Received: 12 November 2021 | Accepted: 25 May 2023

DOI: 10.1111/csp2.12984

CONTRIBUTED PAPER

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

WILEY

Landscapes of nausea: Successful conditioned taste aversion in a wild red fox population

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Funding information
Australian Government Research Training Program; Japan Society for the Promotion of Science, Grant/Award Number: P19084

Abstract

Predation by invasive mammalian species is one of the key drivers of native species' population declines and extinctions. Current management of invasive species focuses on their removal from the landscape. However, total removal can be difficult, costly and even impossible. If eradication is not achieved, reductions in predator numbers are often temporary. New tactics are needed to target predators in situ, to reduce their negative impacts. We test the efficacy of conditioned taste aversion (CTA), a tactic that could reduce the impact of predation on target prey species. By associating nausea with a specific food source, it may be possible to condition an aversion to a target bait, and ultimately to live animals in the wild. To assess if wild invasive red foxes (Vulpes vulpes) can be conditioned to avoid a specific food source, we used baits (fried deboned chicken) containing encapsulated levamisole, an anthelmintic agent known to induce nausea leading to emesis and/or diarrhea at high dosages with no long-term side effects. We buried baits at 30 stations across an open landscape. After treatment, reductions in control baits taken (at least 30%) were observed for 68 days, indicating the use of CTA had successfully reduced bait consumption by red foxes in a wild context. To our knowledge, this study represents the first successful test of CTA to a meat bait in a wild red fox population. Our results suggest that CTA shows promise as a tool to reduce the predation of vulnerable animals providing an alternative tactic to manage the impacts of invasive mammalian predators where eradication is currently impossible.

KEYWORDS

conditioned taste aversion, invasive predator, red fox

1 | INTRODUCTION

Predation is a natural process that plays a role in regulating the density of prey populations (Edwards & Edwards, 2011), as well as maximizing the fitness of individuals (Cowden, 2012). It can, however, be damaging when predators occur outside their natural ranges, where it may bring them into contact with prey ill-equipped to deal with unencountered

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modes of predation (Blumstein & Blumstein, 2006). If the ecological mismatches between the predator and prey are too great, predation can lead to catastrophic declines in prey populations, range restrictions, and even local extinction (Kinnear et al., 2002). The net impact of invasive predators has been identified as contributing to 58% of all bird, mammal, and reptile extinctions globally, with direct predation purported to be the primary driver of declines in native prey populations (Doherty et al., 2016).

Currently, invasive and native predators are managed using a range of lethal and non-lethal tactics that attempt to remove animals from the landscape or manage their impacts. While lethal forms of management, such as shooting, trapping, and poison baiting (Saunders et al., 2010), can result in temporary reductions in predator populations, repeated management interventions are required to keep numbers low (Gentle et al., 2007; Saunders et al., 2010; Treves et al., 2016). Further, it has been suggested that the repeated use of lethal tactics that do not achieve eradication could, in fact, lead to adaptations in the predator population that counteract the control method employed (Allsop et al., 2017; Manning et al., 2021).

Used in isolation, predator culling does not always lead to increased prey survival and can be counterproductive. Predator removal can lead to population expansions of other predators and herbivores (Edwards & Edwards, 2011), disruptions to predator social systems (Doherty & Ritchie, 2017), compensatory immigration (Doherty & Ritchie, 2017; Minnie et al., 2015; Thomson et al., 2000), and increased birth rates (Doherty & Ritchie, 2017; Minnie et al., 2015). Further, some techniques become less effective over time, for example, the use of poison baits can lead to bait resistance or shyness (Allsop et al., 2017). There are also ethical considerations when using lethal management (Doherty & Ritchie, 2017), particularly with the use of poisons such as 1080 that cause significant distress for the target animal over an extended period (Sherley, 2007). This is especially the case when there are negligible measurable positive impacts as a result of management (Mcmanus et al., 2015).

An alternative approach to mitigate the effects of invasive predators could be to use tactics and technologies that reduce the impacts caused by predation, without requiring the removal of the predator (Manning et al., 2021). One potential tactic that reduces predation might be CTA. Conditioned taste aversion is the conditioning of an animal to associate a specific food source with a negative stimulus. This can lead to a reduction in the frequency of consumption, or total rejection of that food after treatment (Ferguson et al., 2021; Snijders et al., 2021). This tactic may be used to deter a predator from consuming a toxic, or threatened, prey species (Indigo et al., 2018; Jolly et al., 2018; Kelly et al., 2018; O'donnell et al., 2010; Price-Rees et al., 2013; Tobajas, Descalzo, Villafuerte, et al., 2020), reduce the predation of nest eggs (Maguire et al., 2009; Nicolaus & Nellis, 1987; Tobajas, Descalzo, Mateo, & Ferreras, 2020), and reduce the predation of livestock (Ellins & Catalano, 1980; Ellins et al., 1977; Gustavson et al., 1974; Horn & Lehner, 1981).

A wide range of species including rats (Rat*tus norvegicus, Rattus rattus*), dogs (*Canis lupus familiarus*), wolves (*Canis lupus*), coyotes (*Canis latrans*), foxes (*Vulpes* spp.), raccoons (*Procyon lotor*), jackals (*Canis aureus*), quolls (*Dasyurus* spp.) and goannas (*Varanus* spp.) have been shown to be susceptible to CTA, using a range of nausea-inducing agents including, thiabendazole, levamisole, lithium chloride, thiram and sodium carbonate (Burns, 1980; Forthman Quick et al., 1985; Gentle et al., 2004; Maguire et al., 2009; Massei et al., 2003a, 2003b; O'donnell et al., 2010; Tobajas et al., 2019b; Tobajas, Ruiz-Aguilera, et al., 2020; Ward-Fear et al., 2017). Methods of inducing CTA include the direct injection of the agent into the center of a food source such as the albumen of eggs or chicken carcasses (Gentle et al., 2004; Maguire et al., 2009), mixing the agent into a food (Massei et al., 2003a), and encapsulation (Sayre & Clark, 2001). Encapsulation aims to prevent the detection of the agent to ensure the predator associates adverse symptoms with the consumption of the food item (Sayre & Clark, 2001). Microencapsulation, where the size of the encapsulated agent particles is minimized, can be used to hide texture cues from the animal more effectively, and prevent the capsule from being accidentally broken open during consumption (Cotterill et al., 2006; Tobajas, Descalzo, Mateo, & Ferreras, 2019).

If CTA is to be useful to managers of invasive predators, CTA needs to be effective in protecting native species in the wild. Further, it also needs to work for a length of time that is practical following its application. Research has identified multiple factors that can affect the strength of aversion induced. These include the agent and dosage used (Gentle et al., 2004; Gill et al., 2000), the type of conditioning stimulus (e.g., live prey are more effective at conditioning aversion than a carcass) (Ward-Fear et al., 2017), and the time between consumption and onset of symptoms (Forthman Quick et al., 1985). Further, an animal's previous experience with the food item and whether an alternate food source (two choice tests) is available post-treatment (Forthman Quick et al., 1985; Mikulka & Klein, 1977; Nolan et al., 1997) can affect how susceptible an individual is to CTA, as well as the time until extinction of aversion.

A significant amount of the research on CTA has been conducted in captivity; however, there is very little research on the potential to use CTA to mitigate the effects of free-ranging predators. Previous work conditioning

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aversion in wild red foxes has produced varied results. For example, while foxes were successfully conditioned to reduce predation of eggs (Maguire et al., 2009; Tobajas, Descalzo, Mateo, & Ferreras, 2020), in a separate study using chicken carcasses, the emetic agent was detected by foxes when injected into a bait allowing foxes to continue consuming untreated baits (Gentle et al., 2004). The aforementioned detection of the agent (levamisole) by wild foxes contrasted with the results seen in captive studies where aversion was successfully elicited for 110–152 days when levamisole was simply mixed in with the food source (Massei et al., 2003a). There has, however, been success in increasing rabbit (*Oryctolagus cuniculus*) survival after translocation in the presence of foxes by presenting foxes with vanilla-scented rabbit baits containing microencapsulated levamisole and distributing vanilla odor within artificial warrens (Tobajas, Descalzo, Villafuerte, et al., 2020). Furthermore, the addition of a novel odor to overshadow or mask the agent (Tobajas et al., 2019a; Tobajas, Descalzo, Villafuerte, et al., 2020) can lead to the overshadowing odor becoming a strong aversive cue via a process known as taste potentiated odor aversion (Baker et al., 2007; Holder & Garcia, 1987).

In this study, we examined the use of CTA to reduce bait consumption by invasive red foxes in South-Eastern Australia. We used encapsulation to hide the odor and taste cues that the nausea-inducing agent (levamisole) may have presented to the fox (Cotterill et al., 2006; Sayre & Clark, 2001). We also set out to determine, once aversion was established, how long it persisted in an open landscape. This is important information that will inform the future development of treatment regimes. We asked:

1. Can wild foxes be conditioned to avoid the consumption of a food item with the use of encapsulated levamisole?
2. How long does the aversion persist in an open landscape?

We discuss our findings in the context of existing invasive predator management and the implications for the reintroduction of native species in the presence of invasive predators.

2 | METHODS AND MATERIALS

2.1 | Study area and design

We conducted our study at Wandiyali-Environa Wildlife Sanctuary (35°26′40″S 149°12′21″ E Figure 1) in South-Eastern Australia. The area is a formerly grazed pastoral property where livestock have been removed and restoration work is ongoing including native vegetation planting and the construction of a predator-proof fence. The property is surrounded by grazed pastoral land containing sheep and cattle, and there is a suburb along its northern boundary. We conducted the baiting from March—June in 2019 over an area of approximately 1.5 km^2.

We installed 30 bait stations (Figure 1), consisting of baits buried in shallow holes (5–10 cm below the surface), monitored by passive infrared cameras positioned approximately 5 m from the baits. We chose locations for bait stations that were relatively free of vegetation to allow the camera to have an unobstructed view of bait take. We placed a single fresh bait at each station every two days. On repeat visits, if the previous bait had not been consumed, it was replaced with a fresh bait. We placed stations at a minimum of 200 m apart to reduce the likelihood of a single animal consuming multiple treated baits before the onset of nausea.

To determine the effect of conditioning, we used a combination of treated baits containing levamisole (99.5%, Bellsouth, Victoria, Australia) in a gelatin capsule (size 1, The Capsule Guy, Adelaide, Australia) and control baits containing an empty gelatin capsule. Our baits consisted of approximately 30 grams of cooked, deboned fried chicken. We chose levamisole as the emetic agent and used a dose of 350 mg per capsule (70 mg/kg [Gentle et al., 2004]) based on an average fox weight of approximately 5 kg [Coman, 1983]). To reduce the risk of detection by foxes during consumption, we embedded the gelatin capsules in the center of whole pieces of chicken. The baiting regime (Table 1) consisted of a single treatment period (treatment) in which we used baits containing levamisole in embedded gelatin capsules, and four separate control periods; one prior to the treatment (pre-conditioning), one immediately after the treatment (Post 1 [baits checked 2–8 days post-treatment], and two others at increasing time intervals posttreatment (Post 2 [baits checked 31–37 days post-treatment] and Post 3 [baits checked 62–68 days post-treatment]). Our experimental design allowed us to test the effects of levamisole during and after the treatment (Table 1). We confirmed that baits were taken by foxes by reviewing the video footage of the bait being removed from the station, and/or through the pattern of disturbance at the bait station.

2.2 | Data analysis

For each station, we recorded whether the bait was taken, the baiting period it was taken in, the date the baits were checked and found to be taken, the station the bait was taken from, if the bait was disturbed but not

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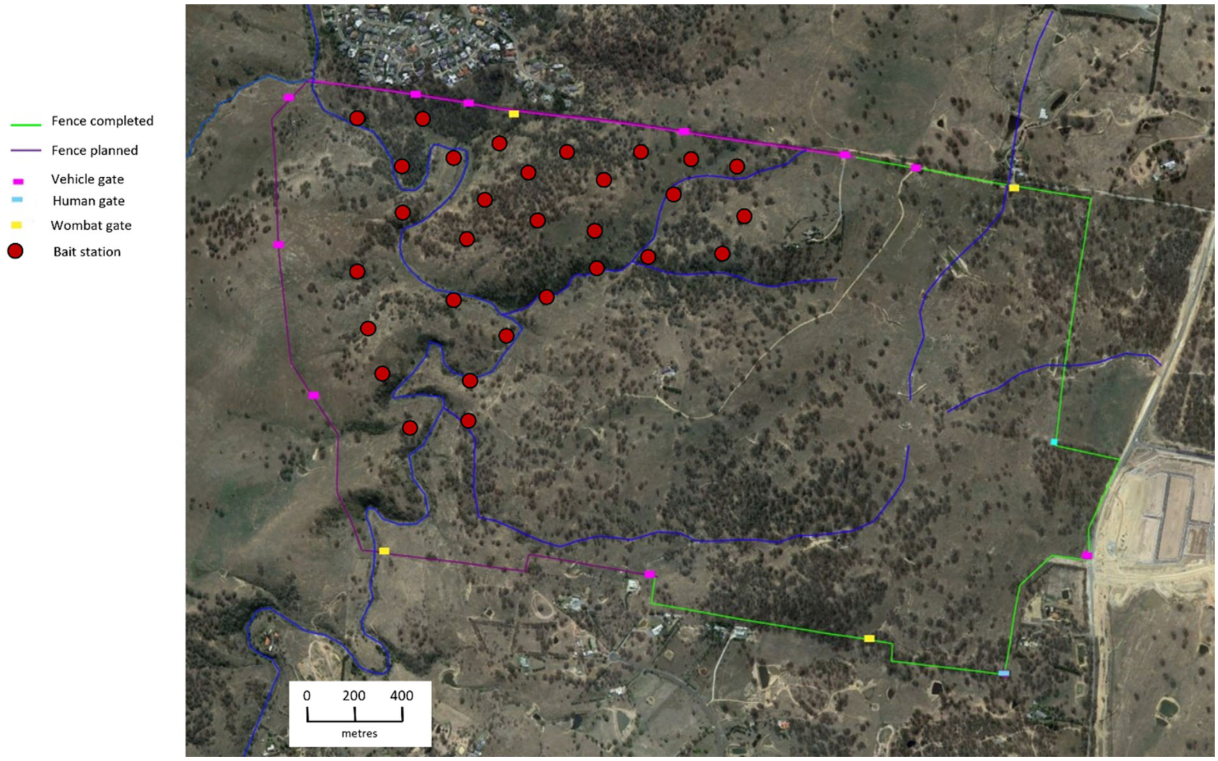

FIGURE 1 Map of Wandiyali–Environa Wildlife Sanctuary showing bait stations and fence construction.

TABLE 1 Baiting regime.

Treatment	Duration	Description	Aim
Control	10 days	Baits containing empty gelatin capsules	Determine baseline fox consumption of baits
Treatment	14 days	Baits containing encapsulated levamisole	Condition aversion in foxes
Post 1	12 days	Baits containing empty gelatin capsules placed immediately after treatment	Determine fox consumption of baits post-treatment
Post 2	8 days	Baits containing empty gelatin capsules were placed 29 days after the treatment	Determine fox consumption of baits post-treatment, and long-term effectiveness of treatment
Post 3	8 days	Baits containing empty gelatin capsules were placed 60 days after the treatment	Determine fox consumption of baits post-treatment, and long-term effectiveness of treatment

removed from the station and, if the bait was disturbed, the distance the bait was moved from the hole.

We fitted a generalized linear mixed model to test for the effect of baiting period on the probability of bait take by foxes. We assumed a binomial distribution with logit link function and included the station as a random effect to account for the repeated measures and variation between sites. We treated the baiting period as a factor and used the preconditioning period as the reference level in the model. We conducted post-hoc Tukey's honest significance test (Tukey, 1949) on the factor levels to determine the significances of their pairwise differences.

We fitted another generalized linear mixed model to test the interaction between baiting period and day (within period). This enabled us to determine whether there was a trend of bait take within each baiting period (for example, whether bait take decreased from day 1 of the treatment period to day 7). We compared model fits using AIC values (Burnham & Anderson, 2002).

Our analyses were performed using the “lme4” (Bates et al., 2016), “MuMIn” (Barton, 2016) and emmeans (Lenth et al., 2020) packages in R (R Core Team, 2016). To plot our results, we used the ggplot2 (Wickham, 2009)

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package in R. We used R Studio (RStudio Team, 2016) as a shell for R.

3 | RESULTS

Over the study period, we presented a total of 750 baits to the local fox population, of which 210 contained encapsulated levamisole. A total of 236 of the control baits, and 34 of the baits containing levamisole were taken. Two control baits were disturbed but left at the station in the Post 1 and Post 2 periods and 29 levamisole-containing baits were disturbed but left at the bait station in the treatment period.

Bait take was lowest during the treatment period, and significantly lower during all three post-treatment control periods compared to the preconditioning period (Table S1 and Figure 2). While the probability of bait take was lowest during the treatment period, it remained at significantly reduced levels relative to preconditioning for 68 days after treatment (Figure 2). In the Post 1 period, bait take was reduced by approximately 30% (69% of pre-treatment levels), and this reduction was maintained into the Post 2 period 31–37 days after treatment (74% of pre-treatment levels). Bait take decreased again from the Post 2 to Post 3 periods by an additional 30% (40% of pre-treatment levels) 60–68 days after treatment.

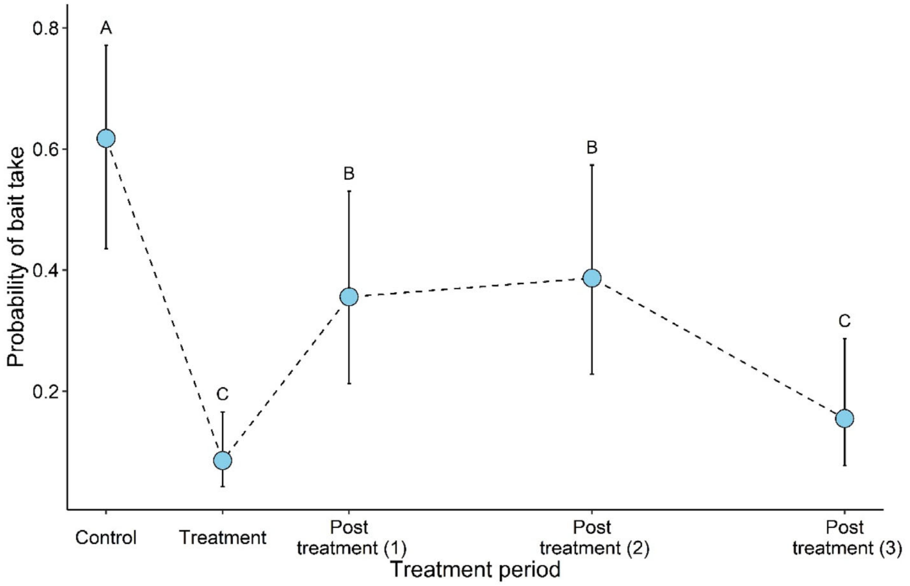

FIGURE 2 The effect of baiting period on the probability of fox bait take with grouping factors indicating significant differences between levels (95% CI, SE).

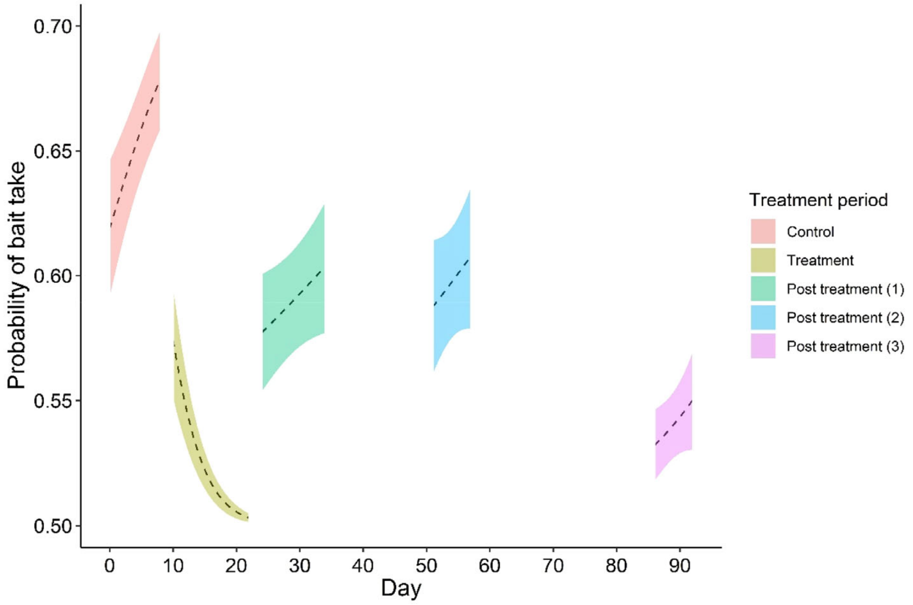

FIGURE 3 Trend in probability of bait-take across each baiting period (95% CI).

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The interactive model of day within period, was a better fit (AICc = 756.43) than the model of period only (AICc = 779.38). This model was not selected as the primary model because we were looking to determine the relative bait take between different baiting periods and not the daily trends in bait take. There was a significant negative trend to daily baits taken by foxes across the conditioning period (Figure 3), while all other periods demonstrated positive trends.

4 | DISCUSSION

Our results demonstrate that free-ranging wild red foxes can be conditioned to reduce their consumption of a target food item in a wild context using CTA. After a treatment period of only two weeks, in which baits containing encapsulated levamisole were placed in the test landscape, subsequent bait take of control baits by foxes was reduced by at least 30%. Furthermore, the reduction in baits taken continued for at least 68 days after treatment. This is an important step in developing a reliable method and treatment regime to elicit CTA in wild foxes, and, as far as we are aware, the first successful test of CTA to a meat bait-only treatment in a wild fox population (but note, Tobajas, Descalzo, Villafuerte, et al., 2020).

4.1 | Can wild foxes be conditioned to avoid the consumption of a food item with the use of encapsulated levamisole?

Our results provide strong support for the use of levamisole to deter foxes from a bait. The immediate decrease in baits taken on day one of treatment probably indicates that aversion was conditioned after a single baiting period (two days). This would be expected if foxes were consuming multiple baits over each baiting period or if aversion was conditioned after a single consumption. The digging up, and subsequent rejection of several control baits by foxes after the treatment, indicates that the reduction in bait take was in part due to an aversion conditioned to the baits, and not an aversion to levamisole per se. It is also possible that the aversion observed was due to foxes no longer visiting bait stations after consuming a treated bait. If this is the case, the reduction in bait take would not be affected by foxes' abilities to detect levamisole. It is also likely that some foxes were able to detect the encapsulated levamisole, and subsequently avoid treated baits while still consuming untreated ones. This is supported by the rise in baits taken from the Treatment period to the Post 1 period and the higher number of disturbed treated baits compared to disturbed control baits (28 treated vs. two controls). The ability of foxes to detect the levamisole is likely in part due to the stability of the gelatin capsules inside of the baits. In early testing, the empty gelatin capsules appeared stable in baits for a period of one week; however, with the introduction of levamisole into the capsules, the integrity of the capsules was affected. Capsules in recovered baits were significantly softer after a period of two days. This may have led to capsules tearing, and subsequent detection of levamisole by foxes. The gelatin capsules themselves may also have been detected by foxes due to the different texture of the meat bait. While it appeared that a higher proportion of foxes were able to detect the levamisole or capsules than were susceptible to conditioning, we have shown that foxes can be conditioned to avoid consumption of a food item in the wild, and refinements to the methodology may allow a greater proportion of foxes to be successfully conditioned.

4.2 | How long does the aversion persist in an open landscape?

Post-treatment, we observed lowered bait take for a period of 68 days at which point the experiment was ceased. A further reduction to bait take was seen in the Post 3 period (60–68 days post-treatment) from an average of 13.75 baits taken every 2 days (Post 2), to 7.5 baits being taken every 2 days (Post 3). We acknowledge that, while the effect of the aversion could have been maintained over the Post 3 period, the additional reduction in baits taken seen from the Post 2, to Post 3 periods may have been caused by other factors (e.g., migration of foxes out of the study site). In order to account for background changes in fox activity, future experiments should include a secondary network of control bait stations containing a different bait type.

4.3 | Treatment regime

The duration of reduced bait take we observed in wild foxes, indicates that it may be possible to condition foxes to avoid consuming a meat bait for a period of at least 68 days in a wild context. If this is the case, to maintain aversion in the fox population, treatment would have to be repeated approximately five times per year. This compares favorably with current lethal baiting regimes where rebaiting may occur 4–12 times per year depending upon the reserve size, perimeter to reserve area ratio and objective of baiting (de Tores & Marlow, 2011; Marlow et al., 2015a, 2015b). Once a duration of aversion can be identified, additional research is required to determine the area that needs to be treated, and the density of baits

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for this tactic to be effective. These parameters are likely to vary depending upon the objective of aversive baiting (e.g., to reduce predation of native animals around vulnerable periods such as breeding or to maintain aversion toward a vulnerable prey species). For a species such as the fox, with a high capacity for movement and migration, large areas may need to be treated (Gentle et al., 2007), or complementary tactics may be required such as establishing aversive baiting in buffer zones to target immigrating individuals (Thomson et al., 2000).

4.4 | Strength and transfer of aversion

A further step is to explore whether the phenomenon we have observed here can be transferred from a food item to a live prey animal. While some successes have been observed in raccoons (*Procyon lotor*) (Nicolaus et al., 1982), coyotes (*Canis latrans*) (Gustavson et al., 1974), varanid lizards (*Varanus* spp.) (Ward-Fear et al., 2017) and northern quolls (*Dasyurus hallucatus*) (O'Donnell et al., 2010) there have also been contradictory results in foxes, coyotes (Gentle et al., 2004; Horn, 1983; Massei et al., 2003a; Smith et al., 2000) and wolves (Tobajas, Ruiz-Aguilera, et al., 2020).

It has been suggested that the behaviors seen in CTA studies involving captive individuals are not transferable to those in the wild. Many captive studies use no-choice tests, where a target predator is not presented with an alternate food item during treatment. This differs from wild situations, where alternative food sources may be available. Further, presenting animals with no choice tests has been shown to increase the rate of extinction of aversion (Mikulka & Klein, 1977). Therefore individual- and population-level impacts of CTA in open landscapes need to be studied further in order to discern the dynamics of prey selection. Irrespective of whether the CTA is wholly transferred to live prey animals, it could still reduce predation events, and be valuable as part of a suite of tactics contributing to the cumulative mitigation of invasive predators' impacts. For example, if a predator species ceases to investigate the cues of a target prey species (i.e., odors and noises), a reduction in predation might be expected, even if the predator still pursues the prey on an incidental encounter. This provides another avenue for the use of CTA with the addition of an overshadowing odor alongside the baits. The odor could subsequently be applied to a prey species or its nest/den to protect it from predation (Tobajas, Descalzo, Villafuerte, et al., 2020; Tobajas, Ruiz-Aguilera, et al., 2020). Alternatively, neutral baits impregnated with the target prey species' odor, may be used to create a strong aversive reaction to the prey species itself.

4.5 | Evolution focused tactics

Our findings indicate that CTA has the potential to modify fox behavior. There is substantial evidence that management and harvesting practices have led to unintended consequences, driving evolution that counteracts their effectiveness (Allsop et al., 2017; Manning et al., 2021; Minnie et al., 2015; Shefferson et al., 2018; Thomson et al., 2000). With greater attention given to evolution-focused tactics, taking animal learning and adaptation into account (Evans et al., 2022; Manning et al., 2021), we may be able to develop fox impact mitigation regimes that minimize the need for culling and removal actions that may lead to undesirable evolutionary consequences (Bischof & Zedrosser, 2009), while still addressing the negative impacts of predator species (Manning et al., 2021). With further refinement, it may be possible to develop CTA regimes that drive desirable evolutionary change in predators.

A key advantage of CTA is that it is nonlethal and based on evolutionary principles (Manning et al., 2021). By considering animal learning and adaptation in response to a new, albeit toxic food, we may be able to artificially create an association between the prey species and nausea. As the tactic takes advantage of animal learning and adaptation, it is unlikely to reduce in efficacy over the long term, which is a potential consequence of any lethal removal approach adopted "(see above)". By either taking advantage of a known response of the fox to a stimulus, (i.e., rejection based upon an imposed cost and/or prevention of reward, e.g., nausea and emesis caused by toxic prey/baits) or by creating an artificial selection that drives the overall population to be less damaging, there would be no avenue that will select for resistance to the approach. Also, parents may pass on the aversion to a particular food item to their young, as observed in rats (*Rattus norvegicus domestica*) (Galef & Clark, 1972; Galef & Henderson, 1972), and there has been speculation that mother coyotes may pass on feeding habits to young via milk (Gustavson et al., 1974).

If CTA can be developed into a reliable management tactic it has the potential for a range of applications in animal conservation, human-wildlife conflict, and agricultural contexts. CTA could allow native prey species to persist in the presence of invasive predator species helping to achieve the long-term goal of co-existence between native prey and invasive predators (Evans et al., 2022). By allowing a low level of predation, the least fit individuals will be removed from the prey population leading to a rebalancing of the ecological mismatch (Evans et al., 2021; Evans et al., 2022; Osmond et al., 2017). In the long term, this may lead to the expansion of native species ranges as their ability to persist in the presence of invasive predators is improved through adaptation

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(Evans et al., 2022). The addition of CTA to the range of tactics currently available will aid in the management of predation, and may reduce, or remove the need for the culling of predators and provide an option where invasive predator eradication cannot be achieved.

ACKNOWLEDGMENTS

A special thanks to Jenny Newport of the ANU for her assistance with logistics and support throughout the study. We would also like to thank the landholders Carolyn Larcombe and Sandy Hume for their advice, assistance and ongoing support. This project was funded through the Australian Government Research Training Program research allocation made available through the Fenner School of Environment and Society, the Australian National University. Further camera traps were provided by the Australian Capital Territory, Parks and Conservation Service. Maldwyn Evans was partly funded by the Japan Society for the Promotion of Science as a Postdoctoral Research Fellow (P19084). This work was conducted under the ANU AEEC ethics protocol A2018/42.

DATA AVAILABILITY STATEMENT

Data will be made available on reasonable request and made publicly available on acceptance of the article.

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How to cite this article: Andrewartha, T., Evans, M., Blencowe, A., Brewer, K., Gordon, I. J., & Manning, A. D. (2023). Landscapes of nausea: Successful conditioned taste aversion in a wild red fox population. *Conservation Science and Practice*, e12984. https://doi.org/10.1111/csp2.12984

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