

THE INDUCIBLE DEFENSES OF LARGE MAMMALS TO HUMAN LETHALITY

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ABSTRACT

1. In the process of avoiding predation, prey are faced with potentially fitness-compromising trade-offs that have implications for their survival and reproduction. The nature and strength of these non-consumptive effects at the population level can be equivalent, or even greater, than consumptive effects.
2. Many prey species have evolved defence mechanisms that are induced by predation risk. These inducible defences can be morphological or behavioural in nature. Extensive research has detected these defences in predator–prey communities across freshwater, marine and terrestrial ecosystems. Among this vast research however, an influential portion of these systems has not been widely considered.
3. Humans inhabit a level in trophic systems above apex predators. In that position, humans have been referred to as a *hyperkeystone* or *super predator* species as they have shown a capacity to consume animals at rates many times higher than any other non-human species. However, the extent to which humans induce adaptive defences in animals is not as clear. Systems involving large mammals may be particularly well-suited for the study of human-induced defences given that these species have been disproportionately exploited (for food and competition) over evolutionary time by humans.
4. To begin this process we first had to examine the context in which large mammals could adaptively evolve inducible defences in relation to human lethality. With the plausibility of these conditions satisfied, we then conducted an extensive review to document the inducible defences that have been detected in large mammals. All of the 187 studies reviewed documented the behavioural plasticity of large mammals to human lethality. No morphological adaptive defences were detected.
5. However, the extent to which the observed behavioural plasticity of large mammals is representative of adaptive inducible defences remains unclear because the fitness trade-offs (i.e. costs), an integral condition for inducible defences to evolve, were implied rather than quantified among close to 92% of this research. We make recommendations for renewed ingenuity in the development of field experiments that can quantify these costs and discuss the implications of human lethality on the ecology, conservation and management of large mammals.

Keywords: Anti-Predator Behavior, Carnivore, Evolution, Inducible Defenses, Human Lethality, Trophic Ecology, Ungulate

1 INTRODUCTION

The decisions that predators make in pursuit of prey and those that prey make to avoid predation have important implications for interspecific interactions, food web dynamics, community structure and evolutionary ecology (Abrams, 1986; Cott, 1940; Dawkins & Krebs, 1979; Edmunds, 1974; Gould, 1977; Paine, 1995). Prey responding to predators can experience both the direct (i.e. lethal or consumptive effects; Paine, 1966; Sih et al., 1985; Taylor, 1984) and indirect effects of predation (Abrams, 1995; Kerfoot & Sih, 1987; Peacor & Werner, 1997). Predator consumption of prey is a direct effect that results in death and the loss of genes from the prey population (Abrams, 2000; Creel et al., 2017; Murdoch et al., 2003; Preisser et al., 2005). To evade predators, prey can make phenotypic changes that typically present costs in the form of fitness trade-offs (Barry, 1994; Relyea, 2002; Ruxton & Lima, 1997; Werner & Peacor, 2003; Zanette et al., 2011). In certain systems, these trait-mediated (Peacor & Werner, 1997; Schmitz et al., 2004; Trussell et al., 2003; Werner & Peacor, 2003), non-consumptive (Brown & Kotler, 2004; Pangle et al., 2007; Peckarsky et al., 2008) or risk effects (Creel, 2011; Creel & Christianson, 2008; Heithaus et al., 2008) have been found to have considerable negative consequences for prey fitness (Cresswell, 2008; Peacor et al., 2013; Peacor & Werner, 2001; Schmitz et al., 1997). of predation (Schmitz et al. 1997; Peacor and Werner 2001; Cresswell 2008; Peacor et al. 2013).

Many phenotypic changes made by prey are defence mechanisms that are induced by predation (Brönmark et al., 1999; Harvell & Tollrian, 1999; Karban et al., 1999). These inducible defences are elicited in response to a previous encounter with a predator (Harvell, 1986, 1990). The origins of inducible defences research involved studies of the spines of rotifers

(*Asplanchna*; Beauchamp, 1952; Gilbert, 1966) and the chemical responses of plants to herbivory (Dicke, 1999; Green & Ryan, 1972; Haukioja, 1980). Importantly, the inducible defences of predation can be morphological or behavioural with subsequent ecological effects (Anholt & Werner, 1999; De Meester et al., 1999; Dodson, 1989; Harvell & Tollrian, 1999). Some classic examples of morphological changes include the evolution of helmets among *Daphnia* (Laforsch & Tollrian, 2004; Tollrian, 1990), thickening and lengthening of the thorns on certain shrubs and trees (Abrahamson, 1975; Young & Okello, 1998), formation of spines on the membranes of the marine bryozoan species *Membranipora membranacea* (Harvell, 1984, 1986; Yoshioka, 1982) and larger body mass in crucian carp *Carassius carassius* subject to piscivory (Brönmark & Miner, 1992). Behaviourally, predation induces a number of defences in prey that often compromise foraging effort (Lima, 1998, 2002; Mangel & Clark, 1988; Sih et al., 1998). These include changes in activity, habitat selection, vigilance and group size (Anholt & Werner, 1999; Dill et al., 2003; Lima & Dill, 1990; Turner et al., 2000; Vos et al., 2002; Ydenberg & Dill, 1986

Immense ecological inquiry has evaluated the role of inducible defences (see Agrawal et al., 1999; Havel, 1987; Karban & Baldwin, 2007; Karban et al., 2014; Tollrian & Dodson, 1999) among plants (Berenbaum & Zangerl, 1999; Van Donk et al., 1999) and animals (Harvell, 1990; Tollrian & Dodson, 1999) via studies in the laboratory, field and theoretical simulations. This research has proven integral to organismal, evolutionary and interdisciplinary assessments of ecology (Harvell & Tollrian, 1999). However, recent research has turned to yet another biological agent that can potentially induce defences in animals: humans. For example, humans are envisioned to be a *hyperkeystone* or *super predator* species inhabiting a position in trophic

systems above apex predators (see Darimont et al., 2015; Oriol-Cotterill et al., 2015a, 2015b; Worm & Paine, 2016). In this role, humans have demonstrated a capacity to consume and exploit animals at rates many times higher than any other non-human species (Barnosky et al., 2011; Darimont et al., 2015; Dirzo et al., 2014; McCauley et al., 2015). Thus, humans have exerted considerable selective pressure on animal populations and altered the evolutionary trajectories of numerous species (Darimont et al., 2009; Liberg et al., 2012; Palumbi, 2001; Reznick et al., 1990).

The inducible defences associated with human lethality might be expected to be probable among large mammalian species (i.e. those with a body weight exceeding 5 kg; see Bourlière, 1975), including large herbivores and large carnivores, which have been disproportionately exploited by humans over evolutionary time (Allendorf & Hard, 2009; Cardillo et al., 2006; Ceballos & Ehrlich, 2002; Darimont et al., 2015; Kuijper et al., 2016; Ripple et al., 2014, 2015, 2016). Humans are a primary contributor to the mortality of large mammals via competition, consumption, killing for sport, killing for products, conflict (retaliatory or preventative killing) and bycatch from poaching for other target species (Chapron et al., 2014; Darimont et al., 2015; Doughty et al., 2015; Macdonald, 2016; Ripple et al., 2014). Here, we discuss the conditions that are necessary for large mammals to adaptively evolve phenotypic changes in response to human lethality (*sensu* Harvell & Tollrian, 1999). Within this context, we clarify the roles of humans as predators, killers and sources of disturbance. We then conducted an extensive review to determine the behavioural and morphological inducible defences of large mammals to human lethality that have been reported in the peer-reviewed literature. Specifically, we discuss the spatial distribution of these studies around the world, the types of

research techniques deployed to assess inducible defences, whether the human cues considered were proxies for lethality and if the costs of the defence mechanisms employed by the large mammals were quantified among this research. We ground the inferences of our study in a discussion of the evolutionary, ecological and conservation implications of mammalian inducible defences to human lethality.

2 THE IMPACT OF HUMANS ON LARGE MAMMALS

It is clear that humans have a capacity to alter the functioning of the natural world like no other species (Benítez-López et al., 2010; Ellis, 2011; Hoy, 1998; Magle et al., 2016; McKinney, 2006; Palumbi, 2001). Humans have transformed ecosystems from natural to built environments, spread diseases and species, changed water, soil and air chemistry, and correspondingly, fundamentally changed the climate of Earth (Davidson & Janssens, 2006; Jones et al., 2018; Lendrum et al., 2018; Parmesan & Yohe, 2003; Smith et al., 2006; Steffen et al., 2011; Venter et al., 2016; Vitousek et al., 1997). Thus, humans have exerted dramatic indirect effects that have led some to contend that the world has advanced from the Holocene to the *Anthropocene* (Crutzen, 2002; Dirzo et al., 2014; Waters et al., 2016). It is also important to distinguish among the direct effects that humans can have on animals. Although widely conflated, these direct effects can be defined either as acts of predation or killing. Here, the distinction principally relates to the consumption of animal biomass.

Predation does not merely imply death. Rather, and using the classic definition provided by Abrams (2000, p. 79), predation describes 'an interaction in which individuals of one species kill and are capable of consuming a significant fraction of the biomass of individuals of another species'. Thus, for an animal to be a predator, it cannot just kill another animal but also must

consume a 'significant fraction' of that animal's biomass. Importantly, the vast majority of instances in which humans lethally affect animals, there is little to no consumption of animal biomass. Vehicle strikes are perhaps the most obvious example. More animals are killed by vehicles each year than by any direct lethal effect of humans (see reviews by Fahrig & Rytwinski, 2009; Trombulak & Frissell, 2000). However, biomass consumption is not a primary component of vehicle strikes and thus, this action should be envisioned to be emblematic of human killing rather than human predation. Other examples of killing include poisoning 'problem' animals, trapping animals for products (i.e. fur), retaliation associated with human-wildlife conflict, culling initiatives for wildlife control or management, and both legal and illegal trophy hunting (Woodroffe & Redpath, 2015; Figure 1). These examples lie in stark contrast to instances in which humans kill animals for the purpose of consuming their biomass (i.e. consumption). Examples of human predation of large mammals include trapping, snaring and hunting with an arrow, spear or firearm (Figure 1). We provide this distinction in human lethality to demonstrate that the portrayal of humans as predators, or indeed *super predators*, should be confined to instances in which consumption of animal biomass is the primary motivation for that lethality.

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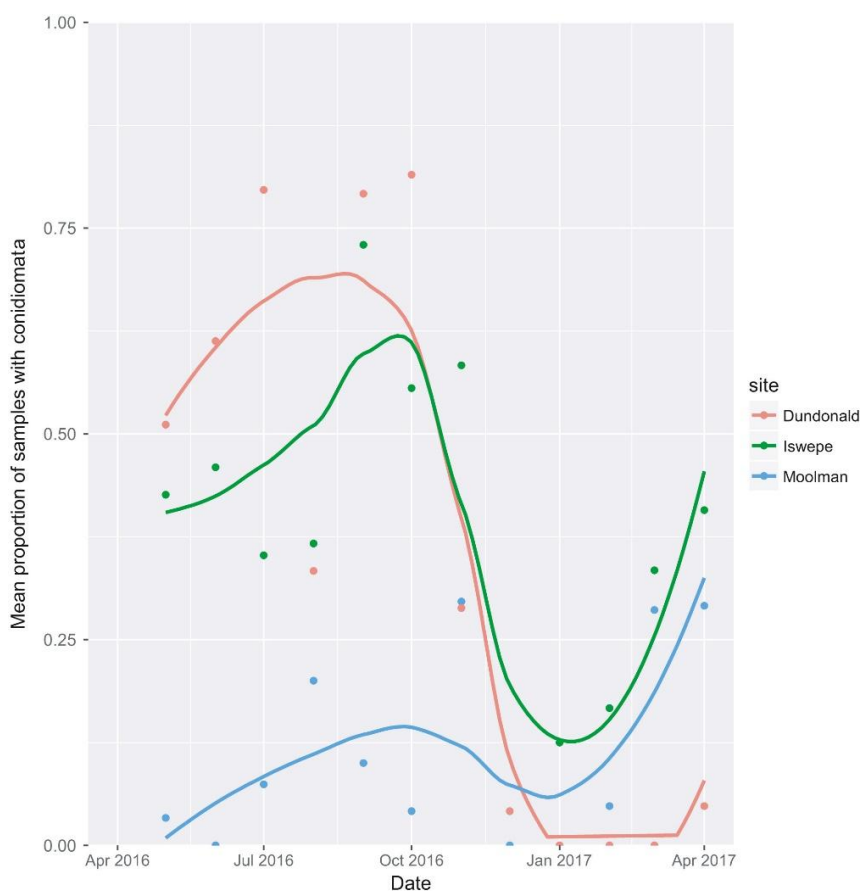


FIGURE 1. Conceptual framework depicting the selective nature, along a spectrum of indiscriminate to discriminate, for human predation in comparison to human killing. Herein, the distinction between predation and killing involves the consumption of animal biomass by the biotic agent (i.e. humans)

We are not suggesting however, that we should necessarily expect variation in the evolution of inducible defences in response to human killing versus human predation. It is certainly possible that there would be variation, but that distinction requires further investigation. Such an assessment is beyond the scope of this paper, but could be the subject of future evolutionary ecological research. Importantly, both forms of human lethality occur along a relative selectivity continuum involving techniques that could be considered indiscriminate to those that could be envisioned as highly selective (Figure 1). And that selectivity has important implications for the

passing of traits to the next generation (Allendorf et al., 2008; Darimont et al., 2009). Here, we examine the potential for inducible defences to evolve in response to human lethality.

3 THE EVOLUTION OF INDUCIBLE DEFENSES

As Harvell and Tollrian (1999) articulate, there are four conditions that are necessary for inducible defences to evolve. The synthesis of these conditions is based on the formative research of many different scholars (see Adler & Harvell, 1990; Harvell, 1990; Sih, 1987 among others). These four conditions require that:

1. The cues describing the presence of the biotic agent are spatio-temporally variable,
2. These cues provide reliable indications of risk,
3. The defenses employed to respond to those risks are effective, and
4. The application of those defenses is costly.

Here, we explore the structure of these conditions assuming that the biotic agent involved is humans and the interaction involves large mammals.

3.1 Cues of human presence

The first condition articulates that the cues of the biotic agent vary in strength across space and time (see Clark & Harvell, 1992; Padilla & Adolph, 1996). It is widely understood that humans leave auditory, visual, chemical and tactile cues of their presence that are perceptible among a wide variety of animals (Burger et al., 1991; Clinchy et al., 2016; Donalby & Henke, 2001; Götmark & Åhlund, 1984; Hampton, 1994; Hettena et al., 2014; McComb et al., 2014). These cues are spatiotemporally variable given the relatively predictable nature of human activity (i.e. typically diurnal and predominantly associated with human activity centres; Barnosky et al., 2012; Clinchy et al., 2016; Foley et al., 2005). Furthermore, large mammals are prone to compensating their behaviours to avoid humans spatially and

temporally (Gaynor et al., 2018; Tucker et al., 2018). Thus, there is good evidence that the first condition associated with the evolution of inducible defences from human actions is satisfied.

3.2 Cues as a reliable indicator of risk

The evolution of inducible defences also depends upon cues providing a reliable indication of risks posed by the biotic agents (Bixenmann et al., 2016; Karban et al., 1999). This notion has been empirically supported via studies documenting the response of large mammals to cues of human activity (Papouchis et al., 2001; Smith et al., 2015; Suraci et al., 2017; Wilmers et al., 2013). Examples include large mammals changing their movement and home range patterns (Šálek et al., 2015; Wang et al., 2017), altering their activity schedules (Carter et al., 2012; Gaynor et al., 2018; Wang et al., 2015), abandoning kills or feeding less (Smith et al., 2017) and choosing different habitat types when perceiving human presence (Gehr et al., 2017; Valeix et al., 2012; Wilmers et al., 2013). Thus, the ways in which large mammals adjust their behaviour in response to human activity suggests that these cues may provide reliable indications of risk.

3.3 Defenses responding to risk are effective

The defences employed by large mammals must also effectively reduce the risk of human interaction. As we have just highlighted in the cues as a reliable indicator of risk section, there is an abundance of evidence that the phenotypic plasticity exhibited by large mammals can effectively lower the risk of lethal interaction with humans. However, as Harvell and Tollrian (1999, p. 6) point out 'the real importance of the inducibility of the character may well have more to do with the importance of responding without error to a changing predator field, than to cost savings'. Further, the effectiveness of the inducible defences is often determined by an array of predators (*sensu* Tallamy, 1985, 1991; Taylor & Gabriel, 1992), rather than one biotic agent (e.g. humans) in isolation. Large herbivores, for instance, are not only subject to predation from humans, but also to predation risk from sympatric large carnivore populations. Thus, the inducible defences of large mammals to human predation may be difficult to

differentiate, particularly given that studies of risk effects in large mammal systems tend to study a fraction of the complexity in the potential trophic interactions (see Montgomery et al., 2019).

3.4 Defenses responding to risk are costly

The defences of large mammals to humans are expected to carry costs in the form of reductions in survival and reproduction (Frid & Dill, 2002) deriving from decreased foraging effort (i.e. the predator-sensitive food hypothesis), increased stress responses (i.e. the predator-induced stress hypothesis; Creel, 2018) or investment in morphological adaptations. However, the extent to which studies examining the inducible defences of large mammals to human predation assess the costs of anti-predator behaviour is unclear. That being said, risks from humans are predicted to be of higher intensity for large mammals when compared to more natural pressures (e.g. prey availability or competitive exclusion; Gehr et al., 2017; Oriol-Cotterill et al., 2015a, 2015b; Smith et al., 2017). Thus, there is good reason to believe that the application of these anti-predator behaviours would carry costs for large mammals.

3.5 Evolutionary time

Of course, for inducible defences to evolve these conditions must be satisfied and the adaptive traits passed down across generations. For instance, animal responses to human predation should be expected to be some combination of genetic pre-dispositions and learned behavioural plasticity (Hendry et al., 2008; Postma, 2014; Whittaker & Knight, 1998). As Harvell and Tollrian (1999, p. 6) highlight, 'Irrespective of the selective factors favoring the evolution of inducible defenses, evolution will not occur in the absence of heritable variation in inducibility'. Given the comparatively long-lived and low reproductive rates (e.g. long generation times) of large mammals, it is necessary to examine whether there has been enough evolutionary time to develop inducible defences to human predation. Humans have been functional components of trophic systems comprised of large mammalian herbivores and competing carnivores for tens of thousands of years (Bird & Nimmo, 2018; Milner-Gulland &

Bennett, 2003). That being said, humans have become more efficient and voracious hunters since the advent of firearms (Allendorf et al., 2008; Milner et al., 2007). Rates of evolutionary change occurring from human predation can be orders of magnitude greater than those associated with natural evolution (Reznick et al., 1990) and researchers have detected population-level trait changes for species that share their landscapes with humans (Hoy, 1998; Van de Walle et al., 2018). Observations of this type might suggest that the evolution of inducible defences in large mammals to human predation would be possible, if heritable, and with that in mind we proceeded to our literature review.

4 MATERIALS AND METHODS

4.1 Literature Review

We conducted a review of peer-reviewed literature (completed in January, 2019) evaluating the suite of defences in large mammals documented in response to human lethality. We focused our assessment on terrestrial large herbivores (i.e. species in the Infra-Order Ungulata and the Order Proboscidea) and carnivores (i.e. species in the Order Carnivora) with a body weigh exceeding 5 kg (Bourlière, 1975). We conducted this review using the Web of Science search engine, with no restrictions on the date range, via the application of the following terms; (human AND ungulate OR elephant OR carnivore) AND (inducible defenses OR hunting OR poaching OR super predation). We analysed all literature deriving from this search and retained those studies with research objectives that were consistent with the scope of our analysis. We then assessed each of the retained studies and recorded the following: (a) the study area, (b) the large mammal species researched, (c) the human cues that were assessed, (d) whether the human cues were indicative of human predation, killing or disturbance, (e) the defence mechanisms employed by these large mammals and vii) whether the costs of the anti-predator behaviours were quantified.

5 RESULTS

In total, there were 392 studies returned from our search of the inducible defences of large mammals to human lethality. Following our initial examination of these studies, we removed just over half ($n = 205$) from consideration given that they: (a) were review or meta-analyses; (b) were theoretical modelling papers; or (c) did not assess inducible defences of large mammals. All of the remaining 187 studies, published between 1958 and 2019, assessed the behavioural plasticity of large mammals to humans (see Appendix S1, Supporting Information for a full list of studies). None evaluated the morphological inducible defences of large mammals.

The retained studies assessed the behaviour of >60 individual species of large mammals inhabiting trophic systems around the world (see Appendix S1, Supporting Information). North America and Europe were the continents where the majority of this research occurred, followed by Africa, Asia and, finally, South America and Australia (Figure 2). Close to half (44%, $n = 83$ of 187) of all studies were based in the United States or Canada (Figure 2). Considering that studies might examine large mammals across several taxonomies, ungulates were the most-common research subjects occurring in 58% ($n = 108$ of 187) of the studies. Carnivorans and proboscideans were considered among 41% ($n = 76$ of 187) and 9% ($n = 16$ of 187) of the studies respectively. Approximately 25% ($n = 46$ of 187) of the studies examined human predation, 17% ($n = 32$ of 187) assessed human killing and 58% ($n = 109$ of 187) quantified humans as sources of disturbance.

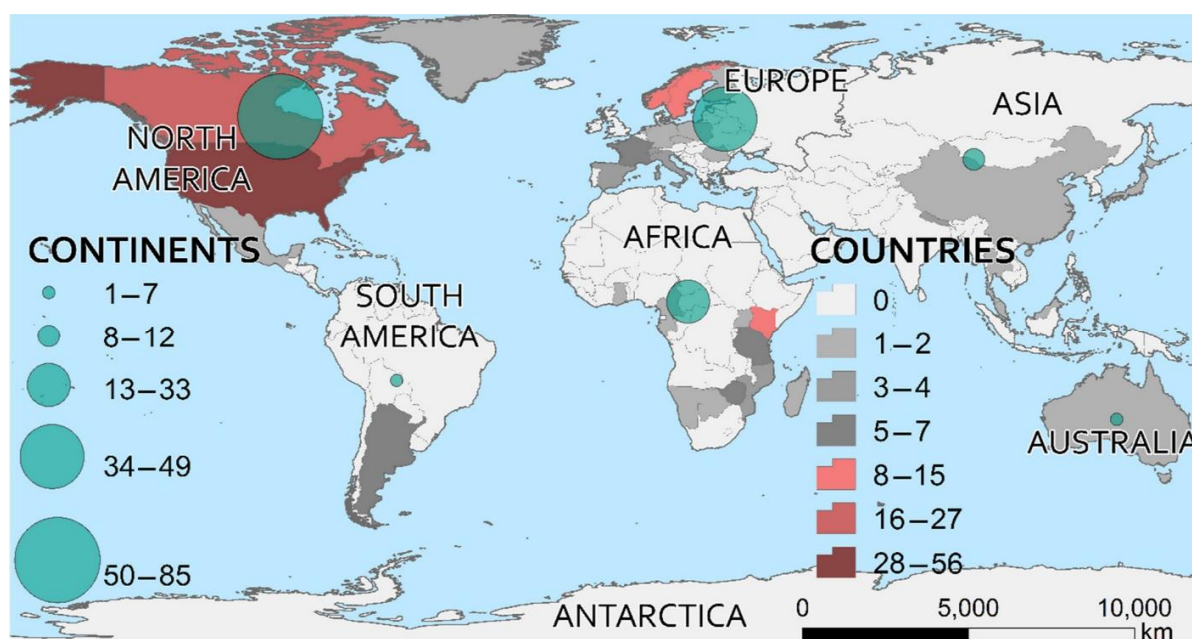


FIGURE 2. The spatial distribution of studies examining the inducible defences of large mammals to human lethality across the world. These data were summarized from a review of the literature published in peer-reviewed journals between 1958 and 2019. Herein, the count of these studies is presented both at the continent and country level

The research subjects also exhibited variation by human action with ungulates being most common among studies of human predation, carnivores being most common in studies of human killing and both carnivores and ungulates being assessed at almost equivalent levels among studies of human disturbance (Figure 3). The five most-commonly studied species were elk/red deer *Cervus elaphus* (13%, $n = 25$ of 187), brown bears *Ursus arctos* (10%, $n = 19$ of 187), white-tailed deer *Odocoileus virginianus* (7%, $n = 13$ of 187), African elephants *Loxodonta africana* (7%, $n = 13$ of 187) and mountain lions *Puma concolor* (5%, $n = 9$ of 187). These five species were research subjects in 42% of all papers evaluated.

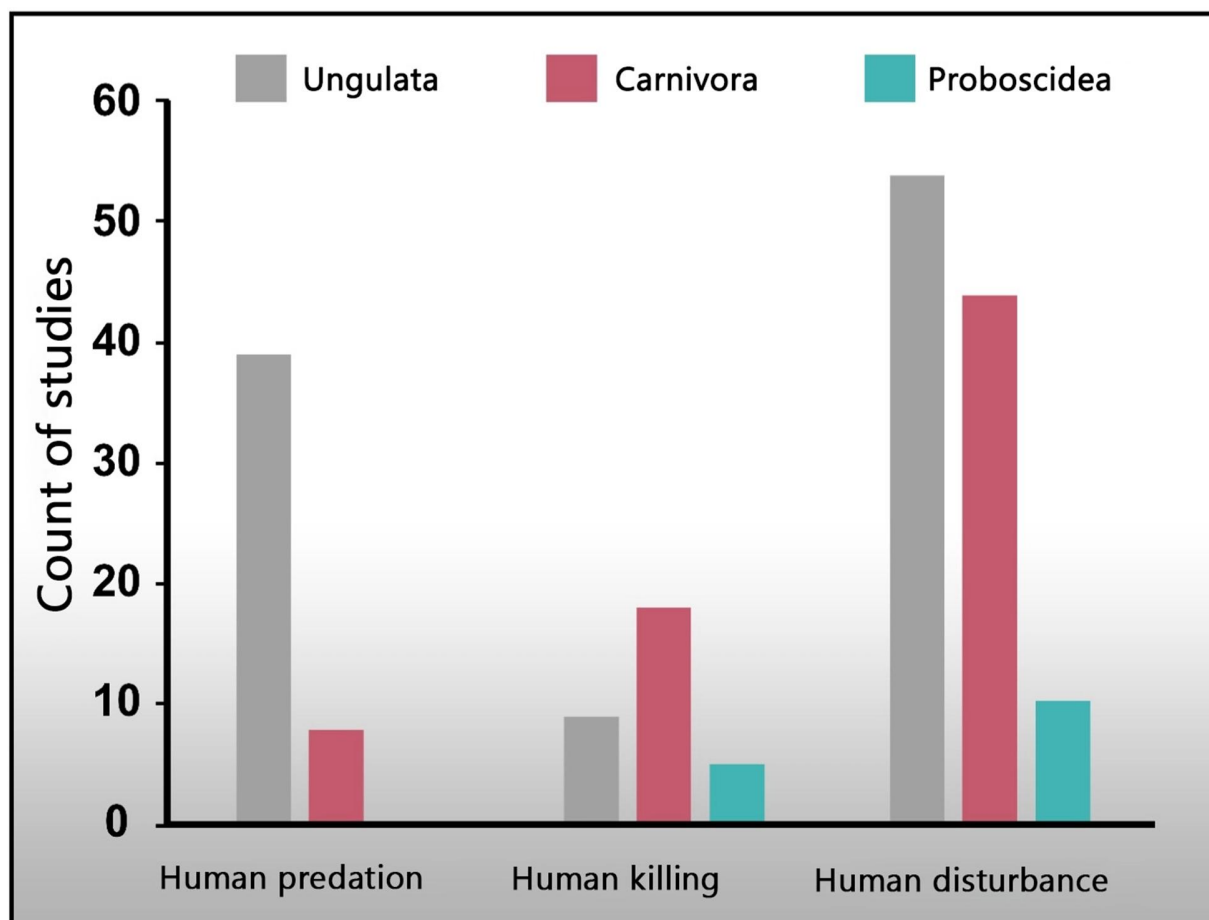


FIGURE 3. Bar chart representing a count of the number of studies published in peer-reviewed journals between 1958 and 2019, featuring species from the Infra-Order Ungulata, the Order Carnivora and the Order Proboscidea, across assessments of human predation, killing and disturbance

There were nine main behaviours that were measured in response to human predation, killing or disturbance (Table 1). While more than one behaviour could have been assessed per study, over 80% of all studies evaluated large mammal space use, movement, flight behaviour or activity changes in relation to human action (Table 1). A number of direct measures and proxies for human predation and killing were used among this literature (Table 2). Examples of direct measures of human predation included detections of hunters, researchers simulating hunting and archer density (Table 2). Direct measures of human killing included vehicle traffic volume on roads, researchers in vehicles and an organized population culling initiative (Table 2). Where disturbance was quantified, large mammal

behaviour commonly related to human land use (53%, $n = 57$ of 108 disturbance studies) or researchers approaching animal subjects either on foot (14%) or in vehicles (7%) to gauge their reaction. Over 70% ($n = 137$ of 187) of the studies that we evaluated identified that hunting of the target species occurred in that ecosystem. Furthermore, 25% ($n = 46$ of 187) of these studies documented that either independently or in tandem with legal hunting, the target species were subject to poaching pressure. There were only 23 studies (12%) that assessed human disturbance in which neither legal nor illegal hunting of the target species was known to occur.

TABLE 1. The categories of behavioural plasticity employed by large mammals in relation to sources of human predation, killing and disturbance detected from a review of 187 peer-reviewed studies published between 1958 and 2019. The 'Other' category includes duration drinking, site visitation rates and site visit duration. We note that a single study could have assessed multiple measures of behavioural plasticity. Hence, the count column exceeds the number of studies and the proportion column exceeds 1.00

Behavioural plasticity	Count	Proportion
Space use	67	0.36
Movement	32	0.17
Flight	27	0.14
Activity	17	0.09
Occupancy	14	0.07
Vigilance	11	0.06
Stress response	7	0.04
Foraging	7	0.04
Group size	6	0.03
Other	4	0.02

TABLE 2. The direct measures of human lethality (either predation or killing) are presented alongside proxies for those mechanisms. The count of the number of times that each factor was used among peer-reviewed studies (published between 1958 and 2019) documenting both human predation and killing is also presented

Super predator	Count	Proportion	Super killing	Count	Proportion
Direct			Direct		
Hunter detections	6	0.13	Traffic volume	1	0.03
Researchers simulating hunting	1	0.02	Researchers simulating hunting in vehicles	1	0.03
Comparison of hunted animals versus unhunted animals	1	0.02	Culling initiative (poisoned bait)	1	0.03
Archer density	1	0.02			
Proxy			Proxy		
Comparison of hunting versus non-hunting season	17	0.36	Road effects	16	0.5
Comparison of hunted versus unhunted sites	11	0.23	Land associated with conflict	6	0.19
Resource selection function of hunter kill sites	5	0.12	Comparison of trophy-hunted versus unhunted sites	5	0.16
Proximity to hunter access points	3	0.06	Land associated with illegal trophy hunting	2	0.06
Relative hunting pressure	1	0.02			
Proximity to roads during hunting season	1	0.02			

The techniques used to assess the behavioural plasticity of the study species in response to human predation, killing and disturbance were predominantly predicated upon the application of telemetry

technology (Figure 4). The next most-common technique was animal observation followed by camera traps (Figure 4). These three techniques were deployed in 89% ($n = 168$ of 187) of all studies. However, the costs associated with large mammal behavioural plasticity were rarely assessed among this literature. Just 16 of these studies (9%) quantified the costs associated with these behavioural modifications (Table 3). There was a high degree of variability in the cost that was evaluated, the human activity that was observed or experimentally assessed to trigger the behavioural response and the directionality of the behavioural responses (Table 3).

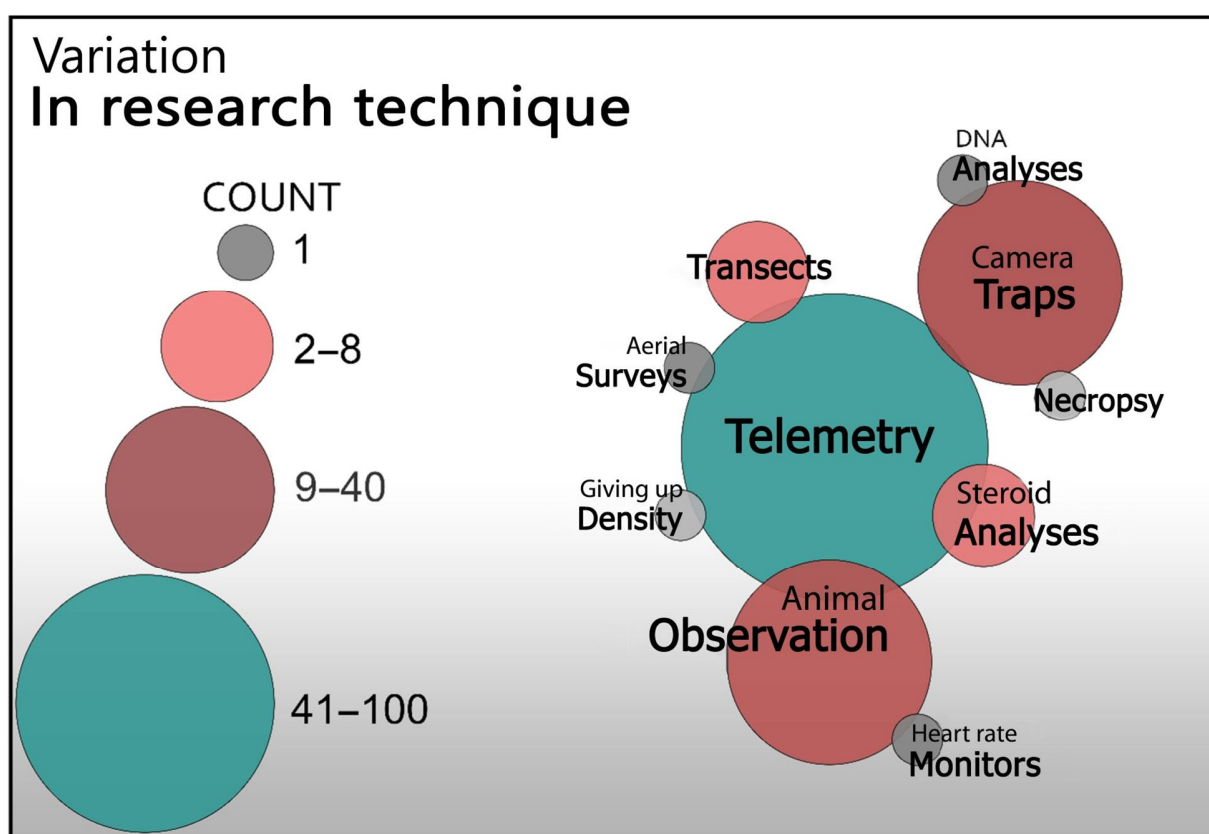


FIGURE 4. Bubble plots showing the variation in research technique used to evaluate the inducible defences of large mammals to human lethality as inferred from studies published between 1958 and 2019

TABLE 3. The cost of the behavioural plasticity of large mammals in response to sources of human predation, killing and disturbance detected from a review of 187 peer-reviewed studies published between 1958 and 2019

Mammal species	Country	Technique	Human activity	Type	Cost evaluated	Reference
<i>Ursus arctos</i>	Sweden	Telemetry	Hunting season	Human predation	Foraging rate ¹	Hertel et al. (2016)
¹ Bear foraging behavior was compared during before, during, and after the hunting season. Bears foraged less efficiently and on lower quality food sources during hunting season.						
<i>Odocoileus hemionus</i>	Canada	Animal observation	Hunted versus control deer	Human predation	Giving up densities ²	Le Saout et al. (2014)
² Comparison of hunted and unhunted sites of a predator-free black-tailed deer population. Hunted deer were found to avoid bait stations and shift browsing pressure.						
<i>Alces alces</i>	Canada	Telemetry	Hunted versus unhunted sites	Human predation	Sex ratio ³	Laurian et al. (2000)
³ The proportion of subadult male moose was found to be higher in hunted sites, in comparison to unhunted sites, interpreted as compensation for lower adult male ratios						
<i>Cervus elaphus</i>	United States	Necropsy	Archer density	Human predation	Vital rates ⁴	Davidson et al. (2012)
⁴ Comparison of archer density at levels of high, low, and none revealed that pregnancy rates were lower for lactating elk in years of high archer density						
<i>Canis lupus</i>	United States	DNA analyses	Harvesting	Human killing	Recruitment ⁵	Ausband et al. (2015)
⁵ Wolf recruitment declined in a period of human harvest when compared to the period directly before harvest						
<i>Cervus elaphus</i>	United States	Animal observation	Researchers on foot	Human disturbance	Cow:calf ratio ⁶	Phillips and Alldredge (2000)

⁶Elk cow:calf ratio declined among treatment elk (those that were repeatedly approached and disturbed by the researchers) when compared to the control elk

<i>Bison bison</i> and <i>Cervus</i> <i>elaphus</i>	United States	Animal observation	Snowmobiles	Human disturbance	Demography ⁷	Borkowski et al. (2006)
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⁷Bison and elk responded to snowmobile disturbance in the moment but no evidence of a demographic impact on these populations over a 35-year period was detected

<i>Cervus</i> <i>elaphus</i>	United States	Telemetry	Researchers on skis	Human disturbance	Energy expenditure ⁸	Cassirer et al. (1992)
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⁸Elk movement in response to researcher disturbance trials conducted on skis showed an average reduction of 5.5% of daily energy intake equivalent to 295 g of forage

<i>Puma</i> <i>concolor</i>	United States	Telemetry	Land use	Human disturbance	Energy expenditure ⁹	Wang et al. (2017)
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⁹Pumas using habitat near to human development increased nighttime activity at a cost of 11.6% for males and 10.1% for females equivalent to 4.0 and 3.4 deer prey/year

<i>Puma</i> <i>concolor</i>	United States	Telemetry	Land use	Human disturbance	Feeding time ¹⁰	Smith et al. (2015)
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¹⁰Consumption time of prey was lower for pumas inhabiting habitat near human development resulting in higher kill rate of prey when compared to less developed areas

<i>Puma</i> <i>concolor</i>	United States	Camera traps	Playback of humans talking	Human disturbance	Feeding time ¹¹	Smith et al. (2017)
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¹¹Playback experiments of human noises led to pumas abandoning kill sites, returning later, and feeding less when compared to playbacks of frog noises

<i>Odocoileus</i> <i>hemionus</i>	United States	Telemetry	Land use	Human disturbance	Fetal survival rate ¹²	Peterson et al. (2017)
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¹²In a drought year, mule deer using habitat with high natural gas activity had higher fetal mortality rates when compared to mule deer using habitat with low gas activity

<i>Ursus arctos</i>	United States	Telemetry	Human activity	Human disturbance	Foraging rate ¹³	Rode et al. (2007)
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¹³Brown bears responded with behavioral plasticity to experimental treatments of bear viewing however, bear body weight and composition was unaffected

<i>Pecari tajacu</i>	United States	Giving up density	Hiking trails	Human disturbance	Foraging rates ¹⁴	Bleicher and Rosenzweig (2017)
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¹⁴Collared peccary avoided food stations near human hiking trails and had lower foraging rates in habitats near human houses

<i>Ursus arctos</i>	Sweden	Telemetry	Land use	Human disturbance	Heart rate ¹⁵	Støen et al. (2015)
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¹⁵Brown bears showed signs of increased stress responses (as measured by lower heart rate variability) when using habitat nearer to human houses during the berry season

<i>Canis lupus</i>	Canada	Telemetry	Land use	Human disturbance	Predation rate ¹⁶	Neilson and Boutin (2017)
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¹⁶Wolf predation rate of moose increased near sources of human disturbance which was attributed to previous land use regimes associated with the mining industry

6 DISCUSSION

By our review of the mammalian defences induced by human lethality, we detected no studies examining morphological defences, but detected a wide variety that assessed behavioural modifications in relation to human predation, killing and disturbance. The extent to which these examples of behavioural plasticity are defences induced by human lethality, however, remains unresolved because the costs associated with these large mammal behaviours tended to be implied, rather than quantitatively assessed among this research. Costs deriving from large mammal behavioural plasticity typically involve trade-offs that compromise foraging effort with potential consequences for survival and reproduction and subsequent implications for population growth and species interactions within the trophic system (Pangle et al., 2007; Ruxton & Lima, 1997; Winnie & Creel, 2017; Zanette et al., 2011). Large carnivores, for instance, may sacrifice hunting efficiency when seeking to avoid potentially risky interactions with humans (see Cristescu et al., 2013; Gehr et al., 2018; Montgomery et al., 2014).

Interestingly, just 16 of the 187 peer-reviewed studies that we evaluated attempted to quantify such costs. These studies examined the impacts of large mammal behavioural adjustments on energy expenditure, foraging rate, reproduction and recruitment, among others (Table 3). Importantly however, only four studies assessed costs of large mammal behavioural responses to human predation. Consequently, one of the four conditions necessary for inducible defences to evolve (i.e. the costliness of the anti-predator responses; Harvell & Tollrian, 1999) has not been widely quantified among this research. At risk here is that the behavioural plasticity that we detected may not actually be costly. Behavioural responses to human action might not result in fitness costs when animals are readily able to recover from the behavioural adjustment or when the distribution of local resources is high enough where the displacement is non-consequential (see Gill et al., 2001). Such observation re-emphasize (see Gill & Sutherland, 2000; Sutherland, 1998) the importance of determining whether the behavioural decisions made by individual animals in regard to human action can scale up to have population-level consequences.

Furthermore, no study within our review evaluated the morphological defences that might be induced by human lethality. We highlight that such morphological adaptations represent an important area of future inquiry on large mammal inducible defences. We suspect that behavioural responses were the only factors assessed among this literature because of the difficulty in attributing the morphological defences in large mammals to human lethality. Morphological adaptations may be challenging to detect because of the vastly diverse ways in which humans hunt large mammals as well as the fact that these species are often subject to lethal pressure from co-occurring non-human predators (Figure 1). Importantly, we are not stating here that no studies captured in our search engine evaluated morphological consequences of human lethality. In fact, we detected 10 studies that examined the impacts of selective hunting on the morphology (i.e. body, horn, antler or tusk size) of large mammals. Harvest-induced selection reduced the size of bighorn sheep *Ovis canadensis* horns (Coltmann

et al., 2003; Pigeon et al., 2016), changed the shape of mouflon *Ovis gmelini musimon* horns (Garel et al., 2007), and promoted higher probabilities of tusklessness in African elephant *Loxodonta africana* populations (Jachmann et al., 1995). Harvest-induced selection for specific traits in animals (e.g. large body size, fierceness or morphological features such large tusks or manes) has resulted in populations evolving phenotypes that are less desirable (see Allendorf & Hard, 2009; Ciuti et al., 2012; Festa-Bianchet & Lee, 2009; Harris et al., 2002; Martinez et al., 2005). This unnatural selection can shape the demography of large mammal populations, trigger harvest-induced trait changes and potentially reduce fitness (Harris et al., 2002; Milner et al., 2007; Mysterud, 2010, 2011; Sforzi & Lovari, 2000). However, these studies were excluded from our examination of inducible defences given that these traits were artificially selected by humans, rather than evolved as a defence against humans.

Although humans do hunt and kill animals, humans are most often agents of disturbance. In their seminal publication, Frid and Dill (2002) contended that animal response to human disturbance stimuli would reflect perceived levels of predation risk (i.e. the risk-disturbance hypothesis). Within this context, inducible defences should be expected to be strongest when humans actually behave as functional predators (i.e. Clinchy et al., 2016; Ordiz et al., 2012; Palumbi, 2001). Thus, it may only be that in systems in which humans have hunted animals over evolutionary time, that disturbance and predation stimuli are synonymous in the mind of an animal (Frid & Dill, 2002). In their review, Hendry et al. (2008) demonstrate that the rates of phenotypic change among wild animals are far greater in response to sources of human disturbance when compared to conditions that would be representative of more natural variation in the environment. There are also important state-dependent processes associated with the response of animals in relation to sources of human disturbance (Beale & Monaghan, 2004; Trimmer et al., 2017). Specifically, animals that are in better body condition have the ability to expend more effort in avoiding, or responding to, sources of human disturbance. Thus, accurate assessments of costs need to consider both the temporal and spatial variability in the biotic

and abiotic conditions in the environment as well as intrinsic conditions of the individual animals (Ydenberg & Dill, 1986).

Quantification of the costs of behavioural plasticity in animals are typically dependent upon experimentation. Experiments that calculate the nature and strength of the indirect effects of predation, for instance, are often associated with comparatively small and controlled research plots featuring the interactions of small (e.g. <1 kg) predator and prey species (Schmitz et al., 2017). Many have highlighted that these types of manipulations may not develop principles that are scalable to larger organisms residing in broader and more complex landscapes (D'Amen et al., 2017; Montgomery et al., 2019; Pearson & Dawson, 2003; Ricklefs, 2008). Thus, undoubtedly, one of the reasons why we did not detect experiments to be common among research exploring the behavioural plasticity of large mammals to human lethality is because conducting experiments in wild systems with highly mobile prey species and fierce carnivore predators is non-trivial (Creel et al., 2017; Winnie & Creel, 2017). Instead, a common approach among large mammalian ecologists to examine interspecies interactions involves the use of telemetry technology (Benson, 2010; Hebblewhite & Haydon, 2010; Whittington et al., 2011). Telemetry was used in over half of all studies (53%, $n = 100$ of 187) featured in this review (Figure 4). Application of this technology is typically associated with the studies of large mammal space use, resource selection and movement (Gray et al., 2017; Moll et al., 2016; Petrunenko et al., 2016). Once again however, these techniques often provide correlative, rather than mechanistic, understandings of the interspecies interactions among large mammals (Gimenez et al., 2014; Paine, 2010; Scheiner, 2013). Thus, an opportunity for future research is to use telemetry technology to detect evidence of behavioural plasticity among large mammals in relation to experimental designs that test various human cues (sensu Smith et al., 2017).

We also found that proxies of human lethality were more commonly used in this literature than direct measures (Table 2). Direct measures often involved researchers moving in such a way to elicit a

behavioural response in the animal subjects. There has been a long history of researchers acting as sources of human disturbance in animal ecology research (see Caro, 2005; Curio, 1993). Within this context however, the application of 'humans as surrogate predators in anti-predator studies is risky but expedient' (Caro, 2005, p. 31). It can be expedient in that the experiments are relatively straightforward to derive and test. However, human subjects are risky in that it can be challenging to quantify whether the response of the animals is attributable to humans perceived to be predators, killers or disturbers. We recommend renewed ingenuity in devising novel field experiments that can effectively quantify the fitness costs of large mammal behavioural plasticity in relation to human actions (*sensu* Boyle & Samson, 1985; Frid & Dill, 2002). Of particular utility will be the use of technology (see Table 3) to track mammal behavioural plasticity in response to experimental, or quasi-experimental, structures simulating various forms of human lethality. Herein, we emphasize the importance of quantifiable and longitudinal estimation of the fitness-related costs of the application of the behavioural responses. We also articulate that the need for these innovations is not restricted to studies of large mammals. Animal community dynamics, more broadly, have not yet effectively accounted for, and quantified, anthropogenic effects (Dorresteijn et al., 2015).

Almost 60% of the studies that we evaluated in this review assessed the behavioural modifications of large mammals to sources of human disturbance. This result is consistent with a variety of research quantifying human action such as human population density or infrastructure (Cristescu et al., 2013; Smith et al., 2015; Steyaert et al., 2016; Støen et al., 2015), tourism (Rode et al., 2007) or human recreational activities (e.g. hiking, biking, snowmobiling; Borkowski et al., 2006; Fortin et al., 2016; Gander & Ingold, 1997; Larson et al., 2016; Rogala et al., 2011; Smith et al., 2017). The literature that we reviewed herein did not enable us to evaluate the validity of the underlying assumption of human activity being indicative of 'predation' cues (see Frid & Dill, 2002). Habituation to non-lethal human presence undoubtedly threatens the premise of this assumption. Wildlife can become

habituated to various sources of human activity (Knight, 2009; Knight & Cole, 1991; Stankowich & Reimers, 2015). However, the rate at which this occurs seems to vary according to prevailing human hunting pressure. In a meta-analysis, Stankowich (2008) identified that flight distance was greater for ungulates inhabiting systems that were hunted, when compared to ungulates in systems without hunting. As Caro (2005, p. 31) remarks 'Humans can affect predator-prey interactions if either prey or predator is differentially fearful of people'. In certain systems, where ecotourism and legal or illegal hunting occur concurrently, tourists may habituate animals to human presence (Bateman & Fleming, 2017; Geffroy et al., 2015) where hunting tends to have the opposite effect (Ciuti et al., 2012). Most of the ecosystems evaluated among this research experienced the simultaneous effects of hunting and ecotourism. Thus, a challenge of future research on this topic relates to the differentiation of interacting effects of benign and lethal human behaviour.

There is hardly a landscape in the world where animals do not regularly encounter humans (Sanderson et al., 2002; Sih et al., 2011; Woodroffe et al., 2005). Although there are benefits of proximity to humans for many species (i.e. nutrient-rich crops, human-mediated refugia from predation/competition or increased abundance of prey; see Berger, 2007; Marshall & Moonen, 2002; Moll et al., 2018) there are important direct and indirect implications that underlie human lethality of large mammals. Large mammal populations across the world have been rapidly declining for decades, with a primary accelerant being negative interactions with humans (Ripple et al., 2014, 2015). For example, consumptive hunting has become an important threat to the population persistence of target animals (Milner-Gulland & Bennett, 2003). Meat dependency has expanded dramatically with an estimated 150 million households in the Global South that regularly harvest wild animals (Nielsen et al., 2018). Consequently, given rapid growth of human populations at the edges of protected areas (Wittemyer et al., 2008), large mammals are now subject to negative anthropogenic effects even within the boundaries of protected areas (see Berger, 2007; Brashares et al., 2001; Loveridge et al., 2017;

Périquet et al., 2015; Watts & Holekamp, 2009; Woodroffe & Ginsberg, 1998). Thus, there are important conservation implications of the lethal interactions of humans and large mammals.

Furthermore, the consequences of highly selective human killing of large mammals can give way to deleterious population-level trait changes (Coltman et al., 2003; Harris et al., 2002). The unnatural selection of bigger, fiercer and bolder large carnivores as trophies, for instance, has been suggested to lead to trait changes in surviving populations (Harris et al., 2002; Milner et al., 2007) with consequences that might destabilize the apex predator position in these trophic systems (Ordiz et al., 2013). Therefore, several scientific recommendations articulate that conservation and management actions should explicitly consider and monitor harvest-driven trait changes in large mammal populations to avoid adverse consequences (Frank et al., 2017; Palkovacs et al., 2018). Such evolutionary traps and source–sink dynamics might indicate maladaptation to human activity (Schlaepfer et al., 2002). These processes have been observed to be prevalent among a vast number of animals (see review Robertson et al., 2013) and are particularly influential among large mammals (Heurich et al., 2018; Pitman et al., 2015; Woodroffe & Ginsberg, 1998). These observations emphasize the importance of considering such selectivity when devising harvest management practices for large mammals.

Finally, we acknowledge the possibility that human-induced environmental change may be too rapid (Trimmer et al., 2017) for inducible defences to evolve among large mammals. Determining whether phenotypic changes can keep pace with the human-dominated 21st century is a fundamental question for all species (see Hendry et al., 2008), but particularly so for long-lived large mammals with comparatively low reproductive rates. Thus, the traits necessary to actualize a rapid evolutionary response to human changes in the environment might not be present in large mammals (see Hendry et al., 2011; Sih et al., 2011). However, our review has highlighted that the prevailing research has not been conducted in such a way so as to capably differentiate among what is simply behavioural plasticity versus adaptive phenotypic changes leading to evolutionary inducible defences among large mammals

in relation to human lethality. Thus, the inducible defences of large mammals to human lethality remains a central need among ecological research with important implications for conservation and management of large mammal populations throughout the world.

AUTHORS' CONTRIBUTIONS

R.A.M. developed all aspects of this analysis. D.W.M. and M.W.H. contributed equitably and substantively to the development of the scope of the analysis, the conceptualization of the design, as well as the writing and editing.

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DATA ACCESSIBILITY

Documentation of the studies considered in this review can be found in the Data Sources section provided in the Supporting Information.

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