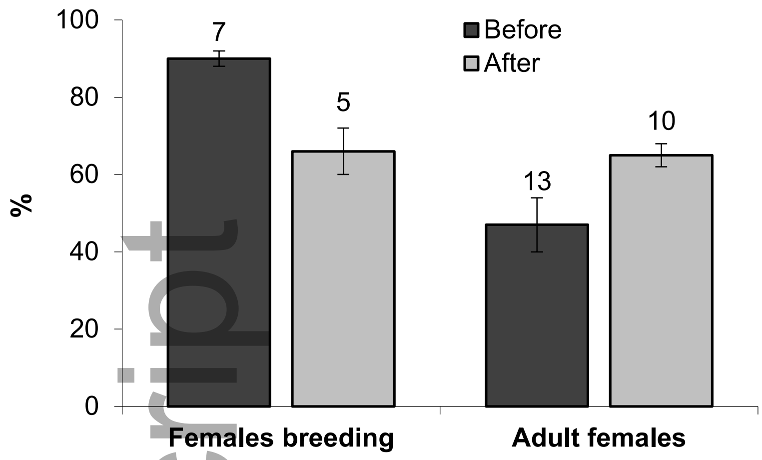
Appendix 1: Timing of demographic sampling relative to irruption phase based on the profile of change in abundance over the period of records for each study site.

Site	Phase sampled	Year sampled	Period of records	Abundance profile	References
Anglesea Golf Course	After	2008	1990s–2019	Concern about increasing abundance and roadkills in 1990s and early 2000s; apparent peak (359 EGK) in 2004; decreased to 142 by 2011.	Inwood *et al.* (2008) Coulson *et al.* (2014)
Darlington*	After	1994	1969–2013	45 introduced in 1969-70; increased to 2000 EGK by 1985; increased further then declined in following 10 years, with high prevalence of parasites and disease; culling program 1994–2013.	Coulson (2001) Ingram (2018)
Government House	Before	1993	1983–1993	12 EGK introduced in 1983; increased to 163 in 10 years; all captured for euthanasia, contraception or translocation in 1993.	Coulson (2001)
D	Before	2014	2000–2015	Concern about increasing abundance and disease; 534 EGK in 2015; all culled in 2015.	Unpublished reports
Gresswell Forest Nature Conservation Reserve	After	2015	2011–2019	Abundance high but stable (201–238 EGK) from 2011 to 2013; crashed to 124 in 2014; rebounded to 194 in 2015; fell further to 97–117 in 2016 to 2019.	Unpublished reports

F	Before	2009	2000–2019	Concern about increasing abundance in 2000s; 450 EGK in 2009; culling program 2009–2019.	Unpublished reports
Plenty Gorge Parklands	Before	2007–2008	1990–2019	Concern about increasing abundance in 1990s & 2000s; 1445 EGK in entire park in 2000; ~2000 in northern half of the park in 2007.	Unpublished reports
Point Lesueur*	After	1994	1969 – 2013	45 EGK introduced in 1969-70; increased to 2000 by 1985; further increase then decline in following 10 years, with high prevalence of parasitism and disease; culling program 1994–2013.	Coulson (2001) Ingram (2018)
Portland Aluminium	Before After	1998 2007	1990 – 2013	Increased steadily to 154 EGK in 1998; reached a peak in early 2000s then decreased; high prevalence of disease; maintained at ~100 by sporadic culling since mid-2000s.	Coulson (2001) Hufschmid *et al.* (2008) Unpublished reports
Puckapunyal Military Area	After	Withheld	1982–2018	Increased slowly in 1980s then rapidly in 1990s: peaked at ~60,000 EGK in 1998 followed by a crash then a cull; irregular culling since early 2000s.	Clarke & Ng (2006) Anderson *et al.* (2007) Unpublished
Serendip Sanctuary	After After After	2007 2009 2013	1995–2016	Increased steadily to 698 EGK in 2006; crashed to 404 in early 2007 then culled; since maintained at lower levels by sporadic culling.	Borland *et al.* (2011) Wilson *et al.* (2013) Unpublished reports
L	Before	2014	2002–2019	7 EGK enclosed in 2002; increased steadily to 25 EGK in 2014 and 97 in 2019.	Unpublished reports

M	After	2013	1980s–2013	8 EGK introduced in early 1980s; increased steadily to 344 in 2005 then decreased; culled in mid-2000s; increased to 310 in 2012; culled in 2013.	Unpublished reports
Tidbinbilla Nature Reserve	After	1997	1963–2003	Increased in the 1960s & 1970s, probably reaching a peak in the early 1970s; fluctuated at lower levels and culled at times from 1976 to 1992; decreased in 1996; culled in 1997; increased again until impacted by fire in 2003.	Bayliss & Choquenot (2002) ACT Government (2010) Unpublished reports
Woodlands Historic Park	Before After	1998 2008	1987–2019	About 30 EGK enclosed in 1987; increased rapidly from 196 in 1991 to 1146 in 1997; culled in 1998; since maintained at lower levels by sporadic culling.	Coulson (2001) Unpublished reports
Yan Yean Reservoir Catchment	After	1992-95	1950s–1999	Concern about increasing abundance in 1950s; 600 EGK culled in mid 1950s; peaked at up to 3000 in 1961; crashed in early 1960s with high parasite prevalence; increased to 2935 in 1975; decreased again to 1770 & 2109 in 1992 & 1995, respectively.	Quin (1989) Arundel et al. (1990) Coulson *et al.* (1999a)

Footnote: * Data for Maria Island as a whole; EGK were introduced to Darlington and subsequently colonised Point Lesueur.


100
80
60
40
20
0
%
7
5
13
10
Before
After
Females breeding
Adult females