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WILDLIFE RESEARCH

Implementing implants: delivery efficiency, contraceptive efficacy and population outcomes in two overabundant kangaroo populations

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ABSTRACT

Context. Overabundant native wildlife can pose serious challenges for managers. The most direct, immediate way to reduce density-dependent impacts is by culling, but lethal control often lacks public support. Fertility control offers a non-lethal management alternative. **Aims.** We conducted two fertility-control projects on eastern grey kangaroos (*Macropus giganteus*), a common and widespread species in Australia. We aimed to evaluate three key components of an integrated fertility-control project, namely, delivery efficiency, contraceptive efficacy and population-level outcomes. **Methods.** The two study sites on the urban fringe of Melbourne, Australia, were small reserves. Both had undergone an irruptive peak and subsequent crash, with negative impacts on animal health. Gresswell Forest (52 ha) is open forest habitat enclosed by a kangaroo-proof fence. Serendip Sanctuary (250 ha) is grassy woodland and retired pasture, with a boundary allowing kangaroo movement onto neighbouring properties. We captured kangaroos with a dart gun at night and treated all healthy adult females with subdermal levonorgestrel implants. **Key results.** Delivery efficiency (catch-per-unit effort) was greater from a vehicle at Serendip Sanctuary than on foot at Gresswell Forest, with only a marginal decline over successive nights at both sites. Background fecundity was 91% at Serendip Sanctuary, but close to zero at Gresswell Forest. Treatment efficacy was high, being 86–100% infertility at Serendip Sanctuary and 96–100% at Gresswell Forest. At Serendip Sanctuary, the proportion of females treated never reached 75%, whereas only one female at Gresswell Forest remained untreated after 3 years. Population density at Serendip Sanctuary exceeded the target range 3 years after culling and fertility control. No culling occurred at Gresswell Forest, but fertility control apparently held population density at a moderate level, albeit much higher than the density target. **Conclusions.** Future management at Serendip Sanctuary and Gresswell Forest will require a sustained fertility-control effort. Further culling may also be required to complement fertility control at Serendip Sanctuary, the larger, open site. **Implications.** Contraceptive efficacy of levonorgestrel is high in kangaroos and implants can be delivered efficiently, but achieving control of a large, open population will be challenging.

Keywords: catch-per-unit effort, culling, fecundity, fertility control, kangaroo, levonorgestrel, overabundance, recruitment, reproduction.

Introduction

Overabundance of native wildlife has long been recognised as a multi-dimensional problem, with potential impacts on agricultural production, ecosystem function, biodiversity conservation, zoonotic diseases, and animal and human welfare (Caughley 1981; Wagner and Seal 1992). These impacts are usually managed by reducing population density, although the relationship between density and impact is rarely a simple, linear function (Norbury *et al.* 2015). The most direct and immediate way to reduce abundance is to cull animals from the population. However, while exotic pest species are routinely culled by lethal means, such as trapping and poisoning (e.g. Elliott and Kemp 2016; Martin and Lea 2020), public support is

Collection: Fertility Control for Wildlife in the 21st Century often lacking for lethal control of native species (van Eeden *et al.* 2020; Drijfhout *et al.* 2022), particularly in conservation reserves (e.g. Martínez-Jauregui *et al.* 2020). Translocation is an appealing alternative for those opposed to lethal control, but the impacts on source and recipient sites and the fate of animals is rarely monitored; the few monitoring studies show that translocated animals often experience poor welfare outcomes (Massei *et al.* 2010; Germano *et al.* 2015; Bradley *et al.* 2022).

Fertility control offers an alternative, non-lethal approach for managing overabundant populations. There have been many developments in this rapidly growing field, beginning with surgical and chemical sterilisation, then more advanced reproductive technologies based on synthetic hormones and, more recently, immunocontraceptive vaccines (Massei and Cowan 2014; Cohn and Kirkpatrick 2015; Asa and Moresco 2019). Despite these biotechnological advances, the uptake of fertility control in wildlife has been slowed by regulatory barriers and inadequate delivery methods (Cohn and Kirkpatrick 2015; Asa and Moresco 2019). Another key consideration is that fertility control acts only on fecundity, so does not reduce abundance instantaneously, and compensatory changes can occur in other vital rates and aspects of behaviour, slowing the effects of reduced fecundity. Consequently, a high proportion of the population may have to be treated to achieve a desired level of abundance (Hone 2004; Ransom *et al.* 2014). To determine the suitability of fertility control for a specific overabundance context, Massei and Cowan (2014) proposed a decision framework with multiple elements for consideration, including public consultation, contraceptive method, field delivery method, potential animal-welfare issues, population responses, budget and timeframe, and program sustainability in the long term.

Kangaroos (*Macropus* spp. and *Osphranter* sp.) are iconic wildlife species and are common and widespread in Australia. They can be overabundant in many situations, resulting in negative impacts on biodiversity values, agricultural production, human health and amenity, as well as welfare of the kangaroos themselves (Coulson 2001, 2007; Descovich *et al.* 2016; Read *et al.* 2021). While the need for kangaroo management is generally understood by the Australian public, the acceptability of lethal control varies widely across Australian society, farmers being the mostly likely to support kangaroo culling (Sinclair *et al.* 2019; van Eeden *et al.* 2019; Drijfhout *et al.* 2020; Boulet *et al.* 2021). Of non-lethal options, translocation and fertility control are generally supported for kangaroo management (Drijfhout *et al.* 2020). Only two translocations of kangaroos have been adequately monitored and documented; both recorded low survival and high dispersal rates after release (Higginbottom and Page 2010; Cowan *et al.* 2020; Thompson *et al.* 2023), suggesting that translocation is not an effective or humane option for kangaroo management.

Fertility control has been under investigation for decades as a non-lethal alternative for kangaroo management. Surgical sterilisation by castration, vasectomy or ovariectomy has been applied to isolated populations (Coulson 2001; Tribe *et al.* 2014; Colgan and Green 2018; Colgan *et al.* 2019). However, synthetic hormones and immunocontraception have been the subject of most research effort, all targeting female kangaroos (Wimpenny *et al.* 2021). Deslorelin, a synthetic GnRH agonist implant, is easily administered, but a single dose gives only 1–2 years of infertility (Herbert *et al.* 2006; Wilson and Coulson 2016). Levonorgestrel, a synthetic gestagen implant, requires minor surgery, but gives at least 7 years of infertility (Coulson *et al.* 2008; Wilson and Coulson 2016). GonaCon, a GNRH-specific immunocontraceptive, can be injected by hand or dart and also gives at least 7 years of infertility (Wimpenny and Hinds 2018), but is not yet commercially available in Australia. Of these alternatives, we used levonorgestrel implants for long-term fertility control of two free-ranging kangaroo populations. We evaluated three of the critical components of a fertility-control program identified by Massei and Cowan (2014): (1) delivery efficiency, measured in terms of catch-effort; (2) contraceptive efficacy, measured as length of action; (3) population-level outcomes, measured as proportion of females treated and population density over time.

Study sites

We conducted this study at two peri-urban reserves in Victoria, Australia. Both sites were managed by Parks Victoria, the state agency responsible for national parks and nature conservation reserves, and both supported populations of eastern grey kangaroos (*Macropus giganteus*) that had displayed one or more symptoms of overabundance (*sensu* Caughley 1981) prior to our research project (Wilson and Coulson 2021).

Gresswell Forest

Gresswell Forest Nature Conservation Reserve (37°42.70′S, 145°4.33′E) is located 14 km north-east of the Central Business District (CBD) of Melbourne, the state capital of Victoria (Fig. 1). Gresswell Forest is 52 ha in area and irregular in shape. It is enclosed by a 1.8-m chain-mesh security fence, which forms an effective barrier to kangaroo movement, and is completely surrounded by medium-density housing. The vegetation of the reserve is a remnant open forest dominated by river red gums (*Eucalyptus camaldulensis*), with shrubby patches dominated by *Acacia* spp. The reserve has a network of walking tracks, which are open to the public at all times.

La Trobe University conducted annual surveys of the kangaroo population from 2011 to 2019 as a student practical exercise. Three student classes independently surveyed the reserve up to a month apart, using the sweep-count method, which is well suited to this small, closed reserve (Coulson *et al.* 2021). However, errors arose in most years when breaks occurred in the line of counters, so affected counts were

Fig. 1. The locations of the two study sites, Gresswell Forest Nature Conservation Reserve and Serendip Sanctuary, in relation to the Central Business District (CBD) of Melbourne, Victoria, Australia. Insets show the vegetation canopy cover and surrounding land use of each study site. Imagery – Google Earth.

discarded and the means of the other two counts were taken as the annual population estimates. The coefficient of variation of these replicate counts ranged from 0% in 2013 and 2018 to 13% in 2019, when only one count worked smoothly. On the basis of these surveys, the population underwent an irruption sequence (Wilson and Coulson 2021), reaching a peak of 4.6 kangaroos per hectare in 2013, followed by a crash to 2.4 ha^{-1} in 2014 (Fig. 2). An implausible rise to 3.7 ha^{-1} in 2015 was followed by a further decline to 1.9 ha^{-1} in 2016 (Fig. 2). In October 2015, Parks Victoria advised residents of neighbouring properties of a plan to cull of an initial cull of 50 kangaroos to improve animal welfare and habitat condition. This was to be followed by fertility control of 25 females and a second cull of about 100 kangaroos to reduce abundance to a density target of 0.5 ha^{-1}. However, the planned cull generated strong public opposition, so Parks Victoria first postponed and eventually abandoned the plan, then commissioned the fertility-control program that forms part of this study.

Serendip Sanctuary

Serendip Sanctuary (38°0.15′S, 144°24.60′E) is located 52 km south-west of the Melbourne CBD (Fig. 1). The sanctuary is 250 ha in area and square in shape. It is bounded by standard stock fencing, which kangaroos can readily cross, and by roads on all sides. Neighbouring properties are low-density residential 'hobby farms' to the east and south, and commercial cropland on the other two sides. The sanctuary has captive-breeding programs for threatened species, education programs for schools, and walk-though enclosures and picnic facilities for the general public. It is open daily from 08:00 to 16:00 hours. The sanctuary has remnant patches of river red gum woodland and ephemeral wetlands. As a former sheep farm, the sanctuary provides a permanent water supply in stock troughs, and abundant forage in cleared areas of improved pasture, although a revegetation program has progressively reduced their area and productivity.

Parks Victoria has surveyed the kangaroo population sporadically since 1995. The surveys were conducted by Parks Victoria staff and volunteers, using a variation of the sweep count method (Coulson *et al*. 2021). The reserve was divided into four habitat blocks; a line of counters surveyed each block before reassembling at the next one, with observers posted at strategic points to record any kangaroos moving between blocks. These composite counts were not replicated. On the basis of these surveys, the population underwent an irruption sequence as it rose from 3.0/ha in 2002 to a peak of 4.5 in 2006, then fell to 2.6 by early

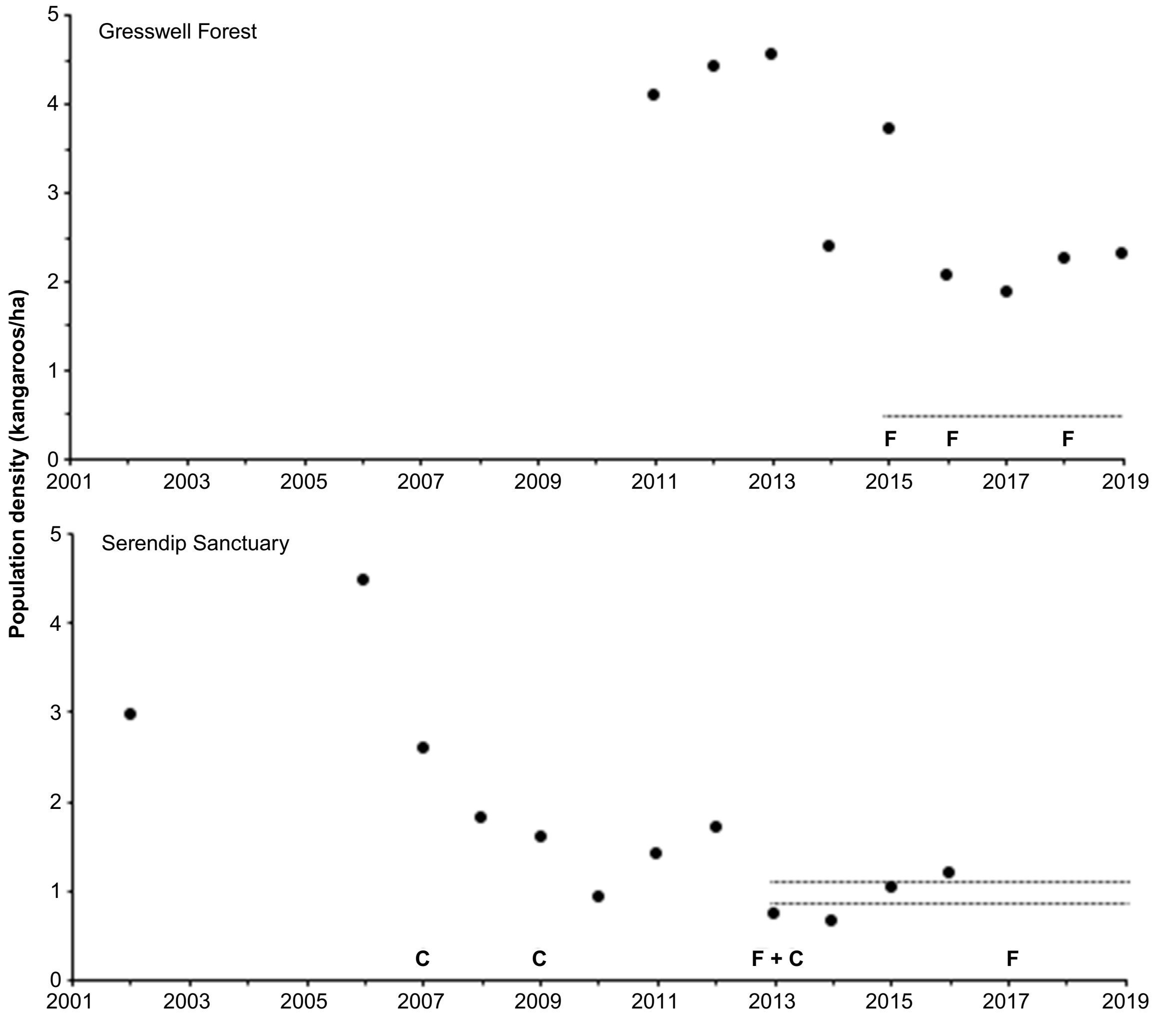

Fig. 2. Population trajectory at Gresswell Forest and Serendip Sanctuary, showing years when surveys of density (circles), fertility control (F) and culling (C) occurred. Population-density data were sourced from La Trobe University for Gresswell Forest and from Parks Victoria for Serendip Sanctuary. Dotted lines show Parks Victoria's target density for each site as a single value for Gresswell Forest and upper and lower limits for Serendip Sanctuary.

2007 (Fig. 2) and was subsequently culled to lower levels (Wilson and Coulson 2021). Deaths during the population crash were attributed mostly to malnutrition and roadkill, but there was also an extremely high prevalence (45%) of 'lumpy jaw' disease (Borland *et al*. 2011). There was some public opposition to culling at Serendip Sanctuary, but nearby residents also voiced concern about the frequent collisions with kangaroos on the surrounding roads. Parks Victoria set a target of 150–200 kangaroos (0.8–1.1/ha) and adopted a combined program of culling and fertility control, which forms part of this study.

Materials and methods

This study had two components: initial capture and treatment of adult female kangaroos, and subsequent monitoring of their reproductive status and proportion in the population. At Gresswell Forest, we captured and treated kangaroos in November 2015, October 2016 and October 2018, and monitored them in 2017, 2018 and 2019 (Table 1). At Serendip Sanctuary, we captured and treated kangaroos in April 2013, which was followed by a cull in May 2013, when only males and untreated females were shot (Table 1). We captured and treated more kangaroos in June 2017 (Table 1). We monitored the population annually from 2014 to 2019, except 2017 (Table 1). Further monitoring was curtailed by prolonged Covid-19 restrictions in Greater Melbourne.

Capture

We captured all kangaroos by tranquilliser darting, sometimes in evening twilight but mostly after dark. Gresswell Forest remained open to the public during the capture and treatment

Table 1. The number of females treated, the proportion of levonorgestrel-treated females breeding (count in brackets) and the mean (±s.e.) proportion of all females that were levonorgestrel-treated each year at Gresswell Forest and Serendip Sanctuary.

	Gresswell Forest			Serendip Sanctuary		
Year	Number treated	% breeding (*N*)	% of all females	Number treated	% breeding (*N*)	% of all females
2013				75		
2014					2 (59)	73 ± 4
2015	30				0 (65)	60 ± 1
2016	26				0 (59)	56 ± 1
2017		14 (47)	89 ± 2	45		
2018	5	8 (52)	84 ± 2		4 (48)	74 ± 2
2019		0 (43)	97 ± 2		0 (37)	69 ± 3

operation, but warning signs were posted at the entrances to the reserve. The capture team operated on foot at Gresswell Forest, walking along the internal tracks to locate kangaroos with the aid of LED head torches at night. Serendip Sanctuary was closed to the public after hours as usual. The team darted from an elevated shooting platform on the tray of a four-wheel-drive utility vehicle at Serendip Sanctuary, driving along service roads and across paddocks to locate kangaroos, using a 100-W spotlight to detect eyeshine and illuminate targets at night. At both sites, the dart operator used a Pneu Dart X-Caliber dart gun fitted with a riflescope for greater accuracy. The gun was powered by 12-g CO_2 cylinders to project a Pneu Dart (Type P, 1 or 2 mL capacity, 3/4″ needle, 13 gauge), with adjustable pressure according to the distance and the size of the target animals, which were adult females.

Our point of aim was the large muscle mass of the upper hind limb (Roberts *et al.* 2010). The darts injected Zoletil 100 (1:1 Zolezapam and Tiletamine, Virbac, Milperra, NSW, Australia) at a dose rate of 5 mg/kg of estimated bodyweight. For the safety of the animals and personnel, we darted kangaroos only in open areas, away from hazards such as water bodies, fences and rough ground, as well as members of the public. We never pursued a target animal or pushed it into a corner. Instead, we approached the target slowly on foot or in the vehicle, moving cautiously into a position to take a shot safely. Although the dart gun had a range of over 50 m, we operated from a range of 20–30 m whenever possible.

The dart operator was accompanied by a spotter, who assisted in locating target animals, estimated bodyweight, measured the range with a laser range-finder, observed the path of the dart through binoculars, retrieved any darts that missed, monitored the movements and demeanour of the target animal after a successful shot, and recorded the outcome (hit/miss), point of impact and time to recumbency. The driver performed these roles at Serendip Sanctuary and a second spotter operated the spotlight alongside the dart operator on the rear platform. We also recorded the duration of the capture effort per night, including short meal and toilet breaks, from first departure to search for kangaroos to the last return from releasing kangaroos at the end of the night.

If the shot missed, we approached again and took a second shot if the kangaroo remained in range. Following a successful shot, we usually withdrew a short distance but kept the kangaroo under continuous observation and guarded it from any disturbance by potential predators or aggressive kangaroos until recumbent and approachable. If a kangaroo was not recumbent after 10 min, we attempted a second shot if the kangaroo was in range. If a kangaroo became recumbent, but not sufficiently sedated, we approached quietly on foot and gave an intra-muscular injection of Zoletil (1 mL) by pole syringe (King *et al.* 2011), or by hand-syringe if possible, applying manual restraint to the kangaroo if necessary. At Gresswell Forest, we either carried sedated female kangaroos to a central processing area in a wheelbarrow or called for a vehicle to collect kangaroos if further away. When a young male kangaroo was darted in error, we left it to recover in a secure location nearby. At Serendip Sanctuary, we loaded one or two sedated kangaroos, regardless of sex, onto the tray of the vehicle and drove back to the central processing area.

Catch-per-unit effort

Catch-per-unit effort is analogous to the functional response of a predator (Van Deelen and Etter 2003), so can be broken into search time and handling time. We recorded search time, which included travel from the clinic to open foraging areas, identification of a target animal and approaching within darting range. We then recorded handling time, which included darting, induction time, locating and retrieving recumbent kangaroos, and return to the clinic. We did not include the time involved in examination, marking and treatment of the kangaroos, which were completed by another team.

Treatment

We established a central field clinic for the treatment team (the implanter and assistant) to process kangaroos under shelter at each site. We set up an operating table under a marquee at Gresswell Forest, and had a similar arrangement under the porch of a building at Serendip Sanctuary. Both clinics were equipped with floodlights for working at night. Once a kangaroo had been delivered to the clinic, the treatment team conducted a general health examination, including assessment of eyes, mouth and pelage, and palpated the mandibles and maxillae for lesions indicative of 'lumpy jaw'. The team also examined pouches, classifying females with everted teats as adults (Poole and Catling 1974) and recording the presence of any young. We used a captive bolt pistol to euthanise any kangaroos judged unsuitable for fertility-control treatment, because they had 'lumpy' jaw' or a serious injury, or were in very poor body condition. At Serendip Sanctuary, we also euthanised young male kangaroos that were darted in error, using the captive bolt pistol, since the culling component of the program started soon after fertility control.

Kangaroos remained sedated and anesthetised for up to an hour after darting, but we gave top-up doses of Zoletil, usually half of the original dose, if required. The implanter made a 3–5-mm incision between the shoulder blades under local anaesthesia (Lignocaine, 20 mg mL^{-1}; Mavlab, Slacks Creek, Qld, Australia) and inserted levonorgestrel implants subcutaneously, as described by Wilson *et al.* (2013), except that we administered five 55-mg implants (Elorn Projects, Gold Coast, Qld, Australia). The incision was then closed with absorbable sutures (J663-h; Johnson and Johnson Medical, Sydney, NSW, Australia), the site was dusted with antibiotic powder (Tricin, Jurox, Rutherford, NSW, Australia), and the female was given a prophylactic intra-muscular dose of antibiotic (Duplocillin, 0.1 mg kg^{-1}, Intervet, Bendigo, Vic. Australia).

We then marked each kangaroo with a paired colour combination of Allflex 'mini' self-piercing swivel ear-tags, which are 52×17 mm in size and weigh 8 g. We dipped the tip of the tag in 70% ethanol and allowed it to air dry before positioning it low in the ear, avoiding cartilage and major blood vessels. The tags were labelled with the kangaroo's ID number by using a permanent tag-marking pen and also bore adhesive reflectors in matching colours to enhance identification by artificial light at night. Sixteen of the kangaroos at Serendip Sanctuary had previously been captured and marked in the same way for studies on efficacy of fertility control agents and costs of reproduction (Cripps *et al.* 2011; Gélin *et al.* 2015; Wilson and Coulson 2016); we treated these females again. In April 2013, we also fitted each kangaroo captured at Serendip Sanctuary with a narrow (15 mm) collar made of a flexible, white PVC material with white adhesive reflectors, and fastened by ratchet rivets with a smooth, rounded profile. These collars typically fell off within a few weeks. They were designed to provide additional, short-term marking to ensure that treated kangaroos were readily identifiable, so they would not be shot by mistake during a cull in the following month. We chose to treat kangaroos prior to the cull to maximise the number of adult females available for capture.

After treatment and marking, we transported each kangaroo to a sheltered release site, away from hazards. There is no reversal agent for Zoletil and recovery can be prolonged, so we spaced kangaroos well apart to minimise the risk of them disturbing each other while recovering. At Gresswell Forest, members of either the capture or treatment transported each kangaroo to its release site in a wheelbarrow. To save time and disturbance at Serendip Sanctuary, a third team (a driver and assistant) used another vehicle to transport kangaroos, often two at a time, to a release area well away from likely capture sites. To further reduce disturbance, we did not monitor recovery during the night, but checked the release area the following morning to confirm that each kangaroo had recovered.

Monitoring

We monitored the efficacy and intensity of fertility-control treatment at Gresswell Forest annually from 2017 to 2019 (Table 1). We searched for kangaroos in the reserve on 4 days from September to November in 2017, 3 days from August to September in 2018 and 4 days from September to November in 2019. Eastern grey kangaroos breed seasonally in southern Victoria, with a peak in January (Quin 1989; MacKay *et al.* 2018), and the resulting young remain in the pouch for about 10 months (Poole 1975), so would be evident as a bulge in the pouch the following winter and spring. We searched in the 2-h period before sunset, when eastern grey kangaroos are more visible as they become active and congregate in open foraging areas (Southwell 1987; Clarke *et al.* 1995). On each search, we walked a zig-zag route along the network of internal paths, so that we covered most of the site. Whenever we encountered a kangaroo, we examined it with the aid of binoculars (12×32; Saxon, Australia) and recorded its sex–age class and reproductive status of females (*sensu* Jaremovic and Croft 1991), and its individual identity if a tagged female. We also assessed its general health in terms of body condition (under-weight, prominent bones, wasted muscles, dull or scruffy coat), mobility (reluctance to hop, stiffness, lameness, shortened or uneven stride, inability to keep up) and 'lumpy jaw' (bulbous lesions around mouth, excessive salivation, reduced foraging). These observations were supplemented by incidental sighting made during capture and release activities.

Annual monitoring of the efficacy and intensity of fertility control at Serendip Sanctuary followed a similar procedure. We searched the sanctuary on 3 days in September 2014, 3 days in August 2015, 3 days in August 2016, 4 days in August 2018 and 3 days in September 2019 (Table 1). We searched in the 2-h period before sunset each year, and also in the 2-h period after sunset in 2014 and 2018, using a 100-W spotlight to detect kangaroos in the dark. We searched for kangaroos from a four-wheel-drive vehicle, driving along service roads and across paddocks, examining kangaroos with the aid of binoculars (12×32; Saxon, Australia) and a spotting telescope (×20–60; Kowa, Japan). Before sunset, we recorded age–sex class, reproductive status of females, identity of tagged females and general health, as above. After sunset, we searched only for tagged females to determine their identity and reproductive status. We also received some reports of tagged kangaroos in paddocks between Serendip Sanctuary and You Yangs National Park (3 km further north), so searched the area several times but were unable to determine their identity or reproductive status.

Results

Catch-per-unit effort

We fired a total of 100 shots over the three capture periods at Gresswell Forest and 205 shots at Serendip Sanctuary. The outcomes of these shots were similar at the two study sites (Table 2), although the miss rate was higher at Serendip Sanctuary and the outcome of another 3% of shots there could not be determined. At each site, a small proportion of shots delivered only a partial dose (Table 2), usually because they hit a body part with little muscle, such as a foot or tail. A similar proportion of shots apparently injected fully, but the kangaroo hopped rapidly out of view and, although it was probably recumbent, could not be found (Table 2). Some shots were our second attempt at the same kangaroo after a miss or partial injection, and we manually injected some kangaroos after partial injections by dart (Table 2). When a dart hit the target area as intended, the kangaroo usually became recumbent, although we could not always see it fall if it moved out of sight. Induction time to recumbency that we observed ranged from 1 to 13 min, with a mean (±s.e.) of 4.1 ± 1.6 min and no difference between the two sites ($t_{150} = 0.569$, $P = 0.570$, 2-tail).

At Gresswell Forest, we captured 63 individual female kangaroos: 10 subadults and 53 adults. We also captured 11 males in error and recaptured four females to replace their implants. We euthanised two females: one had an untreatable dart injury (fractured femur) and the other was severely emaciated. At Serendip Sanctuary, we captured 132 individual females, which were all adults, as well as 14 males. We euthanised all of the males and 11 of the females: nine females had 'lumpy jaw' lesions and two were in very poor condition. Two other females did not recover after release, but were unexceptional in terms of their capture and body condition.

At Gresswell Forest, the nightly catch-per-unit effort of females that were suitable for levonorgestrel treatment ranged from 0.2 to 1.1 females h^{-1} of operation (Fig. 3), with a mean (±s.e.) of 0.7 ± 0.1 females h^{-1}. Although variable, catch-per-unit effort showed a linear decline of 5% per night ($y = -0.051x + 0.978$, $R^2 = 0.253$), from approximately 0.9 to 0.5 females h^{-1} over sequential nights. At Serendip Sanctuary, the equivalent catch-per-unit effort was significantly higher ($t_{19} = 5.052$, $P < 0.0001$, 2-tail), ranging from 0.8 to 2.0 females h^{-1} (Fig. 3), with a mean (±s.e.) of 1.5 ± 0.1 females h^{-1}. Catch-per-unit effort declined by 4% per night from about 1.5 h^{-1} over seven sequential nights in May 2013 ($y = -0.042x + 1.512$, $R^2 = 0.253$), but returned to nightly rates above 1.5 h^{-1} in the second capture period 4 years later (Fig. 3).

Table 2. Darting success as a percentage of total shots fired at Gresswell Forest and Serendip Sanctuary.

Outcome (%)	Gresswell Forest ($N = 100$)	Serendip Sanctuary ($N = 205$)
Hit	84	82
Partial dose	7	8
Second shot	4[A]	6
Manual	3	1
Miss	9	15
Lost	9	3
Unknown	0	3

Values do not sum to 100%. Hits include those injecting a partial dose. Second shots were taken after partial doses and misses if the opportunity arose, and manual captures followed some partial doses if the kangaroo could be approached closely. Lost indicates kangaroos that had apparently been hit but moved out of sight and could not be found.
[A]Includes a third shot at one individual.

Contraceptive efficacy

None of the adult females that we captured at Gresswell Forest had a pouch young, although 19 had an elongated teat indicative of a previous breeding attempt and one had a long, lactating teat supporting a young-at-foot. There were very few untreated females from which to assess natural fecundity during the annual surveys. Of the untreated females, 46 ± 1% (mean ± s.e.) of 4 ± 1 assessed were breeding in the 2017 survey, as were 72 ± 6% of 6 ± 2 in 2018. Only one untreated (non-breeding) female remained in 2019. In contrast, 91% of females at Serendip Sanctuary had a pouch young at the time of capture, and the mean (±s.e.) proportion of untreated females breeding per survey ranged from 85 ± 4% of 50 ± 2 assessed in 2014, to 99 ± 1% of 85 ± 4 in 2016 (Table 1).

The efficacy of levonorgestrel implants varied over time. At Gresswell Forest, the proportion of females breeding declined from 14% in 2017 to zero in 2019 (Table 1). Of the seven females recorded breeding in 2017, three had been implanted in 2015 and four in 2016. The three implanted in 2015 bred again in 2018, as did another female from the 2015 treatment group. These four females were recaptured and given a second set of implants in 2018 and were not recorded breeding again. Efficacy was higher at Serendip Sanctuary (Table 1). We recorded only one female breeding (2%, $N = 59$) in 2014, 1 year after the first round of treatment, and two breeding (4%, $N = 48$) in 2018, the year after the second treatment round (Table 1). The latter two females had been implanted in 2013.

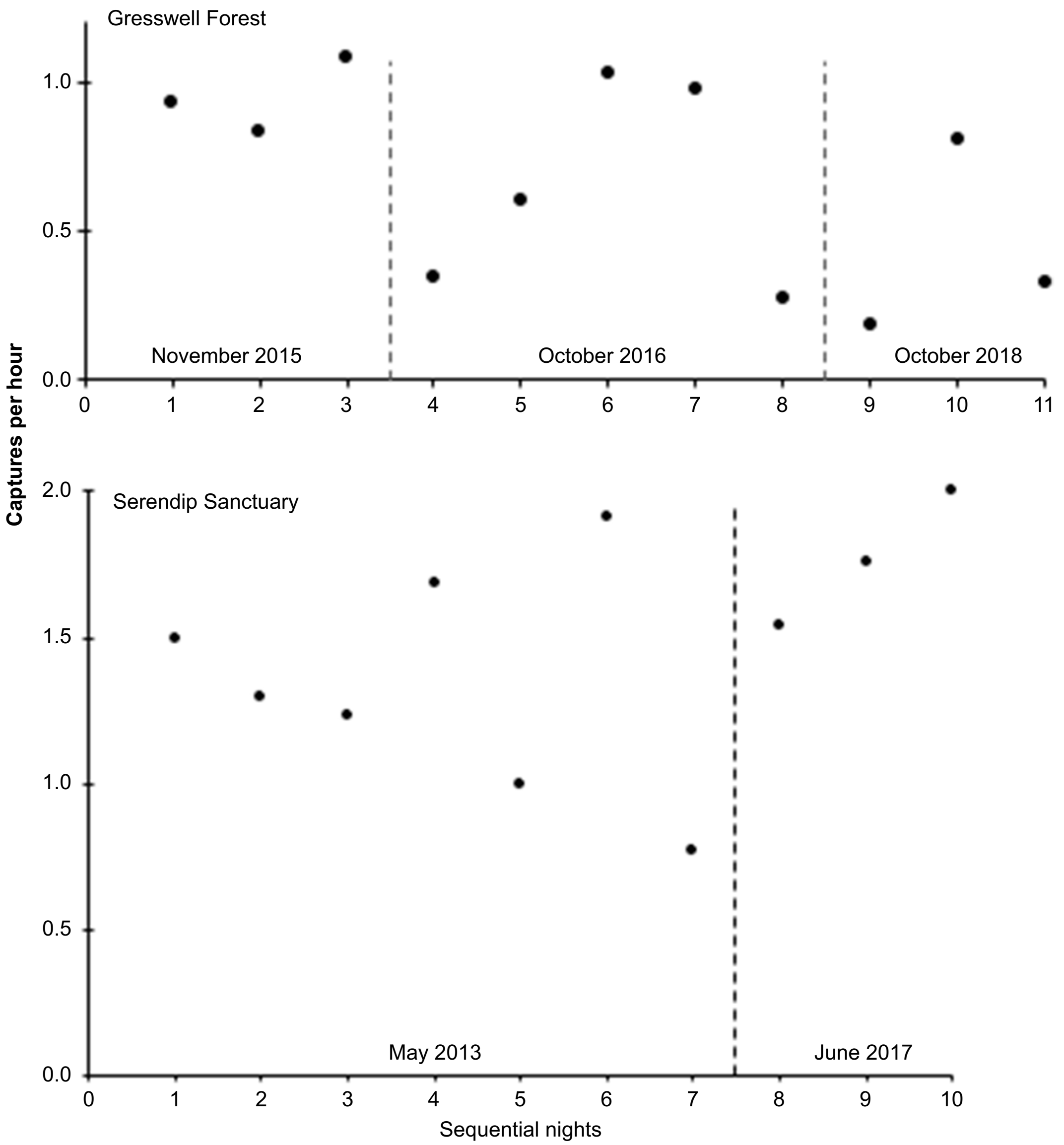

Fig. 3. Catch-per-unit effort, shown as captures of levonorgestrel-treated females per hour over sequential nights at Gresswell Forest and Serendip Sanctuary. Vertical dashed lines mark intervals between rounds of treatment.

Population-level outcomes

At Gresswell Forest, 89% of females had been treated after two rounds of treatment and all but one female had been treated after the third round (Table 1). Population density fell to about 2 ha^{-1} and stayed at that level for the last 3 years (Fig. 2). Only one kangaroo, an adult male, was judged to be in poor condition in 2017. Twelve kangaroos, three of them treated females, were in poor condition in 2018, with prominent ribs, spine and hips, and a dull, scruffy coat. One of these treated females could not be found in 2019, another was still emaciated and had poor mobility, whereas the third had gained condition.

At Serendip Sanctuary, the proportion of females initially treated was lower (73%) and fell further until the second round of treatment, when the proportion treated returned to 74% but fell again the next year. The first round of treatment in 2015 was followed shortly after by a cull, which immediately reduced density from approximately 2 ha^{-1} to less than 1 ha^{-1} (Fig. 2). Population density then rose again; the second round of treatment took place in 2017 but no further population surveys were conducted, so the most recent population outcomes were unknown. Assessing body condition was difficult from a distance, but all kangaroos appeared to be in good health and moved away from the vehicle with ease. However, the carcass of one treated female was found in 2016 with 'lumpy jaw' lesions, and we observed another treated female with obvious 'lumpy jaw' in 2018. We had treated both females in 2013 and did not detect lesions then.

Discussion

Culling and fertility control are typically viewed as lethal and non-lethal alternatives respectively, for the management of overabundant wildlife (Bruce Lauber *et al.* 2007; Cohn and Kirkpatrick 2015). Fertility control is generally preferred over lethal methods by the general public (van Eeden *et al.* 2020; Drijfhout *et al.* 2022), but population models predict that fertility control will rarely reduce abundance as effectively as culling (Barlow *et al.* 1997; McLeod and Saunders 2014). Fertility control alone is even less likely to reduce abundance without significant, sustained management effort (Massei and Cowan 2014; Ransom *et al.* 2014). However, a number of studies have advocated the use of fertility control in conjunction with culling (e.g. Hobbs *et al.* 2000; Pepin *et al.* 2017) for more effective management of abundance. This approach has also been recommended for management of overabundant kangaroos, with initial reduction by culling and ongoing maintenance by fertility control (Wimpenny *et al.* 2021). We adopted this dual approach at one study site (Serendip Sanctuary), whereas the other site (Gresswell Forest) had only fertility control. Contrary to our expectations, abundance at Serendip Sanctuary continued to oscillate and exceeded the management target, whereas abundance at Gresswell Forest fell and remained lower. We evaluated these divergent outcomes in terms of three critical elements of a fertility-control program (Massei and Cowan 2014), namely, delivery efficiency, contraceptive efficacy and population-level response.

We assessed delivery efficiency in terms of catch-per-unit effort. There are some reports of catch-per-unit effort for darting wildlife (e.g. Kilpatrick *et al.* 1996), but this useful measure has not been reported in any kangaroo study. Catch-per-unit effort varied widely from night to night at both sites, although the rate at Serendip Sanctuary was more than double that at Gresswell Forest. The denser vegetation at Gresswell Forest undoubtedly contributed to its lower rate, making it harder to find kangaroos in open areas and to determine their sex, as shown by the erroneous capture of males in 11% of shots, versus 7% at Serendip Sanctuary, and also more difficult to find them after induction, as shown by a higher loss rate at Greswell Forest (Table 2). Catch-per-unit effort underwent a slight (4–5%) linear decline at both sites because an increasing proportion of females were treated and marked, but did not display a characteristic Type 2 response (Real 1977) of ever-diminishing returns because fewer untreated animals remained. The slow and simple decline in catch-per-unit effort suggested that our capture rate was largely unaffected by the availability of untreated kangaroos. It was also noteworthy that catch-per-unit effort returned to high levels during the second treatment round at Serendip Sanctuary, which had a larger population and a permeable boundary, so more females were available to be captured.

Natural fecundity at Gresswell Forest was extremely low. No female had a pouch young at the time of capture and few showed evidence of recent breeding. The regressed teats of many females were indicative of failed reproductive attempts and the 10 subadults captured in error suggested that maturation in these females may have been delayed (Poole and Catling 1974; Quin 1989). These observations were consistent with a population in a post-irruptive phase in eastern grey kangaroos (Wilson and Coulson 2016) following the population crash reported in 2013 (Fig. 2). It was thus difficult to assess efficacy of the levonorgestrel treatment against this low background fecundity. Paradoxically, the only breeding we recorded at Gresswell Forest was in four levonorgestrel-treated females. These females may have been pregnant or had a blastocyst in diapause at the time of treatment, because levonorgestrel does not inhibit gestation or lactation (Nave *et al.* 2000; Wilson *et al.* 2013). However, we suspect that the fault was an expired batch of implants; these females did not breed after they were implanted with fresh implants.

In contrast to Gresswell Forest, natural fecundity at Serendip Sanctuary was high. Over 90% of females were breeding at the time of capture and the fecundity of untreated females was at least 85% over the 6 years of the study (Table 1). This level of fecundity is consistent with the ascending phase of an irruption sequence in this species (Wilson and Coulson 2016). Given this high background fecundity, the efficacy of levonorgestrel treatment was also very high, equivalent to 96–100% infertility over time. The two females recorded breeding in 2014 were probably pregnant or had a diapaused blastocyst in the first round of treatment the year before (Table 1). The two females breeding in 2019 had also been treated in 2013, suggesting that the contraceptive efficacy of the implants had begun to wane after 5 years, as reported in other studies of this species (Coulson *et al.* 2008; Wilson and Coulson 2016).

The population-level effects of fertility control differed between the two sites. At Gresswell Forest, levonorgestrel treatment was almost universal by the third year of the program (Table 1) and was the only form of control applied to this population. Assuming that contraceptive efficacy was high (once the faulty implants had been replaced), levonorgestrel treatment would have contributed to the suppression of population growth and may have curtailed a potential rebound in the period after the irruptive peak, as intraspecific competition lessened and forage availability improved (Wilson and Coulson 2016). However, population density has remained far above the management target of 0.5 ha^{-1} (Fig. 2). A number of kangaroos have also displayed poor body condition at these densities. In response to ongoing grazing pressure by kangaroos, park managers installed a 4-ha exclosure to protect a rare stand of *Banksia marginata* trees and ground-layer vegetation in 2019, reducing the area of kangaroo habitat and increasing the effective population density slightly.

At Serendip Sanctuary, population density fell below the target level of about 1 ha^{-1} after the first round of fertility control and culling in 2013 but rebounded 2 years later and remained above the target since then (Fig. 2). Although levonorgestrel treatment probably dampened this response, there were never more than 74% of females treated in the population (Table 1). Given the very high background level of fecundity, potentially compounded by compensatory effects (Ransom *et al.* 2014), fertility control was incapable of suppressing subsequent population growth. This situation was exacerbated by recruitment. The permit for this project allowed for the euthanasia of pouch young, which is routinely undertaken when kangaroos are captured and treated (e.g. Coulson *et al.* 2008; Wilson *et al.* 2013). However, Parks Victoria elected, on ethical grounds, to allow females to retain their young. Females of this species can attain sexual maturity at 18 months of age (Poole and Catling 1974), giving birth just over a month later (Poole 1975), so can join the breeding population two seasons later. Dispersal may also have reduced the effectiveness of the control program. Female eastern grey kangaroos are generally sedentary (Jaremovic and Croft 1991; Moore *et al.* 2002), but reports of tagged kangaroos beyond the boundary of Serendip Sanctuary suggested that some treated females may have left the site; untreated females may also have entered the population. Both of these factors may also explain the high catch-per-unit effort during the second treatment round.

Taken together, our findings illustrated the necessity of taking a comprehensive approach to develop a fertility-control program (Massei and Cowan 2014). The efficacy of levonorgestrel treatment was high at both sites, although difficult to distinguish from low background fecundity at Gresswell Forest. Catch-per-unit effort was lower at Gresswell Forest than at Serendip Sanctuary, but this small, closed population could be almost entirely treated within budget. However, the inability to also cull this population allowed it to persist at a moderately high density with negative consequences for animal welfare and vegetation condition. Capture was more efficient at Serendip Sanctuary and culling initially reduced density. However, with the budget available, it was not possible to treat a sufficiently high proportion of females to halt the growth of this large, open population. Further culling will be required to meet the management targets, but culls may be smaller in scale and less frequent than would be needed in the absence of fertility control.

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