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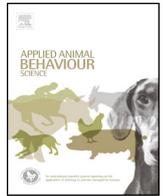


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Repellent application strategy for wild rodents and cottontail rabbits



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ABSTRACT

Effective chemical repellents and repellent application strategies are needed to manage damages caused by wild rodents and rabbits to agricultural resources. For the purpose of comparatively investigating the behavioral response of wild rodents and rabbits to a chemical repellent, we experimentally evaluated the concentration–response relationship of an anthraquinone-based repellent in California voles (*Microtus californicus* Peale), Richardson's ground squirrels (*Urocyon richardsonii* Sabine), deer mice (*Peromyscus maniculatus* Wagner) and cottontail rabbits (*Sylvilagus audubonii* Baird) in captivity. We observed 52–56% feeding repellency for whole oats treated with 10,800 ppm anthraquinone or 18,500 ppm anthraquinone in mice and squirrels, and 84–85% repellency for oats treated with 18,300 ppm anthraquinone or 19,600 ppm anthraquinone in voles and rabbits, respectively. In addition to providing the negative postingestive consequences necessary for conditioned food avoidance, the anthraquinone-based repellent also absorbs ultraviolet (UV) wavelengths that are visible to most wild birds. For the purpose of developing a repellent application strategy to modify the behavior of vertebrate pests, we therefore conducted a conditioned avoidance experiment by offering repellent- and UV-treated food to California voles in a subsequent behavioral assay. Relative to unconditioned test subjects ($P=0.3161$), voles conditioned with the UV, postingestive repellent subsequently avoided whole oats treated only with an UV cue ($P=0.0109$). These behavioral responses to anthraquinone-based repellents and UV feeding cues can be exploited as a repellent application strategy for wild mammals. We discuss potential applications of preplant seed treatments and surface treatments that include postingestive repellents and related visual cues for the protection of agricultural resources associated with mammalian depredation.

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1. Introduction

The opportunistic feeding behavior and fecundity of some wild rodents and rabbits cause economic losses annually to world-wide agricultural production (Gebhardt et al., 2011; Jacob and Tkadlec, 2010; Johnson and Timm, 1987; Pelz, 2003; Salmon, 2008; Witmer and Singleton, 2010). For example, voles (*Microtus* spp. Schrank and *Arvicola* spp. La Cépède) are known to cause damage in the United States of America and Europe to agricultural crops such as alfalfa, peas and wheat, and reforestation efforts (Baldwin et al., 2014; Giusti, 2004; Jacob and Tkadlec, 2010; Sullivan and Sullivan, 2008; Witmer et al., 2007). Ground squirrels (*Spermophilus* spp. Cuvier) cause millions of dollars of damage to alfalfa production in the western United States and Canada (Johnson-Nistler et al., 2005; Proulx, 2010). Ground squirrels caused \$17.9–23.9 million

in crop losses and \$11.9–17.9 million (dollars projected for 2016 valuation) in physical damages to materials such as structures, levees and earthen dams as well as damages to nut crops, tree fruits and rangeland forage (Baldwin et al., 2013; Marsh, 1998). Deer mice (*Peromyscus* spp. Gloger) cause damage to corn, almonds, avocados, citrus, pomegranate and sugar beet crops (Pearson et al., 2000; Witmer and Moulton, 2012). Cottontail rabbits (*Sylvilagus floridanus* Allen) damage tree seedlings, shrubs, hay, soybean and rangeland forage (Dugger et al., 2004; Johnson and Timm, 1987).

Agricultural depredation caused by wild rodents and rabbits is a persistent problem with few cost-effective solutions. Methods to alleviate damage caused by wild rodents and rabbits include behavioral applications (e.g. physical exclusion, chemical repellents) and lethal removal. The need for effective solutions to mammal depredation remains despite prior evaluations of numerous chemical repellents (Agnello et al., 2014; Baldwin et al., 2014; Gurney et al., 1996; Nolte and Barnett, 2000; Nolte et al., 1993; Sutherland, 2003; Williams and Short, 2014). The effectiveness and commercial development of wildlife repellents are dependent upon the repellent's

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efficacy under field conditions, cost relative to expected damages of unprotected resources, environmental impacts, and food and feed safety (Werner et al., 2009). Thus, data regarding efficacy, chemical residues and application strategies are presently needed for the development of non-lethal repellents and the protection of agricultural resources from wild rodents and rabbits.

Although anthraquinone is a naturally-occurring compound that was identified as a promising avian repellent in the early 1940s (Heckmanns and Meisenheimer, 1944), an anthraquinone-based seed treatment (AV-1011; Arkion® Life Sciences, New Castle, DE, USA) was first registered by the United States Environmental Protection Agency for the protection of newly-planted rice in January 2016. Anthraquinone has been used to effectively repel blackbirds (Avery et al., 1997, 1998; Carlson et al., 2013; Cummings et al., 2002a,b, 2011; Neff and Meanley, 1957; Werner et al., 2009, 2011a, 2014b,c), Canada geese (*Branta canadensis* Linnaeus; Blackwell et al., 1999; Dolbeer et al., 1998; Werner et al., 2009), sandhill cranes (*Grus canadensis* Linnaeus; Blackwell et al., 2001), ring-necked pheasants (*Phasianus colchicus* Linnaeus; Werner et al., 2009), European starlings (*Sturnus vulgaris* Linnaeus; Tupper et al., 2014), wild turkeys (*Meleagris gallopavo* Linnaeus; Werner et al., 2014a), horned larks (*Eremophila alpestris* Linnaeus), great-tailed grackles (*Quiscalus mexicanus* Gmelin) and American crows (*Corvus brachyrhynchos* Brehm; Werner et al., 2015).

Relatively few studies, however, have evaluated anthraquinone as a mammalian repellent. Santilli et al. (2005) discovered that wild boar (*Sus scrofa* Linnaeus) consumed 86.5% less corn treated with 0.64% anthraquinone than untreated corn. Werner et al. (2011b) observed 24–37% repellency in black-tailed prairie dogs (*Cynomys ludovicianus* Ord) offered corn seeds treated with 0.5–4.0% anthraquinone. Cowan et al. (2015) observed an aversion to anthraquinone-treated baits in black rats (*Rattus rattus* Linnaeus; 0.1% and 0.25% anthraquinone) and possums (*Trichosurus vulpecula* Kerr; 0.25% anthraquinone). Relative to the consumption of control baits (0.01–0.03% cinnamon, green carrots), the consumption of anthraquinone-treated baits was less in brown rats (*R. norvegicus* Berkenhout; 0.04% and 0.08% anthraquinone) and no different in possums (*T. vulpecula*, 0.08% anthraquinone; Clapperton et al., 2015). Although Hansen et al. (2015) observed that female common voles (*M. arvalis* Pallas) consumed 47% less wheat treated with 5% anthraquinone and chloroform than wheat treated only with chloroform, Hansen et al. (2016a) found no difference in consumption of wheat treated with 15% anthraquinone and chloroform in male common voles and greater consumption of wheat treated with 15% anthraquinone and chloroform in male house mice (*Mus musculus* Linnaeus) relative to wheat treated only with chloroform.

The purposes of this study were to comparatively investigate the behavioral response of wild rodents and rabbits to a chemical repellent, and develop an effective application strategy for the protection of agricultural resources commonly damaged by these wild mammals. Our objectives were to (1) experimentally evaluate the concentration-response relationship of an anthraquinone-based repellent for California voles (*M. californicus* Peale), Richardson's ground squirrels (*Urocitellus richardsonii* Sabine), deer mice (*P. maniculatus* Wagner) and cottontail rabbits (*S. audubonii* Baird), and (2) develop a repellent application strategy by exploiting the behavioral responses of wild rodents and rabbits to anthraquinone-based repellents and associated visual cues.

Most placental mammals (e.g. wild rodents, rabbits) are dichromatic, having two classes of cone photopigment (i.e. long- and short-wave sensitive visual pigments; David-Gray et al., 2002). The short-wave sensitive (SWS) visual pigments of vertebrate cone photoreceptors are divided into two molecular classes, SWS1 and SWS2. Only the SWS1 class is present in mammals. The SWS1 class has been subdivided into violet-sensitive (VS; peak maximum absorbance, or λ_{\max} = 400–430 nm) and ultraviolet-sensitive visual

pigments (UVS, λ_{\max} < 380 nm; Cowing et al., 2002). Although ultraviolet (UV) sensitivity is widespread among animals, UVS visual pigments are considered rare in mammals (Douglas and Jeffery, 2014). Animals without UVS visual pigments, however, will be sensitive to UV wavelengths if they have ocular media that transmit UV wavelengths, as all visual pigments absorb significant amounts of UV if the energy level is sufficient (Douglas and Jeffery, 2014). For the purpose of developing an effective repellent application strategy, we were therefore interested to investigate the conditioned avoidance of UV visual cues subsequent to exposure to an UV, postingestive repellent in California voles.

2. Concentration-response feeding experiments

Four concentration-response feeding experiments were conducted at the headquarters of the National Wildlife Research Center (NWRC) in Fort Collins, Colorado (USA). We live-captured 38 California voles adjacent to commercial artichoke fields in California USA, 28 Richardson's ground squirrels within alfalfa fields in Montana, and 34 deer mice and 30 cottontail rabbits adjacent to NWRC-Fort Collins using appropriate Scientific Collection Permits. We used 8–10 test subjects per treatment group (Werner et al., 2009, 2011b) and thus 3–4 concentrations for each of the four tested species based upon the availability of test subjects subsequent to live-captures. The capture, care and use of all test subjects associated with each experiment were approved by the NWRC Animal Care and Use Committee (NWRC Study Protocols QA-2104, QA-2243, QA-2333; S.J. Werner- Study Director).

All test subjects were offered a maintenance diet for at least one week prior to each of the feeding experiments (i.e. quarantine, holding). For the purpose of comparatively investigating the intra- and interspecific efficacy of a chemical repellent, all test subjects were maintained within individual cages throughout the experiments (quarantine, holding, acclimation, pre-test, test). California voles, Richardson's ground squirrels and cottontail rabbits were maintained within visually-isolated, individual cages (23 × 41 × 18-cm cages for voles, 62 × 50 × 42-cm for ground squirrels, 62 × 50 × 42-cm for rabbits) in an NWRC indoor animal research building. Deer mice were maintained within individual cages (46 × 24 × 19-cm) in the NWRC outdoor animal research facility throughout the experiment to reduce the potential exposure of researchers to hantavirus. Free access to water and environmental enrichment were provided to all test subjects throughout the feeding experiments.

An anthraquinone-based repellent (Avipel® Shield, active ingredient: synthetic 9,10-anthraquinone; Arkion® Life Sciences, New Castle, DE, USA) was used for each of the experiments (Werner et al., 2009, 2010, 2011a,b). Seed treatments for all concentration-response experiments were formulated by applying aqueous suspensions (100 ml/kg) to the test diet using a rotating mixer and household spray equipment (Werner et al., 2014a). The test diet for each of the concentration-response feeding experiments was whole oats.

We hypothesized that repellency would be directly related to repellent concentration during our concentration-response experiments. We operationally defined $\geq 80\%$ repellency as efficacious during our previous laboratory feeding experiments (Werner et al., 2009, 2011a, 2014a,b,c). Thus, we predicted that consumption of efficacious treatments (i.e. threshold repellency) would be $\leq 20\%$ of average, pre-test consumption during the concentration-response experiments.

For each test group, the dependent measure of our concentration-response experiments was calculated as average test consumption of treated test diet relative to average, pre-test consumption of untreated test diet (i.e. percent repellency). The NWRC Analytical Chemistry Unit used high performance liquid

chromatography to quantify actual anthraquinone concentrations (± 10 –100 ppm AQ) among our anthraquinone-treated test diets (Werner et al., 2009, 2011a, 2014a,b,c, 2015). We used non-linear regression procedures (SAS v9.1) to analyze percent repellency as a function of actual anthraquinone concentration (ppm). When non-linear relationships were observed for repellency and repellent concentration ($\alpha \leq 0.05$), we predicted the threshold anthraquinone concentration needed to achieve 80% feeding repellency. We used descriptive statistics ($\bar{x} \pm S.E.M.$) to summarize anthraquinone dosage for observed threshold repellency (mg anthraquinone/kg body mass [BM]).

2.1. California vole feeding experiment

For the purpose of identifying an effective chemical repellent for wild rodents, this experiment involved concentration-response testing of the anthraquinone-based repellent with California voles in captivity. The maintenance diet for California voles included rodent blocks (LabDiet® 5001; Land O'Lakes, St. Louis, MO, USA) and apple slices. Thirty eight California voles (experimentally-naïve) were available for this feeding experiment. All voles acclimated within individual cages for five days (Wednesday–Sunday). During the acclimation period, one food bowl that contained untreated oats (*ad libitum*) was presented on the north side of each cage at 0800 h, daily.

During the three days subsequent to the acclimation period (Monday–Wednesday), one bowl (30.0 g untreated oats) was presented on the north side of each cage at 0800 h, daily. Daily food consumption (including spillage and desiccation) was measured (± 0.1 g) at approximately 0800 h on Tuesday–Thursday. Voles were ranked based upon average, pre-test consumption and assigned to one of four test groups at the conclusion of the pre-test ($n = 8$ –10 voles per group) such that each group was similarly populated with voles that exhibited high–low daily consumption (Werner et al., 2009, 2010, 2011a,b). We randomly assigned test treatments among groups (i.e. experimental units).

On the day subsequent to the pre-test (Thursday), one bowl (30.0 g anthraquinone-treated oats) was presented on the north side of each cage at 0800 h. Voles in Groups 1–4 received whole oats treated with 0.25%, 0.5%, 1.0%, or 2.0% anthraquinone, respectively (target concentrations, wt/wt). Daily food consumption (including spillage and desiccation) was measured at approximately 0800 h on Friday.

2.1.1. Results of California vole feeding experiment

California voles exposed to whole oats treated with 0.25–2.0% anthraquinone exhibited 24–84% repellency during the concentration-response experiment (Fig. 1). Actual anthraquinone concentrations from our anthraquinone-treated oats ranged from 2050–18,300 ppm anthraquinone (Fig. 1). Thus, California voles exhibited 84% repellency for whole oats treated with 18,300 ppm anthraquinone, or 365.0 ± 103.1 mg anthraquinone/kg BM (mean vole BM = 38.1 g). Vole repellency (y) was a function of anthraquinone concentration (x): $y = 26.828 \ln(x) - 174.795$ ($r^2 = 0.95$, $P = 0.0267$). We therefore predicted a threshold concentration of 13,400 ppm anthraquinone for California voles offered treated oats.

2.1.2. Discussion of California vole feeding experiment

The results of this laboratory efficacy experiment suggest that a threshold concentration of 1.3% anthraquinone (wt/wt) can effectively repel California voles from treated food. With regard to the non-lethal management of agricultural crop depredation, anthraquinone-based repellents can be applied as preplant seed treatments for the protection of seeds and seedlings, or as foliar applications for the protection of emergent and maturing seedlings.

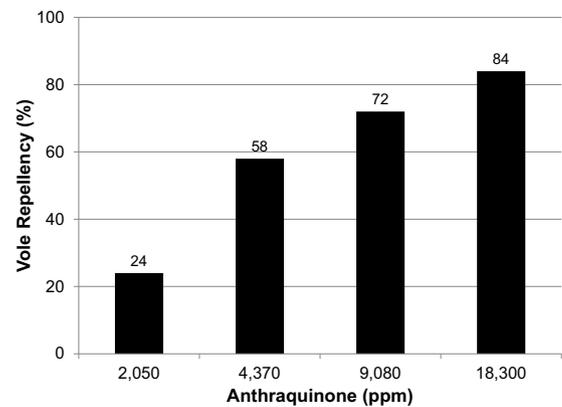


Fig. 1. Mean feeding repellency associated with varying concentrations of an anthraquinone-based repellent (Avipel® Shield; Arkion® Life Sciences, New Castle, DE, USA) offered to California voles (*Microtus californicus* Peale). Repellency represents test consumption (day 4) relative to average, pretreatment consumption (days 1–3) of untreated whole oats ($n = 8$ –10 voles per repellent concentration).

We recommend field efficacy testing of anthraquinone-based seed treatments for alfalfa, peas and wheat, and experimental foliar applications of anthraquinone-based repellents within commercial orchards and reforested stands associated with damages caused by California voles.

2.2. Richardson's ground squirrel feeding experiment

This experiment involved concentration-response testing of the anthraquinone-based repellent with Richardson's ground squirrels in captivity. The maintenance diet for Richardson's ground squirrels included rodent blocks (LabDiet® 5001; Land O'Lakes, St. Louis, MO, USA), apple slices and carrots. We replicated the test procedures of our previous concentration-response experiment with 28 Richardson's ground squirrels (experimentally-naïve) within individual cages (i.e. acclimation, pre-test, test). Test groups 1–3 ($n = 9$ –10 ground squirrels per group) received whole oats treated with 0.5%, 1.0%, or 2.0% anthraquinone (target concentrations, wt/wt), respectively, during the test.

2.2.1. Results of Richardson's ground squirrel feeding experiment

We observed 40–56% feeding repellency among Richardson's ground squirrels offered whole oats treated with target concentrations of 0.5–2.0% anthraquinone (Fig. 2). Actual anthraquinone concentrations from our oat seed treatments ranged from 5380–18,500 ppm anthraquinone (Fig. 2). Ground squirrel repellency was weakly related to actual anthraquinone concentrations ($r^2 = 0.95$; $P = 0.1458$).

2.2.2. Discussion of Richardson's ground squirrel feeding experiment

We observed 56% repellency for whole oats treated with 18,500 ppm anthraquinone in Richardson's ground squirrels. Although we previously defined $\geq 80\%$ repellency as efficacious, synergistic repellency can manifest from optimizing the combination of physiologically-relevant sensory cues and targeted post-ingestive consequences in the formulation of wildlife repellents (Werner et al., 2014b). An efficacious application strategy is needed for foliar and surface applications of chemical repellents for the protection of alfalfa, structures, levees and earthen dams from damages caused by ground squirrels.

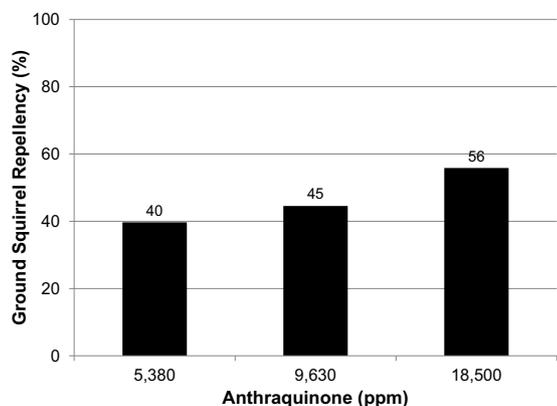


Fig. 2. Mean feeding repellency associated with varying concentrations of an anthraquinone-based repellent (Avipel® Shield; Arkion® Life Sciences, New Castle, DE, USA) offered to Richardson's ground squirrels (*Urocitellus richardsonii* Sabine). Repellency represents test consumption (day 4) relative to average, pretreatment consumption (days 1–3) of untreated whole oats ($n=9$ –10 ground squirrels per repellent concentration).

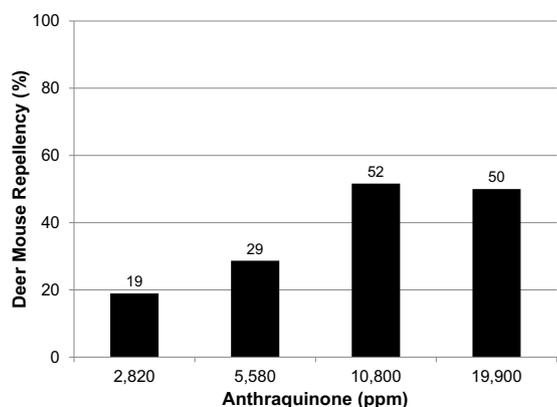


Fig. 3. Mean feeding repellency associated with varying concentrations of an anthraquinone-based repellent (Avipel® Shield; Arkion® Life Sciences, New Castle, DE, USA) offered to deer mice (*Peromyscus maniculatus* Wagner). Repellency represents test consumption (day 4) relative to average, pretreatment consumption (days 1–3) of untreated whole oats ($n=8$ –9 mice per repellent concentration).

2.3. Deer mouse feeding experiment

This experiment involved concentration-response testing of the anthraquinone-based repellent with deer mice in captivity. The maintenance diet for deer mice included rodent blocks (LabDiet® 5001; Land O'Lakes, St. Louis, MO, USA) and apple slices. We replicated the test procedures of our previous concentration-response experiments with 34 deer mice (experimentally-naïve) within individual cages (i.e. acclimation, pre-test, test). Test groups 1–4 ($n=8$ –9 mice per group) received whole oats treated with 0.25%, 0.5%, 1.0%, or 2.0% anthraquinone (target concentrations, wt/wt), respectively, during the test.

2.3.1. Results of deer mouse feeding experiment

Deer mice exposed to whole oats treated with target concentrations of 0.25–2.0% anthraquinone exhibited 19–52% repellency during the concentration-response experiment (Fig. 3). Actual anthraquinone concentrations from our oat seed treatments ranged from 2820–19,900 ppm anthraquinone (Fig. 3). Deer mouse repellency was weakly related to actual anthraquinone concentrations ($r^2=0.89$; $P=0.0580$).

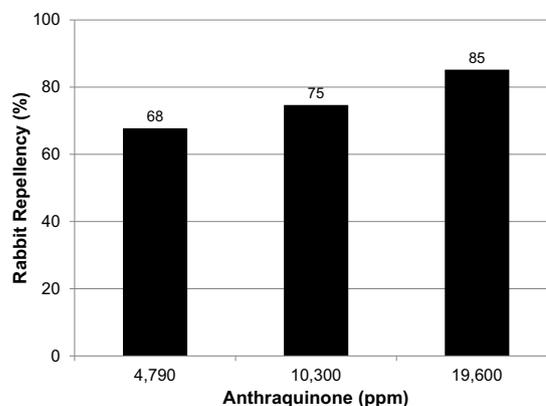


Fig. 4. Mean feeding repellency associated with varying concentrations of an anthraquinone-based repellent (Avipel® Shield; Arkion® Life Sciences, New Castle, DE, USA) offered to cottontail rabbits (*Sylvilagus audubonii* Baird). Repellency represents test consumption (day 4) relative to average, pretreatment consumption (days 1–3) of untreated whole oats ($n=10$ rabbits per repellent concentration).

2.3.2. Discussion of deer mouse feeding experiment

We observed 52% repellency for whole oats treated with 10,800 ppm anthraquinone in deer mice. An efficacious application strategy is needed for the development of repellent seed treatments, and the protection of corn seeds and seedlings from wild rodents (e.g. deer mice). Such strategies can also be formulated as foliar repellent applications for the protection of almonds, avocados, citrus, pomegranate and sugar beet crops associated with depredation caused by deer mouse.

2.4. Cottontail rabbit feeding experiment

This experiment involved concentration-response testing of the anthraquinone-based repellent with cottontail rabbits in captivity. The maintenance diet for cottontail rabbits included Rabbit Chow® (Purina® Mills, St. Louis, MO, USA), apple slices and alfalfa hay. We replicated the test procedures of our previous concentration-response experiments with 30 cottontail rabbits (experimentally-naïve) within individual cages (i.e. acclimation, pre-test, test). Test groups 1–3 ($n=10$ rabbits per group) received whole oats treated with 0.5%, 1.0%, or 2.0% anthraquinone (target concentrations, wt/wt), respectively, during the test.

2.4.1. Results of cottontail rabbit feeding experiment

We observed 68–85% feeding repellency among cottontail rabbits offered whole oats treated with target concentrations of 0.5–2.0% anthraquinone (Fig. 4). Actual anthraquinone concentrations from our oat seed treatments ranged from 4790–19,600 ppm anthraquinone (Fig. 4). Rabbit repellency was weakly related to actual anthraquinone concentrations ($r^2=0.99$; $P=0.0757$). We observed 85% feeding repellency, however, among rabbits offered whole oats treated with 19,600 ppm anthraquinone. Thus, cottontail rabbits were effectively repelled from whole oats treated with a target concentration of 2.0% anthraquinone (Fig. 4), or 149.9 ± 28.1 mg anthraquinone/kg BM (mean rabbit BM = 0.8 kg).

2.4.2. Discussion of cottontail rabbit feeding experiment

We observed 85% repellency for whole oats treated with 19,600 ppm anthraquinone in cottontail rabbits. We recommend field efficacy testing of foliar repellent applications for the protection of tree seedlings, shrubs, hay, soybean and rangeland forage associated with damages caused by cottontail rabbits. Field efficacy experiments should include: (1) application strategies that are specifically developed to protect agricultural crops from mammalian depredation; (2) independent field replicates with

predicted rodent or rabbit damage; (3) varied application rates based upon species-specific threshold concentrations, including untreated controls; (4) pre- and at-harvest analytical chemistry; (5) crop damage measurements; and (6) crop yield measurements (Werner et al., 2011a).

3. Conditioned avoidance experiment with ultraviolet feeding cue

Unlike most tested birds (Aidala et al., 2012; Bennett and Cuthill, 1994; Cuthill et al., 2000), most tested mammals do not exhibit UV vision (Honkavaara et al., 2002; Hut et al., 2000; Jacobs, 1992; Jacobs and Yolton, 1971; Jacobs et al., 1991; Tovee, 1995). Anthraquinone-based repellents provide the negative postingestive consequences and a relevant UV feeding cue necessary to condition avoidance of UV-treated food (Werner et al., 2012, 2014a). We therefore investigated conditioned avoidance of UV-treated food subsequent to anthraquinone conditioning in California voles. Seed treatments for the conditioned avoidance experiment were formulated by applying aqueous suspensions (60 ml/kg) to the test diet using a rotating mixer and household spray equipment (Werner et al., 2012, 2014b).

3.1. Materials and methods

Sixteen California voles (experimentally naïve) were used for this feeding experiment. The maintenance diet (apple slices and LabDiet® 5001, Land O'Lakes St. Louis, MO, USA) and water was again provided to all voles within individual cages, daily. The anthraquinone-based repellent (Avipel® Shield; Arkion® Life Sciences, New Castle, DE, USA) and a titanium dioxide feeding cue (Aeroxide® P25; Acros Organics, Fair Lawn, NJ, U.S.A.) were used for the conditioned avoidance feeding experiment (Werner et al., 2012, 2014a,b). A Genesys™ 2, 336002 spectrophotometer (Thermo Spectronic US, Rochester, NY, USA) was previously used to determine that both the anthraquinone-based repellent and the titanium dioxide feeding cue absorb near UV wavelengths (Werner et al., 2012).

All voles acclimated within individual cages for five days (Wednesday–Sunday; Week 1). Two food bowls (east and west side of each cage) of unadulterated oats were provided throughout the acclimation period. Two food bowls (unadulterated oats on east and west sides of cage) were presented at approximately 0800 h, daily for two days subsequent to acclimation (Monday and Tuesday; Week 2). We ranked cages based upon pre-test consumption, assigned cages to one of two groups, and randomly assigned treatments between groups at the completion of the pre-test.

Two food bowls (east and west side of cage) were presented at approximately 0800 h, daily for two days subsequent to the pre-test (Wednesday and Thursday; Week 2). For the purpose of behavioral conditioning with the UV-absorbent, postingestive repellent, we exposed all voles in the conditioned group (Group 1; $n=8$) to oats treated with 0.25% anthraquinone (target concentration, wt/wt) in both food bowls. We exposed all voles in the unconditioned group (Group 2; $n=8$) to unadulterated oats in both food bowls. We provided two food bowls of the maintenance diet from approximately 0930 h on Friday (Week 2) through 0800 h on Monday (Week 3) to all test subjects.

Two food bowls were presented at approximately 0800 h, daily for four test days (Monday–Thursday; Week 3). For the purpose of preference testing with the UV-absorbent feeding cue subsequent to behavioral conditioning, Groups 1 and 2 received oats treated with 0.2% of the UV cue in one bowl, and untreated oats in the alternate bowl, daily. We randomly located UV-treated oats on the first test day (i.e. east or west side of cage) and thereafter alternated daily throughout the test such that UV-treated and untreated oats

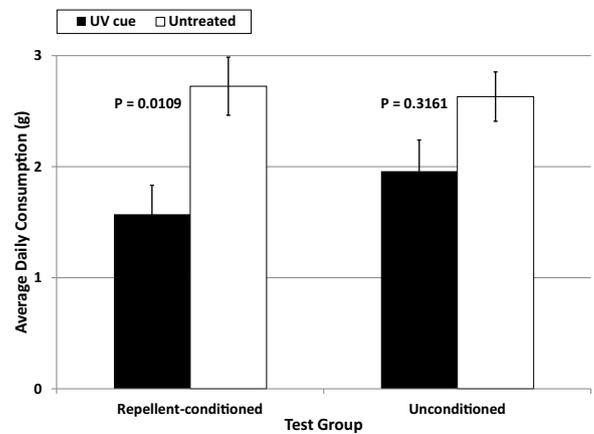


Fig. 5. Mean consumption (\pm S.E.M.) of whole oats offered to California voles (*Microtus californicus* Peale; $n=8$ per test group). Voles were offered untreated whole oats and those treated with 0.2% of an UV feeding cue (active ingredient: titanium dioxide; Evonik Goldschmidt Corporation) throughout the four-day test. The repellent-conditioned test group was exposed to an UV, postingestive repellent prior to the test.

were each offered twice on the east and west side of each cage. We independently measured oat consumption in east and west food bowls in each cage throughout the test (i.e. approximately 0800 h, Tuesday–Friday; Week 3).

The dependent measure of our conditioned avoidance experiment was average (i.e. daily) test consumption of treated and untreated food. After conducting Levene's test for equal variances ($\alpha=0.05$) and affirmatively inspecting the normality of residuals, consumption data were subjected to a Welch's analysis of variance. The group-by-treatment interaction was analyzed using a general linear model (SAS v9.1). We used Tukey-Kramer multiple comparisons to separate the means of the significant interaction ($\alpha=0.05$). Descriptive statistics ($\bar{x} \pm$ S.E.M.) were used to summarize consumption of treated and untreated food throughout the conditioned avoidance experiment.

3.2. Results of conditioned avoidance experiment

The two test groups consumed different amounts of UV-treated and untreated food during the four-day test ($F_{3,67} = 4.48$, $P=0.0063$). Relative to the consumption of untreated oats, voles conditioned with the UV-absorbent, postingestive repellent consumed fewer oats treated only with the UV-absorbent cue throughout the test (i.e. repellent-conditioned, Fig. 5). The repellent-conditioned group consumed an average of 1.6 ± 0.3 g of UV-treated whole oats and 2.7 ± 0.3 g of untreated oats per day, throughout the test (Tukey-Kramer $P=0.0109$).

In contrast, unconditioned voles consumed similar amounts of UV-treated oats and untreated oats throughout the test (Fig. 5). The unconditioned group consumed an average of 2.0 ± 0.3 g of UV-treated whole oats and 2.6 ± 0.2 g of untreated oats per day, throughout the test (Tukey-Kramer $P=0.3161$). Thus, without prior conditioning with the UV-absorbent, postingestive repellent, the UV-absorbent cue was not itself aversive to California voles. Moreover, although California voles are not maximally sensitive to UV wavelengths, voles conditioned with the UV-absorbent, postingestive repellent subsequently consumed less food treated only with the UV-absorbent cue.

3.3. Discussion of conditioned avoidance experiment

Because California voles consumed less of the test diet treated only with the UV-absorbent feeding cue subsequent to condition-

ing with the UV-absorbent, postingestive repellent (i.e. relative to the unconditioned control group; Fig. 5), we observed cue-consequence specificity (Domjan, 1985) for an UV visual cue and a postingestive repellent in a dichromatic rodent. Thus, similar to blackbirds (Werner and Provenza, 2011), California voles cognitively associate pre- and postingestive consequences with visual cues, and reliably integrate visual and gustatory experience with postingestive consequences to procure nutrients and avoid toxins. These visual cues include UV-absorbent and UV-reflective cues for mammalian feeding behavior. The behavioral responses of this study can be exploited as a repellent application strategy for the protection of agricultural resources. This application strategy comprises a postingestive repellent and a feeding cue with visual characteristics sufficiently similar to the repellent such that the repellent concentration can be decreased (i.e. to include 0% of the chemical repellent subsequent to repellent exposure, Fig. 5) whilst maintaining or synergistically increasing repellent efficacy (Werner et al., 2014b).

The repellent application strategy described herein (i.e. UV, postingestive repellent and associated UV visual cue) has implications for several wild rodents and rabbits. Although the spectral sensitivity function peaks at 520 nm in California ground squirrels (i.e. VS visual pigments; *Otospermophilus beecheyi*; Anderson and Jacobs, 1972), the lens of Mexican ground squirrels (*Ictidomys mexicanus*) exhibits λ_{\max} of 265–370 nm (i.e. UVS visual pigments; Cooper and Robson, 1969). In Richardson's ground squirrels, 50% of incident illumination is transmitted at 462 nm and 0.6% of light from 315 to 400 nm is transmitted by the lens (Douglas and Jeffery, 2014). Although shortwave sensitive cones (S) constitute only 5–15% of the cones in deer mice, partial sequencing of the S opsin gene suggested UV sensitivity of the S cone visual pigment (Arbogast et al., 2013). In house mice, 50% of incident illumination is transmitted at 313–337 nm and 81.7% of light from 315 to 400 nm is transmitted by the lens (Douglas and Jeffery, 2014). The maximum optical transmittance (i.e. 94–96%) in albino rabbits was found between 630 and 730 nm; transmittance decreased to 50% at 400 nm and <1% at 380 nm (Algere et al., 1993). In rabbits (*Oryctolagus cuniculus* Linnaeus), 50% of incident illumination is transmitted at 392 nm and 12.7% of light from 315 to 400 nm is transmitted by the lens (Douglas and Jeffery, 2014). Thus, supplemental laboratory and field efficacy testing is recommended for the comparative evaluation and commercial development (e.g. pricing of optimized formulations) of a repellent application strategy comprising an UV, postingestive repellent and an associated UV feeding cue for wild rodents and rabbits.

4. General discussion

We observed 52–56% feeding repellency for whole oats treated with 10,800 ppm anthraquinone or 18,500 ppm anthraquinone in mice and squirrels, and 84–85% repellency for oats treated with 18,300 ppm anthraquinone or 19,600 ppm anthraquinone in voles and rabbits, respectively. We therefore observed considerable interspecific variation in the feeding behavior of these wild mammals offered food treated with the anthraquinone-based repellent. Similarly, we predicted a threshold concentration of 1450–1475 ppm anthraquinone for Canada geese and red-winged blackbirds, 5200 ppm anthraquinone for American crows, 9200 ppm anthraquinone for common grackles (*Quiscalus quiscula* Linnaeus) and 10,450 ppm anthraquinone for ring-necked pheasants (Werner et al., 2009, 2011a, 2015). Thus, anthraquinone repellency is not inversely proportional to the body mass of the target animal and considerable interspecific variation exists for anthraquinone among tested mammals and birds. We therefore

recommend species-specific efficacy testing for each target animal under laboratory and field conditions.

Relative to unconditioned test subjects, voles conditioned with the UV, postingestive repellent subsequently avoided whole oats treated only with an UV cue. Similarly, red-winged blackbirds conditioned with the UV, postingestive repellent subsequently avoided UV-treated food relative to unconditioned blackbirds (Werner et al., 2012). This ultraviolet strategy for repellent applications was recently developed for wild birds associated with agricultural crop depredation (Werner, 2015). Relative to the repellency of food treated only with the anthraquinone-based repellent, synergistic repellency (i.e. 45–115% increase) was observed when 0.2% of the UV feeding cue was combined with 0.02% or 0.035% anthraquinone (wt/wt; Werner et al., 2014b). This ultraviolet strategy for repellent applications is presently being developed for the management of damages caused by wild rodents and rabbits to plant and animal agriculture.

Among the wild mammals that we have experimentally offered food treated with 0.25–2% anthraquinone (wt/wt), the ranked efficacy of anthraquinone-based repellents in order of high–low repellency was cottontail rabbits (68–85% repellency), California voles (24–84% repellency), Richardson's ground squirrels (40–56% repellency), deer mice (19–52% repellency) and black-tailed prairie dogs (24–37% repellency; Werner et al., 2011b). Interestingly, the transmittance of UVA wavelengths (315–400 nm) through the ocular media was estimated to be 13%, 0.6% and 0% in European rabbits (*Oryctolagus cuniculus* Linnaeus), Richardson's ground squirrels and black-tailed prairie dogs, respectively (Douglas and Jeffery, 2014). Thus, the efficacy of this UV, postingestive repellent is directly proportional to the known transmittance of UVA wavelengths in these wild mammals. We therefore recommend additional research for the development of non-lethal, UV repellent application strategies for wild mammals associated with human–wildlife conflicts.

Because inconsistent success has been observed among rodent repellent trials conducted under laboratory and field conditions, a progression of efficacy experiments (i.e. cage, then enclosure, then field studies) has been recommended for the reliable measurement of repellency and the successful development of non-lethal wildlife repellents (Hansen et al., 2016b). We recommend field enclosure experiments to further evaluate anthraquinone-based repellents and ultraviolet application strategies. The results of our current study will enable the design of supplemental field efficacy experiments and the development of non-lethal repellents for wild rodents, rabbits and other wildlife associated with human–wildlife conflicts.

5. Conclusion

This study provided a novel investigation of an anthraquinone-based repellent and related visual cues for wild rodents and rabbits associated with damages to agricultural resources. We observed 52–56% feeding repellency for whole oats treated with 10,800 ppm anthraquinone or 18,500 ppm anthraquinone in deer mice and Richardson's squirrels, and 84–85% repellency for oats treated with 18,300 ppm anthraquinone or 19,600 ppm anthraquinone in California voles and cottontail rabbits, respectively. Relative to unconditioned test subjects, voles conditioned with the UV, postingestive repellent subsequently avoided whole oats treated only with an UV cue. Thus, California voles cognitively associate pre- and postingestive consequences with visual cues, and reliably integrate visual and gustatory experience with postingestive consequences to procure nutrients and avoid toxins. These behavioral responses to anthraquinone-based repellents and UV feeding cues can be exploited as a repellent application strategy for the non-lethal management of agricultural depredation caused by

wild mammals. This application strategy comprises a postingestive repellent and a feeding cue with visual characteristics sufficiently similar to the repellent such that the repellent concentration can be decreased whilst maintaining or increasing repellent efficacy.

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