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RESEARCH ARTICLE

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Management of multiple threats achieves meaningful koala conservation outcomes

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Abstract

1. Management actions designed to mitigate development or anthropogenic impacts on species of conservation concern are often implemented without quantifying the benefit to the species. It is often unclear what combinations and intensities of management actions are required to achieve meaningful conservation outcomes. We investigate whether disease and predator control can reverse population declines of koalas (*Phascolarctos cinereus*).
2. Based on longitudinal monitoring of the epidemiological and demographic status of over 500 animals over 4 years, coupled with an intensive disease and predator management programme, we use survival analyses to estimate annual age-specific survival rates and population growth, and simulations to quantify the benefit of these actions.
3. Predation and disease accounted for 63% and 29% of mortality, respectively, across all years, with wild dog (dingoes or dingo-hybrids: *Canis dingo*, *C. dingo* × *Canis familiaris*), carpet pythons (*Morelia spilota*) and domestic dogs (*C. familiaris*) accounting for 82%, 14% and 4% of confirmed predation mortalities, respectively. In the first 2 years, before disease and dog control had major impact, the population was declining rapidly with annual growth rates of 0.66 and 0.90. In the third and fourth years, after interventions had been fully implemented, the population growth rate had increased to 1.08 and 1.20. The intrinsic survival rate of joeys was 71.2% (excluding deaths resulting from the death of the mother). Adult survival rates varied as a function of sex, age and year.
4. Even in a declining koala population, management actions can achieve meaningful conservation outcomes (population growth rates greater than one). However, benefits may be short-lived in the absence of longer term strategies to manage threats. This work also identifies wild dogs as a major threat to koalas, highlighting the need to better understand how wild dog impacts vary in space and time.
5. *Policy implications*. Offsetting policy that addresses habitat loss alone may achieve little or no meaningful benefit to declining koalas populations. Management must address suites of threats affecting these populations and ensure that the cumulative effects of these actions achieve positive population growth rates.

KEYWORDS
Chlamydia, disease control, koala, offsetting policy, population dynamics, predator control, survival analysis, wild dogs

1 | INTRODUCTION

Legislation governing the management of threatened species often requires that development impacts on those species are minimized on site, with unavoidable impacts being offset in other areas (Quetier & Lavorel, 2011). In practice, it is difficult to quantify impacts on species or ecosystems, or the expected benefits at offset sites because ecological systems are complex, dynamic and often characterized by substantial lag times between a disturbance and its effects (Maron et al., 2012). Quantifying the benefits of management actions requires that appropriate characteristics of the system state are identified, measured, and then compared to the "counterfactual" projection of the state had management not occurred (Gordon, Bull, Wilcox, & Maron, 2015; Maron, Rhodes, & Gibbons, 2013). Arguably, for wildlife populations, best practice involves estimating population dynamics through time, ideally before and after management has taken place, as this provides a mechanistic, evidence-based approach to quantifying impacts and estimating counterfactual states. However, this is rarely done because of the expense of the intensive monitoring required to estimate demographic parameters. As a result, there is often little evidence of the value of mitigation or offsetting actions (Maron et al., 2012). Rather, it is assumed that adequate benefits are realized, which may exacerbate species declines (Gordon et al., 2015).

The koala (*Phascolarctos cinereus*) is an iconic, endemic, herbivorous Australian marsupial that is listed as vulnerable to extinction in Queensland, New South Wales and the Australian Capital Territory under the Environmental Protection Biodiversity Conservation Act 1999 (EPBC Act) since 2012. Northern koala populations in Queensland and New South Wales (approximately two-thirds of the species' range) have declined by 50%–80% in recent decades (de Villiers, 2015; McAlpine et al., 2015; Melzer, Carrick, Menkhorst, Lunney, & John, 2000; Rhodes, Beyer, Preece, & McAlpine, 2015; Seabrook et al., 2011). Several threatening processes are implicated in these declines, including habitat loss resulting from vegetation clearing for development and agriculture, disease, vehicle collisions and dog predation (Dique, Thompson, Preece, Penfold, et al., 2003; Lunney, Gresser, O'Neill, Matthews, & Rhodes, 2007; Melzer et al., 2000; Polkinghorne, Hanger, & Timms, 2013; Rhodes et al., 2011).

Disease has previously been identified as the largest cause of koala mortality in a south-east Queensland population (Rhodes et al., 2011). Chlamydial disease caused by the bacteria *Chlamydia pecorum* and *Chlamydia pneumoniae* is prevalent among koala populations and has important impacts on survival and reproduction (Polkinghorne et al., 2013). It is primarily sexually transmitted, though vertical transmission from mother to joey also occurs. *Chlamydia* infection can be treated with injections of antibiotics if the koala is taken into care. Several vaccines are also in the process of being developed and tested (Kollipara et al., 2012; Waugh et al., 2016). Koalas are also host to other pathogens, including the koala retrovirus (Hanger, Bromham, McKee, O'Brien, & Robinson, 2000; Simmons et al., 2012) and trypanosomes (McInnes, Gillett, Hanger, Reid, & Ryan, 2011; McInnes et al., 2009), though the impacts of these pathogens are currently poorly understood.

An obstacle to developing evidence-based conservation strategies for koalas is the difficulty in studying cryptic arboreal species. Faecal pellet surveys around the base of trees are used to determine koala presence and tree species use (Melzer et al., 2000), and experienced observers can achieve koala detection rates of approximately 60%–75% in some vegetation types, which facilitates population surveys (Dique, Thompson, Preece, de Villiers, & Carrick, 2003). However, from the ground it is difficult to identify individuals unless tagged, or to detect in-pouch joeys, or assess disease status and condition of adults. Hence, detailed demographic data such as age-specific survival and fecundity rates, or disease prevalence rates, are rarely quantified. It is also difficult to determine causes of mortality without tracking individuals at frequent intervals. Estimates of relative mortality rates from incidentally collected data, such as koalas taken to veterinary hospitals or from carcasses recovered from roadsides, are likely to be biased to an unknown degree.

Here, we use frequent longitudinal monitoring data and veterinary assessments of over 500 koalas over 4 years to estimate age- and sex-specific demographic rates, and per capita mortality rates for each source of mortality. We use these parameters to estimate annual population growth rates, with each consecutive year corresponding to increasing levels of key threat (disease and predator) management. The two goals of this work are to establish whether measures taken to offset impacts of development within the study area have been effective, and whether intervention measures can reverse population declines. In doing so, this work establishes a best practice for mitigating development impacts on koala populations and provides valuable new insights into koala population dynamics that can inform future management.

2 | MATERIALS AND METHODS

2.1 | Koala monitoring and treatment

The study took place in the eastern Moreton Bay Region (Queensland, Australia) from 2013 to 2017 in association with an infrastructure (rail line) development project. The study area consisted of a mixture of urban and peri-urban koala habitat remnants, and consisted of lowland coastal vegetation types, including open grassland, shrubland dominated by exotic species and various types of wet and dry open to closed forest generally dominated by mixed eucalypt/paperbark species. A koala management program was established prior to construction to satisfy legislative requirements and meet community expectations regarding protection of koalas. The aims of the program were to minimize the risk of death or injury to koalas during construction, to provide data to inform mitigation, and to offset some of the residual impacts of the development on the koala population using a suite of measures including disease treatment and control, translocation of a small number of koalas, habitat offsetting (creation of new koala habitat) and control of key predators (wild dogs).

Koala captures began in March 2013, 10 months prior to the commencement of vegetation clearing, and ended in June 2016, although monitoring continued until early 2017. During that time, 503 koalas were captured and given veterinary examinations, with most fitted with telemetry devices and monitored after release back into the wild. Although koalas were sometimes retrieved from the ground following illness or injury (e.g. dog attacks), or entered the program via a koala rescue group or wildlife hospital, most captures were made following transect searches to identify untagged koalas in trees. The capture methods used included standard flagging pole methods or live-traps depending on circumstances. All koalas in the study area were monitored with only four detections of untagged koalas (excluding dependent juveniles) occurring during the latter 2 years of the monitoring program.

Following capture, koalas were transported to a veterinary facility and detailed health assessments were conducted under anaesthesia by koala-specialist veterinarians. The most detailed examinations included a physical examination, collection of urine, blood, bone marrow and abdominal fluid samples for laboratory testing, ultrasound imaging (for assessment of kidneys, ureters and bladder, the female reproductive tract and the male prostate), and radiography in the case of suspected trauma injury. Treatment of injured or ill koalas was tailored to each case and typically resolved all traumatic injury, lesions and *Chlamydia* infection (e.g. conjunctivitis, cystitis, rhinitis). Some diseases, such as bone cancers, could not be treated. In cases of severe injury or disease, or a poor prognosis for effective treatment, the animal was euthanased on humane grounds.

After examination and treatment, koalas were released at their point of capture unless conditions were unsuitable (e.g. near a busy road) in which case the animal was released at a tree near the point of capture. Koalas were only released farther from their point of capture in a small number of planned translocations.

Animals were fitted with a near real-time GPS telemetry collar and a backup VHF ankle bracelet to facilitate regular monitoring. Animals were visually inspected from the ground to look for external signs of disease or injury and establish the status of any joeys. In the event of a suspected mortality, an attempt was made to locate the carcass immediately to perform a necropsy and establish cause of death. Animals were recaptured at approximately 6-month intervals (or earlier if justified by field checks or growth rates) for follow-up veterinary examinations.

Further details of protocols can be found in the project's technical report (Hanger et al., 2017). Ethics approvals for all work governing the capture, handling, treatment and monitoring of koalas were issued by the Queensland Department of Agriculture and Fisheries (approvals CA-2012/03/597, CA-2013/09/719, CA-2014/06/777, CA-2015/03/852, CA-2016/03/950). Scientific permits to authorize work on koalas were issued by the Queensland Department of Environment and Heritage Protection (approvals WISP-11525212, WISP-16125415, WISP-13661313, WITK-14173714 and WISP-17273716).

2.2 | Wild dog monitoring and control

"Wild dogs" refer to feral canids that are either dingoes or dingo-hybrids, which are considered pest species in Queensland, but not domestic pet dogs that are free-roaming or have "gone wild". This distinction was based on genetic analysis of 11 samples of DNA recovered from attacked koalas, and visual and behavioural observations. Incidental observations of wild dogs, scat and tracks occurred from the beginning of the project, and regular and widespread wild dog presence was also confirmed through approximately 3,800 camera trap nights occurring from years 1–4. Local wild dog control experts were contracted by the development project to undertake monitoring and control of wild dogs in the study area and surrounding suburbs starting at the commencement of the project. Forty-one wild dogs were removed (live trapped and euthanased) from the study area over the course of the study, resulting in a reduction in the detection of wild dogs from approximately 6–12 detections per month to no detections in the last 12 months of the study.

2.3 | Parameter estimation and modelling

Analysis of koala monitoring data was complicated by the asynchronous entry of koalas into the monitoring programme, the time that animals spent in care receiving treatment and unknown outcomes (right censoring) for some animals. We used survival analysis to quantify mortality rates of joeys and adults and to determine whether death rates differed as a function of age, sex, a year factor and whether the animal was at a translocation site. We quantified survival probabilities using the Andersen–Gill formulation of the Cox proportional hazards model (Andersen & Gill, 1982; Cox, 1972; Cox & Oakes, 1984), which can be expressed in matrix form as:

$$h(t) = h_0(t)\exp(\mathbf{X}\beta) \quad (1)$$

where $h_0(t)$ is the baseline hazard function, $\mathbf{X}$ is a matrix of covariates that does not include an intercept term and β is the vector of parameters to be estimated. The expression $\exp(\mathbf{X}\beta)$ modifies the baseline hazard multiplicatively, hence values of $\exp(\mathbf{X}\beta)$ greater than and less than 1 represent higher and lower mortality rates respectively, relative to the baseline function.

The Cox proportional hazards model can accommodate time-dependent covariates and right-censored records in which the outcome (here mortality) is not known. The Andersen–Gill formulation further accommodates interval censored data (Andersen & Gill, 1982), which in this case corresponded to times when koalas are housed in veterinary facilities and were not, therefore, exposed to threats.

An assumption of this modelling framework is that there was no bias in which animals were censored, and the removal of animals with severe disease or injury was a violation of this assumption. To correct for this bias, we estimated expected survival times for the animals that were euthanased because of severe injury or illness and did not, therefore, die in the field. In 32% of these cases, the injury or condition was so severe that death was imminent and estimates of the survival time had intervention not occurred are likely to be accurate (median 3.5 days; range 0–20 days). A further 32% were assessed to have expected survival times from 20 to 60 days (*M* 47.7 days). The remaining 36% were deemed to have projected survival times that exceeded 60 days (*M* 235 days). All animals in the first and second groups were treated as mortalities using the estimated survival times but the third group was treated as censored.

We estimated prevalence of chlamydial disease and the time between loss of a joey and conception of the next joey ("breeding interval") directly from the monitoring and veterinary exam records.

2.4 | Population modelling

We estimated population growth rates and simulated koala population dynamics using a female-only, age-structured model with an annual time step. There were $k = 12$ age classes, with the first age class corresponding to joeys (age 0–365 days) that were considered to be dependent on their mothers in their first year. Population numbers at time t were assumed to be censused immediately following reproduction, hence recruitment was calculated after mortality and ageing.

Survival into the second age class (N_2) must account for the fact that joeys are dependent upon their mothers, so the death of a mother necessarily results in the loss of the joey:

$$N_2(t+1) = s_1 N_1(t) - \frac{1}{2}\sum_{i=2}^{k}(1-s_i)b_i N_i(t) \tag{2}$$

where $N_i(t)$ is the number of koalas in each age class i at time t, s is a vector of annual per capita age-specific survival rates and b a vector of age-specific per capita birth rates. Thus, the number of animals surviving to age class 2 accounts for mortality among joeys independent of the fate of the mother (s_1) as well as the joeys that are lost as a result of the death of the mother. We assumed an equal sex ratio among neonates (Ellis et al., 2010) and the fraction 1/2 is required to remove males.

In all subsequent age classes ($i \in \{3, \ldots, 12\}$), state transitions are modelled as:

$$N_i(t+1) = s_{i-1} N_{i-1}(t) \tag{3}$$

Recruitment into the first age class at time $t + 1$ is determined from the population of adult females at time $t + 1$:

$$N_1(t+1) = \frac{1}{2}\sum_{i=1}^{k} b_i N_i(t+1) \tag{4}$$

Age-specific annual survival rates were estimated from the survival analysis by fitting a continuous function ($f(x) = a(1-\exp(-cx^d))$, where parameters a, c and d were estimated using maximum likelihood) to observed adult female Kaplan–Meier cumulative survival curves (Kaplan & Meier, 1958) for each of the 3 years of the study (Figure S1). The annual survival rate for age i years, conditional upon having survived to age i–1 years, was then calculated as $s_i = (p(i) - p(i-1))/(1-p(i-1))$, where $p(i)$ is the cumulative probability of mortality (1–survival) at year i, determined from $f(x)$. Survival at age class 12 was assumed to be 0. For joeys, the annual survival rate was estimated directly from the survival curve (see Section 3).

Annual fecundity (per capita birth rate) is not straightforward to estimate for koalas. Unlike mammals in temperate climates, koalas in this region can reproduce at any time of year (Figure 1a; Ellis et al., 2010). This has important implications for population dynamics because, if a mother loses a joey, she can become pregnant again after a short interval. This increases the chance that a female will successfully rear a joey in a given year as she may have more than one attempt. Furthermore, generations of young can overlap because the female can conceive before the previous joey has reached full independence. We estimated annual fecundity by simulating birth, neonate survival and interbreeding intervals, based on observed empirical distributions (see Supplementary material S1 for details). To calculate the realized birth rates (b), we multiplied these theoretical maximum fecundity rates by the observed annual breeding rate of healthy females, which was the proportion of adult females showing evidence of having reproduced in a given year.

Population growth rates are the leading eigenvalues of the Leslie matrices (Caswell, 2001; Leslie, 1945) constructed using Equations 2–4 and the fecundity and survival estimates, for each of the 4 years of the study (Table S3). Population simulations were based on Equations 2–4 and incorporated stochasticity by assuming binomial distributions for survival probabilities and Poisson distributions for reproduction. The initial age distribution of adult females ($n = 100$) was generated by sampling from the observed distributions (Figure S4).

Four stochastic, 10-year population simulation scenarios were evaluated. First, we used the parameter estimates from year 1 to simulate what might have happened to the population had no interventions taken place (the "counterfactual scenario"). Survival was particularly poor in year 1, so this scenario may provide unrealistically pessimistic projections. We therefore evaluated a second, more moderate counterfactual scenario in which survival and reproduction values were calculated as the weighted average of the year 1 and year 2 Leslie matrices, where the weight was drawn at random from a uniform distribution in the range [0, 1]. In the next two scenarios, we used the parameter estimates for each of the 4 years in the corresponding year of the simulation. In the "continued management"

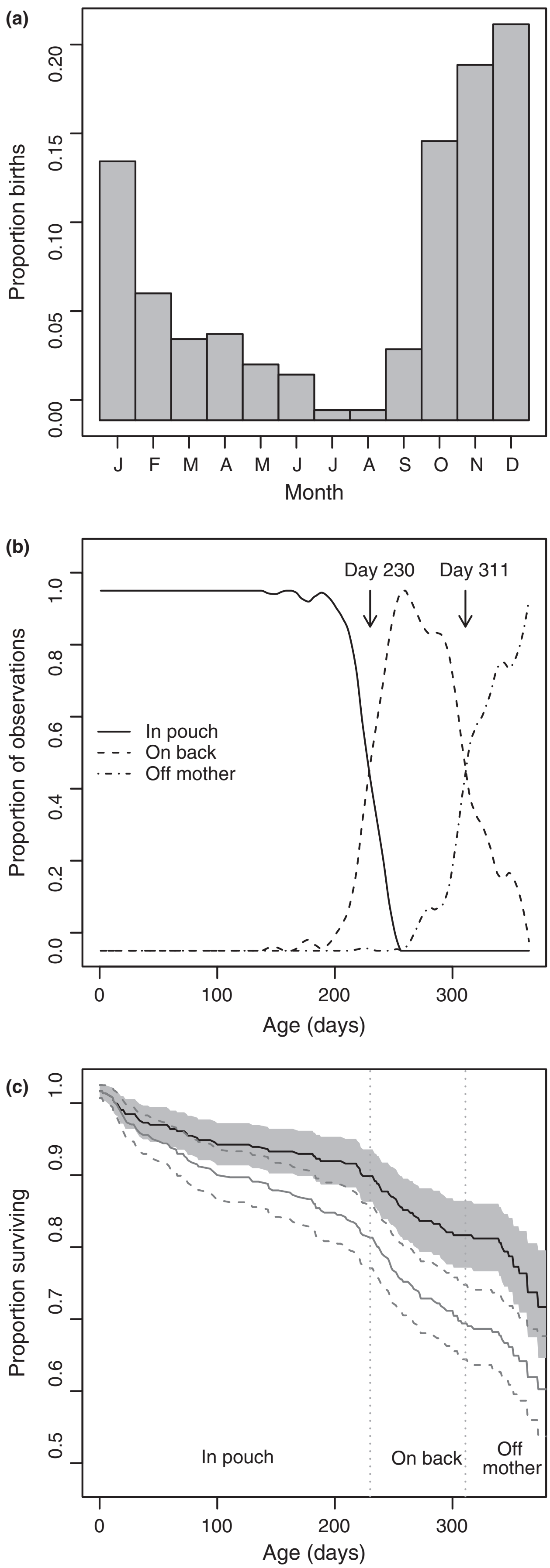

FIGURE 1 (a) Distribution of births by month. Most births (72.6%) occur October–January inclusive, though reproduction throughout the year is possible. (b) Timing of transition of joeys from residing within the mother's pouch to riding on her back and eventually off their mother (but usually nearby and often in the same tree). Lines represent the proportion of joey positions as a function of joey age, based on 2,724 field observations. (c) Cumulative survival probability curves for joeys, quantified with and without mortality arising from the death of the mother (grey lines, dashed confidence intervals and black lines, shaded confidence interval, respectively)

scenario, we then assumed that the conditions in year 3 are maintained from years 6–10, with an average of the year 3 and 4 Leslie matrices in year 5. This scenario represents management that is less intensive than that during the project, hence is able to maintain a positive population growth rate but not the strong growth observed in year 4. Finally, a "phased management" scenario was designed to reflect what may happen to the population as interventions are phased out over the next few years. Specifically, the parameter estimates for years 4, 3 and 2 were applied to years 5, 7, and 9, respectively, with averages between the year 4–3, 3–2 and 2–1 Leslie matrices in years 6, 8 and 10, respectively.

3 | RESULTS

Predation accounted for at least 49.5% of mortality or 62.5% if the suspected (but unconfirmed) predation deaths are included (Table 1). Of the 144 confirmed predation deaths, wild dogs, carpet pythons and domestic dogs accounted for 81.3%, 14.6% and 4.2% of predation mortalities, respectively. We believe it is likely that the 38 suspected but unconfirmed predation events were due to wild dog predation. Wild dogs are more likely to transport and bury the carcass away from the point of predation, thereby making it difficult to find, and the suspected predation events closely track the confirmed wild dog predation events across the 4 years. If true, these percentages would change to 85.2%, 11.5% and 3.3%.

A further 28.9% of mortality was attributed to disease, which included severe chronic cystitis, reproductive tract disease, hypoproteinaemia and anaemia, severe ulcerative dermatitis, acute septicaemia/toxaemia, fungal skin lesions, caeco-colic dysbiosis, severe acute bacterial enteritis and several other conditions. Of these, 62.1% (or 18.0% of total mortality) was attributed to chlamydial disease or complications of treatment for chlamydial disease. The average prevalence of disease in the 4 years of the study was 19.8%, 13.3%, 5.7% and 4.2%, respectively (Figure 2c). Only 8.6% of mortality events were attributable to other causes (Table 1).

We monitored 350 neonates across all years (299 born after the start of monitoring), observing 121 mortalities. Of these mortalities, 68 were attributable to the death of the mother. For the purpose of population modelling, we treat these 68 deaths as censored records in order to estimate only the "intrinsic" survival rates of the joey independent of the fate of the mother. Mortality from the loss of the

TABLE 1 Causes of adult koala mortality, based on monitoring of koalas with telemetry collars and ascertained through necropsy examinations

Cause of death	Year 1	Year 2	Year 3	Year 4	Total	Total (%)
Predation (total)	59	95	25	3	182	62.5
Predation, wild dog	35	68	14	0	117	40.2
Predation, carpet python	9	5	6	1	21	7.2
Predation, domestic dog	3	1	0	2	6	2.1
Suspected predation	12	21	5	0	38	13.1
Disease	32	26	19	7	84	28.9
Trauma, road	3	2	3	1	9	3.1
Trauma, rail	1	0	0	0	1	0.0
Trauma, intermale fighting	0	1	1	2	4	1.4
Other/unknown	2	3	3	3	11	3.8
Total	97	127	51	16	291	

mother is modelled separately in the simulations. For the survival analysis, joeys born before the start of monitoring were omitted as they represent a biased sample (the subset of joeys that had survived until the beginning of the study). Overall intrinsic survival of joeys postgestation to independence (day 365) was 71.2% (65.0%–78.0%) across all animals and years (Figure 1c). Survival rates during the pouch, on back and off-mother stages (Figure 1b) were 87.3%, 90.6% and 90.0%, respectively. When the deaths of the mothers upon which the joeys are dependent are included, survival to independence (day 365) was 59.4% (53.4%–66.1%) and survival during the pouch, on back and off-mother stages was 78.8%, 84.8% and 88.9%, respectively. We found no evidence that neonate survival varied across years, the season of birth or the developmental stage of the joey (survival analysis; Tables S1 and S2).

Mortality risk for adult males was approximately 1.6 times higher than for females (Table 2; Figure 2a). Mortality risk also decreased in each consecutive year of the study as a result of interventions (disease and dog control). Relative to survival in the first year mortality risk was 62%, 85% and 92% lower in years 2, 3 and 4, respectively (Table 2). The hazard was U-shaped with respect to age of adults (Figure 2b) indicating higher risks of mortality for the youngest and oldest individuals. There was no evidence that translocated animals suffered higher or lower mortality rates than residents (Table 2). Tests of nonzero slopes in Schoenfeld residuals were nonsignificant for each variable and globally (Table S4), indicating that the assumption of proportional hazards was not violated (Grambsch & Therneau, 1994).

The mean breeding interval, defined as the number of days between births conditional on the first joey surviving to independence, was 353 days (n = 99, 95% quantiles 334–423 days), implying a mean birth rate of 1.03 young per year. However, this fails to account for the ability of females to conceive again following the death of a joey prior to independence. The mean time interval between loss of a joey and birth of the next joey was 76.4 days (n = 35, median = 44 days, range 0–375 days, Figure S2a) and did not vary seasonally (Figure S2b). Based on simulations (Supplementary material S1), we estimated that the overall annualized fecundity rate after accounting for reproduction following the death of the joey and a breeding rate among healthy females of 90% was 1.10. The average age of first reproduction was 18 months, with 94% (30 of 32) of subadults giving birth before age 2 (we use a value of 80% in the Leslie matrices to account for the fact that later breeders are more appropriately considered to breed in age class 3 in a discrete time model).

Population growth rates were estimated to be 0.659, 0.895, 1.08 and 1.20 in years 1–4 of the study, respectively. Stochastic simulations indicate that without intervention the population may have declined by approximately 90% over a decade under the assumption that dog and disease risks would have continued unabated and that environmental conditions were similar among years (Figure 3a). Conversely, under the continued management scenario, the population would be projected to increase in size by approximately 21% within a decade relative to population numbers at the start of the project (Figure 3b). Under the phased management scenario, population numbers at the end of the projection were estimated to be 57% of population numbers at the beginning of the project (Figure 3c), much greater than the estimated 3% in the counterfactual scenario.

4 | DISCUSSION

This work suggests that the koala population in this area was declining at a substantial rate prior to the introduction of intensive management interventions (dog and disease control). This is consistent with recent regional analyses of long-term trends reporting that koala populations in south-east Queensland have been declining over the last two decades (de Villiers, 2015; Rhodes et al., 2015). Habitat loss, habitat fragmentation, and mortality from predators, vehicle collisions, domestic dogs and disease are all factors implicated in this decline (McAlpine et al., 2015; Melzer et al., 2000; Rhodes et al., 2011, 2015). Of those threats, by far the most significant one identified here was predation by wild dogs.

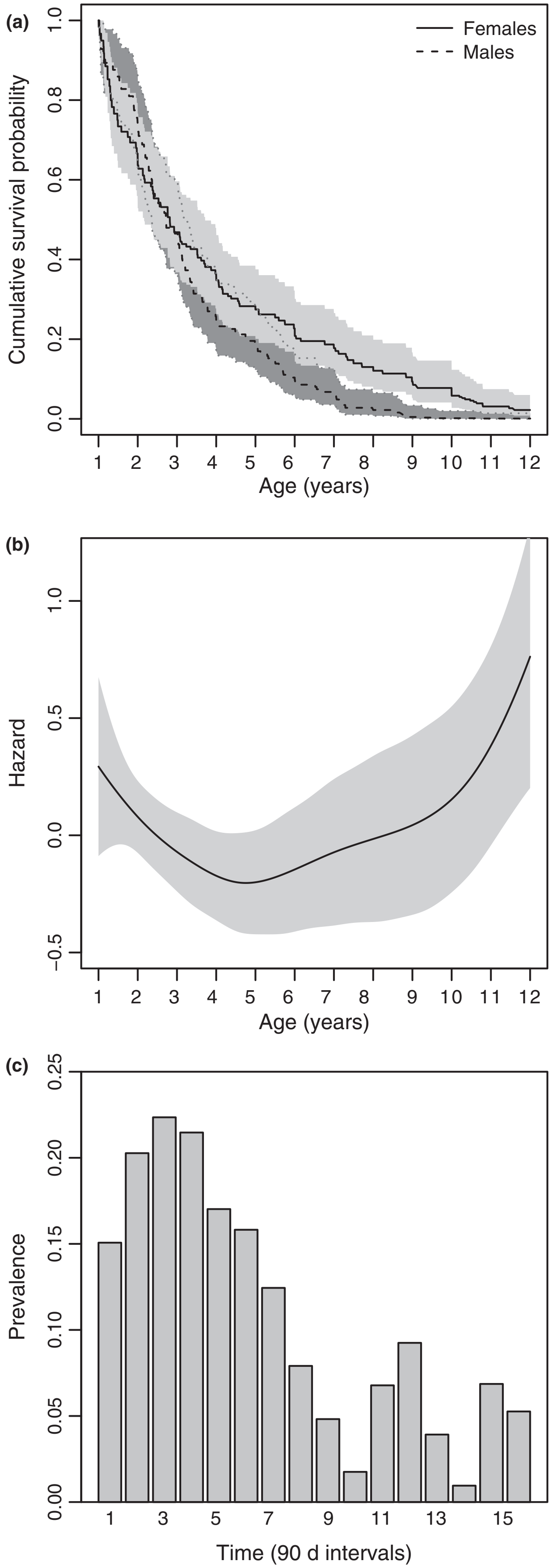

FIGURE 2 (a) Change in mortality risk as a function of age of the koala (for subadults and adults only, starting at 1 year old). (b) Cumulative survival probability curves for adult (>1 year old) males and females (dashed line, dark confidence intervals and solid line, light confidence interval, respectively). Overall, mortality risk for males is approximately 1.6 times larger than that for females. (c) Prevalence of *Chlamydia* infection among adult koalas, calculated in 90 day intervals over the 4-year study

TABLE 2 Cox proportional hazards survival model of adult (n = 441) survival as a function of sex, the year of the study (1–4) and whether the animal was at a translocation site

	Coef	Exp(coeff)	*SE*(coeff)	*z*	*p*
Male	0.47	1.60	0.14	3.31	.00
Translocation	0.27	1.31	0.23	1.15	.25
Year 2	−0.97	0.38	0.18	−5.47	.00
Year 3	−1.91	0.15	0.23	−8.26	.00
Year 4	−2.50	0.08	0.31	−8.03	.00

We estimate that the population could have approached local extinction within a decade in the absence of intensive management. This counterfactual, the estimate of what would have happened in the absence of intervention, establishes a reference baseline for estimating the impact of the development project (Ferraro, 2009). Specifically, the impact is the expected deviation from this counterfactual over a relevant period of time. At a minimum, offsetting should prevent a net detrimental effect relative to the counterfactual. The intervention measures adopted in the first and second year of the project reduced the rate of population decline in the second year, but this was not enough to reverse population declines. Only through further intensive management were positive population growth rates achieved in years 3 and 4. The phased management scenario is a projection of koala population dynamics under the assumption that intervention measures (both disease and dog control) are phased out after year 4 and that the population returns to a rate of decline over the following years. The difference between the population projections under the counterfactual and the phased management scenarios is a measure of the impact of the development project. On this basis, we estimate that intensive management of threats has achieved a substantial net benefit to the koala population and that this benefit was already apparent by the end of the project (year 4).

Habitat loss has occurred (62 ha of land was cleared) but this is not expected to have an important impact on the koala population for two reasons. First, intensive and prolonged searching of the sites for koalas, which were then tagged with telemetry devices, ensured they were located and avoided on each day of vegetation clearing. Second, because koala densities were already low in this area (between 0.15 and 0.25 koalas per hectare in most places) relative to historical densities that have been found in similar habitats (0.2–0.6 koalas per hectare; de Villiers, 2015; Dique, Preece, Thompson, & de Villiers, 2004; Ellis et al., 2013), the loss of habitat is unlikely to

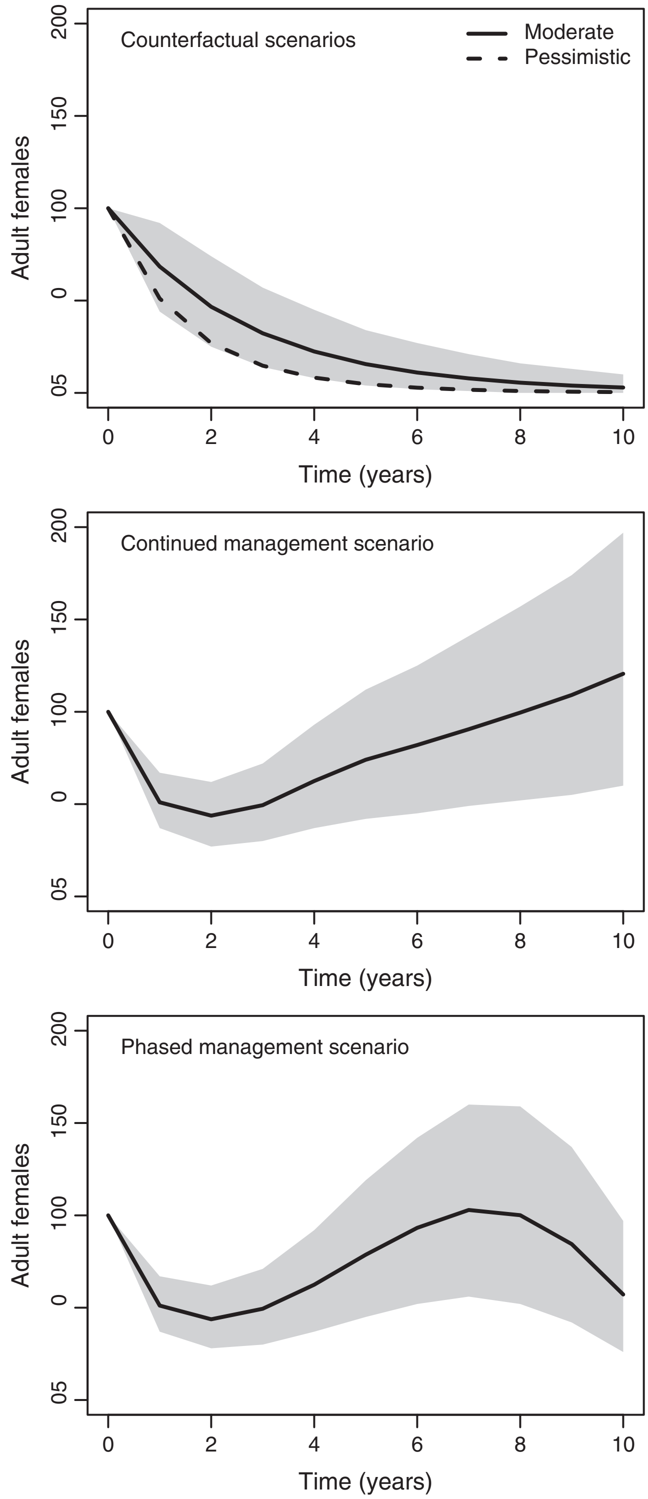

FIGURE 3 Stochastic simulations of adult female koala population numbers (*y*-axis) under three alternative management scenarios. The counterfactual scenario is an estimate of population number had no intervention occurred and indicates a continued population decline (solid line and shaded confidence interval). Under the most pessimistic projection (dashed line), local extinction is expected with 10 years. In the next two scenarios, years 1–4 correspond to observed population growth rates during this project, with year 1 representing predevelopment. The continued management scenario is based on the assumption that dog and disease interventions are maintained in years 5–10, though less intensively than that achieved by year 4 of this project. The phased management scenario is based on the assumption that control measures are phased out after year 4 and the population returns to prior growth rates over the following 5 years. Shaded areas are the 95% confidence intervals

limit the population. Loss of habitat will reduce the carrying capacity of the population (the maximum number of koalas that the area could support), but if the population is well below the carrying capacity, as we suggest, then this limiting effect will never be realized.

A key contribution of this work is providing systematic and reliable assessments of causes of mortality. Incidental sampling procedures, such as the use of veterinary hospital records of sick and injured koalas (e.g. Gonzalez-Astudillo, Allavena, McKinnon, Larkin, & Henning, 2017), may lead to substantial bias in the estimation of the relative importance of different threats. Predation rates are particularly difficult to quantify without intensive monitoring as predation often occurs in places unfrequented by people and the carcass may be undetectable following consumption or burial. Although vehicle collisions and disease are undoubtedly important causes of mortality in this region, this work establishes that predation can be the leading cause of mortality in some populations. Wild dogs, in particular, have not been adequately recognized as a potential major threat to koalas.

It is not clear how representative this koala population may be of other populations in the region as no other population has been studied as intensively. It is likely there is considerable spatial heterogeneity in the distribution of threats. Anthropogenic threats are concentrated in the intensively developed, eastern coastal areas and the prevalence of *Chlamydia* infection is known to vary over this region (Kollipara et al., 2013; Polkinghorne et al., 2013). Less is known about the distribution of wild dogs and carpet pythons in south-east Queensland. Both are generalist predators that may persist in remnant habitat degraded by anthropogenic influences and in urbanized landscapes. Carpet pythons can remain in tree tops for extended periods of time, are difficult to detect and monitor, and are protected by State legislation. Wild dogs can be effectively monitored and controlled, though this requires intensive fieldwork.

Camera trap data provided useful insight into some aspects of wild dog predation. A single male that eluded capture until the end of the study was thought to be responsible for 75 koala deaths. Such behaviour suggests partial reductions in wild dog densities may do little to benefit population dynamics as only a few effective predators are needed to maintain substantial impacts on populations. Although targeting the removal of only the most voracious predators could provide substantial benefit to the koala population, in practice it is exceedingly difficult to identify and then remove these individuals. It is also unclear whether the removal of some animals may change the social structure and behaviour of others.

This project demonstrates that (1) effective control of chlamydial disease is possible, (2) effective control of wild dog predators is possible, (3) together, these effects can secure koala populations in these remnant habitat patches in a heavily human-modified landscape.

Although this study was not an experimental design (there was no control, replication or randomization), we suggest it nevertheless provides a reasonable basis for inferring cause and effect. The intensive monitoring of both koalas and dogs, and immediate investigations into koala deaths and necropsies, provided reliable insight into causes of mortality. Furthermore, the veterinary examinations established that treatment was effective at clearing chlamydial infection and the camera traps and field monitoring provided evidence that wild dog control was effective. Thus, we argue that the management interventions (disease and dog control) were responsible for the decline in mortality rates over the course of the study. We speculate that the severe rates of population decline observed in the first year due to wild dog predation and disease may have been more modest in previous years because: (1) a 35% decline is not sustainable for many years yet koalas appear to have persisted in this study area, and (2) wild dog predation may vary among years depending on the availability of other prey, the density of dogs, dog behaviour, or the movement of dogs to other areas. For example, in the Rhodes et al. (2011) study of a south-east Queensland koala population in the 1990s, wild dog predation appeared to be absent (D. de Villiers pers. comm.).

This study design does not allow us to address is the level of natural interannual variation in survival and reproduction that may arise from environmental variability. The 4 years of this study were representative of typical climatic conditions but multiyear drought and associated bushfire occur in this region and can increase mortality rates in koalas. The population simulations assume that environmental conditions remain similar to those in which monitoring occurred and may, therefore, overestimate population growth rates or underestimate the variation in projected population sizes if adverse years arise.

The purpose of offsetting policy is to mitigate only the impact of specific development projects and often focuses solely on the provision of habitat, such as the number of "koala habitat trees" in the case of the koala (Queensland Government, 2014). In rapidly declining populations below carrying capacity, however, further habitat loss may have negligible effects on population dynamics. In such cases, achieving a net beneficial effect requires addressing the suite of threats impacting a population. This work corroborates the conclusion of Rhodes et al. (2011) that single threats would have to be reduced to implausibly low levels to result in population recovery and addressing multiple threats simultaneously is a key strategy for effective management. Overall, this work constitutes compelling evidence that management actions can achieve meaningful conservation outcomes in declining populations of koalas, specifically that population declines can be reversed. However, this would not have been achieved without detailed studies to quantify the relative importance of threats. Reliance on conventional wisdom to manage threats would have been unlikely to prevent further koala population declines as wild dog management would have been neglected. This work also suggests that the benefits to the koala population achieved during this project could be lost rapidly if the population returns to former rates of decline. Offsetting and mitigation measures arising from development projects must be coupled with long-term management strategies if benefits are to persist. Although it is often difficult to quantify population growth rates in wildlife populations, doing so is a rigorous approach to estimating counterfactuals (what would have happened in the absence of management) and quantifying impacts of management.

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AUTHORS' CONTRIBUTIONS

J.H. led the project. J.H., J.L. and A.R. performed veterinary assessments and treatment. D.V., J.L., A.R. and J.H. collected, interpreted and analysed data. N.F. performed project management and contributed to data collection and analysis. H.L.B. and M.S. performed the statistical analysis and modelling. All authors contributed to writing the paper and approved its publication.

DATA ACCESSIBILITY

Leslie matrices and data required to repeat survival analyses are available from the University of Queensland Data Repository https://doi.org/10.14264/uql.2017.1046 (Beyer & Hanger, 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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