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Kangaroos in peri-urban areas: A fool's paradise?

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Summary **Peri-urban Eastern Grey Kangaroo (*Macropus giganteus*) populations can reach very high densities in areas with remnant native vegetation and adequate pasture. This review summarizes the scientific evidence for the impacts of these high-density peri-urban populations, which predominantly involve threats to human life and livelihood (kangaroo–vehicle collisions), impacts on threatened species and ecosystems and declines in the health of individual kangaroos. The latter two impacts result from an imbalance between the kangaroo population and their food resources. We argue that urban infrastructure is a fundamental driver of many of these inter-related impacts through population fragmentation, isolation and direct mortality of kangaroos on roads. Roads may also act as barriers to movement, isolating populations and promoting this localized overabundance. However, not all peri-urban kangaroo populations attain high densities. Combined with the impacts of climate change on resource availability, peri-urban development has the capacity to push local populations towards extinction in actively urbanizing areas via the impacts of habitat loss and/or fragmentation and road mortality. The successful coexistence of people and kangaroos in these peri-urban environments therefore requires a better understanding of the impacts of urban infrastructure on kangaroo population dynamics, and a better policy framework to promote ecologically sensitive development.**

Key words: *macropod, road ecology, roadkill, urbanization, wildlife disease.*

Implications for Managers

- The long-term trajectory of peri-urban kangaroo populations varies between locations, with both localized overabundance and sustained population declines reported
- Both outcomes likely stem from habitat fragmentation and isolation of populations associated with infrastructure development
- Overabundant kangaroo populations have obvious impacts on people, biodiversity and individual kangaroo welfare, which may necessitate active management
- A stronger policy framework is required to ensure peri-urban developments provide adequate connectivity between kangaroo populations

Introduction

Australia has one of the highest rates of urbanization in the world, with 86% of the population living in urban areas (United Nations 2018). The Eastern Grey (*Macropus giganteus*) and Western Grey (*M. fuliginosus*) Kangaroo overlap with the main urban centres in Australia. The former covers the eastern seaboard and slopes of the Great Dividing Range, including the fringes of Brisbane, Sydney, Canberra, Melbourne and large regional centres (Coulson 2008a); the latter occupies southern Australia, including the outskirts of Adelaide and Perth (Coulson 2008b).

Although detailed ecological studies on peri-urban kangaroo populations are lacking, the management challenges created by urban expansion into kangaroo habitat are well-recognized, forming the subject of numerous reviews (Coulson 2001, 2007; Adderton Herbert 2004; Herbert 2007). These reviews have framed the justification for kangaroo management around Caughley's (1981) classification of problems arising when wildlife are considered overabundant:

1. Threats to human life or livelihood (e.g. kangaroo–vehicle collisions)
2. Depression of the density of another valued species (e.g. a threatened species)
3. Impact on individuals within the population themselves (e.g. poor body condition)
4. Loss of equilibrium between the wildlife population and its food resources

Previously, there was limited empirical data to quantify these four impacts in peri-urban kangaroo populations. Some research gaps have now been filled. Moreover, there has recently been a focus on the *conservation* of peri-urban kangaroo populations, reflecting concerns about

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Ecological Management & Restoration *Linking science and practice*

local extirpation in some areas (Brunton *et al*. 2018a,b). Hence, challenges are occurring at both ends of the management spectrum.

This paper aims to update the current challenges and advances in the biology of peri-urban kangaroo populations, focussing on Eastern Grey Kangaroo as the species that most frequently poses management challenges because of its distribution on the eastern seaboard. Specific aims are to: (i) review advances in knowledge of the biology of peri-urban kangaroo populations; (ii) review scientific evidence for the impacts of (or on) kangaroo populations in peri-urban areas; (iii) discuss the key management challenges associated with peri-urban kangaroo populations; and (iv) identify priorities for future research.

Defining *Peri-Urban* Kangaroo Populations

Previous reviews have emphasized different kangaroo management approaches in urban versus rural areas (Adderton Herbert 2004). Many urban challenges remain, and macropods have on occasion been reported within city centres, including a Swamp Wallaby (*Wallabia bicolor*) hopping across the Sydney Harbour Bridge (Clun 2018). However, kangaroo management issues are predominantly encountered within peri-urban, rather than urban, environments. The *peri-urban* environment forms a transitional zone between 'distinctly urban and unambiguously rural areas' (Simon 2008: 167). In some instances, peri-urban environments represent a temporal transition from rural or undeveloped land to higher density urban environments. In other cases, especially on the outskirts of large regional centres, peri-urban environments will persist over time.

Peri-urban kangaroo management is often viewed through the lens of human stakeholders, with these populations being seen as different from rural populations because the socio-political context drives different approaches to wildlife management (Adderton Herbert 2004). However, it is increasingly recognized that peri-urban populations also differ ecologically. The Eastern Grey Kangaroo occupies a variety of habitats throughout its range, with two key elements being necessary for its survival: shelter from sun, rain, wind and predators, and appropriate food and water sources (Coulson 2008a). The persistence of kangaroos in peri-urban environments will depend on the retention of these two key elements.

Advances in the Knowledge of Peri-Urban Kangaroo Populations

Recent advances in our knowledge of peri-urban kangaroo populations are divided into two main themes: (i) understanding the basic biology of peri-urban kangaroo populations; and (ii) quantifying the impacts of, and on, peri-urban kangaroo populations. Key peri-urban Eastern Grey Kangaroo populations that have been the subject of management and/or research, and their main attributes, are summarized in Table 1.

Biology of peri-urban kangaroo populations

Population densities and trends

Previous reviews focussed on the capacity for peri-urban kangaroo populations to reach high densities, particularly when enclosed (Adderton Herbert 2004). Recent research has reinforced this (Table 1) and highlighted that this phenomenon is not restricted to fenced populations. Populations in excess of five kangaroos per hectare are not uncommon, even in unfenced sites, such as Look At Me Now Headland in New South Wales (NSW; Table 1) and Jerrabomberra East Grassland in the Australian Capital Territory (ACT; Table 1). Conversely, the long-term persistence of some peri-urban populations is uncertain. Brunton *et al*. (2018b) reported a decline of peri-urban Eastern Grey Kangaroo populations in south-eastern Queensland, whilst other populations are similarly at risk of extirpation (Nelson Bay, NSW, Table 1).

Population demography and dynamics

Advances in our knowledge of the demography and dynamics of peri-urban kangaroo populations have predominantly come from long-term studies of marked individuals at Anglesea in Victoria (Coulson *et al*. 2014), and from live surveys and cull samples in the ACT. At these sites, approximately two-thirds of births occur within a three-month window, coinciding with the Austral summer: 66% of young from five reserves in the ACT were born in the 3 months from mid-November (Lucas *et al.* 2021) and 68% of young at Anglesea were born between November and January (Graeme Coulson, Jemma Cripps & Michelle Wilson, unpubl. data). Fecundity is generally high in both rural (Fletcher 2007) and peri-urban kangaroo populations in the ACT, with 54–88% of females at peri-urban parks observed carrying young in late September from 2016 to 2019 (ACT Government, unpubl. data). Fecundity was variable at Anglesea, with lower rates (38–39%) in two years (2008–2009) attributed to the 'millennium drought', followed by 70–76% in the subsequent four years (Coulson *et al*. 2014).

The key causes of mortality are difficult to ascertain in free-living populations. There is little information on age- and sex-specific mortality; however, it is thought that recruitment into populations is relatively low, despite high fecundity rates. At Anglesea, 46% of young tagged in the pouch disappeared from the population (Coulson *et al*. 2014), but it was not known whether they died or dispersed, nor the cause(s) of mortality. The Farrer Ridge Nature Reserve (ACT) population declined from 3.4 to 1.5 kangaroos per hectare between 2015 and 2019 without management intervention, despite high fecundity rates, usually over 80% (ACT Government, unpubl. data; Table 1).

Four longitudinal studies have reported high rates of road mortality for adult kangaroos (Table 2), with between 47% and 88% of known deaths attributed to vehicle collisions. Although these figures may be inflated by a detection bias, as animals hit by cars are more likely to be reported, vehicle collisions clearly represent an important cause of mortality for peri-urban populations.

High site fidelity by females is a common trait of peri-urban populations, with small home ranges reported at Sippy Downs, Queensland (Brunton *et al*.

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Table 1. Peri-urban Eastern Grey Kangaroo populations subject to active management and/or research

Location	Context	Boundary	Size (ha)	Population density [Year]	Population Trend	Management Issue†	Management Technique*	Reference
Mulligans Flat, ACT	Wildlife Sanctuary	Electrified, predator proof fence	485	0.8/ha [2013] 1.29/ha [2019]	High rate of increase maintaining above target densities	2, 3, 4	Culling	[1]
Mulanggari Grasslands, ACT	Urban grassland reserve	High speed roads, suburbs	161	0.71/ha [2008] Maintained at 1 – 1.6/ha [2014-2019]	Stable at target density	2, 4	Culling	[1]
Jerrabomberra East Grasslands, ACT	Urban grassland reserve	Rural properties, high speed roads, nature reserve	233-248	6.98/ha [2014] 3.44/ha [2019]	Immigration maintaining above target densities	1, 2, 4	Culling	[1]
Farrer Ridge, ACT	Urban woodland reserve	High speed roads, suburbs	202	3.07/ha [2007] 1.91/ha [2017] 2.30/ha [2020]	Fluctuating, but maintaining high densities	1, 2, 3, 4	None	[1]
Government House, ACT	Residence, formal and informal gardens	Partially fenced, lake	36 habitat (55 total)	0.33/ha [1983] 4.53/ha [1993] 1.58/ha [2020]	Increased, now stable at target density	1, 2	Culling and Fertility control	[2, 3]
Weston Park, ACT	Urban park	Suburbs, lake, urban parkland	68	1.10/ha [2015] 0.72/ha [2020]	Decreasing	1	Fertility control	[4]
Gold Creek Country Club, ACT	Golf course	Urban roads, suburbs, native bushland	50	2.16 [2015] 2.38 [2019]	Fluctuating	1	Fertility control trial	[4]
Nelson Bay, NSW	Golf course	Native vegetation, suburbs	64	3.4/ha [2012] 1.0/ha [2019]	Decreasing	1,3	Fertility control trial	[5]
Heritage Park, NSW	Suburban development	Motorway, native vegetation	415	1.2 to 1.5/ha [2016]	Increasing	1‡, 3	Fertility control trial	[6,7,8]
Look At Me Now Headland, NSW	Nature Reserve	Suburbs, nature reserve	24	5.0/ha [2018]	Increasing	3	Fertility control trial	[7,8,9]
Sippy Downs, Qld	University campus	Nature reserve, suburbs and road	217	0.39/ha [2010] 0.07/ha [2016]	Decreasing	1,3	None	[10]
Anglesea, Vic.	Golf course	Native vegetation, suburbs	73	4.9/ha [summer 2003/4] 2.0/ha [winter 2010]	Fluctuating	1,3	Fertility control trial	[11,12]
Serendip Sanctuary, Vic	Nature Reserve	Urban and rural properties	250	0.9/ha [2010] 4.5/ha [2016]	Fluctuating	1,3	Culling and fertility control	[13]
Gresswell Forest Reserve, Vic	Nature Reserve	Kangaroo-proof fence	53	4.6/ha (2013) 1.9/ha [2017]	Fluctuating	2,3,4	Universal fertility control	[13]
Woodlands Historic Park, Vic	Nature Reserve	Kangaroo-proof fence	235-400	2.9/ha [1996] 0.6/ha [1998]	Fluctuating	2,4	Fertility control trial, culling	[13]

ACT, Australian Capital Territory; NSW, New South Wales; Vic, Victoria; Qld, Queensland.

[1] ACT Government 2019b [2] Coulson 2001; [3] Government House, unpubl. data; [4] ACT Government, unpubl. data; [5] Catherine Herbert, Georgia Thomas, Phil Murray & Maquel Brandimartia, unpubl. data; [6] Henderson *et al*. 2018b; [7] Henderson *et al*. 2018a; [8] Catherine Herbert, Maquel Brandimarti & Fabiola Silva, unpubl. data; [9] Brandimarti *et al*. In Press; [10] Brunton *et al*. 2018a; [11] Coulson *et al*. 2014 [12] Inwood *et al*. 2008; [13] Wilson & Coulson 2021.

†1, Threats to human life/livelihood (vehicle collisions); 2, Depression of the density of a favoured species; 3, Impact on welfare of individual kangaroos; 4, Loss of equilibrium with food resources.

‡Vehicle collisions and attacks on people.

*Note that the management technique may not necessarily have been responsible for observed changes in the population density.

2018a) and similar observations at Anglesea (Coulson *et al*. 2014), Nelson Bay and Coffs Harbour in NSW (Herbert & Dassis, 2020; Catherine Herbert, Aaron Smith & Mariela Dassis, unpubl. data), and across urban reserves within the ACT (ACT Government, unpubl. data). The seasonal movement of males may vary more between populations. At Anglesea, males roamed throughout the town during the non-breeding season (Coulson *et al*. 2014). In Coffs Harbour, male Eastern Grey Kangaroos had relatively small (<70 ha) home ranges (Henderson *et al*. 2018b), although this may have been influenced by the short tracking duration (≤2 months). Green-Barber and Old (2018) reported larger ranges (~170 ha) for two males tracked for almost two years in Richmond NSW.

The extent to which the growth rates of peri-urban kangaroo populations are density dependent, through a decrease in fecundity and/or increase in mortality, is unclear. There is no real evidence of a density-dependent reduction in fecundity in peri-urban kangaroo populations (Coulson 2007), although the low fecundity rates at Anglesea in 2008/9 may reflect the combined effects of relatively high density (3.53/ha, Coulson *et al*. 2014) and drought. Kangaroo mortality may fluctuate with density (or *per capita* resource

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availability) in some peri-urban environments; however, densities tend to remain high and relatively stable over the long term, as seen in unmanaged reserves in the ACT (ACT Government 2019b). Any density-dependent effects are likely to be through increased death rates of juveniles, especially in the southern parts of the Eastern Grey Kangaroo range. Mass die-offs of juveniles, associated with limited food and high intestinal parasite burdens, have been reported in winter at Yan Yean, Victoria (Arundel *et al*. 1990) and in the ACT (Portas & Snape, 2018). Increased macropod–vehicle collisions have been reported during drought in rural environments (Coulson 1989; Lee *et al*. 2004) and may also contribute to mortality in periods of low resource availability in peri-urban areas.

Physiology and behaviour

Habituation is a common phenomenon in peri-urban areas, where wildlife and humans come into close and frequent contact (Lowry *et al*. 2013). Flight distance has been measured in rural kangaroos (Edwards *et al*. 2013), but there has been no systematic study of habituation in peri-urban settings. However, there is abundant anecdotal evidence of reduced flight initiation distances in peri-urban kangaroos. At Anglesea, for example, most kangaroos could be readily approached and captured on the golf course and nearby school camp, but newly arrived individuals were more wary (Coulson *et al*. 2014). There is also some evidence of kangaroos adapting to the peri-urban environment by modifying their activity patterns. Kangaroos became active earlier in the morning at a peri-urban site than at a more natural site (Green-Barber & Old, 2018), but data from additional sites are needed to confirm a general adaptive response.

The urban environment may also pose a challenge to wildlife and may alter the physiology of an individual through an increase in stress hormones (glucocorticoids). Peri-urban kangaroo populations had elevated stress hormone concentrations compared to rural populations in south-eastern Queensland, whilst the reverse was true in the ACT (Brunton *et al*. 2020). This may account for different population trends in peri-urban kangaroo populations across Australia, but further investigation over a broader range of sites is needed.

Impacts of/on peri-urban kangaroo populations

Evidence for the impacts of, and on, peri-urban kangaroo populations is framed within Caughley's (1981) classification for management problems.

Threats to human life or livelihood

Kangaroo–vehicle collisions. The animal welfare, human safety and economic impacts of kangaroo–vehicle collisions have been well-recognized for decades (Ramp & Roger, 2008; Ramp 2010; Bond & Jones, 2014) and the level of community concern about kangaroo–vehicle collisions is illustrated by the number of sites where this is identified as a key management issue (Table 1).

The economic costs of kangaroo–vehicle collisions are exemplified by insurance company statistics. The estimated total repair cost of kangaroo–vehicle collisions in Australia in 2016/17 was AUD28 million (Huddle 2019). In 2015, the estimated number of kangaroo–vehicle collisions in the ACT alone was 13,895 (Micromex Research 2015, reported in Gordon *et al*. 2021). These figures demonstrate the significant economic impact of kangaroo–vehicle collisions on property and are probably an underestimate of the true cost.

There is surprisingly little information on the rate of human injury and mortality from kangaroo–vehicle collisions. Two studies suggest that approximately 30% of reported macropod–vehicle collisions result in human injury (Coulson 1982; Ben-Ami 2005), and the rate of collisions with animals (mostly macropods) requiring hospital treatment is increasing (Ang *et al*. 2019). Human fatalities are thought to be uncommon (Ramp 2010), but 13 were reported from collisions with macropods in NSW between 1996 and 2005 (Ramp & Roger, 2008). These datasets demonstrate that kangaroo–vehicle collisions pose a definite risk to motorists, particularly motorcyclists (Byard 2020), including death. However, there are no comprehensive estimates of the economic cost of injuries, nor indication of the human fatality and serious injury rate from incidents involving kangaroos. This highlights the need for a better understanding of the factors associated with the risk of a kangaroo–vehicle collision.

There have been numerous studies on road design factors associated with kangaroo 'road-kill hotspots', but the majority have either been in rural areas (e.g. Coulson 1982, 1989, 1997; Ramp *et al*. 2005; Klocker *et al*. 2006) or over small spatial and/or temporal scales in peri-urban areas (e.g. Ramp *et al*. 2006; Green-Barber &

Table 2. Reported known causes of mortality in longitudinal studies of peri-urban Eastern Grey Kangaroo populations. Percentages indicate the fraction of known deaths attributed to each cause.

Site	Mortality	Study Type	Reference
Anglesea, Vic	Roadkill: 47% Other injury: 7% Predation: 5% [n = 78]	Tagged animals, citizen science & police reports	Coulson *et al*. (2014)
Sippy Downs, Qld	Roadkill: 73% Dog attack: 5% [n = 22]	Citizen science (local vet) reports	Brunton *et al*. (2018a)
Weston Park, ACT	Roadkill: 88% Misadventure: 6% Unknown: 6% [n = 17]	Tagged animals, fertility control trial	Claire Wimpenny & Lyn Hinds unpublished
Gold Creek Country Club, ACT	Roadkill: 76% Other injury or illness: 12% Unknown: 12% [n = 17]	Tagged animals, fertility control trial	Claire Wimpenny & Lyn Hinds unpublished

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Old, 2019). More recently, Visintin *et al*. (2016, 2017) modelled the risk of collision with Eastern Grey Kangaroo and Swamp Wallaby across Victoria, showing that collision risk was highest in areas of greatest macropod occurrence, but it is not clear whether there are differential factors associated with risk in rural versus peri-urban areas. Other factors, such as per capita resource availability, may also influence the rate of macropod–vehicle collisions. A comprehensive analysis of larger data sets from a range of peri-urban areas over larger geographical and temporal scales is clearly warranted, building on the approach of Dunne and Doran (2021) for ACT data.

Kangaroo attacks. Kangaroo attacks on people receive less attention than vehicle collisions, but their occurrence, or the perception of risk, is often cited as a key community concern (Coulson 2007; Ballard 2008). For example, the Coffs Harbour northern beaches region reported 40 attacks/serious threats within a 10-year period (Henderson *et al*. 2018b). The few studies on the movement patterns of kangaroos in peri-urban areas demonstrate that kangaroos readily utilize backyards, open spaces and recreational areas (Coulson *et al*. 2014; Brunton *et al*. 2018a; Henderson *et al*. 2018a,b), highlighting the spatial overlap and potential for conflict between people and kangaroos. Moreover, the partly diurnal behaviour of kangaroos frequently places them in contact with people (Henderson *et al*. 2018b), heightening the risk. There is a lack of appropriate reporting mechanisms for these incidents, and hence, actual rates of attacks and near-misses are likely to be under-reported.

Depression of the density of other valued species

High-density kangaroo populations have been associated with shifts in abundance of other species, predominantly exerted by high grazing pressure and consequent changes to grassland structure. The impacts of peri-urban kangaroos on conservation values are well documented in the ACT, where high-density populations coincide with critically endangered ecosystems within a network of peri-urban reserves (ACT Government 2019a). In these environments, kangaroo grazing pressure influences the assemblage of bird species, with differential impacts depending on the life-history traits of the species (Neave & Tanton, 1989; Howland *et al*. 2016b). Reptile abundance, diversity and species richness are also influenced by kangaroo grazing intensity (Manning *et al*. 2013; Howland *et al*. 2014). The best conservation outcomes for a threatened reptile species, the Striped Legless Lizard (*Delma impar*), are predicted to be associated with a kangaroo density of less than 1.3 kangaroos per hectare (Howland & Stojanovic, 2016a). Peri-urban Eastern Grey Kangaroo were implicated in two declines of endangered Eastern Barred Bandicoot (*Perameles gunnii*) at Woodlands Historic Park, Victoria (Coulson 2007; Coulson & Coetsee 2020). Whilst kangaroo grazing is recognized as an important disturbance mechanism to promote floristic diversity in grassy ecosystems, excessive grazing has also been associated with negative impacts on vegetation structure and composition in a range of conservation settings (Neave & Tanton, 1989; Lunt 1991; McIntyre & Stol, 2010).

Impact on individual kangaroos

Baseline health parameters. Brandimarti *et al*. (2020) published a comprehensive overview of blood parameters (haematological, glucose and serum protein) in healthy, free-range Eastern Grey Kangaroo from numerous sites throughout their range, including peri-urban populations. Blood parameters differed between juveniles and adults, but not sexes, yielding Reference Intervals for key blood parameters based on maturity. Site, rainfall, temperature and season all influenced blood parameters, highlighting the need to consider site-specific factors when evaluating kangaroo health. Previous studies involved only captive Eastern Grey Kangaroo (e.g. Vogelnest & Portas, 2008) or small sample sizes from a single site (e.g. Green-Barber *et al*. 2018). However, application of these Reference Intervals requires capture and blood collection, plus expensive laboratory analyses. Additional tools, such as a validated body condition index for live animals, would also be beneficial in assessing health status of peri-urban kangaroo populations.

Disease. Mass die-offs of sub-adult kangaroos (18-24 months of age) have been reported episodically since the 1970s (Coulson 2007), often attributed to the combined effects of low *per capita* food availability combined with decreased fat reserves, increased parasite burdens and low overnight temperatures (e.g. Portas & Snape, 2018).

Disease outbreaks associated with high kangaroo population density are not limited to sub-adults. Borland *et al*. (2012) reported a high prevalence (54%) of oral necrobacillosis ('lumpy jaw') in a high-density population of Eastern Grey Kangaroo on sparse, dry pasture at Serendip Sanctuary, Victoria. Infections were more prevalent in older animals, often associated with clinical evidence of malnutrition. Lumpy jaw is considered a disease of captivity, but the high prevalence at Serendip Sanctuary was associated with drought, limited pasture biomass and heavy faecal contamination when population density was high (3/ha) (Borland *et al*. 2012).

Widespread ill-health and disease have also been reported in a peri-urban Eastern Grey Kangaroo population in the Coffs Harbour region (NSW). High population density (>5/ha) was associated with widespread disease (parasitism and non-regenerative anaemia) and nutritional deficiencies in all age and sex categories (Brandimarti *et al*. 2021). At the same time, kangaroo grazing caused a significant reduction in grass height (Hunter & Hunter 2019), coinciding with a period of limited rainfall (Brandimarti *et al*. 2021). Mass die-offs of sub-adult kangaroos have not occurred in this population, perhaps related to the higher night-time minimum temperatures, compared with die-offs reported in the ACT and Victoria.

Morbidity related to motor vehicle collisions. Kangaroo–vehicle collisions

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clearly pose a threat to the health and welfare of kangaroos injured but not killed by the impact (Bond & Jones 2014). Some authors suggest that up to 9 million macropods are killed throughout Australia per annum (Burgin & Brainwood 2008), but it is not known how many of these animals die instantaneously versus those that later die on the roadside. ACT statistics give some indication of scale: approximately half of the 2,609 ranger call-outs for kangaroos in the 12 months from 1st July 2019 were for injured animals requiring active euthanasia by staff (ACT Government, unpubl. data).

Loss of equilibrium between kangaroos and their food resources

The loss of equilibrium between high-density kangaroo populations and their food resources is inherent in the ill-health and disease described above, as well as the impacts on biodiversity. Mass die-offs of sub-adults have been linked to malnutrition, as have the cases of population-level disease in adults. High kangaroo densities have been negatively correlated with herbage mass in grassy ecosystems in the ACT (McIntyre & Stol, 2010; Howland *et al.* 2014). Experimental manipulations of kangaroo density (McIntyre *et al.* 2014) and grazing exclosures (e.g. Hunter & Hunter 2019) further demonstrate the causative relationship between these variables. Drought and kangaroo grazing often work synergistically to reduce pasture biomass. Long-term climate has an overriding role in driving plant production in more temperate regions (McIntyre *et al.* 2014), and more broadly throughout much of the Eastern Grey Kangaroo range (Robertson, 1987), with significant implications for kangaroo grazing dynamics (Snape *et al.* 2021). Current management of many ACT conservation reserves aims to maintain kangaroo density at a threshold to maintain grassland biomass and minimize risks to endangered ecosystems (ACT Government 2017; Gordon *et al.* 2021), for example Mulligans Flat, Mulanggari Grasslands and Jerrabomberra East Nature Reserves (Table 1).

Discussion

Kangaroos – a matrix-occupying species

Wildlife can be classified according to their ability to survive within urban areas, and the extent of their dependence on habitat fragments: *matrix-occupying* (can occur throughout urban areas), *matrix sensitive* (persist only in habitat fragments within urban areas) and *urban sensitive* (cannot persist in urban areas at all) (Garden *et al.* 2006). Coulson *et al.* (2014) concluded that the kangaroos of Anglesea were *matrix-occupying*, and similar observations have been made in the ACT (ACT Government 2017), Coffs Harbour (Henderson *et al.* 2018b) and South-east Queensland (Brunton *et al.* 2018b), where kangaroos occupy a mosaic of grey and green space. Kangaroos clearly can survive and thrive in some peri-urban environments, but not all. The persistence of kangaroos may be dependent on remnant natural vegetation interwoven with urban development (Brunton *et al.* 2018b). Given the disparate population trends observed in some peri-urban areas, further research is warranted to clearly establish the factors necessary to ensure the survival of Eastern Grey Kangaroo populations in rapidly urbanizing environments.

The paradox of roads

Roads are clearly one of the fundamental challenges for peri-urban kangaroo management, although the effect of motor vehicle collisions at the population level is uncertain. Roadkill is clearly one of the principal causes for mortality in peri-urban populations (Table 2) and is probably linked to the decline and potential extirpation of some populations (Brunton *et al.* 2018a). Other populations are able to sustain high roadkill rates but remain stable or even increase.

Roads also fragment landscapes, acting as barriers to movement and dispersal, thereby isolating populations (Taylor & Goldingay, 2010). Whether this is the case for kangaroo populations is unclear, as there have been no explicit studies of roads as barriers to kangaroo movement or gene flow. Henderson *et al.* (2018b) demonstrated that GPS-collared male kangaroos did not cross a large motorway in a peri-urban area near Coffs Harbour, so it is likely that major roads, at least, are a barrier to kangaroo movement. Major road projects frequently incorporate wildlife barrier fencing, directing animals to safe crossing locations (over- or underpasses), with the intention of reducing wildlife–vehicle collisions (Taylor & Goldingay, 2003). Although there are some reports of kangaroos using road underpasses (Chachelle *et al.* 2016), there is little evidence of their effectiveness at the population level, in terms of maintaining adequate connectivity for regular movement, dispersal and gene flow. Fencing may exacerbate the barrier effects of roads, contributing further to localized overgrazing, overabundance and ill-health, potentially creating a more substantial welfare issue than the initial problem of road mortality. However, fragmentation of habitat by roads or other barriers within the peri-urban matrix also enables localized management targets to be met, at least at some sites (e.g. ACT Government 2017), by delineating individual 'kangaroo management units' (Gordon *et al.* 2021).

The potential downward spiral of ill-health in peri-urban kangaroo populations

The health and welfare of kangaroos and their environment can be compromised in peri-urban areas under certain conditions. We propose that poor health and welfare outcomes are more likely from the combined effects of roads and habitat fragmentation isolating populations, limiting opportunities for dispersal and prolonging high densities. In some, but not all, populations, high densities are unsustainable, causing an imbalance between the population and its food resources, leading to ecosystem degradation and poor animal welfare (summarized in Fig. 1). Declining kangaroo condition may manifest as mass die-offs of sub-adults (by starvation or disease), particularly during winter in more temperate environments, or higher prevalence of disease across age groups. These impacts are exacerbated by drought. It is not

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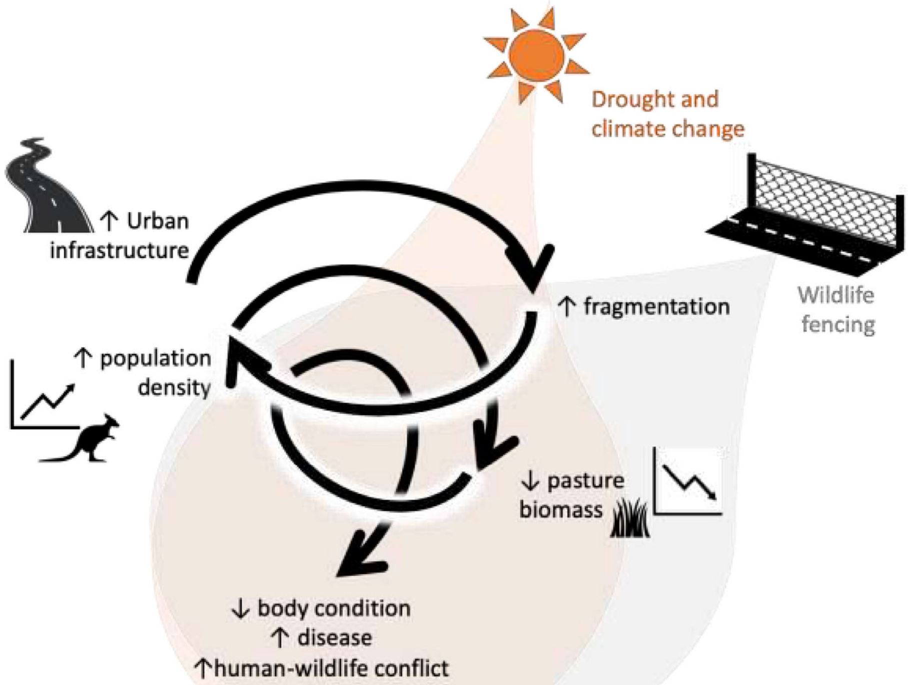

Figure 1. The hypothesized 'downward spiral to ill-health' observed in some peri-urban kangaroo populations, brought about by fragmentation and isolation of populations, artificially elevating density and the severity of localized impacts. These effects are exacerbated by the magnifying effects of drought and climate change, and 'restorative measures' such as the installation of wildlife exclusion fencing. Not all populations progress to the bottom of the spiral, and the reason behind these differential population responses is currently unknown.

entirely clear why some peri-urban kangaroo populations succumb to these effects whereas others do not. Nor is it clear to what extent this is an issue specific to peri-urban populations, as die-offs are also reported on rural land (Portas & Snape, 2018; Wilson & Coulson 2021). Mass mortality is likely to be more obvious in peri-urban areas, because of greater visibility of carcasses and a lower density of predators and scavenging animals.

Further human modifications to the environment, such as the construction of roads, houses, and wildlife exclusion fencing, are likely to exacerbate population fragmentation and amplify these effects in peri-urban areas. The maintenance of adequate green spaces and landscape connectivity in peri-urban areas probably minimizes the likelihood of this downward spiral, as evidenced by the long-term stability of a number of peri-urban populations at relatively high densities (e.g. Anglesea, Jerrabomberra East Grassland, Table 1). Given the significant investments that have been made in wildlife exclusion fencing along major roads in south-eastern Australia, connectivity may become a significant issue for many peri-urban kangaroo populations. Further research on the effectiveness of underpasses and overpasses, with or without barrier fencing, is warranted.

Conclusions

The last two decades have seen advances in our knowledge of the ecological processes operating in peri-urban kangaroo populations, which is an important step in providing an evidence-based framework for evaluating management options. Management challenges are found at both ends of the wildlife management spectrum. Kangaroo–vehicle collisions pose a significant impact on both humans and kangaroos, but we still lack data on population-level effects and appropriate mitigation strategies. We hypothesize that road infrastructure likely contributes to both the decline of some peri-urban populations, and paradoxically, the unsustainably high densities seen in other areas (Fig. 1), through population fragmentation and isolation. Superimposed on this is the over-riding influence of drought and climate change, affecting pasture biomass, and exacerbating the imbalance between the high kangaroo densities and their food resource. In regions where there is insufficient remnant wooded vegetation, urbanization may drive the local extirpation of kangaroo populations. Further research is required to evaluate these hypotheses. If kangaroos are a desired element of the biophysical environment in peri-urban areas, infrastructure development needs to incorporate adequate green space and wildlife movement corridors within a policy framework of ecologically sensitive development.

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