

Declining populations of greater sage-grouse: hunter motivations when numbers are low

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Abstract

As a hunted species becomes increasingly rare, the effort required to locate and harvest an individual tends to increase. As rarity increases, governmental oversight, including changes in hunting regulations and protection of habitats and individuals using mechanisms such as the US Endangered Species Act (ESA), can be used to mitigate extinction risks. However, recent research has demonstrated the existence of a feedback mechanism through which increased rarity may increase hunter demand for opportunities to pursue rare species before the opportunity is lost. This phenomenon, referred to as the anthropogenic Allee effect, may exacerbate exploitation, thereby resulting in disproportionately large effects of harvest on vulnerable species. In 2010, the US Fish and Wildlife Service designated greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) as a candidate for listing under the ESA. Although sage-grouse are a candidate for ESA listing, they are still hunted throughout much of their current range. In 2008, the demand for sage-grouse hunting permits in Utah exceeded their availability, raising questions about why hunters choose to pursue this species. We hypothesized that the pending ESA listing decision increased hunter demand for permits. We surveyed randomly selected hunters who obtained permits to hunt sage-grouse in Utah in 2008–2010 ($n = 838$) to determine their motivations for hunting sage-grouse and determinants of hunter satisfaction. The most commonly reported reasons for hunting sage-grouse were to spend time with family, for tradition and meat. Although the potential ESA listing was not a major motivational factor in 2009 or 2010, the percentage of respondents selecting this option did increase by 7%. Hunter awareness of the ESA listing petition also increased by 18% during this period. Our results provide new insights on the sociological importance and potential threats of hunting rare species.

Introduction

'When a wildlife population is threatened, deliberately killing individuals from it may seem perverse' (Loveridge, Reynolds & Milner-Gulland, 2007). Following the overexploitation of various wildlife species during the 19th century, conservation-minded sportsmen in the late 19th and early 20th centuries advocated for regulated hunting as a means of protecting wildlife populations (Trefethan, 1975). Subsequently, sport hunting of free-ranging wildlife has played a fundamental role in the evolution of wildlife conservation in North America. Pivotal legislation in the US, such as the Pittman-Robertson (PR) Federal Aid in Wildlife Restoration Act of 1937, established critical linkages between hunting and conservation funding (Smith, 1976; Mangun & Shaw, 1984) and most state wildlife management agencies currently depend upon PR funding to

provide revenues for wildlife conservation. However, as populations of some game species decline, largely as a result of habitat loss and fragmentation, society has increasingly questioned the role hunting should play in contemporary wildlife management (Manfredo, Teel & Bright, 2003).

Regulated harvest has traditionally been believed to pose a minor threat of causing species extinction because of the 'law of diminishing returns' [i.e. hunters stop pursuing game if numbers decline to the point that harvest is unlikely (Strickland *et al.*, 1996, although see Connelly, Gammonley & Peek, 2005)]. However, recent research in bio-economic theory has shown that increased rarity may result in increased demand for hunting opportunities by hunters who fear that the opportunity to pursue the species may be lost because of heightened governmental regulations aimed at protecting the species (Courchamp *et al.*, 2006; Gault, Meinard & Courchamp, 2008; Hall, Milner-Gulland &

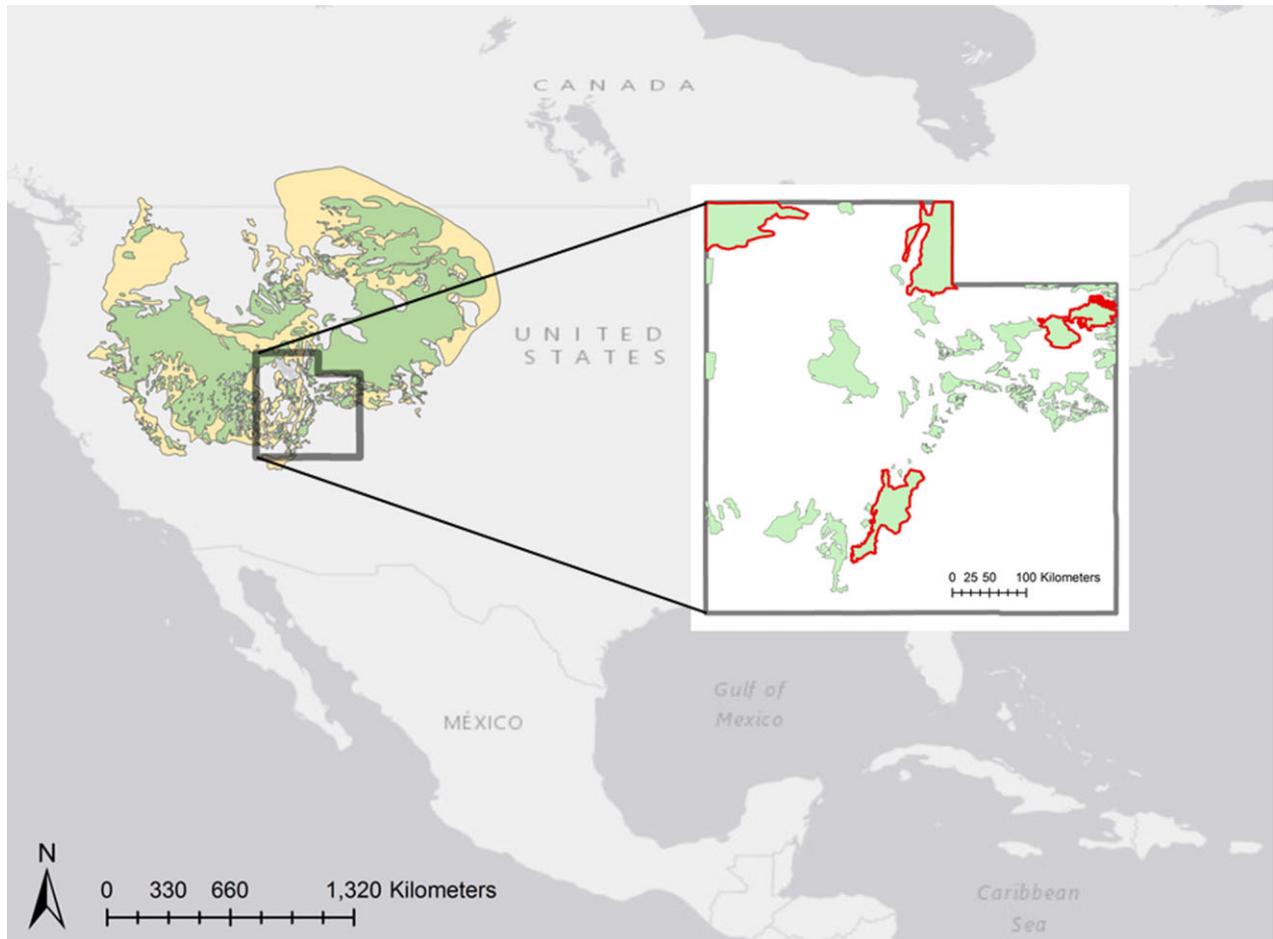


Figure 1 Map of the historic (yellow) and current (green) range of greater sage-grouse in North America. The map inset portrays areas currently occupied by greater sage-grouse in Utah. The four areas where hunting was permitted in Utah during the course of our study (2008–2010) are outlined in red.

Courchamp, 2008; Angulo *et al.*, 2009). These findings, commonly referred to as anthropogenic Allee effect, have increased concerns about the conservation of declining species and the interaction between environmental policy and harvest, particularly for trophy game species (Palazy *et al.*, 2012; Prescott *et al.*, 2012).

Large-scale anthropogenic alteration of biotic and abiotic systems further complicates the conservation of many species. Habitat loss caused by land-use change continues to threaten biodiversity at a global scale (Sala *et al.*, 2000). Contemporary climate change may pose an even greater threat to many species than habitat loss (Thomas *et al.*, 2004). The interactive effects of habitat loss and climate change may prove especially disastrous for species that are unable to adapt or migrate to climate refugia because of a lack of habitat connectivity resulting from habitat loss and/or fragmentation. The cumulative effects of these processes over time may exacerbate population declines of many hunted species thereby increasing public scrutiny of the role of hunter harvest in their management.

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are endemic to western North America and are obligates of sagebrush (*Artemisia* spp.) habitats (Fig. 1; Schroeder, Young & Braun, 1999). Sage-grouse populations experienced range-wide declines throughout the 20th century primarily as a result of habitat loss, fragmentation and degradation (Connelly & Braun, 1997; Knick & Connelly, 2011). During this period of population declines, state wildlife management agencies drastically limited sage-grouse harvest levels and, in some instances, prohibited the harvest of sage-grouse in response to concerns about the impacts of hunting on population trajectories (Rogers, 1964; Connelly, Gammonley & Keegan, 2012).

In addition to the persistent effects of habitat loss and fragmentation, recent research has indicated that sage-grouse populations have already, and will continue to be negatively impacted by projected climate change (Blomberg *et al.*, 2012; Guttery *et al.*, 2013; Caudill *et al.*, 2014). In 2010, the US Fish and Wildlife Service (USFWS) determined that sage-grouse warranted protection under the Endangered

Species Act of 1973 (ESA). However, protection was withheld in favor of species with greater conservation needs (USFWS, 2010). As a result of this 'warranted but precluded' decision, sage-grouse are currently considered a 'candidate species' and, as such, population status must be monitored by USFWS to determine if the species should be promoted to full 'threatened' or 'endangered' status (USFWS, 2010). Despite uncertainty about the long-term viability of this species, sage-grouse are still hunted in 10 of the 11 states in which the species occurs (Reese & Connelly, 2011).

Although hunting was not cited as a high-priority threat by the USFWS (2010), many stakeholders question why state wildlife agencies continue to allow hunters to harvest sage-grouse (Belton, Jackson-Smith & Messmer, 2009; UDWR, 2009). Currently, there is disagreement about the direct effects of hunting on sage-grouse populations. Several authors have attempted to assess the impacts of harvest on sage-grouse populations (Zunino, 1987; Stigar, 1989; Wik, 2002; Connelly *et al.*, 2003; Sika, 2006; Sedinger *et al.*, 2010). However, many of these studies were plagued by confounding factors (small sample sizes, lack of replication) or produced contradictory results regarding whether hunter harvest is additive or compensatory to natural mortality (Reese & Connelly, 2011).

Even given the inconsistent results, the biological impacts of hunting are far better understood than hunter motivations for pursuing this species. Currently, there are no published studies concerning the human dimensions of hunting sage-grouse. Further, because one of the basic tenets of harvest management is that only populations that are large and robust enough to sustain harvest be hunted (Connelly *et al.*, 2005), few opportunities currently exist to study hunters of rare, declining, or ESA candidate species in North America. Reese & Connelly (2011) concluded that the future of sage-grouse harvest management must be guided by both the biological and social implications of hunting this ESA candidate species.

Given recent findings about the interaction of rarity and hunter demand (Angulo *et al.*, 2009) and the potential cumulative threats posed by climate and land-use change on wildlife populations (Sala *et al.*, 2000; Thomas *et al.*, 2004), better information is needed regarding the potential effects of hunting on declining species. Because of their rare dual status as a candidate for ESA listing and a hunted species, we chose to use sage-grouse as a model species to evaluate the effects of real and proposed changes in conservation status and hunting regulations on hunter satisfaction and motivations in order to gain a better understanding of how hunting may affect this and other declining species. Specifically, we hypothesized that the pending ESA listing decision increased hunter demand for sage-grouse hunting permits. Additional objectives of our research were to (1) determine what factors contribute most to sage-grouse hunter satisfaction; (2) gain an understanding of why Utah hunters choose to hunt sage-grouse; (3) to determine if the possibility of heightened protection for sage-grouse has resulted in changes in hunter motivations.

Methods

Survey design and implementation

The Utah Division of Wildlife Resources (UDWR) requires that hunters apply for and obtain special permits to hunt sage-grouse. Hunters who obtained permits were required to pay a \$10 permit processing fee. During the course of our study, only four sage-grouse populations within the state were open to hunting (Fig. 1) and each permitted hunter was allowed to harvest, at most, two birds from one of the four designated populations (UDWR, 2009). The UDWR employs an adaptive harvest management strategy wherein the number of permits available in a given year is a function of the estimated autumn population size, previous hunter participation and harvest success rates (UDWR, 2009). Following the hunting season, UDWR conducts annual surveys of sage-grouse permit holders to determine hunt participation rates, harvest success, number of days hunted, number of birds harvested and hunter satisfaction. In 2008, the demand for sage-grouse hunting permits was so great that the permit application website crashed (the actual number of individuals attempting to access the site is unknown). In response to this unusually high demand for permits, UDWR modified the 2008 survey to include questions concerning motivations for obtaining a permit and factors contributing to hunter satisfaction. Each respondent was allowed to select up to two motivations. Additionally, beginning in 2008, and continuing throughout our study period, UDWR delayed the sage-grouse hunting season by 2 weeks (from mid-September to late September) to allow brood groups additional time to disband in hopes of reducing harvest rates for juveniles and reproductively successful hens (Ellison, 1991). Subsequently, hunters were asked if this regulatory change affected their interest in hunting sage-grouse. Finally, permit holders were asked about their knowledge of the petition to list sage-grouse under the ESA, and their plans to hunt sage-grouse in the future. The survey was modified slightly in 2009 to include additional questions about anticipated participation in upland game bird (i.e. birds other than waterfowl, typically of the order Galliformes or Columbiformes) hunting if the sage-grouse hunt were cancelled, whether a hunt could be satisfactory if the legal limit of two sage-grouse was not harvested and whether a hunt could be satisfactory if no sage-grouse were harvested (Supporting Information Appendix S1).

The UDWR survey sampling protocol required that a minimum of 25% of the permit holders for each of the four hunt areas in the state be contacted. Each permit holder was assigned a permit number and sampling was conducted by randomly selecting from these numbers. Surveys were conducted via telephone interviews during 2008 and 2009. In 2010, the UDWR elected to change the survey method. A sample of permit holders was initially invited to complete the survey online. Hunters who did not complete the online survey within 2 weeks were sent a paper copy of the survey with a pre-addressed postage-paid envelope to return the completed survey. In all years, if a permit holder could not

be reached or refused to participate in the survey, another permittee was randomly selected. The UDWR survey protocol did not include provisions for testing for nonresponse bias. Additionally, UDWR policies do not permit the release of hunter contact information to external parties, thereby precluding other options for testing for nonresponse biases. However, we do not suspect that such a bias existed as it has been shown that post-hunting season surveys generally yield accurate harvest data (Steinert, Riffel & White, 1994) and that even low response rates tend to be adequate to control for response biases (Hammit & McDonald, 1982).

Statistical analysis

Because of the nested nature of the questions (e.g. permit holder who did not participate in the hunt were not asked to respond to hunt-related questions such as the number of sage-grouse harvested), sample sizes varied by survey question. Question-specific sample sizes are presented in Supporting Information Appendix 1. It is possible, even likely, that some hunters were randomly selected to participate in the survey in multiple years, thereby resulting in a possible lack of independence in some responses across years. Unfortunately, the data provided by UDWR did not include a unique identifier that would have allowed us to determine which, if any, hunters responded in multiple years. As such, all responses were treated as independent.

To assess what factors contributed most to hunter satisfaction (objective 1), survey respondents were asked to choose between five levels of satisfaction with their hunting experience (very unsatisfied, unsatisfied, neutral, satisfied and very satisfied). We used cumulative logit models with backward selection to determine which variables influenced hunter satisfaction. Explanatory variables included harvest success, number of days spent hunting and whether the permit holder was aware that sage-grouse had been petitioned for listing under the ESA. Predictor variables were tested for multicollinearity. The number of birds harvested was not used because this response was highly correlated with harvest success.

To address questions concerning hunter motivations (objectives 2 and 3), response frequencies of motivation options (question 8, Supporting Information Appendix S1) were calculated and comparisons of response categories were performed using chi-square tests. All analyses were performed using SAS v9.2 (SAS Institute Inc., Cary, NC, USA).

Results

During the course of the study (2008–2010), the number of permits issued ($n = 1120, 834, 809$, respectively) and number of hunters surveyed ($n = 318, 288, 232$, respectively) varied considerably. Most respondents were males (90%) with an average age of 42 years (range = 9 to 91). Minors (age < 18 years) constituted 14% of survey respondents. Overall, 78% of survey respondents participated in the sage-grouse hunt (2008 = 77.7%, 2009 = 76.0%, 2010 = 81.0%; question 1,

Supporting Information Appendix S1). The median number of days spent hunting sage-grouse was one for all years (question 2, Supporting Information Appendix S1). In 2008, 61% of permit holders who participated in the sage-grouse hunt were successful in harvesting at least one bird (question 3, Supporting Information Appendix S1). The percentage of successful hunters increased to 67% in 2009 and increased to 70% in 2010. In 2008 and 2009, 70% of successful hunters harvested a limit of sage-grouse. This percentage increased to 79% in 2010. Across years, hunters who participated in the sage-grouse hunt harvested an average of 1.7 birds (question 4, Supporting Information Appendix S1).

During 2008–2009, approximately 58% of all survey respondents reported being aware that sage-grouse had been petitioned for listing under the ESA (question 7, Supporting Information Appendix S1). Following the species' designation as 'warranted but precluded' in early 2010, awareness increased to 76%. In 2008, a slightly larger percentage of respondents reported that they planned to obtain a sage-grouse permit during the following year (question 6, Supporting Information Appendix S1) than in 2009 or 2010 (84.6%, 76.0% and 79.3%, respectively).

Approximately 33% of respondents in 2008 reported that the change in sage-grouse hunting season dates had affected their interest in pursuing the species (question 12, Supporting Information Appendix S1). The percentage of respondents who reported that the change in season dates increased their interest was similar to the percentage who reported a decline in interest (15.4% and 17.3%, respectively). Hunting participation rates did not differ between groups who reported an increase or decrease in interest because of changes in season date ($\chi^2 = 0.630, n = 104, \text{d.f.} = 1, P = 0.571$). Additionally, respondents who reported that they were less interested in hunting sage-grouse were no less likely to report intentions of obtaining a permit the following year than were respondents who reported being more interested in pursuing the bird ($\chi^2 = 0.769, n = 104, \text{d.f.} = 2, P = 0.681$).

Fifty-six percent of respondents reported that their level of participation in upland game hunting would not be affected if the sage-grouse hunting season were closed, whereas 10% reported that they would no longer engage in upland game bird hunting if the sage-grouse hunt were cancelled (question 9, Supporting Information Appendix S1). The remaining 34% indicated that elimination of the sage-grouse hunting season would result in them hunting upland game less often.

Logit models for the three combined years of survey data indicated that satisfaction (question 5, Supporting Information Appendix S1) was best explained by whether or not a hunter was successful in harvesting at least one sage-grouse (Table 1, $R^2 = 0.168$). Whether successful or unsuccessful, reported satisfaction reflected the full range of satisfaction levels from 'very unsatisfied' to 'very satisfied' (Table 2). However, unsuccessful hunters were more likely than successful ones to report all levels of satisfaction except 'very satisfied' (Table 2). Successful hunters were 35% more likely to report that they were 'very satisfied' with their hunting

experience than unsuccessful hunters. When permit holders were presented with a hypothetical situation in which they were unsuccessful in harvesting a limit of sage-grouse, 45% responded that they would still be satisfied with their hunt while almost 50% reported that they would be very satisfied (question 10, Supporting Information Appendix S1). When respondents were presented with a situation in which they were unsuccessful in harvesting *any* sage-grouse, 50% reported that they would still be satisfied while over 39% said that they would be very satisfied with their hunt (question 11, Supporting Information Appendix S1).

In 2008, the most commonly cited reason for obtaining a sage-grouse permit was 'meat' (50.6%, Table 3), with 'tradition' (45.3%) being the second most frequently cited moti-

vator (question 8, Supporting Information Appendix S1). Although a small percentage (7.2%) of hunters cited 'other' as a reason for obtaining a permit in 2008, the associated comments indicated that an additional motivation category was needed. Consequently, for the 2009 and 2010 surveys, we added the option of 'To spend time outdoors with family' to the survey. Because of this addition, motivation data from 2008 cannot be directly compared with data from subsequent years. In 2009 and 2010, 'family' was the dominant factor cited for why individuals chose to hunt sage-grouse (74.3% and 67.2%, respectively, Table 3). Although 'listing' was not a primary motivational factor in any year of the study (2008 = 13.8%, 2009 = 10.1%, 2010 = 17.2%), the percentage of respondents who selected this option did increase considerably between 2009 and 2010. This increase between 2009 and 2010 was similar in direction and magnitude to the increase in the percentage of hunters who reported that they were motivated by a view that sage-grouse are a trophy species (2009 = 22.9%, 2010 = 30.6%, Table 3). Across years, respondents who reported being motivated by 'listing' showed a weak evidence of being more likely to report that they were also motivated by the perception of sage-grouse as a trophy species ('trophy': $\chi^2 = 2.401$, $n = 658$, d.f. = 1, $P = 0.121$).

Table 1 Results of backward variable selection for model of greater sage-grouse (*Centrocercus urophasianus*) hunter satisfaction in Utah, USA, 2008–2010

Predictor of satisfaction	Wald χ^2 value	<i>P</i> -value
Aware of status ^a	1.365	0.243
Days hunted ^b	3.244	0.072
Successful ^c	105.279	< 0.001

The final model retained only the effect of successful harvesting at least one sage-grouse. Test statistics and *P*-values are presented for all explanatory variables initially included in the model as these results may aid in the design of similar research. The value in bold is statistically significant.

^aBinary variable indicating whether hunters were aware of the petition to list sage-grouse under the ESA.

^bVariable indicating the number of days spent hunting sage-grouse. Few hunters reported hunting more than 2 days so numbers greater than 2 were rounded down to 2.

^cBinary variable indicating whether a hunter was successful in harvesting at least one sage-grouse.

Table 2 Reported levels of hunt satisfaction for successful and unsuccessful greater sage-grouse (*Centrocercus urophasianus*) hunters, Utah, USA, 2008–2010

Successful	Very unsatisfied	Unsatisfied	Neutral	Satisfied	Very satisfied
No	13.3	13.3	25.2	28.3	19.9
Yes	2.8	2.6	11.9	27.6	55.1

Values reported are the percentage of respondents reporting various levels of satisfaction and hunt success. Percentages are calculated from a sample of 654 hunters who participated in the Utah sage-grouse hunt during our study.

Table 3 Percentage of hunters who reported various reasons for obtaining a greater sage-grouse (*Centrocercus urophasianus*) hunting permit in Utah, USA, 2008–2010

Reasons for obtaining a permit	2008	2009	2010
View them as a trophy game bird (trophy)	29.2	22.9	30.6
Always hunted them (tradition)	45.3	27.8	37.1
Want to harvest one before ESA listing (listing)	13.8	10.1	17.2
New to upland game hunting, giving it a try (new)	19.2	14.2	8.6
Hunt them for meat (meat)	56.0	33.7	19.8
To spend time outdoors with family (family)	NA ^a	74.3	67.2
Other reasons (other)	7.2	2.4	15.5

Percentages within a column do not sum to 100% because hunters were allowed to select up to two motivating factors.

^aIndicated that the associated response option was not applicable (i.e. NA) because of not being included in the survey until 2009.

of ESA listing and the perception of sage-grouse as a trophy species. These findings suggest that for rare or declining game species that are not primarily viewed as high-value trophies, the passage of protective regulations is unlikely to lead to a substantially increased threat from hunting via the anthropogenic Allee effect, provided that harvest is carefully regulated, as with sage-grouse harvest in Utah.

Hunting a declining species

The increased influence of the ESA listing petition in 2010 may be attributable to increased public awareness. However, a search for articles published in Utah newspapers between 1 January 2004 and 1 June 2008 yielded 25 entries that included the words 'sage-grouse' and 'Endangered Species Act' suggesting that many Utah residents had been exposed to information about the decline of sage-grouse prior to our study. Overall, our results suggest that Utah sage-grouse hunters were primarily motivated by affiliation ('family' or 'tradition') and achievement-oriented ('meat' or 'trophy') factors (Decker & Connelly, 1989). These findings are corroborated by other studies (Hayslette, Armstrong & Mirarchi, 2001; Radder & Bech-Larsen, 2008) that highlighted the influence of tradition and companionship/socializing on hunter motivations. We did find weak evidence that respondents who reported being motivated by the perception of sage-grouse as a trophy species were also more likely to report being motivated by the possibility of losing the opportunity to pursue the species if it were listed as threatened or endangered. If the species continues to decline, it is possible that more hunters will be motivated by the threat of ESA listing and/or the desire to harvest a trophy gamebird.

Sage-grouse hunter participation rates declined by 1.6% between 2008 and 2009, continuing a trend documented by UDWR since 2004 (Supporting Information Appendix S2). However, reported participation rates increased by approximately 5.0% between 2009 and 2010. Although it is unclear why this increase occurred, the decision to list sage-grouse as a 'warranted but precluded' in early 2010 may have resulted in higher participation rates among hunters concerned about possibly losing the opportunity to hunt sage-grouse in the near future. Additionally, the highest documented rates of sage-grouse hunter participation in Utah were during the 2005 hunting season (Supporting Information Appendix S2), which was preceded in January of 2005 by a decision by the USFWS that sage-grouse did not warrant ESA protection (UDWR, 2009). This further suggests that the threat of increased regulation and/or increased media coverage of potential regulatory action may lead to increased participation in sage-grouse hunting. An association between increased regulation to protect a species and increased exploitation has previously been documented by other researchers (Rivalan *et al.*, 2007). However, in the years following the high participation rate of 2005 and the rebound of 2010, participation rates declined rapidly, suggesting that the effects of regulatory actions on participation rates are short-lived. Similarly, Koons, Rockwell, & Aubry

(2014) reported that changes in harvest regulations for lesser snow geese (*Chen caerulescens caerulescens*) resulted in a temporary increase in harvest mortality, likely as a result in increased hunter participation rates, followed by a trend in harvest rates declining below the long-term average.

We obtained hunter predictions about whether further regulation (i.e. ESA listing) would affect their future participation in upland game bird hunting. Although most respondents reported that regulations resulting in a cancellation of the sage-grouse hunting season would not lead them to stop participating in upland game hunting, just under half of the respondents did report that termination of the sage-grouse hunt would result in reduced involvement in upland game hunting. We interpret this as evidence that there is a small population of devout sage-grouse hunters but that most hunters would shift the time normally spent pursuing sage-grouse to the pursuit of other upland game species. These results may suggest that wildlife management agencies may be able to impose stringent harvest restrictions for rare species without resulting in a reduction in hunting participation and associated revenues by offering opportunities to pursue more abundant species (Messmer & Enck, 2012).

Hunter satisfaction and the conservation of sage-grouse populations

Most respondents were satisfied with their hunting experience. Unlike other studies, which found that hunter satisfaction was affected by multiple factors (Decker, Brown & Gutierrez, 1980; Hammit, McDonald & Patterson, 1990; Gigliotti, 2000; Frey *et al.*, 2003), our data suggested that the level of satisfaction was primarily influenced by hunter success. Messmer *et al.* (1998) reported a similar relationship for big game hunters in Utah. Early game management philosophy purported that successful hunters were satisfied hunters (Stankey, Lucas & Ream, 1973; Woods & Kerr, 2010). While our data appeared to support this idea, our model explained only 17% of the variation in hunter satisfaction. This suggests that other factors that we did not measure may be better determinants of satisfaction than hunter success (Messmer & Enck, 2012).

Unlike other rare game species in North America [e.g. bighorn sheep (*Ovis canadensis*)], sage-grouse are not viewed as a highly valuable trophy species at a national scale, nor does sage-grouse hunting have strong cultural or spiritual importance as is the case for hunting other ESA listed or candidate species such as the polar bear (*Ursus maritimus*; USFWS, 2008), ringed seal (*Phoca hispida*; NOAA, 2012) and Pacific walrus (*Odobenus rosmarus*; USFWS, 2011) in some Native American cultures (Wein, Freeman & Makus, 1996; Duhaime, Chabot & Gaudreault, 2002; Stirling, 2011).

Although trophy hunting has been shown to have negative evolutionary consequences (Coltman, O'Donoghue & Jorgenson, 2003), individual hunting permits for some trophy species may sell for hundreds of thousands of dollars (Loveridge *et al.*, 2007) thereby producing revenues that may facilitate conservation efforts at a minimal cost to the species being hunted. Some of our respondents reported

being motivated by the perception of sage-grouse as a trophy species and tradition. However, neither of these conditions appeared to occur at the levels documented for other trophy or culturally significant species.

The importance of funding for wildlife research and conservation cannot be ignored. Because the majority of funding for state wildlife management agencies comes from user fees (i.e. PR excise taxes, hunting license sales), these funding sources are essential to the conservation of all wildlife. Until wildlife agencies receive broader public funding, they must continue to balance social, biological and financial factors in addressing conservation concerns with user-based harvest management strategies that provide the majority of the agencies' revenue.

Given these conditions and our findings, conservation strategies for sage-grouse, or other rare or declining species, must carefully weigh the social and biological implications of hunting. The stringent harvest regulations adopted by UDWR that link sage-grouse hunting opportunities to annually estimated population sizes are an effective means of offsetting the threats predicted by the anthropogenic Allee effect hypothesis. However, it is also necessary to recognize that uncertainty about the effects of harvest on sage-grouse still exists. We recommend that if harvest of a species is deemed appropriate, conservative harvest management strategies be established using the best available science and that the long-term stability of the population take precedence over other factors (Connelly *et al.*, 2005).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Utah greater sage-grouse hunting survey 2008–2010.

Appendix S2. Greater sage-grouse hunter participation rates in Utah, 2004–2014.