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Catastrophic cat predation: A call for predator profiling in wildlife protection programs

K.E. Moseby [a,*], D.E. Peacock [b], J.L. Read [a]

[a] The University of Adelaide, North Terrace, Adelaide 5005, Australia
[b] Biosecurity SA, GPO Box 1047, Adelaide 5001, Australia

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ABSTRACT

Introduced predators have been implicated in the decline of many fauna populations around the world and are the main factor responsible for the failure of numerous fauna reintroduction programs. As a result, control of introduced predators is a significant management action implemented in wildlife protection programs, particularly in Australia, New Zealand and on islands. Individual predators are seldom targeted in conservation programs, which usually conduct broad-scale, non-specific predator control based on the assumption that the removal of each individual predator is equally important. In contrast, predator management programs initiated by human–wildlife conflict typically use profiling or specific control techniques to target 'problem' predators. We investigated whether individual domestic cats vary in the magnitude of their predation threat to wildlife by first reviewing published and anecdotal information on incidences where feral cats have had significant impacts on wildlife protection or translocation programs. We concentrated on prey species that were likely to be more challenging to cats based on their size, novelty or behavior. We then used the results from this review to create a profile of cats that were most likely to cause significant problems for challenging prey, and tested this during a translocation of a threatened mammal species. Both the review and translocation suggested that large male cats 3.5 kg or heavier were disproportionally responsible for predation events on challenging prey and possibly implicated in the failure of many protection or reintroduction programs of mammals greater than 1 kg. Some cats within this demographic profile were responsible for multiple prey deaths suggesting that both demography and prior experience may define predators capable of 'catastrophic predation' that threatens prey populations. Current control programs for feral cats and foxes that do not target particular predator profiles may inadvertently avoid controlling individuals most likely to specialize on threatened prey. We call for the application of crime-fighting forensic and aggregate profiling techniques in wildlife protection programs to determine the profile of predators likely to prey on focal wildlife species and to guide the development of control methods that specifically target these individuals.

1. Introduction

Predation and disease transfer by domestic cats, *Felis catus*, present a serious threat to many wildlife species (Jokelainen and Nylund, 2012; Loss et al., 2013) and hence cats are the focus of many eradication and control programs (Bester et al., 2000; Cruz and Cruz, 1987; Nogales et al., 2013; Robinson and Copson, 2014). Introduced predators, including cats, also contribute significantly to the failure of reintroduction programs of small to medium-sized vertebrates in Australia (Christensen and Burrows, 1995; Fischer and Lindenmayer, 2000; Moseby et al., 2011; Short, 2009; Short et al., 1992), New Zealand (Armstrong et al., 2006) and the United States (Shier and Owings, 2006). In Australia, successful reintroductions of mammals such as the greater bilby, *Macrotis lagotis*, bettong, *Bettongia* spp. and stick-nest rat, *Leporillus conditor*, have occurred when species are reintroduced into fenced reserves or islands where exotic cats and red foxes, *Vulpes vulpes*, are absent (Copley, 1999; Moseby et al., 2011; Hayward et al., 2014). In comparison, there is a litany of failed mammal reintroduction attempts, including bandicoots, *Isoodon* spp., mala, *Lagorchestes hirsutus*, and long-haired rats, *Rattus villosissimus* (Christensen and Burrows, 1995; Gibson et al., 1995; Frank et al., 2014) into areas where even low abundance of introduced predators are present.

The efficacy of feral animal control programs implemented to protect wildlife varies widely, with many failing to achieve a satisfactory reduction in predation pressure (Priddel and Wheeler, 2004). For example, with the exception of those cases where eradication has been achieved on islands (Nogales et al., 2004; Parkes et al., 2014) or fenced reserves (Hayward et al., 2014), typical feral cat control in mainland areas fails to provide sustainable protection for vulnerable species (Denny and Dickman, 2010), especially during the critical foundational

* Corresponding author at: P.O. Box 207, Kimba 5641, Australia.
E-mail addresses: katherine.moseby@adelaide.edu.au (K.E. Moseby), david.peacock@sa.gov.au (D.E. Peacock), ecological@activ8.net.au (J.L. Read).

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period of reintroduction programs when animals are often being released into a "predator pit" (May, 1977).

In many cases, the failure of generic introduced predator control to sufficiently reduce predation rates may be in part attributed to disproportionate predation pressure inflicted by specialist hunters. Individual prey specialization has been recorded in many wildlife species including birds (Woo et al., 2008) and sharks (Matich et al., 2011), and recent studies suggest that some felids also develop individual specializations in prey choice (e.g. jaguar, *Panthera onca*, Cavalcanti and Gese, 2010; cougar, *Felis concolor*, Knopff and Boyce, 2007, house cat, *F. catus*, Dickman and Newsome, 2015). Differences in diet could be caused by variations in the sex, age, size or personality of individuals (Brickner et al., 2014; Dickman and Newsome, 2015). These individuals may be less vulnerable to trapping or baiting due to their specific hunting preferences, or their age, size and inherent wariness and acuity. For example, the lack of correlation between coyote control and livestock losses in the US has been associated with the failure of conventional control methods to remove the astute problem alpha coyotes that are primarily responsible for sheep killing (Jaeger et al., 2001).

Predator profiling has long been used for native top-order predators in situations of human- or livestock–wildlife conflict when certain individual bears, *Ursus arctos* (Elfström et al., 2014), cougars, *F. concolor* (Ashman et al., 1983), tigers, *Panthera tigris* (Miller et al., 2013), *Lynx lynx* (Breitenmoser and Haller, 1993; Odden et al., 2006) and jaguar, *P. onca* (Cavalcanti and Gese, 2010) are believed to present disproportionately greater risks than the general population of predators. These individuals are often specifically targeted for control. For example, a 'problem polar bear' is defined as a polar bear, *Ursus maritimus*, that has come into contact with humans, their property, or both, and is destroyed when public safety and property are at stake (Dyck, 2006). A common theme with these 'problem' predators is that evidence suggests that once they have attacked prey of particular concern they are more likely than their naïve conspecifics to 'reoffend'. Vulnerable domestic stock and human safety are more efficiently safeguarded by focusing control efforts, often lethal control, on 'problem' animals and by limited intervention with the remainder of the predator population.

Despite the proven value of predator profiling for management of larger predators, broadscale control of small to medium-sized introduced predators such as red foxes, *V. vulpes*, cats, mongoose, *Herpestes* spp., possums, *Trichosurus* spp., and rats, *Rattus* spp. (Barun et al., 2011; Veitch et al., 2011) typically attempts to reduce the entire population on the assumption that any predator removed will produce a concomitant reduction in predation rate. Roy et al. (2002) reported that generic control of mongoose, *Herpestes javanicus*, failed to prevent uncommon but significant predation events on the rare pink pigeon, *Columbus mayeri*, in Mauritius and called for studies into the behavioral ecology of the mongoose. Several studies suggest that predation pressure of feral cats may also vary intraspecifically due to their size or prior learning (Childs, 1986; Christensen et al., 2012; Kuo, 1930). Dickman and Newsome (2015) identified specialist predators within several populations of feral cats that achieved maximal hunting success when attacking particular prey. Biben (1979) found that the probability of a cat kill decreased with increasing size or difficulty of prey, so relatively challenging prey species may only be tackled by a small fraction of cats or under certain conditions (Leyhausen, 1979).

In order to determine whether certain individual cats are disproportionally responsible for predation impacts on target wildlife species, we reviewed reported individual feral cat predation events on those wildlife species that we assume would be challenging for cats. Although an international study on the preferred prey weight for the house cat suggested 40 g or less (Pearre and Maass, 1998), Fitzgerald and Turner (2000) suggested that Australian cats often consume larger prey. Dickman (1996) proposed that cats in Australia preferred mammalian prey up to 220 g and birds up to 200 g, thus, we defined a challenging prey species as one that was more than 300 g, or 10% of the average female feral cat body weight. Other challenging species included those with high defense capabilities such as species that might defend themselves (i.e. other predators with canines) or those that employ other defense mechanisms (e.g. sharp spines). The characteristics of cats that targeted challenging species were used to develop a potentially 'catastrophic' predator profile that was tested during a reintroduction of a native mammal species, the western quoll, *Dasyurus geoffroii*. This carnivorous marsupial formerly occurred over 70% of the Australian mainland but has declined since European settlement and is now restricted to a small area in south west Western Australia (Morris et al., 2003). It is globally listed as Near Threatened (IUCN red list 2014) and nationally listed as Vulnerable (to extinction) under the Australian Environment Protection and Biodiversity Conservation Act 1999. Results were used to assess the efficacy of current cat control methods in wildlife protection programs and highlight the role that profiling can play in guiding the development of targeted and effective control.

2. Methods

2.1. Review

A literature search was conducted to identify examples where individual feral cats were known to successfully attack and kill challenging prey, were thought to be responsible for catastrophic predation events and where cats had the potential for catastrophic impact but no impacts were recorded. For the purpose of this review we defined catastrophic predation as incidents where a cat or cats caused the significant decline or extinction of prey populations. Cat incursions into fenced protected areas were used to highlight cases where individual cats had low predation impact. We made no distinction between the hunting habits of truly feral cats that live independently of humans, strays that have some human interaction and free-ranging pet cats. Due to the paucity of published information, grey literature, personal communications and published anecdotal reports were also included. Where possible, the individual cat details were sought from practitioners and included. This review is biased towards prey species of conservation concern, many of which are also challenging prey for cats due to their size and novelty, because predation events on these species are most likely to have been closely monitored and reintroduced populations are most at risk of catastrophic predation.

Many of the studies included in our review involve reintroductions of Australian medium-sized native mammal species as introduced predators are thought to be a major factor responsible for the decline and extinction of mammals in the critical weight range of 35 g–5500 g (Burbidge and McKenzie, 1989).

2.2. Predator profiling

2.2.1. Mammal reintroduction

To test the theory that some cats are disproportionally responsible for predation events of challenging prey we utilized the reintroduction of the western quoll to a site within its former range, and monitored post-release predation and survival. Western quolls weigh between 1 and 2 kg and are carnivorous marsupials, feeding on a range of invertebrates, birds, small mammals and reptiles (Rayner et al., 2011). Being a medium-sized carnivore capable of killing prey the size of rabbits, western quolls were predicted to present more challenging prey for cats than the small rodents, rabbits, lizards and birds that constitute the majority of regional cat prey (Holden and Mutze, 2002; Molsher et al., 1999; Read and Bowen, 2001). Western quolls are believed to have become extinct from South Australia's Flinders Ranges in the 1880s (Tunbridge, 1991) possibly due to a combination of disease and predation from introduced cats (Abbott et al., 2014; Peacock and Abbott, 2014). Red foxes (*V. vulpes*) have been successfully controlled in the Flinders Ranges National Park using poison (sodium fluoroacetate) baits since 1994 (de Preu and Pearce, 2006) and more than 7000 camera trap nights conducted during the 10 month reintroduction failed to detect a single fox (DEWNR unpub. data). However, feral cats were detected on cameras in the release area and control was attempted both before and after the reintroduction using a combination of trapping and shooting.

Forty one western quolls were released in April 2014 into the Flinders Ranges National Park in South Australia, 37 from wild populations in Western Australia and four captive-bred animals from the Alice Springs Desert Park. All released quolls were fitted with 25 g radiocollars with mortality sensors triggered after 10 h of inactivity (Sirtrack Pty Ltd, New Zealand) and radiotracked daily by plane or on foot for up to 6 months after release. Any collars detected in mortality mode were immediately located and carcasses retrieved for autopsy by experienced wildlife veterinarians from the Adelaide Zoo (Zoos S.A.). The cause of death and species responsible was ascertained during autopsies or from DNA analysis of swabs taken from the collars and wounds found on carcasses. If the carcass was less than 24 h old, traps were set at the carcass site in an attempt to catch the predator responsible.

The individual cats responsible for quoll kills were identified by a combination of techniques including trapping or sighting individuals at fresh quoll carcasses, identification of quoll remains in stomach contents of trapped cats, matching DNA from saliva found on swabbed collars or carcasses with samples from captured cats (Glen et al., 2010), and direct observation. Where possible, DNA analysis (Wildlife Genetics Laboratory, University of Canberra, Australia) was used to confirm results from trapping and direct observations.

2.2.2. DNA analysis

DNA samples were taken using cotton buds dipped in Tissue Digest (DXT) (Qiagen) and swabbed over the radiocollar and open wounds on the carcasses. Separate swabs were taken for each sample. Samples were stored in the refrigerator and posted to the Wildlife Genetics Laboratory, Institute for Applied Ecology, University of Canberra, Australia where the following procedures were performed. Samples were incubated at 56 °C overnight in 420 μl of Tissue Digest (DXT) and 4.2 μl of DX Digest enzyme. DNA was extracted using the Corbett X-tractor Gene (Qiagen) automated standard swab protocol, following the manufacturer's instructions. DNA was then eluted in 50 μl of elution buffer. Polymerase Chain Reaction (PCR) was undertaken using the universal mtDNA primers CB-J-10612 and CB-N-10920 targeting a highly conserved region of the cytochrome b gene (CYTB) common across a wide range of vertebrates (Kocher et al., 1989). PCR amplifications were performed on a GeneAmp 9700 thermocycler (Applied Biosystems) in 25 μl reactions containing 5 μl of DNA extract, 2.5 μl of FastStartTaq DNA Polymerase PCR Buffer with MgCl2, 2.5 μl dNTPs (2 mM), 1 μl of each primer (10 pm μl^{-1}), 1 μl of BSA (10 mg ml^{-1}) and 1.5U of FastStartTaq DNA Polymerase (Roche Diagnostics). Cycles were as follows: 95 °C for 4 min; >40 cycles of 94 °C for 45 s, 50 °C for 45 s, 72 °C for 1 min; 72 °C for 10 min. Amplification products were visualized under UV using ethidium-bromide stained agarose gels.

To avoid DNA contamination, DNA extraction and PCR set up were performed in a room isolated from amplified DNA with one-way movement between facilities. Direct sequencing of purified products was carried out with BigDye™ Terminator Version 3.1 (Applied Biosystems) following the manufacturer's protocol. Sequences were analyzed on an Applied Biosystems 3130xl genetic analyzer using DNA Sequencing Analysis Software Version 5.3.1 (Applied Biosystems). DNA sequences were compared and edited manually using the program Sequencher 4.6 (Gene Codes). Sequence results usually consisted of mixed profiles that had to be separated out in order to determine whether any potential predator DNA was present. The previously known 'host' mtDNA CYTB sequence, which is available on GenBank, was first subtracted from the mixed profile. If a mixed profile was still evident, then another likely source of DNA contamination, human mtDNA CYTB sequence, was removed. When a single profile was obtained that was neither the 'host' nor human mtDNA CYTB sequence, the BLAST (Basic Local Alignment Search Tool) algorithm was used to search for the most closely matched sequences within the National Center for Biotechnology Information (NCBI) database, GenBank.

Once predator DNA had been positively identified as cat, microsatellite loci were used for individual identification of both swab samples and from tissues of cats that had been trapped. A total of 10 microsatellite loci were used from previously developed multiplex of loci for domestic cats (Butler et al., 2002). GENECAP (Wilberg and Dreher, 2004) was used to detect genotyping errors in the capture-mark-recapture (CMR) data set and to calculate probability of identity P(ID) and probability of identity siblings P(ID)sib (Waits et al., 2001) for the 10 loci. An error-checking and removal procedure was then used which was developed by Paetkau (2003) for use on poor quality samples. Two independent laboratory observers determined consensus genotypes based on strength and confidence in the results. Each locus was amplified at least twice and consensus genotypes were only accepted if 2 heterozygotes and 3 homozygotes were replicated and confirmed through visual inspection by both observers. GENECAP was used to identify samples that produced multi-locus genotypes that differed by only 1 or 2 loci, a potential warning sign that a genotyping error occurred (Paetkau, 2003). Once a consensus genotype for at least 6 microsatellite loci was obtained, the multi locus data set was run through GENECAP. If multilocus genotypes differed by 1–2 alleles, the loci that mismatched were either rerun or scrutinized using the electropherograms from previous runs. This procedure enabled DNA samples from quoll carcasses and collars to be confidently matched (where possible) to DNA samples taken from cats captured in the vicinity of the study area.

2.2.3. Cat sampling

The size and sex of cats responsible for predation events was compared with the general cat population in the release area in order to determine whether specific cat profiles were disproportionately responsible for quoll deaths. Extensive background cat data, sourced primarily by shooting, had previously been collated (Holden, 2000; Holden and Mutze, 2002) and was augmented by data obtained by shooting and trapping of cats within the western quoll release area for 4 months prior to the release and up to 6 months post-release. Captured cats were euthanized then weighed, sexed and checked for reproductive, body and teeth condition. Three transects comprising 7–10 camera traps (Reconyx Hyperfire 550; total 24 traps) spaced 1 km apart, were set along roads within the quoll release area to monitor cat and quoll presence and comparative abundance. The three transects were 2 km and 6 km apart. Cameras were placed on stakes 30 cm above road height and at a 22° angle to the road to maximize detectability of cats (Meek et al., 2014). Camera trap configuration was not designed for robust statistical analysis of cat abundance, rather with the aim of determining if cats were present and comparing long term trends in cat activity to trigger cat control events. Total cat detections were divided by the number of camera trap nights and multiplied by 100 to produce a cat detection rate for each transect. A cat detection was defined as a photograph or series of photographs of a cat that, unless clearly distinguishable, was recorded more than 10 min from the last recorded photograph of an indistinguishable cat on the same camera. Indistinguishable cats detected on a camera within 10 min of a previous detection were considered to be the same detection. The mean detection rate and standard error was then calculated for each month.

3. Results

3.1. Review

We found 20 studies or reports of individual cat predation impacts; 12 instances where individual feral cats were thought to be responsible for catastrophic predation, five instances where cats were known to successfully attack and kill challenging prey and three instances

Table 1
Examples of individual predation events by cats. Mammal prey weights taken from Van Dyck and Strahan (2008) unless specifically stated by author.

Prey species	Prey weight	Cat details (size, sex etc.)	Predation details	Location	Reference
Mammals					
Petrogale assimilis	4.3–4.7 kg		Single cat killed multiple wallabies over 9 months	Queensland, Australia	Spencer (1991)
Lagorchestes hirsutus	1.5–1.7 kg	a) Male 5.1 kg b) Male 4.8 kg	a) 13 (42%) predated b) 14 (56%) predated	Tanami Desert, Northern Territory, Australia	Gibson et al. (1995; 1994)
Pseudocheirus peregrinus	0.7–0.9 kg		Colonies systematically preyed upon by individual cats		Dowling et al. (1994)
Petaurus breviceps	0.11–0.14 kg		Colonies systematically preyed upon by individual cats		Dowling et al. (1994)
Bettongia penicillata	0.75–1.9 kg	Male 5.75 kg	14 (21%) killed before large cat removed, no further deaths despite some cats present	Venus Bay, South Australia	D. Armstrong pers. comm.
Bettongia pencillata	0.75–1.9 kg	Male cats	DNA analysis suggested that all cats known to prey on bettongs were male	Western Australia	Marlow et al. (2015)
Bettongia lesueur	1.28 kg		40 animals translocated, predation believed due to only two or three cats; all animals predated by 60 days.	Gibson Desert, Western Australia	Burrows and Christensen (1995) Christensen and Burrows (1995)
Isoodon auratus	0.3–0.6 kg		40 animals translocated, predation believed due to only two or three cats; all animals predated by 70 days.	Gibson Desert, Western Australia	Burrows and Christensen (1995) Christensen and Burrows (1995)
Macrotis lagotis	0.8–2.5 kg		Two bilbies in same cat stomach, cat with fresh bilby kill with another in stomach. In total 119 confirmed (150 suspected) cat kills at Astrebla Downs NP (Qld, Aust.) in 12 months.		B. Nolan pers. comm. Rich et al. (2014)
Petrogale assimilis	4.3–4.7 kg	c. 5 kg	A single cat killed 45.5% of the young, 14.2% of the subadults, and 4.6% of the adults of a population of unadorned rock-wallabies over a nine month period.	Queensland	Spencer (1991)
Macrotis lagotis	0.8–2.5 kg	Male 3.6 kg and male unknown	Reintroduced population extinct after 18 months, two male cats captured with bilby in their stomach	Arid Recovery, South Australia	K. Moseby pers. obs. 2004
Dasyurus viverrinus	0.7–1.9 kg		Domestic cat in 1876 over a period of one or two weeks "killed and brought home no less than seven full sized native cats" and a feral cat in 1901 killed and ate five quolls: "found the heads of five native cats [in a log with *F. catus* kittens]".	Eastern Australia	Peacock and Abbott (2014)
Onychogalea fraenata *Trichosurus vulpecula*	1.5 kg 1.5 kg	Female 3.4 kg	Lactating female cat killed one *O. fraenata* (juv.) and 2 *T. vulpecula*		Horsup and Evans (1993)
Rattus villosissimus	0.1–0.16 kg		*Rattus villosissimus* (n = 23 and n = 16) reintroduced to 2 cat accessible pens at Wongalara. Rats in each pen believed killed by 1–2 cats.	Northern Territory, Australia	Frank et al. (2014)
Rattus tunneyi	0.066 kg		*Rattus tunneyi* reintroduced to 2 cat accessible pens at Wongalara. Rats in each pen (n = 9 and n = 7) believed killed by same individual cat.	Northern Territory, Australia	Tuft et al. (2014)
Birds					
Anas gracilis	0.3–0.7 kg	Male 1.5 kg	Cat shot swimming out to ducks had grey teal in stomach	Roxby Downs, South Australia	Read and Ebdon (1998)
Strigops habroptilus	1–4 kg		15 cat-killed kakapo in 1981, none after 1982 following commencement of cat control	Stewart Island, New Zealand	Clout and Craig (1995); Powlesland et al. (2006; 1995)
Sula leucogaster	0.9–1.5 kg	Male 3.5 kg	Cat killed 2 Brown booby and predation stopped after offending cat was removed		K. Horikoshi pers. comm.
Non-predation events					
Lagorchestes hirsutus	1.5–1.7 kg	Female ca 3 kg	Cat incursion into the Mala Paddock in 2012. No Mala known to be killed in 2 months	Alice Springs, Australia	J. Clayton pers. comm.
Bettongia lesueur *Macrotis lagotis*	1.28 kg 0.8–2.5 kg	Female 3.5 kg regressed teats	Cat incursion into the Arid Recovery Reserve in March 2008. Cat killed native rodents but did not kill any reintroduced bettongs or bilbies during the 29 days before it was captured.	Arid Recovery, South Australia	K. Moseby pers. obs. 2008
Isoodon auratus *Lagochestes hirsutus*	0.3–0.6 kg 1.5–1.7 kg	Female 3.4 kg	Cat incursion into the Lorna Glen exclosure in 2014. Cat inside for 5 weeks but no record of any killed reintroduced species	Lorna Glen, Western Australia	N. Burrows pers. comm. 2014

where cats had the potential for catastrophic impact but no impacts were recorded (Table 1).

3.1.1. Catastrophic predation of challenging prey by individual cats

The eastern quoll, *Dasyurus viverrinus*, is an aggressive 900–1300 g marsupial predator that would represent a formidable prey for cats yet Peacock and Abbott (2014) document one case of a single domestic cat killing and bringing home at least seven full-sized eastern quolls in a period of 1–2 weeks and another case of a feral cat that had killed and eaten five quolls. Dowling et al. (1994) reported individual pet cats systematically preying on whole colonies of common ring-tail possums, *Pseudocheirus peregrinus*, and sugar gliders, *Petaurus breviceps*, which was believed capable of hastening local extinctions. Spencer (1991) observed and documented what he believed was a single cat killing 45.5% of the young, 14.2% of the subadults, and 4.6% of the adults (mean weight 4.5 kg) of a population of unadorned rock-wallabies, *Petrogale assimilis*, over a nine month period.

Two separate attempts to reintroduce the rufous hare-wallaby, *L. hirsutus*, (mean weight 1.5 kg) to the Tanami Desert, Northern Territory, were thwarted by predation by single cats (Gibson et al., 1995). In the first reintroduction at least 13 (42%) of the 31 reintroduced wallabies, were believed predated by feral cat(s). The removal of a 5.1 kg male cat, with hare-wallaby fur in its stomach, resulted in no further predation. In the second reintroduction, 14 (56%) of the 25 animals were confirmed killed by feral cat(s). Again, eventual removal of a 4.8 kg male cat from the vicinity of the dead animals resulted in cessation of this predation. Similarly, all forty burrowing bettongs, *Bettongia lesueur* (mean weight 1.3 kg), translocated to a 1600 km^2 fox baited area of the Gibson Desert, Western Australia were predated by two or possibly three cats within 60 days (Burrows and Christensen, 1995; Christensen and Burrows, 1995).

Over one fifth (14) of radio-collared brush-tailed bettongs, *Bettongia penicillata* (mean 1.2 kg) were killed at Venus Bay Conservation Park, South Australia (Copley et al., 1999) by 11 months post release despite no predation recorded for the first 7 months. Carcasses were indicative of cat predation and previously unobserved tracks indicated a large cat had moved into the area. Eventual trapping of the suspected cat, a 5.75 kg male, resulted in no additional predation being detected and an associated continued increase in numbers and range of bettongs, despite the continued presence of a few feral cats (D. Armstrong pers. com). Populations of native Australian rats, *Rattus villosisimus* and *Rattus tunneyi*, reintroduced to Wongalara in the Northern Territory, were hunted to extinction soon after release in 2012 and 2014 respectively, believed by only one or two individual cats at each site (Frank et al., 2014; Tuft et al., 2014).

Kakapo, *Strigops habroptilus*, are large (1–4 kg) flightless parrots that are seriously threatened by cat predation. Soon after the population of kakapo was located on Stewart Island in New Zealand, predation by cats on adult radio-tagged kakapo reached 56% per annum in 1981/82. Since cats had been present on Stewart Island for over a century, during which time kakapo could not possibly have survived such predation pressure, the most likely explanation was that one or more cats had learned to kill kakapo, a conclusion supported by the total cessation of cat-killed kakapo after intensive cat control commenced in 1982 (Clout and Craig, 1995; Powlesland et al., 2006).

3.1.2. Cat predation on challenging prey

Cat predation has also been recorded on wallaby species approximately the same weight as cats, including the bridled nail-tail wallaby, *Onychogalea fraenata*, (av wt. 5 kg, Fisher et al., 2001; Horsup and Evans, 1993) and Tasmanian pademelon, *Thylogale billardierii*, up to 4 kg in body mass (Fancourt, 2015).

Despite feral cats typically not preying on large birds (Van Aarde, 1980), some domestic cats and related small felids will occasionally prey on large, difficult-to-subdue birds including eagles, *Aquilla audax*, (adult weight 2–6 kg, Doherty et al., 2015) and sereimas, *Cariama cristata*, (mean weight 1.5 kg, Yanosky and Mercolli, 1994). Only a single duck, a grey teal, was recorded in the stomach of over 2000 feral cats dissected at Roxby Downs (see Read and Bowen, 2001) yet the same 1.5 kg male cat that had consumed the teal was shot whilst swimming out towards other ducks, suggesting that the offending cat had learned to target these unusual and challenging prey (Read and Ebdon, 1998). An individual 3.5 kg male cat was photographed making two kills of brown boobies, *Sula leucogaster*, (mean weight 0.9–1.5 kg, wingspan 1.3–1.5 m) on Hahajima Island, Japan; (Plate 1). Booby kills at the colony ceased after the cat was removed (K. Horikoshi pers. comm.).

3.1.3. Examples of cats not responsible for catastrophic predation

A cat incursion in 2012 into a fenced enclosure protecting the rufous hare-wallaby at Uluru in the Northern Territory did not lead to any known hare-wallaby, *L. hirsutus*, (1.3 kg) deaths despite the cat being present for more than one month. When the cat was finally captured it was an average-sized female cat (approximately 3 kg) (J. Clayton pers. comm.). Similarly, an incursion into the fenced Arid Recovery Reserve in northern South Australia occurred in 2007 and despite following the cat's spoor every day for over a month it was only recorded feeding on small rodents and bandicoots (average wt 40–200 g). The reintroduced burrowing bettongs, *B. lesueur*, and bilbies, *M. lagotis*, within the reserve (Moseby et al., 2011) were not killed but track identification suggested the cat unsuccessfully attempted to catch at least one reintroduced bettong (1–2 kg, K. Moseby pers. obs.). When captured, the cat was found to be a 3.5 kg female. A cat incursion occurred into the Lorna Glen predator-proof exclosure in 2014. The female cat remained inside for 1 month before being removed but there was no record of any killed reintroduced species (N. Burrows pers. comm.).

Our review of cat predation events in wildlife protection programs suggests that, like the variability in threats from predators involved in human–wildlife conflicts, considerable individual and temporal variability exists in the threat posed by cats. In many cases wildlife populations declined over very short time frames after being stable for several months or years. Practitioners attributed this to one or two cats finding and then intensively targeting prey populations. Male cats were responsible for more incidents of catastrophic predation of larger prey than females. The size of cats, notably large adults, was also considered a factor by many conservation practitioners in large scale predation impacts to larger prey. In contrast, female cat incursions into fenced reserves did not appear to cause catastrophic predation of the larger species that are considered to represent challenging prey items.

3.2. Predator profiling

Two sets of cat morphological data collected from the Flinders Ranges National Park were used to assist with determining the profiles of cats that preyed on quolls. The original data set was collected from across the park between 1994 and 1998 by staff and members of the Sporting Shooters Association of Australia (Conservation and Wildlife Management Branch (SA)) and is incorporated in Holden (2000) and Holden and Mutze (2002). Five hundred and sixty six cats (256 male and 310 female) were removed, primarily by shooting (>90%). Cats ranged in weight from 0.7 kg to 5.9 kg with an average weight of 3.2 kg (SE = 0.05). Only 29% of cats weighed more than 4 kg comprised of only 10.6% of the females but nearly half (45.3%) of the males (Fig. 1).

Secondly, seventy cats (26 F, 43 M, 1 unsexed) were removed from the western quoll release area in the 4 months before and 6 months after release. Cats ranged in weight from 0.7 kg to 5.6 kg with an average weight of 3.1 kg (SE = 0.16). All females weighed less than 3.5 kg but half of the males (53%) weighed more than 4 kg (Fig. 2). Cats were removed by cage trapping (57), soft catch foothold trapping (8, Victor size 2 traps, Coast to Coast Vermin Supplies) and shooting (5).

There were 45 cat detections over 2187 remote camera trap nights during the release period from March to August, 2014. Average monthly cat detection rates ranged from 0.9% (SE = 0.9) to 2.2% (SE = 0.29) indicating that cats were present throughout the study period (Fig. 3). There was no noticeable reduction in cat detections over time (Fig. 3).

Of the 41 quolls reintroduced to the Flinders Ranges National Park, 11 died within the first 6 months after release and a further quoll was attacked by a cat. Ten of the 11 deaths were attributed to cat predation (Table 2). The first two quoll deaths occurred 8 and 10 days after release and the collars were found only 100 m apart with identical teeth marks in the leather band. Both collar bands were also severed in the same place suggesting a similar kill style. A large black cat was observed 100 m from the first kill site the night after the first death and was caught the night after the second death in a cage trap less than 5 m from where the quoll remains were found. This 4.25 kg male cat (Cat 1) had quoll remains (foot and tail) in its stomach and was considered responsible for both deaths.

Three deaths then occurred between the 1st and 7th of June, all within a 1 km radius. One carcass from the 2nd of June could be autopsied and the cause of death was cat predation. The other two carcasses had been almost completely consumed with only some bones and collars remaining. Teeth marks were present on the collars. A professional shooter shot a large 5 kg adult male cat (Cat 2) on the 8th June less than 200 m from the site of the autopsied carcass ('Tingle'). Measurements of upper canine separation and one top broken canine matched the type and spacing of puncture wounds recorded during autopsy. Quoll fur was also recorded in its stomach. The DNA analysis confirmed that DNA from this cat matched that found on the autopsied quoll's collar ('Tingle'). This cat was thought to be responsible for the two other deaths ('Rudis' and 'Avon') due to the close timing and

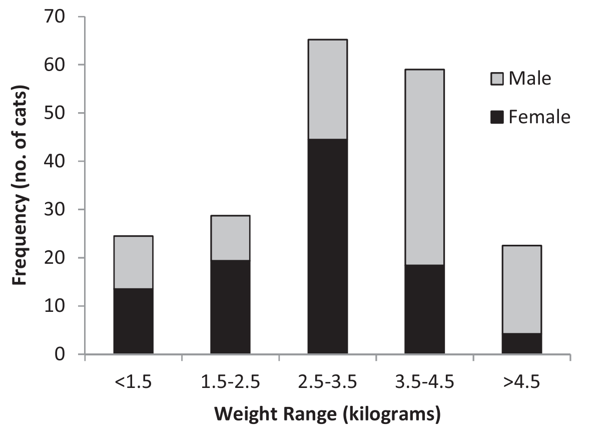

Fig. 1. Frequency of male and female cats captured in each weight category in the Flinders Ranges National Park, South Australia, between 1994 and 1998, n = 556. The western quoll was released into the park in 2014.

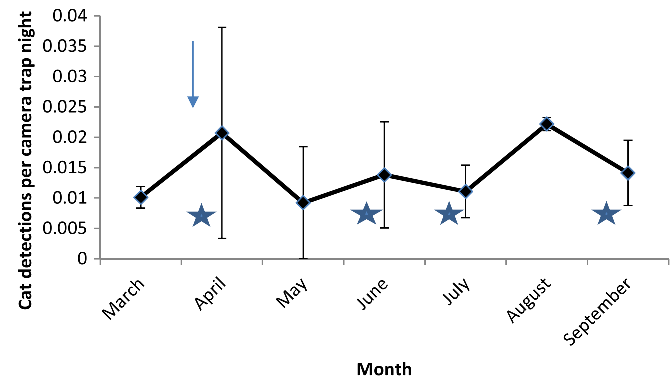

Fig. 3. Average cat detections per month recorded on three remote camera transects set within the western quoll release area in the Flinders Ranges National Park in 2014. Bars denote 1 standard error. Arrow indicates when quolls were reintroduced to the park. Stars indicate months when predation events occurred.

spacing of the kills. Additionally, the quoll fur in the cat stomach is unlikely to have been present since the 2nd of June and most likely represents a more recent kill ('Avon').

On the 26th of June a large tabby cat was scared off a fresh, warm half-eaten quoll carcass ('Kojo') at 2.30 pm. The quoll was being radio tracked during the day and the collar was not yet in mortality mode. A cage trap baited with a rabbit carcass was immediately set at the quoll carcass site and a large tabby cat was in the trap when it was checked 3 h later. This 4.1 kg adult male cat (Cat 3) had quoll in its stomach. The DNA from this cat matched that found on another quoll carcass ('Zamia') found earlier on the 17th of June 4 km away. Due to the proximity and timing of the carcass and the presence of cat DNA found on the collar this cat is also thought to be responsible for the death of 'Narelle' on the 19th of June, 1.5 km from 'Zamia's carcass. Unfortunately individual sequencing of this cat DNA sample could not be conducted due to the small amount of DNA present.

Three more deaths subsequently occurred but only one could be confirmed as a cat predation event. A female quoll ('Toodjay') with denned young was killed during the day and the carcass was still fresh and partially consumed when found that afternoon. The collar was not yet in mortality mode. An autopsy identified puncture wounds in the back of the neck and attributed the death to cat predation. Three nights later a 3.7 kg male (Cat 4) was captured in a soft-catch foothold trap within 200 m of the kill site. Although the cat had an empty stomach, its DNA matched that found on the quoll's ('Toodjay') collar and wounds. The DNA also matched cat DNA found on another quoll collar ('Zeus') recorded 3.5 km away a month earlier. The collar band was broken and the quoll was subsequently captured alive with scars consistent with a cat attack.

There was both a size and sex profile for cats that were known to attack and kill quolls. All cats known to kill quolls were adult males (Table 3). A fisher exact test comparing the proportion of quolls killed by male and female cats (11 vs 0) with the proportion of males and females in the general population trapped during the study (n = 69) found a significant difference between males and females (Fisher exact test, P = 0.0133). The average weight of all cats captured during the study was 3.13 kg (SE = 0.16, n = 70) similar to the average weight recorded from the cats captured in the study area previously (3.16 kg, SE = 0.05, n = 566). There was no significant difference in the weights of cats in the two samples ($t_1 = 0.81$, $P > 0.05$) or in the weights of male cats (3.7 kg, SE = 0.2 vs 3.5 kg, SE = 0.07, $t_1 = 0.38$, $P > 0.05$) so data were combined. The average weight of cats known to kill quolls was 4.26 kg (SE = 0.28), more than 1 kg heavier than the average weight from both studies combined (3.15 kg, SE = 0.07). When only male cats were considered, the average weight of males known to kill quolls was 4.26 kg compared with the average male weight of 3.57 (SE = 0.07). Unfortunately the sample size of cats responsible for quoll killings (4) was too small to facilitate statistical analysis of weight data but when two standard errors were added to the mean, weights did not overlap when using total cat weights and only overlapped by 0.01 when only male cat weights were used. Results indicated that larger than average male cats were responsible for quoll deaths with some individuals known to have killed multiple quolls within a short space of time.

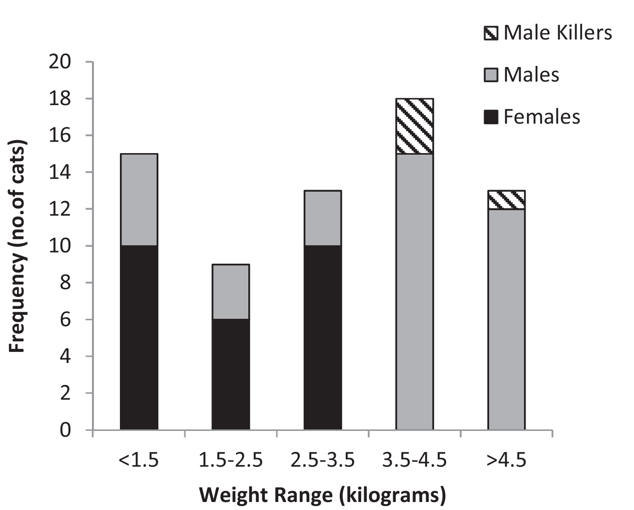

Fig. 2. Frequency of male and female weights for cats captured during the western quoll reintroduction into the Flinders Ranges National Park in South Australia. Male cats responsible for known deaths are also included, n = 70.

4. Discussion

Both the review and reintroduction trial suggest that there are intraspecific differences in cat predation risk to wildlife species, particularly in prey species that present a challenge to cats due to their size or behavior. Our data supports previous suggestions of hunting specializations in domestic cats (Bradshaw, 2013; Dickman, 2009; Mendl and Harcourt, 1988) but is the first study to investigate the profiles of cats responsible for catastrophic predation. The predator profile likely to cause catastrophic predation in our reintroduction trial and other studies of large prey was heavier than average male cats, particularly adult males 3.5 kg or over. Other predator profiles used in human–wildlife conflict have found demography to be an important factor in identifying problem predators. In contrast to our study, young, rather than adult, male predators in species such as lions (Patterson et al., 2003), polar bears (Dyck, 2006) and dingoes (Allen, 2015) are more often

Table 2
The details of 11 western quoll deaths and attacks (*) attributed to cat predation in the first 6 months after release.

Name	Sex	Date of death/attack	Cause of death Autopsy result	Observations	DNA present	Conclusion
Hayden	F	8/04/2014	Collar — no remains	Quoll in cat 1 stomach	Human	Cat 1
Snappi	F	10/04/2014	Collar — no remains	Quoll in cat 1 stomach	Human	Cat 1
Rudis	M	1/06/2014	No autopsy — limited remains	Remains within 1 km of Tingle	European rabbit	Cat 2
Tingle	F	2/06/2014	Cat		Cat 2	Cat 2
Avon	M	7/06/2014	No autopsy — limited remains	Fresh cat scat next to head of carcass	Human	Cat 2
Zamia	M	17/06/2014	Inconclusive	Deep wound on leg	Cat 3	Cat 3
Narelle	F	19/06/2014	Cat	Carcass in rabbit burrow	Cat	Cat 3
Kojo	F	26/06/2014	No autopsy — cat sighted	Cat 3 sighted and captured at fresh carcass. Quoll in stomach	Quoll	Cat 3
Karri	F	14/07/2014	Collar — no remains	Quoll fur and bite marks on collar	Cat 5	Cat 5
Zeus*	M	29/07/2014	Broken Collar — no carcass	Collar broken, Quoll survived attack	Cat 4	Cat 4
Toodjay	F	6/9/2014	Cat	Cat 4 captured within 200 m of carcass within 2 days	Cat 4	Cat 4

characterized as problem animals than their conspecifics because they tend to be more curious, less cautious and maybe more food stressed. Young brown bears are considered to be more likely to become problem bears due to their innate dispersal and fear of conspecifics (Elfström et al., 2014). On the contrary, alpha male and female coyotes (*Canis latrans*) are considered to be primary sheep predators (Conner et al., 1998; Jaeger, 2004). The profile of specialized predators is likely to be prey-specific, varying depending on the size and vulnerability of prey species. Individual wildlife protection programs should develop location-specific profiles of likely potential specialized predators based on prey characteristics and predator life history.

A common theme with ‘problem’ predators in human–wildlife conflict is that evidence suggests that once they have attacked prey of particular concern they are more likely than their naïve conspecifics to ‘reoffend’ (e.g. Diamond, 1989; Baldus, 2004). Our study suggests that some cats were responsible for multiple prey deaths over short periods suggesting that prior experience may be an important component of the profile of cats responsible for catastrophic predation. Alternatively, a potential specialized predator may take some time to find a wildlife colony therefore contributing to a lag effect before a catastrophic predation episode. In situ conservation and reintroduction programs should be prepared to invest considerable effort in targeting a predator as soon as a predation event occurs, as there is considerable evidence to suggest it may quickly reoffend and potentially cause population extinction.

Review results suggest that catastrophic predation by feral or free-ranging domestic cats exacerbates the threat to particular threatened species, even at low population densities of feral cats. Specialist predators may continue to hunt favored prey species even when these prey become very scarce (Molsher et al., 1999). Other instances of a seemingly scarce population of cats causing declines of native animals have been reported (Gibson et al., 1994; Priddel and Wheeler, 2004). Unlike most other pest species, the impacts of predators need not be driven primarily by their abundance, but by other aspects of their ecology. It may be in part the ability of cats to selectively hunt in habitats where prey are vulnerable (McGregor et al., 2015), indulge in surplus killing (Peck et al., 2008), and specialize on particular prey (Ancillotto et al., 2013; Dickman and Newsome, 2015; Fitzgerald, 2000) that makes them so dangerous to some wildlife populations.

Profiling of specialized predators with the potential for catastrophic predation can lead to targeted control efficiencies, as distinct from generic predator control (Burrows et al., 2003; Priddel and Wheeler, 2004) that does not achieve concomitant reductions in predation pressure to focal species. Sinclair et al. (1998) examined the reintroductions of four marsupial species and concluded that in the initial stages of reintroductions ‘the predation should be reduced by at least 90% until a sufficient population has been established’. However this reduction in predation may have been possible through removal of only a few individual predators. The current focus on broadscale population reduction which has been adopted by most threatened species programs (e.g. Priddel and Wheeler, 2004; Moseby et al., 2011) fails to consider the issue of individual problem predators and their tendency to reoffend. Whilst poison baiting can provide landscape scale reductions of considerable magnitude in some circumstances (Johnston et al., 2012; Moseby and Hill, 2011), a reduction in the abundance of specialized predators in the population rather than cat numbers per se is likely to be more important. Some control measures may even inadvertently target individuals that are less likely to predate on challenging wildlife species. Cage traps have been found to catch younger cats and those that scavenge for food whilst leghold traps catch more male cats and hunters (Short et al., 2002). Hungry cats, stray cats or cats found at town dumps are more likely to scavenge than feral cats (Risbey et al., 1999; Short et al., 2002) and are arguably easier to trap or bait using food as lures. At a more arid site, Thomson et al., (2000) also found differences in bait uptake of foxes with younger animals taking baits sooner than older foxes, though this wasn't found at a more mesic site (Thomson and Algar, 2000). The target specificity of control measures needs to be considered when designing wildlife protection programs.

Cats responsible for catastrophic predation, like other ‘problem’ predators in human–wildlife conflict, often require inordinate skill and effort to control. Even when aware of the cat predation of their reintroduced *B. lesueur* and *Isoodon auratus*, Burrows and Christensen (1995, pg. 40) state “despite our best efforts, we were unable to trap, poison or kill the culprits”. In our study, cats preying on quolls were captured only through targeted control rather than during general cat trapping. Conner et al. (1998) also found conventional coyote control to be ineffective at removing problem coyotes. As per livestock protection collars (Burns et al., 1996), there is an urgent need to develop techniques that target specialized predators in wildlife protection programs. Our initial work suggests that large male cats may be disproportionately responsible for catastrophic predation in Australia and New Zealand, however other parameters such as age, body condition, experience and hunger should be examined to improve predator profiles. Christensen and McDonald (2013) and Denny and Dickman (2010) have called for targeted novel cat control and we suggest that until further research is conducted, some of these control methods should be developed to target large, male cats. Targeted control measures are urgently needed to tackle problem predators of medium-sized prey in conservation programs and should focus on both ongoing removal of profiled individuals and an immediate targeted response to predation events. Control measures that focus on mimicking the prey species or attracting specific demographic profiles are likely to be the most successful.

Table 3
The characteristics of cats recorded killing reintroduced western quolls and the number of quoll deaths per cat.

Cat	Color	Sex	Weight (kg)	Date captured	Quoll deaths/attacks
Cat 1	Black	M	4.3	12/4/2014	2
Cat 2	Tabby	M	5.0	8/6/2014	3
Cat 3	Tabby	M	4.1	26/6/2014	3
Cat 4	Tabby	M	3.7	9/9/2014	2
Cat 5	Not captured	M	n/a	n/a	1

We acknowledge that kittens that do not fit the profile of a cat capable of specialized predation of challenging prey may grow and learn to specialize on these prey, hence in confined areas eradication of feral cats would typically be the most profitable approach to protect vulnerable wildlife. Exceptions would include where cats play an important role in limiting populations of other pests (e.g. rats) and where those cats capable of preying on rare challenging prey can be targeted by specific control techniques. Profiling cats with the potential for catastrophic predation will be of most value in prioritizing cat management activities in unbounded regions where eradication of cats is not feasible. Management informed by such profiling may be particularly relevant in capture neuter release programs where profiling may help guide decisions regarding which individuals should be euthanased to protect local wildlife.

5. Conclusion

Introduced predators vary intraspecifically in their predation risk to wildlife populations. Our study was the first to use multiple lines of evidence, similar to those used in criminal investigation, to identify the profiles of cats responsible for catastrophic predation. We call for closer integration between the fields of forensic science and conservation biology to assist in threatened species protection. Criminal, aggregate and DNA profiling is used extensively in crime fighting and data mining applications (Hildebrandt, 2008; Kocsis, 2007) and many human forensic and profiling methods could be adapted to predator profiling for threatened species protection. The recent advancement in trace DNA field sampling at crime scenes (Templeton and Linacre, 2014) suggests that matching DNA from animal carcasses to individual predators is becoming more reliable, and when integrated with forensic evidence (spoor patterns e.g. Taberlet and Luikart, 1999, autopsy results, camera trap images) can accurately identify individuals responsible for predation events. Future studies should focus on identifying the individual physical and behavioral traits of specialized predators in wildlife protection programs, and use of these predator profiles to drive efficient and targeted control.

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