Parameters That Affect Fear Responses in Rodents and How to Use Them for Management

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The strong innate fear response shown by laboratory rodents to predator cues could provide powerful and innovative tools for pest management. Predator cues are routinely used to induce fear and anxiety in laboratory rodents for pharmacological studies. However, research on the fear response induced by predator cues in different species of rodents in the wild has been inconclusive with results often contradictory to laboratory experiments. Potential explanations for this inconsistency include the prey's: (i) physiological state; (ii) parasite load; (iii) differential intensity of perceived threats; (iv) fear learning and habituation; and (v) information gathering. In this review, we first explore current knowledge on the sensory mechanisms and capabilities of rodents, followed by the discussion of each of these explanations within the context of their implications for the use of antipredator response as a pest rodent management tool. Finally, we make recommendations on potential solutions and strategies to resolve issues in rodent management related to these hypotheses.

Keywords: non-consumptive effects, anti-predator response, fear, predator cues, learning, fear conditioning, pest rodents

INTRODUCTION

Worldwide, rodents are prolific and pervasive pests, destroying crops, spreading disease, and causing enormous damage to infrastructure (Mills, 1999; Meerburg et al., 2009a,b). From a conservation perspective, introduced pest rodents have been linked to the demise of many native species around the world, particularly on islands (Atkinson, 1973, 1985; Capizzi et al., 2014). In several developing countries, rodents are considered the main cause of agricultural losses (Makundi et al., 1999). It is estimated that globally 77 million tons of food are lost annually due to rodent pests (John, 2014). In Asia alone, the annual consumption of food crops by rodents could feed 200 million people (Singleton, 2003). Due to rodents, rice harvest in Indonesia is reduced by 15% annually (Geddes, 1992). Tanzania loses US$45 million every year in reduced maize yield (Leirs, 2003) and in some areas of South America, rodent related damage to crops can amount to up to 90% of the total annual production (Rodriguez, 1993). A recent review on the impact of pest rodents in Africa, found that losses fall between 20 and 50% (Swanepoel et al., 2017). Overall, damage to pre and post-harvest crops affects approximately 280 million undernourished people worldwide (Stenseth et al., 2003; Meerburg et al., 2009b). Yet, the number of species of rodents that are consider pests, represents <10% of all the rodents species currently known (Singleton et al., 2007).

In most urban areas around the world, commensal rodents are common and live alongside humans in houses, buildings and other infrastructure such as sewers (Tobin and Fall, 2006). At high densities, rodents contaminate food, damage infrastructure, increase risk of fire by gnawing on electrical wiring and pose a risk to public health as diseases carriers (Tobin and Fall, 2006; Meerburg et al., 2009a; Almeida et al., 2013; Buckle and Smith, 2015). Wherever humans thrive, pest rodents do as well (Barnett, 2001; Lund, 2015).

The most common approach to rodent management follows the well-known framework of Integrated Pest Management (IPM; Singleton et al., 1999; Tobin and Fall, 2006). The IPM model is the combination of all available pest control methods with preventative measures to reduce subsequent pest population increases, while ensuring that these techniques are economically justified and do not pose a risk to human health and the environment (Food Agriculture Organization of the United Nations, 2018). IPM commonly includes monitoring, sanitation, physical interventions (e.g., exclusion, traps, deterrents), and ultimately rodenticides (Kaukeinen, 1994; Singleton et al., 1999; Bennett et al., 2003).

Physical interventions and the use of rodenticides can be particularly difficult to implement, due to difficulties intrinsic to rodent physiology and behavioral adaptations. Most pest rodent species show high levels of neophobia (Barnett, 1958; Barnett and Cowan, 1976; Meehan, 1984), both towards novel objects and tastes (Domjan, 1975; Rusiniak et al., 1979), which results in high levels of "trap-shyness" (Chitty, 1954; Taylor et al., 1974), and low bait acceptance (Brunton et al., 1993; Inglis et al., 1996). Rodents also learn from the experience of conspecifics (Lore et al., 1971); if conspecifics emit signals of distress—e.g., getting caught in a trap—they are less likely to approach the same area later on (Brudzynski and Chiu, 1995; Brechbühl et al., 2013; Haapakoski et al., 2018). Furthermore, the widespread use of rodenticides have induced the development of resistance in rodent populations to first and second-generation anticoagulant poisons (e.g., warfarin, bromadiolone, difenacoum, chlorphacinone; Thijssen, 1995; Pelz et al., 2005; Pelz, 2007; Rost et al., 2009; Buckle, 2013; Meerburg et al., 2014). Concurrently, the widespread use of these poisons can have considerable negative impacts on non-target wildlife (Howald et al., 1999; Eason et al., 2002; Lambert et al., 2007; Walker et al., 2008; Albert et al., 2010; Dowding et al., 2010; Lima and Salmon, 2010; Thomas et al., 2011; Gabriel et al., 2012; Elliott et al., 2014; Coeurdassier et al., 2018; Lohr and Davis, 2018; Rattner and Mastrota, 2018). The development of alternative and innovative ways of managing rodent pests is therefore of high importance.

History can provide inspiration for new and innovative ways to manage rodent pests. One of the oldest methods of controlling rodents is the use of cats. Cats started their domestication serendipitously as commensal relationships with humans, feeding upon the rodents that infested the stored grain of farmers (Clutton-Brock, 1999). Yet, the effect cats have on rodent populations may be more complex that just population reduction. The effect predators have on prey is not only defined by lethal interactions (Taylor, 1984), but also non-lethal effects. For example, in agricultural settings, the protection guard dogs

provide to livestock is through deterrence instead of actual attacks and killing of predators (Hansen and Bakken, 1999; van Eeden et al., 2017). Hence, analogous rodent-deterrence strategies may be of value.

Risk of predation is ubiquitous to almost all taxa, and as such all species show some level of antipredator defense (Freeland, 1991; Caro, 2005). These defenses can be constitutive (e.g., spines in porcupines, thorns in plants; Fraenkel, 1959; Tollrian and Harvell, 1999) or inducible (e.g., morphology in tadpoles, coloration in some crustaceans, and behavioral modifications; Kerfoot and Sih, 1987; Harvell and Tollrian, 1999; Tollrian and Harvell, 1999; Creel et al., 2007; Schoeppner and Relyea, 2009). Constitutive defenses are favored when risk is constantly high and/or defenses are cheap, while inducible defenses are favored when risk is variable and defenses are costly (Tollrian and Harvell, 1999). Inducible defenses allow control on defense expression according to risk level, thus reducing the costs associated with it (Tollrian and Harvell, 1999). Inducible antipredator responses are expected to evolve only if the costs associated with them are offset by their effectiveness in reducing the rate of direct predation.

The antipredator responses and their associated costs drive an evolutionary arms race between predator and prey, and constitute what is known as the "ecology of fear" (Brown et al., 1999), "degree of fear" (Stankowich and Blumstein, 2005), or "cost of fear" (Martin, 2011). The costs of anti-predator responses can include reduced survival (Dudeck et al., 2018; MacLeod et al., 2018); growth (Pangle et al., 2007); fecundity (Ruxton and Lima, 1997; Naidenko et al., 2003; Voznessenskaya et al., 2003; Fuelling and Halle, 2004; Creel et al., 2007) and reproduction (Zanette et al., 2011; Bonnington et al., 2013; Dudeck et al., 2018). More recently, limited evidence have shown that predation risk can drive an increase in current reproductive investment with associated costs to future reproduction (Duffield et al., 2017; Haapakoski et al., 2018). In some extreme cases, fear can induce the development of chronic stress conditions similar to Post-Traumatic Stress Disorders (PTSD) not only in humans, but also in rodents, primates and rabbits (Clinchy et al., 2013). These costs are sometimes more important to the prey population than the lethal effects themselves (Brown and Alkon, 1990; Schmitz et al., 1997; Matassa and Trussell, 2011).

It is theoretically possible to use these non-consumptive costs as a way managing pest rodent populations (Singleton et al., 1999). Pest controllers could manipulate how commensal rodents perceive predation risk to deter them from areas of interest (e.g., crops, food storage facilities). The Landscape of Fear (LOF) framework is a theoretical tool that allows measurement of the way an animal perceives its environment, based on a trade-off between resources and safety, linked to specific areas of available habitat (Laundré et al., 2001), and thus is a spatial representation of the use of habitat by a prey species. This framework has been supported across a wide range of systems (Bleicher, 2017). The LOF is considered the basis in which the use of perceived predation risk as a management tool against pest rodents can be built upon (Krijger et al., 2017).

A major obstacle in the development of a fear-inducing rodent management technique is the variation in anti-predator

responses displayed by wild rats and mice in comparison with their laboratory counterparts. Laboratory rodents respond to a myriad of different predator cues (Vernet-Maury et al., 1984; Blanchard R.J et al., 1991; Dielenberg and McGregor, 2001; Mongeau et al., 2003; Litvin et al., 2007; Kendig et al., 2011; Bowen et al., 2013; Wallace et al., 2013; Yilmaz and Meister, 2013; Ayral et al., 2015), and also demonstrate anxiety-like behaviors, often utilized to model the human condition (Apfelbach et al., 2005; Staples et al., 2008). However, evidence of wild rodents responding to predator cues is inconclusive. Studies with captive wild-type brown rats (*Rattus norvegicus*) (Berdoy and Macdonald, 1991; Macdonald et al., 1999) and wild caught black rats (*Rattus rattus*) (Burwash et al., 1998) showed antipredator responses consistent to those of their laboratory counterparts. Some field studies demonstrated that wild black rats show aversion to fox and cat feces (Banks, 1998), as well as changes in habitat use in the presence of dogs and cats (Mahlaba et al., 2017). In contrast, other studies have shown either no effect of ferret, cat or mongoose odors in black rat visitation (Garvey et al., 2017) and foraging (Bramley and Waas, 2001); and in more extreme cases, black rats were attracted and visitation increased in response to cat body odor (Carthey and Banks, 2016).

Several explanations for the variability in rodent responses to predator cues have been put forward, namely the prey's: (i) physiological state (Abrams, 1994); (ii) parasite loads (Macdonald et al., 1999); (iii) differential intensity of perceived threats (Kavaliers and Choleris, 2001); (iv) fear learning and habituation (Schulte, 2016); and (v) information gathering (Parsons et al., 2017). In this review, we first explore the current knowledge on the sensory mechanisms and capabilities of rodents, followed by the discussion of each of these explanations within the context of their implications for the use of antipredator response as a pest rodent management tool.

SENSORY CAPABILITIES OF RODENTS

Before an animal responds to a predator, it needs to be able to detect its presence. Rodents can detect and respond to visual (Wallace et al., 2013; Yilmaz and Meister, 2013); auditory (Blanchard R.J et al., 1991; Mongeau et al., 2003; Litvin et al., 2007), and olfactory (Vernet-Maury et al., 1984; Dielenberg and McGregor, 2001; Kendig et al., 2011; Bowen et al., 2013; Ayral et al., 2015) predator cues, highlighting that their sensory capabilities are highly tuned to predator detection.

Sight

Laboratory rodents are commonly used as models to study the mammalian visual system (Hughes, 1979; Remtulla and Hallett, 1985; Legg and Lambert, 1990; Berardi and Maffei, 1999; Zoccolan et al., 2009). As rodents are predominantly prey species, they have laterally facing eyes that allow for a panoramic field of view that extends forwards and also covers the back of the animals head, enhancing potential threat detection (Hughes, 1979; Remtulla and Hallett, 1985). Through eye movement alone, rodents are capable of overlapping the fields of view of both eyes to obtain binocular vision, at the loss of a complete panoramic field of view (Wallace et al., 2013). Binocular vision is important

for judging distance (Russell, 1932; Legg and Lambert, 1990) and visual acuity (Hughes, 1979; Remtulla and Hallett, 1985; Zoccolan et al., 2009), while a panoramic monocular vision allows for wide surveillance (Hughes, 1979; Remtulla and Hallett, 1985).

Due to the reliability of visual cues—i.e., seeing a predator is a perfect clue that there is a high risk of predation—most species, including rodents, respond to oversimplified representations of predators (Kavaliers and Choleris, 2001). Some of these representations can encompass only size (Hanson and Coss, 1997; Mathis and Vincent, 2000), shape (Coss and Ramakrishnan, 2000; Emile and Barros, 2009), coloration (Kelley and Magurran, 2003), movement (Yilmaz and Meister, 2013), or frontally positioned eyes (Topál and Csányi, 1994). Rodents in particular, are highly sensitive to movement (Wallace et al., 2013; Yilmaz and Meister, 2013). When exposed to an oversimplified looming stimulus simulating a raptor, laboratory rats maintain overhead binocular vision (Wallace et al., 2013), thus, enabling them to judge the raptor's elevation.

Hearing

Mice and rats are particularly attuned to detect high frequency sounds, often higher than humans have the ability to detect (Heffner and Heffner, 2007, 2008). Accordingly, these rodents commonly produce high-frequency sounds that have been linked to conspecific communication (Portfors, 2007). In laboratory rodents, con-specific high-frequency alarm calls are used to communicate threats (Brudzynski and Chiu, 1995). However, rodents are also capable of detecting lower frequency sounds (Heffner and Heffner, 2007, 2008). Studies in voles and gray squirrels have shown that playback of raptor calls can incite antipredator responses (Bohls and Koehnle, 2017; Lyly et al., 2018).

Smell

In most mammals, olfaction is the most developed sensory system (Eisenberg and Kleiman, 1972), and rodents are no exception (Vernet-Maury et al., 1984; Dielenberg and McGregor, 2001; Kendig et al., 2011; Bowen et al., 2013; Ayral et al., 2015). In contrast with the singularity of visual (i.e., retina) and auditory (i.e., ear) sensing, smells are processed by multiple distinct olfactory systems, involving distinct receptor organs and central neuronal processes involved in detection (Chamero et al., 2012; Ma, 2012). The main olfactory system processes scents and flavors, while the accessory olfactory system processes con-specific and heterospecific chemical cues (pheromones and kairomones) (Ma, 2012).

Predator recognition by olfactory cues does not require cortical information processing (Canteras et al., 2015). Discrimination of different odorants is achieved by the narrow sensitivity to chemical cues from each receptor type in the accessory olfactory system (AOS; Mucignat-Caretta, 2010; Ma, 2012; Canteras et al., 2015; Tromelin, 2016). In laboratory rodents, different predator odors activate receptors from distinct olfactory subsystems (Canteras et al., 2015). Carnivore urine activates TAAR4 neurons in the main olfactory epithelium (Ferrero et al., 2011; Dewan et al., 2013), cat fur activates vomeronasal organ receptors (McGregor et al., 2004), and stoat

anal gland smells activate receptors in the Grueneberg ganglion (Pérez-Gómez et al., 2015). Therefore, activation of specific receptors allows for the recognition of specific predators. In the following section we will describe how after detection and recognition is achieved an appropriate response is induced. Interestingly, rodents are also capable of utilize olfactory signaling from conspecific in order to asses predation risk (Abel, 1991; Kikusui et al., 2001; Haapakoski et al., 2018). And in some cases these pheromones activate similar receptors as predator odors (Brechbühl et al., 2008, 2013).

Sensory Coordination and Response

On predator detection all sensory signals, regardless of their origin (i.e., visual, auditory or chemical), converge in the amygdala (Krettek and Price, 1977; Campeau and Davis, 1995; Chamero et al., 2012; Ma, 2012; Pérez-Gómez et al., 2015). Amygdala signaling initiates sensory and motor response coordination to the predatory threat (Miller and Vogt, 1984) provoking appropriate behavioral and physiological responses (Campeau and Davis, 1995), such as freezing or evasive behaviors. Thus, differences in rodents' antipredator responses are expected to arise because of differences in detection, recognition, or response to predator cues, mediated through complex but converging neural signaling. Modulation of this signaling pathway can occur at every stage based on the individual's internal state, prior experience, or the context, leading to observable variability in antipredator responses.

VARIABILITY IN RODENT RESPONSES TO PREDATOR CUES

Prey's Physiological State

The risk of predation is ubiquitous to all animals (Freeland, 1991; Caro, 2005), however so is the need to forage and acquire resources (Charnov, 1979; Stephens and Krebs, 1986). Yet, laboratory rodents are commonly kept in standard captive husbandry conditions with *ad libitum* access to food and water, and controlled environmental variables such as temperature, humidity and photoperiod (Allmann-lselin, 2000; Hedrich and Bullock, 2004; National Research Council, 2010). In comparison, wild rodents must cope with a variety of environmental factors, while balancing the risk of predation and resource acquisition to optimize their fitness (Abrams, 1994).

Starvation alters the antipredator response in both laboratory (Shoham et al., 2000; Verma et al., 2016) and wild rodents. Starved captive wild-caught Anderson's gerbils (*Gerbillus andersoni allenbyi*) increase foraging despite predation risk (Berger-Tal and Kotler, 2010; Berger-Tal et al., 2010). Free-ranging deer mice (*Peromyscus maniculatus*) (Morris, 1997; Davidson and Morris, 2001) and house mice (*Mus musculus domesticus*) (Ylönen et al., 2002) reduce their foraging at the cost of increased predation risk, when the population density is high driving higher intraspecific competition and thus lower internal energetic state (Bedoya-Pérez et al., 2013).

Relative resource quality also alters the intensity of anti-predator responses (Thorson et al., 1998). Fox squirrels (*Sciurus niger*) (Brown and Morgan, 1995), Namaqua mouse (*Micaelamys*

namaquensis) (Abu Baker and Brown, 2012), Anderson's gerbils (*G. andersoni allenbyi*), the greater Egyptian gerbil (*G. pyramidurn*) (Garb et al., 2000), Merriam's kangaroo rats (*Dipodomys merriami*), and pocket mice (*Chaetodipus* spp.) (Leaver and Daly, 2003) forage more intensely on highly nutritious food regardless of predation risk. Similarly, fox squirrels (*S. niger*), gray squirrels (*S. carolinensis*) (Schmidt et al., 1998), as well as the African unstriped ground squirrel (*Xerus rutilus*) (Fanson et al., 2010), reduce foraging on poor quality food and become more sensitive to predation risk (Bedoya-Pérez et al., 2013).

Other physiological, developmental, and reproductive factors can alter an animal's anti-predator response. For example, immunochallenged white-footed mice (*Peromyscus leucopus*) forage more and are less selective in their habitat use despite the risk of predation (Schwanz et al., 2011, 2012), and Anderson's gerbils (*G. andersoni allenbyi*) and the greater Egyptian gerbil (*G. pyramidurn*) increase foraging efforts during the reproductive season (Kotler et al., 2004). More relevant to rodent management, we know that pest rodents infected with *Toxoplasma gondii* showed a reduced aversion to predators (Berdoy et al., 1995a, 2000; Webster, 2007), we will this discuss this particular case in more detail in the following section.

To exploit anti-predator responses as a pest management tool, it is essential to recognize that wild rodents are not well-fed, homeostatic animals like their laboratory counterparts. If resources are low, and pest rodents are at risk of starvation, these animals are expected to show less-pronounced anti-predator behaviors than those shown by laboratory animals (Abrams, 1994).

Parasite Loads the Case of *Toxoplasma gondii*

Parasite loads can alter an animals perceived predation risk either by altering their internal physiological state (Schwanz et al., 2011, 2012), or through more complex mechanisms involving modulation of neuronal pathways (Berdoy et al., 1995a; Raveh et al., 2011). The complete disruption of anti-predator response in rodents infected by *Toxoplasma gondii* has received wide attention in recent years (Webster, 2007).

Toxoplasma gondii is a parasitic protozoan capable of infecting all mammals, including humans (Hutchison et al., 1969). Domestic cats and other felines are the final host of the parasite, and are the only animals known to shed the parasite's oocyst in their faces (Hutchison et al., 1969). Transmission of the parasite can occur from cat to cat, but more commonly involves an intermediate host, such as a rodent. Here the parasite multiplies and forms cysts in almost every organ, particularly in the brain (Hutchison et al., 1969; Berdoy et al., 1995b). When a cat predates upon an infected rodent, the parasite passes to the final host where sexual reproduction occurs (Berdoy et al., 1995b).

One of the first studies demonstrating a connection between *T. gondii* infections and changes in behavior showed that laboratory rats and mice were cognitively impaired by the parasite (Piekarski et al., 1978). Subsequent studies have showed that *Toxoplasma*-infected rats and mice display deficits in

both learning capacities (Witting, 1979) including novel object recognition (Hutchison et al., 1980; Webster et al., 1994). It was suggested that the reduction in neophobia could cause rats to be more susceptible to predation (Webster et al., 1994). It was later demonstrated that *Toxoplasma*-infected rats are more likely to approach areas with signs of cats, although retaining certain level of innate aversion (Berdoy et al., 1995a). These findings were confirmed by the demonstration that, compared to non-infected rats, *Toxoplasma*-infected rats visited areas treated with cat urine more often that control areas or areas treated with rabbit urine (Berdoy et al., 2000; Webster, 2007).

Toxoplasma gondii likely does not alter the sensory detection of the threat (Vyas et al., 2007a), but instead modifies the learning processes specifically related to cat odor (Vyas et al., 2007a,b). Neurobiologically, *T. gondii* causes epigenetic changes in the DNA methylation in the medial amygdala causing greater expression of arginine vasopressin promoter (Hari Dass and Vyas, 2014). The infection also causes retraction of dendritic processes in basolateral amygdala neurons, reducing the amount of circulating corticosterone (Mitra et al., 2012). A reduction in corticosterone disrupts both the fight or flight response as well-fear memory consolidation (Stephens and Wand, 2012). Behaviorally, infected laboratory rats show reduced anxiety-like behaviors in exploration-based testing, but not during social interaction testing (Gonzalez et al., 2007). This may be because *T. gondii* favors vertical transmission (i.e., cat predation) over horizontal transmission (i.e., infected parents to offspring; Vyas and Sapolsky, 2010). However, research shows that the mechanisms involved in behavioral alterations in male rodents increases sexual arousal (House et al., 2011) and attractiveness (Dass et al., 2011), potentially allowing the parasite to be transmitted sexually and congenitally (Beverley, 1959, 1976; Dass et al., 2011).

In terms of rodent management, undoubtedly *T. gondii* can have profound consequences for the use of anti-predator responses as a tool. However, these consequences are dependent on the prevalence of the infection in the targeted pest rodent population. It is unlikely that this protozoan is the cause of the variation in response between laboratory and field studies, when the prevalence in the field is appreciatively low (Carthey and Banks, 2016). In cases where the prevalence may be high, the disruption of antipredator behavior by *T. gondii* could be used synergistically with predator cues. That is, other management tools (e.g., lethal and non-lethal traps) could be deployed at the same locations as predator cues, thus infected rodents could be removed, while uninfected may be repelled. This method may reduce the prevalence of *T. gondii*, not only in the rodent population, but at the community level. Reductions in the number of infected carriers would benefit non-specific host species that may be vulnerable to the infection, such as humans (Tenter et al., 2000; Dubey and Jones, 2008) and several endangered species that are more susceptible to develop negative symptoms from the infection [e.g., Eastern quoll, *Dasyurus viverrinus* (Fancourt and Jackson, 2014; Fancourt et al., 2014), Tamar wallabies, *Macropus eugenii,* and Bennett's wallabies, *Macropus rufogriseus* (Dubey and Crutchley, 2008)].

Due to the extensive and ever-growing body of knowledge on the mechanisms and potential consequences of *T. gondii,* we have focused on this particular parasite. However, little is known about the potential effects that other parasites may have in the anti-predator behavior of pest rodents. Some evidence suggests that some infections and diseases may have overarching population level consequences such as increase in reproduction (Duffield et al., 2017).

Differential Intensity of Perceived Threats

There are considerable differences between laboratory and field studies in the testing of rodent responses to fear stimuli. Laboratory rodents are usually tested in spatially constrained arenas, where they are presented with a single proximal stimulus. Field or semi-captive studies normally occur at much larger spatial scales, and animals are exposed to varying environmental conditions as well as the specific stimulus of interest. These differences can have important implications to the interpretation of the responses measured (Lima, 1998; Lima and Bednekoff, 1999). Allenbyi's gerbils (*G. allenbyi*) and the greater Egyptian gerbil (*G. pyramidurn*) exposed to Barn owls (*Tyto alba)* at close proximity show a greater reduction in activity than when presented with the same predator in a semi-captive setting (Abramsky et al., 1996). Similarly, house mice (*M. musculus domesticus*) (Dickman, 1992), bank voles (*Clethrionomys glareolus*), and meadow voles (*Microtus pennsylvanicus*) (Perrot-Sinal et al., 1996, 1999, 2000) show a strong aversion and reduce activity when exposed to mustelid odor in relatively small enclosures. Conversely, in large scale enclosures, hairy-footed gerbils (*Gerbillurus tytonis*) (Hughes and Ward, 1993), gray-tail voles (*Microtus canicaudus*) and bank voles (*C. glareolus*) show little to no anti-predator response. This pattern is also observed in other small non-rodent mammals (Ward et al., 1997) and fish (Fraser and Huntingford, 1986; Irving and Magurran, 1997).

Kavaliers and Choleris (2001) suggested that the differences between laboratory and field results may be due to differences in the intensity of the cue. They argue that laboratory animals commonly experience single intense cues while animals in field experiments, although sometimes exposed to the same type of cues, can also assess predation risk by integrating several other relevant cues (e.g., habitat structure, vision, odors, sound) simultaneously (Kavaliers and Choleris, 2001). Thus, the cue of interest (i.e., the cue manipulated by the experimenter) is "drowned out" by the information contained in the other signals. Additionally, it has been suggested that very high predation risk may, counterintuitively, reduce some antipredator responses and increase others (e.g., vigilance vs. time allocation; Lima, 1998). For example, at very high levels of risk, animals are expected to completely avoid an area either by moving away (i.e., habitat partitioning) or by hiding until the risk is reduced (i.e., time partitioning). While at low levels of predation risk, animals may choose to remain in the area but increase vigilance instead (Lima, 1998). This has been demonstrated in desert rodents (Abramsky et al., 1996) and consistently in rats (Blanchard D.C et al., 1991; Blanchard et al., 1993, 1998).

Hence, if a pest rodent management strategy is to be effective, consideration of the intensity and the distribution of the predator cues is essential. Here, we suggest that utilizing a combination of

cues may prove more effective (e.g., predator odor paired with either predator call or conspecific alarm playback).

Fear Learning and Habituation

Before any animal can respond appropriately to reduce its risk of predation, it needs to be able to perceive and estimate such risk. Animals can use ultimate or proximate cues to estimate the risk of predation (Kavaliers and Choleris, 2001). Ultimate cues constitute the actual detection of a predator itself; these could be visual (Magurran and Girling, 1986; Atkins et al., 2017), auditory (Smith et al., 2017; Suraci et al., 2017b), or tactile (Kavaliers and Choleris, 2001). While proximate cues are commonly of a chemical nature, such as odors (Parsons et al., 2017). Ultimate cues convey immediate risk (i.e., the predator is present here right now), while proximate cues convey temporally dependent risk (Parsons and Blumstein, 2010; Parsons et al., 2017) (i.e., the predator was here sometime in the past; Parsons and Blumstein, 2010; Parsons et al., 2017). However, in most cases, these cues are encountered simultaneously—i.e., if an animal sees a predator, it can likely detect the predator by audition and olfaction. By separating the effects of different types of predator cues, each can convey different kinds of information—i.e., presence of a potential threat vs. identity of the threat (Blumstein et al., 2000; Mathis and Vincent, 2000). Ultimate cues of predation are potentially more reliable and convey a good estimate of the actual risk of predation. Proximate cues are more variable in nature, and can provide an underestimation of risk if predators are present, or an overestimation when they are absent (Lima and Dill, 1990; Abrams, 1994; Lima, 1998).

Once a prey animal detects a predator cue it must be able to recognize and assess the risk associated with it, leading to a fear response. In the brain, fear can be categorized in two distinct modes, innate and learnt (Canteras et al., 2015). Innate fear refers to the defensive response to aversive stimuli with no previous experience of such stimulus (Canteras et al., 2015; Parsons et al., 2017). Learned fear is the development of conditioned fear behaviors—i.e., defensive responses to a innocuous stimulus or context, shown after repeated pairings of the innocuous stimulus and an adverse one (Rescorla and Wagner, 1972).

Innate fear is also known as "species memory" or "phyletic memory" (Canteras et al., 2015), and it has been described in a myriad of different taxa: including invertebrates (Dalesman et al., 2007); fish (Berejikian et al., 2003; Vilhunen and Hirvonen, 2003); amphibians (Semlitsch and Reyer, 1992); birds (Veen et al., 2000; Göth, 2001); marsupials (Anson and Dickman, 2013), rabbits (Monclús et al., 2005), rodents (Dielenberg and McGregor, 2001; Bowen et al., 2012, 2013; Parsons et al., 2017); ungulates (Chamaillé-Jammes et al., 2014); and primates (Gould and Sauther, 2007). In mammals, the neurocircuitry that categorizes innate fear responses is initiated by an increase in Fos expression in the posteroventral part of the medial amygdalar (MEApv) and in the dorsomedial part of the ventromedial hypothalamic nucleus (VMHdm) (Pérez-Gómez et al., 2015). The activation of the dorsomedial and central divisions of the VMH (VMHdm/c) are linked with the initiation of a series of context-dependent somatomotor and autonomic defensive behaviors, including generalized passive hiding and freezing

responses, as well as running and jumping (Wang et al., 2015). Innate fear response, and the initiation of autonomic defensive behaviors, could therefore be considered the "default" mechanistic mode of defense when exposed to a novel predator cue. However, the future fear response to the same cue is not always fixed and can be modulated by experience; this is the paradigm of "habituation" (Rankin et al., 2009; Blumstein, 2016). Habituation is the reduction of a natural response to a stimulus as a consequence of repetitive exposure (Davis, 1970; Staddon, 1993). This can represent a major obstacle in the application of anti-predator responses for wildlife management (Bomford and O'Brien, 1990; Koehler et al., 1990; Samia et al., 2015; Blumstein, 2016). Habituation occurs when short-term memory suppresses the natural response to a recent stimulus (Staddon, 1993). Yet, if an animal fails to respond to a stimulus that signals an increase in predation risk, that animal is bound to suffer predation. Thus, it raises questions as to why habituation is widespread among several different taxa and stimuli types (Davis, 1970; Williams et al., 1990; Talling et al., 1998; Nowak et al., 2014) and why animals are not fearful at all times. This is explained by the fact that antipredator responses can be expensive (Ylönen and Brown, 2007; Martin, 2011; LaManna and Martin, 2016), and that not all stimuli can be regarded as honest. There are fundamental differences between the "actual" risk of predation and the "perceived" risk of predation (Creel, 2018), and most species have the cognitive tools to reduce the chances of "false positives" by learning.

After estimating the level of risk, an animal must be able to respond to reduce that risk. There are several stages to the predation process, through which antipredator defenses can act to reduce risks. Prey can reduce the probability of: being detected by the predator; that detection will lead to an attack; that an attack will lead to death or serious injury; and being the individual that is killed (Hamilton, 1971; Turner and Pitcher, 1986; Uetz and Hieber, 1994). To achieve this, animals can: (i) avoid a high risk area (Schmitz et al., 1997; Ojeda and Muñoz, 1999; Wirsing et al., 2008; Mao et al., 2010); (ii) wait until a risk decreases to become active (Lima and Bednekoff, 1999; Kotler et al., 2002; Valeix et al., 2009); (iii) reduce foraging (Brown et al., 1988; Herman and Valone, 2000; Altendorf et al., 2001); (iv) increase vigilance (Childress and Lung, 2003; Cresswell et al., 2003; Fortin et al., 2004; Embar et al., 2011; Iribarren and Kotler, 2012); (v) discourage predation by direct signaling (FitzGibbon and Fanshawe, 1988), (vi) employ active defenses (Corcoran and Conner, 2012); and (vii) aggregate with con-specifics (Hamilton, 1971; Pulliam, 1973; Bowen et al., 2013). In natural systems, these strategies are usually effective in unison (Kotler et al., 2010). Thus, predator defenses can be behavioral (Lima, 1990; Altendorf et al., 2001; Abramsky et al., 2002), morphological (Agrawal and Fishbein, 2006), physiological (Lima, 1998; van Donk et al., 1999), or ecological (Ojeda and Muñoz, 1999; Wirsing et al., 2008; Mao et al., 2010). These defenses are associated with non-consumptive costs and, in order to remain in the population, these costs need to be offset by a reduction in the "actual" risk of predation (Creel, 2018); these costs to risks ratio is what drives habituation.

Laboratory rodents demonstrate defensive responses to predators without previous experience (Parsons et al., 2017).

However, this response is not unchallengeable, as prolonged exposure to predator cues reduces anti-predator behavior in laboratory rats (Williams et al., 1990). Moreover, it is well-understood that varying levels of predation risk can shape wild rodent anti-predator behavior (Brown et al., 1999; Ylönen and Brown, 2007). Thus, rodent antipredator responses seem to be non-binary (i.e., not simply "on and off"), and are shaped by fear learning (Staples et al., 2005).

Fear learning or contextual conditioning involves a different, although related pathway to innate fear neurocircuitry. The current working model for fear learning involves sequential activation, signaling, and feedback, primarily between four brain regions well-characterized for their role in fear acquisition and consolidation (McNally et al., 2011). This model describes how fear learning occurs when the difference between the actual vs. the expected intensity of a aversive unconditioned stimulus is encoded by an error signal (Rescorla and Wagner, 1972). McNally et al. (2011) it mostly involves conditioning with shock rather than with predator-related cues. However other studies have looked at conditioning with cat odor (e.g., Staples et al., 2005). When rats were placed in a context where they previously encountered a predator odor they displayed brain activation in a subset of the regions activated by the predator odor itself: this included the dorsal premammillary nucleus, ventrolateral periaqueductal gray, cuneiform nucleus and locus ceruleus (Staples et al., 2005). Little activation was seen in the amygdala or hippocampus. These results show that stimuli associated with predatory threat come to activate similar brain regions to the threat stimulus itself. If an animal experiences an unexpected aversive stimulus (e.g., predator attack), then the actual intensity of the stimulus will be higher than the expected, thus the stimulus would drive fear learning. Conversely, if an aversive stimulus—e.g., predator attack—was expected—e.g., encounter with a predator cue –, then the expected and actual intensity of aversive stimulus will match, and fear learning does not occur. Finally, when the actual intensity of the aversive stimulus is lower than the expected intensity—e.g., perceived predator cue but predator does not attack– then fear learning extinction occurs— i.e., habituation (Schaller, 1972; McNally et al., 2011).

In mammals, fear learning involves complex neural circuitry within the amygdala (McNally et al., 2011). When an aversive stimulus is detected (e.g., predator attack), this activates spinal and trigeminal dorsal horn neurons that project to the midbrain periaqueductal gray (PAG; McNally et al., 2011). Signaling then travels from the PAG, through the midline and intralaminar thalamus, to the dorsomedial prefrontal cortex (dmPFC) and lateral amygdala (LA) depolarizing pyramidal neurons (McNally et al., 2011). Associative fear learning is achieved when the co-occurrence of the aversive stimulus (e.g., predator attack) with an associated stimulus (e.g., predator cue) strengthen the thalamic and cortical afferent inputs to LA through N-methyl-D-aspartate receptor (NMDA)-mediated long term potentiation (McNally et al., 2011). Consequently, future exposure to the associated stimulus (e.g., predator cue) activates LA projection neurons to the central amygdala (CeA), leading to inhibition of the ventrolateral PAG (vlPAG), and inciting an antipredator response (McNally et al., 2011). Repeated exposures to the associated stimulus alone causes weakening of the auditory thalamic and cortical afferent inputs to LA pyramidal neurons through long term depression at NMDA receptors (McNally et al., 2011).

Learning aids in the recognition of threats, but through conditioning, it is the mechanism by which animals also estimate predation risk (Bolles, 1970; Crawford and Masterson, 1982; Cook and Mineka, 1990; Curio, 1993). There are many examples of different taxa that show certain innate responses to predators: from finches (Curio, 1993), moose (Berger et al., 2001), black-tail deer (Chamaillé-Jammes et al., 2014), Hokkaido deer (Osada et al., 2014), rabbits (Monclús et al., 2005), deer mice (Coss, 1999), ground squirrels (Hirsch and Bolles, 1980), and laboratory mice (Pérez-Gómez et al., 2015). But, more importantly, these innate predator responses can be enhanced or modified through fear learning (Berger et al., 2001). However, individual fear learning requires an animal to experience an adverse predator encounter directly, which may not be conducent to future survival. Thus, to acquired "knowledge" putatively through conspecifics is more advantageous (Russon, 1997).

Social learning occurs when an animal acquires information (i.e., the observer) by witnessing the actions of another, more experienced individual (i.e., the demonstrator; Heyes, 1994; Choleris and Kavaliers, 1999). The first taxa where social learning was characterized was fish (Von Frisch, 1942). Nowadays, social learning has been reported not only in other fish species (Chivers et al., 1995; Mirza and Chivers, 2000; Brown and Laland, 2005), but also birds (Curio et al., 1978; Curio, 1988; Magurran, 1989; Martínez et al., 2017); marsupials (Griffin and Evans, 2003); ungulates (Berger et al., 2001); primates (Cook et al., 1985; Bartecki and Heymann, 1987; Mineka and Cook, 1988; Cook and Mineka, 1990; Srivastava, 1991); laboratory rats (Lore et al., 1971); and mice (Kavaliers et al., 2001a,b; Sanders et al., 2013).

Both individual and social fear learning are widely used in wildlife management programs with species conservation goals (Griffin et al., 2001), yet has been somewhat neglected in the application of fear as a management tool. Schulte (2016) argues that when using artificial predator cue to alter the perceived predation risk by pest animals, a Batesian mimicry type dilemma is difficult to avoid. Batesian mimicry occurs when a non-dangerous species mimics the appearance, smell and/or behavior of a co-occurring dangerous species, thereby protecting itself from the attack of predators that have learned to avoid the dangerous species (Bates, 1861). This type of mimicry is maintained only when the relative frequency of the dangerous species is higher than that of the mimic, thus the predator maintains a conditioned avoidance to the mimic (Duncan and Sheppard, 1965). This argument also brings forward the effect of tolerance as another factor affecting fear response. In a comprehensive review, Blumstein (2016) stablished a clear difference between habituation and tolerance. Habituation is a process that acts at the scale of the individual, with each animal modifying their response to different stimulus based on their associated consequences across repeated exposures (Rankin et al., 2009; Blumstein, 2016). Tolerance, also involving a reduced response to a stimulus, and can emerge through habituation-like processes but also through other ecological pressures (e.g., competition; Owens, 1977; Blumstein, 2016).

Moreover, tolerance through habituation can be transferable to different stimulus—e.g., squirrels inhabiting urban areas reduced their anti-predator response to foxes (Mccleery, 2009).

In a pest management context, the widespread deployment of predator cues (i.e., mimics) in the environment has the potential to overcome the relative frequency of the real predator, thus fear conditioning is lost (Schulte, 2016). Moreover, we would expect pest rodent populations inhabiting urban areas, would be more tolerant to human disturbances, and this tolerance may translate to a reduction in their antipredator response (Mccleery, 2009; Blumstein, 2016). A way of overcoming this dilemma is to maintain conditioning by aversive reinforcement (Kloppers et al., 2005; Leigh and Chamberlain, 2008; Cromsigt et al., 2013). These aversive reinforcements can be administered repeatedly (Huang et al., 1992; Dunsmoor et al., 2007) or be of high intensity (Abrams, 1994; Siegmund and Wotjak, 2007). However, this can be logistically difficult and undesirable (Baruch-Mordo et al., 2011). The implementation of repeated exposures of an intense aversive stimulus can be expensive, has negative animal welfare implications, or be lethal to the target and non-target species (Schulte, 2016). The question then becomes, what aversive reinforcement is required to maintain fear conditioning? One possible solution is to use predator cues that not only incite fear, but can also cause long-term anxiety (Schakner and Blumstein, 2013). This type of response to repeated stimulus is called sensitization and has been reported in seals (Götz and Janik, 2011, 2015), ungulates (Cox et al., 2012), and marsupials (Parsons and Blumstein, 2010). However, to date there is no evidence that rodents would show sensitization to predator cues.

Information Gathering

In a comprehensive review of the role of predator odor in predator-prey interactions, Parsons et al. (2017) suggests that the attraction of prey to some predator smells may be due prey species gathering information either on the identity or temporal characteristics of the scent (Parsons et al., 2017). When an animal approaches the scent of a predator—i.e., predator inspection—it does so in order to obtain information about the actual risk of predation (Fishman, 1999). The animal may gain certain benefits from doing so, namely (i) acquiring information about the nature of the potential threat; (ii) informing conspecifics of the potential threat; (iii) deterring predator attack; and (iv) possibly even advertising one's quality to mates (Dugatkin and Godin, 1992).

Parsons et al. (2017) argues that this phenomenon can confound interpretation of empirical studies testing the repellent potential of predator scents and, as exemplar, describe how hairy-nosed wombats (*Lasiorhinus latifrons*), when presented with dingo (*Canis dingo*) scents, remained within 200 m of the stimulus (Sparrow et al., 2016). However, while still present in the area, wombats stopped their normal digging behavior, thus there was a significant reduction of their impact to human activity (Sparrow et al., 2016).

With the exception of pheromones (i.e., single species communication molecules), most scents are "dose-dependent" (Glimcher, 2010; Vasudevan and Vyas, 2013). Higher concentrations of a specific predator scent may convey higher

or lower predation risk (Schmeisser et al., 2013). However, composition is also important. Scherer and Smee (2016), suggested that most prey species are sensitive to their predators' diet. For example, dwarf hamsters (*Phodopus campelli*) show a stronger anti-predator response when predators fed upon conspecifics (Apfelbach et al., 2015).

Another aspect of information gathering in predator cue inspection is the temporal component. Predator scent is normally complex, and composed of a myriad of different molecules, with different characteristics (Parsons et al., 2017). Each component within this complex mixture react to environmental conditions (e.g., bacterial decomposition, UV light) at different rates and in different manners (Rasmussen, 1988; Muller-Schwarze, 2006), ultimately modifying the chemical profile of the cue over time. Even handling and storage of the chemical cues can alter the way animals perceive them (Hoffmann et al., 2009; Hegab et al., 2014). It is therefore possible that changes in chemical structure of the signal may also change its information over time (Parsons and Blumstein, 2010). Older cues may convey that the predator is not there, and left a long time ago, while fresher cues can convey immediate danger (Hurst and Beynon, 2004; Parsons et al., 2017). However, there is some evidence that these changes may not affect rat responses (*Rattus* spp.) (Bytheway et al., 2013). Alternatively, animals may approach older odor cues since obtaining information from degraded scent may be more difficult, since only the non-volatile components remain (Parsons et al., 2017).

This raises the question; how can predator cues be applied in a rodent management context? The use of predator scent as a rodent management tool requires a better understanding on how these types of cues work. Just as adverse reinforcement is used to prevent habituation, the repeated application of odor cues to maintain their freshness can be logistically expensive and difficult. Current evidence suggest that wild rodents are not affected by aging scent (Bytheway et al., 2013), however, it is important to note that this is based on 1-day old scent. A better understanding is required when, along the aging time-line, anti-predator response disappears. This can help determine the rate at which the scent needs to be re-applied. Note, this is an issue specific to the use of chemical cues. Visual and auditory stimuli (or their pairing with chemical cues), might prove to be more effective.

CONCLUSIONS AND IMPLICATIONS FOR RODENT MANAGEMENT

Pest rodent species adaptability is what has placed them in constant conflict with humans. For humans, rodent populations' cost money, damage buildings, eat crops and transmit diseases. In contrast, rodents are "fighting" for their lives. Thus, it is not surprising that this constant struggle for survival pushes mice and rats to risk safety for food, and has made them very capable of assessing risks across very fine scales.

To use anti-predator responses as a rodent management tool, we need to follow a holistic approach. First, we need to understand that these animal's motivations are strong, thus our

strategy needs to be stronger. It is essential to reinforce our approaches. Using a combination of predator and conspecific cues (e.g., predator odor, paired with predator models, and playbacks of both the predator and conspecifics alarm calls) to simulate high predation risk, but also maintaining the actual risks as high (e.g., repeated simultaneous aversive stimuli), could prevent most of the issues discussed in this review. For example, in agricultural systems, a sentinel system can be applied, where a crop area can be heavily guarded with simulated predators, while another is not, however treated with rodenticide. This can increase rodenticide intake, while reducing widespread use.

However, these are not easy tasks, and economic, logistical, and ethical costs need to be addressed. Yet, some steps in the right direction have been made in other systems. For example, Cromsigt et al. (2013) proposed the use of more intense methods of hunting ungulates (e.g., using dogs, targeting females with calves) in order to induce fear and deter these animals from areas of interest. Regardless of the polemic animal welfare implications, this proposal aims at increasing the intensity of the perceived risk (Cromsigt et al., 2013). Suraci et al. (2017a) have developed a motion triggered systems to playback predator sounds only when an animal approaches the devices, the cue is only used at proximity, intensifying the fear response. The effectiveness of this device has been demonstrated with pumas (*Puma concolor*) (Smith et al., 2017), and raccoons (*Procyon lotor*) (Suraci et al., 2016). One point of caution is the long term consequences of simulated high predation risk deployment are not fully understood, and some have raised doubts about how high this perceived risk should be (Duffield et al., 2017; Haapakoski et al., 2018). Sustained perception of very high risks of predation can drive a cycle of dynamic terminal investment (Duffield et al., 2017), that can have the desired short term deterrent effects, but produce long term population increases.

There are also synergies that can be achieved, if we consider the biological nature of the fear response. For example, the modification of antipredator behavior by *T. gondii* infections could assist with the reduction on the prevalence of *T. gondii*, at the community level, as a tool in conservation programs (Dubey and Crutchley, 2008; Fancourt and Jackson, 2014; Fancourt et al., 2014).

The theoretical framework of using fear as a way of managing pest rodent populations is sound, but it is not in any way simple. Pest rodents, either native or introduced, are embedded within a dynamic ecological system. If anti-predator responses are to be used as a pest management tool, it is essential to recognize that rodent's anti-predator responses are non-binary and rely on complex contextual cues.

AUTHOR CONTRIBUTIONS

FUNDING

ACKNOWLEDGMENTS

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