Received: 19 July 2020 | Revised: 25 January 2021 | Accepted: 18 April 2021

DOI: 10.1111/csp2.447

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access

WILEY

Bettering the devil you know: Can we drive predator adaptation to restore native fauna?

Adrian D. Manning[1] | Tim A. Andrewartha[1] | Anton Blencowe[2,3] | Kyle Brewer[2,3] | Iain J. Gordon[1,4] | Maldwyn J. Evans[1,5]

[1]Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia

[2]Applied Chemistry and Translational Biomaterials Group, School of Pharmacy and Medical Sciences, University of South Australia, Adelaide, South Australia, Australia

[3]Future Industries Institute, University of South Australia, Mawson Lakes, South Australia, Australia

[4]James Hutton Institute, Dundee, UK

[5]Department of Ecosystem Studies, Graduate School of Life and Agricultural Sciences, The University of Tokyo, Tokyo, Japan

Correspondence
Adrian D. Manning, Fenner School of Environment and Society, The Australian National University, Canberra, ACT 0200, Australia.
Email: adrian.manning@anu.edu.au

Abstract

Predation of threatened fauna by native and introduced predators can drive extinction and prevent population recovery. Most predator management involves exclusion or culling. Evidence suggests that exclusion may have detrimental effects on a prey species' predator awareness. At the same time, culling can cause selection of control-resistant predators. There is increasing interest in harnessing evolutionary processes to drive adaptation of threatened fauna to cope, but there is limited attention on trying this from the predator direction. We need to shift the survival advantage away from predators that avoid lethal control, and go on to kill, towards those that demonstrate behaviors that reduce impact on threatened fauna. Instead of driving undesirable predator selection, could we select through management actions desirable traits to make them "less lethal" to threatened fauna? We draw on experimental research on predator aversion that suggests there may be an alternative way to mitigate the impacts of predators, while maintaining the learning opportunities of prey species. Using the case study of the invasive red fox in Australia, we propose a conceptual framework within which future research and management could occur to select for these desirable traits in predators and develop practical regimes for predator impact mitigation.

KEYWORDS

adaptation, conditioned taste aversion, invasive species, pest control, predators, prey, threatened fauna

1 | BETTERING THE DEVIL YOU KNOW

We are currently in the midst of an anthropogenic global biodiversity crisis, which includes population declines and mass extinctions similar to those seen in the previous five mass extinction events (Díaz et al., 2019). The pervasive drivers of the current crisis, the "Anthropocene defaunation" (Dirzo et al., 2014), are direct harvest and overexploitation, habitat loss and modification, invasive species (including diseases), pollution and anthropogenic climate disruption (Young, McCauley, Galetti, & Dirzo, 2016). One key driver, predation by invasive predator species, has been identified as a contributing factor in 58% of all bird, mammal and reptile extinctions, with endemic island fauna the most vulnerable to their impacts (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016). The most extensive damage has been caused by invasive mammalian predators through a combination of direct predation, competition, disease transmission and facilitation (Doherty et al., 2016). In response to this, there have been numerous attempts to manage wildlife to arrest these declines and extinctions; some successful and many not. Examples include managing invasive exotic predators, such as red foxes (*Vulpes vulpes*) and cats (*Felis catus*) in Australia (Saunders, Gentle, & Dickman, 2010); stoats (*Mustela ermine*), weasels (*Mustela nivalis)*, cats, possums (*Trichosurus vulpecula*) and rats (*Rattus* spp.) in New Zealand (Innes, Kelly, Overton, & Gillies, 2010); and American mink (*Neovison vison*) in Scotland (Bryce et al., 2011), and the reintroduction of mammals to their former ranges following local extinction (Armstrong, Seddon, & Moehrenschlager, 2019).

Globally, control of predators—native or exotic—is a widely used management tool to allow other species to persist, or to protect animals with commercial value (Treves & Karanth, 2003). For exotic predators, however, total eradication is either difficult (technically or financially) or impossible. For native predators, control may be undesirable because of the ecological or cultural value of the species. These constraints lead to a key question:

Can we find ways for threatened native fauna to live with predators, thereby achieving conservation or commercial goals?

1.1 | Using evolutionary principles for adaptation of prey species

In recent years, there has been growing interest in ways to make native animals more likely to adapt and survive following reintroduction. One proposed solution is to use evolutionary principles of natural selection to drive reintroduced animals towards predator resistance (Blumstein, Letnic, & Moseby, 2019; Evans et al., 2021; Moseby, Blumstein, & Letnic, 2016; Moseby, Letnic, Blumstein, & West, 2018). It is thought that exposing reintroduced animals to low levels of predation could accelerate the selection for antipredator traits (behavioral, morphological), allowing a viable population of predator-resistant animals to survive in the presence of exotic predators. Crucially, the level of predation should be enough to drive directional selection towards individuals that have predator-resistant traits, but low enough that it does not threaten the viability of the prey population (Evans et al., 2021; Moseby, Letnic, Blumstein, & West, 2019; Osmond, Otto, & Klausmeier, 2017). Finding this balance is challenging and is the subject of increasing research interest.

1.2 | A potential missing piece of the puzzle—Using evolutionary principles for the adaptation of the *predator* species

Despite recent interest in driving the adaptation of *prey* species, there is a conspicuous absence of discussion, and research, on using the same evolutionary principles to drive adaptation of the exotic *predator* species (though there has been work on manipulating predator behavior; see below). Here, we make the argument that we should be approaching this problem of native species predation from both directions—by adapting prey AND predators for coexistence. We use the example of introduced predators in Australia to discuss the potential evolutionary risks of current management techniques and argue for more innovative thinking and strategies for managing exotic predators over the long term.

There is no more unambiguous example of the extinction crisis than the case of Australia; a continent that, globally, has suffered the worst rate of recent mammal extinction (Woinarski, Burbidge, & Harrison, 2015). At least 24 species have been lost since the 19th century, and many only persist on off-shore islands, refugial habitats or fenced sanctuaries (Legge et al., 2018; Woinarski et al., 2015). One of the key drivers of these extinctions events has been the devastating effect of introduced predators on "critical weight range" native mammals that fall between 35 and 5,500 g in size (Johnson, 2006; Woinarski et al., 2015). Introduced cats and foxes represent a significant barrier to the restoration of native mammals "beyond-the-fence," that is, outside predator free islands and fenced sanctuaries (Evans et al., 2021; Legge et al., 2018). This is because of the difficulty of reducing introduced predator populations, through lethal control, to low enough levels, and at large enough scales, permanently for native mammals to re-establish and persist (Evans et al., 2021).

For many native species, the restoration of populations outside predator-proof fenced reserves, in the presence of introduced predators, currently seems very challenging (though with some notable exceptions e.g., Orell, 2004). While there are hopes of new solutions that might lead to the total eradication of feral animals from the continent, such as gene drives that make introduced species infertile (Prowse et al., 2017), these are still some way off. In the meantime, we have little choice but to mitigate the impacts of introduced predators. Current tools include total exclusion with predator-proof fences (Legge et al., 2018) or methods of control (i.e., culling) through shooting, poisoning, trapping, den fumigation and destruction, as well as bounty schemes to increase culling through community participation (Saunders & McLeod, 2007). Evidence suggests that none of these tools of control will result in the total eradication of foxes and cats from the continent of Australia, due to re-invasion from outside control areas (Berry & Kirkwood, 2010; Gentle, Saunders, & Dickman, 2007), and the avoidance of control methods by a proportion of the predator population (Allsop et al., 2017). Control methods can, however, be used to reduce and control introduced predator populations and reduce impacts in the short term (Allsop et al., 2017).

1.3 | Could current predator control efforts be making the problem worse?

Many of the current approaches to controlling introduced predators, could in fact, be making the problem worse in the long term. The phenomenon of animal control driving selection is well understood for hunting (Allendorf & Hard, 2009; Darimont et al., 2009; Stillfried, Belant, Svoboda, Beyer, & Kramer-Schadt, 2015). In fact, human-driven selection is considered one of the most rapid drivers of selection, outpacing many other more "natural" drivers (Darimont et al., 2009). Yet, in the context of introduced predator control, relatively little attention has been paid to this process. While the impacts of conservation actions have been considered (Shefferson et al., 2018), only a few studies have looked at examples in introduced predators. For example, it has been shown that red foxes shift their activity in response to human disturbance (Díaz-Ruiz, Caro, Delibes-Mateos, Arroyo, & Ferreras, 2016), and show compensatory birth effects as a result of non-specific culling (Berry & Kirkwood, 2010; Marlow, Thomson, Rose, & Kok, 2016). Migration in response to culling has also been shown in the red fox (Gentle et al., 2007; Lieury et al., 2015), resulting in source-sink dynamics where animals in source populations, outside of the control area, migrate to areas of higher mortality, known as sinks, created by culling. Other predators have demonstrated similar responses; for example, culling of black-backed jackals (*Canis mesomelas*) has been shown to lead to compensatory birth effects, and increased migration into the control areas (Minnie, Gaylard, & Kerley, 2016). Some preliminary evidence suggests that the most effective control measures can select for animals that avoid that measure (Allsop et al., 2017; Minnie et al., 2016); although the response can be expected to be context-specific. Modeling has shown that undesirable "education" of invasive predators can "create and maintain an uncatchable segment in the population with respect to a given control tool" (p.1234; [Bischof & Zedrosser, 2009]). A logical adaptive consequence of long-term fox control is "control-resistant" or "bait-shy" foxes. That is, individuals that evade each control method and survive, remain lethal to CWR mammals, and can breed and pass on control-avoiding traits to young. If resistance to control is passed on to young, either genetically or through learned behavior, it may mean that control methods reinforce control resistance of fox populations. In short, control without total eradication potentially selects for undesirable traits in introduced predators that in turn makes restoration of native mammals more difficult and expensive (Allsop et al., 2017).

2 | A POTENTIAL SOLUTION?—INTENTIONAL SELECTION TO DRIVE ADAPTATION OF PREDATORS

A successful reintroduction program consists of a suite of animal- and environment-focused tactics (Batson, Gordon, Fletcher, & Manning, 2015). The adaptation of prey species discussed earlier falls within the animal-focused category of tactics. Research in eliciting predator-resistant traits in native Australian mammals is showing some promise (Blumstein et al., 2019; Evans et al., 2021; Moseby et al., 2016; Moseby et al., 2018). However, while total eradication of introduced predators is a long way off on mainland Australia, and tolerances of native animals with lowered densities of predators are not well known, it is not clear that only adapting native animals *ex* or *in situ* will be enough to allow their long-term restoration at a broad scale. This leads naturally to the question: *what environment-focused tactics (*i.e.*, those that relate to making the recipient ecosystems suitable to support the reintroduction of a given species) can be employed to improve the chances of conservation success?* The next logical step, we believe, could be to apply the same evolutionary principles of driving adaptation of prey species (animal-focused tactic) to the predator species (environment-focused tactic). If we accept that we cannot cull all of the introduced predators in a population, could it be possible to manipulate the remaining individuals to be less lethal to native animals? The idea has been proposed of creating "conditioned" wolf (*Canis lupus*) packs that are less lethal to livestock (though shock-collar aversion) and exclude other wolves that are not conditioned (Mech, Fritts, & Nelson, 1996; Schultz, Jonas, Skuldt, & Wydeven, 2005). Could this concept be extended to other canids, like foxes, coyotes (*Canis latrans*) and dingos (*Canis familiaris dingo*), at the population level? It has

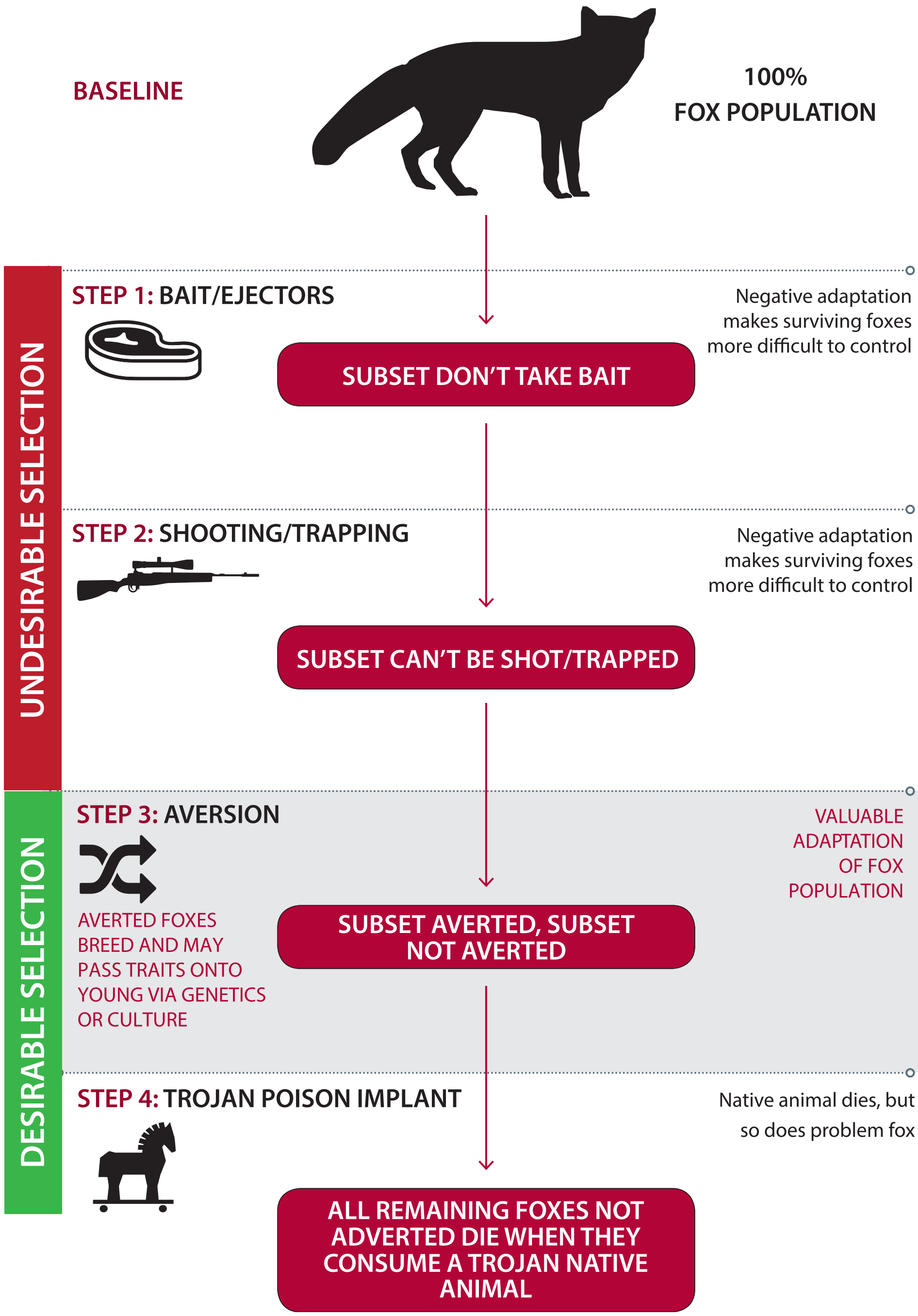

FIGURE 1 A "Bettering the devil" conceptual model for adapting foxes to be less lethal to threatened native fauna. Beginning with a 100% pool of foxes (Baseline), conventional culling methods are employed (as occurs regularly in many places in Australia). Though essential to "knock-down" the population (Step 1 and 2), these techniques can select for "non-desirable" traits in foxes that are not killed. The remaining sub-set of foxes are exposed to "aversive" technologies—that is, those that make them avoid the threatened native fauna of interest such as conditioned taste aversion and shock-collars (Step 3)—reducing predation rates. At the same time, native founders will also be selected/conditioned to be "predator aware." Foxes that are resistant to aversion may go on to kill a native animal of interest containing a toxic implant, but consequently die (Step 4). While this means one native animal dies, the fox cannot go on to kill more or pass on its genes or behavior to offspring. Step 3 and 4 therefore select for individuals with desirable traits, and thus the only foxes that can reproduce in a given area are "less lethal" to the threatened native fauna of interest. This does not mean that native fauna are not preyed upon, but that the pressure on a restored population is lower, and the regime will drive adaptation in prey and predator. The scales over which this approach would be effective would need to be determined by large-scale experimentation

been established experimentally that it is possible to rapidly domesticate the red fox, that is, select for desirable behavioral characteristics (Dugatkin, Trut, & Trut, 2017). It has also been shown that occupation of urban environments by foxes can drive morphological divergence from rural foxes, in a process with similarities to domestication (Parsons et al., 2020). Given this evidence of behavioral and morphological malleability, could this be harnessed to drive desirable characteristics in free-living rural fox populations? For example, if there is selection as a result of control measures, could we select for desirable traits (i.e., less lethal to native animals of concern), the most obvious being an aversion to eating native animals, rather than select for traits that make control measures more difficult and costly, and that ultimately result in failure? In short, we need to shift the survival advantage away from predators that avoid lethal control, and go on to kill, towards those that demonstrate behaviors that reduce impact on threatened fauna.

2.1 | Bettering the devil? The fox in australia

In Figure 1, we outline a conceptual framework for adapting exotic red foxes in situ in the wild, to favor less lethal individuals. Although we use the red fox in Australia as an example, this framework could be adapted to other predators and situations. The approach aims to steer fox populations away from containing "uncontrollable" individuals towards ones that have a lower impact on species of concern (i.e., condition the fox population). If successful, this approach could add to the suite of tactics used to provide beyond-the-fence restoration of CWR species and facilitate their adaptation to the presence of introduced predators. At the same time, we note that logically, some predation of reintroduced mammals by native and exotic predators will be required for prey populations to be able to adapt and survive beyond-the-fence (Moseby et al., 2019; Osmond et al., 2017).

Currently, management efforts focus on control (i.e., culling). If we imagine the total pool of introduced predators in a population (Figure 1, Baseline), under standard pest management, a certain percentage will be removed by the standard control methods (Figure 1, Step 1 and 2). The remaining pool of control-resistant foxes is currently problematic for CWR mammals, other susceptible species and some livestock (Allsop et al., 2017). However, could these foxes be made averse to preying upon the species of interest (Figure 1, Step 3)? Could this remaining pool of foxes, be re-directed to "protect" the prey from other predators through exclusion of conspecifics, as suggested for wolves (Mech et al., 1996; Schultz et al., 2005)?

Two techniques that could elicit aversion (Step 3) to predation of native animals are (a) electric shock-collars and (b) conditioned taste aversion (CTA). Electric shock-collars work by delivering an electric shock (and sometimes an accompanying warning noise) to the predator before they approach livestock (or the farm on which they live). The principle of averting livestock depredation using electric shock collars has been demonstrated in wolves (Schultz et al., 2005) and coyotes (Andelt, Phillips, Gruver, & Guthrie, 1999; Linhart, Roberts, Schumake, & Johnson, 1976). Interestingly, Linhart et al. (1976) elicited coyote aversion to rabbits—an animal of a similar size to many Australian CWR native species. While the technology has been rather cumbersome in the past, developments in GPS, batteries and mobile technology could make this a more feasible option to automate and deploy at broader scales involving more predators in a population. Fitting proximity collars (that initiate a warning then shock if the predator approaches too close) on a portion of the native animal population may also be necessary to develop conditioning of the predator population. The use of "geofences" (GPS delineated virtual fences which cannot be approached without initiating a warning and then a shock) to create "safe zones" for native animals may also be an option. The concept is already used for management of grazing animals (https://nofence.no/en/).

Conditioned taste aversion is the phenomenon whereby sub-lethal illness (nausea, vomiting, malaise), is associated with a food or poison, following consumption by an animal, which subsequently reduces or ceases consumption of that particular food item (Cowan, Reynolds, & Gill, 2000; Macdonald & Feber, 2015). The development of toxins which cause nausea on ingestion has been observed to reduce the level of predation on a prey species in natural systems (Skelhorn & Rowe, 2007). While this adaptation does not protect the individual consumed, the negative symptoms a predator will experience reduces the level of consumption of toxic prey. It has been shown that a predator will learn and modify its level of consumption of a prey species when the toxin burden for that species is artificially altered (Skelhorn & Rowe, 2007). While it will not prevent predation completely, it will lead to predators eating a greater proportion of other prey species where available (Carle & Rowe, 2014; Gustavson, Garcia, Hankins, & Rusiniak, 1974). This could be particularly useful where the alternative prey is also an invasive species, such as rabbits in Australia. This switch was demonstrated by Gustavson et al. (1974) who were able to make coyotes averse to eating sheep while maintaining predation of rabbits. Successful examples of artificially eliciting this aversion to live prey with inanimate baits have also been achieved in many species (Jolly, Kelly, Gillespie, Phillips, & Webb, 2018; Nicolaus, Hoffman, & Gustavson, 1982; O'Donnell, Webb, & Shine, 2010; Ward-Fear, Thomas, Webb, Pearson, & Shine, 2017), including canids (coyotes) (Ellins & Catalano, 1980; Ellins, Catalano, & Schechinger, 1977; Gustavson et al., 1974).

Experiments have shown that fox behavior can be modified with aversive baits containing lithium chloride, with a reduction in San Clemente Island fox (*Urocyon littoralis clementae*) recapture rates seen in comparison to control baits, and reward removal (no bait) on San Clemente Island, California (Phillips & Winchell, 2011). Further, a controlled experiment in which red foxes were fed meat containing chemicals that induce nausea (e.g., levamisole) has shown that they become averse to the meat afterwards (Massei, Lyon, & Cowan, 2003). Similarly, Gustavson, Gustavson, and Holzer (1983) elicited CTA in dingos and new Guinea wild dogs (*Canis familiaris hallstromi*). Figure 2 shows a wild red fox rejecting an untreated meat bait after baiting of a landscape with levamisole-treated bait (Andrewartha, unpublished data). Varying success has been seen in trials with wild fox populations, however, research has shown significant reductions in fox depredation of eggs through conditioned taste aversion (Gentle, Massei, & Saunders, 2004; Maguire, Stojanovic, & Weston, 2009). A reduction in fox depredation of eggs was also seen to increase productivity in a population of partridges in Europe (Tobajas, Descalzo, Mateo, & Ferreras, 2020). Given this, could baits that smell of a native animal be used to "train" wild fox populations to avoid CWR mammals of interest? This has already been demonstrated with free-living raccoons (*Procyon lotor*) (Nicolaus et al., 1982), and an aversion to an overshadowing artificial odor (vanilla) has been demonstrated in captive canids (dogs) (Tobajas et al., 2019), but it is an area that requires further investigation for foxes. Such methods could drive adaptation of less lethal foxes that avoid native animals and, exclude through territoriality, more lethal foxes from elsewhere in the landscape. Some foxes are known to hold territories with an exclusive core home range with little sharing between individuals (Carter, Luck, & McDonald, 2012). If this territoriality resulted in exclusion of nonaverse foxes by averse foxes, even partially, it could augment the other control measures (and coupled with tactics that condition native fauna to avoid predators), and could make the difference between a successful and unsuccessful reintroduction. Further, if aversion was passed on to the young, either genetically or behaviorally, it could potentially have a population-level effect on the introduced predator. Gustavson et al. (1974) speculated that feeding habits of mother coyotes might be transferred to young via milk and early experience of food brought to the den. Such mechanisms have been demonstrated in captive rats (*Rattus norvegicus domestica*) (Galef & Clark, 1972;

FIGURE 2 Non-lethal aversion treatment of wild fox populations has potential to help develop desirable behavioral responses in a population, as part of a multi-tactic management framework. Following treatment of a landscape with levamisole-treated baits, this sequence shows a fox uncovering and interacting (smelling) a bait, before scent marking at the bait station and leaving it unconsumed (Andrewartha, unpublished data). If this response could be transferred to live native animals, it could assist in driving adaptation of foxes to be less lethal to threatened native fauna. Photos: Tim Andrewartha

Galef & Henderson, 1972), and it would be worth testing this phenomenon with a range of predators in a free-ranging situation because it could reinforce population-level conditioning. This would make them less lethal to the native mammals that they have been "conditioned" not to attack. Another advantage of keeping "less lethal" foxes in a given landscape, is that they could prevent compensatory increases in female fox fecundity that has been observed in situations where fox (Berry & Kirkwood, 2010; Marlow et al., 2016) and black-backed jackal (Minnie et al., 2016) numbers have been artificially reduced.

We note that standard control methods (Figure 1, Steps 1 and 2) are likely to continue to be necessary whilst prey species are vulnerable to predation from control-resistant predators. The hope would be that by reducing the effectiveness of the predator and allowing the prey to persist under a reduced predation pressure could establish a balance between predator and prey allowing both to persist in the same landscape while reducing the amount of intervention needed (though this would have to be tested through adaptive management). This would help reduce the risk of selecting for control-resistant foxes.

3 | WHAT ABOUT ANIMALS THAT CANNOT BE CONTROLLED AND CANNOT BE AVERTED? WILL WE JUST SELECT FOR A SUPER-LETHAL, IMPOSSIBLE-TO-KILL FOX?

If individual introduced predators cannot be controlled by conventional means, and cannot be taught to avoid native mammals, there is a real risk of selecting for a population of "super" predators that are the most difficult to control that is, that cannot be culled (Step 1 and 2) or "averted" (Step 3). It has already been suggested that "problem animals" may be responsible for the majority of predation events in some circumstances, and this may be particularly damaging in small populations of a rare species (Jaeger et al., 2001; Moseby, Peacock, & Read, 2015). It is, therefore, essential to develop a technique that can mitigate the impact of these animals (Figure 1, Step 4). The concept of "Toxic Trojans" (Read, Peacock, Wayne, & Moseby, 2016) could provide promise as an ultimate means of removal of control resistant predators (e.g., cats and foxes). This idea makes use of a microchip-sized implant containing a toxicant and a protective coating that can be injected subcutaneously into a native animal. The coating renders the implant inert when under the skin of the native animal, where it can remain stable indefinitely. However, if the native animal is consumed by a predator the implant is exposed to the acidic environment of the predator's stomach, resulting in the dissolution of the implant's protective coating, and the release of the poison, killing the consumer of the native animal. While the individual native animal dies, so does the predator—which prevents further killing of native animals, protects the remaining native animal population, and selects *against* potential problem foxes.

We recognize that there are ethical, research and development challenges to make this conceptual management framework possible. Research needs include proving the in-field viability of adaptive techniques such as aversion and Trojan technologies. Further, there would need to be development of optimal regimes; for example, how often would CTA baits need to be distributed in a landscape to maintain the requisite level of aversion? Aversion techniques are known to require ongoing reinforcement because effects can diminish over time (Linhart et al., 1976; Macdonald & Feber, 2015). How many individuals of a native species would have to be implanted with Trojan implants to drive adaptation towards less lethal foxes? Over what scale would such a regime need to occur to be effective, and be resistant to invasion of naive predators from surrounding areas (noting that maintaining "less lethal" foxes within the control area could theoretically reduce the "sink" caused by lethal control)? Answering questions such as these will require large-scale trials. Nevertheless, what is clear is that new or enhanced strategies are needed to address the difficult challenge of managing exotic predators for threatened fauna restoration. Social license will need to be explored as part of the implementation this framework in the context of an overall benefit for the conservation of threatened species.

Of course, our approach would only protect specific individual native species. It would not protect other native fauna. Arguably, however, other native fauna that have persisted to the present day have been more resilient to fox predation than CWR mammals that are currently locally extinct, and Steps 2 and 3 (Figure 1) would benefit these species by reducing gross fox numbers (Robley, Gormley, Forsyth, & Triggs, 2014). In addition, the ability to reintroduce CWR mammals that bring with them the return of important ecosystem processes may bring greater overall net benefits for biodiversity and ecosystem health.

4 | CONCLUSION

With new technologies and regimes, it may be possible to drive adaptation of predators so that they are less lethal to extant and reintroduced fauna. The fundamental difference between traditional predator management through culling, and the "Bettering the Devil" conceptual framework, is that the former aims to *minimize* the percentage of the population that has learned aversion towards baits (Bischof & Zedrosser, 2009), whereas the latter aims to *maximize* the proportion of a population that has learned aversion towards the bait and/or associated live prey. Furthermore, our conceptual framework aims to minimize the percentage of non-condition averted predators in the population, that is, via elimination from consumption of a native animal containing a Trojan implant, or through exclusion by an averted predator with an established territory. The need for more research on the fundamental science of aversion and impacts on behavior and field logistics has been recognized (Cowan et al., 2000; Macdonald & Feber, 2015). Our framework would enable such research and adaptive practice. With the adaptation of foxes in our Australian example, the only path an individual fox is given to persist and have survival advantage in a landscape would be to be averse to preying upon the native animal of interest. This contrasts fundamentally with standard control measures where the only persisting foxes are those *averse to control* techniques (i.e., those that get away). This idea of *desired* selection rather than *undesired* selection (Figure 1) is fundamental to our framework, that is, that we should be approaching management from an evolutionary perspective. Furthermore, approaches with desired selection in mind might result in predator adaptation that not only exists in the individual, but also potentially in its offspring. This has been demonstrated in carnivores, for example, where aversion to poisonous cane toads (*Rhinella marina*) has been shown to be genetically based in northern quolls (*Dasyurus hallucatus*), a small Australian marsupial carnivore (Kelly & Phillips, 2019).

Here we have given one example of the potential framework that may drive desirable adaptation in predators. However, the concept of desired selection could be applied to many more wildlife management contexts, for example, management of stoats, weasels, cats, possums and rats as threats to native New Zealand birds (Innes et al., 2010), and American mink (*Neovison vison*) in Scotland (Bryce et al., 2011) and bears (*Ursus* spp.), wolves, lynx (*Lynx* spp.), cougars (*Puma concolor*) and coyotes (*Canis latrans*) as threats to domesticated animals in the USA and Europe (Treves, Krofel, & McManus, 2016). Our framework could also be adapted to protect livestock from native or introduced predators, or to adapt reintroduced native predators to minimize conflicts with humans. We believe that research on regimes that drive desirable adaptation could be a potentially fruitful avenue for management of predators. This perspective is timely in light of the growing interest in harnessing ecological processes to drive ecosystem and conservation outcomes and the broader rewilding agenda (Pettorelli et al., 2019) where wildlife and human assets such as livestock or animals of conservation concern, will increasingly come into contact.

ACKNOWLEDGMENTS

Thanks to David Mech for supply of literature. Thanks to Vanessa Bleakley for graphic design work.

CONFLICT OF INTEREST

There are no conflicts of interest.

AUTHOR CONTRIBUTIONS

Adrian D. Manning and Maldwyn J. Evans led the conceptualization and writing of the article. Tim A. Andrewartha, Anton Blencowe, Kyle Brewer, and Iain J. Gordon conceptualized and wrote the article.

ORCID

Adrian D. Manning https://orcid.org/0000-0003-0989-9203
Iain J. Gordon https://orcid.org/0000-0001-9704-0946
Maldwyn J. Evans https://orcid.org/0000-0001-7025-2287

REFERENCES

Allendorf, F. W., & Hard, J. J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 9987–9994.

Allsop, S. E., Dundas, S. J., Adams, P. J., Kreplins, T. L., Bateman, P. W., & Fleming, P. A. (2017). Reduced efficacy of baiting programs for invasive species: Some mechanisms and management implications. *Pacific Conservation Biology*, *23*, 240–257.

Andelt, W. F., Phillips, R. L., Gruver, K. S., & Guthrie, J. W. (1999). Coyote predation on domestic sheep deterred with electronic dog-training collar. *Wildlife Society Bulletin*, *27*(1), 12–18.

Armstrong, D. P., Seddon, P. J., & Moehrenschlager, A. (2019). Reintroduction. In B. D. Fath (Ed.), *Encyclopedia of ecology* (pp. 458–466). Oxford: Elsevier.

Batson, W. G., Gordon, I. J., Fletcher, D. B., & Manning, A. D. (2015). REVIEW: Translocation tactics: A framework to support the IUCN guidelines for wildlife translocations and improve the quality of applied methods. *Journal of Applied Ecology*, *52*, 1598–1607.

Berry, O., & Kirkwood, R. (2010). Measuring recruitment in an invasive species to determine eradication potential. *The Journal of Wildlife Management*, *74*, 1661–1670.

Bischof, R., & Zedrosser, A. (2009). The educated prey: Consequences for exploitation and control. *Behavioral Ecology*, *20*, 1228–1235.

Blumstein, D. T., Letnic, M., & Moseby, K. E. (2019). In situ predator conditioning of naive prey prior to reintroduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*, 20180058.

Bryce, R., Oliver, M. K., Davies, L., Gray, H., Urquhart, J., & Lambin, X. (2011). Turning back the tide of American mink invasion at an unprecedented scale through community participation and adaptive management. *Biological Conservation*, *144*, 575–583.

Carle, T., & Rowe, C. (2014). Avian predators change their foraging strategy on defended prey when undefended prey are hard to find. *Animal Behaviour*, *93*, 97–103.

Carter, A., Luck, G. W., & McDonald, S. P. (2012). Ecology of the red fox (*Vulpes vulpes*) in an agricultural landscape. 2. Home range and movements. *Australian Mammalogy*, *34*, 175–187.

Cowan, D., Reynolds, J., & Gill, E. (2000). Reducing predation through conditioned taste aversion. In L. M. Gosling & W. J. Sutherland (Eds.), *Behaviour and Conservation*, Conservation Biology Series (pp. 281–299). Cambridge: Cambridge University Press.

Darimont, C. T., Carlson, S. M., Kinnison, M. T., Paquet, P. C., Reimchen, T. E., & Wilmers, C. C. (2009). Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(3), 952–954.

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., … Butchart, S. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services*. Bonn, Germany: IPBES secretariat.

Díaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B., & Ferreras, P. (2016). Drivers of red fox (*Vulpes vulpes*) daily activity: Prey availability, human disturbance or habitat structure? *Journal of Zoology*, *298*, 128–138.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*, 401–406.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 11261–11265.

Dugatkin, L. A., Trut, L., & Trut, L. N. (2017). *How to tame a fox (and build a dog): Visionary scientists and a Siberian tale of jump-started evolution*. Chicago: University of Chicago Press.

Ellins, S. R., & Catalano, S. M. (1980). Field application of the conditioned taste aversion paradigm to the control of coyote predation on sheep and turkeys. *Behavioral and Neural Biology*, *29*, 532–536.

Ellins, S. R., Catalano, S. M., & Schechinger, S. A. (1977). Conditioned taste aversion: A field application to coyote predation on sheep. *Behavioral Biology*, *20*, 91–95.

Evans, M. J., Batson, W. G., Gordon, I. J., Belton, E., Chaseling, T., Fletcher, D., … Manning, A. D. (2021). The 'goldilocks zone' of predation: The level of fox control needed to select predator resistance in a reintroduced mammal in Australia. *Biodiversity and Conservation*. https://doi.org/10.1007/s10531-021-02166-y

Galef, B. G., & Clark, M. M. (1972). Mother's milk and adult presence: Two factors determining initial dietary selection by weanling rats. *Journal of Comparative and Physiological Psychology*, *78*, 220–225.

Galef, B. G., & Henderson, P. W. (1972). Mother's milk: A determinant of the feeding preferences of weaning rat pups. *Journal of Comparative and Physiological Psychology*, *78*, 213–219.

Gentle, M., Massei, G., & Saunders, G. (2004). Levamisole can reduce bait monopolization in wild red foxes *Vulpes vulpes*. *Mammal Review*, *34*, 325–330.

Gentle, M. N., Saunders, G. R., & Dickman, C. R. (2007). Poisoning for production: How effective is fox baiting in south-eastern Australia? *Mammal Review*, *37*, 177–190.

Gustavson, C. R., Garcia, J., Hankins, W. G., & Rusiniak, K. W. (1974). Coyote predation control by aversive conditioning. *Science*, *184*, 581–583.

Gustavson, C. R., Gustavson, J. C., & Holzer, G. A. (1983). Thiabendazole-based taste aversions in dingoes (*Canis familiaris* dingo) and New Guinea wild dogs (*Canis familiaris* hallstromi). *Applied Animal Ethology*, *10*, 385–388.

Innes, J., Kelly, D., Overton, J. M., & Gillies, C. (2010). Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology*, *34*, 86–114.

Jaeger, M. M., Blejwas, K. M., Sacks, B. N., Neale, J. C. C., Conner, M. M., & McCullough, D. R. (2001). Targeting alphas can make coyote control more effective and socially acceptable. *California Agriculture*, *55*, 32–37.

Johnson, C. (2006). *Australia's mammal extinctions: A 50,000-year history*. Port Melbourne: Cambridge University Press.

Jolly, C. J., Kelly, E., Gillespie, G. R., Phillips, B., & Webb, J. K. (2018). Out of the frying pan: Reintroduction of toad-smart northern quolls to southern Kakadu National Park. *Austral Ecology*, *43*, 139–149.

Kelly, E., & Phillips, B. L. (2019). Targeted gene flow and rapid adaptation in an endangered marsupial. *Conservation Biology*, *33*, 112–121.

Legge, S., Woinarski, J. C., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J. Q., … Baseler, M. (2018). Havens for threatened Australian mammals: The contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research*, *45*, 627–644.

Lieury, N., Ruette, S., Devillard, S., Albaret, M., Drouyer, F., Baudoux, B., & Millon, A. (2015). Compensatory immigration challenges predator control: An experimental evidence-based approach improves management. *The Journal of Wildlife Management*, *79*, 425–434.

Linhart, S. B., Roberts, J. D., Schumake, S. A., & Johnson, R. (1976). *Avoidance of prey by captive coyotes punished with electric shock*.

Macdonald, D. W., & Feber, R. (2015). *Wildlife conservation on farmland: Conflict in the countryside*. USA: Oxford University Press.

Maguire, G. S., Stojanovic, D., & Weston, M. A. (2009). Conditioned taste aversion reduces fox depredation on model eggs on beaches. *Wildlife Research*, *36*, 702–708.

Marlow, N., Thomson, P., Rose, K., & Kok, N. (2016). Compensatory responses by a fox population to artificial density reduction in a rangeland area in Western Australia. *Conservation Science Western Australia*, *10*(3), 1–10.

Massei, G., Lyon, A., & Cowan, D. P. (2003). Levamisole can induce conditioned taste aversion in foxes. *Wildlife Research*, *30*, 633–637.

Mech, L. D., Fritts, S. H., & Nelson, M. E. (1996). Wolf management in the 21st century: From public input to sterilization. *Journal of Wildlife Research*, *1*, 195–198.

Minnie, L., Gaylard, A., & Kerley, G. I. H. (2016). Compensatory life-history responses of a mesopredator may undermine carnivore management efforts. *Journal of Applied Ecology*, *53*, 379–387.

Moseby, K. E., Blumstein, D. T., & Letnic, M. (2016). Harnessing natural selection to tackle the problem of prey naïveté. *Evolutionary Applications*, *9*, 334–343.

Moseby, K. E., Letnic, M., Blumstein, D. T., & West, R. (2018). Designer prey: Can controlled predation accelerate selection for anti-predator traits in naïve populations? *Biological Conservation*, *217*, 213–221.

Moseby, K. E., Letnic, M., Blumstein, D. T., & West, R. (2019). Understanding predator densities for successful co-existence of alien predators and threatened prey. *Austral Ecology*, *44*, 409–419.

Moseby, K. E., Peacock, D. E., & Read, J. L. (2015). Catastrophic cat predation: A call for predator profiling in wildlife protection programs. *Biological Conservation*, *191*, 331–340.

Nicolaus, L., Hoffman, T., & Gustavson, C. (1982). Taste aversion conditioning in free ranging raccoons (*Procyon lotor*)[alternative method to killing for the control of coyote predation, Oregon]. *Northwest Science*, *56*(3), 165–169.

O'Donnell, S., Webb, J. K., & Shine, R. (2010). Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology*, *47*, 558–565.

Orell, P. (2004). Fauna monitoring and staff training: Western shield review-February 2003. *Conservation Science Western Australia*, *5*, 51.

Osmond, M. M., Otto, S. P., & Klausmeier, C. A. (2017). When predators help prey adapt and persist in a changing environment. *The American Naturalist*, *190*, 83–98.

Parsons, K., Rigg, A., Conith, A., Kitchener, A., Harris, S., & Zhu, H. (2020). Skull morphology diverges between urban and rural populations of red foxes mirroring patterns of domestication and macroevolution. *Proceedings of the Royal Society B*, *287*, 20200763.

Pettorelli, N., Durant, S. M., & du Toit, J. T. (2019). *Rewilding*. Cambridge University Press.

Phillips, R. B., & Winchell, C. S. (2011). Reducing nontarget recaptures of an endangered predator using conditioned aversion and reward removal. *Journal of Applied Ecology*, *48*, 1501–1507.

Prowse, T. A., Cassey, P., Ross, J. V., Pfitzner, C., Wittmann, T. A., & Thomas, P. (2017). Dodging silver bullets: Good CRISPR gene-drive design is critical for eradicating exotic vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170799.

Read, J. L., Peacock, D., Wayne, A. F., & Moseby, K. E. (2016). Toxic Trojans: Can feral cat predation be mitigated by making their prey poisonous? *Wildlife Research*, *42*, 689–696.

Robley, A., Gormley, A. M., Forsyth, D. M., & Triggs, B. (2014). Long-term and large-scale control of the introduced red fox increases native mammal occupancy in Australian forests. *Biological Conservation*, *180*, 262–269.

Saunders, G., & McLeod, L. (2007). *Improving fox management strategies in Australia*. Canberra: Commonwealth of Australia.

Saunders, G. R., Gentle, M. N., & Dickman, C. R. (2010). The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review*, *40*, 181–211.

Schultz, R. N., Jonas, K. W., Skuldt, L. H., & Wydeven, A. P. (2005). Experimental use of dog-training shock collars to deter depredation by gray wolves. *Wildlife Society Bulletin*, *33*, 142–148.

Shefferson, R. P., Mason, C. M., Kellett, K. M., Goolsby, E. W., Coughlin, E., & Flynn, R. W. (2018). The evolutionary impacts of conservation actions. *Population Ecology*, *60*, 49–59.

Skelhorn, J., & Rowe, C. (2007). Predators' toxin burdens influence their strategic decisions to eat toxic prey. *Current Biology*, *17*, 1479–1483.

Stillfried, M., Belant, J. L., Svoboda, N. J., Beyer, D. E., & Kramer-Schadt, S. (2015). When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, *120*, 30–39.

Tobajas, J., Descalzo, E., Mateo, R., & Ferreras, P. (2020). Reducing nest predation of ground-nesting birds through conditioned food aversion. *Biological Conservation*, *242*, 108405.

Tobajas, J., Gómez-Ramírez, P., María-Mojica, P., Navas, I., García-Fernández, A. J., Ferreras, P., & Mateo, R. (2019). Conditioned food aversion mediated by odour cue and microencapsulated levamisole to avoid predation by canids. *European Journal of Wildlife Research*, *65*, 32.

Treves, A., & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, *17*, 1491–1499.

Treves, A., Krofel, M., & McManus, J. (2016). Predator control should not be a shot in the dark. *Frontiers in Ecology and the Environment*, *14*, 380–388.

Ward-Fear, G., Thomas, J., Webb, J. K., Pearson, D. J., & Shine, R. (2017). Eliciting conditioned taste aversion in lizards: Live toxic prey are more effective than scent and taste cues alone. *Integrative Zoology*, *12*, 112–120.

Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 4531–4540.

Young, H. S., McCauley, D. J., Galetti, M., & Dirzo, R. (2016). Patterns, causes, and consequences of Anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics*, *47*, 333–358.

How to cite this article: Manning AD, Andrewartha TA, Blencowe A, Brewer K, Gordon IJ, Evans MJ. Bettering the devil you know: Can we drive predator adaptation to restore native fauna? *Conservation Science and Practice*. 2021;3:e447. https://doi.org/10.1111/csp2.447