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

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20 **Abstract**

21 The critically endangered northern hairy-nosed wombat *Lasiorhinus krefftii* currently exists at
22 only two locations in Queensland. Management, research and monitoring of the species at the
23 main Epping Forest National Park (Scientific) population has occurred over the last four
24 decades using a variety of tools, with the most complete dataset being provided by burrow
25 activity monitoring over that period. Following a series of trap-based surveys in the 1980s and
26 1990s, wombat monitoring has employed DNA profiling of hairs collected remotely on sticky
27 tape set at burrow entrances (since 2000), and passive infrared (PIR) cameras (since 2011).
28 These techniques have produced a wealth of new information on the species. Using this new
29 information, we aim to: 1) summarise the available demographic data and present new
30 estimates using novel techniques for *L. krefftii* at Epping Forest NP; and 2) characterise
31 reproductive patterns and their relationship with environmental factors for *L. krefftii* at Epping
32 Forest NP. We find an ongoing increase in the population size at Epping Forest National Park,
33 supported by healthy levels of reproduction despite periods of poor environmental conditions,
34 notwithstanding the finding that cumulative monthly rainfall six months prior to sampling
35 influenced birth rates. This trend suggests that the population will likely reach carrying
36 capacity in the near future. It is timely to harvest the population to provide founders to a new
37 site to establish an additional population which will also reduce the risk of extinction and help
38 secure the future of the species.

40 **Introduction**

41 The northern hairy-nosed wombat *Lasiorhinus krefftii* is one of the world's most endangered
42 mammals. Prior to the arrival of Europeans in Australia, the species was probably sparsely
43 distributed throughout a huge area of semi-arid eastern Australia from southern New South
44 Wales to northern Queensland. A combination of culling in the Riverina area of NSW to
45 reduce potential habitat for invasive European rabbits, drought, and competition for food with
46 introduced herbivores reduced the species to a single small population in central Queensland
47 by the 1970s (Crossman *et al.* 1994; Swinbourne *et al.* 2016).

50 *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,
52 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
54 Nature Refuge in southern Queensland. Despite a high mortality rate post 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
56 five successful births and a current population of 14 wombats.

58 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
60 Conservation Act 1999*. Current threats and conservation actions are listed in the
Conservation Advice (TSSC 2018).

62 The last population of *L. krefftii* was protected with the gazettal of Epping Forest NP in 1971.
64 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
66 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
68 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
70 2009-10 to establish a second population.

72 *Population trends*

Initial studies of the *L. krefftii* population at Epping Forest NP involved monitoring wombat
74 activity levels at burrow entrances. From 1975 to 1982, around 70% of burrows at Epping
Forest NP were scored as active by Gordon *et al.* (1985), who estimated the population
76 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
78 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.

80 During the first trapping studies of the species, from 1985 to 1989, 70 unique wombats in a
82 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
84 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
86 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.*
88 1997); and demonstrated for the southern hairy-nosed wombat, *L. latifrons* (Walker *et al.*
2008) and the bare-nosed wombat, *Vombatus ursinus* (Banks *et al.* 2002).

90 The recovery in the 1980s was short-lived. Trapping during a protracted drought in the 1990s
92 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
94 estimates: a capture-mark-recapture (CMR) analysis of trapping data in 1993 provided an
estimate of 65 wombats, indicating no population growth had occurred during the drought,
96 given population sizes estimates of 67 in 1985-87 and 62 in 1988-89 (Hoyle *et al.* 1995).

98 Since 2000, population estimates have been based on CMR analysis of detections of
100 individual-specific DNA profiles established from wombat hairs remotely collected at burrow
102 entrances - a technique in the early stages of development at the time of the first wombat
104 conference in Adelaide in 1994 (Taylor *et al.* 1998). The first full 'hair census' analysis in
106 2000 returned a population estimate of 113 individuals and confirmed the male-biased sex
108 ratio recorded during trapping in the 1990s (Banks *et al.* 2003a). Since then, seven more hair
110 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 re-analysis 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.

112 *Trends in survival and reproduction*

Adult mortality levels were low and estimated at less than 8% per year in the 1980s (Johnson
114 1991). Estimates in the 1990s using CMR methods indicated adult mortality levels of around
116 5% in good years (range 0-14%; S. Hoyle, pers. comm.). Life span in the wild can exceed 28
118 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.).

120 The rarity of *L. krefftii*, along with its nocturnal, fossorial and conservative habits, has meant
122 that understanding reproductive patterns has been difficult. The reproductive behaviour of the
124 closely related, and more common, southern hairy-nosed wombat, *L. latifrons*, is better
126 understood. Most *L. latifrons* young are produced during the winter-spring growing season,
128 from July to December (Taggart *et al.* 2007). Following around nine months of pouch life and
130 a further three months of suckling, young-at-foot are weaned in the following spring when
132 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.

134 PIR cameras have provided a non-invasive method to monitor *L. krefftii* at a level not
136 previously possible and enabled long-term data to be collected on individual wombats. For
138 example, observations of a single ear-tagged female *L. krefftii* have provided an indication of
140 the frequency of breeding: she produced five young in the nine years a PIR camera monitored
her burrow (A. Horsup, unpublished 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.

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

146 **The aims of this paper**

148 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
150 reproductive patterns and their relationship with environmental factors for *L. krefftii* at Epping
Forest NP.

152 **Methods**

Epping Forest National Park

154 Located 120 km north-west of Clermont in central Queensland, Epping Forest NP is 2,750 ha
in size, of which 600 ha is considered *optimal* wombat habitat and 1,400 ha is considered
156 *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, unpublished data). The wombat habitat and
158 vegetation of the park are described in DERM (2011).

160 Epping Forest NP is situated in a semi-arid zone on the Belyando river system in the upper
reaches of the Burdekin River catchment. The park was excised from Epping Forest and
162 Waltham 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
164 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
166 Clermont in December, the hottest month, was 34.8°C) and low in winter (the long-term mean
minimum of 6.7°C in July; BOM 2020). Several long-term droughts, lasting up to six years,
168 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
170 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
172 km from the study site; BOM 2019).

174 *Burrow activity monitoring*

The burrows of *L. krefftii* can be single-entranced or multi-entranced, with up to 11 entrances
176 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
178 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
180 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
182 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
184 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.

186

Trapping

188 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
190 considerably depending on monitoring strategies and logistical constraints (Appendix 1).
Wombats were captured in large steel cage traps (60 W x 90 H x 180 L cm) positioned at
192 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
194 to a radio transmitter, ensuring all trapped wombats were processed within two hours of
capture. Wombats were anaesthetised and processed on-site.

196

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; Figure 5).

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

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

216

Hair census

218 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, 220 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 224 in August-October of the census year. All burrows recorded as active during burrow activity monitoring just prior (within three months) of hair collection were taped.

226

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.

238 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_i , and M_{ib} ; 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

246 in individual wombat behaviour, with ‘less catchable’ animals potentially corresponding to
248 smaller individuals that can walk beneath hair tapes, 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
250 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
252 that allows wombats to become either trap-happy or trap-shy after their first capture (model
 M_{tb}). The three mixture models assume the capture probabilities within each group are constant
254 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
256 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
258 each hair census, the best-fitting model was selected using Akaike’s Information Criterion
(AIC).

260

Two goodness-of-fit tests were used to assess the adequacy of the selected model for each year.
262 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
264 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.

266

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

270

Passive infrared camera monitoring

272

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
274 June 2019. An average of 12 (± 4 SD) cameras were set across the park each month at burrow
entrances or water troughs showing signs of high levels of wombat activity. Once wombat
276 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
278 24 hrs 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
280 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).

282

Female wombats with pouch young were classified as having small, medium or large
284 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
286 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);
288 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
290 each pouch young was calculated. We totalled the number of births recorded for each month
to identify any relationship with environmental variables.

292

Modelling environmental effects on reproduction

294

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

296 examined four rainfall variables: total current month rainfall; maximum rainfall event size;
298 number of rain days; and cumulative total rainfall prior to current month. Rainfall over
various time lengths 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
300 current month and one month prior to each survey month. All four variables were calculated
for two, three, six and 12 months prior to the current month.

302

We used generalised additive models (GAMs) to investigate the influence of environmental
304 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
306 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.*
308 *al.* 2009). To account for variation in survey effort over time, number of burrows (log) was
included as an offset in final models (Zuur *et al.* 2014). Notably, the number of burrows
310 surveyed was strongly correlated ($\rho = 1.0$) with, and therefore also accounted for, changes in
population estimates and area surveyed over time.

312

All variables were checked for outliers and collinearity using Pearson correlation coefficients
314 (< 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
316 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
318 combinations (Appendix 3).

320 Data exploration revealed zero inflation within the data; therefore, a zero-inflated Poisson
(ziP) distribution was used, for which the linear predictor specifies the log of the mean of the
322 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
324 candidate models we also calculated the Δ AIC_c (difference between the AIC_c of the model of
interest and lowest AIC_c of all candidate models) and the amount of null deviance explained
326 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
328 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).

330

Results

332

Population size estimates

Estimated population sizes and 95% confidence intervals for all hair censuses from 2000 to
334 2016 are shown in Figure 1 and detailed in Appendix 4. For all eight censuses, the selected
model was a two-point mixture model, namely model *mix.M₀.M₀* for all years except 2010,
336 and model *mix.M₀.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
338 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-
340 group models (*M₀*, *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
342 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.

344

346 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
348 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
350 of the population were well described by the two-point mixture models.

352 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 Figure 1). The
354 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
356 in a chi-square test ($P = 0.75$).

358 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
360 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
362 year from 2000 to 2016, an impressive rate for a relatively slow-breeding species (Figure 1
and Appendix 4).

364

Population structure

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

370

Burrow activity and population estimates

372 Since Epping Forest NP was fenced to exclude cattle in 1981, burrow activity levels have
averaged around 50% per year. The total number of burrows on Epping Forest NP was 75 in
374 1974 and has increased to 493 in 2020, as the population has expanded throughout the park
(Figures 3 and 4).

376

The mean number of active burrows per year is strongly positively correlated with population
378 estimates made on 12 occasions since the recovery program commenced in the early 1970s
($R^2 = 0.87$, $df = 10$, $P < 0.01$; Figure 1). During this period, there has been approximately one
380 active burrow to every wombat.

382

Reproductive patterns

384 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
386 females 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
388 births ($N = 95$) occurred between October and March, preceding and including the summer
wet season (Figure 5).

390

Although breeding rates varied among trapping studies, no correlations were found between
392 annual rainfall totals and the number of females with pouch young ($R^2 = -0.17$, $df = 12$, $p =$
 0.57), lactating ($R^2 = -0.11$, $df = 12$, $p = 0.70$) or non-breeding ($R^2 = -0.14$, $df = 12$, $p = 0.63$;
394 Figure 6).

396 Analysis of the influence of the timing of rainfall showed that only a single GAM (M4)
398 performed better than the null model, with only one variable - cumulative monthly rainfall in
the six months prior to sampling - having a significant effect (edf = 7.15, p = 0.02). When
400 rainfall was below 200 mm, a reduction in births was estimated, indicating a reproductive
threshold in the species (Figure 7). However, because of the limited amount of data available
402 (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.

404 Discussion

Population trends

406 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
408 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
410 Epping Forest NP of 300-400 wombats (Johnson 1991; Steinbeck 1994).

412 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 6 months
414 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
416 increase in availability and quality of food sources (mainly introduced buffel grass, *Cenchrus*
ciliaris) may have benefitted the wombats. *Cenchrus ciliaris* has increased significantly
418 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
420 species *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
422 habitat since 2004 is likely to have improved survival and reproduction rates.

424 There are a number of factors that can impose a negative effect on wombat abundance
including diseases, such as mange (Ruyks *et al.* 2013), competition from other native and
426 exotic species (Wells 1989; Cooke 1998; Taggart *et al.* 2020), human-wombat conflict
(Tartowski and Stellman 1998), drought (Gaughwin *et al.* 1984; Wells 1989; Taggart *et al.*
428 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
430 National Park but can be alleviated to a certain extent by provision of water and
supplementary feed, and control of buffel grass.

432 In 1974, the relationship between the number of active burrows and number of *L. krefftii* was
434 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
436 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
438 population.

440 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,
442 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
444 decline in number of active burrows after cattle were excluded seems to confirm this

446 (Crossman *et al.* 1994). For *L. latifrons*, the relationship is about one active burrow to 0.5
wombats, although this can vary with soil type, region and rainfall (Swinbourne *et al.* 2018).

448 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
450 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
452 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
454 increase in numbers to 96 (revised downwards from the Banks *et al.* 2003a estimate by the
analysis in this paper) from the 1993 estimate of 65 wombats (Hoyle *et al.* 1995; Taylor and
456 Fewster 2017).

458 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
460 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
462 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;
464 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
466 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
468 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
470 seek out new habitat off the park, probably taking them into unsuitable habitat where they
would likely have perished.

472
It is possible that severe drought may have led to female-biased mortality, although we have
474 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,
476 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.
478 Taggart *et al.* 2020 found that several consecutive years of above-average rainfall are
necessary before effective wombat population increase occurs.

480
With the ability of DNA profiling from single hairs to estimate population size and sex ratio,
482 trapping is now rarely necessary. However, as the population expands it is becoming
increasingly difficult to reliably distinguish between individual *L. krefftii*, because genetic
484 bottleneaking has resulted in very low allelic and genotypic diversity, and generation of new
genetic diversity in small populations is negligible (Hartl 1988; Taylor *et al.* 1994). Next
486 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
488 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
490 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
492 inclusion would lead to recording of 'false' genotypes.

494 *Reproductive patterns*

496 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
498 occurs in the subsequent wet season when pasture conditions should be optimal for newly
independent wombats. However, they also noted that this meant the most energy-demanding
phase of lactation coincided with the time of year when pasture productivity was least.

500 This peak of births during the months when pasture growth is optimal matches the seasonal
502 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
504 spend around 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)
506 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,
508 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.
510 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.

512 Our investigation showed that, in *L. krefftii*, cumulative rainfall over the previous six months
514 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
516 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
518 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 understand why *L. krefftii*
520 shows a response threshold to rainfall below 200 mm in the previous six months. *Cenchrus*
ciliaris is known to rapidly respond to rainfall and display response thresholds to increased
522 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
524 support these findings.

526 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
528 evidence of fecundity. Although there were dry years in that period, the provision of water
would have been a major advantage for lactating females (this tagged female has a water
530 trough only 70 m from her burrow).

532 *Recommendations*

It is recommended that burrow activity monitoring be conducted on an annual basis to
534 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
536 activity monitoring is a more cost effective technique for assessing general population trends.
Trapping should only be used to address specific research and recovery objectives because of
538 its impact on wombats and significant use of resources. PIR cameras should continue to be
used to monitor wombat behaviour, reproduction and health.

540 *Conclusions*

542 *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
544 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.
546 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
548 extinction for this species is to create additional, geographically separate and viable *L. krefftii*
populations.

550

Since 1997, there have been several major searches throughout the historic range of *L. krefftii*
552 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
554 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
556 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.*
558 *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!

560

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565 programs and hair censuses over the years. We also acknowledge the major contribution made
566 by the many volunteer caretakers who have lived continuously on Epping Forest NP since
2002. These people have downloaded and edited millions of photos taken on PIR cameras and
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572 census following his pioneering efforts delivering the first one. Thanks to Sarah Sargent for
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588

Conflicts of interest

590 The authors declare no conflicts of interest.

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778 **Appendix 1.** Annual trapping data at Epping Forest NP for years in which there was a
 780 minimum of 10 wombat captures. ‘Unique wombats’ is the total number of unique individuals
 782 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	3,061	0.027	37	18	55	67	3,061	0.080	
1986	19	25	44	43			88	64	152	58			
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	1950	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	12,544	0.048	342

784

786 **Appendix 2.** Examples of wombat features that were recognisable on PIR camera photos,
 788 clockwise from top left: hair loss patterns; distinctive ear nicks; females and juveniles; ear
 tags and pouches.



790

792 **Appendix 3.** Variables included in all candidate models used in generalised additive
 794 modelling. MTmin = Standardised mean monthly minimum temperature; #B = log(number of
 burrows surveyed), TR#m = Standardised total rainfall recorded in # months (0 = current
 month), CR#m = Standardised total cumulative rainfall recorded over # months prior.

796

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)

798

800 **Appendix 4.** Data for all hair censuses from 2000 to 2016 at Epping Forest NP. Population
 802 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.

804

Year	Total burrows	Burrows taped	Individuals sampled	Population estimate	95% C.I.	% Male	% Female
2000	209	193	81	96	80, 114	64	36
808 2001	209	193	73	77	71, 83	55	45
2002	215	195	74	84	73, 97	55	45
810 2005	240	205	91	104	92, 118	52	48
2007	310	251	110	137	111, 168	47	53
812 2010	342	243	100	162	104, 250	53	47
2013	408	354	145	174	155, 196	50	50
814 2016	440	325	170	245	194, 309	46	54

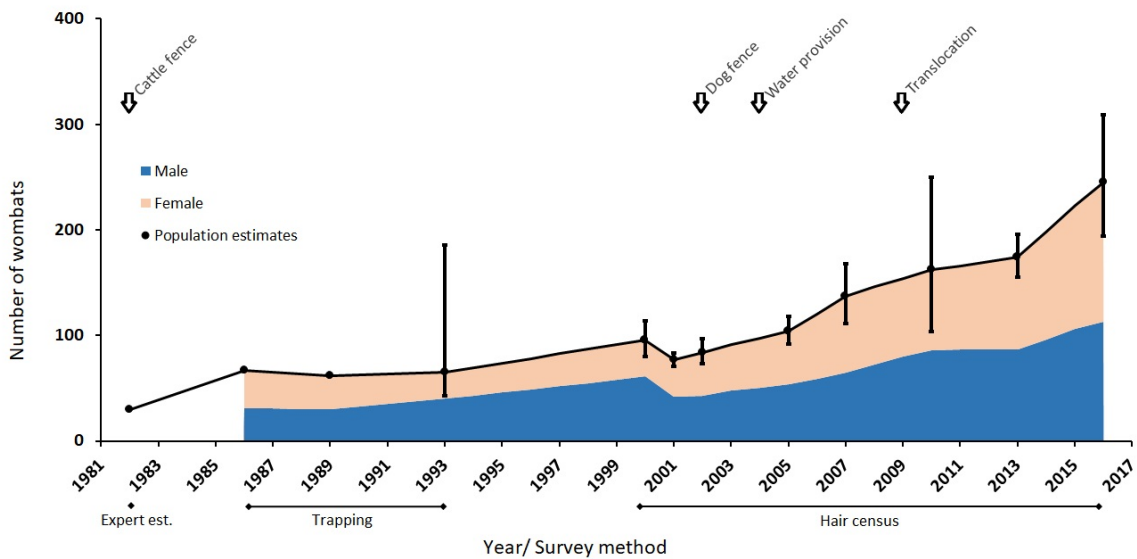
816

818 **Appendix 5.** Breeding data for trapping studies at Epping Forest NP for years in which at
 820 least five females were captured. ‘# Breeding Females’ is the total of ‘Females with PY’
 (number of females with pouch young) and ‘Lactating females’ (females without a pouch
 822 young who were lactating).

824	Trapping year	Females captured	Females with PY	Lactating females	# Breeding females	% Breeding females
	1985	8	1	5	6	75
826	1986	25	6	10	16	64
	1987	12	4	3	7	58
828	1988	12	3	5	8	67
	1989	14	4	1	5	36
830	1993	16	1	3	4	25
	1995	5	1	1	2	40
832	1996	6	0	1	1	17
	1999	13	2	1	3	23
834	2006	7	0	1	1	14
	2010	7	0	1	1	14

836

838

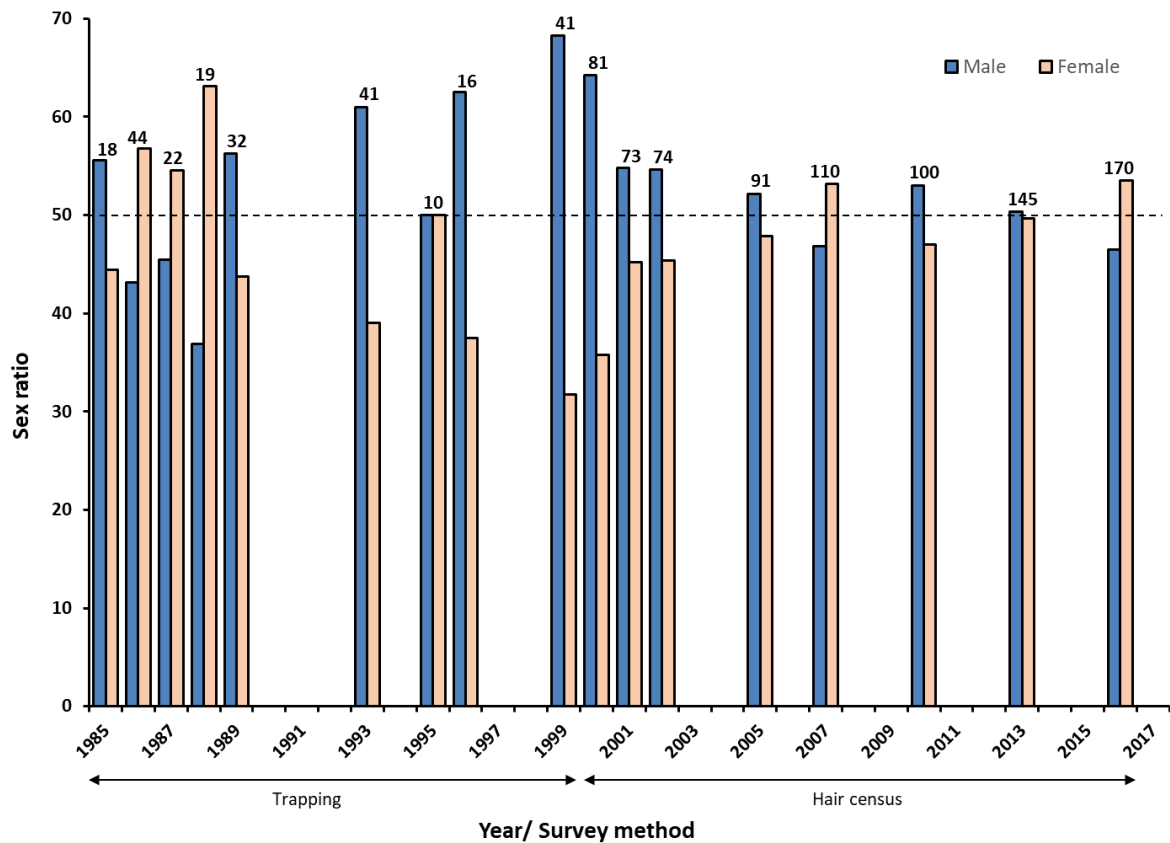


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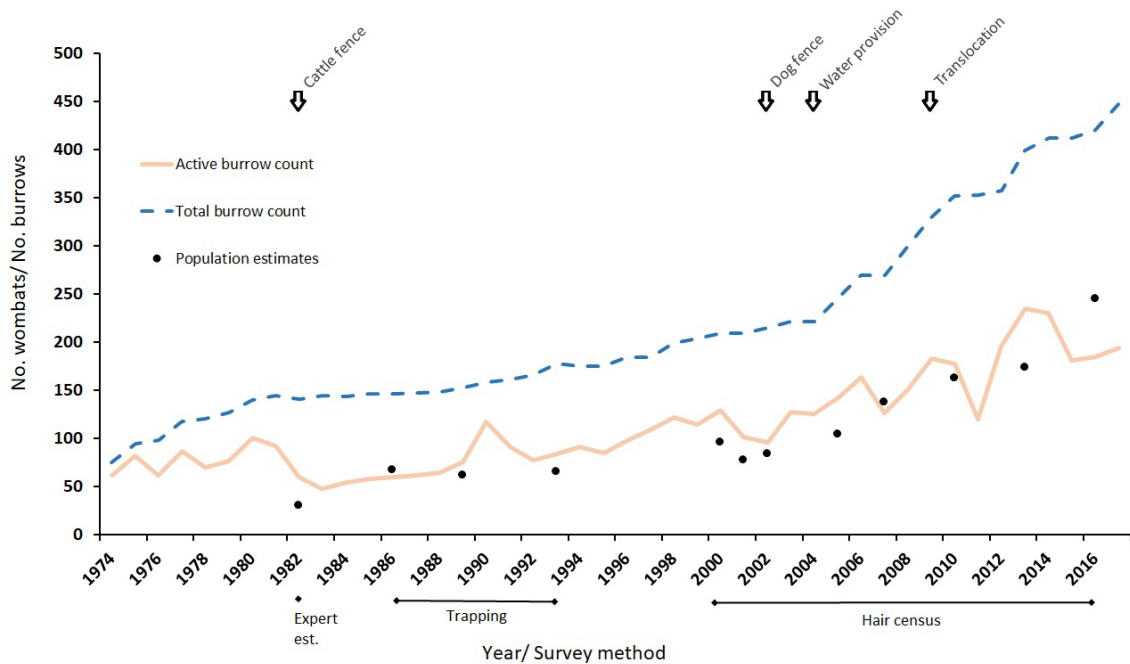
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844

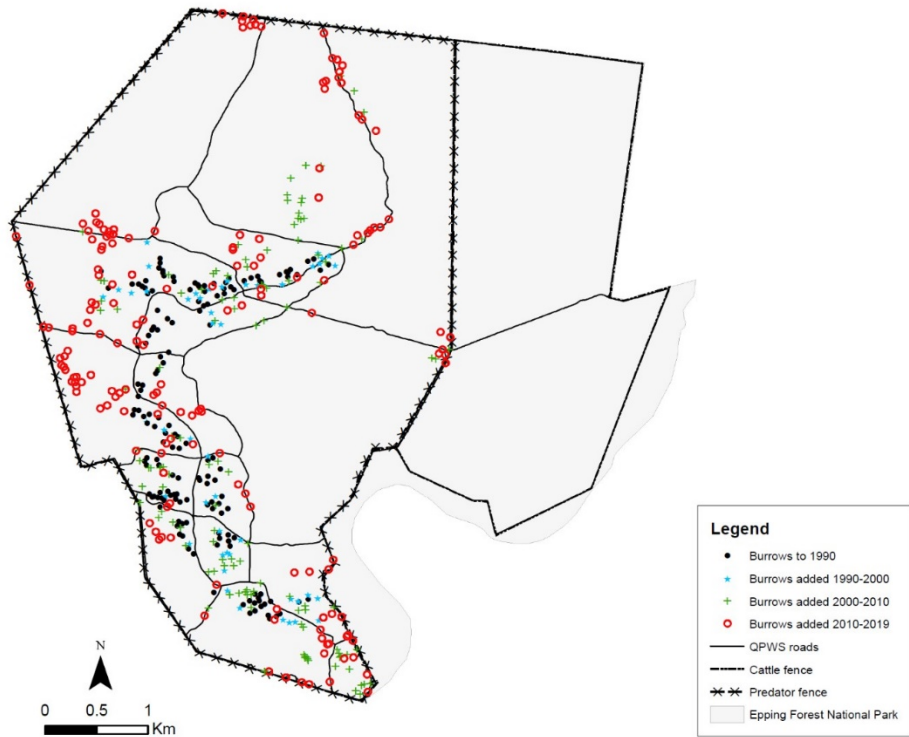
Figure 1. Population estimates for *L. krefftii* at Epping Forest NP based on expert estimation (Gordon *et al.* 1985), trapping (Hoyle *et al.* 1995), and hair censuses (Taylor and Fewster 2017). Sex ratio from 1986 and the timing of significant management actions is indicated.



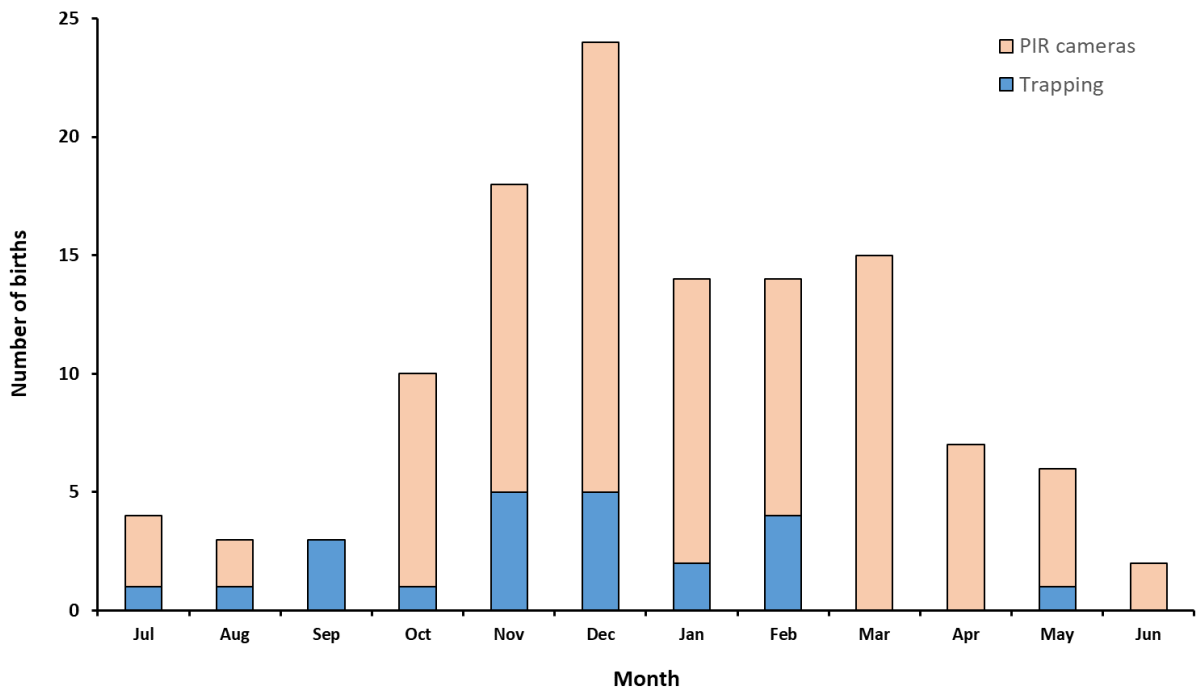
846 **Figure 2.** Sex ratio of the *L. krefftii* population at Epping Forest NP during trapping studies
 848 (1985-1999) and hair censuses (2000-2016). Numbers of unique wombats captured in each
 trapping study and hair census are shown. Dashed line is the 50:50 sex ratio.



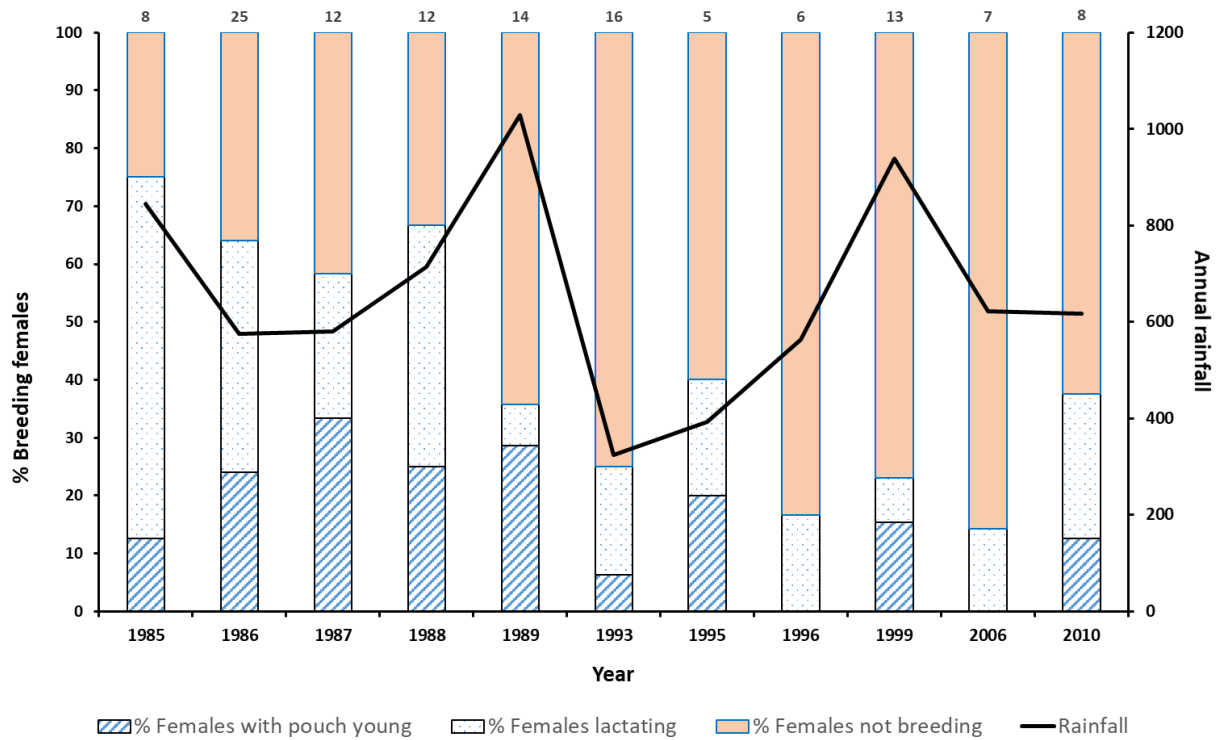
850 **Figure 3.** The total number of burrows (dashed line) and total number of active burrows
 852 (solid line) at Epping Forest NP since burrow monitoring began in 1974. Black dots indicate
 854 when population estimates occurred and the estimated number of wombats. The timing of
 significant management actions is indicated.



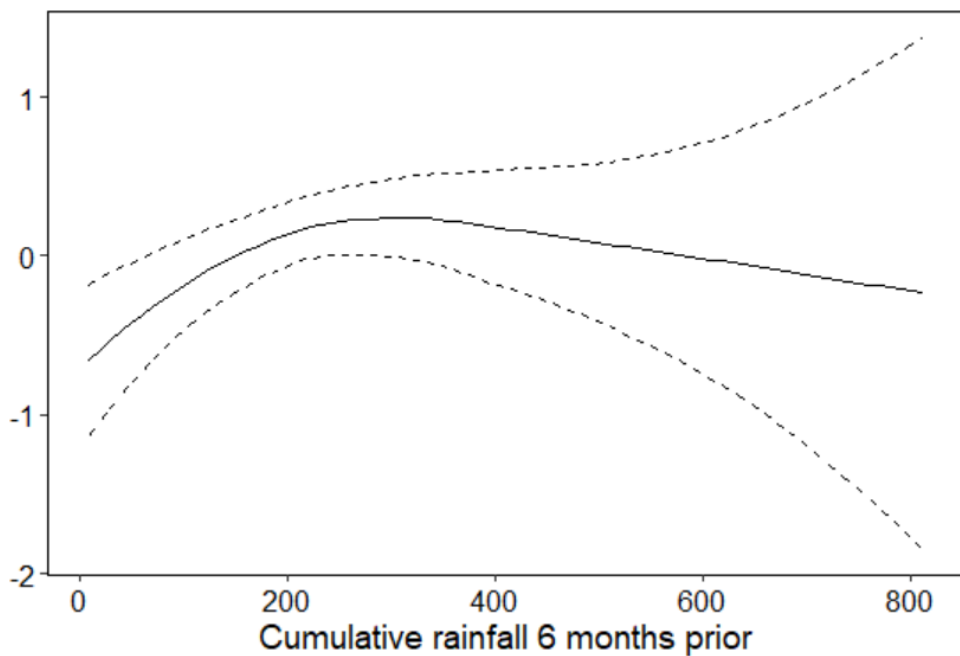
856 **Figure 4.** Map of burrow distribution at Epping Forest NP by decade since monitoring began
 858 in 1974.



860 **Figure 5.** Births per month at Epping Forest NP, determined from trapping (n=24) and PIR
 862 cameras (n=97).



864 **Figure 6.** The relationship between breeding rate and rainfall at Epping Forest NP for years in
 866 which at least five females were captured during trapping studies. Number of females is
 868 shown above each bar.



870 **Figure 7.** Predicted change (GAM smoother) in the likelihood of detecting females with
 872 pouch young over increasing levels of cumulative rainfall during the period 6 months prior to
 874 estimated birth dates. Solid line = GAM model fit; dotted line indicates 95% confidence
 bands.