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A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review

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Abstract

In response to Australia's current extinction crisis, substantial research efforts have been targeted towards some of the most imperilled species. One such species is the northern quoll (Dasyurus hallucatus); a marsupial predator that has recently suffered substantial declines in range and is now listed as endangered. We conducted a systematic review of all literature relevant to the conservation and ecology of northern quolls. We reviewed 143 publications, including research articles, government and industry reports, theses and books, and quantify research effort in terms of topic, location, and publication period. We then summarise research relevant to their taxonomy, genetics, distribution, habitat associations, diet, reproduction, movement, threats, management, and Indigenous knowledge. Research effort was higher in the most recent decade than the previous four combined. Northern quolls in the Northern Territory were the most studied, followed by the Pilbara, the Kimberley, and Queensland populations. The majority of publications focused on northern quoll distribution and habitat, management, and threats; primarily cane toads, predation, and fire. In concluding we provide a non-exhaustive list of 10 future research directions that if pursued, are likely to provide information critical to managing northern quolls in way that minimises future declines.

Introduction

Biodiversity conservation and management is likely to be most effective when derived from a robust evidence base (Salafsky *et al.* 2019). Despite an ever growing amount of ecological information (Bornmann and Mutz 2015), there remains a considerable gap between the science of conservation biology and the on-ground implementation of evidence-based policy (Evans and Cvitanovic 2018; Knight *et al.* 2008; Rose *et al.* 2019). One reason for this is that conservation practitioners can struggle to access, interpret, and synthesise an increasingly dispersed and voluminous body of scientific literature (Pullin and Knight 2005). Similar problems are encountered by researchers, leading to repetition and redundancy in ecological science (Pulsford *et al.* 2016). Systematic literature reviews are one means of overcoming these issues by identifying, selecting, and appraising research on a predefined topic, drawing out evidence-based management implications and critical knowledge gaps for further research (Moher *et al.* 2009).

Australia's contemporary mammal extinction rate is the globe's highest (Woinarski *et al.* 2019a). Yet more Australian mammals are forecast to become extinct within the next two decades (Geyle *et al.* 2018). In response to this crisis, increased research effort has been directed towards Australian species that have suffered population contractions over the last 200 years (Fleming and Bateman 2016). One such species is the northern quoll (*Dasyurus hallucatus*) **—**a medium-sized marsupial predator (240–1120 g) endemic to northern Australia. Prior to European colonisation in 1788, northern quolls were distributed across much of northern Australia (Braithwaite and Griffiths 1994), but have since suffered substantial declines (Fig 1) (Moore *et al.* 2019). As such, northern quolls are listed as Endangered both nationally (TSSC 2005) and globally (Oakwood *et al.* 2016). Due to their ongoing and precipitous decline, much of the research focused on the ecology and conservation of northern quolls has occurred within the last two decades. However, accessing this research can be challenging, largely because it is spread across a diverse and scattered literature (e.g., books, journals, government and consultant's reports, and theses). To help overcome this barrier, we conducted a systematic review of all literature relevant to the ecology and conservation of northern quolls across their entire range.

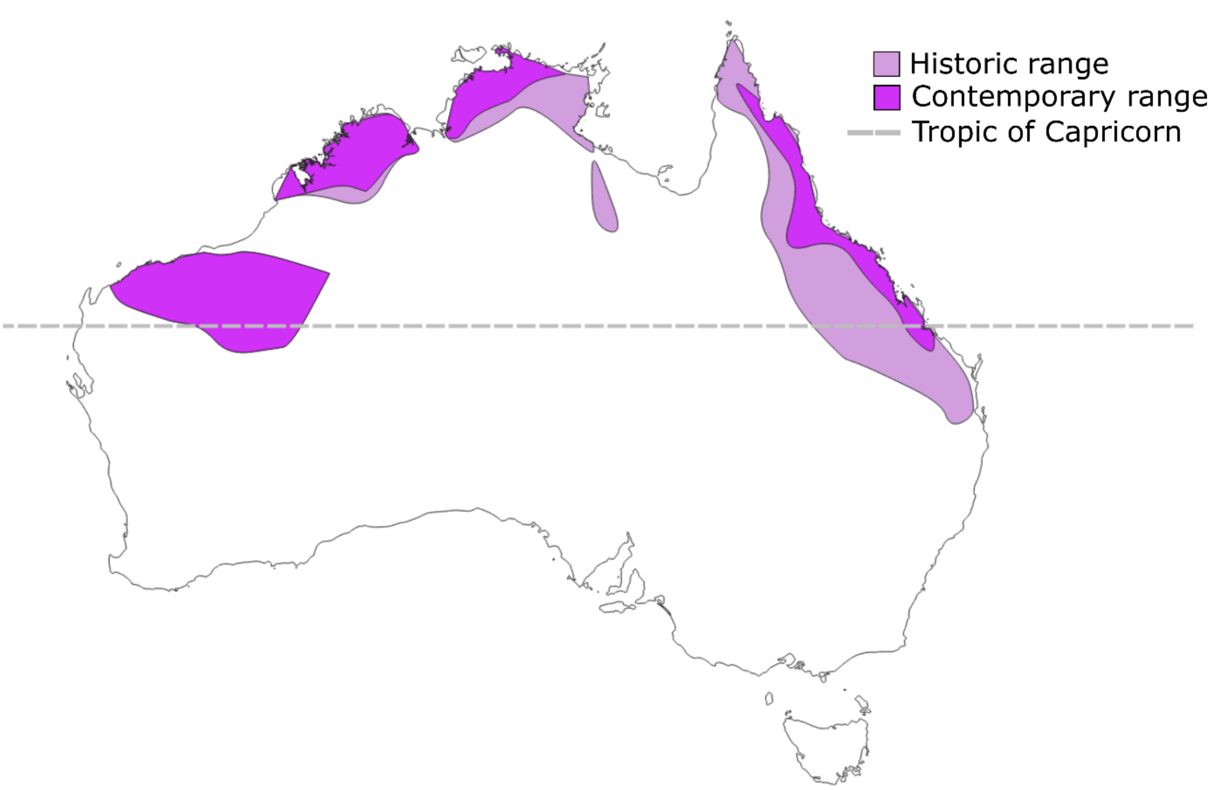

Figure 1. The historic and contemporary range of the northern quoll (*Dasyurus hallucatus*). Figure adapted from (Moore *et al.* 2019). Note that islands occupied by the northern quolls (except Groote Eylandt) are not depicted: these are listed in S1.

The complexities of species conservation are such that multiple disciplinary approaches are often required in order to achieve meaningful progress (Dick *et al.* 2016). With this in mind, we take a deliberately broad approach to our review. We summarise research related to the northern quoll's diet, distribution and habitat associations, genetics and taxonomy, reproduction, movement, and threats and management. We also summarise available Indigenous knowledge related to the northern quoll's ecology. We identify and discuss knowledge gaps throughout, and provide a non-exhaustive list of future research directions for the northern quoll, which if applied, could be useful in providing knowledge critical to improving the conservation of northern quolls.

Materials and Methods

Database compilation

We followed the approach used by Ashman *et al.* (2019) to collate relevant literature for this review. Three electronic databases were searched (Web of Science, Scopus and Google Scholar) on the 17th of August 2020 using the search terms “northern quoll” OR “*Dasyurus hallucatus*”. The search was updated on the 15th of April 2021. Search terms were located in publication title, abstract, keywords and main text. Searches retrieved publications from a range of categories including peer-reviewed literature, Master’ and PhD theses, government and publicly available industry reports, and government action and recovery plans. Publications were reviewed in a three-step process (Fig 2). First, duplicates were removed, then titles and /or abstracts were screened to detect the terms “northern quoll” or “*Dasyurus hallucatus*”, or a reference to a broader community of species that is likely to include northern quolls—for example ‘tropical mammals of Australia’. Last, full texts were reviewed. Publications were excluded if they were not immediately relevant to ecology and conservation of the species. Therefore, for example, publications that focused solely on the physiology or anatomy of northern quolls were removed, unless the publication made explicit reference to the relevance of their findings to ecology or conservation of wild populations (e.g., predator-aversion trials conducted in captivity etc).

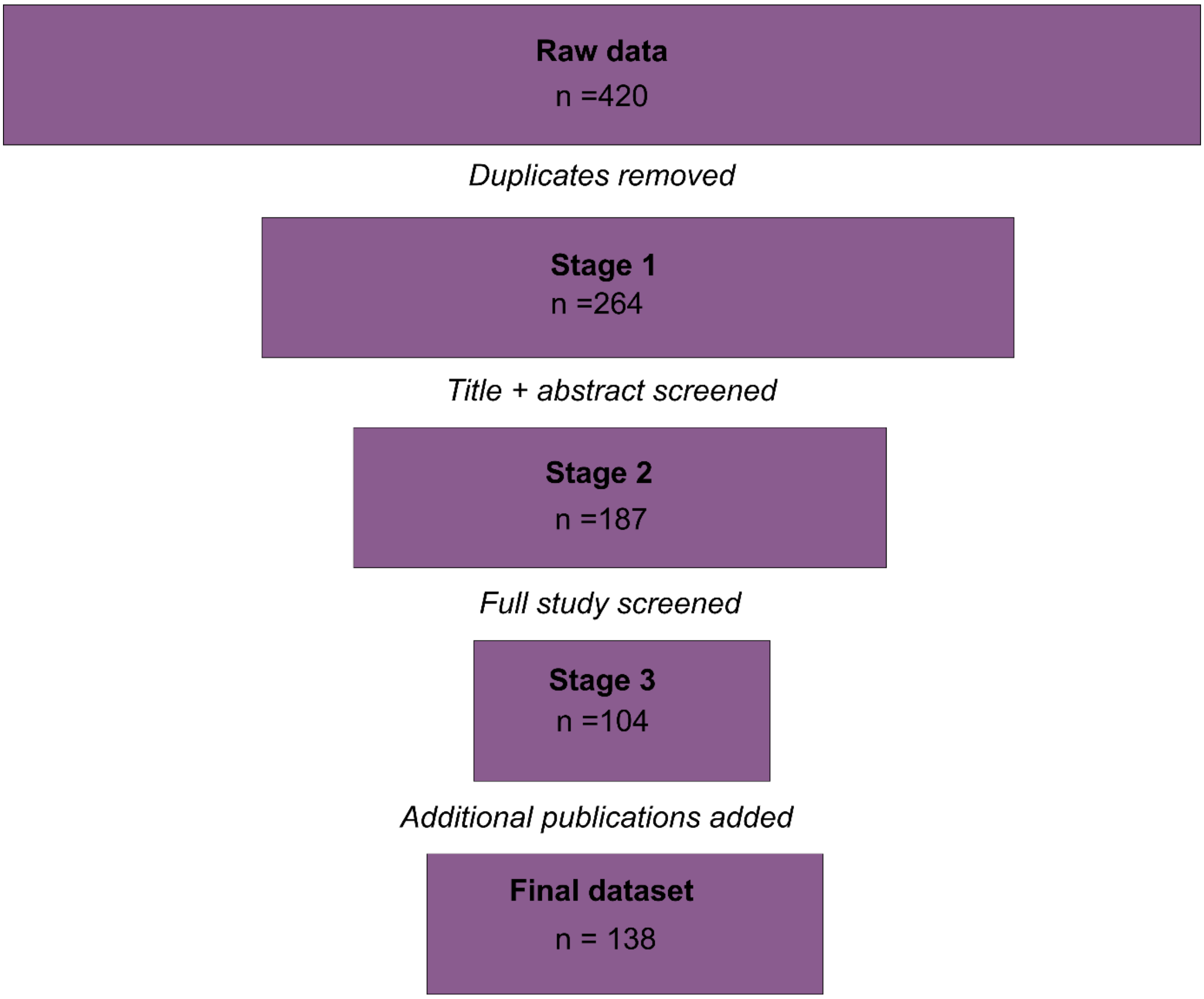

Figure 2. Flow diagram of publications included and excluded from review.

Data retrieved

For each of the 143 publications that were included in the final analysis, we recorded date of publication, study population(s) (if applicable), and study site(s) (if applicable). Study populations were adapted from Moore *et al.* (2019) and comprise four largely spatially segregated units: Queensland, Northern Territory, the Kimberley region of Western Australia, and the Pilbara region (including the neighbouring Little Sandy and Great Sandy Desert bioregions) of Western Australia. We also extracted home range estimates from publications that listed them. We pooled publication dates into six categories: prior to 1980, 1981–1990, 1991–2000, 2001–2010, 2011–2020, 2021–2030. We used decadal increments to categorise publications given they were fine enough to detect changes in research effort through time, but also coarse enough to capture a substantial number of publications within each increment. We then categorised publications into one or more of nine topics, adapted from Ashman et al. (2019):

- Taxonomy and Genetics
- Distribution, declines and habitat associations
- Diet (prey choice, scat composition)
- Reproduction
- Movement
- Threats
- Conservation management (direct management actions, legislation, action and recovery plans)
- Indigenous knowledge
- Miscellaneous (methods, reviews, albinism)

Threats

For publications that included the topic ‘threats’, we categorised the threats examined within the publication according to threat categories adapted from the National Recovery Plan (Hill and Ward 2010). Threat categories adapted from the recovery plan included the introduced and toxic cane toads (*Rhinella marina*), feral cat (*Felis catus*) and dingo/dog (*Canis* spp.) predation, fire, grazing, habitat clearing, mining, disease, feral predator baiting, and vehicle strikes.

Topic summary and future research needs

We provide written summaries for all research topics included in the review, with the exception of ‘behaviour’, which is discussed within the management section, and ‘miscellaneous’, which is discussed throughout. Within summaries, we discuss important findings in context with the ecology and conservation of northern quolls. We also identify and discuss knowledge gaps to highlight areas that may require future research. We finish by providing a non-exhaustive list of ten future research areas that could be useful to refine management action(s) to conserve northern quolls.

Results & Discussion

The temporal distribution of the 143 publications shows a substantial increase in research effort in recent years (Fig 3) (Table S1). The earliest study included in our analysis was published in 1926 (Thomas 1926) and the most recent was published November 2020 (Ondei *et al.* 2020). Most publications were conducted between 2011–2020 (86), and few publications were conducted prior to 1981 (2) (Fig 3). The region with the most publications was the Northern Territory (78), followed by the Pilbara (48), the Kimberley (45), and Queensland (27) (Fig 4). We identified 18 publications which were at least partly lab-based. Each of the nine study topics were represented at least once within publications included in this review (Fig 5). It is important to note that we found a limited amount of grey literature in this review and, as such, a number of environmental impact assessments (and the implications of their findings) were likely missed.

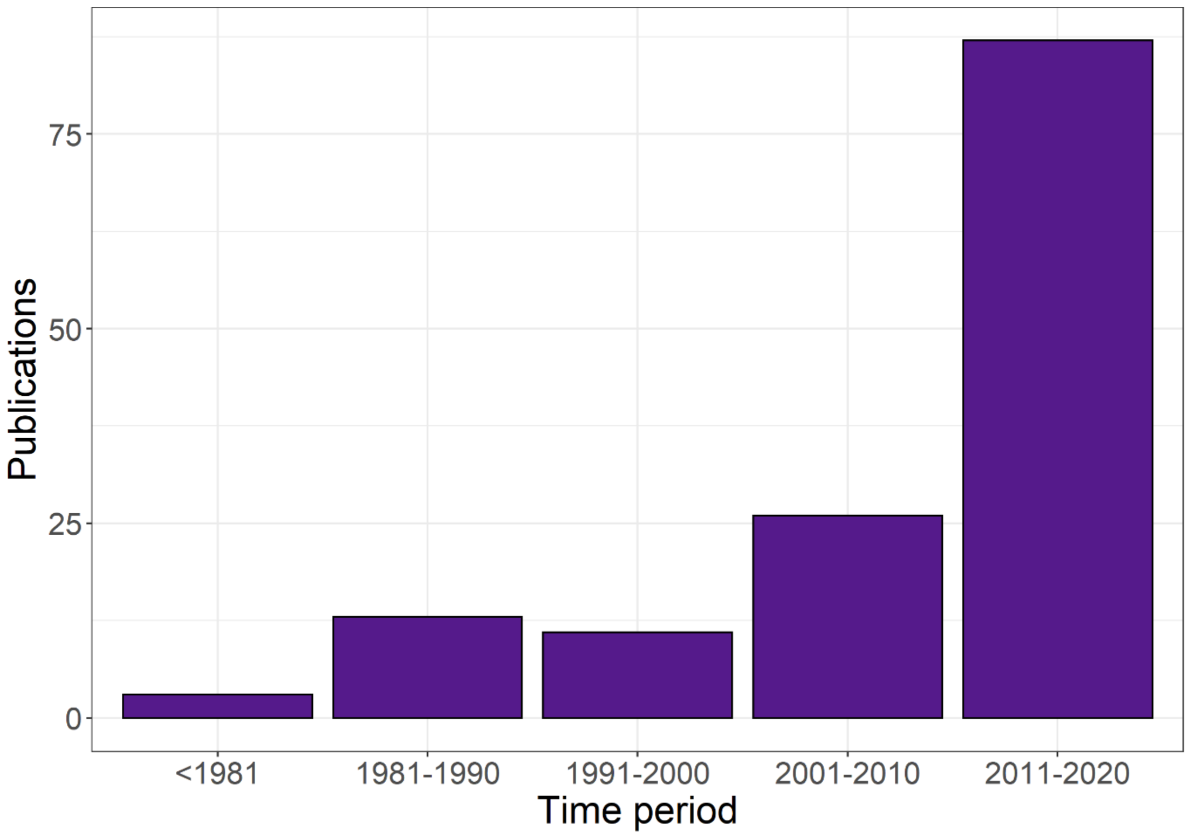

Figure 3 Research relevant to the conservation and ecology of northern quoll (*Dasyurus hallucatus*) categorised by publication date.

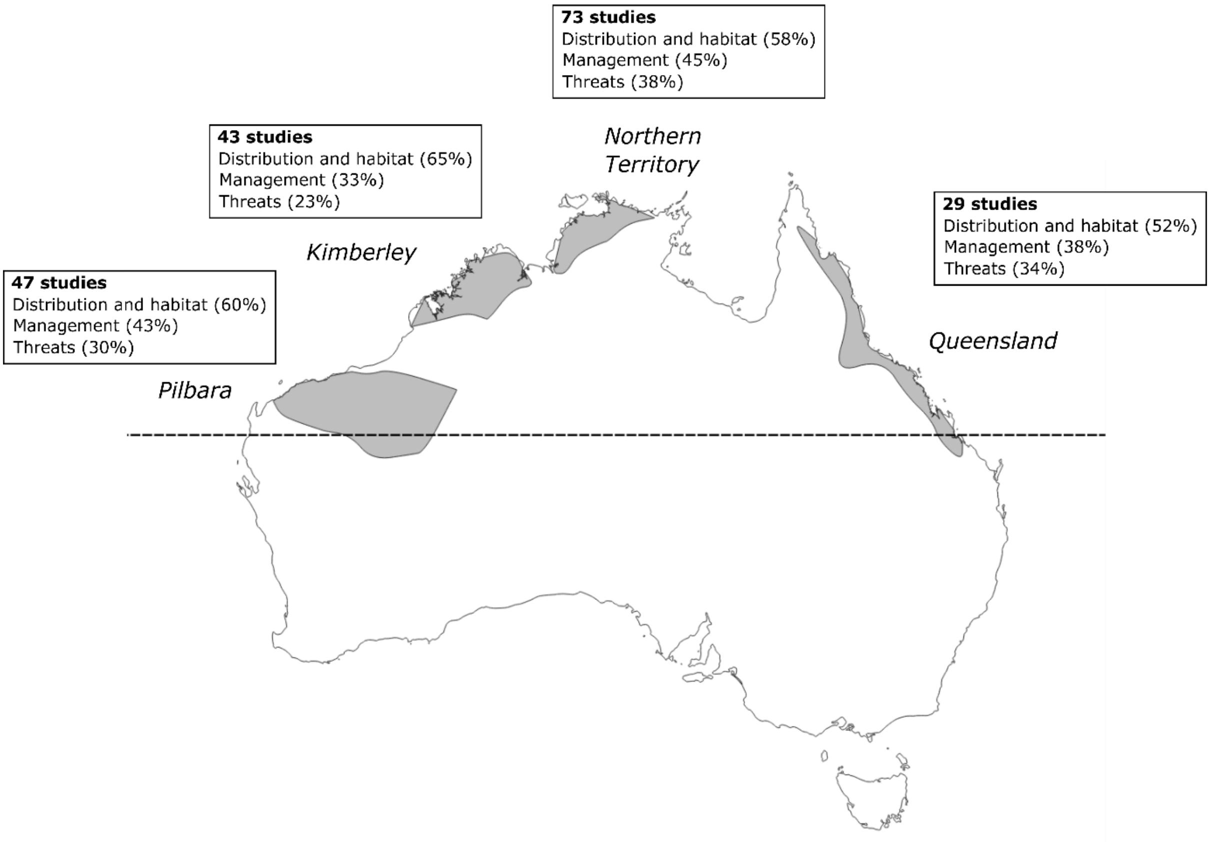

Figure 4. Research relevant to the conservation and ecology of northern quoll (*Dasyurus hallucatus*) mapped by population. Insets represent top three research topics within each populations. Dark grey area represents northern quoll contemporary distribution (prior to year 2000) adapted from (Moore *et al.* 2019).

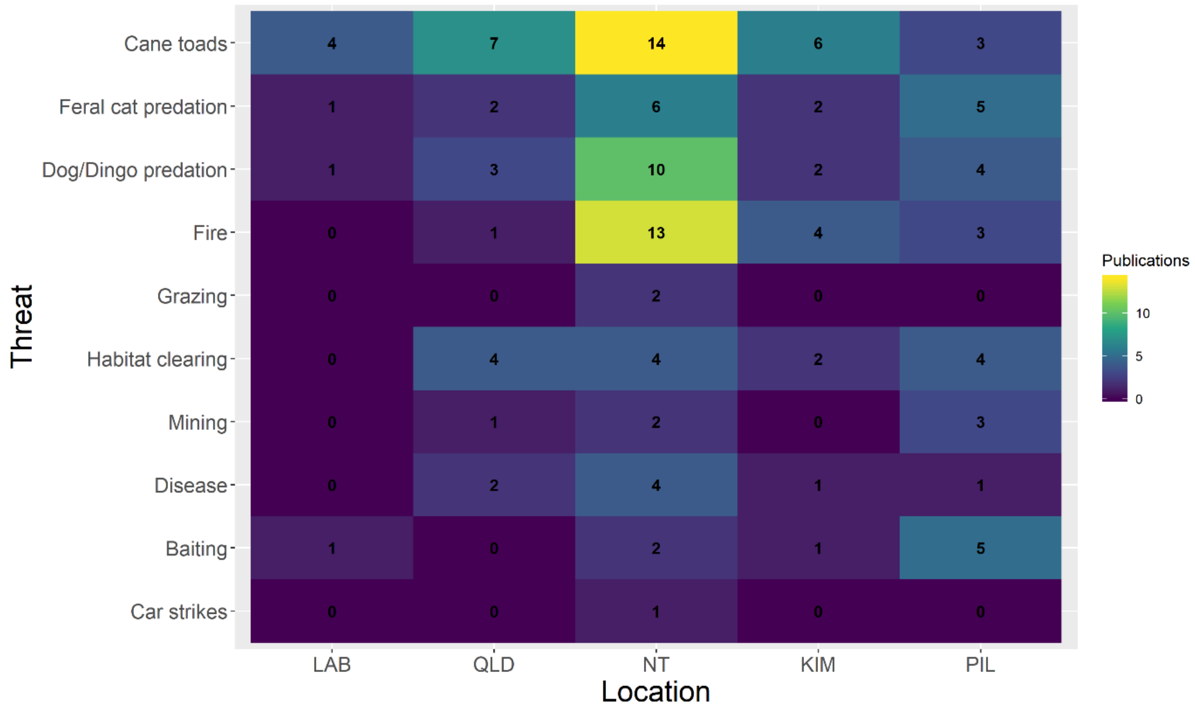

Figure 5. Research relevant to the conservation and ecology of northern quoll (*Dasyurus hallucatus*) categorised by research topic and location.

Taxonomy and genetics

We identified 20 publications relevant to northern quoll taxonomy, covering all major populations. Northern quolls (*Dasyurus hallucatus* Gould, 1842) were described by John Gould (1842) from two specimens collected at Port Essington in the Northern Territory. They are the smallest of six *Dasyurus* species: including the spotted-tailed quoll (*Dasyurus maculatus*), western quoll (*Dasyurus geoffroii*), eastern quoll (*Dasyurus viverrinus*), bronze quoll (*Dasyurus spartacus*), and New Guinean quoll (*Dasyurus albopunctatus*). The latter two species are only found in Papua New Guinea and Indonesia. Northern quolls. The current range of the northern quoll overlaps with the current range of the northern sub species of spotted tailed quoll (*Dasyurus maculatus gracilis*) in North Queensland. In the Pilbara, the northern quolls range overlaps with the historic distribution of the western quoll, as suggested by sub-fossil evidence (Baynes and McDowell 2010).

In 1926, northern quolls were separated into four subspecies, based mostly on the width of the skull at the nasals: *D. h. hallucatus* (Northern Territory to central Queensland); *D. h. predator* (Cape York, Queensland); *D. h. exilis* (the Kimberley); and *D. h. nesaeus* (Groote Eylandt) (Thomas 1926). No Pilbara specimens were included in this examination. While these subspecies are no longer recognised (Jackson *et al.* 2015), there is now genetic evidence to suggest northern quolls in each of the four major populations (Queensland, Northern Territory, the Kimberley and the Pilbara) do represent distinct lineages. Firestone *et al.* (2000) suggest northern quoll cytochrome b sequences from Queensland and the Northern Territory are at least as divergent as those between western quolls and the bronze quoll. Woolley *et al.* (2015) and Hohnen *et al.* (2016b) found that the Northern Territory and Kimberley northern quoll populations are genetically divergent, and How *et al.* (2009) found the same for Kimberley and Pilbara populations. The results of more recent morphological examinations are mixed — Umbrello (2018) found significant differences in skull size, dentition, and external characteristics between Queensland, Northern Territory, Kimberley, and Pilbara populations, while Viacava *et al.* (2020) found few consistent differences. Some island populations separated from the mainland by permanent sea channels (Bigge, Boongaree, Koolan), as well as less permanent channels (Dolphin Island) also appear genetically divergent from mainland populations (How *et al.* 2009). However, this is not the case for the Groote Eylandt population, which genetically aligns with the mainland Northern Territory population (Woolley *et al.* 2015).

The disjunct distribution of mainland northern quolls accompanied by the genetic and morphological differences between populations correspond to biogeographical barriers across northern Australia (Bowman *et al.* 2010). Separating the Queensland and Northern Territory populations is the Carpentaria Gap; a series of clay pans that limit dispersal between Cape York and the rest of the Australian monsoonal tropics for a range of taxa (Bowman *et al.* 2010). For example, the Carpentaria Gap separates a recently described species of glider, *Petaurus ariel*, from its sister species, *Petaurus notatus* (Cremona *et al.* 2020). Similarly, the gap between the Northern Territory and Kimberley populations aligns with the Ord Arid Intrusion, which divides sandstone blocks between Arnhem Land in the Northern Territory and the Kimberley (Bowman *et al.* 2010), and acts as a dispersal barrier for other species that use rocky habitat like rock-wallabies (*Petrogale* spp.) (Potter *et al.* 2012). The Kimberley and Pilbara populations of northern quoll are separated by the Great Sandy Desert—an extensive dune system often implicated in the isolation of both species and populations (Edwards *et al.* 2017).

The taxonomic status of the northern quoll may not yet be fully resolved. Lack of taxonomic clarity has previously hampered conservation efforts in other taxa. In the case of the northern quoll, understanding if populations should be treated as distinct taxonomic units or are genetically similar enough to be intermixed is likely to have important management implications, particularly in relation to cross-population translocations (as discussed in 'management' section). As such, further clarifying the extent to which northern quoll populations differ both genetically and morphologically should be a priority for future research. Other research related to northern quoll genetics are discussed within the 'Management' section.

Distribution, habitat associations, and geographic range contraction

A total of 79 publications were included in the 'Distribution, declines and habitat associations' topic, with the most focused on the Northern Territory population (n = 42), followed by the Kimberley (n = 28), Pilbara (n= 24), and Queensland populations (n = 11) (Fig 5).

Prior to European colonisation, the geographic range of northern quolls incorporated much of northern Australia above the Tropic of Capricorn (90 ° South) and within 200 km of the coastline (but likely extended inward much further (Turpin and Bamford 2015)) (Braithwaite and Griffiths 1994), covering a total area of over 1.2 million km^2. Average annual rainfall across this area varies substantially, ranging from 220 mm in the eastern extent of the Pilbara bioregion, to nearly 4500 mm in the Wet Tropics of northern Queensland (BOM 2020). Similarly, average maximum temperature in the warmest months ranges from 42.1°C in the Pilbara bioregion to 25.5°C in southern Queensland (BOM 2020). Northern quolls naturally occur on at least 32 islands, mostly in the Northern Territory and Kimberley (S1). Many of these are relatively free from human disturbance and lack introduced predators and/or cane toads (How *et al.* 2009; Woinarski *et al.* 2007). In the Northern Territory, northern quolls are particularly associated with large, remote and rugged islands (Woinarski *et al.* 2007), although they are notably absent from two large Northern Territory islands—Bathurst (2600 km^2) and Melville (5786 km^2). In 2003 and 2017, northern quolls were translocated to three islands in the Northern Territory outside of their historical geographic range (Kelly 2018; Rankmore *et al.* 2008) (See management section).

Northern quolls occur across a broad range of habitat types—including tropical and monsoonal rainforest, *Eucalyptus* woodlands, *Eucalyptus* open forests, lowland savanna, vine thickets, on beaches, and amongst human settlements (Begg 1981; Braithwaite and Griffiths 1994; Oakwood 1997; Pollock 1980; Schmitt *et al.* 1989)—but appear most abundant in rugged and rocky landscapes, including rocky hills, patches of granite outcrops, boulder-strewn slopes, rocky creeklines, and gorges (Begg 1981; Braithwaite and Griffiths 1994; Calaby 1973; Ibbett *et al.* 2018; Kitchener *et al.* 1981; McKenzie *et al.* 1975; Oakwood 1997; Olds *et al.* 2016; Pollock 1999; Schmitt *et al.* 1989) (Fig 6). It has been proposed by some that this preference may be due to rocky habitats holding permanent water and potentially greater prey availability than surrounding habitats (Braithwaite and Griffiths 1994; Burnett 1997). By contrast, evidence from other studies suggests diet is unlikely to be a key factor explaining the northern quolls preference for rocky habitat —Oakwood (1997) and Hernandez Santin (2017) found limited evidence that quoll selected rocky habitat based on differences in intrinsic dietary resources. Further, Thomas *et al.* (2021) found quolls occupying rocky habitat consumed a narrower range of prey resources than quolls that occurred in nearby savannah woodland, and also exhibited lower body condition.

Figure 6. Northern quoll habitat. A) Hazelwood Gorge, Queensland , B) East Alligator River, Northern Territory, C) Charnley River Wildlife Sanctuary, the Kimberley, Western Australia, and D) Indee station, the Pilbara, Western Australia. Image credit — Dennis Jeffery, Catherine Marshall, Naomi Indigo, Daniel Bohorquez Fandino.

Another factor linking quolls to rocky habitats is the availability of shelter, particularly dens—small enclosed spaces that northern quolls use as either short-term shelter sites (temporary den) or semi-permeant dwellings used to raise offspring (natal den). Northern quolls den in tree hollows (both alive and dead), termite mounds, logs, and goanna burrows (Oakwood 1997). In more arid regions that lack trees and logs (e.g., the Pilbara), rocky crevices within granite boulder piles and rocky mesas are critical for providing both temporary and natal den sites for northern quolls (Cowan *et al.* 2020b). In addition to providing protection from terrestrial predators such as dingoes and feral cats, rocky dens also provide important protection from climatic exposure. For example, in the Pilbara, Cowan *et al.* (2020b) found rocky dens sites were critical in sheltering from extreme external temperatures, which often exceeded safe temperatures for northern quolls (i.e., >36.5 °C) (Cooper and Withers 2010). In habitats where alternative den sites are available (e.g., tree hollows and logs), females selectively den in rocky habitat, and there is some evidence that females with more rocky habitat within their home range survive longer (Oakwood 1997). Importantly, northern quolls may also prefer rocky habitat because predators like feral cats are less likely to occur here when compared to less structurally complex habitat (Hernandez-Santin *et al.* 2016; Hohnen *et al.* 2016a).

Since European colonization of Australia (1788), and particularly within the past 50 years (Braithwaite and Griffiths 1994), the geographic range of northern quolls has declined by at least 45.2%, and width of their ecological niche has also declined substantially (Moore *et al.* 2019). Declines have been most severe in Queensland, where >400,000 km^2 of former habitat is now unoccupied, constituting a range contraction of >75% (Moore *et al.* 2019). The Northern Territory is the second most affected population, which has experienced a 58% range contraction (115,024 km^2), mostly from the more arid southern extent of their historic distribution (Prior to the year 2000) (Braithwaite and Griffiths 1994; Moore *et al.* 2019; von Takach *et al.* 2020; Ziembicki *et al.* 2013). The Kimberley population has seen a 17% decline, equating to 25,986 km^2 of lost range; (Moore *et al.* 2019), while the Pilbara—the most arid region currently supporting northern quoll populations—has so far seen little to no evidence of decline (Moore *et al.* 2019; Spencer *et al.* 2013).

These broadscale declines in geographic range arise through numerous local declines and extincitons that have been well documented. For example, Burnett and Zwar (2009) found no evidence to suggest northern quolls persist in the southern Mary River catchment north of Brisbane, despite the known occurrence of historic populations. Populations in Far North Queensland have also been subject to substantial decline. For example, Perry *et al.* (2015) and Burnett (1997) found northern quolls are largely absent from sizeable areas of Cape York Peninsula where they once occurred. In the Northern Territory (Ibbett *et al.* 2018) found northern quoll trap success in Kakadu National Park was significantly lower in 2002 than it was in 1980 (Begg 1981), and Woinarski *et al.* (2011b) found northern quoll abundance was lower at sites within Kakadu in 2007–2009 than it was in 2001–2004.

There are clear spatial patterns in the decline and persistence of northern quoll populations. In Queensland, the Northern Territory, and the Kimberly, topographically simple landscapes that receive low rainfall and are distant from permanent water have seen extremely severe declines (Burnett 1997; Moore *et al.* 2019; Pollock 1999; Radford *et al.* 2014; Woinarski *et al.* 2008), and areas that would have historically been marginal habitat have seen the greatest declines (Moore *et al.* 2019). Hence, extant populations tend to occur in topographically rugged areas with high annual rainfall (Moore *et al.* 2019). The extent of decline across populations corresponds with the length of time that the population has co-occurred with the introduced cane toad (see threat section). Persisting mainland populations of northern quolls now exist on the Central Mackay coast, Wet Tropics, Einasleigh Uplands and Cape York Peninsula bioregions in Queensland, the Arnhem Plateau, Darwin Coastal Plain, Daly Basin, Pine Creek bioregions, and Groote Eylandt in the Northern Territory, the Central and North Kimberley bioregions, and the Pilbara bioregion.

Diet

We identified 29 publications that examined the diet of the northern quoll, representing all study populations, with the most publications conducted in the Northern Territory. A large number of these publications (n = 14) focused on the consumption of cane toads, or baits designed to kill cats and dingos (n = 7) by quolls, and are discussed in the 'threats' section below. In general, northern quolls are omnivorous, opportunistic foragers, consuming a range of invertebrate, vertebrate, and plant species. Research examining sex-based dietary differences is scarce; however, there is some evidence that females northern quoll consume less vertebrate prey items than males, probably because females are typically smaller in mass (Oakwood 1997).

Invertebrates are a dominant feature in the diets of northern quolls across all populations, with beetles (Coleoptera), grasshoppers (Orthoptera), ants (Hymenopterans) and spiders (Arachnida) appearing most frequently within scats (Dixon and Huxley 1985; Dunlop *et al.* 2017; Oakwood 1997; Pollock 1999; Radford 2012). Indigenous people from Arnhem Land in the Northern Territory also observed northern quolls feeding on *wai* (worms), grubs, and moths (Dixon and Huxley 1985). In Kakadu National Park (Northern Territory), Oakwood (1997) found invertebrate consumption peaked in the early dry-season, coinciding with the arrival of juveniles into the population. In the Pilbara, invertebrate occurrence in the northern quoll diets decreases with the occurrence of rodents and plant material, potentially indicating invertebrates may be a staple food item, but not always preferred (Dunlop *et al.* 2017).

A diverse range of vertebrate prey also appear in the diet of northern quolls, including rodents (*Melomys burtoni , Pseudomys delicatulus, Pseudomys hermannsbergensis, Rattus rattus, Rattus sordidus, Zyzomys argurus*), rabbits (*Oryctolagus cuniculus*), other dasyurids (*Dasykaluta rosamondae, Ningaui timeleyai, Pseudantechinus* sp., *Sminthopsis macroura, Sminthopsis youngsoni*), gliders (*Petaurus* spp.), possums (*Trichosurus vulpecula*), bandicoots (*Isoodon auratus, Isoodon macrourus*), bats (Nyctophilus spp., *Rhinonicteris aurantia*), birds, lizards (Scincidae spp., Agamidae spp., Varanidae spp., Gekkonidae spp.), snakes, and frogs (Dixon and Huxley 1985; Dunlop *et al.* 2017; Oakwood 1997; Pollock 1999; Radford 2012). Larger mammals including kangaroos (*Osphranter* spp.), cows (*Bos taurus*), cats (*Felis catus*) and dogs/dingoes (*Canis* spp.) have also been recorded in northern quoll scats (Dunlop *et al.* 2017), presumably consumed as carrion. In the Kimberley, northern quolls consume a larger proportion of larger prey, such as golden bandicoots (*Isoodon auratus*), in recently burnt habitats, potentially because hunting this prey is easier when vegetation cover is reduced (Radford 2012).

Plant material has been recorded in the diet of northern quolls in the Northern Territory (Oakwood 1997), the Kimberley (Radford 2012), and the Pilbara (Dunlop *et al.* 2017), and is typically comprised of fleshy fruits, seeds, and flowers. In the Northern Territory, Oakwood (1997) found fruits from wild grape plants (*Ampellocissus acetose*) were the most common plant material to appear in northern quoll diets, with peak consumption occurring in the late-dry to early-wet season. In the Pilbara, native figs (*Ficus* spp.) were the most frequently recorded plant group within northern quoll scats, occurring within 16.1% of total scats measured (Dunlop *et al.* 2017).

Reproduction

We identified 16 publications related to northern quoll reproduction. Northern quolls typically breed during the dry season — between June and July in Queensland, May and June in the Northern Territory, June to October in the Kimberley, and July to September in the Pilbara. Variation in the timing of breeding also occurs within population and between years, mostly as a result of variation in rainfall (Braithwaite and Griffiths 1994; Oakwood 2000; Schmitt *et al.* 1989).

Male northern quolls are known to exhibit semelparity—a reproductive strategy where animals only breed once in their lifetime—characterized by increased levels of testosterone followed by rapid condition loss, with individuals rarely living longer than 11 months (Oakwood *et al.* 2001), although survival varies.

In the Northern Territory, most male quolls die within two weeks of mating (Dickman and Braithwaite 1992; Oakwood 2004a), although a small percentage may survive to a second breeding season (Begg 1981; Schmitt *et al.* 1989). Female survival is also very low in the Northern Territory (typically less than ~ 40% between years), although they can survive for up to three years (Braithwaite and Griffiths 1994; Cremona *et al.* 2017b; Oakwood 2000). In the Kimberley, Schmitt *et al.* (1989) found 4% of males and 37% of females survived to reach a second breeding season. In the Pilbara, just over 5% of males and 40% of females survive to a second breeding season (Hernandez-

Santin *et al.* 2019). On Groote Eylandt, Heiniger *et al.* (2020) found 0% of males and 39.6% of females survived to their second year. They also found 8.7% of females survived to their third year.

A consequence of large annual die-offs in the adult population of northern quolls is that the likelihood of population persistence is heavily reliant on offspring survivorship. For example, in the Pilbara, an increase in mean juvenile mortality of 5% could potentially result in a 20% decline in overall population size (Moro *et al.* 2019). One strategy northern quolls may use to increase juvenile survival is polyandry—where females mate with multiple males to increase genetic diversity among offspring, conferring a group net fitness benefit. For example, a recent study found that 100% of examined northern quoll litters (*n* = 16) had young sired by multiple males, and in some litters, every offspring was fathered by a different male (Chan *et al.* 2020).

It's possible that risks associated with semelparity are likely counterbalanced by benefits derived from reduced competition between males and offspring in areas where resources are limited. As such, Cook (2010b) suggest male die off may be less pronounced in populations where resources are plentiful. However, more recent studies suggest this may not necessarily be the case — Heiniger *et al.* (2020) found complete semelparity was observed in northern quoll populations on Groote Eylandt, where resources are sufficient to support high quoll densities. Further research may be required to better understand the evolutionary drivers of semelparity in northern quolls.

Following mating, females undergo a gestation period of between 21–25 days before giving birth (Oakwood 2000). Mothers have between five and nine nipples (normally 8) (Begg 1981; Braithwaite and Griffiths 1994). Although up to 17 young can be born (Nelson and Gemmell 2003), nipple number determines the maximum number of young that can be carried after birth. Braithwaite and Griffiths (1994) found that, on average, females that lived closer to creeklines—areas that are more productive than surrounding habitat, and likely more conducive to reproduction—had more nipples than females that lived further from creeklines. Once young are attached to a nipple, mortality over the following three months ranges from less than 2% (Oakwood 2000) to 86% (Braithwaite and Griffiths 1994). Young are deposited in dens at roughly two and a half months of age (Oakwood

2000), are independently foraging at four months, and are trappable by five months of age (Oakwood 1997). Young are weaned by six months and disperse shortly thereafter (Oakwood 2000).

We found little information regarding northern quoll reproduction in Queensland. For example, no research included in this review documented whether quolls in Queensland show evidence of complete or partial annual male die-off, as observed in other regions (Oakwood *et al.* 2001). Documenting the post-breeding survival rate of northern quolls in Queensland will allow managers to better estimate the risk of Queensland sub-populations becoming locally extinct.

Movement

We identified 11 publications that investigated the movement ecology of northern quolls, which were spread across all regions (Figure 5). Seven of these publications included home range estimates, calculated using three different methods (Delimiting Supposed Home Range, Minimum Convex Polygon, and 95% Minimum Convex Polygon) (Table 1). Across all home-range publications, a general trend appears to be that male home ranges are typically larger than female home ranges, especially in the breeding season, when males move large distances in search of females. In the Northern Territory, Oakwood (2002) found that males occupied a much larger home range (84 ± 16 ha) than females (34.8 ± 6.4 ha). The difference was largest in the breeding season when males expanded their home-range to seek mating opportunities (Oakwood 2002). These males also travelled further between dens (average = 1.9 km) than females (average = 1.2 km). Similarly, on Groote Eylandt (Northern Territory), Heiniger *et al.* (2020) found the average home range of male northern quolls (215 ± 58.4 ha) to be four times larger than that of females (53.1 ± 38.8 ha), although this was largely due to male quolls expanding their home ranges by an average of 300% during the breeding season. Prior to the breeding season beginning, average home range sizes were larger for females (79.0 ± 58.8 ha) than they were for males (72.9 ± 24.4 ha) (Heiniger *et al.* 2020).

Table 1. Northern quoll (*Dasyurus hallucatus*) home range estimates (ha) sourced from publications included in review. MCP refers to minimum convex polygon. DSHR refers to Delimiting Supposed Home Range.

Author	**Location**	**Female**	**Male**	**Data type**	**Method**
Oakwood (2002)	Northern Territory	34.8 ± 6.4 *n* = 7	84.1 ± 16 *n* = 8	VHF	MCP
Heiniger et al. 2020	Northern Territory (Groote Eylandt)	53.07 ± 38.77 *n* = 10	215.4 ± 58.24 *n* = 29	GPS	MCP
Schmitt *et al.* (1989)	Kimberley	2.30 ± 1.20 *n* = 7	1.80 ± 1.60 *n* = 2	TRAP	DSHM
Cook (2010b)	Kimberley	7 ± 2 *n* = 11	64 ± 37 *n* = 11	VHF	MCP
King (1989)	Pilbara	168 ± 32.25 *n* = 4	464.75 ± 200.245 *n* = 4	VHF	MCP
Cowan *et al* (2020)	Pilbara (Red hill)	13.8 ± 6.6 *n* = 10	301.4 ± 108.9 *n* = 10	VHF	MCP
Cowan *et al* (2020)	Pilbara (Yarraloola)	32.5 ± 10.7 *n* = 10	931.1 ± 259.9 *n* = 11	VHF	MCP
Hernandez-Santin *et al* (2020)	Pilbara	34 *n* = 1	193 ± 55 *n* = 8	GPS	95 % MCP

In the Kimberley, (Cook 2010a) found home ranges were on average larger for males (64 ± 37 ha) than females (7 ± 2 ha). Maximum distance between dens was also greater for males (1.2 km) than females (0.4 km). Schmitt *et al.* (1989) found quolls moved further between successive trap locations in the breeding season (104 ± 99 m) when compared to the non-breeding season (61 ± 82 m). In the Pilbara, average male home range estimates were between 2.7 and 28.6 times larger than female home range estimates (Table 1). Similar to the Northern Territory and Kimberly populations, male quolls in the Pilbara appear to move further in the breeding season when compared to the non-breeding season (Hernandez-Santin *et al.* 2020; Oakwood 2002; Schmitt *et al.* 1989). Although we did not find any direct measurements of home range for northern quolls in Queensland, Burnett *et al.* (2013) provides a mean half maximum distance moved for 25 individuals (334.6 m), suggesting a crude circular home range estimate of 35 ha.

Lab-based publications investigating northern quoll locomotion have found northern quolls tend to sacrifice speed in favour of manoeuvrability in order to avoid making mistakes (Amir Abdul Nasir *et al.* 2017; Wynn *et al.* 2015). On Groote Eylandt, northern quolls with greater agility when moving around corners are more likely to survive their first 21 months of life than quolls that move slower around corners, potentially because they are better at avoiding predators such as dingoes, feral cats and birds of prey (Rew-Duffy *et al.* 2020).

Although male-biased dispersal is common in other dasyurids, evidence for this in northern quolls is limited (Oakwood 2002). Further research is required to better understand patterns in northern quoll dispersal. However, there is evidence that male northern quolls disperse further than females (Oakwood 2000) and male consecutive dens can be up to 4 km apart (Cook 2010b). In the Kimberley, genetic data suggests that habitats with higher annual rainfall and lower topographical ruggedness are likely to facilitate increased dispersal between sub-populations (Hohnen *et al.* 2016b).

Threats

A total of 70 publications included the topic ‘threats’, most of which were focused on northern quolls in the Northern Territory (*n* = 40), with substantially fewer publications focused on the Pilbara (*n* = 18), the Kimberley (*n* = 17) or Queensland (*n* = 9) (Fig 7).

Figure 7. Research relevant to threatening processes for northern quolls (*Dasyurus hallucatus*) categorised by threat and location. Threat categories were derived from the ‘National Recovery Plan for the Northern Quoll’ (Hill and Ward 2010).

Cane toads

The most commonly investigated threat was cane toads (*n* = 22). In 1935, cane toads (*Rhinella marina*) were introduced to a research station near Cairns, Queensland, Australia (17°04'S 145°47'E) (Lever 2001). From there, toads quickly expanded their distribution into other parts of Queensland. Cane toads first invaded the Northern Territory in the 1980s (Freeland and Martin 1985), reached Kakadu National Park in 2001 (Woinarski *et al.* 2002) and progressed through to Western Australia around 2009.

Like some other native predators, northern quolls that attempt to consume cane toads rapidly succumb to their novel and potent defensive toxins (Shine 2010). Oakwood (2004b) found 31% of radio-tracked quoll mortalities in Kakadu were likely caused by cane toads, while O'Donnell *et al.* (2010) found 29%, and Jolly *et al.* (2018a) found 85% of toad-naïve quolls and 18% of toad-trained quolls died as a result of consuming cane toads.

In Far North Queensland, Burnett (1997) presented anecdotal evidence that cane toads were the cause of northern quoll extirpation from 1983 and 1995. While northern quoll populations in the Northern Territory exhibited declines prior to toad arrival (Ibbett *et al.* 2018; Woinarski *et al.* 2001; Ziembicki *et al.* 2013), rapid declines, often to extirpation, followed the invasion front (Woinarski *et al.* 2010a; Woinarski *et al.* 2011b). In the Kimberley, Indigo (2020) found northern quoll populations declined by 86–96% following toad arrival, despite these populations being repeatedly exposed to TBZ-laced cane toad sausages—a technique shown to elicit toad-aversion in captive quolls (see management section). Despite these declines, there is evidence that northern quolls can co-exist successfully with cane toads, and most of this evidence comes from Queensland, where toads and quolls have co-existed for over 80 years (Sabath *et al.* 1981). While it has been confirmed that Queensland northern quolls (and likely all other populations of northern quolls) are not physiologically resistant to cane toad toxins (Ujvari *et al.* 2013), natural variation in quoll behavioural responses to toads may have made some quolls less vulnerable to toad related mortality than others (see management section).

Predation

Feral cats and dingoes are considered the most threatening predators to northern quolls across the majority of their range (Hill and Ward 2010), and this was reflected in the number of northern quoll publications that included reference to feral cat or dingo/dog predation (*n* = 15 and *n* = 21, respectively). Feral cats were introduced onto the Australian mainland with the arrival of the 'first fleet' of British colonists in 1788 (Abbott 2008), and as such northern quolls have had limited evolutionary exposure in order to adapt to feral cats as predators (< 240 years). By contrast, northern quolls have co-existed with dingoes across their entire historical range for at least 3081 to 3348 years (Balme *et al.* 2018). This suggests the impacts of dingoes, and potentially their close relatives, domestic dogs, are unlikely to threaten the persistence of northern quolls on their own, but instead are amplified when acting in conjunction with other threats such as changing fire regimes and predation from feral cats (Geary *et al.* 2019b). Another introduced predator, the red fox (*Vulpes vulpes*), is also likely to predate on northern quolls in some areas of their southern distribution (Cramer *et al.* 2016), however foxes are not present in the majority of the northern quolls range (Saunders *et al.* 2010).

In the Mackay Bowen region of Queensland, Pollock (1999) recorded eleven occurrences of quoll mortality as a result of domestic dogs and one record of predation by a black-headed python (*Aspidites melanocephalus*). This author also recorded predation by domestic or feral cats; but the number of quolls killed was not recorded. Cat predation on northern quolls in Queensland has also been recorded in the Rockhampton and Cape Upstart regions (Burnett pers. comm., 2020). In Kakadu National Park, Northern Territory, Oakwood (2000) tracked 9 of 15 radio-tracked quolls to their death as a result of predation (dingo = 4, feral cat = 2, owl = 1, king brown snake, *Pseudechis australis* = 1, olive python, *Liasis olivaceus* = 1). Similarly, Jolly *et al.* (2018a) found at least 7 of 19 quolls were killed by dingoes. However, this number is likely to underrepresent the threat of dingo predation to quolls in this instance. Most quolls that were tracked to their death (*n* = 10) died rapidly after release (< 4 days) due to toad consumption, reducing the opportunity for dingo predation to occur. Cremona *et al.* (2017a) found 3 of 4 quolls tracked to their death likely died of dingo/dog predation. In the Pilbara, Cowan *et al.* (2020a) found 6 of 41 collared northern quolls died as result of feral cat predation and two from dingo predation.

In a behavioural study, quolls from mainland Queensland were shown to recognise and avoid the scent of cats and dingoes, as did their captive born young, suggesting a genetic basis for predator recognition, including recognition of the introduced feral cat (Jolly *et al.* 2018b). However, quolls that had been translocated to Astell Island to conserve them against the impacts of cane toads appeared to have lost the ability to recognise dingoes and cats, after only 13 generations (Jolly *et al.* 2018b). The capacity of northern quolls to detect their predators could explain why Hernandez-Santin *et al.* (2016) found northern quolls avoided areas used by feral cats. The loss of antipredator traits observed on Astell Island may explain the role of dingo predation in the rapid extirpation of quolls during a reintroduction attempt (Jolly *et al.* 2018a). Unfortunately, any attempts to train quolls to recognise dingoes as predators in captivity failed to impart predator aversion on quolls prior to reintroduction (Jolly *et al.* 2020).

Fire

A large number of publications (*n* = 24) considered the impacts of fire on northern quolls. We found no publications that recorded evidence of northern quoll mortality as a direct result of fire, however, we did find evidence from several populations that fire can have negative impacts on northern quoll populations. In the Northern Territory, Begg (1981) found that fire delayed northern quoll breeding and reduced the mean number of young that left the pouch, Oakwood (1997) found 55% of female northern quolls perished soon after fire in Kakadu, and Kerle and Burgman (1984) found that although northern quolls were common just after fire (< 1 year), they declined in the following year. Corbett (2003) and Andersen *et al.* (2005) found northern quolls were more abundant at unburnt sites than burnt sites, and Griffiths *et al.* (2015) predicted fire frequencies of over one fire per year would cause substantial decline in northern quoll populations. Griffiths and Brook (2015) found modelled recruitment was 20% lower after a late season fire.

In the Kimberley, Radford *et al.* (2015) found northern quolls were less abundant at sites with larger extents of habitat burnt within the previous year, high fire frequency, and increasing distance to the nearest unburnt patch. Ondei *et al.* (2020) found northern quolls were only detected at rainforest sites, which burn less frequently than adjacent savanna sites, where no northern quolls were detected.

Finally, in the Pilbara; Hernandez-Santin *et al.* (2016) found northern quolls were negatively associated with habitat that had been recently burnt.

There are multiple mechanisms that could explain observed negative impacts of fire on northern quolls. It is possible that food may be scarce immediately following fire, which reduces overall habitat suitability. For example, in the Kimberley, Radford and Andersen (2012) found the total number of invertebrates—a key prey item for northern quoll—declined by 80–90% in the week following fire. However, this same study found invertebrates were rapidly restored following the first wet season after fire, and there was no significant difference in invertebrate numbers between pre- and post-fire sessions within a year (Radford and Andersen 2012). This study also found quolls benefited from small scale fires by consuming an increased proportion of vertebrate prey, which were likely more vulnerable to quoll predation post-fire, given vegetation cover was reduced.

Another probable mechanism is that fire increases predation risk, as a result of reduced ground-layer vegetation cover (Kerle and Burgman 1984; Oakwood 1997). Interactions between fire and predation have previously been implicated in the decline of numerous Australian mammals (Hradsky *et al.* 2017; Leahy *et al.* 2016; McGregor *et al.* 2017; Woinarski *et al.* 2010b), particularly for species including northern quolls that fall within a critical weight range (CWR) of species most vulnerable to predation from feral cats, foxes and dingoes (Woinarski 2015).

It is important to note that some publications have not found fire to have a negative impact on northern quolls. Woinarski *et al.* (2004) found northern quolls near Darwin in the Northern Territory were more common at sites burnt annually, compared to sites that were long unburnt. In the Kimberley, Cook (2010a) found fire had little impact on northern quoll home range size, even when an animal's entire home range was burnt. These contrasting results highlight that the impact of fire on northern quolls is likely to be context specific. This is demonstrated by Radford *et al.* (2020), who found northern quolls declined under prescribed burning in woodland habitats, but increased under prescribed burning in sandstone habitat. Additional research is required to further investigate the contextual impacts of fire on northern quoll populations across their range

Grazing

Overgrazing by feral and managed livestock has long been implicated in the decline of Australia's mammal fauna (Woinarski *et al.* 2011b). Here, we identified 11 publications which discuss the impacts of over-grazing on northern quolls. The primary mechanism by which over-grazing is thought to impact northern quolls is through the removal of ground-level vegetation, which likely exposes quolls to increased levels of predation (Oakwood 1997). Additionally, factors such as water-hole contamination and soil-erosion caused by stock, as well as extensive tree-removal are likely to impact northern quolls. Braithwaite and Griffiths (1994) suggest the combined impacts of grazing by feral ungulates are highly likely to have contributed to the decline of northern quolls across their range and similar assessments are also made elsewhere (Oakwood 1997; Radford *et al.* 2014; Woinarski *et al.* 2011b). However, it is important to note that quolls do appear to persist at some sites where heavy grazing occurs (Hill and Ward 2010, Moore pers comms.; Woinarski *et al.* 2008). In these locations, it is possible that quolls may benefit from reduced fire frequency and intensities as a result of cattle minimising fuel loads (Hill and Ward 2010), and reduced predation as a result of dingo baiting.

Habitat clearing

We identified six publications that discussed the impact of habitat clearing on northern quoll populations. Habitat clearing has been implicated as a factor in northern quoll declines prior to the year 2000, particularly in Queensland and the Northern Territory (Braithwaite and Griffiths 1994; Hill and Ward 2010; Jones *et al.* 2014). However, despite the subsequent introduction of environmental legislation such as the *Environment Protection and Biodiversity Conservation Act 1999* (*EPBC Act*) designed to protect species from such direct human impacts, habitat clearing is likely continuing to threaten northern quoll populations. For example, in the period 2000–2017, an estimated 1.6 million hectares of potential northern quoll habitat was legally cleared (Ward *et al.* 2019). Northern quolls may be particularly sensitive to direct habitat loss because they require large areas (at least 220 km^2) to maintain populations (Brook *et al.* 2011), they show strong negative responses to habitat fragmentation (Rankmore 2006), and because hollows and logs used for shelter are removed during land clearing and take many years to form (Woinarski and Westaway 2008).

Mining

There were few publications (*n* = 6) that investigated the response of northern quolls to disturbance as a result of mining/resource development. This was surprising, especially for the Pilbara population, where the scale of overlap between mining activity and northern quoll habitat is likely to be greatest—91% of the Pilbara bioregion is occupied by mining tenement (Environmental Protection Authority 2014). Here, rocky ridges and mesas, which are thought to be important habitat for northern quolls, are frequently destroyed by mining companies targeting deposits of iron-ore and gold (Cramer *et al.* 2016). Surrounding granite outcrops are also quarried for rail formation ballast, rock armour for port infrastructure and basic raw materials for road construction. We found two publications from the Pilbara which examined the impact of mining-related habitat clearing on quolls, including a government report that found northern quolls persist at two rocky sites located in close proximity to a recently installed rail line (Dunlop *et al.* 2015), and a Masters thesis with similar findings at the same sites (Henderson 2015).

In addition to destroying habitat, mining activity can also impact species by introducing contaminants into the environment which can bioaccumulate, reducing the health of animals within affected areas (Nawab *et al.* 2015). For example, Amir Abdul Nasir *et al.* (2018b) found airborne manganese dust from Groote Eylandt Mining Company (a BHP Billiton subsidiary) was absorbed by northern quolls living in close proximity to mining operations. Groote Eylandt quolls accumulated manganese within their hair, testes and brain. Quolls with higher manganese body burdens were slower at manoeuvring around corners than manganese free quolls, which may reduce their capacity to capture prey and escape predators (Amir Abdul Nasir *et al.* 2018a).

Other threats

Other potential threats or sources of mortality for northern quolls are vehicle strikes (Oakwood 1997) and toxoplasmosis. However, Oakwood and Pritchard (1999) found no evidence of toxoplasmosis from 28 road-killed quolls in Kakadu National Park. Although it is clear from this review that northern quolls are exposed to multiple threats across their range, our understanding as to whether such threats to quolls are coincidentally or causally linked is poorly understood, and this can limit our capacity to manage threats effectively (Doherty *et al.* 2015). For example, while targeted baiting for larger predators such as canids or foxes may result in short-term alleviation of pressure from one predator on the northern quoll (Jolly *et al.* 2018a), in the long-term it could potentially increase predation by mesopredators, such as feral cats (Marlow *et al.* 2015). Additionally, total isolation from predators (i.e. in havens) can cause rapid evolutionary loss of antipredator traits that may not be easily reinstated (Jolly and Phillips 2020; Jolly *et al.* 2018b). Similarly, while it has been suggested that fire may increase the susceptibility of northern quolls to predation (Oakwood 1997), our understanding as to how the timing, scale or intensity of fire influences predator-prey relationships remains limited for most ecosystems and species (Geary *et al.* 2019a). Recognizing and understanding how these threats interact may facilitate more targeted management interventions potentially leading to more desirable conservation outcomes (see Geary *et al.* 2019b).

Indigenous knowledge

Incorporation of Indigenous people and their knowledge into management actions is listed in three of eight recovery plan objectives for northern quolls (Hill and Ward 2010). Further, a recent study found 63% of the northern quolls current range, as defined by the IUCN, occurs within Indigenous peoples' lands (O'Bryan *et al.* 2019). We identified eight publications that incorporated Indigenous knowledge as part of this review, two of which included indigenous rangers or ranger groups as co-authors (Jolly *et al.* 2021; Kelly *et al.* 2020).

The name ‘quoll’, is derived from an indigenous name for northern quolls, ‘Je-Quoll’, recorded by Joseph Banks near Cooktown in North Queensland, 1770 (Beaglehole 1963). Other names were used by Indigenous peoples to describe northern quolls across Northern Australia, and many of these are recorded by (Abbott 2013). Using local Indigenous vernacular names may help acknowledge the strong connections Aboriginal people share with Australia’s fauna and flora that were honed over thousands of years of coexistence.

The most comprehensive summary of Indigenous knowledge about northern quolls is provided by Oakwood (1997). Like other quoll species (Attenbrow and Attenbrow 1987), northern quolls were consumed as food by Aboriginal people in Australia. However, there are mixed reports as to their palatability (Oakwood 1997). For example, northern quolls were considered "good tucker" by the Gunwinggu people of West Arnhem Land (Goodfellow 1993). By contrast, *barkuma* (northern quolls) were not enjoyed as much by people of East Arnhem Land due to the *buggan tumero* (big smell) of the flesh (Dixon and Huxley 1985). Indigenous people of East Arnhem Land mentioned northern quolls as being numerous in *diltji* (open forest with grass) and also along beaches where cover is available, where they are said to shelter in hollow fallen logs and amongst stone.

In the Sir Edward Pellew Group of Islands of the Northern Territory, *karnbulanyi* (male northern quoll) or *a-kaliba* (female northern quoll) were also used as a food source (Bradley *et al.* 2006). Yanyuwa elders from the Pellew islands said northern quolls were once common, but younger people are less familiar with the species, and some of these island populations of quolls have been extirpated (Woinarski *et al.* 2011a). Interestingly, the terms *karnbulanyi* and *a-kaliba* were later also used to describe feral cats (Bradley *et al.* 2006). Ziembicki *et al.* (2013) used Indigenous knowledge collated through a series of interviews across multiple communities in the Northern Territory to assess the extent and timing of regional mammal declines. This collation of information across communities found that range contractions were particularly pronounced for northern quolls, with the majority of decline recognised to have occurred in the 20 years prior to interviews taking place (1985–2009), and in the south of their range. Both cane toads and feral cats were implicated by observers as contributing factors in the declines, along with changing fire regimes associated with the cessation of Indigenous land management practises (Ziembicki *et al.* 2013).

There is significant Indigenous knowledge of the northern quoll across Australia (Abbott 2013, authors' pers. obs.). While some traditional knowledge has been included in a handful of publications, there is a great potential for future integration into research and management of the remaining northern quoll populations. Recently, some research groups have worked very closely with Indigenous rangers and Traditional Owners to improve the conservation of northern quolls in northern Australia. Despite our review surfacing limited publications including Indigenous knowledge, there are other ways in which Indigenous people and their knowledge are actively involved in researching and conserving northern quoll populations, and it is important that this is acknowledged. One way is through Indigenous ranger programs, such as the Dhimurru, Jawoyn, Kenbi, Warddeken, and Marthakal ranger programs in the Northern Territory, the Uunguu ranger program in the Kimberley and Martu ― Kanyirninpa Jukurrpa and Budadee programs in the Pilbara.. As part of these programs, Indigenous people play an important role in surveying and monitoring northern quolls, typically on lands with which they share a strong cultural connection, lands which are part of the Indigenous land estate (Jacobsen *et al.* 2020).

Conservation management

In 1993, despite recognition of a potential national decline in geographic range of 10–50%, the conservation status of northern quolls was recognised as 'apparently stable' in an action plan for the conservation of Australian marsupials and monotremes (Kennedy 1992). Four years later, a similar action plan listed northern quolls as 'lower risk (near threatened)' (Maxwell *et al.* 1996). In 2005, the northern quoll was listed as Endangered under the *EPBC Act*, which enacts legal responsibility for consideration in environmental impact assessments, and management actions, such as the development of conservation advice and a recovery plan. Northern quolls were later listed as

Critically Endangered in the Northern Territory, and Endangered in Western Australia, but have remained listed as 'Least Concern' in Queensland. In 2010, a strategic set of management priorities for the northern quoll was outlined in the 'National Recovery Plan for the Northern Quoll' (Hill and Ward 2010), which included eight specific objectives: (1) prevent cane toads from reaching offshore islands where northern quolls are present; (2) foster the recovery of northern quolls in populations where they coexist with cane toads; (3) halt northern quoll declines in areas where cane toads are present; (4) or absent; (5) maintain secure populations for future translocations; (6) increase knowledge of disease; (7) reduce the impacts of feral predators on northern quolls; and (8) raise public awareness of the plight of the northern quoll.

We have identified four primary management actions which have so far been applied and documented in detail that aim to achieve these objectives. These are: 1) the use of islands as reserve populations through translocations, 2) cane toad control and aversion techniques, 3) feral predator control, and 4) the creation of artificial habitat.

Islands

Islands can be important tools for species conservation by harbouring species at risk from threats present on the mainland (Ringma *et al.* 2018). The translocation of northern quolls to three islands (Astell Island, Pobassoo Island, and Indian Island) off the coast of Northern Territory between 2003 and 2017 (Jolly and Phillips 2020; Kelly *et al.* 2020; Rankmore *et al.* 2008) has produced several positive outcomes. On Astell and Pobassoo islands, northern quoll populations increased from a total of 64 to 5600 individuals in the five years that followed translocations (Rankmore *et al.* 2008) and populations appeared to maintain genetic diversity at least in the short-term (Cardoso *et al.* 2009). Whilst both translocated populations exhibited some decline following their initial booms, both have now stabilised with high survival and recruitment rates compared to mainland populations (Griffiths *et al.* 2017).

In contrast to the Astell and Pobassoo Island translocations, the Indian Island population declined sharply within a year of individuals being released and is now unlikely to be viable (Kelly *et al.*

2020). In addition to cane toad related mortality, the failure of the Indian Island translocation was likely contributed to by the extremely unfortunate timing of two major stochastic events (fire and cyclone) in the establishment year (Kelly *et al.* 2020). It is plausible, had the timing of these events been different, the introduced quoll population on Indian Island may have taken a different trajectory (Kelly *et al.* 2020). The primary purpose of the Indian Island translocation, rather than establishing an insurance population, was to experimentally measure a selection of toad-smart genes and, thus, test the effectiveness of targeted gene flow (see below) (Kelly *et al.* 2020). This also probably influenced the fate of the population, as the experiment required quolls to be released onto an island with a resident toad population and a release cohort with appropriate population demographics (i.e., proportion of toad-smart individuals) meaning release numbers were small (n = 54).

Where quolls have been introduced to island arks for the purposes of setting up insurance populations, the success rate has been 100% (Griffiths *et al.* 2017). However, it's important to consider that an objective of northern quoll island introductions is to create insurance populations which can be used for future mainland reintroductions (Hill and Ward 2010). As such, it will be important for those planning future island translocations to consider the impacts of isolation on quolls in terms of both genetic diversity (Cardoso *et al.* 2009) and predator naivety (Jolly and Phillips 2020) in order to maximise the success of future mainland reintroductions. Translocation planners should also consider the impact northern quolls may have on prey species occupying islands that quolls are translocated to, which, in the short-term, are unlikely to be equipped with appropriate behaviours to avoid being predated on by quolls (Jolly *et al.* 2021). Given the right circumstances, translocations to mainland locations within the northern quoll's historic range could also be considered. This could include properties managed in terms of both predators and fire by conservations organisation such as the Australian Wildlife Conservancy and Bush Heritage Australia, or through the Australian Government's Indigenous Protected Areas program.

Cane toad control and aversion techniques

Although established toad populations are largely impossible to eradicate with existing tools (Tingley *et al.* 2017), several publications have assessed the feasibility of controlling the spread of cane toads by capitalizing on their vulnerability to desiccation and blocking access to large artificial water bodies (Brook *et al.* 2011; Gregg *et al.* 2019; Southwell *et al.* 2017; Tingley *et al.* 2013; Tingley *et al.* 2017). Southwell *et al.* (2017) suggest barriers blocking toad access to water between the Kimberley and the Pilbara could be constructed for $4.5 million AUD, with such a mechanism potentially capable of stopping toad invasion from the Kimberley to the Pilbara region, even for scenarios with extremely high rainfall. Initial field trials have been successful, with toads surviving a maximum of 5 days without access to surface water under the conditions where barriers would be installed (Gregg *et al.* 2019). However, it is important to note that the WA governments and pastoral industries desire to drought-proof the north-west pastoral industry through the increased development of alternative agriculture practises (new crops and fodder) and intensification in pastoral diversification such a central pivot irrigation (e.g. La Grange region) will limit the effectiveness of strategies based on rendering water sources inaccessible to toads. Similarly, this method of restricting toad movement will not address breaches in biosecurity procedures which enable toads to reach the Pilbara with plant nursey stock and fresh food produce from the Kimberley and Northern Territory growing regions and as hitchhikers with tourists and industrial/mining equipment.

In populations where cane toads are already established, northern quolls are now ‘toad-smart’ and are less willing to depredate toads than quolls that have no previous exposure to toads (Kelly and Phillips 2017). This behaviour has been shown to be heritable, with offspring of toad-smart quolls being shown to innately avoid cane toads on their first encounter, suggesting rapid adaptive response in a small number of toad-impacted populations (Kelly and Phillips 2017; Kelly and Phillips 2019). To induce similar toad-smart behaviour in toad-naïve quolls, conditioned taste aversion (CTA) trials have recently been used to alter northern quoll predatory behaviour in captivity (Cremona *et al.* 2017b; Indigo *et al.* 2018; Jolly *et al.* 2018a; Kelly *et al.* 2018; O’Donnell *et al.* 2010; Webb *et al.* 2015) and have shown promise. CTA techniques used to train quolls to avoid toads typically use cane toad flesh laced with a nausea inducing dose of thiabendazole that deters quolls from subsequently eating cane toad flesh once released. Quolls trained with the toad sausages generally avoided the consumption of live and dead toads when tested in captivity (Indigo *et al.* 2018) and survived longer in the wild then toad-naïve quolls (Jolly *et al.* 2018a; O'Donnell *et al.* 2010).

Despite the success of CTA trials on lab-trained quolls, buffering wild northern quolls against cane toads using CTA techniques has proved more difficult. For example, recent unpublished research found CTA trials conducted within and adjacent to Mornington Wildlife Sanctuary in the Kimberley did not reduce toad impacts on the quoll population (Indigo 2020). Several contributing factors are thought to be potentially responsible for the failure of these trials, including: i) the decay of toad aversion with time since CTA exposure (Indigo *et al.* 2018); ii) ineffective delivery rates of the toad sausages; and iii) ineffective dose rates of thiabendazole within sausages (Indigo 2020). Although it has been demonstrated that intergenerational persistence of CTA trained quolls can occur in the wild following translocation (Cremona *et al.* 2017b), the mechanism by which toad-avoidance behaviour is transmitted across generations (genetic or cultural) remains unclear. Decerning the transmission mechanisms is made considerably more difficult by the fact a certain proportion of quolls, irrespective of training, have a natural tendency to avoid attacking cane toads (Kelly and Phillips 2017). The efficacy of CTA as a management strategy is largely dependent on a single factor: whether quolls can confer the learnt toad-aversion lesson between generations via trained mothers teaching their young (cultural transmission). Unfortunately, there is currently no evidence that quolls have the ability or tendency to train their young to avoid cane toads (Indigo *et al.* 2021), and thus quoll populations that now appear naturally adverse to toads (e.g Queensland northern quolls) likely transmit this behaviour between individuals genetically. Recently, population viability models demonstrated that without a cultural transmission rate of >70%, for which there is no evidence, CTA is unable to prevent local extinction (Indigo *et al.* 2021).

Another cane toad mitigation strategy that could be implemented as part of future northern quoll management efforts is targeted gene flow, where quolls with heritable toad-smart genes are introduced into naïve populations to enhance their adaptive capacity (Kelly and Phillips 2016; Kelly and Phillips 2019). In 2017, the first and only trial of targeted gene flow in northern quolls involved releasing 54 CTA trained northern quolls onto toad infested Indian Island. The released quolls were composed of toad-smart genotypes from Queensland, hybrid toad-smart and toad-naïve genotypes (Qld ×NT) and toad-naïve genotypes from Northern Territory. The aim of the trial was to test if selection pressure in the form of cane toads would drive toad smart genes to spread throughout the introduced quoll population with each generation. Although northern quolls failed to establish a population on Indian Island (details discussed above), genetic data collected the year after the translocation indicated selection toward toad-smarts had occurred after only a single generation (Kelly 2018; Kelly *et al.* 2020). The study also demonstrated the successful hybridisation of Qld and NT northern quolls, with viable F2 hybrids and backcrosses observed, suggesting outbreeding depression (a potential barrier to the success of targeted gene flow) is not an issue for this species (Kelly *et al.* 2020).

Feral predator control

Dingo and wild dog control has occurred across much of mainland Australia for well over a century (Allen and Sparkes 2001). Dingo control is particularly common in pastoral areas and is mostly conducted via the deployment of meat baits containing 1080 (sodium monofluoroacetate) (Twigg *et al.* 2000). Sodium monofluoroacetate is a poisonous compound produced naturally by plants in the genus *Gastrolobium*, which mostly occurs in the southwest region of Western Australia. While it is typically most lethal to animals without an evolved tolerance, this depends on both the dose rate and number of baits consumed (McIlroy 1981; McIlroy 1982). Using aircraft to deploy baits (aerial baiting) has dramatically increased the scale at which predator control can feasibility be implemented (Thomson 1986).

At sites where 1080 baits are deployed, dingo densities are often reduced (Thomson 1986; Twigg *et al.* 2000). Although northern quolls will eat 1080 baits (Calver *et al.* 1989), the baits themselves do not appear to negatively affect quoll population sizes (King 1989). However, due to differences in their evolutionary history with plants containing sodium monofluoroacetate (mostly occuring in the south-west of Australia), some populations of northern quoll are likely to be more susceptible to 1080 than others (Twigg *et al.* 2003). Whilst dingo control may reduce dingo-related mortality in quolls, by potentially leading to mesopredator release (Crooks and Soulé 1999; Ritchie and Johnson 2009) of feral cats, it may also have complex and unintended indirect effects (Brook *et al.* 2012; Dickman *et al.* 2009). However, there is conflicting evidence regarding whether feral cats are indeed released following dingo control in northern Australia (Brook *et al.* 2012; Kennedy *et al.* 2012; Leo *et al.* 2019; Stobo-Wilson *et al.* 2020)

Similar to dingoes, cats can also be controlled using poison baits, albeit to date much less effectively (Algar *et al.* 2007), and with the risk of unintentionally killing dingoes (e.g Wysong *et al.* 2020). New baits engineered specifically for cats such as Eradicat™ , Curiosity™ and Hisstory™ are now being trialled (Johnston *et al.* 2020; Johnston *et al.* 2013; Woinarski *et al.* 2019b) and have so far shown no signs of obvious impacts on northern quolls (Ranges 2017). A five-year trial is currently underway investigating the impact of a large-scale Eradicat™ baiting program on northern quolls, as well as other species vulnerable to cat predation such as Rothschild's rock wallabies (*Petrogale rothschildi*) and Pilbara olive pythons (*Liasis olivaceus barroni*) (Morris *et al.* 2015). Preliminary results suggest feral cat baiting does have a positive effect on northern quoll populations (Palmer 2019) without any direct impacts to the quolls themselves (Cowan *et al.* 2020a; Moro *et al.* 2019). However, confounding factors related to rainfall and fire justify the need for more sophisticated analyses to get an accurate measure of the impact of feral cats on northern quolls.

Artificial habitat

Northern quolls, among many other CWR species in Australia, require structural complexity in the form of logs, tree hollows, termite mounds, or rocky outcrops to use as refuges (Oakwood 1997a), and reductions in habitat complexity as a result of fire or habitat clearing can expose these species to increased rates of predation (Oakwood 1997a, Palmer pers comm). One way of mitigating these effects may be through the use of artificial refuges (Cramer *et al.* 2016), which provide quolls with shelter from predation and climatic exposure where natural refuges have been removed. So far, artificial refuges designed for northern quolls have been deployed in several locations across the Pilbara bioregion (Cowan *et al.* 2020b; Cramer *et al.* 2016) and have achieved mixed success. For example, Cowan *et al.* (2020b) found that although artificial refuges closely replicated the thermal conditions created by natural dens, the surrounding environment was typically less complex, potentially contributing to greater feral cat visitation and lower prey availability. While it is possible that improving restoration efforts in the area surrounding refuges may increase their suitability for northern quolls, this has yet to be tested.

Future research directions

Northern quolls have been the subject of considerable research, much of which has improved our understanding of their threats and provided a useful basis for conservation management. However, the species remains threatened and continues to decline, with more resolute and strategic management required. Further research that addresses key knowledge gaps can contribute significantly to improving the effectiveness of conservation management for the northern quoll, and hence its overall conservation outlook. Here, we provide a non-exhaustive list of future research directions based on knowledge gaps evident from our review. If applied, each could be used to fine-tune and redirect management actions to improve conservation outcomes for northern quolls.

We acknowledge that a separate but overlapping set of research priorities have been identified for the Pilbara population (Cramer et al. 2016), including: (i) develop appropriate and standardised survey and monitoring methods (ii) improve our understanding of habitat requirements, (iii) better understand the population dynamics of the northern quoll in the Pilbara, (iv) better understand key threats (cane toads, feral predators, mining infrastructure) and the interactions of these threats, and (v) determine the ability of the northern quoll to recolonise disturbed areas or colonise artificial habitat. We reiterate the importance of these research priorities to the conservation of Pilbara northern quolls.

1. Resolving taxonomy

While no subspecies of northern quoll are currently recognised, several publications have found clear genetic distinctions among the four major populations based on microsatellite data, which are separated from one another by established biogeographic boundaries. Determining if major populations should be treated as distinct taxonomic units is likely to be critical in informing future management interventions such as targeted gene flow and genetic rescue, where quolls from one population are translocated to another (see management section). The use of more recently available genetic techniques, such as genome-wide single nucleotide polymorphisms (SNPs) analysis, is likely to be important in addressing whether these genetic divergences warrant taxonomic recognition and/or whether significant evolutionary units should be assigned to populations and managed differently

2. The status of Queensland northern quolls

The Queensland population of northern quoll previously occupied a larger area than any other northern quoll population, and has since undergone larger decline than any other northern quoll population (Moore et al. 2019), yet we found a disproportionally small number of publications on Queensland northern quolls (although research in Queensland is ongoing). Queensland northern quoll have not been comprehensively surveyed, and there are no published studies which provide estimates of abundance or density for this population. An explanation for this could be that northern quolls remain listed as 'least concern' under the Queensland Nature Conservation Act (1992), and therefore research funding provided by the state government for threatened species have so far not been available. While acknowledging northern quoll research currently underway in Queensland (e.g Burnett et al.; Trewella et al.) we suggest an increased research effort is valid given the scale of declines that have occurred here. Further research may assist in elucidating if persisting northern quoll populations are stable, declining, or expanding.

3. Understand mechanisms allowing the persistence and resistance of northern quoll populations during cane toad invasions

In contrast to a trend of severe and rapid decline following the arrival of cane toads, some northern quoll populations do survive the initial wave of a toad invasion. However, apart from a small selection of broad-scale habitat predictors (Woinarski *et al.* 2008), we have little knowledge of population-specific characteristics that best predict a population's short-term likelihood of surviving a toad invasion. Understanding the initial patterns of persistence may be useful in forecasting the probability of quoll population persistence in areas yet to be invaded by cane toads (southern Kimberley, Pilbara), potentially allowing us to prioritise the management of these areas. Such lessons are likely to both improve our understanding of the mechanisms and circumstances underlying a quoll populations' persistence following cane toad invasion, but may also provide us with an increased mechanistic understanding of how these impacts and recoveries may play out in populations of other Australian predators that are threatened with extinction via the impacts of cane toads.

In addition to investigating factors facilitating quoll persistence through cane toad invasions, an important future research direction may be to assess if there are any signs of recovery. Have northern quolls returned to sites from which they were previously lost, and if so, what population/habitat characteristics have allowed for this return? Answering these questions is likely to provide information critical to the success of future assisted recolonizations—currently one of our most promising tools for conserving northern quolls (discussed above). Addressing these questions will first require the re-surveying of sites at which northern quolls have previously been confirmed to be absent following cane toad invasion (of which there are now many) to investigate whether recoveries have occurred. Secondly, the physical and genetic characteristics of the recolonising quolls, along with the make-up of the recolonised habitat should be compared with sites where quolls have remained absent. Given northern quolls in Queensland have co-existed with cane toads for longer than any other northern quoll population, it is likely that post-cane toad recolonization events are most likely to occur here. As such, we recommend future studies addressing this questions focus on the Queensland population.

4. Quantifying the impacts of mining

Mining activity occurs across the northern quolls entire range, including important cane toad-free populations, such as Groote Eylandt and the Pilbara bioregion. Yet, few publications (see threats section) have investigated the impact of mining on northern quoll populations. As such, determining the extent to which mining activity is likely to influence the persistence of northern quoll population should be addressed in future research. This is especially true for the Pilbara populations, where overlap between the northern quolls geographic range, and mining tenure is high (Cramer *et al.* 2016). In relation to mining activity specifically, Cramer *et al.* (2016) identify the impacts of linear infrastructure on northern quoll movement and the ability of the northern quoll to recolonise disturbed areas or artificial habitat as key research areas. In addition to these areas, we suggest future studies investigate secondary impacts of mining activity on northern quoll populations, such as increased predator densities surrounding mining camps, as a result of increased resource subsidies (e.g., food, water).

5. Population isolation and genetic rescue

A consequence of the northern quolls recent geographic decline is that many populations are now smaller and more isolated. Inbreeding and loss of genetic diversity is often unavoidable in small, isolated populations, increasing their extinction risk due to inbreeding depression (i.e. loss of fitness from low genetic diversity) and lowered adaptive potential (Frankham *et al.* 2017; Ralls *et al.* 2020). Island populations of northern quolls are particularly exposed to these risks – and previous work has shown they have lower genetic diversity compared to populations on the mainland (Cardoso *et al.* 2009). We recommend future studies expand on this work by including additional sites – both on islands as well as the mainland populations (Flanagan *et al.* 2018). Where isolated quoll populations are showing signs of genetic degradation, we would be wise to consider mixing populations via translocation, to increase genetic diversity and adaptive potential of these degraded populations(Aitken and Whitlock 2013; Frankham 2015; Whiteley *et al.* 2015).

6. Unwinding interacting threats

Northern quolls face multiple co-occurring threats across their range; however, limited research has investigated if and how these threats interact synergistically. Publications of other native mammals occurring in northern Australia demonstrate that threats may be compounding and management that addresses only single threats may be ineffective (Legge *et al.* 2019). Better understanding northern quoll 'threat webs'—a group of co-occurring threats that may have additive or non-additive impacts on each other—may improve land managers' ability to focus efforts toward ultimate threats, rather than proximate threats, hopefully with improved conservation outcomes (Geary *et al.* 2019b). Understanding the synergetic impacts of predation, fire, and grazing, on northern quolls is likely to be particularly important to their conservation, given each of these threats occurs in tandem across the majority of their existing range. Among these threats, we suggest isolating the impacts of feral cats be investigated as a matter of priority, given the scale at which they are likely to impact not only northern quolls, but also their role in driving Australia's broader mammal declines (Woinarski *et al.* 2019b).

An important tool in untangling these threats is the use of manipulative experiments, where at least one threat within a system is artificially controlled (typically as part of conservation management activities), such that its relative impact on northern quolls populations can be measured in context to co-occurring threats. While experiments of this nature are already under way (eg. Palmer 2019), opportunity for further research in this area is likely to exist in areas where threat management (e.g., controlled burns, predator baiting) within northern quoll habitat is planned or actively occurring already.

7. Predicting the impact of climate change

Climate change poses an extreme risk to global biodiversity (Steffen 2009), yet we found little mention of the threat in literature related to northern quolls. Across the northern quolls geographic range, the impacts of climate change are likely to include increased temperatures, rainfall variability, increased proportion of extreme rainfall events and less frequent cyclones (NESP 2018). While projected changes to total annual rainfall are uncertain, decreases in total rainfall are more likely than increases (NESP 2018). Measuring the extent to which changes in rainfall will impact resource availability and breeding success for northern quoll, among other northern Australian mammals, has obvious implications for the conservation of the species. In addition to changes in rainfall, average temperatures across Northern Australia will continue to increase and there will be more days with extreme maximum temperatures (NESP 2018). Understanding if these changes will lead to increased northern quoll mortality as a result of thermal stress, and the implications this would have for population persistence, should be a future research priority. More broadly, identifying potential climate refugia for northern quolls—areas that they will likely persist in under various climate change scenarios—where management efforts can be concentrated should also form a future research focus.

8. Further incorporation of Indigenous knowledge

Recognition of the knowledge held by the Indigenous people of Australia, often termed ‘two-way’ or ‘right-way’ science, has improved our ecological understanding of species on many occasions (Bohensky *et al.* 2013; Butler *et al.* 2012; Horstman and Wightman 2001; Telfer and Garde 2006). There is significant Indigenous knowledge of the northern quoll across northern Australia (Abbott 2013, authors personal communications). While some traditional knowledge has been included in a handful of publications (Dixon and Huxley 1985; Woinarski *et al.* 2011a; Ziembicki *et al.* 2013), there is a large potential for future integration into research and on-ground management of the remaining northern quoll populations, and potentially the detection of new isolated populations in remote areas of the Western Desert.Given that such a large proportion of the known distribution of northern quolls is on Traditionally Owned Indigenous land, future research and conservation endeavours should seek to be more inclusive of Indigenous stakeholders and aim to incorporate increased involvement of Indigenous people in such efforts.

9. Harnessing the heritability of toad avoidance behaviour

Individuals within quoll populations that survive the initial invasion of toads and continue to persist in sympatry with toads do so because they are innately unwilling to attack toads (Kelly and Phillips 2017; Moore *et al.* 2019). Thus, if populations can avoid local extinction, natural selection should be rapidly acting upon heritable toad-averse traits. Harnessing the heritability of this behaviour forms the basis of targeted gene flow strategies (discussed above). Initial targeted gene flow trials using northern quolls have documented some encouraging results, however, additional research required to enhance this technique such that it can be applied on a broader-scale. This may be achieved by utilizing recent advancements in genetic technology to identify areas of the quolls genome that are most useful in predicting toad adverse behaviours in quolls. Future research in this area may also include attempting additional translocation trials, where captively bred quolls with genetic tendances to avoid toads are inserted into quoll populations predicted to be impacted by invading cane toads.

10. The role of artificial refuges

Initial trials have shown some potential for quolls to make use of artificial refuges in areas of disturbed or degraded habitat (Cowan et al. 2020b). However, this approach is not yet proven, and further research is required to determine whether artificial refuges can be a viable management tool for future northern quoll conservation. For example, evidence that northern quolls willingly use artificially constructed refuges as breeding habitat is currently lacking. Further trials, potentially incorporating differing complimentary actions (i.e., invasive predator control), are therefore required in order to address this knowledge gap. We also still have a limited understanding of the dimensions of artificially constructed den sites that maximise northern quoll useability. For example, existing artificial refuges range from 9–150 m^2 in size, but offer shallower crevices compared to those northern quolls use in natural habitat (Cowan et al. 2020b). Future experiments should aim to test different sizes or arrangements of artificial refuges to determine how differences in these variables alter the thermal conditions of the refuges, and northern quoll use and survival. We also recommend that artificial refuges are trialled for northern quolls in habitats impacted by disturbances other than mining, such as fire and intense grazing, such has already been trialled for smaller dasyurids (Bleicher and Dickman 2020).

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Conflict of interests

The authors declare no conflict of interests

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