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Review

Diagnosing species decline: a contextual review of threats, causes and future directions for management and conservation of the eastern quoll

Bronwyn A. Fancourt

School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tas. 7001, Australia.
Email: Bronwyn.Fancourt@utas.edu.au

Abstract. Diagnosing the cause of a species' decline is one of the most challenging tasks faced by conservation practitioners. For a species approaching extinction, it is not possible to go back in time to measure the agents that operated at various stages of the decline. Accordingly, managers are often restricted to measuring factors currently affecting residual populations, which may not be related to factors that operated earlier in the decline, and inferring other mechanisms from different lines of evidence. In this review, I adopt a methodical diagnostic framework to comprehensively evaluate the potential causal factors for the decline of the eastern quoll (*Dasyurus viverrinus*) in Tasmania, and propose a hypothesis as to the cause of decline. Potential causal agents were gleaned from two key sources: factors implicated in the eastern quoll's historical demise on the Australian mainland, and factors that changed during the recent period of quoll decline in Tasmania. The three most likely candidate causal agents were investigated over 4 years to evaluate their likely contribution to the decline. Here, I synthesise the findings from this recent research to advance a hypothesis as to the cause of the eastern quoll decline in Tasmania. I suggest that a period of unsuitable weather reduced quoll populations to an unprecedented low abundance, and that populations are now too small to overcome established threat intensities to which they were robust when at higher densities. Residual small populations are inherently more susceptible to demographic, environmental and genetic stochasticity and are unlikely to recover without management intervention. I propose a study design to experimentally test this hypothesis, and outline priority areas for future research and actions to guide in the future management and conservation of the species. This case study illustrates an approach by which practical species conservation problems might be solved and recovery strategies may be better informed, thereby ensuring positive conservation outcomes for threatened species.

Additional keywords: *Dasyurus viverrinus*, weather, climate change, disease, toxoplasmosis, feral cat, Tasmanian devil, mesopredator release, predation, competition, fox, 1080.

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Introduction

Diagnosing the cause of a species' decline is one of the most challenging tasks faced by conservation practitioners (Caughley 1994). For some species, a decline in abundance may simply be part of a natural population fluctuation from which the species will recover without management intervention (Krebs *et al.* 2001). Alternatively, it may indicate a more concerning trajectory towards extinction (O'Grady *et al.* 2004). A population decline may result from a contraction in a species' range, or a decline in abundance within an existing range (Rodríguez 2002). Different threats and mechanisms can operate at different temporal and spatial scales, in succession or simultaneously, such that contemporary agents of decline may be unrelated to or disconnected from the original cause of decline (Elliott and Brook 2007). Often, several threats act together to produce synergistic effects that are greater than the sum of the contributions of each threatening process in isolation (Brook *et al.* 2008), complicating attempts to tease apart causal agents from mere associations. Accordingly, before appropriate conservation strategies can be developed, managers need to understand the factors that determine and limit the species' distribution and abundance.

To identify the agent(s) responsible for a species decline, Caughley (1994) proposed four key steps:

(1) Gain an understanding of the species' natural history, ecology, context and status;
(2) List all the conceivable agents of decline;
(3) Measure and contrast the agents where the species is now, and where the species used to be, to identify putative causal agents of decline; and
(4) Test the hypotheses produced to confirm agents are causal and not merely associated with the decline.

While Caughley's (1994) diagnostic framework provides a solid scientific foundation to simplify many complex and difficult investigations, its application and the usefulness of any insights gained may be limited in some cases. For example, step 3 inherently requires that the species' decline is still ongoing, or has not yet reached a state where all populations have declined or become locally extinct, thereby facilitating comparison between populations that have declined and those that have not. Additionally, for a species undergoing decline, the final step in the extinction vortex may be unrelated or disconnected from the original cause of decline (Brook *et al*. 2008). For a species approaching extinction, it is not possible to go back in time to measure the agents that operated at various stages of the decline, unless these records were maintained before the decline became apparent. In many cases, managers are restricted to measuring those factors currently operating on residual populations (which may or may not be related to factors operating earlier in the decline), and inferring other mechanisms from different lines of evidence (Hillborn and Mangel 1997; Elliott and Brook 2007).

In this review, I adopted Caughley's (1994) diagnostic framework to investigate and evaluate the key threats and processes that have contributed to the recent decline of the eastern quoll in Australia's island state of Tasmania. I used this approach for two reasons. First, the decline of the eastern quoll is still in progress, and some populations have not (yet) declined. This allowed the mechanisms of decline to be directly studied by comparing declining and non-declining populations. Second, by comparing declining with non-declining populations or comparing populations in different stages of decline, I could identify factors associated with the decline and study their effects. I commenced by reviewing existing knowledge on the species' natural history, ecology, context and status, and identified potential threats and key knowledge gaps. I then compiled a comprehensive list of potential agents of decline. For each agent, I collated all available anecdotal and observational evidence to assess its likely contribution to the recent decline. The three most likely candidate causal factors were then selected as part of a 4-year multidisciplinary investigation to further identify and quantify any potential causal links. Here I synthesise findings from this recent research to formulate a hypothesis as to the cause of the decline, and propose an experimental design to test this hypothesis. Finally, I conclude by outlining priority areas for future research, and recommend actions to guide in the future management and conservation of the species.

Natural history, ecology, context and status

The eastern quoll (*Dasyurus viverrinus*) is an endangered medium-sized carnivorous marsupial that was formerly widespread throughout south-eastern Australia, but now survives only in the island state of Tasmania. Populations on the Australian mainland declined rapidly around the late 1800s and early 1900s (Wood Jones 1923; Peacock and Abbott 2014). The species persisted in relatively low densities within a greatly reduced range, until the last confirmed sighting in Sydney in 1963 (Dickman *et al*. 2001). In contrast to its mainland extirpation, the eastern quoll continued to thrive in Tasmania (Green 1967) where it was considered stable and secure (McKnight 2008). However, the species has recently undergone rapid and severe population decline across the Tasmanian mainland (Fancourt *et al*. 2013), although North Bruny Island still supports a stable, high-density population (Fancourt *et al*. 2015*b*). A combination of trapping and spotlight surveys indicated statewide declines of more than 50% in the 10 years to 2009 with no sign of recovery (Fancourt *et al*. 2013; Fancourt 2015*a*). The reasons for this recent and ongoing precipitous decline are not currently understood.

The eastern quoll is sexually dimorphic with a mean adult body mass of 1250 g (900–2000 g) for males and 850 g (700–1100 g) for females (Godsell 1983; Jones and Rose 2001). Females are seasonally polyoestrous, with highly synchronous births in June–July each year. This highly synchronous breeding typically results in a 3- to 4-fold increase in population abundance around November and December each year, when independent juveniles first emerge from their natal dens. Population abundance typically remains high until after the May–June mating season, after which populations usually return to pre-weaning abundance (Godsell 1983). The more mobile males cover a mean home range of around 44 ha compared with 35 ha for females (Godsell 1982; Godsell 1983; Bryant 1986), although larger home ranges have been observed in subalpine areas (M. Jones, pers. comm). Annual mortality appears high (Godsell 1983), although the causes remain unclear and speculative (Dickman *et al*. 2001). Maximum life expectancy is around 3–4 years in the wild (Godsell 1983).

The eastern quoll is widespread throughout most of Tasmania. It occurs primarily in the drier agricultural regions in the eastern half of the island, although it is infrequently observed in low densities in open habitat throughout the wetter west of the island (Fancourt *et al*. 2015*a*). It is commonly associated with forest-pasture interfaces that provide open grasslands for foraging at night, adjoining natural forest habitat where quolls den in hollow logs, under rocks and in underground burrows during the day (Godsell 1983). It also occurs in subalpine buttongrass moorlands, sedgelands and a mix of wet and dry sclerophyll forest, but is notably absent from large tracts of rainforest (Rounsevell *et al*. 1991; Taylor and Comfort 1993; Fancourt *et al*. 2013). The diet consists mostly of invertebrates, although birds, small mammals, reptiles, fruit and carrion are also eaten, depending on season and location (Blackhall 1980; Godsell 1983; Jones and Barmuta 1998).

The ecological interactions between eastern quolls and their potential predators and competitors are not well understood. Eastern quoll remains have been found in roost and nest sites of masked owls (*Tyto novaehollandiae*) (Mooney 1993), and cats (*Felis catus*) are known to kill eastern quolls (Peacock and Abbott 2014; Fancourt *et al*. 2015*b*), although the frequency and impacts of predation on quoll populations are not currently known. Tasmanian devils (*Sarcophilus harrisii*) are known to scavenge dead quolls (Jones 2000), but it is unclear whether devils or spotted-tailed quolls (*Dasyurus maculatus*) hunt or kill eastern quolls. Some dietary overlap between eastern quolls and feral cats may be inferred from species-specific dietary studies (e.g. Blackhall 1980; Godsell 1983; Jones and Barmuta 1998; Lazenby 2012). However, these Tasmanian studies are limited both spatially and temporally, and no studies have investigated the diets of sympatric cats and quolls in Tasmania. Therefore, the extent to which eastern quolls may compete with feral cats for resources is largely unknown.

Potential agents of decline

In compiling a list of potential agents of decline, I have drawn on two main lines of evidence: (1) agents implicated in the eastern quoll's demise on the Australian mainland; and (2) factors that have recently changed in Tasmania that broadly correlate temporally with the period of eastern quoll decline. Each factor is considered in detail below.

Climatic variables

Population eruptions and declines have been anecdotally reported in eastern quolls since the 1800s, both in Tasmania and on the Australian mainland (Peacock and Abbott 2014). These observations lend support to the hypothesis that marked fluctuations may simply be part of the species' natural history, but the mechanisms driving these fluctuations are not understood. The duration of weather (short-term climatic conditions over months or a few years) differs from climate (long-term climate means, typically over 30–50 years or longer). Accordingly, weather and climate will potentially impact different species in different ways. Short-term weather fluctuations can result in sudden marked changes in a species' distribution and abundance (Parmesan *et al*. 2000; Whitfield *et al*. 2007). Unfavourable climatic conditions may contribute to population declines by exceeding a species' physiological tolerances (Root 1988), limiting food resources (Thomas *et al*. 1996) or disrupting reproduction and completion of life cycles (Woodward *et al*. 1990). Furthermore, climate change can exacerbate extrinsic threats such as disease or competition for limited food resources (Pounds *et al*. 2006). For short-lived species such as the eastern quoll, variation in short-term weather, or weather extremes, would likely be a greater contributor to rapid population declines than changes in long-term climatic means.

Extreme weather is a candidate agent in the eastern quoll decline. The recent decline in Tasmania broadly coincides with 'the millennium drought' (2001–2009), the longest uninterrupted series of years with below median rainfall in south-east Australia since at least 1900 (van Dijk *et al*. 2013). If weather extremes drive episodic fluctuations in quoll abundance, the recent decline may be temporary and recovery could ensue without management intervention when weather conditions return to normal. Alternatively, the recent decline could represent a cumulative or permanent trajectory towards extinction. Therefore, as a first step, it is imperative that the nature of the decline be determined by investigating if the distribution and abundance of eastern quolls are sensitive to short-term variation in climatic variables (i.e. weather), and if shifting weather patterns can explain the recent decline.

Feral cats

Predation by feral cats is considered to be the most significant factor in Australia's recent mammalian extinctions, and is also regarded as the factor affecting the largest number of threatened and near-threatened mammal taxa in Australia (Woinarski *et al*. 2014). Since the 1860s, there have been reports of domestic cats killing quolls (Peacock and Abbott 2014), indicating that feral cats are capable of killing adult and juvenile eastern quolls. However, most historic observations involve domestic cats, and the extent to which feral cats may have contributed to historic quoll declines on the mainland is unknown. Domestic cats were first introduced to Tasmania in 1806, while the earliest records of feral cats are from the 1840s (Abbott 2008). Accordingly, cats and quolls have not only co-existed but thrived together in Tasmania for over 200 years, without any known significant negative effects on populations of either species. This suggests that feral cats are unlikely to have been a major contributor to the recent quoll decline. However, cats are capable of killing prey much larger than eastern quolls (Fancourt 2015*b*), and several studies suggest that feral cats sometimes act in conjunction with a range of other variables such as alteration of habitat, fire, drought and disease to contribute to the decline of native taxa (Oakwood 2000; Burbidge and Manly 2002; Abbott 2006; McGregor *et al*. 2014). This lends support to the hypothesis that variables such as 'the millennium drought' (Tasmanian Planning Commission 2009*a*; van Dijk *et al*. 2013), in combination with ongoing habitat changes (Forest Practices Authority 2012), may have been enough to unsettle the historic balance between these species in favour of cats, possibly contributing to the recent eastern quoll decline.

Of particular note is the decline of the Tasmanian devil due to the spread of the fatal Devil Facial Tumour Disease (DFTD) (Hawkins *et al*. 2006). As the largest terrestrial mammalian carnivore on mainland Tasmania, it has been hypothesised that devils historically suppressed feral cats, through aggressive encounters, competition and possibly predation (Jones *et al*. 2007). If this is the case, then the ongoing loss of devils might reduce predation or competition pressure on feral cats, potentially allowing them to alter their spatial and temporal activity and possibly increase in abundance. Indeed, a recent study suggested that an increase in cat sightings following devil decline in north-eastern Tasmanian might be linked to eastern quoll declines (Hollings *et al*. 2014). While the interactions between devils, cats and eastern quolls have not been investigated, any increase in feral cat abundance or activity may exert additional pressure on smaller predators such as the eastern quoll, possibly through increased predation, exploitation or interference competition, or exposure to diseases such as toxoplasmosis. Accordingly, feral cats are a candidate contributor to the recent quoll decline.

Disease

Numerous historical accounts refer to an unspecified disease that affected eastern quolls on the mainland commencing around the mid-1860s, with the number of accounts peaking between 1890 and 1910 (Peacock and Abbott 2014). In some areas, local quoll populations seemingly disappeared within a matter of weeks or months (Peacock and Abbott 2014), although some populations persisted in relatively low densities in a few isolated areas until the 1950s or 1960s (Lindsay 1962; Wakefield 1964; Seebeck 1984). Many have speculated as to the identity of the candidate pathogen or disease: mange, heavy ectoparasite burdens, bubonic plague, a distemper-like virus, and toxoplasmosis have all been suggested (Peacock and Abbott 2014).

There is some evidence that the mainland disease was not host-specific. While the exact causative agent(s) is unknown, several accounts refer to disease affecting a range of native animals at that time, including possums, phascogales, bettongs, wallabies, kangaroos and koalas (Lindsay 1962; Lunney and Leary 1988; Curson and McCracken 1989; Recher *et al*. 1993; Abbott 2006; Peacock and Abbott 2014). There is currently no evidence for a pathogen that is not host-specific being involved in the eastern quoll's recent Tasmanian decline, and comparable declines in a range of Tasmanian marsupials have not been observed. The only confirmed disease-induced species decline during the period of quoll decline is that of the Tasmanian devil due to the spread of DFTD (Hawkins *et al*. 2006). While the close relatedness of eastern quolls to devils may imply a similar susceptibility, the cell line responsible for this infectious cancer is considered highly unlikely to grow in other species (McCallum and Jones 2006). To date, no cases of DFTD have been confirmed in any related species.

Toxoplasmosis, the disease caused by the pathogen *Toxoplasma gondii*, has been posited by some as the disease possibly responsible for the historic eastern quoll declines on the Australian mainland (Shepherd and Mahood 1978; Cross 1990; Freeland 1993; Recher *et al*. 1993). *T. gondii* is an intracellular coccidian parasite with a worldwide distribution (Hill *et al*. 2005; Dubey 2010). Infection by *T. gondii* can result in overt clinical disease (Dubey and Frenkel 1972; Innes 1997; Dubey 2010), with fatalities observed in many wildlife species (Work *et al*. 2000; Szabo *et al*. 2004; Jokelainen and Nylund 2012; Howe *et al*. 2014). Some Australian marsupials are especially susceptible to toxoplasmosis (Obendorf and Munday 1983; Canfield *et al*. 1990; Innes 1997; Bettiol *et al*. 2000). In Australia, feral, stray and domestic cats are the only definitive host that can excrete the environmentally persistent *T. gondii* oocysts that are a major source of infection for many intermediate hosts (Dubey *et al*. 2004). As the mainland decline of quolls occurred after the introduction of cats, it was considered plausible that toxoplasmosis may have been the disease responsible.

While cats have been in Tasmania for over 200 years (Abbott 2008) with no obvious negative effect on eastern quoll populations, several stressors such as drought or habitat loss in recent years may have triggered recrudescence of latent infection into overt disease, which may be contributing to the recent quoll decline. Furthermore, if the abundance of feral cats has increased following devil decline, this would increase the prevalence of the pathogen in the environment, presenting an increased risk of exposure to susceptible wildlife. Indeed, a pilot study in 2010 found higher prevalence of *T. gondii*-specific IgG antibodies at two sites where quolls had declined compared with a site with a stable population (Fancourt 2010). Accordingly, toxoplasmosis is a candidate agent in the recent quoll decline.

Foxes

The red fox (*Vulpes vulpes*) has been implicated as a major factor in the extirpation of eastern quolls on mainland Australia (Jones and Rose 2001), largely because the pattern of quoll decline broadly coincided spatially and temporally with the fox's geographical range expansion. Additionally, eastern quolls fit within the critical weight range or 'CWR' of prey species that have been most affected by foxes on the mainland (Burbidge and McKenzie 1989). However, first-hand accounts of foxes killing quolls are scarce (Peacock and Abbott 2014), and predation (as distinct from scavenging) has typically only been inferred from historical anecdotal evidence of quoll remains around fox dens (*The Australasian* 9 December 1905: p.1404) or foxes chasing quolls (*The Argus* 11 June 1884: p.3).

However, it seems more likely that disease, rather than fox predation, accounted for the major decline in quoll populations on the Australian mainland around 1890–1910. An extensive review of historical accounts (Peacock and Abbott 2014) has revealed numerous accounts of quoll decline that predate the introduction or local establishment of foxes (Abbott 2011), and several accounts of quoll hyperabundance postdating fox establishment in some regions. Foxes probably contributed to the final demise of the remaining quoll populations that persisted in low densities for the 50–60 years following the disease epidemic.

Foxes are also unlikely to have been a major contributor to the recent decline of eastern quolls in Tasmania. Foxes were recently introduced to Tasmania (Saunders *et al*. 2006; Sarre *et al*. 2013), presenting an imminent threat, should they become established, to a range of CWR species, including the eastern quoll. However, the estimated low density of foxes and the absence of any new fox evidence since July 2011 (Invasive Species Branch 2013) suggests that foxes are likely to be functionally absent from the island.

Poisoning

Some poisons with potential to affect the eastern quoll are still in use in Tasmania. Strychnine, cyanide and phosphorus were historically used to poison eastern quolls directly (as predators of domestic poultry) and indirectly (as non-target consumers of rabbit baits), or by secondary poisoning of quolls scavenging carcasses of poisoned rabbits (Lunney and Leary 1988; Peacock and Abbott 2013). While the widespread use of these poisons has now ceased, sodium fluoroacetate (compound 1080) has, in recent decades, been the leading method of strategic control of foxes and wild dogs ubiquitous throughout much of the Australian mainland (Glen *et al*. 2007). In Tasmania, 1080 has been used to control the browsing impacts of herbivores since the 1950s, predominantly delivered as poisoned carrot baits that did not present a significant risk to non-target carnivores (Statham 2005). However, the introduction of foxes around 15 years ago led to the commencement of fox baiting programs in Tasmania in 2002 (Saunders *et al*. 2006). Fox baits initially comprised dried kangaroo meat baits poisoned with 1080, with commercially prepared Foxoff® baits being utilised from around 2006–7 (Nick Bates, Department of Primary Industries, Parks, Water and Environment (DPIPWE) pers. comm.). Both bait types are specifically designed to target carnivores and therefore present a novel risk to the eastern quoll through possible non-target poisoning (McIlroy 1981; McIlroy 1986; King *et al*. 1989).

For eastern quolls, the lethal dose (LD_{50}) of 1.5 mg kg^{-1} of 1080 (King *et al*. 1989) would mean that an average 0.85 kg female (Godsell 1983) would need to consume less than half of one 35 g Foxoff bait (3 mg of 1080) to be fatal, possibly even less to kill any nursing young. This is much less than the 90 g of non-poisoned baits consumed in one sitting by eastern quolls in captive trials (Belcher 1998). Laboratory-derived sensitivities, however, reflect a given set of variables such as ambient temperature, diet, stress and energy levels unlikely to be reflective of conditions experienced by wild animals in the landscape. For example, Oliver and King (1983) found that mice (*Mus musculus*), guinea-pigs (*Cavia porcellus*) and brushtail possums (*Trichosurus vulpecula*) were up to five times more sensitive to 1080 at higher and lower temperatures (from 4 to 33°C) than at ambient temperatures used in laboratory trials to establish an LD_{50}. As ambient temperatures in Tasmania are much lower than those used in deriving the LD_{50} for the species, laboratory trials may provide only weak theoretical evidence of whether 1080 baiting presents a realised risk to species in the landscape.

While eastern quolls might be highly vulnerable to mortality from fox baits in the landscape, fox baiting does not appear to have significantly contributed to the recent quoll decline, essentially because declines occurred prior to baiting at many sites. Field-based sensitivity studies have not been performed for the eastern quoll; however, a preliminary review of 1080 fox baiting operations in Tasmania revealed that while quoll declines broadly correlated temporally with the commencement of fox baiting on the island, they did not correlate spatio-temporally. Several quoll populations declined in areas that were either not baited, or were only baited several years after quolls had already declined in that area, indicating that some other factor was responsible for the recent decline. For example, eastern quoll trap success at Bronte Park reduced from 21% to 0% between 2004 and 2011 (Fancourt *et al*. 2013), but baiting only commenced at this site in July 2012. More broadly, statewide quoll declines were recorded around 2003–04 (Fancourt *et al*. 2013), yet less than 10% of the species' distribution had been baited prior to 2010 (C. Elliott, Invasive Species Branch, unpubl. data).

Rodenticides are another potential agent in the recent quoll decline. In recent decades, the active ingredient in rodenticides changed from the first generation anticoagulants (FGAs: e.g. warfarin) to the second generation anticoagulants (SGAs: predominantly brodifacoum and bromadiolone) (Eason *et al*. 2002). During the 1990s, the patent on brodifacoum expired, and its availability and use increased rapidly thereafter (Eason *et al*. 2002). It became widely used in over-the-counter rodenticides that target commensal rodents, but is also increasingly applied in agricultural systems (Eason *et al*. 2002). Rodenticides may result in primary poisoning through unintended ingestion of baits by non-target species, and can also result in secondary poisoning of carnivores that eat poisoned prey or scavenge on their carcasses (Eason and Spurr 1995; Alterio 1996). Brodifacoum in particular has been implicated in increasing numbers of non-target deaths in a range of wildlife species (Eason and Spurr 1995; Stone *et al*. 1999; Thompson *et al*. 2014; Poessel *et al*. 2015). The persistence and potency of the SGAs means that the risk of primary and secondary poisoning from these toxins is greater than that associated with FGAs. In some species, brodifacoum can persist in the liver for more than 8 months (Eason *et al*. 2002). Accordingly, sub-lethal doses of brodifacoum can rapidly bioaccumulate to reach toxic levels, presenting a much higher risk to a range of non-target species. The increasing use of brodifacoum over recent decades (and its widespread use in agricultural areas frequented by eastern quolls) points to its potential contribution to quoll declines. However, given its widespread use and unrestricted availability (e.g. supermarkets), I am unable to ascertain if increased use of brodifacoum is spatially and temporally associated with the recent quoll decline. Future research should evaluate the risk of such poisoning to eastern quolls.

Persecution

Eastern quolls were commonly persecuted throughout recent history, but current persecution levels are unlikely to present a significant threat. Historically, quolls were persecuted as agricultural pests, both on the mainland (Wood Jones 1923; Bennett 1990; Peacock and Abbott 2013) and in Tasmania (Backhouse 1843; Green 1967). Green (1967) considered that when predation on domestic poultry and stock became excessive, population control of quolls (and devils) became a necessary part of 'good pasture and stock management'. Eastern quolls are now legally protected. There may still be cases of individual quolls being killed, but it seems unlikely that ongoing persecution would be sufficient to have driven eastern quolls to their recent decline.

Habitat modification

Certain changes in land use may present a threat to quoll habitat availability. While land clearing has been implicated in the historic decline of the eastern quoll on the mainland and in Tasmania (Green 1967; Lunney and Leary 1988), eastern quolls frequently use open areas (Godsell 1983; Jones and Barmuta 2000; B. Fancourt, pers. obs.). In fact, eastern quolls often benefit from pasture establishment and improvement that is typically accompanied by increases in the pasture grubs and other agricultural pests, such as rodents, that form a substantial part of the species' diet (Green 1967; Blackhall 1980; Godsell 1983). However, conversion of agricultural land or natural forest into monocultures such as timber plantation reduces either foraging or denning habitat for the species. Tasmania has undergone extensive conversion of large tracts of agricultural and natural vegetation into *Eucalyptus* species plantations during the period of quoll decline (Tasmanian Planning Commission 2009*a*; Forest Practices Authority 2012). Accordingly, habitat modification remains a potential contributor to the recent decline and requires further investigation.

Road mortality

Eastern quolls are highly susceptible to road mortality, but this is unlikely to be a significant contributor to the recent decline. Quolls often use roads and tracks for long-distance travel, and they opportunistically scavenge roadkills, often becoming casualties in the process (Jones 2000; B. Fancourt, pers. obs.). Road mortality can have a dramatic impact on local quoll populations in a relatively short period of time (Jones 2000). However, there have been no significant expansions of road networks in Tasmania, and therefore while localised losses may still occur, road mortality is unlikely to be a significant contributor to recent statewide declines in the eastern quoll.

Investigation of candidate causal factors

Based on the review of potential agents of decline, I focused on more detailed investigations of two key events that may have elevated the effects of three of the potential agents: (1) extreme weather events such as the millennium drought; and (2) the potential mesopredator release of feral cats following the decline of the Tasmanian devil. Accordingly, the three candidate causal factors investigated were: (1) weather variables; (2) toxoplasmosis; and (3) possible mesopredator release of feral cats leading to increased predation and/or competition with quolls.

Weather variables

Through the use of temporally explicit species distribution models (SDMs), Fancourt *et al*. (2015*a*) provided evidence that short-term variability in weather likely contributed to the decline of the eastern quoll in Tasmania. They used SDMs to reconstruct variation through time in the distribution of climatically suitable range for the species between 1950 and 2009. Recent fluctuations in quoll abundance (indexed by statewide transect counts) were related to changes in weather across its range, including a sharp decline between 2001 and 2003 (Fig. 1). However, while weather conditions improved after 2004, there was no corresponding recovery of quoll abundance. Fancourt *et al*. (2015*a*) suggest that fluctuations in weather account for the species' recent decline in Tasmania, but that recovery is now being inhibited by factor(s) unrelated to weather.

Toxoplasmosis

Fancourt *et al*. (2014) demonstrated that despite a high susceptibility to *Toxoplasma gondii* infection, eastern quoll populations do not appear to be limited by the cat-borne parasite or its resultant disease, toxoplasmosis. While *T. gondii* infection of quolls was five times higher at sites where they had declined than at the North Bruny Island site where quoll populations were stable, infection did not reduce quoll survival or reproduction, either directly or indirectly (Fancourt *et al*. 2014). The prevalence of *T. gondii* in feral cats (the parasites' definitive host) did not differ among regions (Fancourt and Jackson 2014), and therefore did not contribute to the differing prevalence of infection observed among quoll populations. However, the higher prevalence of *T. gondii* infection in quolls at declined quoll sites signalled higher cat activity at those sites (Fancourt *et al*. 2014), lending support to the hypothesis that cats may be contributing to quoll declines and inhibiting population recovery through non-disease-related mechanisms such as predation or competition.

Mesopredator release of feral cats

Fancourt *et al*. (2015*b*) investigated the influences of top-down effects on abundance and activity patterns among sympatric carnivores (devils, feral cats and eastern quolls) throughout

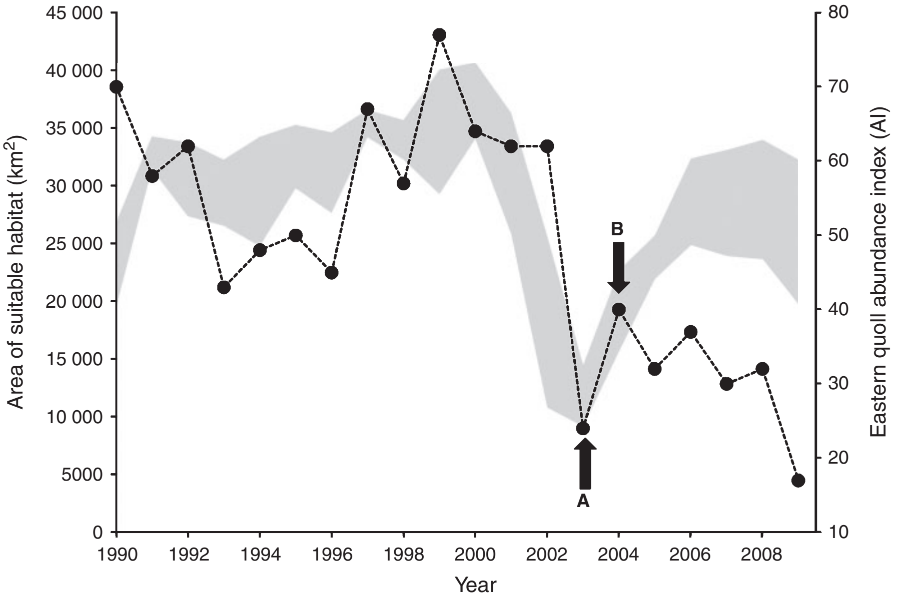

Fig. 1. Temporal variation in area of environmentally suitable habitat and quoll abundance in Tasmania from 1990 to 2009. Grey shading represents the total area of core habitat across all 12 months for each year (left axis). Width of shading indicates variability of suitable area within each year (lower and upper bounds of shading represent the months with the lowest and highest amounts of suitable habitat respectively). Black dots represent the quoll abundance index (AI), being the total number of eastern quoll sightings recorded in annual spotlight surveys across all transects ($n = 147$) surveyed every year from 1990 to 2009 inclusive (right axis). Arrows indicate (A) identified changepoint in mean quoll AI, and (B) identified changepoint in relationship between area of suitable habitat and quoll AI. Figure replicated from Fancourt *et al*. (2015*a*).

the eastern quoll's range. They found no evidence of a negative relationship between devil and cat abundance, and also no evidence of higher cat abundance in areas where devil populations had declined the longest, suggesting that mesopredator release of feral cat abundance had not occurred following devil declines. Cats and devils used the same sites, although there was evidence suggestive of temporal avoidance of devils by cats. Cat and devil activity showed marked temporal separation, with reduced separation and increased nocturnal cat activity observed in areas where devils had declined the longest. Cats and quolls used the same sites, and there was no evidence that cat and quoll abundance were negatively related. However, temporal overlap in cat and quoll activity was higher in summer than in winter, implying a high risk of predation for juvenile quolls, which emerge in summer. Fancourt *et al*. (2015*b*) suggest that predation of juvenile quolls by cats may be inhibiting low-density quoll populations from recovering their former abundance following weather-induced decline, but that this is independent of devil decline.

Hypothesised cause of decline

Based on the results outlined in this review, I advance a hypothesis on the cause of the recent decline of the eastern quoll in Tasmania. I suggest that a period of unsuitable weather reduced quoll populations to an unprecedented low abundance, and that populations are now too small to withstand threats to which they were robust when at higher densities. Eastern quolls appear to be trapped in a 'predator pit' (Krebs 1996; Sinclair *et al*. 1998): environmental conditions have caused a sudden collapse in abundance, leading to a significant per capita increase in predation pressure on small surviving quoll populations, thereby preventing quolls from increasing their abundance when environmental conditions improved, and possibly contributing to further declines. Accordingly, the recent decline does not appear to be temporary and recovery is unlikely without management intervention.

The reduced abundance of eastern quolls during 2002–03 may be unprecedented in recent history, and may have taken abundance below a critical density threshold from which recovery is difficult or improbable. Throughout the 60-year modelling period (1950 to 2009), the total area of climatically suitable habitat fell below 15 000 km^2 in only 34 months, with the 18 months from July 2002 to December 2003 representing the longest consecutive period below 15 000 km^2 (Fancourt *et al*. 2015*a*). In the absence of consistent and reliable abundance records back to 1950, I cannot determine whether 2002–03 was the first instance of such low quoll abundance during this period. However, the unprecedented reduction in core habitat during the 60-year period modelled and the historic correlation between climatically derived habitat suitability and quoll abundance suggests that the low abundance observed during 2002–03 may have also been unprecedented in this 60-year period.

The inability of eastern quoll populations to recover does not appear to have resulted from any new threat or even an increase in threat intensity, but rather an inability to overcome existing levels of threat and attain positive population growth from their current low densities. Small populations are inherently more vulnerable to demographic, environmental and genetic stochasticity (Shaffer 1981; Gilpin and Soulé 1986; O'Grady *et al*. 2004; Willi *et al*. 2006). At their former high abundance, quoll populations may have been able to withstand a certain level of mortality from predation, road mortality, non-target poisoning and a range of other pressures without resulting in population level impacts that threaten local population persistence. However, the same threat intensities may have a disproportionately larger impact on populations that comprise fewer individuals. As quolls are annual breeders and can only produce a maximum of six young per year, their natural reproductive potential is too low to expect the species to return to a viable population threshold without management intervention, either through a reduction in predator intensity, or through supplementing quoll populations to increase local densities, or a combination of both.

Testing the hypothesis: a proposed experimental approach

I recommend that an applied experimental approach be used to test my hypothesis. Field research that focuses on the manipulation of a small set of likely causal factors will provide more compelling evidence on causality than will modelling built on untested assumptions. Investigations should measure the *in situ* response of site-specific population growth rates to two distinct but possibly interacting predictor variables: eastern quoll population size and intensity of cat predation.

While the direct or indirect mechanisms responsible for the weather-induced quoll decline are not currently understood, the greatest impact on the species' viability lies in the resultant reduced population size and the higher risk of extinction that imperils small populations. The inability of small populations to recover unassisted has been observed in numerous species (Newsome *et al*. 1989; Kerle *et al*. 1992; Westemeier *et al*. 1998). To quantify the effect of population size on population growth rates, several low-abundance quoll sites should be supplemented by the introduction of new individuals sourced from captive breeding colonies, insurance populations or the high abundance wild population on Bruny Island. The number of individuals introduced to each site should be large enough to potentially overwhelm current predation intensity (Sinclair *et al*. 1998) and facilitate a positive rate of population growth under the current suite of threats.

The hypothesis that feral cat predation of juvenile eastern quolls is contributing to the inability of low-abundance quoll populations to recover should also be tested. Different species will exhibit different population responses at varying densities of predators or prey. For example, some species such as the eastern barred bandicoot (*Perameles gunnii*) in Victoria appear to have no stable population density in the presence of exotic predators (Backhouse *et al*. 1995; Sinclair *et al*. 1998), whereas fox predation on black-footed rock wallaby (*Petrogale lateralis*) populations has a depensatory effect (inversely dependent on prey density), destabilising wallaby populations when habitat loss or weather reduce them to below a threshold density (Sinclair *et al*. 1998). This latter example parallels the hypothesis that feral cats are contributing to the suppression, preventing recovery of quoll populations following a weather-induced decline below some critical threshold. To test this hypotheses, cat densities should be reduced before juvenile quoll emergence each year at sites with low quoll abundance, and population changes monitored to determine whether survival of juvenile quolls increases, and if quoll populations are able to achieve a positive rate of population increase under reduced predation intensity.

The recommended study design is presented in Fig. 2. Several low-density quoll sites should be divided into the four treatment groups: (1) control sites; (2) quoll supplementation sites; (3) feral cat removal sites; and (4) sites where quoll populations are supplemented and feral cats are removed. Quoll populations at each site should be regularly monitored before, during and after quoll supplementation and/or cat removal. This will enable population growth rates to be compared among treatments by using a series of planned contrasts to quantify the individual effects of each predictor (Fig. 2, contrasts A and B), together with incremental and synergistic effects of the predictors on population growth rates (Fig. 2, contrasts A *v.* C and B *v.* C). Temporal and spatial activity profiles of quolls and cats should also be monitored to determine any behavioural differences among treatments. The spatial scale for these ‘site’ manipulations should be large enough to encompass multiple home ranges of both species, and span multiple years to ensure temporal scales are sufficient to detect any population response.

The development of models of multiple causes may help to determine the relative contribution of each variable to population growth and persistence. However, the usefulness and reliability of any model output assessing population viability will depend on the accuracy and rigour of its inputs (Beissinger and Westphal 1998; McCallum 2000). In data-dependent models, uncertainties in input variables translate to uncertainties, possibly amplified, in model output; reliable estimates will only be found after collecting and interpreting appropriate experimental raw data in the field (Pielou 1981; Beissinger and Westphal 1998; Linnell and Strand 2000). At present, there are no quantitative data on the effects of cat predation on eastern quoll populations, nor on the relationship between quoll population size and viability. Accordingly, to model the relative contribution of each of these variables based on current assumptions, either as univariate or multivariate contributors, would likely produce relatively meaningless predictions and may lead to misdirected and wasted management effort and potentially the loss of the species (Ferson and Burgman 1995). The most compelling evidence to support a hypothesis of cause and effect would come from longitudinal manipulative experimental testing, as I have proposed here. The findings from these experiments should then be used to develop models of multiple causes using an information-theoretic approach (Burnham and Anderson 2002), to determine the relative contribution of each factor to the population growth rate and its effect on population viability.

Management options for conservation of the eastern quoll

The findings from this study have important implications for the future management and conservation of the eastern quoll. The proposed study design outlined above should be commenced as a matter of high management priority, incorporating quoll translocations to low-density Tasmanian sites and targeted cat control. Additionally, the following sections provide a comprehensive list of recommended management actions. Some actions will form an integral part of the recommended study design, while others are complementary and will assist in the interim conservation of the species while experimental studies are performed.

Do nothing

One option is to not assist the eastern quoll in recovering its former abundance, but this is not recommended. Prior to its mainland extirpation, the eastern quoll was considered widespread and sometimes overabundant throughout its range in south-eastern Australia (Peacock and Abbott 2014), illustrating that the species can rapidly descend from overabundance to extinction. While it is possible that the species may recover unassisted in Tasmania, the findings from this review suggest that this is highly unlikely. The recent loss of the Christmas Island pipistrelle (*Pipistrellus murrayi*) illustrates how inaction or delayed action can result in the extinction of a species, and that decisions must be made while there is still an opportunity to act (Martin *et al*. 2012).

In situ *management*

Monitoring

The importance and value of ongoing monitoring adequate to detect significant changes in eastern quoll populations cannot be overstated. The species’ decline was first detected

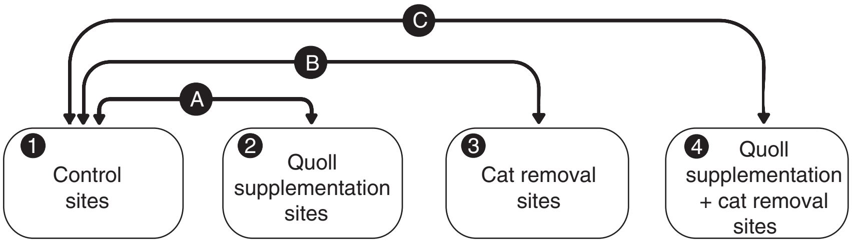

Fig. 2. Recommended experimental design to test the hypothesis of eastern quoll decline advanced in this review. 1–4: treatment groups. A–C: Planned contrasts to compare differences in population growth rates due to (A) quoll supplementation, (B) cat removal and (C) quoll supplementation and cat removal.

through the Tasmanian state government's annual spotlight surveys (Tasmanian Planning Commission 2009*b*). While these surveys were primarily established and designed to monitor wallaby and possum species subject to harvesting (Driessen and Hocking 1992), the survey method was considered valuable for monitoring long-term trends of less frequently recorded species, including the eastern quoll (Driessen and Hocking 1992). Trends in survey data were used to highlight the species' plight (Colyer *et al*. 2008), prompting investigations to confirm the decline (Fancourt *et al*. 2013) and subsequently identify the cause(s) of decline (Fancourt 2015*a*) within a reasonable timeframe. Long-term trends from these spotlight surveys have now been confirmed for the eastern quoll, using trapping surveys (Fancourt *et al*. 2013) and camera surveys (Fancourt *et al*. 2015*b*). In the absence of alternative monitoring protocols for the species, spotlight surveys should continue as an interim form of monitoring, and be extended to include the high-abundance population on North Bruny Island. However, given the parlous status of the species, more robust monitoring techniques such as trapping and camera surveys are warranted to ensure that conservation of the species is adaptive. Trapping surveys enable collection of demographic data and biological samples, but are labour-intensive and restricted in their spatial coverage. However, camera surveys are less invasive, relatively inexpensive, less labour-intensive than trapping surveys, and do not require proximity to roads. They provide more extensive datasets than the vehicle-based spotlight surveys conducted one night a year along roads. Importantly, camera surveys enable detection probability to be incorporated into any estimates of species occupancy or relative abundance, and facilitate assessments of behavioural responses such as spatial and temporal activity patterns that are not discernible using techniques such as spotlight or trapping surveys. Camera surveys should also be extended to sites not surveyed as part of the current investigation in Fancourt (2015*a*), to potentially identify any other relic high-density quoll populations that warrant intensive management.

While the North Bruny Island population is isolated from many of the pressures currently threatening populations on mainland Tasmania, its isolation and the island's small area (362 km^2) also renders it extremely vulnerable to catastrophic events such as bushfires or the introduction of a novel disease. This population is already at risk of inbreeding depression (Hedrick and Kalinowski 2000) due to its low genetic diversity (Cardoso *et al*. 2014), further compounding the vulnerability to threats such as infectious disease. Monitoring and active management of this population is critical to the conservation of the species in the wild. While the North Bruny Island population experienced the same period of unsuitable weather during 2002–03, populations likely recovered due to the lower threat intensities on the island compared with mainland Tasmania (e.g. lower cat densities, reduced road mortality, reduced competitive pressures from large predators such as devils, etc.). Accordingly, monitoring quoll populations through future periods of unsuitable weather, and any subsequent recovery, will be informative as to the hypotheses postulated in this review. Management actions should focus on monitoring this key population, retaining or increasing its genetic variation and ameliorating threatening processes on the island.

Feral cat control

The seasonal removal of feral cats from sites supporting low densities of eastern quolls may allow quolls to emerge from the 'predator pit' and recover their former abundance (Fancourt *et al*. 2015*b*). Additionally, if certain individual cats specialise on quolls as prey (Caro 1980; Dickman and Newsome 2015), their removal could have a disproportionately positive impact on quoll populations. However, the converse may also apply if a single quoll specialist cat remains after all other cats are removed, as a large numerical reduction in cats would only result in a minimal reduction in predation risk. Limited management resources should concentrate removal efforts in October–November each year, thereby reducing predation intensity over summer when vulnerable juvenile quolls first emerge from their natal dens. If successful, such control should not only assist eastern quoll recovery, but could also assist in reducing predation intensity on a range of vulnerable prey species.

The total eradication of cats is not a realistic objective in an area as large as Tasmania, but control programs should aim at reducing cat abundance in priority areas when and where sensitive prey species are most vulnerable. While the total removal of predators from islands can be achieved, successful outcomes typically require large investments of resources (Courchamp *et al*. 2003; Nogales *et al*. 2004; Campbell *et al*. 2011; Robinson and Copson 2014). Such efforts are unlikely to be economically and logistically feasible in large areas of continuous landscapes. Furthermore, targeted cat removal programs in open populations can sometimes result in temporary localised increases in cats due to reinvasion from surrounding areas (Lazenby *et al*. 2015). Accordingly, sustainable ecosystems need to be managed in the presence of predators, possibly by reducing predator abundance so that species can develop appropriate anti-predator responses, such as spatial or temporal partitioning of resources, thereby adapting to live sympatrically with their predators (Lima and Dill 1990; Creel *et al*. 2005). Coexistence is a prerequisite for biodiversity persistence (Linnell and Strand 2000), but for some species in some ecosystems, coexistence may not be possible (Backhouse *et al*. 1995; Sinclair *et al*. 1998).

Devil declines

Compounding the threats posed by feral cats are the shifting ecosystem dynamics following the disease-induced decline of the devil. While an increase in cat sightings in the north-east of the state has been linked to declining devil abundance following DFTD arrival (Jones *et al*. 2007; Hollings *et al*. 2014), studies to date have found no evidence supporting the hypothesis that devil and cat abundance are negatively related, or that cat abundance has increased following devil decline (Lazenby 2012; Saunders 2012; Troy 2014; Fancourt *et al*. 2015*b*). However, the mechanisms by which devils could suppress cats may be more subtle, with some evidence supporting the hypothesis that cats may avoid devils temporally (Lazenby and Dickman 2013; Fancourt *et al*. 2015*b*). Similar temporal avoidance has been observed in other carnivores such as weasels (*Mustela altaica*), which exhibit diurnal activity that contrasts with the crepuscular/nocturnal activity of larger sympatric carnivores such as the stone marten (*Martes foina*) and the red fox (*Vulpes vulpes*) (Bischof *et al*. 2014). Differences in cat activity with increasing time since DFTD arrival suggest that cats may be becoming more nocturnal as devils decline, with similar differences observed among sites with and without devils (Fancourt *et al*. 2015*b*). If this is the case, then shifting cat activity presents an emerging threat to nocturnal species such as eastern quolls that may have rarely encountered cats before devil decline. In this way, predation risk from feral cats may increase further as devils continue to decline, even without an increase in cat abundance. The monitoring of devil and cat populations before, during and after DFTD arrival in the disease-free areas of western Tasmania would help clarify whether devils at higher densities can suppress cats numerically, and whether temporal differences observed in in Fancourt *et al*. (2015*b*) are a response to devil decline or merely reflect pre-existing differences between regions due to other factors that may differ regionally. If devils do suppress cat activity, restoration of devil populations may help ameliorate any predation intensity on nocturnal species such as the eastern quoll.

Other local threatening processes

Ongoing efforts to eradicate the introduced fox should continue as a high-management priority in Tasmania (Sarre *et al*. 2013). As there has been no confirmed fox evidence in Tasmania since July 2011 (Invasive Species Branch 2013), the Fox Eradication Plan is currently in its final stage of operations, with a focus on statewide monitoring and incursion response (Department of Primary Industries Parks Water and Environment 2014). Should foxes become established, the increased predation intensity could not only threaten current low-density quoll populations with extinction, but would likely result in the widespread decline of CWR species, as seen on the Australian mainland (Woinarski *et al*. 2014).

Other potential threats identified, such as habitat loss and non-target poisoning from fox baits and rodenticides, should also be investigated to better understand their impact on eastern quoll populations. I did not consider these factors to be highly likely candidate-causal agents in the recent decline, but they may act in combination with other factors to produce synergies that may amplify negative impacts (Brook *et al*. 2008), particularly on current small quoll populations. Dietary studies should be undertaken to understand the extent to which feral cats compete with eastern quolls for resources. Demographic modelling should also be performed to identify which key life stages appear to differ between declined and stable quoll populations, thereby helping to reveal the causal agents' mode of action.

Climate change

The decline in eastern quoll abundance appears to be linked to an unusual period of unsuitable weather (Fancourt *et al*. 2015*a*), and the frequency, severity and duration of extreme weather events are predicted to increase over coming decades as a result of anthropogenic-driven climate change (White *et al*. 2010; IPCC 2013). The predicted increase in minimum winter temperatures and increased frequency and intensity of extreme rainfall events will gradually erode environmental suitability for eastern quolls (Fancourt *et al*. 2015*a*). Furthermore, the increasing frequency of these unfavourable events will increase the frequency with which populations will be reduced. If quoll populations are unable to recover unassisted under current threat intensities, subsequent extreme weather events may compound the problem and drive current small populations to extinction.

While Fancourt *et al*. (2015*a*) identified the weather variables that are important to the likelihood of quoll occurrence (the minimum temperature of coldest month and precipitation of the wettest quarter), further investigation is required to understand how these variables affect eastern quolls, including how they may interact with other threats. For example, do minimum winter temperatures affect seasonal breeding cues, or determine food resources? An understanding of these mechanisms will help managers decide on actions to ameliorate impacts on quoll populations. The broader causes of climate change are driven by global processes and therefore cannot be adequately managed at the local population scale. Therefore, management should focus on reducing the intensity of current threats such as feral cats, non-target poisoning, habitat loss and road mortality to increase the likelihood of quoll recovery following weather-induced declines in abundance.

Ex situ management

Insurance populations

The establishment of insurance populations should be considered a high-management priority to insure conservation of the species. Insurance populations would serve three main purposes: (1) to provide individuals to supplement current low-density populations in Tasmania; (2) to numerically and genetically ensure against the loss of the species in the wild; and (3) to be a source of founder individuals for future mainland translocations. The species readily adapts to captive management and breeds well in captivity (Bryant 1988). The Tasmanian Quoll Conservation Program currently houses around 70 individuals across four Tasmanian sites, with plans to increase capacity in the near future (W. Anthony, pers. comm.). Additionally, the use of large, fenced predator-free reserves such as the. Mt Rothwell Conservation and Research Centre in Victoria facilitates the conservation of wild-living, self-sustaining eastern quoll populations while minimising their dependence on humans, thereby allowing quolls to better retain their natural instincts and behaviours. These free-range sanctuaries, once established, are less management- and resource-intensive than smaller-scale captive breeding colonies in zoos and wildlife parks. Given the species' small, overlapping home ranges of between 35 and 44 ha (Godsell 1983), large populations can be maintained within fenced sanctuaries of modest size.

Insurance populations should be managed as a metapopulation, with individuals being transferred between sanctuaries to minimise deterioration of genetic variation for the species (Franklin and Frankham 1998). Care must also be taken in sourcing founder individuals from current low-density wild populations in Tasmania. While genetic diversity in insurance populations is desirable, it should not be at the expense of reducing wild populations to such low abundance as to render them unviable and functionally extinct, as occurred with wild source populations of eastern barred bandicoots in Victoria (Todd *et al*. 2002).

Mainland translocations

Reintroductions of eastern quolls into parts of their former distribution on the Australian mainland should also be considered as medium- to long-term goal, but only once mainland insurance populations have been established. The use of predator-proof fenced sanctuaries enables free-range insurance populations to increase in the absence of predation by foxes, cats and wild dogs. By comparison, translocations to unfenced sites are considered high-risk. For example, while fox baiting may reduce fox predation for many threatened species and allow them to recover (Murray *et al*. 2006), for eastern quolls, the risk of poisoning from fox baits could possibly equal, or even exceed, the threat of fox predation (King *et al*. 1989). Additionally, sites managed for predator control are typically national parks, reserves or forestry management areas that incorporate a high proportion of forested habitat and contain very little open grassland to provide the habitat preferred by eastern quolls. In Tasmania, the highest likelihood of eastern quoll occurrence exists outside of national parks and reserves, typically in farmland and more open, sparsely forested grasslands (Godsell 1983; Fancourt *et al*. 2015*a*). Accordingly, founder individuals for translocations into unfenced, high-risk sites on the Australian mainland should be sourced only from genetically managed mainland insurance populations, and only once they are established and at sufficiently high abundance to enable harvesting without jeopardising viability of insurance populations. Given the parlous status of the species in Tasmania, founder individuals for high-risk translocations should not be sourced from wild populations in Tasmania until recovery has been assured, with low numbers of opportunistically wild-sourced individuals being prioritised to maintain genetic diversity of insurance populations.

An understanding of population demographics and factors that affect eastern quoll population growth rates (such as differing population size, sex ratios and predator densities) should be considered in such translocations. Many reintroductions have failed as a result of too few founder individuals being introduced (Short *et al*. 1992; Christensen and Burrows 1995; Gibson *et al*. 1995; Pietsch 1995; Soderquist 1995), often because the species of interest is endangered and the availability of founder individuals is limited. To maximise the likelihood of success, it is important that the appropriate number of individuals is reintroduced to facilitate a net population increase. Sinclair *et al*. (1998) provide a list of important factors that should be considered before undertaking such reintroductions, including estimating the boundary density (the lowest density at which the reintroduced species and its predators can coexist without a net reduction in population size), and whether per capita predation rates increase or decrease at low densities of the reintroduced species. The recommended study design outlined above would quantify these key rates for eastern quolls, thereby enabling determination of the minimum number of individuals to be reintroduced.

Conclusion

This review provides a comprehensive synthesis of the threats and hypothesised cause of decline of the eastern quoll. It highlights priority areas for future research, and recommends appropriate management actions to assist in the conservation of the species. Importantly, this review provides an important resource to ensure conservation strategies and management actions are informed, thereby ensuring conservation of the eastern quoll.

The decline of the eastern quoll demonstrates how multiple threatening processes can interact to bring about the decline of a common species and inhibit its recovery. Effective conservation strategies require an in-depth understanding of the nature of the decline, the agents responsible and their mode of action. However, diagnosing the cause of a species' decline is difficult, as confounding variables and mechanisms can operate at different temporal and spatial scales such that contemporary agents of decline are often unrelated or disconnected from the original cause of decline. Consequently, conservation practitioners are repeatedly forced to act in the absence of evidence-based information about the threats to a species and how those threats may interact. Accordingly, management actions are often based on untested assumptions and hypotheses. However, this may lead to misdirected and wasted management effort, inappropriate conservation strategies and, potentially, the loss of the species. The approach outlined in this review will assist conservation practitioners in solving practical conservation problems, and will ensure that recovery strategies are better informed, thereby increasing the likelihood of positive conservation outcomes for threatened species.

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