Biological Conservation 197 (2016) 47–52

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Discussion

Improving habitat for game animals has mixed consequences for biodiversity conservation

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ARTICLE INFO

Article history:
Received 7 October 2015
Received in revised form 26 February 2016
Accepted 27 February 2016
Available online 9 March 2016

ABSTRACT

Habitat alteration to benefit hunted species has been implemented for centuries. These practices are most prevalent on public and private lands where management is funded through hunting licenses and hunting tourism. Habitat management for game species is globally widespread and can take diverse forms — e.g. tree reduction to enhance forage for deer in the United States and burning moorlands in Scotland to increase habitat for wading birds. Yet the effects of these practices on non-targeted animals are poorly understood. Given limited funding for conservation and increasing threats to biodiversity, understanding the shared benefits and unintended consequences of game management for other species is important. To quantify and characterize existing studies on this topic, we synthesized scientific literature that measured the effects of game management on non-targeted animals. We found surprisingly few studies ($n = 26$), and the outcomes of these studies illustrated that, through diverse mechanisms, game management can have positive, negative or no effect on non-target taxa. Our analysis suggests that the explicit evaluation of the effects of game management on other species is rare but warranted, offering opportunities to advance ecological understanding and conservation of both target and non-target species. We propose a research agenda to fill knowledge gaps and catalyze a conversation about an approach to wildlife management that affects a large fraction of public and private land.

1. Introduction

In the aftermath of early industrialization, many animal populations declined globally due to habitat loss, overexploitation, and pollution (Leopold, 1933; Sotherton, 1998; Vitousek et al., 1997). As awareness of this loss reached policy-makers and the public, preserving and improving habitat quality for wildlife, particularly hunted species, became a priority in North America (Leopold, 1933), Europe (Phillips, 2004) and colonial-ruled countries in Africa (Phillips, 2004). In many cases, manipulating natural communities to improve habitat quality for these species has been remarkably successful at reversing population declines among harvested species. For example, at the turn of the century land preservation (e.g., U.S. National Wildlife Refuge system), game laws (e.g., U.S. Lacey Act), and habitat management (e.g., forest restoration) stabilized many populations of declining North American mammals (Leopold, 1933; U.S. Fish and Wildlife Service, 2006). Similarly, reinstating natural processes (e.g., prescribed fire) in heather moorlands — has restored populations of commonly hunted wading birds throughout the UK (Brennan and Kuvlesky, 2005; Pack et al., 2013; Tharme et al., 2001). Habitat altering practices are widely implemented and well funded across the globe. For example, 58% of the land area in Scotland is managed for hunting (HUNT, 2015a), hunting estates cover approximately 80% of the Spanish territory (HUNT, 2015b), and hunting influences the management of 94% of the land in Slovenia (HUNT, 2015c).

More recently, however, both game and non-game species are faced with novel anthropogenic pressures, such as climate change (Parmesan and Yohe, 2003), as well as rapid rates of habitat loss and fragmentation from energy development (Jones et al., 2015; Northrup and Wittemyer, 2013) and urbanization (McKinney, 2002). Due to the synergistic effects of these changes (Foley et al., 2005) and the continued practice of manipulating habitat for game species across private and public lands, we argue that evaluating the effects of game management on biodiversity is warranted.

1.1. Hunting and conservation

We recognize that hunting provides diverse and substantial economic (PACEC, 2006; Schulz et al., 2003; U.S. Fish and Wildlife Service, 2014), social (Heberlein et al., 2008; Mangun, 1992), and ecological (Lindsey et al., 2006) benefits, and that habitat management for hunted species has advanced the fields of ecology and conservation biology (Leopold, 1933). We are not advocating that hunting be reduced or prohibited on either public or private lands. Nor do we set out to

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http://dx.doi.org/10.1016/j.biocon.2016.02.032
0006-3207/

diminish the dedication of the large number of hunter-based special interests groups and state and federal agencies to the conservation of both game and non-game animals (North American Bird Conservation Initiative, 2014; Lebbin et al., 2010). Rather, because game management has the potential to have a significant impact on biodiversity by altering habitat structure, food availability and intra- and inter-specific interactions on large tracts of land (Arroyo and Beja, 2002; Leopold, 1933), we suggest conservationists objectively examine the ecological consequences of the game management paradigm that remains so prevalent.

Funding for the management of game species often exceeds spending on all other species, including those that are threatened and endangered. In the U.S., the state of Washington spends approximately $18.6 million biennially to maximize hunting opportunities and sustain game animal populations — compared to $13.3 million on non-game species protection (Anderson and Larson, 2013). The state of Minnesota budgeted $206.2 million in 2014–2015 for game management and the protection of game species (Minnesota Division of Natural Resources, 2013), whereas non-game wildlife management is funded through a $179.8 million budget that is split among parks and zoos (Minnesota Division of Natural Resources, 2013). These examples illustrate funding scenarios for game management and non-game management in just two U.S. states; these values are likely to vary substantially among hunted species and regions of the world.

Because traditional funding support for wildlife conservation has come almost exclusively from user fees and taxes on goods for hunting (Mangun, 1992); there is an enormous economic incentive for state and federal agencies to manage for game species on public lands (Draycott et al., 2008). Hunting licenses in the U.S. totaled approximately $790 million in 2013 (U.S. Fish and Wildlife Service, 2013), and the special U.S. excise taxes and duties on hunting gear under the Wildlife Restoration Act generate approximately $550 million annually (Corn and Gravelle, 2013). In 2014, the U.S. distributed $1.1 billion dollars from these excise tax revenues to state fish and wildlife agencies for fish and wildlife management (U.S. Fish and Wildlife Service, 2014). In the UK, hunters spend approximately $16.3 million annually on hunting licenses and firearm certificates (PACEC, 2006). Hunting generates $83.8 million annually from reindeer licenses alone in Iceland (Matilainen and Keskinarkaus, 2010). Hunting upland game birds in Scotland is reported to contribute $365 million annually to the Scottish economy (Irvine, 2011). Hunting tourism results in approximately $68.3 million of revenue annually in South Africa, $27.6 million in Tanzania, $18.5 million in Zimbabwe and $12.6 million in Botswana (Lindsey et al., 2006; Pack et al., 2013). Further, private landowners have an economic incentive to manage their lands specifically for game species, because recreational hunting by paying clients provides important supplemental income (Sage et al., 2005).

1.2. Objectives

Although land ownership and funding mechanisms vary (Pack et al., 2013), strategies to increase the populations of hunted species have been implemented for centuries on every continent except Antarctica (Arroyo and Beja, 2002; Damm, 2008; Leopold, 1933; Pack et al., 2013; Redford and Bodmer, 1995). Despite the long history, ubiquitous use, and global relevance of these practices, information on the extent of habitat manipulation is largely lacking, making it difficult to quantify the ecological consequences of game management (Arroyo and Beja, 2002). We systematically surveyed the scientific literature to evaluate the state of knowledge on this topic. Specifically, we address the following research questions: 1) How many studies have investigated the effects of game management strategies on non-target species?, 2) What proportion of these studies document positive, negative or no effect of various game management activities on non-target taxa?, and 3) What are the mechanisms underlying these effects? We draw on this literature review to identify potential sources of conflict and synergy between game management and biodiversity conservation, and we conclude by discussing priorities for research, policy and practice.

2. Approach

To quantify the number of previous papers on this topic, and the frequency of results that demonstrated positive, negative or no effect of game management on non-target taxa, we searched the scientific and gray literature using multiple combinations of relevant keywords (see online Appendix for keywords and search criteria). We limited the scope of our search to empirical studies that investigated the effects of habitat management for terrestrial game species (native and introduced) on native terrestrial animals. We define direct effects as the direct and unmediated impact a management activity has on the demography or behavior of an individual species or group of species. In contrast, indirect effects of habitat alteration on a species/group are mediated through changes in abundance of another taxa; these can include apparent competition, trophic cascades (predator–prey interactions), or a change in the physical or chemical properties of the habitat by this species/taxa (Moon et al., 2010).

3. Results and discussion

Our examination of the literature found remarkably few articles ($n = 26$) that directly evaluated the effect of game management practices on non-targeted wildlife (Fig. 1, Table A1). These articles measured the effects of game management on diverse non-targeted taxa that included birds (81%), mammals (23%), herptiles (4%) and/or arthropods (8%). A total of 43 relationships were reported; 40% of these effects were positive for non-targeted species, 37% were negative, and the remaining 23% found no effect (Table A1). In the following sections, we draw on these studies to highlight several mechanisms through which game management affects non-target animals.

3.1. Positive effects

Managing land for game species has several documented shared benefits for non-targeted species. Many protected areas and the full suite of wildlife they support would have been degraded in the absence of hunting and active land preservation for the benefit of game species (Tharme et al., 2001). In addition, some management practices that closely mimic ecological processes – e.g. prescribed fire and mechanical removal of forest cover as an alternative to natural wildfires – have demonstrated positive effects on animal communities adapted to natural disturbance regimes (Arroyo and Beja, 2002; O'Meara et al., 1981; Radke et al., 2008; Tapper, 1999).

Previous studies demonstrate that managing specifically for game species can act as an umbrella to conserve habitat for a large number of non-game species (Hanser and Knick, 2011; Karl et al., 2005). For example, Hanser and Knick (2011) found that maintaining sagebrush-dominated plant communities as habitat for greater sage grouse (*Centrocercus urophasianus*) in the Western U.S. will likely protect habitat for 13 non-game passerine birds. Similarly, Idaho's Wildlife Management Areas provide valuable habitat for a variety of non-game species — i.e. reptiles, birds and non-game mammals (Karl et al., 2005). These benefits to non-targeted species are likely a function of the broad range of habitats that are protected within those areas (Hanser and Knick, 2011), rather than the consequences of specific management practices.

In some cases, habitat alteration to create new vegetation communities that benefit game species – e.g., woodlands converted to grasslands – also benefits species that prefer the new habitat characteristics resulting from the management practice. For example, removing shrub species from wetlands in the Great Lakes region of the U.S. maintains high-quality habitat for game birds, such as sharp-tailed

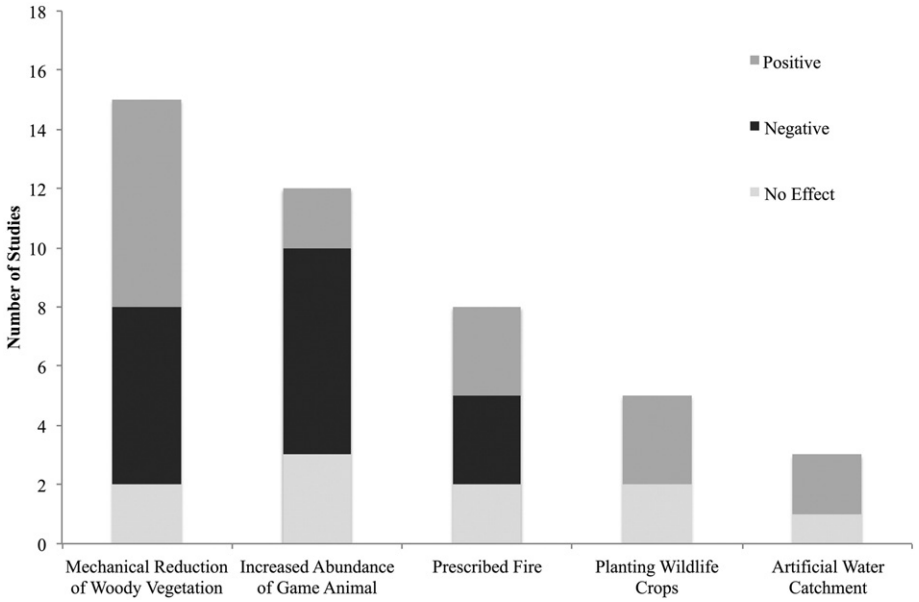

Fig. 1. The number of studies that examine the effect of game management on non-target species and met the selection criteria for our review (online Appendix). The frequency of studies reporting positive, negative or no effect of several types of game management on non-target species are illustrated. See Table A1 for a full list of studies and taxonomic groups.

grouse (*Tympanuchus phasianellus*), and simultaneously increases the abundance of non-game bird species that require open wetland habitat, such as Le Conte's sparrow (*Ammodramus leconteii*) and sedge wren (*Cistothorus platensis*) (Hanowski et al., 1999).

Artificial supplementation of food and water has also had potential benefits for non-targeted wildlife species (Table A1). Planting game crops – non-agricultural crops that attract game species – is a common tool employed by European farms to increase and diversify farm income through hunting (Sage et al., 2005). Studies in Europe found that farms that planted "game crops" had a positive effect on non-game birds, more so than nearby conventional farms (Caro et al., 2015; Parish and Sotherton, 2004; Sage et al., 2005). Construction of water catchments is a common game-habitat improvement technique throughout the southwestern U.S. (Lynn et al., 2008). In Arizona, native bats, mammalian predators, and rodents were observed using water catchments more often than the games species for which they were designed, such as mule deer (*Odocoileus hemionus*), Gambel's quail (*Callipepla gambelii*), and dove (*Zenaida* spp.) (O'Brien et al., 2006). Equipped with a better understanding of the factors associated with shared benefits of game management for non-targeted species, land managers may be able to strategically implement management practices that account for these factors — an approach that could increase populations of hunted species while also protecting the full suite of biodiversity under their stewardship.

3.2. Negative effects

Habitat manipulation to benefit game species can have direct or indirect negative effects on non-targeted species through diverse mechanisms, including competition for resources, trophic cascades, and inter-specific interactions (Table A1). For example, the increased abundance of wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), and aoudad sheep (*Ammotragus lervia*), decreased the available resources for closely related native species of high conservation concern in Spain and across the Iberian Peninsula (Acevedo et al., 2007; Lozano et al., 2007). In the UK, Newson et al. (2012) found that the increase of three commonly hunted deer populations – Reeves' muntjac (*Muntiacus reevesi*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*) – corresponded with substantial declines in the abundance of chiffchaff (*Phylloscopus collybita*), common nightingale (*Luscinia megarhynchos*), willow warbler (*Phylloscopus trochilus*), willow tit (*Poecile montanus*) and song thrush (*Turdus merula*). These five species are associated with dense understory vegetation that was significantly reduced due to browsing by the ungulates. Similarly, the overabundance of elk at the National Elk Refugee in Wyoming, USA, increased browsing pressure and decreased habitat availability for migratory shorebirds and songbirds that depend on vegetation cover (Matson, 2000).

Removing or reducing tree cover and shrub cover has been shown to have negative effects on non-target species that prefer woodland and shrubland habitats (Brown et al., 2014; Gruver and Guthery, 1986; Kozicky and Fulbright, 1991; O'Meara et al., 1981; Tharme et al., 2001; Yahner, 1984, 1993). For example, mosaic-like clear-cutting of forest for ruffed grouse (*Bonasa umbellus*) management in Pennsylvania had a positive effect on the abundance of some birds such as blue-jays (*Cyanocitta cristata*), but decreased the abundance of red-eyed vireo (*Vireo olivaceus*) and ovenbird (*Seiurus aurocapilla*) — both forest obligate birds (Yahner, 1984, 1993). Although, habitat management for game species can benefit non-targeted species with similar habitat preferences, these studies demonstrate that game management can also have an adverse effect on species that thrived under original conditions.

3.3. No effect

In some cases game management practices had no significant detectable effect on non-targeted species (Table A1). For example, Radke et al. (2008) found no short-term effect of prescribe fire on lizard abundance in central Texas, and Petersen and Best (1987) found no positive or negative effects from small mosaic-like prescribed fires on non-target bird species that preferred open habitats. In both studies fire was used as a management tool to improve habitat conditions for game species. As aforementioned, creating artificial water catchments and planting wildlife crops were shown to have positive effects on non-targeted species (Caro et al., 2015; O'Brien et al., 2006; Parish and Sotherton, 2004; Sage et al., 2005), but also had no effect on some non-targeted species in studies by Lynn et al. (2006) and Stoate (2002).

4. Recommendations for science, policy, and practice

Land managers are frequently faced with the challenge of managing for both game species and non-game species with limited funding and

limited access to information needed to make science-based decisions (Noon et al., 2009). Our examination of the literature suggests that few studies explicitly measure how game management practices affect non-game wildlife. Greater scientific scrutiny of game management practices by game and non-game scientists could provide greater shared benefits to hunters, hunted species, and other biodiversity.

4.1. Priorities for research

To remedy these knowledge gaps, we offer a shortlist of ecologically intriguing and policy relevant questions intended to guide future research on this topic (Table 1). In addition to direct effects, it is likely that mechanisms, such as competitive interactions, predator–prey dynamics, trophic cascades, and changes in ecosystem function (Levin et al., 2009; Osmond et al., 2004), are driving the interactions between game management and non-targeted species. Applying principles of community ecology and ecosystem science to game management research provides an unprecedented opportunity to advance science while also building the foundation for well-informed land management practices.

A study reporting that habitat management for endangered non-game species provided complimentary benefits for game species suggest that research on this related topic is also warranted (Masters et al., 1996). In western Arkansas, pine-bluestem habitat restoration and red cockaded woodpecker (*Picoides borealis*) management (low intensity prescribed fire) increased preferred forage of white-tailed deer (*Odocoileus virginianus*; Masters et al., 1996). This outcome suggests that there may be additional untapped opportunities for management actions that are mutually beneficial for both games species and species of highest conservation concern.

Finally, obtaining publically available data on funds spent on management activities for particular game and non-game species is often difficult, and these values are likely to vary substantially by management activity, taxonomic group, and region (Anderson and Larson, 2013; Mangun, 1992). We recommend compiling and comparing these data in regions where both game management and biodiversity conservation are a priority. This, combined with a better understanding of the ecological costs and benefits of managing for hunted species, would enable land managers and society to more fully evaluate public investment in game and non-game management.

Table 1
Priorities for future research: questions that will enhance understanding of the potential unintended consequences of game management practices on non-targeted species.

A research agenda for assessing the consequences of game management on biodiversity
Through what mechanisms does habitat management that increases the abundance of a single game species have direct or indirect effects on non-target species?
Are these mechanisms predictable based on the characteristics of the game and non-game species, and/or the characteristics of the ecosystem?
Does food and water supplementation for game species have broad co-benefits for non-game species, or do some species (e.g. introduced plants or animals) benefit at the expense of others?
Does habitat manipulation designed to mimic natural disturbance (e.g. mechanical clearing or prescribed burns in lieu of wildfire) have differential effects on game and non-game species?
Do the long-term effects of habitat manipulation for game species on non-targeted animal communities differ from measured short-term effects?
Is there a threshold in the extent or intensity of habitat manipulation, which precipitates a state-shift in the community composition of non-game species?
Are hunted species effective surrogate species? Does large-landscape conservation designed to benefit hunted species provide sufficient viable habitat for native non-game species?

4.2. Revisiting funding sources for conservation

We suggest that conservationists revisit available funding streams for conservation. Hunters and anglers traditionally pay the user fees and taxes that support wildlife programs. Today, however, there are less people engaged in recreational hunting, as evident in a steady decline of license sales in the U.S. (Brown et al., 2000; Enck et al., 2000; Mangun, 1992; Schulz et al., 2003) and throughout Europe (Heberlein et al., 2008). In contrast, an increasingly large number of land users participate in non-consumptive wildlife recreation. For example, in the U.S., 13.7 million people consider themselves "hunters", compared with the 71.8 million people that consider themselves "wildlife watchers" (U.S. Fish and Wildlife Service, 2012). Nearly half (48%) of all Americans participate in an outdoor recreational activity (not including hunting) at least once per year (Cordell, 2012). Similarly, participation in non-consumptive wildlife recreation has been steadily increasing in Europe over the last 15 years (Bell et al., 2007). To reflect these national and global trends, one alternative funding stream for wildlife management could be a non-consumptive tax on recreational goods (e.g., the proposed U.S. Teaming with Wildlife Act of 2009). While such a tax may not be viable or desirable in every context, exploring new ways to diversify the funding stream for conservation could reduce pressure on public and private landowners. In addition to managing for game species, land managers would have additional resources to direct towards the diverse ways that society values natural, intact ecological communities.

4.3. Mixed consequences of game management: implications for practice

Previous studies demonstrate that all types of game management have mixed consequences for non-targeted species (Fig. 1; Table A1). For example, removing shrub species from wetlands in the Great Lakes region of the U.S. to maintain habitat for sharp-tailed grouse increased the abundance of non-game bird species that require open wetland habitat, such as Le Conte's sparrow and sedge wren, but decreased the abundance of birds that prefer shrubland habitats — i.e. veery (*Catharus fuscescens*), gray catbird, Nashville warbler (*Oreothlypis ruficapilla*), yellow warbler (*Setophaga petechia*), brown-headed cowbird (*Molothrus ater*) and American goldfinch (*Spinus tristis*). This study and the cumulative findings of our review, demonstrate that game management can have the unintended effect of benefiting some species at the expense of others. Thus, the benefits gained by improving habitat for game species should be weighed against the predicted impacts to the species of greatest conservation concern in a particular ecoregion (Arroyo and Beja, 2002). Incorporating more consistent monitoring of non-target effects into game management projects would help managers detect, and where feasible and appropriate, mitigate for unintended consequences on biodiversity.

5. Conclusion

For decades, the assumption that land management practices that benefit hunted species also positively affect all wildlife species has been relatively unexamined (Johnson et al., 1994). We found that fewer than 30 studies, globally, have addressed this topic, and the direction of the effects they report are not consistent. In light of limited funding for biodiversity conservation (Primack, 2010) and alarming rates of extinction (Pimm et al., 2014), understanding how game management affects other species, and particularly those of conservation concern, is critical. Habitat management intended to benefit hunted species should be designed to experimentally test the consequences of these actions on both game and non-game species. By understanding and acknowledging costs and benefits to diverse species, public and private landowners can more effectively implement management practices that collectively increase populations of hunted species while also protecting the full suite of biodiversity.

Acknowledgments

The authors would like to thank J. Tack, L. Stinson, C. Larson, G. Shannon, J. Northrup, B. Gerber, L. Cordes, P. Williams, K. Wilkins, and three anonymous reviewers for their valuable comments and discussion that improved this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.02.032.

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