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Review

Ungulates and Their Impact on Reptiles: A Review of Interspecific Relationships

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Abstract: Several ungulate species are showing increasing population patterns within their geographical distribution ranges, leading to constant interactions with other animal species. Varying densities and activities of different ungulates may result in diverse impacts on other coexisting species groups, including large numbers of threatened species, such as reptiles. In this study, we performed an analysis of the available literature to investigate the impacts of ungulates on reptiles. We aimed to reveal the diversity of: (1) the geographical and environmental distribution of related investigations; (2) the ungulate and reptile species involved; and (3) the characteristics of interactions (direct or indirect, positive or negative) from 69 publications. Our results show that the most papers were reported from the Americas (42%) and Australia (28%). The proportions of studies were balanced for wild ungulates (53%) and livestock (47%). Wild boar (*Sus scrofa*) was found to be the most problematic species on reptiles whereas reptiles which suffered the harshest impacts were Squamates (i.e., lizards, and snakes). Ungulate activities (e.g., digging by wild boar) may directly harm reptiles (consuming or killing them) or indirectly affect them by modifying their habitats or destroying their hideouts. Some preferential effects were also noted (e.g., by moderate livestock grazing or when wild ungulates are prey for large reptiles). Published livestock impacts were mainly indirect and mostly negatively linked to overgrazing. We conclude that it is important to manage and monitor the densities of ungulates to minimize their negative impacts on reptile species, especially in case of wild boar and grazing livestock, but also to maintain their moderate beneficial effects (e.g., as prey basis).

Keywords: deer; lizard; overgrazing; reptiles; rooting; snake; ungulate effects; wild boar

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1. Introduction

Recently, world ecosystems have been experiencing a significant increase in the population of several ungulate species in numbers and their geographic range sizes, especially in the northern hemisphere [1,2]. The increase in ungulate communities is closely related to human socio-demographic modifications in addition to the increasing availability of unused, abandoned lands and rural agricultural areas, which result in abundant food supply for ungulates [3]. The lack of native predators [4], strict hunting legislation and declining numbers and aging of hunters [5,6] may also play a significant role in the current increasing populations of ungulates.

Despite the ever-changing climatic conditions affecting biodiversity across the globe some ungulates are thriving and gaining stable populations (i.e., wild boar, *Sus scrofa*), red deer (*Cervus elaphus*), wildebeest (*Connochaetes* spp.) or reindeer (*Rangifer tarandus*)) [6–9]. Although the dense populations of ungulates may bring financial benefits for conservation and society through tourism and hunting [10] they may also cause cascading effects on their ecosystem [11]; ungulates with high reproductive capabilities [12] may exert significant impacts on various wildlife species (e.g., insects, birds, and other mammals in an ecosystem).

Different ungulate species can follow different foraging strategies and feed on diverse food items [13] (e.g., they may graze, browse or do both, they can even consume animal food). Furthermore, when feeding they prefer certain habitat patches [14–16], plant species and plant parts and feed at specific heights within the available vegetation strata [17]. Consequently, their various feeding behaviour (including selective feeding, trampling and defecating) generates diverse changes in the vegetation patterns and animal communities of the habitats [18,19].

Reptiles are one of the most ecologically and evolutionarily remarkable classes of living creatures, having colonized nearly every part of the globe, including the seas and some of the world's most harsh and environmentally fragile environments [20]. Many reptile species share similar habitats with ungulates [21] mainly in terrestrial environments. Within the animal taxa, reptiles face strong declines globally [22,23] and their populations are tremendously fragmented [24]. Reptile species may be directly and indirectly impacted by the presence of dense populations of ungulates through grazing (by both livestock and wild ungulates), trampling, and opportunistic predation [25]. A high level of ungulate disturbances can homogenise the areas and destroy favoured habitat patches of reptiles [26]. However, preferential effects of ungulates can also establish appropriate heterogeneous habitat or can modify insect or small mammal prey availability and foraging opportunities for reptile species [27]. From the other side, large-bodied reptiles (e.g., Komodo dragon, *Varanus komodoensis*) may have a direct negative impact on ungulates but lack of these ungulates as prey may be a significant threat to them [28].

Monitoring of ungulate populations and their effects in the ecosystems is crucial to mitigate the threats to herpetofauna and mainly enhance the beneficial outcomes from ungulate presence. For a better understanding of the usual mechanisms and concerned species, we performed a systematic analysis of literature and investigated the direct and indirect effects of ungulates on reptiles from a global perspective. Our main research questions were: (1) in which geographical ranges and habitat types were ungulate-reptile interactions mainly reported; (2) which species (ungulate vs. reptile) were involved in these interspecific relationships; (3) what is the nature of revealed effects; direct or indirect and positive or negative for the participants of these interactions?

2. Materials and Methods

2.1. Literature Search and Paper Selection

We performed a broad literature search on the Web of Science database (Clarivate; https://www.webofknowledge.com; accessed on 1 June 2022) and SCOPUS (Elsevier; https://www.scopus.com; accessed on 10 December 2022), in accordance to the guidelines of Preferred Reporting Items for Systematic Reviews and Meta-Analyses–PRISMA (http://www.prisma-statement.org; accessed on 10 December 2022) for bibliographic surveys [29]. We searched the whole database and retrieved articles published in English from 1990 through 2022 using a combination of keywords/nomenclature, i.e., Total Search = ((impact* OR effect* OR grazing* OR browsing* OR rooting* OR trampling*) AND (Squamat* OR herpetofauna* OR reptile* OR snake* OR tortoise* OR alligator* OR crocodile* OR lizard* OR turtle*) AND (ungulate* OR hoofed* OR deer* OR wild boar* OR pig* OR livestock* OR elephant* OR antelope* OR gazelle* OR horse* OR peccari*)) searching in the titles, keywords and abstracts of the potential sources.

We considered only peer reviewed papers, other reports such as websites, newspapers, newsletters were excluded. We managed to obtain 1181 scientific articles from our entire literature search. We found four review papers which we used to extract additional publications from the references listed which were not found by our search. We selected these papers when the title of the source suggested it has data or information about the impact of ungulates on reptiles.

All of the identified records were screened by their title and abstract. For articles which were not excluded but were unavailable to the public and we had no direct access to them, we contacted the authors requesting for full papers. The retrieved scientific articles were read thoroughly in details, searching for investigations and descriptions on ungulate-reptile interactions. Following this assessment for eligibility, we found that 69 papers (5.8% of the initial articles) reported clearly impacts of ungulates on reptiles, either direct or indirect. Within the 69 papers, some studies reported more than one type of impact, hence, in total we analysed 75 interactions. Since the reports on this topic were relatively limited, we did not specify or filter the years of publishing during the further analyses.

2.2. Data Extraction and Analysis

From the articles retrieved through our broad literature search, we extracted the following information: the country/continent where the study was carried out, the type of habitat, study approach (i.e., observational (direct observation in the field, e.g., [30]), descriptive (short- and long-term correlational studies, e.g., [31]) or experimental (manipulation of impacting factor, using exclusion and inclusion methods, e.g., [32])), the ungulate and reptile species of interest of the studied interaction, the nature of impact caused by ungulates (direct or indirect and negative or positive from the point of view of reptiles). We identified the conservation status of the affected reptiles according to IUCN Red List (https://www.iucnredlist.org; accessed on 30 June 2022). Ungulates were further grouped as wild and domestic ones, furthermore, we split them by their digestive system and foraging characteristics. Based on the latter three main groups were distinguished: (1) foregut fermenter Herbivores (Ruminants); (2) hindgut fermenter Herbivores; and (3) monogastric Omnivores.

We categorized an impact as positive for reptiles: (1) when ungulates are prey to reptiles; (2) when ungulate activities benefit the reptiles either directly or indirectly and this was stated by results of the original source. We further distinguished impact as negative for reptiles: (1) when ungulate species intentionally or opportunistically prey on reptiles (e.g., if wild boar predates on snakes during rooting); (2) when ungulate activity significantly modifies the habitat characteristics (e.g., ungulates destroy habitat of reptile species by rooting or trampling) leading to a decrease in reptile density.

First, we analysed the spatial and temporal trends in the number of publications appeared in the studied topic. To describe the different types of effects of ungulates on reptile species, we paired ungulates with reptiles they have impacted based on all reported interactions. Furthermore, we listed the different ungulate-reptile pairs studied and calculated the number of cases of their mentioning. We also analysed the findings on wild ungulates and livestock and on the three digestive/foraging categories separately and compared the relative proportion of their negative and positive; direct and indirect effects on reptile species. The frequency distribution of these categories and impact types were evaluated by Pearson's Chi-squared test with Yates's continuity correction. Additionally, we calculated the odds ratio of the most informative category combinations to quantify the strength of the potential associations (e.g., whether wild ungulates tend to exert more direct impacts than livestock). If the value is higher than 1, the event is more likely to occur in the first group (e.g., wild ungulates do have more direct impacts on reptiles) and vice versa [33].

3. Results

3.1. Spatiotemporal Patterns of Research, Species Involved

The relatively low quantity of original research articles (n = 69) shows that studies focusing on ungulate-reptile interactions are scarce.

From our literature search results we can reiterate that studies on ungulate-reptile interactions have been gaining increasing attention by the scientific community in the last decade as there are more recent (2010–2021; n = 41) and fewer older papers (1973–2009; n = 32) (Figure 1). More attention was given to livestock interaction with reptiles as opposed to wild ungulates in the 1973–2002 period (n = 12 and n = 7, respectively). Whereas wild ungulates and their interactions with reptiles have been researched more intensively in the past two decades (n = 30 and n = 20, respectively). We found that 64% (n = 44) of the papers published a descriptive study, 29% (n = 20) of them published experimental research, and direct observational publications constituted 7% (n = 5).

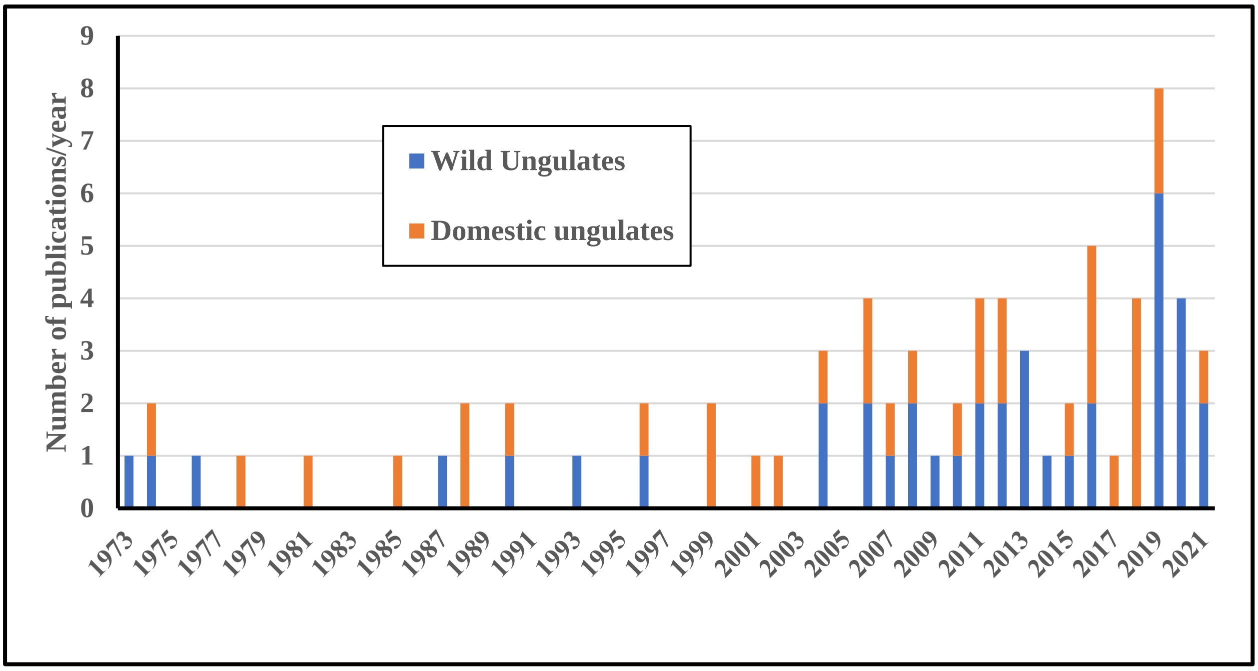

Figure 1. Number of publications per year (n = 73, including review papers) focusing on the impact of wild and domestic (livestock) ungulates on reptile species based on the selected publications of the search.

The geographical distribution of the studies shows that 42% (n = 29) of investigations were conducted in the Americas, 28% (n = 19) in Australia, and only 13% (n = 9) in Europe, 12% (n = 8) in Africa, 4% (n = 3) in Asia and 1% (n = 1) in Oceania, excluding Australia (i.e., New Zealand, Figure 2).

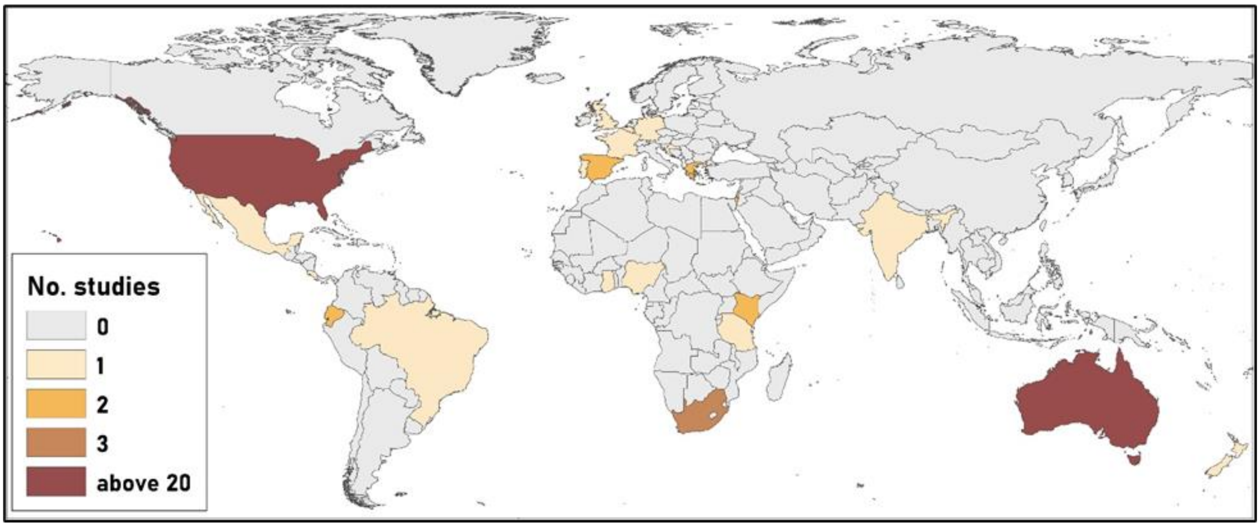

Figure 2. The distribution (by percentage number of papers, n = 69) of researches by countries which reported ungulate impacts on/interactions with reptiles. The remaining four papers are accounted for the review studies which did not specify the geographical location of the study.

We found that 59% (n = 41) of the studies were conducted dominantly on terrestrial landscapes in mixed habitats (usually a mosaic of different macro- and microhabitat types;

shrublands, grasslands, forest, woodlands, etc.). The remaining 41% (*n* = 28) took place in homogenous habitats; 21% on grasslands, 12% in forests, 6% on wetlands and 2% on shrubby areas. In some occasions studies were carried out near and linked to aquatic ecosystems; for example, in case of nest predation by wild boar on sea turtles.

Fifteen ungulate species (13 Artiodactyla, 2 Perissodactyla) were mentioned in the literature and 47 species of reptiles were affected by them (Appendix A Table A1); 34% (*n* = 16) of those reptiles have high conservation value according to IUCN Red List wherein 13% of 47 species (*n* = 6) are Endangered ones, 11% (*n* = 5) have a Near Threatened status, 6% (*n* = 3) are Vulnerable and 4% (*n* = 2) of the reptiles are Critically Endangered (Appendix A Table A1). *Sus scrofa* was stated as the most problematic species among many other wild ungulates to a variety of reptile species. *Bos taurus* and *Ovis aries* were dominantly studied livestock ungulates according to our results and had more revealed interactions with reptiles than other livestock species.

3.2. Comparison between Wild and Domestic Ungulates

Studies on impacts were balanced between wild ungulates and livestock in terms of their interactions with reptiles, showing a proportion of 53% and 47% (*n* = 40 and *n* = 35, respectively) (Figure 3). We found that 61% of the interactions (*n* = 46) showed examples on indirect ungulate impacts and 39% of them (*n* = 29) were direct effects. Livestock caused indirect impacts on reptiles more frequently than wild ones (63%; *n* = 29 vs. 37%; *n* = 17), and the reverse was found for the direct impacts (Figure 3A). The indirect impacts mostly included overgrazing and/or overbrowsing by livestock (i.e., removal of understorey) whereas the dominant direct impact was found to be the predation by wild ungulates. For both ungulate species groups negative effects on reptiles were much more common (livestock 48%; *n* = 28 vs. wild ungulates 52%; *n* = 30) (Figure 3B).

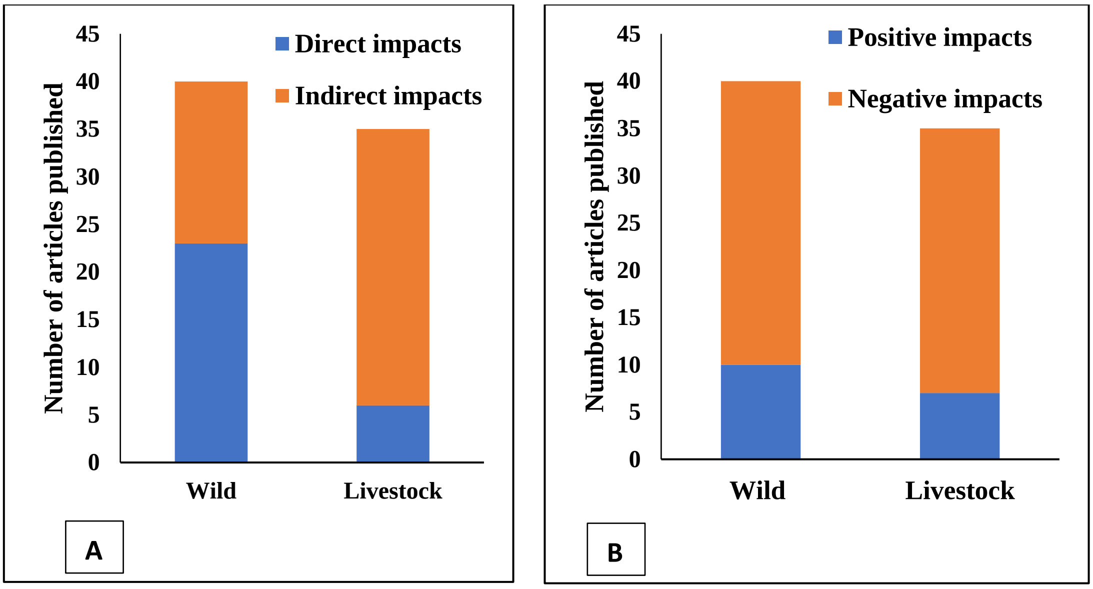

Figure 3. Different types of impacts (**A**: direct and indirect or **B**: positive and negative, respectively) on reptiles by wild and domestic ungulates based on the reported 75 interactions between 1973 and 2021.

Our results show that wild ungulates have one main characteristic type of direct and negative impact on reptiles, which is predation (reported when ungulates directly killed the reptile or remains of reptiles were found in the stomach content) (Figure 4, Appendix A Table A1). Their indirect and negative impacts were mainly related to drastic changes in habitat and vegetation by overgrazing activities causing a decrease in reptile richness. However, the indirect and positive impacts by wild ungulates also included grazing/browsing and in some cases their local overabundance (i.e., overutilisation of the area with their combined effects), when high density of ungulates changed the vegetation cover making it suitable for reptiles. Direct positive impacts of wild ungulates were also recorded; these are the situations when wild ungulates are preyed upon by large-bodied reptiles.

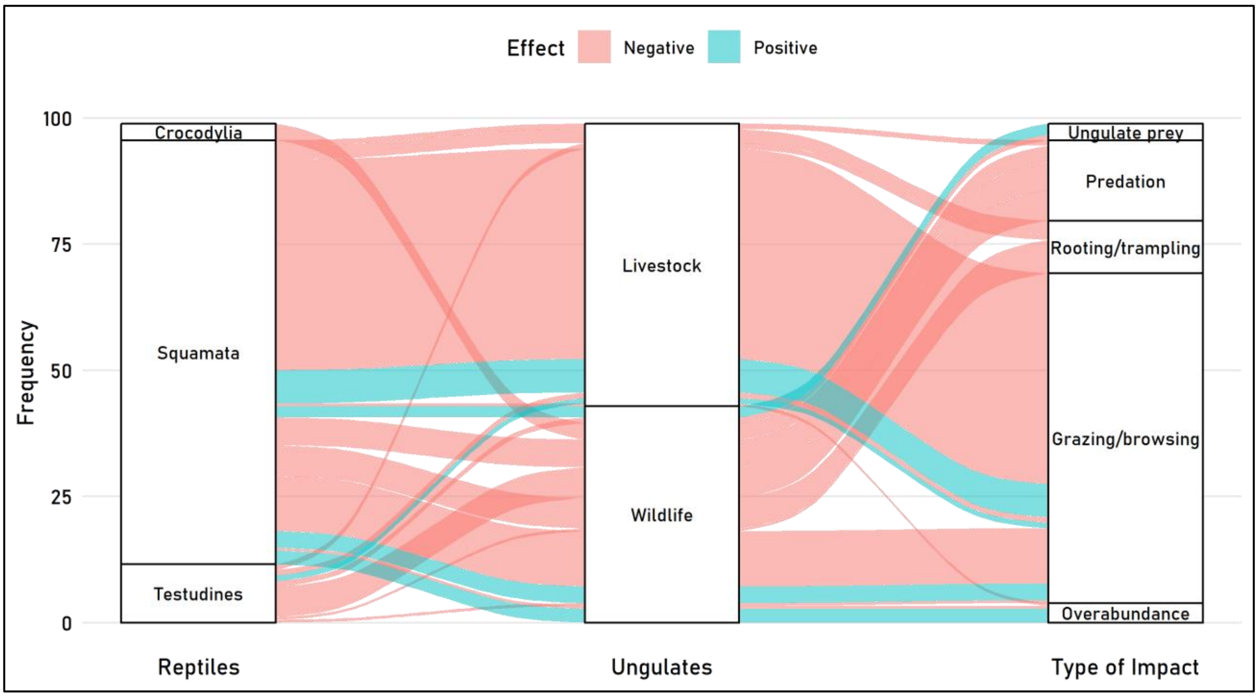

Figure 4. The distribution patterns (frequencies) of publications showing the different types of impacts/interactions of ungulates (wild ones and livestock separately) on/with different orders of reptiles.

Similarly, to wild ungulates, in the case of livestock, the indirect and negative impacts dominantly featured overgrazing, meanwhile their indirect positive impacts comprised of maintaining preferential vegetation characteristics by moderate grazing. However, there are currently no statements on domestic ungulates in the role of prey for reptiles or as their predators (Figure 4, Appendix A Table A1).

Squamates (i.e., lizards and snakes) were the most negatively affected reptiles by ungulates, variedly impacted by both, wild ungulates and livestock (Figure 4). Occasionally, ungulates had positive impacts on Squamates, when they provided their prey or through grazing effects. In the second case, in highly dense vegetation, ungulates browsing and grazing created open spaces to allow light penetration on the ground, leading to the increased abundance of reptiles. Crocodylia (i.e., alligators) endured only negative impacts, came from wild ungulates; specifically, *Sus scrofa* predation on their nest. Testudines (tortoises and turtles) were affected mainly negatively (and primarily by wild ungulates through predation of adults and the nests (destroying eggs and killing hatchlings)).

There was a significant difference in the nature of impacts on the reptiles by wild ungulates and livestock (Tables 1 and 2). Impacts by wild ungulates tend to be more often direct than in case of livestock. This can be related to the fact that the proportion of predation on reptiles by wild ungulates was significantly higher than in the case of livestock. However, the proportion of grazing/browsing impacts was higher for livestock than for wild ungulates.

Table 1. The results of Pearson's Chi-square tests with Yates continuity correction on ungulate-reptile interactions comparing wild ungulates and livestock. *** $p < 0.001$.

	Wild ungulates		*Livestock*		χ^2 (df)	*p*
	N	**%**	**N**	**%**		
Effect					0.06 (1)	0.811
Positive	10	13.4	7	9.3		
Negative	30	40	28	37.3		
Nature of impact ***					11.17 (1)	0.000
Direct	23	30.7	6	8		
Indirect	17	22.6	29	38.7		
Impact type						
Ungulate prey	5	6.7	0	0	2.89 (1)	0.089
Grazing/browsing ***	8	10.7	30	40	29.67 (1)	0.000
Predation ***	16	21.3	1	1.3	12.65 (1)	0.000
Overabundance	4	5.4	1	1.3	0.59 (1)	0.439
Rooting/trampling	6	8	3	4	0.25 (1)	0.618
	Direct		*Indirect*			
Effect					3.03 (1)	0.08
Positive	3	4	14	18.7		
Negative	26	34.7	32	42.6		

Table 2. Odds ratios and their 95% confidence intervals of the specific combinations of ungulate impact type vs. ungulate species groups (wild ungulates or livestock); the nature (direct or indirect) of ungulate impact vs. positive ungulate effects.

Comparison		**Odds Ratio**	**95% Confidence Interval**
Effect: *Positive*	*Wild ungulates*	1.33	0.4–3.9
Impact nature: *Direct*	*Wild ungulates*	6.53	2.2–19.3
Impact type: *Ungulate prey*	*Wild ungulates*	11	0.6–206.6
Impact type: *Grazing/browsing*	*Livestock*	24	7.1–81.6
Impact type: *Predation*	*Wild ungulates*	22.67	2.8–182.7
Impact type: *Overabundance*	*Wild ungulates*	3.78	0.4–35.5
Impact type: *Rooting/trampling*	*Wild ungulates*	1.88	0.4–8.2
Impact nature: *Direct*	Effect: *Positive*	0.26	2.2–19.3

3.3. Comparison between Ruminants and Monogastric Ungulates

A significant amount of ungulates in the reviewed studies were ruminant domestic ungulates, thus the majority of impacts were related to them (Tables 3 and 4). The importance of Ruminants is huge in shaping reptile (especially Squamata) communities, the majority of articles reported this combination of interactions. Ruminants tended to show more indirect effects than direct ones. Meanwhile, the opposite was found for omnivores.

Independent of the attributes of the digestive system of ungulates, all of them exerted mostly negative impacts. However, this association was not turned out as significant. Regarding to Omnivores, almost all of their effects came out as a negative one to reptiles and the vast majority of these were direct ($\chi^2 = 4.77$, df = 1, $p = 0.03$; Odds-ratio: negative × direct: 37; CI = 1.35–1015.3). Due to the low number of cases, it is hard to prove associations for Hindgut fermenter herbivores and their effects on reptile populations, but their impacts were reported mostly as negative. The impact types of Ruminants were the most diverse and expressed both negative and positive effects to reptiles.

The bulk of predation impacts were related to Omnivores (eating reptiles or eggs), and it affected every taxonomic order of the reported reptile species. While Ruminants were mainly involved in grazing and browsing impact of which a part was reported as positive for reptiles. Rooting or trampling nearly equally distributed among the three ungulate foraging groups, but trampling was more characteristic to Ruminants and Hindgut fermenter herbivores; while rooting was mainly caused by wild boar (i.e., Omnivores (Tables 3 and 4)).

Table 3. The results of Pearson's Chi-square tests with Yates continuity correction on ungulate-reptile interactions grouped by the digestive system and foraging characteristics of ungulates (i.e., foregut fermenter herbivores (Ruminants); hindgut fermenter herbivores and monogastric Omnivores). *** $p < 0.001$.

	Ruminants		***Omnivores***		***Hindgut fermenters***		χ^2 **(df)**	***p***
	N	**%**	**N**	**%**	**N**	**%**		
Domestication status ***							40.03 (2)	0.000
Livestock	35	46	0	0	0	0		
Wild	12	16	22	29	7	9		
Nature of impact ***							25.14 (2)	0.000
Direct	10	13	18	24	1	1		
Indirect	37	49	4	5	6	8		
Effect							4.69 (2)	0.09
Positive	15	20	2	3	1	1		
Negative	32	42	20	26	6	8		
Impact type ***							53.93 (10)	0.000
Ungulate prey	4	5	1	1	0	0		
Grazing/browsing	34	45	0	0	4	5		
Predation	1	1	16	21	1	1		
Overabundance	4	5	1	1	0	0		
Rooting/trampling	4	5	3	4	2	3		

Table 4. Odds ratios and their 95% confidence intervals of the specific combinations of domestication status, nature and outcome of impact, ungulate impact type vs. ungulates categories based on their digestive system and foraging characteristics.

Comparison		**Odds Ratio**	**95% Confidence Interval**
Foraging group: *Ruminant*	*Livestock*	161.88	9.2–2855.3
Foraging group: *Omnivore*	Impact nature: *Direct*	17.6	4.9–62.6
Foraging group: *Ruminant*	Impact nature: *Indirect*	7	2.5–19.8
Foraging group: *Omnivore*	Effect: *Negative*	4.21	0.9–20.2
Foraging group: *Ruminant*	Effect: *Negative*	0.25	0.06–0.9
Foraging group: *Omnivore*	Impact type: *Predation*	141.33	15.1–1263
Foraging group: *Ruminant*	Impact type: *Grazing/browsing*	16.35	4.8–56.2

4. Discussion

The sporadic geographical distribution of studies suggests that ungulate-reptile interactions receive significantly different levels of attention globally by scientific community. Relative to the reptile diversity of the continents, an increasing number of studies is expected from Asia, Africa or South-America. Previous researches reported distinct impacts and interactions between ungulates and reptile communities on different continents. For example, in Australia, where all ungulates are non-native and the ecosystems are more sensitive to their effects, the studies revealed significant impacts in the form of grazing effects by livestock (e.g., cattle; *Bos taurus*) [34–36] or predation by wild ungulates (i.e., wild boar on marine turtles) [37], meanwhile in Asia the predation of reptiles on ungulates (Komodo dragon on Javan rusa, *Rusa timorensis*) [38] was a particular interspecific relationship. Although the largest part of the studies was a descriptive one providing mainly correlational information, the significant number of experimental studies (by manipulation of ungulate presence) also support the various ungulate effects on reptiles by more reliable methodologies of impact assessments.

We found that 59% of the studies took place in heterogenous habitats types (a mixture of shrublands, open grasslands, woodlands, wetlands, and riparian habitats). Mixed or mosaic areas are typical habitats for reptiles [39], and therefore studies are important in supporting the habitat management and species conservation efforts.

Our results show that ungulates may be significantly problematic to reptiles and to their habitat especially if they occur in high densities; similar conclusions were drawn by Graitson et al. [40] in the case of wild boar. Ungulates may cause more harmful than beneficial impacts to reptiles. The most disruptive ungulate species was found to be the wild boar. Our data showed that wild boar can have tremendous impacts on reptiles due to their rooting/digging behaviour which may result in opportunistic feeding of reptiles and change the habitat structure or decrease preys (lizard, amphibians and other invertebrates) for reptiles in the ecosystem. Since many different reptile species were affected by their foraging behaviour, it would be hard to state which ones were mostly impacted, as this is also dependent on the effort of scientific research conducted on specific reptile species. However, it is clear that coexistence of reptiles with ungulate populations, especially with wild boar, and mainly in case of their high density, will result in several negative effects [41]. A recent analysis demonstrated that wild pigs threaten 672 taxa in 54 different countries across the globe, most of them being listed as critically endangered or endangered, and some additional ones have been driven to extinction as a direct result of impacts from wild pigs [42].

Our results reflect that both direct and indirect ungulate effects can shape the reptile communities but that indirect effects that are less obvious and more difficult to detect are more common. This is consistent with previous studies (e.g., by Larson and Paine) [43]. We found that the indirect impacts are more dominant by livestock than wild ungulates and mainly related to grazing. Livestock grazing is the most widespread land-use on Earth, and can also have some negative effects on biodiversity [44] including reptiles [45]. Indirect impacts by livestock and wild ungulates primarily include overgrazing, which often affects the abundance of reptiles [36].

Positive impacts by ungulates on reptiles were seldom, but we could also reveal some favourable situations (for example, the presence of ungulates may favour some arthropods [46], which can provide prey basis for reptiles). In terms of indirect interactions shaping habitat characteristics by ungulate activities has a special significance and can also lead to favourable conditions. Reider et al. [47] mentioned that collared peccary (*Pecari tajacu*) is an important agent that affects leaf litter structure and promotes the increase in occurrence of terrestrial reptiles. Even abundant ungulates may also result in positive impacts for reptiles; in abandoned areas, they can contribute to halting forest encroachment and maintaining the required habitat heterogeneity, creating a suitable habitat for reptiles [48]. Similarly, in a recent study in an urban area, it was also demonstrated [49] that wild boar rooting enhances sand lizard (*Lacerta agilis*) populations in dry grasslands, likely by creating a mosaic of bare ground, litter, sparse and dense vegetation. Positive direct impacts were linked to wild ungulates, being potential prey to large-bodied reptiles such as the above-mentioned Komodo dragon preying on Javan rusa [38] or the African python (*Python sebae*) feeding on kob (*Kobus kob*) [30]. Conversely, in such cases reptiles may also cause negative impacts on rare/endangered ungulate species, therefore management of populations or the impact of large-bodied reptiles should also be taken into consideration.

However, the significant number of reptiles with high conservation value affected by ungulates is alarming and should not be ignored. Many of ungulate species are continuously increasing and this proliferation of wild and domestic ungulates may be locally detrimental for reptile species coexisting with them. Effective management should function to monitor the dynamics of ungulates in order to ensure fewer negative impacts on reptile communities. Similarly, close monitoring of ungulates should take place in ecosystems where ungulates such as deer are prey to large-bodied reptiles. Further research and reporting by the scientific communities are encouraged to better understand the diversity of investigated ungulate-reptile interactions. Overgrazing by livestock and wild boar foraging activities tend to be the most problematic impacts on reptiles from ungulates. Therefore, well-planned grazing regimes by livestock and effective control of abundant ungulates, especially wild boar outside its native geographical range, need to be considered in habitats of vulnerable reptile species. Instead of total eradication of ungulate effects promoting moderate ungulate impact is recommended to maintain their beneficial effects without causing damaging impact on reptile communities.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. List of ungulate and reptile species (common and Latin name) mentioned in the scientific papers. Each ungulate is paired with reptile it has impacted and *vice versa*. Type of the reported impact (kind of ungulate activity and whether direct or indirect and positive or negative to reptiles) and the papers publishing them are demonstrated. *"−" = Negative impact, "+" = Positive impact. IUCN Conservation status: Least Concern* $^{(LC)}$*, Endangered* $^{(EN)}$*, Critically Endangered* $^{(CR)}$*, Vulnerable* $^{(VU)}$*, Data deficient* $^{(DD)}$ *and Near Threatened* $^{(NT)}$.

Ungulate Species (Latin Name)	Ungulate Species (Common Name)	Reptile Species (Latin Name)	Reptile Species (Common Name)	Type of Impact	+/−	Number of Times Pairs Mentioned in Publications	Authors
Axis axis	Chital deer	*Lacerta viridis* ^{LC}	Green lizard	(Indirect) **Grazing**—deer removes understorey (habitat) of lizards	−	1	Mohanty et al., 2016
Bos taurus	Cattle	*Centrochelys sulcata* ^{EN}	African spurred tortoise	(Indirect) **Grazing**—cattle reduce food for spurred tortoise	−	1	Petrozzi et al., 2018
Bos taurus	Cattle	*Clemmys muhlenbergii* ^{CR}	Bog turtle	(Indirect) **Grazing**—cattle remove cover for turtles	−	1	Tesauro and Ehrenfeld, 2007
Bos taurus	Cattle	*Iguana iguana* ^{LC}; *Lygodactylus sp.* ^{LC} *and Tiliqua scincoides* ^{LC}; *Phrynosoma platyrhinos* ^{LC}	Green iguana; Dwarf gecko and Common blue-tongued skink; Desert horned lizard	(Indirect) **Competition** (interference)—for space-use between reptiles and cattles	−	3	Mitchell, 1999; Neilly et al., 2018; Newbold and Macmahon, 2008
Capra hircus	Domestic goat	*Hemidactylus turcicus* ^{LC}	Mediterranean house gecko	(Indirect) **Grazing**—goat removes under-storey/cover (habitat)	−	1	Pafilis et al., 2013

Table A1. *Cont.*

Ungulate Species (Latin Name)	Ungulate Species (Common Name)	Reptile Species (Latin Name)	Reptile Species (Common Name)	Type of Impact	+/−	Number of Times Pairs Mentioned in Publications	Authors
Equus asinus	Feral burro	*Gopherus agassizii* ^{CR}	Mojave Desert tortoise	(Indirect) **Grazing**—overgrazing by abundant burros reduce population density of tortoises	−	1	Berry et al., 2020
Kobus kob	Kob	*Python sebae* ^{NT}	African rock python	(Direct) **Predation**—python feeds on kob as prey	+	1	Antwi et al., 2019
Loxodonta africana	African elephant	*Lygodactylus. spp.* ^{LC} *and Tiliqua scincoides* ^{LC}	Dwarf gecko and Common bluetongue skink	(Indirect) **Grazing**—bare soil after grazing increases mortality for gecko and skink	−	2	Gordons et al., 2021; Nasseri et al., 2011
Odocoileus virginianus	White-tailed deer	*Python bivittatus* ^{VU}	Burmese python	(Direct) **Predation**—deer as prey for python (remains of 3 deers in stomach of the python)	+	2	Boback et al., 2016; Boback et al., 2020
Odocoileus virginianus	White tailed deer	*Thamnophis sirtalis* ^{LC}	Common garter snake	(Indirect) **Presence**—ungulates increase abundance of garter snakes through augmenting their invertebrate prey density	+	1	Greenwald et al., 2008
Ovis aries and Bos taurus	Sheep and Cattle	*Carlia tetradactyla* ^{LC}*, Morethia boulengeri* ^{LC} *and Ctenotus spaldingi* ^{LC}	Southern rainbow-skink, Boulenger's snake-eyed skink and Straight-browed ctenotus	(Indirect) **Grazing**—sheep and cattle remove cover for the skinks	+	1	Kay et al., 2017
Ovis aries and Bos taurus	Sheep and Cattle	*Cryptoblepharus pannosus* ^{LC}*, Hemiergis talbingoensis* ^{LC}*, Christinus marmoratus* ^{LC}	Ragged snake-eyed skink, Victoria three-toed earless skink and Marbled gecko	(Indirect) **Grazing**—sheep and cattle remove cover for the skinks	−	1	Kay et al., 2017
Ovis aries	Domestic sheep	*Lacerta viridis* ^{LC}	Green lizard	(Indirect) **Grazing**—sheep removes cover for the lizards	−	1	Smith et al., 1996
Ovis aries	Domestic sheep	*Tiliqua adelaidensis* ^{EN}	Pygmy bluetongue lizard	(Indirect) **Grazing**—sheep removes cover for the lizards	−	3	Brown et al., 2011; Kazmaier, 2001; Nielsen and Bull, 2016
Sus scrofa	Wild boar	*Alligator mississippiensis* ^{LC}	American alligator	(Direct) **Predation**—nest predated by wild boar	−	2	Campos and Mourão, 2014; Elsey et al. 2012
Sus scrofa	Wild boar	*Anolis carolinensis* ^{LC}*, Storeria occipitomaculata* ^{LC} *and Sceloporus undulatus* ^{LC}	Green anole, Red-bellied snake and Eastern fence lizard	(Direct) **Predation**—reptile species as prey for wild boar	−	1	Jolley et al., 2010
Sus scrofa	Wild boar	*Blanus cinereus* ^{LC} *and Psammodromus algirus* ^{LC}	Iberian worm lizard and Algerian sand racer	(Direct) **Predation**—reptile remains found in stomach content of wild boar	−	2	Abáigar, 1993; Briedermann, 1976
Sus scrofa	Wild boar	*Chelodina longicollis* ^{NT}	Eastern long-necked turtle	(Indirect) **Rooting, Trampling**—wild boar destroys turtle's habitat	−	1	Doupé et al., 2009
Sus scrofa	Wild boar	*Chelodina rugosa Ogilby* ^{NT}	Northern snake-necked turtle	(Direct) **Predation**—wild boar kills turtles	−	2	Fordham et al., 2006 and 2008

Table A1. *Cont.*

Ungulate Species (Latin Name)	Ungulate Species (Common Name)	Reptile Species (Latin Name)	Reptile Species (Common Name)	Type of Impact	+/−	Number of Times Pairs Mentioned in Publications	Authors
Sus scrofa	Wild boar	*Malpolon monspessulanus* ^{LC}	Montpellier snake	(Direct) **Predation**—Montpellier snake as prey for wild boar	−	1	Ballouard et al., 2021
Sus scrofa	Wild boar	*Chelonia mydas* ^{EN}	Green sea turtle	(Direct) **Predation**—sea turtle as prey for wild boar	−	2	Engeman et al., 2019; Nordberg et al., 2019
Sus scrofa	Wild boar	*Geochelone elephantopus* ^{EN}	Galápagos giant tortoise	(Direct) **Predation**—wild boar killed adult tortoises	−	1	MacFarland et al., 1974
Sus scrofa	Wild boar	*Kinosternon hirtipes* ^{LC}	Rough-footed mud turtle	(Direct) **Predation**—turtle as prey for wild boar	−	1	Platt et al., 2019
Sus scrofa	Wild boar	*Natator depressus* ^{DD}, *Lepidochelys olivacea* ^{VU} *and Eretmochelys imbricata* ^{EN}	Flatback turtle, Olive ridley turtle and Hawksbill turtle	(Direct) **Predation**—turtle nests predated by wild boar	−	1	Whytlaw et al., 2013
Sus scrofa	Wild boar	*Natrix natrix* ^{LC}	Grass snake	(Direct) **Predation**—snake remains found in stomach content of wild boar	−	1	Tucak, 1996
Sus scrofa	Wild boar	*Storeria occipitomaculata* ^{LC}	Red-bellied snake	(Direct) **Predation**—snake remains found in stomach content of wild boar	−	1	Scott, 1973
Sus scrofa	Wild boar	*Testudo hermanni* ^{NT}	Hermann's tortoise	(Direct) **Predation**—tortoise remains found in stomach content of wild boar	−	1	Vilardell et al., 2012
Sus scrofa	Wild boar	*Tropidurus jacobii* ^{LC} *and Pseudalsophis steindachneri* ^{NT}	Santiago lava lizard and Painted racer	(Direct) **Predation**—reptile remains found in the stomach content of wild boar	−	1	Coblentz and Baber, 1987
Sus scrofa	Wild boar	*Varanus komodoensis* ^{EN}	Komodo dragon	(Direct) **Predation**—wild boar providing prey to dragon	+	3	Ariefiandy et al., 2020; Jessop et al., 2019 and 2020
Sus scrofa	Wild boar	*Vipera berus* ^{LC}	Common European viper	(Indirect) **Rooting**—wild boar foraging behaviour reduces common viper abundance in the area	−	1	Graitson et al., 2019
Tapirus terrestris ^{VU}	Lowland tapir	*Chelonoidis denticulata* ^{VU}	Yellow-footed tortoise	(Direct) **Predation**—tortoise as prey for tapir	−	1	Edison and David, 2020

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