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Foraging theory provides a useful framework for livestock predation management.

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Abstract

A societal shift toward plant dominant diets and a reduction in livestock rearing could have broad social, environmental and conservation benefits. Livestock husbandry, however, has a wealthy cultural history, strong support and high consumer demand. It is therefore likely to continue as a major land use and conservation issue for predators. From a producer's perspective, the primary goals of livestock protection are maximising, or at least maintaining, production by minimising losses and mitigating detriment to stock welfare. Lethal removal of predators remains a commonplace solution. Such management measures are questionable as they raise animal welfare and conservation concerns, risk inhibiting ecological processes, are often expensive, and in some circumstances, exacerbate livestock predation problems. Non-lethal alternatives can facilitate co-existence between livestock farmers and predators, ideally reducing the ecological impact of pastoralism and achieving conservation goals. The need for rigorous study of non-lethal approaches has however been recently highlighted. Tools and methods involved in livestock protection, as well as the theoretical basis of how we perceive and manage the problem, require deeper consideration. Non-lethal approaches require knowledgeable implementation and an effective decision making system is a prerequisite for successful practice. Livestock predation and its prevention are fundamentally influenced by the underlying principles of foraging ecology and risk theory. We propose that manipulating elements of Brown's (1988) quitting harvest rate model provides a useful conceptual framework for reducing livestock predation and encouraging coexistence.

Keywords

Livestock; Non-lethal; Foraging; Predation; Harvest rate, Risk

Introduction

While perhaps politically and industrially unfavourable, there is justifiable discourse and concern regarding the social and environmental footprint of the livestock industry (Westhoek *et al.* 2014; Hallström, Carlsson-Kanyama & Börjesson 2015). Public concern with livestock welfare presents a longstanding contention (Deemer & Lobao 2011). Resource efficiency and issues relating to health and nutrition present direct concerns for effectively meeting nutritional needs of a growing human population through livestock products (Baroni *et al.* 2007; Westhoek *et al.* 2014; WWF 2016). Disease transmission and antibiotic resistance pose additional health concerns for humans, livestock and wildlife (Thompson 2013; Gottdenker *et al.* 2014; Hudson *et al.* 2017). Pastoralism's freshwater consumption and land use are also intensive, with habitat modification, ecological degradation, emissions, effluent and contribution to climate change all providing grave concerns (Baroni *et al.* 2007; Westhoek *et al.* 2014; Hallström, Carlsson-Kanyama & Börjesson 2015). Alongside indirect implications for wildlife conservation, livestock directly compete with and have replaced much wild biodiversity (Bar-On, Phillips & Milo 2018).

Some champion the potential conservation benefits of well managed livestock but often neglect to place such benefits in context, failing to draw comparisons with unmodified systems (Franzluebbers *et al.* 2012). The overall benefits for wildlife conservation are however contentious; livestock grazing, for example, can adversely affect species conservation, ecosystem structure, function and composition (Reading & Jofre 2015; Eldridge *et al.* 2016; Sharps *et al.* 2016). Livestock biomass now far exceeds that of wild mammals and competition for forage can negatively impact both wild herbivores and their predators (Latham 1999; Bar-On, Phillips & Milo 2018).

Native predators can be completely excluded from pastoral landscapes or exterminated altogether, e.g. large carnivores in the British Isles (Brown, McMorran & Price 2011). Cultural and social bias against predators may often exist in rural areas, regardless of personal experience with livestock predation (Chavez, Gese & Krannich 2005). Actual impacts can be small relative to other factors including disease, birthing problems, weather and accidents (Breck & Meier 2004; Dar *et al.* 2009). A small proportion of producers in predation hotspots may, however, absorb the majority of losses, increased husbandry costs and decreased animal performance (Breck & Meier 2004; Shelton 2004). Damage to livelihoods can reduce support for conservation initiatives (Anthony 2007; Anthony, Scott & Antypas 2010). Livestock predation often results in disproportionate deaths of the animals deemed responsible and persecution of predators is common (Meriggi & Lovari 1996; Shivik 2006; Eggermann *et al.* 2011). Lethal control of predators to pre-empt or in response to livestock predation has become common management in many contexts (Macdonald & Baker 2004; Treves *et al.* 2006).

The simplest way to resolve many of these problems would be to substantially reduce livestock production and move to plant dominant diets on a societal level (Eshel *et al.* 2014; Poore & Nemecek 2018). Changing consumer habits should not be overlooked as a potential nature conservation tool. Suitable damage related taxation may offer some assistance to this end (Springmann *et al.* 2017). Discouraging unnecessary consumption and encouraging financial divestment by consumers offers an additional route to achieving sustainability (Ripple *et al.* 2017). Such a large-scale transition may, however, prove difficult where habitat, technology, international trade, culture, affluence or knowledge makes livestock products one of few viable food production methods or an easily accessible dietary option. Livestock farming also has a long and enduring cultural significance (McClure 2015; Holmes 2016; Pitikoe 2017). High levels of meat, egg and dairy consumption are prevalent in many societies and a global shift away from this is currently unlikely, with human populations and demand for animal products increasing globally (Kearney 2010; Westhoek *et al.* 2014). Livestock production is likely to continue as a major land use and livestock predation remains an issue for both pastoralists and conservationists.

The ecological impacts, efficiency and morality of lethal control are questionable (Treves, Krofel & McManus 2016). Lethal control of predators and decline in their numbers can result in loss of ecological services and stability (Wallach *et al.* 2010; Ripple *et al.* 2014). Lethal control may not always be economically viable if loss of regulatory services by predators results in high costs where wild herbivores compete for forage with domestic stock (Wicks & Allen 2012). Lethal control can also disrupt social structure, exacerbating livestock predation problems (Wallach *et al.* 2009), or lead to compensatory reproduction, thereby minimising the effect of control (Minnie, Gaylard & Kerley 2016; 2017). A range of non-lethal alternatives exist that can assist mitigation of livestock predation problems and encourage coexistence (Shivik 2006; Stone *et al.* 2017). Societal preference for coexistence has led to greater adoption of such approaches (Chapron *et al.* 2014). Non-lethal livestock predation management can, although may not always, be equally or more effective than lethal control of predators (McManus *et al.* 2015; Stone *et al.* 2017; van Eeden *et al.* 2018a). Some non-lethal tools have been well tested but further robust experimentation is required to assess efficacy, encourage producer adoption and guarantee return on investments (Eklund *et al.* 2017; Scasta, Stam & Windh 2017; van Eeden *et al.* 2018b).

We refer readers to van Eeden et al. (2018b) for a useful synthesis of the current evidence base but recognise that in practice, one approach is rarely used in isolation of others, effectiveness will be context dependent and action is still required while the necessary testing of tools is conducted. Practitioners require a holistic and adaptive management system to more easily and effectively implement non-lethal programmes across a broad range of contexts. Applying existing scientific theory to real world issues should prove productive for both study and practice. The predation and protection of livestock are fundamentally influenced by the principles of both foraging and risk theory. We propose that Brown's (1988) quitting harvest rate model provides a useful theoretical framework for managing livestock predation and achieving conservation goals.

Brown's (1988) quitting harvest rate model as a management framework

Foraging theory suggests animals attempt to make the best of foraging scenarios by trading-off costs against benefits (Emlen 1966; MacArthur & Pianka 1966; Charnov 1976). Decisions to prey upon livestock instead of wild prey may be based in energetics (Polisar *et al.* 2003), but there is little evidence of predators preferentially hunting livestock where it has been tested (Lyngdoh *et al.* 2014; Hayward *et al.* 2017). Brown's (1988) quitting harvest rate model provides a useful framework with which to examine the mitigation of livestock harvest by predators. Where food patches are depletable, animals should abandon patches once gains (H) become equal to or fall below costs (Brown 1988;

Brown & Kotler 2007). The concept is described in the equation H = C + P + MOC, where H = harvest rate (food gain per unit time), C = energetic costs (to obtain food), P = predation costs (cost/likelihood of losing fitness by interacting with predators) and MOC = missed opportunity costs (food or fitness enhancing benefits available elsewhere) (Brown 1988; Brown & Kotler 2007). Like Berger-Tal et al. (2009), we also included risk of injury (RI) or mortality (e.g. from objects like electric fencing, terrain ruggedness, the stock themselves, or a device worn by stock) as an additional cost that may be incurred during livestock predation but discuss it alongside P for ease of discussion and implementation.

From a producer's perspective, the primary goals of livestock protection are maximising, or at least maintaining, production by minimising losses and mitigating detriment to stock welfare. Practitioners and wildlife managers should aim to manipulate predator foraging behaviour to reduce livestock predation; intentionally causing predators to quit livestock patches more quickly and harvest less, or ideally, no stock (Table.1). Ideally, livestock could be made so unprofitable comparable to wild prey that they become less preferable and are rarely preyed upon. Here we highlight considerations that may offer some utility but should be contemplated only in relation to individual context by giving thought to all model components.

Harvest rate (H)

Initial harvest rate (H) of livestock patches could be reduced to increase how quickly predators give up on livestock patches. Predators can be attracted to anthropogenic food subsidies, adapting their behaviour to utilise them (Ciucci *et al.* 1997; Newsome *et al.* 2014; Morehouse & Boyce 2017). Refuse sites in pastoral areas are likely to attract predators and lead to increased conflict (Wilson *et al.* 2006; Kolowski & Holekamp 2008). Removal of carcasses, livestock pits or waste dumps in the vicinity of livestock would provide sensible starting points to reducing patch attractiveness. Herd size (i.e. food availability) may also provide an attractant. Farms with larger herds may be more likely to experience livestock predation (Treves *et al.* 2004; Bradley & Pletscher 2005; Pimenta *et al.* 2017).

Herd size could potentially be reduced, although there is likely an economic disincentive to do so (Pimenta *et al.* 2017).

Missed opportunity costs (MOC)

Costs to predators of foraging in livestock patches can also be increased. Raising or ensuring high missed opportunity costs (MOC) relative to livestock patches should accelerate giving up on livestock. Often overlooked as a mitigation measure, ensuring viable wild prey populations (e.g. via harvest regulations, habitat restoration, reinforcement or reintroduction) is pivotal in sustaining large carnivore populations and minimising livestock predation (Meriggi & Lovari 1996; Polisar *et al.* 2003; Barja 2009). Predators will increasingly target livestock, which increase in relative value, as wild prey decline (Kolowski & Holekamp 2006). Low energy state foragers also tend to take higher risks (Brown 1988; Brown, Morgan & Dow 1992). Ensuring higher predator energy states by maintaining suitable wild prey stocks could reduce the marginal value of livestock as a food source.

Livestock production and the maintenance of wild prey stocks are however most likely best kept somewhat apart. Abundant wild prey in pastoral areas could cause increased livestock predation (Stahl *et al.* 2001; Bradley & Pletscher 2005; Amirkhiz *et al.* 2018). Carnivores are attracted to high quality habitat and conflicts may be more likely to occur where human activities, including livestock farming, overlap (Wilson *et al.* 2006; Odden *et al.* 2008). Livestock could be kept away from preferable wildlife habitat or better protected where this is not feasible. Habitat improvement and suitable limitation to wild herbivore harvest could also be employed in areas set aside from pastoralism. Excepting large land owners, this will require regional level intervention. Livestock producers can however make their properties less attractive to wild herbivores, e.g. protecting hay supplies, using livestock guardian dogs, *Canis lupus familiaris*, or hazing habituated wildlife (Bradley & Pletscher 2005; Kloppers, St. Clair & Hurd 2005; Gehring *et al.* 2010).

Seasonal declines in wild prey availability (MOC) driven by environmental conditions, seasonal migrations and prey habitat use, especially if coinciding with increased stock availability can lead to prey switching and increased livestock predation (Cavalcanti & Gese 2010; Valeix *et al.* 2012). In a similar fashion the relative value of livestock may increase following seasonal predator food demand and decreases in wild prey vulnerability due to maturing young (Ciucci & Boitani 1998). Practitioners should accordingly increase other costs (C, P or RI) and avoid increasing potential attractants (e.g. young livestock) during these more vulnerable periods.

Energetic cost (C)

The energetic cost (C) of preying on livestock could be increased, especially during periods of vulnerability. Fencing can provide an energetically costly barrier for carnivores to overcome. Fencing, albeit a barrier to wildlife movements, likely reduces losses; however its general efficacy will depend on the problem carnivore's abilities, fence maintenance and the presence of other fence damaging wildlife (Breitenmoser *et al.* 2005; McManus *et al.* 2015). Keeping livestock in predator proof corrals at night can efficiently minimise losses, although crowding can necessitate additional health care, and poor maintenance risks severe losses (Breitenmoser *et al.* 2005; Schiess-Meier *et al.* 2007; Weise *et al.* 2018). Corrals and fencing can also be made more disruptive through the addition of perceived or real injury related risk via fladry (Fig.1) and/or electric current (Musiani *et al.* 2003; Lance *et al.* 2011).

Livestock attributes could also affect the energetic costs of predation. Young, sick and injured animals may incur minimal energetic costs to hunt and can thus be more vulnerable to predation (Chavez & Giese 2006; Cavalcanti & Gese 2010). Producers should monitor and be mindful of herd vulnerability relative to alternative wild prey sources, targeting additional interventions accordingly. Vulnerable livestock, such as sheep, *Ovis aries*, can also be bonded to or housed with herd animals possessing better defensive capabilities (greater aggression, size, strength, armament). For example, llama's, *Lama glama*, long-horned cattle, *Bos taurus*, or donkeys, *Equus africanus*, can provide protective services by increasing injury related risk (RI) and the energetic costs (C) of accessing livestock (Smith *et al.* 2000b). Stock breed could perhaps be altered by selecting more agile or defensive breeds, which retain anti-predator behaviour. Anti-predator defence could also be encouraged within current stocks, for example, some producers attribute fewer wolf, *Canis lupus*, related livestock losses to keeping protective mother cows and encouraging defensive herding behaviour, instead of removing protective mothers and allowing herds to fragment across remote areas (H.Z. Anderson, Tom Miner Basin Project, *Pers comm*).

Predation risk (P) and risk of injury (RI)

There is good evidence to suggest that animals assess and respond to risk (Lima & Dill 1990; Creel & Christianson 2008; Heithaus *et al.* 2009). Fear ecology suggests such interactions may affect landscape use and foraging (Brown, Laundré & Gurung 1999; Brown & Kotler 2007; Laundré, Hernández & Ripple 2010). The mesopredator release hypothesis suggests predators too have things to fear (Crooks & Soulé 1999; Ritchie & Johnson 2009; Newsome *et al.* 2017). Humans are a key factor that alters the context within which predators exist (Haswell, Kusak & Hayward 2017). Humans may be viewed as super predators whose presence provides substantial risk to carnivores, consequently modifying predatory behaviour (Smith *et al.* 2017).

Increase in perceived or actual predation costs (P), as well as risk of injury (RI) from other causes, have received most attention in the development of non-lethal mitigation strategy (See Breitenmoser et al. (2005) and Shivik (2006) for comprehensive reviews). Wild animals, especially predators, can be particularly sensitive to new stimuli; scare devices using disruptive mechanisms such as neophobia, irritation or pain have consequently been utilised as primary repellents (Shivik, Treves & Callahan 2003; Shivik 2006). Secondary repellents establish a link between a behaviour and a negative outcome through aversive conditioning, e.g. electronic training collars worn by predators or taste aversion collars worn by livestock (Shivik, Treves & Callahan 2003; Shivik 2006). Excessive use of primary repellents risks habituation whereas secondary repellents can require substantial logistical effort and may need to be regularly reinforced to remain effective (Smith *et al.* 2000a; Shivik 2006). Harassment (e.g. rubber bullets) may offer simple implementation but linking aversion and behaviour might prove difficult and thereby limit effectiveness; consistent secondary repellents such as electrified fladry may however prove more efficacious in both application and reinforcement

(Shivik 2006). Use of primary and secondary repellents will depend on local laws, additional conservation concerns, and the ethical views of the practitioner.

Manipulating risk perception could still prove useful alongside the provision of direct threats. Visual assessment of habitat and its interaction with escape strategies provides one means by which animals may assess and respond to risk (Wirsing, Cameron & Heithaus 2010; Kuijper *et al.* 2013; Camacho 2014). Landscape characteristics, such as vegetative cover or woodlands adjacent to pastures, can be associated with higher levels of livestock predation (Ciucci & Boitani 1998; Stahl *et al*. 2001). Mapping risk hotspots could provide an effective decision making tool (Treves *et al.* 2004).

Animals also assess risk through auditory means (Berger, Swenson & Persson 2001; Lynch *et al.* 2015). Many technological scare devices work through visual or auditory disruptive stimuli, e.g. flashing lights, high beam lights, air horns, propane cannons, and sometimes through a combination, e.g. radio activated guard (RAG) boxes. Repellents such as flashing lights can significantly reduce predation but may not be effective against all carnivores (Ohrens, Bonacic & Treves 2019). Practitioner strategy will need to be context specific as well as adaptive. For example, when nocturnally flashing lights were applied to livestock bomas (protective night pens) in Kenya, Lions, *Panthera leo*, switched to attacking bomas where intervention was not implemented, and subsequently, when installation of lights increased, shifted to diurnal attacks (Lesilau *et al.* 2018).

The scent of dominant predators can communicate increased risk to carnivores (Leo, Reading & Letnic 2015; Haswell *et al.* 2018). Manipulation of scent could be useful in manipulating predator landscape use but may not always yield intended outcomes due to the context in which scent is encountered (Jones *et al.* 2016). Placement of scent manipulations could ideally be optimised if context relations are understood, i.e. what scent to place, when, where and how much. Identifying effective components of olfactory communication such as producer diet or social status and their associated compounds could also improve effectiveness (Parsons *et al.* 2018).

Direct presence of predation and injury risk are likely to elicit stronger responses than cues such as olfaction alone (Scheinin *et al.* 2006; Vanak, Thaker & Gompper 2009). Livestock guardian animals may provide multiple benefits through olfactory and auditory risk cue provision as well as direct presence (van Bommel & Johnson 2012; McManus *et al.* 2015). Livestock guardian dogs (Fig.2) can increase predation risk (P) and intimidate predators by protecting stock directly or creating landscapes of fear when used in a patrolling manor (Rigg 2001; Hansen, Staaland & Ringso 2002; Rigg *et al.* 2011). Guardian dogs may protect livestock without entirely excluding predators from foraging nearby (Allen *et al.* 2017). In some circumstances, the use of dogs may be spatially or seasonally problematic depending on wildlife sensitive periods, farming practices and other landscape users e.g. hikers or hunters. Livestock guardian dogs show good potential in mitigating pastoral wildlife conflict but the most effective methods for their use requires further investigation (Gehring, VerCauteren & Landry 2010; Gehring *et al.* 2010; Lescureux & Linnell 2014).

Conclusions

Scientific theory can offer useful frameworks for applied conservation issues. Understanding patterns and processes involved in livestock predation, developing effective ways to mitigate predation and rigorously testing non-lethal deterrents have been identified as areas requiring advancement (Breck & Meier 2004; Purcell *et al.* 2012; Eklund *et al.* 2017). All could be assisted by inclusion of foraging theory and risk ecology frameworks as part of study design and theoretical underpinning for management decision making.

It is important to understand that there is no 'silver bullet' strategy (Treves *et al.* 2006). Interactions between species are context-dependent (Haswell, Kusak & Hayward 2017). Success of non-lethal tools will vary in time and space depending on the structure of the quitting harvest rate model in a given scenario. There will of course also be scenarios where animals don't follow the model or non-lethal tools aren't applied correctly. Habituation to repellent devices can also prove problematic (Musiani *et al.* 2003; Shivik 2006; Lance *et al.* 2011). Adaptive, location and time specific management strategies are likely to prove most effective in ensuring protection techniques do not lose risk value (Stone *et al.* 2017; van Eeden *et al.* 2018a). Understanding changes in model components will also help with timing management interventions, e.g. increase in P in unison with seasonal fluctuations of MOC and predator nutritional needs. Identifying areas where predation likelihood is higher and circumstances tip the equation in favour of harvest will prove additionally useful (Treves *et al.* 2004; Treves & Rabenhorst 2017). Foraging theory can provide a useful framework for studying and managing livestock predation. If components of Brown's (1988) model are understood and can be manipulated through management practices then it should be feasible to tip the equation in favour of coexistence.

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Compliance with ethical standards

The authors declare that they have no conflict of interest in the authorship of this article. Use of product or corporation names is for descriptive purposes only and implies no endorsement by any author or affiliation.

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Table 1. Management options for reducing livestock predation utilising Brown's (1988) quitting harvest rate model, H = C + P + MOC. H = harvest rate, food available per unit time, C = energetic costs, P = predation costs, MOC = missed opportunity costs, alternative fitness enhancing activities e.g. foraging elsewhere, we also add RI = risk of injury. Predators should give up foraging from patches of livestock when the available gains (H) are equal to or less than the costs (C + P + RI + MOC). Managers can manipulate and alter components of the model in order to manipulate predator behaviour, reducing livestock harvest or preventing it beginning in the first place.

Livestock predation management

Decrease H

Reduce herd size, remove carcasses, remove anthropogenic food sources, any intervention which increases the time taken for predation

Increase MOC

Ensure wild prey stocks
- Ensure suitable habitat and access to forage
- Decrease wild herbivore harvest
- Keep wild prey and livestock separate
- Deter wild prey from pastoral areas

Monitor seasonal fluctuations in wild prey
- Increase P, RI or C if wild prey stocks decline, become less accessible to predators or if predator food needs increase e.g. when predator young are weaned

Increase P or RI

Guardians
- Use when possible. Humans, dogs or other animals e.g. donkeys
- Use stock with natural defences
- Ensure appropriate numbers and behaviour
- Increase use when needed e.g. during mobile grazing

Scare devices / risk cues e.g. air horn
- Avoid predator habituation
- Use sporadically and when most needed
- Ensure stock are not startled by devices and are habituated

Aversive conditioning e.g. taste aversion collars worn by stock
- Ensure reinforcement

Increase C

Fencing
- Use corrals when vulnerable e.g. at night or during lambing
- Consider solid stationary or electric mobile corrals as well as positioning
- Apply additional deterrents (P or RI) when needed e.g. fladry

Livestock attributes
- Use more agile & less docile livestock
- Use stock with natural defences e.g. armament or behaviour
- Breed for attributes
- Herding regime, dispersed or herded

Guardian patrols
- Increase when needed e.g. when predator young are weaned

Additional considerations

Terrain
- Avoid known hotspots or landscape contexts where livestock predation is more likely
- If unavoidable increase P, RI or C

Predator monitoring
- Avoid areas well visited by predators e.g. known breeding sites
- Increase P, RI or C when predators are in the vicinity

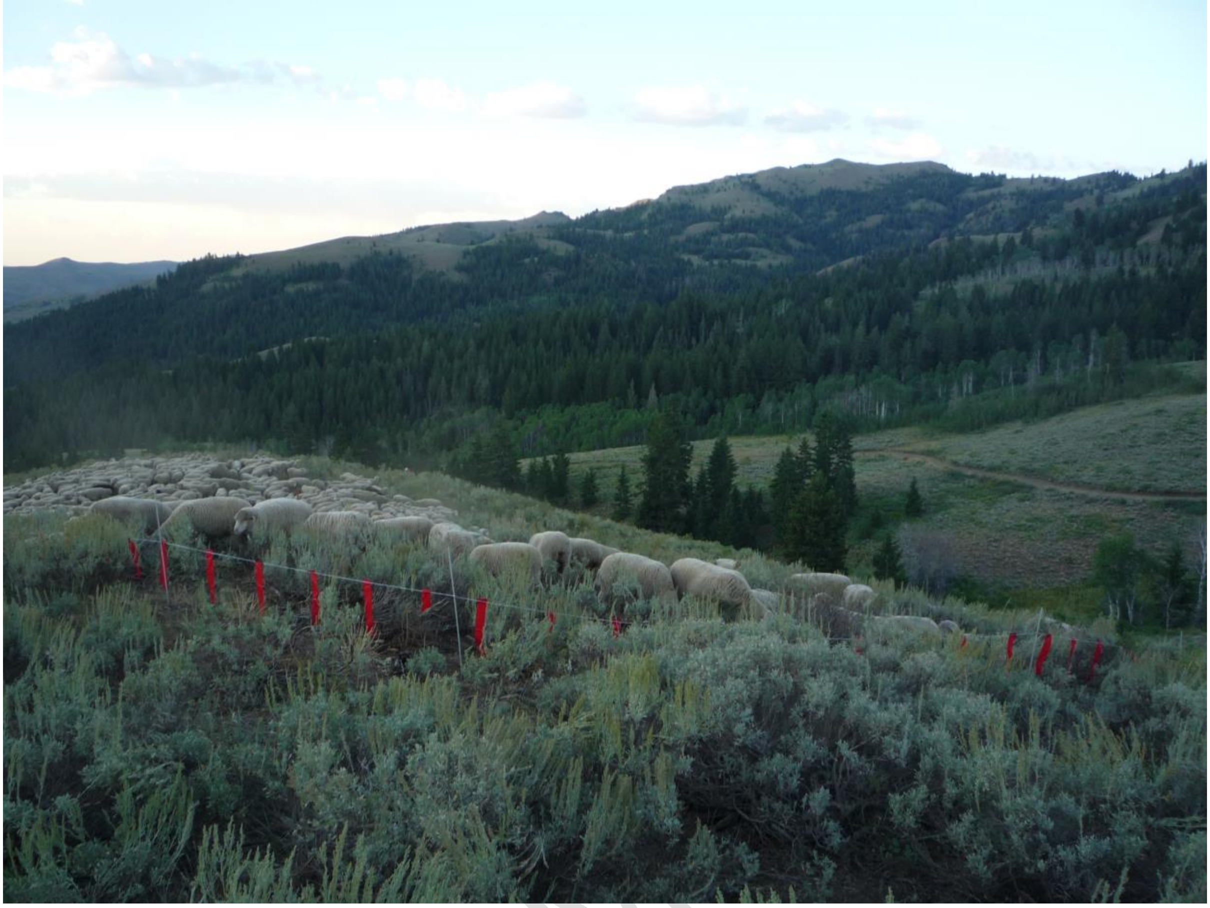

Fig 1. Sheep in a temporary night time corral made of electrified fladry as part of the wood river wolf project in Blaine County, Idaho.

Fig 2. Livestock guardian dogs can be raised with and kept with stock or used in a patrolling capacity with a handler or range rider. Karakachan female pictured, a rare breed being conserved by S. Sedefchev, Bulgarian Biodiversity Preservation Society, Semperviva.