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Domestic ungulates in protected areas and the potential for indirect interactions via shared predation

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ABSTRACT

In many parts of the world, protected areas harbour permanent livestock that range freely with native herbivores. These domestic animals are typically an undesirable ecosystem component because they pose a challenge to park managers and biologists who wish to maintain 'natural' species interactions and diversity. Studies dealing with livestock in protected areas have primarily focussed on interactions such as competition for food resources with native herbivores, habitat degradation, and human-carnivore conflicts caused by livestock depredation. The negative effects of such interactions are a major threat to the survival of many mammalian prey and predator species. However, the role of indirect interactions between native herbivores and domestic prey, via their common enemy, has received comparatively little attention and poses a significant knowledge gap in understanding the net impacts of domestic prey on native herbivores. We present our perspectives on ignored or missed indirect interactions in livestock–native ungulate systems, and suggest some management actions for understanding these systems and minimising conflicts. A broader understanding of indirect interactions among livestock, native herbivores and their predators will aid in more informed protected-area management.

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Livestock in protected areas

Livestock are typically an undesirable ecosystem component and pose a challenge to park managers and biologists who wish to maintain species interactions and diversity of natural systems (Das 2008; Wangchuk 2002). Nevertheless, several conservation areas around the world contain (or are next to) permanent human settlements with livestock, and in many, livestock greatly outnumber native ungulates (Mishra 1997; Tumenta et al. 2013; Li et al. 2013; Aryal et al. 2014; Schulz, Printes, and Oliveira 2014; Constant, Bell, and Hill 2015; Kuiper et al. 2015; Li et al. 2015; Sharma, Bhatnagar, and Mishra 2015; Shehzad et al. 2015). Livestock in conservation areas have a variety of negative effects on native flora and fauna (Prins 1992; Bagchi and Ritchie 2010). They may compete for food resources with native ungulates, transmit diseases, modify vegetation, and reduce the diversity and nutritional quality of forage (Mishra and Rawat 1998; Prins 2000; Bagchi, Goyal, and Sankar 2003; Bagchi, Mishra, and Bhatnagar 2004; Madhusudan 2004; Bagchi and Mishra 2006; Martin et al. 2011).

We used the International Union for Conservation of Nature and Natural Resources' (IUCN) Red List of threatened species to gain insight into how conservation organisations approach livestock. The Red List documents 129 mammalian species in protected areas that fall under the IUCN's major threatened categories (critically endangered, vulnerable, endangered or near threatened) where the presence of livestock is considered a major threat to native diversity (IUCN 2013, Figure 1). Ninety species of large ungulates (>5 kg) are threatened by livestock populations through competition for food and habitat degradation. Out of this list, 60 face major threats that require considerable management intervention. Efforts to minimise these impacts are usually aimed at reducing contact with native herbivores, in order to minimise competition and prevent disease transmission (Kilpatrick, Gillin, and Daszak 2009).

Conservation and management in systems where domestic prey coexist with large carnivores often target controlling human-carnivore conflict precipitated by carnivore predation on livestock and on humans

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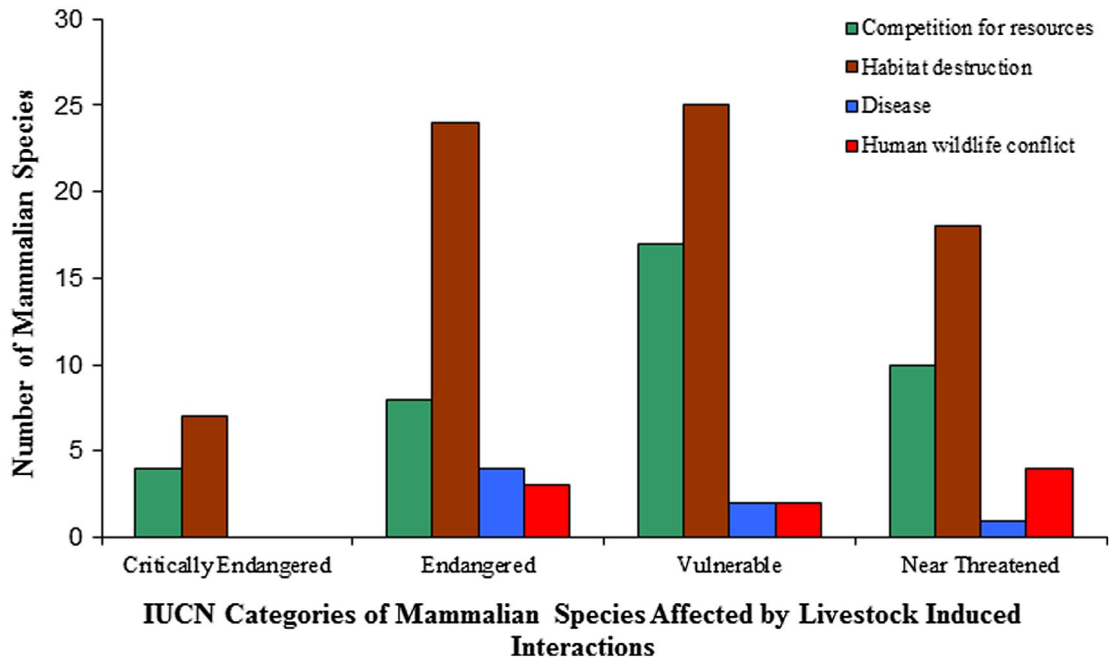

Figure 1. IUCN Red List threat categories of mammalian species in protected areas as affected by livestock induced interactions (IUCN, 2013, search criteria in Appendix A).

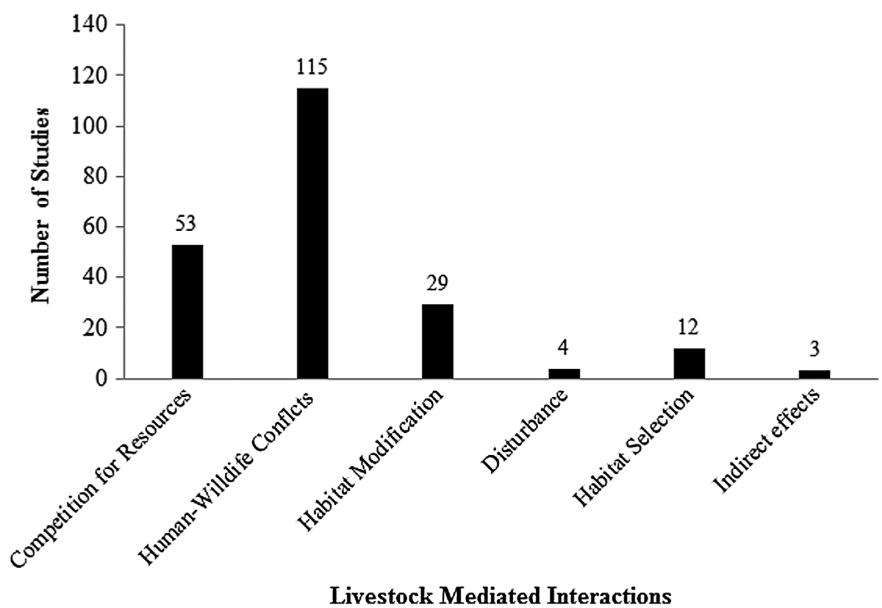

Figure 2. Number of research publications related to livestock-mediated interactions (n=276, see search criteria in Appendix B) involving native ungulates and predators in conservation areas. Numbers at the top of the bars represent the number of published papers.

(Patterson et al. 2004; Saberwal et al. 1994; Karanth and Madhusudan 2002; Treves and Karanth 2003; Ogada et al. 2003; Inskip and Zimmermann 2009; Meena et al. 2011; Dickman, Macdonald, and Macdonald 2011). Indeed, our review of research publications dealing with livestock-mediated interactions reveals more attention to human-wildlife conflict than to all other categories combined (Figure 2). Wildlife invariably loses in encounters with humans and fully 21 carnivore species (>5 kg) are threatened by human–carnivore conflicts associated with livestock predation (IUCN Red List). Financial compensation for livestock loss is a typical response, despite social determinants playing a greater role in attitudes toward carnivores (Naughton-Treves, Grossberg, and Treves 2003; Banerjee et al. 2013; Meena, Macdonald, and Montgomery 2014).

Studies focussed on predation ecology in livestock systems often concentrate on quantifying the proportional contribution of each prey species, domestic and native, to the diet of the predator (Bagchi and Mishra 2006; Meena et al. 2011; Odden, Nilsen, and Linnell 2013; Banerjee et al. 2013; Shehzad et al. 2015). This approach does not assess the possibility of livestock-mediated indirect interactions via shared predation (*sensu* Holt 1977; Holt and Lawton 1994). For example, increased grazing in a particular habitat by domestic prey may attract predators to that area, which in turn can affect habitat selection by other wild ungulate prey in the system (Aryal et al. 2014; Constant, Bell, and Hill 2015; Kuiper et al. 2015). Failure to consider the indirect interactions that are mediated by a common predator, can lead to incomplete understanding of foraging decisions by prey animals and the resulting net interactions among prey. Here, we make a case for conservation to include a range of predator-mediated indirect interactions that are missed or ignored in livestock-dominated systems.

Carnivores in the mix: Shared predation and indirect interactions in livestock systems

For many ecosystems, livestock is the dominant prey (both in number and biomass) consumed by native carnivores

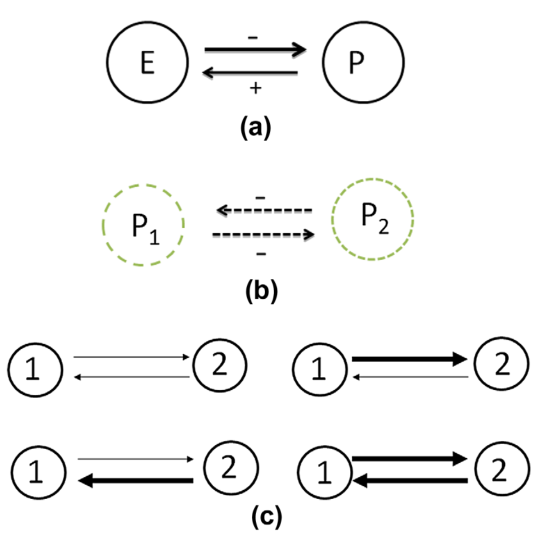

Figure 3. (a) Direct trophic interaction (i.e. predation) between a predator (E) and prey (P). (b) Resource competition (dashed lines) between two prey species (P_1 and P_2) resulting in mutual negative effects (an indirect effect mediated by resource consumption that might be enhanced by direct interference between prey species; the prey species' underlying direct consumer-resource interaction is omitted for clarity). The "-" and "+" signs represent negative and positive effects respectively. (c) Magnitude of the direct effects between each two-species interactions (species 1 and species 2). Thin and bold arrows represent small and large effects on one another respectively.

(Muhly et al. 2010; Shehzad et al. 2015). When generalist carnivores feed on both domestic and native prey, there is considerable potential for indirect interactions (Wootton 1994; Abrams and Matsuda 1996; Vijayan et al. 2012). These interactions will often be driven by changes in the predator's foraging behaviour in response to two prey types. Functional responses and depredation rates may depend upon the relative densities of native and domestic prey as well as their combined densities in the system (Meriggi and Lovari 1996; Odden, Nilsen, and Linnell 2013; Suryawanshi et al. 2013; Gervasi et al. 2013).

The many differences between domestic and native prey allow us to postulate several kinds of shared predator-mediated indirect interactions for livestock-dominated systems. These indirect interactions can be complex, depending upon whether the direct effect between predator and prey is small or large. For example, imagine a system with two competing prey and one predator. This system includes two types of common interactions that are well addressed in literature: (a) the basic direct predator–prey interaction, where predators benefit from consuming prey (a typical '+, –' effect, Figure 3a), and (b) resource competition, where two prey species compete and have a reciprocal negative effect caused by reducing a common resource ('–, –' an indirect effect mediated through the prey species' consumer–resource interaction, Figure 3b). However, the magnitude of these effects for each two-species interaction will vary. For instance, if we imagine that the effect of a prey species, on the other, is small or large (Figure 3c), each species pair can display four different 'levels' of interaction. The variety of potential outcomes will expand considerably if the magnitude of interactions varies continuously. The net interactions will also vary when we overlay other mechanisms on top of the prey-consumer dynamics (e.g. behaviours associated with the 'landscape of fear', *sensu* Brown, Laundre, and Gurung 1999; Laundre, Hernandez, and Ripple 2010; or variations in livestock husbandry, Tumenta et al. 2013; Constant, Bell, and Hill 2015).

For simplicity, we restrict our examples of the possible predator-mediated, indirect interactions to systems containing one predator and two prey species (native and domestic). We briefly describe three underlying mechanisms under which the different interactions are likely to occur in natural areas:

(a) Apparent mutualism: reciprocal positive interaction ('+, +')

A predator feeding on a single prey species will normally have a strong negative effect on that species' survival and population dynamics (Figure 4a). However, when it feeds on two prey species, the net 'indirect' prey–prey

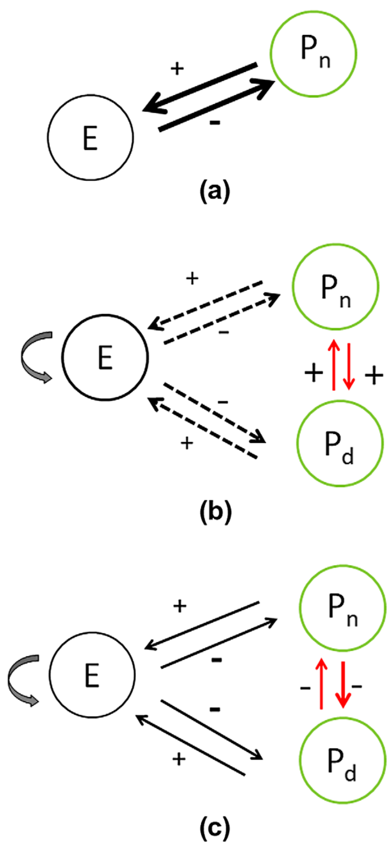

Figure 4. Conceptual representation of different indirect interactions (*sensu* Holt 1977, 1984) between domestic (P_d) and native prey (P_n) via their shared predator (E), (potential changes in competition between prey not included). Direct effects (black lines) between the common enemy and prey represent trophic interactions. Line weight (thin and thick) and dashed lines represent effects of high and low magnitude respectively. The "-" and "+" signs represent negative and positive effects. Red arrows represent indirect prey-prey effects mediated by their common enemy. Grey curved arrows signify that the predator population is self-regulated (or controlled externally as through hunting or other forms of mortality). For simplicity, potential changes in competition between prey are not included in the interactions. (a) One predator consuming a single native prey species. (b) Apparent mutualism between native and domestic prey caused by shared predation that reduces predation pressure on both prey species. (c) Apparent competition between native and domestic prey leading to higher predation on both prey species. The presence of one (often the domesticated) prey species increases predation rate on the second.

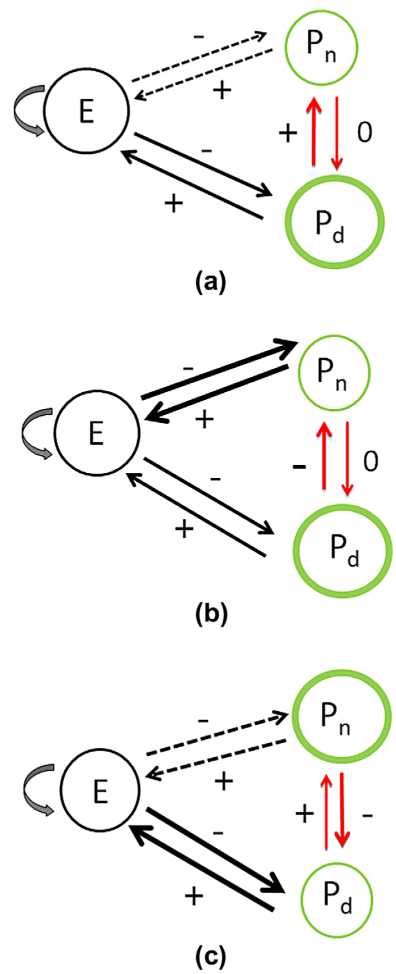

Figure 5. Possible density-dependent modulated asymmetric or non-reciprocal interactions between native (P_n) and domestic (P_d) prey via their shared predator (E). The "-", "+" and "0" signs represent negative, positive and zero effects respectively. Bold circles represent higher densities of prey. Line weight (thin and thick) and dashed lines represent effects of high and low magnitude respectively. Grey curved arrows document the essential feature that the predator population is self-regulated (or controlled externally). For simplicity we only show the density effect of one prey species on another. Potential changes in competition between prey are not included in the interactions. (a) A strong positive indirect effect of P_d on P_n will occur if domestic prey is preferred by predators and if they also exist at high density (reduced predation on native prey). The low density of native prey has no effect on the domestic prey (+, 0). (b) A strong negative indirect effect of P_d on P_n will occur if high density of domestic prey increases predation on native prey. The interaction will be asymmetrical if P_n has no (or marginal) effect on the predation of domestic prey (-, 0). (c) A strong negative indirect effect of P_n on P_d, and a positive indirect effect of P_d on P_n will occur if domestic livestock are attacked preferentially while the high density of native prey increases predator activity in the area (+,-).

interaction can be positive due to risk dilution (red arrows, +, +, Figure 4b). The positive indirect effect emerges if predators respond only to total prey abundance. The time spent searching and killing one prey type is unavailable to search for and attack the other prey (Holt 1977; Holt and Lawton 1994; Holt and Kotler 1987). Under these conditions, the negative effects of predation are shared between the two prey species and will be lower than when either species is preyed on alone. Reciprocal positive interactions between livestock and native ungulates may be much more common than currently assumed, because the density of generalist predators in many of these systems is regulated by factors other than prey abundance (curved arrow,

Table 1. Summary of some major indirect interactions (between one predator and two prey species) that are likely to occur in livestock-dominated protected areas, their outcomes for stakeholders and preferred management actions. $E \times (P_n \times P_d)$ represents indirect interactions, E = common enemy/predator, P_n = native prey, P_d = domestic prey. The symbol '+' represents a positive effect on one prey, '–' represents a negative effect on one prey and '0' represents no effect on one prey.

Community	Indirect interactions	Outcomes	Preferable management action
$E \times (P_n \times P_d)$	+, +	Desirable by stakeholders (livestock settlors and park authorities) but will increase resource competition at some level	Ceiling on livestock stocking level
	+, –	Desirable by park authority but not by livestock settlors,aggravated human-carnivore conflict due to increase in livestock killing	Compensation for livestock loss, protect livestock from carnivores
	+, 0	Desirable by park managers and livestock settlors	None
	0, –	Human carnivore conflict between livestock settlors and park authority	Compensation for livestock loss, protect livestock
	–, +	Native prey decline, not desirable by park authority,conflicts between livestock settlors and park management	Restrict livestock population, relocate the settlements protect native prey
	–, –	Not desirable by stakeholders, human carnivore conflicts, Increase in conflict between livestock settlors and park authorities	Restrict livestock population, relocate settlements, protect native prey and livestock, compensation for livestock
	0, 0	Desirable by stakeholders	None

Figure 4b). Removal of the carnivore from the system may result in negative interactions between the prey species and likely asymmetry that favors the domestic prey.

(b) Apparent competition: reciprocal negative interaction ('–, –')

Reciprocal negative effects can occur when an increase in the number or activity of one prey species attracts a common predator (or increases its functional response), thus inflating predation risk and reducing the habitat quality for the coexisting, second prey species (Holt 1977; Holt and Kotler 1987). Coexisting prey species will be impacted whenever one prey species induces changes in the aggregation, distribution and behaviour of predators (Solomon 1949; Holling 1959). Predators attracted to high-quality patches where livestock are sympatric with native ungulates can be expected to encounter both prey species more frequently than otherwise, such that both experience higher than normal predation rates (Figure 4c). The indirect positive effect associated with reduced resource competition that emerges from a smaller population of competitors is over-ridden by high predation rates on both species.

(c) Density (dependent) modulated non-reciprocal or asymmetrical interactions ('0, +', '0, –' and '+, –')

Consequences of shared predation between coexisting prey species may not always be reciprocal or symmetrical. The interactions may be driven by density-dependent predator–prey interactions or prey behaviour, such as reduced predation through aggregation (Hamilton 1971) and heightened group vigilance (Pulliam 1973), that emerge through social aggregation. For example, a '+, 0' interaction can occur between prey when the density of one prey species is higher than the other, and is thus consumed preferentially. When coexisting with a more abundant prey, predation on the less abundant prey species is thus less than what would occur if it was alone (a strong positive indirect effect). The less-abundant species' low density is inconsequential to the dynamics of the abundant one (Figure 5a).

A '–, 0' interaction may occur if the presence of prey species 1 increases the predator attack rate on species 2 (provided that 2 has no effect on 1; Figure 5b). Such an interaction is very likely if one of the prey types differs substantially in nutritional quality from other prey or yields lower food value (e.g. smaller size or longer handling time than the other prey). A third possible asymmetrical interaction can occur when a predator preferentially attacks and consumes the prey species that is most profitable ('+, –'). Such an effect may be especially common where abundant, low-value (e.g. small body size) native prey coexist with large and vulnerable domestic prey (Figure 5c).

Differences in prey association, as well as accessibility and availability of livestock as a prey item for the shared predator, are likely to yield asymmetrical indirect interactions (see review by DeCesare et al. 2010). Further, the common predators' functional response is likely to be idiosyncratic to each predator and prey type. For example, kill rates on domestic sheep by European lynx (*Lynx lynx*) are higher where sheep co-occur with few roe deer (*Capreolus capreolus*) than where roe deer density is high (Odden, Nilsen, and Linnell 2013). The number of native prey species coexisting with livestock, and the number, characteristics and breed of livestock species may also influence the predator–prey interaction. Since in diverse prey–predator systems, both predation (top-down) and resource limitation (bottom-up) regulate herbivore populations (Sinclair, Mduma, and Brashares 2003), the presence of livestock may pose a unique challenge to native ungulates. First through competition for limited food resources, but secondly through diluting predation risk. Coexisting native prey may, however, be able to optimise the respective costs and benefits through habitat choice (Vijayan, Morris, and McLaren 2012), and simplify what would otherwise require more complicated management.

Conservation challenges and management in livestock systems

Which type of interaction emerges when livestock coexist with native ungulates? Generalisation of outcomes is difficult, because the approach to pastoral systems varies throughout the world. Ecological characteristics, such as size and behavioural differences between native and domestic prey, their spatial-temporal overlap, relative densities and accessibility, will dictate the direction and magnitude of indirect interactions. Outcomes are also influenced by social factors, such as programs that compensate ranchers and pastoralists for livestock losses (Dickman, Macdonald, and Macdonald 2011; Banerjee et al. 2013), and the level at which herders guard their livestock. For example, ranch systems more typical of the Americas and Australia, where livestock are maintained separately from wildlife in fenced environments, differ from traditional grazing in many protected areas in Asia and Africa which contain permanent human settlements where native prey are sympatric with livestock. Human response to carnivore–livestock interactions (in the 'landscape of coexistence', *sensu* Oriol-Cotterill et al. 2015) can play a major role in determining the outcome of predation in a livestock-dominated system.

That the interactions in the systems we describe may be more complex than generally addressed by conservation and management policies is evident. The challenge for managers is to detect and monitor indirect effects of livestock–prey–predator interactions and accordingly devise management strategies. Some key interactions and an overview of preferable management actions are listed in Table 1. Some indirect effects can be detected by quick and careful observations and comparisons on adaptive behaviours of native prey in the presence and absence of domestic prey in their natural habitats (i.e. time spent foraging, duration of anti-predator response like vigilance, group formation and habitat selection, *sensu* Caro 2007; Kotler, Morris, and Brown 2007; Ale and Brown 2009; Morris et al. 2009). The 'giving up densities' technique (GUDs; Brown and Kotler 2004) provides a strong behavioural indicator of patch use and the level of predation risk faced by the native prey (e.g. see Kotler, Gross, and Mitchell 1994; Iribarren and Kotler 2012). Shared predator foraging behaviour and habitat choice can be monitored by tracking carnivore movement (GPS collars, camera trapping; Kuiper et al. 2015; Sharma, Bhatnagar, and Mishra 2015). It might also be possible to detect such effects through the behaviours of domestic prey and their human attendants (level of guarding) and to reduce negative indirect interactions similarly by attentive management involving relocation or spatial segregation of livestock, or aggregation of human pastoral settlements.

The solutions we suggest are echoed in Du Toit's (2011) call for 'bold experimentation' and steering away from 'orthodoxy' in approaching inter-specific relationships between livestock and wild prey. We encourage the same path forward for investigating the role of predator-mediated indirect interactions in livestock-dominated conservation systems. Only then will we be able to perceive the true impacts of livestock on native herbivores and their wild carnivore prey.

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Disclosure statement

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