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A mechanistic understanding of repellent function against mammalian herbivores

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Abstract

Background: Browsing repellents are widely used to deter large herbivores from consuming plants of ecological, economic and aesthetic importance. Understanding how these repellents function on a behavioural mechanistic level is critical to predicting effectiveness. Here, we illustrate how these mechanisms can be tested, by exposing a model mammalian herbivore, the fallow deer, to different concentrations of a commercial chemical repellent (HaTe2) in two-choice feeding trials.

Results: The repellent acted as a defensive chemical for the food by both reducing visitation and the amount consumed. Deer favoured the less defended feeders before ingesting any food, suggesting that the repellent altered olfactory and/or visual cues. Deer also consumed less of the more defended food when choosing between low and high repellent feeders than no and low repellent feeders, indicating that the repellent modified flavour and/or sensation. Repellent effectiveness declined with increased exposure, suggesting that consumption had no negative post-ingestive effects, and thus, deterrence was not caused by a conditioned aversion or irritation. Instead, this pattern suggests that deer learned, through repeated sampling of repellent-treated food, that there was no adverse physiological effect of ingesting it.

Conclusions: These results imply that HaTe2 repellent will not be effective over prolonged periods or in the absence of alternative untreated food. Understanding the mechanisms driving repellent function using two-choice trials could help practitioners decide whether a particular repellent is likely to be effective against mammalian herbivory in their management scenario.

Keywords: Browse, Foraging decisions, Forestry, Ungulate, Wildlife damage

Background

Plants and herbivores interact in a complex and reciprocal manner: plants influence the health and distribution of herbivores, while herbivory modifies the composition and structure of plant communities (Augustine and McNaughton 1998). These interactions can have far-reaching consequences for other plants and animals by influencing the availability of resources (Nuttle et al. 2011; Pedersen et al. 2007; Stephan et al. 2017), the success of revegetation efforts (Austin et al. 1994; Stutz et al. 2015) and productivity in agriculture and forestry (Putman and Moore 1998). One method for reducing damage by abundant mammalian herbivores is the application of chemical repellents to deter herbivores from
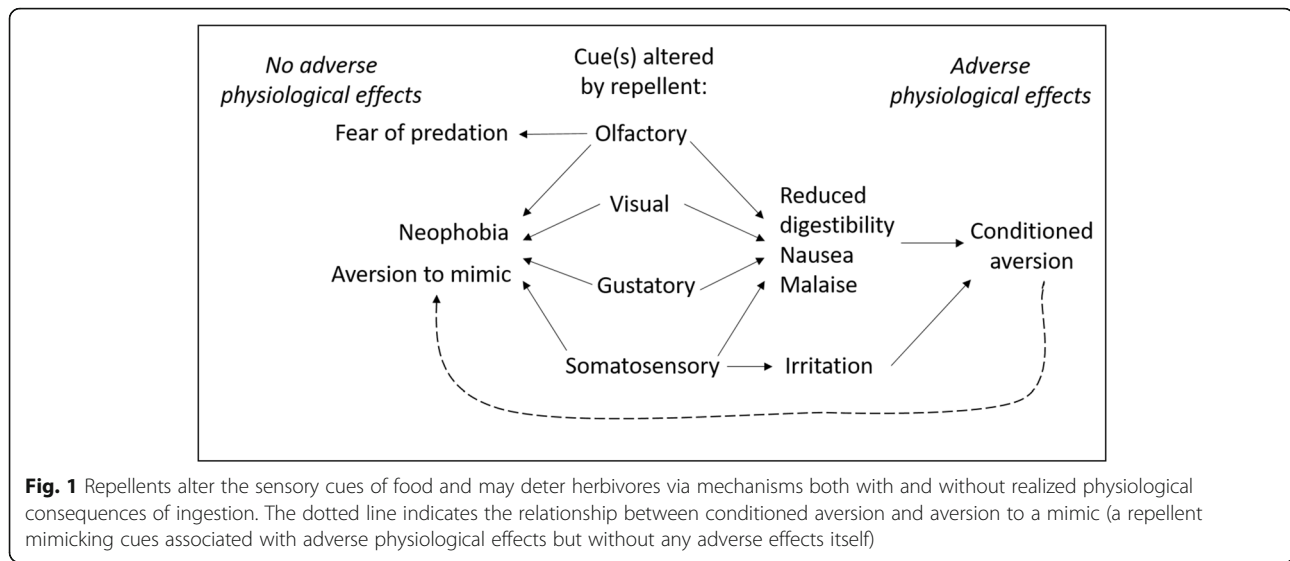
high-value plants such as those used in cropping, timber production, restoration and gardening. While several commercial wildlife repellents are available, and some products have been tested for effectiveness (e.g. Conover 1984; El Hani and Conover 1998; Nolte 1998; Novellie and Bigalke 1981), we have an incomplete understanding of the behavioural mechanisms that underlie repellent function (or malfunction) in deterring mammalian herbivores from consuming plants.

Repellents may deter herbivores via one or more mechanisms that reduce the appeal of plants and thus influence foraging decisions. Kimball et al. (2009) defined four 'modes of action' for mammalian herbivore repellents: neophobia, irritation, flavour modification and conditioned taste aversion. We propose an extension of this framework that disentangles the sensory cues altered by repellents from the behavioural and physiological mechanisms that drive deterrence (Fig. 1).

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Fig. 1 Repellents alter the sensory cues of food and may deter herbivores via mechanisms both with and without realized physiological consequences of ingestion. The dotted line indicates the relationship between conditioned aversion and aversion to a mimic (a repellent mimicking cues associated with adverse physiological effects but without any adverse effects itself)

Repellents often change the smell and appearance of food, and these cues are apparent before the food is tasted. Once the animal takes a bite, it experiences the flavour and feeling of the food in its mouth and this can also be modified by a chemical repellent. The association, or not, of these cues with previous experiences and adverse physiological effects determines how effectively the repellent deters herbivores from consuming treated food (Kimball and Taylor 2010).

Repellents that do not cause any adverse physiological effects rely on cues that induce innate or learned avoidance behaviours. For example, those based on neophobia take advantage of the fear of novel stimuli (Cassini 1994; Villalba and Provenza 2000). However, if a repellent only consists of a novel taste, texture, smell or colour, without any negative post-ingestive consequences, its effectiveness generally decreases with exposure time as animals learn to incorporate it in their diet (Nolte 1999). This is probably a consequence of post-ingestive learning (Arnould and Signoret 1993; Provenza 1995), in combination with the continuous sampling behaviour of mammalian herbivores (Provenza et al. 1998), with the speed of learning depending on an animal's nutritional status and the availability of alternative food (Provenza 1995).

Another category of repellents is based on herbivores' innate fear of predation, often induced using odour cues from predator urine and faeces, or sulphurous compounds associated with predation (Bean et al. 1997; Pfister et al. 1990; Sullivan et al. 1985; Woolhouse and Morgan 1995). Much like the repellents based on novelty, those based on fear of predation are infrequently reinforced by experience; unless predation pressure is high, there are relatively few opportunities to associate the cue with the presence of a predator or a predation

event in the herd. Their effects can thus be short-lived, particularly in the absence of alternative food (Murray et al. 2006).

In contrast, repellents that cause pain or discomfort on contact with the mouth, nose or eyes generally have immediate deterrent effects (Beauchamp 1997; Mason 1998), possibly because these irritants mimic the compounds released during tissue damage (Clark 1997). There is some evidence that repellents containing compounds that activate the trigeminal system, such as capsaicin, deter mammalian herbivores from consumption when applied at high concentrations, but hunger appears to reduce the deterrent effect (Andelt et al. 1992; Andelt et al. 1994).

Animals experiencing sensory cues associated with malaise or gastrointestinal distress, such as those indicating the presence of tannins or lithium chloride, can develop conditioned aversions (Burritt and Provenza 1989; Provenza 1996; Provenza et al. 1990). The effects of these repellents are typically long-lasting as repeated sampling by herbivores reinforces the negative association between flavour and consequence. Conditioned aversions may even extend to mimicking cues associated with experiences of negative post-ingestive effects (Massei et al. 2007).

A single repellent may employ one or a combination of sensory cues and behavioural mechanisms to deter herbivores from consuming treated plants. A large number of repellents exist and have been tested for efficacy in the field, but we currently do not have a mechanistic understanding of how these repellents operate to deter herbivores. This is important for predicting repellent effectiveness under variable field conditions and the factors that could lead to failure. Our objective was to develop a simple behavioural experiment for determining

the mechanisms of deterrence and modes of action employed by commercial repellents.

We used two-choice feeding trials to quantify the behavioural responses of a model mammalian herbivore, the fallow deer (*Dama dama*), to food varying in repellent concentration. We chose the commercial repellent HaTe2 (Fluegel GmbH, Germany), a black viscous liquid comprised of ethanol, balsam resin and black pigment. Given that the repellent altered the appearance, smell and possibly taste and texture of food, we hypothesised that the mechanisms behind its deterrent function would be twofold: first by reducing the frequency with which animals chose the food and second by reducing the amount of food they ingested as a function of repellent concentration. For each sensory and behavioural mechanism that could be involved in deterring food consumption, we specified the foraging behaviour that we would expect from the deer (Table 1). Some modes of action are more robust than others; thus, understanding how a chemical repellent functions at the behavioural level is critical for predicting its performance as a herbivore deterrent.

Methods

Experimental design

We used seven adult female fallow deer that were born in 2000 and had been hand-reared, making them amenable to conducting individual paired-choice feeding trials. They were held in a 4-ha enclosure at Tovetorp Research Station (Stockholm University, south-central Sweden). The enclosure comprised a sloping meadow with low-lying shallow waterbodies and a variety of trees including spruce *Picea abies*, Scots pine, silver birch *Betula pendula*, downy birch *Betula pubescens*, Norway maple *Acer platanoides*, rowan *Sorbus aucuparia*, aspen *Populus tremula*, alder *Alnus glutinosa*, hazel *Corylus avellana*, oak *Quercus robur* and small-leaved lime *Tilia cordata*. The deer had ad libitum access to water, minerals and a salt stone throughout the study period (26th of January to 26th of February, 2016). The food consumed

during trials constituted more than their normal daily intake, so no additional food was provided on trial days.

Fallow deer were offered a choice between food treated with different concentrations of HaTe2 repellent. We used Renfor pellets (manufacturer: Lantmännen, Nyköping), a product specifically designed for cervids that contains dried beet pulp and molasses, oats, wheat, malt sprouts, distiller's grains, corn, rapeseed and sodium chloride (crude protein = $100 \, \text{g kg}^{-1}$, energy = $11.2 \, \text{MJ kg}^{-1}$). We used a hand-pressurized spray bottle to apply the repellent to pellets at three wet-weight concentrations: high ($70 \, \text{g kg}^{-1}$), low ($7 \, \text{g kg}^{-1}$) and control (none applied). Testing occurred with one individual at a time led to the entrance of a triangular pen in a corner of their enclosure. Animals were presented with two clay bowls (feeders, 23 cm in diameter) at 20 cm apart, containing 200 g of food each in one of two repellent combinations: no and low, or low and high. We expected that adding repellent would alter the food quality perceived by deer by artificially increasing defence against herbivores. The level of defence was expected to be lowest in feeders with no repellent and highest in feeders with high repellent concentration; the defence of low repellent feeders should then be relative to the alternative feeder offered. Both positive and negative simultaneous contrasts have been previously demonstrated in fallow deer (Bergvall and Balogh 2009) and are potentially important when applying repellents in forests because this may create contrasts between treated and untreated plants, with the untreated plants themselves having variable levels of natural plant defences.

We randomly allocated treatments and the position of the feeders (left/right). The trial endpoint was when the animal had eaten all the food in one of the feeders. The remaining feeder was then removed and food weighed. During each trial, we also recorded at which feeder the animal initiated feeding and the number of times they switched feeders. The former indicates whether or not deer used visual and/or olfactory cues at a distance to

Table 1 The expected foraging responses of fallow deer for each potential mechanism of repellent function. Deer were exposed to two-choice food trials with no and low or low and high concentrations of repellent (more repellent = more defended)

Mechanisms	Expected foraging response
Sensory cues altered	
Olfactory/visual	-Fewer trials involve consumption from more defended feeder in pair
	-More likely to initiate consumption at less defended feeder in pair
Gustatory/somatosensory	-Shift between feeders more often when consumption initiated at more defended feeder in pair
	-Consume more from less defended feeder in pair
	-More selective for less defended feeder in more defended (low-high) pair
Adverse physiological effects	
Yes	-More selective for less defended food with exposure
No	-Less selective for less defended food with exposure

select feeders, while the latter suggests the level of indecision or satisfaction with their current choice. We performed one two-choice trial per day with each of the seven fallow deer for 10 days, except one individual (#7) which only participated in seven trials (thus $N = 67$). Deer were involved in trials for a maximum of four consecutive days, followed by a break of at least 5 days before trials recommenced.

Statistical analyses

We tested whether initial feeder choice was a function of relative repellent concentration within two-choice pairs (less or more), the type of two-choice pair (no-low or low-high) and their interaction. We fitted a generalized linear model (GLM) specifying a binomial response variable (initial feeder = 1, otherwise = 0, for each of the two feeders in a trial) with logit link function. We could not include trial day and animal identity as random effects because in this logistic model, each level of these factors necessarily consisted of equal numbers of 0's and 1's (i.e. where one bowl was chosen first, the other was not). A model that included these random effects as interaction terms with relative defence failed to converge.

To test if the first feeder chosen in a trial had any effect on the number of times each deer switched between feeders, we fitted a generalized linear mixed effects model (GLMM) specifying a Poisson response distribution with log link function. We included relative defence and pair type as fixed effects, as in the previous model. We also included trial day and animal identity as random effects, accounting for potential effects of uncontrollable conditions on a trial day (e.g. temperature, cloud cover, environmental noise) and of consistent foraging behaviours by individual deer (Bergvall 2009).

We used a linear mixed effects model (LMM) to test how relative defence and type of two-choice pair affected food consumption, including trial day and animal identity as random effects. Here, we also included trial day as a continuous fixed effect to determine whether the amount consumed by deer in a trial changed over consecutive trials.

Repellents often become less effective at deterring herbivores with increasing exposure. We therefore tested how selective deer were across the five replicates of the two types of two-choice pair. We divided the amount consumed from the less defended feeder in each pair (no in no-low and low in low-high) by the total consumption across both feeders in each trial. We then fitted a LMM with the treatment replicate number as a continuous fixed effect and animal identity as a random effect.

We performed all statistical analyses using the 'lme4' package (Bates et al. 2015) in R version 3.2.2 (R Core Team 2016). We report the significance of the type II

Wald chi-square tests derived using the 'car' package (Fox and Weisberg 2011). Quantile-quantile plots were checked for approximation of normality.

Results

All the deer consumed food from at least one feeder in each trial. In no-low pairs ($N = 33$ trials), deer consumed food from both feeders in 70% of trials, exclusively from no-repellent feeders in 27% of trials and exclusively from low-repellent feeders in 3% of trials. In low-high pairs ($N = 34$ trials), deer consumed from both feeders in 59% of trials, exclusively low-repellent feeders in 35% of trials and exclusively high-repellent feeders in 6% of trials.

First feeder selected

When presented with a choice between two feeders with no and low, or low and high concentrations of HaTe2 repellent, fallow deer were more likely to initiate trials at the less defended feeder in the two-choice pair (relative defence, $\chi^2_1 = 5.07$, $P = 0.024$; Fig. 2). There was no interaction between relative defence and pair type ($\chi^2_1 = 0.24$, $P = 0.621$); pair type itself was not of interest as probabilities of selection within pairs were equal to 1 ($\chi^2_1 = 0$, $P = 1$).

Number of feeder shifts

Deer changed feeders more often when they started the trial at the more defended feeder (relative defence of first feeder, $\chi^2_1 = 7.84$, $P = 0.005$; Fig. 3). The pair type and its interaction with relative defence of first feeder were not significant (pair, $\chi^2_1 = 0.10$, $P = 0.752$; interaction, $\chi^2_1 = 0.91$, $P = 0.339$).

Amount consumed

There was a significant interactive effect of relative defence and pair type on the amount consumed by deer: consumption from the more defended feeder was greater
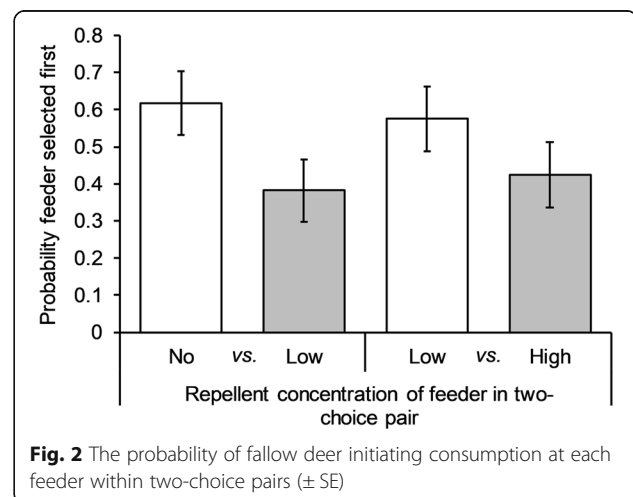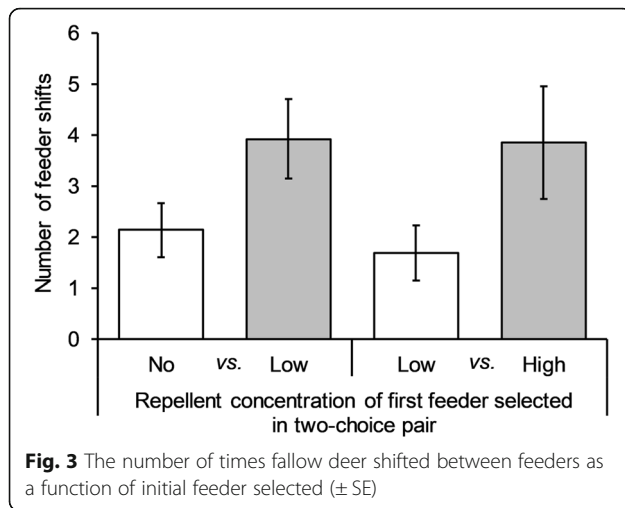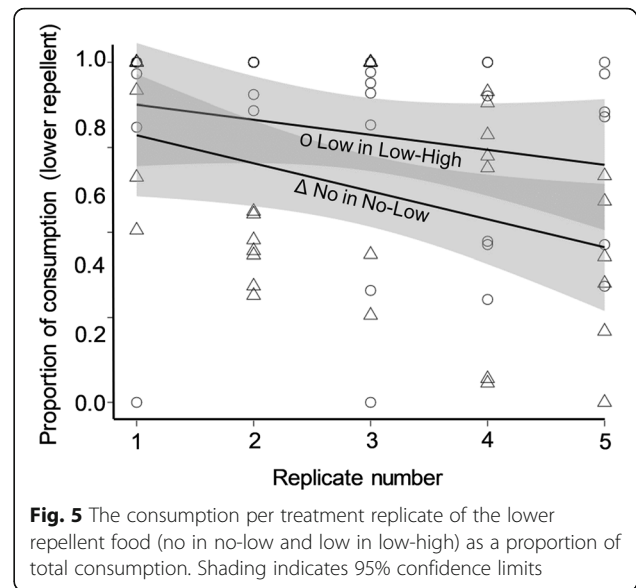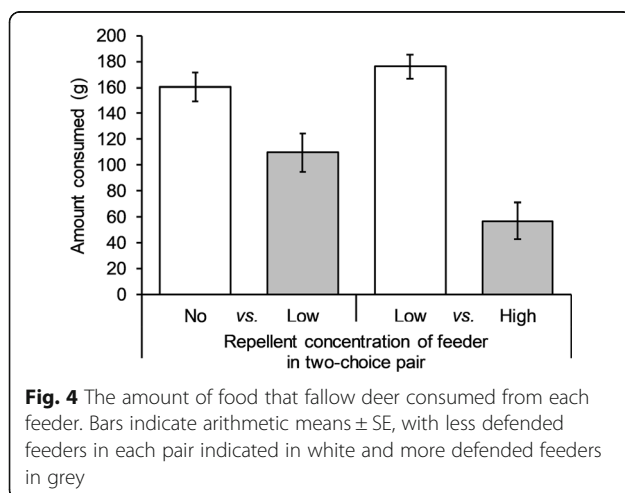

Fig. 2 The probability of fallow deer initiating consumption at each feeder within two-choice pairs (± SE)

Fig. 3 The number of times fallow deer shifted between feeders as a function of initial feeder selected (± SE)

in no-low pairs than in low-high pairs, while consumption from the less defended feeder was greater in low-high pairs than in no-low pairs (interaction, $\chi^2_1 = 7.30$, $P = 0.007$; Fig. 4). Overall, deer ate more from the less defended feeders in each pair (relative defence, $\chi^2_1 = 44.42$, $P < 0.0001$). Pair type and the number of trials that deer completed had no significant effect on the total amount of food consumed by deer in a trial (pair, $\chi^2_1 = 2.66$, $P = 0.103$; trial day, $\chi^2_1 = 1.44$, $P = 0.230$).

Selectivity as a function of exposure

The proportion of consumption comprising lower repellent food was greater in low-high than no-low repellent pairs (pair, $\chi^2_1 = 5.71$, $P = 0.017$; Fig. 5). Selectivity for the lower repellent food decreased with the number of trials each deer was exposed to in both types of two-choice pairs (replicate, $\chi^2_1 = 5.79$, $P = 0.016$). The rate at which selectivity decreased over time was not significantly different between pair types (interaction, $\chi^2_1 = 0.70$, $P = 0.402$).

Fig. 4 The amount of food that fallow deer consumed from each feeder. Bars indicate arithmetic means ± SE, with less defended feeders in each pair indicated in white and more defended feeders in grey

Fig. 5 The consumption per treatment replicate of the lower repellent food (no in no-low and low in low-high) as a proportion of total consumption. Shading indicates 95% confidence limits

Discussion

Browsing by large herbivores can cause significant damage to plants that are important in forestry, agriculture and restoration, yet chemical repellents to deter browsing are not well understood from a behavioural perspective. Using simple two-choice trials with captive fallow deer, we demonstrated the mechanisms of deterrence operating behind a commercial herbivore repellent, HaTe2. We found evidence of both reduced visitation to more defended (higher repellent) feeders and reduced consumption while there. The patterns of consumption from differentially defended pairs of feeders supported a mechanism that included pre-ingestive cues (olfactory and/or visual) and lacked adverse physiological consequences post-ingestion. The two-choice tests therefore provided critical information about the contexts in which the repellent is likely to be effective.

In the majority of trials, the deer consumed food from both feeders but, consistent with our predictions, they chose the higher repellent (more defended) food less often and very rarely consumed the higher repellent food exclusively. Deer were more likely to initiate consumption at the lower repellent (less defended) feeder, showing some ability to differentiate between more and less defended feeders prior to tasting. They may have used visual or olfactory cues coupled to food quality to select the first feeder in a trial. Fallow deer are known to be able to use colour to discriminate between visual stimuli (Birgersson et al. 2001). In addition, there is mounting evidence that colour and odour are important cues used to detect and assess palatable food plants by mammalian herbivores that consume green vegetation, not just for those consuming fruits and fungi (Schmitt et al. 2018; Stutz et al. 2016; Stutz et al. 2017).

When deer did initiate feeding at the more defended feeder, they were more indecisive, switching more often between feeders. This behaviour is consistent with that observed when applying compounds extracted from birch bark (*Betula* spp.) to food; in a two-choice experiment consisting of test and control feeders, fallow deer switched feeders more often when test feeders contained higher concentrations of the extract (Bergvall et al. 2013). We suggest that repellent residue on the tongue may have made subsequent comparisons with the other feeder in the pair more difficult.

The absolute amount that deer consumed during trials did not differ significantly between no-low and low-high pairs. However, the repellent had the effect of suppressing intake of the more defended food, with deer eating a greater amount from the less defended feeder in both treatment pairs (no in no-low and low in low-high pairs). This is consistent with the idea that repellents are more effective when there are alternative (better) food options available (Kimball et al. 2002; Provenza 1995). Consumption of the more defended food was higher in no-low than low-high pairs, suggesting that the repellent modified flavour (odour, taste and texture) and that flavour intensity played a role in food selection (Villalba and Provenza 2000).

The effectiveness of the repellent declined over time in both two-choice pairs, with deer becoming less selective for the less defended feeder in each pair as trials progressed. This suggests that consumption of HaTe2 repellent in food did not have significant post-ingestive consequences for fallow deer (Kimball et al. 2009). Alternatively, the effects of toxins or digestibility-reducing compounds in the repellent may have been partly negated by the high nutritional value of the food compared to natural forage. Detoxification, deactivation or elimination of toxic and anti-nutritional compounds require nutrients and water and thus can be achieved more quickly when food is nutrient-rich (Illius and Jessop 1995; Provenza et al. 2003). The deer may therefore have learned over successive trials that the cost of ingesting the more defended food was not very high; as a result, they may have reduced their effort in selecting between feeders and instead attempted to maximize total intake or rate of intake. This could have implications for the use of repellents near supplementary feeding stations; animals feeding from stations would have enhanced detoxification abilities, decreasing the effectiveness of repellents applied to surrounding trees (Provenza et al. 2003; Timmons et al. 2010).

Conclusions

Our study provides evidence that HaTe2 repellent altered both pre- and post-ingestive cues perceived by deer and suggests that these cues were not coupled with significant physiological consequences. This has implications for the effectiveness of the repellent both temporally and spatially: herbivore deterrence is likely to decrease with prolonged exposure to the repellent and with lower availability of alternative feeding options nearby. As a result, the repellent may not be appropriate in some contexts or require application patterns to be modified by, for example, using rotations of different repellents to maintain novelty, leaving some plants untreated as sacrificial feed or providing supplementary feed.

Decisions about applying herbivore-repelling chemicals to plants over large areas, such as in forestry and agricultural operations, should be informed by the behavioural mechanisms responsible for the deterrent effects. We demonstrated how simple two-choice feeding trials can be used to understand herbivore responses to repellents. The characteristics of the herbivores and plants in an area will influence these responses and thus the effectiveness of a repellent. For example, the effectiveness of a repellent will likely be lower where the nutritive value of the plant is high relative to other available food, there is little alternative food or the herbivore density is high. We therefore suggest that this type of experimentation could be used to select effective mechanisms of plant protection for particular management scenarios and reduce the risk of repellent failure in large-scale field applications.

Authors' contributions
UAB conceived and designed the experiment. LV and RSS performed the experiment. RSS analysed the data and wrote the manuscript; all other authors provided editorial advice. All authors approved the final version of the manuscript.

Availability of data and materials
The datasets generated and/or analysed during the current study will be available in the Mendeley Data repository (https://doi.org/10.17632/ycdr6yr3dx.1).

Ethics approval and consent to participate
Research procedures were approved by the Swedish National Board for Laboratory Animals (Dnr 14–14).

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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Stutz *et al. Ecological Processes*   (2019) 8:25

Page 8 of 8

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