Uso de repelentes olfativos como alternativa de control no letal para el manejo de carnívoros silvestres.

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RESUMEN BIOGRÁFICO

Nací en 1985 en Santiago. Durante toda mi vida sentí un gran interés en dedicarme a la ciencia y al medio ambiente. Me titulé de Bióloga Ambiental en 2012 y desde entonces tuve la oportunidad de trabajar en diversos proyectos de consultoría y educación. En 2014 comencé a formar parte de lo que hoy es el Instituto Jane Goodall Chile, donde me desempeño como Directora de Proyectos. En el año 2016 ingresé al Laboratorio de Conservación Biológica donde pude desarrollar mi investigación en el área de conservación de carnívoros en ambientes fragmentados por la actividad humana y en conflicto con la vida silvestre. En el futuro me interesa continuar trabajando para que el desarrollo humano se realice en armonía con la naturaleza, a través de la investigación, acción y educación.

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RESUMEN GENERAL

Los carnívoros poseen grandes rangos de distribución y una alta demanda de proteínas en su dieta, por lo que entran frecuentemente en conflicto con productores de ganado alrededor del mundo, ya que el ganado representa una presa abundante, fácil de capturar y energéticamente rentable para los carnívoros. Por este motivo los carnívoros se han vuelto quizás las especies más severamente amenazadas por el control letal, haciendo urgente el desarrollo de estrategias de control no letal que permitan compensar en parte la perdida de hábitat y faciliten su coexistencia en ambientes antropogénicos con la población humana. Los repelentes primarios ofrecen una alternativa de fácil acceso, en mamíferos los repelentes utilizados por más tiempo han sido aquellos dirigidos al gusto u olfato. Basados en el uso de componentes naturales o artificiales, estos repelentes buscan generar señales que indiquen a los animales que una fuente de alimento no es palatable o bien hay un riesgo inminente próximo a ellos y por ello deberían evitar ese alimento. En este contexto, en el primer capítulo realizamos una revisión bibliográfica para contextualizar el uso de repelentes primarios en mamíferos y particularmente para analizar su efectividad en especies carnívoras y omnívoras. Por un lado, mientras los repelentes si logran un efecto en los herbívoros, los antecedentes disponibles no sugieren un efecto repelente consistente en las especies carnívoras u omnívoras, quienes responden a diferentes señales químicas o semioquímicas, comparadas con aquellas que repelen a los herbívoros. Sin embargo, nuestra revisión sugiere que el uso de un arreglo más complejo de olores de un depredador podría repeler a carnívoros más pequeños. En el segundo capítulo utilizamos *olor corporal completo* de perro maremma para analizar la densidad de abandono de alimento de los zorros en un sistema de ganadería extensiva en Isla Riesco en Magallanes. Efectivamente el olor a maremma reduce el consumo de alimento de los zorros. Este efecto estaría asociado a la amenaza por competencia que representaría la presencia del maremma para los zorros.

GENERAL ABSTRACT

Carnivores, because their large ranges of distribution and a high demand for protein in their diet, frequently come into conflict with livestock producers around the world, as cattle represent an abundant, easy-to-catch, and energy-efficient prey for carnivores. For this reason, carnivores have perhaps become the most severely threatened species by lethal control, making urgent the development of non-lethal control strategies that compensate in part for the loss of habitat for carnivores and facilitate their coexistence in anthropogenic environments with the human population. Primary repellents offer an easily accessible alternative, in mammals the repellents used for the longest time have been those directed to taste or smell. Based on the use of natural or artificial components, these repellents seek to generate signals that indicate to the animals that a food source is not palatable or there is an imminent risk close to them and therefore should avoid that food. In this context, in the first chapter we conducted a literature review to contextualize the use of primary repellents in mammals and particularly to analyze their effectiveness in carnivorous and omnivorous species. While repellents do have an effect on herbivores, the available antecedents do not suggest a consisting repellent effect on carnivorous or omnivorous species, which responding to different chemical or semiochemical signals, compared with those that repel herbivores. However, our review suggests that the use of a more complex arrangement of odors from a predator could repel small to medium carnivores. In the second chapter, we used full body odor of the Maremma dog to analyze the density of food abandonment of foxes in an extensive livestock system in Isla Riesco in Magallanes. Indeed, the smell of maremma reduces fox food consumption. This effect would be associated with the threat of competition that would represent the presence of the maremma for foxes.

GENERAL INTRODUCTION

A human-wildlife conflict occurs when the needs and behavior by either wildlife or humans has a negative impact on the other and ultimately generates conservation conflicts (Madden 2004; Redpath 2013). For example, predation of livestock by wild carnivores is a widespread problem and although losses to predators are usually small relative to the numbers held, in many cases they can account for a significant proportion of livestock mortality (Baker et al., 2008). In this context, the most immediate response to carnivore predation involves lethal control. Lethal control is frequently unselective and perceived losses seem to have no relation to predator abundance (Graham et al., 2005; McManus et al., 2015; Ripple et al., 2014; Treves et al., 2006; Treves et al., 2016).

Counterproductively, lethal control can lead to compensatory reproduction in carnivore populations, and when completely extirpated, the ecological vacancy of a given species could be filled in by other carnivores (Treves et al., 2016). The complexity of this scenario is that both, carnivores and livestock need protection (Shivik & Martin, 2000). In this sense, non-lethal managing techniques are an alternative that can reduce predation and be economically advantageous, for example a study in Easter Cape Province in South Africa shows that even when lethal methods are cheaper to implement, overall economic losses from predation are lower when farmers used non-lethal methods (McManus et al., 2015). Furthermore, non-lethal strategies, as virtual fences to control animal movement without creating a real physical barrier, has more social support than lethal control (Jachowski et al., 2014). However, the adoption of non-lethal techniques depends on both, proven efficacy and the willingness of producers and authorities to implement them in relation to their cost and availability (Baker et al., 2008). In the case of carnivores, the effectiveness of non-lethal strategies such as virtual fencing depends on the understanding of predator behavior associated with risk perception (Blackwell et al., 2016). Here we review the efficacy of primary odor and taste repellents intended to manipulate predatory activities and behavior in mammals. Then, we will use this background to experimentally test its usefulness in the context of extensive livestock farming in Isla Riesco, Magallanes.

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CHAPTER I

A REVIEW ON THE EFFECTS OF PRIMARY REPELLENTS USED TO REDUCE WILDLIFE HUMAN CONFLICTS WITH MAMMALS.

ABSTRACT

The use of primary repellents as a non-lethal managing tool for wildlife in conflict with human interests has been widely studied for herbivores, but not so much in the case of carnivore species. Primary repellents that target on olfactory and gustatory systems, do not require individual learning and are easy to access, their formulations are based on secondary metabolites of plant defense against herbivory, bitter taste substances, essential oils and sulfur compounds with strong nauseous smells, irritant components as capsaicin, blood and several predator odors as urine, feces and other secretions. Nevertheless, the repellency ratios which with animals respond to this repellents, differs significantly among herbivores and carnivores or omnivores. Herbivores seem to be negatively affected to some extent by all type of repellents altering their feeding behavior and movements, probably related to their evolutionary history with semiochemical cues as found in plant defenses and predator odors that are indicative of food quality and risk of predation. In the case of carnivores and omnivores, there is a negative repellency effect but the very few existing studies did not allow identifying which types of repellents were most relevant for this species. By all matters, ecological context and biologically meaningful olfactory and taste cues should be considered for the use and development of primary repellents. And in the case of carnivores there is still much research to do finding proper alternatives for primary repellents.

INTRODUCTION

The development of non-lethal strategies to manage human-wildlife conflicts is a challenge being addressed through the use of aversive or disruptive techniques, which rely on visual, auditory, taste and olfactory cues. Among these cues, chemical and semiochemical repellents have being used to induce fear, cause irritation or even sickness if they are ingested, altering feeding behavior or limiting the movement of target animals, aiming to reduce human-wildlife conflict produced by animal-vehicle collisions, crop damaging and livestock predation (Mason, 1998; Mason et al., 2001; Jachowski., 2014). Nevertheless, despite the potential to reduce human-wildlife conflicts, the effectiveness of chemical and semiochemical repellents has not always been tested to assess if they do reduce herbivory over crops, or predation upon livestock.

In general, two types of chemically-based repellents are available, and their action modes will vary according to the active ingredients of the formulation (Mason, 1998), their formulations can be based in plant metabolites and essential oils, animal waste and odors or other types such as sulfur components or chemicals with bitter or malodourous characteristics. Primary repellents provoke immediate aversion to the taste or odor, through sensory irritation or nuisance, either by direct contact or olfaction. No learning by the targeted species is required to be effective (Rogers et al., 1974; Mason, 1991, Coleman et al. 2006). Primary repellents can be based on chemicals or semiochemicals, which are odors that can mediate intra and inter-specific interactions, such as urine, anal secretions, feces, or sulfur odors, are often used to induce fear (Mason, 1998; Müller-Schwarze, 2006; Nielsen et al., 2015; Schulte, 2016). Herbivores in particular rely on semiochemicals as a cue for predation risk, preventing them from entering an area where they might find a predator (Mason, 1998; Nolte et al., 1994; Coleman et al., 2006). Secondary repellents on the other hand are based on chemical compounds that can generate learned aversion to a particular food, color or smell as the result of a post-ingestion effect causing discomfort or sickness (Rogers et al., 1974; Gill et al., 2000). In general, secondary repellents used to modify behavior on carnivores have only initial success and decreased effectiveness in the long term (Mason et al., 2001; Shivik, 2006, Smith et al, 2000; Nielsen et al., 2015). In the case of herbivores, a significant amount of damage to vegetation or crops can occur in the time it takes the animals to associate the malaise with the treated food (William & Short, 2014). Further, when alternative food sources are scarce or not especially palatable, herbivores and carnivores would still feed on the preferred food source even though it is treated with secondary repellents (Mason, 1998; El Hani & Conover, 1995; William & Short, 2014).

Regarding the efficacy of chemical and semiochemical primary repellents in wildlife management, there are mixed results among taste and odor repellent (Beauchamp, 1995; Mason, 1998; De Nicola et al., 2000; Smith et al., 2000; Mason et al., 2001; Coleman et al., 2006; Williams et al., 2006; Walter et al., 2010). Odor and irritating repellents seem to be effective in herbivores (Mason et al. 1998, Walter et al. 2010). Taste repellents based on secondary metabolites naturally occurring in plants for defense against browsing and grazing, like phenolics, alkanoids and terpenoids, would influence herbivores feeding behavior through bitter taste or toxic effects (Müller-Schwarze, 2006). Although some herbivores have developed metabolic defenses against secondary metabolites, these still reduce the feeding and probability of herbivory, hence helping to reduce the conflict with humans (Freeland & Janzen, 1974; Iason, 2005). In the case of repellents based on predator odor against prey species such as herbivores is expected they respond intensively with an innate fear reaction (Nolte et al., 1994; Apfelbach et al., 2015; Brown, 2010; Rosen et al., 2015).

In the case of carnivores, chemical repellents causing irritation by direct sniffing and tasting seem to be effective only until they dissipate and if the food source is completely impregnated (Mason, 2001). On the other hand, bitter and distasteful substances are expected to be good candidates for repellents, because they are associated with the immediate identification of unpalatable or toxic food, without involving previous experiences or learning (Beauchamp, 1995). Nevertheless, in the case of odor repellents based on predator urine, feces or sulfur odors coming from these wastes, showed no evidence of fear induction on carnivores, hence no repellent effect (Mason, 1998; Mason 2001). Probably because carnivores are often at the top of the food chain, and this olfactory stimuli might be dissociated from fear experiences, contrary to what happens with herbivores as prey species, so it is likely to be meaningless and therefore resulting in a poor repellent (Beauchamp, 1995). However, carnivores might actually fear to interfere with each other while hunting for the same prey, because they fear risk themselves to severe injuries or death if confrontation with conspecifics or other bigger carnivores occurs (Brown, 2010). In this sense, as mammalian signal odors mediating communication are complex mixtures of compounds of different volatilities (Gorman & Trowbridge, 1989) and only waste odors from predator urine or feces might not be enough as a cue to other carnivores. Studies with rats (Blanchard et al., 2001, Bytheway et al., 2013; Masini et al., 2005) suggest that a more complex arrangement of odors from a known predator specie, including cell skins, bacteria, fur, feces, urine, saliva and several glands secretions in one olfactory cue (whole body odor), could trigger a consistent avoidance or stress behavior, even in carnivores as the red fox (Leo et al. 2015).

In this context and despite the mixed results, there has been no empirical analysis of semiochemical or chemically based primary repellents comparing effectiveness among formulations, targeted sensory systems and if the target specie is a carnivore or herbivore. Here we review the existing publications on the subject and aim to compare their effect on terrestrial mammals to stablish an appropriate framework for the development of future semiochemical or chemically based primary repellents that serve as tools to reduce the human wildlife-conflict.

METHODS

We surveyed the Web of Science database using the keywords “repellent”, “deterrent”, “deter” and “repel”. We focused on terrestrial mammals and included publications dealing with the use or development of chemical or semiochemical primary repellents to deal with herbivore and carnivore mammals, excluding reviews and commentaries. First, as a measure of repellents efficacy, we collected all available empirical data measuring a) the amount of food consumed by target species exposed to a repellent, b) the number of trespassing events in an area treated with a repellent, and c) the approach distance to a repellent source or the time spent in a treated area, with a BACI approach, before and after a chemical or semiochemical repellent was applied.
Then weadded 0.1 to every value and calculated a repellency ratio between measures using the repellent over the control situation (repellent/control) and standardized it by using ln in order to avoid over dispersion (after Moreira-Arce et al. 2018):

$$\text{Repellency ratio} = \text{Ln}\left(\frac{\text{with repellent}}{\text{control}}\right)$$

If the ratio was zero there was not difference among compared feeding, time spent, movement or trespassing in areas treated with repellents, when the ratio is below cero the repellent has an effect reducing food consumption, movement, time spent or trespassing, and when the ratio is above 1 it had the opposite effect.

To analyze repellency effect, we first conducted a Kruskall-Wallis test for all terrestrial mammals, comparing the repellency ratio among repellents according to sensory system (taste, smell, irritant), strategy (antifeedant or biofencing) and formulation (plant-based, animal scent-based or other formulations) and we conducted Dunn's test as a post-hoc analysis. Then we compared the repellency ratio among herbivores and carnivores-omnivores. Finally, we performed a sign test to assess the significant effect of repellents specifically on carnivore-omnivore species comparing the observed ratio to zero (i.e. no effect).

RESULTS

We retrieved 80 publications that included quantitative information about the effect of chemical or semiochemical primary repellents up to march 2018 (Appendix 1). 85% of the studies focused on evaluating the effectiveness of repellents upon herbivore species and only 15% of them focused on carnivores or omnivores. Cervids, lagomorphs, rodents and macropods were the most frequently studied among herbivores while mustelids, boars, rats and canids among carnivores and omnivores. Regarding to the strategy of repellents, 73% of them were aimed as antifeedant and 27% were aimed to manipulate animal trespassing movement trough biofencing.

Values below 0 in Fig. 1 indicate that primary repellents do have a repellent effect in treated areas when considering all species of mammals. When analyzing the effect of all repellents upon carnivores-omnivores solely, we found that there is a negative effect different from 0 (S-statistic = 20, n = 55, p-value = 0.05). Comparing the effect of repellents among sensory systems, including odor repellents (n=278), taste repellents (n=52) and irritant repellents affecting both smell and taste (n=51), there was a significate difference (H=11.7, p-value < 0.05) with taste repellents being 1.5 times more repellent than irritant repellents (z=2.54, p-value < 0.05) and 1.1 times more repellent than odor repellents (z=2.55, p-value < 0.05). There are also significate differences on the effects of the repellents according to formulations, including animal based (n=89), plant based (n=160) and other formulations (n=114) (H=11.27, p-value < 0.05), with animal scent-based (z=-2.51, p-value <0.05) and plant based (z=3.19, p-value < 0.05) having almost twice the repellent effect of repellents with other formulations. In relation with the strategy of the repellents, antifeedant (n = 274) were over two times more repellent than biofence repellents (n = 97) repellents (H = 5.94, p-value < 0.05). All repellents regardless the target sensory system, formulation or strategy they used, do reduce food consumption, movement, time spent or trespassing of animals, but overall plant-based and antifeedant repellents seem to be the most effective ones on mammals.

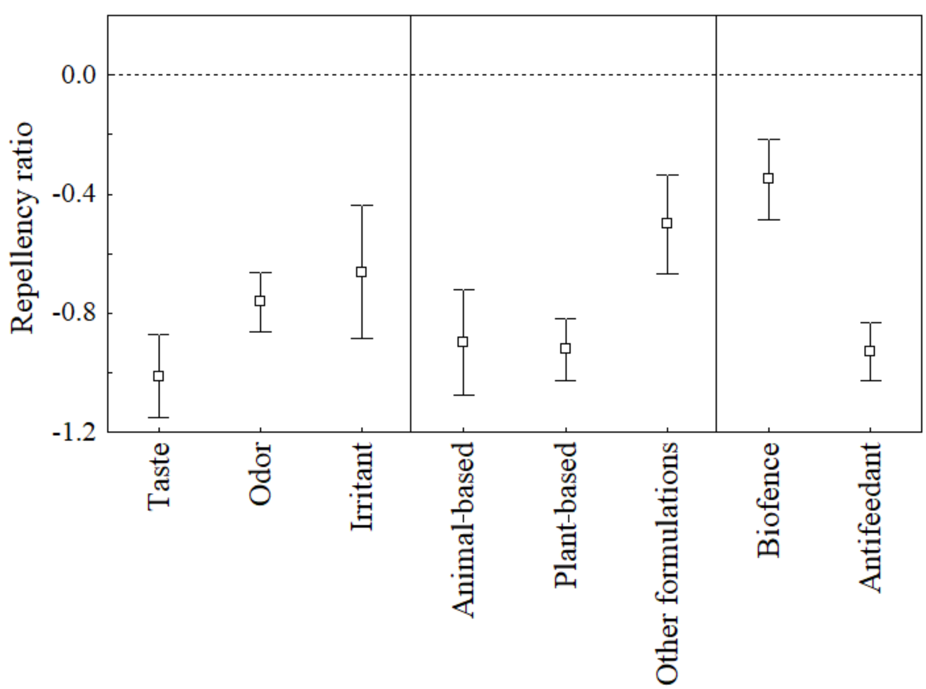

Figure 1. Repellency ratio of primary repellents in all mammal species, according to target sensory system (Taste, Odor or Irritant), formulation (Animal scent-based, Plant-based or Other formulations) and strategy (Biofence or Antifeedant). Figures are mean ± one standard error.

But when comparing the effects of the different repellents among carnivores-omnivores, there was no negative effect of repellency in any of them. Possibly, due to the small sample size when we separate repellents by target sensory system, formulation or strategy. On the contrary, herbivores seem to be deter by all types of repellents (S-statistic = 35, n = 316, p-value < 0.05).

On the other hand, comparisons of the effects of repellents among herbivores and carnivores-omnivores (Fig.2) we found a significant difference among the repellency ratios, with the effect odor repellents on herbivores being over 40 times more than the repellent effect on carnivore-omnivores (H=16.42, p-value <0.05). The repellent effect of animal based repellents on herbivores (Fig. 3) is close to 3 times more than the repellent effect on carnivore-omnivores (H= 9.46, p-value <0.05), while plant based repellents on herbivores are near 14 times more repellent than on carnivore-omnivore species (H=11, p-value <0.05).

In the case of biofence repellents (Fig. 4), they are up to 4 times more effective on herbivores than carnivores-omnivores (H= 9.68, p-value <0.05) and antifeedant repellents are twice more effective on herbivores than carnivore-omnivores (H=7.76, p-value <0.05). No differences in the repellency ratio among herbivores and carnivores-omnivores were found for taste repellents (H=2.60, p-value=0.11), irritant repellents H=3.43, p-value=0.06) and repellents of other formulations (H=1.64, p-value=0.20).

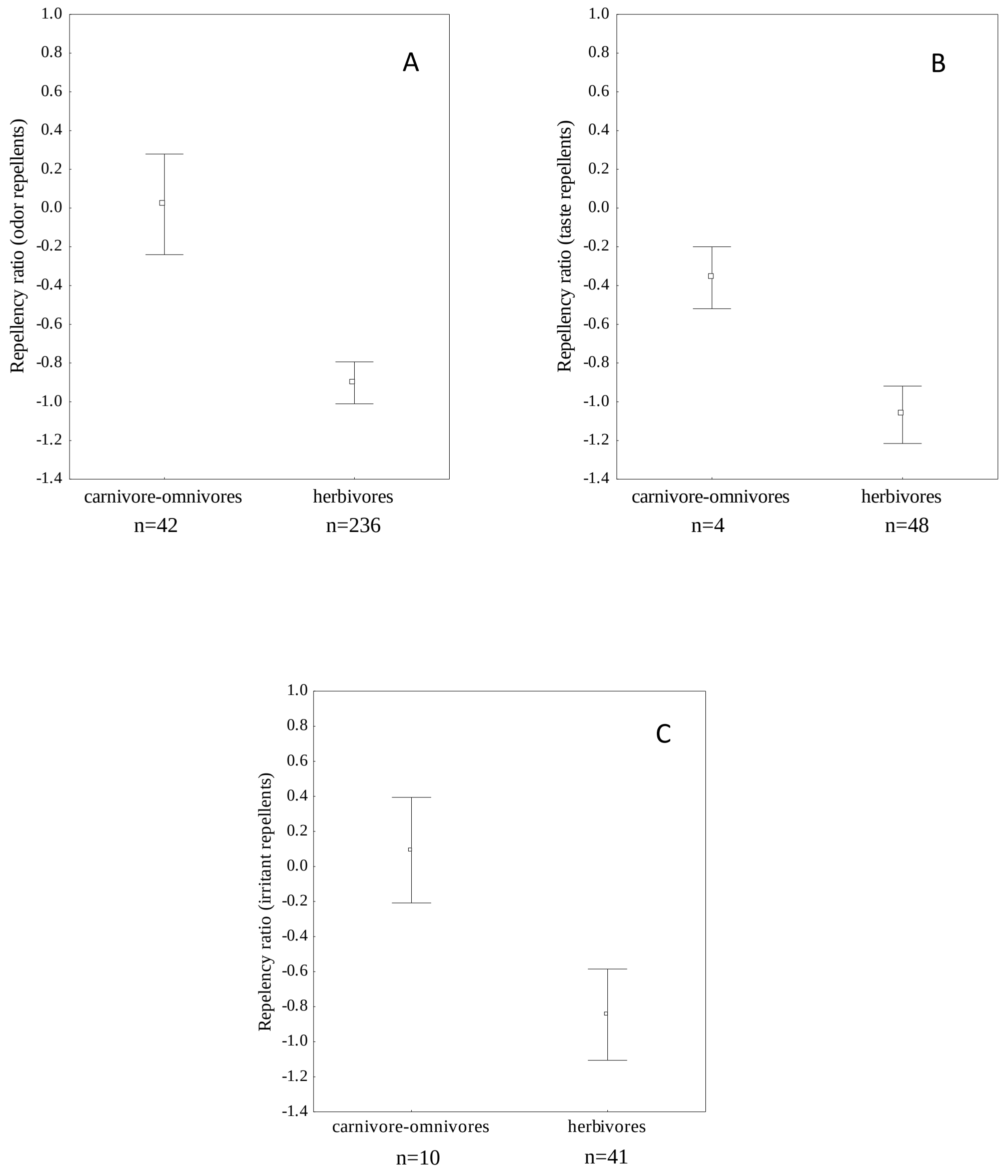

Figure 2. Comparison among herbivores and carnivores, of the repellency ratio of primary repellents according to affected sensory system. Odor repellents (A), taste repellents (B) and irritant repellents (C). Figures are mean ± one standard error.

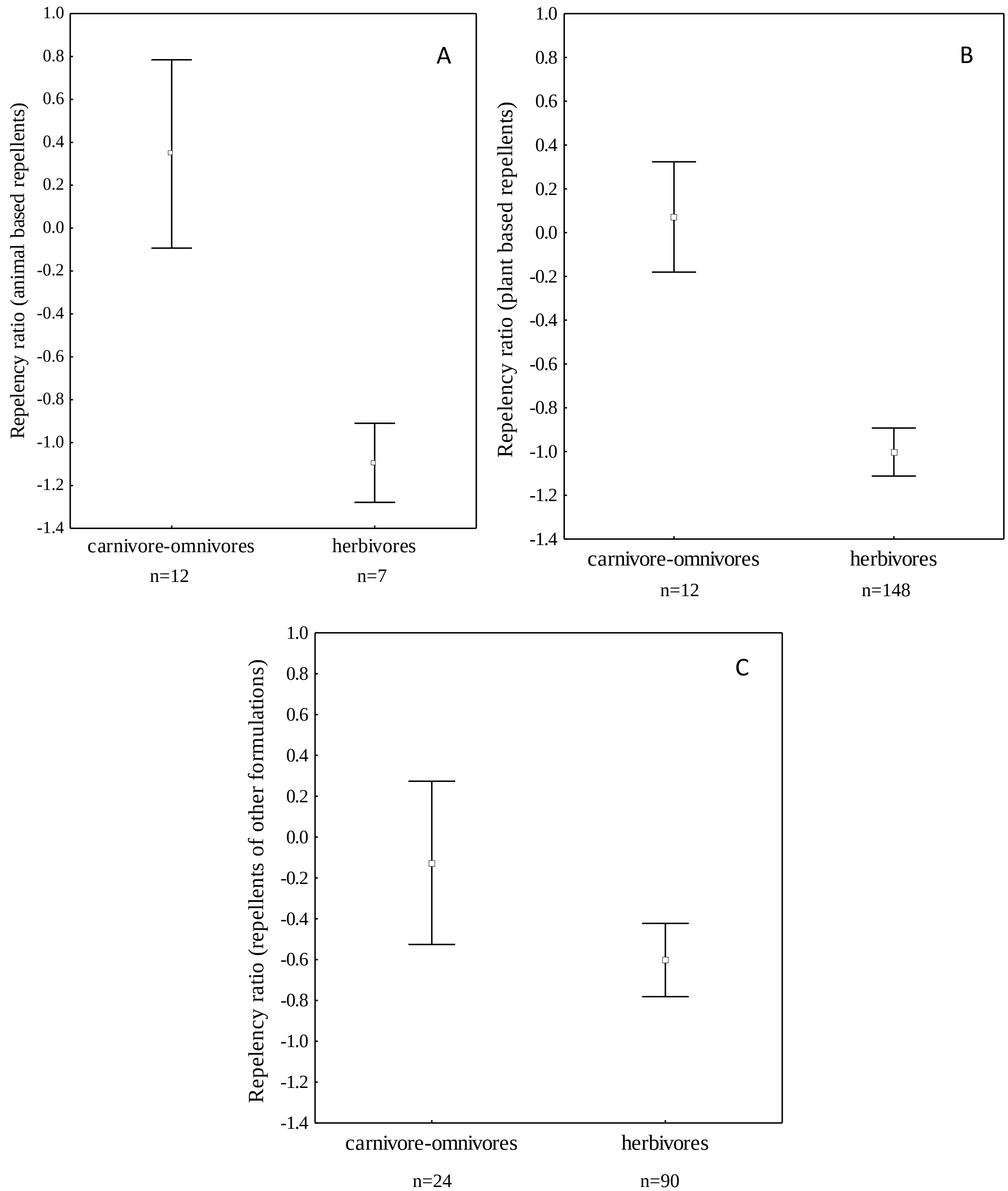

Figure3. Comparison among herbivores and carnivores, of the repellency ratio of primary repellents according to type of formulation. Animal based repellents (A), plant based repellents (B) and other types of formulations (C). Figures are mean ± one standard error.

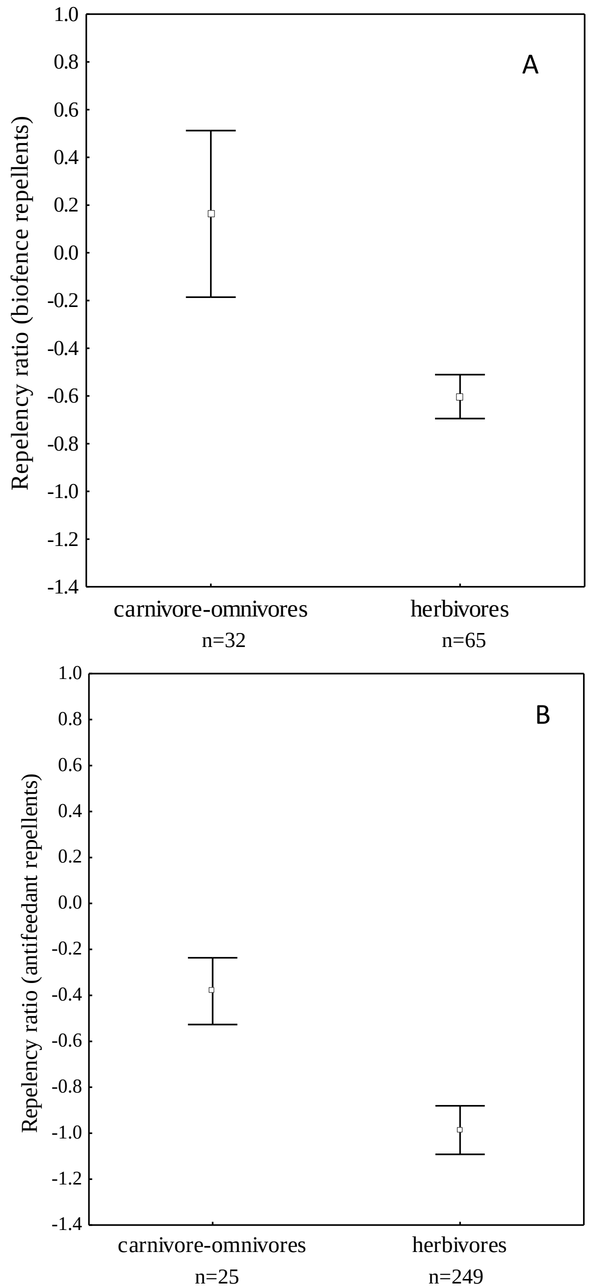

Figure 4. Comparison among herbivores and carnivores, of the repellency ratio of primary repellents according to the repellent's strategy. Biofencing repellents (A), antifeedant repellents (B). Figures are mean ± one standard error.

DISCUSSION

Chemical and semiochemical primary repellents have a consistent negative effect on herbivores food consumption, trespassing and approaching; on the contrary, this repellent effect is not the same in carnivore-omnivore species. In the case of antifeedant repellents, they seem to be effective for carnivore and herbivore species, formulations can include secondary metabolites, essential oils, capsaicin derivatives, blood, sulfurous or predator odors and bitter agents, by themselves or in mixtures, aiming to discourage food consumption either by taste, smell or irritation; but there is a significate less among of studies in carnivore species. In general, plant-based repellent were the most frequently used repellents among the reviewed studies and they are mostly based in the use of secondary metabolites and essential oils to deter feeding trough smell, taste or irritation, but mainly in herbivores. Secondary metabolites of plants can affect mammals in several ways, such as toxicants reducing digestibility or altering the quality of plants as food and in consequence modifying foraging behavior of animals (Iason, 2005). Aversion linked to taste in herbivores has been developed in the evolutionary time to cope with secondary metabolites, and it does not require individual learning to avoid food (Müller-Schwarze, 2006). In fact when comparing to carnivores, herbivores have much more aversive taste receptor, possibly due to the variety of plant defenses they face (Lunceford & Kubanek, 2015).

In the case of animal scent-based repellents, they are mostly aimed to deter herbivores, the formulations include feces, urine or gland secretions from predator species, odor cues for which herbivores essential response is avoidance (Apfelbach et al., 2005, Canteras et al., 2015). Prey species have developed a very low odor threshold in order to identify and avoid volatile sulfur compounds or thiols found in rancid food and carnivore excretions (Li et al., 2016). Blood also has an evolutionarily conserved chemosignal identified as E2D, which triggers avoidance in herbivore species but has a luring effect on carnivores (Arshamian et al., 2017). In this sense, such an innate avoidance response of herbivores to all these odor cues conveys that the use of scent based repellents reduce the likelihood of conflict with humans. But in the case of carnivores and omnivores, there is no such evolutionary story of repellency with cues like secondary plant metabolites, blood, sulfurous or predator odors, which has made very difficult to find a proper cue to trigger food or spatial avoidance in these species, especially trough olfaction.

In the human-wildlife conflict with predator species, biofence repellents would be a particularly useful tool to discourage carnivores from approaching to areas where they would be in conflict with humans, reducing the chances of encountering and preying livestock. But so far in the reviewed studies, biofence repellents seem not to be effective for carnivores, probably due to the fact that the composition of repellents used is mostly based in scents to which herbivores respond because there is biological meaning on them, but they have no biological meaning for carnivores. Only one field study (Leo et al., 2015) resulted in reduced food consumption of red foxes (*Vulpes vulpes*), using dingo (*Canis lupus dingo*) "whole body odor" as more complex arrangement of odors including urine, feces, skin cells, hair and glandular secretions, which will have biological meaning to red fox, a smaller carnivore that sometimes is predated by dingo. In this sense, this odor cue would be an appropriated signal of the presence and not only wastes of a bigger known predator indicating risk of injury or death by predation or competition to smaller predators (Brown, 2010; Leo et al., 2015).

Overall, is important to consider that chemical and semiochemical signals as deterrents would only gain meaning according to the previous experience, the evolutionary and natural history of the recipient and the environmental context in which they are located in the development of any primary repellent (Thiessen & Rice, 1976; Beauchamp, 1995; Griffin et al., 2001). In this review we focused on taste and olfactory systems, but the same principle should also apply to visual and auditory cues if they are aimed to be used as non-lethal strategies to manage wildlife conflicts, as all cues must have biological meaning to the target animals in order to generate the needed avoidance response that will make of these non-lethal strategies an effective alternative to wildlife retaliation.

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CHAPTER II

WHOLE BODY ODOR OF LIVESTOCK GUARDIAN DOG DISCOURAGES FOOD CONSUMPTION BY FOXES IN AN EXTENSIVE LIVESTOCK FARMING HABITAT IN THE SOUTH OF CHILE.

ABSTRACT

When native predators prey on livestock, a conflict occurs that results in a significant economic loss. A practice widely used to counteract these losses, is the use of livestock guardian dogs. However, the mechanism by which these dogs manage to deter native predators is poorly understood. In this chapter we perform a field study in Isla Riesco from the Magallanes Region in the Chilean Patagonia, deepening in this deterring mechanism to try to establish if these dogs are perceived as a threat by smaller native predators such as culpeo and gray foxes. For this we evaluated if the livestock guardian dog's whole body odor clue, represents a biologically meaningful cue of their presence to foxes, allow them to assess risk and determine whether the intrusion in the dog's territory to prey on the livestock, exceeds or not the cost of being seriously injured. On the other hand citronella oil, which is frequently used in several repellents formulations, was used as an olfactory cue with no biological meaning. Overall the livestock guardian dog whole body odor clue had a negative effect on fox's food consumption, meaning they were willing to abandon more food in the presence of this odor, while citronella oil had no effect. Horizontal and vertical vegetation cover also influenced food consumption and horizontal cover particularly had a negative effect on fox presence in the experimental stations. We conclude that the complex odor arrangement of the livestock guardian dog cue and the vegetation cover are useful tools for the carnivore-livestock conflict management.

INTRODUCTION

One of the oldest and most frequent conflicts in the world occurs between humans, their livestock and wild carnivores. Given their protein-rich diet and wide ranges of distribution, wild carnivores frequently prey on domestic livestock (Treves & Karanth, 2003). Lethal control of carnivores is the first and most commonly used resource to protect livestock from carnivores regardless its low effectivity (Treves & Karanth, 2003; Moreira-Arce et al., 2018). Currently at least 30% of terrestrial carnivores are threatened by retaliation (Moreira-Arce et al., in press). In fact, retaliatory persecution has led to a decline in carnivore populations, threatening them with local extinctions (Ripple et al., 2014). On the other hand, alternative non-lethal practices, instead of eliminating predators, seek to reduce the problem altering the predatory behavior of carnivores, through olfactory and taste repellents, sound and visual deterrent devices, conditioning to aversive stimuli, and the use of livestock guardian dogs (Shivik, 2006).

The use of different breeds of dogs as protectors of livestock reduces the number of livestock losses and attacks perceived by farmers on their herds (Rigg, 2001; Eklund et al., 2017). The mechanism by which livestock guardian dogs effectively protect the herd is yet poorly understood, but livestock guardian dogs do interrupt the hunting behavior of native predators, diverting the attack when approaching to livestock (Coppinger et al., 1988). The reduction in livestock losses despite the presence of predators is expected to change the attitude towards the management of wild carnivores and also reduce hunting as a mean of control, allowing the coexistence of native predators in productive systems surroundings.

In grazing areas, dogs would represent a large predator, whose presence might modify the local distribution and behavior of smaller predators, like foxes (van Bommel & Johnson, 2016). In this context, it is assumed that when a carnivore, and particularly solitary ones, have to face a larger carnivore, runs the risk of suffering serious injuries, which might affect its ability to hunt, increasing the risk of starvation and reducing its chances of survival (Brown, 2010). Therefore carnivores, should avoid confronting livestock guardian dog. Understanding the behavioral mechanisms underlying this interaction provides information that could be translated into a management tool, identifying which sensory abilities would allow a native carnivore to avoid or move away from areas of potential danger, thereby reducing both the likelihood of predation and conflict (Greggor et al., 2016).

The use of primary odor repellents is another non-lethal alternative, accessible and frequently use for managing foxes and dogs in rural and urban areas. Smell based repellents using urine or ammonium (like "Predator Pee" ®, "Coyote Mist" ®, "Yard Cover" ® and "Scoot Fox Repellent" ® among others), aim to create an artificial territorial barrier simulating the presence of a bigger carnivore be it hetero or conspecific, through an olfactory cue. Another type of smell-based repellents use nauseating odors intended to distract or confuse individuals, disabling them to perform an appropriate risk assessment, forcing them to leave the area in the face of uncertainty. For example "Get Off My Garden" ®, widely recommended in the UK, is based in citronella oil, that has a high content of citronellol, a terpenoid that would cause intense discomfort in dogs when they smell it (Huebner & Morton, 1964; Baser & Buchbauer, 2015). In the case of citronella oil empirical studies suggesting is avoided to some extent by wolverines (Landa & Tømmerås, 1997) and increase risk assessment behavior in mice (Kemble & Gibson, 1992; Garbe et al., 1994; Kemble & Bolwahnn, 1997).

Evidence of carnivores avoiding areas or food with urine or feces from another carnivore is variable (Masini et al., 2005; Shivik et al., 2011). In fact, these excretions might not be the best cue of the presence of a large predator (Mason, 1998; 2001), and could be perceived only as waste produced by the occasional passage of an individual and not necessarily as intentional territorial marks which would evidence a constant presence of the predator in the area (Leo et al., 2015).

Nevertheless, other odor cues would generate a stronger behavioral and physiological stress response. For example rats, which are omnivorous s that frequently prey on birds, reptiles and smaller mammals, when exposed to skin odors from a bigger predator such as a cat, ferret or dog, abandon more food, increased their defensive behavior and activate hormonal and neural responses to stress, but didn't respond in the same way to waste odors like feces or urine from the same predator species (Blanchard et al., 2001; Masini et al., 2005). A more recent study on red fox (*Vulpes vulpes*) used "whole body odor", a complex odor arrangement from urine, feces, skin cells, hair and glandular secretions, from a natural predator such as dingo (*Canis lupus dingo*) and conspecifics; Foxes abandoned higher amounts of food in the presence of the dingo odor (Leo et al., 2015).

This could mean that to elicit an aversive response in omnivores and carnivores, a more complex and biologically meaningful arrangement of odors is required instead of only single excretion odors, providing much more information that can be encoded by the receiver of the signal (Gorman & Trowbridge, 1989; Nolte et al., 1994; Apfelbach, 2015). Such a complex odor cue would represent more realistically the presence of a carnivore, hence an imminent threat by proximity (Leo et al., 2015). In such conditions, smaller animals should reduce foraging times, increase surveillance time and eventually abandon a food patch to reduce the risk of being preyed or injured, even when food is available and accessible (Lima & Dill, 1990).

Food abandonment occurs when the energy reward is less than the cost of being injured or preyed. The density of abandoned food or giving up density (GUD) represents a quantitatively, empirically-supported tool to evaluate the compromises between foraging and the risk of predation (Brown, 1988; Brown & Kotler, 2004; Verdolin, 2006).

On the other hand, habitat characteristics can also influence an animal's perceived predation risks affecting its foraging behavior (Verdolin, 2006). Vegetation cover affects visibility and olfactory communication among terrestrial animals. Stationary objects like trees may generate fluctuations in air velocity causing turbulences that will modify air currents, affect flow patterns and even odor concentration (Muller-Schwarze, 2006). A major advantage is that olfactory signals can work in darkness, around obstacles and depending on the odor volatiles composition and climate, may last from seconds to months. Therefore, olfactory signals enable animals to communicate with others still in its absence (Muller-Schwarze, 2006; Apfelbach et al. 2015)
In this sense, managing wild carnivores with scent based repellents as a non-lethal strategy, needs to consider ecological aspects as animal behavior, the complexity of the odor cue and the habitat characteristics, if is intended to work as a biofencing strategy to discourage carnivores approaching and passaging through areas where livestock graze or give birth.

Chilean Patagonia is a prime sheep producer region, accounting for 57% of the total national sheep production, generating 80% of sheep meat at national level (ODEPA 2018). In this region, 42% of the livestock ranches are affected by predation upon lambs by Puma (*Puma concolor*), South American Gray Foxe (*Lycalopex griseus*) and Andean Fox (*Lycalopex culpaeus*). Foxes alone are responsible for sheep deaths in at least 54% of farms (INE 2017); which translates into a significant economic loss at a regional scale to which many farmers respond in the first instance with lethal control, and a few producers have implemented the use of livestock guardian dogs of the Maremma breed.

An adult healthy male Maremma can weight up to 45 kilograms, while the biggest culpeo foxes weight up to 13 kilograms, and gray foxes only 5 kilograms as a maximum. This difference creates a disadvantage to native foxes when facing the Maremma dog, with a high risk of being severely injured or killed in a confrontation due to their small sizes. In this scenario, we would expect that the whole body odor of Maremma dogs could reinforce the cues for risks triggering a landscape of fear for culpeo and gray foxes, which ought to modify their local distribution and behavior, hence reducing options of attacks on livestock and reducing the conflict, facilitating their coexistence (Crespín & Simonetti, 2018). To test this hypothesis, we conducted a field experiment in a livestock farm in Isla Riesco, Andean Patagonia. We aimed to assess the repellent effect of the whole body odor of livestock guardian dogs as a non-lethal strategy to manage native foxes.

We selected a local producer that has been using Maremma sheep dog to protect their livestock, this way the foxes would have previous experience encountering the dog; on the other hand, we used citronella oil, a nauseating odor, as another repellent alternative. If these odors are perceived as meaningful signals we expect a significant effect increasing GUD (reduced food consumption) and altering behavior (foraging, vigilance, walking, marking and exploring). Habitat characteristic was considered through vegetation cover, as a covariate to odor treatments that could impact the transmission of the odor cue to the foxes.

METHODS

Study site.

The study was carried out during May 2017 at Anita Beatriz sheep farm, Isla Riesco, Region of Magallanes. At this ranch, like others in the region, *L. culpaeus* and *L. griseus*, do prey on sheep, and Maremma livestock guardian dogs are being used to protect livestock with positive results perceived by farmers.

Olfactory treatments.

To obtain the olfactory cue corresponding to the whole body odor of maremma sheep dog, we follow the methodology described by Leo et al. (2015) and Bytheway et al. (2013), which consists of using white cotton towels of 700 gr/cm^2 that were left for a month in the resting place of a set of maremma dogs, allowing the towels to be impregnated with skin oils, dandruff, sweat, saliva, anal excretions, remains of urine and feces. Then, towels were stored in airtight bags at -20 ° C until their use in the field. We used citronella oil (*Cymbopogon winteranius*) as a second olfactory treatment. This essence was sprayed on white cotton towels and subjected to the same treatment previous to store them until their use in the field. Control treatment consists of clean towels of the same material and stored in the same way. In the field, we stablish 9 experimental stations 400 m apart. At each station, towel pieces of 12 x 12 cm were placed inside a white plastic dispenser with holes in the base and adhered to a 60 cm wood pole, one pole placed in each cardinal point of the station, 5 meters away from a central container with food. We used only one odor treatment per station and they were randomly assigned every day, with 3 replicates for each treatment including controls. All experimental stations remained without olfactory cues and free food access during the first 48 hours to allow the habituation of foxes, as there is evidence of neophobic behavior in *Lycalopex* (Travaini et al., 2013). On the third day, towels with the odor treatments were placed, no station got the same treatment two nights in a row to avoid spatial habituation. A trap camera was placed pointing to each food container to record the visit of foxes during 24 hrs.

Food consumption and habitat characteristics.

As an experimental approach to measure the repellency effect of odor treatments, we establish foxes giving up density (GUD) in presence of citronella oil, maremma whole body odor and controls. For this, each experimental station had a food source (plastic container staked to the ground) containing 500 g (646 pellets) of Pro Plan® adult food Medium breeds, which corresponds to twice the suggested portion for wild animals, presuming they could have a greater energy expenditure than that of domestic animals. Food was renewed daily for a total of 6 days; during that period food left behind on the previous night in each station was collected, counting the number of remaining pellets to stablish GUD.

To assess if habitat characteristics could influence the repellency effect of odor treatments, we used vegetation cover as an approximation. We measured the horizontal vegetation cover surrounding each experimental station around the food container and we estimated the total cover by shrubs and trees. For the vertical cover, a rod of 3 meters high was placed every one meter along the 5 meters of the tape (in the 4 cardinal points) and then measured the height of the vegetation touching the rod in centimeters.

Statistical analysis for fox presence and food consumption.

We used Kruskal-Wallis test to stablish if there were differences in the presence of foxes associated to odor treatments, which we consider as the number of times a fox was seen on camera trap with at least 30 minutes apart. Then we used GLM with binomial distribution to stablish if the vegetation cover had any effect on the fox presence in the experimental stations.

To test if there was a repellency effect from maremma whole body odor or citronella oil reducing the number of pellets consumed by foxes compared to the control, we used the count of the number of pellets consumed as an approximation of GUD and zero-inflated Poisson (ZIP) models to include all 9 stations. We used the number of pellets eaten by foxes as the dependent variable, the fixed effect was the odor treatment (control, citronella oil, livestock guardian dog), and horizontal and vertical vegetation covers were included as covariates. Finally multi-model inference was used to assess the most plausible model explaining the change in food consumption.

Fox behavior.

Based on Leo et al. (2015), we used the video recordings of fox visits to analyze the effect of odor treatments in the foraging behavior and risk assessment behavior of foxes. We constructed an ethogram (Table 1) and used it to analyzed all videos with fox presence with JWatcher software (Blumstein & Daniel, 2007) were all scored behaviors were treated as mutually exclusive as suggested by Blumstein & Daniel (2007), data was extracted as the mean proportion of time in sight an individual allocated to each behavior.

PCA analysis was used to select the number of variables that explained most of the variation. Finally, we used Kruskal-Wallis stablish differences in foraging and risk assessment behavior between odor treatments. All analyses were conducted in the computer program R (R Development Core Team 2013).

Table 1. Ethogram set up to score the behavior of culpeo and gray foxes, based on Leo et al. (2015)

Behavior	Description
Walking	Moving on for legs (without considering the speed)
Foraging	Head down eating directly from the food container or the ground
Vigilance	Still, head up, ears pricked, looking, sniffing the air and/or looking
Exploring	Still, head down sniffing the food or ground
Exploring the signal	Head up, sniffing towards the signal or directly on it
Marking	Urinating or rubbing on the food container

For ethical reasons, this study was carried out in areas within the farm where sheep were recently excluded, to avoid attracting predators to sectors being used by sheep during the trial.

RESULTS

Fox presence.

Foxes visited stations regardless of odor treatments, but when incorporating vegetal cover, horizontal vegetation cover had a significant negative effect on fox presence at the experimental stations (Table 2, Figure 1).

Table 2: Model selection for the presence of foxes. GLM are ranked in ascending order based on AICc values; there are also reported the values for parameters K, log-likelihood values (logLik), AICc differences (Δi) and Akaike weights (Wi).

Model	K	logLik	AICc	Δ AICc	W_i
horizontal cover	2	-38.57	81.32	0.000	0.674
vertical cover + horizontal cover	3	-38.57	83.49	2.171	0.228
vertical cover	2	-41.02	86.21	4.884	0.059
odor treatment + vertical cover + horizonta cover	5	-38.46	87.82	6.502	0.026
odor treatment	3	-41.43	89.20	7.882	0.013

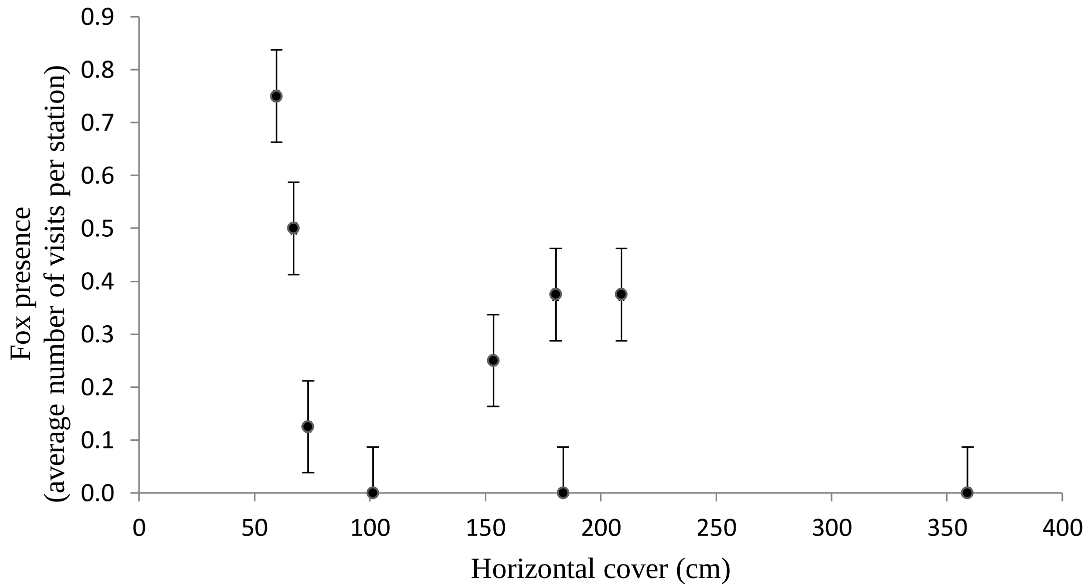

Figure 1. Fox presence in relation to horizontal cover vegetation. Average visits to an experimental station decrease as horizontal vegetal cover increases.

Food consumption in response to odors treatments and vegetation cover.

Overall, average food consumption was lower in stations with maremma whole body odor (Figure 2). The most parsimonious ZIP model, included odor treatments and vegetation cover (Table 3). Maremma whole body odor as well as horizontal cover had both significant and negative effects on food consumption by foxes. On the contrary, vertical cover had a positive effect on reducing food consumption, and citronella oil had no repellent effect at all.

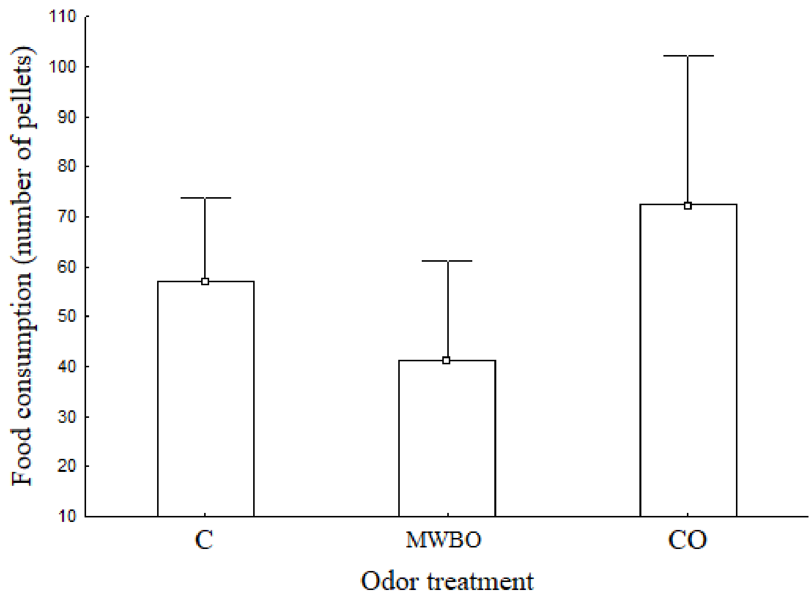

Figure 2. Food consumption in odor treatments. Control (C), maremma whole body odor (WBO) and citronella oil (CO) (n=18 counts). Mean food consumption and ± one standard error.

Table 3. Model selection for the food consumption by foxes. ZIP are ranked in ascending order based on AICc values; there are also reported the values for parameters K, log-likelihood values (logLik), AICc differences (Δi) and Akaike weights (Wi).

Model	K	logLik	AICc	Δ AICc	W_i
odor treatment + horizontal cover + vertical cover	10	-199.45	423.14	0.000	1
odor treatment + horizontal cover	8	-325.52	669.70	246.566	0
odor treatment + vertical cover	8	-380.63	779.93	356.794	0
odor treatment	6	-447.97	909.44	486.302	0

Fox behavior.

We selected 19 videos for the behavioral analysis. These videos registered the behavior of at least 6 different individuals of *L. griseus* and 3 from *L. culpaeus*. Foraging behavior had the most importance contribution to the first principal component (PC1), which explained 53% of the variance, while vigilance behavior had the most important contribution to the second principal component (PC2), which explained 38% of the variance. Together PC1 and PC2 accounted for 91% of total variance. On the other hand, walking behavior was second in importance in both axes and had a negative correlation to PC2. However, there are no significant differences in the proportion of time allocated to vigilance, foraging and walking behavior among odor treatment or vegetation cover.

Nevertheless, despite marking behavior had little contribution to PC1 and PC2, this behavior was recorded over food containers from two different culpeo foxes at two separate stations on different days and time, exclusively under the maremma whole body odor treatment, which could indicate competition between foxes and maremma dogs.

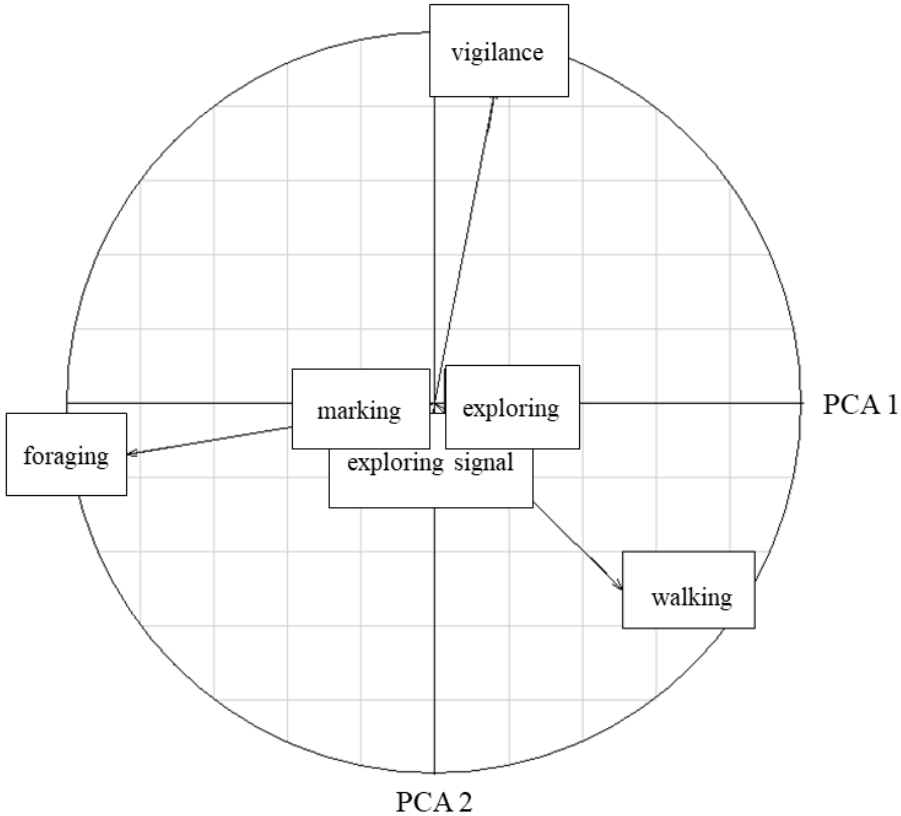

Figure 3. Principal component analysis for behavioral variables. PC1 explains 53 % of variance and PC 2 explains 38% of variance. Foraging, vigilance and walking had the most important contribution.

DISCUSSION

Non-lethal managing techniques are imperatives to allow coexisting with wild carnivores and mitigate the human-wildlife conflict (Blackwell et al., 2016; Shivik, 2006). In this sense, maremma whole body odor, has a repellent effect and reduces food consumption by foxes, suggesting that foxes could recognize the scent as a threat. Therefore, this odor would have a biological meaning, acting as an indicator of habitat quality to foxes, because the risk of confrontation overcomes the reward of the available food and could incite the avoidance of the area (Brown & Kotler, 2004). On the other hand, citronella oil having no effect on food consumption would indicate that is not provoking the presumed nauseating effect on foxes and in consequence is not disabling them to do a proper risk assessment.

Compounds secreted by predators are most likely detected by the vomeronasal system, and odors that contribute with scarce biological information as might be the citronella oil, would be most likely detected by the main olfactory system. This way both odor cues are perceived in different structures and would send signals to different parts of the brain (Wyatt, 2003; Muller-Schwarze, 2006; Sbarbati & Osculati, 2006; Rosen et al., 2015). Hence it seems there is no reason why these two different cues could provoke a similar repellent effect on foraging and behavior. Therefore the nauseating odor like citronella oil might not be a biofencing against foxes.

Along with the type of odor signal, the environmental context is important for its effect (Thiessen & Rice, 1976; Muller-Schwarze, 2006; McEvoy et al., 2008). In a first instance, vegetation cover would be explaining fox presence at the experimental stations, because those stations with more horizontal cover had less visits from foxes. But once that foxes arrived to a station, along with the maremma whole body odor treatment influencing food consumption, vegetation also plays a part. Horizontal and vertical vegetation cover had opposed effects on food consumption, the more horizontal cover the less the foxes eat, but the more vertical cover the more foxes eat. Horizontal cover could be favoring the repellent effect of the maremma whole body odor by preventing the fox from seeing the approaching, making riskier to stay. Instead, when facing tall trees but less or no bushes, even doe the fox can smell the dog, it can also see if it is really near or not. Besides, dense horizontal cover might be generating turbulent air currents which can disperse the smell within the surroundings and not necessarily take the smell far away from the area where its needed, as it happens with laminar air flows in a scattered group of trees (Muller-Schwarze, 2006). On the other hand, despite we intended to avoid habituation by renewing and periodically moving the olfactory signals, in natural environments habituation might be caused rather by aging olfactory cues (Apfelbach et al. 2015). Nevertheless due to climate conditions of Isla Riesco with low temperatures, hence low vapor pressures, would help decrease compounds evaporation and aging of the odor cue, therefore reducing the chances of odor loss (Muller-Schwarze, 2006; Apfelbach et al. 2015).

Regarding behavior, as expected, vigilance and foraging were the most important behavioral variables we could identify. But we weren't able to find any effects of odor treatments or vegetation cover on these variables, possibly due to sample size. However, marking behavior did occur probably as a result of the presence of maremma whole body odor treatment. One fox neck rubbing on the food container and another individual urinated on the food container from a different station on different days. This behavior might be indicating a potential competition between foxes and the livestock guardian dog, the maremma dog in Isla Riesco probably interfering with native foxes who might perceive maremma as a bigger threatening competitor with which confrontation should be avoided (Hugie & Dill, 1994; Brown & Kotler, 2004; Brown, 2010). Another field study found evidence of spatial and temporal avoidance of maremma dog from red foxes (*Vulpes vulpes*), in which there was a low probability of finding both species at the same site and within a same period of time (van Bommel & Johnson, 2016). In this sense, results support that the risk of encountering and confronting a bigger competitor and possible predator would play an important role in habitat selection for mesocarnivores

On the other hand, for ethical reasons, the implementation of this first experimental study could not put in risk any sheep by attracting foxes with food near the pasturelands with sheep or in calving season. Future studies should test if the maremma whole body odor effect is replicable in different seasons due to changing environmental conditions as wind intensity, temperature and humidity could influence odor dispersion.

Effective scent-based repellents must be specific for carnivores, the odor cue must have biological meaning to the target species and its use should contemplate the local context along with habitat characteristics. Therefore the use of the repellency effect of the maremma whole body odor cue to play with the expectations of risk on foxes must consider the influence of habitat configuration in order to generate the effect of a riskier habitat to foxes and trigger avoidance, because odor dispersion can be influenced by changes in the air currents provoked by vegetation cover. These two aspects, repellent and vegetation cover, are useful and complementary tools to the use of livestock guardian dogs on the task of mitigating the human-wildlife conflict.

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GENERAL DISCUSSION

In the human-wildlife conflict, the development of an effective biofence strategy could be a useful alternative to lethal-control strategies. To be effective, scent based repellents need to be appropriate in an ecological context and consider natural history of target species, their behavior and habitat characteristics of the species involved. Regarding the possibilities to use odor cues to avoid carnivore-livestock conflicts, carnivores would respond to cues indicating the presence of other bigger carnivores that might injure or kill them in a confrontation, hence avoiding the areas where they perceive the scent to escape from the risk.

Maremma whole body odor used as an olfactory primary repellent negatively affects food consumption in native foxes. The used of this odor might reinforce previous experience of native foxes with the maremma dog, which provides a biological meaning to the odor cue and would enhance the dog's presence effect. In this sense, foxes don't need to learn to avoid the cue because they have interacted with the dog in previous occasions, instead whole body odor plays with the expectations of foxes from encountering the dog, foxes don't know if maremma dog is close or not, but the risk of a confrontation with the maremma dog is a real possibility.

Habitat characteristics has an important role in repellents effect, whole body odor from maremma could increase risk perception in areas with more horizontal cover, because this vegetation obstructs the visual field, a fox can smell the dog but it would not be able to anticipate dog's approaching, playing with its expectations of confrontation.

Therefore, the use of maremma whole body odor in the proper environmental context might work as a deterrent for foxes. Studies on a larger spatial and temporal scale would be helpful to determine if maremma whole body odor could be used to reduce attacks on livestock and therefore the conflict with native carnivores, allowing the coexistence with wild species in a more sustainable scenario.

APPENDIX 1: PRIMARY REPELLENTS USED TO REDUCE WILDLIFE-HUMAN CONFLICTS WITH MAMMALS.

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