

Predation services: quantifying societal effects of predators and their prey

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Conservation of predators – especially large carnivores and those that potentially pose threats to humans – can be controversial among stakeholders who must coexist with them. What is often overlooked, however, are the direct and indirect ecosystem services and disservices predators provide as a result of consumption of herbivores (“predation services”). We used a theoretical predator–prey–economic model to examine when predators are likely to provide a net service to society, by comparing services/disservices to a predator-free counterfactual scenario. We found that net predator services were strongly dependent on how per-capita services and disservices of predators and prey changed with abundance (ie assumed marginal value [MV] functions of service/disservice). We suggest that further empirical research is needed into MVs of services/disservices of wildlife, because transferring net services among locations – a common practice – is problematic unless MV functions are known. Rigorously quantifying services/disservices of predators could improve conservation and management outcomes by increasing effective communication to diverse stakeholders.

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Predators, especially large carnivores, continue to be among the most politically and socially polarizing of all wildlife, in part because some people perceive them as costly consumers of livestock while others see them as beneficial regulators of wild ecosystems (Treves and Karanth 2003). In reality, predators, as with all wildlife species, can provide ecosystem services and disservices that are likely to flow to different groups of people at different times and to change depending on the

social–ecological context (Figures 1 and 2; Seoraj-Pillai and Pillay 2017). Moreover, the services and disservices of any wildlife species, including predators, include some that are direct (eg disservices such as livestock damages from predators; van Eeden *et al.* 2017), and others that are indirect via trophic interactions (eg services provided by predators consuming damaging prey; Figure 1; O'Bryan *et al.* 2018). For predators, which are generally rare relative to their herbivore prey but which can strongly influence lower trophic levels through top-down effects (Estes *et al.* 2011), indirect services and disservices provided by predation have the potential to outweigh direct service/disservices (Gilbert *et al.* 2016), but comparisons of such effects are uncommon.

As practitioners and researchers seek to increase the viability of predator conservation in the Anthropocene, improving the valuation of the direct and indirect services and disservices of predators has become a pressing research need (Gilbert *et al.* 2016; O'Bryan *et al.* 2018). Although the use of economic tools and concepts to assign a human-centered (ie instrumental) worth to nature remains somewhat controversial – primarily due to the argument that nature is intrinsically valuable regardless of whether humans recognize or benefit from it (Farber *et al.* 2002) – such approaches are increasingly relied upon as decision-support tools in conservation and natural resource decision making. Nonmarket valuation tools can, at least in part, bridge this divide, allowing for quantification of metrics like “existence values”, in which people’s “willingness to pay” for the continued existence of a natural resource is measured even if they may never directly interact with the resource in question (Fisher *et al.* 2015). This is, however, still a fundamentally human-centered and capitalistic viewpoint. Given that the futures of more and more ecosystems are dependent on human decision making, human-centered tools like economic valuation will doubtless play increasingly prominent

In a nutshell:

- Predators and their prey can both provide ecosystem services and disservices (that is, benefits and costs) to society
- Through the act of predation on prey, predators fundamentally provide indirect services/disservices (“predation services”), which are currently not well understood or quantified
- To calculate net services of predators and prey, scientists must determine the relationship between animal abundance and the “marginal value” of services/disservices provided (defined as the value of the service/disservice per additional animal added to the population)
- If marginal values of services/disservices vary with animal abundance, the net services of predator populations will be more difficult to calculate, and caution should be used when transferring values of services/disservices to new locations or ecological conditions

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Figure 1. A predator – in this case, the American black bear (*Ursus americanus*) – can perform (a) direct disservices (eg bears eating trash, a common conflict behavior); (b) direct services (eg a tourist engaging in bear viewing); and (c) indirect “predation” services or disservices (eg impacts resulting from bear predation on deer [*Odocoileus* sp], such as regulating an overabundant herbivore population or reducing deer-hunting opportunities).

roles as hard trade-offs are contemplated. Indeed, while nature may often be perceived to be “priceless”, having an intrinsic value beyond that which can be characterized using economic tools, treating it as such in public discourse and policy making can instead result in an implicit value of zero in many decision processes. Improved approaches to the valuation of nature will therefore likely improve conservation outcomes, particularly if used to measure hidden services not currently valued, and if applied rigorously and transparently even in the face of ecological and socioeconomic complexity.

Some services/disservices, such as the direct disservices of depredating livestock or attacks on humans, are relatively easy

to quantify, and as a result are also the focus of much controversy, as well as research and mitigation or compensation efforts (Dickman *et al.* 2011). However, predators can also provide a range of direct services, including recreational hunting, tourism opportunities, and cultural and identity services (Muhly and Musiani 2009; Carter *et al.* 2012; Penteriani *et al.* 2016). In addition, the indirect services provided by predators, such as those deriving from consumption of damaging prey, are an emerging research frontier (Gilbert *et al.* 2016; O'Bryan *et al.* 2018; Braczkowski *et al.* 2018; Dee *et al.* 2019). These indirect services can be substantial when herbivorous prey species cause harm to valuable plants, such as crops, seedlings of forestry trees, residential landscaping (Côté *et al.* 2004; Gilbert *et al.* 2016), forage plants shared with domestic livestock (Ranglack and du Toit 2015), or plants of cultural importance or necessary for subsistence (eg traditional foods used by Indigenous groups). Predators can also have indirect disservices when they consume valuable wild prey, including reductions of prey existence and viewing services (Naidoo *et al.* 2016), hunting/meat services (Chen 2016; Naidoo *et al.* 2016), cultural/spiritual services, and enhancement of habitat for other animals via beneficial grazing effects. Although the indirect disservices of predators are well known to stakeholders (eg hunters who value wild ungulates), they are rarely considered by researchers (but see for example Elbroch *et al.* 2017).

Our objective here was to help fill this research gap through the use of a theoretical predator–prey–economic model as a heuristic tool to consider predator services and disservices to society, by comparing services/disservices in a predator–prey–plant model when predators are present to a counterfactual scenario in which predators are absent. We translated trophic relationships into services and disservices to humans by incorporating the direct services and disservices of predators, as well as the services and disservices of prey consumed by predators. Moreover, we considered different assumptions about

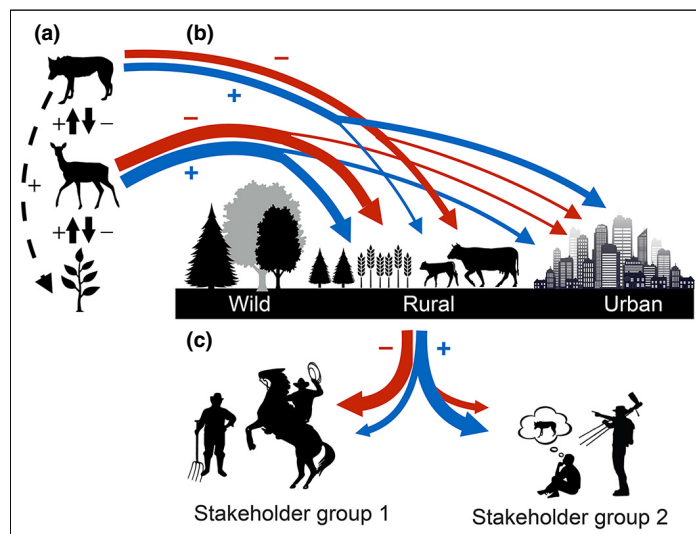


Figure 2. Conceptual diagram of how (a) a tri-trophic system consisting of predators, herbivores, and plants can interact directly (solid black arrows) and indirectly (dashed black arrow) in ways that increase (+) and decrease (–) each other’s abundance, which can provide direct and indirect services (blue arrows) and disservices (red arrows) that are (b) distributed across landscapes unequally, resulting in (c) services/disservices that differ by stakeholder group.

how the per-capita services and disservices (ie the marginal value [MV] of services/disservices; Fisher *et al.* 2015) of predators and prey are related to their respective abundances (Panel 1; WebTable 1).

Addressing MVs of services/disservices in predator–prey systems is especially important for economic valuation of predators because their net service depends not only on their own service and disservice MVs but also on those of their prey. Ensuring that this estimation is accurate is extremely important because the per-animal or per-unit-area services/disservices of a species are often extrapolated from one study location to a broader landscape or new locations altogether (Richardson and Loomis 2009; Boyles *et al.* 2011). This extrapolation is called a “benefit transfer”, and while potentially very useful, it depends heavily on the assumption that the factors that influence service/disservice values are similar in the original and transferred locations, an assumption that is not always correct (Richardson and Loomis 2009). Although rarely employed, disservices could also be transferred in a similar way, with similar assumptions. Overall, when undertaking these service/disservice “value transfers”, it is critical that the underlying assumptions, such as the functional form of the MVs for services/disservices, be examined and met (Figure 3; Panel 1).

We conducted a series of predator–prey simulations using three basic MV relationships (Figure 3; Panel 1) that seemed reasonable given the limited examples available in the literature (Panel 1). We demonstrate that net services or disservices of predators are largely determined by marginal services/disservices of both predators and prey, underscoring the need to understand MVs of services/disservices across different trophic levels and different social–ecological contexts. A better understanding of these services/disservices can enhance our knowledge of the services and disservices provided by predators in landscapes shared with humans, and improve the design and sustainability of conservation interventions, such as compensation programs and market-based approaches (Treves and Karanth 2003).

■ Methods

To explore the importance and effects of different MV functions of predator–prey services/disservices on the net

services of predators, we compared the effects of three likely functional relationships for the MV of wildlife, although numerous other, more complex relationships are also possible (eg thresholds, multimodal distributions, and so on; Putman *et al.* 2011; Bleier *et al.* 2012; Khorozyan *et al.* 2015). Specifically, we examined (1) a constant MV, in which no matter how many animals there are in the population, each new animal added to the population has the same value; (2) a linear MV, in which each new animal has an incrementally (constantly) increasing disservice or service value as abundance increases; and (3) an exponential MV, in which the value of each new animal escalates or diminishes in a nonlinear way with abundance (Figure 3; Panel 1; WebTable 1). From each of these three relationships between MVs and animal abundance, we arbitrarily set the maximum service of a single predator and prey animal at \$1 and the maximum disservice of each at \$0.90 (such that services/disservices would be visibly different in figures). For exponential marginal relationships, a minimum per-capita disservice of predator and prey was set at 0.001 of the maximum services/disservices, so that the curved relationship had a positive minimum/maximum (eg the services curve could not go below zero; Panel 1). We then calculated expected total services and disservices of the predator and prey populations across a range of animal abundances produced by our predator–prey models (see WebPanel 1). Because many large-bodied herbivore populations are density dependent, with vital rates (eg survival, reproduction) that decline as the population approaches carrying capacity (Bowyer *et al.* 2014), we included an herbivore population that was limited by nutritional carrying capacity (K). We used predator–prey difference equations, with ratio-dependent predation rates and values based on wolf (*Canis lupus*) and moose (*Alces alces*) life-history characteristics, as developed and described by Eberhardt (1998). Our models were deterministic, although demographic and environmental stochasticity would be interesting avenues for exploration in future analyses. Details about our modeling approach are presented in WebPanel 1.

To determine the services and disservices of predators, researchers must choose the correct “control” for comparison. Because many debates about predators hinge on the question

Panel 1. What is a marginal value, and why does it matter?

An individual animal can provide both services and disservices (benefits and costs) to society. The value of the service/disservice of adding one more animal to the current population is the “marginal value” (MV) in economic terms, or the slope or coefficient if we think of a generalized linear equation of cost–benefit dependent on abundance. The MVs of wildlife can vary widely. For example, for herbivorous prey, depredation of crops increases with population density (Bleier *et al.* 2012), and per-capita depredation may also increase with density if wild forage plants become depleted, causing increased consumption of crops (Putman *et al.* 2011). Likewise, predators

increase livestock depredation if the density of wild herbivores drops below a threshold (ie less total wild food available; Khorozyan *et al.* 2015). Other factors could also cause non-constant and nonlinear marginal services/disservices for wildlife, such as humans placing greater value on rare wildlife than on more common species (Chen 2016; Dee *et al.* 2019). MVs affect how we can “transfer the value” of the population under study to a different location. As the relationship between MV and animal abundance becomes increasingly complex, more information is needed for a value transfer (Figure 3).

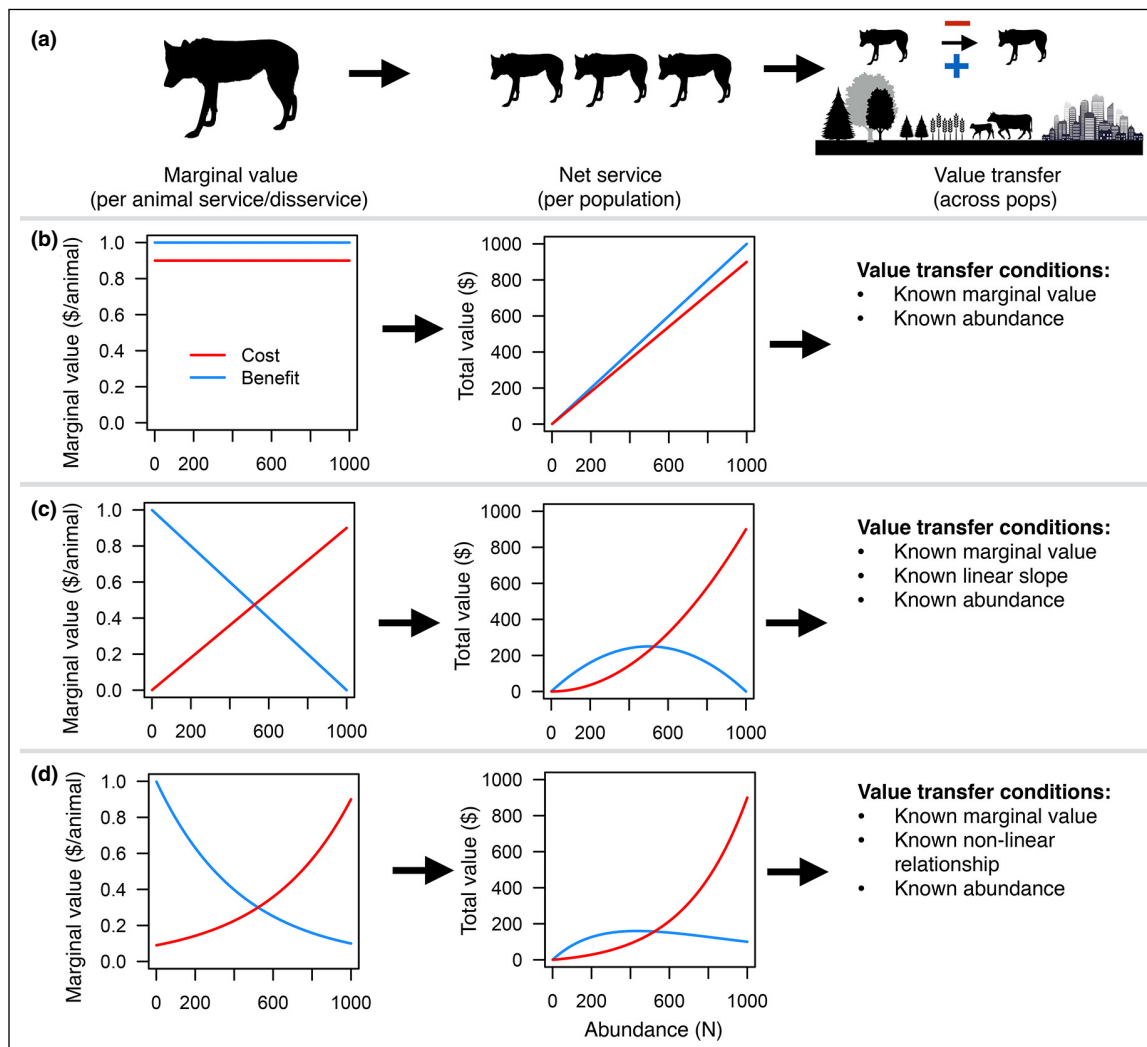


Figure 3. We used three functional forms to operationalize different marginal values (MVs) of wildlife in our theoretical model; here, we illustrate (a) the constraints on rigorous value transfers, including (b) a constant MV (eg if bears attack humans, but each additional bear in a population is just as likely to attack); (c) a linear MV (eg if each additional elk [*Cervus canadensis*] in a population linearly decreases the supply of wild forage plants shared with cattle); and (d) an exponential MV (eg if the viewing service of an individual tiger [*Panthera tigris*] to tourists is much higher when tigers are rare rather than common). The marginal service/disservice (blue line/red line) does not necessarily describe the same species at the same time.

of if they should persist, be reintroduced, or be allowed to recolonize naturally in a given landscape, we represented the control as a predator-free counterfactual scenario. To generate a predator-absent counterfactual comparison, we used the same predator-prey model but set predator abundance to zero, permitting prey population size to be entirely dictated by nutritional carrying capacity. This allowed us to compare outcomes associated with predator-free prey abundances to those with both predators and prey present (Figure 4). By comparing the predator-free and predator-present scenarios, we could then use different MV-abundance relationships, per-predator and per-prey, to calculate predator direct services and disservices, as well as predator indirect services and disservices (Panel 1; Figures 4–6). Predator indirect disservices were calculated as the “foregone services” of the prey that did not exist in the predator-present scenario compared to the predator-free

scenario (Figure 4c, graph [i]). Likewise, predator indirect services were calculated as the “avoided disservices” of the prey that did not exist in the predator-present scenario compared to the predator-free scenario (Figure 4c, graph [ii]).

Results

We found that the forms of the functional relationships between MVs of services/disservices and animal abundance had a strong effect on the total services and disservices of predators and prey, and subsequently on the net services of predators.

Direct services and disservices of predators and prey were strongly affected by MV-abundance relationships (Figures 5 and 6). Constant marginal services/disservices produced total direct services and disservices that scaled directly with abundance. In contrast, linear marginal services/disservices, in

which per-capita disservices increased with abundance and per-capita services decreased with abundance, produced total direct services and disservices that changed much more dramatically with abundance. Exponential marginal relationships produced even more dramatically escalating total disservices and declining total services with abundance than did linear relationships.

As a result, the net service (sum of direct and indirect services and disservices) of predators varied across marginal relationships, and with abundance of predators and prey (Figure 6). Net services of predators could be positive (constant MV; Figure 6d) or primarily negative (linear and exponential MV; Figure 6, e and f), but were all dominated by the indirect services and disservices of predators via consumption of prey, accrued through either avoided disservices or foregone services of prey that were consumed, compared to the predator-free counterfactual (Figures 5 and 6).

Discussion and conclusions

The services and disservices of predatory wildlife affect many facets of human lives. Comprehensively measuring predation services and disservices and evaluating how different conditions affect service/disservice values therefore have profound consequences for how we manage for human–wildlife coexistence in shared landscapes. Previous research has primarily focused on the direct disservices of predators to humans (eg livestock loss), often overlooking their direct services, indirect services/disservices, or the variation in services/disservices as functions of predator and prey abundances. Here, using deterministic predator–prey–economic models, we demonstrate how slightly different assumptions regarding the marginal (per-capita) services and disservices of predators and their prey can strongly affect the resulting net services of predators. The variation in model outcomes illustrates that the misattribution of services and disservices or imprecision in the measurement of MVs of services/disservices can potentially lead to ineffective or even counterproductive conservation policies. Below, we discuss the implications of differing marginal services/disservices to contemporary conservation policy making, and future research directions to better characterize the role that predators have in our lives.

Accurate and holistic valuation of predatory wildlife could help increase social tolerance and improve prospects for their conservation. For instance, there is currently a lack of equity between who pays for the disservices versus who reaps the benefits of the services of predators, such that rural populations typically bear many more disservices than do urban

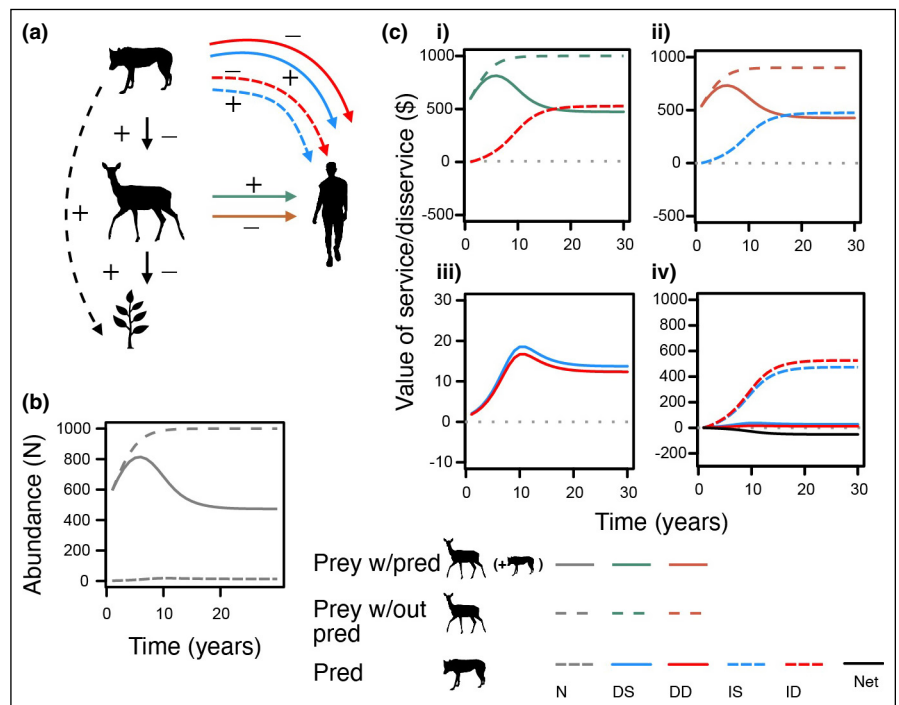


Figure 4. The predator–prey–economic model assumes (a) trophic interactions (both + and –) among predators, prey, and plants can be direct (black solid arrows) and indirect (black dashed arrow), and determine the indirect services (IS) and indirect disservices (ID) of predators (dashed blue and red lines), which result from the direct services (DS) and disservices (DD) of their prey (green and orange solid lines); (b) predator-associated services and disservices were calculated by comparison to a predator-free counterfactual model of abundance (N); and (c) predator ID are the result of foregone services of prey (i), predator IS are the result of avoided disservices of prey (ii), predator DS and DD are dependent only on predator abundance (iii), and predator net service (Net) is calculated from the DS, IS, DD, and ID of predators (iv).

populations. Redistributing services and disservices among stakeholders should lead to better conservation outcomes, but to do so would require accurate quantification of the disparities in space and time. Furthermore, transfers of wildlife services/disservices (almost entirely services, based on the literature to date) from an original study system to a new system, although a common approach (eg Richardson and Loomis 2009) should be undertaken only with great care, especially for predatory wildlife where many services/disservices depend on the prey eaten. For example, the per-hectare economic value of pest suppression by insectivorous bat species has been estimated for cotton-dominated landscapes in Texas (Boyle *et al.* 1998), but due to variation in both predator (bat) and prey (crop pest) species outside of this study region, it would be inappropriate to extrapolate this value across the entirety of the US (Fisher and Naidoo 2011). Likewise, for large predators that are gradually recolonizing portions of their historical ranges, it is problematic to assume that the net services or disservices in their current ranges will transfer to those newly occupied areas. In the province of Trento, Italy, public opinion has switched from widespread acceptance of brown bears (*Ursus arctos*) – reintroduced to the mixed-use region ~20 years ago – to growing opposition to their presence due to increasing bear depredation of livestock and damage to local

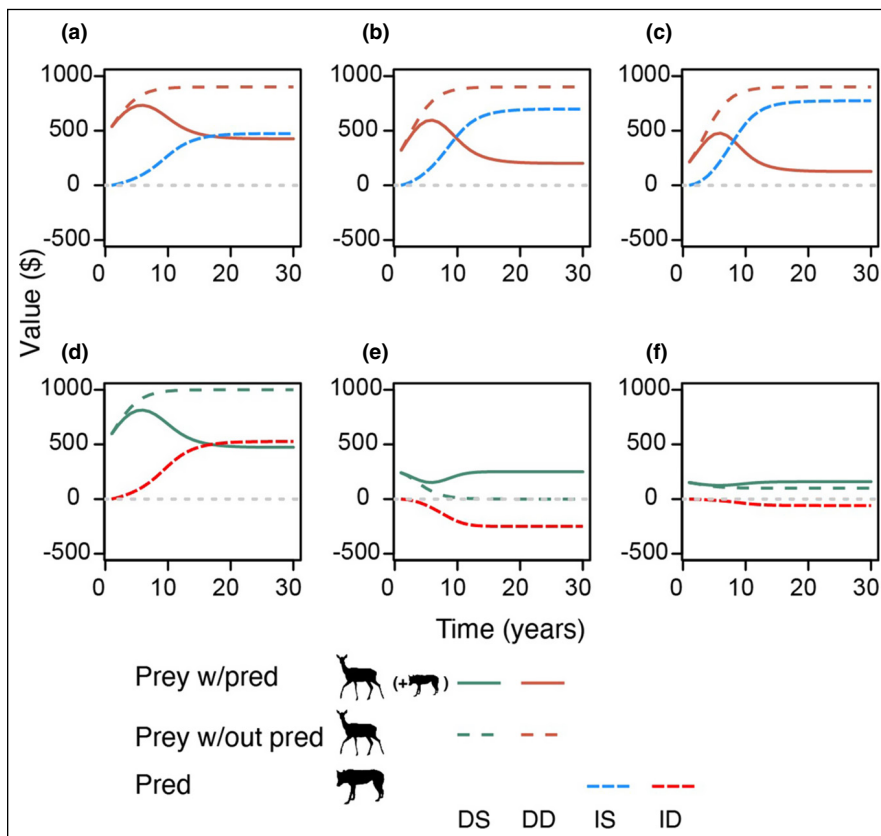


Figure 5. Predator–prey populations that fluctuate through time-steps provide indirect services of predators (a–c) due to avoided disservices of prey eaten, and indirect disservices of predators (d–f) due to foregone services of prey eaten, which differ dependent on whether the MVs of services/disservices of each predator and prey are constant (a and d), linear (b and e), or exponential (c and f). Colors are the same as those described in the Figure 4 caption.

apiaries (Tosi *et al.* 2015). However, we might expect a different mixture of services and disservices associated with the recent arrival of brown bears that dispersed from Trento to the nearby Swiss National Park, where approximately 150,000 tourists visit each year (Perino *et al.* 2019). Similarly, the net services and disservices of wolves reintroduced into the North Rocky Mountains of North America shift as animals from those populations disperse into areas with different prey bases and social contexts (Carter *et al.* 2019).

We suggest that value transfers could be problematic if (1) MV relationships with abundance are not known; (2) MVs of services/disservices are not constant with animal abundance/density, and density of predators and prey are not known; and/or (3) stakeholder and landscape contexts are markedly different (see Panel 1). For example, per-capita disservices of predators differ by an order of magnitude across their ranges in Europe (Bautista *et al.* 2019), and invasive predators can be devastating to native biodiversity outside of their native range (Doherty *et al.* 2016). Finally, because the indirect services of predators are likely dramatically underestimated, greater effort to comprehensively evaluate predation services can also influence how we communicate the services of predators to society. Recent work highlights the often-overlooked indirect services of predatory wildlife. This includes several cases where

reductions in herbivore abundance from predation result in economic services to people, including reductions in vehicle collisions (Gilbert *et al.* 2016) and reduced disease transmission to humans and livestock (Braczkowski *et al.* 2018; O'Bryan *et al.* 2018). Assessing and mainstreaming these services in social discourse about predators in shared landscapes could improve human tolerance of these animals (Carter and Linnell 2016). For instance, adult men in Costa Rica who knew more about bat natural history and ecosystem functions (seed dispersal and flower pollination) were less likely to harbor intentions to indiscriminately kill bats (Reid 2016).

It is also very important to correctly identify the counterfactual against which wildlife species' services and disservices should be calculated. It is tempting to compare the services and disservices of controversial wildlife, such as predators, to those generated by a slightly higher or lower abundance (eg compared to a previous year's services and disservices of a predator species; “would we experience fewer livestock depredations and harvest more elk [*Cervus canadensis*] if there were fewer wolves next year?”). Although this could be useful in some applied situations, the ultimate counterfactual is the absence of the species altogether (eg compared to the total absence of the predator species) – in the wolf/

elk example, there would be no livestock depredations in the absence of wolves, but also high elk populations, resulting in enhanced hunting and viewing opportunities for elk but also increased disservices of crop depredation, vehicle collisions, disease transmission, and so on. For predators that regulate prey abundance, this could lead to very different calculations if prey populations increase rapidly in the absence of predators and prey marginal services/disservices vary with abundance. In reality, this “counterfactual” is the status quo for many parts of the world where predators have been extirpated or have experienced large contractions in range size, although recent natural and assisted recolonization of predator-absent landscapes also highlights the utility of this counterfactual.

As practitioners and researchers seek to use real-world valuations of carnivores to enhance coexistence on shared landscapes, we stress that our models are merely a starting point for analysis of linked wildlife and human systems that include predators. The relationships we modeled are an oversimplification of many of the nonlinear relationships of wildlife services and disservices that occur in the real world (Bautista *et al.* 2019). Next steps in extending our models could include empirical and/or theoretical efforts to incorporate the effects of stochastic environments on predator–prey–plant dynamics,

marginal services/disservices that have different relationships with abundance, multiple direct and indirect services and disservices, and services and disservices that fluctuate in space and/or time in response to ecological and social change (eg differences in stakeholder groups, livestock, and wildlife communities; Carter *et al.* 2019).

Real-world social–ecological systems are far more complex than the first-pass sources of complexity we discuss above. On the ecological side, the dynamics of multi-predator multi-prey assemblages have proven extremely difficult to predict, and become even less tractable when considering climate and other environmental fluctuations, source–sink dynamics among metapopulations, and other sources of uncertainty. In terms of the socioeconomic system, predation services/disservices across shared landscapes inherently depend on human behavioral responses to wildlife (Penteriani *et al.* 2016), which can shift over time and could in turn have feedbacks to wildlife abundance and MV functions (Farber *et al.* 2002). Indeed, changing human behavior is a promising avenue for reducing disservices and increasing services (eg adoption of nonlethal deterrence of predators that prey on livestock or ungulates that depredate crops, more widespread use of payment-for-services and other incentive-based programs; Dickman *et al.* 2011).

Given these many sources of ecological and social complexity in coupled social–ecological systems, it would be unwise to use valuation tools and/or models to attempt to manage for some static “optimum” abundance of predators or prey based on net value to society (Farber *et al.* 2002). Rather, such tools could be used to better identify inequities in who pays the costs versus who reaps the benefits of wildlife, and when services/disservices must be locally evaluated versus transferred. In addition, inherently high levels of uncertainty in these complex, coupled systems also suggest that maintaining large areas as unmanaged “reservoirs” of natural predator–prey dynamics would be prudent as a hedge against current and future uncertainty (eg Robinson 1993).

Economic valuation tools are increasingly used to derive a “common currency” for predatory wildlife based on their services and disservices, and therefore sources of complexity should be acknowledged and incorporated. As we demonstrate here, predators’ strong indirect effects via regulation of prey should be included in valuation efforts, and their socioecological context also carefully considered before transferring their net services to any other systems. Rigorously doing so will help ensure that wildlife valuation remains a valuable tool for decision makers, managers, and conservation practitioners into the future.

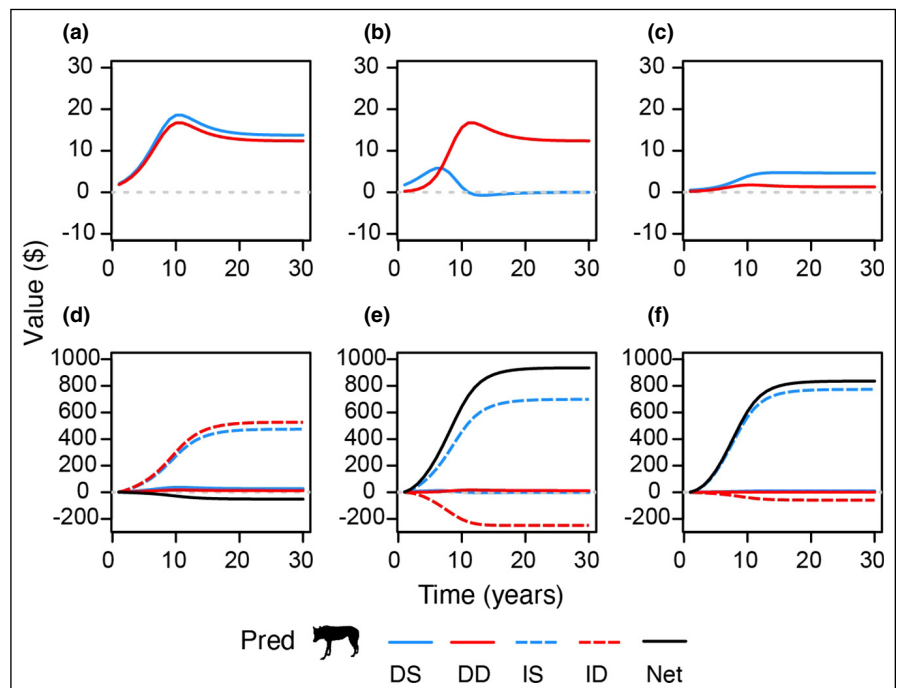


Figure 6. Predator populations have differing direct predator services/disservices (a–c) and net services (d–f) dependent on whether the MVs of services/disservices are constant (a and d), linear (b and e), or exponential (c and f). Colors are the same as those described in the Figure 4 caption.

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■ Supporting Information

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