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Corrigendum

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The authors apologise for a referencing error in this paper. The citation and reference for Nutting and Wooley were listed with the incorrect year of 2009. This should have been 1965. The complete and correct reference is provided below.

Nutting, W., and Woolley, P. (1965). Pathology in *Antechinus stuartii* (Marsupialia) due to *Demodex* sp. *Parasitology* **55**(2), 383–389. doi:10.1017/S0031182000068852

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Review

Conservation of quolls (*Dasyurus* spp.) in captivity – a review

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Abstract. Quolls are carnivorous marsupials in the family Dasyuridae with characteristic white spots. They are distributed throughout Australia and New Guinea, but uncommonly seen due to their mostly nocturnal solitary nature, and large home ranges. All Australian quolls are listed as 'near threatened' or 'endangered' at state, national and international levels, largely due to human-induced threats. Threats include introduced predators, habitat loss through clearing and modifications including changed fire regimes, disease, human persecution, vehicle collisions and accidental or targeted poisoning by humans and cane toads (*Rhinella marina*). Conservation efforts that have focussed on reducing introduced predators, and minimising the impact of cane toads, have aided some translocations, hence species recovery in some local areas of Australia has occurred. Where species conservation has required captive breeding for translocation, successful captive management has been crucial. We summarise research conducted in captivity on aspects of birth and development, health and disease, and blood and nutrition parameters of quolls, and suggest future directions for research. Further research on captive and wild quoll populations will benefit future translocations, reintroductions and conservation through increased knowledge, improved maintenance and husbandry of captive colonies, and monitoring of wild populations.

Keywords: captive breeding, carnivore, conservation, dasyurid, endangered species, marsupial, quoll, reintroduction, semelparity, translocation.

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Introduction

Carnivorous mammals play a significant role in nutrient cycling in the environment, insect and vertebrate population regulation, and carrion removal by scavenging on dead animals (Estes *et al.* 2011; Wilson and Wolkovich 2011; Ripple and Beschta 2012; Ripple *et al.* 2014). Thus, carnivorous mammals are important to conserve because of their significant role in the ecosystem. Methods for conserving carnivores include *ex-situ* practices such as captive breeding colonies for translocations/reintroductions and zoological displays for educational purposes, as well as *in-situ* practices such as management of threats, long-term monitoring, reintroductions and translocations.

In Australia, native species in the Dasyuridae family are predators consuming and controlling vertebrate and invertebrate fauna population numbers (Dickman 2014). Within this family are quolls (*Dasyurus* spp.), medium-sized carnivorous marsupials. Quolls inhabit a diverse range of habitats and are the largest extant marsupial carnivores on mainland Australia and New Guinea. There are six species of quoll, the bronze quoll (*Dasyurus spartacus*), western quoll (*D. geoffroii*), New Guinean or New Guinea quoll (*D. albopunctatus*), eastern quoll (*D. viverrinus*), northern quoll (*D. hallucatus*) and spotted-tailed or tiger quoll (*D. maculatus*) (see Table 1 for description of each species). We conducted this review on quolls to summarise recent conservation efforts, and highlight gaps in our knowledge where additional research, particularly in captive populations, will aid their conservation. The methodology used for this review involved utilising literature amassed previously, as well as using formal databases to locate new literature. We used the common and Latin species names to search GoogleScholar and ScienceDirect databases and limited our searches to peer-reviewed journal articles. Whilst initially there were no limitations on the literature included, we chose to limit the literature incorporated to focus the review on current conservation efforts in the field, and how information gained through captive studies (diet and nutrition, reproduction and development, and health and disease) can be used to support future conservation efforts.

Geographic distribution

The geographical distribution of most quoll species has contracted from their historic range since European settlement. The eastern quoll (Fig. 1) was formerly distributed throughout south eastern mainland Australia including New South Wales (NSW), Victoria, and South Australia (SA), but was thought to have

Table 1. Description and morphometrics of all quoll species

Quoll species	Body length (cm)	Body mass (g)	Description	References
Eastern quoll	45	Males 900–1900, females 700–1100	There are two coat colour variations (black or fawn), both with white-spots, and no spots on tail. Colour variations can occur in any family group and are independent of sex and parent coat colour. Limited in distribution to Tasmania. Eastern quolls are the only species of quoll lacking a hallux (first digit) on the hind foot.	Jones (2008); Jones *et al.* (2014)
Spotted-tailed quoll	76	Males 1500–5000, females 900– 2500	Rufous brown to dark brown colour, covered in white spots over the body and tail. Belly fur is a pale brown to cream colour. Largest species of quoll and the most arboreal.	Jones *et al.* (2001); Belcher *et al.* (2008)
Northern quoll	37	Males 340–1120, females 240–690	Brown with white spots covering the body up to the base of the tail and creamy white belly. Striations are present on their footpads and they have a V-shaped upper incisor row.	Oakwood (2008); Jones *et al.* (2014)
Western quoll	40	Males 710–2185, females 615–1130	Brown with white spots and a creamy white belly. Lack striations on their footpads and limited in distributed to Western Australia.	Serena and Soderquist (2008); Jones *et al.* (2014)
Bronze quoll	30.5–38	700–1000	Dark, golden-brown coat colour with minute white spots, dark golden-bronze feet and a dark tan tail. Lack of striations on their footpads. Limited in distributed to New Guinea.	Flannery (1995*a*); Jones *et al.* (2014)
New Guinea quoll	23–35	500–700	The New Guinea quoll differs from the bronze quoll by having a less hairy tail, a larger hallux and is smaller in size. Striations are present on their footpads and they have a U-shaped upper incisor row. Limited in distributed to New Guinea.	Flannery (1995*b*); Jones *et al.* (2014)

Fig. 1. Eastern quolls exhibiting the two colour morphs.

Fig. 2. Spotted-tailed quoll. Note the spots visible on the tail (bottom left).

become extinct in the mid-1960s, and is now restricted to Tasmania (Jones *et al.* 2014). Frankham *et al.* (2017) however recently described the genetic status of a road-killed eastern quoll collected in 1989 from Barrington Tops, NSW, suggesting the species likely persisted longer than previously thought in isolated areas of mainland Australia.

The spotted-tailed quoll (Fig. 2) was previously distributed along the east coast and into the semiarid zone of eastern Australia, several of the Bass Strait Islands and Tasmania. Although it is still distributed in most of these areas it has declined and become extinct in SA and on the islands in Bass Strait (Jones *et al.* 2014). It is now regarded as common only in the New England Tablelands and parts of south-eastern NSW, far-north Queensland and Tasmania.

Spotted-tailed quolls have been described as two distinct subspecies. The subspecies *D. maculatus maculatus* was formerly distributed from south-east Queensland, eastern NSW, Victoria, SA, Tasmania and some Bass Strait islands (Maxwell *et al.* 1996). The population of this subspecies in Queensland has dramatically decreased in the last 25 years and the species is now regarded as rare. The largest numbers in NSW occur on the mid-north coast from the Hunter to Coffs Harbour, and the New England Tablelands (Maxwell *et al.* 1996).

The other subspecies, *D. m. gracilis* resides mostly in upland notophyll vine forest and in lower numbers at lower altitude notophyll and mesophyll forests (Maxwell *et al.* 1996). *D. m. gracilis* formerly occurred throughout the wet tropics of

Queensland, but it is now believed to be extinct from the Atherton and Evelyn Tablelands, and patchily distributed in the south of the state (Maxwell *et al.* 1996).

Although the northern quoll is now restricted to northern Australia, in the past it occurred from the Pilbara to south-eastern Queensland, and inland as far south as Alexandria in the Northern Territory (NT) (Oakwood *et al.* 2016). Recent declines have been observed in eastern and southern Queensland, the Cape York Peninsula, low rainfall areas in the NT, the south east and south west Kimberley (Maxwell *et al.* 1996; Oakwood *et al.* 2016), and the Pilbara (Maxwell *et al.* 1996). A particularly severe population decline has occurred in Kakadu National Park National Park (Burnett 1997). The northern quoll has also been recorded on Groote Eylandt, Marchinbar Island, Inglis Island and Vanderlin Island, and translocated to Astell and Pobassoo Islands (Woinarski *et al.* 2007; Hill and Ward 2010; Griffiths *et al.* 2017).

Western quolls were previously distributed across 70% of Australia, with the exception of the NT and Tasmania (Morris *et al.* 2003). The eastern subspecies, *D. geoffroii geoffroii*, was recorded at Peak Downs in eastern Queensland, in NSW on the Liverpool Plains, and Mildura. In NSW unconfirmed reports have been noted north of Broken Hill (1996), between Broken Hill and Menindee (1988), and north west of Tilpa (1990) (Woinarski and Burbidge 2019). No further investigations have been made to verify the identity of any of these individuals as western quolls, because spotted-tailed quolls have been noted to occur in central west NSW and it is presumably assumed to be the species in the area, however mammal survey techniques have not been undertaken to specifically target the western quoll in western NSW (Woinarski and Burbidge 2019).

The western subspecies (*D. geoffroii fortis*) is naturally restricted to the central and southern wheatbelt in WA and was believed to consist of less than 10 000 individuals (Maxwell *et al.* 1996). However due to translocations and fox control most populations have stopped declining (Woinarski and Burbidge 2019). It occurs in small populations, with the translocated Julimar State Forest population estimated at less than 100 individuals (Woinarski and Burbidge 2019).

The bronze quoll is the larger of the two quoll species occurring in New Guinea (Flannery 1995*a*). It is limited in its woodland distribution to the Trans-Fly ecoregion (Flannery 1995*a*) across an area of 26 000 km^2 in New Guinea, but described as common in the area by locals (Leary *et al.* 2016). In comparison, little is known about the smaller New Guinea quoll, which inhabits rainforests above 1000 m altitude (and sometimes lower altitudes) (Flannery 1995*b*).

Despite both western quoll subspecies currently being recognised, Woinarski *et al.* (2014) suggests there are no western quoll subspecies, and that the western quoll may be the same species as the bronze quoll. Woinarski *et al.* (2014) made these suggestions based on mitochondrial DNA evidence reported in Firestone (2000) that found less divergence in the DNA sequences of the mitochondrial control region between the western and bronze quolls compared with different populations of spotted-tailed quolls. Thus, further investigations into the classification of quoll species is required to confirm the precise taxonomic classification of both the western quoll and the bronze quoll.

Conservation efforts in the field

All quolls are threatened by a range of factors including predation and competition from introduced predators such as European red foxes (*Vulpes vulpes*), feral cats (*Felis catus*) and potentially wild dogs (*Canis lupus*), loss of habitat through land clearing and modification (Rankmore and Price 2004; Oakwood 2008; Jones *et al.* 2014), and more specifically, disease, human persecution, vehicle collisions and through targeted or secondary poisoning (Jones *et al.* 2014).

The conservation status of quolls ranges from 'near threatened' to 'endangered' (Table 2). The northern quoll is listed as 'endangered'. The population has been estimated to have declined by more than 50% in the last 10 years and is expected to continue to decline due to habitat degradation and/or destruction, introduced predators and cane toads (Oakwood *et al.* 2016). The impact of cane toads on northern quolls has been mixed. Some northern quolls in toad-infested areas show a lack of interest in toads, naturally disregarding them as prey items, compared with naïve quolls in areas where toads have not yet reached, which will readily attacks toads (Kelly and Phillips 2017). This naivety has led to conditioned taste aversion training being trialled in captive and wild northern quolls (O'Donnell *et al.* 2010; Indigo *et al.* 2018). After trial reintroductions of taste aversion quolls into Kakadu National Park, parentage analysis indicated that 'educated' quolls, and their offspring, were surviving and reproducing (Cremona *et al.* 2017). It may also be possible to train naïve quolls *in situ* ahead of the cane toad front.

The northern quoll has a National Recovery Plan (Hill and Ward 2010) that largely recommends focusing on translocations and maintaining populations on off-shore islands free of cane toads (as well as managing fire regimes) to conserve the species. Several northern quoll translocations have been conducted to date. Sixty-four northern quolls were translocated to Astell (11 males and 34 females) and Pobassoo (8 males and 11 females) islands, NT, in March 2003 (Hill and Ward 2010; Griffiths *et al.* 2017). Juvenile animals were sourced from Kakadu National Park, and the Darwin rural fringe, NT, for the translocation. Subsequent surveys in April–July 2003–2005, October–December 2006–2009 and a final survey in October 2014, confirmed resident populations were established (Griffiths *et al.* 2017).

There are current efforts to reintroduce and translocate two of the other four quoll species in Australia into current and former habitats as a method of conservation. Reintroduction of eastern quolls on mainland Australia has been suggested by several groups but is largely dependent on fox control (Jones *et al.* 2014). Eastern quolls have been reintroduced into fenced areas at Mulligans Flat near Canberra, ACT (https://mulligansflat.org.au/), and Mt Rothwell, Victoria (http://mtrothwell.com.au/). Eastern quolls (20) were also translocated into Booderee National Park, NSW in April 2018, the first reintroduction of the species onto mainland Australia, with the aim of a further 40 per year in 2019 and 2020 (R. Brewster, pers. comm.). Within a few months after introduction 40% of the quolls had died from predation, and another 40% died from unexpected threats (Robinson *et al.* 2020).

Live trapping studies in the 1980s suggested less than 6000 western quolls remained in the wild and a recovery plan was implemented (Orell and Morris 1994). There was an updated

Table 2. Reproductive parameters of quolls (*Dasyurus* spp.)

Quoll species	Litters born (days)	Gestation (days)	Maximum # young	Teat detachment (days)	Left in den (weeks)	Weaned (weeks)	Sexual maturity (months)	Longevity	Reference
Eastern	May–Aug	19–24	6	59–65		23–26	12	2 years in the wild	Hill and O'Donoghue (1913); Green (1967); Merchant *et al.* (1984); Fletcher (1985); Bryant (1988); Jones (2008)
Spotted-tailed	Jun–Aug	20–21	6	35–49		18–21	11		Conway (1988); Belcher *et al.* (2008)
Northern	Jun–Aug	21–26	8	60–70	8–9	24	11	3 years, but mostly 1 year	Nelson and Smith (1971); Begg (1981); Braithwaite and Griffiths (1994); Oakwood (2000)
Western	May–Sept	16–18	6	Unknown	9	22–24	11	5 years in captivity, 3 years in wild	Serena and Soderquist (1988); Soderquist and Serena (1990)
Bronze	Unknown	Unknown	7–8	Unknown	Unknown	Unknown	Unknown	Unknown	Van Dyck (1987); Woolley (2001)
New Guinea	Unknown	Unknown	6	Unknown	Unknown	Unknown	Unknown	Unknown	Woolley (2001)

National Recovery Plan for the western quoll published in 2012 (Department of Environment and Conservation 2012) and there have been many successes. Perth Zoo has been heavily involved in breeding western quolls, and the success of the program, and their subsequent relocations, led to the quoll species being reclassified from 'endangered' to 'vulnerable' under the *Environmental Protection and Biodiversity Conservation Act 1999* and IUCN criteria (Perth Zoo 2018). To date, Perth Zoo have released 315 western quolls into Julimar State Forest, Lake Magenta Nature Reserve, Cape Arid National Park, Mount Lindsay National Park and Kalbarri National Park (Morris *et al.* 2003; Harley *et al.* 2018; Perth Zoo 2018). Baiting with sodium fluroacetate (1080) has been particularly effective at reducing fox numbers and aiding successful translocations and hence facilitated western quoll recovery (Morris *et al.* 2003; Serena and Soderquist 2008).

Western quoll relocations have also occurred in WA's Rangeland Restoration project and Dirk Hartog National Park (Jones *et al.* 2014). Thirty-eight western quolls were initially reintroduced into the Flinders Ranges, SA, in 2014 (Commonwealth of Australia 2015). In total, 93 western quolls were translocated (R. Brewster, pers comm.). Although some cat predation has been evident (Moseby *et al.* 2015), cat control is allowing the population to persist (R. Brewster, pers. comm.). In May 2018, 12 (8 male and 4 female) western quolls were introduced into the Arid Recovery Reserve (fenced area) in SA (Beerkens 2018; West *et al.* 2020).

There are no confirmed reintroductions planned for the spotted-tailed quoll. Burnett and Marsh (2004) however advocated for further research on human-wildlife conflicts, their ecology, control of introduced eutherian predators and cane toads, habitat restoration, and captive management and translocation. The National Recovery Plan for the spotted-tailed quoll (2016) outlines more research is required into quoll biology and ecology, reducing habitat loss, managing introduced predators, reducing deliberate killing and road kill-related deaths, and assessing the risk of cane toads and climate change (Department of Environment, Land, Water and Planning 2016).

No conservation plans have been developed for either of the New Guinean species of quoll. The bronze quoll is listed as 'near threatened', however there is not enough information to categorise it as 'vulnerable', as it was listed in 1996 (Leary *et al.* 2016). Although not directly targeted by hunters, hunting dogs and feral cats are known to kill bronze quolls (Leary *et al.* 2016). Other threats to bronze quolls include habitat change due to invasive weed incursions, for example, *Mimosa* spp., and changed fire regimes (Leary *et al.* 2016).

The New Guinea quoll is locally common, and not protected, however declines have occurred in areas with increasing human impacts (Woolley *et al.* 2016). There have also been some suggestions that cats have impacted the species but this is speculative (Flannery 1995*b*).

Conservation efforts in captivity

Conservation efforts such as reintroductions and translocations often rely on breeding captive populations of animals to be used in the reintroduction, therefore it is important to employ effective husbandry techniques and appropriate management strategies while animals are in captivity. Housing and breeding animals in captivity to aid translocation programs require the maintenance of effective gene pools, management of disease, and that animals be supplied with nutritionally appropriate diets to maximise health and reproductive efforts. In the following sections we have therefore summarised what is known about these aspects of quoll biology, both in the wild and in captivity, and based on this information highlight the gaps in our knowledge in terms of captive management. Increasing our knowledge of quoll biology will support future translocation efforts.

Diet and nutrition of quolls

Quolls are carnivorous and eat a range of items from invertebrates to vertebrates. The smaller-sized quolls (e.g. eastern and northern quolls) in the genus tend to be more insectivorous whereas the larger spotted-tailed quoll is more carnivorous. Insects make up the majority of food items consumed by eastern quolls, followed by birds and small mammals (Blackhall 1980; Godsell 1982). Favoured insect groups include beetles (Coleoptera) and moths (Lepidoptera). Blackhall (1980) identified that plant material made up to 60% of some scats analysed and included grasses, bracken (*Pteridium* spp.), clover (*Trifolium* spp.), *Eucalyptus* spp. and blackberry (*Rubus* spp.). Northern quolls primarily favour beetles (Coleoptera) and grasshoppers (Orthoptera); however, rodents appear to be an important food source, with cane rats (*Rattus sordidus*) present in the diet at one site (Pollock 1999). Western quolls rely heavily on small to medium-sized mammals such as *Antechinus* spp., brush-tailed phascogales (*Phascogale tapoatafa*), house mice (*Mus musculus*), black rats (*Rattus rattus*), southern brown bandicoots (*Isoodon obesulus*) and European rabbits (*Oryctolagus cuniculus*) (Soderquist and Serena 1994; Glen *et al.* 2010). Soderquist and Serena (1994) found invertebrates were the main dietary component in the diet of western quolls, whereas Glen *et al.* (2010) found mammals followed by invertebrates were the main dietary components. Occasionally they will consume larger carrion as well (Soderquist and Serena 1994). The spotted-tailed quoll predominantly relies on medium-sized mammals (500–5000 g) such as European rabbits, brushtail possums (*Trichosurus* spp.) and common ringtail possums (*Pseudocheirus peregrinus*). They also consume birds, invertebrates, and small mammals such as *Antechinus* spp. and bush rats (*Rattus fuscipes*) (Belcher 1995; Glen and Dickman 2006; Belcher *et al.* 2007; Dawson *et al.* 2007; Jarman *et al.* 2007). Spotted tailed-quolls have been observed eating a road-kill wombat (*Vombatus ursinus*) and red-necked wallaby (*Macropus rufogriseus*) (Belcher *et al.* 2007). Quolls are likely targeting food for the most energetic gain; however, this would likely be compromised with handling time and food availability (Fisher and Dickman 1993; Rychlik and Jancewicz 2002).

A range of factors affect prey choice in the wild including age of the animal, seasonal abundance of prey items, environmental conditions and locality. Age plays a role in prey choice of spotted-tailed quolls with bush rats, invertebrates, reptiles and common ringtail possums consumed significantly more by subadults than adults, and rabbits consumed more by adults than subadults (Belcher 1995). Insects and reptiles are a more frequent prey item in warmer months as opposed to during winter for spotted-tailed quolls and western quolls (Belcher 1995; Glen and Dickman 2006; Jarman *et al.* 2007; Glen *et al.* 2010). In Gippsland, Vic., medium-sized mammal intake peaked in winter whereas bird intake peaked in spring and summer in the diet of spotted-tailed quolls (Belcher 1995). The higher incidence of mammals in the diet is likely attributed to seasonal availability of food items. However, it also coincides with the breeding season, a time that is energetically costly for quolls. Similarly a preference for vertebrates (nutrient rich foods) during the breeding season occurs in another dasyurid marsupial, the red-tailed phascogale (*Phascogale calura*) (Stannard *et al.* 2010). A higher intake of nutrient rich foods would be beneficial for lactating animals. Recent fire in a spotted-tailed quoll habitat caused the population to consume significantly more lagomorphs in the 2 years following the fire (Dawson *et al.* 2007). The increase in rabbit and hare consumption was positively correlated to their abundance post-fire. In spotted-tailed quolls, males tend to consume larger prey than females; however, sex does not appear to have a significant impact on prey choice (Glen and Dickman 2006; Belcher *et al.* 2007).

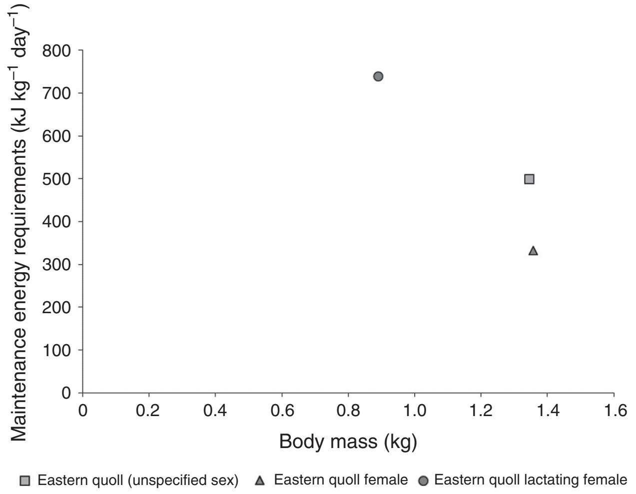

Fig. 3. Eastern quoll maintenance energy requirements (kJ kg^{-1} d^{-1}) for lactating and non-lactating animals. Data from (Green and Eberhard 1979; Green *et al.* 1997).

Nutrition has not been studied in detail in quolls and little is known about their nutritional requirements. Digestive efficiency for eastern quolls is above 80% for macronutrients and energy when maintained on meat diets of chicken necks, kangaroo mince and rats (Green and Eberhard 1979; Stannard and Old 2013). Estimated mean daily digestible energy intake for eastern quolls is 545 kJ kg^{-1} day^{-1} and is the minimum daily energy required to maintain a constant body mass (Green and Eberhard 1979). Energy requirements tend to follow the general marsupial trend of higher body mass equating to lower energy requirements per unit of body mass (Fig. 3) (Hume 1999). During lactation, energy requirements are approximately double that of non-lactating animals in eastern quolls (Fig. 3) (Green *et al.* 1997) which is similar to the red-tailed phascogale during late lactation (Stannard and Old 2015). The increase in energy demands in eastern quolls coincides with changes in milk composition at around 9 weeks postpartum when lipids increase in the milk (Green *et al.* 1997). Approximately 4080 kJ are provided to each pouch young from birth to the start of weaning (Green *et al.* 1997).

Table 3. IUCN and conservation status of quolls

IUCN status from IUCN version 3.1. National conservation status based on EPBC Act 1999. State conservation status based on NSW Biodiversity Conservation Act 2016, Vic. Flora and Fauna Guarantee Act 1988, South Australian's National Parks and Wildlife Act 1972, Western Australia's Biodiversity and Conservation Act 2016, Northern Territory Parks and Wildlife Conservation Act, Queensland Nature Conservation Act 1992, Tasmanian Threatened Species Protection Act 1995

Quoll species	IUCN status	Australian national conservation status	Australian state conservation status	Reference
Spotted-tailed	Near Threatened	Varies – state and subspecies specific		
D. m. maculatus			Endangered (mainland population), Vulnerable (Tas.)	Woinarski *et al.* (2014)
D. m. gracilis			Endangered	
Bronze	Near Threatened			Leary *et al.* (2016)
New Guinea	Near Threatened			Woolley *et al.* (2016)
Northern	Endangered A2ce + 3ce + 4ce	Endangered	Critically endangered (NT), Endangered (WA)	Oakwood *et al.* (2016)
Western	Near Threatened	Near threatened	Extinct (NT), Presumed extinct (NSW), Extinct in the wild (Qld), Endangered (SA), Vulnerable (WA)	Woinarski *et al.* (2014)
Eastern	Endangered A2b	Endangered	Endangered (NSW and SA), Threatened (Vic.)	Burbidge and Woinarski (2016)

Eastern quolls drink very little water in captivity (Green and Eberhard 1979) and likely meet their hydration needs through food consumption. Presumably the other quoll species would similarly obtain most of their water from food. Further research is needed to determine nutrient and energy requirements of all six species of quoll, especially given the lack of dietary studies for bronze and New Guinea quolls. These data could then be used to formulate nutritionally appropriate diets for animals in captive breeding programs.

Reproduction and development

There is variation in the reproductive characteristics of quolls such as length of gestation and sexual maturity (see Table 3). Quolls breed seasonally with breeding occurring May to August, and most young born June–July (McAllan 2003; Jones 2008; Oakwood 2008). However breeding is believed to be controlled by photoperiod (McAllan 2003) and captivity influences time of birth (Conway 1988).

Little is known about the reproduction and development of the bronze and New Guinea quolls, hence they require further investigation. Most western quoll young are born to first year mothers, due to those individuals representing over half the population, and these individuals also produce the largest litters (Serena and Soderquist 2008). Woolley (2001) suggested the bronze quoll is a seasonal breeder, and that there were clear distinctions in size and weight of specimens examined, thus possibly two cohorts (Leary *et al.* 2016). In contrast to other quoll species, the New Guinea quoll appears to breed throughout the year (Woolley 1994). Woolley (1994) suggested breeding occurred throughout the year in female New Guinea quolls based on museum specimens collected throughout most months of the year exhibiting evidence of lactating. Further indirect support for New Guinea quolls breeding throughout the year is based on juveniles and sub-adults being captured throughout the year (Woolley 1994). Litter size of New Guinea quolls is 4–6 (Flannery 1995*b*).

Spotted-tailed quolls are known to hiss, and during the mating season, click softly (Belcher *et al.* 2008). Spotted-tailed quolls are solitary; however, only females are territorial but tolerate their female offspring. Males are not territorial and range over large areas with both males and females (Belcher *et al.* 2008). Spotted-tailed quolls exhibit multiple paternity within a litter, although larger males are more likely to sire offspring because they compete physically (Glen *et al.* 2009).

Pouch appearance is a reliable indicator of reproductive status in the spotted-tailed quoll based on a comparison of it to plasma and faecal hormone levels, and vaginal smears (Hesterman *et al.* 2008). The secretions, colour and size of the pouch were correlated with vaginal cytology and sexual steroids, with the pouch reaching maximal size, colour and secretions during the follicular phase just prior to copulation, and becoming glandular post-ovulation (Hesterman *et al.* 2008).

Gemmell *et al.* (2002) and Nelson and Gemmell (2003) described birth in the northern quoll, whereby the mother stood on all fours with the hind legs raised slightly higher than the front legs. It was initiated by a release of around 20 mL of fluid, and within 10 min a small gelatinous mass appeared. Nelson and Gemmell (2003) observed births of 17, 16, 6, 16, 13 and 11 young from six quolls, and Gemmell *et al.* (2002) observed 18 young attached to teats and hairs in the pouch of one quoll. The next day, Gemmell *et al.* (2002) observed only eight young attached to teats, and the remainder dead and abandoned. Both Gemmell *et al.* (2002) and Nelson and Gemmell (2003) thus confirmed quolls are superovulators, and capable of supernumerary birth of young.

A further study by Nelson and Gemmell (2005) of birth in the northern quoll found there was an increasing temperature gradient from the urogenital sinus, to the skin between the urogenital sinus and pouch, and to the pouch. Therefore, a temperature gradient was suggested to play a role in aiding transit of the newborn from the urogenital sinus to the pouch (Nelson and Gemmell 2005). Further, Nelson and Gemmell (2005) found hair formed a tunnel from the urogenital sinus to the pouch and may also aid the newborn in its transit to the pouch.

Like other marsupials, the young are born largely undeveloped (Nelson *et al.* 2003). By contrast, quoll forelimbs are well developed at birth, and although the head and neck moves side to side, it allows the young to move forward and grasp hair on the way to the teat (Nelson *et al.* 2003). At birth the elbow joint is not yet developed and a full extension of the forelimb is not yet possible (Nelson *et al.* 2003). The digits of the paws extend and flex allowing the hair of the mother to be gripped, but if no hair is gripped the digits still extend and flex (Nelson *et al.* 2003). The young fully attach to the teat once they reach it, with the lips forming the anchorage (Nelson *et al.* 2003). By day 30, the forelimb becomes fully functional (Nelson *et al.* 2003). Nelson *et al.* (2003) stated the northern quoll is less developed than gray short-tailed opossums (*Monodelphis domestica*) (Carnegie stage 21) at birth.

Northern quolls are partly semelparous, with some males exhibiting post-mating mortality in some areas, whilst others can breed again in a second season (Dickman and Braithwaite 1992; Braithwaite and Griffiths 1994; Oakwood 2000). Semelparity is characterised by increased androgens, fur loss, weight loss and increased parasite burden (Oakwood *et al.* 2001). In captivity however, male northern quolls can live for up to 6 years (Jackson 2003), and this is not unlike other semelparous marsupials that are known to live longer in captivity despite becoming infertile (Stannard *et al.* 2013*a*).

Although we have a reasonable understanding of quoll physical development after birth, most species lack specific developmental growth charts. Serena and Soderquist (1988) have described the growth and development of western quolls based on crown–rump length and head width, but this was limited to five captive litters, hence much larger numbers of individuals are required. Wild specimens were also included, but ages were unable to be determined and only estimates made (Serena and Soderquist 1988). Ideally western quolls from more diverse locations and genetic differences should also be included, as we know there are differences in growth rates based on maternal nutrition in other marsupial species (Stannard and Old 2015).

Green and Scarborough (1990) measured preserved spotted-tailed quoll young and constructed an estimated growth curve, like those of the Tasmanian devil (*Sarcophilus harissii*) and extinct Tasmanian tiger (*Thylacinus cynocephalus*) (Old 2015), but are limited to developmental features, as ages of the young were unknown (Green and Scarborough 1990). Developmental growth charts of other species will likely be helpful as guides, such as those developed for the tammar wallaby (*Macropus eugenii*) (Poole *et al.* 1991), red-tailed phascogale (Foster *et al.* 2006) and stripe-faced dunnart (*Sminthopsis macroura*) (Frigo and Woolley 1997). Once more fully developed, quoll species specific developmental charts can then be used to monitor the development and estimate the ages of young during routine monitoring both in captivity and in the wild and would provide a further mechanism for monitoring reproductive and translocation success.

Additional information on the factors affecting the likelihood of semelparity occurring in northern quolls would be advantageous to determine which individuals may breed in a subsequent year. More information on the factors affecting semelparity in the wild and captivity would support efforts to maintain genetic viability and diversity in all populations and be particularly beneficial for translocation programs where individuals with a range of ages may be released and may suggest which animals are the most likely to be able to successfully breed. Further information on bronze and New Guinea quoll reproduction and litter size would aid our understanding of the biology of these species.

Health and disease

Investigations have been made into haematology, blood biochemistry and morphology of blood cells. The haematology of western quolls, eastern quolls and northern quolls (Parsons *et al.* 1971*a*; Melrose *et al.* 1987; Schmitt *et al.* 1989; Svensson *et al.* 1998; Stannard *et al.* 2013*b*; Fancourt and Nicol 2019), blood biochemistry of western quolls, eastern quolls, spotted-tailed quolls and northern quolls (Parsons *et al.* 1971*b*; Parsons and Guiler 1972; Schmitt *et al.* 1989; Svensson *et al.* 1998; Stannard *et al.* 2013*b*; Fancourt and Nicol 2019), and the morphology of eastern quoll (Stannard *et al.* 2013*b*), spotted-tailed quoll, northern quoll and western quoll blood cells (Clark 2004) have been investigated.

Melrose *et al.* (1987) found very high haemoglobin and erythrocyte counts but low mean cell volumes in eastern quolls. Basophils were absent in eastern quolls, however eosinophils contained some basophilic granules (Melrose *et al.* 1987). Ring-form leucocytes were also commonly observed in eastern quolls (Melrose *et al.* 1987; Stannard *et al.* 2013*b*).

A study by Parsons and Guiler (1972) found many enzymes (except serum amylase) were higher in spotted-tailed quolls, compared with other marsupials and eutherians, especially serum acid phosphatase. Melrose *et al.* (1990) similarly described eastern quolls as having higher levels of phosphofructokinase, glyceraldehyde dehydrogenase and phosphoglycerate kinase, but lower levels of enolase and 2,3-diphosphoglycerate, compared with other marsupials; however, no reasons for these differences were attributed. Further studies have been conducted by Stannard *et al.* (2013*b*) on eastern quolls and found serum enzymes differed based on season. Alkaline phosphatase activity also varied according to age (Stannard *et al.* 2013*b*). Likewise, Fancourt and Nicol (2019) found significant differences in free-ranging eastern quolls, particularly in serum biochemistry, between the sexes in different seasons and ages. Schmitt *et al.* (1989) also found northern quolls had reduced haematocrit and plasma albumin (in males only), and reduced numbers of leucocytes but higher levels of haemoglobin and cortisol in both sexes during the dry season, which coincided with the timing of post-mating male semelparity.

One recent study has validated stress hormones in relation to field capture and transfer of western quolls into captivity (Jensen *et al.* 2019). This newly developed non-invasive monitoring tool can now be used by managers to monitor the success of western quoll translocations into the field. Furthermore, it will aid translocation management decisions when choosing individual quolls for translocation, as decisions can now be based on measurements of stress for each individual quoll held in captivity. Non-invasive routine monitoring of stress levels in captive western quolls will also benefit their health, welfare and potentially reproductive output whilst held in captivity. Further development and validation of this technique is required before it could be utilised to monitor stress levels in other quolls, as the technique is species specific.

Quolls presumably have similar rates of cancers to that observed in other dasyurids and marsupials (Attwood and Woolley 1973; Munday 1978; Straube and Callinan 1980; Canfield *et al.* 1990; Stannard and Old 2014). In general, Dasyurids have been noted as particularly susceptible to development of neoplasms. Twin and Pearse (1986) have described a mammary carcinoma and a malignant mixed salivary tumour in a wild eastern quoll. A range of other cancers have been described in quolls, and the reader is referred to Canfield *et al.* (1990) for more specific details and a summary of those types identified.

Recent studies on Groote Eylandt have found high levels of Mn (from mining on the island) in northern quoll hair, testes and brains, presumably impairing reproductive and neurological functions as observed in other species (Amir Abdul Nasir *et al.* 2018). Further studies are required to confirm if these high levels of Mn are impacting the quoll population.

A limited number of studies have investigated parasites of quolls (see Table 4). Toxoplasmosis has been identified in western quolls (Haigh *et al.* 1994; Parameswaran 2008), spotted-tailed quolls (Hollings *et al.* 2013) and eastern quolls (Hollings *et al.* 2013; Fancourt *et al.* 2014), whereas a small number of additional spotted-tailed and northern quolls investigated were not seropositive (Smith and Munday 1965; Oakwood and Pritchard 1999). Fancourt *et al.* (2014) investigated the link between toxoplasmosis seroprevalence and reduced reproduction or survival in eastern quolls and found despite high prevalence in some populations that toxoplasmosis appeared to have little to no impact.

The presence of trypanosomes have been investigated in western quolls but were absent in 18 blood samples from wild-caught specimens (Paparini *et al.* 2011). However, trypanosomes have been reported in western quolls previously (Smith *et al.* 2008), as well as spotted-tailed quoll (Botero *et al.* 2013). Botero *et al.* (2013) identified trypanosome isolates from spotted-tailed quolls using molecular techniques and found they were closely related to *T. copemani* and *T. gilletti*. One further endoparasite has been described in quolls. Trichinella has been identified in spotted-tailed quolls and eastern quolls (Obendorf *et al.* 1990).

Fleas have been identified on quolls and include *Uropsylla tasmanica*, *Xenopsylla vexabilis*, *Acanthopsyllidae rothschildi rothschildi*, *Psgiopsylla hoplia*, *Stephanocircus dasyuri* and *Stephanocircus harrisoni* (Dunnet and Nardon 1974; Obendorf 1993; Oakwood and Spratt 2000; Vilcins *et al.* 2008). *Uropsylla tasmanica*, found on spotted-tailed quolls, is the only flea species with a larval stage that burrows into the skin of its host, and therefore is also endoparasitic (Williams 1986; Obendorf 1993; Vilcins *et al.* 2008).

Lice have been identified on northern quolls (Schmitt *et al.* 1989). Semelparous males were described as heavily infected with *Boopia uncinata* compared with non-semelparous males and females (Schmitt *et al.* 1989).

Acari (ticks and mites) have been found on quolls. Ticks observed on quolls include *Ixodes fecialis* on western quolls, eastern quolls and spotted-tailed quolls, *Ixodes tasmani* on eastern quoll and spotted-tailed quolls, *Ixodes holocyclus* and an *Ixodes* (*Sternalixoes*) sp. nymph on the spotted-tailed quoll, *Ixodes antechini* on the eastern quoll and *Haemaphysalis humerosa* on the northern quoll (Roberts 1970; Vilcins *et al.* 2008). The common marsupial tick (*Ixodes tasmani*), *I. fecialis*, paralysis tick (*I. holocyclus*) and *H. humerosa* have been associated with various hosts, however *I. antechini* appears more restricted in its host range and mostly associated with dasyurid hosts (Roberts 1970). The mites *Dasyurochirus* nr. *major*, *Labidopygus australiensis*, *Myocoptes musculinus*, two species of trombiculid mite, and demodectic mites, have been identified on spotted-tailed quolls (Fain and Domrow 1972; Holz 2008; Vilcins *et al.* 2008; Nutting and Woolley 2009).

Although disease and parasites have been investigated in some quoll species, the impact of these diseases and parasites on the wider populations is largely unknown. Given quolls are mostly threatened or endangered, diseases and parasites may present an emerging threat to quoll conservation, especially with the advent of climate change, where parasites and disease prevalence are expected to increase (Dantas-Torres 2015; Short *et al.* 2017). Furthermore, quolls in captivity can be monitored for disease threats and treated regularly to reduce parasite loads, thus enhancing immunological fitness. However, during translocation quolls are likely to be re-introduced to potential disease and parasite threats, and the stress induced due to translocation may further enhance these threats. Gaining further knowledge of quoll immunity, host-pathogen and host-parasite interactions, and the times and situations when quoll hosts may be more susceptible to these threats will enhance the success of translocations in the longer term.

Conclusions and future directions

Recovery programs for some species of Australian quolls have been relatively successful with increases in population numbers and releases into areas of their former range. Further success of these programs may see conservation statuses downgraded, as has occurred for the western quoll. However, translocations often require rigorous monitoring and actions to prevent loss of individuals post-release, ongoing predator control, and possibly implementation of other threat mitigation strategies. Furthermore, they are heavily reliant on funding and cooperation from a range of agencies including zoological and wildlife parks, national parks and other non-government organisations. Recovery programs for other quoll species will likely require similar resources. Reintroductions onto islands where they were formerly distributed may also be beneficial in creating further wild insurance populations as suggested in Legge *et al.* (2018).

Overall success of reintroduction and translocation programs are also heavily reliant on gaining a good understanding of the biology of the species involved, and often includes successfully breeding and maintaining captive populations of the species pre-release. Successful *ex-situ* breeding relies on providing nutritionally appropriate diets. Diet choice in quolls is influenced by age and breeding season, whilst energy requirements double during late lactation for females. Hence it is likely that changes

Table 4. Parasites of quolls

Parasite	Quoll species	Reference
	Endoparasites	
Toxoplasmosis gondii	Western	Haigh *et al.* (1994); Parameswaran (2008)
	Spotted-tailed	Hollings *et al.* (2013)
	Eastern	Hollings *et al.* (2013); Fancourt *et al.* (2014)
Trypanosomes	Western	Smith *et al.* (2008)
	Spotted-tailed	Botero *et al.* (2013)
Trichinella	Spotted-tailed	Obendorf *et al.* (1990)
	Eastern	Obendorf *et al.* (1990)
Nematoda		
Baylisascaris tasmaniensis	Spotted-tailed	Green and Scarborough (1990)
	Ectoparasites	
Fleas		
Uropsylla tasmanica	Spotted-tailed	Williams (1986); Obendorf (1993); Vilcins *et al.* (2008)
Xenopsylla vexabilis	Spotted-tailed	Obendorf (1993); Oakwood and Spratt (2000)
Acanthopsyllidae rothschildi	Spotted-tailed	Dunnet and Nardon (1974); Obendorf (1993); Oakwood and Spratt (2000); Vilcins *et al.* (2008)
Pygiopsylla zethi	Spotted-tailed	Vilcins *et al.* (2008)
Psgiopsylla hoplia	Spotted-tailed	Dunnet and Nardon (1974)
Stephanocircus dasyuri	Spotted-tailed	Dunnet and Nardon (1974); Vilcins *et al.* (2008)
Stephanocircus simsoni	Spotted-tailed	Dunnet and Nardon (1974)
Stephanocircus harrisoni	Spotted-tailed	Vilcins *et al.* (2008)
Lice		
Boopia uncinata	Northern	Schmitt *et al.* (1989)
Ticks		
Ixodes fecialis	Western	Roberts (1970)
	Spotted-tailed	Roberts (1970)
	Eastern	Roberts (1970)
Ixodes fecialis	Western	Roberts (1970)
	Spotted-tailed	Roberts (1970)
Ixodes tasmani	Eastern	Roberts (1970)
	Spotted-tailed	Roberts (1970); Vilcins *et al.* (2008)
	Eastern	Roberts (1970); Vilcins *et al.* (2008)
Ixodes holocyclus	Spotted-tailed	Roberts (1970); Vilcins *et al.* (2008)
Ixodes (*Sternalixoes*) sp. nymph	Spotted-tailed	Roberts (1970); Vilcins *et al.* (2008)
Ixodes antechini.	Eastern	Roberts (1970); Vilcins *et al.* (2008)
Haemaphysalis humerosa	Northern	Roberts (1970)
Mites		
Dasyurochirus nr. *major*	Spotted-tailed	Fain and Domrow (1972); Holz (2008); Vilcins *et al.* (2008); Nutting and Woolley (2009)
Labidopygus australiensis	Spotted-tailed	Fain and Domrow (1972); Holz (2008); Vilcins *et al.* (2008); Nutting and Woolley (2009)
Myocoptes musculinus	Spotted-tailed	Fain and Domrow (1972); Holz (2008); Vilcins *et al.* (2008); Nutting and Woolley (2009)
Neotrombicula novaehollandiae	Spotted-tailed Eastern	Domrow and Lester (1985)

need to occur in captive diet regimes that correspond with the life history events to ensure quolls in *ex-situ* breeding populations are healthy and meeting their nutrient requirements. It is possible there are other notable changes in nutrient requirements over the lifetime of a quoll (e.g. difference in young versus old animals), however more data is required to determine the significance of these changes and how to incorporate them into captive dietary regimes.

Baseline blood data is available for some species of quoll and can be used to assess levels of health in these species in captivity, in translocations programs and in wild free-ranging populations. The data has shown that parameters such as alkaline phosphatase as well as other serum enzymes are affected by season, age, sex and hence must be taken into account when monitoring health of individuals. Other methods of assessing health and welfare in captivity should be investigated to aid management of the species, and include the documentation and development of growth charts, continued documentation and investigation of parasites, and aspects of health and disease such as the impacts of stress and semelparity on reproductive outputs.

Conflicts of interest

The authors declare no conflicts of interest.

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