

REVIEW

Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour

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Summary

1. Anthropogenic structures such as those associated with energy development are a major threat to wildlife as a result of direct and indirect effects on populations. Species already imperilled as a result of habitat loss and alteration also may be the most threatened by rapidly increasing energy development, and these added pressures could lead to species extinctions and further declines in biodiversity.
2. Of particular concern are tetraonids (grouse spp.) which have life cycles that require large, intact habitats to persist. We searched the peer-reviewed literature to assess impacts of six anthropogenic structures (i.e. oil and gas, fences, wind turbines, buildings, roads and power lines) on grouse survival and displacement behaviour across four different time periods in a grouse life cycle (i.e. year around, lekking, nesting and brooding).
3. We used 5 studies that examined a total of 23 study–structure combinations to assess displacement behaviour in grouse and found an average effect of -1.40 (95% CI: -1.50 , -1.31), indicating that anthropogenic structures displace grouse. Similarly, we used 9 studies examining a total of 17 study–structure combinations to assess survival and found an average effect of -1.11 (95% CI: -1.33 , -0.88), indicating a negative effect of structures on grouse survival.
4. Oil and gas structures had the greatest negative effect on displacement behaviour ($\bar{E} = -2.41$, 95% CI: -3.28 , -1.54), and of the periods of the life cycle examined, lek attendance was most affected ($\bar{E} = -4.85$, 95% CI: -6.39 , -3.31).
5. *Synthesis and applications.* This data-driven synthesis reveals an overall negative effect of anthropogenic structures on grouse displacement behaviour and survival. Specifically, grouse were displaced and had lower survival in the presence of oil and gas structures and the presence of roads resulted in displacement behaviour. Too few studies existed to examine the specific effects of wind turbines and fences on displacement behaviour and the impact of wind turbines, fences, buildings and power lines on survival, which emphasizes the need for research assessing the influence of these structures on wildlife. Future management should focus on limiting the amount of oil and gas and road development in areas occupied by extant grouse populations, and if unavoidable, new infrastructure should be placed at low densities away from known lekking locations as leks appear sensitive to disturbance from anthropogenic structures.

Key-words: avoidance behaviour, bird collision, Hedges' d , oil, gas, *Tetraonidae*, wind turbine

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Introduction

Despite a United Nations Millennium Goal to reduce the rate of biodiversity decline by 2010, most indicators of the state of biodiversity continue to show declines, and pressures on biodiversity have increased (Butchart *et al.* 2010). A rapidly increasing human population and per capita energy demand have led to increased energy development and land-use change, much of which is occurring in previously unfragmented ecosystems that support imperilled species (Lior 2008). The resulting increases in human infrastructure, particularly those associated with energy development and extraction, represent a major threat to wildlife populations (De Lucas *et al.* 2008; Miller *et al.* 2014). Recent estimates indicate that monopole wind turbines in the United States kill between 140,000 and 328 000 birds annually (Loss, Will & Marra 2013), and it is hypothesized that the effects on bat populations may be equal to or exceed those on birds (Kunz *et al.* 2007; Arnett *et al.* 2008). Collision fatalities with anthropogenic structures are frequently implicated in biodiversity loss resulting from bird and bat deaths, but indirect impacts such as fragmentation of habitat and disruption of migration corridors can also negatively affect wildlife populations (Bhattacharya, Primack & Gerwein 2003; Forman *et al.* 2003; Waller & Servheen 2005; Jenkins, Smallie & Diamond 2010; Degregorio, Weatherhead & Sperry 2014). Improving our understanding of how human infrastructure affects wildlife populations, particularly those in decline, is necessary to reduce future biodiversity loss and to maximize effective conservation efforts.

The effects of anthropogenic structures can vary greatly dependent upon spatial and temporal distribution of structures and both within and among species (De Lucas *et al.* 2008; Ferrer *et al.* 2012). For that reason, it is necessary to examine the impacts of structures on multiple species, regions, times of the year and across different life stages to fully understand the direct and indirect effects of structures on wildlife (Burger *et al.* 2012; Belaire *et al.* 2014; Loring *et al.* 2014). When these issues are addressed, we can begin to solve problems stemming from conflicting ecological and industrial goals through risk assessments and spatial planning (Carrete *et al.* 2009; Miller *et al.* 2014). However, despite planning tools and continued efforts to mitigate for negative effects of anthropogenic structures on wildlife, population decline for many species has accelerated (Kunz *et al.* 2007; Pearce-Higgins *et al.* 2009).

Anthropogenic structures are known to cause direct wildlife mortality as a result of collisions (Kunz *et al.* 2007; Stewart, Pullin & Coles 2007; Jenkins, Smallie & Diamond 2010; Stevens, Reese & Connelly 2011). Specifically, fences, power lines, roads and wind turbines have all been associated with collision mortality (Bevanger 1998; Baines & Andrew 2003; Wolfe *et al.* 2007; Kocielek *et al.* 2011; Rioux, Savard & Gerick 2013). Rates of

collision vary greatly with type of structure, species density and placement of the structure on the landscape. For instance, the Altamont Pass Wind Resource Area in California kills >1000 raptors per year (Smallwood & Thelander 2008), and reported rates of collisions with deer fences in Europe and livestock fencing in the United States have been relatively high for low flying grouse species (Bevanger & Brøseth 2000; Wolfe *et al.* 2007). In Norway, for example, capercaillie and black grouse (see Table 1 for scientific names) mortalities from power line collisions are near 90% and 47% of the take associated with legal hunting harvest, respectively (Bevanger 1995). Perhaps an even greater threat than direct loss of wildlife associated with collisions are the potential negative effects associated with habitat loss and avoidance behaviour.

Both direct and indirect effects (e.g. collisions and avoidance, respectively) have been associated with anthropogenic structures, but indirect effects can be much harder to quantify (Patten *et al.* 2005; Kuvlesky *et al.* 2007; Pruett, Patten & Wolfe 2009). In many cases, avoidance or displacement may have greater repercussions on reproductive output at the population level than direct mortality because moving animals away from preferred pathways can incur great energetic costs (Chamberlain *et al.* 2006; Zeiler & Grunschachner-Berger 2009; Pearce-Higgins *et al.* 2012). Additionally, anthropogenic structures erected near breeding grounds can alter site fidelity behaviour and disrupt breeding cycles when animals are forced into novel environments. For example, nearly all grassland grouse breed on communal display areas referred to as leks and they exhibit strong site fidelity to areas around lekking locations (Fuhldendorf *et al.* 2002). As a result of site fidelity behaviours, the immediate effect of development is not always apparent and may exhibit a lag as survival of persisting individuals wanes over time (Walker, Naugle & Doherty 2007; Harju *et al.* 2010). Evidence documenting the decline of lekking grouse species after the construction of energy structures exists for many species (Hanowski, Christian & Niemi 2000; Zeiler & Grunschachner-Berger 2009; Harju *et al.* 2010).

Indirect habitat loss resulting from anthropogenic structures can affect wildlife behaviour and limit the amount of usable space, thereby reducing carrying capacities (Madsen *et al.* 2009; Pruett, Patten & Wolfe 2009). Structures may alter animal behaviour by creating corridors and perches for predatory species (Slater & Smith 2010). However, type, size, amount of time present and density of structures all influence the magnitude of a response (Lyon & Anderson 2003; Aldridge & Boyce 2007; Pearce-Higgins *et al.* 2009; Harju *et al.* 2010). Yet, research in this area is highly variable with some structure types having had exhaustive amounts of investigation, while others have received almost none. Furthermore, wildlife varies greatly in their responses to structures dependent upon the period of their life cycle, home range sizes and many other factors. Of particular concern are tetraonids (grouse spp.) which have complex life histories that require large, intact

Table 1. Nineteen recognized grouse species, their population estimate, population status and population trend

Common name	Scientific name	Pop. estimate ^a	Status ^b	Trend ^b
Black Grouse*	<i>Tetrao tetrix</i>	22 500 000	Least concern	Decreasing
Black-billed Capercaillie	<i>Tetrao urogalloides</i>	>1 000 000	Least concern	Decreasing
Western Capercaillie*	<i>Tetrao urogallus</i>	7 500 000	Least concern	Decreasing
Caucasian Black Grouse	<i>Tetrao mlokosiewiczi</i>	<85 000	Near threatened	Decreasing
Chinese Grouse	<i>Bonasa sewerzowi</i>	Not quantified	Near threatened	Decreasing
Hazel Grouse	<i>Bonasa bonasia</i>	2 800 000	Least concern	Decreasing
Ruffed Grouse	<i>Bonasa umbellus</i>	3 700 000	Least concern	Decreasing
Dusky Grouse	<i>Dendragapus obscurus</i>	3 000 000	Least concern	Decreasing
Sooty Grouse	<i>Dendragapus fuliginosus</i>	Not quantified	Least concern	Decreasing
Greater Prairie-Chicken*	<i>Tympanuchus cupido</i>	<700 000	Vulnerable	Decreasing
Lesser Prairie-Chicken*	<i>Tympanuchus pallidicinctus</i>	30 000	Vulnerable	Decreasing
Sharp-tailed Grouse*	<i>Tympanuchus phasianellus</i>	1 200 000	Least concern	Decreasing
Greater Sage-Grouse*	<i>Centrocercus urophasianus</i>	<150 000	Near threatened	Decreasing
Gunnison Sage-Grouse	<i>Cetrocercus minimus</i>	<3000	Endangered	Decreasing
White-tailed Ptarmigan	<i>Lagopus leucurus</i>	2 000 000	Least concern	Decreasing
Willow Ptarmigan*	<i>Lagopus lagopus</i>	40 000 000	Least concern	Decreasing
Rock Ptarmigan*	<i>Lagopus muta</i>	8 000 000	Least concern	Decreasing
Siberian Grouse	<i>Falco pennis falcipennis</i>	Not quantified	Near threatened	Decreasing
Spruce Grouse	<i>Falco pennis canadensis</i>	Not quantified	Least concern	Stable

*Species included in meta-analysis.

^aWe report the mid-point of population estimates.

^bAll status and trend listing information was gathered from BirdLife International 2012. IUCN Red List of Threatened Species. version 2012.2.

habitats to persist (Johnsgard 1983; Storch 2007). The high conservation status of many grouse species together with their broad geographic range (Table 1; BirdLife International 2012) means that grouse represent a suitable suite of species to synthesize our understanding of the impacts of anthropogenic structures. Ideally, this information can then be used in the planning and development of structures to minimize the impacts on native wildlife.

There are nineteen grouse species that occur throughout much of the Northern Hemisphere and they inhabit a variety of environments including grassland, steppe, tundra and forest. Grouse possess a variety of morphological, physiological and behavioural adaptations that allow them to occupy seasonal changes in northern latitudes without having to migrate, which in turn, makes them highly susceptible to landscape changes (Johnsgard 1983; Storch 2007). As a result, many grouse have become imperilled as demands for development increase in once unfragmented landscapes. For example, in North America, four species are listed as near threatened, vulnerable or endangered, and in Eurasia, three species are considered near threatened according to the International Union for Conservation of Nature Red List (Table 1; BirdLife International 2012). Of particular concern are the grouse species that inhabit non-forested ecosystems because they have evolved in landscapes that are relatively void of tall vertical structures, meaning that anthropogenic structures erected in these landscapes could have significant impacts on their behaviour.

We demonstrate the influence of anthropogenic structures on grouse species globally by synthesizing the current peer-reviewed research and calculating *Hedges' d* as a

measure of the effect of structures on grouse. We also used mixed-model meta-analysis techniques to assess the effects on specific periods of the life cycle and the effects of different structure types when the number of studies permitted. Additionally, we emphasize the current gaps in literature and give research recommendations to help improve our understanding of the influence of anthropogenic structures on grouse and other wildlife. To do this, we examined the effects of six anthropogenic structure types on grouse behaviour and survival throughout their life cycle. Specifically, we evaluated the impacts of wind turbines, oil and gas structures, fences, roads, buildings and power lines on the behaviour and survival of grouse during the lekking, nesting, brooding and overall annual (i.e. home ranges and annual survival) periods of their life cycles.

Materials and methods

SEARCH STRATEGY

We conducted a search of the peer-reviewed literature using the Web of Science data base and Google™ Scholar in July of 2012. We included only those studies published in peer-reviewed journals or edited book series (e.g. Studies in Avian Biology). We focused on studies that investigated the effects of anthropogenic structures on grouse vital rates (e.g. survival) and displacement (e.g. shifting home ranges). Our search terms included combinations of anthropogenic structures such as roads, fences and buildings in addition to terms associated with energy such as oil and gas, wind and turbine (Table 2). We also identified additional sources by searching the literature cited of the papers that were included in our review. We had no temporal limitations on our

Table 2. Search terms and number of publications resulting from searches in Web of Science and Google Scholar to locate articles reporting research on the influence of anthropogenic structures on grouse survival and displacement. Searches conducted in July 2012

Specificity	Relevant structures	Search term(s)	Search results (Number of publications)
Broad	All	Grouse*	2401
Mid	All	[(grouse* and energy*), (grouse* and energy development*)]	139
	All	[(grouse* and structure*), (grouse* and anthropogenic*), (grouse* and avoidance*)]	280
Fine	Wind	[(grouse* and wind*),(grouse* and turbine*)]	24
	Oil and gas	[(grouse* and oil*),(grouse* and (natural) gas*)]	76
	Power lines	[(grouse* and transmission line*),(grouse* and powerline*)]	8
	Fences	(grouse* and fence*)	27
	Roads	(grouse* and road*)	39
	Buildings	(grouse* and building*)	9

In cases of irregular plurals, “*” allows search engines to retrieve all forms of the root word.

search, and our search was focused on work published in or translated to the English language.

STUDY INCLUSION CRITERIA

Initial assessment of studies included all papers that mentioned grouse and structures in the title, abstract or keywords. This allowed us to retain the maximum number of potential papers investigating grouse and structures, while eliminating some from the initial search. Next, we excluded all papers that did not include some direct measure of grouse and structures (i.e. papers that did not collect data), thus eliminating all review-style papers or summaries that made observations and gave management recommendations without directly measuring survival rates or displacement behaviours. Finally, for inclusion in our analyses, studies had to measure survival and reproduction or displacement behavioural responses at two or more levels. For example, there must be a treatment and a control, a gradient of structural densities, a before and after, or some similar comparison.

DATA EXTRACTION

We included data examining multiple periods of the grouse life cycle that described survival and displacement responses. Therefore, a study investigating nest survival and brood survival could be used to investigate each period of the life cycle in our analyses. Similarly, studies that reported outcomes for geographically separated replicates within a study were considered independent and used in analyses. Our justification for this rationale is twofold. First, many grouse species have different habitat requirements for different periods of the life cycle (e.g. lekking, nesting and brooding), meaning that examining the influence of anthropogenic structures on each period during the life cycle has the potential to yield different and important results. Secondly, the limited number of published papers on this topic makes the information within each study too critical to disregard. Finally, there was one study that examined two different species and we treated each species independently and included them both in the analysis.

META-ANALYSIS

We assessed the effects of anthropogenic structures on grouse survival and displacement, using a technique that combines mea-

sures of effects from multiple, individual studies into an estimate of average effect which then determines significance. In order to calculate an average effect size across studies, we first had to standardize the data from individual studies by generating an effect size for each. We used the mean, standard deviation and sample size from a control and treatment group. Field studies do not always lend themselves to a conventional treatment and control methodology. For this reason, we used multiple classifications to split study data into two groups that represented a highly impacted group and a non-impacted group. Using these data, we then calculated *Hedges' d* as our measure of effect size which is the difference in survival or behaviour (i.e. two separate analyses) between sites with and without structures. *Hedges' d* is calculated by dividing the difference in means of the control and experimental groups by the pooled standard deviation and then multiplying it by a constant (*J*) that corrects for biases associated with small sample sizes. In general, an effect size of <0·2 is low, an effect size near 0·5 is moderate, and an effect size >0·8 is high (Cohen 1988).

We calculated weighted average effect sizes and total heterogeneity of variance after determining a *Hedges' d* score for individual studies. Average effect size, (\bar{E}), is a measure of the mean calculated across each of the studies where each study is weighted by the reciprocal of its sampling variance. This helps account for the imprecision associated with small sampling sizes and the resulting high amount of error associated with the estimated means (Lipsey & Wilson 2000). Confidence intervals (CI) were then calculated for the average effect size using the overall variance calculated by weighting each study based on sample size. This allowed us to determine whether the effect was significant (i.e. the CI does not overlap 0). We also calculated the total heterogeneity of the studies (Q_T), to determine whether variance among effect sizes is greater than expected by sampling error alone (Gurevitch & Hedges 1993). The Q statistics are a type of weighted sums of squares test (i.e. similar to an analysis of variance) and use a chi-square distribution to determine significance (Gurevitch & Hedges 1993). The Q statistics can have low power when sample sizes are small so an investigation of explanatory variables even in the presence of insignificant Q statistics may be necessary.

Our initial fixed-effects models, without partitioning of categorical variables, showed significant amounts of total heterogeneity (Q_T). Therefore, we identified structure type and period of the life cycle as categorical variables to test for differences among the

effect sizes using a mixed model that allowed for random effects. Random-effects mixed models are commonly used for ecological data because they allow for heterogeneity among studies rather than sampling error alone (Pullin & Stewart 2006). Mixed models in this case are analogous to analysis of variance because they include random variation among studies within a group and fixed differences between groups (Rosenberg, Adams & Gurevitch 2000). We used six structure categories (buildings, roads, power lines, oil and gas structures, wind turbine and fences) and four periods of the grouse life cycle (nesting, brooding, lekking, annual survival). There had to be at least two results in each category for it to be included in mixed-model calculations. After running mixed models, we further tested for differences between categories (i.e. structures and period of the life cycle) using a Q_B test which is similar to an analysis of variance and indicates whether there are significant differences in the response of grouse between periods of the life cycle and structures.

We addressed the 'file drawer problem' which is the tendency for only significant results to get published, by calculating fail-safe numbers for our analyses. A fail-safe number indicates the number of non-significant, unpublished (i.e. missing) studies that would need to be added to a meta-analysis to reduce an overall statistically significant result to non-significant (Rosenthal 1979). Non-significant results are often overlooked in the sciences; therefore, this number is intended to focus on the number of studies with non-significant outcomes that never get reported, rather than the number of studies with opposing, significant trends needed to reverse our findings. An effect is generally considered robust if the fail-safe number is greater than $5n + 10$, where n is the original number of studies (Rosenthal 1991). All meta-analytic methods were conducted using METAWIN 2.1 (Rosenberg, Adams & Gurevitch 2000).

Results

Our search resulted in 3003 papers investigating grouse (Table 2). We found 24 peer-reviewed papers that examined the influence of anthropogenic structures on grouse survival or displacement and reported statistical outcomes (Table 3). Of the 24 total papers, the majority focused on greater sage-grouse (41%) followed by ptarmigan spp. (22%), lesser prairie-chicken (15%), black grouse (7%), capercaillie (7%), sharp-tailed grouse (4%) and greater

prairie-chicken (4%). Research on lesser prairie-chickens has addressed the most types of structures, while research on greater prairie-chickens and sharp-tailed grouse has examined the fewest (Table 3). Despite reporting statistical outcomes, only 12 of the 24 papers had a research framework that allowed for an inclusion in our meta-analysis. The primary reason for exclusion of relevant studies was a lack of proper controls or a before–after framework. We included one study that examined multiple grouse species and five studies that examined the influence of more than one type of structure, and two studies were included in analysis of displacement behaviour and survival.

We examined five studies that investigated a total of 23 structure–study combinations (i.e. each study could examine fences, turbines, oil and gas wells, buildings, roads or power poles) with a fixed-effect model and found evidence that structures cause displacement of grouse ($\bar{E} = -1.40$, 95% CI: -1.50 , -1.31). However, our general model examining the impacts of structures on displacement indicated underlying structure in the data would be better suited for mixed models ($Q_T = 323.59$, d.f. = 22, $P < 0.05$). Mixed-model results showed that oil structures (mixed effect $\bar{E} = -2.41$, $k = 7$, 95% CI: -3.28 , -1.54) and roads (mixed effects $\bar{E} = -1.70$, $k = 8$, 95% CI: -2.50 , -0.90) had statistically significant effects and caused displacement (Fig. 1). Additionally, all periods in the grouse life cycle showed displacement from structures with lekking and nesting periods most influenced, respectively (mixed effects $\bar{E} = -4.85$, $k = 3$, 95% CI: -6.39 , -3.31 ; mixed effects $\bar{E} = -1.60$, $k = 11$, 95% CI: -1.90 , -1.30) (Fig. 2). Furthermore, there were differences in the responses to structures dependent upon the period of the grouse life cycle ($Q_B = 112.68$, d.f. = 2, $P < 0.05$), and responses were significantly different between structure types ($Q_B = 8.13$, d.f. = 3, $P < 0.05$).

We used nine studies that reported rates for a total of 17 structure–study combinations in a fixed-effect model to examine the influence of anthropogenic structures on grouse survival, and found anthropogenic structures

Table 3. Number of journal articles that reported research evaluating the influence of anthropogenic structures on survival or displacement behaviour of different grouse species

Species	Structure						TOTAL
	Oil and gas	Wind turbines	Buildings	Roads	Power lines	Fences	
Greater Sage-Grouse	11		2	6	1		20
Lesser Prairie-Chicken	2		2	4	4	1	13
Sharp-tailed Grouse				1			1
Greater Prairie-Chicken				1		1	
Black Grouse		1			1	3	5
Capercaillie		1		1	1	3	6
Ptarmigan spp.		2	1		2	3	8
TOTAL	13	4	5	12	10	10	

The total column represents total number of articles in which a structure type was included in a study. The number of individual articles reporting a study of structures is fewer (e.g. one article might investigate multiple structures).

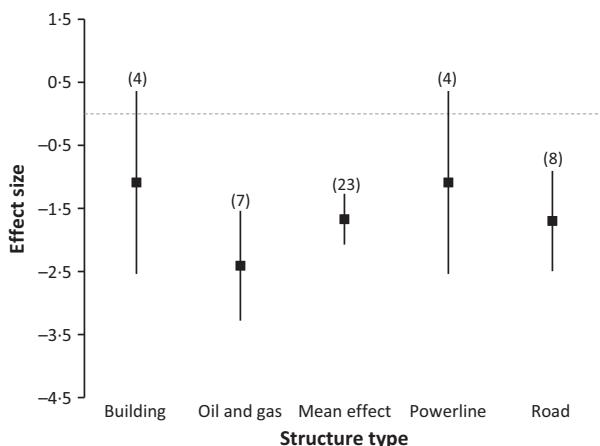


Fig. 1. Effect sizes (square) and 95% confidence interval (line) from mixed-effects models of anthropogenic structures affecting displacement behaviour in grouse. Positive effect size indicates that grouse were attracted to structures, while negative effect size indicates displacement of grouse.

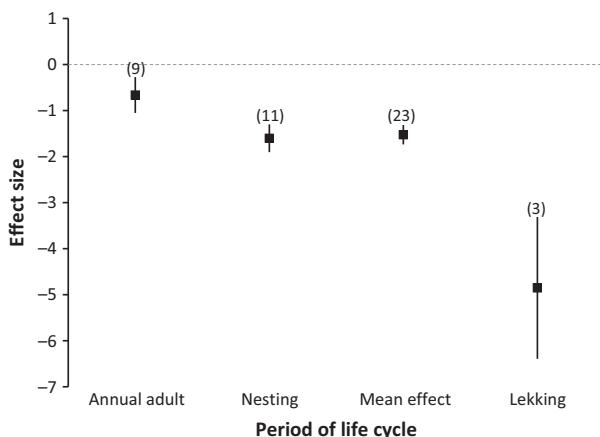


Fig. 2. Effect sizes (square) and 95% confidence interval (line) from mixed-effects models examining periods during the grouse life cycle affected by anthropogenic structures. Positive effect size indicates increased activity near structures, while negative effect sizes indicates decreased activity (or increased distance from structure).

negatively affect grouse survival rates ($\bar{E} = -1.11$, 95% CI: -1.33 , -0.88). However, our general model examining the impacts of structures on survival also indicated that underlying structure in the data that would be better suited for mixed models ($Q_T = 888.92$, d.f. = 16, $P < 0.001$). Mixed-model results indicated that both lek attendance and annual adult survival were negatively influenced by the presence of structures, respectively (mixed effects $\bar{E} = -6.10$, $k = 11$, 95% CI: -9.02 , -3.31 ; mixed effects $\bar{E} = -1.60$, $k = 11$, 95% CI: -1.90 , -1.30). There was no significant difference in the magnitude of responses between lekking and annual survival ($Q_B = 1.44$, d.f. = 1, $P > 0.05$). Unfortunately, too few studies exist to examine the effects of structures on nest or brood survival (i.e. one reported for each)

or the differences in survival resulting from varying structure types (i.e. most studies only focus on oil and gas, and multiple studies for other structures do not currently exist).

We tested for publication bias using Rosenthal's fail-safe number and found our displacement results were robust to publication bias (fail-safe = 8230). Mixed-model analysis of displacement was also robust (fail-safe structure = 629; fail-safe life cycle periods = 2107). Finally, our survival results were robust to publication bias with fail-safe products of 1820 and 120 for our general linear and mixed models, respectively.

Discussion

Anthropogenic fragmentation of native ecosystems has contributed to biodiversity loss, and one major source of current fragmentation is the development of energy infrastructure in previously unfragmented landscapes (Obermeyer *et al.* 2011; Laurence & Balmford 2013). In many cases, species losses have increased as a result of either direct mortality with structures (Bissonette 2002; Jenkins, Smallie & Diamond 2010; Loss, Will & Marra 2013), or displacement into novel environments as a result of avoidance behaviour, which can be exhibited through a lag effect in species with high site fidelity (Walker, Naugle & Doherty 2007; Fahrig & Rytwinski 2009; Degregorio, Weatherhead & Sperry 2014). Our data-driven synthesis on the response of grouse to anthropogenic structures indicated that grouse may be particularly sensitive to structures associated with energy development. We found that nearly all structures examined resulted in declines of grouse survival and caused displacement behaviour. This universal response regardless of structure type, period of life cycle studied or the species of grouse is a strong indication of the susceptibility of grouse to human threats and gives merit to the use of extreme caution where plans for energy development and grouse populations overlap. While it is hard to quantify a minimally important difference for wildlife populations, the upper limits of our confidence intervals for our pooled effects indicated that grouse populations near structures have 1.50 standard deviation units greater probability of being displaced than populations without structures. Similarly, the upper confidence interval for the pooled effects of survival indicates that grouse populations in environments with structures have 1.33 standard deviation units greater probability of decreased survival. This additive mortality is likely detrimental at a population scale when combined with the annual variation associated with survival rates from climatic constraints and hunting in some populations.

We found that oil and gas structures had the greatest negative effect on displacement behaviour. Oil structures pose several threats to wildlife. Structures can act as perch sites for predatory raptors (Ellis 1984) or can cause noise pollution near breeding areas. A study in Wyoming found greater sage-grouse declines of 73% and 29% at leks with

broadcasted road noise and oil and gas drilling noises, respectively, when compared to control (no noise) leks (Blickley, Blackwood & Patricelli 2012). Researchers hypothesized that noise from anthropogenic structures may mask the noise of approaching predators, leaving animals susceptible to higher rates of predation, or the decline could be associated with avoidance (i.e. displacement) of noisy areas and a subsequent shift to less affected areas.

Our data revealed displacement behaviour associated with roads. Roads are a barrier to many forest and shrubland species that avoid open spaces such as road clearings (Summers, McFarlane & Pearce-Higgins 2007), and roads are typically associated with all types of energy development (i.e. wind turbines, oil and gas wells) allowing them to occur more frequently on the landscape than other structures (Pitman *et al.* 2005; Hagen *et al.* 2011). In our analysis, we treated all roads the same despite their surface substrate or level of traffic; however, most roads that were described in studies were gravel or unimproved, two-tracks. We used this inclusive grouping (i.e. classified all roads the same) to prevent losing data presented on limited road types (i.e. gravel versus paved). A broad classification of roads was the most conservative approach and should have dampened the overall effects. Thus, assuming that roads with minimal traffic have low displacement, there are likely some road types in these studies that are causing high levels of displacement.

Of the portions of the life cycle we investigated, lek-site persistence was most affected by anthropogenic structures. For example, black grouse abandoned leks after wind farm construction in Austria (Zeiler & Grunschachner-Berger 2009), sharp-tailed grouse left lek sites in Minnesota after road cutting (Hanowksi, Christian & Niemi 2000) and greater sage-grouse vacated leks near oil and gas development in Wyoming (Harju *et al.* 2010). Oil and gas development directly removes native vegetation, thereby decreasing useable space, but perhaps more importantly, oil and gas structures can also create perches for aerial predators (Ellis 1984). Similarly, power line poles provide perch sites for predators (Lammers & Collopy 2007) and efforts have been taken to reduce the attractiveness of power poles as predator perches (Prather & Messmer 2010; Slater & Smith 2010). In addition to raptor perch sites, power lines pose a direct threat to many avian species from collision mortality (Jenkins, Smallie & Diamond 2010) and may be especially threatening when constructed in areas of high animal use such as migration corridors or breeding grounds (Rioux, Savard & Gerick 2013).

Survival during all periods of the life cycle we examined decreased in the presence of anthropogenic structures. Published research of the effects on nest survival and brood survival was too scarce to examine, but for lek attendance and annual survival, we found significant declines in the presence of structures. Grouse are mostly non-migratory in nature and develop high site fidelity

associated with annual reproductive activities. As a consequence, annual survival and lek attendance can both be affected as structures can increase fragmentation and alter predator dynamics. For example, increases in mesopredator abundances are common in fragmented habitats and could be the mechanism driving declines in environments with energy structures (Prugh *et al.* 2009).

Much variation exists in the types of structures and focal species investigated, and many studies are not designed with a control treatment or a before and after framework that allowed for inclusion in meta-analysis. For example, greater sage-grouse investigations in areas of oil and gas development overwhelmingly dominate the literature on responses to anthropogenic structures. Additionally, at the time of our analysis, there were no published studies examining the influence of wind turbines on grouse behaviour or survival in the United States; this represents a major void in research given the rapid expansion of wind energy (Kiesecker *et al.* 2011; Obermeyer *et al.* 2011). However, since the completion of our analysis, additional research has examined wind energy (Winder *et al.* 2013) and found minimal impacts on greater prairie-chickens. In Europe, research is more diverse, with multiple studies examining fences (Catt *et al.* 1994; Baines & Summers 1997; Janss & Ferrer 1998; Bevanger & Brøseth 2000; Baines & Andrew 2003), power lines (Bevanger 1995, 1998; Bevanger & Brøseth 2001) and wind turbines (Gonzales & Ena 2011; Douglas, Bellamy & Pearce-Higgins 2012; Pearce-Higgins *et al.* 2012). Across all regions, there is a lack of research investigating survival in response to structures with many more publications reporting displacement behaviour.

There are many research gaps that currently exist in the literature examining the influence of anthropogenic structures and as a result, our analysis is biased by what is available. Additionally, it is important to think about potential biases that may stem from current paradigms, academics or related funding biases. For example, our data inclusion for the United States is confined primarily to open rangeland species of the western United States with no research investigating the influence of structures on forest dwelling species. One can reasonably assume that anthropogenic structures in a structurally diverse forested ecosystem would have less of an effect on avoidance behaviour than structures in open rangeland, but this is an area of research that warrants investigation. Furthermore, variation in species-specific responses to anthropogenic structures is likely to exist with some species exhibiting greater sensitivity to structures than others. We intentionally combined all grouse species to emphasize the general trend associated with anthropogenic structures.

Management and policy implications

Two over-arching conclusions resulting from this systematic and data-driven synthesis can be confidently made.

First, nearly all types of anthropogenic structures that we assessed resulted in displacement behaviour and/or decreased survival of grouse. Therefore, continued energy development is expected to amplify population declines of grouse and associated wildlife. However, effects of energy development on wildlife can be minimized (Kiesecker *et al.* 2011; Obermeyer *et al.* 2011). Fortunately, there are spatial planning tools available and more being created to aid energy developers in avoiding high-priority habitats. Additionally, it is possible that land managers can utilize disturbances such as fire and grazing to influence wildlife use of areas with high densities of structures, which may reduce some of the negative effects associated with survival. Secondly, research is lacking for impacts of anthropogenic structures on many species. At the time of our analysis, there were no studies investigating the effect of wind energy on grouse in the United States, a major concern given the United State's Department of Energy's goal of providing 20% of the nation's energy from wind by 2030 (DOE 2008). Recently, however, research from a wind energy project in the central United States has published results that show variable effects on greater prairie-chickens dependent upon the time of year and period of the life cycle (Winder *et al.* 2013, 2014; McNew *et al.* 2014). Europe has a broader base of literature examining structures, but there is still an overall lack of survival data and more before/after control designs should be conducted in both regions. In the future, it continues to be the responsibility of scientists to support policymakers with data elucidating human impacts on wildlife, and this examination of anthropogenic structures provides clear evidence that human development is negatively affecting some species of wildlife, while the potential effects on the vast majority of species are still unknown. We suggest land managers try to work with energy companies to prevent structure development near areas important to breeding activities (e.g. lek sites), and efforts should be made to try and reduce the density of anthropogenic structures erected in unfragmented rangelands when all other options (i.e. alternate locations) have been exhausted.

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Data accessibility

All data used in this study have been sourced from published studies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Studies used in the analysis of grouse displacement behaviour and survival in response to anthropogenic structures. Table includes the grouse species, period of the life cycle, type of anthropogenic structure, and whether the study was included in the displacement or survival analysis.