OWNERSHIP, MORALITY, AND WILDLIFE CONSERVATION

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ABSTRACT

This dissertation is an interdisciplinary investigation of three morally contested dimensions of wildlife conservation: Who, if anyone, should own wildlife? What moral obligations, if any, do people have to conserve other species? What types of governance reform could help address contemporary conservation challenges? In Chapter 1 I describe the context for this dissertation. Wildlife conservation and governance must change to meet ecological challenges and social expectations, but the scope and direction of change required are contested. Much of the discourse on the future of wildlife conservation in the United States (U.S.) revolves around the concept of wildlife as a public trust. Nevertheless, disagreement over what it means for wildlife to be a public trust and competing interpretations of the concept's implications can exacerbate rather than ameliorate conflict over the future of wildlife conservation. Chapters 2 and 3 offer practically orientated guidance to scholars and wildlife professionals interested in the potential of public trust thinking (PTT) to inspire socially and ecologically responsible wildlife governance reform. Chapter 2 outlines PTT's foundation principles, and chapter 3 describes challenges and opportunities in applying PTT to wildlife governance in the U.S. Chapter 4 presents

results of an empirical study of moral attitudes about wildlife ownership among people living in the U.S. Variation in moral attitudes can help explain why some wildlife conservation activities are more morally acceptable than others. Chapter 5 shows that ownership (defined as respect for possession) is a powerful but overlooked cooperative solution to resource conflict throughout the biological world. It consists of a literature review of ownership across disciplines and a new evolutionary game-theoretic model of how ownership arrangements can emerge and remain stable. Chapter 6 investigates whether the theory of evolution by natural selection can explain why conservation ethics (moral beliefs, intuitions, attitudes, and norms regarding other species) exist and why they vary. It consists of eco-evolutionary models of adaptive conservation behavior, and proposes that an evolutionary perspective might help resolve persistent moral debates over the value of other species. To better understand and address contemporary conservation challenges, we need to better understand morality. And to better understand morality, we need to incorporate evolution. Wildlife conservation approaches that go with the grain of evolved dispositions and harness our capacities for sustainable behavior are less likely to be morally contested, so are especially likely to succeed.

BIOGRAPHICAL SKETCH

Darragh Hare was born in Lanark, Scotland, in 1979. He grew up in Larkhall, South Lanarkshire, a former mining, textile, and weaving town on the rivers Avon and Clyde. Darragh was fortunate to receive continuous love, encouragement, and frank advice from his older brother, Paul, his parents, Ian and Sally, and an enduring group of childhood friends. In 2001 Darragh graduated from the University of Glasgow with an M.A. (Hons) in philosophy, with concentrations in moral and political theory. During his first year at university, Darragh met his best friend and strongest supporter, Lorraine, who is also from Larkhall. They married in 2005.

Throughout his undergraduate studies, Darragh worked in a clothing factory and a local pub. After graduating, he worked for two years as a researcher in the recently re-established Scottish Parliament. He spent the next seven years working in and around the Scottish and UK political systems, always keen to forge links between people producing research and people looking to apply it. Darragh worked on a variety of research and cross-sectoral dialogue projects at Glasgow Caledonian University, Liverpool Hope University, Heriot-Watt University, the University of Edinburgh, the University of Glasgow, and the University of Cambridge. From 2007-2011 he coordinated the Scottish Policy Innovation Forum, a network of academics, policy makers, NGO officials, and business people, based in the Law School at the University of Glasgow. Darragh's experiences at the interface of research, policy, and practice inspired him to become an academic.

In 2010 Darragh helped organize a series of workshops on diversity and pluralism across disciplines. During these workshops, he met Dr. Bernd Blossey. Despite their different disciplinary backgrounds, Darragh and Bernd quickly discovered a strong intellectual connection through their personal commitments to biodiversity conservation and interests in the ecological and evolutionary foundations of human behavior. Bernd suggested that Darragh come to Cornell to transform his curiosity into expertise by studying for a PhD in natural resources as a member of the Blossey lab. This graduate work led Darragh down fascinating and unforeseen scientific paths, where he met a host of wonderful mentors and collaborators. He would not have succeeded without their generous and patient guidance.

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Several people contributed to the articles that comprise this dissertation. Dr. Kern Reeve helped me add deep theoretical rigor to my ideas and showed me how to see the world from an entirely new, much clearer, perspective. His mentorship profoundly shaped my intellectual development. Dr. Andrea Dávalos gave up far too much of her time to help me as I stumbled through various components of my research. Dr. Erika Mudrak taught me with much patience and good humor to enjoy concepts and techniques I had previously struggled to understand. Ann Forstchen, Chris Smith, and Dr. Cindi Jacobson helped me understand the wildlife conservation and governance landscape in the United States. Their tireless commitment to

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My brother, Dr. Paul Hare, and my mum, Sally, supported and believed in me from a distance. My late dad, Ian, taught me to look as far and aim as high as I possibly can. I could not have achieved any of this work without my wife Lorraine's unwavering confidence, gentle patience, and boundless love. I aspire to be as kind and giving a partner to her as she is to me.

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CHAPTER 1

INTRODUCTION

The moral dimensions of wildlife conservation are unavoidable. People believe we should conserve wildlife for a variety of reasons (Berry et al., 2016). However, sometimes these reasons conflict (Chan et al., 2016; Noss, Nash, Paquet, & Soulé, 2013; Tallis & Lubchenco, 2014), and disagreements over precisely what we should conserve and why can impede effective conservation (Mace, 2014). Even when we agree that we should conserve wildlife, we often disagree about how to achieve it, for example the appropriate roles of government, non-governmental organizations, and members of the public (Redpath et al., 2017). In most places, government has substantial responsibility for wildlife conservation, and enacts laws, policies and regulations to manage relationships between people and wild organisms (Freyfogle & Goble, 2009). Nevertheless, deciding exactly which laws, policies, and regulations to enact also requires answering difficult moral questions about whose interests should be represented in conservation and whom conservation should benefit (Baynham-Herd, Redpath, Bunnefeld, Molony, & Keane, 2018; Decker et al., 2016; Lute, Navarrete, Nelson, & Gore, 2016).

In this dissertation I draw on insights and techniques from across disciplines to investigate three morally contested issues in wildlife conservation: What types of governance reform could help address contemporary conservation challenges? Who, if anyone, should own wildlife? What moral obligations, if any, do people have to conserve other species?

Understanding how moral conflict arises and how it affects the feasibility of different strategies for wildlife conservation will be essential if we are to overcome contemporary conservation challenges. These challenges include addressing biodiversity decline (Urban, 2015; WWF, 2016) while solving institutional problems such as improving public participation, and responding to socio-cultural changes such as shifting demographics and associated shifts in people's values regarding wildlife (Hare, Smith, Forstchen, & Decker, 2018; López-Bao, Chapron, & Treves, 2017). A growing number of scholars and wildlife professionals propose that the concept of a public trust could help guide transformation to more socially and ecologically responsible wildlife conservation in the United States (U.S.) and elsewhere (Blackmore, 2017; López-Bao et al., 2017; Treves et al., 2017, 2018). These proposals are controversial, and there are significant disagreements over exactly what the concept of a public trust implies for wildlife conservation reform.

In chapter 2 of this dissertation Bernd Blossey and I review the literature on the concept of a public trust for wildlife and other natural resources. We distinguish between public trust thinking (PTT) and the public trust doctrine (PTD). PTT offers a vision for wildlife governance reform that emphasizes public ownership, long-term sustainability, broad public participation, and avoidance of preferential treatment of special interests. Elements of PTT feature in environmental ethics and resource management traditions around the world and over time. PTD is a legal expression of PTT in common-law traditions. Distinguishing between PTD and PTT provides a means of thinking creatively about wildlife governance reform. Nevertheless, serious challenges impede comprehensive application of PTT to wildlife conservation in the

U.S. In chapter 3, Dan Decker, Chris Smith, Ann Forstchen, Cynthia Jacobson, and I offer practically oriented guidance for wildlife conservation professionals by outlining eight conceptual, structural, institutional, and societal challenges to comprehensively applying PTT. We sketch potential solutions, and argue that overcoming these eight challenges will require cooperation among governmental and nongovernmental partners, supported by diverse engaged members of the public.

In chapter 4, Bernd Blossey, Andrea Dávalos, Erika Mudrak, and I investigate moral attitudes about wildlife ownership among people living in the U.S. Who, if anyone, should be obligated to conserve wildlife? Should private landowners have the right to decide which species live or die on their property? To what extent should government have authority to influence wildlife conservation on private land? We document subtle variation in respondents' moral attitudes about wildlife ownership according to the organism in question, whether that organism is on public or private land, which specific right or responsibility of ownership is under consideration, and demographic characteristics of respondents. Our results can help explain why some wildlife conservation activities are more morally acceptable than others.

In chapter 5, Kern Reeve, Bernd Blossey and I take a more panoramic view of ownership across the biological world. How and why does ownership evolve? Do any other species own things? We distinguish between possession and ownership and present species-neutral criteria for ownership, defined as respect for possession. We derive this simple behavioral definition of ownership primarily from research across disciplines on human systems of ownership, which vary widely but all involve respect for possession. We review the literature on resource conflict and cooperation across

species and argue that ownership is a powerful cooperative solution to tragedies of the commons and problems of collective action. We discuss how ownership unites previously described behaviors across taxa and present a new game-theoretic model to demonstrate an additional way in which individual ownership can evolve.

In chapter 6, Bernd Blossey, Kern Reeve, and I argue that the theory of evolution by natural selection can help explain why humans care about other species. Building upon recent insights that morality evolves to secure fitness advantages of cooperation, we propose that conservation ethics could be adaptations that support cooperation between humans and non-humans. Natural selection will favour traits for selectively conserving other species to optimize inclusive fitness benefits to humans. Our models provide new insights into persistent moral debates over the value of biodiversity by helping explain why conservation ethics exist and why they vary. From this evolutionary perspective, human and non-human interests are not necessarily at odds.

In chapter 7 I reflect upon how these collaborative, interdisciplinary projects connect. I argue that to better understand and address contemporary conservation challenges, we need to better understand morality. And to better understand morality, we need to incorporate evolution.

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CHAPTER 2

PRINCIPLES OF PUBLIC TRUST THINKING[1]

Abstract

Public trust thinking (PTT) offers a philosophical orientation toward natural resources and a means of addressing persistent and emerging challenges in environmental conservation. It has inspired laws and policies around the world and is receiving increasing attention among scholars and natural resource practitioners. Nevertheless, attempts to develop and implement PTT are hampered by lack of clarity: no clear single statement of principles that unite PTT's diverse expressions exists. We address this need by synthesizing PTT literature across academic disciplines. We identify four areas that are in need of development and offer five principles that characterize PTT: (1) Human well-being is dependent on benefits provided by ecosystems; (2) Certain resources are not suitable for exclusive private ownership; (3) All beneficiaries are equal; (4) Future generations should be considered in current resource management decisions; and (5) Trustees are bound by fiduciary obligations and are publicly accountable.

Introduction

Public trust thinking (PTT) seeks to guarantee that the benefits provided by ecosystems are available to everyone, including future generations (Weiss, 1992; Wood, 2009). It asserts that a group of elected or appointed trustees holds certain

[1] Hare, D., & Blossey, B. (2014). Principles of public trust thinking. *Human Dimensions of Wildlife*, *19*(5), 397–406.

natural resources in trust in the interests of all current and future citizens, who are beneficiaries of the trust (Sagarin & Turnipseed, 2012; Scott, 1999). Trustees are charged with overseeing trust resources in a manner that ensures long-term viability and does not privilege any individuals, groups or uses (Horner, 2000; Sax, 1970). In turn, beneficiaries are entitled to hold trustees to account if they are deemed to be in abrogation of their obligations (Blumm & Guthrie, 2012; Sax, 1970).

PTT has inspired laws, policies, and environmental ethics around the world that share fundamental normative aspirations but differ in scope, antecedents, and institutional arrangements (Blumm & Guthrie, 2012; Sand, 2014; Takacs, 2008). Applications of PTT have developed along various trajectories: trust resources range from water to wildlife to atmosphere, are located in different elements of the law, and apply at different levels of governance. India's public trust arrangements, for example, are derived from the constitutional right to a healthy environment, extend to all natural resources, and apply to the Union Government (Blumm & Guthrie, 2012; Takacs, 2008). This is different from U.S. public trust arrangements that were originally intended to facilitate commerce (Cohen, 1992; Ryan, 2001), apply to state governments, and extend to different resources in each state (Slade, 2008).

PTT is not a single, neatly demarcated set of ideas or precepts. Rather, it is an orientation toward natural resource governance that uses the concept of trusteeship to frame human stewardship of natural resources. Elements of PTT have arisen and evolved separately in various cultures at different times. Some manifestations share roots in Roman and English law (Blumm & Guthrie, 2012); others with separate ancestries have converged over time (Weiss, 1984; Wilkinson, 1988). Sand (2014)

describes concepts of trusteeship in French and German civil law, in rules for access to land and wildlife derived from customary law in Scandinavia, and in the mandates of statutory agencies in Italian public law. Elsewhere, Sand (2004) points to parallels between PTT and Islamic *waqf* and the *moramati* in African customary law. Wilkinson (1988) identifies elements of PTT in rules governing natural resource (mostly water) use in ancient China as well as in customary traditions in Africa, the Middle East, and North America. Consonance between PTT and some Native American attitudes toward the use of land and resources is further developed by Wood (2014). Weiss (1984) perhaps goes furthest in identifying the appeal of PTT across cultures and over time, claiming that the notion of trusteeship of natural resources enjoys "nearly universal recognition and acceptance" (p. 500).

The public trust doctrine (PTD) is a common law codification of PTT that can be traced to Roman Law (Sax, 1970). PTD made its way to the United States via English law and exists as a feature of environmental law in several other former parts of the British Empire, such as Australia, Canada, India, Kenya, Nepal, Pakistan, South Africa, Sri Lanka, and Tanzania (Blumm & Guthrie, 2012; Sand, 2004; Takacs, 2008; Wood, 2012). Applications in Asia, Africa, and South America appear stronger and more ambitious than in the United States (Blumm & Guthrie, 2012), where it has been disdained as ineffectual or redundant by proponents as well as critics (Blumm & Guthrie, 2012; Cohen, 1992; Horner, 2000; Huffman, 2008; Wood, 2007).

Beyond this wide geographical distribution of PTD, PTT inspires natural resource governance in countries not historically part of the British Empire, including Brazil, Ecuador, Eritrea, France, Germany, Italy, Nepal, the Philippines, Sweden, and

Switzerland (Blumm & Guthrie, 2012; Sand, 2014; Takacs, 2008; Wood, 2012). Furthermore, PTT has been proposed as a foundation for international and transnational governance. Bosselmann, Brown, and Mackey (2012) envision a transnational "World Environment Organization" charged with trustee obligations, while Sand (2004) describes how the concept of trusteeship for common global resources was advanced within the United Nations but eventually swamped by bureaucracy. PTT finds expression in the World Commission on Environment and Development's (1987) definition of sustainability and in a number of international agreements and treaties (Sand, 2014; Turnipseed et al., 2010).

We propose that PTT offers a useful means of situating growing attention to PTD within a broader context that reflects the development of public trust governance in a variety of institutional frameworks. We offer five foundational principles that characterize PTT distilled from scholarly writings on public trusteeship in law, policy and governance. This list is not intended to be exhaustive, but to describe a family of ideas that can be discerned within a diverse and somewhat amorphous literature.

Principle 1: Human Well-Being Is Dependent on Benefits Provided by Ecosystems

A rapidly increasing literature documents the dependence of humans on benefits derived from ecosystems (Millennium Ecosystem Asessment, 2005). These benefits accrue whether beneficiaries are aware of them or not and go beyond the interests and uses trustees have historically sought to balance (Decker et al., 2014). PTT has been advanced as a potential solution to contemporary environmental challenges including atmospheric pollution (Coplan, 2010; Wood, 2012), wildlife

conservation (Jacobson, Organ, Decker, Batcheller, & Carpenter, 2010; Meyers, 1989), marine ecosystem governance (Turnipseed, Crowder, Sagarin, & Roady, 2009), and access to potable water (Takacs, 2008) and ecosystem services (Ruhl & Salzman, 2007). Protecting ecosystems generally, not just specific components or uses, should be a priority for trustees (Bosselmann et al., 2012; Weiss, 1992; Ruhl & Salzman, 2007; Wood, 2013).

Historically PTT has been used to protect valuable public interests by ensuring access to specific places and resources they contain, and its justification has changed in line with societal needs (Cohen, 1992). These changes are reflected in the history of PTD. In medieval England PTD was used to ensure common access to forests and huntable animals (Blumm & Paulsen, 2013; Rose, 1986; Sax, 1980), and in the early United States it was used to ensure access to shorelines and navigable waters that would facilitate trade and commerce (Lazarus, 1986; Ruhl & Salzman, 2007; Ryan, 2001). The contemporary environmental justification for PTD was first articulated by Sax (1970), who argued for expansion of PTD to a wider range of natural resources and uses, providing legal traction for conservation and environmental protection.

Principle 2: Certain Resources Are Not Suitable for Exclusive Private Ownership

PTT encapsulates "populist impulses" (Wood, 2013) to treat certain natural resources as "inherently public" (Rose, 1986) or " . . . so intrinsically important to every citizen that their free availability tends to mark the society as one of citizens rather than of serfs" (Sax, 1970, p. 484). In this respect, PTT asserts that exclusive private ownership of these resources is inappropriate. Flowing water, the atmosphere

and organisms that travel across landscapes do not easily lend themselves to private ownership because they are difficult to demarcate or contain, and in many places these are designated trust resources (Meyers, 1989; Rose, 1986, 1998). However, PTT's rejection of private ownership is not absolute. In some cases, granting property rights to private actors can be consistent with the interests of all beneficiaries, and therefore does not violate PTT. For example, privately held fishing or hunting licenses, catch shares (Turnipseed et al., 2010), water rights (Blumm & Schwartz, 1995), or atmospheric pollution permits (Coplan, 2010) can be legitimate ways to allocate access to, but not exclusive ownership of, trust resources, as long as trustees retain regulatory oversight of the allocation process in keeping with their public trust responsibilities. Young (2011) presents a flexible approach to property rights that is attuned to relevant social and environmental factors and can generate public benefits.

The conviction that some resources are inherently public means that trustees or government agencies cannot abandon, sell, transfer, delegate, or alienate them (Horner, 2000; Rose, 1986; Sax, 1980; Torres & Bellinger, 2014). Using trust resources to achieve a public purpose is not enough—trustees should also make resources available for use by beneficiaries (Sax, 1970) without jeopardizing long-term resource viability (Weiss, 1992). Trustees must ensure that access to and benefits from trust resources are allocated fairly among beneficiaries: they must not privilege particular individuals or groups among current beneficiaries (Weiss, 1992; Horner, 2000; Wood, 2013), or current generations over future generations (Brady, 1990; Weiss, 1992).

PTT's disavowal of exclusive private ownership makes it vulnerable in two

key respects. First, PTT is inconsistent with regard to which types of ownership it does endorse. Ownership is not a binary choice between private and not private, but includes alternative designations such as public (owned by the state), common (owned by everyone), ownerless (owned by no one) (Coquillette, 1979), and combinations thereof (Geisler, 2000). PTT's inconsistent endorsement of ownership types could be construed as confusion or uncertainty, but it is possible that multiple ownership types are compatible with PTT. Second, a rejection of exclusive private ownership contradicts economic orthodoxy (Brewer & Libecap, 2009; Cohen, 1992) and demonstrable successes in conservation based on private property rights (Goldman, Tallis, Kareiva, & Daily, 2008). PTT has encountered significant resistance from advocates of economic efficiency and private property rights (Brewer & Libecap, 2009; Cohen, 1992; Huffman, 2008; Jaunich, 1994; Lazarus, 1986). Attempts to extend it to additional resources could place further constraints on private action (Takacs, 2008; Wood, 2013) and provoke political backlash (Sagarin & Turnipseed, 2012).

Principle 3: All Beneficiaries Are Equal

Trustees are charged with managing trust resources to the advantage of all beneficiaries, including future generations (Barnes, 2006; Weiss, 1992; Wood, 2009). Trustees' decisions affect all beneficiaries including those who express no interest or who are unaware of the impacts of resource management decisions on their lives (Decker et al., 2014) and those yet to be born. It is therefore imperative that trustees consider impacts of their decisions in the broadest terms. Policies or management

practices that privilege individual beneficiaries or groups are inconsistent with PTT (Horner, 2000; Jacobson et al., 2010; Wood, 2009).

Proponents of PTT are critical of contemporary environmental governance geared towards special interests rather than long-term interests of all beneficiaries (Jacobson, Decker, & Carpenter, 2007; Jacobson et al., 2010; Torres & Bellinger, 2014). Horner (2000) argues that individuals with no direct public accountability, often representing powerful interests, make decisions on behalf of the public's wildlife. Bruskotter et al. (2011) echo Horner's critique, highlighting state-level policies toward wolves in the United States that give higher priority to hunting and ranching interests than to broader social and environmental goals. Such regulatory capture affects not only wildlife conservation, but environmental governance in general (Barnes, 2006; Wood, 2013).

Scholars and practitioners have called for changes to funding models for wildlife agencies that have become financially dependent on consumptive interests (Jacobson et al., 2007, 2010). Consumptive interests are legitimate and must be considered by trustees. However, as societal interests in wildlife and expectations of agencies change, an over-weighted focus on traditional interests is increasingly untenable and threatens agency relevance (Jacobson et al., 2010). State wildlife agencies have implemented significant outreach campaigns to gather information on diverse interests of beneficiaries in order to meet public trust responsibilities (Boggess & Jacobson, 2013). Identifying and understanding the interests of beneficiaries is a necessary first step in meeting public trust responsibilities. However, truly fulfilling public trust responsibilities implies delivering important social and ecological

outcomes, such as meaningful participation by a broad range of citizens in the development of policies that successfully conserve natural resources.

In addition to difficulties associated with balancing diverse values expressed by citizens, trustees must also consider two groups of beneficiaries not revealed by agency outreach campaigns: current beneficiaries who express no preferences but are nevertheless affected, and future generations. The role of trustees is therefore not only to act on preferences expressed by beneficiaries participating in decision-making processes but to consider these interests alongside those of silent beneficiaries, current and future.

Principle 4: Future Generations Should Be Considered in Current Resource Management Decisions

PTT sees trust resources as a "natural inheritance" (Wood, 2013) passed from generation to generation (Weiss, 1992; Horner, 2000; Meyers, 1989; Rose, 1998). This commitment to future generations can be identified in environmental ethics of many cultures, and therefore provides a strong moral foundation for PTT (Weiss, 1984; Sand, 2014; Wilkinson, 1988; Wood, 2013). Decisions on natural resource use have material effects on future and current generations, and PTT holds that no generation is entitled to exhaust or degrade resources it has inherited from previous generations and holds in trust for future generations (Brady, 1990; Weiss, 1992).

PTT's intergenerational commitment has been confirmed in numerous legal rulings in the United States and internationally (Blumm & Guthrie, 2012; Slade, 2008; Takacs, 2008). Trustees are required to strike a difficult balance not only between

competing current interests, but also between current use and conservation for future generations (Weiss, 1984; Horner, 2000; Rose, 1986). Intergenerational justice presents two difficulties for PTT: predicting needs of future beneficiaries and representing their interests in contemporary decisions. Trustees face a problem of asymmetry in balancing often explicit current interests with unknown interests of future generations. However, the role of trustees is not to anticipate and provide specifically for interests of future generations, but to allow them to make their own determinations according to their own needs and values (Brady, 1990; Scott, 1999). Trustees are therefore obligated to maintain or enhance a diverse resource base for future generations that is in no worse condition than when the current generation inherited it, while not imposing any unreasonable burdens on the present generation's ability to meet its needs (Weiss, 1992).

Principle 5: Trustees Are Bound by Fiduciary Obligations and Are Publicly Accountable

Managing trust resources for the advantage of all beneficiaries implies fiduciary obligations (Sagarin & Turnipseed, 2012; Smith, 2011; Torres & Bellinger, 2014; Wood, 2012) of trustees, requiring them to act on behalf of beneficiaries, not simply in accordance with their own preferences (Horner, 2000; Scott, 1999; Watson, 2013).

Trustees' fiduciary obligations to beneficiaries are given legal force in PTD, which provides specific mechanisms for beneficiaries to hold trustees to account if they are deemed to be in abrogation of their obligations (Horner, 2000; Smith, 2011).

Trustees are individuals with legal mandates for managing trust resources, usually elected members of a legislature or appointed agency or commission leaders, and directly accountable to beneficiaries. Trust managers are civil servants employed by agencies in various capacities, directly accountable to trustees but only indirectly accountable to beneficiaries. The distinct roles, responsibilities, and entitlements of trustees and trust managers are essential to effective public trust governance, but are often poorly understood and can generate significant legal and operational difficulties (Smith, 2011). Open accountability mechanisms differentiate PTD from paternalistic approaches, democratizing environmental governance by making sure that decision-makers are directly accountable to the public (Sax, 1970). While the right to hold to account provides an essential check on trustee decision-making (Horner, 2000), it varies widely in application. Citizen standing ranges from very broad, for example in India, where a suit brought against the Minister for the Environment by an individual citizen saw its Supreme Court overturn a major economic development decision (Blumm & Guthrie, 2012; Takacs, 2008), to very narrow, for example in North Carolina, where only the state government can enforce public access rights to trust resources, not individuals or citizen groups (Sagarin & Turnipseed, 2012).

It can be instructive to imagine public trusts as broadly analogous to private or charitable trusts (Weiss, 1984; Coplan, 2010; Scott, 1999). Fiduciary obligations require trustees to protect trust resources and adopt a greater aversion to risk than acting on one's own behalf (Scott, 1999). Like all trusts, public trusts require a strong legal foundation and must be enforceable by courts (Wood, 2013). However, there are important differences between public trusts and private or charitable trusts. For

example, as citizens, trustees and trust managers are also beneficiaries of a public trust. While private or charitable trusts seek to ensure that trustees are not personally affected by their decisions, this is unavoidable in public trusts.

While the purpose of private trusts is often to maximize financial gains for beneficiaries, converting trust resources into financial capital does not reflect PTT's commitment to long-term environmental conservation (Scott, 1999) and could violate the inherent publicness of trust resources. More meaningful insights into good public trusteeship might be derived from comparisons with charitable trusts, which do not require specific named beneficiaries, often serve a common or public good and are impartial to the needs of different generations of beneficiaries (Weiss, 1984). While private and charitable trusts can help guide public trustees, they are not identical to public trusts. Comparisons should therefore be treated as indicative, not literal.

Significant tension exists between PTT's commitment to equal consideration of future generations of beneficiaries and its assertion of the right of beneficiaries to hold trustees to account. Future beneficiaries are of course unable to hold present trustees to account, so their interests might be overlooked in a way that is less likely than for well-informed and engaged current beneficiaries. Barnes (2006) and Weiss (1984) suggest mechanisms for indirect participation, whereby trustees are appointed to look out specifically for the interests of future generations and to make representations accordingly.

Areas of PTT That Require Further Development

In this section we highlight four elements of PTT that require further

development to strengthen its intellectual foundations and increase its relevance for practical application. Each implies a significant role for human dimensions research.

Clarity on Ownership

Ownership occupies a fundamental role in PTT. At present this is only negatively defined: PTT is clear in its rejection of exclusive private ownership but does not endorse any particular alternative. Common ownership, public ownership and nonownership, coupled with government trusteeship, are each at least in principle compatible with PTT. Research on the relative merits of different ownership designations under PTT, undertaken by scholars in collaboration with resource management practitioners, could shed useful light on this important but understudied area of PTT. Understanding the ability of trustees and trust managers to meet their public trust responsibilities under different ownership designations, and documenting the attitudes of beneficiaries towards different types of ownership could be especially useful.

Performance Metrics for Public Trust Policies

Social and ecological indicators could be used to assess whether trustees are meeting their obligations. Any system of performance metrics is likely to be imperfect and potentially controversial, and significant financial and personnel resources would be required to monitor the status of trust resources. But such metrics would be indispensible in making informed decisions and providing useful guidance for trustees, trust managers, beneficiaries, and the judiciary. Forstchen and Smith (this issue) argue

that state wildlife agencies in the United States must integrate more and better human dimensions research into their activities in order to meet their public trust obligations. Organ et al. (2014) suggest important areas for social scientific research to address current challenges in wildlife trust administration. Similarly, human dimensions research could support more effective beneficiary participation in identifying social and ecological indicators and evaluating trustee performance.

Obligations to Conserve and Grow Trust Resources

Some scholars advocate conservative, risk-averse management of trust resources requiring trustees only to preserve trust resources, not to grow them (Sagarin & Turnipseed, 2012; Scott, 1999). But it is not clear how this should be interpreted: preserving trust resources could preclude any nonrenewable resource use, and contradicts common aspirations to increase and improve resources. For example, wildlife conservation is often concerned with species recovery, not simply sustaining present numbers and distributions. Effective trusteeship could require significant changes to current species composition and abundance, such as reintroducing extirpated species or those in decline, reducing pressure created by overabundant species, and protecting vulnerable species or communities. Identifying baselines against which obligations to conserve or grow resources would require a careful combination of ecological data and social data on beneficiaries' preferences and tolerance limits.

Anthropocentrism and Nonhuman Beneficiaries

Wildlife is established as a public trust resource in many jurisdictions (Blumm & Guthrie, 2012; Blumm & Paulsen, 2013), and even those who are skeptical of the expansion of PTT accept its legitimacy in relation to wildlife (Huffman, 2008). However, that wildlife is a "resource" that exists to satisfy human needs is not a universally accepted ethical position. The belief that humans have obligations to other species finds public support (de Groot, Drenthen, & de Groot, 2011) and is evident in contemporary debates in environmental conservation (Cafaro & Primack, 2014). Incorporating the welfare of other species is not unheard of in PTT. Barnes (2006) advocates appointing a trustee with a specific remit to represent nonhuman species. Weiss (1984) welcomes the possibility that trustees' fiduciary obligations could extend to other species, and Meyers (1989) advocates consideration of nonhuman interests. The Florida Fish and Wildlife Conservation Commission, a champion of PTT, sees its role as "(M)anaging fish and wildlife resources for their long-term well-being and the benefit of people," explicitly acknowledging the well-being of nonhuman species in its mission statement (myfwc.com/about/overview/). However, redesignating wildlife from trust resources to beneficiaries would represent a significant alteration of trust relationships.

Conclusion

Natural resource professionals and scholars are increasingly turning their attention to public trusteeship as a promising means of addressing social and ecological inadequacies of contemporary environmental governance. PTT offers a

broader context for this proliferating attention than the narrower, primarily legal context provided by PTD. However, some key aspects of PTT remain understudied and poorly defined. These present a varied and exciting set of questions that can be addressed by scholars in close partnership with practitioners working with various natural resources in different social and ecological contexts.

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CHAPTER 3

APPLYING PUBLIC TRUST THINKING TO WILDLIFE GOVERNANCE IN THE UNITED STATES: CHALLENGES AND POTENTIAL SOLUTIONS[2]

Abstract

Public trust thinking (PTT) promises to inspire ecologically and socially responsible wildlife governance in the United States, but its application is not straightforward. We describe eight broad challenges to comprehensive application of PTT including: increasing authority and capacity; overcoming resistance to change; achieving fair consideration of all public interests; facilitating broad public participation; and fulfilling commitments to future generations. We discuss potential solutions including: distributing responsibilities for public wildlife conservation among governmental and nongovernmental entities; adopting an expansive definition of "wildlife;" promoting an inclusive interpretation of PTT among public wildlife professionals; rejuvenating relationships between the public and wildlife agencies; and increasing public participation and accountability in decision-making processes. Efforts to address challenges in specific socioecological contexts should be led by people working in those contexts. Achieving comprehensive application of PTT will require collaboration and cooperation among governmental and nongovernmental partners, supported by diverse and engaged members of the public.

[2] Hare, D., Decker, D. J., Smith, C. A., Forstchen, A. B., & Jacobson, C. A. (2017). Applying public trust thinking to wildlife governance in the United States: challenges and potential solutions. *Human Dimensions of Wildlife*, *22*(6), 506–523.

Introduction

Public trust thinking (PTT) is a philosophical orientation toward natural resources that emphasizes public ownership, long-term sustainability, broad public participation, and avoidance of preferential treatment of special interests (Hare & Blossey, 2014). Elements of PTT exist in natural resource management traditions in several cultures now and historically (Sagarin & Turnipseed, 2012; Sand, 2014; Weiss, 1992; Wilkinson, 1988). A well-known expression of PTT is the public trust doctrine (PTD), a feature of common-law systems around the world (Blumm & Guthrie, 2012; Takacs, 2008) including the United States. PTD places enforceable legal obligations on governments to conserve natural resources in the interests of all current and future members of society (Horner, 2000; Sax, 1970). PTD is a central component of environmental law in the United States and underpins wildlife law in most states (Blumm & Paulsen, 2013).

Although courts throughout the United States have repeatedly ruled that PTD applies to wildlife (Blumm & Wood, 2013), public wildlife agencies have been criticized for failing to comprehensively fulfill their PTD obligations (Horner, 2000; Treves et al., 2017; Wood, 2004). Effective public trusteeship of wildlife is inhibited in part by the absence of explicit trust documents specifying in detail the legal terms of the public trust in wildlife and clearly stipulating governmental obligations and public rights (Freyfogle & Goble, 2009; Horner, 2000).

In addition to calls for clearer legal guidance and comprehensive enforcement of PTD (Rodgers et al., 2013; Wood, 2013), some wildlife practitioners and scholars are advancing PTT as a potential solution to persistent and emerging challenges

affecting wildlife conservation in the United States (Decker et al., 2016; Forstchen & Smith, 2014; Jacobson, Organ, Decker, Batcheller, & Carpenter, 2010; Smith, 2011). Proponents of an inclusive interpretation of PTT are enthusiastic about its potential to produce favorable socioecological outcomes (Bruskotter, Enzler, & Treves, 2011), foster more responsive, even-handed, and participatory mechanisms of public engagement (Decker et al., 2014, 2015; Forstchen & Smith, 2014; Pomeranz et al., 2014), and overcome systemic biases and structural impediments to fair and effective public wildlife governance (Decker et al., 2016; Jacobson et al., 2010; Treves et al., 2017). Public wildlife professionals who approach their work in broader terms of PTT rather than PTD could bring practices and procedures into line with these aspirations without necessarily relying on legal interventions, including in places where the application of PTD to wildlife is unclear or contested (Blumm & Paulsen, 2013; Redmond, 2009).

Nevertheless, several conceptual, structural, and institutional impediments currently impede full realization of these aspirations. We identify eight general challenges and discuss potential solutions (Table 3.1) to support wildlife professionals applying PTT in specific socioecological contexts.

Table 3.1. Potential solutions to challenges. "Challenge" identifies the corresponding challenge in the text, with some divided into subcategories. "Potential solution" briefly states how each challenge could be overcome. "Possible paths to solution" suggests means of achieving possible solutions. Efforts to address challenges in specific socioecological contexts should be led by people working in those contexts.

Challenge	***Potential solution***	***Possible paths to solution***
1a Concepts and definitions – "wildlife."	Expansive definition of "wildlife."	Adopt a definition of "wildlife" that can accommodate all non-domesticated taxa. Implement this definition in law and policy to enable proliferation throughout public wildlife conservation.
1b Concepts and definitions – "fairness between generations."	Establish effective agreement on the definition of "fairness between generations" for types and rates of wildlife uses.	Negotiate a general framework for considering future generations in wildlife decisions that is neither overly restrictive nor overly permissive with regard to current use. Produce guidelines for trustees in setting limits or thresholds for current practices that could significantly impinge upon future generations. Effects of current activities on immediate future generations are clearer than for distant future generations, and can be more specifically taken into account (see 6c).
2a Authority and capacity – trustee responsibilities.	Renewed emphasis on trustee responsibilities of elected and appointed officials at all levels of government.	Emphasize trustee responsibilities of elected and appointed officials at all levels of government. Ensure that legislators retain trustee responsibilities even when they delegate responsibility to appointed officials such as state wildlife commissioners. Establish mechanisms for incorporating wildlife considerations into legislators' broader responsibilities across policy domains.
2b Authority and capacity – coordinated wildlife conservation.	Mechanisms for coordinating public wildlife conservation across public and private land.	Establish partnerships with private landowners (individuals, NGOs, for-profit organizations) that can harmonize wildlife conservation activities across public and private land. Identify voluntary, incentive-based, and regulatory mechanisms for promoting wildlife conservation on private land.
3 Roles and responsibilities of trust administrators.	Coordinated activities across sectors and levels of government, recognizing contributions of non-governmental entities.	Identify arrangements that can increase effectiveness by leveraging capacities and resources of partners across levels of government and sectors. Devise workable arrangements for synchronizing activities and distributing responsibilities while retaining oversight by trustees, avoiding special interest exclusivity, and respecting the autonomy of local and tribal governments and non-governmental partners.

Table 3.1 *continued*

Challenge	*Potential solution*	*Possible paths to solution*
4a Impartiality – real and perceived bias.	Productive, respectful relationships with individuals and groups holding historically underserved perspectives.	Develop communication between trust administrators and historically excluded beneficiaries (see 6a and 6b). Emphasize inclusivity of perspectives, values, and interests implied by PTT as a desirable feature of modern wildlife governance, and crucial roles of individual beneficiaries and groups in an optimally functioning public trust in wildlife.
4b Impartiality – financial dependence.	Broad-based funding for public wildlife conservation.	Remove financial dependence of SFWAs on consumptive activities and user groups. Explore the possibility and suitability of generating revenues from nonconsumptive wildlife activities.
4c Impartiality – commissions.	Diversity of interests represented on state wildlife commissions.	Increase transparency of selection and appointment mechanisms for state wildlife commissions. Establish rules to ensure diversity of interests and prevent dominance by any particular interests.
5a Institutional resistance – communicating inclusive interpretation of PTT.	Communicate inclusive interpretation of PTT in ways likely to reach and resonate with wildlife professionals across sectors.	Communicate an inclusive interpretation of PTT and its justification in print and online media, in-person training, and professional meetings. Justify comprehensive application of PTT, especially to constituencies that might resist change. Identify thought leaders across sector to advocate for change using appropriate rhetoric in different settings. Incorporate PTT into undergraduate, graduate, and professional training syllabuses.
5b Institutional resistance – agency culture.	Broad recognition and representation of diverse values and interests among public wildlife agency employees (trust managers).	Emphasize to all public wildlife agency employees the legitimacy of all public values and the importance of incorporating broad interests in fulfilling public trust responsibilities. Implement decision-making processes that dampen or preclude common cognitive biases, and allow for continuous improvement through evaluation and learning. Encourage individuals with non-traditional wildlife interests to consider careers in wildlife agencies, and make agencies appealing career options for such individuals. Take advantage of training and hiring opportunities to broaden agency skill sets to increase diversity and inclusivity.
6a Public adoption – communication with beneficiaries.	Meaningful engagement with beneficiaries aware of their roles, rights, and responsibilities in public trust governance.	Communicate to beneficiaries their importance in effective, participatory public trust administration. Promote awareness of the benefits of wildlife conservation to all people and accentuate public rights and responsibilities in shaping decisions and holding trustees to account.

Table 3.1 *continued*

Challenge	*Potential solution*	*Possible paths to solution*
6b Public adoption – increased beneficiary participation.	Additional means of including beneficiaries in wildlife decisions.	Broaden beneficiary participation, for example, through citizen juries for systematic public deliberation of particularly important wildlife issues, or fixed-term citizen-trustees.
6c Public adoption – immediate future generations.	Participation by young people in wildlife decisions.	Establish youth commissions with two-way mechanisms of communication with state wildlife commissions. Facilitate input from youth commissions on current wildlife issues, establish mechanisms for youth commissions to recommend issues for consideration by trustees, and encourage trustees to report publicly how they considered impacts on immediate future generations.
7a Measurement and accountability – performance metrics.	Clear ecological and social performance metrics for trust administrators.	Create iterative processes by which beneficiaries (individuals and groups) can negotiate with trust administrators appropriate performance metrics, levels of risk, and decision triggers. Include mechanisms for adaptation to socioecological change (e.g., new issues arising, existing issues becoming more or less urgent).
7b Measurement and accountability – monitoring and evaluation.	Appropriate, efficient, and responsive systems of public accountability.	Build on negotiations outlined in 7a to establish meaningful, viable evidence-based systems of monitoring, measuring, and evaluating trustees' performance that are efficient and responsive, and reflect trustees' legal obligations to consider the interests of all beneficiaries.
8 Legitimizing decision-making processes.	Fairer, more trustworthy, and ultimately more legitimate decision-making processes.	Openly and honestly communicate costs and benefits of transition to more comprehensive application of PTT. Adapt and correct when goals, practices, and processes deviate from PTT and beneficiaries' express preferences (see 7a and 7b). Inform beneficiaries of risks of decision alternatives, as well as risks associated with making no change.

Challenge 1. Clarifying definitions and concepts

The vocabulary associated with PTT for wildlife can be opaque (Table 3.2). Some key terms remain unsettled, including the definition of "wildlife" and the concept of fairness.

Table 3.2. Definitions of terms associated with PTT for wildlife in the U.S.

Public trust doctrine (PTD) A common-law tradition that places specific legal obligations on government to manage natural resources including wildlife for public benefit and protect them for use by future generations.
Public trust thinking (PTT) A philosophical approach to natural resources including wildlife that emphasizes public ownership, long-term sustainability, broad public participation, and avoidance of preferential treatment of special interests.
Trustees Elected and appointed government officials with legal responsibility for trust resources, ultimately accountable to beneficiaries.
Trust managers Conservation professionals working in public wildlife agencies, who act as agents of and are ultimately accountable to trustees.
Trust administrators Trustees and trust managers collectively.
Beneficiaries All current and future members of society.
Fiduciary obligation Responsibility to act in the interests of beneficiaries, not self-interest.
State fish and wildlife agencies (SFWAs) Public agencies at the state level with responsibility for fish and wildlife conservation.
Public wildlife agencies Public agencies at all levels of government with responsibility for fish and wildlife conservation.

What is wildlife?

PTT implies an expansive definition of "wildlife" (Meyers, 1989), possibly encompassing all non-domesticated taxa and acknowledging the interdependence of species (Soulé, 1985). Conservation efforts that extend mostly or exclusively to game animals or to charismatic, imperiled, or economically important species reflect objectives and values of wildlife conservation inconsistent with an inclusive interpretation of PTT. Realistically, not every species can be the subject of focused management attention at all times, but under an expansive definition of "wildlife" no species or taxonomic group could be categorically excluded from trustees' responsibility should it come to require attention.

Achieving such an expansion could be difficult because no public wildlife agency has jurisdiction over all species, let alone land uses that affect habitat (challenges 2 and 3). State legislatures have historically assigned different levels of

protection to different categories of species (Freyfogle & Goble, 2009), and some state fish and wildlife agencies (SFWAs) have authority for only some species (Blumm & Paulsen, 2013). Therefore, SFWAs' ability to expand public conservation programs to "all species for all people" (Decker et al., 2016) could be legally constrained, and might generate difficulties for public wildlife agencies already dealing with limited financial and staff resources. Expanding attention to a broader suite of species could be unpopular among traditionally privileged beneficiaries and interest groups. Engaging beneficiaries whose values and interests have not previously been adequately represented, for example individuals or groups who do not hunt, trap, or fish, or otherwise do not subscribe to the dominant approach to wildlife conservation (Feldpausch-Parker, Parker, & Vidon, 2017; Peterson & Nelson, 2016) could pose additional difficulties (challenges 5 and 6).

To address these challenges wildlife practitioners across sectors will have to reach a broad consensus regarding the scope of wildlife conservation efforts. In many places, State Wildlife Action Plans (teaming.com/state-wildlife-action-plans-swaps) and Landscape Conservation Cooperatives (lccnetwork.org) are expanding the scope of conservation and engaging broader perspectives, consistent with PTT. Precise metrics (challenge 7) would enable evaluation of how these and other public conservation initiatives are performing in relation to beneficiaries' aspirations and the principles of PTT, and help identify areas for improvement.

What is fairness?

Under PTT, fairness is construed as equal consideration (Bruskotter et al.,

2011; Horner, 2000) among all current beneficiaries and among generations of beneficiaries (Hare & Blossey, 2014; Weiss, 1992). Advocates of an inclusive interpretation of PTT emphasize that all values and interests in wildlife are legitimate (Decker et al., 2016; Hare & Blossey, 2014; Horner, 2000), so trust administrators should facilitate comprehensive public participation in wildlife decision-making processes and avoid privileging special interests (Bruskotter et al., 2011; Decker et al., 2015; Jacobson et al., 2010; Pomeranz et al., 2014). This commitment to fairness and inclusion acknowledges that not all beneficiaries will be fully satisfied with every wildlife decision, but seeks to consider all beneficiary perspectives and prevent long-run systemic biases. Social scientific research can help trust administrators understand values, preferences, and interests of beneficiaries who do not directly participate in formal engagement processes, and therefore better represent them in decisions (Forstchen & Smith, 2014).

Fairness among current beneficiaries is possible in principle, if not typically achieved (Treves et al., 2017; Wood, 2013; challenges 4, 5, and 6), but fairness between generations is more complicated. Moral obligations to future generations are notoriously thorny: it is impossible to know which particular individuals will be alive in future or predict their values and preferences, and some scholars question whether the current generation has any moral obligations to future generations (Gosseries, 2008; Parfit, 1984; Sagoff, 1988). Nevertheless, environmental ethics across cultures include strong moral commitments to future generations (Callicott, 1994; Weiss, 1992; Wood, 2013), and groups making collective decisions tend to allocate resources to future generations (Hauser, Rand, Peysakhovich, & Nowak, 2014).

Considering future generations also creates practical difficulties for trustees. Future beneficiaries cannot participate in current decisions or hold trustees to account, and identifying discount rates to prevent aggregate interests of all future people swamping those of people alive today can be complex and controversial (Arrow et al., 2013). It is reasonable to assume that future beneficiaries' general preferences will include viable socioecological systems (Zakaras, 2016), but the typical formulation of conserving options for future generations without predicting their specific values or preferences (Scott, 1999; Weiss, 1992) provides little practical guidance.

Obligations to conserve wildlife for future beneficiaries (Wood, 2004) could require trustees to limit or prohibit wildlife-related activities that threaten species or populations (Meyers, 1989), for example, consumptive or nonconsumptive activities that disturb vulnerable populations or habitats. However, prohibiting current activities that do not threaten species or populations could breach obligations to current beneficiaries. Wildlife policies and practices that seek to maintain current species assemblages or minimum viable population levels might often be insufficient (Wood, 2004). Trust administrators could better satisfy fiduciary obligations to both current and future beneficiaries by restoring and enhancing wildlife resources as much as possible, for example, by reversing declines of native species, creating refugia and migration corridors, controlling deleterious impacts of non-native species, and improving wildlife health in the broadest sense (Decker, Schuler, Forstchen, Wild, & Siemer, 2016).

Focusing on the immediate future generation could offer trustees a pragmatic approach less vulnerable to difficulties usually associated with obligations to future

generations (Zakaras, 2016). Young people alive today are specific individuals, their values and preferences are less uncertain, and it is impossible to deny moral obligations to them. Incorporating existing young people's interests into decisions would provide a rolling time horizon that does not extend so far into the future that discount rates become problematic. Formally engaging young people in wildlife decision-making processes (challenge 6) could enable trust administrators to better consider future beneficiaries, broaden beneficiary participation, and help produce the next generation of informed, engaged conservation advocates.

Challenge 2. Increasing authority and capacity

PTT places responsibility for public wildlife conservation on government, but public wildlife agencies often lack powers required to conserve wildlife. For example, public wildlife agencies can influence, but seldom control, final decisions about economic development, land use, energy, water, public health, and fiscal policy, all of which have significant implications for wildlife conservation. Wildlife trusteeship is an aspect of sovereignty (Meyers, 1989), so legislators have duties to enact laws that protect wildlife (Wood, 2004). Because states have substantial responsibility for wildlife (Bean & Rowland, 1997; Sax, 1970), this applies particularly to elected and appointed officials at the state level. In practice, state legislators typically delegate administrative responsibilities for fish and wildlife management decisions to wildlife commissioners (Nie, 2004), moving responsibility for wildlife from the core to the periphery of state government. Making sure that the public and legislators are aware that elected and appointed officials are wildlife trustees with fiduciary obligations to

all beneficiaries, and establishing mechanisms for incorporating wildlife considerations into decisions across policy domains, could elevate the importance of wildlife conservation. However, legislators weigh competing pressures and responsibilities across several policy domains that can take priority over wildlife conservation and complicate accountability (challenges 3 and 7).

A separate and perhaps broader difficulty stems from trust administrators' limited ability to influence actions on private lands (Freyfogle & Goble, 2009), which are crucially important for wildlife conservation (Hilty & Merenlender, 2003; Jenkins, Houtan, Van, Pimm, & Sexton, 2015). Under the Endangered Species Act (1973), the U.S. Fish and Wildlife Service has authority to protect endangered species on private land, but private property rights generally supersede the ability of government to impose expectations for wildlife conservation on landowners (Freyfogle & Goble, 2009). Landowners may engage in wildlife conservation through voluntary or incentive-based programs to enhance habitat (Goldman, Tallis, Kareiva, & Daily, 2008; Rissman, 2013), or adversely affect wildlife conservation or public access to wildlife by using or developing land in ways consistent with private property rights but inconsistent with PTT for wildlife (Freyfogle & Goble, 2009).

Public wildlife agencies often reach productive partnerships with private landowners (Lauber, Connelly, Niederdeppe, & Knuth, 2014; Rissman, 2013), and federal initiatives such as the U.S. Department of Agriculture's Environmental Quality Incentives Program (nrcs.usda.gov/wps/portal/nrcs/main/national/programs/financial/eqip/) and Conservation Stewardship Program (nrcs.usda.gov/wps/portal/nrcs/main/national/pro-

grams/financial/csp/) provide incentives for wildlife conservation on private land. Many significant parcels of land are controlled by nongovernmental organizations (NGOs) whose missions clearly resonate with PTT, such as land trusts, and some individual landowners acknowledge a responsibility to conserve wildlife on their land (Raymond & Olive, 2008) and elect to manage their properties for broad conservation outcomes. Nevertheless, given the diverse motivations for private landownership (Ferranto et al., 2013), it would be unrealistic to expect all private landowners to ascribe high priority to wildlife conservation on their land.

Effective wildlife planning and implementation are complicated by issues of authority, responsibility, and cooperation across a mosaic of landownership types (Jenkins et al., 2015). One measure of success for PTT would be to inspire and support coordination across property boundaries (Knight & Landres, 2013), helping to integrate productive private lands with effective wildlife conservation (Jacobson & Haubold, 2014; Kretser, Glennon, & Smith, 2014), for example, through partnerships across sectors, scales, and levels of government (challenge 3).

Challenge 3. Clarifying roles and responsibilities of trust administrators

Uncertainty about who is responsible for wildlife trust administration impedes effective application of PTT (Smith, 2011). At the state level, trust administrators are trustees (elected and appointed officials with ultimate legal responsibility) and trust managers (public wildlife professionals, acting as agents of trustees), all of whom have fiduciary responsibilities under PTD (Horner, 2000; Smith, 2011). Elected officials, appointees, and civil servants at all levels of government have public trust

responsibilities (Blumm & Schaffer, 2015; Torres & Bellinger, 2014; Wood, 2004) but may be unaware of, or otherwise not fulfill, those responsibilities (Horner, 2000; Wood, 2013).

The structure and authorities of SFWAs largely reflect the historical context in which they were established (Gill, 1996; Nie, 2004), rather than a purposeful intent to implement PTT or the PTD. Accordingly, public wildlife agencies may not currently have the funding, capacity, legal authority, or organizational flexibility to operate in ways consistent with PTT (Decker et al., 2016; Jacobson & Decker, 2008; Jacobson et al., 2010), for example, authority to protect habitats critical for the survival of many species (Oehler, 2003). In principle, such limitations could be addressed by legally expanding public wildlife agencies' responsibilities and authorities to help them meet their fiduciary responsibilities to all beneficiaries.

However, expanding agencies' authorities and responsibilities would not necessarily solve, and could potentially exacerbate, difficulties of cooperation across levels of government. Tensions between state and federal agencies, largely motivated by divergent interpretations of jurisdiction and authority, already inhibit collaborative wildlife conservation (AFWA, 2014). Tribal governments have jurisdiction over wildlife across substantial areas of land, and tribal members may have off-reservation treaty rights (Freyfogle & Goble, 2009) that could be in tension with state or federal agencies' interpretation of their PTD responsibilities. Other (non-wildlife) state agencies, for example, those responsible for zoning, water, transportation, and economic development have significant regulatory control over land use with implications for habitat conservation and connectivity, as do local governments.

Scholars interested in PTT have focused on SFWAs as the primary governmental actors in public trust administration, leaving the roles of federal, municipal, and tribal governments understudied by comparison. Federal, state, and municipal governments have responsibilities to overlapping but different publics, creating uncertainty about who should be considered beneficiaries of any given decision: citizens of a municipality, state, or the United States (Epstein, 2016), or those affected by the decision in question, regardless of location or citizenship (Zakaras, 2016). Tribal governments, whose wildlife authority is not derived from state or federal governments (Freyfogle & Goble, 2009), might conceive of their wildlife conservation responsibilities in terms of PTT (Torres & Bellinger, 2014; Wood, 2013) but are not legally obliged to do so.

Nevertheless, expanding public wildlife agencies' responsibilities and authorities might not be the most efficient, effective, or politically expedient means of reforming wildlife governance. Modern wildlife conservation is a collaborative endeavor involving nongovernmental actors such as private landowners, for-profit organizations, nonprofit organizations, and community groups. In many circumstances, NGOs already augment the work of public wildlife agencies and help them meet public trust obligations indirectly through pursuing their organizations' conservation goals, or directly by providing financial and operational support (Kretser et al., 2014; Kretser, Schiavone, Hare, & Smith, 2016; Lauber et al., 2014). In other circumstances, local governments engage for-profit or not-for-profit organizations to undertake wildlife management activities under permits issued by SFWAs, and nongovernmental entities lead successful conservation initiatives with public wildlife

agencies playing supporting roles (Lauber et al., 2014). Extending trust manager status to some nongovernmental partners, overseen by trustees, could increase the overall capacity, resources, and scope of public wildlife trusteeship (Decker et al., 2016). This partnership approach would distribute public trust responsibilities more broadly, and augment public wildlife conservation by drawing on existing nongovernmental networks and collaborations. Innovative partnerships would recognize the autonomy and harness the capacity of partners across sectors and levels of government.

Partnerships that bring together multiple diverse interests to meet specific conservation objectives identified in conjunction with beneficiaries could help improve public participation, legitimacy, measurement, and accountability (challenges 6 and 7). Partnering with organizations that primarily represent only a subset of beneficiaries could challenge the ability of trustees to avoid privileging (or appearing to privilege) special interests (Kretser et al., 2016; Lauber et al., 2014) and thereby reduce public confidence in trust administrators. Contracts clearly specifying roles and obligations of partners and stipulating specific delegated conservation activities would ensure that trustees retain ultimate oversight. Such a partnership approach might appeal to trustees keen to increase capacity for public wildlife conservation, but potential nongovernmental partners might be disinclined to assume the additional oversight and responsibilities that would accompany trust manager status. Increased financial disclosure might not appeal to individual or corporate landowners or NGOs, and could potentially compromise NGOs' ability to raise funds by conflicting with donors' desires for anonymity (Kretser et al., 2016). Mechanisms and standards of public accountability could be difficult to apply to nongovernmental partners that do

not claim broad public missions, or derive their mandate directly from members' interests in particular species, systems, or issues.

Challenge 4. Practicing impartiality and avoiding bias

PTT's aspiration for wildlife governance to reflect the full suite of societal values (Decker et al., 2016; Horner, 2000) is not always achieved in practice. Trust administrators at the state level have historically served interests of some beneficiaries more than others (Feldpausch-Parker et al., 2017; Nie, 2004). SFWAs therefore have longer-established relationships with certain beneficiaries or interest groups, such as hunters, trappers and anglers, or commercial interests such as ranching, farming, and fishing (Gill, 1996; Jacobson & Decker, 2008), who as a result often enjoy special access to agency officials. Many of these same groups provide significant income to SFWAs through license purchases and tax revenues from sales of hunting and angling equipment (Jacobson et al., 2010), and many SFWA staff personally identify with hunters and anglers, or at least are perceived to (Vernon & Clark, 2016). These special relationships are reinforced by some appointment systems stipulating that members of state wildlife commissions represent particular interests (Nie, 2004).

It is therefore not surprising that certain beneficiaries and interest groups believe that they are entitled to preferential treatment by SFWAs (Vernon & Clark, 2016), and in some cases receive it through agency decisions that favor them in the long run, or commissions that are constituted in a way that guarantees them a dominant voice in policy deliberations (Horner, 2000; Nie, 2004). Historically underserved beneficiaries and groups might find it difficult to engage with public

wildlife agencies when they do not see their values represented in those agencies' activities or cultures. This could diminish the confidence those and other beneficiaries place in agencies and trust administrators whose mandate is to serve all members of society.

Cultivating productive, respectful channels of communication with and among beneficiaries holding diverse perspectives, values, and interests may be difficult (challenges 5 and 6), but is within the control of public wildlife agencies. Structural changes such as removing dependence on hunting, angling, and shooting revenues (Jacobson, Decker, & Carpenter, 2007) and ensuring that commission appointment systems produce trustees who will represent beneficiaries broadly (Horner, 2000) fall under the control of legislators.

Challenge 5. Overcoming institutional resistance to change

Comprehensive application of PTT will require significant changes to contemporary priorities and practices in public wildlife governance (Forstchen & Smith, 2014; Jacobson et al., 2010). Change is likely to be slow even if trust administrators readily adopt PTT, due to time required to substantially adjust policies, budgets, processes, and practices to reflect legal obligations and societal expectations for considering all beneficiary interests (Decker et al., 2016). Change will be slower if trust administrators are unwilling to move away from the status quo based on concerns about the impact of change on them personally or professionally. Bias in favor of the status quo is not particular to public wildlife professionals (Kahneman, Knetsch, & Thaler, 1991), and can be stronger when existing arrangements favor a decision

maker's own interests (Diekmann, Samuels, Ross, & Bazerman, 1997). The effects of this and other cognitive biases (Iftekhar & Pannell, 2015) could be mitigated by altering choices available to decision makers (Milkman, Chugh, & Bazerman, 2009), and providing opportunities for evaluation and learning to improve future decisions (Conroy & Peterson, 2013).

The rationale for comprehensive application of PTT might be evident to those who have been critical of the status quo with regard to wildlife governance and would welcome reform. Others might be skeptical of whether trust administrators will embrace PTT more than superficially (Treves et al., 2017), given public wildlife agencies' historical alignment with particular special interests. Nevertheless, public wildlife agencies are likely to remain central to public wildlife conservation, so it is essential that they fairly accommodate all beneficiary perspectives to avoid perpetuating or magnifying problems of bias and exclusivity (challenge 4).

Creating an institutional culture genuinely committed to the aspirations of PTT will require trust administrators fully willing to embrace diverse values and make decisions reflecting that diversity. Champions and thought leaders across sectors (including universities, professional societies, and interest groups) could communicate benefits of an inclusive interpretation of PTT to peers, colleagues, staff, and all beneficiaries, including those who are skeptical of change. Public wildlife agencies could actively welcome historically underrepresented perspectives into core activities by communicating openly with historically underserved beneficiaries, employing individuals with diverse perspectives more representatives of all beneficiaries, and providing education and training for new and existing staff. Colleges and universities

could support inclusivity by teaching governance in core undergraduate and graduate wildlife classes, and in education and outreach activities with wildlife professionals.

Challenge 6. Promoting public adoption of PTT

In addition to responsive trust administrators genuinely committed to diverse beneficiary values, optimally functioning public trust administration requires informed beneficiaries, aware of their entitlements and obligations, engaging throughout wildlife decision-making processes from information gathering, through planning and implementation, to mechanisms of appeal and accountability (Decker et al., 2016; Hare & Blossey, 2014). However, it is not clear whether members of the public are aware that they are beneficiaries of a public trust in wildlife and the rights and responsibilities that status implies. Moreover, opportunities for engagement vary among states (Blumm et al., 2014; Sagarin & Turnipseed, 2012), possibly reflecting that states do not embrace PTD to the same extent (Blumm & Paulsen, 2013; Redmond, 2009). Inconsistent or insufficient beneficiary engagement favors individuals and groups with particular interests in wildlife, reinforcing difficulties of exclusivity (challenges 4 and 5).

Trustees are obliged to consider the interests of beneficiaries who do not or cannot express their interests in wildlife issues (Hare & Blossey, 2014), but merely inferring the interests of such beneficiaries can at best be a partial substitute for active, meaningful engagement. Trust administrators should not interpret absence of engagement by beneficiaries as indifference toward or tacit support for their actions. Rather, it is incumbent upon trust administrators to establish and maintain

constructive, informative dialogue with all beneficiaries (Forstchen & Smith, 2014; Vernon & Clark, 2016), and provide opportunities to exchange knowledge, express values, and explore multiple possible courses of action (Chase, Decker, & Lauber, 2004; Crowley, Hinchliffe, & Mcdonald, 2017; Klijn & Edelenbos, 2013). Trust administrators could help overcome historical difficulties of engaging only a subset of beneficiaries through communication campaigns conveying clearly to all beneficiaries, especially those who do not subscribe to established approaches to wildlife management or who are apathetic to wildlife issues, that the public trust exists and depends on participation by all beneficiaries.

Established methods of beneficiary participation, for example, public meetings, trust administrators attending gatherings of beneficiaries (e.g., homeowners' associations, outdoor recreation clubs, schools and colleges, and citizen science initiatives), or online or in-person listening sessions, in which beneficiaries and trust administrators identify important issues and work together to develop recommendations for trustees to consider, will remain important. These methods will be more effective and will better satisfy the aspirations of PTT when trust administrators acknowledge and incorporate broader perspectives, and traditionally excluded beneficiaries are willing to enter into dialogue with trust administrators (challenges 7 and 8).

Devising additional methods of participation could create opportunities for more and different beneficiaries to contribute to wildlife decisions. For example, citizen juries (Proctor & Drechsler, 2006) in which randomly selected or representative groups of beneficiaries systematically hear arguments for alternative

courses of action and make informed recommendations to trustees. This deliberative approach could be especially useful for particularly contentious issues, such as those involving controversial species. Fixed-term rolling appointments of citizen-trustees, individuals randomly chosen from the electorate with no formal allegiance to any special wildlife interest, on state wildlife commissions would enable broader beneficiary representation beyond specific or contentious issues.

Trust administrators could engage immediate future generations by establishing youth wildlife forums, comprised of a small group of young beneficiaries (e.g., 15–18-year-olds). Two-way communication between youth wildlife forums and state wildlife commissions would ensure that immediate future generations participate in wildlife governance, and commissions could report publicly on how they incorporate youth forums' representations into policies and decisions. Participation by young people promises improved democratic outcomes as well as benefits to participants (Frank, 2006). Careful attention to how youth forum members are recruited and trained, the issues they consider, and the processes by which they consider them (Matthews, 2001) would help deliver these promises.

Challenge 7: Increasing focus on performance, measurement, and accountability

PTT envisions a vital role for beneficiaries in determining whether trust administrators are fulfilling their obligations (Hare & Blossey, 2014; Sax, 1970). Individual beneficiaries and groups can make personal representations to trust administrators, but such feedback is unsystematic and not necessarily representative of beneficiaries more generally. Public wildlife agencies routinely engage beneficiaries

in nonconfrontational ways, but because formal feedback loops between beneficiaries and wildlife trustees are largely exercised through elections, ballot initiatives, and court cases; public accountability for wildlife trusteeship can be bound by the timing of election cycles or courts (Smith, 2011).

During elections, signals from the wildlife arena can become swamped among other issues, and legal action is often retrospective, after relationships have been fractured and resources have been degraded (Wood, 2013). Ballot initiatives can take important wildlife decisions out of the hands of trustees (Williamson, 1998), effectively circumventing public trusteeship. Nevertheless, large numbers of people cast votes either in favor of or opposition to wildlife-related ballot initiatives, which often take the form of values-based challenges to existing or proposed wildlife policies or practices (Vucetich, Bruskotter, Nelson, Peterson, & Bump, 2017). This suggests that a significant proportion of beneficiaries care about and are willing to express opinions on wildlife issues, but choose to do so without engaging directly with public wildlife agencies. By facilitating conversations with and among as many beneficiaries as possible, in which historically underrepresented opinions and values are treated equally alongside all others, trust administrators could make decisions more inclusive and therefore more consistent with PTT, potentially reducing the frequency of ballot initiatives and facilitating public deliberation of important wildlife decisions.

Stark disagreements over the content and direction of wildlife decisions highlight a need for clear metrics against which beneficiaries can assess trustees' performance (Hare & Blossey, 2014), as well as transparent decision-making processes and mechanisms for beneficiaries to challenge decisions that fall short of

trust standards (Horner, 2000). Systematic measurement, evaluation, accountability, and reporting processes through which trust administrators and beneficiaries can communicate efficiently and in a timely manner could improve the sensitivity and responsiveness (adaptability) of the system, sharpen conservation objectives, and increase confidence in and credibility of public wildlife governance.

Exact performance metrics, how they are measured, and by whom are open questions. Metrics should be negotiated between beneficiaries and trust administrators, sensitive to socioecological context (Crowley et al., 2017), and revisable to accommodate socioecological change. Some metrics are likely to be relevant in all jurisdictions, but others might vary according to the nature and context of local wildlife issues. Metrics should reflect and formalize trustees' obligations to all beneficiaries under PTD, and incorporate ecological and social dimensions (Bixler et al., 2016), such as wildlife population numbers, habitat quality and availability, wildlife impact on humans, accommodation of multiple and diverse interests, and quality and breadth of public engagement and representation. Efficient measurement and accountability processes would not require beneficiaries to approve every decision, but to identify acceptable limits within which trust administrators can confidently operate. For example, defining particularly important wildlife issues, agreeing acceptable levels of risk, and negotiating decision triggers (Addison, Cook, De Bie, & Bennett, 2016) to guide management interventions. This would actively involve beneficiaries in wildlife planning, and require trust administrators to monitor, measure, and report progress toward specific ecological and social targets identified in conversation with beneficiaries.

Challenge 8. Legitimizing decision-making processes

More comprehensive application of PTT to wildlife governance in the United States could improve its legitimacy: recognition by beneficiaries that trust administrators have justified authority to make decisions on their behalf (Beetham, 1991). Although trustees are expected to be impartial, wildlife decision making in the United States is inherently political, from how trustees are elected and appointed, to policies they pursue and specific decisions they make. Some level of disagreement about the direction of and justifications for wildlife decisions is therefore unavoidable, and need not be destructive (Crowley et al., 2017). Beneficiaries who meaningfully participate and are confident that trustees fully consider their values and interests will be more likely to recognize decision-making processes as fairer, more trustworthy, and ultimately more legitimate (Earle & Siegrist, 2008; Klijn & Edelenbos, 2013; Rudolph & Riley, 2014; Van Ryzin, 2011), even if they do not agree with eventual decisions.

Increasing the volume and scope of information used in decision making and evaluation would require additional time, funding, and human resources, reducing agencies' ability to act quickly or address as many issues as they might like. Although listening to outside perspectives can generate less biased decisions (Milkman et al., 2009), increased beneficiary participation could also create a larger number of disappointed beneficiaries when decisions go against preferences they have communicated to trust administrators. Moreover, radical reorganization or reorientation of governance arrangements could lead to short-term declines in trust as beneficiaries become uncertain about what to expect from trust administrators

(Thomas, 1998). Such negative impacts of change may eventually be offset if better-informed, participatory processes generate decisions with broader support (Forstchen & Smith, 2014; Van Ryzin, 2011), and provide trust administrators with greater license to operate within general parameters negotiated between trust administrators and beneficiaries. Uncertainty is unavoidable in natural resource management, so every decision involves some risk (Conroy & Peterson, 2013). Recognizing and informing beneficiaries of the inherent risks of decision alternatives, including the risks associated with making no change, will allow trust administrators to negotiate paths forward with beneficiaries informed of potential positive and negative consequences of different courses of action. Increased legitimacy could reduce retrospective legal challenges, freeing up resources that could be invested in other aspects of wildlife conservation, and enable trust administrators to make bolder, proactive wildlife decisions.

Conclusion

None of these challenges alone is likely to stall continued development of PTT or its application to wildlife governance in the United States. Nevertheless, each of them has the potential to diminish the effectiveness of PTT in achieving benefits articulated by its proponents: favorable socioecological outcomes, more responsive, even-handed, participatory public engagement, and fair and effective public wildlife governance. Overcoming these interlinked impediments could help realize PTT's aspirations for more ecologically and socially responsible wildlife governance. Doing so will require significant changes to many practices and processes of wildlife conservation, and the

philosophical orientation upon which they are founded. It will only be achieved through committed collaboration and cooperation among governmental and nongovernmental partners immersed and invested in specific conservation issues, supported and legitimized by diverse beneficiaries engaged throughout decision-making processes.

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CHAPTER 4

WHOSE WILDLIFE? MORAL ATTITUDES ABOUT WILDLIFE OWNERSHIP IN THE UNITED STATES

Abstract

Who, if anyone, should have obligations conserve wildlife? Should private landowners have the right to decide which species live or die on their property? To what extent should government have authority to influence wildlife conservation on private land? What rights and obligations should individual members of the public have with regard to wildlife on public land? These are moral questions about wildlife ownership. Understanding how members of the public answer them could provide important insights into the viability of different approaches to wildlife conservation, such as those based on governmental authority or those based on landowner autonomy and market-based incentives. We investigated moral attitudes about wildlife ownership among adults living in the United States (U.S.) using two online studies. Respondents' moral attitudes about who, if anyone, should own wild organisms varied depending on the organism in question, whether it was on public or private land, and the specific ownership right or responsibility under consideration. Respondents agreed that government should have obligations to conserve wildlife on both public and private land, and also that private landowners should have obligations to conserve wildlife on their land. Respondents agreed that private landowners should have rights to kill and transfer (collect and sell) wild organisms on their land, but disagreed that government should have rights to kill or transfer organisms on either public or private land. Patterns in our results reveal that moral attitudes sometimes contradict legal

ownership designations in the U.S. A more detailed understanding of people's moral attitudes about wildlife ownership could illuminate the moral acceptability of alternative approaches to wildlife conservation and governance, and so help identify approaches that will be more – or less – likely to succeed.

Introduction

> *It is well settled that wild animals are not the private property of those whose land they occupy, but are instead a sort of common property whose control and regulation are to be exercised 'as a trust for the benefit of the people'.*
>
> (Geer v Connecticut, 1896).

Wildlife conservation, sustaining wild organisms and their habitats, is morally contested (Baynham-Herd, Redpath, Bunnefeld, Molony, & Keane, 2018; Lute, Navarrete, Nelson, & Gore, 2016). In the United States (U.S.), much of this contestation centers around which rights and responsibilities people should have with regard to wild organisms, and to whom those rights and responsibilities should belong (Manfredo, Teel, Sullivan, & Dietsch, 2017; Peterson, Lopez, Mertig, & Liu, 2011; Slagle, Bruskotter, Singh, & Schmidt, 2017; Vernon & Clark, 2016). Who, if anyone, should be obligated to conserve wild organisms? Should private landowners have the right to decide which organisms live or die on their property? To what extent should government have authority to influence what happens to wildlife on private land? Should anyone have the right to collect and sell living wild organisms? What rights and obligations should individual members of the public have with regard to wildlife

on public land? These are moral questions about wildlife ownership: who should get to decide what happens to wildlife (Cahoon, 2001; Lueck, 1995; Peterson et al., 2011; Robbins & Luginbuhl, 2005).

Competing answers to these questions illuminate notoriously acute tensions between governments' responsibilities to conserve wildlife and private landowners' rights to determine what happens on their land (Freyfogle & Goble, 2009; Hare, Decker, Smith, Forstchen, & Jacobson, 2017; Watson, 2013). Understanding how members of the public answer these questions could provide important insights into the moral acceptability, and therefore legitimacy (Beetham, 1991; Boyer & Petersen, 2012; Hare et al., 2017), of alternative proposals for wildlife governance reform, such as those based on governmental authority and regulation versus those based on landowner autonomy, private ownership, and market-based incentives (Decker et al., 2016; Peterson et al., 2011; Watson, 2013; Wilson, Hayward, & Wilson, 2017).

In the U.S., people in charge of state and federal wildlife agencies have legal obligations to conserve wildlife in the interests of all current and future members of the public, not in their own interests or in the interests of particular segments of society (Decker et al., 2016; Hare & Blossey, 2014; Horner, 2000). However, public wildlife agencies tend to employ a narrow definition of "wildlife," restricting their attention primarily to species that have been the focus of historical conservation challenges or controversies (Freyfogle & Goble, 2009), most often huntable animals, but also migratory, economically important, or endangered species (Horner, 2000; Nie, 2004; Robbins & Luginbuhl, 2005). Moreover, public wildlife agencies regulate interactions between people and some wild organisms intensively (for example by

protecting rare or endangered species), others less intensively (for example by allowing people to kill some animals they consider to be a nuisance), and some not at all (for example microorganisms and non-endangered plants, small mammals, and invertebrates). Public wildlife agencies regulate only a small fraction of people's total interactions with wild organisms, and often fall short of societal expectations – and arguably legal obligations – to conserve all species for all members of the public (Decker et al., 2016).

Public wildlife agencies are experiencing increasing pressure to address biodiversity decline (Urban, 2015) in ways that are responsive to all societal values and interests (Decker et al., 2016; Dietsch, Teel, & Manfredo, 2016; Hare et al., 2017; López-Bao, Chapron, & Treves, 2017; Treves et al., 2017). Fully meeting these contemporary conservation challenges will require coordinated conservation on public and private land (Jenkins, Houtan, Pimm, & Sexton, 2015). One way to achieve this could be for agencies to employ a more expansive definition of "wildlife" that could encompass all non-domesticated taxa (Hare et al., 2017). But even if agencies were to broaden their taxonomic focus, they currently have limited ability to influence wildlife conservation on private land, except in relation to endangered species (Raymond & Schneider, 2014). Approximately 60 per cent of land in the U.S. is privately owned (Nickerson, Ebel, Borchers, & Carriazo, 2011), and much of it is critically important for wildlife conservation (Jenkins et al., 2015). Private landowners legally own some wild organisms, such as non-endangered plants and trees, because they are considered part of their land (i.e., their property). Furthermore, landowners can decide what happens to all unregulated organisms on their land, so effectively (if not legally) own

those organisms (Cahoon, 2001; Freyfogle & Goble, 2009). Although many private landowners manage their land for wildlife conservation, they have no legal obligations to do so and may have incentives not to do so (Ferranto et al., 2013; Wilson et al., 2017).

It is difficult to see how public wildlife agencies will be able to meet contemporary conservation challenges without expanding their ability to influence conservation on private land. However, any proposal to expand government authority for wildlife on private land could be unpopular, particularly among people who consider private property rights more important than species conservation (Teel & Manfredo, 2010), who believe landowners have a moral obligation to conserve wildlife on their land (Raymond & Olive, 2008), or who would perceive increased governmental authority as threat to their values and lifestyles (Manfredo et al., 2017). Nevertheless, leaving wildlife decisions in private landowners' hands precludes public oversight of many activities on private land that could be detrimental to wildlife conservation.

Better understanding why wildlife ownership is morally contested could shed light on possible ways to overcome these tensions and improve conservation outcomes. However, little empirical research has explicitly measured moral attitudes about wildlife ownership in the U.S. Residents of two counties along the Texas-Mexico border who answered a single question about who should own wildlife on private land were fairly evenly divided between those who supported public ownership (39%), private (landowner) ownership (29%), or were neutral (33%) (Peterson et al., 2011). This demonstrates remarkable variation in moral attitudes towards wildlife

ownership even among people within a relatively small geographical area responding to an inquiry only about wildlife on private land.

We believed that the ambiguity of "wildlife" and "ownership" might also account for variation in moral attitudes about wildlife ownership. Wildlife is a broad category that could mean different things to different people, and people assign different moral values to and support different management approaches for different species (Lute & Attari, 2017; Piazza, Landy, & Goodwin, 2014; Slagle et al., 2017). Ownership is not a single right but a "bundle of sticks" (Hohfeld, 1913); a set of rights and responsibilities that can be held by a single individual or organization, or allocated among several (Gerhart, 2014; Plummer & Fitzgibbon, 2004; Rissman, 2013). Rights and responsibilities associated with wildlife ownership could include the right to kill, the right to transfer (collects and sell), and the obligation to conserve. But whether such rights and responsibilities exist at all, and whether they are allocated to government (public ownership) or landowners (private ownership) varies from place to place (Aggarwal & Elbow, 2006; FAO, 2002; Robbins & Luginbuhl, 2005). Tensions between landowner autonomy and legitimate public authority for wildlife on private land are often conflicts over the allocation of such rights and responsibilities (Redpath et al., 2017; Robbins & Luginbuhl, 2005; Watson, 2013). In addition to these debates about *who* should own wildlife, some question whether *anyone* should own wildlife, because categorizing organisms as property may enable people to treat them in morally questionable ways (Francione, 2015; Leopold, 1949).

We investigated moral attitudes about government, individual, and non-ownership of wildlife (who, if anyone, should have rights and responsibilities

regarding non-domesticated animals and plants) among adults living in the U.S. We expected support for different ownership types to vary according to the organism in question, whether that organism is on public or private land, and the specific right or responsibility under consideration. Because of a deep cultural commitment to property rights in the U.S. (Ely, 2008; Hoffman, 2018) we expected respondents to agree that who owns the land should also own the wildlife on that land. This would manifest as support for private (individual landowner) ownership of wildlife on private land and government ownership of wildlife on public land. It would also manifest as lack of support for individual ownership on public land and lack of support for government ownership on private land. We expected respondents to agree that no one should own organisms perceived to be wilder, more intelligent, more capable of experiencing pleasure, more capable of making decisions, and more wide-ranging (Donaldson & Kymlicka, 2011; Francione, 2015; Peterson, Peterson, & Peterson, 2016; Starmans & Friedman, 2016). We expected respondents who own more land, and who grew up or currently live more rurally to be more supportive of individual ownership and less supportive of government ownership of wildlife on private land (Peterson et al., 2011). We expected respondents who are male, older, less educated, and who identify as more politically conservative to be less supportive of government ownership of wildlife on private land (Manfredo et al., 2017).

Methods

We hosted two online studies on Qualtrics (www.qualtrics.com). In study 1 we characterized people's perceptions of 33 different organisms, because we expected

people's moral attitudes to vary depending on the organism in question. This allowed us to select organisms systematically for inclusion in study 2, in which we investigated moral attitudes about wildlife ownership.

For both studies, we recruited adults living in the U.S. via Amazon Mechanical Turk (MTurk, www.mturk.com). MTurk is a respondent recruitment service that allows researchers to access large and demographically diverse convenience samples that are not representative of the U.S. public but improve significantly upon traditional convenience samples (Berinsky, Huber, & Lenz, 2012; Mason & Suri, 2012). We restricted access to MTurk users who had completed at least 50 previous assignments with an approval rating of at least 95%, and we did not allow the same user to participate more than once in either study. We minimized self-selection bias towards MTurk users with particular interests in wildlife by advertising our study simply as "Please give us your opinions for an academic research project" (Robbins, Franks, & von Keyserlingk, 2018). We pretested both studies for clarity and comprehensibility among colleagues not involved in the study. We provided all respondents in each study the same brief introductions (Appendix A and B). To avoid influencing respondents' answers we did not define key terms in these introductions or elsewhere in the studies.

We recruited 998 respondents for study 1 and paid each 75¢ in Amazon credit to answer sets of questions about three organisms (Appendix A) and complete a short demographic questionnaire (Appendix C). We recruited 1250 respondents for study 2 and paid each 60¢ in Amazon credit to respond to six questions (Appendix B) and complete the same short demographic questionnaire we used in study 1. Cornell

University Institutional Review Board staff approved this research as exempt (protocol number 1407004842), and all respondents gave informed consent before answering any questions.

Study 1: Characterizing organisms

We selected 33 common terrestrial organisms (eight mammals, seven plants, seven birds, six invertebrates, and five herptiles) native to the U.S. that adults would likely be familiar with. We sought to vary heterotrophic level, home range size, and body size as much as possible within each group (Table 4.1 and Appendix D.) We used a combination of seven-point Likert scales and six-point ordinal scales to measure respondents' perceptions of organisms according to 20 characteristics that might influence moral attitudes towards them (Table 4.2 and Appendix A).

Table 4.1. Cluster analysis results and adjusted familiarity scores for all 33 organisms in study 1.

Organism	*Scaled adjusted familiarity*	*Cluster*
oak	0.15	1
moss	-0.01	1
pine	-0.42	1
redwood	-0.62	1
cattail	-0.72	1
fern	-0.77	1
birch	-0.95	1
spider	0.94	2
grasshopper	0.60	2
bat	-0.14	2
raccoon	-0.16	2
yellowjacket	-0.22	2
garter snake	-0.45	2
toad	-0.58	2
rattlesnake	-1.04	2
vole	-2.41	2
deer	1.88	3
squirrel	1.28	3
hummingbird	0.95	3
bumblebee	0.92	3
cardinal	0.74	3
eagle	0.72	3
owl	0.60	3
bluejay	0.51	3
mountain lion	0.27	3
woodpecker	0.23	3
lady bug	0.21	3
bear	0.20	3
fox	0.10	3
dragonfly	0.07	3
crow	-0.05	3
lizard	-0.92	3
salamander	-0.93	3

Table 4.2. Organism characteristics for study 1. Left-hand column lists 20 characteristics, right-hand column lists corresponding measurement item, using crows as an example. Items were identical for all organisms except for the organism name.

Organism characteristic measured	*Item*
Perceived familiarity with organism	I am familiar with crows
Perceived economic value	Crows are good for the economy
Perceived ecological value	Crows are good for the ecosystem
Perceived cultural importance	Crows are culturally important
Perceived nuisance	Crows are a nuisance
Perceived harmfulness to humans	Crows are harmful to humans
Perceived intelligence	Crows are intelligent
Perceived capacity to suffer	Crows can experience pain and suffering
Perceived capacity to experience pleasure	Crows can experience pleasure and enjoyment
Perceived capacity to make own decisions	Crows can make their own decisions
Perceived cooperativeness	Crows cooperate with each other
Perceived wildness	Crows are wild
Perceived beauty	Crows are beautiful
Perceived charisma	Crows are charismatic
Perceived scariness	Crows are scary
Perceived disgustingness	Crows are disgusting
Perceived harmfulness to non-humans	Crows are harmful to other animals and/or plants
Perceived moral considerability	Humans have moral obligations to crows
Perceived mobility	How much space does a crow use in a normal day?
Perceived heterotrophic type	How does a crow obtain its energy?

We randomly assigned each respondent to answer questions about three organisms. We first asked respondents whether they knew the study organism. If they answered yes, we asked them to answer all 20 subsequent questions about that organism (Appendix A). If they answered no, we provided an alternative randomly selected organism. All questions for each study organism were identical except for the name of the organism (Appendix A). To prevent priming effects, we randomized the order in which each respondent saw the 20 questions.

To check whether respondents did in fact know an organism after answering

questions about it, we asked them to identify it from photographs of all study organisms from the same class (mammal, bird, plant, invertebrate, or herptile). We sourced images of study organisms with creative commons licenses permitting unrestricted use on Flickr (www.flickr.com), and credited Flickr users whenever we used their images (Appendix D). We began with 2994 completed sets of questions, three from each respondent. To ensure data quality, we removed 583 sets of responses because respondents had failed to identify the organism in question, failed a randomly-inserted attention check, or had taken too short or too long to complete the task (Appendix E). Our final data set contained a total of 2414 completed sets of responses, an average of 73 for each study organism (min=42, max=99).

We checked for correlations between all 20 characteristics (Appendix A) across all 33 study organisms. Respondents' perceptions of organisms' capacity to experience pain and suffering was strongly positively correlated with their perceptions of organisms' capacity to experience pleasure and enjoyment ($r = 0.794$, Appendix A), much higher than the correlation coefficient for any other pair. We removed perceived capacity to experience pain and suffering because it had the lower variance of the two. We used the kmeans function in R Studio to conduct a 3-means cluster analysis on the remaining 19 variables to separate study organisms into three clusters of organisms with similar characteristics.

We created a "scaled adjusted familiarity" index for all 33 organisms (Table 4.1). This index equally combines the number of completed sets of questions about that organism in our final data set with the mean value of how familiar respondents reported themselves to be with that organism. Scaled adjusted familiarity values

greater than 0 indicate that the organism is more familiar than average, values less than 0 indicate that the organism is less familiar than average (mean = 0, maximum = 1.88, minimum = -0.241). We selected the organism in each cluster with the highest standardized adjusted familiarity score (Table 4.1) as the representative organism from that cluster: oak, spider, and deer. Each representative organism had a positive adjusted familiarity value (oak 0.15, spider 0.94, deer 1.88), indicating that respondents were more familiar with these organisms than most other study organisms.

Study 2: Moral attitudes about wildlife ownership

We measured respondents' moral attitudes about wildlife ownership using experimental vignettes (Atzmüller & Steiner, 2010). Each vignette combined a short description of a realistic hypothetical scenario involving wildlife with a normative statement proposing one possible ownership type (Figure 4.1). In these vignettes we manipulated four experimental factors: location (public or private land); organism (oak, spider, or deer); specific ownership right or responsibility (obligation to conserve, right to kill, and right to transfer); and ownership type (individual ownership, government ownership, and non-ownership). This 2x3x3x3 design generated a total of 54 possible combinations (Figure 4.1 and Appendix B). We constructed a unique vignette for each of these 54 combinations to produce a full factorial, between-subjects design. Each vignette consisted of a short scenario describing organisms on either public or private land, and a statement proposing that either an individual, government, or no one should have either an obligation to

conserve, a right to kill, or a right to transfer (defined as collect and sell) the organisms in that location (Figure 4.1).

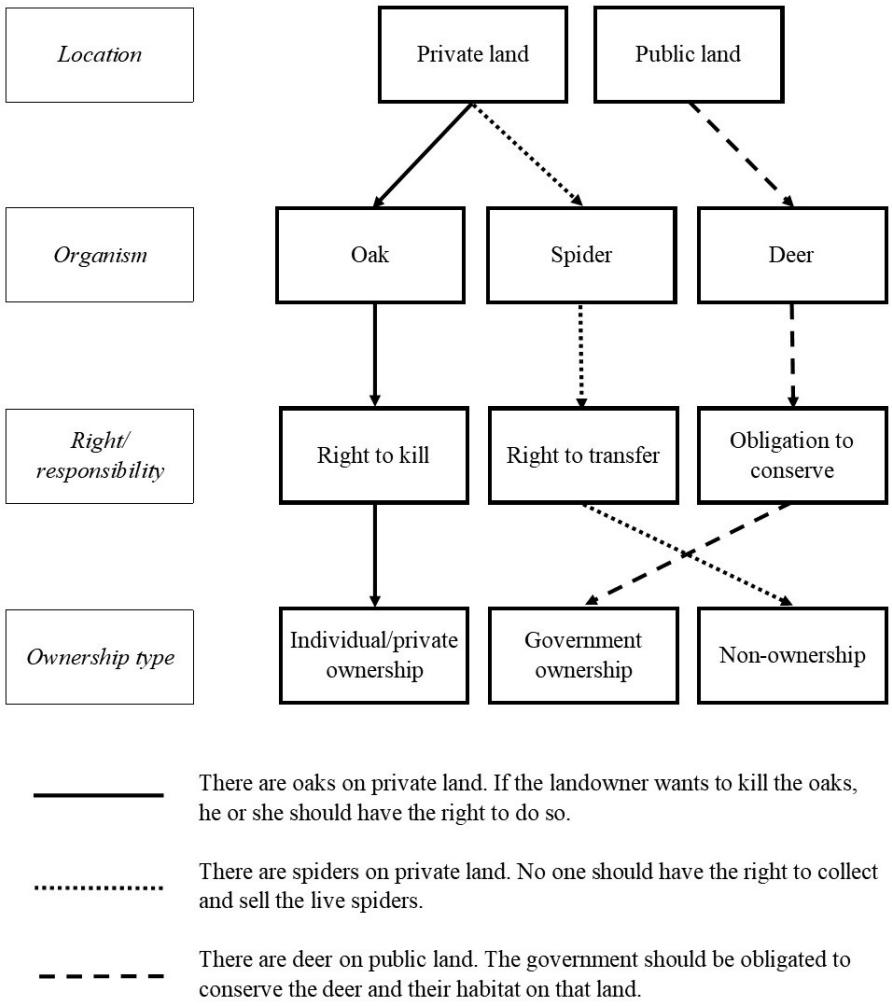

Figure 4.1. Factors and levels for all 54 factor combinations and vignettes in study 2. Solid, broken, and dotted lines show three sample combinations, with corresponding vignettes.

We used the design of experiments function in JMP Pro version 13.1.0 to randomly organize these 54 vignettes into nine sets of six. We randomly assigned each respondent to one of the nine sets of vignettes and measured their moral attitudes

about wildlife ownership as degree of agreement with the normative statement in each vignette using seven-point Likert scales (strongly agree – strongly disagree, with the additional option of "I don't know"). To prevent priming or anchoring effects, we randomized the order of vignettes within sets. We began with 7500 responses to vignettes, six from each respondent. We removed 454 responses because respondents had failed to identify the organism in question, failed an attention check, or had taken too short or too long to complete the task, or did not complete the task at all (Appendix E). Our final data set contained 6044 responses, an average of 111 for each vignette (min=90, max=130, Appendix B).

We fitted a linear mixed effects model using the lmer function from the lme4 package in RStudio. We included main, two-way, and three-way interaction effects of our experimental variables: location, organism, and right or responsibility of ownership, and a random effect of respondent to account for the same individuals responding to multiple vignettes. Because no demographic variables were strongly correlated and their generalized variance inflation factors were all low (<1.5), we included them as main effects. We used analysis of variance (ANOVA) to quantify all main and interaction effects on people's support for individual, government, or non-ownership of wildlife across all experimental combinations.

Results

Study 1

Cluster 1 consisted of all the plants and no other organisms. Cluster 2 consisted of animals that respondents tended to perceive as worse for the economy, scarier, more

of a nuisance, more harmful to humans, less intelligent, less charismatic, less worthy of moral consideration, and using less space in a normal day. Cluster 3 consisted of animals that respondents tended to perceive as better for the economy, less scary, less of a nuisance, less harmful to humans, more intelligent, more charismatic, more worthy of moral consideration, and using more space in a normal day (Table 4.3). In general terms, we might think of these clusters as "plants," "nasty animals," and "nice animals," respectively.

Table 4.3. Cluster means for all 19 organism characteristics in cluster analysis. Values for each cluster represent averages across all organisms in that cluster.

Organism characteristic	***Cluster 1***	***Cluster 2***	***Cluster 3***
Familiar	5.65	5.57	5.79
Good for economy	4.64	3.72	4.23
Good for ecosystem	6.14	5.51	5.88
Culturally important	4.81	4.13	4.93
Nuisance	2.22	4.29	2.98
Harmful to humans	1.88	3.59	2.64
Intelligent	2.34	4.53	5.22
Experience pleasure	2.43	4.84	5.51
Make decisions	2.21	5.20	5.57
Cooperate	3.02	4.80	5.14
Wild	5.73	6.17	6.17
Beautiful	5.81	4.05	5.77
Charismatic	2.78	3.24	4.41
Scary	1.62	3.78	2.76
Disgusting	1.76	3.45	2.08
Harmful to animals and plants	2.20	3.99	3.34
Moral obligations	4.29	3.95	4.72
Movement	1.29	3.18	3.98
Heterotrophic level	1.08	3.84	3.70

Study 2

Respondents' moral attitudes about individual, government, and non-ownership of wildlife depended on each of our experimental factors (Table 4.4). Respondents agreed that in certain circumstances people should have the right to kill, the right to transfer (collect and sell), and the obligation to conserve wildlife (Figure 4.2). However, exactly who should have these rights and responsibilities varied according to the organism in question as well as whether that organism is on public or private land (Table 4.4, Figure 4.2).

Table 4.4. Type III analysis of variance for linear mixed effects model of moral attitudes towards wildlife ownership. "Stick" is shorthand for right or responsibility. Significance codes: *** p < 0.0001, ** p < 0.001, * p < 0.05 at 95% confidence level.

	Sum Sq	***Mean Sq***	***NumDF***	***DenDF***	***F value***	***Pr(>F)***	
Location	2.41	2.41	1	5944.9	0.819	0.365516	
Stick	111.09	55.55	2	5766.6	18.9034	6.56E-09	***
Organism	4.52	2.26	2	5924.7	0.7689	0.46359	
Owntype	281.85	140.93	2	5872.1	47.9604	< 2.2e-16	***
Sex	11.21	11.21	1	962.5	3.8167	0.051032	
Age	59.16	4.23	14	958.3	1.4381	0.128586	
Education	51.39	12.85	4	963	4.3722	0.001653	**
Income	38.8	4.31	9	965.7	1.4671	0.15543	
Acres_home	8.63	4.32	2	956.2	1.4689	0.23069	
Acres_own	40.34	13.45	3	958.9	4.5757	0.003443	**
Rural_current	24.26	4.04	6	961.6	1.3762	0.221095	
Rural_past	41.29	5.9	7	960.1	2.0072	0.051452	
Politics	49.23	7.03	7	960.8	2.3935	0.019775	*
Location:Stick	66.87	33.44	2	5611	11.3795	1.17E-05	***
Location:Organism	14.05	7.02	2	5836.9	2.3907	0.091659	
Location:Owntype	856.94	428.47	2	4953.7	145.8186	< 2.2e-16	***
Stick:Organism	73.71	18.43	4	5103	6.2711	4.97E-05	***
Stick:Owntype	938.94	234.74	4	5588.6	79.8862	< 2.2e-16	***
Organism:Owntype	134.86	33.72	4	5775.2	11.4742	2.81E-09	***
Location:stick: Organism	3.05	0.76	4	5727.5	0.2594	0.904031	
Location:Stick: Owntype	413.21	103.3	4	5314.6	35.1565	< 2.2e-16	***
Location:Organism :Owntype	118.65	29.66	4	5489.5	10.0953	3.86E-08	***
Stick:Organism: Owntype	1025.86	128.23	8	5748.9	43.6406	< 2.2e-16	***

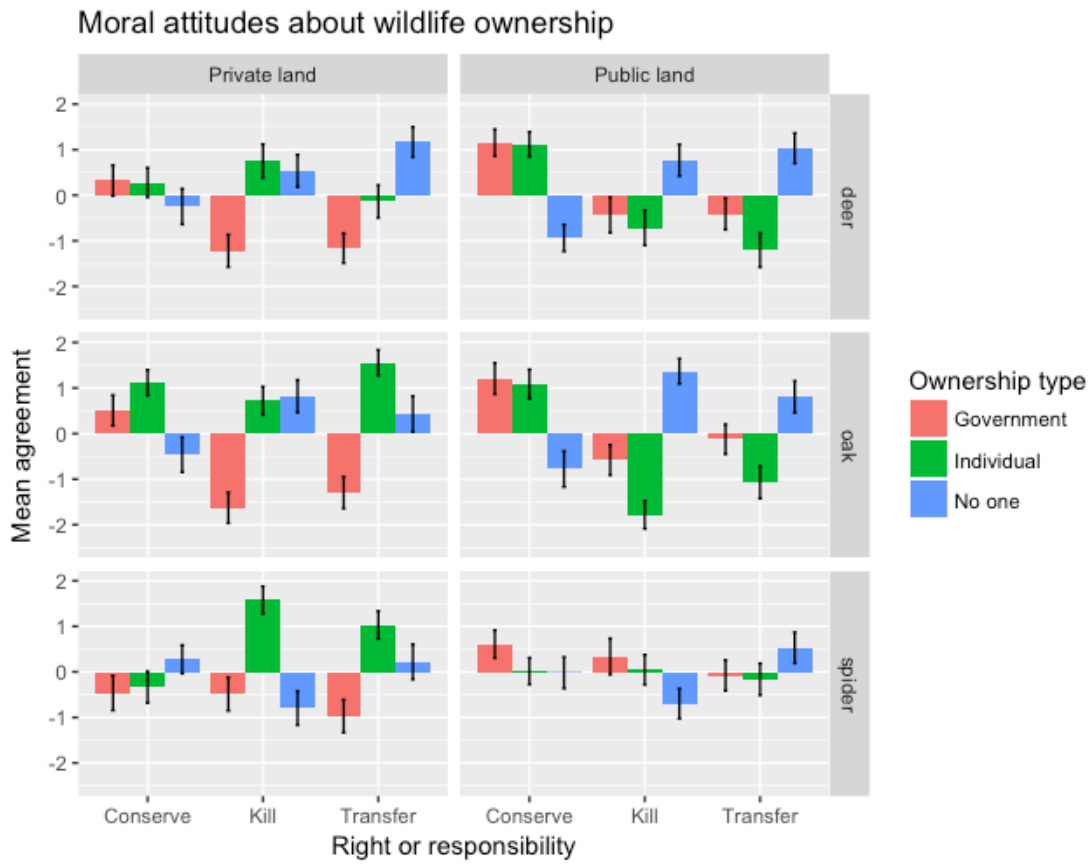

Figure 4.2. Support for government, individual, and non-ownership of wildlife across all experimental conditions. Each bar corresponds with a single combination of experimental factors. Bar height indicates agreement with the moral statement about wildlife ownership in the corresponding vignette. Positive values indicate agreement, negative values indicate disagreement, and neutral values indicate indifference (neither agreement nor disagreement). Data are means ± 95% CI.

Respondents generally agreed that individuals should own wildlife on their land (private ownership). Individual landowners should have a right to kill all three representative organisms, the right to transfer oaks and spiders, and an obligation to conserve oaks and deer (but not spiders) on their land (Figure 4.2). Government should have an obligation to conserve all three organisms on public land. However, government should not have a right to transfer any of the three organisms from public

land, or a right to kill oaks and deer on private land. No one should have a right to kill oaks or deer on public land. Government should have an obligation to conserve all three organisms on public land, as well as oaks and deer on private land. Individual members of the public also have an obligation to conserve oaks and deer on public land. Support for non-ownership did not correspond with organisms that were perceived as more intelligent, more capable of experiencing pleasure, more capable of making decisions, or more wide-ranging: in certain conditions, support for non-ownership of oaks was stronger than for spiders and deer (Figure 4.2).

Respondents across the political spectrum agreed that who owns land should also own the wildlife on that land (private individuals on private land, and government on public land), although their attitudes were markedly stronger for private land (Figure 4.3). Respondents with less formal education were both more supportive of individual ownership and more opposed to government ownership of wildlife on private land than respondents with more formal education (Figure 4.4). Respondents who owned more land were more supportive of individual ownership on private land (Figure 4.5). We found no effect of respondents' age, sex, or whether they grew up or currently live rurally on their moral attitudes towards wildlife ownership (Table 4.4).

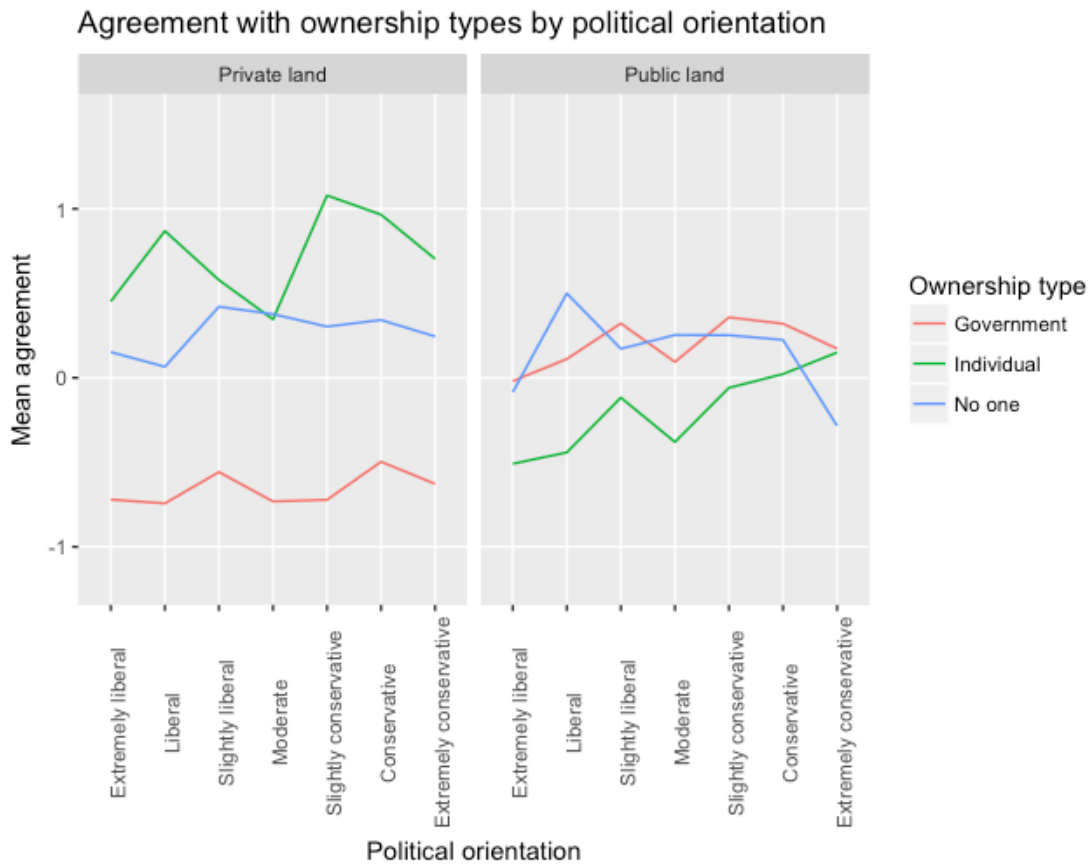

Figure 4.3. Mean agreement with each ownership type on public and private land by political orientation. Line heights show mean agreement with moral statements proposing each ownership type, averaged across all levels of organism and right or responsibility. Positive values indicate agreement, negative values indicate disagreement, and neutral values indicate indifference (neither agreement nor disagreement).

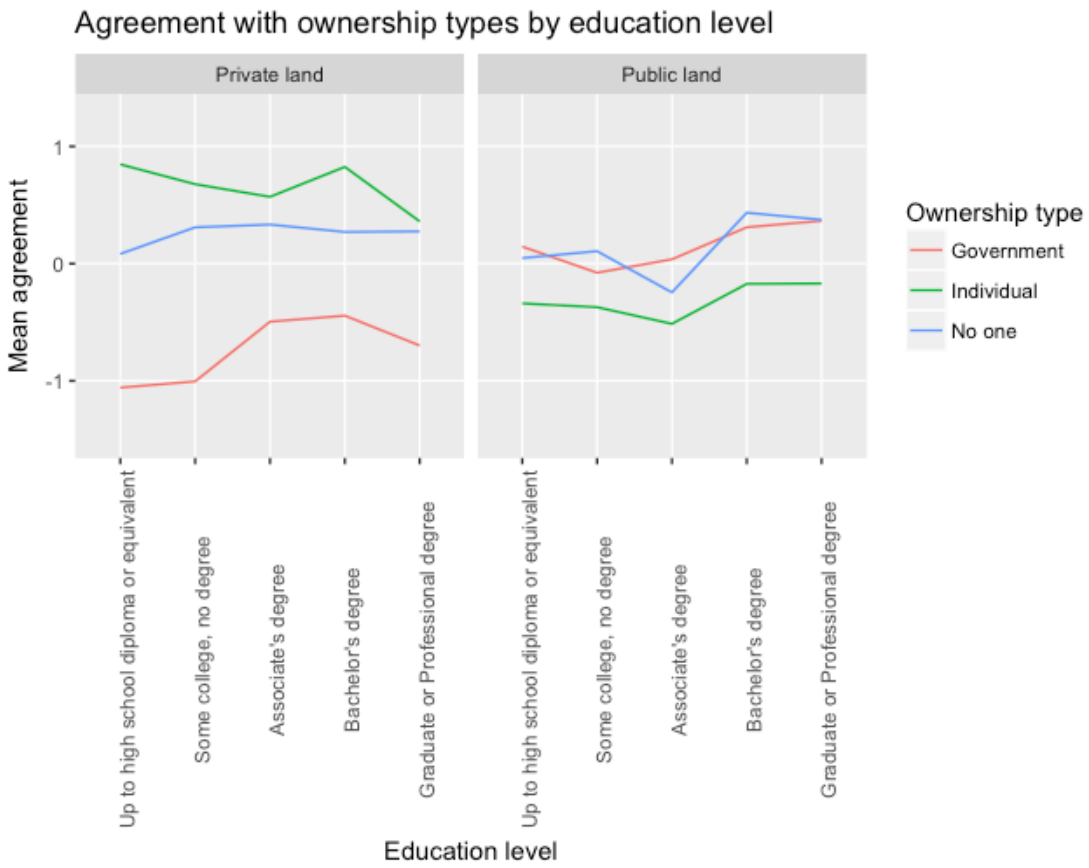

Figure 4.4. Mean agreement with each ownership type on public and private land by education level. Line heights show mean agreement with moral statements proposing each ownership type, averaged across all levels of organism and right or responsibility. Positive values indicate agreement, negative values indicate disagreement, and neutral values indicate indifference (neither agreement nor disagreement).

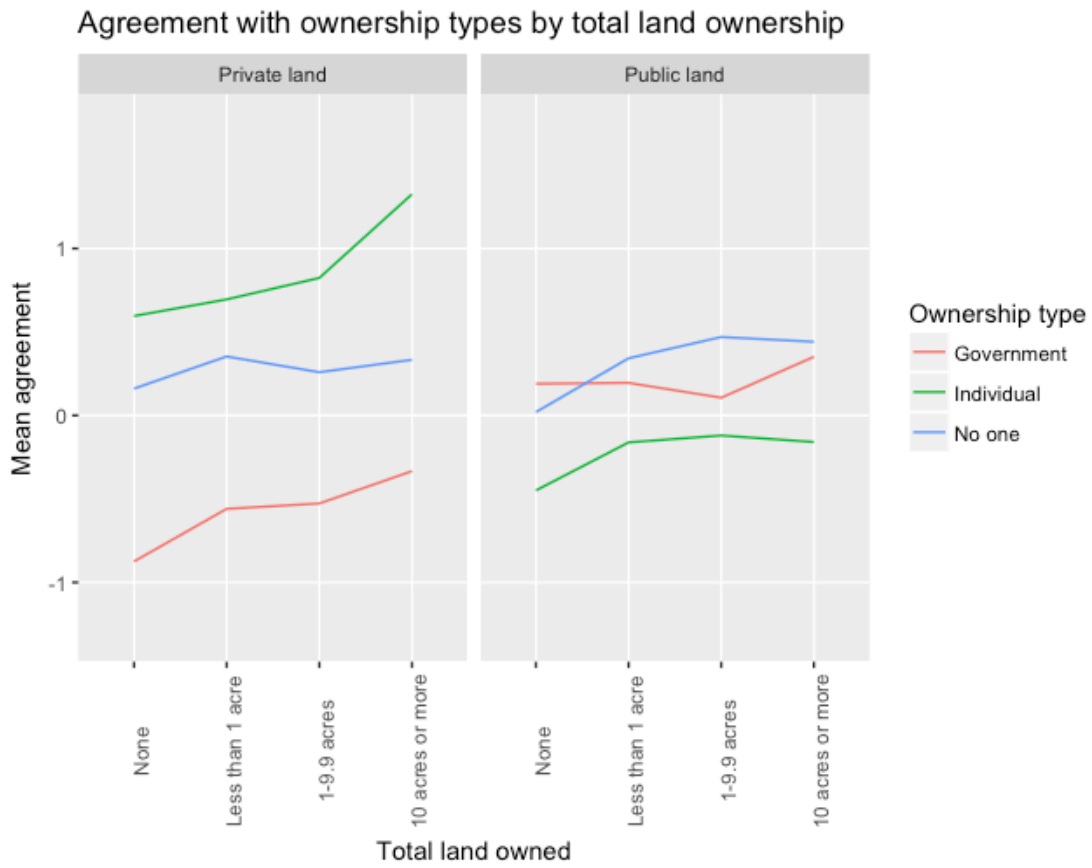

Figure 4.5. Mean agreement with each wildlife ownership type on public and private land as a function of total amount of land owned. Line heights show mean agreement with moral statements proposing each ownership type, averaged across all levels of organism and right or responsibility. Positive values indicate agreement, negative values indicate disagreement, and neutral values indicate indifference (neither agreement nor disagreement).

Discussion

Adults living in the U.S. think in nuanced ways about different wild organisms, and this contributes to their moral attitudes about who, if anyone, should own those organisms. Respondents agreed that both individuals and government should have obligations to conserve wild organisms on both public and private land. In certain circumstances, individuals and government should have a right to kill or transfer wild organisms, but in other circumstances no one should have those rights.

Respondents' moral attitudes reflect complexities of real-world ownership systems, in which rights and responsibilities are context-dependent and can be distributed among various individuals and organizations (Carruthers & Ariovich, 2004; Geisler & Daneker, 2000). However, respondents' moral attitudes sometimes do not correspond with existing legal ownership designations in the U.S.

Patterns in our results reveal considerable moral disagreement about who should have rights and responsibilities with regard to wildlife, for example whether landowners should have a right to kill spiders or deer on their land, or whether anyone should have an obligation to conserve spiders or oaks on public land. Moral disagreement is evident in differences in mean responses to the ownership proposition in each vignette (Figure 4.2). These differences exist because moral attitudes about different types of wildlife ownership depend on location, right or responsibility, and organism as well as interactions between them. Substantial variance around means indicates disagreement between respondents about who should own wildlife in specific scenarios. These forms of disagreement could contribute to moral contestation regarding wildlife conservation and governance in the U.S. (Dietsch et al., 2016; Lute & Attari, 2017; Manfredo et al., 2017; Peterson et al., 2016).

In study 1 our analysis assigned deer, oaks, and spiders to different clusters, indicating differences in how people perceive those organisms (Table 4.2). Nevertheless, in study 2 respondents' attitudes towards deer and oak were strikingly similar across almost all combinations of location and right or responsibility (Figure 4.2). But for some reason respondents' attitudes towards spiders are different. Respondents agreed that both individuals and government should have an obligation to

conserve oaks and deer on private and, especially, public land. However, they were largely indifferent about rights and responsibilities regarding to spiders on public land, and agreed that no one should have an obligation to conserve them on private land. Similarities in respondents' attitudes towards deer and oaks are especially intriguing given taxonomic (a mammal and a plant) and ecological (how they obtain energy, how far they move) differences.

We emphasize that our results in study 2 only apply to deer, oaks, and spiders, not to other organisms in their respective clusters. It is an open question whether other organisms from the same clusters would have elicited identical responses. For example we would expect people not to have identical moral attitudes about owning organisms as diverse as toads, raccoons, or grasshoppers (all of which are "nasty animals", cluster 2), as they have about owning spiders. However, we would expect that moral attitudes would be more similar for organisms from the same cluster than for organisms from different clusters.

Patterns in our results from study 2 contradict legal ownership designations in the U.S., where on private land oaks belong to the landowner, deer do not, and spiders are mostly unregulated so are owned by no one (Cahoon, 2001; Freyfogle & Goble, 2009). These legal ownership designations may have arisen due to differences in how far organisms move, with private property rights in static organisms but not wide-ranging organisms being more economically efficient (Lueck, 1995). However, our results show that an organism's mobility alone does not determine moral attitudes about who should own it. If that were true, we would expect moral attitudes about owning oaks to be similar to moral attitudes about owning spiders because neither

moves far compared to deer. Instead we found consistent similarities in moral attitudes about owning oaks (which are static) and deer (which are more wide-ranging).

Where organisms reside had a strong effect on moral attitudes towards ownership of wild organisms (Figures 2-5). Importantly, our results reveal agreement that whoever owns the land should have rights and responsibilities regarding wildlife on that land. This is especially noticeable in relation to the right to kill organisms: individuals should have the right to kill all three organisms on their own land, but not on public land. This again contradicts legal arrangements, for example the U.S. Supreme Court's influential pronouncement that it is "well settled that wild animals are not the private property of those whose land they occupy" (*Geer v Connecticut*, 1896).

However, our results reveal that people disagree that government should have corresponding rights to kill organisms on public land – in fact, no one should have the right to kill oaks or deer on public land (Figure 4.2). This surprising and potentially controversial finding implies that many common activities in public forestry and wildlife management appear morally unacceptable. However, this finding might reflect that our vignettes were not detailed enough to capture nuances in people's moral attitudes about this particular aspect of wildlife ownership. Future studies could investigate whether this finding remains robust in more refined hypothetical scenarios. For example, more detailed experimental vignettes could manipulate alternative reasons why government proposes to kill organisms on public land (e.g. for timber production, habitat provision, or to benefit other species), or who specifically is allowed to kill those organisms (e.g. SFWA officials, members of the public with

hunting licenses, or private companies contracted by government agencies). Vignettes that describe such activities using less provocative words than "kill", for example "harvest", might elicit less moral opposition.

We were not surprised to find strong moral opposition to government rights on private land (Hoffman, 2018; Raymond & Olive, 2008). However, we were surprised to find general apathy or even antipathy towards government rights on public land. If this finding does hold after further investigation, it could provide new insights into why public wildlife management projects that involve killing wildlife on public land, for example lethal control of ungulates (Vernon & Clark, 2016), predators (Olson et al., 2015), and many other species (Bergstrom et al., 2014), often provoke moral opposition. Such opposition might stem not only from concern about animal welfare or killing *per se*, but because it violates a moral belief that no people should have the right to kill certain organisms on public land. Identifying characteristics that make it more or less acceptable to kill particular organism on public land would illuminate additional nuances in people's moral attitudes about wildlife.

In some scenarios, respondents morally objected to treating wildlife as property (Francione, 2015; Leopold, 1949). However, agreement that no one should own a wild organism did not depend on any perceived characteristics of the organism, such as wildness (Peterson et al., 2016), space use, moral considerability, cognitive or intellectual capacities (Donaldson & Kymlicka, 2011), or ability to make its own decisions (Starmans & Friedman, 2016). Instead, agreement depended on the specific combination of where the organism is and the right or responsibility under consideration.

Peterson et al. (2011) found that people living along the Texas-Mexico border who own more land were more likely to support private ownership of wildlife on private land (Figure 4.5). Similarly, study 2 respondents who owned more land were also more likely to favor private ownership of wildlife (individual ownership on private land), suggesting that this relationship applies beyond Peterson et al.'s specific geographical focus. However, this finding did not generalize to respondents who lived on larger parcels of land but did not own them. This may be because people who own more land may especially able to profit from privatized wildlife (Peterson et al., 2011) or wildlife-related activities on their property (Macaulay, 2016). It might also indicate that, because land ownership brings increased taxes and liability, owners of larger amounts of land believe they should have commensurate entitlements or privileges in relation to wild organisms on their land. However, unlike Peterson et al. (2011), we found no effect of whether respondents grew up or currently live rurally on their moral attitudes about wildlife ownership (Table 4.4).

We asked a non-representative sample of the adult U.S. population about wildlife ownership in hypothetical scenarios, so our findings are not fine-grained enough to guide specific wildlife policies or programs. However, our results suggest that wildlife governance reforms based purely on expanded government authority or restrictions on landowner autonomy are likely to be morally unacceptable. At first glance this may call into question public wildlife agencies' ability to meet contemporary needs to conserve wildlife on private land (Jenkins et al., 2015). However, public agencies have many options for influencing conservation on private land that do not necessarily constrain landowners' autonomy (Kamal, Grodzińska-

Jurczak, & Brown, 2015). Some recent proposals for wildlife governance reform highlight the potential for public wildlife agencies to partner with private landowners (Decker et al., 2016; Kretser, Glennon, & Smith, 2014; Lauber, Connelly, Niederdeppe, & Knuth, 2014). Partnerships that appeal to private landowners' moral responsibilities to conserve wildlife on their land could be more morally acceptable, and therefore more legitimate (Beetham, 1991; Boyer & Petersen, 2012; Hare et al., 2017) than claims of government authority to conserve wildlife on private land.

Respondents agreed that someone should have an obligation to conserve wild organisms in every scenario except those concerning spiders on private land. This suggests that respondents generally endorse a conservation ethic that prioritizes organisms they perceive to be better for people and ecosystems (plants and "nice animals", Table 4.3) (Hare, Blossey, & Reeve, 2018). Respondents disagreed about who should conserve wild organisms and where, not whether anyone should conserve them. Conservation approaches that resonate with people's moral attitudes could channel this moral support for conservation into outcomes that address biodiversity decline and are more socially acceptable.

Conclusion

Our results reveal nuanced patterns in people's moral attitudes about wildlife ownership, which might contribute to moral contestation over wildlife conservation in the U.S. A more detailed understanding of people's moral attitudes about wildlife ownership could illuminate the moral acceptability of alternative approaches to wildlife conservation and governance, and so help identify approaches that will be

more – or less – likely to succeed.

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CHAPTER 5

EVOLUTIONARY ROUTES TO STABLE OWNERSHIP[3]

Abstract

Ownership can evolve in potentially any species. Drawing on insights from across disciplines, we distinguish between possession and ownership and present species-neutral criteria for ownership, defined as respect for possession. We use a variant of the tug-of-war evolutionary game to demonstrate how ownership can evolve in the form of a new, biologically realistic strategy, Restraint With Retaliation (RWR). In our game, resource holding potential (RHP) is assumed to be equal between interactants, and resource holding asymmetry determines whether ownership is adaptive. RWR will be evolutionarily stable when the ratio of resource holdings between interactants is relatively low, but not when this ratio is sufficiently high. We offer RWR as one evolutionary route to ownership among many, and discuss how ownership unites previously described behavioural phenomena across taxa. We propose that some but not all mechanisms of territory formation and maintenance can be considered ownership, and show that territories are not the only resources that can be owned. We argue that ownership can be a powerful cooperative solution to tragedies of the commons and problems of collective action throughout the biological world. We advance recent scholarship that has begun to investigate the biological importance of ownership, and we call for a comprehensive account of its evolutionary

[3] Hare, D., Reeve, H. K., & Blossey, B. (2016). Evolutionary routes to stable ownership. *Journal of Evolutionary Biology*, *29*(6), 1178–1188.

logic and taxonomic distribution. We propose that ownership should be considered a fundamental, unifying biological phenomenon.

Introduction

Possession and ownership are intimately connected, but they are crucially different. Separating these two concepts is of fundamental importance in understanding social relations concerning the partitioning of resources among humans (Ellis, 1985; Macpherson, 1978; Rose, 1985) and, we propose, individuals of potentially any species. Possession describes a relationship between an individual and a resource. For example, an individual might possess a space by occupying it or a food item by holding it. Ownership, on the other hand, describes a relationship between individuals with regard to a resource (Carruthers & Ariovich, 2004; Macpherson, 1978; Stake, 2004). For example, an individual will own space or a food item only when potential competitors respect its possession. Ownership therefore emerges from interactions that satisfy the following criteria:

1. A possesses a resource
2. B respects A's possession of that resource.

Ownership is a widespread and possibly universal human phenomenon (Brown, 1991; Carruthers & Ariovich, 2004; Ellis, 1985) that varies along multiple axes such as types of things that can be owned, entities that can be owners, and rules and norms that pertain to ownership (Carruthers & Ariovich, 2004; Cole, 2002; Cole & Ostrom, 2012; Ostrom, 1990). The pervasiveness of human ownership suggests an evolutionary basis: ownership – respect for a potential competitor's possession of a

resource – can be adaptive. A reasonable candidate for the evolutionary value of ownership is directly and indirectly increasing fitness by reducing conflict over resources (Russ, Comins, Smith, & Hauser, 2010; Stake, 2004). Ownership therefore lies on a continuum between competition and cooperation and as such is amenable to analysis from a game-theoretic perspective (Bowles & Choi, 2013; Gintis, 2007; Sherratt & Mesterton-Gibbons, 2015).

In human societies, ownership is a collective agreement that can reduce conflict, maximize individual and group benefits and prevent tragedies of the commons (Hardin, 1968; Ostrom, 1990). Because humans are not alone in encountering problems of collective action or potential tragedies of the commons (Dionisio & Gordo, 2006; Gersani & O'Brien, 2001; Levin, 2014; Rankin, Bargum, & Kokko, 2007), it would be surprising to find that ownership is an exclusively human behaviour. Although the acquisition and division of resources has been the subject of extensive biological investigation, the relational nature of ownership, differentiated from mere possession, is underappreciated in biology. This is remarkable given the attention that evolutionary biologists have paid to cooperation generally (Axelrod & Hamilton, 1981; Dudley, 2015; Nowak, 2006; Sachs, Mueller, Wilcox, & Bull, 2004; West, Griffin, & Gardner, 2007), and the importance of ownership in reducing conflict, averting tragedies of the commons and securing public goods among humans (Cole, 2002; Hardin, 1968; Ostrom, 1990). Recent contributions have signalled the potential evolutionary importance of ownership throughout the biological world and stress the need for closer examination of respect for possession among nonhumans (Sherratt & Mesterton-Gibbons, 2015; Strassmann & Queller, 2014). These insights

have advanced the discourse on nonhuman ownership beyond conceptual and exploratory contributions (Archer, 1986; Boehm, 2004; Brosnan, 2011; Ellis, 1985; Fredlund, 1976; Gintis, 2007; Stake, 2004) and limited experimental studies (Kummer & Cords, 1991; Russ et al., 2010; Sigg & Falett, 1985). The possibility that ownership is a widespread behavioural strategy is worthy of focused investigation.

A number of established behavioural phenomena satisfy our criteria for ownership. An early and still influential model of ownership is the Bourgeois strategy (Maynard Smith, 1982), in which possessors of a resource escalate aggression against intruders, which in turn flee from aggressive possessors, thereby respecting possession. (Note that we refer to 'possessors' instead of the typical designation of 'owners', because ownership, in our restricted definition, emerges only when potential competitors respect possession. The standard designation of 'ownership' (Maynard Smith, 1982) in behavioural ecology often conflates ownership and possession.) Extensions of Bourgeois are also evolutionarily stable under more complex conditions and when additional alternative strategies are available (Sherratt & Mesterton-Gibbons, 2015). Other behaviours that satisfy our criteria for ownership emerge from various types of territorial interactions. Examples include the dear enemy phenomenon (Fisher, 1954), winner and loser effects (Morrell & Kokko, 2003), learning through repeated contests or negotiations (Stamps & Krishnan, 2001; Switzer, Stamps, & Mangel, 2001), fighting ability (Morrell & Kokko, 2003; Pereira, Bergman, & Roughgarden, 2003) and value asymmetry (Gintis, 2007).

Using a previously unexamined set of theoretical conditions, we present an additional route by which ownership can evolve and remain stable. We use a variant of

the tug-of-war evolutionary game (Reeve, Emlen, & Keller, 1998) and show that purely selfish strategies lead to unfavourable fitness pay-offs and a tragedy of the commons (Rankin et al., 2007). Beginning with asymmetry in resource holdings between interactants of equal resource holding potential (RHP) (Parker, 1974), we analyse the conditions under which an individual can be expected to raid (i.e. compete for the resources another possesses) or not to raid (i.e. respect the other's possession of those resources). We describe the conditions under which ownership – defined as mutual respect for possession between interactants, manifested in decisions not to raid – will emerge, persist and break down. Restraint With Retaliation (RWR), a conditionally cooperative strategy that satisfies our criteria for ownership, emerges as an evolutionarily stable strategy (ESS) in games with any number of interactants. Importantly, in our raiding game, it is the ratio of resources held by interactants that determines whether ownership will be favoured, not differences in RHP, because we assume this to be equal.

Our model complements and expands upon existing models of how potential competitors partition contestable resources. It offers a biologically realistic yet straightforward process by which ownership will evolve. We discuss how a relational understanding of ownership, although not widely acknowledged among nonhumans, unites a range of established behaviours across taxa. We strengthen and deepen emerging scholarship that has begun to explore the biological significance of ownership, and discuss some implications of considering ownership a fundamental biological phenomenon.

Model

Our raiding game follows Dugatkin & Reeve's (2014) tug-of-war framework. In a tug-of-war game, interactants choose how much to invest in competition, at some other fitness expense, with outcomes depending on relative instead of absolute magnitudes of investments. We assume that there are pairwise interactions in which each interactant can choose whether to raid a divisible resource possessed by the other. Each individual is assumed to have evolved the flexible abilities to assess the value of the resource possessed by the other and to behave in ways that maximize its expected pay-off at the end of interactions. Suppose individual 1, who possesses a resource of value v_1, is raided by individual 2, who possesses a resource of value v_2. We assume that individual 1 will attempt to mount an optimal level of resistance x to counter the observed raiding effort y of individual 2 in a sequential game. We make the realistic assumption that individuals will adaptively choose their investments in raiding and resistance efforts rather than pay fixed costs for these efforts, responding to Hinsch & Komdeur's (2010) call for more mechanistically realistic and explicit models of resource partitioning. Raiding and resistance efforts determine the costs paid by individuals, and these costs are deducted from the resource obtained or defended, thereby reducing its net value. This framework applies to interactions between individuals who each possess some amount of the contested resource (possessor–possessor interactions) as well as interactions in which one individual possesses none (possessor–intruder interactions). Our model can accommodate the case in which $v_2 = 0$, that is interactions in which individual 2 arrives at a resource currently possessed by individual 1 and holds no prior resource of its own.

We always assume that interactants are of matched competitive ability (RHP), so as to rule out explanations of respect for possession due to competitive asymmetries between the interactants, as in other models such as those offered by Pereira et al. (2003), Morrell & Kokko (2003) and Hinsch & Komdeur (2010). For convenience, we assume that ecological and/or timing constraints allow only one raiding initiation for each individual, so as to rule out conventional tit-for-tat-like solutions for the maintenance of respect for possession.

Using tug-of-war theory, the pay-offs w_1 and w_2 to individuals 1 and 2, respectively, after individual 2 attempts to raid individual 1, can be written as

$$w_1 = \left(\frac{x}{y+x}\right) v_1 - x$$

$$w_2 = \left(\frac{y}{y+x}\right) v_1 - y + v_2 \qquad (1)$$

Because the interaction is sequential, we first solve for the optimal resistance effort of individual 1, using $\partial w_1/\partial x = 0$, which reveals a single fitness maximum at $x^* = (v_1 y)^{1/2} - y$. The optimal resistance response $x^*$is then substituted into the raider's pay-off w_2, and we solve $\partial w_2/\partial x = 0$, which reveals a single fitness maximum for the raiding effort at $y^* = v_1/4$. Substituting the latter value for the previous expression for x^* yields an optimal resistance effort of $x^* = v_1/4$. These solutions predict that the fraction of disputed resource gained by a raider will, on average, be ½. This is what we would expect given our assumption that interactants are competitively equal.

Thus, each time a raid takes place, the optimal raiding effort and the optimal

resistance effort are the same and equal to $v_1/4$. For these optimal raiding and resistance efforts, the net pay-off to the raider is $v_1/4 + v_2$ and the net pay-off to the raided individual is $v_1/4$.

Now we are in a position to examine the net payoffs for varying rules for raiding versus respect for possession. First, we consider the individual pay-offs in a population in which everyone engages in raiding (one raid allowed per interactant), corresponding to a rule of no respect for possession. We assume a pair of individuals with the same resource holdings as above. Each party will do better if it is the first raider, but we assume no asymmetry in the ability to initiate the first raid. Thus, there is a probability ½ that individual 1 will raid individual 2 first and a probability ½ that the reverse will occur. If individual 1 raids first, it follows from the optimal raiding and resistance models above that, after the first raid, individual 1 gets the net pay-off $v_2/4 + v_1$ and individual 2 gets the net pay-off $v_2/4$. Then, upon the subsequent raid of individual 1 by individual 2, individual 1 gets the final net pay-off $(1/16)(4v_1 + v_2)$ $[= (1/4)(v_2/4 + v_1)]$ and individual 2 gets the final net pay-off $(1/16)(4v_1 + 5v_2)$ $[= (1/4)(v_2/4 + v_1) + v_2/4]$.

Had individual 2 initiated the first raid instead of individual 1, it follows from symmetry that individual 1 would have received the final net pay-off $(1/16)(4v_2 + 5v_1)$ and individual 2 would have received the final net pay-off $(1/16)(4v_2 + v_1)$. The overall expected net pay-off to individual 1 over both the above possible cases is thus $(1/2)[(1/16)(4v_1 + v_2)] + (1/2)[(1/16)(4v_2 + 5v_1)] = (1/32)(9v_1 + 5v_2)$ and that to individual 2 is $(1/2)[(1/16)(4v_1 + 5v_2)] + (1/2)[(1/16)(4v_2 + v_1)] = (1/32)(9v_2 + 5v_1)$.

From these final pay-off expressions, we can conclude that, in a population with no respect for possession, a focal individual with an initial possessed resource v_i will have a higher final average net pay-off after mutual raiding with an interactant with possessed resource v_j only if $v_j > 23v_i/5$, that is only if the adversary's initial resource was more than four times greater in value than the focal individual's resource.

Because the individual with the initially more valuable resource would seek to avoid the cost of mutual raiding, we consider whether it might benefit from a rule of not raiding unless its interactant's resource is of sufficiently greater value than its own. Such a rule, which we call Restraint, would represent a basic strategy of conditional respect for possession. However, if an individual playing Restraint were in a population of unconditional raiders, it would be raided and end up with a net pay-off equal to just $v_1/4$, lower than its net pay-off for having engaged in mutual raiding $(1/32)\ (9v_1 + 5v_2)$, which is necessarily less than $v_1/4$ because $9/32 > 1/4$. Restraint could therefore not spread in a population of unconditional raiders, despite the fact that everyone in such a population receives a much lower pay-off than in a population in which everyone respects possession. This is a prime example of the tragedy of the commons and raises the question: Is there any raiding-restraint rule that could avert a tragedy of the commons and spread in a population of mutual raiders?

We now consider a mutant rule that we name 'Restraint With Retaliation' (RWR). In this rule, the individual with the initially greater resource holding does not initiate a raid unless it has been raided. In a population of unconditional raiders, an RWR rule-player will be raided first, then it will retaliate, ending up with a net pay-off

of $(v_1/4) + (v_1/4 + v_2)/4 = (5/16)\, v_1 + v_2/4$. This pay-off always exceeds the pay-off for randomly initiated mutual raiding $(1/32)\,(9v_1 + 5v_2)$. Respect for possession in the form of RWR yields a higher expected pay-off than outright scramble, so the RWR rule would spread in a population of unconditional raiders.

The question remains, however, whether RWR can be evolutionarily stable when everyone plays it. RWR can in fact become an evolutionarily stable rule if it is modified to include assessment of the value of one's own initial resource relative to that of a neighbour. In a pairwise interaction, suppose that the modified RWR rule adopted by both players is 'Don't raid your neighbour unless its resource is more than twelve times as valuable as your own or unless it raids you'. We can show that this RWR rule is evolutionarily stable. If a rare mutant raider with initial resource v_2 enters a population of RWR rule-players, and its neighbour has initial resource v_1, it will raid and be raided in retaliation, yielding a final net pay-off of $(v_1/4 + v_2)/4$. This pay-off will be higher than its pay-off for not raiding, v_2, only if $v_1/v_2 > 12$. If indeed $v_1/v_2 > 12$, the mutant's pay-off will be exactly the same as for an individual playing the RWR rule, because the RWR strategist will raid and experience retaliation as well. If, on the other hand, $v_1/v_2 < 12$, the mutant raider would receive a smaller final net pay-off than an RWR player in the same situation, because the latter would not raid and receive the higher net pay-off v_2. It follows that a rare mutant unconditional raiding rule could not spread in a population of RWR rule-players.

In a population of RWR rule-players, there will be a complete lack of raiding, and therefore mutual respect for possession, so long as no individual holds resources more than twelve times the value of any other individual. If two individuals' resource

holdings differ more than 12-fold, the individual with the initially smaller resource will raid and experience retaliation by the individual with the initially larger resource. Thus, the RWR rule leads to the stable maintenance of respect for possession whenever interactants' resource holdings are not too asymmetrical in value. When resource holdings are sufficiently asymmetrical, mutual raiding will occur until resource holdings return to a level at which respect for possession will become stable again.

Expanding our asymmetrical tug-of-war model to more than two parties leads to a slightly modified RWR rule. Suppose that there are n equally matched neighbours exhibiting a range of initial resource holdings. We might expect a strong incentive for the one with the smallest resource to raid the one with the largest resource. However, suppose that all others are playing a modified RWR rule in which there is mutual respect for possession unless (i) any neighbour has a resource at least of value k^* times any other's resource (whereupon it is raided) or (ii) if another individual in the group is observed to raid someone else (whereupon the raider is raided). If a rare mutant raider with initial resource v_2 enters a group of such RWR rule-players, and its target has initial resource v_1, it will raid and be raided in retaliation by everyone else (which will benefit each of the RWR rule-players), yielding a final net pay-off of $(v_1/4 + v_2)/4^{n-1}$. This pay-off will be higher than its pay-off for not raiding, v_2, only if $k = v_1/v_2 > k^* = 4^n - 4$. Thus, using the logic developed above, the modified RWR rule will be an ESS and lead to stable mutual respect for possession as long as $k < k^*$ for all group members.

In our model, stable respect for possession does not depend on differences in

fighting ability. RWR is similar to, but not exactly the same as, the classical tit-for-tat strategy that stabilizes cooperation when there are repeated games each described by a Prisoner's Dilemma pay-off matrix. RWR, unlike tit-for-tat, depends critically on retaliation reducing the pay-off for the original defection. This difference arises because the structure of our raiding game is different from an extensive form Prisoner's Dilemma game (Figure 5.1). In an extensive form Prisoner's Dilemma game with two sequential decisions, one for each party, the evolutionary stable rule is for both parties to defect rather than to cooperate (Figure 5.1). However, RWR is stable in our raiding game because (i) defection (raiding) is costly enough that it can only be used once and (ii) defection (raiding) extends the interaction sequence (by just one step) by triggering retaliation that in turn greatly reduces the pay-off of the original defection (Figure 5.1). Thus, although tit-for-tat evolves against a fixed background of future repeated interactions, RWR can be stable because it actually extends the number of interactions when defection occurs and subsequent interactions reduce initial pay-offs for defection.

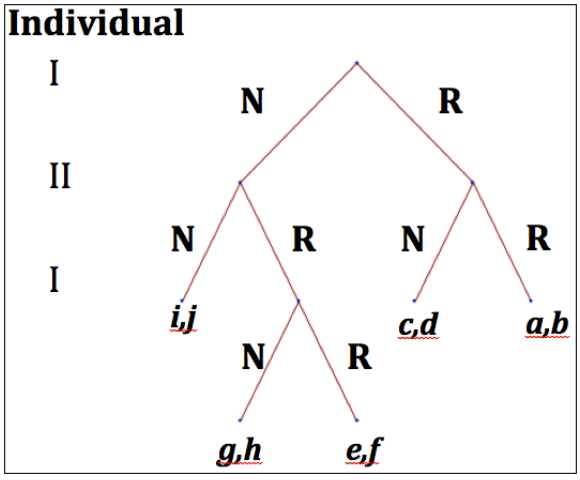

Figure 5.1. Extensive form representation of the raiding game between two individuals, 1 and 2. Terminal payoff pairs are structured as (payoff to 1, payoff to 2). R = Raiding, N = not raiding (respect for possession). For either player, raiding is always favoured if one is raided when raiding success is modelled as a tug-of-war, so $b > d$ and $e > g$. However, not raiding (respect for possession) can be favoured over raiding in the absence of being raided when disparities in initial resource holdings are low or moderate, because in such cases tug-of-war theory yields $j > f$ and $i > a$. This is because raiding carries a fitness cost. This game structure is different from that of an extensive form Prisoner's Dilemma, in which mutual defection (the equivalent of mutual raiding) would always be favoured. (Note: Individual 1 is not given the option to raid at the left-most terminal node, because this situation is the same as the root node of the overall game.)

Moreover, RWR is not vulnerable to neutral invasion through drift by Restraint, even though the pay-offs for RWR and Restraint would be identical in a population of RWR rule-players. So long as a small number of unconditional raiders are maintained in the population, which we would expect through mutation selection balance, RWR would provide a higher pay-off than Restraint, thus preventing its spread. Such 'phenotypic defectors' (Lotem, Fishman, & Stone, 1999) can also stabilize reciprocating conventional tit-for-tat-like strategies in an iterated Prisoner's Dilemma framework, indicating a counterintuitive role for occasional defection in enhancing the long-term stability of cooperation (Sherratt & Roberts, 2001).

Results

Our model begins with initial conditions that are common across the biological world: resources are frequently distributed unequally among individuals that face a decision whether to settle for what they have (respect one another's possession) or to compete for a larger proportion of the overall resource (raid). Our model provides several predictions for the partitioning of divisible resources between interactants of equal RHP engaged in an asymmetric tug-of-war.

We improve upon Hinsch & Komdeur's (2010) explanation of resource division. Whereas their simulations assume that both raiding and defending have fixed costs, our model allows both to be selected as continuous variables. By allowing for adaptive plasticity in the level of defensive and aggressive effort invested by all interactants, our model stabilizes the partitioning of resources. For simplicity, we examine the expected pay-offs for sequences of one possible raid and retaliation. After any such sequence, the interactants find themselves once again in the initial conditions, facing the choice between raiding and respecting possession. However, if they have raided and retaliated, they will both now have a smaller amount of the disputed resource because they have used up some of those resources to 'fund' their raiding and defensive efforts. There is nothing to stop interactants raiding and retaliating more than once, but if they do, it will progressively compound the costs of fighting, and reduce both interactants' expected pay-offs in the long run. Thus, even though our model is made simple by assuming time and energy for only one raid (aggressive or retaliatory) per player, any rule that is sufficient to discourage an initial raid in the one raid per player game will be sufficient to discourage raiding in multiple

raids per player games.

Ownership in the form of RWR is ESS when resource holding asymmetries between interactants are low or moderate, but not when resource holding asymmetries are sufficiently large. If initial resource holding asymmetries do not exceed the critical ratio k^*, ownership will be stable from the outset and will persist as long as asymmetries remain below k^*. However, if increases in resource holding asymmetries over time lead to a situation in which $k \geq k^*$, mutual raids are expected to break out and continue until a more equal distribution is attained. Waves of mutual raiding therefore act as sorting processes that return relative resource holdings to a stable state (i.e. in which $k < k^*$). The same logic can also account for how individuals initially come to possess resources and therefore how resource holding asymmetries arise. When a new shareable resource (e.g. a territory, food source, nutrient supply or potential mates) becomes available, an initial period of scramble will give way to a stable state, most likely without fully equal division of the resource among all members of the population. Such processes are frequently observed in the biological world. Our model predicts that the transition from scramble to peaceful equilibrium will take place when $k < k^*$. Nevertheless, RWR is not stable under conditions of scramble when $k \geq k^*$, or in all possessor–intruder interactions. Alternative explanations (discussed below, such as RHP asymmetries) are required to explain respect for possession in such circumstances.

The value of k^* is $4^n - 4$, meaning that it increases exponentially with the number of interacting individuals. In a two-player scenario, $k^* = 12$, meaning that a mutant raiding strategy would not beat RWR unless v_1 is more than 12 times greater

than v_2. However, the geometric function determining k^* means that it rises steeply with each additional interactant: increasing the number of interactants raises the critical value below which possession will be respected, and therefore broadens the conditions under which RWR is ESS.

The modified RWR strategy that is stable in an n-player game presents three important implications for the emergence and maintenance of ownership in populations: (i) ownership becomes more likely as group size increases, (ii) a form of third-party enforcement emerges because raiders will be raided in turn by everyone, not just the originally raided individual, strengthening the conditions under which ownership is evolutionarily stable, and (iii) a single instance of raiding will trigger retaliation that will spread through a population like an infection process.

Our model therefore predicts a stabilizing effect of additional interactants that does not rely on specialist policing individuals: the presence of additional interactants increases the likelihood of a raiding individual being raided in return, increasing the potential costs of raiding. Because repeated outbreaks of mutual raiding will reduce the fitness pay-offs to all interactants, raiding will not be favoured. Ownership in the form of RWR averts a tragedy of the commons by reducing the costs of selfish investment in competition by all interactants, thereby increasing overall fitness within a population.

Discussion

We propose that ownership is a widespread behavioural phenomenon that has been hiding in plain sight. Differentiating ownership from possession offers sharper

concepts for the study of cooperation and its evolution, exposing an underappreciated distinction at the root of many interactions. Possessive behaviours such as calls, displays, marking and willingness to aggressively defend a resource can be understood as claims to ownership. But such claims alone do not constitute ownership, which is contingent upon respect of these claims by potential competitors. This relational understanding of ownership requires us to look beyond the overt possessive behaviour of resource possessors, and also pay attention to the behaviour of nonpossessors. Ownership will often take the form of 'hidden' interactions (i.e. an absence of challenges) rather than more obvious competitive interactions.

Our model shows one process by which ownership, mutual respect for possession, can emerge and be maintained in a population, reducing conflict and averting a tragedy of the commons. Our findings support insights from the social sciences and the humanities on the foundational importance of possession to ownership and the significance of distinguishing between the two (Carruthers & Ariovich, 2004; Ellis, 1985; Macpherson, 1978; Rose, 1985), and reinforce biological contributions that acknowledge the importance of respect for possession among nonhuman species (Archer, 1986; Gintis, 2007; Kokko, Lopez-Sepulcre, & Morrell, 2006; Russ et al., 2010; Sherratt & Mesterton-Gibbons, 2015; Stake, 2004).

Our model allows for the possibility that ownership arrangements can be maintained within a population even when possession is not respected in every interaction. Whether ownership arrangements exist within a population is therefore not an all-or-nothing proposition but a function of the frequency of respect for possession. Ownership arrangements emerge and become more firmly established within a

population as the frequency of respect for possession increases. This increase might manifest not simply as a linear quantitative change but a phase transition: as variation in resource holdings decreases, there is a point at which social relations within a population may suddenly change in type from outright scramble or mutual raiding to peaceful respect for possession. The obverse also applies: if variation in resource holdings becomes sufficiently high, ownership arrangements will suddenly break down and be replaced by mutual raiding.

We omitted differences in RHP and degree of relatedness from our models so as not to confuse our analysis of what is driving respect for possession. By allowing resource holdings to vary while keeping RHP equal and relatedness effectively zero, we illuminate the crucial importance of relative resource holdings to the evolution of stable ownership. This does not mean that RHP is irrelevant in the evolution of ownership, but that asymmetries in RHP are not necessary to explain how stable respect for possession can be maintained. We discuss below how asymmetries in RHP can be sufficient to explain respect for possession in many situations. Nevertheless, we acknowledge that a more complete and biologically realistic model would incorporate both differential RHP and a relatedness coefficient. Both are likely to influence the conditions under which individuals are willing to raid: we would expect individuals with relatively lower RHP to be less likely to raid as the potential costs of raiding would be higher, and we would expect a positive relationship between relatedness and the value of k^*. Differential RHP has previously been accommodated in a tug-of-war framework (Dugatkin & Reeve, 2014), and the structure of that framework lends itself to the incorporation of a relatedness coefficient. Both RHP and relatedness should be

given consideration in subsequent treatments of the evolution of ownership.

Our model shows an exponential relationship between the number of interactants and the breadth of conditions under which ownership in the form of RWR will be evolutionarily stable: the more interactants, the higher the value of k^* and therefore the higher the likelihood that possession will be respected. This has intuitive appeal because it implies a sociality effect whereby ownership arrangements will be more stable in species in which larger numbers of individuals known to one another frequently interact. However, the value of k^* rises steeply with each additional interactant, meaning that even in relatively small groups k^* might become so high that it would almost never be exceeded by k. We would expect real-world examples to include some feature that arrests the geometric growth of k^*. We propose that this purpose is served by n denoting the number of interactants whose resource holdings any given individual can assess, not the total number of individuals in a population. If so, the actual value of k^* in any given population will be determined by a combination of population size and individual recognition abilities of the species in question (Dávid-Barrett & Dunbar, 2013). This calls attention to a possible connection between the stability of ownership arrangements and the evolution of group size and structure. If the costs of adding another individual to a group are outweighed by the benefits of more stable ownership arrangements (i.e. a lower probability of being raided), this will influence the likelihood of 'outsiders' opting to try to join a group, as well as 'insiders' allowing new individuals to join (Higashi & Yamamura, 1993).

In addition to these direct implications of our model, our treatment of the evolution of ownership raises considerations for several branches of biology. In what

follows, we demonstrate that RWR is not the only way that ownership can evolve. Rather, ownership can emerge from a variety of initial conditions, by different mechanisms, and can apply to potentially any species.

Ownership and territoriality

Studies of territoriality explain how divisions of space arise and are maintained among conspecifics. Typical definitions of territoriality emphasize the importance of aggressive defence against conspecific intruders in securing exclusive use of an area (Davies, 1980; Kaufmann, 1983; Maher & Lott, 1995). However, escalated conflict between possessors and intruders indicates that possession is not respected, but contested, violating the second criterion for ownership. All-out scramble or frequent aggressive defence against intruders is therefore evidence of the absence of ownership.

Territorial arrangements can arise and persist when possession is not habitually respected. For example, Hinsch & Komdeur's (2010) simulations show that stable territories can be maintained even when possessors must continuously defend their territories against intruders. When the value of a territory is high, it will be adaptive for territory possessors to retain possession by repeated costly fighting. However, even in the face of assured aggressive defence, the incentive to raid can be so strong that intruders will continue to raid (i.e. not respect possession), leading possessors eventually to flee under sustained intense pressure. Similarly, Stamps & Krishnan (2001) show how territorial arrangements can arise under the assumption that individuals will fight when they visit the same area at the same time. They theorize that more aggressive individuals will end up with exclusive access to larger territories

after fights with less aggressive individuals, but when both players are aggressive, each will end up with exclusive access to relatively smaller territories. They also demonstrate that it can pay for territory possessors to cede parcels of space to 'nagging' neighbours who persistently invite defensive effort at territory boundaries. In each of these cases, space is divided and territories are formed, but as a result of repeated aggressive contestations, not respect for possession. Territorial partitioning is not always ownership.

However, some processes of territory formation and maintenance can be considered ownership. A well-known example is the Bourgeois strategy (Maynard Smith, 1982), which will be evolutionarily stable against unconditionally aggressive (Hawk) or unconditionally fleeing (Dove) strategies in simple contests over resources, as long as the cost of injury in mutual fighting is greater than the value of the contested resource. In a population of Bourgeois strategists, possession is habitually respected and ownership exists. Nevertheless, there are problems with Bourgeois as a realistic model of ownership. First, under the same conditions in which Bourgeois is an ESS, an anti-Bourgeois strategy (fleeing possessors and aggressive intruders) can also be an ESS (Gintis, 2007). However, anti-Bourgeois conventions are very rarely observed, suggesting the original theoretical framework is missing some important components (Kokko et al., 2006; Sherratt & Mesterton-Gibbons, 2015). Second, a population of Bourgeois strategists can be invaded by Assessor strategies that escalate aggression when the Assessor accurately perceives itself to be stronger (of greater RHP) than its opponent, regardless of who possesses the resource (Parker, 1974). Finally, the original discrete strategy game framework neglects the possibility that the

level of aggression is a continuous variable whose values can be flexibly chosen by both possessor and intruder, a possibility implemented theoretically by Gintis (2007).

Beyond the Hawk/Dove/Bourgeois framework, the literature on territoriality provides several examples of behavioural strategies that satisfy our criteria for ownership. Morrell & Kokko (2003) describe how winner and loser effects can lead to the emergence of mutually respected boundaries. Individuals that have won a fight in a particular place are more likely to return than losers, effectively taking ownership of that area when it becomes uncontested by nonreturning losers. Switzer et al. (2001) similarly show how territory possessors can 'train' repeat intruders to stay away through aggressive territorial defence. Possessors recoup the energetic costs of territory defence in the long run by retaining exclusive use of a territory, whereas intruders suffer fighting costs with no subsequent pay-off. Intruders learn the location of territory boundaries and come to respect them. Pereira et al. (2003) describe how foragers will negotiate peaceful divisions of space or 'socially stable territories', even when individuals differ in fighting ability (RHP). These socially stable territories are conditional upon availability of resources: under the conditions of scarcity, individuals with inferior fighting ability will be evicted. This shows another process by which ownership arrangements can collapse, although in Pereira et al.'s model it is overall resource availability that determines the tipping point, whereas in ours it is asymmetry in resource holdings.

Another example of ownership is provided by the dear enemy effect (Fisher, 1954), which is observed in many taxa and is characterized by peaceful mutual respect of territorial boundaries by neighbours (Temeles, 1994; Ydenberg, Giraldeau, & Falls,

1988). Dear enemy arrangements arise because mutually respected boundaries reduce the energetic costs associated with territorial maintenance. Initial territorial negotiations carry up-front costs, which are offset by long-term reduction in the costs of continuous territorial maintenance. Once territories have been negotiated between neighbours, it is beneficial not to have to renegotiate with a new neighbour (Krebs, 1982). Unknown intruders threaten to completely undermine stable territorial arrangements. Dear enemies will therefore not only respect one another's possession but help to defend neighbours' territories from unknown intruders (Getty, 1987). However, the dear enemy phenomenon is not ubiquitous. It is most commonly associated with species in which individuals live alone or in small groups. An opposite phenomenon, where 'nasty neighbours' display more intense aggression towards neighbours, has also been documented in group-living species in which small groups run the risk of being outnumbered and dispossessed by larger neighbouring groups (Müller & Manser, 2007). Dear enemies have ownership arrangements, but nasty neighbours do not.

Studies of territoriality provide fruitful insights into the existence and variety of ownership behaviours in nonhumans and suggest that a wide variety of species could exhibit ownership (e.g. the range of species in which the dear enemy phenomenon applies, reviewed by Ydenberg et al., 1988). Nevertheless, due to its emphasis on the partitioning of space by animal species, the literature on territoriality can only reveal a partial view of the overall taxonomic distribution of nonhuman ownership. Ownership can potentially exist whenever there can be competition for resources, and a complete account of the biological distribution of ownership would

extend to all taxa and all ownable resources. A strength of our tug-of-war model is that it is neutral with respect to both taxa and resources. Our raiding game can explain not only the partitioning of space, but also of other contestable, divisible resources such as mates, food sources and resource flows that change location over time such as bodies of water or patches of sunlight.

Ownership beyond space

Another partial view of the extent of nonhuman ownership is offered by empirical studies explicitly examining respect for possession. However, these are few and have primarily focused on individual ownership of food items among captive primates. Sigg & Falett (1985) show that *Papio hamadryas* (hamadryas baboons) respect potential competitors' possession of food items. In their experiments, males always respected the possession of other males, even subordinates, although respect for possession was not observed as frequently in female–female or male–female dyads. Ownership of food items has subsequently been observed in *Macaca fascicularis* (long-tailed macaques) (Kummer & Cords, 1991) and *Macaca mulatta* (rhesus monkeys) (Russ et al., 2010). Such explicit empirical investigations have the additional benefit of revealing specific rules pertaining to ownership conventions, for example the types of cues that signify possession and the extent to which RHP or hierarchical position influences the probability of respect for possession. In all three species, physical possession was necessary, but not always sufficient, for ownership. The nuances discernable in this limited set of observations highlight the complexities of real-world ownership conventions and therefore the value of incorporating a

relational understanding of ownership more fully into the conceptual toolkits of behavioural ecology and evolutionary biology.

Ownership and the tragedy of the commons

In a tragedy of the commons, purely self-interested behaviours diminish and eventually exhaust shared resources (Hardin, 1968). Beyond Hardin's initial concern with human pressure on natural resources, the tragedy of the commons has attracted significant attention as a problem of collective action throughout the biological world (Dionisio & Gordo, 2006; Rankin et al., 2007). The term has taken on a broader definition in evolutionary biology, but its logic is identical: 'a situation in which individual competition reduces the resource over which individuals compete, resulting in lower overall fitness for all members of a group or population' (Rankin et al., 2007: 643).

Hardin initially proposed private or government ownership as the only solutions to tragedies of the commons in humans. Subsequent studies of natural resource governance demonstrate that Hardin's prescriptions were overly narrow, crucially overlooking systems of collective ownership (Ostrom, 1990). Nevertheless, these studies confirm that ownership arrangements, in various forms, are key to solving tragedies of the commons (Cole & Ostrom, 2012). In our species-neutral model, RWR offers another example of how ownership can avert a tragedy of the commons by reducing the defensive investment of all players. This signals a potentially very rich avenue of inquiry into the relationship between ownership and the evolution of cooperation and collective action across taxa. Rankin et al.'s (2007)

review of nonhuman tragedies of the commons offers a rich source of cases in which the existence of nonhuman ownership can be investigated. Furthermore, beyond nonhuman analogues of individual ownership and private property (Dionisio & Gordo, 2007; Gintis, 2007; Strassmann & Queller, 2014), we might also consider systems of collective ownership among nonhumans. Pereira et al.'s (2003) models illustrate the conditional sharing of space among foragers, and Frank's (1996) work on mutual policing demonstrates how systems of collective internal control can limit the degradation of shared resources. The dear enemy phenomenon shows that a group of neighbouring owners will exclude outsiders from an area. Although we presented our model as an explanation of the behaviour of individuals, it could also explain the behaviour of groups engaged in a tug-of-war. Such an extension could only apply to groups of individuals with closely overlapping interests. For groups whose members have divergent interests, a more complex model would be required to account for the potential of free-riding. Empirical examples of collective ownership could include the division of resources such as home ranges or feeding areas by group-living species such as *Pan troglodytes* (chimpanzees) (Luncz, Mundry, & Boesch, 2012) and *Panthera leo* (African lions) (Mosser, Kosmala, & Packer, 2015).

Ownership and escalated aggression

Although ownership arrangements are characterized by the absence of overt escalated aggression, violence can play an important part in their emergence and maintenance. We have discussed how ownership of space can be the result of initial contests during which individuals negotiate or learn the size of territories and the

location of boundaries. In these cases, initial escalated aggression and outright conflict are an important component of the sorting processes that produce long-term stable and peaceful territorial arrangements. The costs of initial conflict pay off in the long term. Nevertheless, not all ownership arrangements require initial conflict. 'Common sense' reasons not to compete, such as large cost of fighting relative to the value of the resource in question or high likelihood of losing a fight to a possessor with superior RHP, can be sufficient to drive respect for possession (Morrell & Kokko, 2003). But in other situations, such as respect for subordinates' possession in Sigg and Falett's hamadryas baboon experiments, differences in RHP or direct costs of fighting do not determine the division of resources. Something subtler is at play.

Eswaran & Neary (2014) propose that humans have an 'innate, biological sense of property rights', a possibility echoed by Gintis (2007). Gintis locates this unlearned sense of property rights in the endowment effect, the propensity of possessors to value a resource more highly than nonpossessors, which he claims can be observed in many species. This value asymmetry provides an evolutionary basis for Bourgeois behaviours with possessors more willing to engage in agonistic behaviour than intruders. The endowment effect can therefore help to explain why seemingly paradoxical arbitrary conventions such as anti-Bourgeois are observed so infrequently.

Ownership arrangements associated with the endowment effect, Bourgeois, Assessor or RWR neither arise from nor are maintained by escalated aggression, but involve hidden interactions in which individuals have a propensity to respect possession rather than to compete. Nevertheless, such propensities not to compete have likely also been selected for due to the costs of ancestral conflict, and can be

considered a ghost of competition past (Connell, 1980).

Ownership refers to a set of behavioural conventions governing the partitioning of resources that do not require to be constantly maintained by aggressive interactions. Nevertheless, in the examples we have considered, punishment or enforcement is a critical component of ownership. Ownership arrangements either emerge from initial costly interactions or are underpinned by the threat of punishment in response to intrusion. RWR and Bourgeois do not eschew conflict entirely, but employ it under certain circumstances. Without the willingness to punish intruders, resource possessors would effectively always play Dove, a strategy that can never be evolutionarily stable (Maynard Smith, 1982). This is consistent with the evolutionary importance of punishment and sanctions to the maintenance of prosocial norms (Axelrod, 1986; Clutton-Brock & Parker, 1995). Punishment in the form of retaliation plays two important roles in our raiding game: it increases the costs of raiding, thereby promoting respect for possession, and keeps RWR robust against neutral invasion through drift by Restraint.

Aggressive defence by resource possessors and enforcement by third parties ultimately serve the same sanctioning function (Clutton-Brock & Parker, 1995). Specific mechanisms of enforcement of ownership arrangements will depend on the social characteristics of the species in question (Roos, Gelfand, Nau, & Carr, 2014) and will be revealed by close empirical study of particular nonhuman ownership conventions. Third-party enforcement might take several forms, including centralized authority exercised by dominant individuals, dedicated policing by individuals whose functional role within a society is to enforce particular behaviours, and nonhierarchical

enforcement by all members of a group. RWR falls within this last category, as retaliation for raiding will be delivered by all interactants rather than a subgroup or an individual.

Conclusions

We propose that ownership should be considered a common and powerful biological phenomenon, to which there are many evolutionary routes. Nevertheless, the significance of ownership as a distinct and potentially unifying behavioural category has not yet received the focused attention it requires. We presently lack a comprehensive account of instances of ownership among nonhumans, or a complete and overarching evolutionary explanation for its evolution. Understanding the individual and group benefits of reducing defensive investments and averting tragedies of the commons are likely to account for a significant proportion of the evolutionary value of ownership. We encourage further mathematical contributions on the origins, functions and adaptive advantages of ownership. We look forward to enhancements and refinements of RWR and the model we present in this paper, as well as explanations of how ownership can evolve within additional theoretical frameworks.

Ownership is related to but fundamentally different from well-established behavioural concepts such as territoriality. Articulating in greater detail how these concepts are connected will be an important conceptual exercise, and promises to provide additional understanding of how evolution has moulded competition, cooperation and division of resources. We encourage researchers in all disciplines to devise creative approaches for investigating the existence of nonhuman ownership and

to re-examine established behaviours that might meet the relational criteria for ownership. We welcome empirical elucidation of the diversity of ownership expressions across taxa: which species exhibit ownership, the types of resources that can be owned, specific ownership rules, mechanisms of enforcement and the possibility that groups and not individuals can be owners. We anticipate that the characteristics that differentiate ownership arrangements will be every bit as instructive as the criteria we have proposed for uniting them.

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CHAPTER 6

VALUE OF SPECIES AND THE EVOLUTION OF CONSERVATION ETHICS[4]

Abstract

The theory of evolution by natural selection can help explain why people care about other species. Building upon recent insights that morality evolves to secure fitness advantages of cooperation, we propose that conservation ethics (moral beliefs, attitudes, intuitions, and norms regarding other species) could be adaptations that support cooperation between humans and non-humans. We present eco-evolutionary cost-benefit models of conservation behaviours as interspecific cooperation (altruism towards members of other species). We find that an evolutionary rule identical in structure to Hamilton's rule (which explains altruistic behaviour toward related conspecifics) can explain altruistic behaviour towards members of other species. Natural selection will favour traits for selectively altering the success of members of other species (e.g. conserving them) in ways that maximize inclusive fitness return benefits. Conservation behaviours and the ethics that evolve to reinforce them will be sensitive to local ecological and socio-cultural conditions, so will assume different contours in different places. Difficulties accurately assessing costs and benefits provided by other species, time required to adapt to ecological and socio-cultural change, and barriers to collective action could explain the apparent contradiction between the widespread existence of conservation ethics and patterns of biodiversity

[4] Hare, D., Blossey, B., & Reeve, H. K. (2018). Value of species and the evolution of conservation ethics. *Royal Society Open Science 5*: 181038.

decline globally.

Introduction

Why should we care about biodiversity loss and ecological change? Which species should we conserve, and why? Are species valuable simply because they contribute to human well-being, or also for their own sake? To what extent should people consider the interests of non-humans in conservation? How we answer these enduring moral questions will influence our impacts on ecosystems that support human and non-human life (Mace, 2014). Our answers will depend on how we understand the causal origins and scope of human morality, and how we interpret relationships between humans and other species.

Claims that humans have profound moral concern for other species might ring hollow as human activities continue to drive biodiversity declines globally (Dirzo et al., 2014; Urban, 2015; WWF, 2018). Nevertheless, conservation ethics (individual-level moral beliefs, attitudes, and intuitions as well as population-level social norms regarding other species) appear to be widespread. Concerns about unsustainable human impacts on ecosystems (Barnosky et al., 2012; Millennium Ecosystem Assessment, 2005; Ripple et al., 2016; Rockström et al., 2009; Urban, 2015) and calls for concomitant recalibration of values and institutions (Dannenberg & Barrett, 2018; Diaz et al., 2018; Levin, 2006; Martin, Maris, & Simberloff, 2016; Ostrom, 2010) suggest that moral dimensions of ecological change and biodiversity loss resonate deeply. Moral commitments to protect, conserve, and respect other species are evident in social norms and cultural traditions around the world and over time (Berkes, 2012;

Callicott, 1994; Fatheuer, 2011; Pungetti, Oviedo, & Hooke, 2012), and in contemporary individual moral beliefs, attitudes, and intuitions, across societies (de Groot, Drenthen, & de Groot, 2011; Fox & Xu, 2017; Gamborg & Jensen, 2016; Teel & Manfredo, 2010). However, fundamental disagreements about why conservation is important and the nature of human obligations to other species (Chan et al., 2016; Kareiva & Marvier, 2007; Soulé, 2013) cast doubt on whether conservation ethics will be able to inspire actions that successfully reduce or reverse biodiversity loss globally.

Members of the public in several countries believe that non-human species have both instrumental value (derived from benefits they provide to humans) and intrinsic or non-instrumental value (over and above benefits they provide to humans) (Sandler, 2012), but assign them different relative importance (Arias-Arévalo, Martín-López, & Gómez-Baggethun, 2017; de Groot et al., 2011; Fox & Xu, 2017; Gamborg & Jensen, 2016; Lute, Navarrete, Nelson, & Gore, 2016; Teel & Manfredo, 2010; Vucetich, Bruskotter, & Nelson, 2015). Even conservation professionals, united by a foundational commitment to the value of biodiversity, are divided over which species are valuable, what type of value they have, and to whom they are valuable (Chan et al., 2016; Holmes, Sandbrook, & Fisher, 2017; Hunter, Redford, & Lindenmayer, 2014; Marvier, 2014; Noss, Nash, Paquet, & Soulé, 2013). Despite recognition that simple categories such as instrumental and intrinsic value cannot capture the full diversity of conservation ethics (Chan et al., 2016; Sandbrook, Scales, Vira, & Adams, 2011), and calls for unity between opposing moral justifications for conservation (Green et al., 2015; Hunter et al., 2014; Pearson, 2016; Tallis & Lubchenco, 2014), philosophical differences persist and impede conservation efforts (Marvier, 2014).

Thoughtful reflection and debate about moral justifications for biodiversity conservation, informed by empirical research, can provide crucial guidance on balancing human interests with interests of other species. However, conservation ethics at the level of both individual attitudes and social norms have deep and complex psychological and cultural roots, so can be stubbornly resistant to change (Amel, Manning, Scott, & Koger, 2017; Manfredo et al., 2016). Continuing to rehearse arguments about "correct" moral justifications for conservation is likely to deepen entrenched positions rather than inspire solutions. Because human behaviour reflects evolved solutions to adaptive challenges that arise in particular social and ecological environments (Alvard, 1995; Berkes, 2012; Gadgil, Berkes, & Folke, 1993; Gibson & Lawson, 2015; Smith & Wishnie, 2000), a fresh approach that integrates ecology and evolution into our understanding of human morality could provide novel insights into the origins of and justifications for conservation ethics.

Research across disciplines indicates that morality (beliefs, attitudes, intuitions, and norms about what is right and wrong) is a set of adaptations favoured by natural selection to regulate behaviour in ways that promote mutually beneficial cooperation (Brosnan, 2014; Curry, 2016; Curry, Chesters, & van Lissa, 2018; Tomasello, 2016) in recurrent non-zero-sum interactions (i.e. when it is possible to produce "win-win" outcomes). In such interactions, cooperators receive more favourable fitness outcomes than non-cooperators (Maynard Smith, 1982). Cooperation is therefore favoured over non-cooperation within groups of frequently interacting individuals, and groups of cooperators outcompete groups of non-cooperators, so traits promoting adherence to cooperative rules are more likely to persist and spread (Dugatkin & Reeve, 1994).

Cooperation is so evolutionarily powerful that it is a fundamental component of the behavioural repertoires of group-living species (Axelrod & Hamilton, 1981), and explains much of how human societies are structured (Bowles & Gintis, 2011). Moral beliefs, attitudes, and intuitions nudge individuals towards cooperative behaviours, bolstering fitness advantages of cooperation (Tomasello, 2016; Van Lange, Balliet, Parks, & Van Vugt, 2014).

While so far the evolutionary study of morality has focused on moral behaviour towards members of the same species, its basis in cooperation suggests that it could also explain moral behaviour towards members of other species. Interspecific cooperation is widespread (Kiers et al., 2011; Raihani, Thornton, & Bshary, 2012), and humans frequently cooperate with other species, from gut microbiota that keep us healthy, to animals that help us make a living, to plants we cultivate and animals whose habitats we maintain. There is therefore no *a priori* reason why morality could not evolve to promote fitness advantages of interspecific cooperation.

To investigate this possibility, we develop general evolutionary cost-benefit models of interspecific cooperation that can apply to human conservation behaviour. Specifically, we ask whether altruism (improving another's fitness at some initial fitness cost to oneself (Hamilton, 1964)), a form of cooperation observed in many taxa and a defining feature of human morality (Curry, 2016; Trivers, 1971), can also be adaptive (i.e. ultimately increase inclusive fitness) when directed towards members of other species, even if they have not been naturally selected to conditionally repay the altruistic act. Just as many aspects of morality have evolved to promote cooperation in recurrent social interactions within groups of humans, so might conservation ethics

have evolved to promote cooperation in recurrent ecological interactions between humans and members of other species. A foundational account of how and why conservation behaviours evolve could help explain why conservation ethics exist and why they vary, and shed light on the apparent contradiction between the widespread occurrence of conservation ethics and patterns of biodiversity decline globally.

Models

1. Conservation behaviours as interspecific altruism

Conservation behaviours involve an individual of one species paying some cost to take an action that will benefit at least one individual of another species (Alvard, 1995; Ruttan & Borgerhoff Mulder, 1999), for example by restraining consumption, modifying environments, or directly providing resources. Conservation behaviours can therefore be considered altruistic because one individual pays an initial personal fitness cost to provide a benefit to one or more others (Hamilton, 1964). Like any other behaviour, conservation behaviours will be favoured by natural selection if they ultimately increase the inclusive fitness of individuals who engage in them, and will spread in a population if they increase the inclusive fitness of individuals who engage in them relative to individuals who do not (Hamilton, 1964). Because inclusive fitness takes into account the fitness of an altruist's relatives as well as the altruist's personal fitness, an altruist need not receive any personal fitness gains for altruism to evolve and spread. Behaviours can spread genetically, culturally, or through gene-culture interactions (Creanza, Kolodny, & Feldman, 2017), so long as transmission rules have evolved to maximize inclusive fitness. Interactions described by our models

do not necessarily involve humans (Appendix F), so we make no assumptions about the species to which interactants belong.

We model conservation behaviours as actions taken by individuals. In reality groups of individuals can exhibit coordinated conservation behaviours, but because selection will work on differential inclusive fitness outcomes among individuals, we restrict our models accordingly. In the discussion we explore the implications of this restriction. In order to capture a broad range of realistic conservation behaviours, we allow recipients of conservation behaviours to be individuals or groups such as populations.

We begin by asking whether it could ever be adaptive for a focal individual to take some action that will alter the success, a, of a recipient of a different species by an amount x. (Table 6.1 contains detailed definitions of all variables in our models.) The action in question will carry some initial personal fitness cost, c, to the focal individual. Altering the recipient's success will affect the focal individual's inclusive fitness, w, scaled by the "ecological relatedness", r, between the focal individual and the recipient. Ecological relatedness is a multiplier that converts change in the recipient's success into change in the focal individual's inclusive fitness. Increasing a recipient's success will generate a positive return effect on the focal individual's inclusive fitness when r is positive, and a negative return effect when r is negative. For example, crops could have a positive r value, because increasing their success is likely to provide positive inclusive fitness returns, whereas poisonous plants, pathogens, or dangerous animals could have a negative r value because increasing their success might provide negative inclusive fitness returns by amplifying the risks

they present. The absolute value for r represents the strength of positive or negative return effects on the focal individual's inclusive fitness.

Table 6.1. Definitions, possible conditions, and explanations for all model variables, grouped by model and listed in the order they appear in text.

Model	*Variable*	*Definition*	*Possible conditions*	*Explanation*
1. Conservation behaviours as interspecific altruism	a	baseline success of recipient	always positive	recipient will always have some baseline level of success
	x	amount by which focal individual changes recipient's success from its baseline success, a	positive	increases recipient's total success above baseline success (altruism, conservation)
			negative	decreases recipient's total success below baseline success (spite, persecution)
			neutral (zero)	does not change recipient's total success from baseline success
	c	fitness cost of *doing something*	always positive	*doing something* will always carry some fitness cost to focal individual
	w	inclusive fitness of focal individual	always positive	focal individual will always have some inclusive fitness

Table 6.1 *continued*

Model	*Variable*	*Definition*	*Possible conditions*	*Explanation*
1. Conservation behaviours as interspecific altruism	r	ecological relatedness between focal individual and recipient, i.e., a multiplier that converts x (change in recipient's success, a) into change in focal individual's inclusive fitness, w. This can be expressed in two equivalent ways: (i) average effect on the focal individual's inclusive fitness, w, of altering recipient's success by an amount x; and (ii) slope of the expected return on focal individual's inclusive fitness, w, as a function of the change of amount x in recipient's success	positive	increasing recipient's success generates a positive return effect on focal individual's inclusive fitness; decreasing recipient's success generates a negative return effect on focal individual's inclusive fitness
			negative	increasing recipient's success generates a negative return effect on focal individual's inclusive fitness; decreasing recipient's success generates a positive return effect on focal individual's inclusive fitness
			neutral (zero)	increasing or decreasing recipient's success generates no return effect on focal individual's inclusive fitness
	z	focal individual's baseline inclusive fitness, regardless of whether it *does something* or *does nothing*	always positive	focal individual will always have some baseline inclusive fitness

Table 6.1 *continued*

Model	*Variable*	*Definition*	*Possible conditions*	*Explanation*
2. Indirect effects of downstream ecological interactions	r'	net ecological relatedness between focal individual and recipient, incorporating all downstream ecological effects	positive	increasing recipient's success generates a positive return effect on focal individual's inclusive fitness; decreasing recipient's success generates a negative return effect on focal individual's inclusive fitness
			negative	increasing recipient's success generates a negative return effect on focal individual's inclusive fitness; decreasing recipient's success generates a positive return effect on focal individual's inclusive fitness
			neutral (zero)	increasing or decreasing recipient's success generates no return effect on focal individual's inclusive fitness
	u	proportion of initial investment that alters success of downstream recipients; quantifies strength and sign of indirect effect on downstream recipient of investment in initial recipient	positive	when effect on initial recipient (x) is positive, indirect effect on downstream recipient is also positive; when effect on initial recipient is negative, effect on downstream recipient is also negative
			negative	when effect on initial recipient (x) is positive, effect on downstream recipient is negative; when effect on initial recipient is negative, effect on downstream recipient is positive

Table 6.1 *continued*

Model	*Variable*	*Definition*	*Possible conditions*	*Explanation*
3. Continuous effort and nonlinear returns	y	level of effort required to alter recipient's success	always positive	higher value for y means that the focal individual invests more effort in altering recipient's success
	d	determines whether investment increases or decreases recipient's success	positive	increased investment increases recipient's success
			negative	increased investment decreases recipient's success
	v	determines how sensitively an increasing investment affects the recipient's success	always positive	higher value for v amplifies effects of investment on recipient's success (minimal non-zero *y* scaled to be 1 or greater)
	c	determines cost rate of investment y	positive	higher values for c indicate a higher cost for a given investment, y
	t	determines how sensitively an increasing investment affects the focal individual's cost	always positive	higher value for t increases the cost of investment (minimal non-zero *y* scaled to be 1 or greater)
	y^*	optimal level of effort	always non-negative	by investing y^*, focal individual maximizes its net inclusive fitness; corresponds with dashed lines in Figure 6.1

It will be adaptive for the focal individual to take an action that alters the recipient's success when:

$$z + r(a + x) - c > z + ra \quad (1)$$

where z is the focal individual's baseline inclusive fitness, regardless of whether it *does something* or *does nothing*. The left hand side of this inequality represents the focal individual's inclusive fitness, w, for *doing something* ($w = z + r(a + x) - c$)

and the right hand side represents the focal individual's inclusive fitness for *doing nothing*, i.e. not taking the action in question ($w = z + ra$).

The inequality simplifies to:

$$rx > c \qquad (2)$$

Therefore it will be adaptive for a focal individual to take an action that affects a recipient's success (*do something*) when ecological relatedness between the recipient and the focal individual, multiplied by the strength of effect on the recipient's success, exceeds the cost of taking the action under consideration. We call this the adaptive conservation rule (ACR). We do not assume that the focal individual consciously calculates costs and benefits, only that selection will favour traits that promote *doing something* when ACR is satisfied and *doing nothing* when ACR is not satisfied.

2. Indirect effects of downstream ecological interactions

Actions that positively or negatively affect the success of members of one species are likely also to have positive or negative indirect effects on the success of members of additional species ecologically connected to the first (Estes et al., 2011; O'Bryan et al., 2018; Sheehy, Sutherland, O'Reilly, & Lambin, 2018). These indirect effects will also impact the focal individual's inclusive fitness, so will determine whether *doing something* will be adaptive.

Suppose a focal individual alters the success of an initial recipient by an amount x, which in turn affects the success of n other "downstream" recipients belonging to additional species. The *i*th such downstream recipient experiences an indirect effect of the focal individual's action $u_i x$, that positively or negatively changes the downstream recipient's success from its baseline success, a_i, to $a_i + u_i x$,

where u quantifies the strength and sign of indirect effects. Each such downstream recipient provides an inclusive fitness return $r_i(a_i + u_i x)$ to the focal individual. The initial recipient, indexed as zero, provides a return $r_0(a_0 + u_0 x)$ to the focal individual. We conservatively assume that all such returns additively combine. Returns might multiplicatively combine, which would amplify the effects of downstream interactions. Under this additive assumption, the total (net) fitness return to the focal individual is

$$\sum_{i=0}^{n} r_i * (a_i + u_i x) \quad (3)$$

where $u_0 = 1$.

Since taking the action with effect x necessarily entails a cost c to the focal individual, then the action will be favoured if

$$\sum_{i=0}^{n} r_i * (a_i + u_i x) - \sum_{i=0}^{n} r_i\, a_i > c \quad (4)$$

which simplifies to

$$\sum_{i=0}^{n} r_i\, u_i x > c \quad (5)$$

This is equivalent to ACR if we define the initial recipient's net ecological relatedness r' to the focal individual as

$$r' = \sum_{i=0}^{n} r_i\, u_i \quad (6)$$

entailing that altering the success of the initial recipient species by x is favored if $r'x > c$, just as in the simple formulation of ACR in model 1. This reformulation of ACR is more ecologically realistic because it accommodates positive and negative indirect effects on all downstream recipients (i.e. broader cascading effects on the ecological community), which will mediate the net inclusive fitness consequences of *doing something*.

3. Continuous effort and nonlinear returns

Models 1 and 2 treat conservation behaviours as discrete acts of investment in members of other species (*doing something*). However, it would be more realistic to model conservation behaviours as investments of continuously varying effort, y, in altering a recipient's success, and to allow costs of and returns on such investments to be nonlinear continuous functions.

For example, increasing effort might affect the recipient's success nonlinearly, according to the function dy^v, where d and v are constants, $v > 0$. By replacing x in model 2 with this new function, dy^v, the return inclusive fitness benefit to the focal individual for *doing something to an extent y* would be $r'(a + dy^v)$. Negative values for d represent investments that decrease the recipient's success, and positive values for d represent investments that increase the recipient's success. If $0 < v < 1$, then increasing investment will have diminishing marginal effects on the recipient's success, and if $v > 1$, increasing investment will have accelerating marginal effects on the recipient's success. Increasing investment might also affect the cost to the focal individual nonlinearly, according to the function cy^t, where c and t are positive constants. If $0 < t < 1$, then increasing investment will yield diminishing increases in costs, and if $t > 1$, increasing investment will yield accelerating costs.

By further modifying model 2 to also account for nonlinear costs of investment, the focal individual's net inclusive fitness becomes

$$w = z + r'(a + dy^v) - cy^t \qquad (7)$$

This retains the basic structure of models 1 and 2 but is more realistic because it incorporates nonlinear costs as well as non-linear inclusive fitness returns of

investments.

If costs rise faster than benefits of investment as investment increases ($t > v$), the focal individual's net inclusive fitness will reach a peak at an intermediate optimal level of investment (Figure 6.1). Natural selection will favour investing at this optimal level, y^*, which is given by

$$y^* = e^{ln[r'dv/(tc)]/(t-v)} \quad (8)$$

The optimal level of investment increases as the product of benefit-related parameters $r'dv$ increases and as cost-related parameters c and t decrease.

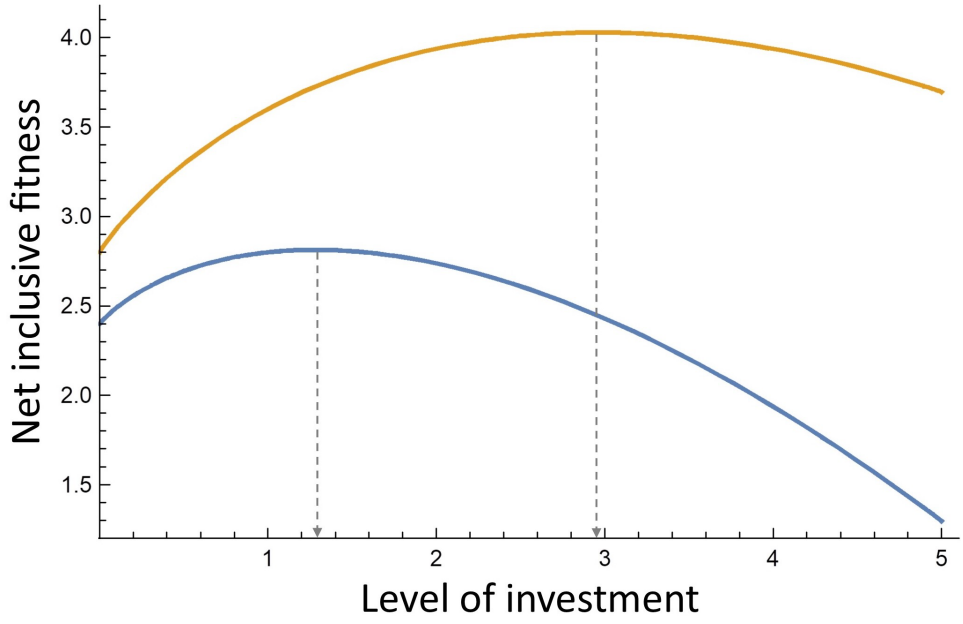

Figure 6.1. Net inclusive fitness returns for continuous investment of effort under different conditions of net ecological relatedness. Nonlinear net inclusive fitness, w, returns for level of effort, y, such that $w = z + r'(a + dy^v) - cy^t$. For the blue curve, values are set to: $r' = 1.4, a = 1, c = 1, d = 1, t = 1.3, v = 1$. For the orange curve, all values are the same except $r' = 1.8$. Higher r' (orange curve) yields greater net inclusive fitness returns for a given level of investment. Dashed vertical lines indicate optimal level of investment y^*, which increases as net ecological relatedness, r', increases. Focal individuals can maximize inclusive fitness returns by focusing their investments in members of species with higher r'.

Results

Any action that alters the success of members of another species will also generate return effects on the inclusive fitness of the individual taking that action (unless net ecological relatedness r' is exactly zero). Natural selection will operate on different strategies for altering the success of members of other species, favouring those strategies that produce the greatest net inclusive outcomes. Net inclusive fitness outcomes will reflect the cost of taking an action as well as the sum of all direct and indirect return effects. Additive indirect ecological effects (incorporated into r') could increase or decrease the magnitude of direct effects (represented by r), in some cases strongly enough to reverse the sign from positive to negative or negative to positive.

ACR represents a general rule for maximizing net inclusive fitness outcomes of altering the success of members of other species. Adaptive strategies under ACR (Figure 6.2) include paying a cost to positively affect a recipient's success (altruism, positive value for x, conservation behaviours) as well as paying a cost to negatively affect a recipient's success (spite, negative value for x, persecution behaviours) (West & Gardner, 2010). Similarly, in model 3, optimal levels of investment increase the greater the degree that investment increases the success of beneficial species (positive values for both r' and d) or depresses the success of harmful species (negative values for both r' and d). Optimal strategies will be sensitive to non-linear payoff functions (Figure 6.1) to prevent over-investment in a recipient, i.e., affecting a recipient's success so much that doing so produces a net negative inclusive fitness outcome for the focal individual.

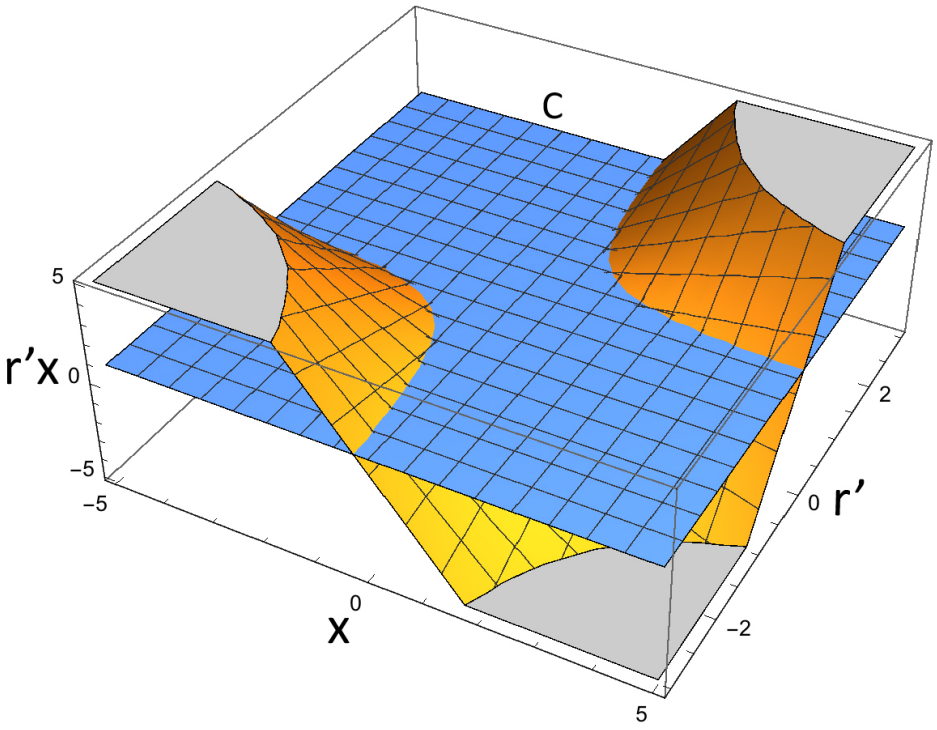

Figure 6.2. **Adaptive strategies under the adaptive conservation rule (ACR).** Regions in which *doing something* is favoured because $r'x$ (net ecological relatedness multiplied by effect of a given action on the recipient's success) exceeds cost, c. Orange surfaces are $r'x$ and blue plane is c. *Doing something* is favoured in both scenarios in which orange surfaces lie above the blue plane. In the first scenario (upper right quadrant) it will be adaptive for the focal individual to increase the recipient's success (i.e. engage in conservation behaviour). In the second scenario (lower left quadrant) it will be adaptive for the focal individual to decrease the recipient's success (i.e. engage in persecution behaviour). For simplicity this figure uses notation from model 2.

ACR is homomorphic to Hamilton's rule (Hamilton, 1964), which explains why individuals will act altruistically towards conspecifics. Hamilton's rule states that it will be adaptive for a focal individual to pay a cost to provide some benefit to a recipient, so long as benefits to the recipient multiplied by genetic relatedness between the two is greater than the cost to the focal individual ($rb > c$). When Hamilton's rule is satisfied, altruistic individuals pay a personal fitness cost but receive a net inclusive fitness gain. The same is true when ACR is satisfied: expected inclusive fitness

consequences of *doing something* exceed expected inclusive fitness consequences of *doing nothing*, so *doing something* is favoured even though it involves an initial personal fitness cost. However, in our interspecific models the factor that scales effects of investments to the focal individual's inclusive fitness is ecological relatedness, not genetic relatedness. Genetic relatedness is a fixed probability that individuals share alleles, but ecological relatedness and net ecological relatedness can each take on different values in different contexts.

Models 1 and 2 provide a general theory of the inclusive fitness value of genetically unrelated organisms, and model 3 explains how focal individuals can maximize their inclusive fitness returns by selectively affecting the success of members of other species. Under all three formulations of ACR, focal individuals can maximize their inclusive fitness by working harder to alter the success of members of species with larger absolute values of ecological relatedness (r or r'). This includes increasing members of other species' success when net ecological relatedness (r') is positive, and decreasing their success when net ecological relatedness is negative.

Discussion

By describing how natural selection can favour interspecific cooperation in the form of ACR, we demonstrate one way in which selective conservation behaviours can be adaptive. Our models therefore reveal a possible evolutionary basis for conservation ethics: adaptive conservation behaviours will spread in a population and conservation ethics will evolve to bolster resultant fitness advantages. Like morality more generally (Curry, 2016; Tomasello, 2016), conservation ethics could be rooted in

cooperative behaviour.

Interspecific cooperation

By showing that *doing something* can be adaptive when values for r' and x are low, when effects are indirect, and when no specific return behaviour is required, our models extend the logic of Hamilton's rule to a broader set of biological conditions. When ACR is satisfied, return inclusive fitness benefits, scaled by net ecological relatedness, exceed initial personal fitness costs of altruistic behaviours. Such return benefits unite ACR mathematically with two established evolutionary accounts of altruism, although they differ in precisely how the actor obtains return benefits: reciprocal altruism (Trivers, 1971), in which return benefits result from repeated interactions among conditionally reciprocating altruists; and kin-selected altruism (Hamilton, 1964), in which return benefits accrue to altruists through relatives sharing the gene for altruism. Without return benefits, altruistic behaviours would incur costs but provide no inclusive fitness gains, so would not be favoured by selection.

We do not intend our models to replace existing explanations of mutualism, in which species co-evolve specific behaviours to provide benefits to each other (Leigh, 2010). Previous studies have described the mathematics of mutualism (Ferriere, Bronstein, Rinaldi, Law, & Gauduchon, 2002; Foster & Wenseleers, 2006; Leigh, 2010; Zink, 2015), some of which have also drawn parallels to Hamilton's rule (Frank, 1994; Queller, 2012). Because our models do not assume that the focal individual and recipient belong to species that interact frequently or have been under selection to provide reciprocal benefits, they apply more broadly than just to mutualisms. Our

models can accommodate mutualisms, which would emerge through strong positive selection for higher values for r. Our models are distinctive because they can (i) extend to antagonistic behaviours towards members of other species, represented by negative values for x and d, (ii) take into account indirect effects on an indefinite number of downstream species and ecological interactions, so extend beyond interactions between a focal individual and recipients of a single different species, and (iii) apply to an adaptive form of unilateral interspecific altruism, i.e., cases in which recipients have not necessarily evolved specific behaviours to provide return benefits (sometimes referred to as by-product mutualism (Leigh, 2010)). Even without such specific behaviours, in our models inclusive fitness benefits can accrue to the focal individual by virtue of broader direct and indirect ecological consequences of investing in a recipient's success within a larger ecological community. Inclusive fitness gains could offset the cost of an initial investment when return benefits accrue to the focal individual (short-term reduction but lifetime increase in the focal individual's personal fitness) or to the focal individual's relatives (lifetime reduction in focal individual's personal fitness but net inclusive fitness gain through increased fitness of relatives).

Ecology, local adaptation, and cultural diversity

Although our models could apply to cooperation between interactants of potentially any species, we are especially interested in whether they can explain observed patterns in human conservation behaviours and ethics. ACR sheds light on some factors that may have influenced our ancestors' conservation behaviours and

continue to influence our own. Acting in accordance with ACR would help humans maximize inclusive fitness benefits of direct and indirect interactions with the species they encounter, so conservation behaviours will over time become adapted to local ecologies (Berkes & Turner, 2006; Boivin et al., 2016; Turner & Berkes, 2006). We propose that conservation ethics are also part of this dynamic system, regulating individual and collective behaviours in ways that promote and reinforce adaptive strategies for interacting with members of non-human species.

From this perspective, conservation ethics are not intellectual luxuries divorced from or imposed upon ecology, but components of evolved survival strategies sensitive to ecological and socio-cultural conditions. We emphasize that local adaptation does not necessarily imply evolved genetic differences among human populations with different conservation ethics, because local adaptation could reflect a general adaptive rule for (consciously or unconsciously) flexibly assessing costs and benefits of different behaviours in different socio-cultural and ecological contexts. Individuals could acquire particular expressions of that rule through trial and error or observing others. Innate or culturally acquired propensities to favour certain species over others encoded in beliefs, attitudes, and intuitions could promote adaptive conservation behaviours at the level of the individual. Social norms, formal and informal rules that regulate behaviour within groups, could reflect long-run costs and benefits of acting altruistically towards members of other species and reinforce adaptive individual conservation behaviours at the population level.

We do not suggest that conservation behaviours and ethics will always and everywhere be perfectly fine-tuned to local conditions. Difficulties accurately

assessing costs and benefits other species provide, time required to adapt to ecological and socio-cultural change, and barriers to collective action might cause conservation ethics to be suboptimal. These factors could help explain the apparent contradiction between the widespread existence of conservation ethics and patterns of biodiversity decline globally.

A key prediction of our models is that conservation ethics will be geared towards conserving locally important species (those with a high positive value for r or r'). People conserve species of particular local importance to human well-being by assigning them special cultural status, for example corn (*Zea mays*) among the Q'eqchí and Poqomchí peoples of Alta Verapaz in Guatemala (Mariscal, 2014), and fig trees (*Ficus spp.*) in several societies in Africa and Asia (Gadgil et al., 1993). By repeatedly selecting for traits that provide greatest return benefits, for example through dispersal, cultivation, intensification, or domestication (Jackley, Gardner, Djunaedi, & Salomon, 2016; Levis et al., 2017; Mohlenhoff & Codding, 2017; Zeder, 2017), people could consciously or unconsciously increase r or r' values of species over time.

Local adaptation implies that different human populations could assign a given species different moral status depending on its local r' value, which will reflect social and cultural practices as well as ecological community composition. Differential r' values could potentially explain why moral attitudes towards other species vary between and within human societies (Lute, Bump, & Gore, 2014; Macdonald et al., 2015; Teel & Manfredo, 2010). For example, in India people who live in close proximity to species that can negatively impact their well-being, such as tigers (*Panthera tigris*) and king cobras (*Ophiophagus hannah*), appreciate those species less

than people who live further from them (Kanagavel, Raghavan, & Veríssimo, 2014).

Our models also predict that under some conditions selection will favour anti-conservation behaviours (i.e. decreasing a recipient's success through persecution or extirpation, Figure 6.2). Model 3 predicts that people will invest more effort in conserving or persecuting species when doing so will provide greater net inclusive fitness advantages (right-shifted peaks on net inclusive fitness return curves, Figure 6.1) because of larger absolute magnitudes of ecological relatedness. We would therefore expect persecution ethics to evolve and perhaps find expression in people's support for efforts to limit deleterious effects of invasive or other species that disrupt established ecological dynamics (Crowley, Hinchliffe, & McDonald, 2017; Lute & Attari, 2017). In extreme cases, acting in accordance with ACR could lead people to extirpate categorically harmful species (negative values for r and r'), such as the bacterial agent of anthrax (*Bacillus anthracis*).

Political tensions regarding presence and abundance of controversial species such as large carnivores could reflect their differential r and r' values to different people. Although large carnivores can be extremely politically divisive, people tend to express favourable moral attitudes towards them (Goldman, de Pinho, & Perry, 2010; Lute et al., 2016; Macdonald et al., 2015), and invest large amounts of money and effort in conserving them despite significant habitat requirements and difficulty of effective conservation interventions (Packer et al., 2013; Weise, Stratford, & Van Vuuren, 2014). Large investments will be worthwhile from an evolutionary perspective when the net inclusive fitness benefits are sufficiently high. For example, this could apply to conserving or restoring large carnivores because they provide

public health benefits (O'Bryan et al., 2018) or increase community diversity by exerting top-down structuring effects that regulate consumer species at lower trophic levels (Ripple et al., 2014). People develop practices and technologies including physical deterrents and monitoring systems that mitigate harmful effects of large carnivores such as intense predation on domestic animals or other beneficial species (Lichtenfeld, Trout, & Kisimir, 2015; Shivik, 2006). These practices and technologies effectively diminish large carnivores' negative r values and thereby increase their r' values.

If conservation ethics are locally adapted, we would expect justifications for why certain behaviours towards members of other species are right or wrong, required or forbidden also to vary between human societies. Such justifications form part of societies' larger worldviews, including their cosmology, their interpretation of the place of humans in nature, and their more general moral systems (Berkes, Colding, & Folke, 2000; Diaz et al., 2018), for example different religious expressions of moral responsibilities towards non-humans (Bhatia, Redpath, Suryawanshi, & Mishra, 2017). Justifications for conservation can be scrutinized in terms of ethical assumptions and internal consistency, whether they emphasize economic value (McCauley, 2006), instrumental value (Schröter et al., 2014), intrinsic value (Maguire & Justus, 2008), or avoidance of supernatural punishment (Smith & Wishnie, 2000). From an evolutionary standpoint, justifications that effectively promote adaptive conservation behaviours can persist regardless of whether they are able to withstand rigorous philosophical or logical scrutiny.

Over time, adaptive conservation behaviours become supported by rules of

thumb, heuristics that condense complex local ecological knowledge into clear and simple guidance (Gadgil et al., 1993), and social taboos, informal prohibitions of particular behaviours (Colding & Folke, 2001). Across societies, rules of thumb and social taboos permanently or seasonally restrict access to locally important species and protect places associated with high biodiversity (Acheson & Gardner, 2010; Berkes, 2012; Colding & Folke, 2001; Gadgil & Berkes, 1991; Jones, Andriamarovololona, & Hockley, 2008; von Essen, 2017; Wood, Brandt, Pidgeon, & Radeloff, 2015). Such conservation-oriented rules of thumb and taboos safeguard benefits from local ecosystems but do not always originate from deliberate attempts to conserve species or communities (Colding & Folke, 2001). In this respect, they are functionally similar to rules promoting other adaptive behaviours, such as incest avoidance and food taboos, which have evolved across human societies to minimize risks associated with inbreeding and food-borne illness (Henrich & Henrich, 2010; Thornhill, 1991). Justifications for such rules regulate behaviour to maximize fitness in particular socio-cultural and ecological contexts, even though they often include no mention of adaptive advantages and are not always fully consciously understood by people who adhere to them (Henrich, 2015).

Obvious and non-obvious benefits

Benefits other species and biodiversity more generally provide to humans can be subtle and diffuse (Mace, Norris, & Fitter, 2012; Millennium Ecosystem Assessment, 2005; O'Bryan et al., 2018). As long as feedbacks between an individual's behaviour, ecological consequences, and inclusive fitness are sufficiently

strong, natural selection will favour conserving species with a sufficiently positive r' value, even when those species' apparent direct impact on humans is neutral or negative. Errors in ascertaining benefits provided by some species (overlooking non-obvious benefits, and therefore miscalculating r') could lead to actions that are detrimental to human well-being. Historical examples of such errors include extirpations of apex consumers that initiated trophic cascades resulting in significant changes to herbivore and autotroph populations (Estes et al., 2011), and attempts to eradicate scavengers or microbial communities that were beneficial to human health (Dethlefsen, McFall-Ngai, & Relman, 2007; O'Bryan et al., 2018). In these cases, people negatively affected the success of species with positive r' values, an action that could not satisfy ACR (Figure 6.2).

Because r represents direct benefits, we would expect natural selection to favour moral beliefs, attitudes, and intuitions promoting conservation of species with obviously high r values, such as those based on instrumental value to humans. To prevent mistakes of focusing exclusively on r, especially when r', which incorporates indirect ecological benefits, is vastly more positive, we would also expect natural selection to favour beliefs, attitudes, and intuitions promoting conservation of species whose benefits to humans are not obvious or even completely opaque. Assigning such species intrinsic or non-instrumental value could serve this purpose. People across societies do assign intrinsic or non-instrumental value to species, ecosystems, or "nature" more generally, although specific articulations vary (Choy, 2018; de Groot et al., 2011; Lute et al., 2016; Vucetich et al., 2015). Moral maxims urging respect for members of non-human species for reasons other than their immediately obvious

instrumental value have emerged in several traditions and schools of thought. They are expressed in terms appropriate to the society from which they emerge, for example mechanistic views of ecology (such as Leopold's injunction to keep every cog and wheel (Leopold, 1949) or Ehrlich and Ehrlich's disappearing airplane rivets metaphor (Ehrlich & Ehrlich, 1981)), kinship or community among humans and other species (such as in worldviews across cultures (Berkes, 2012; Callicott, 1994; Fatheuer, 2011; Qirko, 2017)), and direct calls for moral consideration of non-human interests (such as arguments for animal rights (Donaldson & Kymlicka, 2011) or criticisms of conservation agendas based purely on human interests (Chan et al., 2007; Noss et al., 2013)).

We would expect evolved conservation ethics to promote conservation of keystone species (Simberloff, 1998), whose structuring effects on ecosystems mean that their r' value is likely far more positive than their apparent impacts on human well-being might suggest. This could apply even to species that can be directly harmful (for example, by killing or injuring humans) and indirectly harmful (for example, by competing for prey species) but indirectly beneficial, such as large carnivores or venomous snakes. Human societies often give special protection to keystone species, for example through formal legal protections for top predators (Epstein, Lopez-Bao, & Chapron, 2015) and informal cultural protections for plants that provide food and habitat for a variety of other species (Berkes et al., 2000; Colding & Folke, 2001; Gadgil et al., 1993; Wood et al., 2015). Psychological dispositions such as assigning awe or charisma, reinforced by ascribing special cultural status (Macdonald et al., 2015; Pooley, 2016), could help conserve dangerous

species that pose direct threats but provide net benefits to humans through their broader ecological effects ($r' > r$).

Contemporary global conditions

If human societies were always to evolve more or less independently from each other, nuanced, locally adapted conservation behaviours would emerge through individual and social learning and be passed on to successive generations within groups (Bentley & O'Brien, 2015; Gadgil et al., 1993). Occasional environmental shocks could further refine locally adapted conservation behaviours (Berkes & Turner, 2006) and the ethics that support them (Acheson & Gardner, 2010). Continuous strong feedbacks between human behaviour, ecological consequences, and inclusive fitness could mean that ecological knowledge would become richer, conservation behaviours would become more deeply embedded in local traditions, and conservation ethics would become more refined and precisely adapted as a function of residence time. Traditional ecological knowledge is often the product of enduring associations between people, non-human species, and ecosystems (Berkes, 2012; Berkes et al., 2000), and comprises rich ecological expertise as well as moral components such as correct ways to relate to locally important species and places (Artelle et al., 2018; Houde, 2007; Jones et al., 2008; Kelbessa, 2005).

During the past few hundred years, human societies have become larger and more globally interconnected. As a result, people have encountered unfamiliar species and assemblages (Dawson et al., 2017; Hobbs, Higgs, & Harris, 2009), as well as unfamiliar cultural variants such as religious and economic practices whose adoption

might impact local ecological and socio-cultural relationships by altering land use, institutions, or livelihood strategies (Bentley & O'Brien, 2015; Mattison, Smith, Shenk, & Cochrane, 2016). Modern technologies have enabled faster and more intensive environmental exploitation (permitting substantially larger values for x), often with colossal negative effects on biodiversity (Dirzo et al., 2014; Rockström et al., 2009; WWF, 2016). During or following periods of rapid or substantial change, we would expect mismatches between the species people act to conserve and those it would be most advantageous to conserve. Cultural adaptation could help calibrate conservation behaviours and ethics to new or changing conditions more quickly than genetic adaptation.

Contemporary global conditions, many of which are associated with anthropogenic climate change (Boivin et al., 2016; Dirzo et al., 2014), are evolutionarily novel and could have loosened feedbacks between individual behaviours and ecological consequences (for example, melting polar ice caps due to land use change and increased consumption in lower-latitude cities). Contemporary global conditions have also created situations in which people experience negative consequences of others' environmentally harmful behaviour, even when they live far apart (for example, disproportionate costs of sea-level rise, deforestation, and biodiversity loss borne by people in lower-consumption regions). Selection pressures associated with ACR will be weaker when feedbacks are looser, because harmful consequences will not necessarily be borne by the people who cause them or their relatives. In extreme cases, when feedbacks are effectively non-existent, ACR may not regulate environmentally destructive behaviour, so selection could favour

environmental exploitation and jeopardize the survival of non-human populations and human populations who rely on them.

Collective action for conservation

Our models focus on decisions made by an individual. However, when a focal individual is a member of a group and benefits of conservation are available to other (possibly not genetically related) group members, that individual must incorporate additional considerations into decisions about whether to *do something*. For example, should the focal individual be the first to pay the cost of conservation behaviours? Should the focal individual pay the cost of conservation at all, or let others pay it and still reap the benefits? These are considerations about whether to cooperate with other group members (contribute to the cost of conservation) or defect (not contribute to cost of conservation), and require game-theoretic analysis. Incentives to defect could delay or derail effective conservation efforts.

Three general collective action scenarios could be particularly helpful in explaining why groups may struggle to conserve non-human populations, species, or communities, even when doing so would benefit every individual in the group. In such scenarios, conservation ethics derived from ACR might not be sufficient to motivate conservation. First, prisoner's dilemmas, in which an individual's optimal strategy is to defect unless group members are likely to encounter each other again and are able to keep track of and punish defectors (Axelrod & Hamilton, 1981; Ostrom, 1990). In prisoner's dilemmas, people are more likely to cooperate in small, stable groups and with people whom they are likely to encounter again. However, people are more likely

to defect in large, continuously changing groups in which group members rarely or never encounter each other again, making it difficult to track and punish defection (Van Cleve, 2015).

Second, public goods games, in which individuals will cooperate when the factor multiplying the sum of individual investments in an overall public good is sufficiently high relative to group size. In such scenarios, people would be most likely to pay the costs to conserve organisms with higher r or r' values because those provide largest return benefits. Public goods scenarios are especially relevant because they create opportunities for free-riding, in which defectors reap the benefits of others' cooperation. Efforts to coordinate conservation among diffuse groups of people, for example of organisms with large home ranges or migration routes, would increase opportunities for free-riding. Furthermore, wide-ranging species could have different r or r' values in different places, and low values in some places would potentially reduce the likelihood of coordinated conservation across large spatial scales. Collective action for conservation has typically been modelled as public goods games or prisoner's dilemmas, revealing how individual defection can generate large-scale environmental degradation (Dannenberg & Barrett, 2018; Hardin, 1968; Johnson & Levin, 2009; Levin, 2014; Ostrom, 1990).

Third, brave leader games (Shen, Reeve, & Herrnkind, 2010), in which everyone would benefit from conservation but no one benefits if no one pays the cost. In such scenarios, the initial cooperator pays a disproportionately high share of the cost and risks that cost being wasted if no one else follows. A "brave leader" will eventually emerge when the costs of not cooperating become sufficiently high, but

there can be a significant time lag before a brave leader will come forward. After a brave leader does emerge, other cooperators will follow and groups will contain a mixture of cooperators and defectors. Because both lag time and ratio of cooperators to defectors depend on the specific magnitude of costs and benefits, we would expect to see brave leaders emerge sooner and a higher proportion of people within groups willing to conserve organisms with higher r or r' values.

Implications for value of species debates

Integrating ecology and evolution into our understanding of conservation ethics can help explain why conservation ethics exist, why they vary, and why people assign greater value to some species than others. Recent conceptualizations of the value of biodiversity recognize that non-human species have direct and indirect positive effects on human well-being (Diaz et al., 2018; Mace et al., 2012; Millennium Ecosystem Assessment, 2005; O'Bryan et al., 2018). We formalize such effects in the form of r and r'. In our models natural selection operates upon a specific kind of instrumental value that incorporates indirect ecological effects and is measured in inclusive fitness.

Because selectively increasing the success of members of other species can sustain or increase the benefits they provide to humans, altruism towards members of other species may also be altruism towards humans (Wyatt, West, & Gardner, 2013). In a fundamental biological sense, human and non-human interests are not necessarily at odds. This win-win logic could help assuage moral divisions within the conservation community about the extent to which conservation should prioritize

benefits to humans or non-humans. An evolutionary perspective suggests that diverse conservation ethics have evolved to promote adaptive cooperation with members of other species in different socio-cultural and ecological contexts. Employing a variety of context-appropriate moral justifications and emphasizing commonalities between conservation ethics (Green et al., 2015; Hunter et al., 2014; Sandbrook et al., 2011; Tallis & Lubchenco, 2014) could therefore appeal to a larger and more diverse group of people and so help make conservation efforts more effective. Celebrating and sustaining local traditions, practices, and moral justifications for biodiversity (Artelle et al., 2018; Diaz et al., 2018) could ultimately engender more favourable conservation outcomes than promoting universal approaches or single "correct" moral justifications.

Conclusion

Established scholarship on conservation ethics empirically documents the values people attach to other species, and philosophically evaluates moral justifications for conservation. These approaches are important for describing the content of moral beliefs, attitudes, intuitions, and norms regarding other species, and scrutinizing assumptions underlying alternative conservation agendas. By integrating ecology and evolution into the study of conservation ethics, we offer complementary insights into the adaptive value of cooperating with members of other species and propose an explanation for the apparent contradiction between widespread conservation ethics and patterns of biodiversity decline globally. A comprehensive evolutionary understanding of why conservation ethics exist, why they vary, and their limitations could inform more effective efforts to conserve the diversity of life of

which we are part – a moral aspiration across cultures, and a win-win outcome for humans and non-humans.

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CHAPTER 7

CONCLUSION

The moral dimensions of wildlife conservation are unavoidable. To better understand and address contemporary conservation challenges, we need to better understand morality. And to better understand morality, we need to incorporate evolution. I have attempted to do that in this dissertation.

I believe that all aspects of human behavior – from our intuitions to our institutions – have been sculpted by evolution. I also believe that natural selection is currently acting on our environmental behaviors as we struggle to adapt to socio-cultural and ecological change at multiple scales. I therefore do not see wildlife conservation as a social process separate from and grafted onto ecological processes. Rather, I see all individual and collective environmental behaviors as ecological interactions with consequences upon which natural selection will operate.

While working on PTT and the evolution of ownership I became aware of an emerging evolutionary account of the origins and purposes of morality, derived primarily from scholarship in evolutionary theory, psychology, and animal behavior (Brosnan, 2014; Greene, 2013; Tomasello, 2016; Van Lange, Balliet, Parks, & Van Vugt, 2014). One recent element of this scholarship, the theory of morality as cooperation (MAC), proposes that morality (individual-level thoughts, beliefs, intuitions, and attitudes, and social norms about what is right and wrong) is a set of adaptations to promote cooperation and resolve conflict in recurrent challenges in social life (Curry, 2016).

MAC draws attention to the moral dimensions of ownership by proposing that ownership is one of seven foundational domains of morality. Empirical tests of MAC indicate that that ownership is a fundamental component of moral systems across cultures (Curry, Mullins, & Whitehouse, 2019), and a key component of people's moral psychology (Curry, Chesters, & van Lissa, 2018). This is because ownership (respecting possession) can resolve conflict – a point my co-authors and I make in some detail in chapter 5. While we were working on that project, we independently noticed several connections between ownership and morality. We reflect upon a few of these, for example how ownership can solve potential tragedies of the commons, and the relationships between resource inequality and ownership instability (chapter 5). Nevertheless, I believe we are only beginning to uncover the evolutionary significance of ownership as a form of cooperation, and corresponding links to morality. For example, in chapter 4 we emphasize the complexity of ownership as a bundle of sticks, control of which can be concentrated in a single individual or distributed among many individuals. Such complexity is currently missing from theoretical and empirical evolutionary work. If they are to provide a comprehensive evolutionary account of ownership, future evolutionary models and empirical studies will have to incorporate the bundle of sticks as well as other observed nuances in ownership arrangements such as inheritance rules, voluntary transfers, collective forms of ownership, and different enforcement mechanisms.

The cooperative evolutionary account of morality can also shed new light on persistent moral problems in biodiversity conservation. My co-authors and I found that it can help explain why people have moral beliefs about the value of other species, as

well as why those beliefs vary (chapter 6). In doing so, we also expanded the cooperative account of morality from cooperation between individuals of the same species to cooperation between members of different species. Chapter 6 complements existing empirical work on environmental ethics, which documents the various types of value people attach to other species and therefore illustrates how proximate psychological mechanisms can support conservation behaviors (Batavia et al., 2018; Bhatia, Redpath, Suryawanshi, & Mishra, 2017; de Groot, Drenthen, & de Groot, 2011; Kanagavel, Raghavan, & Veríssimo, 2014; Lute, Bump, & Gore, 2014; Vucetich, Bruskotter, & Nelson, 2015). Our evolutionary theory of conservation ethics does not compete with these studies but drills beneath debates about intrinsic, instrumental, and other values (Chan et al., 2016; Marvier, 2014; Noss, Nash, Paquet, & Soulé, 2013; Sandler, 2012) to reveal possible ultimate reasons (Tinbergen, 1963) why people value other species at all.

I believe that in time evolutionary theory will shed light on many more aspects of environmental morality and governance, including core concepts in PTT. The principles of PTT crop up in environmental ethics and natural resource management systems around the world and over time (Sagarin & Turnipseed, 2012; Takacs, 2008; Weiss, 1984; Wilkinson, 1988; Wood, 2012). Moreover, scholars and conservation practitioners argue that better applying these principles could help solve a host of contemporary environmental problems, from local to global scales (Blackmore, 2017; Giacomelli, Hare, Blossey, & Gibbert, in review; López-Bao, Chapron, & Treves, 2017; Sand, 2014; Torres & Bellinger, 2014; Treves et al., 2017, 2018; Wood, 2013). Why do principles of public control, fair and equitable access, and conservation for

future generations recur across societies throughout history? And why do they still resonate so strongly across cultures? I believe the answer is that these principles are adaptive: they help promote survival by resolving conflicts over natural resources and promoting long-term viability of ecosystems. People who live in societies that organize their environmental relationships according to such principles have higher inclusive fitness than people who live in societies that do not. That is not to say the specific principles of PTT are the only principles that help people live sustainably, survive, and reproduce – if that were so, we would expect little or no moral contestation over environmental governance strategies or the "correct" justification for environmental conservation. However, environmental practices inspired by these principles have proved successful enough for the principles to become established in social norms and stand the test of time. We as environmental scholars should pay attention to the tenacity and longevity of these principles, and examine whether there is evidence that they provide adaptive advantages, and if so in which socio-cultural and ecological circumstances.

Investigating human environmental behavior and morality from an evolutionary perspective can help explain why people behave sustainably in some situations but not in others (Johnson & Levin, 2009; Van Lange et al., 2014; Van Vugt, Griskevicius, & Schultz, 2014). This in turn could help us design wildlife conservation approaches that go with the grain of evolved psychology and harness our capacities for sustainable behavior. Such approaches are less likely to be morally contested and therefore more likely to be legitimate (Boyer & Petersen, 2012), so will be especially likely to succeed.

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APPENDICES

Appendix A: Measuring organism characteristics

Instrument for measuring organism characteristics in study 1 (using crows as indicative species). Items for each study organism were identical except for the name of the organism. To prevent priming effects, we randomized the order of items 2-18 along with an attention check question for every respondent.

	By participating in this study you will help us understand people's attitudes about wildlife. If you participate, you will see photographs of plants and animals. Participation is voluntary and you can choose to stop at any point during the study. You will receive payment for your participation if you complete the study, which includes answering some mandatory questions. We will not identify any individual participants from their answers. We will not report personal details of anyone who participates in the study, and we will only analyze and report answers in general terms. By clicking "Next" below and carefully answering a few short questions (approximately 15 minutes), you indicate that you voluntarily agree to participate in this study. Cornell Institutional Review Board office staff has approved this research as exempt (protocol number 1407004842). Please email cdh232@cornell.edu if you have any questions.
1	Do you know what a crow is?
	On this page you will see some general statements about crows. Please indicate how strongly you agree or disagree with each statement. If you are indifferent, please select "neither agree nor disagree". If you do not know whether you agree or disagree, please select "I don't know". You will then see two multiple choice questions about crows. For each question, please select the option that you believe is most accurate. If you are not sure, please select the option that seems most reasonable to you. If you do not know, please select "I don't know". Your responses will help us understand how people think about crows.
	Item
2	I am familiar with crows
3	Crows are good for the economy
4	Crows are good for the ecosystem
5	Crows are culturally important
6	Crows are a nuisance
7	Crows are harmful to humans
8	Crows are intelligent
9	Crows can experience pain and suffering
10	Crows can experience pleasure and enjoyment
11	Crows can make their own decisions
12	Crows cooperate with each other

Continued

	Item
13	Crows are wild
14	Crows are beautiful
15	Crows are charismatic
16	Crows are scary
17	Crows are disgusting
18	Crows are harmful to other animals and/or plants
19	Humans have moral obligations to crows
20	How much space does a crow use in a normal day?
21	How does a crow obtain its energy?

We asked respondents whether they knew the organism in question (item 1), with the option to answer either yes or no. If they answered yes, we asked them to respond to items 2-21 regarding that organism. If they answered no, we did not ask them to respond to any more items about that organism.

We measured respondents' level of agreement with items 2-19 using seven-point bipolar Likert scales (strongly disagree – strongly agree) with an additional option "I don't know." We coded those responses as ordinal categories (strongly disagree = -3, neither agree nor disagree = 0, strongly agree = 3).

We measured respondents' perceptions of how much space an organism uses (item 20) using six ordinal response categories with the additional option "I don't know." Ordinal ranks correspond with increasing space use.

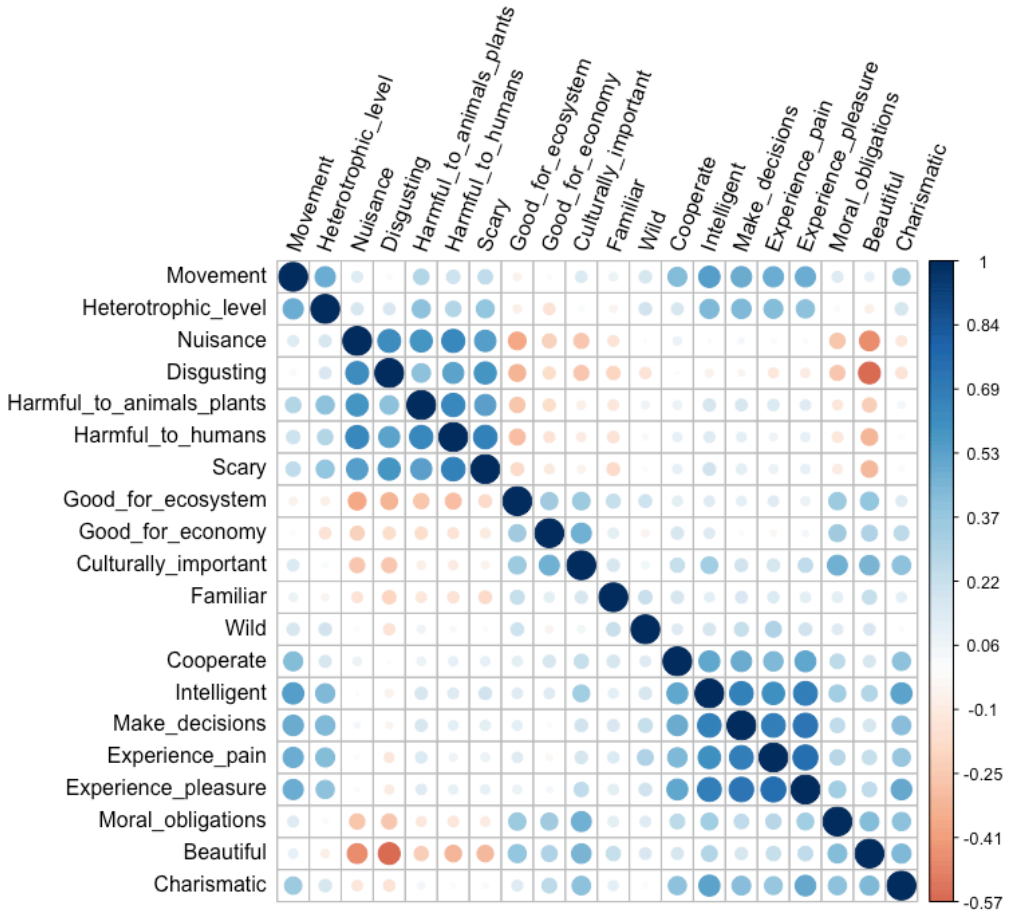
Response categories	***Ordinal rank***
Stays in one place	1
Less than 0.5 acres	2
0.5-0.99 acres	3
1-9.9 acres	4
10-99 acres	5
100 acres or more	6

We measured respondents' perceptions of how an organism obtains its energy (item 21) using six ordinal categories the additional option "I don't know." Ordinal ranks correspond with increasing heterotrophic level.

Response categories	***Ordinal rank***
Eats only plants	2
Eats mostly plants but some animals	3
Eats plants and animals equally	4
Eats mostly animals but some plants	5
Eats only animals	6
Obtains its energy some other way	1

We inserted an attention check question ('If you are reading this question, select "strongly agree"'). Possible responses were identical to those for items 2-18: seven-point bipolar Likert scales (strongly agree – strongly disagree) with an additional option "I don't know."

Correlation plot for all 20 characteristics across all 33 organisms in study 1. Blue circles indicate positive relationships, red circles indicate negative relationships. Circle size and color intensity indicate the strength of each relationship.



Appendix B: Measuring moral attitudes about wildlife ownership

Sample instrument for measuring moral attitudes about wildlife ownership (using six vignettes randomly assigned to vignette block 1 as indicators). To prevent priming effects, we randomized the order of vignettes within each block along with an attention check question for every respondent.

	By participating in this study you will help us understand people's attitudes about wildlife. If you participate, you will see photographs of plants and animals. Participation is voluntary and you can choose to stop at any point during the study. You will receive payment for your participation if you complete the study, which includes answering some mandatory questions. We will not identify any individual participants from their answers. We will not report personal details of anyone who participates in the study, and we will only analyze and report answers in general terms. By clicking "Next" below and carefully answering a few short questions (approximately 15 minutes), you indicate that you voluntarily agree to participate in this study. Cornell Institutional Review Board office staff has approved this research as exempt (protocol number 1407004842). Please email cdh232@cornell.edu if you have any questions.
	On the next few pages you will read short descriptions of scenarios involving people and wildlife. These scenarios will include a statement about who, if anyone, should have rights and obligations towards wildlife. Please indicate how strongly you agree or disagree with each statement. If you are indifferent, please select "neither agree nor disagree". If you do not know whether you agree or disagree, please select "I don't know". Your responses will help us understand how people think about wildlife.
	Item
1	There are deer on public land. If the government wants to collect and sell the live deer, it should have the right to do so.
2	There are deer on public land. The government should have an obligation to conserve the deer and their habitat on that land.
3	There are spiders on public land. No one should have the right to collect and sell the live spiders.
4	There are deer on private land. The landowner should have an obligation to conserve the deer and their habitat on that land.
5	There are oaks on public land. No one should have the right to kill the oaks.
6	There are spiders on private land. The landowner should have an obligation to conserve the spiders and their habitat on that land.

Summary results for mean support across all 54 experimental conditions, showing factor combinations and number of responses to each vignette (N), as well as mean agreement, standard deviation (SD), and standard error (SE).

Ownership type	*Stick*	*Organism*	*Location*	*N*	*Mean agreement*	*SD*	*SE*
Government	Conserve	deer	Private	130	0.32	1.94	0.17
Government	Conserve	deer	Public	123	1.15	1.64	0.15
Government	Conserve	oak	Private	118	0.51	1.84	0.17
Government	Conserve	oak	Public	97	1.21	1.69	0.17
Government	Conserve	spider	Private	97	-0.46	1.89	0.19
Government	Conserve	spider	Public	110	0.61	1.61	0.15
Individual	Conserve	deer	Private	121	0.28	1.80	0.16
Individual	Conserve	deer	Public	118	1.12	1.49	0.14
Individual	Conserve	oak	Private	130	1.12	1.62	0.14
Individual	Conserve	oak	Public	104	1.09	1.66	0.16
Individual	Conserve	spider	Private	123	-0.33	1.94	0.17
Individual	Conserve	spider	Public	126	0.02	1.66	0.15
No one	Conserve	deer	Private	93	-0.25	1.89	0.20
No one	Conserve	deer	Public	130	-0.94	1.70	0.15
No one	Conserve	oak	Private	93	-0.46	1.86	0.19
No one	Conserve	oak	Public	90	-0.78	1.88	0.20
No one	Conserve	spider	Private	127	0.28	1.77	0.16
No one	Conserve	spider	Public	103	-0.02	1.77	0.17
Government	Kill	deer	Private	96	-1.22	1.76	0.18
Government	Kill	deer	Public	95	-0.43	1.91	0.20
Government	Kill	oak	Private	105	-1.63	1.74	0.17
Government	Kill	oak	Public	117	-0.58	1.81	0.17
Government	Kill	spider	Private	109	-0.49	1.94	0.19
Government	Kill	spider	Public	104	0.34	2.03	0.20
Individual	Kill	deer	Private	109	0.75	1.94	0.19
Individual	Kill	deer	Public	95	-0.72	1.88	0.19
Individual	Kill	oak	Private	125	0.72	1.76	0.16
Individual	Kill	oak	Public	111	-1.78	1.63	0.15
Individual	Kill	spider	Private	97	1.58	1.49	0.15
Individual	Kill	spider	Public	130	0.05	1.90	0.17
No one	Kill	deer	Private	125	0.54	2.00	0.18
No one	Kill	deer	Public	108	0.77	1.82	0.18
No one	Kill	oak	Private	111	0.82	1.90	0.18
No one	Kill	oak	Public	122	1.37	1.55	0.14
No one	Kill	spider	Private	97	-0.79	1.85	0.19

Continued

Ownership type	***Stick***	***Organism***	***Location***	***N***	***Mean agreement***	***SD***	***SE***
No one	Kill	spider	Public	119	-0.70	1.82	0.17
Government	Transfer	deer	Private	117	-1.16	1.80	0.17
Government	Transfer	deer	Public	120	-0.41	1.91	0.17
Government	Transfer	oak	Private	108	-1.30	1.83	0.18
Government	Transfer	oak	Public	96	-0.13	1.61	0.16
Government	Transfer	spider	Private	108	-0.97	1.90	0.18
Government	Transfer	spider	Public	128	-0.08	1.91	0.17
Individual	Transfer	deer	Private	125	-0.14	2.03	0.18
Individual	Transfer	deer	Public	103	-1.20	1.92	0.19
Individual	Transfer	oak	Private	111	1.56	1.49	0.14
Individual	Transfer	oak	Public	109	-1.07	1.85	0.18
Individual	Transfer	spider	Private	130	1.03	1.75	0.15
Individual	Transfer	spider	Public	110	-0.16	1.85	0.18
No one	Transfer	deer	Private	125	1.17	1.86	0.17
No one	Transfer	deer	Public	120	1.03	1.84	0.17
No one	Transfer	oak	Private	93	0.43	1.90	0.20
No one	Transfer	oak	Public	109	0.81	1.83	0.18
No one	Transfer	spider	Private	105	0.22	1.99	0.19
No one	Transfer	spider	Public	119	0.53	1.87	0.17

Appendix C: Respondent demographics

In both studies, we measured respondents' demographic characteristics according to 12 factors. Where possible, to enable us to compare our sample to the most recent publicly available data on the U.S. population, we adapted item wording and response categories from the 2016 American Community Survey (ACS), conducted by the U.S. Census Bureau (https://www.census.gov/programs-surveys/acs/about.html). Our demographic questionnaire included 7 questions from ACS, one question borrowed from American National Election Studies (ANES, https://electionstudies.org/), and 5 questions we created.

Demographic questionnaire for studies 1 and 2

On this page you will see some general questions about your background. Your answers will be confidential. We will not use them to identify any individual participants. By answering these questions as accurately as you can, you will help us understand how people from different backgrounds think differently about wildlife.

Characteristic	**Item**	**Response categories**	**Source**
Sex	What is your sex?	Male Female	ACS
Age	What is your age?	15 to 19 years 20 to 24 years 25 to 29 years 30 to 34 years 35 to 39 years 40 to 44 years 45 to 49 years 50 to 54 years 55 to 59 years 60 to 64 years 65 to 69 years 70 to 74 years 75 to 79 years 80 to 84 years 85 years and over	ACS
ZIP code	What is your ZIP code?	U.S. ZIP code	Our question
Hispanic or Spanish origin	Are you of Hispanic, Latino, or Spanish origin?	Yes No	ACS

Continued

Race	What is your race? (Mark one or more boxes)	White Black or African Am. American Indian or Alaska Native Asian Indian Japanese Native Hawaiian Chinese Korean Guamanian or Chamorro Filipino Vietnamese Samoan Other Asian (for example Hmong, Laotian, Thai, Pakistani, Cambodian) Other Pacific Islander (for example Fijian, Tongan) Some other race	ACS
Education	What is the highest degree or level of school you have COMPLETED? Mark one box. If currently enrolled, mark the previous grade or highest degree received.	Less than high school diploma High school diploma or equivalency (e.g. GED) Some college, no degree Associate's degree Bachelor's degree Graduate or Professional degree	ACS
Income	What was your total household income during the PAST 12 MONTHS? (If your household income was a loss, you can enter a negative number)	Less than $10,000 $10,000 to $14,999 $15,000 to $24,999 $25,000 to $34,999 $35,000 to $49,999 $50,000 to $74,999 $75,000 to $99,999 $100,000 to $149,999 $150,000 to $199,999 $200,000 or more	ACS
Acreage	How many acres is your home on?	Less than 1 acre 1-9.9 acres 10 or more acres	ACS
Land ownership	How much total land do you own?	None Less than 1 acre 1-9.9 acres 10-99 acres 100 acres or more	Our question

Continued

Current rurality	How would you describe the area where you currently live?	Very urban 2 3 4 5 6 Very rural I don't know	Our question
Growing up rurality	How would you describe the area where you grew up?	Very urban 2 3 4 5 6 Very rural I don't know	Our question
Political orientation	When it comes to politics do you usually think of yourself as…	Extremely liberal Liberal Slightly liberal Moderate or middle of the road Slightly conservative Conservative Extremely conservative I don't know	ANES

Descriptive statistics of respondents' demographics for studies 1 and 2, and US Census data for 4 variables.

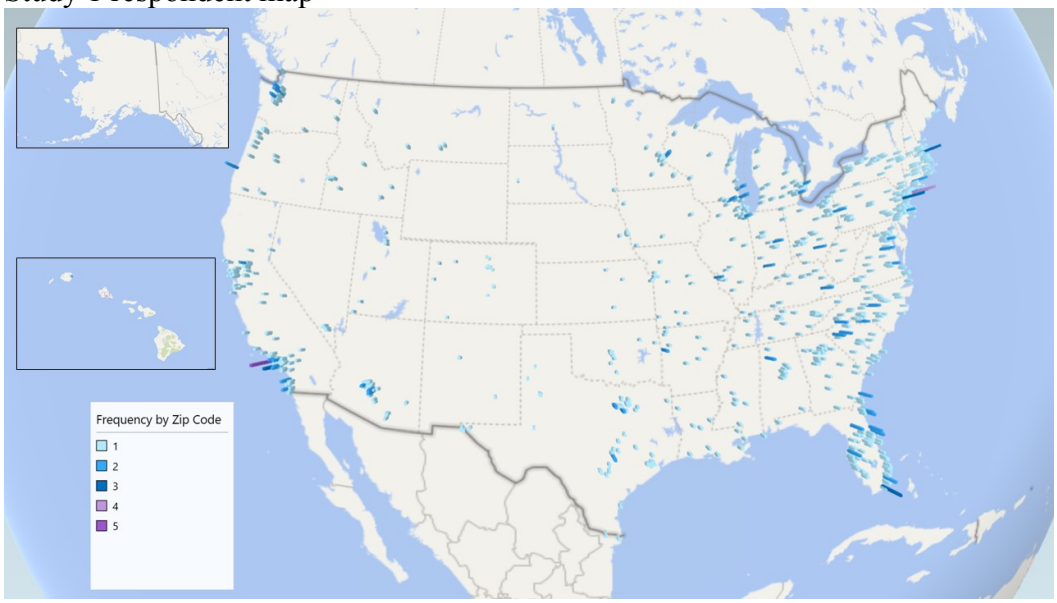
Variable		*Study 1(%)*	*Study 2(%)*	*ACS (%)*
Sex	Male	52.0	57.6	49.2
	Female	48.0	42.4	50.8
Age	15 to 19 years	1.1	0.8	6.9
	20 to 24 years	8.5	9.7	6.7
	25 to 29 years	20.7	23.0	8.0
	30 to 34 years	20.2	24.9	6.0
	35 to 39 years	15.4	15.0	9.3
	40 to 44 years	9.4	7.7	5.7
	45 to 49 years	6.9	5.1	4.9
	50 to 54 years	5.2	4.7	6.5
	55 to 59 years	4.7	4.3	6.2
	60 to 64 years	3.9	1.8	5.3
	65 to 69 years	2.5	1.7	3.9
	70 to 74 years	1.0	1.0	2.7
	75 to 79 years	0.1	0.2	1.6
	80 to 84 years	0.2	0.1	0.9
	85 years and over	0.0	0.2	1.3
Education	Less than High school diploma	0.2	0.3	13.0
	High school diploma or equivalency	11.0	10.0	27.5
	Some college, no degree	25.3	22.0	21.0
	Associate's degree	13.6	10.5	8.2
	Bachelor's degree	39.0	43.9	18.8
	Graduate or Professional degree	10.1	13.3	11.5
Income	Less than $10,000	6.5	4.5	6.7
	$10,000 to $14,999	5.8	3.9	4.8
	$15,000 to $24,999	10.2	9.3	10.0
	$25,000 to $34,999	13.9	14.4	10.0
	$35,000 to $49,999	18.0	19.8	13.0
	$50,000 to $74,999	23.0	22.0	17.7
	$75,000 to $99,999	11.9	13.5	12.3
	$100,000 to $149,999	7.0	8.5	14.0
	$150,000 to $199,999	3.0	3.1	5.8
	$200,000 or more	0.8	1.2	6.4
	Median household income (dollars)	35,000-49,999	35,000-49,999	57617.00

Continued

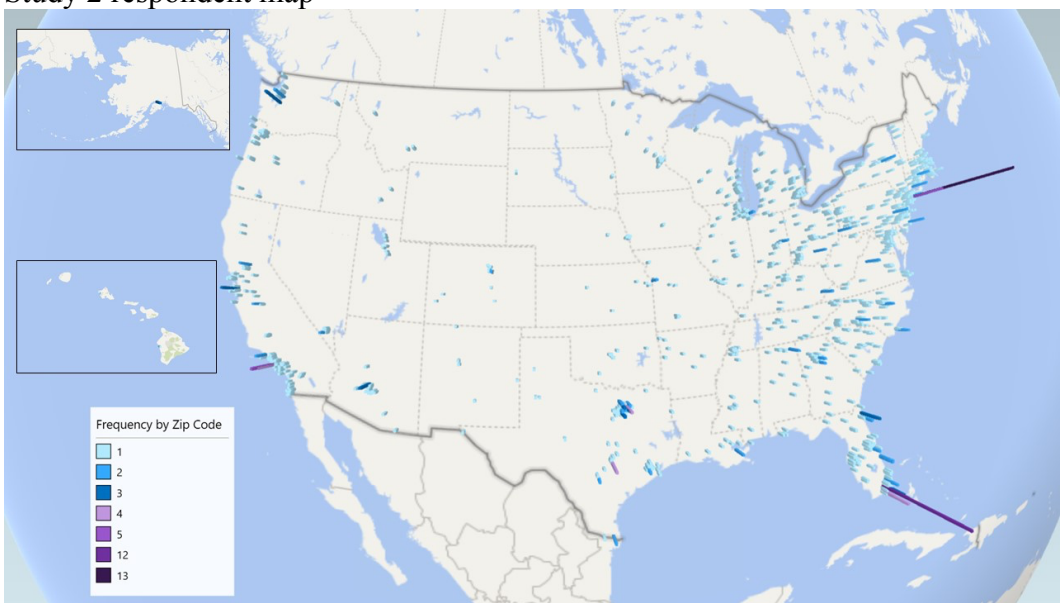
Variable		***Study 1(%)***	***Study 2(%)***	***ACS (%)***
Acres home	Less than 1 acre	77.4	76.3	Not reported
	1 to 9.9 acres	20.0	21.7	
	10 acres or more	2.4	2.1	
Total land	None	44.0	39.0	Not reported
	Less than 1 acre	35.4	40.2	
	1 to 9.9 acres	17.3	17.0	
	10 to 99 acres	2.5	3.3	
	100 acres or more	0.7	0.5	
Rural current	Very urban	14.6	14.6	Not reported
	2	17.0	13.7	
	3	19.8	18.7	
	4	17.1	17.1	
	5	13.8	16.6	
	6	9.9	10.4	
	Very rural	7.9	9.0	
Rural past	Very urban	13.5	12.1	Not reported
	2	13.3	13.0	
	3	16.4	18.0	
	4	17.6	17.5	
	5	14.9	15.3	
	6	13.6	13.2	
	Very rural	10.1	10.5	
Politics	Extremely liberal	13.7	10.3	Not reported
	Liberal	26.8	27.3	
	Slightly liberal	15.0	12.8	
	Moderate or middle of the road	17.3	20.1	
	Slightly conservative	10.6	10.1	
	Conservative	11.7	13.6	
	Extremely conservative	4.3	5.1	

For each study we used Microsoft Excel to create a map of respondents by ZIP code. Bar locations are respondents' ZIP codes, bar height and color are frequency counts of respondents in that ZIP code.

Study 1 respondent map



Study 2 respondent map



Appendix D: Organisms and images

organism	*class*
vole	mammal
squirrel	mammal
bat	mammal
fox	mammal
deer	mammal
raccoon	mammal
cougar	mammal
bear	mammal
pine	plant
oak	plant
redwood	plant
birch	plant
moss	plant
fern	plant
cattail	plant
hummingbird	bird
cardinal	bird
blue jay	bird
owl	bird
crow	bird
eagle	bird
woodpecker	bird
bumblebee	invertebrate
yellow jacket	invertebrate
dragonfly	invertebrate
lady bug	invertebrate
grasshopper	invertebrate
spider	invertebrate
garter snake	herptile
rattlesnake	herptile
salamander	herptile
toad	herptile
lizard	herptile

We sourced images of study organisms on Flickr (www.flickr.com). We used only images with creative commons licenses permitting unrestricted use. We credited Flickr users whenever we used their images.

Bat
Kelly Colgan Azar on Flickr

Bear
Jethro Taylor on Flickr

Deer
Blake Matheson on Flickr

Fox
wplynn on Flickr

Mountain lion
digitalART2 on Flickr

Raccoon
Sergey Shpakovsky on Flickr

Squirrel
watts_photos on Flickr

Vole
Chimp82 on Flickr

Birch
Plant Image Library (close),
Maggie_and_her_camera (distant) both on Flickr

Cattail
ruffin_ready on Flickr

Fern
Robyn Turner on Flickr

Moss
coniferconifer on Flickr

Oak
CamelliaTWU (close),
wlcutler (distant) both on Flickr

Pine
Harum.koh (close), scott.zona
(distant) both on Flickr

Redwood
Plant Image Library (close), campsjc (distant) both on Flickr

Blue jay
Mr.TinDC on Flickr

Cardinal
DrPhotoMoto on Flickr

Crow
Jon. D. Anderson on Flickr

Eagle
Bill Chitty on Flickr

Hummingbird
coltfan909 on Flickr

Owl
Mark Chambers on Flickr

Woodpecker
ebeckes on Flickr

Bumblebee
Jason Means on Flickr

Dragonfly
jwinfred on Flickr

Grasshopper
platycryptus on Flickr

Ladybug
treegrow on Flickr

Spider
Livingston Frost Photography on Flickr

Yellowjacket
Mean and Pinchy on Flickr

Garter snake
carla kishinami on Flickr

Lizard
aspidoscelis on Flickr

Rattlesnake
amdubois01 on Flickr

Salamander
DaveHuth on Flickr

Toad
brian.gratwicke on Flickr

Appendix E: Data screening

Study 1

We began with 2994 responses, three from each of our 998 respondents. We removed 264 responses because respondents reported they did not know the organism in question (and did not answer questions for that organism).

Before performing statistical analyses we inspected data for each completed set of organism items, and excluded every set for which we found evidence that the respondent did not complete it reliably, using three screening measures. (1) After answering items about a particular organism, we asked respondents to identify it from photographs of all study organisms from the same class (mammal, bird, plant, invertebrate, or herptile) (Appendix D). If respondents did not correctly identify an organism from its photograph, we removed their responses regarding that organism from our data set. We removed 140 responses because respondents failed to identify an organism from its photograph. (2) If people took what we considered to be too short (less than 31.5 seconds, 1.5 seconds per item) or too long (longer than mean response time for 21 items plus three standard deviations, 351.96 seconds) to respond to items about an organism, we removed their responses for that organism. (3) We inserted an attention check randomly among the 18 Likert-scale organism characteristics items. This attention check ('If you are reading this question, select "strongly agree"') looked identical to all other Likert scale items. We removed 65 responses because respondents failed the attention check. We removed 121 total responses based on timing, 68 short responses and 53 long responses. Our final data set therefore contained 2414 responses.

Study 2

We began with 7500 unique responses to vignettes, six from each of our 1250 respondents. We removed 42 responses from seven respondents who failed to finish the survey completely. We removed all "I don't know" responses to vignettes, 131 responses in total. Before performing statistical analyses we inspected data for each completed survey response (vignette set and demographic questions), and excluded every set for which we found any evidence that the respondent did not complete it reliably, using three screening measures. (1) After responding to vignettes, we asked respondents to identify one of the three organisms (oak, spider, or deer) from photographs of all organisms from the same class used in study 1 (plant, invertebrate, or mammal) (Appendix D). If respondents did not correctly identify an organism from its photograph, we removed all of their responses from our data set. We removed 694 responses because respondents failed to identify an organism from its photograph. (2) If people took what we considered to be too short (less than 120 seconds) or too long (longer than mean plus three standard deviations, 2151 seconds) to submit their completed task on MTurk, we removed all of their responses from our data set. We removed 449 total responses based on timing, 281 short responses and 168 long responses. (3) We inserted an attention check randomly within each vignette set. This attention check ('If you are reading this question, select "strongly agree"') looked identical to all other items in the set. We removed 140 responses because respondents failed the attention check. Our final data set therefore contained 6044 responses.

Appendix F: Measuring model parameters[5]

We focus on how our models apply to human conservation behaviours. However, interactions described by our models are not necessarily restricted to humans. They could therefore provide a framework for studying interspecific altruism more generally, as well as the value of one species to another. It would be possible to experimentally manipulate interactions between two species, and measure the value of members of species B (recipient) to members of species A (focal individual). This approach would permit researchers to evaluate, for example, the value of particular plant species to leafcutter ants (*Atta* or *Acromyrmex* spp.), the value of particular pollinators to plants they pollinate, or the value of particular prey species to predators.

Researchers could independently measure key model parameters:

What to measure	**Corresponding model parameter**
(i) Baseline inclusive fitness of a focal individual who does not invest in a recipient and receives no benefit from a recipient	z
(ii) Effect of a focal individual's investment on a recipient's success (difference between how well the recipient does with or without an investment)	x
(iii) Inclusive fitness change (over and above z) for a focal individual who receives a return benefit from a recipient but does not itself invest in the recipient	rx
(iv) The value in (iii) above, divided by the value in (ii) above ($rx \div x$)	r
(v) Difference between the inclusive fitness change of an individual that receives a return benefit but does not invest in a recipient, and the inclusive fitness change of an individual that receives a return benefit and does invest in a recipient	c

[5] Hare, D., Blossey, B., & Reeve, H. K. (2018). Value of species and the evolution of conservation ethics. *Royal Society Open Science 5*: 181038. Supplementary material.