

# High mortality and small population size prevent population recovery of a reintroduced mesopredator

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## Keywords

mammal decline; mesopredator; predation; population viability analysis; resource subsidies; Vortex; anthropogenic; reintroduction.

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## Abstract

Northern Australia's native mammal fauna has undergone a severe decline in recent decades. Putative factors include altered fire regimes, cat predation, poisoning by cane toads and disease. Populations of northern quolls, *Dasyurus hallucatus* severely declined following cane toad invasion and have not recovered. We monitored a population of northern quolls in Kakadu National Park that was supplemented with 'toad-smart' individuals, to determine whether cane toad poisoning or predation was preventing population recovery. The population increased after supplementation, but crashed in March 2012, coincident with a high level of trap disturbance by canids. Canid predation was the major source of mortality for radio-tagged quolls. We used population viability analyses (PVA) to explore how changes in mortality influenced the likelihood of extinction. With no management, the quoll population has a 48% chance of extinction over the next 20 years. Sensitivity analyses highlighted small population size and high mortality as the main reasons for the population failing to recover. We then explored whether population supplementation or reducing mortality could increase the likelihood of persistence. One year of supplementation increased the probability of population survival over 20 years from 51.6% to 81.7%. Continuing supplementation for 3 or 5 years increased the probability of population survival to 96.5% and 98.1% respectively. Similarly, a 2.5% reduction in the rate of mortality for juveniles and adult females increased the probability of population persistence over 20 years to 83.6%. Further reductions in mortality of 5% and 10% increased the probability of survival to 92.2% and 99.4% respectively. The results of the PVA suggest that small interventions could have a significant positive effect on population survival. We hypothesize that predation from food-subsidized canids is preventing the recovery of quoll populations. Future management actions to reduce mortality, via improved fire management, or through population supplementation, are necessary to ensure the persistence of the northern quoll.

## Introduction

The small mammals of northern Australia are facing an extinction crisis of international significance with 19 species declining since 1970 and some declining to <90% of their abundance (Woinarski *et al.*, 2011; Fisher *et al.*, 2014). The factors driving this decline have occurred indiscriminately of land tenures, and in relatively intact landscapes (Fisher *et al.*, 2014; Murphy & Davies, 2014; Woinarski, 2015). Putative causal factors responsible for mammal declines include changed vegetation structure as a result of introduced herbivores and altered fire regimes, predation by feral cats *Felis catus*, invasion of the toxic cane toad *Rhinella marina* and novel disease (Woinarski *et al.*, 2010, 2011). However, there is

consensus that changed fire regimes are driving declines (Fisher *et al.*, 2014; Woinarski, 2014). Fire is a pervasive element of the wet-dry tropics, and both fire frequency and intensity influence the abundance and diversity of vertebrate fauna (Woinarski, Risler & Kean, 2004; Andersen, Woinarski & Parr, 2012). Evidence suggests that most mammals survive the immediate effects of a fire by utilizing shelters (Legge *et al.*, 2008), but are impacted by the indirect effects of fire in the subsequent months (Andersen *et al.*, 2012). Fire influences the structure and species composition of vegetation assemblages (Russell-Smith, Ryan & Cheal, 2002; Woinarski *et al.*, 2004), and frequent, intense fires reduces shelter and refugia for prey species (Vigilante & Bowman, 2004), exacerbating the effects of predation. Feral

cats can travel up to 12.5 km from their home ranges to hunt in recently burnt habitat (McGregor *et al.*, 2016), and have been identified as an important contributor to post-fire mortality of small mammals (Leahy *et al.*, 2016). Dingoes *Canis dingo* (Crowther *et al.*, 2014) also show increased activity after fire (Leahy *et al.*, 2016), however, the role of dingoes and other free-living canids in the current small mammal decline in Northern Australia is less clear (Woinarski *et al.*, 2011; Fisher *et al.*, 2014; Ziemnicki *et al.*, 2015).

The northern quoll *Dasyurus hallucatus* is a carnivorous marsupial that has experienced a severe decline and range contraction across northern Australia over the past three decades (Braithwaite & Griffiths, 1994). This historical decline has been part of the broad-scale small mammal decline in northern Australia and largely attributed to changes in vegetation structure resulting from altered fire regimes increasing predation pressure (Woinarski *et al.*, 2010). The northern quoll is a small, omnivorous marsupial with a short lifespan. The species exhibits a die-off typical of semelparous dasyurids of small size (up to 300 g; Oakwood, Bradley & Cockburn, 2001). After mating, male quolls exhibit loss of condition and generally have an increased parasite burden, and most do not survive to mate in a second breeding season. Female northern quolls are also short-lived with most surviving to breed in only one season and a very small proportion survives to a third (Begg, 1981; Schmitt *et al.*, 1989). Population survival of species with a short lifespan is strongly influenced by fluctuations in juvenile survival (Ferguson & Lariviere, 2002). Low juvenile survival in any given year, due to external factors, can result in recruitment failure and the immediate decline of the population. Northern quolls are opportunistic predators and consume reptiles, mammals, amphibians and fruiting plants according to availability (Oakwood, 1997). The opportunistic feeding habits of quolls make them particularly vulnerable to the invasion of a toxic vertebrate, the cane toad *Rhinella marina*.

In Kakadu National Park (KNP), quoll populations crashed following the invasion of the highly toxic cane toad (Woinarski *et al.*, 2011). Quolls lack immunity to toad toxins (Ujvari, Oakwood & Madsen, 2013), and quolls that attack or ingest large toads die rapidly (Burnett, 1997; O'Donnell, Webb & Shine, 2010). Ten years after toads invaded, quoll populations have not recovered in parts of KNP. Poisoning by cane toads or predation by feral cats and dingoes could be preventing small populations from increasing. Predation is a major source of mortality for quolls causing 56–60% of adult mortality (Oakwood, 2000, 2003). Small populations are vulnerable to extinction, and to facilitate recovery, we need to disentangle the factors responsible for mortality and population decline (Caughley, 1994).

To mitigate the effects of cane toads on quolls, we used conditioned taste aversion to train quolls to avoid eating cane toads. A pilot study revealed that most quolls learnt to avoid consuming toads after ingesting a single toad, and those animals had higher short-term survival in the wild than did untrained controls (O'Donnell *et al.*, 2010). In 2009, we trained captive bred quolls to avoid eating cane toads and introduced these 'toad-smart' quolls to East Alligator region

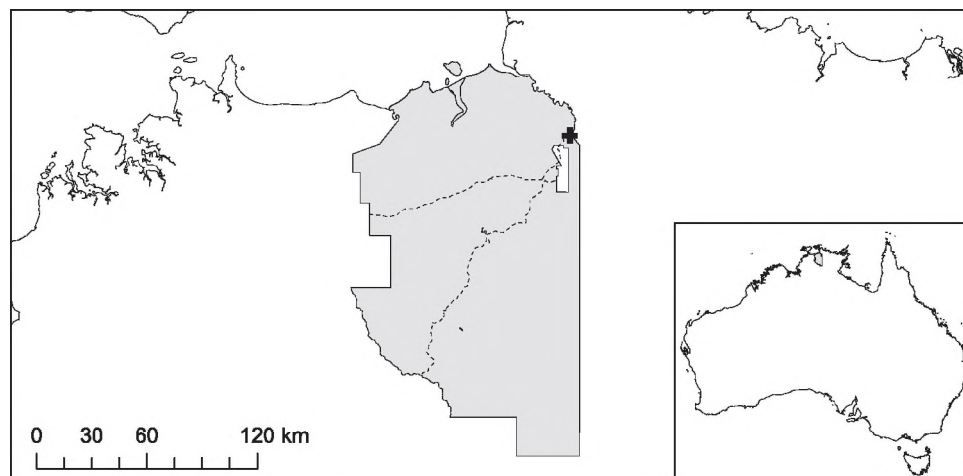
of KNP. Subsequent genetic parentage analysis showed that some offspring of the toad-smart females survived to reproduce in a toad-infested landscape (Cremona *et al.*, 2017). This novel approach provided us with a unique opportunity to examine whether poisoning by cane toads or predation, was preventing the recovery of northern quolls.

We monitored the population at East Alligators for 3 years following the introduction of 'toad-smart' quolls. In late 2012, we radio-tagged 16 quolls to determine sources of mortality. In spite of our novel intervention, the population failed to recover. Demography data, obtained from the population in KNP, was used to model the fate of the quoll population through population viability analyses (PVA). Simulations of population viability are an effective tool for projecting outcomes of habitat catastrophes as well as improvements such as the outcomes of conservation efforts (Boyce, 1992). Here, we use PVA to investigate the reasons behind the population's failure to thrive and to model the effects of future conservation interventions.

## Materials and methods

We trained 50 captive-born quolls at the Territory Wildlife Park (Berry Springs, NT, Australia) to avoid toads as prey, by offering them small dead toads coated with the nausea-inducing chemical, thiabendazole (O'Donnell *et al.*, 2010). We released 19 of these animals (11 males, 8 females) in December 2009 and another 31 (17 males, 14 females) in February 2010 in a toad-infested area of KNP (12°25'S, 132°56'E; Fig. 1). Part of the wet-dry tropics, the area is highly seasonal and has a distinct wet and dry season. Approximately 1400 mm of rain falls annually, usually between November and March. High rainfall causes the study site and surrounding area to be completely isolated and inaccessible to the public.

After reintroduction, trapping occurred for a minimum of three nights (except in March 2012) on 15 occasions between December 2009 and May 2013, with at least 5400 trapping nights. We placed traps in suitable locations (under ledges, beside crevices) in the late afternoon, baited them with a mixture of peanut butter, honey and oats, and checked them within 2 h of sunrise the following morning. When we captured a quoll, we recorded its sex, mass, reproductive status and microchip number (new animals were injected with a microchip). Given the northern quoll's highly synchronized breeding season and short lifespan (males live for ~1 year and females 2–3 years) age was estimated via the time of year, reproductive maturity, body mass and condition. The Cormack–Jolly–Seber (CJS) (Cormack, 1989) method was used to derive apparent survival estimates from the mark-recapture data using program MARK v9.9 (White & Burnham, 1999), as the fate was unknown for all individuals. We also did not use Pollock's Robust Design, as the study did not satisfy the assumptions of this method, being an open population (Kendall, 2001). Quolls were separated into four groups; juvenile females, adult females, juvenile males and adult males. Quolls were classified as juvenile or adult on their first capture. Eighteen candidate models were compared where survival ( $\Phi$ ) and recapture ( $p$ )



**Figure 1** Location of the study site within Kakadu National Park.

were group specific ( $g$ ), sex specific (Sex), time dependent ( $t$ ) or constant ( $\cdot$ ). Model averaging (Burnham & Anderson, 2002) was used to obtain annual survival estimates for the PVA.

Radio-tracking of quolls was undertaken for 3 months in 2012–2013 as part of a study examining den selection. Collars with very high frequency radio-transmitters weighing <5% of each animal's body mass (Model: BD-2C; Holohil Systems Ltd., Carp, ON, Canada) were fitted to adult female quolls and juvenile quolls >100 g using polyvinyl chloride (PVC) tubing and cotton (Soderquist, 1993). Two threads of cotton were threaded through the PVC tubing and tied to secure the collar. This design enabled the cotton thread to break if the collar became too tight. Completed collars weighed between 4 and 11 g, depending on the size of the transmitter. When fitted with a collar, quolls were radio-tracked on a daily basis, before noon. If an animal was tracked to the site of its death, the cause of death was determined by a post-mortem examination, based on criteria used by Oakwood (2003).

We used demographic data from our target population to construct a PVA using VORTEX 9.9 (Lacy, 1993). The input values along with the information source for the basic model are shown in Table 1. Due to insufficient data, environmental variation was set at zero. This may underestimate extinction risk, since stochastic processes cause instability in small populations (Lacy, 1993; Glen & Dickman, 2013). Hence, the importance of environmental variation in the model up to 10% was tested using sensitivity testing. The model and predicted population survival was not sensitive to changes in environmental variation (Fig. S1).

We examined two intervention scenarios; the first is population supplementation, whereby five adult males and five adult females are released into the population annually for 1, 3 or 5 years. The second scenario involved modelling a reduction in mortality across all age and sex classes except adult males. Adult males were excluded from the mortality reduction due to the fact that they are short-lived and rarely live longer than a year (Oakwood, 2000). We modelled mortality reductions of 2.5%, 5% and 10% (Table 2).

We used sensitivity testing to examine the sensitivity of the model to its parameters and estimated the response of population survival to changes in mortality of up to 5% in each direction for each age and sex class.

## Results

### Population monitoring and radio-tracking

Following their reintroduction, seven female quolls established territories on the study site. The population remained stable for the next 12 months. In March 2012, trapping was abandoned after two nights due to high levels of trap disturbance by dingoes and free-ranging dogs. This was the first occurrence of trap disturbance during the study and coincided with seasonal closure of the area to tourists due to wet-season flooding. In the following trapping session, only one adult female was captured at the study site (Fig. 2).

Sixteen quolls (two adult females, eight juvenile females and six juvenile males) were tracked intermittently over the 3-month period. Of the 16 radio-tracked quolls, four juveniles were tracked to the site of their death. Three of these quolls were located in open woodland adjacent to rock outcrops and had evidence of canid predation as they were largely uneaten and bite size was larger than what would be expected from cat predation as per Oakwood (2003). One quoll died of unknown causes.

### Demography

The results of the CJS identified three models with  $\Delta AIC_c < 2.0$ , suggesting that these three models were well supported by the data (Table S1) (Burnham & Anderson, 2002). The best supported model was  $\Phi(\text{Sex}) p(\cdot)$  in which monthly survival was affected by sex (independent of age) and recapture was constant. In this model, female survival was significantly higher than male survival ( $89.3\% \pm 2.3$  and  $76.4\% \pm 4.4$  respectively; Table S2). In order to obtain mortality data for use

**Table 1** Parameter inputs and information sources for the basic VORTEX population model for *Dasyurus hallucatus*

Parameter	Value	Source
Scenario settings		
No. of years	20	
No. of iterations	1000	
Extinction definition	Only one sex remains	
No. of populations	1	
Species description		
Inbreeding	N/A	
Reproductive system		
Mating system	Polygynous	(Oakwood, 2002)
Age at first offspring (years)	1	(Begg, 1981)
Maximum age of reproduction (years)	3	(Begg, 1981)
Maximum no. of progeny per year	8	(Oakwood, 2000)
Sex ratio in the pouch (% males)	50	(Oakwood, 2000)
Reproductive rates		
% adult females breeding	91	(Begg, 1981)
Offspring per female per year (mean $\pm$ sd)	7.3 $\pm$ 0.9	(Oakwood, 2000)
Mortality rates		
Annual juvenile female mortality (%)	72.2	(Table S3)
Annual juvenile male mortality (%)	93.9	
Annual adult female mortality (%)	76.3	
Annual adult male mortality (%)	94.8	
Mate monopolization		
% males in breeding pool	100	
Initial population size		
Age distribution	Stable	
Initial population size	12	Average population over the past year
Carrying capacity		
Carrying capacity ( <i>K</i> )	50	(Oakwood, 2003)

**Table 2** Input parameters for reduced mortality scenario

	Baseline mortality (%)	−2.50%	−5%	−10%
Juvenile female	72.2	69.7	67.2	62.2
Juvenile male	93.9	91.4	88.9	83.9
Adult female	76.3	73.8	71.3	66.3
Adult male	94.8	94.8	94.8	94.8

**Table 3** Estimates of apparent survival using model averaging

	Monthly survival	SE	Annual survival (%)
Juvenile female	0.8986825	0.026835	27.75
Adult female	0.8869035	0.0261338	23.69
Juvenile male	0.7924504	0.0574597	6.13
Adult male	0.7813733	0.0608768	5.18

in the PVA, estimates of survival across sex and age classes were calculated using model averaging (Table S3).

### Population viability modelling

The base VORTEX model demonstrates the vulnerability of this population with a  $48.4\% \pm 0.016$  SE probability of population extinction over the next 20 years. The average time to extinction was  $3.96 \pm 0.150$  SE years.

Population survival was most sensitive to changes in juvenile mortality, especially juvenile males. Even small increases in mortality of juvenile males had a strong negative influence on population survival (Fig. 4).

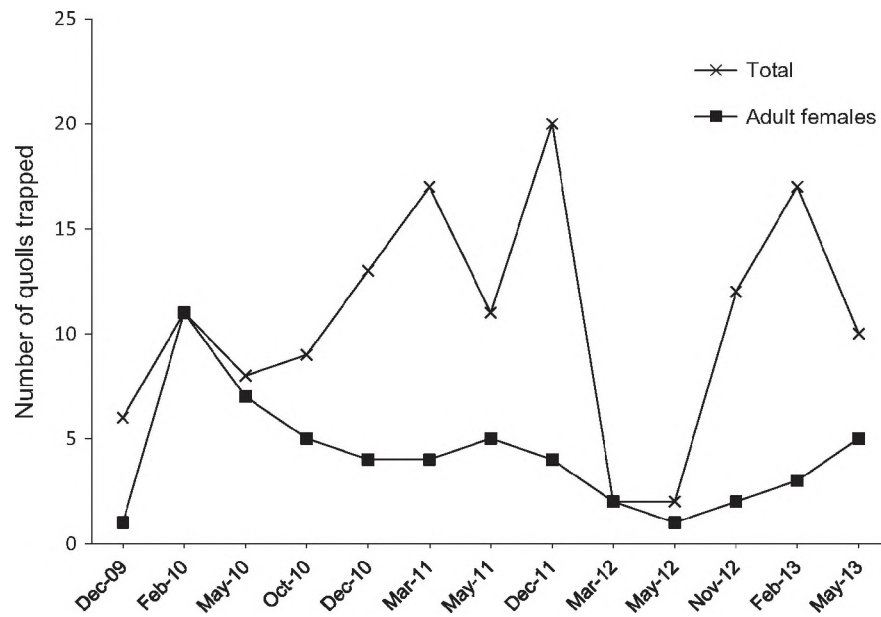
Population supplementation had a substantial effect on probability of population survival and effective population size (Fig. 3a,c). One year of supplementation increased the probability of population survival over 20 years from 51.6% to 81.7%. Continuing supplementation for 3 or 5 years increased the probability of population survival to 96.5% and 98.1% respectively.

Small changes in mortality strongly influenced the probability of population survival and effective population size (Fig. 3b,d). A 2.5% reduction in the rate of mortality for juveniles and adult females increased the probability of population persistence over 20 years to 83.6%. Further reductions in mortality of 5% and 10% increased the probability of survival to 92.2% and 99.4% respectively.

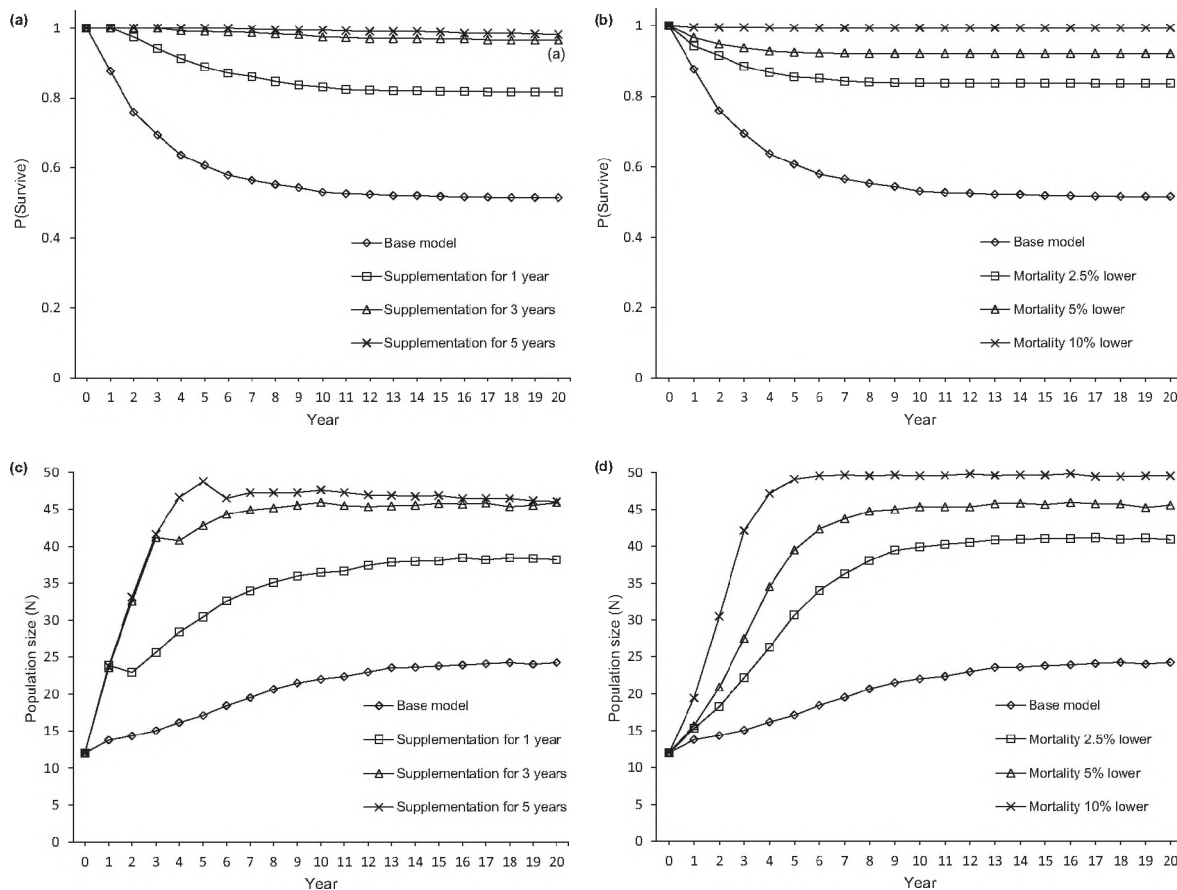
### Discussion

Translocation of animals is widely used as a conservation tool (Seddon *et al.*, 2014), but success rates are often poor, especially when threatening processes are not removed (Fischer & Lindenmayer, 2000). In our study, we identified a key threatening process (cane toad poisoning) and





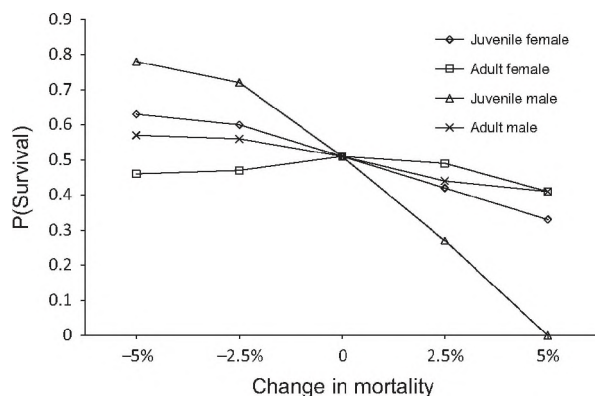
**Figure 2** Number of individually marked quolls captured during each trapping session.



**Figure 3** Simulated survival and effective population size curves for the population of quolls with supplementation (a and c respectively) and reduced mortality (b and d respectively).

ameliorated it by introducing 'toad-smart' quolls to supplement a near-extinct population. Two years after our intervention, the population increased in late 2011. Subsequent genetic analyses confirmed that some offspring of introduced females survived and reproduced, suggesting that 'toad-smart' traits were transferred to offspring (Cremona *et al.*, 2017). However, in early 2012, the population experienced a severe crash coinciding with observations of elevated dingo densities on the study site. Radio-tracking revealed that canid predation, not cane toad poisoning, was the major source of mortality for radio-tagged juvenile quolls. Although the small number of animals tracked to their site of death is insufficient to draw conclusions on a population scale, it nonetheless revealed an unforeseen source of mortality (canid predation) that exerted strong effects on population viability. In this respect, our study is not alone; predation is responsible for many failed reintroduction attempts in Australia (Moseby *et al.*, 2011). Indeed, a reintroduction of burrowing bettongs involving over 100 animals failed due to dingo predation (Moseby *et al.*, 2011). Below, we discuss the broader implications of our research, and make recommendations for future translocations of northern quolls.

The incorporation of PVA in reintroduction biology is a valuable tool for guiding management (Seddon, Armstrong & Maloney, 2007). In our study, sensitivity testing revealed the importance of juvenile male mortality in influencing population viability (Fig. 4). This is likely due to the already high mortality of juvenile males, and the male 'die-off' after their first reproductive season (Oakwood *et al.*, 2001). In a short-lived mammal with high annual mortality, such as the northern quoll, increases in juvenile male mortality may push towards comprehensive mortality and result in recruitment failure. Therefore, male survival may be more important than female mortality in influencing population survival in a small population. The importance of male survival may also be significant in other small populations with male-biased mortality. For example, the risk of local extinction in small fragmented populations of African lions *Panthera leo* may be intensified by increased adult male mortality due to trophy hunting (Barthold *et al.*, 2016).



**Figure 4** Sensitivity testing: changes in mortality in all classes and their effect on population survival.

Our results also fit with theoretical predictions on the fate of small populations; demographic processes can be a more immediate risk than genetic diversity in driving population extinction (Lande, 1988; Wootton & Pfister, 2013). However, given the high mortality rate and rapid extinction of the modelled population, it is likely that reduced genetic diversity could also adversely affect population viability. For example, recent modelling of a threatened bettong, the woylie *Bettongia penicillata ogilbyi* revealed that inbreeding depression was detrimental to the population when combined with high predation (Pacioni *et al.*, 2017).

In the last decade, there has been a growing interest in the reintroduction of apex predators to restore ecosystem functioning (Seddon *et al.*, 2014). By regulating the density of mesopredators, apex predators can provide positive benefits for smaller prey species (Ritchie & Johnson, 2009; Ripple *et al.*, 2014). However, the density of apex predators in a trophic cascade strongly alters their trophic impact. Predator numbers are usually regulated by a density-dependent response to a shortage of resources, enabling predator and mesopredator numbers to achieve a stable state (Smith & Quinn, 1996). Providing resource subsidies to predators has various direct and indirect ecological effects including changes in predator abundance, demography, sociality and increased predation or competitions with co-occurring species (Newsome *et al.*, 2015). Generalist predators frequently take advantage of the availability of anthropogenic resources and the provision of superabundant food results in high-density predator populations (Bino *et al.*, 2010; Newsome *et al.*, 2013b). In Australia, human resources can influence dingo occurrence (Newsome *et al.*, 2013a), and dingoes can consume relatively more small mammals when supplemented by human resources (Newsome *et al.*, 2014).

The quoll population crash we observed in March 2012 coincided with cyclonic flooding coupled with the absence of anthropogenic resources provided by the high number of tourists that visit Kakadu between May and October. The seasonal nature of tourism causes a disparity in human occupation and consequently the availability of anthropogenic resources between high and low seasons (Rudihartmann, 1986). Many areas have patches of high resource availability due to tourism. For example, in North America, the presence of anthropogenic food in black bear scats is correlated with the number of visitors to Yosemite National Park (Greenleaf *et al.*, 2009). When these human-provided resources decrease in availability, predators increase predation on prey species to compensate. In northern Ethiopia, increases in hyena predation on donkeys coincided with Christian fasting periods and the resulting reduction in availability of anthropogenic waste (Yirga *et al.*, 2012). Refuse facilities, campground rubbish and road kill are anthropogenic food sources that support high numbers of dingoes (Newsome *et al.*, 2013a). In this study, the absence of human food subsidies and a decreased foraging area caused by cyclonic flooding likely forced dingoes to converge on the remaining refuges of small mammals. We propose that elevated canid predation is likely playing a role in the decline of small mammals in KNP.

Our PVA showed that successful conservation of northern quolls requires a reduction in mortality rates within the population. We propose that canid predation is high in this population and therefore conservation efforts should focus on reducing the impacts of canids on quolls in Kakadu. One way to do this would be to re-establish appropriate fire regimes in the park, which would provide more cover for juvenile quolls during the dispersal phase, when they are most vulnerable to dog predation. In KNP, mammal declines have been linked to inappropriate fire regimes (Woinarski *et al.*, 2010). Frequent fires reduce the understorey shrubs and hollow logs thereby minimizing shelter for small mammals and increasing the risk of predation (Russell-Smith *et al.*, 2002). In a previous study, all predation events by dingoes on quolls occurred in open areas with little vegetation cover (Oakwood, 2000). Hence, high fire frequency likely exacerbates canid predation on quolls, preventing population recovery.

Restricting the availability of anthropogenic food resources could also help to reduce canid predation on vulnerable species (Newsome *et al.*, 2013b). For example, preventing access to food waste reduced populations of overabundant foxes in Israel (Bino *et al.*, 2010). In KNP, rangers could remove road kill or carcasses of culled feral animals, and could bury or burn campground rubbish to reduce anthropogenic food subsidies. Fencing refuse facilities and installing predator proof bins at campgrounds could also help to restrict predator access to food subsidies. For example, the installation of food storage lockers and bear-proof waste disposal facilities in Yosemite NP has decreased the prevalence of anthropogenic foods in bear scats (Greenleaf *et al.*, 2009). Considering the average extinction time for quolls in our analyses was 3.96 years, a rapid approach to management is necessary. In order to conserve the few quolls that remain in this population, culling or neutering free-ranging canids to limit the population may be necessary.

Our population simulations suggest that with no management, the quoll population in at East Alligator region of KNP has a 48% risk of extinction in 20 years. The high probability of extinction for the quoll population emphasizes the importance of immediate conservation action. The two scenarios examined in the PVA had similar results suggesting that conservation intervention would have a substantial effect on the imperilled population. Northern quolls occur and exist in good numbers on 10 islands off the coast of the Northern Territory and successful translocation has established populations on an additional two islands (Rankmore *et al.*, 2008). Supplementation is therefore a feasible conservation action for quolls in mainland Australia. However, given that we reintroduced 22 female quolls and had a maximum of seven establish at the study site, it is likely that we would need to supplement the population with at least 50 quolls, preferably from wild populations co-occurring with dingoes (e.g. from Groote Eylandt) to ensure that five of each sex establish within the population.

In conclusion, our monitoring study and PVA model demonstrates the dire circumstances for one of the few remaining populations of northern quolls in the Northern

Territory. The impending extinction crisis reinforces the need to explore all factors responsible for mammal declines; in this respect, increased predation by subsidized apex predators has so far been overlooked (Ziembicki *et al.*, 2015). It is extremely important not to undervalue the role that dingoes play as trophic regulators (Letnic, Ritchie & Dickman, 2012); nonetheless, we must acknowledge that dingoes are predators and in the absence of alternative food sources, subsidized apex predators can prey on native species and contribute to their extinction.

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## Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Sensitivity testing: changes in mortality in all classes and their effect on population survival.

**Table S1.** Full set of mark-recapture models compared using program MARK.

**Table S2.** Monthly survival and recapture probability estimates from model ' $\Phi(\text{Sex}) p(\cdot)$ '.