

Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know?

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TOPICAL REVIEW

Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know?

OPEN ACCESS

RECEIVED

19 May 2015

REVISED

22 August 2016

ACCEPTED FOR PUBLICATION

14 October 2016

PUBLISHED

11 November 2016

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¹ Author to whom any correspondence should be addressed.E-mail: schieltz@princeton.edu and dir@princeton.edu**Keywords:** livestock, wildlife, grazing, livestock–wildlife interactions, mammal, ungulateSupplementary material for this article is available [online](#)**Abstract**

More than a quarter of earth's land surface is used for grazing domestic livestock. Livestock grazing is generally assumed to negatively affect wildlife, however, a number of studies have found positive impacts as well. We conducted an evidence-based review of the existing literature using a series of livestock- and wildlife-related search words to systematically query Google Scholar and Web of Science. A total of 807 sources were included in the final list, including 646 primary sources which reported original data. The majority of studies were conducted in North America (338) or Europe (123), with many fewer from Africa (57), Australia (54), Central/South America (43), or Asia (31). Most studies examined birds (330) and mammals (262), with fewer including reptiles (91) or amphibians (58). We extracted further information from studies that included mammals on positive, negative, and neutral effects of livestock grazing on mammals. We found that livestock change vegetation structure and cover in ways important to small mammals, while ungulates may be affected more by interference competition and changes in forage quantity and quality. Community-level total abundance of small mammals typically declines with grazing. Species richness of small mammals either declines or stays the same, as many studies found a change in species composition from ungrazed to grazed sites while the number of species remained similar. Individual species responses of small mammals vary. Voles, harvest mice, cotton rats, and shrews show consistently negative responses to grazing while deer mice, kangaroo rats, ground squirrels, and lagomorphs show positive or variable responses. In general, species adapted to open habitats are often positively affected by grazing, while species needing denser cover are negatively affected. Studies of wild ungulates are more variable in methodology and quality than those for small mammals. We found more negative ($n = 86$) than positive ($n = 34$) ungulate responses overall, however, most studies have been on browsers and mixed feeders, namely deer and elk, and there is little available data for other groups. Although data is limited, several of the grazing species in Africa may show a trend toward positive responses, suggesting possible facilitation. For a number of species, responses varied by season. We find a strong need for additional research on ungulates of varying diets and body sizes, especially in the developing world, and across longer time scales to examine possible tradeoffs between competition and facilitation from livestock.

1. Introduction

Cattle and other livestock graze more than a quarter of the planet's total land surface, making livestock grazing the most ubiquitous human activity on earth in land area used (Steinfeld *et al* 2006, Robinson

et al 2014). Livestock production is generally thought of as detrimental to wildlife and many people assert that livestock have had a dramatic negative impact on global biodiversity. In some regions of the world, overgrazing has indeed reduced the density and biomass of plant and animal species, reduced

biodiversity, and altered ecological succession, nutrient cycles, and landscape heterogeneity (Kauffman and Pyke 2001).

However, this is not always the case. A number of studies have found that grazing can sometimes have positive effects on wildlife. In contrast to intensive crop production agriculture, grazing lands are also considered critical to conservation because they provide vital habitat for wildlife outside of formally protected areas and preserve open space and connectivity in ecosystems (FAO 2009, du Toit *et al* 2010). In a number of systems, conservation efforts are increasingly aimed at managing land for livestock–wildlife coexistence.

The effects of cattle grazing on vegetation and soil dynamics have been extensively studied (Milchunas and Lauenroth 1993, Belsky and Blumenthal 1997, Holechek *et al* 1999, Stahlheber and D'Antonio 2013). They have also been the subject of much controversy due to conflicting results or limitations of small-scale experiments. Recent reviews have concluded that, in general, managed livestock grazing at light to moderate intensities can have positive impacts on rangeland vegetation compared with grazing exclusion (Holechek *et al* 2006), though uncertainties remain concerning how spatial movements of livestock influence these processes (Briske *et al* 2008).

Livestock impacts on wildlife are perhaps even less well resolved. Impacts can be direct, such as interference competition as a result of the physical presence of livestock on shared rangelands, or indirect through changes they create in vegetation. These changes include primary influences like herbage removal or trampling and higher order effects such as changes in vegetation structure, productivity or composition (Kauffman and Pyke 2001). Vegetation changes created by livestock will then influence wildlife via factors such as food quality and quantity, cover from predators, or availability of nesting sites. There may also be cascading effects through a food chain by altering prey abundance for higher trophic levels.

Different vegetation changes are likely to be of varying importance to different types and species of wildlife based on fundamental properties like body size and diet. First, small-bodied species are vulnerable to a range of predators and influences on cover may be more important to them than to large-bodied species which have fewer predators or do not use crypsis to hide from them (Sinclair *et al* 2003).

Changes in food availability will likely be important to all animals, but may manifest in different ways. Research on resource partitioning of plant food along a quality/quantity axis suggests variation in herbivore body size promotes coexistence (Demment and Van Soest 1985, Illius and Gordon 1987, Gordon and Illius 1996, Olff *et al* 2002). Smaller animals have higher metabolic rates relative to their size than larger animals (Kleiber 1947) and thus need to eat higher quality food. For herbivores, this means that small

species select the rarer, but more nutritious parts of plants such as new leaves or young shoots while avoiding high-fiber components like stems. Large herbivores need to consume a greater total amount of food but have a higher tolerance for low quality forage and can be less selective (Bell 1971, Jarman 1974, Belovsky 1997, Kartzinel *et al* 2015).

Grazing by livestock generally reduces quantity, but sometimes improves quality of vegetation by removing old forage and stimulating new growth (Georgiadis *et al* 1989). Therefore, the effect of livestock grazing on native herbivores can be negative, through exploitative competition, or positive, as a result of facilitation. Wild herbivores of differing body sizes are predicted to respond differently to this trade-off between forage quantity, quality, and predation (Hopcraft *et al* 2010, 2012).

Diets can also vary based on the type of plant matter consumed and herbivores are generally classified into three major groups: browsers, which eat the leaves, shoots, or fruits of woody plants and shrubs; grazers, which eat grass; and intermediate mixed feeders, which eat both grass and browse. Though these are often treated as separate categories, in reality, most species fall somewhere on a continuum between a pure grazer and a pure browser. Livestock can change vegetation composition (Augustine and McNaughton 1998) and may shift the relative proportions of grasses, forbs, and browse available to wildlife, depending on the species of livestock used. Large-bodied grazers like cattle will need a greater total quantity of forage per animal, but will be less selective than smaller-bodied sheep. Goats are similar in size to sheep but eat more browse. In some parts of the world, camels are also an important or growing stock type and camels are pure browsers.

Wildlife responses can also manifest in a number of forms. At the community level, there could be a shift in diversity or species composition of wildlife present. At the individual species level, there can be proximate changes in wildlife behavior, such as use of an area or diet selectivity, which may lead to demographic changes in age structure, sex ratios, survival or fecundity. Over time, these changes may alter population sizes and growth rates, including extremes such as local extinction. We expect that very few studies examine all of these responses, especially the population level changes which require long-term monitoring to truly detect.

Perhaps the most important factor governing all of these changes is stocking rate, or livestock grazing intensity. While many studies simply compare 'grazed' to 'ungrazed' conditions, grazing is not an all or nothing proposition and the intensity of grazing is likely to be of utmost importance. Ecological theory suggests that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent, a concept known as the intermediate disturbance hypothesis (Grime 1973, Horn 1975, Connell 1978).

In the context of grazing, this suggests that plant diversity may be greater at a light or moderate level of grazing than with either grazing exclusion or heavy grazing. Research has also found that for some plant species grazing can stimulate net primary productivity, with the maximum stimulation at intermediate grazing intensities (McNaughton 1983, 1985). If this holds true for the plant community in any given site, the wildlife communities that depend on these plants may also show similar patterns and be found in greatest diversity or abundance at intermediate grazing intensity. This response may be habitat-specific, however, and depend on factors such as environmental moisture and evolutionary history of grazing (Milchunas *et al* 1988).

Many individual studies have been conducted on the responses of select wildlife species to livestock grazing and a number of reviews have targeted certain taxa of wildlife in specific habitats or geographic locations. Reid *et al* (2013) provide a good narrative review of the many issues surrounding global livestock impacts on biodiversity. Reviews by Prins (1992, 2000) provide additional discussion of competition between wildlife and humans with livestock, particularly in Africa. However, to date, there has not been a comprehensive systematic review examining the effects of livestock on a broad array of wildlife around the globe and under different conditions.

This review attempts to address that gap by collating and assessing the evidence for positive, negative, and neutral impacts of domestic livestock on various taxa of wildlife around the world. The factors considered here include the style and intensity of management system employed, the region of the world and habitat types studied, the taxa of wildlife examined, the type of wildlife responses measured, and the mechanisms suggested to explain effects of livestock on wildlife. This will allow an examination of whether gaps exist in the current literature in factors such as geographic coverage or wildlife taxa studied to date. This review also seeks to identify broad patterns and highlight areas for further study concerning the question: under what conditions might livestock benefit wildlife and under what conditions are livestock expected to negatively impact wildlife?

2. Methods

2.1. Search protocol and initial inclusion criteria

This review examined the effects of livestock grazing on vertebrate wildlife, including mammals, birds, reptiles, and amphibians, but not fish. The purpose of the review was to collate the evidence for positive, negative, and neutral effects of livestock grazing on wildlife abundance, demography, diversity, or behavior. The impacts of wildlife on livestock production were not a focus of this review. Therefore, studies which investigated the effect of wildlife on livestock,

Table 1. Search words used in search engines Google Scholar and Web of Science.

Livestock-related words	Wildlife-related words
Livestock	Wildlife
Cattle	Bird*
Sheep	Mammal*
Goat	Reptile*
Graz/grazing	Amphibian*

but not the reverse were not included. For a recent review of effects of large herbivores on arthropods, which were not included in this paper, see van Klink *et al* (2015).

The above keywords (table 1) were used to search the electronic databases Google Scholar and Web of Science. Every combination of a livestock-related word from the left column and a wildlife-related word from the right column were used as searches. Searches were conducted from 11 May 2015 to 1 February 2016.

Because of the broad nature of these words, many combinations resulted in a very large number of hits. For example, searching 'livestock' and 'wildlife' yields about 240 000 results in Google Scholar and over 13 000 results in Web of Science. Therefore, in order to generate a list of relevant sources, it was necessary to use several levels of filtering to exclude non-relevant sources.

For each search, results were sorted by 'relevance' (as defined by the search engine being used). We then examined the first 200 query results for each combination of a livestock-related search word and a wildlife-related search word, in each search engine. Therefore, we examined 5000 total results from Google Scholar and 5000 from Web of Science. There was overlap in some titles between searches, so we kept note of how many total relevant articles we obtained from each search as well as how many new relevant articles we found in each search, i.e. those not already identified from a previous query.

A first step of exclusion was to eliminate some material based on title alone if a title was clearly not relevant to the specific question being addressed in this review. If a title did seem relevant, or if it was unclear from the title alone, the abstract was then examined. Only articles whose title and abstract were relevant were then included in the first list of possible sources. Literature cited lists for these relevant articles were then also searched to find additional sources not identified in our primary web searches. All relevant sources were then read, at which point further exclusion criteria were applied before specific analyses were conducted.

Only sources with at least the title and abstract available in English were used. Therefore, we are likely missing some articles published in other languages, which may bias this review geographically somewhat.

Several broad areas of research which appeared in many of the searches were mostly excluded because of lack of relevance, such as those pertaining to disease, diet overlap, and predation. While potential disease transmission between livestock and wildlife is an important factor to consider in many systems, for this review we are interested only in sources which detail a quantifiable effect of livestock on wildlife. Therefore, titles which focused only on disease diagnosis, pathways of transmission, or disease prevention or control without quantifying the effect of disease on wildlife were not included. Most studies of disease transmission between wildlife and livestock focused on disease effects on livestock only.

Additionally, numerous studies investigated diet overlap between domestic and wild herbivores, but did not measure any realized impact on wildlife based on this potential overlap. Similarly, a number of studies measured changes in vegetation created by grazing and discussed these in the context of wildlife habitat, but did not actually measure a wildlife response. Therefore, these studies were not included. Large carnivores are mostly excluded from this review because the majority of studies on livestock–carnivore interactions focused only on human–carnivore conflict and livestock depredation by predators. However, studies which focused on the effect of livestock on wild carnivores through changes in the abundance or vulnerability of their prey were included.

We also note that this review focused on effects of *managed* livestock only. Feral livestock have been known to cause severe negative effects on wildlife, especially on islands (Phillips *et al* 2012), but studies of feral livestock are not included here. This review also did not include studies which focused on the effects of human activities related to ranching, such as fencing or construction of new water developments, but not the effect of livestock themselves on wildlife. For example, the effect of constructing new livestock watering ponds on frog abundance was not included. However, the effect of livestock grazing around ponds, whether natural or artificial, was included. Therefore, negative effects from activities such as shooting or poisoning of predators or competitors, but not a result of livestock themselves, are not captured in this review.

2.2. Data extraction, further inclusion/rejection criteria

All studies included in the list of relevant sources were then examined more closely and the following information extracted:

- (1) Reference source: journal article, report, conference proceedings, book chapter, thesis
- (2) Article type: primary literature, mathematical model, review/commentary
To avoid duplication, a thesis was generally only included when the data were not published

elsewhere, such as in a journal article or conference paper. Review papers and commentary articles were used to identify other studies we may have missed in our initial searches. However, these articles were not used directly in the following further data extraction methods.

For primary literature that contained data and results from original research, we also extracted the following information.

- (3) Study type : determined as one of the following
 - a. Controlled experiment: where treatments were created or variables manipulated for the purpose of testing the effect of livestock grazing
 - b. Natural experiment: where authors used some kind of existing variation in livestock on the landscape (e.g. ranches with different stocking rates; grazed versus ungrazed adjacent properties) as treatments to specifically examine the effect of this livestock factor
 - c. Correlational study: where authors used a gradient or continuum of existing variation in some livestock or grazing factor, often in combination with other environmental correlates or co-factors
- (4) Livestock type(s): cattle, sheep, goats, other
- (5) Comparison type(s): grazing intensity, land use, grazing system (such as rotational versus continuous), livestock type, grazing timing (such as spring versus fall grazing)
- (6) Treatment categories included: e.g. grazed, ungrazed or no, light, heavy grazing intensity, as defined by the authors of that study
- (7) Whether any special grazing systems other than continuous grazing (such as deferred-rotation or short duration grazing) were considered in the study and what they were
- (8) Duration of study (in years)
- (9) Geographic Region: North America, Central/South America, Europe, Africa, Asia, Australia
- (10) Location, narrowed to country and in North America to state or province
- (11) Habitat type, as described by the authors
- (12) Wildlife class: mammal, bird, reptile, amphibian.

2.3. Extraction of positive, negative, and neutral effects on mammals

Our initial list of all relevant sources included several comprehensive reviews detailing positive and negative effects of livestock grazing on various groups of birds, though mostly from North America. See especially Saab *et al* (1995), Briske *et al* (2011) and Hartway and

Mills (2012), but also Kirsch *et al* (1978), Bock *et al* (1993) and Tewksbury *et al* (2002).

However, in general, such reviews were not available for mammals, although see (Jones 2000, Tabeni and Ojeda 2003, Chaikina and Ruckstuhl 2006, Briske *et al* 2011). Mammals are an important taxon to consider because they span a large range of body sizes and diet types. As livestock are also mammals, there is reason to believe that livestock grazing may have a significant impact on mammalian wildlife, particularly other ungulates with which they may compete directly for food. Small mammals which depend on vegetative cover may also be strongly affected.

Therefore, we then took the subset of primary sources which looked at mammals and extracted information on positive, negative, and neutral effects of livestock on wild mammals. We first noted what general types of mammals were included in each study: small mammals (including rodents, shrews, and lagomorphs), ungulates, carnivores, primates, kangaroo, or other. Then, individual effects were extracted from each study.

For small mammals, all of the controlled experiments were included as well as most of the natural experiments, but correlational or observational studies were not used, as grazing was often confounded with other factors. For ungulates, over half of the studies were categorized as correlational. Therefore, in order to obtain a large enough sample of responses, we first extracted responses from the controlled and natural experiments, then relaxed the criteria to include many of the correlational studies as well. Some correlational studies were still excluded because they did not focus on livestock grazing itself, but rather on effects of land use change or human settlement. Only studies which attempted to isolate the effect of livestock grazing apart from other human influences were used.

Effects on mammals were noted as being either at the species level, such as differences in abundance or pasture use by an individual species, or at the community level, such as differences in diversity or total abundance for a number of species in aggregate.

For studies of grazing intensity, we looked for wildlife differences between treatments that varied in intensity of grazing. That is, when an idle or ungrazed treatment was part of the study it was compared to each of the grazed treatments. In cases where there was no ungrazed treatment, we looked at the effect of increasing grazing intensity (e.g. light versus heavy). Positive and negative responses were noted when the authors found a statistically significant difference in the variable of interest between treatments or with increasing grazing intensity. A wildlife result was considered positive if sites with grazing had higher abundance or diversity than ungrazed sites, or if those variables increased with increasing grazing intensity. A result was negative if wildlife abundance or diversity declined with grazing. If no significant difference was

seen between treatments, the response was listed as neutral. For a few of the older studies, authors did not use modern statistical analyses, so a positive, negative, or neutral response was determined based on how authors worded their conclusions in the text. When possible, we also verified that the data in any tables presented matched this conclusion.

For studies that contained more than one grazing treatment or intensity level (such as no grazing versus light, moderate, and heavy grazing), we also noted whether all grazing treatments studied were positive or negative compared to the ungrazed control or if the wildlife response depended on intensity. For example, a species might increase in abundance relative to ungrazed sites with moderate grazing, but decline in abundance relative to ungrazed at heavy grazing intensity. We then also explicitly noted whether a response showed support for the highest values being found at intermediate grazing intensity or not.

For the few comparisons dealing with grazing system or livestock type, we noted whether wildlife abundance or diversity was higher under one system, grazing time period, or livestock type over the other.

3. Results

3.1. Characterization of included studies

We compiled a final list of 807 relevant sources: 11 books, 50 book chapters, 48 conference papers, 606 journal articles, 57 reports, 32 theses, and 3 other.

This included 646 primary sources, 10 mathematical models, and 151 review or commentary sources (including 2 meta-analyses).

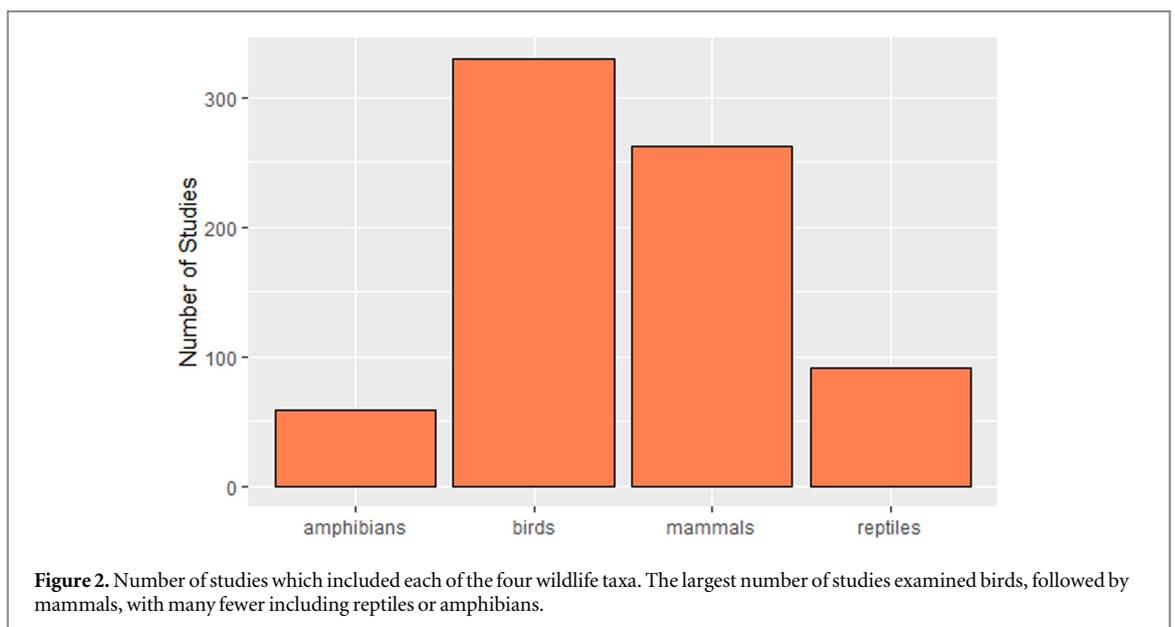
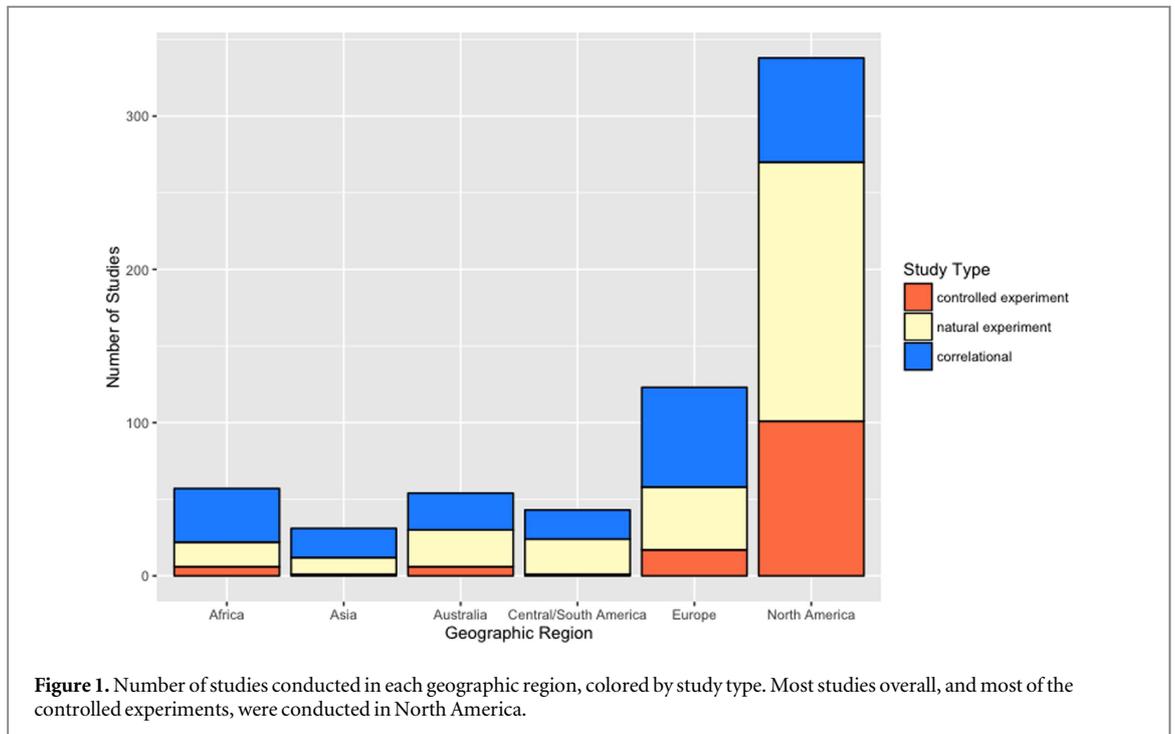
For primary sources only:

Study type: Only 132 studies could be considered an attempt at a controlled experiment, though many lacked more rigorous standards such as adequate replication. 284 studies fell into the category of natural experiment and 230 were purely correlational or observational.

Geographic locations: Most studies were from North America ($N = 338$) followed by Europe (123), with many fewer studies from Africa (57), Australia (54), Central/South America (43), or Asia (31) (figure 1).

Wildlife taxa: Most studies examined birds ($N = 330$) and mammals (262), with fewer including reptiles (91) or amphibians (58) (figure 2). Note numbers do not add up to 646 because some studies examined more than one taxon.

Livestock type: The majority of studies ($N = 381$) investigated cattle grazing only. Another 134 studies included cattle along with other livestock, principally sheep, but also goats, horses, donkeys, buffalos, yaks and pigs. In most of these studies, all livestock types were lumped together and not directly compared to one another. (Only 21 studies explicitly tested the effect of grazing by different livestock types on



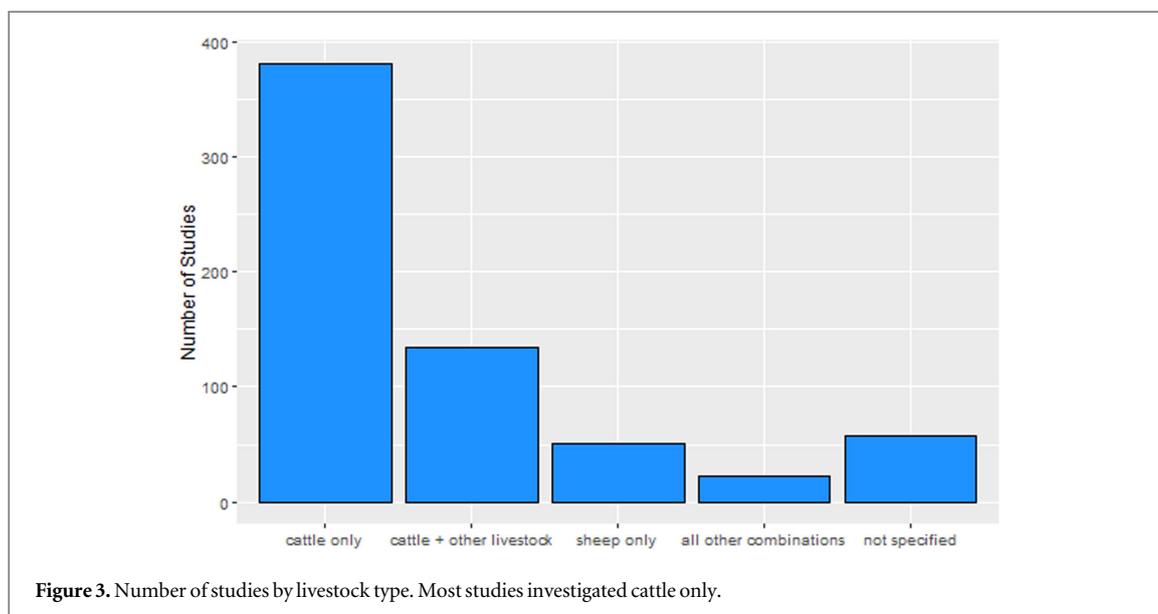
wildlife.) 51 articles investigated sheep grazing only. 57 articles did not specify the type of livestock involved (figure 3).

Duration of studies: In some cases the authors did not specify study duration or it was difficult to determine from the description. In other cases, two or more separate wildlife surveys were conducted a number of years apart, but not during the intervening period. Of 632 studies where we were able to determine study length, 38% ($n = 245$) lasted one year or less, many of which encompassed only a single sampling period at each site, with no repeats or follow up surveys. Greater than 63% lasted two years or less ($n = 403$, including the 245 of one year or less duration).

More details on all of the above results can be found in the supplemental data file containing a list of all primary studies and the study type, livestock type (s), comparison type(s), duration of study, geographic region, location, and wildlife class(es) extracted from each.

3.2. Mammal results

For the 262 studies that examined mammals: 140 included small mammals, 111 included ungulates, 26 included carnivores, nine kangaroo family, seven primates, and 11 other (bats, panda, echidna, possum, aardvark).



We extracted positive, negative, and neutral responses from a total of 182 studies, 110 from North America, 21 from Europe, 19 from Africa, 14 from Asia, 10 from Australia, and 8 from South America.

These studies produced over 600 wild mammal responses. Only nine comparisons from seven studies looked at differences between grazing systems. Only three showed effects of livestock type. The rest investigated variation in grazing intensity. Of the grazing intensity comparisons, 109 were at the community level, virtually all from small mammals, and >500 were at the individual species level. At the species level, 352 were from small mammals, 146 from ungulates, and 10 for carnivores.

3.2.1. Small mammals

For the community-level responses, 60 responses from 41 studies looked at small mammal total abundance and 49 responses from 34 studies examined small mammal diversity, usually in the form of species richness, though some also calculated Shannon diversity index or evenness scores.

The effect of livestock grazing on community-level small mammal abundance was found to be predominately negative. All geographic areas had a greater number of negative responses than positive ones. Summed across all geographic areas, we found 8 positive, 34 negative, and 18 neutral responses of community-level small mammal abundance to livestock grazing (table 2). If we make a null prediction that there should be an equal number of positive, negative, and neutral responses, we find the observed number of responses in each category to be highly significant (chi-squared = 17.2, $df = 2$, $p < 0.001$). Both an excess of negative responses and a paucity of positive responses compared to the null contribute to this high chi-squared value.

For small mammal species richness, responses were again found to be more negative than positive in

each geographic region, but with a higher number of neutral responses. Summed across all geographic areas, we found 1 positive, 26 negative, and 22 neutral responses of small mammal richness to livestock grazing (table 2). The higher number of neutral responses reflects the fact that many studies found a change in species composition from ungrazed to grazed sites, but the overall number of species remained relatively unchanged. Again compared to a null prediction of equal number of responses in each category, we find the observed distribution to be highly significant (chi-squared = 22.08, $df = 2$, $p < 0.0001$), predominately as a result of there being only one positive response.

Detailed tables of all community-level small mammal responses with study citations can be found in supplementary tables S1 and S2.

Though total community small mammal abundance generally shows a negative response to grazing, individual species responses vary considerably. Table 3 shows trends in individual species responses summarized by taxonomic Order, Family, and Genus for some Families. We find that some taxonomic groups, such as voles, harvest mice, cotton rats, and shrews, show consistently negative responses to grazing (combined 3 positive, 77 negative, 18 neutral responses; chi-squared = 93.67, $df = 2$, $p < 0.001$) while others, such as deer mice, kangaroo rats, ground squirrels, and lagomorphs, are more likely to show positive or variable responses (combined 58 positive, 26 negative, 35 neutral responses; chi-squared = 13.73, $df = 2$, $p = 0.001$), consistent with the different lifestyles and habitat requirements of these species.

Virtually all of the studies looked at changes in a species' abundance with grazing. Less than ten studies focused on other types of responses such as growth rate, activity budgets, diet selection, body mass, survival, sex and age ratios, or number of fetuses in the population. Therefore, there is currently not enough

Table 2. Community-level small mammal total abundance and diversity responses to grazing. Positive = increase with grazing, negative = decrease with grazing, neutral = no change.

Community small mammal Abundance				Community small mammal Species Richness			
GeoRegion	Positive	Negative	Neutral	GeoRegion	Positive	Negative	Neutral
Africa	0	2	2	Africa	0	4	1
Australia	1	3	1	Australia	0	1	2
Europe	1	5	2	Europe	0	1	4
North America	6	24	13	North America	1	20	15
Total	8	34	18	Total	1	26	22

Table 3. Species-level small mammal responses to grazing, summarized taxonomically. Some families or genera show consistent negative responses to livestock grazing while others show more positive or variable responses.

Order	Family	Genus ²	Description	Positive	Negative	Neutral	
Rodentia	Cricetidae	total	voles, New World rats and mice	33 ³	90	38	
		<i>Clethrionomys</i>	bank and red-backed voles	0	2	2	
		<i>Lagurus</i>	sagebrush vole	0	3	0	
		<i>Microtus</i>	voles	3	32	8	
		<i>Neotoma</i>	woodrats	0	1	3	
		<i>Onychomys</i>	grasshopper mice	3	3	5	
		<i>Peromyscus</i>	deer mice and others	27	16	18	
			deer mouse (<i>P. maniculatus</i>) only	26	13	15	
		<i>Reithrodontomys</i>	harvest mice	0	17	2	
		<i>Sigmodon</i>	cotton rats	0	11	0	
		Dipodidae		jumping mice	0	3	2
		Geomyidae		pocket gophers	3	4	0
		Heteromyidae	total	pocket mice, kangaroo rats	19	20	16
			<i>Chaetodipus</i>	pocket mice	1	7	1
			<i>Dipodomys</i>	kangaroo rats	11	3	10
			<i>Perognathus</i>	pocket mice	7	10	5
		Muridae			3	17	7
		Nesomyidae		African mice	0	3	1
		Sciuridae		prairie dogs, chipmunks, squirrels	15	9	8
Eulipotyphla	Soricidae		shrews	0	12	6	
Macroscelidea	Macroscelididae		elephant shrews	0	2	1	
Dasyuromorphia	Dasyuridae		planigales, dunnarts	0	1	4	
Lagomorpha	Leporidae		rabbits, hares	13	8	6	
		Total		86	169	89	

² Only Genera with at least 3 responses shown.

³ 26 of the 33 (+) responses are from one species, deer mouse (*Peromyscus maniculatus*).

data to draw conclusions about the effect of grazing on behavioral, demographic, dietary, physiological, and life history responses of small mammals.

The most-studied species, by far, is the deer mouse (*Peromyscus maniculatus*), with 54 responses (26 positive, 13 negative, 15 neutral), followed by the western harvest mouse (*Reithrodontomys megalotis*) with 14, and the field vole (*Microtus agrestis*) with 12. A full list of responses and citations for each species is found in supplementary table S3.

3.2.2. Ungulates

We extracted positive, negative, and neutral responses of ungulates from 74 studies: 41 from North America, 12 from Asia, 11 from Africa, 7 from Europe, and three from South America. The types of wildlife responses

measured in ungulates were more varied than they were for small mammals. Instead of being limited to changes in abundance, ungulate responses fell into four broad categories which we labeled as follows:

- (1) Site use: differences in wildlife density between sites or relative use between pastures that vary in grazing intensity, or changes in distribution or habitat selection in response to livestock introduction
- (2) Food: effects of livestock on diet selection, nutrients, foraging efficiency, or percent time spent feeding versus resting or traveling
- (3) Health: effects of livestock presence or stocking rate on parasite loads, weight gain, or fat stores

Table 4. Responses of wild ungulate species to livestock grazing. Numbers of positive, negative, and neutral responses (extracted from 74 individual studies) are summarized for groups of similar species and grouped by diet type: browsers, intermediate mixed feeders, and grazers. Families highlighted in orange are the non-ruminants. All others are ruminants.

	Order, Family	Subfamily	Species	Positive	Negative	Neutral
Browsers	ARTIODACTYLA					
	Bovidae	Bovinae	nyala, kudu, eland	2	4	1
	Cervidae	Capreolinae	mule and white-tailed deer	6	27	15
	Moschidae		musk deer	0	1	0
	All browser responses (N = 56)			8	32	16
Mixed feeders	Antilocapridae		pronghorn	0	2	2
	Bovidae	Aepycerotinae	impala	2	2	0
	Bovidae	Antilopinae	Thomson's, Grant's gazelle	2	0	0
	Bovidae	Caprinae	ibex	0	2	1
	Bovidae	Caprinae	bighorn sheep, bharal, argali	1	7	4
	Camelidae		guanaco, vicuna	0	3	0
	Cervidae	Cervinae	chital, elk, red deer, muntjac, sambar deer	10	18	8
	Suidae		warthog, wild boar	4	1	2
	PROBOSCIDEA					
	Elephantidae		African, Asian elephant	0	4	1
All mixed feeder responses (N = 76)			19	39	18	
Grazers	Bovidae	Alcelaphinae	hartebeest, topi, tsessebe, wildebeest	3	5	0
	Bovidae	Bovinae	gaur, banteng, Cape buffalo	0	4	0
	Bovidae	Reduncinae	puku, waterbuck	0	2	0
	PERISSODACTYLA					
	Equidae		kiang, plains zebra	4	4	1
	All grazer responses (N = 23)			7	15	1
Grand Total				34	86	35

- (4) Demography: differences in young:adult ratios or survival with variation in livestock grazing intensity

Total numbers of positive, negative and neutral responses, of all types, are summarized in table 4, with species grouped by diet type into browsers, mixed feeders, and grazers. We also distinguish between animals with different digestive systems by highlighting the non-ruminant families in orange. All other, non-highlighted species are ruminants. We found that grazers have been much less studied than browsers or mixed feeders, with only 23 total grazer responses compared to 56 and 76 responses for the other two groups, respectively. Within the browser and mixed feeder groups, some species have also been studied much more than others. Three species, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and elk (*Cervus Canadensis*), account for nearly 44% of all the work done, with a combined 68 responses out of the total 155. Non-ruminants account for only 21 of the responses. The remaining 134 responses are from ruminant species.

Summed for all species together, we found more negative effects of livestock grazing on wild ungulates ($N = 86$) than positive (34) or neutral (35) responses, but responses do vary by diet type and species. Browsers, represented mostly by mule and white-tailed deer, showed a preponderance of negative responses (32) compared to positive ones (8). Across all diet types, the only family to show more positive than negative responses overall was Suidae, represented by two non-ruminant species, warthog and wild boar. A few other families or subfamilies showed possible trends toward positive or an equal number of positive and negative responses, namely equids (family Equidae), impala (*Aepyceros melampus*), Antilopine and Alcelaphine antelopes, and European red deer (*Cervus elaphus*), but sample sizes are small for all of these groups.

The full table of all species responses, response types, and study citations can be found in supplementary table S4. All of the following results discussed in this section refer to supplementary table S4.

Of the four categories of response listed above, changes in site use were the most studied ($N = 93$), followed by feeding (15), demography (7), and health

(3). As mentioned above, cervids have been the most studied group to date, especially mule deer, white-tailed deer, and elk. With respect to changes in site use, these species often, but not always, reduced use of pastures or shifted their distribution to steeper slopes or less preferred habitat types once livestock were introduced.

For a number of species, responses were both negative and positive, varying by season. Therefore, one area deserving further research is the possible balance between facilitative impacts of livestock grazing on improving forage quality for wild ungulates during certain times of year with competitive interactions at other times, in relation to the growing season of the vegetation. We found that many studies were conducted in only one season or did not quantify differences in responses between seasons. However, for those studies that did specifically compare responses between different times of year, we found three cases where a species responded positively in both seasons, three cases where a species responded negatively in both seasons, and 19 cases where the response changed from negative or neutral to neutral or positive between different times of year, with approximately equal numbers of positive and negative responses overall (22 positive, 19 negative, 9 neutral responses).

For example, in Africa, several species including warthog, topi, wildebeest, and plains zebra showed a negative response during the dry season, but a positive response in the wet season (Bhola *et al* 2012). In Europe and North America, a number of studies found that ungulates avoided livestock when they were present on pastures, but preferred previously grazed sites once forage re-grew (see supplementary table S4). Effects of livestock on wild ungulate feeding also varied. In one study, fecal nitrogen was lower in white-tailed deer feces collected from treatments with cattle in February during the winter, but higher with cattle in August and October following plant growth (Jenks *et al* 1996). In another study on deer, grazing had no effect on dietary nutrients, a negative effect on digestibility, and a positive effect on foraging efficiency (Thill *et al* 1987).

For the few studies that investigated demography and health, responses were again variable. Young to adult ratios decreased in bharal (*Pseudois nayaur*) (Mishra *et al* 2004, Suryawanshi *et al* 2010), showed no difference in chital (*Axis axis*) (Dave and Jhala 2011), and increased in red deer (*Cervus elaphus*) (Gordon 1988) in response to livestock grazing. In white-tailed deer, reproductive rates and fawns surviving to yearling age both decreased with an increase in stocking rate (McMahan and Ramsey 1965, Jenks and Leslie 2003). In contrast, the proportions of newborn warthog (*Phacochoerus africanus*) and juvenile topi (*Damaliscus lunatus jimela*) were higher in grazed ranches with shorter grasses and lower predation risk than in a protected reserve (Bhola *et al* 2012).

For health, donkeys as surrogate zebras gained more weight and had fewer parasites when grazing with cattle than alone (Odadi *et al* 2011a). However, in chital, helminth loads were higher with sympatric cattle than without in scrub forest, but showed no difference in dry deciduous forest (Dharmarajan *et al* 2003). White-tailed deer from areas with cattle had lower carcass weights and fat attributes in February, but there was no difference in August with moderate grazing (Jenks and Leslie 2003).

Note that because most veterinary or disease-related studies did not meet the inclusion criteria, one known area of negative effects missing from this review is the evidence of respiratory disease and fatal pneumonia in bighorn sheep caused by contact with domestic sheep. See reviews in Krausman *et al* (1996), Schommer and Woolever (2008), Wehausen *et al* (2011), mathematical models in Clifford *et al* (2009), Cahn *et al* (2011), and Carpenter *et al* (2014), and additional data in Shannon *et al* (2014) and Sells *et al* (2015).

3.2.3. Intermediate grazing intensity

At the individual species level, small mammals tended to either continually decrease or increase with increasing livestock grazing intensity, depending on their habitat requirements for either dense cover or open or bare ground (supplementary table S3). Therefore, we found only twelve cases where a small mammal species' abundance was highest at intermediate grazing intensity and thirty-eight cases where abundance was highest at either no or heavy grazing. For ungulates, namely white-tailed deer, mule deer, and elk, we found four cases where site use was highest at intermediate grazing intensity, nine cases where no grazing was best for site use, feeding or demography, and one case where heavy fall grazing by cattle had the highest site use by mule deer the next year. Because most studies only compared grazed to ungrazed conditions, there is little data available to investigate this hypothesis at the community level.

4. Discussion

4.1. Study attributes and limitations

During the initial search for relevant articles, many studies were identified which stated a perception or opinion that livestock grazing has had a certain effect on wildlife or discussed effects of livestock on wildlife habitat attributes. However, upon closer inspection, we found that a large number of these studies did not actually quantify effects of livestock on wildlife. Our final list of relevant studies includes only those that actually measured wildlife responses to livestock grazing. The full list of 807 sources, including reviews and commentary articles, can be found as a supplemental All Citations document.

Within this final list, there is great variation in study design and quality. Many studies compared only grazed versus ungrazed conditions, and the intensity of grazing is often not reported (a limitation also noted by Briske *et al* 2011). A review by Barrett *et al* (1999) of existing literature on California rangelands points out that grazing is most often treated as a yes or no proposition, but is really a complex process where timing, frequency, duration, season of use, and intensity matter. The terms 'grazing' and 'overgrazing' are not defined in most of the statements where they are used.

Measures of grazing intensity that are reported also come in different forms: for example, number of animals per hectare versus percent utilization of the vegetation. This makes comparing studies to one another difficult. What is considered 'moderate' grazing in one study may be very different from what is considered 'moderate' in another. Additionally, very few studies were judged to be attempts at a controlled experiment where livestock numbers or systems were intentionally manipulated, and even many of these lacked elements such as adequate replication.

The final list of relevant sources also shows clear biases in geography, livestock type, and wildlife taxa studied to date, with most coming from North America on cattle, birds and mammals. Far fewer studies have been done in the developing world, in Africa, Asia, and Central and South America, even though these regions support large livestock populations and many people in these regions rely on livestock for their livelihoods (Robinson *et al* 2014). Livestock types other than cattle have also been poorly studied, despite large or growing populations in some regions of the world.

Many different livestock grazing systems have also been developed and implemented around the world (see Bryant *et al* 1982 for examples in the USA and South Africa), but their impacts on wildlife are not well known. Effects of different grazing systems on soils and vegetation have been conducted, but rigorous comparisons of wildlife responses are rare. We found only seven studies that looked for differences in wildlife responses between grazing systems. Briske *et al* (2011) also conclude in their review that the limited number of available studies does not permit generalizations concerning wildlife responses to grazing systems and when or where or for which species positive, negative, or neutral responses may be predicted.

4.2. Positive, negative, and neutral effects of livestock on wildlife

Reid *et al* (2013), in a book chapter titled 'Global Livestock Impacts on Biodiversity', assert that the impacts of livestock on biodiversity are principally negative, although there are some positive impacts as well. A number of authors, however, see more room for positive impacts of livestock, given 'proper' management, where livestock could even be used as a

tool to manage rangelands for ecosystem health or wildlife habitat (Holechek *et al* 1982, Urness 1982, Severson 1990, Severson and Urness 1994, Bleich *et al* 2005, Vavra 2005, Derner *et al* 2009, Augustine *et al* 2011, Briske *et al* 2011). However, it is often unclear what constitutes 'proper' management, and whether this means simply setting an 'appropriate' stocking rate of livestock to avoid overgrazing, or if more ongoing adaptive management is necessary to promote positive impacts of livestock at certain times of year, while minimizing negative impacts at other times.

Severson (1990) outlines four general categories of strategies for using livestock to enhance wildlife habitat: (1) Alter the composition of the forage base; that is, change the proportions of plant species present and perhaps cause the introduction of others, (2) Increase the productivity (available forage) of selected species in the forage base, (3) Increase the nutritive quality of the forage, or (4) Alter the structure of vegetation.

These four categories of change are likely to be of varying importance to different types and species of wildlife. We found generally that changes in cover and vegetation structure are important to small mammals, though in taxon or species-specific ways, while ungulates may be affected more by interference competition from the physical presence of livestock and by changes in forage quantity and quality, as discussed in more detail in the sections below.

4.3. Small mammals—species and community-level responses

We found that overall small mammal abundance at the community level generally declines with grazing (34 negative responses), although occasionally increases (8 positive responses), while individual species responses vary dramatically. Community species richness either declines (26 negative responses) or stays the same (22 neutral responses), but rarely increases with grazing (only 1 positive response). We believe all of these results derive from the interplay between the lifestyle and habitat requirements of individual small mammals and the effect that livestock grazing has on changing the architecture of the vegetation.

According to Grant *et al* (1982), the general composition of grassland small mammal communities is determined primarily by structural attributes of the habitat. However, as different small mammals require different types and levels of vegetation for escape hiding cover and food sources, the presence of livestock benefits some species and hinders others. Therefore, some authors conclude that livestock grazing, when used as a habitat manipulation tool, is very wildlife species-specific in its benefits (Fulbright and Ortega-Santos 2006).

We found that there is species-specificity in response to grazing, but some general patterns emerge

as well. Species adapted to more open habitats are often positively affected by livestock grazing, while species needing denser cover or specific vegetation structure are negatively affected, as seen in Bock *et al* (1984). This leads to the patterns seen in table 3, where certain families or genera of small mammals show consistent negative responses while others are more likely to show positive responses to grazing. Some of the species known to show positive responses to grazing were considered pests by early ranchers in North America.

A number of other authors have noted this general pattern as well. Many members of the family Cricetidae are more frequent in ungrazed areas, while some members of the family Heteromyidae do better with low cover. Jones *et al* (2003) developed a conceptual model of habitat relationships among rodents which says that cricetids, specifically the genera *Sigmodon*, *Baiomys* and *Reithrodontomys*, dominate areas with the most and tallest ground cover. Among heteromyids, pocket mice (*Chaetodipus* and *Perognathus*) are common in areas of intermediate cover and kangaroo rats (*Dipodomys* spp.), are abundant in areas with the most bare soil. They conclude that in relatively mesic grasslands, livestock grazing will drive the rodent community toward one dominated by heteromyids instead of cricetids. In more arid landscapes, grazing favors kangaroo rats over pocket mice.

While cover for protection from predation is often cited as the mechanism for small mammal responses (Powell *et al* 2000), other studies have concluded that effects of livestock on food quantity and quality (Keasing 1998, Keasing and Young 2014) or negative effects of trampling on the suitability of soils for building predator-inhibiting burrow systems (Torre *et al* 2007) may be just as, or more important for some species. Overall, small mammals that require little vegetative cover and have general diets appear to be more resilient to grazing (Johnston and Anthony 2008). For example, the deer mouse is one of the most widespread and generalized of all North American rodents. In many studies it was the most common small mammal trapped in both the grazed and ungrazed habitats.

However, even within a species, responses to grazing may vary depending on habitat. Fulbright and Ortega-Santos (2006) assert that direct impacts of livestock grazing on wildlife depend largely on stocking rate, climate, and soils because vegetation responses to herbivory vary across environment gradients and gradients of grazing pressure. They conclude that livestock grazing may increase plant diversity and animal densities in humid bioclimatic zones, but may reduce plant diversity and wildlife densities in semiarid habitats. Hanley and Page (1982) also found that in xeric habitats grazing reduced the diversity of plant growth forms and small mammals, while the opposite was true in mesic habitats where grazing increased the diversity of both. Moulton *et al* (1981) found that grazing had the least effect on small mammal associations

in shortgrass and the greatest effect on associations in riparian woodland. Grant *et al* (1982) found that grazing had the greatest (negative) effect in tallgrass and montane habitats, and relatively little effect at shortgrass and bunchgrass sites.

From our review of species studied to date, there appears to be a greater number of small mammal species which decline with grazing than increase with it. Therefore, livestock grazing will often lead to a decline in community-level small mammal abundance as well. However, depending upon the mix of species in any particular habitat, total abundance may sometimes increase in communities dominated by positively-responding species. Species richness can also decline with grazing, as some species disappear from grazed sites. However, sometimes there is instead a change in species composition from ungrazed to grazed sites while the overall number of species remains relatively the same, but hardly ever increases.

4.4. Ungulates

Our review of ungulate responses to livestock grazing shows some interesting patterns and also highlights needs for future research. Several factors are hypothesized to be important for predicting individual ungulate responses to grazing, including the diet type, digestive system, and body size of both the livestock and wild ungulate species involved. In table 4, we grouped species by diet type in order to investigate whether these groups are affected differently by livestock grazing, as is predicted from theory.

First, we found that the majority of studies have been conducted on just a few species of cervids, mostly from North America. Therefore, most responses were from browsers and mixed feeders, with less data available on wild grazers. Diet overlap should be highest between two animals in the same feeding guild and of similar body size, who may thus compete most strongly for food. Given that most of the studies conducted so far have been on cattle, a large grazer, it is perhaps surprising that our review found so many negative responses exhibited by browsers, namely mule deer and white-tailed deer. We believe several factors may be at play here. A number of these negative responses appear to be due to interference competition, where ungulates are responding to the physical presence of livestock, rather than immediate changes in forage quantity or quality. Several authors noted that deer and elk would actively avoid livestock in shared pastures or shift their use of sites as soon as livestock were introduced, a response they referred to as 'social intolerance'. In North America, where livestock often roam freely in pastures without being actively herded during the day or corralled at night (as they are in Africa) this impact may be chronic.

However, other authors did suggest negative effects of livestock on food quantity and quality as the mechanism for negative responses by cervids. In some

locations, this appears to be as a result of overgrazing or heavy cattle intensity, where cattle compete with deer for food, especially at high stocking rates and with low rainfall. Though deer are considered browsers and cattle grazers, a number of studies observed deer eating some grass and cattle utilizing browse plants. Therefore, in some habitats or in times of forage scarcity, diet overlap and exploitative competition between cattle and deer may be higher than expected. This may be especially true when livestock and wild ungulates share pastures year-round.

In contrast, cattle use of pastures during only certain parts of the year may possibly promote facilitation. Our review found that when responses between seasons were specifically investigated, many cases ($n = 19$) showed a negative or neutral response in one season, but a shift to a neutral or positive response in another, rather than uniformly positive ($n = 3$ cases) or negative ($n = 3$) responses in both seasons. For example, Willms *et al* (1979) found that heavy fall grazing by cattle increased mule deer use of the pasture the next year. He concluded that the mechanism explaining this result is that fall cattle grazing removed mature forage, making spring forage more attractive to deer. Yeo *et al* (1993) also found a positive response by mule deer, which selected habitats previously grazed by cattle. He, too, suggested that cattle improved forage productivity and availability for deer.

The one study that did compare white-tailed deer responses to variation in both grazing intensity and livestock type (Merrill *et al* 1957) found results consistent with the prediction of decreased competition between two ungulates of dissimilar diet type and size. Merrill found that deer showed the strongest negative response to grazing by goats, a similar-sized animal that also eats large quantities of browse, followed by sheep. In contrast, treatments that included cattle, a large-bodied grazer, showed less negative effects and perhaps even an increase in deer site use at light stocking levels as a result of range improvement.

Chaikina and Ruckstuhl (2006), in their review of positive and negative effects of cattle grazing on ungulates, also noted that the majority of studies focused on deer, even though diet overlap between deer and cattle is relatively small. They conclude that future research should concentrate more on investigating the effects of cattle on ungulates that consume graminoids as part of their diets, because the impact of grazing should be greater for this group. We similarly found that wild grazers have been relatively under-studied (less than 15% of all responses, 23 of 155, are from grazers) and believe this group of ungulates deserves more attention. We also add that two important factors to consider when comparing wild to domestic grazers are body size and mode of digestion (ruminant versus non-ruminant).

One explanation for why so many grazing species coexist in African savannas is that they divide up food resources based on body size. Smaller animals have

higher metabolic rates relative to their size than larger animals (Kleiber 1947). This has important implications for the energy requirements and diet choices of different species; small animals are more constrained by the quality of their food, while large animals are more constrained by the quantity of forage available (Belovsky 1997).

However, this relationship is complicated by differences in digestion (Demment and Van Soest 1985). Rumination allows foregut fermenters to obtain more energy per gram of food, but limits intake when feeding on poor quality forage. Theory then predicts that a non-ruminant can tolerate lower quality forage for its size and should select a diet similar to that of a much larger ruminant (Illius and Gordon 1992). This relationship between body size, digestion, and preference for quality versus quantity of grass has been found in response to burning of grasslands (Sensenig *et al* 2010). Recent research has also shown that zebra, a large non-ruminant, can facilitate cattle by removing stems and improving forage quality at certain times of year (Odadi *et al* 2011a, 2011b).

Therefore, we predict that cattle may facilitate smaller-bodied grazers, especially ruminants, by removing old, tall, poor quality grass and stimulating new growth, but may compete with large-bodied grazers in times of resource limitation if they remove too much forage. Though grazers as a class and African and Asian species in general have been little-studied to date, the work that has been done so far partially supports these predictions. In table 4, we found that certain families or subfamilies, namely suids and smaller and medium-sized antelopes, showed possible trends toward positive or an equal number of positive and negative responses. Meanwhile, large grazers in the subfamily Bovinae, which are most similar to domestic cattle, showed exclusively negative responses. Similarly, Bhola *et al* (2012) found that small-sized herbivores, requiring short, nutritious grasses, were more abundant in ranches than a protected reserve in both the wet and dry season. Medium-sized herbivores moved seasonally between landscapes. Larger-bodied herbivores, requiring bulk forage but less susceptible to predation, were more abundant in the reserve than the ranches.

Wild grazer responses may also be contingent on time of year and condition of the vegetation. This can be seen in the results from Bhola *et al* (2012) where warthogs, wildebeest, topi, eland, and plains zebra seemed to prefer grazed ranches in the wet season, but moved to the protected reserve in the dry season. As mentioned above, a number of studies of mule deer, elk, and red deer (*Cervus elaphus*) showed negative responses when cattle were present, but later preferred sites that had been previously grazed by cattle over those that had not. These results also seem to support the hypothesis that cattle can sometimes improve vegetation quality for some species (facilitation), dependent on rainfall and growing season, but may

reduce forage quantity to the point of competition during the non-growing season. Jenks *et al* (1996) found lower fecal nitrogen levels in white-tailed deer sharing land with cattle in February, indicating possible competitive interactions in winter, but higher dietary quality in summer for deer exposed to cattle, suggesting that cattle can facilitate growth of early successional plants. Therefore, it may be the net effect of both facilitative and competitive interactions over the course of a year or an animal's lifetime that is most important in structuring populations.

Our review also found that non-ruminants have been little studied, accounting for less than 14% of all responses measured (21 out of 155). However, we do note some possible interesting patterns from the limited data available. In table 4, suids were the only family to show more positive than negative responses. This may be due in part to their classification as omnivores, capable of a varied diet and dealing well with disturbance. Warthogs also use a unique kneeling stance while feeding that enables them to get low to the ground and eat very short grass. Equids showed an equal number of negative and positive responses to date and, as mentioned above, may compete with livestock during the dry season while being facilitated by them in wet seasons. Elephants showed almost exclusively negative responses, but we hypothesize that this may be the result of a behavioral response to avoid humans, especially in Africa where poaching is a threat.

Overall, most studies have examined only short term responses, such as a shift in use of sites with and without cattle during one or a few seasons. However, the long term population-level consequences of short term changes in behavior, diet, or even health caused by livestock grazing are not well known. Because of the long life spans and generation times of most of these species, population level changes in abundance have only been investigated at the coarsest level.

For example, in Africa, authors have attempted to correlate declines in wildlife population sizes over several decades to increases in livestock numbers over that same time period. However, many other related and unrelated variables were also changing over this period. A number of these studies concluded that land use changes, drought effects, and poaching are among the potential factors that may have been most responsible for declines (Ottichilo *et al* 2000a, 2000b). Kiffner *et al* (2015) assert that areas used for livestock keeping in Africa can maintain high wildlife species richness and that direct and indirect effects of agricultural and settlement expansions are the main drivers of species richness loss. Georgiadis *et al* (2007) found that, where favored, diverse and abundant wild herbivores can thrive even when sharing the landscape with a slightly higher biomass density of livestock. Where not favored, only a few resilient wild species (e.g. gazelles and plains zebra) persist with high densities of livestock.

Future research on a variety of ungulate species and livestock types, especially in regions other than North America will add valuable data to the field to help confirm or revise the patterns evident so far. A more detailed examination of the mechanisms leading to these responses and the particular conditions under which they are likely to occur is especially needed. Chaikina and Ruckstuhl (2006) note that there is a great degree of inconsistency in methodology among different ungulate studies, which makes comparisons difficult. This is something we found to be true as well and advocate for developing more standard methods that can be repeated and compared across studies.

4.5. Non-mammalian wildlife responses

From the numerous reviews conducted on birds, we see that responses of birds parallel those of small mammals. As stated by Briske *et al* (2011), bird responses to stocking rate are well recognized as being species dependent and can be positive, negative, or neutral within any one location and treatment comparison. This species-dependency of bird responses is well-supported in our search of the literature. See especially Saab *et al* (1995), but also Bock *et al* (1993) and Tewksbury *et al* (2002) for reviews of bird species that show positive, negative, neutral, or mixed responses to grazing.

Principal mechanisms for the effect of livestock grazing on birds, according to Fuller and Gough (1999), are: (1) loss of preferred vegetation types, (2) alteration of food supplies and (3) alteration of predation pressure. Powell *et al* (2000) assert that livestock use influences bird populations primarily by influencing the kind, amount, and structure of vegetation. As with small mammals, livestock activity appears to promote birds that favor open, disturbed habitat, and has a negative effect on those that prefer closed, undisturbed areas (Bock *et al* 1984). Passerine birds are particularly sensitive to changes in the shrub and tree component.

A few bird species show clear positive relationships and close associations with livestock, such as cowbirds (*Molothrus* spp.), cattle egrets (*Bubulcus ibis*), and barn swallows (*Hirundo rustica*). This association is attributed to increased feeding opportunities on insects provided by the livestock (either an increase in insect abundance or by making the prey easier to obtain) and in the case of barn swallows, perhaps also by increased nesting sites via the barns in which livestock are kept. Because cowbirds are nest parasites on other bird species, the increase of cowbirds associated with livestock can lead to a decrease in other birds. This has led to the use of livestock removal as a management technique to reduce parasitism of host nests. However, it is unclear if removal or reduced stocking of cattle actually leads to a decrease in cowbirds.

Responses of reptiles also seem to parallel those of small mammals, with some species tending to decrease

with grazing while others increase. At the community level, reptile responses may also depend on the habitat. For example, Rotem *et al* (2016) found that reptile diversity increased with grazing intensity at mesic sites, but decreased with grazing at arid ones. They conclude that grazing, by reducing vegetation cover, increases habitat heterogeneity in the dense mesic sites and decreases habitat heterogeneity in the arid sites. Thus, the same direction of habitat alteration caused by grazing may have opposite effects on biodiversity and community composition in different climatic contexts.

4.6. Intermediate grazing intensity

As mentioned above, many studies examined only grazed versus ungrazed conditions, and, therefore, do not provide an opportunity to examine the intermediate grazing hypothesis, especially in mammals. There is some indication that intermediate grazing intensities may be beneficial for birds in some contexts. Piana and Marsden (2014) found that moderate cattle densities may benefit some raptor species and help maintain the high raptor diversity in their study area. Prior *et al* (2011), studying reproduction in the meadow pipit (*Anthus pratensis*), found that offspring sex ratio varied significantly between grazing treatments, where the proportion of sons was lowest in the ungrazed and intensively grazed treatments and highest in treatments grazed at low intensity. They contend that these results support growing evidence that too much grazing, or the complete removal of livestock from upland areas, is detrimental for common breeding birds. In general, more work needs to be done investigating a range of grazing intensities and in different habitat contexts.

5. Conclusion

From the many individual studies that have investigated wildlife responses to livestock grazing, this review has identified patterns as well as gaps in our current knowledge. Broad patterns that emerge include the importance of fundamental properties such as body size, lifestyle, and diet in controlling wildlife responses to livestock grazing. Vegetation structure and cover appear most important for small mammals, birds, and reptiles, while forage quantity and quality, along with interference competition from livestock presence, drive ungulate responses. Among small mammals, species that need denser cover for protection generally decrease in abundance with grazing, while species adapted to open habitats increase. For ungulates, results are more complicated. These studies are more variable in methods and quality than those for small mammals, and there is geographic bias and a lack of data in several key areas. Most studies have been done in North America on browsers and mixed feeders, namely deer and elk, which show a majority of negative responses to livestock grazing

resulting from habitat restriction or a decline in diet nutritional quality. These observations from the New World when applied to the Old World are partially supported. We see similar negative responses to livestock grazing from large browsers and mixed feeders. However, as body size gets smaller and studies focus on grazing species, the results appear to change. Although data is limited, several of the grazing species in Africa such as zebra, warthog and smaller-bodied antelopes show a trend toward positive habitat use responses, suggesting possible facilitation. For a number of species, responses varied by season with negative responses to livestock grazing found at one time of year, but positive responses seen in another. If livestock are to be used as a tool for habitat or ecosystem management, factors such as body size, diet type, and seasonality need to be taken into account. However, we currently have an incomplete picture of ungulate responses. Africa may be different from North America because of its longer co-evolutionary history of wildlife with people and their herds of livestock, but more studies are needed to investigate this. Therefore, we find a strong need for additional research on ungulates of varying diets and body sizes, especially in the developing world. Particular attention should be paid to any changes in responses across seasons or environmental conditions, where tradeoffs in competition and facilitation may occur over time. Future data of this sort will be critical for informing wildlife-conscious livestock management around the world.

Acknowledgments

We thank two anonymous reviewers for their helpful comments in strengthening an earlier version of this manuscript. This work was partially funded by National Science Foundation Grants CNS-1453428, CNS-1248080 and IIS-0705311-III-CXT to D I Rubenstein, the Princeton University Department of Ecology and Evolutionary Biology and the Class of 1877 Fund, and the Princeton Environmental Institute Grand Challenges Program. We also thank David Pappano for assistance in creating figures.

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