UC Agriculture & Natural Resources
Proceedings of the Vertebrate Pest Conference

Title
Plant secondary chemicals as non-lethal vertebrate repellents

Permalink
https://escholarship.org/uc/item/5132n4f9

Journal
Proceedings of the Vertebrate Pest Conference, 17(17)

ISSN
0507-6773

Authors
Watkins, Richard W.
Cowan, David P.
Gill, Elaine L.

Publication Date
1996

PLANT SECONDARY CHEMICALS AS NON-LETHAL VERTEBRATE REPELLENTS

RICHARD W. WATKINS, and **DAVID P. COWAN**, Central Science Laboratory, London Road, Slough, Berkshire, SL3 7HJ, United Kingdom.

ELAINE L. GILL, Central Science Laboratory, Tangley Place, Worplesdon, Surrey, GU3 3LQ, United Kingdom.

ABSTRACT: Few effective repellents are currently available for the non-lethal management of vertebrate pests. This is perhaps not surprising considering the ad hoc nature of past applications which assumed that the target pest species would have the same attraction/aversion preferences as man. A more rational approach is to identify compounds that have real biological significance for the pest species. Plants have evolved an array of defense chemicals (secondary plant compounds) that inhibit the feeding of vertebrate herbivores, because they are either innately aversive or they generate a conditioned aversion. These compounds are, therefore, ideally suited for use in the reduction of feeding damage to crops, forest plantations and stored food products. Several of these novel plant-derived materials (e.g., cinnamamide) are already undergoing commercial evaluation. This approach facilitates the use of a number of systems to increase a plant's resistance to attack: topical application of the defense compound, systemic stimulation of the plants own resistance mechanisms and genetic enhancement. The two latter systems will enable the utilization of potent repellents that are not commercially viable for topical application and to concentrate their expression in the most palatable and vulnerable tissues. This paper also discusses work undertaken to improve our knowledge of the feeding strategies of target species. A proper understanding of these behaviors is essential before it will finally be possible to predict the field conditions under which a repellent will be effective.

KEY WORDS: chemical repellents, pest management, aversive conditioning, food aversion, birds, mammals

INTRODUCTION

Plants are a promising source of pharmacologically active compounds including a number which can be used to manipulate the behavior of animals. This paper examines the potential of plant-derived compounds as non-lethal repellents for the management of pest species. This includes a review of the types of plant-derived repellents available, their mode of action, methods of application and factors which influence their efficacy in the field.

WHY REPELLENTS?

Traditional methods of reducing pest problems by population control are becoming increasingly controversial in terms of humaneness and target specificity. Active-hunting methods are labor-intensive and, therefore, rarely cost-effective, and there are only a few examples where such control programs have been successful (Gosling and Baker 1989). Poison baiting is the most widely used method of lethal control. However, the use of poison has four major disadvantages: 1) control is only temporary as the area is often rapidly re-invaded by the target species; 2) the target species may develop a resistance to the bait formulation; 3) the bait may not be accepted in the presence of other familiar alternative foods; and 4) there is the risk of inadvertent poisoning of non-target species (Sullivan et al. 1988).

Repellents offer an alternative, non-lethal method of reducing damage by pests, by causing the animal to avoid certain foods or vacate a given area. For vertebrate pests, repellents can be visual (e.g., scarecrows), auditory (e.g., ultrasound), physical (e.g., netting, electric fences), or chemical (e.g., cinnamamide, methyl anthranilate) (Mason and Clark 1992). Physical exclusion techniques are often costly to install and maintain, while audio and visual scarers are either ineffective or the initial aversion is rapidly overcome owing to the lack of reinforcement of the stimuli (Lund 1988). In some cases the animal may even learn to associate the stimuli with a good food source, and what was an aversive stimulus becomes an attractive one (I. R. Inglis, pers. comm.). Chemical repellents, if used appropriately in relation to the biology of the target species, are less likely to be compromised by these effects.

SOURCES OF CHEMICAL REPELLENTS

Chemical repellents, often in combination with other pest management techniques, are now taking their place in the environmentally friendly scheme of integrated pest management (Feare 1995). However, it seems likely that they have yet to reach their full potential for a number of reasons. The development of this field was initially stalled by our limited knowledge of pest behavior and the parameters which determine the efficacy in the field of any putative repellent. Compounds were put forward as candidate repellents simply on the basis that they tasted bad to humans. These compounds, such as the bitter agent denatonium benzoate, have limited effectiveness with rapid habituation and, thus, poor performance in the absence of high quality alternative food (Nolte et al. 1994). Other strategies for the selection of a repellent involved screening of compounds from other agricultural applications such as insecticides (Woronecki et al. 1981) and fungicides (Avery and Decker 1991). These chemicals rely on sub-lethal toxic effects to establish aversions to their taste and as a result birds may ingest a lethal dose while learning to avoid the food (Crocker and Perry 1990).

A more rational approach to the search for effective repellents is to consider materials that are biologically meaningful for the target species. Recent successes in the identification of effective molecules are the result of detailed study and exploitation of the semio-chemicals involved in inter- and intra-specific chemical communication. A number of these repellents have found commercial application (Sullivan et al. 1990b). These compounds function as warnings that an aggressive conspecific (scent marks: Novotny et al. 1993) or a predator (predator odors: Sullivan et al. 1990a; Woolhouse and Morgan 1995) is close by. It is, therefore, likely that habituation to these aversive chemical signals will be slow. However, both conspecific and predator odors may require reinforcement by encounters with live animals to have a long-term effect (Muller-Schwarze 1994). Semio-chemical repellents are likely to be more effective in applications that seek to reduce general activity in an area, e.g., moles (*Talpa europaea*) (Gorman and Stone 1989). Many pest management problems, however, relate to consumption of food crops, trees and stored food products by, for example, rabbits (*Oryctolagus cuniculus*), voles (e.g. *Microtus agrestis*), and pigeons (*Columba palumbus*) (Gill 1992a; Lane 1984). A number of plant secondary compounds, in contrast to semio-chemicals, have evolved to protect the plant against such damage. One could thus take advantage of the "arms race" between plants and herbivores and identify chemicals whose specific function is to repel animals from eating plant material.

WHY PLANT DEFENSE COMPOUNDS?

Plants are continuously exposed to attack by vast numbers of pest organisms and as a consequence have evolved an array of defense systems for their protection. A number of these systems have a profound effect on food-plant selection by herbivores (Provenza 1995). These defense systems can be divided into those based on physical and morphological adaptations (e.g., thick cell walls, seed coats, thorns and hairs) and those based upon biochemical adaptations (secondary compounds). It is the latter group which are the most promising potential source of vertebrate repellents.

These secondary metabolites may be unpleasant to taste, poisonous, malodorous, or produce anti-nutritional effects. They can be advertised to the herbivore as exudates on the exterior surface or be located within the plant, to be released only when the tissue is damaged. In many cases these substances protect the plant from damage without causing the herbivore any significant, long-term harm. This may reflect a balance that must be maintained in order to minimize any selection pressure on the herbivore: The rate of adaptation of a herbivore to a plant defense-characteristic will be slower when it has less effect on herbivore fitness (Gould 1988). Consequently, many of the defense chemicals produced by plants can be exploited as agents for the non-lethal management of pests.

Not all secondary metabolites are equally effective as defenses against herbivory, and none provides complete protection (Reichardt et al. 1987). Identification of potential repellents is made difficult because the causal relationship between inhibition of feeding and the presence of a class of secondary metabolite (e.g. resins, phenolics, tannins and alkaloids) can be hard to prove. Phytochemicals belonging to similar chemical classes do not necessarily have similar activities; camphor contributes to the defense of white spruce (*Picea glauca*), but the structurally related monoterpene, bornyl acetate, is ineffective (Sinclair et al. 1988). The situation is further complicated by the additive or synergistic effects of different metabolites and the spatial and temporal variations in their secondary metabolite chemistry. In addition, animals have evolved anatomical, physiological and behavioral strategies to counter these plant defenses (Lindroth 1988).

The range of secondary metabolites is immense; there are as many as 30,000 plant secondary compounds that were originally thought to be waste products but many are now suspected of having a defensive role (Harborne 1982). The three main classes within this natural armoury are: phenols, nitrogen-containing compounds, and terpenoids.

PHENOLS

Phenolic compounds are a diverse class of phytochemicals. They range from simple compounds such as phenol and the hydroxy-cinnamic acids, through complex anthocyanin pigments to the polymeric condensed tannins. With regard to mammalian and avian herbivory, the plant polyphenols that have attracted the most attention are the tannins. These polyphenols deter feeding primarily because of their characteristic astringency and anti-nutritional effects (Cooper and Owen-Smith 1993; Bennett and Wallsgrove 1994). Low molecular weight phenols also have a protective role as feeding deterrents (Greig-Smith and Wilson 1985). Capsaicin, the pungent principle found in Capsicum peppers, is a highly effective mammalian repellent causing irritation to the oral cavity (Mason et al. 1991; Mason et al. 1992). Snowshoe (*Lepus americanus*) and mountain hares (*L. timidus*) do not feed on balsam poplar (*Populus balsamifera*) twigs because of the presence of 2,4,6-trihydroxydihydrochalcone (Reichardt et al. 1990b) and the extremely low palatability of the Alaskan green alder (*Alnus crispa*) is due to two related compounds, pinosylvin and pinosylvin methyl ether (Clausen et al. 1986). Platyphylloside, a phenolic glycoside, strongly inhibits the digestion of the apical twigs of Betula pendula by ruminants (Palo et al. 1985). In willows (*Salix* spp.) an array of phenolic glycosides such as salicortin, acetyl salicortins, picein, and saldroside deter feeding by mammals (Tahvanainen et al. 1985). A number of phenolic glycosides are metabolized when the plant tissue is disrupted, producing compounds (e.g., trichcoparpogenin and 6-hydroxycyclo-hexanone) that deter feeding of hares on quaking aspen (*Populus tremuloides*) and balsam poplar (Clausen et al. 1989; Reichardt et al. 1990b). Coniferyl and cinnamyl derivatives, which are found at high concentrations in plant resins (e.g., *Styrax tonkinensis*), bud scales and seed husks, have been shown to deter feeding in a number of bird species (Jakubas et al. 1992; Avery and Decker 1992).

NITROGEN-CONTAINING METABOLITES

The distribution of nitrogen-containing metabolites in plant families is relatively sporadic. One reason for this restricted distribution is that the supply of nitrogen to the plant is often limited. Even when these compounds are produced by plants in response to herbivore damage their production is limited. However, in the plants where they are found, their low concentration is offset by their high potency (Barbosa and Krischik 1987).

Alkaloids are found in the leaves, leaf buds, and seeds of a small number of plant families, most notably the Leguminosae, Liliaceae, Solanaceae and Amryllidaceae. There is strong evidence in the literature that the primary role of all alkaloids is one of chemical defense (Wink 1987; Bennett and Wallsgrove 1994); the use of nicotine as an insecticide and fungicide demonstrates its value to the defense of the plant. Tissues with high nutritional value, such as seeds, buds, and young leaves, contain high concentrations of these compounds. To exploit these tissues, herbivores have to overcome the bitter taste of these compounds (even at very low concentrations) and cope with the pharmacological effects which include vomiting (e.g., ipecacuanha alkaloids) and anti-cholinesterase activity (e.g., steroidal alkaloids) (Frischknecht et al. 1986).

Plant proteins may also have a role in plant defense. Trypsin inhibitors from legumes have direct antinutritional activity through their effects on digestive enzymes, although their ability to inhibit feeding by vertebrates has yet to be demonstrated. Lectins are a diverse group of proteins classified on the basis of their ability to bind to specific carbohydrate ligands. The defensive role of lectins relies on their ability to interact with the glycoconjugates, on either the epithelial cells in the digestive tract of nematodes, insects, snails, and higher animals or on the surface of the micro-organisms (Pusztai, 1991). Lectins are found in seeds and vegetative tissue such as tubers, roots, phloem and leaves. The bark of at least two tree species, elderberry (*Sambucus nigra*) and false acacia (*Robinia pseudoacacia*) contain high concentrations of lectins (Peumans et al. 1986). These proteins are powerful aversive agents, causing adverse effects on the stomach and small intestine almost immediately after ingestion and may contribute to the defense of trees against bark stripping by voles and deer (Pusztai et al. 1990).

TERPENOIDS

The largest and, structurally, the most diverse class of secondary plant metabolites includes the terpenes and the allied sesqui-, di-, tri-, and poly-terpenoid compounds. In addition to their many vital metabolic roles, terpenoids represent a major defense in plants against vertebrates (Reichardt et al. 1990a). These compounds are thought to deter herbivory by reducing palatability and digestive efficiency due to bactericidal effects on gut microbes. The association between feeding aversion and the deleterious effects of terpenoids has been clearly demonstrated. Snowshoe and mountain hares reject terminal parts of birch twigs containing high concentrations of the triterpenoid, papyriferic acid (Reichardt et al. 1984). In addition, D-pulegone, a terpene which can be readily isolated from pennyroyal (*Mentha pulegium*), has been shown to be highly aversive to birds (Mason 1990). It appears that <1% of the known terpenoids have been investigated for their feeding-deterrent or toxic properties. Thus, the role of terpenoids in plant-herbivore interactions and as a source of new repellents is a fertile field for future research.

MODE OF ACTION: INNATE OR LEARNED

The aversive response to some repellents is innate, a property that is the result of past evolutionary pressures to develop sensitivity to particular odors or tastes. Foods that are toxic usually taste bitter or cause irritation to the buccal cavity. For example, mammals show aversive orofacial responses to quinine and chili peppers despite having no prior experiences with these tastes (Chambers and Bernstein 1995).

Experience can also play a critical role in the response to a repellent. An initial preference for treated food is reversed when the post-ingestional consequences of eating the food are negative. The compound causes some form of transient upper-gastrointestinal discomfort or illness such as nausea or vomiting, which the individual then associates with the taste of the compound, or, if the compound has no taste, another salient cue within the food (Provenza 1995). The animal then becomes conditioned to avoid that cue in future encounters. In agriculture, this latter type of repellency has been successfully used to induce prey avoidance behavior in mammalian and avian predators (Conover 1990) and to train livestock to avoid certain plant species (Burrit and Provenza 1990).

Innate aversions appear to be weaker and more easily broken than conditioned aversions (Greig-Smith 1985). The effects of ingesting an innately repellent compound are often neutral and consequently any initial aversion may be lost and even reversed following repeated exposure. Millions of people use chili peppers as an essential flavoring ingredient, having "acquired a taste" for the burning sensation experienced following ingestion of the active constituent, capsaicin. Innately repellent compounds also appear to have a narrow spectrum of activity. Compounds that are aversive to mammals (e.g., capsaicin) are not aversive to birds at similar concentrations and vice versa (e.g., methyl anthranilate). This appears to be the result of physiological differences in the oro-sensory systems (taste, odor, trigeminal) of these taxa (Mason et al. 1992). This differential activity has a number of practical applications. For example, methyl anthranilate can be used to treat cattle feed in order to inhibit the feeding of avian pests but not livestock (Mason et al. 1985).

Repellents that are effective against both mammals and birds are unusual, and recent work suggests that such agents should, ideally, have innate activity and be able to generate a conditioned aversion (Crocker and Perry 1990; Gill et al. 1995b). About ten years ago scientists at the UK's Ministry of Agriculture, Fisheries and Food began to investigate the plant chemicals that underlie preferences of one avian pest species, the bullfinch (*Pyrrhula pyrrhula*) for varieties of pear-tree (*Pyrus communis var. sativa*). The flower-buds of certain varieties of pear-tree were prone to attack while other varieties, in the same orchard, remained undamaged. Captive birds were

presented with seeds treated with flower-bud extracts from a number of cultivars. There was a clear inverse relationship between the concentration of one class of phenolic compounds, the cinnamic acids, and the palatability of the flower-bud extract (Greig-Smith 1985). When these compounds and their derivatives were presented individually to the birds, several proved to be effective feeding deterrents both in the laboratory and in the field (Crocker and Reid 1993; Watkins et al. 1995).

The response to cinnamamide, the most potent cinnamic acid derivative, has been studied in detail. Cinnamamide, produces an instant (innate) aversive response in birds, consumption falling to 20% of normal consumption when treated food was first presented (Figure 1). However, studies with the chestnut-capped blackbird (*Agelaius ruficapillus*) and rock doves (*Columba livia*) suggests that the compound also has post-ingestional activity (Gill et al. 1994; Watkins et al. 1995). Birds show behavioral signs of malaise following ingestion of treated food and at high concentrations (>0.26% w/w) the palatability of the food is reduced following repeated exposure, a response indicative of a conditioned aversion. It is, therefore, unlikely that there will be an extinction in the response to cinnamamide since the animal will incur some form of physiological cost if it ignores the oral stimulus.

Figure 2. Mean percent normal (pre-trial) consumption (n = 6) of cinnamamide-treated food (0.8% w/w) by house mice (*Mus domesticus*) over the course of a three-day short-term, no-choice trial. For experimental protocol refer to Gurney et al. (1996).

APPLICATIONS

Non-lethal repellents derived from plant secondary compounds potentially have many agricultural and environmental applications (Mason and Clark 1992) and several are undergoing commercial evaluation. Topical applications of these repellents are being used to prevent bird damage to crops (Cummings et al. 1995; Gill et al. 1995a), inhibit non-target wildlife from consuming potentially toxic granular pesticides and chemically treated seeds (Mason et al. 1993; Watkins et al. 1996b), and prevent gnawing damage to electrical cables by rodents (Kurata et al. 1994).

However, the use of topical applications can be problemmatic: some compounds have poor persistence, due to weathering and chemical/biological degradation, and spray formulations often do not penetrate the crop canopy to protect the most palatable and vulnerable tissues (e.g., meristem). The choice of secondary compounds opens up opportunities to overcome these issues by helping plants to help themselves. The levels of secondary compounds in plants can increase significantly within a few hours of being damaged by the herbivore. These induced defense systems have been studied extensively in response to microbial infection and insect feeding (Bennett and Wallsgrove 1994). However, until recently, the dynamic defense response to grazing by vertebrates has received little attention. New studies have demonstrated that the production of phenylpropanoids, a class phenolic compound commonly found in plants, can be stimulated by the systemic application of metabolic precursors. The phenolic precursor, L-phenylalanine, when applied as a solution to the roots, was observed to increase significantly the phenolic pool in oilseed rape to 13% above the levels determined for the control plants. These treated plants were significantly more resistant to damage by feral pigeons than untreated plants (Scanlon et al. in prep.). This, to our knowledge, is the first report of increased resistance to vertebrate pest damage following systemic application of precursors for plant defense compounds.
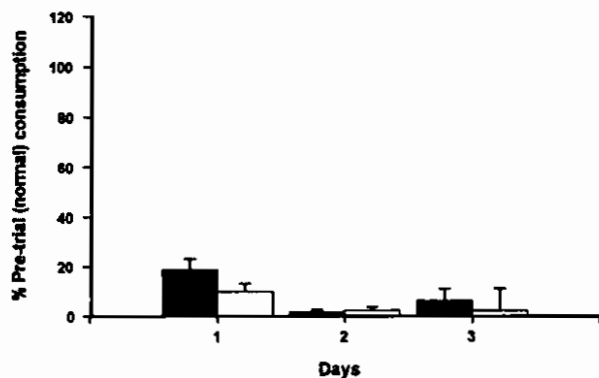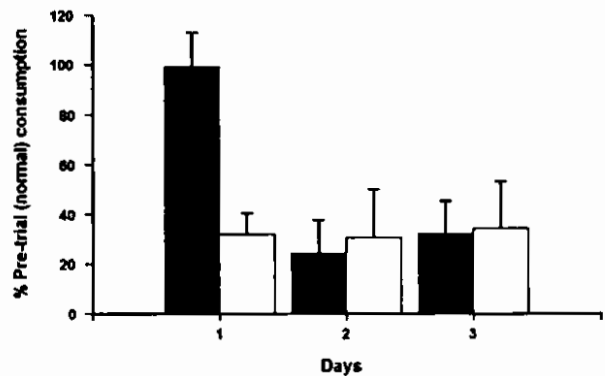
Figure 1. Mean percent normal (pre-trial) consumption (n = 5) of cinnamamide-treated food (0.8% w/w) by rock doves (*Columba livia*) over the course of a three-day short-term, no-choice trial. For experimental protocol refer to Watkins et al. (1995).

In contrast, the response in mice (*Mus domesticus*) was delayed, indicative of a conditioned aversion. Consumption of cinnamamide-treated food (0.8% w/w) remained at normal (pre-trial) levels for a short period (three hours) before a marked decline to 17% of normal (pre-trial) consumption was observed (Figure 2). This observation was confirmed by subsequent experiments where animals intubated with cinnamamide (160 mg/kg) developed a strong and persistent aversion to what had been a preferred flavor (saccharin). Subsequently, this aversion remained undiminished for the entire course of the trial (64 days) (Watkins et al., in prep.).

This approach can potentially be taken one stage further. Breeding for resistance against pests is being pursued by farmers because modern, intensively managed plantations often represent a sizeable investment to the grower. As a result, growers are now focusing their attention on novel damage alleviation mechanisms, in particular the genetic enhancement of resistance by selective breeding and biotechnology. The enhancement of resistance to vertebrate damage by screening for resistant cultivars such as bird-resistant forms of sorghum and sunflowers (tannic acid and related astringents) (Greig-Smith 1985) and herbivore-resistant tree provenances (terpenes and phenols) (Gill 1992b) continues apace. The use of genetic insertion technology in this area is still in its infancy. However, this technology should enable us to utilize defense compounds that cannot be synthesized in vitro and has the potential to rapidly increase the fitness of the planting stock, as it has done for disease and invertebrate resistant plants (Boulter et al. 1990; Coghlan 1996). This, in turn, will be reflected in a reduction in the cost of establishing crops, an improvement in the yield and quality of the final product, and a reduction in the application of potentially toxic pesticides.

Plant secondary compounds have the potential to provide effective and humane solutions for the management of pest species. Previously, however, the effectiveness of an application may have been compromised in relation to the foraging behavior of the target species. For any application to be successful the costs imposed by the repellent on an animal (e.g., internal malaise) must be high enough to encourage the animal to change its foraging goal and seek alternative food or harborage. Foraging costs can be manipulated by using a more "aggressive" repellent and/or providing a more favorable foraging alternative, from an animal's point of view, as a diversion. It may be unnecessary to treat the whole crop to make foraging elsewhere a more beneficial option for the pest species. For instance, many species prefer to feed at the edge of crops to minimize the risk of predation. Treatment of only the edge of the crop can reduce total damage as the animals choose safer but, perhaps, less nutritious alternatives (Gill et al. 1995b). The development of optimal foraging models that have the potential to address the question, "Under what conditions will the repellent be effective?" demands that investigators take a more holistic approach to their research. Both the physiological cost imposed by the repellent and the cost-benefit decisions that animals have to make when foraging for food in the natural environment need to be defined. In the case of plant-derived repellents, it is fortunate that much of this information can be gleaned by studying the impact of herbivores on plants which already utilize the compound in their defense.

In conclusion, many of the plant secondary compounds described above merit further investigation with the aim of producing commercially viable non-lethal applications that can compete and/or complement established control techniques. If this goal can be achieved, we can look forward to a benign but powerful armory of natural weapons against vertebrate pests.

LITERATURE CITED
AVERY, M. L., and D. G. DECKER. 1991. Repellency of fungicidal rice seed treatments to red-winged blackbirds. J. Wildl. Manage. 55:327-334.

AVERY, M. L., and D. G. DECKER. 1992. Repellency of cinnamic acid esters to captive red-winged blackbirds. J. Wildl. Manage. 56:799-804.

BARBOSA, P., and V. A. KRISCHIK. 1987. Influence of alkaloids on feeding preference of eastern deciduous forest trees by the gypsy moth *Lymastria dispar*. Amer. Naturalist 130:53-69.

BENNETT, R. N., and R. M. WALLSGROVE. 1994. Tansley review No 72. Secondary metabolites in plant defense mechanisms. New. Phytol. 127:617-633.

BOULTER, D., G .A. EDWARDS, A. M. R. GATEHOUSE, J. A. GATEHOUSE, and V. A. HILDER. 1990. Additive protective effects of different plant-derived insect resistance genes in transgenic tobacco plants. Crop Prot. 9:351-354.

BURRIT, E. A., and F. D. PROVENZA. 1990. Food aversion learning in sheep: persistence of conditioned taste aversion to palatable shrubs (*Cerocarpus montanus* and *Amelanchier alnifolia*). J. Anim. Sci. 68:1003-1007.

CHAMBERS, K. C., and I. L. BERNSTEIN. 1995. Conditioned flavor aversions. Pages 745-773 *in* R. L. Doty, ed. Handbook of olfaction and gustation. Marcel Dekker Inc. New York.

CLAUSEN, T. P., J. P. BRYANT, and P. B. REICHARDT. 1986. Defense of winter-dormant green alder against snowshoe hares. J. Chem. Ecol. 12:2117-2131.

CLAUSEN, T. P., P. B. REICHARDT, J. P. BRYANT, R. A. WERNER, and K. POST. 1989. Chemical model for short-term induction in quaking aspen (*Populus tremuloides*) foliage against herbivores. J. Chem. Ecol. 15:2335-2345.

COGHLAN, A. 1996. Aphids give snowdrop gene the cold shoulder. New Sci. 149 (2011): 18.

CONOVER, M. R. 1990. Reducing mammalian predation on eggs by using conditioned taste aversion to deceive predators. J. Wildl. Manage. 54:360-365.

COOPER, S. M., and N. OWEN-SMITH. 1993. Condensed tannins deter feeding by browsing ruminants in a South African savanna. Oecologia 67:142

CROCKER, D. R., and S. M. PERRY. 1990. Plant chemistry and bird repellents. Ibis 132:300-308.

CROCKER, D. R., and K. REID. 1993. Repellency of cinnamic acid derivatives to rooks and chaffinches. Wildl. Soc. Bull. 21:456-460.

CUMMINGS, J. L., M. L. AVERY, P. A. POCHOP, J. E. DAVIS, D. G. DECKER, H. W. KRUPA, and J. W. JOHNSON. 1995. Evaluation of a methyl anthranilate formulation for reducing bird damage to blueberries. Crop Prot. 14:257-259.

FEARE, C. J. 1995. The role of agricultural change in integrated pest management. Pages 376-380 in J. A. Bissonette and P. R. Krausman, eds. Integrating people and wildlife for a sustainable future. Widlife Society, Bethesda.

FRISCHKNECHT, P. M., J. V. DUFEK, and T. W. BAUMANN. 1986. Purine alkaloid formation in buds and developing leaflets of Coffea arabica; an expression of an optimal defense strategy. Phytochemistry 25:613-616.

GILL, E. L., M. B. SERRA, S. B. CANAVELLI, C. J. FEARE, M. E. ZACCAGNINI, A. K. NADIAN, M. L. HEFFERNAN, and R. W. WATKINS. 1994. Cinnamamide prevents captive Chestnut-capped Blackbirds (Agelaius ruficapillus) from eating rice. Int. J. Pest Manage. 40:195-198.

GILL, E. L., D. P. COWAN, and R. W. WATKINS. 1995a. Pilot study of the potential of the repellent cinnamamide to reduce Woodpigeon damage to oilseed rape. Home Grown Cereals Authority (HGCA), London. OS12E.

GILL, E. L., R. W. WATKINS, J. E. GURNEY, C. B. SCANLON, J. D. BISHOP, C. J. FEARE, and D. P. COWAN. 1995b. Cinnamamide: a non-lethal chemical repellent for birds and mammals. Denver Wildlife Research Centre Symposium Proceedings: Repellents in Wildlife Management (in press).

GILL, R. M. A. 1992a. A review of damage by mammals in north temperate forests: 2. Small mammals. Forestry 65:281-308.

GILL, R. M. A. 1992b. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry 65:363-388.

GORMAN, M. L., and R. D. STONE. 1989. Repelling moles. Pages 81-97 in R. J. Putman, ed. Mammals as pests. Chapman & Hall, London.

GOSLING, L. M., and S. J. BAKER. 1989. Demographic consequences of differences in ranging behaviour of male and female coypus. Pages 155-167 in R.J. Putman, ed. Mammals as pests. Chapman and Hall, London.

GOULD, F. 1988. Evolutionary biology and genetically engineered crops. BioScience 38:26-33.

GREIG-SMITH, P. W. 1985. Deter birds the tasteful way. New Sci. 108:38-40.

GREIG-SMITH, P. W., and M. F. WILSON. 1985. Plant secondary chemicals as non-toxic bird repellents. Pages 74-76 in Research and development report: Agricultural Science Service. M.A.F.F. London.

GURNEY, J. E., R. W. WATKINS, E. L. GILL, and D. P. COWAN. 1996. Non-lethal mouse repellents: evaluation of cinnamamide as a repellent against commensal and field rodents. Appl. Anim. Behav. Sci. (in press).

HARBORNE, J. B. 1982. Insect feeding preferences. Pages 147-185 in Introduction to ecological biochemistry. Academic Press, London.

JAKUBAS, W. J., P. S. SHAH, J. R. MASON, and D. M. NORMAN. 1992. Avian repellency of coniferyl and cinnamyl derivatives. Ecol. Applic. 2:147-156.

KURATA, M., Y. ICHIKAWA, M. TOYA, I. TAKAHASHI, and Y. OKUI. 1994. Resin molding composition for preventing damage by animals. U.S.A. Patent No. 5,322,862. 22 pp.

LANE, A. B. 1984. An enquiry into the responses of growers to attacks by pests on oilseed rape (Brassica napus), a relatively new crop in the United Kingdom. Prot. Ecol. 7:73-78.

LINDROTH, R. L. 1988. Adaptations of mammalian herbivores to plant chemical defenses. Pages 163-204 in K. C. Spencer, ed. Chemical mediation of coevolution. Academic Press, New York.

LUND, M. 1988. Ultrasound devices. Pages 407-409 in I. Prakash, ed. Rodent pest management. CRC Press, Boca Raton.

MASON, J. R., J. F. GLAHN, R. A. DOLBEER, and R.F. REIDINGER. 1985. Field evaluation of dimethyl anthranilate as a bird repellent livestock feed additive. J. Wildl. Manage. 49:636-642.

MASON, J. R. 1990. Evaluation of D-pulegone as an avian repellent. J. Wildl. Manage. 54:130-135.

MASON, J. R., N. J. BEAN, P. S. SHAH, and L. CLARK. 1991. Taxon-specific differences in reponsiveness to capsaicin and several analogues: Correlates between chemical structure and behavioural aversiveness. J. Chem. Ecol. 17:2539-2551.

MASON, J. R., L. CLARK, and P. S. SHAH. 1992. Taxonomic differences between birds and mammals in their responses to chemical irritants. Pages 311-317 in R. L. Doty and D. Muller-Schwarze, eds. Chemical signals in vertebrates VI. Plenum Press, New York.

MASON, J. R., L. CLARK, and T. P. MILLER. 1993. Evaluation of a pelleted bait containing methyl anthranilate as a bird repellent. Pestic. Sci. 39:299-304.

MASON, J. R., and L. CLARK. 1992. Nonlethal repellents: the development of cost-effective, practical solutions to agricultural and industrial problems. Proc. Vertebr. Pest Conf. 15:115-129.

MULLER-SCHWARZE, D. 1994. Chemical repellents for beaver: new leads. Pages 479-484 in R. Apfelbach, D. Muller-Schwarze, K. Reutter, and E. Weiler, eds. Chemical signals in vertebrates VII, Pergamon, Oxford.

NOLTE, D. L., J. R. MASON, and S. L. LEWIS. 1994. Tolerance of bitter compounds by an herbivore, Cavia porcellus. J. Chem. Ecol. 20:303-308.

NOVOTNY, M. V., S. D. HARVEY, and B. JEMIOLO. 1993. Farnesenes and related substances for mouse control. U.S.A. Patent No. 5,252,326. 20 pp.

PALO, R. T., K. SUNNERHEIM, and O. THEANDER. 1985. Seasonal variation of phenols, crude protein and cell wall content of birch (Betula pendula Roth.) in relation to ruminant in vitro digestibility. Oecologia 65:314-318.

PEUMANS, W. J., M. NSIMBA-LUBAKI, W. F. BROEKAERT, and E. VANDAMME. 1986. Are

bark lectins of elderberry (*Sambucus nigra*) and black locus (*Robinia pseudoacacia*) storage proteins? Pages 53-63 *in* L. M. Shannon and M. J. Crispeels, eds. Molecular Biology of Seed Storage Proteins and Lectins. Proceedings of the 9th Annual Symposium in Plant Physiology, UCR, Riverside.

PROVENZA, F. D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. J. Range Manage. 48:2-17.

PUSZTAI, A., S. W. B. EWEN, G. GRANT, W. J. PEUMANS, E. J. M. VANDAMME, L. RUBIO, and S. BARDOCZ. 1990. Relationship between survival and binding of plant lectins during small intestinal passage and their effectiveness as growth factors. Digestion 46:308-316.

PUSZTAI, A. 1991. Plant lectins. J.D. Phillipson, D. C. Ayres, and H. Baxter, eds. Cambridge University Press, Cambridge. 264 pp.

REICHARDT, P., T. CLAUSEN, and J. BRYANT. 1987. Plant secondary metabolites as feeding deterrents to vertebrate herbivores. Pages 37-42 *in* F. D. Provenza, J. T. Flinders, and E. D. McArthur, eds. Symposium on plant-herbivore interactions. Snowbird, Utah.

REICHARDT, P. B., J. P. BRYANT, T. P. CLAUSEN, and G. D. WIELAND. 1984. Defense of winter-dormant Alaska paper birch against snowshoe hares. Oecologia 65:58-69.

REICHARDT, P. B., J. P. BRYANT, B. J. ANDERSON, D. PHILIPS, T. P. CLAUSEN, M. MEYER, and K. FRISBY. 1990a. Germacrone defends labrador tea from browsing by snowshoe hares. J. Chem. Ecol. 16:1961-1970.

REICHARDT, P. B., J. P. BRYANT, B. R. MATTES, T. P. CLAUSEN, and F. S. CHAPIN. 1990b. The winter chemical defense of balsam poplar against snowshoe hares. J. Chem. Ecol. 16:1941-1960.

SINCLAIR, A. R. E., M. K. JOGIA, and R. J. ANDERSEN. 1988. Camphor from juvenile white spruce as antifeedant for snowshoe hares. J. Chem. Ecol. 14:1505-1514.

SULLIVAN, T. P., D. S. SULLIVAN, D. R. CRUMP, H. WEISER, and E. A. DIXON. 1988. Predators and their potential role in managing pest rodents and rabbits. Proc. Vertebr. Pest Conf. 13:145-150.

SULLIVAN, T. P., D. R. CRUMP, H. WIESER, and E. A. DIXON. 1990a. Comparison of release devices for stoat (*Mustela erminea*) semiochemicals used as montane vole repellents. J. Chem. Ecol. 16:951-957.

SULLIVAN, T. P., D. R. CRUMP, H. WIESER, and E. A. DIXON. 1990b. Responses of pocket gophers (*Thomomys talpoides*) to an operational application of synthetic semiochemicals of stoat (Mustela erminea). J. Chem. Ecol. 16:941-949.

TAHVANAINEN, J., E. HELLE, R. JULKUNEN-TIITTO, and A. LAVOLA. 1985. Phenolic compounds of willow bark as deterrents against feeding by mountain hare. Oecologia 65:319-323.

WATKINS, R. W., E. L. GIL, and J. D. BISHOP. 1995. Evaluation of cinnamamide as an avian repellent: Determination of a dose-response curve. Pestic. Sci. 44:335-340.

WATKINS, R. W., H. J. MOSSON, J. E. GURNEY, D. P. COWAN, and J. P. EDWARDS. 1996b. Cinnamic acid derivatives: novel repellent seed dressings for the protection of wheat seed against damage by the field slug, *Deroceras reticulatum*. Crop Prot. (in press).

WINK, M. 1987. Chemical Ecology of quinolizidine alkaloids. Pages 524-533 *in* G. R. Waller, ed. Allelochemicals: Role in agriculture and forestry. American Chemical Society, New York.

WOOLHOUSE, A. D., and D. R. MORGAN. 1995. An evaluation of repellents to suppress browsing by possums. J. Chem. Ecol. 21:1571-1583.

WORONECKI, P. P., R. A. DOLBEER, and R. A. STEHN. 1981. Response of blackbirds to mesurol and sevin applications on sweetcorn. J. Wildl. Manage. 45:693-701.