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**Research Article**

# Multi-year impacts of environmental stress on the abundance and reproduction of a large social herbivore, the Eastern Grey Kangaroo (*Macropus giganteus*)

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## Abstract

**The abundance of herbivores has broad effects on the surrounding ecosystem, yet herbivores are also limited by the carrying capacity of their environments. This balance can be interrupted by climate change-induced extreme weather events causing unprecedented environmental degradation. We conducted an 8 yr study of individually identified eastern grey kangaroos (*Macropus giganteus*) in the wild, following reproduction, sociality, and the general fate of animals from 1 yr to the next. During this period, the landscape experienced extreme rainfall fluctuations, including one of the worst droughts on record followed by prolonged, extreme high rainfall. We found that these large deviations in annual rainfall significantly increased the likelihood of permanent disappearances (through mortality or, less likely, dispersal) and reduced reproduction. Some of these adverse impacts were moderated by size, body condition, and sociality of an individual, indicating varying vulnerability to environmental stressors for certain individuals. Furthermore, some sex and age classes contributed disproportionally to population recovery through reproduction post-environmental stress. These findings reveal how the demography of a wild population could play a critical role in determining local extinction risk and recovery as environmental stressors intensify with the worsening climate crisis.**

**Keywords** extreme precipitation, long-term study, macropod behavior, population decline, reproductive success, social affiliations

As the Anthropocene continues, mean global temperature and frequency of extreme phenomena such as drought and flooding are predicted to rise (Intergovernmental Panel on Climate 2023). The capacity of species to adequately respond to these extreme changes will be crucial for their survival, and knowledge of how animal species behave during extreme environmental events is of vital importance to wildlife conservation efforts (Maxwell et al. 2019). Large herbivores are particularly vulnerable to increased fluctuations in rainfall (Georgiadis et al. 2003), which can impact reproduction (Ogutu et al. 2014), body condition (Turner et al. 2012), and survival (Mills et al. 1995). For example, drought can cause large shifts in reproductive success and population abundance as large herbivores struggle to survive with limited water or reduced green vegetation (Abraham et al. 2019).

The Eastern Grey Kangaroo (*Macropus giganteus*) is the second largest herbivore in Australia, and its abundance can have widespread effects on the surrounding ecosystem. For example, grazing by kangaroos can detrimentally reduce groundcover (Letnic et al. 2009) or increase flora and fauna species richness (Fensham et al. 2011). These effects are contingent on the carrying capacity of the environment, which fluctuates with rainfall. As rainfall declines and feed is reduced, overgrazing ultimately reduces kangaroo numbers (Caughley et al. 1984) through mortality, reduced reproduction, or dispersal as animals attempt to move to more hospitable areas (Pedler et al. 2021).

The effects of drought on kangaroos have been a focus of much research, particularly in arid and semi-arid environments, where droughts are common (Caughley et al. 1985; Juillard and Ramp 2022). In these areas, prolonged drought has resulted in mass mortality events for several species (Pedler et al. 2021). Conversely, increased rainfall and subsequent pasture health lead to improved body condition in red kangaroos (Moss and Croft 1999) and juvenile survival in eastern grey kangaroos (Plaisir et al. 2022). However, non-arid kangaroos are less adept at surviving in dry conditions than arid species, potentially putting these populations at a higher risk should a drought occur (Dawson et al. 2000). Any environmental stressor that decreases vegetation quality or quantity can have a serious impact on the body condition of herbivores (Searle et al. 2015). Body condition in itself can affect fecundity (Widiyono et al. 2020) and survival (Hempson et al. 2015),

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particularly in larger animals (Issac 2005) and younger members of a species (Hamel et al. 2009). However, there are little data reflecting the impact of prolonged deviations in rainfall over several years on the within population dynamics of kangaroos, such as the vulnerability of different classes of animals to stress.

Furthermore, differences in the sociality of individuals within the same population could influence individual responses to environmental stress defined as an adverse environmental factor that has a negative impact on a wild population (e.g., Cairns 2013). There is evidence that gregariousness allows greater behavioral flexibility that can help buffer against rapidly changing environments (Komdeur and Ma 2021). For instance, many animals adjust the size of social groups according to resource availability (Bond et al. 2019; Chen et al. 2022). Female eastern grey kangaroos who associate more with one another are also more likely to reproduce than less social females (Campbell and Ord 2023). The mechanism of impact from an environmental stressor on wild populations is therefore likely to be a complex interaction of individually specific factors including the body condition, size, age, and sociality of an individual. Identifying which of these factors are influential in determining population resilience under stress is difficult without the capacity to track the condition, reproduction, and survival of different classes of individuals within the population.

In this study, we examined the impact of large deviations in annual rainfall over several years on a wild population of eastern grey kangaroos. By following individual animals over many years, we determined the reproduction, sociality, and general fate of individuals from one year to the next in response to prolonged and severe drought followed by several years of unusually high annual rainfall. Our study essentially leverages the natural experiment of oscillating environmental conditions to test how major fluctuations in annual rainfall affect the population dynamics of this iconic species. By doing so, our data offer broad insights into how large keystone herbivores may respond to adverse environmental variability. In particular, our goal was to assess how different classes of individuals of a large social herbivore responded to severe environmental stress, in order to identify the likely mechanism by which that stressor induced large fluctuations in observed population abundance.

## Methods

### Study population

Data from this study were taken from an annual survey of wild eastern grey kangaroos at a remote field site near the locality of Wollar in the New South Wales (NSW) Central Tablelands. This area is classified as having a humid sub-tropical climate according to the Köppen-Geiger climate classification (Peel et al. 2007) and consists of predominantly dry sclerophyll forest (State Government of NSW and NSW Department of Climate Change 2020), surrounding a cleared grassland valley historically used for cattle farming. A water trough provided a permanent water source in all years.

Annual surveys were conducted over 3 to 4 consecutive days for 8 yr (2015 to 2022). The survey took place mostly in the Austral spring or early summer (September to December), except for 2016 where it took place in winter (July). The survey was conducted by the last author using an established protocol from Campbell and Ord (2023), involving observations being made for approximately 3 h twice-daily at dawn and dusk, alternating among 3 hides positioned around the open grassland perimeter.

The survey consisted of exhaustively photographing every individual within the population and later individually identifying every animal within the population from the high-resolution images (see “Individual Identification”). Images were taken using a 200 mm lens on a Canon EOS 7D digital SLR. An effort was made to take multiple photos of each kangaroo to provide images that could be used for both individual identification and to adequately measure proportional body height and condition (see “Body size and condition”).

The data obtained from this survey provided extensive information on the specific individuals present in the population from one year to the next along with their probable age, sex, and reproductive state (Campbell and Ord 2023). Social groups can also be identified from photographs (Campbell and Ord 2023) and network analysis was used to determine the sociality of each animal within the population based on proximity associations observed in photographs (see “Measure of sociality”).

Rainfall has been recorded at the site daily for the last 19 yr and was used to calculate a site-specific annual rainfall average.

### Individual identification

Over the 8 yr of the study, 5,022 photographs were taken of a total of 159 individuals. To individually identify the kangaroos in these images, we applied the method outlined in Campbell and Ord (2023). This procedure used the computer software I3S Contour (Reijns 2013) to help identify individuals based on the unique shape of their ears. This method allowed the continual observation of an individual from 1 yr to the next and often followed their growth from a juvenile or sub-adult to a sexually mature adult. In the case of females, it was also possible to determine the years in which they had medium or large pouch young, which resulted in an obvious pouch bulge and was usually confirmed with the head of the joey being visible.

Individuals observed in a given year were classified into the following sex and reproductive categories: males (kangaroos with visible male sex organs or sexually dimorphic muscular structure); females with young (kangaroos with a visible pouch bulge indicating the presence of a large/medium pouch young, or who were seen to be nursing young-at-foot); females without young (kangaroos with a visible pouch opening but no pouch bulge); sub-adults (kangaroos who were larger than young-at-foot but did not yet have defining sexual characteristics); young-at-foot (joeys who were permanently out of the pouch but still nursing); and unknown (adult kangaroos that could not be confidently identified as male or female).

### Body size and condition

Body size and body condition were calculated from measures taken from photographs using ImageJ version 1.0 (Schneider et al. 2012). Height estimates were measured as a proportional scale relative to all other individuals identified in the population within a given year. This measure was achieved by first selecting the kangaroo anticipated to be the largest animal in a given year (subsequently benchmarked at a proportional height of 100%) and then scaling all other individuals within that year relative to this individual. Height estimates were further facilitated by metal posts positioned in various locations throughout the study area that could be used to provide an absolute measure of height based on 0.5 and 1 m marked intervals on these posts. The following set of criteria were used in selecting images to take estimates of body height. First, the image had to be of individuals unobstructed by other animals or vegetation with at least 1 other individual in focus. Second, each kangaroo compared had to be the same distance to the observer (i.e., standing side-by-side to each other). Third, kangaroos being compared had to both be standing bipedally.

In most instances, height was taken from the base of the foot to the top of the head (excluding ears) using the measuring tool in ImageJ. This measure was converted to a proportion relative to the largest other animal within the image, which was in turn compared relative to the largest animal in the population. In the small number of cases where full body height could not be measured, we inferred body height based on the length of the foreleg, which was positively correlated to body height ($n = 20$, $R^2 = 0.88$, $P < 0.001$). Supplementary Data SD1 and figures therein have additional details on the validation of these methods. A single observer (N.E.C.) made all assessments of height.

Body condition was quantified using a novel index developed for this study that uses the ratio of the widest (W) part of the arm (the forearm muscle) to the narrowest (N) part of the arm (the bony wrist), or the W:N ratio. This ratio was loosely modelled on the hip-to-waist ratio used to calculate obesity in humans (Gadekar et al. 2020), although our condition measure realistically indexes both fat and muscle. Wild animals are likely to be leaner than their captive counterparts (Klimentidis et al. 2011), and kangaroos have a higher rate of muscle than similar sized non-native herbivores (Tribe and Peel 1963). This is particularly true for males whose forelimb muscles grow faster than other muscles, likely due to the use of forelimb muscles in male-male aggression (Warburton et al. 2013). In the case of the kangaroo W:N ratio, an animal in better condition would have a larger W:N ratio—larger forearm to bony wrist—than an animal in poorer condition (i.e., the bony wrist is expected to remain similar in size, with the forearm width fluctuating over months to years as a function of the capacity of an animal to sustain itself with feed). To ensure consistency and robustness of body condition measurements, only images in which the target individual was in focus were used. The individual also had to be stationary and the entire arm unobscured in the photograph and resting against the body to ensure the distance of the forearm and wrist relative to the camera was consistent.

As kangaroos display sexual size dimorphism and males have a much wider range of body size compared to other individuals (Toni et al. 2021) males, females, sub-adults, and joeys were grouped separately in statistical analyses to determine the range of conditions exhibited by each sex/age category. See Supplementary Data SD2 and SD3 for validation methods of body condition estimates for adult females.

## Measure of sociality

Sociality was calculated using the package "igraph" version 1.4.1 (Csardi and Nepusz 2006) in R version 3.0.1 (Team 2021). For each year of the survey, a social network graph was created to show all associations between individuals in that year. Kangaroo associations were measured by their presence at approximately 3 m distance from each other (estimated as 2 to 3 body lengths). This spacing has been shown to be conservative in comparison to other kangaroo studies, yet appropriate for accurately determining strong associations amongst kangaroos (Campbell and Ord 2023). The eigenvector centrality score for each kangaroo was then calculated from these social network graphs.

## Statistical analysis

All analyses were conducted using R version 3.0.1 (R Core Team 2021). Model assumptions were confirmed to have been met using the "check_model" function in the package "performance" version 0.10.2 (Lüdecke et al. 2021). Additional model parameters (e.g., 95% confidence intervals) were calculated using "jtools" version 2.1.0 (Long 2020).

First, we developed a longitudinal plot of all individuals within the population using "ggplot2" version 3.4.2 (Wickham 2016). This plot illustrates the presence and absence of each individually identified kangaroo from one year to the next. This plot also highlights the sex of individuals and breeding status of females in each year that they were observed.

Second, we ran generalized linear mixed models using the package "lme4" version 1.1–31 (Bates et al. 2015) to test the effect of annual rainfall in the previous year on the likelihood of a kangaroo remaining in the population the following year. We focused on rainfall in the previous year because there is likely to be at least a 6-mo "lag" between changes in rainfall and the subsequent population change in kangaroos (Caughley et al. 1984). This model used a binomial error distribution and included a random intercept for individual identity (ID). Annual rainfall was first mean-centered based on the 19 yr average for the field site (667 mm), then converted to an absolute value per 100 mm. This conversion was made to assess the effect of both negative and positive deviations in annual rainfall from the 19 yr average. The rescale to per 100 mm provided better resolution of statistical parameter estimates (NB: effect sizes and $P$-values were not affected by this rescale). Absolute mean-centered annual rainfall was included in the model as a factor. An additional factor for sex/reproductive category (i.e., females with young, females without young, males, sub-adults, juveniles) determined the extent to which certain individuals of different sex and age class (e.g., male vs female, young vs adult) were more or less likely to be observed in the population from one year to the next. A first model also considered factors for social centrality and population size, as well as an interaction between reproductive category and absolute mean-centered rainfall, but none of these factors were found to be statistically distinguishable from zero and were subsequently removed from the final model.

Third, to identify factors likely to influence the probability of reproduction in adult females (coded as 0 when no pouch young or young-at-foot were observed, or 1 when young or young-at-foot were observed for a given female), we applied a generalized linear mixed effects model, with a random intercept for female ID and factors for body condition (W:N ratio), proportional height, absolute mean-centered rainfall in the previous year, centrality, and population size. An interaction term between body condition and rainfall was also considered in the model. An additional model was run on data excluding 2016, where the annual survey had been conducted in winter. The result from this model is reported in Supplementary Data SD4 and was qualitatively unchanged to findings inclusive of all years and is not discussed further.

Finally, we examined factors likely to influence body condition by implementing separate linear mixed models for each sex and age category (adult males, adult females, and sub-adults and young-at-foot combined). All models included a random intercept for ID and initially had factors for absolute mean-centered rainfall in the previous year, proportional height, centrality, and population size—and in the case of females, whether they were identified to have young, and its interaction with rainfall. Final models ultimately focused on those factors found to have effects that were statistically distinguishable from zero.

# Results

## General population dynamics

Over the 8 yr period (2015 to 2022), a total of 159 individual kangaroos were identified within the population: 84 females; 37 males; 17 sub-adults; 10 young-at-foot; and 11 adults of unknown sex (Fig. 1). The annual population size ranged from 34 (the year following peak drought) to 72 individuals (a year of average annual rainfall; Fig. 2). The population was exposed to a severe 3 yr drought which reached its peak in 2019, followed by a further 3 yr of unusually high rainfall (Fig. 2). Population size fluctuated dramatically and as an apparent function of annual rainfall in the previous year (Fig. 2). Some kangaroos were known to drop in and out of the population on occasion, but absences during drought tended to correspond to permanent disappearances either from mortality (most likely) or dispersal (Fig. 1). For example, of the 57 kangaroos observed during the drought year of 2019, 21 were never seen again in the 3 consecutive years that followed, a loss of over a third of the animals from the population (Fig. 1). Furthermore, the gradual increase in numbers post-drought (following 2020) can largely be attributed to the arrival of new individuals through reproduction by remaining females in the population, but also to some extent by the appearance of new adult males dispersing into the population (Fig. 1).

## Factors impacting individual persistence in the population

Females with young had 12 times greater than even odds of being present in the population in any given year (Table 1; NB: these data are specific to females with medium to large pouch young), while females without young and adult males had less than half these odds of remaining in the population (Table 1). Sub-adults and young-at-foot had statistically comparable odds of being present in the population as females with young (Table 1). Deviations in average rainfall had a statistically distinguishable effect on permanent disappearances from the population (likely through mortality but potentially dispersal as well) and the effect was consistent across reproductive categories (Table 1). Specifically, for every 100 mm deviation away from the 19 yr average, there was a 61% increase in the chances of permanent disappearance for any given individual from the population (Table 1).

## Factors impacting female reproduction

There were even odds of a female having visible pouch young in any given year (Table 2). These odds increased with female body size, with the chances of reproduction improving by approximately 10% for every 0.1 increase in proportional size (i.e., ~10% increase in body size relative to other individuals in the population as a whole; Table 2). Given that proportional height is likely to reflect growth (see Supplementary Data SD5), and subsequently age (female kangaroos grow indeterminately throughout their lives; Quesnel et al. 2018), this outcome would be consistent with older females being more likely to reproduce than younger females. As rainfall deviated from the mean, the odds of reproduction decreased (Table 2). More social females also had a greater likelihood of reproducing in any given year than females that tended to be more isolated from other individuals (Table 2). Finally, females in better condition (those with higher W:N values) were more likely to be observed with young in years following large deviations in annual rainfall than females of poorer condition (Table 2). Population size had no discriminable effect on the chances of female reproduction in any given year (Table 2).

## Factors impacting body condition

Male body condition and subadult/young-at-foot body condition were not predicted by any variable, including deviations in annual rainfall in the previous year, population size, or any other factor (Table 3). In contrast, there was a statistically distinguishable effect for the interaction between rainfall and reproduction on female body condition (Table 2). Specifically, females in better condition were those that were more likely to be observed with young in years following large deviations in annual rainfall compared to females in poor condition (Table 3).

# Discussion

After tracking individuals for almost a decade, we found all classes of kangaroo less likely to persist in the population following extreme deviations in annual rainfall (Table 1). For large herbivores consuming sizeable amounts of vegetation daily (Georgiadis et al. 2003), large drops in rainfall disrupt water sources, cause displacement, and lead to starvation as the vegetation itself suffers. Eastern grey kangaroos of all sexes and ages have an increased likelihood of both dispersal (presumably to find food) and mortality (either from starvation or from an increased likelihood of vehicle collision during dispersal) during drought years (Hill 1982; Lunney et al. 2018). The population showed some post-drought recovery (Fig. 2), primarily from reproduction by surviving individuals and to some extent immigration of new adult males (of the 34 individuals who appeared in the population after 2020, 17 were juveniles and sub-adults likely born into the population while 9 were males who presumably dispersed into the population from elsewhere; collectively this represented over 75% of new individuals in the population; Fig. 1). The population had access to a permanent water source at the study site (a water trough), suggesting that permanent disappearances during drought likely reflected declining food availability from the impact of drought on the growth of ground vegetation. The mechanism for disappearance following excessive rainfall years is less clear.

Disappearances were most common among males and females without young (Table 1). Adult male eastern grey kangaroos in their prime or pre-senescent states (males who were likely nearing the end of their reproductive years) are known to have lower survival than females (Bergeron et al. 2023). This pattern is typical for other sexually dimorphic species as well, including fur seals (Negro et al. 2010) and Roe Deer (Lemaître et al. 2018). As males (and to a lesser extent, sub-adults; King et al. 2015) also tend to move between populations more often than females (Coghlan et al. 2017), our findings could reflect increased dispersal as well. We therefore cannot be certain whether male disappearances were primarily from death or dispersal, but we can conclude disappearances were otherwise permanent (animals did not return in later years). Given that extreme deviations in rainfall were state-wide, even if disappearances were from dispersal, these animals were unlikely to have ranged far enough to settle in environments not similarly impacted by rainfall conditions. For females without young, the implications of disappearance were less clear. Female eastern grey kangaroos are mostly philopatric (Neaves et al. 2017) and females of other macropod species (red kangaroos) are even less likely to disperse during drought periods (Norbury et al. 1994). Nevertheless, female dispersal is not unknown, and our findings might instead reflect females with young being less likely to disperse when caring for dependent young.

Reproduction also declined following extreme deviations in rainfall (Table 2), a trend shared with several African ungulate species

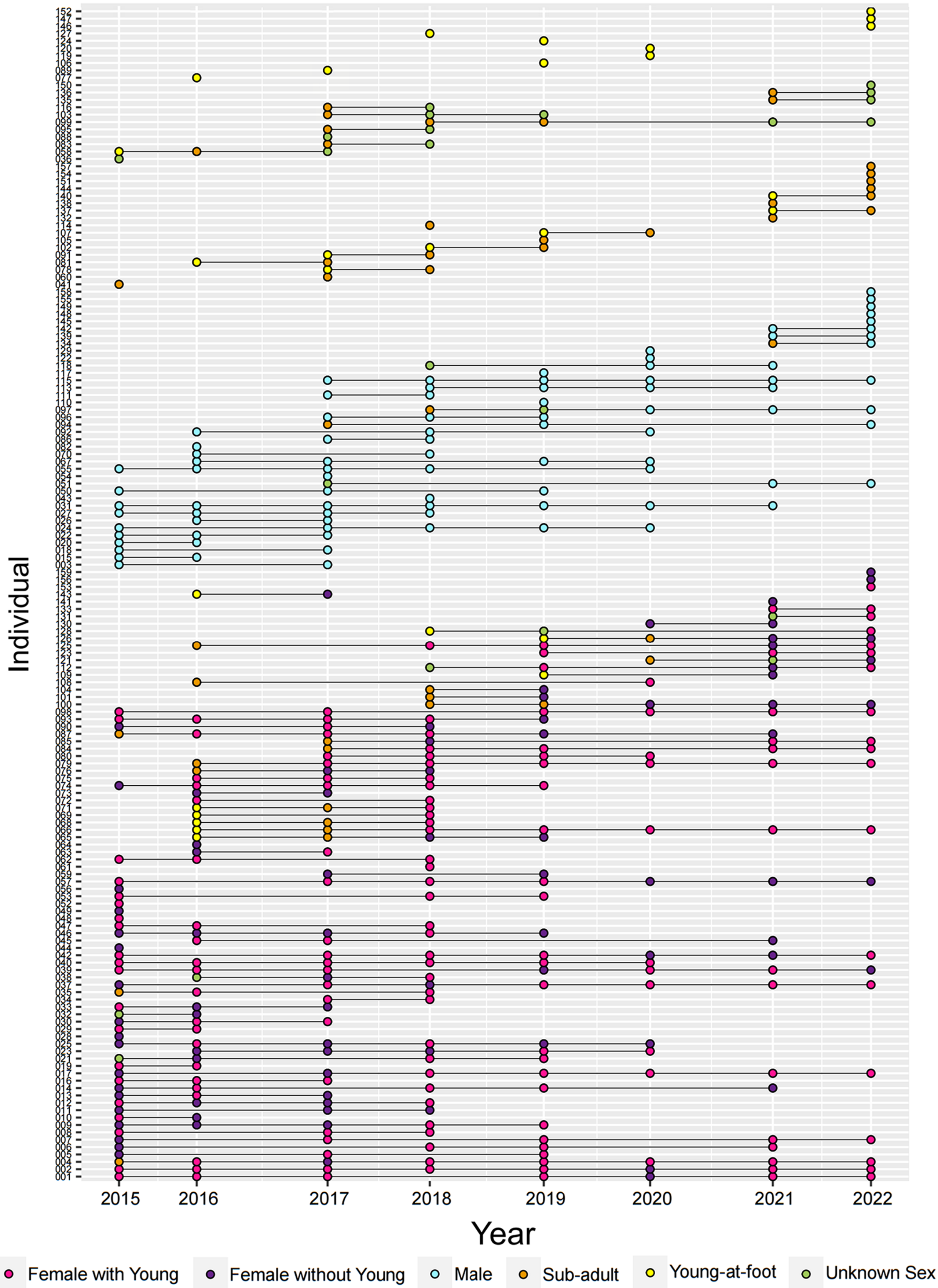


**Fig. 1** Demography of individual eastern grey kangaroos. The spacing of annual survey periods on the x-axis reflects the number of weeks from monitoring starting in 2015. Each dot point shows the year a particular individual was observed and its general age, sex, and reproductive status (in the case of females).

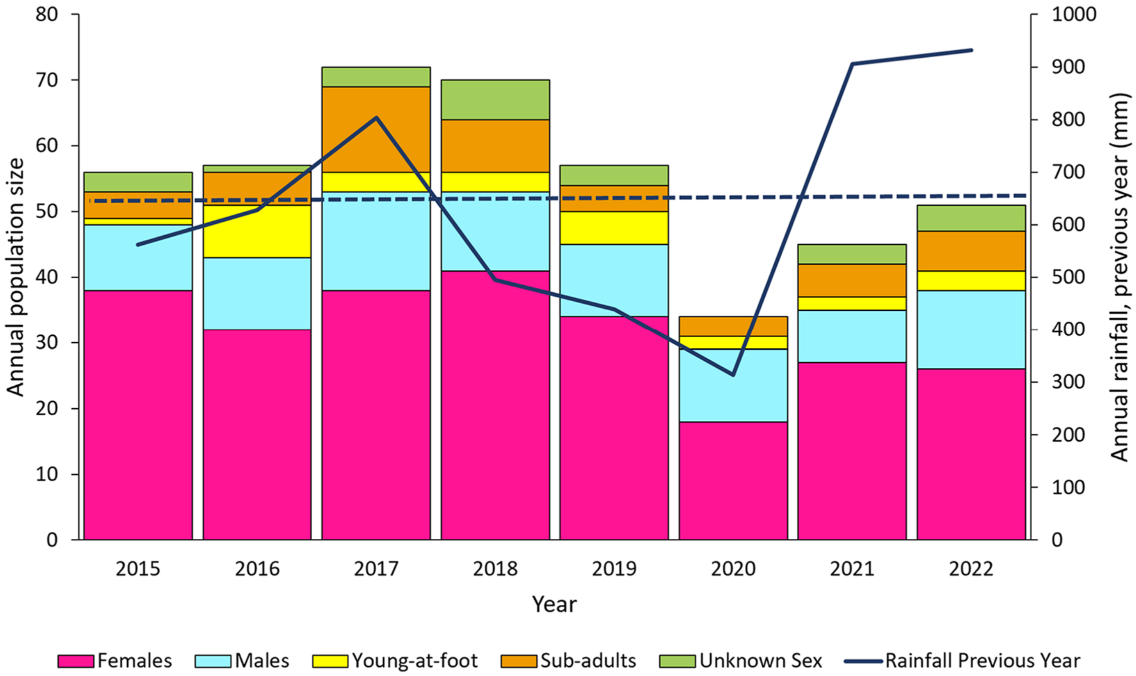


**Fig. 2** Fluctuations in population size and annual rainfall from the previous year. The dashed line shows the 19 yr average annual rainfall (667 mm), which was used to benchmark annual deviations in rainfall in statistical analyses.

**Table 1** The odds and odds ratio of eastern grey kangaroos remaining in the population in the following year, as a function of reproductive category (females with young, females without young, males, sub-adults, young-at-foot, and individuals of unknown sex) and annual rainfall (absolute mean-centered).

| Variable | Estimate (95% confidence range) | z | P |
|---|---|---|---|
| | Odds | | |
| **Intercept (females with young)** | 11.5 (5.2, 25.8) | 5.95 | <0.001 |
| | Odds ratio | | |
| **Females without young** | 0.42 (0.22, 0.8) | −2.64 | 0.008 |
| **Males** | 0.47 (0.25, 0.9) | −2.3 | 0.02 |
| **Sub-adults** | 0.68 (0.3, 1.56) | −0.92 | 0.36 |
| **Young-at-foot** | 0.64 (0.22, 1.87) | −0.81 | 0.42 |
| **Unknown sex** | 0.43 (0.15, 1.23) | −1.57 | 0.12 |
| **Rainfall (absolute mean-centered)** | 0.61 (0.44, 0.85) | −2.9 | 0.004 |

The original model contained an interaction between reproductive category and rainfall but it was found not to have a statistically distinguishable effect from zero and subsequently removed from the final model.
$n_{\text{individuals, observations}}$ = 159, 390.

**Table 2** The odds and odds ratio of female eastern grey kangaroos having young in a given year, as a function of her body condition, height, and sociality (centrality), and controlling for rainfall in the previous year (absolute mean-centered) and population size (see also Supplementary Data SD2).

| Variable | Estimate (95% confidence range) | z | P |
|---|---|---|---|
| | Odds | | |
| **Intercept (reproduction)** | 24.59 (0.001, 897188.49) | 0.6 | 0.55 |
| | Odds ratio | | |
| **Body condition** | 0.07 (0.003, 1.5) | −1.7 | 0.09 |
| **Percentage height (per year)** | 1.1 (1.03, 1.16) | 3.06 | 0.002 |
| **Population size** | 1.02 (0.98, 1.06) | 0.76 | 0.45 |
| **Centrality** | 11.99 (1.06, 136.2) | 2.004 | 0.05 |
| **Rainfall (previous year)** | 0.16 (0.03, 0.77) | −2.28 | 0.02 |
| **Body condition × previous year rainfall** | 1.65 (1.01, 2.66) | 2.02 | 0.04 |

$n_{\text{individuals, observations}}$ = 84, 184.

(Ogutu et al. 2014). Females who were more social and those with larger relative body sizes had greater reproductive success (i.e., were more likely to have medium-large pouch young or unweaned young-at-foot; Table 2). Body size, especially among young females, is also positively associated with fecundity (Quesnel et al. 2018), while sociality has been shown to increase as females become mothers (Campbell and Ord 2023). Additionally, females with higher body condition were more likely to reproduce in the years following rainfall deviations (Table 2). Body condition at the onset of an environmental stressor is a key determinant of reproduction, as females with no young (or young which were too small to detect using visual observations) showed a greater body condition decline in a post-drought environment (Moss and Croft 1999). Our data suggest that certain females in the population—those who are more social and in better starting condition—have the potential to contribute more to overall population growth. By extension, any loss of these females could disproportionally impact population persistence, resulting in a greater vulnerability to local extinction. Breeding females are important in population recovery for all species, but

**Table 3** The extent to which body condition of (a) female, (b) male, and (c) juvenile eastern grey kangaroos in a given year reflects changes in population size or deviations in annual rainfall in the previous year (absolute mean-centered).

| Variable | Estimate (95% confidence interval) | *T* | df | *P* |
|---|---|---|---|---|
| **(a) Females only** | | | | |
| **Intercept (females with young)** | 3.24 (2.80, 3.69) | 14.26 | 222.97 | <0.001 |
| **Females without young** | 0.39 (−0.10, 0.88) | 1.55 | 223.92 | 0.12 |
| **Population size** | −0.005 (−0.01, 0.002) | −1.46 | 223.85 | 0.15 |
| **Rainfall in the previous year (absolute mean-centered)** | −0.03 (−0.09, 0.03) | −0.9 | 225.34 | 0.37 |
| **Rainfall in the previous year × reproduction** | 0.08 (0.004, 0.15) | 2.06 | 22.48 | 0.04 |
| **$n_{\text{individuals, observations}}$ = 84, 245** | | | | |
| **(b) Males only** | | | | |
| **Intercept (body condition)** | 3.34 (2.85, 3.83) | 13.38 | 80.42 | <0.001 |
| **Population size** | −0.01 (−0.009, 0.007) | −0.31 | 82.97 | 0.76 |
| **Rainfall in the previous year (absolute mean-centered)** | −0.03 (−0.08, 0.02) | −1.28 | 82.96 | 0.21 |
| **$n_{\text{individuals, observations}}$ = 37, 86** | | | | |
| **(c) Sub-adults and young-at-foot only** | | | | |
| **Intercept (body condition)** | 3.28 (2.55, 4.02) | 8.75 | 67 | <0.001 |
| **Population size** | −0.003 (−0.01, 0.008) | −0.47 | 67 | 0.64 |
| **Rainfall in the previous year (absolute mean-centered)** | 0.003 (−0.06, 0.07) | 0.12 | 67 | 0.92 |
| **$n_{\text{individuals, observations}}$ = 27, 70** | | | | |

The original model contained factors for height, sociality (centrality), and an interaction term between rainfall in the previous year and reproduction (for females only), which were not found to be significant and subsequently removed from the final model.

particularly for eastern grey kangaroos who can simultaneously carry a fertilized embryo, pouch young, and nurse young-at-foot when conditions are favorable (Poole 1975).

While the environmental events that underpin our study were historically unusual—the worst drought in Australia's recorded history followed by several years of abnormally high rainfall—the magnitude of such oscillations in conditions like rainfall are expected to become progressively worse under the climate crisis (Abrahms et al. 2023; Intergovernmental Panel on Climate 2023). Our multi-year study provides some insight on the potential impact of such events on wild populations. Of special note was the combined effect of both drought and excessive rainfall on permanent disappearances among all classes of kangaroo (either through mortality or attempted dispersal). Drought has been long recognized as a significant stressor on wildlife populations (e.g., Hill 1982; Lunney et al. 2018; Abraham et al. 2019; Maxwell et al. 2019), whereas the consequences of unusually high and prolonged rainfall events has been less appreciated. Our data show that both extreme reductions and elevations in rainfall are largely equivalent forms of stress, at least on large herbivores who are often ecologically important species in many ecosystems.

Overall, however, the average condition of animals in the population was consistent from one year to the next (Table 3; Supplementary Data SD6) even in drought years where persistence decreased dramatically (Table 1; Fig. 2). We suspect the maintenance of body condition in remaining animals reflects a reduction in overall population density, which resulted in remaining animals having sufficient feed to maintain condition. Remaining animals also had access to a permanent water source in all years (the presence of a water trough, a holdover from historic cattle farming in the area). In macropods, measuring body condition has previously required the physiological assessment of captured (usually sedated) individuals (Brandimarti et al. 2021), a process that can lead to capture myopathy, a severe physiological shock in response to stress (Vogelnest 2019). These limitations are compounded in the case of longer-term studies, where animals are captured multiple times, increasing both the stress to the animal and the cost and time involved for the researcher. Visual body condition scores are widely used (Best et al. 2015; Menz et al. 2017; Juillard and Ramp 2022), but these are largely subjective and potentially vary by researcher. The aim of our body condition index was to circumvent these issues and provide a simple, noninvasive, quantitative means of measuring body condition from photographs. We have validated this index using captive females as a benchmark of good body condition and confirmed that the range of body conditions exhibited by wild females was considerably wider than captives (as predicted) and this was unlikely to have occurred by chance (see Supplementary Data SD2). Despite this broader range of body conditions in the wild, we suspect it unlikely that animals will be observed in extremely poor condition given these animals would presumably be quickly removed from the population by predation. Although our validation provides a reasonable confirmation of the utility of the W:N ratio for measuring body condition in eastern grey kangaroos (at least in females), further work is needed to extend the method to other macropod species. Our current data do suggest that it has considerable potential as a noninvasive means of determining general body condition for elusive species monitored remotely via camera traps, and over the long term to evaluate the overall health of the population and its potential capacity to persist through adverse environmental change.

Despite the depth of information obtained from this population of eastern grey kangaroos, it is important to acknowledge some limitations. Our approach of obtaining a representative "snapshot" of the population each year is a common and cost-effective strategy for multi-year monitoring, enabling researchers to track the fate of individuals within a population over multiple years with minimal disturbance (Piefke et al. 2021; Toni et al. 2021; Campbell and Ord 2023). However, the noninvasive nature of the photographic survey means only medium/large pouch young can be adequately detected via a visible bulge in the pouch of a mother. The result is a likely underestimate of individual reproduction, given that some females could still have small (undetected) pouch young. Furthermore, our capacity to monitor the survival of individual young between years was limited by data collection through annual surveys conducted over several days rather than weeks or months. Despite this, our snapshot sampling was still adequate for tracking the fate of individuals from one year to the next, including the development of young-at-foot into sexually mature adults (e.g., Fig. 1; Supplementary Data SD4). More intensive monitoring would be achieved by increasing the frequency of surveys to several times a year (if financial resources permit). Although our study was focused on a single population, other studies on large herbivores show similar findings of certain individuals within a population being more prone to disappearance through morality or dispersal (Negro et al. 2010; Ogutu et al. 2014; Lemaître et al. 2018). This pattern infers at least some translational potential of identified factors from a longitudinal study of a single population to other populations or species.

By extension, understanding which individuals are most affected by adverse environmental conditions, and why, has broad implications for wildlife management. Across Australia, multiple state and local initiatives are attempting to manage kangaroo populations, including fertility control (Wimpenny et al. 2021; Coulson and Wilson 2023) and conservation culling (Gordon et al. 2021). For these programs to work effectively, wildlife managers need a solid understanding of population dynamics over time, including sex and age structure, dispersal, and the environmental factors that shape reproduction and survival (Dawson 2012). This need is becoming increasingly urgent as climate change accelerates and weather patterns become more extreme and less predictable (Abrahms et al. 2023). Multi-year population-level studies, such as ours, provide vital data for building predictive models that can anticipate how wildlife will respond to a rapidly changing climate. Similar efforts are underway globally, with long-term studies on Red Deer (Clutton-Brock and Sheldon 2010) and Bighorn Sheep (Festa-Bianchet et al. 2019), providing comparable insights into how environmental variability impacts demographic processes. Together, these studies highlight the universal importance of individual-based monitoring for managing wildlife populations in an area of environmental uncertainty. While population averages can obscure important variation, individual level data can reveal specifics such as the cohorts most vulnerable to unpredicted environmental factors. These insights are essential not only for guiding effective management practices but also for safeguarding the long-term resilience of native species in an uncertain future.

## Author contributions

Nora Campbell (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing—original draft, Writing—review & editing), Katherine Moseby (Conceptualization, Formal analysis, Methodology, Supervision, Writing—review & editing), and Terry J. Ord (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing—review & editing)

## Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1**. The odds and odds ratio of remaining in the population the following year as a function of reproductive category (females with young, females without young, males, sub-adults, young-at-foot and kangaroos of unknown sex) controlling for rainfall (absolute mean-centred), sociality (centrality), and population size, with an interaction term between reproductive category and rainfall.

**Supplementary Data SD2.** Graphs displaying the standard deviation and range in body condition of wild female eastern grey kangaroos is consistently greater than observed for a healthy captive population. The upper panel (a) shows the distribution of standard deviations and ranges of W:N in the wild population in a "good" year compared to those in the lower panel (b) in a "bad" year. The histograms show the distribution of 100 random samples of 23 female eastern grey kangaroos from the wild population under study. Benchmarked against this by the red line is the observed standard deviation and range of W:N estimated for the healthy, well-fed population at Symbio Wildlife Park. The associated *P*-value represents the proportion of the random samples from the wild population that fall below the observed standard deviation/range of the healthy captive population at Symbio. The associated percentage value indicates the percentage random draws from the wild population pool that have a standard deviation or range that was larger than the captive population.

**Supplementary Data SD3.** A graph displaying the body condition of females across years. The dashed line represents the average body condition of the captive kangaroos used as a measure of 'healthy' body condition (3.57). Not the tendency for individuals of poor condition to disappear from the wild population following the worse periods of drought (2019 onwards). This implies only animals in better condition survive in the population following drought.

**Supplementary Data SD4.** The odds and odds ratio of a female eastern grey kangaroos having young in a given year, as a function of her body condition, height and sociality (centrality), and controlling for rainfall in the previous year (absolute mean-centred) and population size. This analysis was conducted with the winter survey in 2016 excluded from the data.

**Supplementary Data SD5.** A graph displaying the proportional height of 5 representative females who were seen for a minimum of 6 years. Their heights increase through growth over the years, with only minor deviations.

**Supplementary Data SD6.** The extent to which body condition of (a) female, (b) male and (c) juvenile eastern is predicted by population size, rainfall in the previous year (absolute mean-centred), height, sociality (centrality), and population size, with an interaction term between rainfall in the previous year and reproduction (for females only).

**Supplementary Data SD7.** A graph displaying the proportional heights of individuals appropriately delineates individuals by sex and general age category (males, females with young, females without young, sub-adults and young-at-foot).

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## Conflict of interest

None declared.

## Data availability

Data are available via Dryad Digital Repository and can be accessed through the following link: https://datadryad.org/stash/share/VriDoTXnXS7HbHrANMX355Kv8k1RtgRu4y5r2WcQ4D0

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