Demographic trends and reproductive patterns in the northern hairy-nosed wombat (*Lasiorhinus krefftii*) at Epping Forest National Park (Scientific), central Queensland

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Abstract.   The critically endangered northern hairy-nosed wombat (*Lasiorhinus krefftii*) currently exists at only two locations in Queensland. Management, research and monitoring of the species at the main Epping Forest National Park (Scientific) population has occurred over the last four decades using a variety of tools, with the most complete dataset being provided by burrow activity monitoring over that period. Following a series of trap-based surveys in the 1980s and 1990s, wombat monitoring has employed DNA profiling of hairs collected remotely on sticky tape set at burrow entrances (since 2000), and passive infrared (PIR) cameras (since 2011). These techniques have produced a wealth of new information on the species. Using this new information, we aim to: (1) summarise the available demographic data and present new estimates using novel techniques for *L. krefftii* at Epping Forest NP; and (2) characterise reproductive patterns and their relationship with environmental factors for *L. krefftii* at Epping Forest NP. We find an ongoing increase in the population size at Epping Forest National Park, supported by healthy levels of reproduction despite periods of poor environmental conditions, notwithstanding the finding that cumulative monthly rainfall six months prior to sampling influenced birth rates. This trend suggests that the population will likely reach carrying capacity in the near future. It is timely to harvest the population to provide founders to a new site to establish an additional population, which will also reduce the risk of extinction and help secure the future of the species.

Introduction

The northern hairy-nosed wombat (*Lasiorhinus krefftii*) is one of the world's most endangered mammals. Prior to the arrival of Europeans in Australia, the species was probably sparsely distributed throughout a huge area of semiarid eastern Australia from southern New South Wales to northern Queensland. A combination of culling in the Riverina area of New South Wales to

reduce potential habitat for invasive European rabbits, drought, and competition for food with introduced herbivores reduced the species to a single small population in central Queensland by the 1970s (Crossman *et al.* 1994; Swinbourne *et al.* 2016).

Lasiorhinus krefftii currently occurs in two Queensland locations. The last natural population occurs at Epping Forest National Park (Scientific) (Epping Forest NP) in central

Queensland, with approximately 245 animals (Taylor and Fewster 2017). In 2009 and 2010, the second population was established through the translocation of 15 individuals to Richard Underwood Nature Refuge in southern Queensland. Despite a high mortality rate after release (seven wombats in the first 3.5 years), there have been no further deaths of translocated animals. In 2016, an additional male was introduced to stimulate breeding in the population, resulting in five successful births and a current population of 14 wombats.

The species is listed as Endangered in Queensland under the *Nature Conservation Act 1992*, and as Critically Endangered nationally under the *Environment Protection and Biodiversity Conservation Act 1999*. Current threats and conservation actions are listed in the Conservation Advice (TSSC 2018).

The last population of *L. krefftii* was protected with the gazettal of Epping Forest NP in 1971. Monitoring of the wombat population has been continuous since 1974 (Gordon *et al.* 1985) and has included measuring burrow activity, live trapping, genetic censusing based on remote collection of wombat hair, and PIR camera monitoring. Several key management events have occurred since gazettal, including the construction of a cattle fence around the population in 1981, construction of a dog fence in 2002, placement of permanent caretakers on the park since 2002, provision of permanent water in 2004 and the translocation of 15 individuals in 2009–10 to establish a second population.

Population trends

Initial studies of the *L. krefftii* population at Epping Forest NP involved monitoring wombat activity levels at burrow entrances. From 1975 to 1982, approximately 70% of burrows at Epping Forest NP were scored as active by Gordon *et al.* (1985), who estimated that the population contained only 20–30 wombats, perilously close to extinction. A major decline in the number of active burrows occurred when the park was fenced to exclude cattle in 1981. Crossman *et al.* (1994) attributed this to a reduction in the size of wombat feeding ranges in response to the higher availability of food after the removal of cattle.

During the first trapping studies of the species, from 1985 to 1989, 70 unique wombats in a roughly equal sex ratio were captured, implying a substantial increase in the population size since the study by Gordon *et al.* (1985). The recovery of the population was attributed to the exclusion of cattle from Epping Forest NP in 1981 and the consequent increase in the quality and quantity of food available to the wombats. Trapping also suggested that female-biased dispersal was occurring, with 50% of females dispersing, while few males did so (Johnson and Crossman 1991). This trend has subsequently been confirmed for *L. krefftii* (Taylor *et al.* 1997), and demonstrated for the southern hairy-nosed wombat (*Lasiorhinus latifrons*) (Walker *et al.* 2008) and the bare-nosed wombat (*Vombatus ursinus*) (Banks *et al.* 2002).

The recovery in the 1980s was short-lived. Trapping during a protracted drought in the 1990s revealed declines in breeding rates and a significant skewing of the sex ratio towards males (Horsup 1998). These negative demographic trends were reflected in reduced population estimates: a capture–mark–recapture (CMR) analysis of trapping data in 1993 provided an estimate of 65 wombats, indicating that no population growth had occurred during the drought, given population size estimates of 67 in 1985–87 and 62 in 1988–89 (Hoyle *et al.* 1995).

Since 2000, population estimates have been based on CMR analysis of detections of individual-specific DNA profiles established from wombat hairs remotely collected at burrow entrances – a technique in the early stages of development at the time of the first wombat conference in Adelaide in 1994 (Taylor *et al.* 1998). The first full 'hair census' analysis in 2000 returned a population estimate of 113 individuals and confirmed the male-biased sex ratio recorded during trapping in the 1990s (Banks *et al.* 2003a). Since then, seven more hair censuses have provided population and sex ratio estimates, as documented in a series of unpublished reports. Those reports employed the same statistical approach as Banks *et al.* (2003a) to standardise the analysis and identify trends in population size, although that approach is now known to produce upwardly biased population estimates. Hence, one of the goals of the current paper is to report on a reanalysis of the data from all hair censuses using newly developed statistical models (Taylor and Fewster 2017). This paper presents these new estimates and clarifies overall population trends, as we now understand them.

Trends in survival and reproduction

Adult mortality levels were low and estimated at less than 8% per year in the 1980s (Johnson 1991). Estimates in the 1990s using CMR methods indicated adult mortality levels of approximately 5% in good years (range: 0–14%; S. Hoyle, pers. comm.). Life span in the wild can exceed 28 years according to trapping and hair census records (Taylor 2012). The oldest captive *L. krefftii* was more than 30 years old when it died at Epping Forest Station (J. Dennis, pers. comm.).

The rarity of *L. krefftii*, along with its nocturnal, fossorial and conservative habits, has meant that understanding reproductive patterns has been difficult. The reproductive behaviour of the closely related, and more common, southern hairy-nosed wombat, *L. latifrons*, is better understood. Most *L. latifrons* young are produced during the winter–spring growing season, from July to December (Taggart *et al.* 2007). Following approximately nine months of pouch life and a further three months of suckling, young-at-foot are weaned in the following spring when pasture conditions are optimal. There is evidence that a similar pattern of reproduction occurs for *L. krefftii* (although shifted to coincide with the northern wet season), with most births occurring between October and March (Crossman *et al.* 1994). Early trapping studies also suggested that 50–75% of *L. krefftii* females breed in any one year (Crossman *et al.* 1994). However, as the species is very trap-shy, the ability to collect more detailed reproductive data for individual animals was limited prior to the advent of PIR cameras.

PIR cameras have provided a non-invasive method to monitor *L. krefftii* at a level not previously possible and have enabled long-term data to be collected on individual wombats. For example, observations of a single ear-tagged female *L. krefftii* have provided an indication of the frequency of breeding: she produced five young in the nine years that a PIR camera monitored her burrow (A. Horsup, unpubl. data). This period followed eight years of mostly above-average rainfall (range: 420–1293; 20-year mean: 546 mm) and included mostly

below-average rainfall (268–803 mm). The intervals between births for this female were 23, 28, 16 and 25 months, respectively, for an overall mean interval of 23 months between births.

This paper combines existing reproductive data with new data extracted from millions of PIR camera photos to determine the environmental factors that influence breeding events and to clarify the breeding patterns of *L. krefftii* at Epping Forest NP.

The aims of this paper

The purpose of this paper is to (1) summarise the available demographic data and present new estimates using novel techniques for *L. krefftii* at Epping Forest NP, and (2) characterise reproductive patterns and their relationship with environmental factors for *L. krefftii* at Epping Forest NP.

Methods

Epping Forest National Park

Located 120 km north-west of Clermont in central Queensland, Epping Forest NP is 2750 ha in size, of which 600 ha is considered *optimal* wombat habitat and 1400 ha is considered *suitable* (Steinbeck 1994). In 1989, *L. krefftii* occupied 300 ha of the park (Johnson 1991); by 2019, this had increased to 800 ha (A. Horsup, unpubl. data). The wombat habitat and vegetation of the park are described in DERM (2011).

Epping Forest NP is situated in a semiarid zone on the Belyando river system in the upper reaches of the Burdekin River catchment. The park was excised from Epping Forest and Walthum cattle stations in 1971, although grazing continued on the park until 1981, when it was fenced to exclude cattle. The climate is warm to hot with a mean annual rainfall of 576 mm that is summer-dominated (72% falls from November to March) and unpredictable. Mean monthly temperatures are high in summer (the long-term mean maximum temperature for Clermont in December, the hottest month, was 34.8°C) and low in winter (the long-term mean minimum was 6.7°C in July) (BOM 2020). Several long-term droughts, lasting up to six years, have been recorded in the area in recent decades (Gordon *et al.* 1985). The most recent severe drought was from 1992 to 1997 (ABC 2020). Since 1999, rainfall data have been collected on-site. Prior to 1999 data were collected at Epping Forest cattle station (3 km from the study site) and temperature data from the closest working weather station at Clermont Airport (105 km from the study site: BOM 2019).

Burrow activity monitoring

The burrows of *L. krefftii* can be single-entranced or multi-entranced, with up to 11 entrances recorded at the largest warren complex. Activity monitoring of *L. krefftii* burrows has occurred at varying intervals on Epping Forest NP since 1974 and constitutes the longest continuous monitoring program for the species. Burrow activity monitoring is carried out by two people over seven mornings at all known burrows and causes little or no disturbance to the wombats. Each morning for seven days, all new and established burrows are marked and mapped. Burrows, including all entrances, are recorded as 'active', 'visited' or 'inactive' according to the presence of wombat tracks, digging, fresh dung and urine, and the state of the burrow (collapsed, partially collapsed, open). An 'active' burrow shows clear signs of entry by a wombat in at least one entrance. 'Visited' burrows have fresh wombat signs near at least one entrance but show no signs of entry by a wombat.

Trapping

Demographic and reproductive data were collected at irregular intervals during wombat trapping at Epping Forest NP from 1985 to 2017. Trap effort within individual surveys varied considerably depending on monitoring strategies and logistical constraints (Appendix 1). Wombats were captured in large steel cage traps (60 cm W × 90 cm H × 180 cm L) positioned at openings in permanent fences constructed around active burrows. Trigger lines set 50 mm above the trap floor activated both trap doors. Since 1993, the trap mechanism was connected to a radio transmitter, ensuring that all trapped wombats were processed within 2 h of capture. Wombats were anaesthetised and processed on-site.

Body measurements (weight, total length, head length, head width, neck girth, chest girth, tibia length and pes length) were recorded for all captured wombats. Wombats were classed as adult if total body length was greater than 1 m (Crossman *et al.* 1994). Reproductive status of adult wombats was assessed through observations on lactation and pouch condition in females and the size of testes and accessory glands in males (D. Taggart, pers. comm.). Large, furred joeys were removed from the pouch for measurement of head length, pes length and total length. To minimise disturbance, the length of smaller joeys from nose to tail base was approximated using a tape measure wrapped around the outside of the pouch. Pouch young size was used to estimate birth month with reference to growth and development patterns established for *L. latifrons* (Taggart *et al.* 2007).

All wombats independent of the pouch were tattooed with a three-digit number in the ear (right, males; left, females). From 1995 onwards, a microchip was implanted subcutaneously in the intrascapular region of all independent wombats. Wombats were monitored in a recovery crate (45 cm W × 85 cm H × 110 cm L) until they showed no on-going effect of the anaesthetic and then released down their burrow of capture.

Sex ratio data are presented for trapping studies where at least 10 wombats were captured, and for all hair censuses.

Hair census

The hair census technique replaced live trapping as a method to estimate population size in 2000. Hair censuses were undertaken at Epping Forest NP in 2000, 2001, 2002, 2005, 2007, 2010, 2013 and 2016. During a hair census, wombat hairs with attached follicles were collected on double-sided sticky tape (Tesa Tape #4970) strung across the entrances of all active burrows. Hair tapes were set at a height so that wombats passing under them would leave some hairs stuck to the tape. Hair samples were collected over seven consecutive nights in August–October of the census year. Tape was set in all burrows recorded as active during burrow activity monitoring just prior (within three months) of hair collection.

DNA was extracted from the follicles of single hairs and DNA profiling in the laboratory was used to identify and sex individual hair donors (Sloane *et al.* 2000; Banks *et al.* 2003a; White *et al.* 2014). A genotyping error rate of 0.08% was recently estimated using repeat genotyping of a random selection of hair samples

(Taylor and Fewster 2017). A conservative approach was taken to declaring new individuals: genotypes detected only once and differing by only a single allele from another genotype were closely scrutinised. This included extra rounds of genotyping with additional markers in an effort to distinguish between genotyping error and high genetic similarity in such situations. The resulting data based on hair capture may be treated similarly to actual captures of wombats, and separately used to estimate wombat population size and sex ratios. The genetic data are available from the authors on request.

To estimate population size, a capture history was compiled for each declared individual, specifying its pattern of capture and non-capture over the seven nights surveyed within each year. Data for different years were analysed separately. Six closed-population capture–recapture models were fitted to the data for each year. These comprised three models in which all animals are assumed to share the same set of capture probabilities (models M_0, M_t, and M_{tb}: Otis *et al.* 1978), and three models known as two-point mixture models that allocate animals to two different groups, one group corresponding to 'more catchable' animals and the other to 'less catchable' animals (model M_h: Pledger 2000). The notion of catchability allows for differences in individual wombat behaviour, with 'less catchable' animals potentially corresponding to smaller individuals that can walk beneath hair tapes without touching them, individuals that favour undiscovered burrow exits, or individuals that share a burrow with a large wombat that habitually exits the burrow first and sometimes breaks the tape. The three simpler models assume a single capture probability for all nights (model M_0), a different capture probability for each night (model M_t), or a different capture probability for each night along with a behavioural response to capture that allows wombats to become either trap-happy or trap-shy after their first capture (model M_{tb}). The three mixture models assume that the capture probabilities within each group are constant across nights (mix.$M_0.M_0$), vary across nights (mix.$M_t.M_t$) or are constant for one group and vary for the other group (mix.$M_0.M_t$). Parameters governing capture probabilities, behavioural effects, and group membership are estimated along with population size in each model. Models were fitted by maximum likelihood using custom code written in *R* (R Core Team 2015). For each hair census, the best-fitting model was selected using Akaike's Information Criterion (AIC).

Two goodness-of-fit tests were used to assess the adequacy of the selected model for each year. The first test compared the frequency distribution of the number of nightly captures among wombats, where each wombat may be caught between 1 and 7 times, with the distribution predicted by the fitted model. The second test compared the maximised likelihood value with the distribution of values obtained if data were simulated from the fitted model.

Data on males and females were pooled for a joint analysis of each hair census. The six models were also fitted to the single-sex data within each year, to cross-check the results from the pooled data.

Passive infrared camera monitoring

Passive infrared (PIR) cameras (Bushnell; Browning) were used to collect data on wombat behaviour, activity and reproductive patterns at Epping Forest NP from November 2011 to June 2019.

On average, 12 (± 4 s.d.) cameras were set across the park each month at burrow entrances or water troughs showing signs of high levels of wombat activity. Once wombat activity was detected at a burrow or water trough, the camera was usually left there permanently to continuously monitor individual wombats, where possible. Cameras operated 24 h per day and were set on still capture or a combination of still and video capture. Cameras were usually placed at least 300 m apart. All female wombats with pouch young were recorded and individually identified via distinctive markings (ear tags, hair loss, ear nicks), size and location (see examples of recognisable wombat features in Appendix 2).

Female wombats with pouch young were classified as having small, medium or large pouches. To ensure consistency, scoring was completed by the same experienced (30 years working with wombats) individual (A. Horsup). The ages of pouch young were estimated using the development timetable established by Taggart *et al.* (2007) for *L. latifrons*. Small pouches were deemed to contain pouch young that were 2 months old (range 1–3 months); medium pouches, a 5-month-old pouch young (range 4–6 months); and large pouches, an 8-month-old pouch young (range 7–9 months). Based on these estimates, the birth month of each pouch young was calculated. We totalled the number of births recorded for each month to identify any relationship with environmental variables.

Modelling environmental effects on reproduction

Using the PIR camera data between 2011 and 2019, we examined the effect of two temperature variables: monthly mean minimum and maximum temperature. We also examined four rainfall variables: total current month rainfall; maximum rainfall event size; number of rain days; and cumulative total rainfall prior to current month. Rainfall over various periods was assessed to identify any lag in reproduction caused by primary productivity pulses (Noy-Meir 1973). The first three rainfall variables were calculated for the current month and one month prior to each survey month. All four variables were calculated for 2, 3, 6 and 12 months prior to the current month.

We used generalised additive models (GAMs) to investigate the influence of environmental variables because initial data exploration showed clear non-linear relationships between response and predictor variables (Zuur *et al.* 2014). To account for known seasonal variation in births, we included the average minimum monthly temperature. All continuous covariates were standardised to account for the different measurement scales among covariates (Zuur *et al.* 2009). To account for variation in survey effort over time, the logarithm of the number of burrows was included as an offset in final models (Zuur *et al.* 2014). Notably, the number of burrows surveyed was strongly correlated ($\rho = 1.0$) with, and therefore also accounted for, changes in population estimates and area surveyed over time.

All variables were checked for outliers and collinearity using Pearson correlation coefficients (<0.70) and variance inflation factors (<3; Zuur *et al.* 2014). If two variables were correlated, we retained the variable considered most ecologically relevant to wombat reproduction. Where no ecological priority could be applied, variables were retained and included in five candidate models (including the null model) that assessed all viable combinations (Appendix 3).

Data exploration revealed zero inflation within the data; therefore, a zero-inflated Poisson distribution was used, for which the linear predictor specifies the logarithm of the mean of the Poisson component. We ranked candidate models based upon the Akaike's Information Criterion (AIC) corrected for small sample size (AIC_c) (Burnham and Anderson 2002). For all candidate models we also calculated the ΔAIC_c (difference between the AICc of the model of interest and lowest AIC_c of all candidate models) and the amount of null deviance explained by the model (% dev) (Burnham and Anderson 2002; Zuur *et al.* 2009). All models that performed better than the null model were presented for interpretation. All analyses were generated and plotted using packages *mgcv* (Wood and Scheipl 2014), *MuMin* (Barton 2014) and *ggplot2* (Wickham 2009) in the statistical program *R* (R Core Team 2015).

Results

Population size estimates

Estimated population sizes and 95% confidence intervals for all hair censuses from 2000 to 2016 are shown in Fig. 1 and detailed in Appendix 4. For all eight censuses, the selected model was a two-point mixture model, namely model mix.$M_0.M_0$ for all years except 2010, and model mix.$M_0.M_t$ in 2010, with the time-varying probabilities belonging to the more-catchable group. In each case, the top model had an AIC score between 3.4 and 7.1 points lower than the second-ranked model, which was always an alternative two-point mixture model. Goodness-of-fit tests indicated model adequacy in all cases. In contrast, the single-group models (M_0, M_t, and M_{tb}) exhibited a severe lack of fit, highlighting the importance of controlling for heterogeneity in capture probability among wombats when estimating population size. Notably, the 2000 CMR estimate of 113 wombats made by Banks *et al.* (2003a) is revised to 96 by this analysis, although the male-biased sex ratio is unchanged.

For most surveys, there was close concordance between the estimated population size from the pooled data, and the sum of the male and female estimates, with the discrepancy being fewer than six individuals for seven of the eight surveys. A higher discrepancy of 21 individuals for the 2013 survey was due to a high-variance estimate from the male-only data in that year. The general closeness of results suggests that both the male and female portions of the population were well described by the two-point mixture models.

The hair census estimate for 2016 was 245 wombats (95% confidence interval 194–309). The upward trend in the size of the Epping Forest population is continuing (see Fig. 1). The single-sex analyses estimated 122 males and 117 females, which sums to 239 wombats, close to the pooled-data estimate of 245. The implied sex ratio does not differ significantly from parity in a Chi-square test ($P = 0.75$).

Wombat numbers, as determined by hair censuses at Epping Forest NP, have continually increased since 2000, with the exception of a decline in 2001 and 2002 caused at least in part by dingo predation of at least seven wombats (Banks *et al.* 2003b), and probably more, whose remains were undetected. Overall, the population increased at a mean annual rate of 6% per year from 2000 to 2016, an impressive rate for a relatively slow-breeding species (Fig. 1 and Appendix 4).

Population structure

The estimated sex ratio of the population has fluctuated considerably from 1985 to 2016 (Fig. 2). The sex ratio apparently did not depart significantly from parity during trapping in the 1980s, became significantly male-biased during trapping in the 1990s, and returned to parity from around 2001 onwards.

Burrow activity and population estimates

Since Epping Forest NP was fenced to exclude cattle in 1981, burrow activity levels have averaged approximately 50% per year. The total number of burrows on Epping Forest NP was 75 in 1974 and has increased to 493 in 2020, as the population has expanded throughout the park (Figs 3, 4).

The mean number of active burrows per year is strongly positively correlated with population estimates made on 12
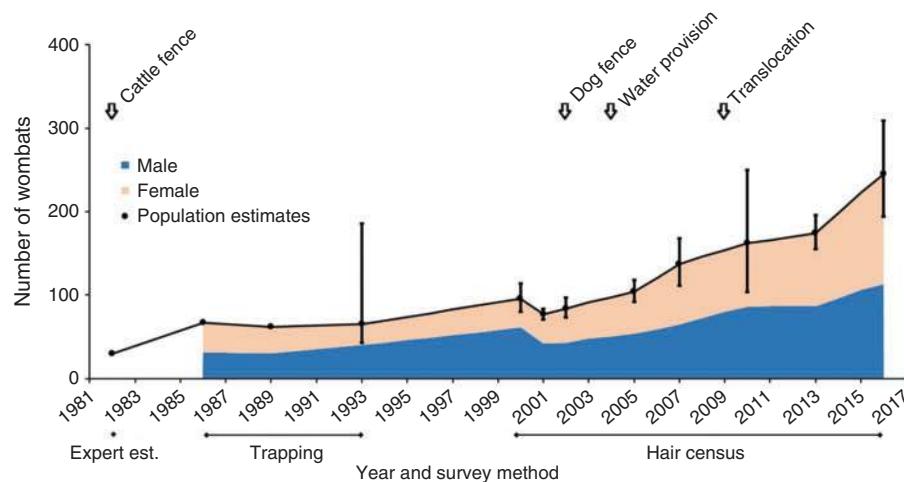
Fig. 1. Population estimates for *L. krefftii* at Epping Forest NP based on expert estimation (Gordon *et al.* 1985), trapping (Hoyle *et al.* 1995), and hair censuses (Taylor and Fewster 2017). Sex ratio from 1986 and the timing of significant management actions are indicated.
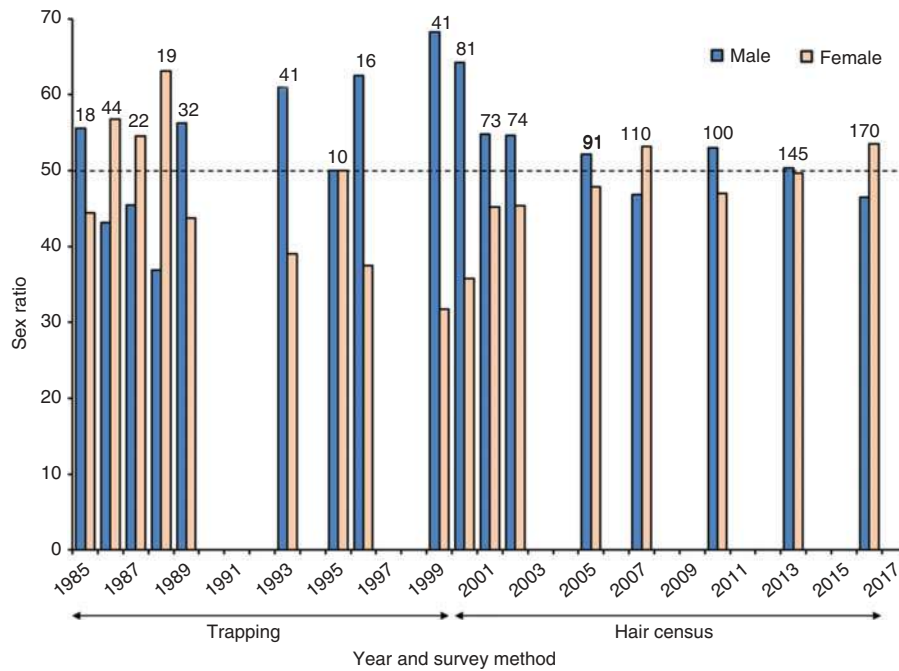
Fig. 2. Sex ratio of the *L. krefftii* population at Epping Forest NP during trapping studies (1985–99) and hair censuses (2000–16). Numbers of unique wombats captured in each trapping study and hair census are shown. Dashed line indicates the 50:50 sex ratio.
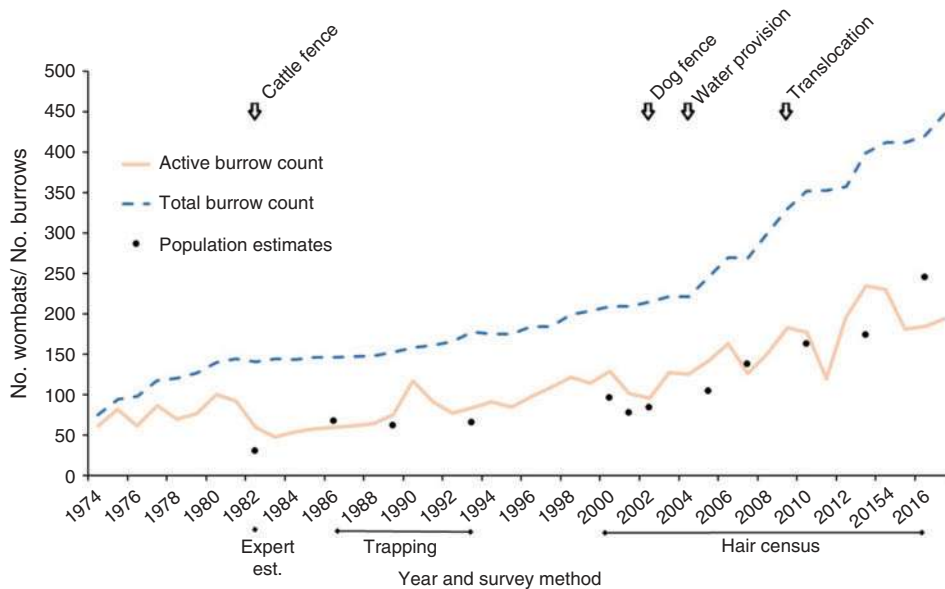
Fig. 3. The total number of burrows (dashed line) and total number of active burrows (solid line) at Epping Forest NP since burrow monitoring began in 1974. Black dots indicate when the population was estimated, and the estimated number of wombats. The timing of significant management actions is indicated.

occasions since the recovery program commenced in the early 1970s ($R^2 = 0.87$, d.f. = 10, $P < 0.01$) (Fig. 1). During this period, there has been approximately one active burrow to every wombat.

Reproductive patterns

The 33 years and 12 544 trap nights at Epping Forest NP yielded 598 captures of wombats, involving 147 individuals. Of these, 47% ($N = 69$) were female (Appendix 4) and these females
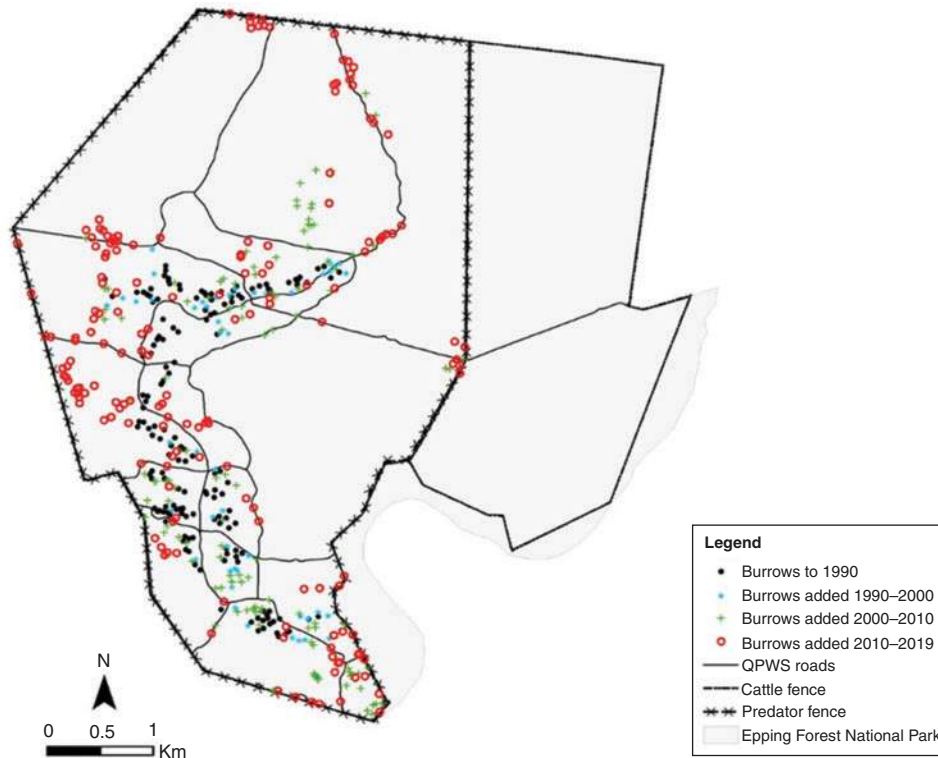
Fig. 4. The distribution of burrows at Epping Forest NP by decade since monitoring began in 1974.
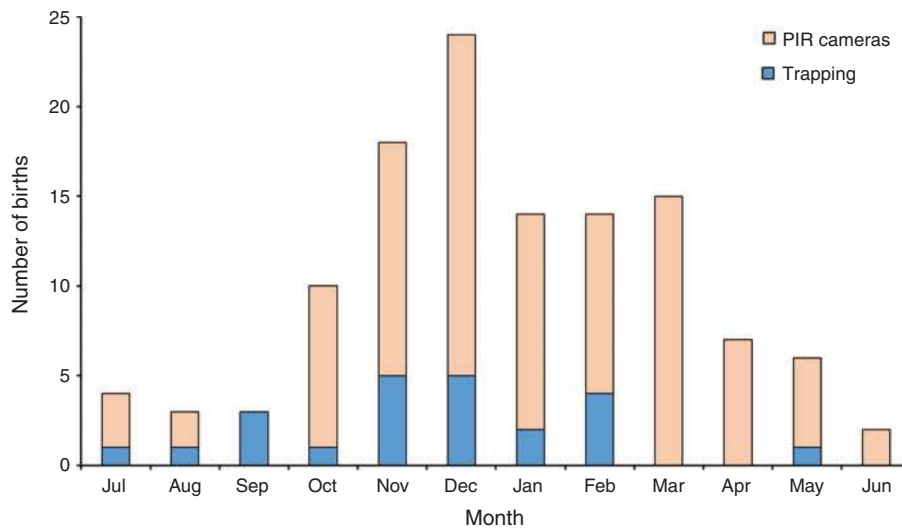
Fig. 5. Births per month at Epping Forest NP, determined from trapping ($n = 24$) and PIR cameras ($n = 97$).

carried only 24 unique pouch young (Appendix 5). Birth estimates generated by remote camera data have added another 97 unique births to the data set. Almost 80% of all births ($N = 95$) occurred between October and March, preceding and including the summer wet season (Fig. 5).

Although breeding rates varied among trapping studies, no correlations were found between annual rainfall totals

and the number of females with pouch young ($R^2 = -0.17$, d.f. = 12, $P = 0.57$), lactating ($R^2 = -0.11$, d.f. = 12, $P = 0.70$) or non-breeding ($R^2 = -0.14$, d.f. = 12, $P = 0.63$) (Fig. 6).

Analysis of the influence of the timing of rainfall showed that only a single GAM (M4) performed better than the null model, with only one variable – cumulative monthly rainfall in the six months prior to sampling – having a significant effect
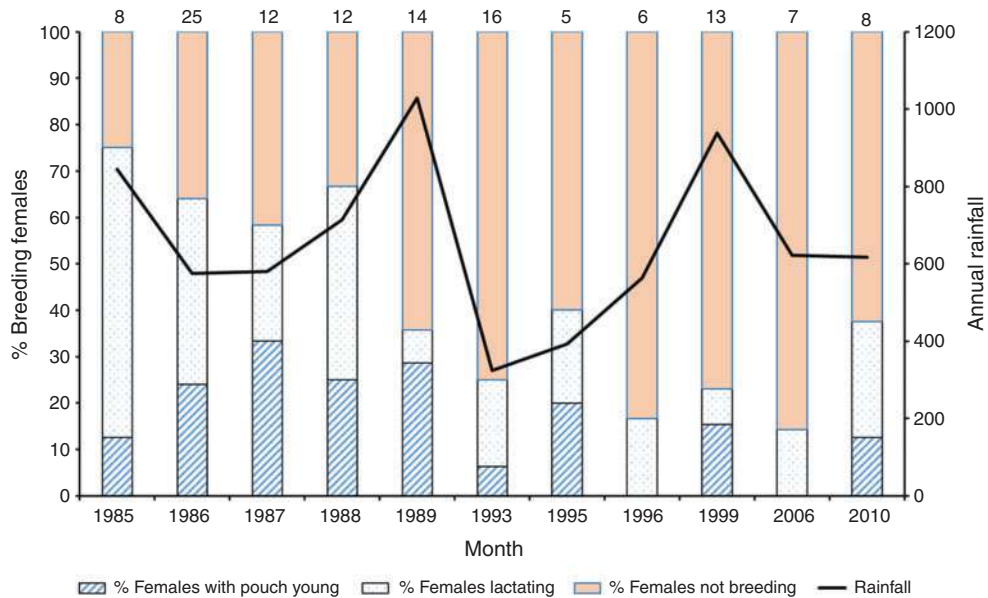
Fig. 6. The relationship between breeding rate and rainfall at Epping Forest NP for years in which at least five females were captured during trapping studies. Number of females is shown above each bar.
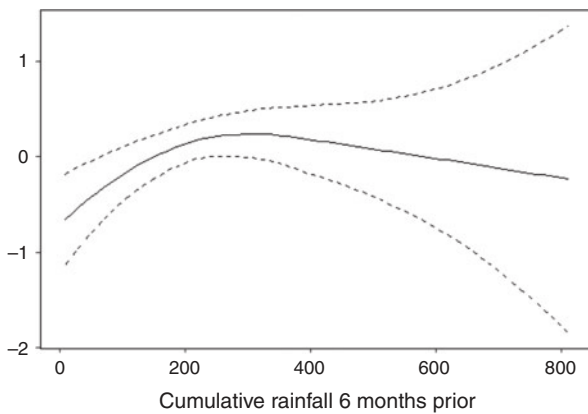
Fig. 7. Predicted change (GAM smoother) in the likelihood of detecting females with pouch young over increasing levels of cumulative rainfall during the period six months prior to estimated birth dates. Solid line = GAM model fit; dotted lines indicate 95% confidence bands.

(estimated d.f. = 7.15, $P = 0.02$). When rainfall was below 200 mm, a reduction in births was estimated, indicating a reproductive threshold in the species (Fig. 7). However, because of the limited amount of data available ($n = 12$) for periods with high rainfall (>400 mm), caution should be used when interpreting predictions above this rainfall level due to the large confidence intervals.

Discussion

Population trends

Wombat numbers at Epping Forest NP have increased eight-fold since 1974, from 30 to 245, despite a six-year drought, the likely dispersal of female wombats off-park prior to predator fencing, a significant predation event, and the removal of 15 individuals

for translocation. Importantly, the latest population estimate is approaching the predicted carrying capacity at Epping Forest NP of 300–400 wombats (Johnson 1991; Steinbeck 1994).

Several factors have likely contributed to the upward trend. First, the negative effect of trapping on the health and body weight of *L. krefftii* captured more than once within six months was highlighted by Hoyle *et al.* (1995). Thus, the reduction in frequency and intensity of trapping since 1999 may have contributed to enhanced survival and breeding. Second, the increase in availability and quality of food sources (mainly introduced buffel grass, *Cenchrus ciliaris*) may have benefitted the wombats. *Cenchrus ciliaris* has increased significantly across the park (Back 2013), reducing species diversity and creating significant fuel loads. However, when green and actively growing, it is more nutritious than some of the native grass species that *L. krefftii* normally eats (*Aristida* spp., *Enneapogon* spp.: Horsup 2003). Finally, the construction of the predator fence in 2002 and the provision of water throughout all wombat habitat since 2004 is likely to have improved survival and reproduction rates.

There are a number of factors that can impose a negative effect on wombat abundance, including diseases, such as mange (Ruykys *et al.* 2013), competition from other native and exotic species (Wells 1973; Cooke 1998; Taggart *et al.* 2020), human–wombat conflict (Tartowski and Stellman 1998), drought (Gaughwin *et al.* 1998; Wells 1973; Taggart *et al.* 2020), declining native grasslands, and future climate change (Marshall *et al.* 2018). The latter three are potentially problematic for the northern hairy-nosed wombat at Epping Forest National Park but can be alleviated to a certain extent by provision of water and supplementary feed, and control of buffel grass.

In 1974, the relationship between the number of active burrows and the number of *L. krefftii* was unclear. This relationship is now well understood at Epping Forest NP, with roughly

one active burrow to each wombat. This strong association means that burrow activity monitoring should continue to be used to monitor *L. krefftii* population trends. A simple technique, it creates no stress for the wombats and can provide early warning of problems in the population.

Based on the 80–100 active burrows recorded by Gordon *et al.* (1985) from 1974 to 1982, there were possibly more wombats on Epping Forest NP than the estimated 20–30. However, given cattle were still present until 1981, the number of active burrows was probably higher than normal because the wombats required larger home ranges to find enough to eat. The decline in number of active burrows after cattle were excluded seems to confirm this (Crossman *et al.* 1994). For *L. latifrons*, the relationship is approximately one active burrow to 0.5 wombats, although this can vary with soil type, region and rainfall (Swinbourne *et al.* 2018).

A major advantage of trapping over burrow activity monitoring is that it provides information on health and body condition, sex ratio and reproductive status. Sex ratios at Epping Forest NP were equal throughout the 1980s and highly skewed towards males throughout the 1990s. It was hoped this bias was an artefact of trapping, with males being more trappable than females, perhaps influenced by the long drought from 1992–97. However, a male bias was also evident in the first hair census in 2000. The 2000 census also documented a significant increase in numbers to 96 (revised downwards from the estimate of Banks *et al.* (2003*a*) by the analysis in this paper) from the 1993 estimate of 65 wombats (Hoyle *et al.* 1995; Taylor and Fewster 2017).

By the 2001 and 2002 hair censuses, the sex ratio had returned to parity and remained essentially equal through to 2016. The prevention of dispersal by females following the construction of the predator fence in 2002 is considered the most likely reason for the return to parity, although there is no direct evidence for this. The trend for females to disperse at Epping Forest NP was first detected by Johnson and Crossman (1991) during trapping and this trend has since been confirmed in the two other wombat species (Banks *et al.* 2002; Walker *et al.* 2008). In the 1980s, female dispersal off-park may have been uncommon because wombat numbers were still low, suitable habitat on park was readily available, food was plentiful following the removal of cattle in 1981 and rainfall was good. In the early 1990s, numbers may have recovered enough that there was increasing pressure for space within the occupied burrow complexes. The beginning of the severe 1990s drought in 1992 and the subsequent reduction in food quantity and quality may have encouraged females to seek out new habitat off the park, probably taking them into unsuitable habitat where they would likely have perished.

It is possible that severe drought may have led to female-biased mortality, although we have no evidence for this. Certainly, the drought reduced breeding rates in the population in the 1990s, as detected during trapping studies (Horsup 1998). In *L. latifrons* in South Australia, poor winter–spring rainfall (equivalent to wet season rainfall for *L. krefftii* at Epping Forest NP), has a significant effect on the abundance of *L. latifrons* in the following winter–spring. Taggart *et al.* (2020) found that several consecutive years of above-average rainfall are necessary before effective wombat population increase occurs.

With the ability of DNA profiling from single hairs to estimate population size and sex ratio, trapping is now rarely

necessary. However, as the population expands it is becoming increasingly difficult to reliably distinguish between individual *L. krefftii*, because genetic bottlenecking has resulted in very low allelic and genotypic diversity, and generation of new genetic diversity in small populations is negligible (Hartl 1980; Taylor *et al.* 1994). Next-generation sequencing approaches are being explored to access genome-wide variation with the aim of improving the specificity of DNA profiles. Although such approaches are becoming routine, it is not known if they will work with the small amounts of DNA recovered from single, remotely collected hairs and this requires investigation. If the approach requires the use of multiple hairs from a tape, it will be essential that it allows for the identification and exclusion of pooled samples (i.e. those consisting of hairs from multiple individuals), whose inclusion would lead to recording of 'false' genotypes.

Reproductive patterns

A seasonal pattern of reproduction in *L. krefftii* centred on summer rainfall (the 'wet season') was first reported by Crossman *et al.* (1994), who suggested this was timed so that weaning occurs in the subsequent wet season when pasture conditions should be optimal for newly independent wombats. However, they also noted that this meant that the most energy-demanding phase of lactation coincided with the time of year when pasture productivity was lowest.

This peak of births during the months when pasture growth is optimal matches the seasonal breeding pattern of *L. latifrons*: most births occur in spring (August–October), which is when most rain falls in South Australia (BOM 2020). This pattern means that young wombats, who spend approximately nine months in the pouch and a further three months suckling, are beginning to eat solid food 12 months after birth, in the next wet season/spring. Taggart *et al.* (2005) pointed out that when female wombats breed seasonally in response to variable environmental conditions, such as rainfall, the exact timing of reproduction may vary from year to year, indicating potential impacts of unknown variables or more fine-scale response to rainfall than can be detected when using annual totals. This appeared to be the case at Epping Forest NP. Although nearly 80% of all births at Epping Forest NP were estimated to have occurred from October to March, births did occur in all months of the year.

Our investigation showed that, in *L. krefftii*, cumulative rainfall over the previous six months increased the number of pouch young seen in the population. It is likely that the sustained flush in primary productivity caused by rainfall helps to improve body condition and therefore increase reproductive output across the population. This pattern has been shown in *L. latifrons* in South Australia where the amount of annual winter and spring rainfall is strongly linked to population trends the following year (Taggart *et al.* 2020). This causal relationship and the dominance of *C. ciliaris* at Epping Forest NP may also help to explain why *L. krefftii* shows a response threshold to rainfall below 200 mm in the previous six months. *Cenchrus ciliaris* is known to rapidly respond to rainfall and show response thresholds to increased access to water (Ward *et al.* 2006). Further studies, examining the correlation between the amount of new grass growth, rainfall and reproductive output in *L. krefftii* would help to support these findings.

Although we know little about individual patterns of reproduction, the camera observations of a tagged female *L. krefftii*

who produced five young from 2011 to 2019 provides some evidence of fecundity. Although there were dry years during that period, the provision of water would have been a major advantage for lactating females (this tagged female has a water trough only 70 m from her burrow).

Recommendations

It is recommended that burrow activity monitoring be conducted on an annual basis to determine general population trends and be supported by genetic monitoring every 3–5 years. Genetic monitoring provides more detailed and accurate demographic data, while burrow activity monitoring is a more cost-effective technique for assessing general population trends. Trapping should be used only to address specific research and recovery objectives because of its impact on wombats and significant use of resources. PIR cameras should continue to be used to monitor wombat behaviour, reproduction and health.

Conclusions

Lasiorhinus krefftii has recovered from about 30 wombats in one population in the early 1980s to more than 250 wombats in two populations by 2020. However, the species is still highly vulnerable to extinction given that 95% of individuals exist at one site, Epping Forest NP. A disease outbreak, major wildfire or flood could cause the extinction of this population. To reduce this risk, existing protective measures for the Epping Forest NP population should be continued and intensified where possible. The highest priority to reduce the risk of extinction for this species is to create additional, geographically separate and viable *L. krefftii* populations.

Since 1997, there have been several major searches throughout the historic range of *L. krefftii* where over 120 properties have been assessed for their habitat suitability. To date, the success of these searches has been the establishment of the second colony at Richard Underwood Nature Refuge and a short-listing of several potential sites. *Lasiorhinus krefftii* has specific habitat requirements, including deep sandy soils with 10–20% clay content and a year-round food supply. Finding an area of intact habitat large enough to support a self-sustaining population is very challenging; however, the search continues. The increasing numbers of *L. krefftii* at Epping Forest NP means the population is approaching the site's carrying capacity and that we must be ready to act. What a good conservation problem to have!

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

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Appendix 1.   Annual trapping data at Epping Forest NP for years in which there was a minimum of 10 wombat captures

'Unique wombats' is the total number of unique individuals captured in each year and cannot be summed because of repeat captures in different years. 'All wombat captures' is the total of all captures in each year. There are no data for the number of trap nights in 1988 or for the number of nights of trapping for 1985–89

Date	Unique wombats						All wombat captures						Nights trapping
	Male	Female	Total	% male	Trap-nights	Capture rate	Male	Female	Total	% male	Trap-nights	Capture rate	
1985	10	8	18	56			37	18	55	67			
1986	19	25	44	43	3061[A]	0.027[A]	88	64	152	58	3061[A]	0.080[A]	
1987	10	12	22	45			18	21	39	46			
1988	7	12	19	37			15	26	41	37			
1989	18	14	32	56	974	0.033	27	21	48	56	974	0.049	
1993	25	16	41	61	1850	0.021	61	30	91	67	1950	0.047	79
1995	5	5	10	50	690	0.014	12	13	25	48	690	0.036	29
1996	10	6	16	63	990	0.016	19	17	36	53	990	0.036	43
1999	28	13	41	68	2371	0.017	39	21	60	65	2371	0.025	85
2006	5	7	12	42	464	0.026	6	7	13	46	464	0.028	20
2009	17	4	21	81	1272	0.017	21	5	26	81	1272	0.020	51
2010	3	9	12	25	772	0.016	3	9	12	25	772	0.016	35
Total							346	252	598	58	12544	0.048	342

[A]Cumulative totals from 1985 to 1987.

Appendix 2.   Examples of wombat features that were recognisable on PIR camera photographs. Clockwise from top left: hair loss patterns; distinctive ear nicks; females and juveniles; ear tags and pouches.

Appendix 3.   Variables included in all candidate models used in generalised additive modelling

MTmin, Standardised mean monthly minimum temperature; #B, log(no. of burrows surveyed); TR#m, standardised total rainfall recorded in # months (0 = current month); CR#m, standardised total cumulative rainfall recorded over # months prior

Model ID	Model composition
M0	Births ~ MTmin + offset(#B)
M1	Births ~ MTmin + TR0m + TR1m + TR2m + TR3m + TR6m + CR12m + offset(#B)
M2	Births ~ MTmin + TR0m + CR2m + TR3m + TR6m + TR12m + CR12m + offset(#B)
M3	Births ~ MTmin + TR0m + CR3m + TR6m + TR12m + CR12m + offset(#B)
M4	Births ~ MTmin + TR0m + TR6m + CR6m + TR12m + CR12m + offset(#B)

Appendix 4.   Data for all hair censuses from 2000 to 2016 at Epping Forest NP

Population estimates and 95% confidence intervals are presented for pooled male and female data using the selected two-point mixture model for each year. The percentage of male and female wombats was calculated using the number of male and female genotypes

Year	Total no. of burrows	No. of burrow staped	No. of individuals sampled	Population estimate	95% C.I.	% Male	% Female
2000	209	193	81	96	80, 114	64	36
2001	209	193	73	77	71, 83	55	45
2002	215	195	74	84	73, 97	55	45
2005	240	205	91	104	92, 118	52	48
2007	310	251	110	137	111, 168	47	53
2010	342	243	100	162	104, 250	53	47
2013	408	354	145	174	155, 196	50	50
2016	440	325	170	245	194, 309	46	54

Appendix 5.   Breeding data for trapping studies at Epping Forest NP for years in which at least five females were captured

'No. of breeding females' is the total of 'No. of females with PY' (number of females with pouch young) and 'No. of lactating females' (females without a pouch young who were lactating)

Trapping year	No. of females captured	No. of females with PY	No. of lactating females	No. of breeding females	% breeding females
1985	8	1	5	6	75
1986	25	6	10	16	64
1987	12	4	3	7	58
1988	12	3	5	8	67
1989	14	4	1	5	36
1993	16	1	3	4	25
1995	5	1	1	2	40
1996	6	0	1	1	17
1999	13	2	1	3	23
2006	7	0	1	1	14
2010	7	0	1	1	14