Non-lethal control of fox predation: the potential of generalised aversion

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Abstract

Traditionally, game-keepers and agriculturalists have controlled predators using lethal methods, but there are circumstances under which these may be ineffective or inappropriate for animal welfare or conservation reasons. Generalised aversion is potentially a form of non-lethal control, in which predators are conditioned to avoid foul-tasting bait, causing them subsequently to generalise this avoidance to similar, but untreated, prey, thereby affording it protection. In this exploratory study, a group of captive red foxes (Vulpes vulpes) was successfully conditioned to avoid untreated milk after drinking milk containing Bitrex™, a bitter substance that they were unable to detect except by taste. Our foxes were members of a family group and so housed together to reduce stress, and therefore the individuals' responses to the various treatments may not have been independent. As a result, we combined data from the three animals, and our most conservative analyses consider the sampling population to be this fox group; we do not make inferences about foxes in general, but confine them to this fox-group. This trial was a pilot to reveal the potential for future work on wild animals. Successful application of generalised aversion to non-lethal predator control has far-reaching implications for the sport hunting industry, nature reserve management and the conservation of threatened predators requiring control, as well as clear animal welfare benefits.

Keywords: *animal welfare, Bitrex™, conditioned taste aversion, generalised aversion, red fox, repellency*

Introduction

Predators such as red foxes (*Vulpes vulpes*) and mustelids frequently conflict with game-bird management through consumption of eggs, chicks and adult birds (Reynolds *et al* 1988). Predators also kill threatened native species; for example, on nature reserves in the UK, red foxes predate fragmented populations of red grouse (*Lagopus lagopus*) and terns (*Sterna* spp) (see Baker & Macdonald 1999).

Traditionally, game-keepers have controlled predators by lethal methods such as shooting, poisoning and kill-trapping (Tapper 1992), and the Royal Society for the Protection of Birds uses shooting to control foxes on its reserves where necessary (RSPB 1994). However, there are circumstances under which lethal methods are inappropriate for animal welfare or conservation reasons and, in any case, their efficacy in preventing losses remains a matter of debate (Cadbury 1989; Newton 1993; Macdonald *et al* 2000).

Of course, killing a predator is not itself an animal welfare issue, but some lethal control methods are considered to be inhumane. Tapper (1992) considers shooting to be the most humane method of killing foxes, and Baker and Harris (1997) agree that, providing that the relevant codes of practice are followed, cruelty is not an issue. However, Harris (1997), for example, believes hunting to be at least as cruel as banned methods such as poisoning and gassing. In addition, although welfare problems associated with snaring can be minimised by following the guidelines for their use, Baker and Harris (1997) believe that snaring should be banned because of widespread abuse, which results in trapping a large proportion of non-target species such as badgers and cats.

Historically, lethal control has had a devastating impact on some predators' populations (eg Langley & Yalden 1977) and may therefore be particularly dangerous on nature reserves, or elsewhere where the predator is itself endangered or protected (Macdonald *et al* 1999). An example of this conservation dilemma was illustrated recently in Java, Indonesia, where it was decided not to intervene in a situation where the threatened Asiatic wild dog, or ajag (*Cuon alpinus*), was preying on a dwindling population of endangered wild cattle, or banteng (*Bos javanicus*) (Sillero-Zubiri & Laurenson 2001).

Furthermore, lethal control can be expensive, as it must be conducted over a long period to counter immigration and density-dependent compensations in predator breeding success or survival (Cadbury 1989; Reynolds *et al* 1993; King 1994). There is, therefore, a need for alternative control techniques.

A variety of non-lethal measures to reduce predation has been used or tested, with varying rates of success (Reynolds & Tapper 1996; Baker & Macdonald 1999). Electric and conventional fencing, wardening and habitat management (such as provision of cover) can significantly reduce predation on nesting birds, but they are expensive and may have a negative impact on other wildlife (eg Minsky 1980; Green & Cadbury 1987; Holloway & Young 1991). In general,

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there has been very little follow-up of translocated animals, and almost no data exist on the subsequent levels of predation after translocation of predators (Linnell *et al* 1997). Scaring devices have sometimes been shown to be effective (eg Pfeifer & Goos 1982; Linhart *et al* 1984), and although supplementary feeding has had some success in reducing predation, its usefulness is variable and limited to small areas and short time periods (Avery & Winder 1987; Lindstrom *et al* 1987; Durdin 1992). Fertility control, repellents and conditioned taste aversion (CTA) still require considerable research before they can be applied in the field (Tuyttens & Macdonald 1998; Reynolds 1999; Cowan *et al* 2000).

Classic CTA develops when an animal learns to avoid specific foods by associating them with illness (Garcia & Hankins 1977). To form a CTA, a predator must ingest a noxious prey item and correlate the resulting illness with the consumption of that prey after a single dose or a small number of doses (Nicolaus & Nellis 1987). CTA retains an association between the conditioned and unconditioned stimuli — the food taste and illness, respectively (Cowan *et al* 2000). This apparently takes place in the medulla of the brainstem (Reynolds & Nicolaus 1993). Stimulus of a CTA depends on the severity and nature of the illness (Nachman & Ashe 1973), the time between the conditioned and unconditioned stimuli (Garcia & Koelling 1966), the salience of the conditioned stimulus (Garcia *et al* 1974) and whether it is novel or familiar (Riley & Tuck 1985). Both the development and the duration of CTAs are highly complex and are influenced by social and environmental factors, individual variation, prey-recognition cues, stimulus reinforcement, length of training period and choice of aversive agent (Nicolaus *et al* 1983; Gustavson & Gustavson 1985; Dimmick & Nicolaus 1990; Semel & Nicolaus 1992; Avery & Decker 1994).

A process quite distinct from CTA is that whereby animals may be repelled by noxious odours or tastes (eg Atkinson & Macdonald 1994). In this context, the important distinction between CTA and repellency is that in repellency the noxious stimulus is detected, and avoided, afresh at each encounter, whereas in CTA the subject subsequently rejects the prey even when it is untainted by the aversive agent. Here, we deal with a predator control process with features similar to both repellency and classic CTA, but different from both.

Aversive behaviour in general might be exploited to modify the feeding behaviour of species to meet wildlife management objectives (Cowan *et al* 2000). We tackle the question of whether a conscious association between a foul taste that cannot be detected until the bait is taken into the mouth, and food cues other than taste (ie odour, appearance), can produce an aversion that is generalised to similar, but untainted, bait. We term the outcome of this process 'generalised aversion'. Similarities in the processes involved mean that this type of aversion may be viewed as a subset of CTA. For example, the mechanism of any learning that

takes place is likely to be through classical conditioning (by forming an association between two stimuli — in this case, the bitter taste and cues related to the consumption of milk, and, in the case of classic CTA, illness and the food taste). The main feature which differentiates this kind of aversion from other CTAs is the form of the unconditioned stimulus. In classic CTA this is the physiological response of nausea/vomiting, whereas in the context of this study it is the animal's reaction to a foul taste.

Generalised aversion has, potentially, a great advantage over both classic CTA and repellency, on the one hand because the immediate experience of foul taste on sampling involves no ambiguity as to which prey is associated with the negative experience, and on the other hand because it may confer protection upon untreated prey. The disadvantage of generalised aversion (and of repellency, but not of classic CTA) is that the predator has only to lick untainted prey to discover the fraud — the hope is that it will be discouraged from doing so because the unpalatable prey are so foul.

Our trial aimed to induce in captive red foxes a generalised aversion to milk by exposing them to milk tainted with Bitrex™, which is odourless, but is one of the bitterest known substances (Emsley 1985). Milk was selected as an appropriate test medium for four reasons. First, it was unlike the other foods that the foxes were receiving at the time (their basic diet consisted of rabbits, fowl and occasionally canned dogfood), so they should be less likely to confuse the effects of conditioning between foods. Second, the Bitrex™ could be thoroughly dissolved in the liquid, facilitating even distribution throughout the bait. Third, they appeared to like untreated milk, and initially drank it very quickly, making it more straightforward to detect a change in their behaviour. Finally, it was impossible for them to carry it off or to play with it, so it was easy to determine clearly whether it had been consumed or left in the bowl. We first determined the minimum concentration of Bitrex™ that deterred foxes from drinking, and then successfully induced in the foxes a generalised aversion that resulted in them avoiding untreated milk. Our trial was a pilot for future work on wild animals.

Methods

Experimental animals

A litter of three orphaned wild-born female red foxes (*Vulpes vulpes*) was hand-reared from three days old. From weaning, they were housed together on deep litter in a roofed pen (dimensions 5 m × 6 m × 3 m), and fed (from the ground) each morning on their normal, untreated, basic diet (rabbits, fowl and canned dogfood); fresh water was freely available. The animals were provided with a kennel for sleeping, logs to jump on and cover in which to hide.

Trials began when the animals were six months old, and ran continuously for 70 days, between 29th September and 7th December 1996. After completion of the trials, the animals were kept as pets.

Table 1   Trial sequence, treatment phases within trials, and milk treatment in each.

Trial	Treatment phase	Number of days	Bait
Baseline	Baseline	8	Untreated milk
Dosage	400 ppm	5	Treated milk
	1000 ppm	10	Treated milk
	2000 ppm	8	Treated milk
	4000 ppm	9	Treated milk
Conditioning	Conditioning	8	Treated milk
	Partial Reinforcement	2	Treated and untreated milk
	Post-Conditioning	20	Untreated milk

Bitrex™

Bitrex™ (Macfarlan Smith Ltd, Edinburgh, UK) is an extremely bitter-tasting N-substituted lignocaine derivative, known as denatonium benzoate (chemical name N-[2-[2,6-dimethyl phenyl)amino]-2-oxoethyl]-N,N-diethylbenzen-emethanaminium benzoate; available from MacFarlan Smith, Edinburgh, UK). Bitrex™ is commonly used in everyday products such as shampoos and cleaning materials to deter humans (through its bitter taste) from consuming otherwise harmful substances. Previous studies have demonstrated that Bitrex™ can be repulsive to various mammals at particular concentrations (Kaukeinen & Buckle 1992; Andelt et al 1994; Kleinkauf et al 1999), while preliminary trials suggest that it functions as a generalised aversive agent on dogs (Macfarlan Smith Ltd, unpublished data).

Experimental design

Foxes were tested together, in their usual enclosure (to eliminate any stress which might result from housing individually). The animals were presented with 0.5 pint (227 ml) of milk, on some occasions untreated, and on others laced with varying quantities of Bitrex™, in one plastic dog bowl (20 cm diameter), and 227 ml untreated tinned dogfood in another. Each bowl was securely attached to a paving slab (to prevent tipping), and bowls were placed 1.5 m apart, at one end of the enclosure. To control for a possible positional preference between the bowls, milk and canned dogfood were alternated between the two positions each night. At approximately 2300h each evening, the handler entered the pen briefly to charge the bowls with the appropriate bait, first removing any milk or dogfood remaining from the previous 24 h period, and washing the bowls thoroughly. The foxes had 24 h access to the bowls and were left undisturbed for this period.

Three consecutive trials were conducted (Table 1). In the Baseline trial (eight days), all milk was untreated, this providing a historical control for comparison with subsequent trials. The Dosage trial aimed to establish the concentration of Bitrex™ that deterred foxes from drinking the milk. Solutions of Bitrex™ in milk were presented at 400 ppm (over five days), 1000 ppm (10 days), 2000 ppm (eight days) and 4000 ppm (nine days) by mass. The trial began at 400 ppm and the dose was increased until effective at deterring the foxes from drinking the milk (see results). The Conditioning trial was split into three consecutive phases:

Conditioning (eight days), Partial Reinforcement (two days), and Post-Conditioning (20 days). A dose of 4000 ppm was found to be effective at deterring foxes, and was presented in the milk throughout the Conditioning phase. During the Partial Reinforcement that followed, Bitrex™-treated milk and untreated milk were offered simultaneously in the two bowls (no experimental canned dogfood was offered during this phase, but foxes continued to be provided with their normal, basic diet). This was followed by Post-Conditioning, during which all milk was untreated.

Behavioural observations

During trials, the foxes were observed using video surveillance (Stewart et al 1997) under infra-red lights mounted 3 m from the bowls. The animals were allowed to habituate to the experimental set-up for a week before the trials commenced, and their activities were then filmed for up to 16 h each night.

From the tapes, the bait presentation time, and the time at which the bowl was emptied (or, if this happened sooner, the time the recording finished — giving a minimum time for which the bowl remained unemptied) were recorded for each bowl on each night. The handler also noted whether the bowls were empty 24 h later, when he returned to replenish them. Start and stop times were recorded (in seconds) for each occurrence of each behaviour.

Six main behaviours were of interest: drink, eat, take, taste, sniff and bury. Each of these constituted an 'approach' to the bait, while drink, eat, take and taste also provided an opportunity to 'sample' the bait. Drinking, eating or tasting were classed as 'consumption' (for the purposes of calculating consumption rate and number of consumption bouts), while sniffing or burying were classed as 'pre-sampling' activities, if performed prior to the first sampling event (drink, eat, take or taste).

During tasting, the fox visibly sampled bait with tentative individual tongue movements, distinguishing it from drinking or eating. Details of the foxes' activities at the bowls could be seen clearly, but if there was any doubt regarding whether an animal sniffed or tasted bait, it was assumed to have tasted (and was therefore recorded as sampling the milk). Any error therefore tended to under-estimate the length of time for which a bait 'survived' without being sampled. 'Take' events occurred when a fox removed dogfood from the bowl, whilst 'bury' events involved hooking

Table 2   Median responses of foxes to untreated milk in the Baseline trial, and to milk containing four concentrations of Bitrex™ in the Dosage trial [interquartile range] (n). Medians with the same superscript letter are not significantly different (at P < 0.05) for pairwise Kruskal-Wallis tests. df = 1 for all comparisons.

Behavioural variable	Bitrex™ treatment				
	0	400 ppm	1000 ppm	2000 ppm	4000 ppm
Time to empty bowl (s)	132[a] [126-163] (8)	8859[b] [1134-10424] (5)	12467[b] [8570-14180] (10)	10856[b] [8307-18534] (5)	86319[c] [64893-89698] (8)
Number of pre-sampling activities	0[a] [0-0] (8)	1[bc] [0-1] (5)	0[ac] [0-1] (10)	1[bc] [0-2] (5)	2[b] [1-10] (6)
Time to first approach (s)	1[a] [0-2] (8)	6[ab] [1-28] (5)	13[b] [7-16] (10)	24[b] [19-39] (5)	26[b] [14-37] (6)
Time to first sample (s)	1[a] [0-2] (8)	20[bc] [4-91] (4)	14[b] [10-16] (8)	414[bc] [13-3606] (4)	37[c] [35-509] (5)
Time to first drink (s)	1[a] [1-3] (8)	34[b] [28-1216] (3)	188[bc] [49-327] (2)	12764[bc] [6420-19108] (2)	37094[c] [3600-39168] (5)
Time between approach and sample (s)	0[a] [0-0] (8)	1[bc] [0-4] (4)	0[ac] [0-0] (8)	374[bc] [0-3558] (4)	14[b] [1-502] (5)
Time between sample and drink (s)	0[a] [0-1] (8)	27[ac] [0-1069] (3)	174[bc] [34-313] (2)	9158[bc] [12-18304] (2)	36475[b] [3565-36585] (5)
Consumption rate (s h⁻¹)	4001[a] [3500-4479] (8)	75[b] [70-2606] (3)	140[bc] [118-162] (2)	1[bc] [0-1] (2)	1[c] [1-4] (5)
Consumption bouts per hour	374[a] [318-423] (8)	56[b] [32-188] (3)	34[bc] [21-47] (2)	1[bc] [0-1] (2)	1[c] [1-4] (5)

bedding into the bowl with the nose. 'Sniff' events took place within approximately 5 cm of the bowl or contents.

Video and statistical analysis

From the video data, we obtained nine measures of the foxes' responses to milk or food. These were: time to empty the bowl (s); number of pre-sampling activities; time to first approach (s); time to first sample (s); time to first drink/eat (s); time lag between the first fox approaching the milk bowl and the first fox sampling the milk (s); time lag between the first fox sampling the milk and the first fox drinking the milk (s); consumption rate (s h⁻¹); and number of consumption bouts in the first hour after presentation. Median values were calculated to represent the behaviour of the foxes on each night. Consumption rate was calculated by adding together the length of time (s) spent 'consuming' by each of the three foxes in the first hour after bait presentation. The number of 'consumption' bouts was calculated in a similar way. Both consumption measures were also calculated for each fox individually over each trial or phase.

The number of foxes tested was small (three) and, because they were housed together, the responses of individual animals to the various treatments may not have been independent. As a result, we combined data from the three animals, thereby avoiding the assumption that the behaviour of one fox is not influenced by that of the others. Some behavioural variables were also analysed on a 'per individual' basis, and results closely mirrored those of the combined data. Attention is drawn to this in the appropriate parts of the results section. Our most cautious analysis then considers the sampling population to be this fox group, and we do

not make inferences about foxes in general, but confine them to this fox group.

All statistical comparisons were made using Kruskal-Wallis tests (Seigel & Castellan 1988). For each of the Dosage and Conditioning trials, we tested first for a difference across phases within a trial and then between phase pairs. Statistical tests were applied using SAS software (SAS Institute Inc 1988).

Results

Dosage trials: establishing deterrent concentrations

For each variable, comparisons were made across the Baseline phase and each treatment phase in the Dosage trial. Then, for each variable, we compared each phase pair to produce Table 2.

The time taken by foxes to empty the milk bowl differed significantly across the phases ($\chi^2_{[4]} = 28.73$, $P < 0.001$). Foxes took significantly longer to finish milk treated with each concentration of Bitrex™ than untreated milk in the Baseline trial (Table 2). The foxes finished 227 ml of Bitrex™-treated milk within 7 h 2 min 20 s each night at concentrations of 400 ppm, 1000 ppm and 2000 ppm. However, on six of the eight days on which the milk was treated at 4000 ppm, the bowl still contained milk after 24 h, and foxes took significantly longer to empty the bowl at this concentration than at any of the lower concentrations.

The number of pre-sampling activities performed by foxes differed significantly across the phases ($\chi^2_{[4]} = 13.21$, $P = 0.01$). There were significantly more pre-sampling activities (sniffing or burying the bowl) when milk was

Table 3   Median responses of foxes to untreated milk during the Baseline trial, and to untreated milk during the Partial Reinforcement and Post-Conditioning phases of the Conditioning trial [interquartile range] (n). Medians with the same superscript letter are not significantly different (at P < 0.05) for pairwise Kruskal-Wallis tests. df = 1 for all comparisons.

Behavioural variable	Baseline trial	Conditioning trial phase	
		Partial Reinforcement	**Post-Conditioning**
Time to empty bowl (s)	132[a] [126-163] (8)	39064[b] [1543-76585] (2)	8967[b] [4269-27210] (18)
Number of pre-sampling activities	0[a] [0-0] (8)	1[b] [1-1] (1)	2[b] [2-5] (13)
Time to first approach (s)	1[a] [0-2] (8)	11[ab] [3-18] (2)	15[b] [7-19] (13)
Time to first sample (s)	1[a] [0-2] (8)	6938[b] [23-13853] (2)	45[b] [24-115] (13)
Time to first drink (s)	1[a] [1-3] (8)	6938[b] [23-13853] (2)	109[b] [55-289] (13)
Time between approach and sample (s)	0[a] [0-0] (8)	6928[b] [5-13850] (2)	26[b] [5-108] (13)
Time between sample and drink (s)	0[a] [0-1] (8)	0[a] [0-0] (2)	0[a] [0-37] (13)
Consumption rate (s h⁻¹)	4001[a] [3500-4479] (8)	0[b] [0-306] (2)	225[b] [132-288] (13)
Consumption bouts per hour	374[a] [318-423] (8)	16[b] [0-33] (2)	26[b] [19-31] (13)

treated with 400 ppm, 2000 ppm and 4000 ppm Bitrex™ than when milk was untreated in the Baseline. The times elapsing before the first fox approached, sampled and drank the milk also differed significantly over the phases ($\chi^2_{[4]} \geq 15.87$, $P \leq 0.003$). Foxes took longer to approach Bitrex™-treated milk at doses of 1000 ppm, 2000 ppm and 4000 ppm than untreated milk in the Baseline (Table 2). Foxes took longer to sample and to drink Bitrex™-treated milk at each of the concentrations than untreated milk in the Baseline.

The time lags between the first approach and the first sample, and between the first sample and the first drink, both differed across the phases ($\chi^2_{[4]} \geq 11.76$, $P \leq 0.019$). Each of these lags was significantly greater for most concentrations of Bitrex™ than for untreated milk (Table 2).

The rate of milk consumption and the number of consumption bouts per hour both differed significantly across the phases ($\chi^2_{[4]} \geq 16.93$, $P = 0.002$). Foxes spent a significantly lower proportion of their time consuming milk treated with Bitrex™ at each treatment concentration than they did consuming untreated milk in the Baseline trial, and performed significantly fewer consumption bouts in the first hour when presented with treated milk compared with untreated milk (Table 2). Data for these two measures for individual foxes followed broadly similar patterns.

Dosage trials: effect on interest in dogfood bowl

Figures given here for behaviour associated with dogfood are in the format '(median [interquartile range])'. The time elapsing before the first fox sampled canned dogfood differed significantly across the phases ($\chi^2_{[4]} = 19.49$, $P < 0.001$). Foxes sampled dogfood significantly more quickly when the alternative milk was treated at 400 ppm (0 s [0–1], n = 5; $\chi^2_{[1]} = 5.37$, $P = 0.021$) or 1000 ppm Bitrex™ (1 s [0–2], n = 10; $\chi^2_{[1]} = 5.75$, $P = 0.017$), than they did during the Baseline when the milk was untreated (4 s [2–8], n = 8). However, the time elapsed before sampling the dogfood no longer differed significantly from the Baseline when milk was subsequently treated at 2000 ppm

(2 s [2–3], n = 5, $\chi^2_{[1]} = 0.70$, $P = 0.415$) or 4000 ppm Bitrex™ (10 s [3–19], n = 6, $\chi^2_{[1]} = 1.5$, $P = 0.214$).

Conditioning trial: inducing a generalised aversion

For each variable, comparisons were made across all phases when untreated milk was available (Baseline, Partial Reinforcement and Post-Conditioning). Then, for each variable, we compared phase pairs to produce Table 3.

We obtained 24 h information on seven of the eight Conditioning days. The bowl contained (treated) milk after 24 h on six of these occasions. The time taken by foxes to empty the bowl of untreated milk differed significantly across the Baseline, Partial Reinforcement and Post-Conditioning phases ($\chi^2_{[2]} = 16.59$, $P < 0.001$). After Conditioning, foxes took significantly longer to finish their untreated milk in the Partial Reinforcement ($\chi^2_{[1]} = 4.39$, $P = 0.036$) and Post-Conditioning ($\chi^2_{[1]} = 16.01$, $P < 0.001$) phases than they had during the Baseline trial (Table 3).

The number of pre-sampling activities differed significantly across the phases ($\chi^2_{[2]} = 16.30$, $P < 0.001$). Foxes carried out significantly more pre-sampling activities (sniffing or burying the bowl) when untreated milk was presented during the Partial Reinforcement ($\chi^2_{[1]} = 8.0$, $P = 0.005$) and Post-Conditioning ($\chi^2_{[1]} = 15.25$, $P < 0.001$) phases than when it was presented during the Baseline trial (Table 3). The times elapsing before the first fox approached, sampled and drank the milk each differed significantly across the phases ($\chi^2_{[2]} \geq 13.12$, $P \leq 0.001$). Although the time taken to approach untreated milk during Partial Reinforcement was not quite significantly longer than during the Baseline ($\chi^2_{[1]} = 3.05$, $P = 0.081$), it was significantly longer during Post-Conditioning ($\chi^2_{[1]} = 12.7$, $P < 0.001$; Table 3). Foxes took significantly longer both to sample and to drink untreated milk during Partial Reinforcement ($\chi^2_{[1]} \geq 4.50$, $P \leq 0.034$) and Post-Conditioning ($\chi^2_{[1]} \geq 14.23$, $P < 0.001$) than during the Baseline trial (Table 3). During the Baseline, foxes sampled milk within 1.5 s, on average, but on the final day of the Conditioning phase, no fox sampled or drank Bitrex™-treated milk during 12 h 8 min 3 s of recording.

The following day (the first of Partial Reinforcement), untreated milk was available, but no fox sampled it during 3 h 50 min 53 s of recording; however, on the next day, the individual foxes sampled untreated milk after 23 s, 24 min 13 s, and 24 min 57 s, respectively. Bitrex™-treated milk remained unsampled on both Partial Reinforcement days.

The time lag between the first approach and the first sample differed across the phases ($\chi^2_{[2]} = 15.83$, $P < 0.001$). This was not the case for the time lag between the first sample and the first drink ($\chi^2_{[2]} = 2.82$, $P = 0.244$) (Table 3). The time lag between the first approach and the first sample was greatest during Partial Reinforcement for both treated and untreated milk, and, for untreated milk, was significantly greater during Partial Reinforcement and Post-Conditioning than during the Baseline trial ($\chi^2_{[1]} \geq 8.89$, $P \leq 0.003$). In contrast, following Conditioning, the time lag between sampling and drinking returned to zero for untreated milk during both Partial Reinforcement and Post-Conditioning. Compare the time lag between sampling and drinking for treated milk (Table 2) and for untreated milk (Baseline in Table 2, and Table 3).

The rate of milk consumption and the number of consumption bouts per hour both differed significantly across the phases ($\chi^2_{[2]} \geq 15.11$, $P < 0.001$). The proportion of time foxes spent consuming untreated milk, and the number of consumption bouts within the first hour of presentation, were significantly lower during Partial Reinforcement and Post-Conditioning than during the Baseline trial ($\chi^2_{[1]} \geq 4.36$, $P \leq 0.037$) (Table 3). Data for these two measures for individual foxes followed broadly similar patterns.

For both milk and dogfood, there were no statistically significant differences between bowl positions in the time taken to empty the bowl ($\chi^2_{[1]} \leq 1.33$, $P \geq 0.25$), number of pre-sampling activities ($\chi^2_{[1]} \leq 1.07$, $P \geq 0.30$), or time elapsing before approaching ($\chi^2_{[1]} \leq 3.49$, $P \geq 0.06$), sampling ($\chi^2_{[1]} \leq 1.47$, $P \geq 0.23$), or drinking (or eating) ($\chi^2_{[1]} \leq 0.55$, $P \geq 0.46$), during either the Baseline or the Post-Conditioning phase.

Discussion

We found that Bitrex™ was distasteful to foxes at all concentrations, but increasingly so as concentrations rose. Overall, the time taken to empty the bowl increased with increasing concentration, and consumption decreased. In the Baseline trial, there was no time lag between sampling and drinking — foxes simply drank the milk without tasting it first. The lag increased significantly with the 1000 ppm, 2000 ppm and 4000 ppm phases of the Dosage Trials, suggesting that tasting Bitrex™ milk at these concentrations made foxes more reluctant to drink it. At the lower concentrations of Bitrex™ (400 ppm and 1000 ppm), foxes sampled dogfood more quickly than during the Baseline trial, suggesting that aversion to Bitrex™-tainted milk caused them to turn to alternative food.

Although the foxes found Bitrex™ distasteful, they finished treated milk within 8 h on every occasion when presented with concentrations up to and including 2000 ppm.

However, at a concentration of 4000 ppm, some milk remained in the bowl after 24 h on most nights. Up to 4000 ppm, foxes were prepared to sample, and later drink, treated milk, but, as the concentration rose, they were increasingly reluctant to drink after sampling.

Having determined a deterrent concentration of Bitrex™ in milk, we then successfully established, in this fox group, a generalised aversion to milk. After Conditioning, foxes took significantly longer to sample and to drink untreated milk. Untreated milk thus had a longer 'survival' period than it had in the Baseline. The conclusion that foxes displayed generalised aversion rests on two assumptions: first, that foxes did not detect the taint of Bitrex™ remotely; and second, that they did not first test rejected milk by licking it. Corruption of either of these assumptions would indicate repellency rather than generalised aversion.

Analytical chemists regard Bitrex™ as non-volatile, and at least some dogs were unable to smell it in milk insofar as they exhibited generalised aversion to untreated milk following conditioning with Bitrex™ (Macfarlan Smith Ltd, personal communication 1996). Seemingly, a small minority of dogs and about 5% of humans cannot taste Bitrex™, so we may also expect genetic variation in the capacity of wild canids to taste it. A possibility that cannot yet be excluded, but which seems improbable, is that during the process of synthesis a residue of some detectable solvent contaminates Bitrex™ and provides an osmic flag to its presence on bait. Analytical chemists working on the purification of Bitrex™ estimate that any such contamination would be unlikely to exceed the vanishingly small concentration of 2 ppm, a concentration likely to challenge the sensitivity of even the vulpine nose under field conditions.

These observations about the chemical nature of Bitrex™ are borne out by the foxes' behaviour in our trials. On the first night of Partial Reinforcement, both treated and untreated milk remained untouched for the duration of recording, and milk remained in both bowls 24 h after presentation. The time lag between the first fox sampling and drinking milk was greatest at 4000 ppm during the Dosage trial, whilst the time lag between approaching and sampling the milk peaked some days later, during the Partial Reinforcement phase of the Conditioning trial. The time between first approach and first sample was greater after Conditioning than during or before, whereas the time between sampling and drinking was not. Thus, after Conditioning, foxes were less likely to sample the (untreated) milk, but once they did so, they could tell immediately that it was not tainted. The observed increase in the time lag between approaching and sampling milk could not therefore have been a response to smell, and so the foxes' rejection of palatable milk during the Post-Conditioning period demonstrates generalised aversion.

It is not possible to say how good a model hand-reared foxes might provide for those reared in the wild. Also, wild and captive foxes may be subject to different motivations. For example, wild foxes will experience varying and possibly extreme hunger levels and may be prepared to take greater risks, for example, eating potentially unpalatable food.

However, in some ways, the captive conditions under which we evaluated Bitrex™ as an aversive agent were likely to provide a more severe test than would have been the case for a fox in the wild, which would be free to move on to alternative food sources, with the prey in turn having the opportunity to escape. To facilitate establishment of an effective dose (one which foxes would not drink), we provided foxes with 24 h access to the milk. To ensure an equally demanding test of any aversion achieved, it was considered necessary to continue this regime during Post-Conditioning. Therefore, the foxes were kept in close proximity to the milk for up to 24 h, so that the untreated milk probably provided a great and constant temptation, potentially sufficient to 'crack' their resolve, and expose the fraud during Post-Conditioning. Keeping the animals together during the trials, as we did, may also have acted to enhance direct competition and create opportunities for social facilitation.

On the other hand, the captive nature of this work ensured that each fox was regularly exposed to treated milk throughout the Conditioning Phase, more reliably perhaps than would be likely in the wild. However, the fact that the foxes were successfully conditioned under these circumstances offers support for the potential of trials in the wild with more realistic bait. The promising results of this exploratory study suggest that the next logical step is to test the generalised aversion process with a wild population. We have further developed our methods for this purpose and related work is now underway with wild animals.

Animal welfare implications

The welfare and other rewards of exploiting generalised aversion against a range of predators could be considerable. Killing a predator is not itself an animal welfare issue, but some of the methods regularly used are judged to be inhumane (Baker & Harris 1997; Harris 1997). In Britain alone, about 20 million pheasants are hand-reared for shooting each year and, to protect this industry, large numbers of mammalian and avian predators are killed. At least 100 000 foxes are killed annually on British farms largely in the interests of preserving game (Macdonald *et al* 2000; Tapper 1992). Feral cats (*Felis sylvestris catus*), American mink (*Mustela vison*), stoats (*Mustela erminea*) and weasels (*Mustela nivalis*) are also legally killed in Britain for gamebird protection.

It is also frequently judged necessary to control predators such as foxes in nature reserves, particularly in areas where there are ground-nesting birds (eg Forster 1975; Minsky 1980; Haddon & Knight 1983). Lethal control in protected areas may be difficult or inappropriate because of the danger to non-target animals, the rarity of some predators, the general desirability of maintaining a community as a whole rather than protecting one or two species, and public feeling. There was an outcry when English Nature decided to control foxes and corvids lethally at Stiperstones National Nature Reserve in Shropshire, when red grouse (*Lagopus lagopus*) numbers at the reserve became critically low (Wall 1993). Local nature lovers questioned the ethics

of killing one species to protect another (Anon 1993; Strange 1993).

Although generalised aversion will probably last for only a short period of time, this may nevertheless be sufficient for the protection of pen-reared game birds (Hill & Robertson 1988; Leif 1994). The same may apply to some rare ground-nesting birds in nature reserves, which are at risk only during the breeding season. Successful establishment of generalised aversion in captive foxes suggests that this may be a potentially important tool in non-lethal predator control.

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