MAMMALIAN HERBIVORE REPELLENTS: TOOLS FOR ALTERING PLANT PALATABILITY

Bruce A. Kimball, USDA/APHIS/WS/National Wildlife Research Center, Monell Chemical Senses Center, 3500 Market Street, Philadelphia, PA 19104, USA & Jimmy D. Taylor, USDA/APHIS/WS/National Wildlife Research Center, 321 Richardson Hall, Corvallis, OR 97331, USA describe approaches to repelling mammalian herbivores

Introduction

Mammalian herbivores are responsible for significant damage that may total billions of dollars to a variety of agricultural products, including crops, landscape ornamentals, and timber. The challenge of the resource manager is to minimize the conflict between herbivore and human activity while recognizing that consuming plant material is the herbivore's function in the ecosystem. Diet selection by herbivores is the product of many distinct behaviors occurring in concert. Among these are behaviors that do not arise directly from plant-animal interaction; e.g. predator avoidance, habitat selection, competition, territoriality, etc. However, diet selection is strongly influenced by the interaction of the consequences of consumption (or prior consumption) and the flavor of a food, i.e. palatability. In other words, herbivory is strongly influenced by the interaction of plant chemistry and herbivore processing of phytochemicals. Likewise, herbivore responses to repellents are strongly influenced by the repellent agent and the physiological responses these agents produce in the herbivore.

A number of deterrents have been employed for the protection of agricultural resources (Nolte 1999). Guard animals, exclosures, supplemental feeding, and a laundry list of chemicals (including animal products such as egg, blood, urine, etc.) have been tested and incorporated into tools intended to repel herbivores from select resources. Here, we focus on the modes of action of these chemical repellents. Current research suggests that mammalian herbivore repellents promote feeding avoidance behavior via four mechanisms: 1) neophobia; 2) irritation; 3) conditioned aversion; and 4) flavor modification. These mechanisms are employed singly or in combination in numerous commercial formulations. Many chemical repellents registered for use in the United States are applied directly to plant tissues (i.e. "contact repellents"). To the herbivore, these repellents are a collection of taste, odor, visual and tactile cues much in the same way plants are characterized by these sensory qualities. Furthermore, the sensory cues of repellents are associated with the postingestive consequences of their consumption – precisely in the same manner that plant cues and consequences are integrated by the herbivores.

We review diet selection as it underlies interactions of herbivores with plants and repellent agents. For discussion, we define production crops as those planted on a rotational basis with expectation of an economic return. This includes the fields of agriculture, agronomy, agro-forestry, horticulture, silviculture, and viticulture. Further, we define repellents as products applied to crop systems for the chief purpose of reducing damage caused by foraging activities.

Mammalian damage to production crops

Wildlife species are integral components of farmlands in the United States which comprise over 372 million ha (NASS 2009). Many agricultural producers value wildlife on their farms, even spending time and money to improve wildlife habitat (Conover 1994, 1998). Despite positive benefits of wildlife, landowners/producers also experience costs (Conover 1997) and report lost income due to wildlife damage (Conover 1994; Wywialowski 1994). Herbivory by mammals contributes to decreased crop/forest production along with impacts from insects, birds, disease, and other climatic and edaphic factors. Herbivory may occur throughout the production cycle and is dependent on several factors (see foraging behavior below) including the mammals' size and foraging height. On agricultural crop producing farms, ungulates (deer such as *Odocoileus* spp., elk – *Cervus canadensis*) are the most obvious vertebrate browsers/grazers, although lagamorphs (such as cottontail rabbits – *Sylvilagus* spp.), bears (such as the black bear – *Ursus amercianus*), and numerous rodent species can cause significant damage. Unlike annual agricultural crops, trees may be damaged several times throughout a rotation. Voles (*Microtus* spp.), pocket gophers (*Thomomys* spp.), and mountain beaver (*Aplondontia rufa*) clip newly planted seedlings in the Pacific Northwest immediately after planting, while deer and elk retard vertical growth by browsing terminal stems. After stand establishment and crown closure, trees are susceptible to girdling by North American beaver (*Castor canadensis*), black bear, and mountain beaver.

Surveys of mammalian damage to agriculture may provide accurate estimates of crop loss, but they are expensive and resource intensive (Craven *et al.* 1992). For this reason, estimates of wildlife-related loss often rely on landowner estimates (Conover 1994, 1998; Wywialowski 1994; Irby *et al.* 1997). Nevertheless, producers are often good predictors of the occurrence of wildlife damage (Wywialowski 1996) and their estimates have been statistically similar to on-the-ground estimates of crop loss (Tzilkowski *et al.* 2002). In a 1995 study in Pennsylvania, average wildlife related loss to corn yield was 0.48 m³/ha (5.5 bu/ac) with white-tailed deer (*Odocoileus virginianus*) accounting for 73% of that loss valued at $36.82/ha ($14.90/ac) (Tzilkowski *et al.* 2002). A survey of wildlife-related loss in the top 10 corn producing states in

1993 revealed a loss of $91.6 million (US), <1% of the total harvested corn crop ($13.3 billion) (Wywialowski 1996). White-tailed deer, birds, and unidentified wildlife accounted for 0.23%, 0.19%, and 0.27%, respectively.

Diet selection

Mammals have a variety of energy requirements, including basal metabolism, locomotion, thermoregulation, and reproduction. To meet these needs, digestion and metabolism combine to release energy from ingested foods. Primary plant metabolites (carbohydrates, starches, lipids, and proteins) are the universal constituents of plant cells and tissues that provide this energy. At the same time, plants have evolved chemical defenses to defend against herbivores, pathogens, and competing plants. Evidence suggests that the distribution and abundance of these defenses resulted, in part, from selective pressures exerted by herbivores (Berenbaum 1995). These defenses, often termed secondary plant metabolites, differ from primary metabolites in that they do not contribute directly to plant growth and are idiosyncratic in distribution.

Chemical Senses. In addition to serving as nutrients or antifeedants, chemical constituents in plants contribute to the flavor and visual characteristics of the plant. Vision, taste, olfaction, flavor (taste and olfaction in concert), and somatosensation (pain and texture) provide sensory information about the food. Although mammals experience only a small number of unique tastes (e.g. sweet, sour, salt, bitter, and umami), the contribution of odorants elicit a much greater variety of hedonic qualities. When the stimulus is in the mouth, odor contributes to the flavor profile via retronasal detection. Odors are also detectable before being placed in the mouth (orthonasal detection) and can serve as important cues that provide much information to the receiver before having to taste the food.

Importantly, the plant metabolites that produce postingestive feedbacks in herbivores and those serving as flavor cues may not necessarily be one in the same. In particular, it is unlikely that the compounds contributing to the flavor of a particular food are themselves elicitors of negative consequences (Provenza & Balph 1990). For example, possum (*Pseudocheirus* spp, *Trichosurus* spp) intake of *Eucalyptus* leaves is correlated with the concentration of 1,8-cineole in the leaves (Lawler *et al*. 1999). However, another phytochemical, jensenone, is responsible for the negative consequences arising from ingestion of *Eucalyptus* leaves (Lawler *et al*. 1999). Thus, cineole is the flavor cue that possums associate with jensenone-induced consequences of ingesting *Eucalyptus* leaves.

Processing of Plant Secondary Metabolites. Herbivores are equipped with a series of biochemical cycles to contend with toxins and antifeedants. Mammalian detoxification involves three steps: primary metabolism, conjugation, and elimination. Deleterious plant compounds are transformed into more polar compounds by primary metabolism and conjugation. Primary metabolism, or Phase I biotransformation, involves enzymatic oxidation, reduction, or hydrolysis (Sipes & Gandolfi 1993). Conjugation, or Phase II biotransformation, principally results in the formation of toxin-glucuronic acid conjugation products (Foley *et al*. 1995). Elimination of the toxin is enhanced because the non-polar, foreign species is covalently bonded to a polar, endogenous compound (Sipes & Gandolfi 1993).

Detoxification allows herbivores to utilize the nutrient content of plants while circumventing the plants' chemical arsenal. However, detoxification reactions proceed at finite rates. When the rate of toxin adsorption exceeds the rate of detoxification, toxins accumulate in bodily tissues and toxic effects are observed (Klaassen & Rozman 1993). Though detoxification effectively eliminates toxins from the body, it is a costly biochemical process. Production of glucuronic acid for conjugation comes at the expense of daily energy requirements (Illius & Jessop 1995). Acid-base homeostasis is also disrupted by detoxification (Foley *et al*. 1995). Maintaining acid-base balance has a significant metabolic cost because production of buffering bicarbonate is achieved via protein catabolism (Illius & Jessop 1995). Thus, the nutrient content of foods ingested also impacts the ability of an herbivore to tolerate toxins. Increased nutrient intake is likely to increase the animal's ability to detoxify plant compounds (Illius & Jessop 1995; Foley *et al*. 1995).

Three Sources of Memory. It is imperative that animals maximize intake of primary plant metabolites while minimizing toxin ingestion. To accomplish this, they are equipped with the machinery to recognize and respond behaviorally to the phytochemicals they encounter. There are three facets of this machinery: anatomical and physiological traits bestowed by evolution; transgenerational knowledge learned from mother; and individual experience (Provenza 1995b). These three "sources of memory" permit herbivores to learn about the postingestive consequences of diet selection.

Many anatomical and morphological factors dictate which plants are suitable for foraging and at what rate plant parts can be ingested (Illius & Gordon 1993). The size and shape of the animal's mouth, teeth, digestive system, appendages, as well as visual acuity, basal metabolic rate, etc, are intrinsic properties granted them by their parents and generations of natural selection. Thus, evolution represents the first foraging constraint for herbivores (Provenza 1995b). Mother also has immense influence on the behavior of her offspring (Provenza 1995b). Animals may gain knowledge of plant phytochemicals by watching and imitating mother. Offspring are not likely to ingest foods rejected by mother and prefer those foods that mother ingests (Nolte *et al*. 1990). Chemical information regarding mother's diet can even be passed to her offspring in-utero (Nolte & Mason 1995). Nutrients, toxins, and flavor components of foods ingested by mother are passed through the placenta, allowing fetuses to learn about foods simultaneously with mother. Information about the flavor of mother's diet can also be transmitted to her offspring during lactation through mother's milk (Galef & Sherry 1973).

Social influences also impact foraging. In simple cases, the mere presence of an individual near food increases the likelihood that conspecifics will eat food located there (Galef 1996). Individuals (observers) may also learn of the consequences of a particular food by watching the behavior of conspecifics that consume the item (demonstrators). However, individual experiences can rapidly extinguish socially-formed preferences for a food (Galef & Whiskin 2001). Social influences may be important to introduce patterns of behavior,

while individual experiences dictate if the preference or aversion should be maintained.

Learning about Consequences. When an animal ingests a food, information regarding the flavor of that food and the physiological effects of ingestion are processed (Provenza *et al.* 1992). Preferences or aversions for the flavor of the food arise directly from the postingestive consequences. Preferences are formed for foods that produce energy when metabolized or are otherwise beneficial. Conversely, aversions to foods are formed when ingestion of that food has a negative effect on the individual. Foods that cause emetic malaise shortly after ingestion are very effective in producing aversions to that food (Garcia *et al.* 1985). Aversions can also be formed for nutrient-deficient foods, even if they contain no toxins (Provenza 1995a).

It has been stated that taste or flavor aversions potentiate aversions to other cues (Provenza *et al.* 1992). In other words, foraging behaviors result from cognitive processes that integrate the flavor and consequence of the eating the food with other attributes such as sight, smell, texture, or context. Thus, experienced animals can avoid deleterious foods by sight or odor alone, without having to ingest them again. Cognitive learning allows animals to learn that certain behaviors (e.g. food handling) positively impact palatability of the food. For example, Pikas (*Ochotona princeps*) cache food in haypiles for use in winter (Dearing 1997b). Chemical analyses of haypile contents indicate that this behavior serves two important purposes having direct effects on palatability. First, storage of certain plants causes the levels of some of the secondary metabolites to decrease (Dearing 1997a). Second, presence of some plants containing high-levels of phenolics in the haypiles assists in preserving the haypile contents during months of storage.

Palatability. The individual fitness of an animal depends significantly on its ability to ingest a nutritious diet. Thus, food preferences based on the phytochemical content of the prey items have long been recognized. For example, nutrient maximization per unit foraging time is the basis of optimal foraging theory (Macarthur & Pianka 1966). Conversely, the deterrent role of secondary plant metabolites on the feeding strategies of mammals was elucidated by Freeland and Janzen in 1974. In practice, plants contain both primary and secondary metabolites and herbivores assess both the positive and negative consequences of food ingestion simultaneously. Palatability is the term that describes this interplay of flavor and postingestive feedback. Palatability incorporates chemical constituents of the forage, foraging constraints, and animal experience with the food. Palatability does not emphasize only what an animal eats (optimal foraging) or what an animal does not eat (plant defense). Rather, both of these important determinants of diet selection are considered.

Palatability is determined by the animal's physiological condition, the chemical characteristics of the food, and the animal's prior experiences with that food (Provenza 1996). Within the framework of the animal's cognitive world, palatability is another term for the learned association between flavor of the food and consequence of ingestion. Associative processes such as this were implicated in animal behavior over 100 years ago (Thorndike 1898). According to Thorndike, "In the higher animals the bodily life and preservative acts are largely directed by these associations. They, and not instinct, make the animal use the best feeding grounds, sleep in the same lair, avoid new dangers and profit by new changes in nature". Simply, palatability dictates what animals eat (diet selection), which influences behavior, which impacts palatability.

Altering palatability with repellents

From the herbivore's point-of-view, repellents are just another collection of chemical signals and consequences that must be processed like any suite of chemicals they encounter while foraging. Taste, olfaction, vision, and touch permit herbivores to detect the chemosensory attributes of repellents. Inputs from evolution, mother, and conspecifics dictate whether or not these cues are meaningful in the context of foraging. If the repellent is ingested, postingestive consequences are integrated with the sensory attributes and learning processes will dictate how the individual herbivore will perceive the repellent the next time it is encountered. In this context, repellents are simply an extension of natural plant metabolites.

Odor and Repellency. Repellent stimuli that are not applied directly to the food are disassociated from the food source and can be referred to as "vapor repellents." Vapor repellents do not contribute to the flavor of the repellent stimuli and are detectable at variable distances from the source. At the same time, odors of contact repellents (applied topically to the plant or food source) similarly deliver cues detectable from a distance. Nolte and Wagner evaluated the "effective distance" of vapor repellents by placing apple cubes at regular intervals in two directions (180°) from a repellent-treated conifer seedling (Nolte & Wagner 2000). Using multiple repellent products, deer were provided access to the test apparatus so that consumption of apple cubes and browsing of the treated seedling could be monitored to evaluate the proximity at which deer would approach the repellent. For all repellents tested, including blood and egg-based repellents that afforded complete protection to the seedling, the mean distance was less than 1 m and the range included 0 cm (Nolte & Wagner 2000). Thus, odor alone delivered as a vapor repellent is unlikely to afford significant protection. This is also why browsing of new growth is frequently observed on previously treated plants. However, odor can be an important cue that advertises the presence of a contact repellent. In fact, all sensory modalities provide information to the herbivore regarding not only the presence of the stimuli, but also the possible consequences (neophobia, irritation, conditioned aversion, and flavor modification) of ignoring the signal.

Neophobia. Repellents that employ the neophobia mechanism prey on the herbivore's fear of unknown consequences. However, when there are no negative consequences associated with the stimuli, neophobia responses are subject to habituation and the cues will not be avoided for extended periods (Nolte 1999). In an experiment with captive deer, a sachet of meat and bone meal was only moderately effective as a feeding deterrent (Kimball *et al.* 2009). Tremendous variation among the test subjects was observed in response to the sachet treatment and habituation was evident after repeated exposures. Placement of vapor repellents near a food source does not reduce intake as effectively as topical treatment of the food

with the same odor source (Swihart *et al.* 1991). White-tailed deer demonstrated persistent avoidance of conifers treated topically with predator urines, while avoidance declined when the urines were presented in tubes attached to the plants. The authors concluded that flavor modification was a probable cause for the increased effectiveness of predator urines as contact repellents (Swihart *et al.* 1991). Similarly, sachets of capsaicin and meat and bone meal were more effective at reducing deer browse when the contents of the sachet dripped onto the conifer plants (Wagner & Nolte 2001).

Irritation. Effective contact repellents are those that impart additional consequences beyond mere neophobia. One such consequence is associated with activation of the trigeminal system. Peripheral (oral/nasal/ocular) contact with repellents that activate the trigeminal system results in pain. Trigeminal irritants are often taxon-specific (Mason *et al.* 1991). Capsaicin is a well-known trigeminal irritant in mammals, while birds are insensitive. Chemical irritation is a concentration-dependant effect and high concentrations of the irritant are frequently required to deter herbivory (Andelt *et al.* 1994). In a recent study, a 0.14% capsaicin solution was highly effective at reducing deer intake of a test diet, even when the diet was highly preferred (Kimball *et al.* 2009).

Conditioned Aversion. Malaise is another negative consequence of ingesting certain repellents. Affective and cognitive processes allow herbivores to learn about the negative consequences and avoid the repellent stimuli at future encounters. Lithium chloride is often used in laboratory studies to condition taste aversions in many vertebrate species (Riley & Tuck 1985). Thiram (tetramethylthiuram disulfide) is a fungicide used in several commercially-formulated repellents to condition aversions (Nolte & Wagner 2000). Chronic thiram exposure produces anemia and nausea (Maita *et al.* 1991). As with all toxins that condition aversions, herbivores must have experience with thiram to elicit avoidance behavior through learning processes. It is necessary to treat every plant in the immediate area with the repellent because the negative consequences are associated with the treatment, not with plants in general. Repeated exposures to the repellent may also be required for aversions to form (Kimball & Nolte 2005). Thus, considerable damage to plants may occur before repellency is observed with the conditioned aversion mechanism. In previous studies with mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus nelsoni*), consumption of thiram-treated foods in cafeteria-type tests decreased daily in four and five day experiments as it took repeated exposures for subjects to develop an aversion to the familiar food (Andelt *et al.* 1991, 1992).

Flavor Modification. Numerous compounds have been used to impact palatability without eliciting pain or malaise. For example, bitter agents are employed in several repellent products to alter the palatability of treated plants. It has been widely held that rejection of bitter taste is an evolutionary response to toxins (Scott & Mark 1987; Bachmanov & Beauchamp 2007). Denatonium benzoate is one such compound used in repellent formulations. Although apparently effective for omnivorous species, products which rely on bitter taste as the sole mode of action are not effective herbivore repellents (Wagner & Nolte 2001). Studies such as these raise familiar questions about the reliability of bitter taste *per se* as a warning of toxicity (Nolte *et al.* 1994; Glendinning 1994). It is

probable that commercial use of bitter agents as repellents for herbivores is not based on scientific evaluation, but rather has considerable anthropomorphic motivation ("if it tastes bad to me, deer must not like it").

Animal-based Repellents. Blood and egg are further examples of repellent ingredients that do not cause pain or malaise yet are effective herbivore repellents (Kimball *et al.* 2008). Hydrolyzed casein (HC) is a similar animal-based stimulus that produces long-lived avoidance in a variety of herbivores (Kimball & Nolte 2006; Figueroa *et al.* 2008). These animal-based ingredients are non-toxic (i.e. unlikely to condition aversions) and may be nutritious (e.g. blood is an excellent source of limiting amino acids such as methionine). Yet, blood is strongly avoided by deer, even when applied to highly nutritious foods (Kimball *et al.* 2009). It is unlikely that observed avoidance is mediated by neophobia alone. When applied directly to food items, animal-based repellents do not appear to be subject to habituation – even upon repeated exposure. Deer avoided test diets treated with HC for 16 consecutive days when offered alongside two alternative diets (Kimball *et al.* 2005). Furthermore, when HC-treated diets were offered in single-choice tests, deer avoided the test diet in eight consecutive daily testing periods.

Reduced intake of foods treated with animal-based products has been characterized as a "fear" response (Nolte 1999). However, there is some question whether predator avoidance or flavor modification is the actual mechanism for intake reduction by these animal-based repellents (Chabot *et al.* 1996; Kimball & Nolte 2006). Although increased vigilance is a likely response to predator cues, limiting intake is not an effective strategy for reducing predation risk. Other non-feeding responses to predator odors, such as heart and respiration rates, have only occasionally been measured in mammals. A recent study with horses indicated that predator odors affected sniffing and vigilance behaviors in horses, but increased heart rates occurred only when the odors were presented in conjunction with a sudden auditory cue (Christensen & Rundgren 2008). Rabbits also demonstrated increased vigilance, weight loss, and stress hormone responses to fox feces present in the testing apparatus, but time spent feeding and total food intake remained stable (Monclus *et al.* 2005). Elk responses to predator odors included increased heart rate and oxygen consumption (Chabot *et al.* 1996). However, habituation to odors occurred in the absence of feedback. Snowshoe hares (*Lepus americanus*) similarly habituated to predator odors in the absence of other predator cues (Sullivan *et al.* 1985).

Innate avoidance of conspecifics feces has been well studied in sheep (Hutchings *et al.* 1998). In controlled experiments, sheep foraged fecal-contaminated swards in a manner which minimized parasitism. The individuals own parasite load dictated trade-offs between exposure to parasites and nutrition (Hutchings *et al.* 2000). Subjects with greater incentive to feed were more likely to risk exposure to fecal-contaminated swards. Hutchings *et al.* concluded that avoidance of feces is an evolved behavioral strategy that employs odor as an important cue in identifying potential pathogens (Hutchings *et al.* 1998). Thus, avoidance of foods adulterated with animal products may be a product of an evolutionary "memory" (Kimball *et al.* 2009). Animal proteins are an excellent media for microbes that are not only potential sources of toxin-

producing pathogens (DeVault *et al.* 2003), but are likely to be incompatible with the native gut microflora of herbivores. It would be highly adaptive for herbivores, characterized by complex stomachs and long hindguts, to evolve a strategy for recognizing potential toxins and pathogens before suffering the consequences of ingestion. Conversely, mammals characterized by simple stomachs and short hindguts (i.e. carnivores) can be expected to ignore this threat. In a comparative study with multiple species, greater avoidance of casein hydrolysate (an animal protein) was observed among herbivores than omnivores (Field *et al.* 2009).

Repellent use in practice

Use of chemical repellents is socially appealing because they offer a potential non-lethal alternative to reduce plant damage (i.e., browse). Because deer (*Odocoileus* spp.) are the most common source of damage, most commercial repellent products are marketed to reduce deer browse. However, repellents may affect other mammals (Nolte & Wagner 2000; Figueroa *et al.* 2008). In general, repellents have short-term effects and are influenced by numerous factors such as animal density, food availability, and climatic conditions (e.g., temperature extremes, rainfall). A recent evaluation of ten commercially-available deer repellents in Connecticut concluded that no repellents prevented 100% of browse damage and that usage is a trade-off among effectiveness, cost, ability to follow recommended reapplication schedule, and the types of plants to be protected (Ward & Williams 2010).

The relative effectiveness of any one repellent mechanism (neophobia, irritation, conditioned aversion, or flavor modification) may depend on the individual herbivore's motivation to consume the protected resource. When alternative foods are available, repellents with no consequences may provide significant protection. Conversely, when alternative foods are insufficient, actual consequences to the consumer may be required to reduce browsing effectively. In a recent study, deer were offered the choice of two test diets differing in energy content (Kimball *et al.* 2009). Each of four different repellents (representing each of the four mechanisms) appeared to be effective when applied to the less preferred food. Conversely when the high energy diets were treated with repellents, only blood (flavor modification) and capsaicin (irritation) demonstrated significant repellency (Kimball *et al.* 2009). Highly motivated animals will ignore even the most effective repellent products. In a winter application of various repellents and netting, deer destroyed nets and consumed dormant, repellent-treated trees (Milunas *et al.* 1994). The controversial practice of employing "lure crops" or supplemental feed in association with repellent treatments may be necessary in extreme situations (see TWS, 2007 for a summary of the management concerns associated with supplemental feeding).

Effective herbivore repellent formulations require two qualities: 1) persistence of residues applied directly to the plant; and 2) physiological or evolutionary consequences for the herbivore. As investigation of new and improved repellent formulations proceeds, it is important to consider the underlying behavioral mechanisms in play for plant-herbivore interactions as well as the evolutionary history of the herbivore. An anthropomorphic approach ("if it tastes bad to me, deer must not like it") is unlikely to yield insightful information regarding the protection of agricultural resources.

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Bruce Kimball is a research chemist with the USDA-APHIS-WS National Wildlife Research Center (NWRC) and conducts his research at the Monell Chemical Senses Center in Philadelphia, PA. Bruce received his M.S. (Chemistry) from Arizona State University and Ph.D. (Ecology) from Colorado State University. His research is conducted at the interface of ecology and chemistry, with a focus on animal behavior and the chemical signals that identify friend, foe, and food. The goal of his research is to understand wildlife behavior better and develop tools to minimize wildlife damage to agricultural resources.

Jimmy Taylor is a supervisory research wildlife biologist with the USDA-APHIS-WS National Wildlife Research Center (NWRC) and is located on the campus of Oregon State University in Corvallis, OR. Jimmy received his M.S. (Wildlife Science) and Ph.D. (Forest Resources) from Mississippi State University. His research is conducted at the human-wildlife interface and focuses on defining impacts and developing strategies to reduce mammalian damage in forested and riparian ecosystems.