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ANIMAL AGENCY IN WILDLIFE CONSERVATION AND MANAGEMENT

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ABSTRACT

Wildlife conservation and management (WCM) practices have historically drawn from a wide variety of academic fields, yet have been slow to engage with emerging conversations about animals as complex beings, whose individuality and sociality influence their relationships with humans. Here, we propose an explicit acknowledgement of wild, non-human animals as active participants in WCM. We first review a wide selection of past WCM interventions and outcomes to highlight common assumptions regarding wildlife that underpin many present approaches to WCM. These interventions insufficiently consider animal learning, decision-making, individuality, sociality, and relationships with humans, leading to unanticipated management outcomes. To address these shortcomings, we synthesize theoretical advances in the fields of animal behavioral sciences, animal geographies, and animal legal theory that present helpful concepts for reconceptualizing animals and their relationships with humans within WCM. From these, we construct the concept of *animal agency*, which we define

as the ability of animals to actively influence conservation and management outcomes through their adaptive, context-specific, and complex behaviors that are predicated on their sentience, individuality, lived experiences, cognition, sociality, and cultures, in ways that shape and reshape shared human–wildlife cultures, spaces, and histories. We highlight contemporary conservation practices that incorporate facets of animal agency. We conclude by providing guidance for incorporating animal agency into future conservation problem solving.

INTRODUCTION

In the face of unprecedented transformations to the biosphere, wildlife conservation and management (WCM) must constantly evolve. We define WCM as the practice and study of wildlife conservation, management, and human–wildlife interactions that intersect with the broad fields of human–animal studies. (We use ‘wildlife’ and ‘wild animals’ interchangeably to refer to non-human animals that live somewhat autonomously from humans, are self-sufficient, and possess the freedom to reproduce). WCM draws from diverse disciplines to accomplish its goals of protecting and preserving wild animals to ensure their survival and wellbeing while considering the wellbeing of humans who share landscapes with them. Many WCM interventions—from international policies like CITES, to national Protected Areas, to local restoration—are notable successes that can credit their formulation and effectiveness to theories and concepts absorbed from various scholarships (e.g., population dynamics and ecological modeling, monitoring and evaluation, applied statistics, genetics, and geospatial sciences). The practice of WCM has also broadened to include humanities and social sciences (Manfredo 1989; Moon et al. 2019), engage with various forms of expertise and values (Lawrence 2010; Tengö et al. 2014), and consider possibilities for coexistence between humans and wildlife in human-dominated landscapes (Woodroffe et al. 2005; Carter & Linnell 2016; Pooley et al. 2017; Frank et al. 2019; Hodgson 2020).

Yet, WCM practices have been slower to uptake key findings from a wide range of disciplines that engage with the complexity of animals’ lives and behaviors, their relationships with each other and with humans, and the ways in which these relationships shape our shared world. Despite the emergence of novel WCM approaches that challenge anthropocentric perspectives (e.g., Washington et al. 2018; Büscher & Fletcher 2019; Celermajer et al. 2020; Wallach et al. 2020; Brakes et al. 2021), and the celebration of animals’ personhood by respected conservationists (e.g., Jane Goodall) and in the public imagination (Manfredo et al 2020), many contemporary WCM policies and practices are still based on assumptions that wild animals respond passively to reconfigurations of complex human systems, without considering their influence in shaping these systems.

In this paper, we propose an explicit acknowledgment of wildlife as active participants in WCM contexts. We do so by surveying recent work in the fields of animal behavioral sciences, animal geographies, and animal legal theory. Though emerging from distinct theoretical and epistemological backgrounds, these fields share an

interest in understanding the complexity of animals, their relations to their environments and to humans, and how these dynamics can and should shape humans' treatment of non-human animals. By highlighting convergences of these fields towards similar sensitivities to animals and human-animal relationships, we examine the implications of considering *animal agency* as an integral part of developing nuanced and effective approaches to the practice of WCM. We define animal agency in WCM as the ability of animals to actively influence conservation and management outcomes through their adaptive, context-specific, and complex behaviors that are predicated on their sentience, individuality, lived experiences, cognition, sociality, and cultures, in ways that shape and reshape shared human–wildlife cultures, spaces, and histories. The modalities of practice presented here have been part of various global communities for centuries as many nonwestern traditions attribute agency to animals (Watts 2013; Hornborg 2015). However, this holistic definition of agency remains underexplored in the majority of current WCM practices.

We critically evaluate conceptual assumptions that underpin dominant forms of WCM, and illustrate the potential for enriching our views of animals to improve WCM outcomes. For instance, animal agency shares some influences and positions in common with compassionate conservation (Wallach et al. 2020), convivial conservation (Büscher & Fletcher 2019) and ecological justice (Kopnina & Washington 2020), which grapple with the intrinsic value and personhood of all sentient beings and humans' ethical obligations to them. We argue that animal agency can offer a useful lens to understand the successes, challenges, and spaces for growth in novel and established approaches. Doing so, we aim to complement and support scholarly work reimagining more just and effective WCM futures (Bhattacharyya & Slocombe 2017; Ampumuza & Driessen 2020; Batavia et al. 2020; Toncheva & Fletcher 2021).

CHALLENGES IN WILDLIFE CONSERVATION AND MANAGEMENT

SCRUTINIZING WCM: WHY DO INTERVENTIONS PRODUCE UNEXPECTED OUTCOMES?

Understanding how WCM activities have unintended outcomes for wild animals and humans can help illuminate shortcomings and address future challenges emerging from increased and novel human-wildlife interactions. Table 1 provides a sample of scenarios where WCM practices produced unanticipated results. This review compiles and synthesizes peer-reviewed publications that evaluate WCM interventions, with targeted searches concerning

commonly used intervention methods (e.g., translocation, re-introduction, fencing). While not a comprehensive list, it is indicative of the diversity of species, practices, and outcomes associated with mainstream WCM. This review was augmented by the authors' prior research involving interactions between humans and leopards, white-tailed deer, macaques, and wolves. Drawing on the examples in Table 1, we identify common assumptions about animals uniting these examples (full citations to Table 1 sources are in Appendix 1). The assumptions outlined below are not held by all conservationists or applied in all management scenarios, but nonetheless represent pervasive ideas in WCM across a wide span of species, contexts, and time.

Table 1. Selected wildlife conservation and management interventions, their intended goals, and actual outcomes. The final column (“Assumptions”) refers to three common managerial assumptions made in WCM practice: animal behaviors are rigid and homogeneous (A1); wildlife exhibit idealized wild behavior and prefer pristine habitats (A2); and human–wildlife relationships are of marginal or secondary importance (A3). Full references to cited works are in Appendix 1.

Species and Management method	Expected management or conservation outcomes	Actual outcomes of interventions	References	Assumptions
African Elephant (<i>Loxodonta africana</i>) Lethal control , Multiple locations	<ul style="list-style-type: none"> Reduction in crop-raiding once so-called problem animal is killed Human communities will be appeased as problem animals are controlled 	<ul style="list-style-type: none"> Number of raiders did not decrease because other individuals replaced removed raiders Problem animal misidentified Continued community hostility toward elephants and conservation efforts 	Hoare 2001; Hoare 2012	A1
African Elephant (<i>Loxodonta africana</i>) and Asian Elephant (<i>Elephas maximus</i>) Translocation , Multiple locations	<ul style="list-style-type: none"> Reduction in crop raiding once so-called problem animal is translocated Elephants will stay at release site and will not (re)occupy new/original sites Elephants will thrive and cease to break fences if moved to native habitat 	<ul style="list-style-type: none"> Animals tried to return to their home range Stressed individuals show PTSD symptoms Increased mortality New conflicts around release site Fence breaking escalated in original location and spread to new location 	Hoare 2001; Pinter-Wollman 2009; Fernando et al. 2012; Evans & Adams 2018; Shaffer et al. 2019	A1, A2
Asian Elephant (<i>Elephas maximus</i>) Non-lethal deterrents , South Asia	Elephants will avoid threatening sounds/spotlights	Elephants developed tolerance for deterrents and returned to area	Shaffer et al. 2019	A1
African Elephant (<i>Loxodonta africana</i>), Exclusion through fencing , Multiple locations	Elephants will remain outside of fences and not enter human spaces	<ul style="list-style-type: none"> Elephants returned to human spaces and crossed/broke fences Fences funneled high number of elephants creating conflict with surrounding communities 	Hoare 2012	A1
African Elephant (<i>Loxodonta africana</i>), Detusking , Kenya	Once detusked, elephants will not break fences	Fence breaking reduced but detusked elephants developed new techniques to break fences	Mutinda et al. 2014	A1
Kangaroo Rat (<i>Dipodomys</i>	Translocations of individuals to newly restored areas will re-establish populations	Translocations ignored established neighborhood relationships	Greggor et al. 2016	A1

<i>stephensi)</i> , Translocation , USA		resulting in low reproduction and survival rates		
Rhesus Macaque (<i>Macaca mulatta</i>), Translocation , India	• Translocation from cities to rural areas will provide less disturbed habitat and reduce/remove nuisance macaque population from urban sites	<ul style="list-style-type: none"> Individuals quickly colonized nearest human settlements Individuals continued to behave aggressively towards humans and native macaques Site of capture (urban New Delhi) was repopulated Residents split over morality of intervention 	Govindrajan 2015; Kumar et al. 2013	A1, A2, A3
Coyote (<i>Canis latrans</i>), Non-lethal deterrents , USA	Use of plastic collars around the necks of sheep will reduce number of attacks on sheep and other domesticated animals	Coyote adapted their attack behavior to the hindquarters of the sheep	Blackwell et al. 2016	A1
European Badger (<i>Meles meles</i>), Culling , UK	Culling will reduce the reservoir of TB infection in wild badgers (considered the underlying source of increased infection rates across species)	Cull survivors explored unoccupied territories and deposit infected feces in new locations, contributing to disease spread	MacDonald 2016; Cassidy 2012	A1
Brown Bear (<i>Ursus arctos</i>) Hunting , USA	Hunting will control bear population	Increase of longer maternal care among bear population and potentially slower reproduction to avoid hunting exposure	Van de Walle et al. 2018	A1
Black Bear (<i>Ursus americanus</i>) Translocation , Canada	Translocation will reduce interactions between humans and habituated bears in residential areas	<ul style="list-style-type: none"> Low survival of translocated bears Bears returned frequently to site of release 	Landriault et al. 2006	A1, A2
Wolf (<i>Canis lupus</i>) Translocation , USA	Translocation will reduce predation on livestock and encounters with humans	Most translocated wolves left release areas and traveled to or through areas of livestock production	Fritts et al. 1984	A2
Wolf (<i>Canis lupus</i>), Culling , USA	Culling will reduce predation of wolves on livestock and conflicts with humans	Predation increased as culling led to social disruption and fragmentation of packs and less efficient hunting	Brainerd et al. 2008; Borg et al. 2015; Fernández- Gil et al. 2016	A1
Wolf (<i>Canis Lupus</i>), Re-introduction , Europe	Wolves will colonize areas of low human population density across Europe	Spontaneous rewilding in more densely populated areas	Drenthen 2016	A1, A2
White-tailed Deer (<i>Odocoileus virginianus</i>), Hunting , USA	Hunting will control overabundant deer population	<ul style="list-style-type: none"> Deer ranges shifted away from roads during the hunting season, avoiding areas of greater human activity Altered deer behavior during hunting season affected endangered Florida panther 	Kilgo et al. 1998	A1, A2, A3
Leopard (<i>Panthera pardus</i>) Translocation , India	Translocation from peri-urban areas to core of protected areas will reduce leopard population density, and minimize attacks and encounters with humans	<ul style="list-style-type: none"> Individuals traveled long distances to return to original range Social disruption at sites of capture and release Increased attacks on humans 	Athreya et al. 2011	A1, A2

Bengal Tiger (<i>Panthera tigris tigris</i>), Reintroduction , India	Reintroduce tiger population in undisturbed protected areas	Tiger reintroduction displaced leopards into human-dominated environments, increasing conflicts with humans	Mondal 2012	A1
Bottlenose Dolphin (<i>Tursiops truncatus</i>) Reintroduction from captivity , USA	Dolphins will thrive in the wild and supplement endangered or threatened populations, or reestablish a population in former range	Many individuals did not survive	Wells et al. 1998	A1, A2
Horses (<i>Equus ferus</i>), Culling , USA	Removal of feral horses	<ul style="list-style-type: none"> • No removal of horses after years long conflict between Ozark residents and National Park Service • Conflicts between groups emerged from differences in representation of and attachment to horses 	Rikoon 2006	A3
Multiple species, Community displacement , Multiple locations	Displacement of human communities from protected areas will reduce detrimental anthropogenic impacts	<ul style="list-style-type: none"> • Absence of critical anthropogenic activities resulting in loss of landscape and species diversity • Loss of indirect monitoring leading to encroachment by more destructive actors • Increased pressure on natural resources at sites of settlement • Negative attitudes toward conservation 	Rangarajan & Shahabuddin 2006; Fabricius & de Wet 2002; Cerneia & Schmidt-Soltau 2003	A3
Beluga whale (<i>Delphinapterus leucas</i>), Hunting quotas , Canadian Arctic	Imposition of quotas on beluga whale hunting and tightening of hunting restrictions will maintain robust stocks of beluga	<ul style="list-style-type: none"> • Hunting above quota in response to restrictions seen as unfair, scientifically unsound, rigid, and ignorant of Inuit perceptions of beluga sentience • Criminalization of subsistence hunting with detrimental cultural, economic, and nutritional impacts for the Nunavik Inuit—threatening the survival of Inuit culture and relationship with beluga • Other important factors for the decline of beluga populations were underexplored (e.g., disease, pollution, loss of habitats, net entanglement) 	Tyrrell 2007; Tyrrell 2008	A3

Assumption 1: Animal behaviors are rigid and homogeneous

Many WCM strategies assume that a species or individuals' behavior in one context will remain largely unchanged in another; and that individuals of the same species show uniform behaviors (Table 1). Yet, in practice, animals including wolves, coyotes, elephants, and leopards frequently exhibit plasticity of behavior unanticipated by WCM interventions. Testing a predictive model for wolf habitat suitability in Wisconsin (developed by Mladenoff et al. 1995), Mech (2006) demonstrated that the model was a “poor predictor of wolf re-colonizing locations in

Wisconsin, apparently because it *failed to consider the adaptability* of wolves. Such models should be used cautiously in wolf-management or restoration plans" (Mech 2006 :874, emphasis ours). Yet such models often underlie wolf management strategies (e.g., Michigan DNR 1997; Wisconsin DNR 1999).

Relatedly, many WCM efforts are predicated upon the assumption that interventions will not fundamentally reshape animal decision-making (Swaisgood 2010). This assumption often undermines reintroduction efforts of captive-bred individuals, as captivity profoundly influences behavior and decision-making, and therefore survival rates in reintroduction programs (Jule et al. 2008). Further, disruption of the social fabric of animal communities by culling, translocation, and reintroduction can impair the survival and longevity of targeted species (Teixeira et al. 2007). For example, culling elephants can lead to the breakdown of social systems among the impacted population, driving the emergence and spread of hyper-aggressive behaviors (Bradshaw et al. 2005).

Assumption 2: Wildlife exhibit idealized wild behavior and prefer pristine habitats

Many WCM efforts assume that animals will return to an idealized state of wildness if offered appropriate environments. Translocation and reintroduction of leopards, macaques, elephants, and dolphins illustrate this point (Table 1). Emerging from the assumption that wild animals inherently prefer undisturbed or pristine habitats and that these preferences are fixed (Osiko et al. 2004), habitat preference is understood to be directly correlated with habitat quality, which itself is assumed to have a direct relationship with the level of human disturbance or human population density. This relationship is used in wildlife population models that underlie many WCM decisions (Battin 2004). However, real world habitat preferences and resource selection among individual animals contradict certain outcomes predicted by these population models (Nielsen et al. 2002; Osiko et al. 2004), as do the results of numerous wildlife reintroduction and translocation programs where animals attempt to return to disturbed sites.

Assumption 3: Human–wildlife relationships are of marginal or secondary importance

Although human dimensions are recognized and integrated in WCM scholarship and practice (Manfredo 1989; Treves et al. 2006; Bennett et al. 2017), WCM efforts often fail to consider differences in the ways human individuals, communities, and cultures view and value animals. Most WCM approaches are based on species' biological, ecological, or economic value, thus classifying them as overabundant, invasive, endangered, game, etc.

However, to many people wildlife may be sentient beings, kin, deities, or community members (e.g., Tyrrell 2008; Borish et al. 2021; Nair et al. 2021). By narrowly considering human–animal relationships, WCM practice often overlooks traditions that engage with wildlife as unique individuals or cultural entities that are distinct from but related to humans—discounting the shared histories, geographies, and dependencies that create these relationships.

The exclusion of complex human–wildlife relationships from WCM practice results in unanticipated outcomes that run counter to the objectives of contemporary conservation—to protect threatened species with the support of local communities. For example, the failed removal of feral horses in the Ozark Riverways, intended to restore native ecosystems, was partly due to a disregard for the horses’ local historical, cultural, and emotional significance (Rikoon 2006). In the Canadian Arctic, Inuit cultures consider beluga whales sentient beings that are deeply connected to communal practices. However, state-sponsored plans that included rigid quotas on whale hunting ignored Inuit knowledge of and relationships with whales. This engendered a breakdown of Inuit livelihoods and cultural identity and a distrust of co-management, contributing to decisions to exceed state-imposed hunting quotas (Tyrrell 2007, 2008).

ACKNOWLEDGING THE ROLE OF AGENCY IN ANIMALS : CONTRIBUTIONS FROM THREE DISCIPLINARY TRADITIONS

Our review of common assumptions and unanticipated outcomes highlights key shortcomings in conceptualizations of wildlife in WCM that come from a shared historical lineage. Western scientific thought, heavily influenced by Judeo-Christian views of man’s dominion over nature, has a long history of treating animals as automata dating back at least to Descartes’ treatise on animals in the 16th century (Crist 2013). Animals are considered inferior and subordinate to humans, lacking emotion, free will, self-consciousness, or personhood. Although societies across space and time—ranging from the European middle ages to contemporary world religions—have acknowledged animal sentience, and laboratory studies increasingly demonstrate personality and empathy in animals, the cartesian perspective has carried through to contemporary western conceptualizations of wildlife. Current WCM approaches perpetuate the idea that humans can control and contain animals; as soon as wildlife leave designated spaces or exhibit novel behaviors, they are viewed as overabundant, out-of-place, or problematic. As a result, these approaches often devalue habitats that are not pristine or untrammeled, and strive to excise behaviors outside of

those observed in idealized conditions. These practices routinely exclude communities that consider animals as sentient beings (Berkes 2012). In doing so, WCM efforts can delegitimize relationships and spaces characterized by more complex human–animal engagements (Blaser 2009; Borish et al. 2021) and dismiss forms of knowledge about animals that are not deemed scientific (Saberwal 2000).

DISCIPLINARY OVERVIEW

Below we present a selected review of recent scholarship in three fields that reconceptualize animals and their relationships with humans: animal behavior, animal geographies, and animal legal theory. These fields question many of the premises of contemporary WCM discussed above. Here, we do not present a comprehensive literature review but highlight concepts that could enrich WCM.

Animal behavioral sciences

Animal behavioral sciences explore why animals act the way they do through studies of expression, intelligence, learning abilities, culture, sociability, cognition, and the range and flexibility of these characteristics.

Throughout the 20th century, behaviorism—which considered behavior strictly as a response to stimuli—strongly influenced the study of animal psychology. Some branches of behavioral sciences have since taken a more comprehensive view of behavior and its drivers—understood to be influenced by personality, temperament, experience, mood, attitudes, social context, etc. (Levitis et al. 2009). For instance, the field of cognitive ethology focuses on the study of animal intelligence and demonstrates that animals' thoughts, feelings, and social systems are more developed than previously thought (Waal 1989; Bekoff 2002). Drawing from Darwin's theory that the difference between animals and humans is in degree, not kind, cognitive ethologists engage with “all ways in which animals take in information about the world through the senses, process, retain and decide to act on it” (Shettleworth 2001: 278). While originating in higher primate studies, animal ethological research has broadened to engage with species ranging from ants to cetaceans (Shettleworth 2010; MacDonald & Ritvo 2016; Brakes et al. 2021). Doing so, these studies contribute to rejecting the static view of animals as passively occupying existing environments (Barua & Sinha 2017).

Animal geographies

Animal geographies have emerged over the last 20 years as a rich and heterogeneous sub-discipline (Buller 2014) to respond to the "deafening silence about nonhumans" in social theory (Wolch & Emel 1995: 632). Building on methodologies and frameworks from geography (including actor-network theory, posthumanist, Feminist, Marxist, Indigenous, and cultural geographies), animal geographers also draw from diverse animal-centric fields including animal ecology and behavioral sciences (Wolch & Emel 1995; Lorimer & Srinivasan 2013; Barua & Sinha 2017).

Animal geographers are interested in the multiple ways animals intersect with human societies (Urbanik 2012) and complicate mainstream views of animals: they reject utilitarian representations of animals as objects and resources under human control with no influence on human lives. By exploring the various temporal, spatial, and place-based relationships among humans and animals, animal geographers consider the geographies of animals themselves, their active participation in the construction of landscapes (Wilbert & Philo 2000), and their heterogeneous, fluid, intertwined subjectivities (Holloway 2007; Govindrajan 2018). They critically examine the ways in which dominant discourses on animals are rooted in capitalist traditions that commodify non-humans and devalue their relationships to humans (Wolch & Emel 1995). The literature explores human relationships with companion animals (Haraway 2008), farmed animal welfare (Miele 2011) and wild species (Dempsey 2010; de Silva & Srinivasan 2019; Ampumuza & Driessen, 2020; Toncheva & Fletcher 2021). In the context of WCM, animal geographers consider wild animals as political actors engaged in WCM through their relationships with humans and other species (e.g., Boonman-Berson et al. 2016; Evans & Adams 2018).

Animal legal theory

Animal legal theory has its roots in animal philosophy, which has long established that animals possess sufficiently similar mental and emotional capacities to those of humans, and therefore should be given similar moral consideration (Singer 1975; Regan 1983; Jamieson 2018).

Foundational work in animal legal theory argues for inherent rights for all organisms and questions the western legal status of animals as objects, solely the property of humans (Stone 1972; Francione 1995). Drawing from animal ethics and political animal philosophy, animal legal theorists view animals as sentient beings having moral standings, subjective experiences, and abilities to shape their own and others' lives; therefore possessing

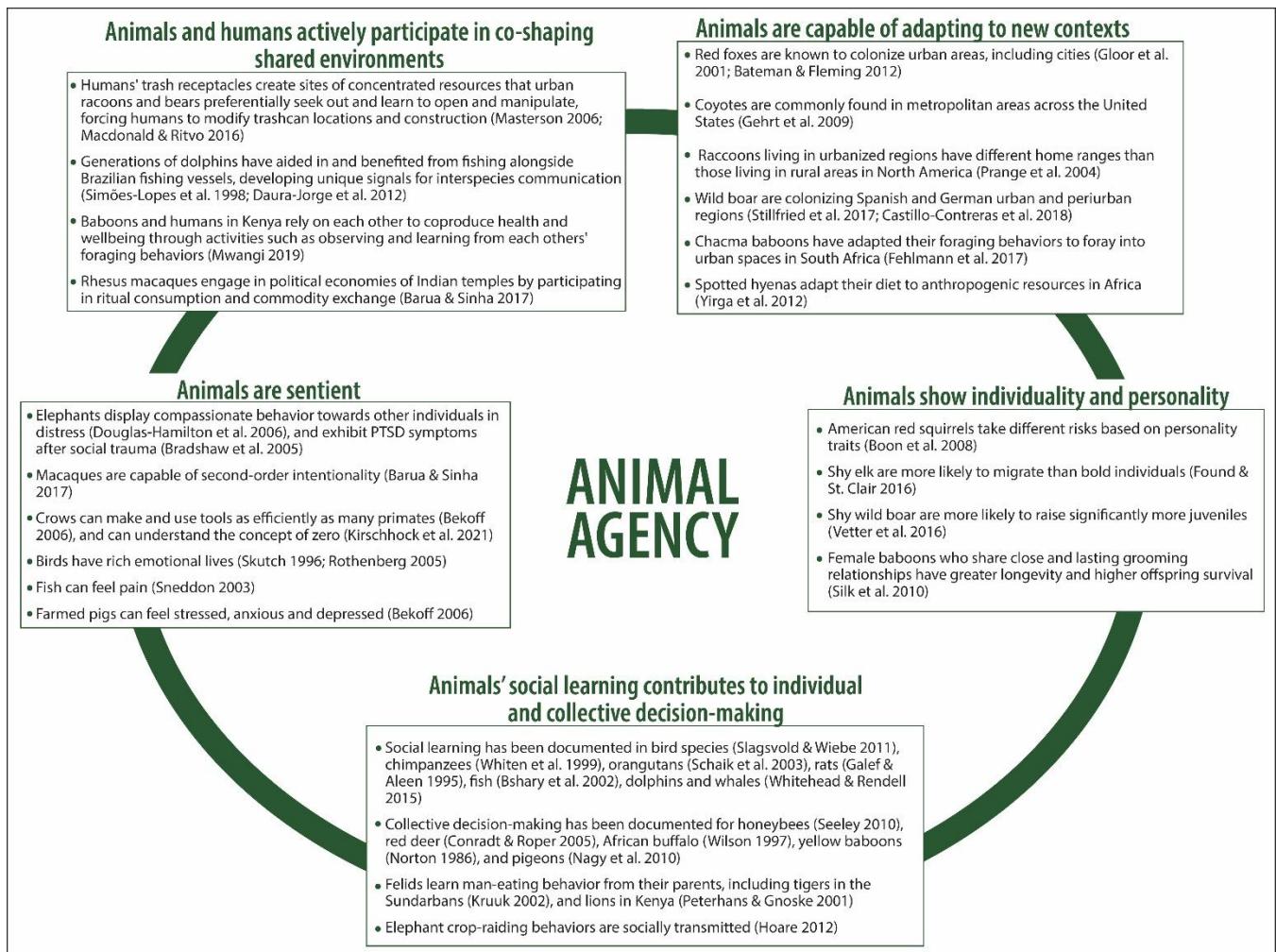
individual and collective interests that should be represented within human institutions and included within decision-making regarding governance of spaces (Regan 1983; Rowlands 1997; Wise 2000; O’Sullivan 2011; Garner 2013; Cochrane 2018; Celermajer et al. 2020). Animal legal theory has moved from a conceptual academic interest to a field with tangible consequences for and benefits to animals through shaping outcomes in legislation and litigation (e.g., Cohen 2006; Dunn & Rosengard 2017).

Much of the theory and practice of animal law exists on a spectrum from animal welfare on one end (concerning the responsibilities of humans toward protecting animals’ best interests) to animal rights on the other (a deontological position that animal interests are inherent and inviolable, which legal systems should be designed to defend, as is the case with human rights). Some animal legal philosophers go further by asserting that animals have agency—they are not only aware of their surroundings and interactions, but proactively shape them—a concept which animal law and philosophy as a whole have been slow to embrace (Jamieson 2018).

KEY LESSONS FROM DIVERSE DISCIPLINES

The collective findings from these fields challenge assumptions that underpin many mainstream WCM approaches. Below we outline five conceptual contributions that have implications for the ways animals are protected, managed, and treated in WCM practice. Figure 1 summarizes selected case studies that illustrate each of these concepts. Full citations to sources in figure 1 are in Appendix 1.

Figure 1. Selected examples that illustrate important components of animal agency. Full references to cited works are in Appendix 1.



Animals are sentient

Animals are sentient, that is, they have feelings and intelligence. Many species possess a shared sense of morality, empathy, and justice (Bekoff & Pierce 2017). Numerous behavioral studies of bird and mammal species identify expressions of empathy and emotions including fear, pain, and distress (Masson & McCarthy 2016). Animals are also reflective and capable of “remembering the past and planning for the future” (Kaplan 2016: 201).

Animals are capable of adapting to new contexts

The behavioral plasticity of animals allows them to adapt and habituate to different conditions. Animal behaviorists, geographers, and legal theorists demonstrate that animals can modify behaviors when faced with change, including human disturbance (Griffin et al. 2017), by drawing on past experiences and interests (Gullo et al. 1998; Hodgetts & Lorimer 2015; Donaldson & Kymlicka 2016). Notably, generalist species adapt to anthropogenic changes by

finding novel ways to exploit resources in human-dominated landscapes (Devictor et al. 2008, Fig. 1). Experiences can also be learned and transmitted over generations (Berger 2008).

Animals show individuality and personality

Individuals from the same population can have personality traits that set them apart from others. Behavioral scientists have established that in most studied species, individuals exhibit idiosyncratic behavioral differences (Réale et al. 2010; Dall & Griffith 2014; Blackwell et al. 2016; Merrick & Koprowski 2017). Both genetic and non-genetic factors drive these differences (Réale et al. 2007; Honda et al. 2018) and influence the decisions individuals take (Réale et al. 2010).

Animals' lived experiences and social learning contribute to individual and collective decision-making

All three disciplines provide strong evidence for the sociality of animals, which allows them to develop distinct languages (Bekoff 2002) and the capacity for collective decision-making. Social behavior varies across time and space producing communication idioms and cultures (Waal 1999; Bekoff 2002; Laland & Janik 2006). In fact, there is growing evidence that animal culture, defined as “information or behavior—shared within a community—which is acquired from conspecifics through some form of social learning” (Whitehead & Rendell 2015 :12) exists in a wide range of wild animals (Brakes et al. 2021).

Animals and humans actively participate in co-shaping shared environments

Animal geographers and animal legal theorists understand human–animal interactions as a product of complex relational processes in which humans and animals are active participants. Both fields recognize animals' influence in shaping the natural world—as agents of ecological processes—but also in co-shaping humans' socio-economic, cultural, and political worlds (Hobson 2007; Dempsey 2010). For example, female bottlenose dolphins have had lasting and complex relationships with fishermen in Brazil—these individuals have socially learned cooperative foraging tactics, benefitting both dolphins and humans (Simões-Lopes et al. 2016; Bezamat et al. 2020). Rhesus macaques participate in the political economies of Indian temples by engaging in ritual consumption and commodity exchange with humans (Barua & Sinha 2017). Beluga whales, polar bears and caribou, enmeshed in the cultural and socio-economic lives of many communities in the Arctic, have shared enduring relationships developed over

centuries (Kishigami 2005; Tyrrell 2007; Borish et al. 2021). Elephants in Sri Lanka are what Lorimer (2015) calls a companion species as they have co-evolved with people over millennia such that “their genetics, anatomies, behaviors, feelings, social groupings, and wider ecologies all bear a human signature. At the same time, the language, culture, religions, agriculture, and economies of their human co-inhabitants carry a pachyderm trace” (Lorimer 2015: 23). Even slugs’ activities in domestic gardens shape fine-scale geographies and humans’ relationships with their shared environments (Ginn 2014).

Animals have been considered guardians, deities, companions, rivals, nations, community members, or co-conspirators that contribute in direct and indirect ways to the survival of both human cultures and wild species (Blaser 2009; Nadasdy 2007; Lorimer 2015; Bhattacharyya & Slocombe 2017; Nair et al. 2021). These views acknowledge animals’ intentions, emotions, and cultures that they share with humans in a common social, spiritual, and ecological world (Umeek/Atleo 2011). While often associated with non-western, pre-colonial traditions (Berkes et al. 2000), it is worth noting that meaningful relationships with animals that engage with their personhood and shared culture also exist throughout western societies, often in vastly divergent ways (e.g., hunters (Kelly & Rule 2013) and animal rights advocates (Rudy 2011)).

WHAT DOES IT MEAN FOR WILDLIFE TO HAVE AGENCY?

Our review draws attention to the need for greater recognition of wild animals' complexity and intentions in their interactions with humans in WCM contexts. The concept of animal agency captures this complexity. The term agency can be broadly understood as “the capacity to produce a phenomenon or modify a state of affairs” (Jepson et al. 2011 :230). Although the term agency is used differently across disciplines (see Nash 2005; Teubner 2006; Steward 2009; Jepson et al. 2011; Carter & Charles 2013; Jamieson 2018), we integrate findings from the three fields to build a definition for animal agency in WCM contexts that encompasses the complexities discussed above.

We define animal agency as the ability of animals to actively influence conservation and management outcomes through their adaptive, context-specific, and complex behaviors that are predicated on their sentience, individuality, lived experiences, cognition, sociality, and cultures, in ways that shape and reshape shared human–wildlife cultures, spaces, and histories. Adopting animal agency as a lens in WCM interventions helps moving

beyond perceptions of wildlife as manipulable objects, recognizes animals' active participation in WCM efforts, and gives valence to worldviews that have long incorporated dimensions of animal agency into their engagements with the environment.

INTEGRATING ANIMAL AGENCY INTO WCM SCIENCE AND PRACTICE - CHALLENGES AND OPPORTUNITIES

Practically, barriers exist to engaging agency in WCM practice. We highlight two here. First, incorporating facets of animal agency into modeling and predicting animal behaviors is challenging (Budaev et al. 2019). Quantitative, automata-based methodologies are well established, scalable, parsimonious, and inexpensive (Budaev et al. 2019). In contrast, acknowledging animal agency introduces non-uniformity, uncertainty, and complexity at the modeling, planning, and implementation stages. Integrating agency into predictive models can require more complex, expensive, and computationally intensive simulations (Budaev et al. 2019). Second, although many practitioners implicitly recognize animals' agency (e.g., Boonman-Berson et al. 2016), there are structural and institutional challenges to widespread application in WCM—such as the difficulty in updating established systems of practice and policy, and the entrenchment of cartesian approaches by those occupying higher levels of power (Jacobson & Decker 2006). Despite these challenges, facets of animal agency are already integrated into, and can be further explored within, existing and emergent WCM practices.

INCORPORATING ANIMAL AGENCY IN CONSERVATION PRIORITIZATION

Conservationists closely consider metrics that treat animals primarily as quantifiable stock when defining conservation priorities and measuring success (e.g., viability, endemism, population size, genetic diversity (Brakes et al. 2019)). However, WCM efforts that only consider tangible and measurable components of animal life at the expense of less tangible, more plastic aspects (e.g., behavioral traits, cultural diversity) ignore essential characteristics of individuals, groups, and ecosystems that contribute to survival.

Integrating animal agency into WCM strategies can help identify and conserve agentic qualities essential for species' survival (Blumstein & Fernández-Juricic 2010; Smith & Blumstein 2013; Berger-Tal et al. 2016; Greggor et al. 2016). Applied conservation behavior research has expanded to explicitly consider how individuality, personality, and learning produce heterogeneous responses across individuals, and their implications for ecological

and population-scale processes (Merrick & Koprowski 2017; Brakes et al. 2021). Personalities of animals can influence metrics as fundamental as population estimates. For example, individuals that are less perturbed by human presence are more likely to be counted (Biro 2013). Bold and exploratory individuals tend to exhibit greater tolerance for noise, human activity, and other forms of disturbance. They are more likely to make use of conservation infrastructures (e.g., nest boxes, artificial habitats, etc.), come into conflict with humans, transmit and acquire zoonotic diseases, and colonize new areas (Found & St. Clair 2016; Greggor et al. 2016; Merrick & Koprowski 2017; Honda et al. 2018). Coupling data on personality and behavioral traits associated with habituation to humans and disturbance tolerance with population and genetic diversity data can help identify vulnerable, isolated populations (Riley et al. 2014). Similarly, incorporating learning and behavioral diversity into landscape connectivity and dispersal modeling has serious implications for conservation corridor planning, as models have strikingly different results when including different behavioral characteristics (Elliot et al. 2014). By inquiring how individuals, groups or populations engage with and respond to landscapes, an agency-based approach illuminates how animals shape contexts to meet their needs under different scenarios, potentially altering conservation outcomes. For example, different populations of bears have developed attune behaviors towards humans based on the varying degrees of protection across Bulgarian regions (Toncheva & Fletcher 2021). Coupling agency-based framings that consider wildlife's behavioral plasticity and decision-making with well-established practices to understand spatial patterns—such as tracking with GPS collars, wildlife cameras, and satellite images—are also worth greater exploration to identify vulnerable individuals.

Animal agency can also enrich WCM priorities, including the preservation of animal social systems and culture (Marzluff & Swift 2017; Brakes et al. 2019, 2021), as advocated for in animal culture conservation approaches (Laiolo & Jovani 2006). Culture can impart crucial survival skills that contribute to the persistence of social groups and potentially whole populations. For example, accounting for dolphins' and wolves' social systems were key to successful reintroduction programs (Milstein 1995; Ferguson 1996; Wells et al. 1998). African elephant matriarchs accumulate knowledge regarding their social and ecological environment, transmitting information crucial to group survival (Mccomb et al. 2001). Yet traditional approaches prioritize younger individuals' reproductive potential (Brakes et al. 2019). These studies demonstrate the importance of not only protecting genetic

diversity and reproductive capacity but also cultural and social systems for species survival. These ideas are gaining traction in conservation biology (Griffin et al. 2000; MacDonald 2016) and informing human–wildlife conflict management (Greggor et al. 2017; Marzluff & Swift 2017; Brakes et al. 2021)—such as identifying culturally significant units in the protection of small and endangered populations (e.g., Whitehead et al. 2004; Ryan 2006). Further, practitioners and conservation institutions have recognized the importance of cultural traits not only at the individual and group level, but also at the population and species level (Brakes et al. 2021). For example, the Convention on the Conservation of Migratory Species of Wild Animals is exploring the implications of conserving cultural traits such as clan culture among sperm whales and nut-cracking culture in banded mongooses for the preservation of these species (CMS 2017, 2018).

MANAGING WILD ANIMALS WITH THEIR AGENCY IN MIND

Viewing animals as active participants allows us to reconsider *how* conservationists and wildlife managers can engage in WCM. Practical WCM experiments are already considering various facets of animal agency (although different terminology might be used), with findings that suggest avenues forward for animal agency-centered WCM.

Linking cognitive science, animal cognition and evolutionary ecology, an increasing number of behavioral ecologists incorporate animal personalities, life histories, emotions, learning abilities, and motivations to better model animal adaptive decision-making (Budaev et al. 2019). These approaches informing WCM strategies show promising results. For example, in traditional husbandry, carcasses of animals killed by predators or accidents are generally quickly removed. However, this may actually limit the ability of domesticated animals to learn about predators and the importance of avoiding dangerous areas (Marzluff & Swift 2017).

Animal decision-making is also emphasized in the kincentric ecology approach (Bhattacharyya & Slocombe 2017) that foregrounds multi-species collaborative management in shared socio-environmental systems. To manage human–seagull conflict, the city of Leiden in the Netherlands experimented with seagull–human collaboration in negotiating nesting locations that met both seagull and human needs (Meijer 2016). In doing so, managers acknowledged the role seagulls can play in management efforts through “interspecies decision-making” (Meijer 2016 :64). Other examples of humans leveraging the participation of animals in conservation include

beavers' involvement in watershed management (Woelfle-Erskine & Sarna 2013) and captured elephants in mitigating human–animal conflicts (Münster 2016). These examples illustrate the possibilities that emerge by considering animals as agents of territorialization able to occupy human-modified environments, and as creative participants in adaptive experimentation.

Other contemporary management strategies are noteworthy for their consideration of animal agency within more traditional paradigms. Using deterrence mechanisms (“strikes”), a wildlife management approach in Colorado intended to teach black bears to avoid human spaces. Although this initiative assumed uniform bear behavior, wildlife managers whose role it was to implement strikes, often bent the rules and used their intimate knowledge of bear autonomy and individuality to decide which animals to target (Boonman-Berson et al. 2016). This example demonstrates the need to experiment with context-specific, adaptive strategies that leverage existing, carefully nurtured human–animal relationships (Boonman-Berson et al. 2016). It also speaks to recent discussions regarding the moral implications of making decisions in WCM. For example, Batavia et al. (2020) argue for considering the concept of moral residue within WCM, recognizing the ethical challenges of WCM and encouraging conservationists to sit with the emotional dimension of their missions. Finally, this example illustrates that many managers know that animals have agency and implicitly acknowledge it by integrating it into management practice, despite institutional norms and discourses that discount its importance.

Further, viewing animals as active participants within conservation policymaking raises pertinent questions of whose knowledge is valuable in understanding and representing animals' perspectives, interests, and rights (Toncheva & Fletcher 2021). Considering agency encourages us to more closely examine worldviews that have been perceived as lacking scientific rigor, but are products of decades or centuries of integration between human and non-human lives. Many management practices are rooted in human–wildlife reciprocal relationships and derived from multi-generational experience-based knowledge (e.g., Kideghesho 2009; Mukul et al. 2012; Toncheva & Fletcher 2021). For instance, Rayne et al. (2020) show how Indigenous knowledge systems in Aotearoa New Zealand can improve outcomes of conservation efforts, such as the translocation of under-studied species. In the Canadian Arctic, Inuit hunters' knowledge of muskoxen and caribou life histories, population dynamics, and body conditions was crucial to conserve these species (Tomaselli et al. 2018). In Bulgaria, experience-based knowledge

of local communities (and especially hunters) is key to cohabitation with bears. There, humans and bears have developed relations of mutual “trust” and “respect” through repeated, non-conflictual, peaceful encounters (Toncheva & Fletcher 2021). This type of knowledge can enrich conservation policymaking and potentially inform the appointment of human “trustees” to advocate for animal rights within WCM efforts (Cochrane 2018). In the same vein as Etuaptmumk (Mi’kmaw for “Two-Eyed Seeing”, Bartlett et al. 2012) which advocates for the coexistence of various knowledge paradigms, we argue that animal agency can support the development of hybrid deductive and inductive reasoning and address complex issues with all available and critical sources of information necessary to face the ongoing loss of global biodiversity. Further, recognizing the many ways of being with and viewing animals is necessary to avoid trivializing or alienating communities directly impacted by WCM interventions. This is particularly important in the case of Indigenous Peoples who have been marginalized through centuries of colonial conservation approaches, resulting in the loss of shared human–animal worlds. While it is crucial to be attentive to the ways local knowledge can be misunderstood, simplified or instrumentalized, centering animal agency in conservation practices can contribute to efforts that respect and recognize the approaches of Indigenous Peoples—who currently manage or have tenure rights over $\frac{1}{4}$ of the world’s land surface, representing about 40% of the world’s terrestrial protected areas (Garnett 2018; Artelle et al. 2019).

Finally, integrating animal agency into conservation allows more nuanced discussions of, and can potentially augment, existing and emergent practices. WCM will always be an endeavor held in tension by different goals, worldviews, and ontologies of what is worth conserving and how to conserve it. Engaging with animal agency will not remove the challenge of balancing different views or easily solve ecologically, politically, and culturally fraught conservation challenges that inherently involve tradeoffs (see for example Oommen et al. (2019) and their critique of compassionate conservation). The degree to which each facet of the animal agency concept needs to be engaged may vary among species, ecological systems, and local contexts. For these reasons, we argue that considering animal agency can draw attention to, and spur conversations about, fundamental questions and tensions that often go unspoken in mainstream WCM. Driving questions may include: how will humans and wildlife engage with and affect different WCM efforts? Is there room for WCM plans to adapt as diverse humans and animals learn from each other? How can plans incorporate more than the biological value of a species? Are the human

communities most closely engaged with animals able to contribute and grow their knowledge and expertise under this management regime? How can their relationships be honored, maintained, and supported? What animal cultural traits and relationships does this make room for, and what does it inhibit? How will these interventions produce new interspecies relationships, cultures, and politics? We encourage managers and stakeholders interested in exploring the ramifications of an animal agency lens to ask these questions within contexts described in Table 1.

These questions have relevance regardless of whether managers use mainstream WCM approaches or emergent practices, and can help WCM practitioners evaluate plans, develop scenarios, engage with other stakeholders, make room for surprises, and imagine multiple futures. We thus present animal agency as a concept with the potential to connect wildlife, Indigenous and local communities, scholars, conservationists, and wildlife managers to enhance context-specific and adaptive WCM practice. These approaches have the potential to create spaces for better collaboration, inclusion, and well-being for both animals and humans.

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APPENDIX 1

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