REVIEW PAPER



Threats to Australia's rock-wallabies (*Petrogale* spp.) with key directions for effective monitoring

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Abstract

Rock-wallabies (Petrogale spp.) are one of Australia's most speciose genera of mammals, irregularly distributed across much of the continent and its offshore islands. The 25 taxa in the genus Petrogale (17 species and 8 subspecies) have specialised ecological requirements that render them vulnerable to numerous threats. Many rock-wallaby populations have declined severely, and most species and subspecies are experiencing ongoing declines in population size, distribution and their conservation status. Despite an explicit recognition of the need for conservation management, some species are not monitored and a consensus on the most appropriate methods for ongoing population monitoring has proven elusive. We reviewed the available literature to understand the conservation issues and threats most relevant to Petrogale spp. We also reviewed rock-wallaby monitoring programs with the aim of identifying which are most informative of population trends, and most suitable for guiding better management responses. Major threats to rock-wallabies include predation by introduced cats and foxes, competition from introduced herbivores and overabundant native herbivores, changed fire regimes and loss of genetic diversity. There are synergisms that exacerbate these threats. While live-trapping gives comprehensive population data, camera traps have proven popular for collecting data over long periods, have minimal animal welfare impacts, and can simultaneously collect data on some significant cooccurring threats (feral predators and herbivores). A variety of rock-wallaby monitoring programs are current in Australia, but few adequately provide the range of data necessary for informed conservation. Monitoring programs should consider incorporating multiple methods to ensure the range of information necessary for successfully conserving rockwallabies is obtained.

Keywords Competition · Decline · Extinct · Mammal · Predator · Survey

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Introduction

Australia's terrestrial mammal fauna is the world's most distinctive (Holt et al. 2013). Persistent isolation from other land masses has helped generate extraordinary levels of endemism, with approximately 87% of species found only on the continent (Woinarski et al. 2014). Linked with this isolation and endemism are inherent vulnerabilities to a range of novel threats (Woinarski et al. 2015). A significant proportion of species have declined since European colonisation and approximately one-third of global mammal extinctions over the past 400 years have occurred in Australia (Woinarski et al. 2015). This nationwide deterioration of biodiversity is ongoing (Woinarski et al. 2015) and occurring against a backdrop of inadequate monitoring of threatened species, meaning the declines of many species remain poorly quantified (Scheele et al. 2019).

Among the most speciose of Australia's endemic mammal radiations are the rock-wallables (Petrogale spp.), a group of 25 taxa (17 species and 8 subspecies) broadly distributed across the continent (Eldridge et al. 2010; Potter et al. 2014) (Fig. 1a). Most species are allopatric and have restricted geographic ranges (Eldridge 2008). Rock-wallabies have unique morphological, ecological and behavioural adaptations tailored towards exploiting rocky outcrops that make them spatially restricted within broader distributions (Eldridge 2008). They are also relatively sedentary with limited daily ranging movements (Eldridge et al. 2001; Piggott et al. 2005). These traits of specialised ecology, and restricted ranges are frequently associated with vulnerability to decline and extinction (Gaston 1998). Although no extinctions of rock-wallabies have been documented since European colonisation, many taxa within the group face significant threats and are declining in distribution and abundance (Woinarski et al. 2014). Of 16 species whose conservation status has been assessed by the International Union for Conservation of Nature (IUCN), five are currently considered Least Concern, five as Near Threatened, three as Vulnerable and three as Endangered (Table 1). Population trend information given in the IUCN Red List (IUCN 2020) indicates that no species are considered to be increasing, only two species are considered stable, seven species are undergoing continuing decline and seven species have unknown trends. This is indicative of a lack of, or inadequate, monitoring for many of the taxa, and the need for ongoing conservation management intervention coupled with assessments of the success of such management.

Declines and extinctions among Australia's modern mammals generally commenced in the south, reaching the north by the 1960s and somewhat coinciding with the expansion of feral predators and pastoralism, and interruption of Indigenous land management (Woinarski et al. 2011, 2015). Among rock-wallabies, McCallum (1997) suggested there was a north–south gradient in the status of rock-wallabies with southern species and populations under threat, while northern taxa were secure. However, ongoing revisions of taxonomy and conservation status have meant this pattern no longer holds. Six of seven species or subspecies now listed as Endangered or Critically Endangered under the Federal *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) occur in northern Australia (*P. coenensis, P. concinna concinna, P. concinna canescens, P. concinna monastria. P. lateralis kimberleyensis* and *P. persephone*) (Fig. 1b, Table 1). Almost all southern and central Australian taxa are Vulnerable, but so is one northern taxon (*P. sharmani*) (Fig. 1b, Table 1).

Rock-wallabies are a subject of ongoing scientific interest (Eldridge 2011). Their conservation hinges on many of the same factors pertinent to the broader Australian mammal fauna (Woinarski et al. 2014, 2015). However, the specialised ecology of rock-wallabies means that threats may interact and affect rock-wallabies in unique ways (Pearson and Kinnear 1997). Conversely, the rugged nature of their habitat ameliorates some threats (e.g. protection from

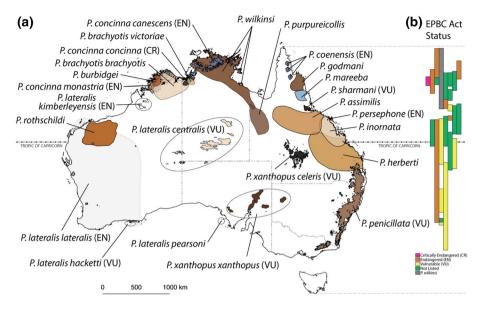


Fig. 1 a Distributions of 25 *Petrogale* taxa (17 species and 8 subspecies), in Australia. The dotted line surrounding light grey shading in the west of the map encompasses all scattered populations of *P. lateralis lateralis*; **b** north–south distributions of *Petrogale* taxa EPBC Act conservation status. Each of the 25 bars represents the approximate latitudinal distribution of a distinct species or subspecies; pink=Critically Endangered (CR), orange=Endangered (EN), yellow=Vulnerable (VU), green=not listed, grey=recently recognised *P. wilkinsi*. Distributional data were generated from Potter et al. (2014), Commonwealth of Australia (2020), and IUCN (2020).

intense late season fires, reduced grazing pressure from livestock) that have led to losses of native mammal species in surrounding less rugged areas (Gibson and Cole 1996).

There has been a long and prominent history of monitoring of some rock-wallaby species as a key mechanism to demonstrate the outcomes of threat management, particularly control of a main predator, the introduced red fox *Vulpes vulpes* (Kinnear et al. 1988, 1998, 2010; Sharp et al. 2014). The evidence built on such monitoring of conservation success has led to long-term and large-scale fox-baiting programs.

Ongoing taxonomic revisions (Potter et al. 2014; Eldridge and Potter 2019), and the declining conservation status for *Petrogale* spp., warrant an examination of the available literature to summarise current knowledge and identify gaps in conservation actions and monitoring. Furthermore, we aimed to review which monitoring methods have been most effective for determining changes in their conservation status, so rock-wallaby populations can best be tracked to avoid further declines.

Methods

We used Web of Science, Scopus and Google Scholar search engines to identify publications focused on ecology, genetics, conservation and monitoring of *Petrogale* taxa. Using the search terms 'Petrogale' and 'rock-wallaby', we identified relevant literature published between 1960 and 2020 (March). We searched reference lists of primary sources, and viewed materials citing primary and secondary sources. Duplicates were removed in R (R

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Table 1

Taxon	Common name	EPBC Act 1999	IUCN red list
Petrogale assimilis	Allied rock-wallaby	1	LC
Petrogale brachyotis brachyotis	Short-eared rock-wallaby (Kimberley)	I	LC
Petrogale brachyotis victoriae	Short-eared rock-wallaby (Victoria River District)	I	
Petrogale burbidgei	Monjon	I	NT
Petrogale coenensis	Cape York rock-wallaby	EN	EN
Petrogale concinna concinna	Nabarlek (Victoria River District)	CR	EN
Petrogale concinna canescens	Nabarlek (Top End)	EN	
Petrogale concinna monastria	Nabarlek (Kimberley)	EN	
Petrogale godmani	Godman's rock-wallaby	I	NT
Petrogale herberti	Herbert's rock-wallaby	I	LC
Petrogale inornata	Unadorned rock-wallaby	I	LC
Petrogale lateralis lateralis	Black-flanked rock-wallaby, Moororong, Black-footed rock-wallaby	EN	ΛΩ
Petrogale lateralis hacketti	Recherche rock-wallaby	ΝŪ	
Petrogale lateralis pearsoni	Pearson Island rock-wallaby	I	
Petrogale lateralis centralis	Warru, central Australian rock-wallaby	VU	
Petrogale lateralis kimberleyensis	Wiliji, West Kimberley rock-wallaby	EN	
Petrogale mareeba	Mareeba rock-wallaby	I	TN
Petrogale penicillata	Brush-tailed rock-wallaby	VU	ΝU
Petrogale persephone	Proserpine rock-wallaby	EN	EN
Petrogale purpureicollis	Purple-necked rock-wallaby	I	NT
Petrogale rothschildi	Rothschild's rock-wallaby	1	LC
Petrogale sharmani	Mount Claro rock-wallaby, Sharman's rock-wallaby	ΛU	ΝŪ
Petrogale wilkinsi	Wilkins's rock-wallaby, Eastern short-eared rock-wallaby	I	I
Petrogale xanthopus xanthopus	Yellow-footed rock-wallaby (SA and NSW)	ΛŪ	NT
Petrogale xanthopus celeris	Yellow-footed rock-wallaby (central-western Queensland)	VU	

4141

Core Team 2018) using *revtools* (Westgate 2019). We then screened results for eligibility by manually examining titles and abstracts and eliminating literature focused solely on parasitology, anatomy, palaeontology, genetic sequencing methods, animal husbandry, and introduced populations in Hawaii and New Zealand. Results included articles published as peer reviewed papers, books, and grey literature.

We manually classified the primary and secondary research foci of each publication in our final list into topics corresponding to: ecology (behaviour, diet, distribution, habitat and habitat modelling, home range, reproduction); conservation (conservation status, management, recovery planning, reintroduction, threats, and translocation); genetics (population, ecological and evolutionary genetics, systematics and taxonomy, phylogeography); and monitoring (methods for establishing presence-absence, and estimating abundance).

Results

Our database searches located 611 papers. We excluded 264 papers because they were not directly focussed on *Petrogale* spp. or because they were focussed on topics outside the focus of this review (e.g. parasitology and animal husbandry). After applying filters, our final dataset contained 344 papers. The primary research foci of these were ecology (145), conservation (115), genetics (69) and monitoring (16) (Fig. 2). Studies focused on a single species were strongly biased towards three species: *Petrogale lateralis* (77); *P. penicillata* (95); and *P. xanthopus* (53) (Fig. 2). Eleven of 25 taxa had been the primary research foci in only four or fewer publications (Fig. 2). One species (*P. godmani*) featured in phylogenetic publications that focused on multiple *Petrogale* taxa; however, we were unable to locate any publications that were explicitly focused on this species.

Threats

Fifty papers in our literature review included a detailed focus on threats to rock-wallaby conservation. Key threats identified were: predation by introduced predators (foxes *Vulpes*, *vulpes*, and cats *Felis catus*); competition from over-abundant introduced herbivores (e.g. *Capra aegagrus hircus*) and native herbivores (e.g. *Osphranter robustus*); reduced genetic diversity; and unsuitable fire regimes.

Predation

Predation by foxes and cats is a leading driver of extinction and decline in Australian mammals (Woinarski et al. 2015). Our literature review revealed 121 papers with mention of foxes and/or cats as a major threat for rock-wallabies. Across southern parts of Australia where foxes were reportedly most common, they were considered to be the primary threat to rock-wallabies and numerous studies clearly demonstrated their impacts (Kinnear et al. 1988; McCallum 1997; Pearson and Kinnear 1997; Sharp 2002; Pearson 2013). In the Western Australian Wheatbelt region, foxes were responsible for the extirpation of *P. lateralis lateralis* colonies (Kinnear et al. 1988) and have caused a 'landscape of fear' in surviving populations that limits foraging distances from shelter (Pentland 2014). Sighting ratios of Rothschild's rock-wallaby on islands without foxes and those with foxes were 62:1, and after fox control, sightings increased by almost 26 times (Kinnear et al. 2002). In the Coturaundee and Gap Ranges, New South Wales, foxes were baited around *P. xanthopus*

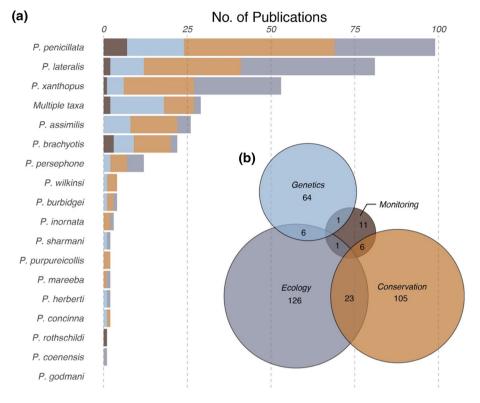


Fig. 2 Rock-wallaby publications and topics of study: a divided into the primary topics of genetics, ecology, conservation and monitoring per species; and b Venn diagram depicting overall research focus for literature included in the review. Circles depict primary research topics, and overlaps represent secondary topics that are shared between primary topics

xanthopus colonies between 1995 and 1998. Subsequent monitoring revealed that populations of rock-wallabies increased by an estimated 600% after baiting before plateauing in 1998 (Sharp 2002).

Feral cats pose a well recognised predation threat to Australian mammals including rock-wallabies (Woinarski et al. 2015). In more southern parts of Australia, fox baiting can release cats from competition and enable them to become a primary driver of rock-wallaby decline (Kinnear et al. 2017). Numerous studies have documented predation of *Petrogale* spp. by feral cats (Woolley et al. 2019). Hair from *P. lateralis centralis* was recorded in the stomach of a feral cat in the Northern Territory's West MacDonnell Ranges (Paltridge et al. 1997). In the Anangu Pitjantjatjara Yankunytjatjara Lands in arid Central Australia, a feral cat was shot at the carcass of a freshly killed *P. lateralis centralis* and remains were found in the stomachs of another four individuals (Read et al. 2018). The authors postulated these were examples of cats directly preying on rock-wallabies during a season of food stress, rather than scavenging carrion (Read et al. 2018). Evidence of predation by feral cats on rock-wallabies also has been documented for *P. assimilis* (Spencer 1991), *P. persephone* (Eldridge 2012), *P. rothschildi* (Anderson et al. 2021), and inferred for *P. penicillata* (Doherty et al. 2015). Woolley et al. (2019) incorporated published and unpublished records of cat predation or consumption on *P. purpureicollis, P. rothschildi*, and *P.*

xanthopus. Using camera traps, the Northern Territory Government's Department of Environment and Natural Resources recorded images of a cat killing an adult eastern shorteared rock-wallaby (*P. wilkinsi*, mean adult body mass 3 kg) (Dahlstrom 2019).

The predation pressure on young rock-wallabies that disrupts recruitment appears to be the key mechanism that drives declines (Spencer 1991; Sharp et al. 2006, 2014; Ward et al. 2011a). For example, in New South Wales, low population sizes of *P. xanthopus xanthopus* were attributed to low juvenile survival rates, and following fox baiting, a marked increase in the proportion of juveniles and subadults occurred (Sharp et al. 2014). In South Australia's Anangu Pitjantjatjara Yankunytjatjara Lands where foxes are rare, cats were believed to be the cause of similar low juvenile survival (51%) and an estimated 88% range contraction (Ward et al. 2011a, b; Read et al. 2018). In tropical north Queensland, Spencer 1991 collected evidence indicating a single cat had killed eight *Petrogale assimilis* over a 9-month period. The animal was a significant predator on young rock-wallabies, killing five of 11 young at foot present in the colony.

To the best of our knowledge, the impact of dingoes or wild dogs on rock-wallaby populations has not been specifically studied and is little understood. A review of dingo diets (Doherty et al. 2019) found that at least seven species of rock-wallabies were consumed. In desert areas with no wild dog control, dingoes are potentially major predators of rockwallabies. For example, Ngaanyatjarra people have identified dingoes as significant predators of *P. lateralis centralis* in the Warburton region of Western Australia (Pearson and Ngaanyatjarra Council 1997). However, at least in northern Australia, dingoes occur far less frequently in rugged rocky areas (such as those favoured by rock-wallabies) than in areas with less rugged topography (Stobo-Wilson et al. 2020).

Maintaining dingo populations has been suggested as a means of limiting fox and feral cat populations (and hence predation of rock-wallabies) by avoiding meso-predator release (Finke and Denno 2004). However, any control that dingoes may exert has been insufficient to prevent widespread disappearance of desert rock-wallaby populations (Pearson 1992; Pearson and Ngaanyatjarra Council 1997). The use of the Eradicat 1080 bait (Algar and Burrows 2004) designed for feral cats, has resulted in effective control of feral cats, dingoes and foxes in the Calvert Ranges of Western Australia and this resulted in a dramatic increase in the size of the *P. lateralis lateralis* population (McGilvray and Kendrick 2012, A. Whittington, pers. comm.). The overall predation pressure from exotic, naturalised and native predators needs to be considered in management actions, especially for small and isolated populations of rock-wallabies that are more prone to extinction.

Competition

We identified 27 papers that considered the role of competition from introduced or native herbivores as a significant threat for Australia's rock-wallabies. The availability of foraging resources can exert strong bottom-up effects on *Petrogale* spp. populations (Lethbridge and Alexander 2008; Sharp and McCallum 2014). Competition for these resources with introduced herbivores such as feral goats (*Capra hircus*), European rabbits (*Oryctolagus cunic-ulus*), cattle (*Bos taurus*, *B. indicus*), donkeys (*Equus asinus*), horses (*E. equus*) and camels (*Camelus dromedarius*) thus represents a potential threat to rock-wallabies (Read and Ward 2011). Feral goats are the most frequently recognised threat in this context because they frequent rocky habitats and have high dietary overlap with species of *Petrogale*. (Dawson and Ellis 1979; Allen 2001; Sharp and McCallum 2014; Creese et al. 2019). However, direct evidence of their influence on rock-wallaby populations remains poorly documented.

Extensive goat control over a fifteen-year period in New South Wales failed to influence populations of *P. xanthopus xanthopus* (Sharp et al. 1999), although this may have been because the removal of thousands of individuals during that period resulted in no detectable decrease in goat numbers (Sharp et al. 1999; Sharp and McCallum 2014). A study of *P. xanthopus xanthopus* movements in the Flinders Ranges found that following the control of foxes and goats, wallaby home ranges decreased in size and this was attributed to the reduction in competition (Hayward et al. 2011).

Goats often shelter in rocky habitats by night and by day venture out to feed in the adjacent lowlands (Sharp and McCallum 2014). These grazing patterns can lead to the formation of grazing halos around rocky habitats, where the intensity of resource consumption increases with proximity to rock-wallaby colonies (Sharp and McCallum 2014). Rocky outcrops similarly provide ideal locations in which rabbits shelter, and build warrens, that presumably also leads to reduced forage around colonies of rock-wallabies (Read and Ward 2010).

Overabundant native macropods also have impacts on rock-wallaby colonies. Euros (*Osphranter robustus*) in particular, can reach high densities in pastoral landscapes adjoining rock-wallaby habitat (Lavery et al. 2017). Although they are not spatially restricted to escarpments like rock-wallabies, euros increase in abundance with increasing proximity to these features (Sharp and McCallum 2014; Lavery et al. 2017). Dietary overlap between euros and *P. lateralis lateralis* was found to be low compared to goats and rock-wallabies, but probably increases when food resources are limited (Creese et al. 2019). During times of food stress, rock-wallabies are likely to be at a significant disadvantage because, unlike euros, they are less able to exploit extensive lowland habitats and must withstand increased competition for nutritious plants in the escarpments (Sharp and McCallum 2014). Ultimately, competition from native and introduced herbivores can reduce the fitness of adult rock-wallabies and their ability to successfully rear young (Sharp and McCallum 2014).

Fire

Alterations to Indigenous burning regimes in Australia have caused widespread shifts from smaller scale patchwork burns to larger scale fires in some biomes, resulting in both direct and indirect impacts on native species (Legge et al. 2008; Woinarski et al. 2011). Studies on the specific short- and long-term consequences of altered fire regimes are generally lacking for rock-wallabies (Pearson 2013). In terms of direct consequences, instances where large-scale fires have caused direct mortality have been documented (e.g. *Petrogale lateralis hacketti*) (Pearson and Kinnear 1997; Pearson 2013; Piggott et al. 2018). Fires in Watagan State Forest, New South Wales also caused temporary abandonment of a *P. penicillata* colony which re-established several years later (DECC 2008). However, rock escarpments tend to interrupt the spread of bushfires and the heavily dissected rock structure can somewhat buffer rock-wallaby populations from direct mortality (Pearson 2013; Piggott et al. 2018).

Like many Australian mammals, fire probably has the greatest implications for rockwallaby conservation indirectly though changes to habitat structure and abundances of preferred plant food species rather than via direct mortality (Telfer & Bowman 2006; Woinarski et al. 2011, 2015; Tuft et al. 2012). Large fires burnt escarpment habitat for *P. lateralis kimberleyensis*, causing long-term damage to rock figs (*Ficus platypoda*) that provided important shelter and food to the species (Pearson 2013; WWF Australia & Nyikina Mangala Rangers 2018). Appropriate burn regimes were considered critical for conservation of *Petrogale concinna* and *P. wilkinsi* in the monsoon tropics of northen Australia by maintaining a diverse flora including fruit-bearing browse species, and encouraging pulses of resprouting grasses (Telfer and Bowman 2006). In Warrumbungle National Park, New South Wales fine-scale burns created patchworks of post-fire vegetation ages that optimised foraging resources for *P. penicillata* (Tuft et al. 2012).

Genetic diversity

Genetic processes such as inbreeding depression, genetic drift, and accumulation of deleterious mutations can increase extinction risk and become increasingly significant when population sizes decrease (Eldridge et al. 1999; Gaggiotti 2003). Many *Petrogale* spp. exist as metapopulations of geographically distinct colonies inter-connected via the occasional dispersal of individuals (Eldridge et al. 2001; Ruykys and Lancaster 2015). These metapopulation dynamics help avoid detrimental genetic processes, so the local extinction of colonies can have rippling implications for subspecies and species as a whole. Ruykys and Lancaster (2015) and West et al. (2018) examined genetic diversity of *P. lateralis centralis* in South Australia's Anangu Pitjantjatjara Yankunytjatjara Lands. The authors found little evidence of inbreeding among colonies, small-scale dispersal between colonies and large proportions of adults in the population producing offspring, all of which helped maintain high genetic diversity. When single colonies are isolated and are small, the loss of genetic diversity can be considerable. Eldridge et al. (1999) found *P. lateralis* colonies isolated on offshore islands (over time scales of thousands of years) comprised extremely low genetic diversity, and that this was likely to place them under significant risk of local extinction.

Interacting threats

Predation, competition, altered fires regimes, and reduced genetic diversity each independently threaten rock-wallabies to varying degrees across Australia. But these factors also frequently interact, generating compound impacts on *Petrogale* spp. populations (Pearson and Kinnear 1997; Pentland 2014).

There is evidence to suggest that rock-wallaby populations were formerly more widely distributed in the landscape, contracting to rocky area refuges following the arrival of threats associated with European colonization (Menkhorst 1995). The presence of rocky landscape features is now a prerequisite for the distribution of rock-wallables, but animals will nonetheless intermittently travel between outcrops and frequently venture out to forage in peripheral habitats (Pearson 1992; Jarman and Capararo 1997; Eldridge et al. 2001; Ward et al. 2011b). Foxes and cats focus their hunting efforts at the edges of colonies, and cat activity deep within rocky habitats is low (Hernandez-Santin et al. 2016; Hohnen et al. 2016; WWF Australia and Nyikina Mangala Rangers 2018). Under these landscapescale patterns of predation, wallabies reduce the risks of being killed by foraging closer to refuges and shelter points (Tuft et al. 2011; Pentland 2014). Reducing predation pressure through poison baiting can restore foraging beyond refuges (Sharp 2002; Kinnear et al. 2010). However, sustained exposure to predation risk can also instil a pervasive fear of predation that persists long after the threat has been reduced. Populations therefore remain confined to refuges and rarely expand into adjacent habitats (Pentland 2014; Kinnear et al. 2017).

Adjacent (non-rocky) habitats are important for providing additional resources to sustain healthy populations (Pearson 1992; Kinnear et al. 1998, 2017). At levels of

population saturation and during good seasons, individuals move out from outcrops into surrounding vacant habitat and also disperse between colonies thereby maintaining functional metapopulations (Norton et al. 2011). When confined solely to outcrops, rock-wallabies can severely overgraze, and their populations can then crash (Kinnear et al. 2017). High densities of rabbits can sustain higher densities of cats and foxes near the rock-wallaby refuges, thus increasing the threat of predation for rock-wallabies (Read and Bowen 2001). Where feral herbivores (goats, rabbits) denude vegetation, rock-wallabies an be forced to forage further afield further exacerbating predation (Dawson and Ellis 1979) (Fig. 3).

Appropriate fire regimes can promote plant resources that are favoured by rock-wallabies, but benefits can be negated by the foraging of native or introduced herbivores (Tuft et al. 2012). Large-scale uncontrolled wildfires can also increase predation by cats and foxes, which travel long distances to target prey in the recently burnt areas where refuges are scarce (McGregor et al. 2014; Hradsky et al. 2017). However, this may be less of an issue for species of rock-wallaby that can take some refuge in topographically complex habitats.

Locally abundant colonies can create false perceptions that the broader status of a species is secure (Pearson and Kinnear 1997). However, many colonies have been extirpated and some remain with precariously small populations (Lim and Giles 1987; Read and Ward 2010). Local extirpations and gradual and cumulative range contractions are significant because they weaken important metapopulation dynamics and compound the vulnerability of species to threatening processes (Lunney et al. 1997). Moreover, effective dispersal is central to the maintenance of genetic diversity, and reduced colony connectivity or colony extirpation can reduce long-term viability of species (Ruykys and Lancaster 2015; Piggott et al. 2018).

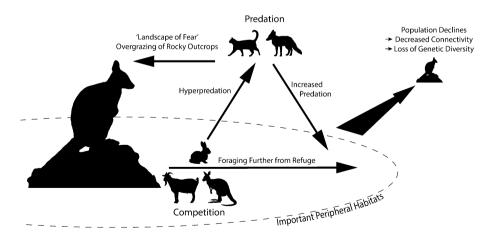


Fig. 3 Conceptual diagram of some of the interacting threats facing rock-wallabies. Introduced herbivores (rabbits) can support elevated populations of feral predators (cats and foxes). Competition (e.g. goats, rabbits, euros) can increase the need to forage further from refuge, increasing exposure to predation. Population declines and losses of colonies impact metapopulation dynamics to the detriment of species persistence. Predators can create a landscape of fear that cause rock-wallabies to remain among rocky outcrops. Predator control can lead to increased rock-wallaby numbers and overgrazing of rocky refugia

Monitoring

We identified 16 papers with a primary or secondary focus on monitoring. The majority of monitoring efforts have been directed towards three species (*P. lateralis, P. penicillata*, and *P. xanthopus*) that most often exist as discrete, localised colonies across well-defined extents of habitat. As a result, our review of methods used in rock-wallaby monitoring reflect approaches most relevant for these discrete and localised colonies. Many of the rock-wallaby species and subspecies found in northern Australia instead occur with no apparent habitat discontinuity, and this consideration is likely to influence the effectiveness of the measures discussed.

Our review identified direct counts, camera traps, mark-recapture, faecal pellet counts and faecal DNA analysis as methods employed to monitor rock-wallaby populations (Table 2). Nocturnal behaviour and the predilection of rock-wallabies towards remote, steep and rugged terrain can mean they are difficult to observe directly and obtaining estimates of population size and trends can be extremely challenging (Norton et al. 2011). As a result, the methods and standards of *Petrogale* spp. monitoring have been highly variable.

Direct counts

Ten studies used variations of directly counting individuals as a method to monitor populations. Burbidge (2008) compared direct count methods for estimating relative abundance (daytime searches of shelters, dusk observations, and nocturnal spotlight transects). Dusk observations and spotlight surveys were deemed inadequate because estimated numbers were markedly lower than the results of daytime searches. Moreover, spatial coverage achieved with dusk observations and spotlight surveys was limited. Daytime shelter searches provided more accurate abundance estimates but the method was problematic in that it disturbed resting animals, was difficult to standardise, there was high likelihood that individuals were regularly missed, and results were thus highly variable. The ability of this method to detect population changes was uncertain (Burbidge 2008).

Sharp et al. (2006) and Norton et al. (2011) made direct counts from a hide located at distance from a *P. xanthopus xanthopus* colony in New South Wales. Animals were counted during a one-hour period following dawn to take advantage of wallabies sunning themselves on exposed ledges after cold winter nights. Maximum daily counts were averaged across winter surveys to derive a mean number of wallabies seen each season. Comparisons with population estimates made using mark-recapture and Jolly-Seber modelling indicated this technique for direct counts provided a suitable index of population size (Sharp et al. 2006). However, spatial coverage was an issue and individuals moving out beyond the main colony into surrounding habitat were inadvertently missed leading to underestimates of total population size (Norton et al. 2011).

Aerial counts from helicopters have been used to monitor population trends of *P. penicillata* and *P. xanthopus xanthopus* (Lim et al. 1992; Sharp et al. 1999). Depending on the location, aerial surveys can be more cost effective than ground-based techniques, and negate problems associated with the inaccessible country in which rock-wallabies are found (Lethbridge and Alexander 2008). However, aerial detectability of rock-wallabies can vary widely with vegetation cover, observer experience, time of day, aircraft height and speed, and habitat type (Caughley 1974; Lethbridge and Alexander 2008). Diurnal aerial surveys invariably miss a substantial proportion of these primarily nocturnal species that shelter

Method Direct counts	Variation	Droc	Cone	Framnles
Direct counts		F105	COILS	глашриса
	Daytime transects/searches of shelters (Most suitable for presence- absence)	Estimates of abundance were more accurate than those obtained from dusk observations and spotlight surveys	Challenging over rough terrain Difficult to standardize spatially and temporally Individuals are regularly missed Results remain inconsistent compared to methods such as mark-recapture	(Burbidge 2008)
	Dusk stationary observations (Most suitable for presence- absence)	1	Estimates significantly lower than daytime searches Low spatial coverage	(Burbidge 2008)
	Stationary counts from hides (dawn) Good relative abundance index— (Most suitable for presence- absence) ture and Jolly–Seber modelling ture and Jolly–Seber modelling	Good relative abundance index— estimates similar to mark-recap- ture and Jolly–Seber modelling	Low spatial coverage Estimates low compared to aerial counts because of spatial coverage Less suitable for absolute abun- dance estimates—population estimates lower than those from Jolly–Seber modelling	(Sharp et al. 2006; Norton et al. 2011)
	Spotlight surveys (Most suitable for presence- absence)	Petrogale spp. are nocturnal and animals are likely to be more active during this period	Estimates significantly lower than the for daytime searches Low spatial coverage	(Burbidge 2008)
	Aerial counts (Suited for population estimates)	Can be very cost effective depend- ing on proximities to aircraft bases Negates problems associated with the inaccessible rocky country	Detectability can vary widely with habitat type, vegetation cover, observer experience, time of day, aircraft height and speed Underestimates likely where rock- wallabies take shelter in response to aircraft noise before being detected Occupational Health and Safety concerns associated with operat- ting aircraft in complex rocky thororranhies	(Lethbridge and Alexander 2008; Lim et al. 1992; Sharp et al. 1999; Lim and Giles 1987)

Table 2 (continued)	(
Method	Variation	Pros	Cons	Examples
Mark recapture	Trapping (Suited for population estimates)	Robust population estimates Valuable demographic, health, dis- ease and morphological data, and DNA samples can be collected	Animal welfare risk from capture myopathy Trapping rates highly variable between species and sites, and success at a single site can be vary between individuals and across time periods Labour intensive, considerable trap- ping effort often required	(Robinson et al. 1994; Sharp et al. 2006; Sharp and McCallum 2010; Bluff et al. 2011)
	Observation of natural markings (Suited for population estimates)	Robust population estimates using Schumacher method and Schnabel method	Schumacher and Schnabel estimates (Vernes et al. 2011) assume a closed population and are less suitable for long-term monitoring In complex habitats, animal identi- fication can be difficult leading to inaccurate estimates may not be applicable for species with relatively little colour pat- terning Low spatial coverage	(Vernes et al. 2011)

Table 2 (continued)				
Method	Variation	Pros	Cons	Examples
Camera traps	Motion activated transects (Most often used for presence- absence)	Can be deployed over extended periods Data on extent of threats from intro- duced predators and herbivores also captured Can generate useful understanding of temporal activity	Difficult to accurately estimate abundance without individual recognition Relative abundance indices vary between species, and can be inconsistent temporally and spatially Reduced detection when the ambi- ent temperature is similar to rock- wallaby body temperature Processing images is time consum- ing	(West et al. 2016; Bluff et al. 2011; WWF Australia and Nyikina Man- gala Rangers 2018)
	Time lapse photographs (Applicable for population esti- mates)	Accurately estimates colony size in certain situations Can generate useful understanding of temporal activity	Results variable Accurate estimates of minimum number known to be alive relies on all animals being photo- graphed at the same time Estimated number of individuals lower than estimates derived using SLR photography	(Gowen and Vernes 2014)
Faecal pellet counts	Fixed plots (Best suited to presence-absence)	Pellets easy to locate, identify, with long life-span on rocky substrates Can provide information on tempo- ral and spatial habitat use Efficient for determining presence across many potential sites	Difficult to estimate population size Establishing the date of animal presence is not possible without repeat sampling Rigid sampling periodicity or time calibration needed or misinterpre- tation of the data can occur	(Jarman and Capararo 1997; Telfer et al. 2006; Bluff et al. 2011; Nor- ton et al. 2011; Ward et al. 2011b)

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Table 2 (continued)	(]			
Method	Variation	Pros	Cons	Examples
Faecal DNA	(Not viable at present)	Can simultaneously provide data on Variability between individuals in demographics of colonies, genetic the quality or availability of faec diversity, metapopulation dynam-DNA DNA ics, and colony long-term viability Analysis of large numbers of samics, and colony long-term viability The success of trial studies for this method have not been success-fully repeated	Can simultaneously provide data on Variability between individuals in (Piggott et al. 2004, 2005, 2018) demographics of colonies, genetic the quality or availability of faecal diversity, metapopulation dynam- DNA DNA ics, and colony long-term viability Analysis of large numbers of samples can be costly The success of trial studies for this method have not been success-fully repeated	(Piggott et al. 2004, 2005, 2018)

during the day in caves and crevices. Moreover, the noise from helicopters can elicit a sheltering response in *P. penicillata* that may cause them to be missed in counts (NPWS 2002). To cater for these variables and the significant proportion of animals that can be missed, a correction factor is often applied to aerial surveys (e.g. × 4.6, Hayward et al. 2011).

Mark-recapture

Mark-recapture methods can provide robust means to monitor populations and estimate abundance (Krebs 1999). We identified nine studies that used this method of monitoring. For *Petrogale* spp., mark-recapture methods demand considerable effort to trap and mark animals with ear tags (Sharp et al. 2006; Sharp and McCallum 2010; Bluff et al. 2011; Willers et al. 2011), colour-coded collars (Robinson et al. 1994), or passive integrated transponder (PIT) tags (Bluff et al. 2011). There are important welfare considerations associated with trapping *Petrogale* spp. due to their risk of death from capture myopathy (Vogelnest and Woods 2008; West et al. 2016). Furthermore, mark-recapture studies of rock-wallabies can be complicated because of relatively low and highly variable rates of trapping success, and trap success may decline to impractical levels as population density diminishes. At two P. xanthopus xanthopus colonies in New South Wales success varied between 0.08 unmarked individuals per trap night at one colony, and 0.008 per trap night at a second colony (Norton et al. 2011). Approximately 0.006 unmarked individuals were caught per trap night at a small P. penicillata colony in Victoria (Bluff et al. 2011). Trapping of P. lateralis centralis at two sites in the Anangu Pitjantjatjara Yankunytjatjara Lands returned results of 0.06–0.15 new animals per trap night (Ward et al. 2011a).

Vernes et al. (2011) developed a mark-recapture protocol without the need to capture animals and generated accurate abundance estimates of P. penicillata. Rock shelter habitats were surveyed with SLR cameras, binoculars and spotting scopes. Wallabies were photographed and sketched, and natural markings such as colour patterns and scars were used to develop individual animal profiles. The method enabled identification of 91.7% of wallaby sightings and generated consistent population estimates using Schumacher and Schnabel method (Krebs 1999), and counts of minimum number of animals known to be alive (Vernes et al. 2011). Estimating abundance across four sites incorporated a total time commitment of approximately 37 h to identify and resight wallables, spread out over 10-day period and divided between four colonies. Capture-recapture methods using the Schumacher and Schnabel method are less suitable for long-term monitoring because they assume a closed population and require short time periods over which animals are assigned an identity and resignted (Vernes et al. 2011). Counts must therefore be constrained to discrete episodes such that each can conform to the closed population assumption. At one site where habitat was more complex, clearly viewing wallabies became challenging and new individuals were still being detected late in the sampling period. This led to wide confidence limits for abundance estimates (Vernes et al. 2011). This technique is only likely to be useful with very small, discrete populations due to issues with visually identifying and separating individuals.

Camera traps

Seven of the studies in our literature review employed camera traps for monitoring, primarily for detecting presence/absence, or to generate relative abundance indices (usually number of photograph events per 100 camera trap nights). Camera traps provide the added benefits of generating temporal activity profiles that can be used to guide the timing of additional data collection (Gowen and Vernes 2014). However, relative abundance indices do not account for variability in detection probabilities and can be inconsistent temporally and spatially (Sollmann et al. 2013).

The calculation of abundance estimates from camera traps has thus far relied on individual recognition either via deliberately marking animals (West et al. 2016), or recognising natural markings (Gowen and Vernes 2014). Marking individuals with ear tags or colour coded collars is entirely feasible for reintroduction trials (West et al. 2016), but difficult with wild animals because of low and variable trapability and accompanied by risks to the health of study animals via capture myopathy (Norton et al. 2011).

Gowen and Vernes (2014) used camera traps with a different approach to estimate colony size. Multiple cameras were placed at distance from the colony to encompass nonoverlapping views of the rock faces. Time lapse settings were used to capture simultaneous images every 10 min. Data from all cameras were then used to estimate the minimum number of animals known to be alive. The method generated an accurate population size estimate for a small colony (estimated four individuals) that was adequately covered by the numbers and positions of camera traps deployed (Gowen and Vernes 2014). However, results across the four colonies surveyed were variable and the estimated number of individuals was 32.5% lower than estimates derived from mark-recapture methods (Vernes et al. 2011). This approach is also likely implausible for colonies that occupy larger, less clearly defined habitat extents such as the extensive rock plateaus found in northern Australia.

Faecal pellet counts

Our literature review identified four studies that used pellet counts as a monitoring method. Rock-wallabies produce distinctive faecal pellets that usually preserve well, are easy to locate, and can be readily distinguished from those of other macropod genera (Jarman and Capararo 1997; Telfer et al. 2006). Mean pellet counts thus provide a suitable technique to determine *Petrogale* spp. presence/absence and, in some situations, an index of colony of size (Norton et al. 2011; Ward et al. 2011b). Faecal pellet counts can also provide detailed representation of temporal and spatial habitat use (Jarman and Capararo 1997; Norton et al. 2011).

When multiple *Petrogale* spp. co-occur regionally (e.g. *P. concinna*, *P. brachyotis* and *P. burbidgei*), differentiating between species is challenging. In addition, information on abundance is problematic because defecation and decomposition rates are largely unavailable and can vary with climate and weather (Norton et al. 2011). Nonetheless, regular monitoring of fixed faecal pellet plots can determine whether populations are stable, increasing or decreasing (Jarman and Capararo 1997; Norton et al. 2011). Faecal pellet counts aiming to estimate abundance or population trends require recurrent sampling of many quadrats to generate robust data. Moreover, rigid sampling periodicity or time calibration is important to avoid variable accumulation and decomposition periods affecting interpretation of the data (Norton et al. 2011).

Faecal DNA

We identified four studies that employed faecal DNA for population monitoring. Non-invasive sampling of faecal DNA has proven useful for monitoring *P. penicillata* in New South Wales (Piggott et al. 2005, 2018). The method can follow a mark-recapture protocol with sampling of faecal pellets spaced appropriately to reasonably cover a colony and repeated over flexible intervals of days to months. Population estimates generated by Piggott et al. (2018) were consistent with those from pellet counts, and the authors demonstrated additional major advantages for monitoring. Individual animals could be identified and profiled using their DNA, enabling the demographics of colonies and sex ratios to be understood and tracked along with population trends. Furthermore, genetic diversity could be assessed allowing an understanding of broader metapopulation dynamics beyond the colony, and long-term viability of the colony to be assessed.

One drawback for this method is that the quality and quantity of faecal DNA produced varies between individuals and this can introduce biases whereby some animals are detected more frequently than others (Piggott et al. 2005). Moreover, the consumables, expertise and time needed for processing and analysing DNA is currently expensive. Most importantly, most subsequent attempts to repeat the protocol of (Piggott et al. 2005, 2018) have failed to produce consistent results. The use of faecal DNA analysis for monitoring rock-wallabies is thus not recommended at present.

Additional considerations

The standard of rock-wallaby monitoring in Australia has been variable, largely focussed on three species, and for many species has been below the average quality of monitoring for Australian threatened mammals (Scheele et al. 2019). Moreover, few studies have stipulated the survey effort necessary to detect either presence-absence or significant population changes with confidence. Because many *Petrogale* spp. exist as large, patchy metapopulations, collaboration across government jurisdictions can be an integral part of effective monitoring. Consistently managing and sharing monitoring data and reporting between organisations, and maintaining appropriate legislative support across jurisdictions are likely to be especially important (Ward et al. 2011b; Woinarski 2018; Lindenmayer et al 2020).

Discussion

Thirteen (out of 25) rock-wallaby taxa are classified as threatened under Australia's *Environment Protection and Biodiversity Conservation Act 1999*. These are distributed across the country and include both southern, central and northern threatened taxa.

Research and monitoring has been heavily biased toward *P. lateralis*, *P. penicillata*, and *P. xanthopus*. For 11 species we were able to encounter only four or fewer publications and we were unable to encounter any research with an explicit focus on one of those species (*P. godmani*). This taxonomic research bias also incorporates geographic and ecological biases. *Petrogale lateralis*, *P. penicillata*, and *P. xanthopus* are primarily distributed in southern parts of Australia and tend to occupy discrete rocky outcrops. In contrast, rock-wallabies with limited research attention tend to be distributed in northern Australia, and many occupy larger, less clearly defined habitat extents such as extensive rock plateaus. Limited research may thus reflect the occurrence of these taxa in less easily defined colonies, in more difficult to access regions of Australia. Greater focus on these taxa is much needed and in a monitoring context will reveal novel insights and challenges in addition to those identified via studies focused on more discrete habitats.

The value and importance of close Indigenous involvement and guidance in rock-wallaby monitoring and conservation has long been recognised and could provide a means to overcome knowledge gaps for data deficient northern taxa (Pearson and Ngaanyatjarra Council 1997). Ethno-ecological knowledge is deep for many species and can greatly complement and extend scientific approaches (Telfer and Garde 2006). Furthermore, at least 52% of Australia is Indigenous land, or lands under Indigenous land use agreements (Renwick et al. 2017), and a large proportion of land on which *Petrogale* spp. occur is thus managed by Indigenous organisations. It is clearly essential that rock-wallaby monitoring protocols should be co-developed with leadership and guidance from Indigenous communities, and where possible be designed to match the strengths, capabilities and skills of landowners and managers. The incorporation of multiple methods conducted in tandem will strengthen monitoring protocols, and also ensure a range of complimentary data are available for use by different organisations, personnel, and skill sets.

The range of threats to rock-wallabies identified in our literature review were those more widely considered pivotal in the decline of Australian mammals since European colonisation (introduced predators, herbivores and changed fire regimes). However, the specialised ecology of rock-wallabies means these threats interact to affect rock-wallabies in specific ways. Although rock-wallabies are associated with rocky landscape features, threats in the surrounding lowland habitats are also important.

Of the range of techniques employed for monitoring rock-wallabies, no method was clearly most suitable for gathering the range of data needed to accurately track populations and inform management. Successful monitoring requires a clear understanding of purpose (e.g. assessing the impact of threats, maintenance of genetic variation, the response to management actions such as predator control) and sufficient sampling to provide relevant data.

A key constraint of the available options used to date is that they predominantly establish the presence or absence of rock-wallabies. Presence-absence monitoring across many discrete colonies will highlight distributional change, but these data are generally not suitable for following changes in the sizes of populations, nor for revealing demographic parameters including juvenile recruitment, survivorship, or breeding success that provide indications about stability and persistence of populations. Each of the monitoring methods identified in this review had considerable limitations and for the foreseeable future, detailed rock-wallaby monitoring will require the deployment of multiple complementary methods.

Some rock-wallaby species have been the beneficiaries of substantial management investment; others have been largely neglected. Given there is much commonality in ecological requirements and threats across rock-wallaby species, there is much opportunity to more broadly apply management practices that have been found successful at local scale to populations elsewhere. Monitoring management efficacy is crucial to enable such extrapolation with confidence, and more monitoring, and more consistent and insightful approaches to monitoring of rock-wallaby populations will help prioritise those species and populations that most require management. National coordination of protocols and sharing of monitoring data for Australia's rock-wallabies would be highly beneficial. The continued development and coordination of monitoring must pivot on close and respectful collaborations between Indigenous people, government, private conservation agencies, and private land-holders, to harness respective strengths and skills and improve rock-wallaby conservation and associated social benefits. Author contributions All authors contributed to the conception and design of this review. Literature searches, data analysis, and preparation of the first manuscript draft were performed by TL. All authors developed subsequent versions of the manuscript by critically revising the work and drafting and editing text. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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