



Review

Evaluating the efficacy of predator removal in a conflict-prone world

Robert J. Lennox^{a,*}, Austin J. Gallagher^{a,b,c}, Euan G. Ritchie^d, Steven J. Cooke^a^a Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada^b Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA^c Beneath the Waves, Inc., Miami, FL 33133, USA^d Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Victoria 3125 Australia

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ABSTRACT

Predators shape ecosystem structure and function through their direct and indirect effects on prey, which permeate through ecological communities. Predators are often perceived as competitors or threats to human values or well-being. This conflict has persisted for centuries, often resulting in predator removal (i.e. killing) via targeted culling, trapping, poisoning, and/or public hunts. Predator removal persists as a management strategy but requires scientific evaluation to assess the impacts of these actions, and to develop a way forward in a world where human-predator conflict may intensify due to predator reintroduction and rewilding, alongside an expanding human population. We reviewed literature investigating predator removal and focused on identifying instances of successes and failures. We found that predator removal was generally intended to protect domestic animals from depredation, to preserve prey species, or to mitigate risks of direct human conflict, corresponding to being conducted in farmland, wild land, or urban areas. Because of the different motivations for predator removal, there was no consistent definition of what success entailed so we developed one with which to assess studies we reviewed. Research tended to be retrospective and correlative and there were few controlled experimental approaches that evaluated whether predator removal met our definition of success, making formal meta-analysis impossible. Predator removal appeared to only be effective for the short-term, failing in the absence of sustained predator suppression. This means predator removal was typically an ineffective and costly approach to conflicts between humans and predators. Management must consider the role of the predator within the ecosystem and the potential consequences of removal on competitors and prey. Simulations or models can be generated to predict responses prior to removing predators. We also suggest that alternatives to predator removal be further developed and researched. Ultimately, humans must coexist with predators and learning how best to do so may resolve many conflicts.

1. Introduction

Predators can influence ecosystems through top-down control of the distribution and abundance of other species (Estes et al., 2011; Mills et al., 1993; Newsome et al., 2017; Pace et al., 1999). The loss of predators can therefore have profound ecological effects in certain contexts, including disease outbreaks, biodiversity loss, and ecosystem state changes (Myers et al., 2007; Ripple et al., 2014). There is evidence to suggest that ecological communities can exhibit dramatic shifts following the loss of predators (Crooks and Soulé, 1999; Pech et al., 1992; Ritchie and Johnson, 2009; Wallach et al., 2010), including changes at other trophic levels (Anthony et al., 2008; Atwood et al., 2015; Suraci et al., 2016). Although predators occur among diverse animal taxa (e.g., arthropods, molluscs, teleosts, raptors, canids, mustelids, etc.), vertebrate predators frequently conflict with humans, and many species are

threatened (Ripple et al., 2014); they are therefore the focus of this paper.

Many predatory vertebrates are vulnerable to disturbances because they generally have slower life histories, higher investment in parental care, lower abundances, and patchy distributions (Purvis et al., 2000). Yet, predators are challenged by a perception of being a threat to human interests or safety. Indeed, predators can be considered hazardous to domesticated animals (Gusset et al., 2009; Mishra, 1997; Oli et al., 1994), prey species of economic importance (Dalla Rosa and Secchi, 2007; Henschel et al., 2011; Weise and Harvey, 2005), or human safety via direct conflict (Dickman, 2010; Gore et al., 2005; Loe and Röskopf, 2004; Penteriani et al., 2016). Consequently, predators are often negatively perceived and persecution of vertebrate predators has a long history (Bergstrom et al., 2014; Kruuk, 2002; Reynolds and Tapper, 1996; Treves and Naughton-Treves, 1999). Competition with

* Corresponding author.

E-mail address: robert.lennox@carleton.ca (R.J. Lennox).

predators yielded many institutionalized campaigns against them dating back to ancient Greece and Rome, a trend that pervaded through medieval Europe and was exported to North America with emigrants in the 1700s (Reynolds and Tapper, 1996 and references therein). Today, state, regional, and agency-led programs to systematically control predator populations exist. Predator removal is carried out systematically via a number of methods and across various geographic scales (Bergstrom et al., 2014; Reynolds and Tapper, 1996), including poison baiting, trapping, hunting, and culling or via bounty or reward systems in public hunting or fishing events, but may also be more haphazard as retaliation for encroachment or interaction with humans or their property (e.g., farmer killing a wolf encroaching on their herds; e.g. Bergstrom et al., 2014; Treves and Karanth, 2003).

The significance of predators in ecosystems is well established yet their removal remains a component of the management toolbox. Owing to a lack of clarity pertaining to how and when removal can be expected to be successful, it may be difficult for management agencies to decide whether to proceed with predator removal when confronted with a problem. Furthermore, there is mounting opposition from advocacy groups (especially animal rights) and conservation-aware citizens that provide social inertia and pressure on animal control (van Eeden et al., 2017), which may complicate and influence decision-making (see Wallach et al., 2015). The science of predator removal therefore could benefit from an objective evaluation to identify successes and failures to both inform decision-making and identify lingering research gaps across multiple taxa (Treves et al., 2016; Eklund et al., 2017). Syntheses of this topic have focused on using meta-analysis, particularly for nesting birds (Côté and Sutherland, 1997; Smith et al., 2010, 2011), but it is challenging to apply such an approach across taxa and research paradigms (i.e., motivations). In this review, we evaluated these two competing hypotheses by considering of the available evidence for predator removal to determine whether predator removal is successful for wildlife conservation and management. We reviewed relevant literature and evaluated outcomes. In doing so, we propose a definition of success that can be applied to predator removal programs and we provide examples of success and failure in predator removals based on the following motivations 1) protection of domestic species, 2) preservation of prey species (e.g. economically important species or species at risk), and 3) mitigating risks of direct human-wildlife conflict. We conclude by considering evidence for the costs of failure in predator removal and a discussion of alternatives to predator removal. Although there are social and economic motivations associated with predator removal (Reynolds and Tapper, 1996; Engeman et al., 2002; Eklund et al., 2017; Swan et al., 2017), we focus on the ecological motivations aiming to synthesize perspectives on this practice. In this context, we refer to removal interchangeably with killing or lethal control. Removal may also refer to translocation, however, translocating predators has generally been demonstrated as ineffective for reducing conflicts (Athreya et al., 2011; Linnell et al., 1997; but see Hazin and Afonso, 2014). We focus on examples of aquatic and terrestrial vertebrate predators and ecosystems that include urban and rural areas. Moreover, we restrict the scope of this review to native predators. Invasive species are a global threat to biodiversity (Doherty et al., 2016) and the problems associated with biological invasions, although not necessarily unique or distinct from the problems that create nuisance predator conflict, are sufficiently different from a conservation and management perspective (see Doherty and Ritchie, 2016). Specifically, we incorporated evidence from published and gray literature on a variety of predatory taxa and from studies with varied predator removal motivations.

2. Approach

Based on preliminary searches and our perceptions regarding the quality of the evidence base (i.e., most studies had replication or included appropriate controls) we opted to conduct a qualitative

literature review rather than a systematic review. Because the scope of our paper was broad, we used general search terms of the title, keywords, and abstract of papers in the Scopus search engine: “predator removal*”, “cull”, and “predator control” to identify relevant literature (asterisks are wildcards in the Scopus search engine). Reference lists in identified literature were consulted for additional resources and searches were repeated in Google Scholar. Articles were appraised at the title and then abstract level for inclusion in a synthetic table. Referring to our definition of success (see below), we sorted literature into successful and failed applications of predator removal and by the objective of the study in removing predators. All searches, filtering and analysis were conducted by the same individual (R.J.L.) following input from co-authors. Bibliometric analyses were conducted in R (R Core Team, 2017). Figure plotted using the ggplot2 package (Wickham, 2009). Included studies were stored in a table (Supplementary material) with the predator species, motivation for removal, study duration, experimental method, our evaluation of success or failure (or equivocality), the removal method, a description of the study, and a citation (if not included in main text).

2.1. Defining successful predator removal

Success is a difficult outcome to define in predator removal because the motivations may be variable and idiosyncratic. Although we define success in the context of ecological responses, we acknowledge that successful predator removal must also consider the socioeconomic dimensions. For governments, the decision to implement predator removal may be a balance between satisfying demands of constituents for safety or prosperity against national or international agreements to protect species and economic externalities associated with wildlife, particularly ecological integrity. Nonetheless, we approach it from a conservation perspective insofar as removal must not cause long-term change or damage to the ecosystem while demonstrably benefiting the prey species, be they domestic animals (e.g. reduced rates of depredation), species at risk (e.g. increased local abundance or population growth rate) or of economic concern (e.g. increased harvest yield), or humans (e.g. reduced conflict or fear from predators). From an ecological and management perspective, we propose that successful predator removal would *reduce predator population to a size (or demographic state) that would not negatively impact the persistence of that population or its competitive status relative to mesopredators, but still provide demonstrable benefits to the prey species following predator removal* (Table 2).

Correlative methods used to evaluate success broadly match population trends of predator and prey species and ascribe outcomes (in terms of predator or prey densities) to the removal. Correlative approaches may lack the power to identify mechanisms (at least in the short term) driving population dynamics (Grubbs et al., 2016; Marcström et al., 1988) but can still provide insight into processes underlying prey population dynamics, particularly where experiments are infeasible. This can be observed in open marine systems where marine mammal culling programs may be tested by measuring correlations with fishery yields (Bax, 1998; Morissette et al., 2012). Shortcomings of retrospective analyses and correlational studies render it difficult to identify evidence supporting any positive effects accrued from predator removal, particularly in the context of different problems that arise where predator removal is being considered as a management strategy.

Experimental approaches to predator removal have more power to detect main effects on livestock depredation or species recovery. Controlled experiments using reference sites may be necessary but before-after-control-impact (BACI) studies can be useful to relate demographic trends to predator removal; however, BACI cannot account for changes to the environment that occur over time (e.g. Hervieux et al., 2014). Marcström et al. (1988) monitored grouse (*Bonasa bonasia*, *Lagopus lagopus*, *Tetrao tetri*) and capercaillie (*Tetrao urogallus*) populations across eight years, the first four with fox (*Vulpes vulpes*) and

marten (*Martes martes*) removal followed by four years without killing. Although removal improved nesting success and increased adult density over time, the authors still cautioned that factors other than predator removal could have stimulated the increases. Simulations can be useful, such as Martin et al. (2010), in which the number of removed raccoons (*Procyon lotor*) necessary to achieve oystercatcher productivity (*Haematopus palliatus*) was simulated, suggesting that the specific number targeted should depend on the density of raccoons. Ernest et al. (2002) similarly used simulation to calculate the number of mountain lion removals necessary to reduce extinction risk of bighorn sheep (*Ovis canadensis*). Such frameworks are one solution for testing the efficacy of predator removal programs prior to implementation.

Attributing predator removal to livestock depredation, species recovery, or direct conflict with humans is complicated when the measurement of outcomes is restricted to relatively short intervals after predator removal. The period immediately following the action of predator removal is the period most likely to indicate a reduction in predator density and conflict and an increase in prey density, but this may decrease at longer post-treatment intervals (e.g. Engeman et al., 2006; Magella and Brousseau, 2001; Sagor et al., 1997; van Eeden et al., 2018). Short-term increases to nesting success or juvenile survival fail to consider density-dependence that manifests in the longer-term and cannot demonstrate success of predator removal when there is no demonstrated benefit to the population in subsequent years. Several studies observed increased nesting success of ducks following predator removal (Garretson and Rohwer, 2001; Pearse and Ratti, 2004; Pieron and Rohwer, 2010), but a longer-term study conducted by Pieron et al. (2013) found that benefits to nesting did not carry over to the breeding population and therefore the latter studies provided no evidence to support predator removal (see meta-analysis by Côté and Sutherland, 1997). Although removal must generally be sustained (e.g. seasonally or annually) for benefits to be realized, success must be demonstrable and persistent over time (Bergstrom et al., 2014; van Eeden et al., 2018). Moreover, the benefits must outweigh the costs (Chessnes et al., 1968). A lack of longer term monitoring to determine whether predator removal was effective limits the power to interpret whether it was a successful intervention (van Eeden et al., 2018).

3. Synthesis

Our searches identified 141 empirical studies in which predator removal was studied by haphazardly culling predators with traps, guns, or poisons ($N = 87$), selectively removing predators ($N = 10$), controlled removal (i.e. a pre-specified number; $N = 21$), observing a natural decrease ($N = 1$), or in a simulation ($N = 10$). Studies were conducted on data from 1 to 78 years (mean \pm SD = 9 ± 12 years). Most studies ($N = 104$) were conducted to evaluate whether predator removal could improve prey populations, followed by studies determined to evaluate impacts on domestic animals ($N = 28$) and direct interactions with humans ($N = 8$).

We evaluated a large number of these studies ($N = 37$) to have equivocal results, for example owing to a lack of statistical analysis, poor control to detect main effects, or because the study did not include sufficient information with which to make a determination about success (Fig. 1). Frequently, this arose because predator removal resulted in increased breeding success without evidence that this contributed to subsequent increases in the population. Although the scope of a study may have intentionally been focused on briefer time scales or questions, for our purposes and based on our definition of success we could not describe such results as indicative of success. Most studies we evaluated we determined to have failed ($N = 67$) owing to direct evidence that predator removal had either not succeeded in limiting the predator population or had no statistical demonstration of success in reducing livestock losses, increasing prey densities, or mitigating direct conflict with humans (Fig. 1). Studies that were successful ($N = 36$) demonstrated that predators were agents of additive mortality and that their

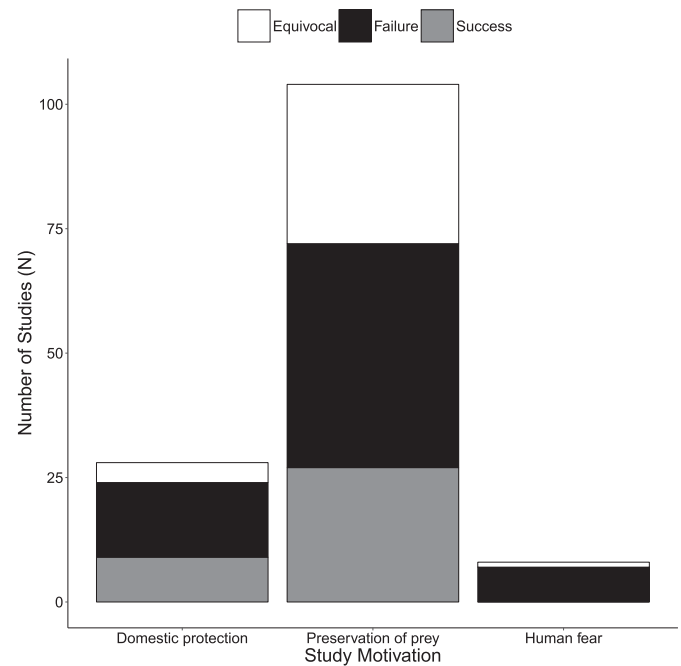


Fig. 1. Bibliometric summary of studies reviewed in this paper based on the three motivations for predator removal and the outcome. Studies are summarized in Table S1. Success was evaluated based on the definition in Table 2. Shading indicates our evaluation of the study as representing a success, failure, or equivocal outcome. Equivocality was ascribed for studies with inconclusive study design to determine success based on our definition.

removal resulted in subsequent increases in prey.

An important caveat of this bibliometric approach is that studies that were deemed to be successful or failed may have been so because of some idiosyncrasy in the sampling protocol that could not be expected to be consistent among studies. When measurements were made (e.g. when prey abundance was measured) and when interventions were undertaken (e.g. what season the predator was removed in) could influence the outcome and the determination of success or failure. Successes or failures could also emerge consistently for similar taxa that were overrepresented in the literature, a limitation of the vote-counting approach that we used to present percentages.

The numbers presented in this bibliometric analysis are intended only to represent relevant information and a summary of published literature and are not intended to provide evidence for or against predator removal without further context. Below, we discuss factors associated with success and failure in predator removal with the objective of introducing more context, nuance, and interpretation of the literature covered in our bibliometric review along with other research focused on the relationship between predators and their prey in an effort to address the question of predator removal from a conservation perspective.

4. Factors contributing to success and failure

4.1. Resulting in success

A prevailing hypothesis is that predator removal can be implemented to achieve wildlife management objectives. We predicted that predator removal would be successful in some contexts, specifically, when implemented as a solution for short-term conservation challenges in which the return or replacement of the predator population in the long-term is not necessarily relevant to success (see Table 1).

Table 1

In our literature review we identified outcomes of experiments that yielded success or failure given three motivations for removing predators and based on our definition of success (see Table 2). Here we review 11 of the common outcomes of predator removal, two of which we considered to be successful and nine of which we considered to result in failure. Rows are populated with examples of the predator removed and references to literature demonstrating the given outcome for different motivations. References without species are those that removed multiple predators or predators were generalized (e.g. in a simulation). Refer to Table S1 for a comprehensive review of the appraised literature.

Outcome	Evaluation	Protection of domestic animals	Preservation of prey	Mitigating risks of direct conflict
Removal of “problem predators” known to instigate conflict reduces future conflict	Success	<ul style="list-style-type: none"> • <i>Canis latrans</i>: Blejwas et al., 2002, Till and Knowlton, 1983 • <i>Canis lupus</i>: Blejwas et al., 2002 • <i>Lynx lynx</i>: Stahl et al., 2001 • <i>Canis lupus</i>: Bradley et al., 2015 • <i>Lynx lynx</i>: Herfindal et al., 2005 • <i>Pogonius cromis</i>: George et al., 2008 	<ul style="list-style-type: none"> • <i>Arctocephalus pusillus</i>: Makhado et al., 2009 • <i>Larus michahellis</i>: Sanz-Aguilar et al., 2009 	
Measurable reduction in conflict or improvement in prey demographics while maintaining predators in the ecosystem	Success		<ul style="list-style-type: none"> • <i>Arctocephalus pusillus</i>: Weller et al., 2016 • Fletcher et al., 2010 • <i>Canis latrans</i>: Smith et al., 1986; Reynolds et al., 2010 • <i>Canis lupus</i>: Bjorge and Gunson, 1985; Boertje et al., 1996, Gasaway et al., 1983, Hayes et al., 2003, Hervieux et al., 2014, Keech et al., 2011, Potvin et al., 1992 • Greentree et al., 2000 	
Conspecifics immigrate, replace predators, and conflict persists	Failure	<ul style="list-style-type: none"> • <i>Canis lupus</i> (Wielgus and Peebles, 2014 [refuted by Poudyal et al., 2016], Fernández-Gil et al., 2016) • <i>Caracal caracal</i> Bailey and Conradie, 2013; Conradie and Piesse, 2013) • <i>Puma concolor</i> (Peebles et al., 2013), <i>Canis dingo</i> (Allen, 2014, 2015) • McManus et al., 2015, Palmer et al., 2005 • <i>Canis lupus</i>: Chapron and Treves, 2016 • <i>Puma concolor</i>: Cooley et al., 2009 • <i>Ursus arctos</i>: Swenson et al., 1997 	<ul style="list-style-type: none"> • Amundson et al., 2013, Ellis-Felege et al., 2012, Littlefield and Cornely, 1997 • <i>Canis latrans</i>: Knowlton, 1972 	
Removal was equally or less effective than non-lethal alternatives	Failure			<ul style="list-style-type: none"> • <i>Puma concolor</i>: Peebles et al., 2013, Teichman et al., 2016 • <i>Ursus americanus</i>: Obbard et al., 2014 • <i>Ursus arctos</i>: Artelle et al., 2016 • <i>Ursus thibetanus</i>; Huygens et al., 2004 • Wetherbee et al., 1994
Predator population becomes imperilled by introgression with congenetic species or suffers depensation due to superadditive mortality	Failure		<ul style="list-style-type: none"> • <i>Canis lupus</i>: Eggemann, 2015 • <i>Epinephelus itajara</i>: Frias-Torres, 2013 • <i>Larus cachinnans</i>: Bosch, 1996 	
Unknown mechanisms of compensatory mortality reveal short-term success (e.g. improved nesting or hatching rates) but no evidence of increases in abundance or density in subsequent years	Failure			
Conspecifics increase reproductive rate, predator population increases, and conflict persists	Failure			
Density independent conflict yields no benefits of removing predators on the incidence of conflict	Failure			
Disappearance of a predator releases a mesopredator from competition, which maintains depredation	Failure		<ul style="list-style-type: none"> • <i>Canis dingo</i>: Wallach et al., 2010 • <i>Canis lupus</i>: Rutledge et al., 2012 • <i>Corvus brachyrhynchos</i>: Clark et al., 1995 • <i>Lynx lynx</i>: Palomares et al., 1995; Bodey et al., 2011, Prugh and Arthur, 2015 • Packer et al., 2003 	
Loss of predators deregulates pathogens within populations, resulting in increased disease-related mortality of prey	Failure			

Table 2

Proposed maxims of predator removal summarizing important findings about successful applications of predator removal for management.

1	Predator removal is an interdisciplinary topic necessitating consideration of ecological, economic, sociological, political, and other dimensions.
2	Failure to consider ecological issues when initiating predator removal can harm the ecosystem.
3	From an ecological perspective, successful predator removal would reduce predator population to a size (or demographic state) that would not negatively impact the persistence of that population or its competitive status relative to mesopredators, but still provide demonstrable benefits to the prey species following predator removal.
4	The functional response of the predator is essential to consider because it influences the rate of depredation of prey species.
5	Targeted removal of problem individuals may be an effective application of predator removal (Swan et al., 2017), as opposed to indiscriminate or retaliatory killing, but it is logistically difficult to confidently identify culprit predators (Stahl et al., 2002).
6	Killing predators seems to generally result in an increase of local depredation of livestock resulting from demographic compensation via increased birth rates of predators (Knowlton, 1972), immigration (Sagor et al., 1997), or release of mesopredators/invasive species (Wallach et al., 2015).
7	Among humans, there are broad demographic differences in attitudes towards predators, with support for predator removal generally from older and more rural individuals (Andersone and Ozolinš, 2004; Lüchtrath and Schraml, 2015).
8	Justifiable objectives for removal, especially the number to be removed, are necessary in planning predator removal rather than haphazard killing. Understanding the demographics and population dynamics of the predator is therefore essential. Adaptive management approaches can be applied to attempt sustainable removal that does not imperil the predator population (e.g. Martin et al., 2010).
9	Whether predator removal is actually effective at reducing conflicts or satisfying human attitudes towards predators is essential to its overall success as a management practice but the evidence for it is either equivocal or deficient.
10	There are increasing examples of non-lethal alternatives to predator removal, although many require scientific validation (Ogada et al., 2003; Okemwa, 2015).
11	Evidence that conflicts are mechanistically linked to depredation is important before beginning predator removal, along with evidence that predator removal will resolve the conflict, which can be tested via simulation (e.g. Morissette et al., 2012).
12	Coexistence with predators is possible and the most sensible way forward, but interdisciplinary research is necessary to continue to refine understanding of the human dimensions of predator removal (Carter and Linnell, 2016; Johnson and Wallach, In Press; Woodroffe et al., 2005).

4.1.1. Protection of domestic animals

When predators encroach on property or property development intersects with predator ranges, the presence of predators can become problematic if they threaten production animals (e.g. farms, ranch land, aquaculture facilities). Apex predators such as sharks, wolves (*Canis lupus*), dingoes (*Canis dingo*), lions (*Panthera leo*), tigers (*Panthera tigris*), cougars (*Puma concolor*), jaguars (*Panthera onca*), and leopards (*Panthera pardus*), for example, can affect the livelihoods of pastoralists, but so too can mesopredators (Davis et al., 2015) such as coyotes (*Canis latrans*), jackals (*Canis spp.*), crows (*Corvus corax*) and red foxes (*Vulpes vulpes*).

Predator removal can acutely reduce conflict when known predators are dispatched, but removals must often be of sufficient frequency or magnitude that they actually affect the population size or structure of the predator such that immigration does not compensate for removal (Bjorge and Gunson, 1985; Herfindal et al., 2005; Landa et al., 1999). For example, Bradley et al. (2015) found that wolf removal was successful at reducing livestock depredation if the entire pack was eliminated. Wagner and Conover (1999) killed coyotes and found that pastures with removal experienced slower rates of lamb depredation following removal (but see Treves et al., 2016 Supplementary material). In some cases, the success of predator removal is highly concentrated and neighbouring areas will suffer increased pressure; this may be a success on a small spatial or temporal scale but in general it would not achieve the desired outcomes (Santiago-Avila et al., 2018). Whether predators are actively targeting livestock or are encountering them opportunistically can affect success of the removal program. Odden et al. (2013) suggested that increased sheep production and decreased roe deer (*Capreolus capreolus*) density triggered a shift by lynx (*Lynx lynx*) towards sheep depredation, a type III functional response (i.e. preferentially targeting abundant species) that supports either lynx removal or roe deer conservation/supplementation. Moreover, there are different patterns of depredation for male and female animals. Males are generally more frequent livestock predators than females among solitary species, requiring selective removal to be successful (Felids: Odden et al., 2002; polar bear *Ursus maritimus*: Stenhouse et al., 1988).

Individuals within a population can differ in their propensity to depredate livestock for many reasons. Selective removal of individuals known to depredate livestock could be most effective in reducing future problems than haphazard culling (e.g. Woodroffe and Frank, 2005), the challenge being to accurately identify the offending individuals (Stahl et al., 2002; Swan et al., 2017). In our bibliometric review, we ascribed success to 40% of selective removals ($N = 10$) and only 19% in which

predators were non-selectively removed by haphazard culling ($N = 87$) or public hunts ($N = 11$). Blejwas et al. (2002) found that only selective removal of coyotes following depredation events reduced subsequent depredations and not pre-emptive or non-selective removal. Some predators socially transmit knowledge that livestock are prey (e.g. to offspring; Mondolfi and Hoogesteijn, 1986) and systematic removal of known predators could instill wariness in predators by “hunting for fear” (Cromsigt et al., 2013) or social transmission of risk (e.g. invasive lionfish; Côté et al., 2014). In spite of a long history of predator persecution, we did not identify examples that support this, suggesting more research is needed to address this question.

4.1.2. Preservation of prey species

When prey species or populations are declining in abundance, there may be added pressure for managers to take remedial action (Lessard et al., 2005; Reynolds and Tapper, 1996). This is particularly true of economically important species that are hunted or fished or those that are at risk of extinction. Most examples of success were from studies aiming to preserve prey, although not on a relative basis as only 26% were deemed to be successful.

Many of the most important terrestrial game species are herbivores whose populations may be moderated by depredation. Removing predators can release prey species from predation and, so long as mortality from those predators is additive and not compensatory, the prey species could increase in following years and re-establish a higher abundance. The most successful examples of preserving prey by removing predators emerge from studies of predator removal in northern ecosystems with fewer trophic linkages and more direct influences of predators. Jarnemo and Liberg (2005) correlated roe deer (*Capreolus capreolus*) population growth to a disease outbreak that reduced red fox density and released the deer from predation. Moose and caribou (*Rangifer tarandus caribou*) survival has also improved following removal of wolves as demonstrated by several studies observing increases in prey abundance (Boertje et al., 1996; Hayes et al., 2003; Gasaway et al., 1983; Keech et al., 2011).

Prey species suffering from depensation may specifically benefit from predator release (e.g. Liermann and Hilborn, 2001; Stephens and Sutherland, 1999). For example, cormorant (*Phalacrocorax auritus*) culling preceded yellow perch (*Perca flavescens*) abundance increases in Lake Huron, suggesting that removing the predators assisted in rebound of its prey. Although human intervention is generally the mechanism for small population size of prey species, the added pressure of predation can still be linked to depensation (Gascoigne and Lipcius, 2004; Kramer and Drake, 2010; Liermann and Hilborn, 2001). Juveniles of

species at risk such as marine turtles (Gascoigne and Lipcius, 2004) and salmon (*Oncorhynchus* sp.; Wood, 1987) that rely on safety in numbers to saturate predators during migration can undergo rapid declines from depredation (Hervieux et al., 2014; Liermann and Hilborn, 2001) and predator removal may facilitate increased juvenile survival and recruitment to such populations (Engeman et al., 2006; Pichegru, 2013; Hervieux et al., 2014; Makhado et al., 2009). However, it is not universally effective and alternate actions may have higher success than predator removal (Ratnaswamy et al., 1997). Improving juvenile survival may be a relevant management outcome for some species, but it does not necessarily improve population growth rate or abundance when there is density dependent or otherwise compensatory mortality and therefore studies that only observed increased egg hatching or juvenile densities were evaluated as equivocal without longer-term investigation (see Pieron et al., 2013). Considering generalist predators that consume fewer prey at smaller prey densities (type III functional response characterized by a logistic-type relationship between prey density and prey consumption, in which depredation is low until prey achieve a relatively high density and predators begin targeting that species), predator removal will not likely have a considerable effect because they would more likely switch to alternative prey instead of expending energy pursuing the rarer prey species (Murdoch, 1969; e.g. Middlemas et al., 2006). Specialization may also occur within species, in which cases the selective removal of specialized individuals can be an effective application of predator removal to release prey from depredation pressure (Sanz-Aguilar et al., 2009). Although predator removal may be effective when problems arise because of specialization, removal is not necessarily the most effective management option; alternatives such as exclosures may be more effective for reducing depredation and recovery of species at risk and should be tested (Rimmer and Deblinger, 1990; Reynolds and Tapper, 1996; Smith et al., 2011; Stringham and Robinson, 2015). However, the logistics of fencing off entire areas (e.g. breeding sites) to exclude predators are questionable and the long-term consequences can also be destructive (Hayward and Kerley, 2009).

4.1.3. Mitigating risks of direct human-wildlife conflict

Direct human-wildlife conflict has stimulated efforts to kill predators after attacks or a pre-emptive strike against future conflict (Gallagher, 2016). Few examples in the literature were identified that studied predator removal for relieving direct conflict between humans and predators ($N = 8$), with no examples of success. Fukuda et al. (2014) was determined to provide equivocal evidence for predator removal because it lacked proper control. However, they provide a salient example for future research in which predators that attack humans may learn to target them, in which case removing individual animals that have attacked humans could reduce future conflict (e.g. saltwater crocodiles *Crocodylus porosus*). There is a threat of animals habituating to humans, which may lead to more direct conflict in subsequent years and require removal of problem individuals (Linnell and Alleau, 2016). Predators infected with rabies or other diseases that increase conflict may also require lethal control (Linnell and Alleau, 2016). However, there is limited evidence that targeted killing of animals that have a history of interacting with humans reduces future conflicts, probably because such events are rare to observe, precluding experimentation or analysis (Swan et al., 2017).

4.2. Resulting in failure

The prevailing alternate hypothesis that we tested in conducting this literature review was that predator removal is not an effective tool for conservation or management of ecosystems. We reviewed the literature to identify research that described experiences or experiments with predator removal that have yielded perverse impacts on the ecosystem, or failure to achieve the desired objectives, which were different depending on the motivation for predator removal. Thus, we have divided

this section into the familiar subheadings based on those motivations (see Table 1).

4.2.1. Protection of domestic animals

Protecting domestic animals by removing predators should reduce the rate of depredation on those domestic animals (Eklund et al., 2017). However, predator removal efforts fail when depredation rates do not respond to culling because the predator population compensates or is replaced by another predator. When there are multiple predatory species, Kissui (2008) found that pastoralists had difficulty identifying which species was responsible for livestock depredation and that higher visibility of lions during daytime caused them to be incorrectly accused. Targeted killing of leopards and caracals (*Caracal caracal*; Bailey and Conradie, 2013; Conradie and Piesse, 2013), cougars (Peebles et al., 2013), dingoes (Allen, 2014, 2015), and wolves (Wielgus and Peebles, 2014 [refuted by Poudyal et al., 2016]; Fernández-Gil et al., 2016) designed to reduce livestock depredation actually increased depredation in subsequent years (but see Bradley et al., 2015). Removal of adults may have triggered compensation via rapid replacement by immigrants in open systems (e.g. Baker and Harris, 2006; Bjorge and Gunson, 1985; Lieury et al., 2015; Sagør et al., 1997), enhanced local juvenile survival (Kemp, 1976; Peebles et al., 2013), or increased reproductive rates (Knowlton, 1972; Pitt et al., 2001). These demographic responses maintain or increase the number of local predators, stabilize the probability of further conflict, and represent distinct failures (Boyce et al., 1999; Sacks et al., 1999). Demographic responses of predators to culling may therefore render predator removal largely ineffective unless removal is so extensive that it alters predator demography on a broad scale, perhaps to impose an alternative stable state (Greentree et al., 2000; Herfindal et al., 2005). Removal can imperil the predators by accelerating their population declines if mortality is additive (or even super-additive; Creel and Rotella, 2010), for example when it instigates increased poaching (Chapron and Treves, 2016) or infanticidal behaviour (e.g. cougar: Cooley et al., 2009; grizzly bear *Ursus arctos*: Swenson et al., 1997; lion: Packer et al., 2009). Removal can also isolate remaining individuals, resulting in increased dependence on livestock in the absence of a group that would otherwise target wild prey (Bjorge and Gunson, 1985) or result in hybridization and degradation of genetic integrity (Rutledge et al., 2012). Short of predator eradication, removal generally does not protect domestic animals in the long-term.

Extensive removal of predators or eradication of top predators can also release subordinate species from competition (i.e. mesopredator release; Crooks and Soulé, 1999). Mesopredators can be of equal or greater possible or perceived threat to livestock and may be invasive species that become difficult to remove (Gross, 2008; Wallach et al., 2010), with cascading changes at other trophic levels (Hebblewhite et al., 2005; McPeck, 1998; McClanahan and Muthiga, 1988; Ritchie and Johnson, 2009). Mesopredator release can undermine predator removal and sustain depredation of domestic animals. In some cases, multiple mesopredators replace one extirpated top predator, complicating further control efforts.

4.2.2. Preservation of prey species

Removing predators theoretically reduces the extent to which prey species are removed from a population (e.g. Weller et al., 2016) given an assumption that predation contributes to additive and not compensatory mortality of the prey species, and therefore removal of the predators will directly contribute to an increase in prey (e.g. Flaaten, 1988). Evidently, this presupposes negligible effects of bottom-up processes (see Grange and Duncan, 2006; Elmhagen and Rushton, 2007), that the prey would not be limited by density-dependent resource limitation, and that prey is limited by a specific predator (Frias-Torres, 2013; Parker, 1984). However, most acknowledge both forms of regulation are simultaneously important in ecosystems and the relative importance of top down vs. bottom up control can shift in relation to productivity (Oksanen et al., 1981). Despite repeated efforts to connect

predation to declines of economically important fishes, evidence for such a relationship is tenuous (Anon., 1986; Trzcinski et al., 2006). Eggemann (2015) also suggested that wolf depredation of moose (*Alces alces*) is density independent, meaning that reduced pack size could not succeed to increase moose escapement availability to hunters (also Kauhala et al., 2000). Similarly, Serrouya et al. (2017) showed that removing moose was effective for recovery of caribou in British Columbia because of apparent competition between wolves and caribou; although moose removal was not compared to wolf removal, this shows how predators can be incorrectly persecuted if alternative solutions to maintaining prey densities are not explored. Using Ecopath with Ecosim for mass balanced simulation based on foraging arena theory, Morissette et al. (2012) tested whether marine mammal removal would increase fishery yield and suggested that it would more likely lead to reductions than increases because of limited actual competition between fisheries and whales (see also Gerber et al., 2009). Yodzis (1998) also predicted a decline of fisheries yields during cape fur seal (*Arctocephalus pusillus*) culling programs that were proposed to increase yields. Lessard et al. (2005) simulated seal removal and predicted an increase in Pacific salmon smolt survival but suggested that it might increase predatory fish populations, which would replace the seals in depredating the smolts; generalist predators such as seals often regulate multiple populations within a community and removing these predators can lead to disequilibrium in the ecosystem.

The trophic position of the predator contributes to its functional response to changes in prey, an important factor when considering removal (Bowen and Lidgard, 2013). Removing a mesopredator will most likely yield compensatory depredation by other mesopredators (Clark et al., 1995). Elimination of a top predator could release herbivores from control, resulting in extensive damage to landscapes and changes to habitat suitability that cause shifts in the community (Bertness et al., 2014; Ripple and Beschta, 2006). Hunters can compensate for predation mortality but will generally remove highly fit phenotypes (Allendorf and Hard, 2009) whereas predators target weak or diseased prey (Genovart et al., 2010; Krumm et al., 2010; Quinn and Cresswell, 2004); loss of predators can then proliferate disease within prey populations (Packer et al., 2003) and can spill over to infect domestic animals (Cross et al., 2007). Even when removal is successful in the short-term, compensatory processes may regulate predator populations such that removal is ineffective in the long-term (e.g. Donehower et al., 2007). Long-term studies or simulation models are necessary to detect effects of predator removal on prey (see Costa et al., 2017).

4.2.3. Mitigating risks of direct human-wildlife conflict

Predatory animals are often perceived as threats to human safety in spite of infrequent interactions and small odds of actual conflict relative to many other habitual activities such as driving cars (Slovic, 1987). According to the social amplification of risk framework, empirically rare events contribute disproportionately to concern among the public and lead to economically, socially, or ecologically illogical responses (e.g. fear of flying; Kaspersen et al., 1988). This framework could be applicable to human-wildlife conflict if the perceived risk of direct attack on humans is higher than the actual risk. Sharks are often victimized by social amplification of risk, which has resulted in publicized and prominent state-sponsored programs that aim to cull sharks near beaches (e.g. Wetherbee et al., 1994; Gallagher, 2016). The major failure of shark culling programs, however, has been exemplified by a lack of evidence that it actually decreases attacks (Wetherbee et al., 1994), arising in part because many large predatory shark species are migratory and therefore there is a low probability that locally-based actions will be effective once they cease and sharks from surrounding and more distant areas move into these managed areas continually (Holland et al., 1999). Gray and Gray (2017) found limited support among patrons for lethal control of sharks. Correspondingly, we found no research asking whether culling programs actually affected the perception of risk by patrons; safety is difficult to guarantee, and a

perception of safety may encourage reckless behaviour (e.g. ignoring key risk factors associated with shark attack) that increases the likelihood of negative encounters with sharks (e.g. swimming offshore). The legacies of such efforts could instead just be negative public perception of the animals, increased fear, and impoverished conservation status of the targeted species. Perversely, Teichman et al. (2016) found that human-cougar conflict was higher in areas of cougar trophy hunting yet Gilbert et al. (2017) suggested that economic value of cougar populations exceeds the costs because they control deer populations that cause costly collisions with vehicles. Skonhoft (2006) discussed this in terms of Scandinavian wolves, suggesting there is an equilibrium possible between the economic losses of lucrative moose depredated by wolves (*Alces alces*) and gains in terms of reduced vehicle-moose collisions and damage to foliage caused by moose browsing in the winter, emphasizing the value of maintaining predators and the costs of predator removal.

There was no direct evidence that removing predators changes outcomes for human-wildlife conflict. Obbard et al. (2014) found no influence of black bear removal on future conflict with humans and Artelle et al. (2016) perversely observed that removal of grizzly bears was followed by no difference in future conflicts rather than a reduction. Although data in Artelle et al. (2016) do not suggest causality, it does indicate that removal was not successful at mitigating conflicts. Treves et al. (2010) further suggested that the number of black bears (*Ursus americanus*) killed by hunters did not reduce, and was actually correlated with increases in, reports of conflict in subsequent years (although it is relevant to note that complaints were not necessarily related to predatory activity of bears, but also property damage). Apparently, overlap between humans and black bears increases during poor years when urban resources aggregate the animals, meaning that removal of predators in these years has disproportionately high impact on the population (Baruch-Mordo et al., 2014).

5. Discussion

We evaluated the two opposing hypotheses considering the (a) success or (b) failure of predator removal as in the conservation and management of ecosystems. We selected a qualitative approach to testing these hypotheses by searching for published evidence of success and failure. We identified examples of success but ultimately found much more consistent evidence for failure (Table 1). Evidence that removing predators achieved conservation-sound outcomes was context-specific (see Section 4.1). Removing predators presumes that ecosystem-level responses are predictable (Ramsey and Norbury, 2009), yet theoretical and empirical evidence often suggests the contrary (Bax, 1998; Ruscoe et al., 2011; Yodzis, 2000). An exception may exist in ecosystems where predators and prey are very closely linked (e.g. northern terrestrial ecosystems) or the prey are suffering from compensatory population declines associated with depredation by predators with a type II functional response. Although predators can influence ecosystems (Holt et al., 2008; Nelson et al., 2004), other factors can make the ultimate response of an ecosystem unpredictable, even with rigorous scientific evaluation. The full range of complexity at the ecosystem scale is poorly understood, especially as it pertains to processes such as parasites in ecosystem dynamics (Roche et al., 2012). This was observed consistently in study designs, which were often either short in duration or lacking in control, rendering it difficult to avoid type I error.

Many governments are responsible for establishing and maintaining protected areas, zoning property (for agriculture or developing buffers), and formulating wildlife management regulations (Rands et al., 2010; Treves et al., 2017). Strong policy based on available evidence can contribute to effective conservation of predators in many ways, including the establishment of suitable regulations and protected areas (Linnell et al., 2001). However, predators are important components of the landscape not just in designated areas but also in areas of human

use (Dorresteijn et al., 2015; Gilbert et al., 2017; Kuijper et al., 2016; López-Bao et al., 2017). When conflicts arise, retaliatory killing by local stakeholders may be understandable but can undermine conservation efforts for both predators and the broader ecosystem. It is important to accurately document the movements and actions of depredating species and maintain records of conflicts to determine the appropriate course of action and to advance the science of predator conflict to develop resolutions. In its present form, our findings suggest that success in predator removal is highly contextual and should not be assumed by management without rigorous testing.

5.1. Alternative actions for managing human-predator conflict

Human-predator conflict challenges managers because depredation can be damaging to some livelihoods and traumatic for individuals (e.g. pastoralists, aquaculturists, fishers; Butler, 2000; Graham et al., 2005; Mishra, 1997; Patterson et al., 2004). Attitudes of retaliation (Holmern et al., 2007; Kissui, 2008; Thorn et al., 2012) are understandable, even though conflicts tend to be isolated incidents (Cozza et al., 1996; Chavez and Gese, 2005). Economic losses to depredation are, however, generally less than those attributable to other sources of mortality such as disease (Breck and Meier, 2004; Frank, 1998; Mazzolli et al., 2002; Mizutani, 1999; Kissui, 2008; Rasmussen, 1999). Livestock often comprises smaller components of the diet of predators than assumed by some pastoralists (Allen, 2015; Boast et al., 2016; Davis et al., 2015). Kaltenborn and Brainerd (2016) suggested that restoration of predators to large population sizes and then opening recreational hunting seasons could be a more effective alternative to balance socioeconomic objectives. However, sustainable harvest limits are incalculable without demographic data (Packer et al., 2009; Treves, 2009). Moreover, human harvests tend not to be non-selective for problem predators (Sunde et al., 1998) or can undermine conservation (Creel and Rotella, 2010). Where livestock comprise a more important food source for predators, conservation or restoration of native prey sources could mitigate losses (Meriggi and Lovari, 1996; Odden et al., 2013). Husbandry practices can alternatively reduce conflict with wildlife without ecological issues or social controversy (e.g. Jackson and Wangchuk, 2004; Johnson and Wallach, 2016). Fencing is already used by pastoralists (Hayward and Kerley, 2009) with variable success (Eklund et al., 2017). Birthing of calves during a short period may facilitate predator satiation, reducing depredation on farms (Palmeira et al., 2008). Calves can also be kept centralized and away from edges (Palmeira et al., 2008). Deterrent devices (e.g. fladry) also hold promise for reducing depredation (Ogada et al., 2003; Okemwa, 2015), evidenced by a 93–97% reduction in depredation of aquaculture sites using a non-lethal deterrent by seals (Götz and Janik, 2016). In scientific study, predator removal should be tested against realistic alternatives because in some cases deterrents are just as effective (Harper et al., 2008; Ratnaswamy et al., 1997) and may be more economical (McManus et al., 2015). When conflicts do arise, the costs can be offset with subsidies (Bulte and Rondeau, 2005; Dickman et al., 2011; Mishra et al., 2003). Challengingly, some governments do not have the resources to support conservation initiatives or compensate farmers for losses and in others, the systems are not developed to properly address the problems (Chen et al., 2015). In developing countries, this leads to continued persecution of predators, maybe out of bare necessity to maintain herds in some cases (Dar et al., 2009), but improved education and validation of effective alternatives hold promise for resolving conflict.

When prey species decline, hunters may support and lobby for predator removal (Franzmann, 1993) and conservation movements may support protection of species at risk by controlling their predators. Species persistence is considered a priority of conservation science and is often nested within the laws of regional and national management plans. Predator removal may appear to be a logical solution for maintaining adult populations and increasing juvenile survival during species declines; however, our results clearly show that studies are needed

to demonstrate this (Oro and Martínez-Abraín, 2007). Deterrents or barriers can reduce predator access to endangered species and may be more effective and economical in many scenarios (Shivik, 2006; Smith et al., 2011; Yurk and Trites, 2000). Emerging solutions that use sensory modalities to mitigate predation can also yield promising results, for example, Neves et al. (2006) tested taste aversion methods of reducing nest predation of endangered roseate tern (*Sterna dougallii*). Guardian animals have also shown promise for livestock (Meadows and Knowlton, 2000; Smith et al., 2000; van Bommel and Johnson, 2012) and species at risk (King et al., 2015).

The willingness to pay for hunting/fishing for large predators may be high, species of recreational importance tend to have higher acceptability and be better conserved, and illegal hunting can undermine ecological, economic, and sociological objectives of wildlife management. Therefore, managed hunts or fisheries targeting predators have been proposed as a solution to reduce poaching, maintain stable predator populations, fund conservation initiatives, and increase acceptability of some predators (Creel et al., 2016; Gallagher et al., 2016; Kaltenborn and Brainerd, 2016; Lindsey et al., 2007). Sportspeople and guides can keep watch for illegal activity, particularly in remote areas and activity can also reduce predator activity (Harper et al., 2008). The result of such managed hunts would, however, probably result in random, rather than targeted, removal that would not likely have any effect on the rate of predator conflict (Packer et al., 2009; Treves, 2009) unless it can be confidently applied to maintain a smaller predator population without resulting in depensation.

5.2. Social and economic costs of failure

Killing by people is the largest threat to the conservation of many predators (Kissui, 2008; Ripple et al., 2016; Woodroffe and Ginsberg, 1998). In spite of the problems with implementing predator removal for management, human-wildlife conflict persists (Treves and Karanth, 2003) and predator persecution and removal will likely continue, particularly when there is direct conflict between a human and a predator. Research on human attitudes towards predators is plentiful, relating demographics to perception of predators (e.g. nationality, gender, age; Andersone and Ozolinš, 2004; Lühtrath and Schraml, 2015). Attitudes towards predators depend greatly on exposure and experience as well as cultural values towards wildlife, for example, rural people tended to favour control more than urban dwellers (Andersone and Ozolinš, 2004).

It should be possible to quantify the carrying capacities and demographics of predators to maintain a smaller population of predators to limit conflicts, although in general we found that this is likely only possible via continued intervention (e.g. Landa et al., 1999). Careful calculation and monitoring would be essential for this because of unanticipated changes in demography arising from human-induced mortality and the potential for additive or super-additive (rather than compensatory) mortality following intervention that imperils the predators (Creel and Rotella, 2010). Indeed, Bradley et al. (2015) found that partial wolf pack removal was effective for mitigating livestock depredation while maintaining wolves in the northern Rocky Mountains; however, more rigorous methods can be implemented to calculate removal targets. The justification for predator removal targets and how they are defined is often weak and idiosyncratic. Strategies can include controlled removal with a stated goal (e.g. 50% reduction), haphazard culling (e.g. opportunistic removal), or selective removal (e.g. removing problem individuals), with variation in the expected outcomes. In Western Australia, the social licence and evidence for culling has recently been questioned (Legge et al., 2017). Simulation to determine the optimal number of predators to be removed to achieve conservation objectives can assist with validating predator removal prior to implementation (Ernest et al., 2002; Martin et al., 2010).

Modern management of predator conflicts must include stakeholders (Breitenmoser, 1998) and consider predators in an ecosystem

context rather than as individual species in conflict with humans. There is limited evidence that retaliation against a species or pre-emptive culling decreases conflicts or generates a sense of security in landscapes where predators exist. This points to a failure to consider the broader-scale processes that regulate predator populations and ecosystems (Berlow, 1999) as well as a lack of understanding of the human dimension of attitudes towards wildlife that promote negative perceptions. Moreover, it ignores the positive impacts of predators and intact ecosystems by regulating herbivores, mesopredators, and disease. Predator removal can also disconnect public perceptions of nature by acclimating people to manipulated and arguably depauperate ecosystems (Wallach et al., 2015), an outcome that can shift baselines and reduce support for conservation initiatives (Chapron and Treves, 2016). This problem is exemplified in coyote control, where Berger (2006) calculated a long-term expenditure of over a billion dollars for coyote removal programs in the United States that were intended to improve the sheep farming industry and wool production had no measurable benefits across 78 years of data.

5.3. Study context and future research directions

Evaluating the contribution of predators and the success of predator removal to conservation efforts has been attempted elsewhere in the ecological literature. Meta-analysis is well suited to this problem because it reduces type II error (compared to vote-counting approaches) and weights studies by their sample size; however, it can be overly influenced by few studies with large sample sizes. Whereas meta-analysis is suited to analyzing studies with similar intervention, endpoint, and subjects (Eysenck, 1994; see Smith et al., 2010, 2011 for effective examples of this), it is constraining for broad topics such as predator removal (Haddaway et al., 2015), which is conducted for many different reasons on a variety of taxa, making it difficult to generate reliable numerical assessments that could be considered relevant across socioecological contexts. Instead, we opted for a qualitative review with bibliometric analyses to reveal successes and failures with appropriate consideration to context. There are lessons to be gained from viewing many different, often disparate predator removal attempts through a common lens and identifying how varying inputs (e.g. motivations, taxa) contribute to outcomes to address future problems that arise. Provided that future studies on this topic address some of the deficiencies in experimental design noted here, there is potential to improve the quality of the evidence base such that meta-analysis within the context of a systematic review should be possible and will help to ensure evidence-based environmental management in the future (Sutherland et al., 2004).

6. Conclusion

Human-wildlife conflict will persist with direct impacts on ecosystems globally. Desire to manage predator populations will therefore continue in spite of growing conservation concern for many predators (and in some cases, recovery of their populations; Curtis et al., 2014).

Our review suggests that the success of predator removal depends on the motivation and design of the effort because of the variability in success identified across studies. More research is needed to determine whether predator removal reduces direct conflict with humans or human fear. However, there was some circumstantial support that removing predators facilitated prey recovery and some evidence that it assisted with protection of domestic animals. Nonetheless, a main takeaway from this review is the inconsistencies and idiosyncrasies of outcomes. Predator control should be pre-empted by research to justify the action and set removal targets, with anticipated outcomes stated and follow-ups planned to evaluate the action. Alternative actions may be equally or more effective and should be studied in parallel when possible. Some studies are not designed to detect main effects of predator removal and are instead retrospective and correlative because

predator removal may not always be motivated by conservation (Treves et al., 2016). How the decision to remove predators is arrived at typically remains unclear. Although much can be learned from experimental approaches (e.g. Lieury et al., 2015), they can be costly, ethically controversial, and require the removal of predators for didactic purposes. Simulation approaches or predictive modelling have the potential to become increasingly useful tools prior to implementing removal in order to project whether the predator removal is likely to achieve the desired outcomes (e.g. Martin et al., 2010; Morissette et al., 2012; Yodzis, 1998). However, such efforts need to consider and account for many potentially confounding external variables such as food availability and competition in order to conclude whether predator removal is likely to be successful as well as the potential for immigration compared to compensation (Creel et al., 2015).

6.1. Promoting coexistence

Coexistence with predators is the desired way forward for many (Bergstrom, 2017; Carter and Linnell, 2016; Johnson and Wallach, 2016; Woodroffe et al., 2005), and there are increasing examples that predators can persist even among dense human populations (Chapron et al., 2014; Elliot et al., 2016; Gilbert et al., 2017). Indeed, predators play important ecological roles in rural areas and even in urban regions (Gilbert et al., 2017). We propose that paradigms positing predator persecution as a positive management intervention require reassessment (see also Graham et al., 2005). However, interdisciplinary approaches that consider socio-ecological perspectives (e.g.; Bisi et al., 2007; Elliot et al., In Press; Hill, 2015; Kaltenborn et al., 2006) will be integral for determining how human perceptions, values, and attitudes towards predators are shaped, and how they can be accounted for to meet the needs of humans and predators and minimise conflict in an increasingly crowded landscape.

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