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REVIEWS

Stop Jumping the Gun: A Call for Evidence-Based Invasive Predator Management

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Abstract

Invasive mammalian predators are major drivers of species extinctions globally. To protect native prey, lethal control is often used with the aim of reducing or exterminating invasive predator populations. The efficacy of this practice, however, is often not considered despite multiple practical and ecological factors that can limit success. Here, we summarize contemporary knowledge regarding the use and challenges of both lethal control and alternative approaches for reducing invasive predator impacts. As the prevailing management approach, we outline four key issues that can compromise the effectiveness of lethal control: release of herbivore and mesopredator populations, disruption of predator social systems, compensatory predator immigration, and ethical concerns. We then discuss the relative merits and limitations of four alternative approaches that may enhance conservation practitioner's ability to effectively manage invasive predators: top-predator conservation or reintroduction, maintaining habitat complexity, exclusion fencing, and behavioral and evolutionary ecology. Considerable uncertainty remains regarding the effectiveness of management approaches in different environmental contexts. We propose that the deficiencies and uncertainties outlined here can be addressed through a combination of adaptive management, expert elicitation, and cost-benefit analyses. Improved management of invasive predators requires greater consideration and assessment of the full range of management approaches available.

Introduction

Invasive mammalian predators are responsible for many vertebrate extinctions globally (Medina *et al.* 2011; Woinarski *et al.* 2015). Feral cats *Felis catus*, for example, are implicated in at least 14% of insular bird, mammal, and reptile extinctions (Medina *et al.* 2011), and along with the introduced red fox *Vulpes vulpes*, have contributed to the extinction of more than 20 Australian mammals (Woinarski *et al.* 2015). Nine invasive predators feature in the list of 100 of the World's Worst Invasive Alien Species (Lowe *et al.* 2000), and reducing their impacts is considered essential for conserving threatened species.

The most common approach to achieving this goal is to reduce predator population size using lethal control,

such as shooting, trapping, and poison baiting. Such approaches form a core component of conservation policy and practice in all regions where invasive predators threaten biodiversity. Despite the prominence of lethal control across the globe, a number of practical (Newsome et al. 2014; Lieury et al. 2015), ecological (Ruscoe et al. 2011; Colman et al. 2014), and ethical (Wallach et al. 2015) concerns have recently been raised regarding this approach. Further, lethal control is often assumed to benefit biodiversity, with little scrutiny of the actual efficacy of such programs (Reddiex et al. 2006; Walsh et al. 2012). This is concerning given the limited resources typically available for conservation programs and the high costs associated with lethal control. For example, Reddiex et al. (2006) estimated that AU\$21.3m was spent on labor costs alone for red fox control in Australia in 1998-2003. A rare example where the cost-efficiency of concurrent management approaches has been assessed involves the yellow-eyed penguin *Megadyptes antipodes* in New Zealand (Busch & Cullen 2009). The penguin's population growth rate was improved through intensive management (involving medical care, supplementary feeding, and predator trapping) at a cost of NZ\$68,600 per nest, whereas trapping alone (NZ\$35,200) or revegetation (infinite cost due to negative results) did not improve population growth rates (Busch & Cullen 2009).

Given that successful eradication of invasive predators is limited to closed systems, methods are needed that increase the ability of native prey to coexist with predators in open systems (i.e., outside of islands and fenced reserves). We currently lack a cohesive understanding of this important topic because the issues are generally only considered in isolation. Here, we provide new insights by summarizing contemporary knowledge on the use of both lethal control and alternative approaches for reducing the impact of invasive predators on native species. As the prevailing management approach, we outline four key issues that can compromise the effectiveness of lethal control: release of herbivore and mesopredator populations, disruption of predator social systems, compensatory predator immigration, and ethical concerns. We then discuss the relative merits and limitations of four alternative approaches that may enhance conservation practitioner's ability to effectively manage invasive predators: top-predator conservation or reintroduction, maintaining habitat complexity, exclusion fencing, and behavioral and evolutionary ecology. We do not prescribe strict management guidelines because it is not feasible or useful given the complex social-ecological systems in which invasive predator management takes place. Rather, we propose that current uncertainty in invasive predator management can be addressed through a combination of adaptive management, expert elicitation, and cost-benefit analyses. Since lethal control is an essential part of island eradications (Russell et al. 2016), our discussion mainly focuses on mainland and large island situations where eradication is difficult.

Consequences of lethal control

Mesopredator- and herbivore-release

Top-predators are keystone species that regulate the distribution, abundance, and behavior of their prey species and often intraguild competitors as well (Ritchie & Johnson 2009). Consequently, removing predators through lethal control can release subordinate species from suppression and cause unintended negative impacts (Ruscoe *et al.* 2011; Colman *et al.* 2014). Top-predators

can be native, such as wolves Canis lupus in North America and dingoes Canis dingo in Australia, or introduced, such as feral cats on many islands, hence such terms are ecosystem context dependent (Ritchie et al. 2012). Long-term poison baiting in Western Australia has reduced introduced red fox densities, but at some sites this has also resulted in higher cat activity and related predation of threatened mammals (de Tores & Marlow 2012; Department of Parks and Wildlife 2015; Marlow et al. 2015). Similar programs have since been launched in other parts of Australia, and although preliminary results are encouraging (e.g., Robley et al. 2014), the longterm impact on cat populations and their impacts are unknown. In New Zealand forests, the abundance of rats Rattus rattus increased following removal of possums Trichosurus vulpecula, as did mouse Mus musculus abundance when rats were removed, thus demonstrating competitive release of sympatric invasive species (Ruscoe et al. 2011). Killing predators can also have strong impacts on large herbivores, small prey species, and vegetation structure and composition (Dexter et al. 2013; Colman et al. 2014). Such cascading impacts have often not been predicted and have resulted in overall negative outcomes for biodiversity, despite the original intentions of management interventions (Bergstrom et al. 2009; Ruscoe et al. 2011). As such, it is essential that integrated, multispecies approaches are used for management of pest animal species. Multispecies approaches can help prevent

damaging trophic cascades that have occurred where single introduced species have been controlled without sufficient consideration of changes to species interactions (Bergstrom *et al.* 2009; Ruscoe *et al.* 2011).

Disruption of predator social systems

Carnivores are characteristically territorial, and many species have complex social systems (Macdonald 1983). For these species, culling programs may inadvertently remove dominant individuals from populations and disrupt their social systems. Wallach et al. (2009) showed that where lethal control was practiced, dingo abundance fluctuated with rainfall-driven environmental productivity, most likely because control removed dominant individuals and destabilized pack social structure and population regulation. Dingoes are typically poisoned to protect livestock from predation, but studies show that poison baiting can actually result in greater calf losses (Allen 2013) and lower productivity due to increased grazing by native kangaroos Macropus spp. released from predation (Prowse et al. 2014). In the United Kingdom, culling of badgers Meles meles to reduce bovine tuberculosis risk in cattle actually resulted in higher disease incidence due to the disruption of badger social states and increased ranging activity of surviving individuals and risks to anin

(McDonald *et al.* 2008). These subtle impacts have rarely been considered in lethal control programs, but have high potential to cause more damage than good to both ecological and agricultural systems.

Compensatory immigration

Given high costs and other logistical constraints, lethal control is generally focused on a subset of a landscape surrounded by an area subjected to less intense or no control at all. Logistical constraints that may limit the effective area of lethal control include needing to check traps daily, avoiding areas populated by humans, not dispensing poisons near watercourses, reducing risks to nontarget species (both domestic and native), and the remoteness and inaccessibility of many regions. By their nature, invasive predators are typically highly mobile and have good dispersal abilities. This means that predators can quickly invade areas where previously resident individuals have been removed-a process termed compensatory immigration (Lieury et al. 2015; Minnie et al. 2016). In south-eastern Australia, feral cat numbers increased during a culling program and then stabilized to precull levels following the cessation of control (Lazenby et al. 2014). The authors posited that this occurred because culling removed dominant resident cats, which allowed younger and/or previously subordinate individuals from surrounding areas to invade the vacated territories (Lazenby et al. 2014). A related phenomenon is increases in predator population size due to enhanced juvenile survival following culling of adults, such as that seen in feral ferrets Mustela furo in the United Kingdom (Bodey et al. 2011). These examples, and others (Gentle et al. 2007; Newsome et al. 2014), illustrate how short-term, uncoordinated, or pulsed lethal control can be ineffective. Although, there are other examples where long-term lethal control has reduced predator populations and benefited native species (e.g., Robley et al. 2014).

Ethical considerations

Culling of pest animals to protect biodiversity raises complex ethical dilemmas (Wallach *et al.* 2015; Russell *et al.* 2016). Prioritizing the conservation of species over the value of individual animals is often used to justify culling programs. But this logic is challenged when culls fail to have a positive impact on the species they aim to protect, or worse, cause more damage than good (Bodey *et al.* 2011; Marlow *et al.* 2015). Additional concerns include wasting limited conservation funds on ineffective culls, and risks to animal welfare due to potentially inhumane control techniques (Littin *et al.* 2014). Lethal control will continue to be an important part of predator management, hence it is important that the ethics of this practice are well justified with evidence.

Alternative approaches

Top-predator conservation and reintroduction

Native top-predators contribute to ecosystem function and resilience by regulating herbivore and mesopredator populations (Ripple et al. 2014). However, many large carnivores are declining due largely to habitat loss and persecution by humans aiming to reduce damage to livestock (Ripple et al. 2014). Such declines can compound the problems of already stressed ecosystems (Doherty et al. 2015). On the other hand, recovery of native toppredators can reduce invasive predator populations, such as declines in introduced mink Neovison vison following the recovery of otters Lutra lutra in England (Bonesi et al. 2006). Approaches that can aid the persistence and recovery of native top-predators include protective legislation, supportive public opinion, and nonlethal tools (e.g., guardian animals, discussed below) (Chapron et al. 2014). Government policy or legislation for mandatory use of lethal control by landholders must be reviewed if such progress is to be achieved. Another promising endeavor is reintroductions of native top-predators into areas of their former range (a form of rewilding) (Ritchie et al. 2012), such as otters in the United Kingdom (Bonesi & Macdonald 2004) and the proposed reintroduction of Tasmanian devils Sarcophilus harrisii to mainland Australia (Hunter et al. 2015).

Positive management of top-predators is a contentious issue due to potential social, economic, and environmental conflicts. This means that prior to management actions taking place, potential conflicts should be formally considered, perhaps using decision theory approaches that can help optimize outcomes in complex situations (e.g., Driscoll et al. 2010). In addition, studies using similar methodologies have produced divergent conclusions regarding the ecological impacts of dingoes in Australia (Dickman et al. 2014), and additional experimental studies are therefore required to help resolve scientific conjecture that currently hinders advances in predator management (Newsome et al. 2015). In some cases, native top-predators may also depredate threatened species (Oakwood 2000) or livestock (Potgieter et al. 2013), and this should be considered in any rewilding plans. Guardian animals are one solution that can reduce local-scale predation by both native and introduced predators of livestock and threatened species (van Bommel 2010).

Maintaining and restoring habitat complexity and ecological refuges

Reductions in habitat complexity through fire, grazing, and land clearing can worsen the impacts of predators by removing protective cover for prey species (Leahy et al. 2016). The maintenance of ecological refuges through less intense grazing and patchy fire (e.g., via appropriate prescribed burning) may increase the ability of native fauna to coexist with predators (Doherty et al. 2015). Accordingly, conservation practitioners should consider habitat protection, revegetation projects, and grazing and fire management as crucial and complimentary components of predator abatement plans. Landscape-scale fire and grazing experiments in northern Australia show that appropriate management of these two processes can conserve habitat refuges and boost native mammal populations, even in the absence of direct control of feral cats (Kutt & Woinarski 2007; Legge et al. 2011). The use of prescribed fire presents logistical constraints with regard to controlling fire size and intensity, and protecting human lives and property. Multicriteria decision-making approaches may help resolve potential conflicts between societal and environmental values (Driscoll et al. 2016).

In some cases, artificial refuges or nest exclosures may provide a stopgap to temporally diminish predation pressure (reviewed in Smith *et al.* 2011). Nest exclosures are particularly attractive because they need only be used during the nesting season, hence reducing time and labor commitments. Although, their effectiveness should be assessed experimentally for individual species (Lettink *et al.* 2010), especially since exclosures can lead to nest abandonment and higher adult mortality (e.g., Pearson *et al.* 2012). Further, it is important to acknowledge that nest exclosures are usually deployed over relatively small areas and may be costly.

Exclusion fencing

The creation of predator-free reserves using exclusion fencing is an effective, albeit costly, method for conserving populations of threatened species unable to withstand even very low levels of predation. Fencing has high construction costs (e.g., \sim AU\$10,000 km⁻¹; Bode *et al.* 2012) and requires ongoing monitoring and maintenance to prevent predator incursions. Additionally, fencing can cause by-catch and death of native animals (Ferronato *et al.* 2014) and this should be managed appropriately. Further considerations include reducing inbreeding and potential overpopulation of species within enclosures. Decision support tools can help identify optimal locations for fences subject to economic, ecological, and political constraints (Bode *et al.* 2012). For the

conservation of threatened reptiles in New Zealand, Norbury *et al.* (2014) estimated that exclusion fencing was most cost-effective for areas < 1 ha in size, whereas a "leaky" fence was most cost-effective for areas 1–219 ha, and trapping most cost-effective for areas > 219 ha. Similarly, for protection of eastern barred bandicoots *Perameles gunnii*, Bode & Wintle (2010) used a return on investment framework to demonstrate that the most efficient fence design, and hence cost, varied with exclosure size. To elucidate the relative merits of exclusion fencing in different contexts, additional cost-benefit analyses across a range of locations, predators, and prey species are needed.

Behavioral and evolutionary ecology

An exciting new frontier in conservation and pest management is using behavioral and evolutionary ecology to better understand the mechanisms behind predators' impacts on prey, and ultimately to increase prey survival. Predator avoidance training has had limited success at increasing the survival of reintroduced threatened species, particularly where the predator is introduced (Moseby et al. 2016). As an alternative, Moseby et al. (2016) propose that in situ encounters between wild predator and prey populations could promote natural selection of appropriate prey defensive traits. Whether such approaches can lead to improved outcomes for threatened species remains to be determined, although at the Arid Recovery reserve in South Australia, 350 burrowing bettongs Bettongia lesueur are coexisting with three feral cats inside a 24 km² exclosure, and possibly increasing their vigilance behavior (K. Moseby, personal communication).

Using intraspecific behavioral variation—"animal personalities" (Wolf & Weissing 2012)-to understand and predict predation events is another area that requires further research. The failure of reintroduction attempts for threatened species is commonly caused by only a few individual predators, perhaps due to specialized hunting behavior (Moseby et al. 2015). Lethal control such as baiting (Thomson et al. 2000) or cage trapping (Short et al. 2002) may paradoxically target younger or less efficient hunters that are less of a threat to vulnerable prey species. Profiling of "problem" predators may help target control efforts toward those individuals most likely to compromise threatened species reintroductions (Moseby et al. 2015). However, even if problem predators can be reliably identified, and importantly removed from populations, it remains uncertain how long such benefits to prey would persist before other problem predators might arise. This is because although predator populations are likely to be composed of different individuals that vary in their behavioral traits, they may also display behavioral plasticity in response to the presence/absence of conspecifics and intraspecific competition.

Tackling uncertainty

Given the identified limitations and uncertainties, determining when, where, and how to manage invasive predators remains a considerable challenge for conservation practitioners and the development of effective pest management policy. There exists a strong need to increase the quality and amount of information available regarding the effectiveness of management approaches in different environmental contexts. Such information is essential for determining whether management interventions meet their intended objectives (e.g., the increase in a threatened species' population, or ecosystem recovery, following invasive predator control), provide return on investment, and ultimately improve the conservation status of species we are trying to protect. However, the design of many management programs may impede practitioners' ability to answer these questions. For example, Reddiex & Forsyth (2006) found that 67.5% of pest animal control programs in Australia did not monitor pest or resource (e.g., threatened species) responses to management interventions, nor did they involve a nontreatment area (experimental control).

We propose that the deficiencies and uncertainties outlined here can be addressed through a combination of adaptive management (AM), expert elicitation, and cost-benefit analyses. Rather than discussing the known barriers to adoption of AM and possible solutions (see Westgate et al. 2013; Williams & Brown 2016), we focus on how AM can be applied to predator management. An AM approach would involve: (1) definition of management goals, (2) development of management approaches to achieve these goals, (3) experimental implementation of two or more management approaches (including doing nothing as an option), (4) monitoring and analysis to evaluate the relative merits and limitations of different approaches, and (5) iterative modification of management strategies to improve management outcomes (Parkes et al. 2006; Westgate et al. 2013).

Two tools that are increasingly being used to inform decision making in conservation science and are particularly well suited to a "learning by doing" approach are expert elicitation (Martin *et al.* 2012) and Bayesian networks (BNs) (Nyberg & Marcot 2006). Other decision theory and optimization approaches are also likely to be useful here (e.g., Bode *et al.* 2012), although we use BNs as an exemplary analytical approach. BNs represent causal and correlative interactions between variables as a network of nodes, and we envisage that a BN would be

involved in all stages of the AM approach. The initial network diagram could be developed during steps 1 and 2 through expert elicitation, which serves dual purposes of engaging with stakeholders and gaining information that can reduce system uncertainty. The experimental manipulation and monitoring in steps 3-4 could be designed to address particular nodes and uncertainties in the network. Lastly, the new information could be used to update and refine the model (step 5), and increase confidence in the use of different management approaches. Two relevant examples include the use of BNs to assess bird responses to grazing and fire (Howes et al. 2010) and evaluation of feral cat management options with regard to stakeholder values (Loyd & DeVore 2010). Incorporating cost-benefit analyses into this framework will also help guide management by assessing the suitability of different techniques across a range of environmental contexts (Busch & Cullen 2009; Bode & Wintle 2010; Norbury et al. 2014).

Robust experimental monitoring of both predator and prey species should be used in steps 3 and 4 to obtain the most reliable information regarding management effectiveness. For example, Lettink et al. (2010) used a randomized and replicated before-after, control-impact design to show that predator control, but not artificial refuge supplementation, increased skink Oligosoma maccani survival in New Zealand. Such a design could be used in Australia to, for example, assess the population response of small mammals to different combinations of prescribed fire (e.g., patchy or uniform) and predator control (e.g., poison baiting or not). Where economic and/or logistical constraints prevent replicated and randomized experimental manipulations, quasi- and natural experiments should also be considered as alternatives (Hone 2007).

We reiterate that it is not feasible or useful to prescribe strict guidelines for invasive predator management. However, there are key principles that should underlie all management programs: (1) the aim should be to reduce predator damage to species and ecosystems, rather than merely reduce predator numbers per se; (2) it is necessary to demonstrate, rather than assume by association, predator damage to species and ecosystems; (3) a combination of management approaches can be used and should be considered; (4) the control of one species can affect others; and (5) management actions should be evidence-based.

Conclusions

We identified potential key limitations in both the prevailing approach of lethal control to reduce invasive

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predators' impacts on native species and alternative approaches such as exclusion fencing and top-predator restoration. Remedying this situation necessitates urgent and careful assessment of the full range of options available to managers prior to any interventions, and this should involve economic, environmental, and social considerations. Some of the management approaches discussed (e.g., nest exclosures and exclusion fencing) are relatively small scale and intensive in nature compared to, for example, the larger areas over which lethal control is often conducted. This point reiterates the fact that no approach is without limitations; effective and efficient management requires different combinations of techniques depending on local context. Improved management of invasive predators requires greater consideration and assessment of the full range of management approaches available.

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