



Responses of Vertebrate Wildlife to Oil and Natural Gas Development: Patterns and Frontiers

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Abstract

Purpose of Review Anthropogenic activities can lead to the loss, fragmentation, and alteration of wildlife habitats. I reviewed the recent literature (2014–2019) focused on the responses of avian, mammalian, and herpetofaunal species to oil and natural gas development, a widespread and still-expanding land use worldwide. My primary goals were to identify any generalities in species' responses to development and summarize remaining gaps in knowledge. To do so, I evaluated the directionality of a wide variety of responses in relation to taxon, location, development type, development metric, habitat type, and spatiotemporal aspects.

Recent Findings Studies ($n = 70$) were restricted to the USA and Canada, and taxonomically biased towards birds and mammals. Longer studies, but not those incorporating multiple spatial scales, were more likely to detect significant responses. Negative responses of all types were present in relatively low frequencies across all taxa, locations, development types, and development metrics but were context-dependent. The directionality of responses by the same species often varied across studies or development metrics.

Summary The state of knowledge about wildlife responses to oil and natural gas development has developed considerably, though many biases and gaps remain. Studies outside of North America and that focus on herpetofauna are lacking. Tests of mechanistic hypotheses for effects, long-term studies, assessment of response thresholds, and experimental designs that isolate the effects of different stimuli associated with development, remain critical. Moreover, tests of the efficacy of habitat mitigation efforts have been rare. Finally, investigations of the demographic effects of development across the full annual cycle were absent for non-game species and are critical for the estimation of population-level effects.

Keywords Amphibians · Birds · Mammals · Natural gas development · Oil · Wildlife

Introduction

Global demand for energy continues to increase [1, 2], and substantial portions of that demand will be met with natural gas extraction and on-going oil production [3, 4]. In particular, unconventional oil and natural gas extraction is becoming a major energy sector worldwide [1], though currently is conducted primarily within the USA and Canada [2, 5]. New

extraction technologies are facilitating rapid development in previously pristine landscapes, which has raised concerns for sensitive species [3, 4, 5, 6]. Similar to other forms of human-induced rapid environmental change, the process of extracting fossil fuels has the capability to rapidly and extensively transform landscapes before wildlife can adapt [6, 7]. Landscape changes that result from oil and natural gas development include habitat loss, fragmentation, and alteration; chemical pollution, and the addition or amplification of novel stimuli such as human traffic, noise, and light [5, 6, 8, 9]. Delineation of the effects of such changes is therefore timely and critical for the effective mitigation of habitats, and wildlife conservation.

My review was preceded by several thorough and insightful reviews on various aspects of energy development and wildlife, which set the stage for the examination of progress and remaining frontiers. Most examinations of development effects at the time of previous reviews documented negative effects of extraction activities [1]. Empirical studies, however,

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were conducted primarily within North America, albeit very few within the forests of the eastern USA [1, 2]. Moreover, studies were biased taxonomically towards non-volant mammals and, to a lesser extent, birds [1, 2]. Species of economic importance such as ungulates and greater sage-grouse received more focus in field studies than non-game species [1, 2, 9]. Mammalian responses were primarily behavioral, including space use and patterns of movement, whereas avian evaluations centered on changes in abundance within the vicinity of development [1]. Few generalizations about patterns of wildlife responses to oil and natural gas development had emerged, however, and effects were characterized as area and species specific [1].

Authors of previous reviews articulated many frontiers in understanding, in addition to addressing geographic and taxonomic gaps. Because energy development simultaneously alters landscapes in many ways, authors reasoned that the disentangling of responses to multiple factors deserved further attention [2], as did the quantification of both direct and indirect effects [5, 10, 11]. Accordingly, from a methodological standpoint, researchers encouraged the incorporation of baselines (e.g., before-after, control-impact designs) such that the effects of development could be isolated definitively [5, 11]. Another insightful suggestion with clear implications for management was the examination of potential thresholds above which responses to development occur [1]. Physical habitat changes such as those imposed by development, moreover, do not occur in isolation. Thus, understanding the cumulative effects of oil and natural gas development in combination with other contemporary stressors such as climatic variability also is critical [1, 6]. From a spatiotemporal perspective, authors emphasized the analysis of effects at multiple spatial scales and across sufficient time periods such that potential lag effects could be detected [5, 11]. The importance of studying a species across the full annual cycle also was articulated, so that ultimately demographic effects can be connected to actual population dynamics [1, 4]. Finally, oil and natural gas development has a finite lifespan, and operators are usually required to implement reclamation measures following well completion. The efficacy of potential mitigation measures, however, had received little study [1, 5].

Herein, I revisit and build upon existing reviews of the effects of oil and natural gas development on vertebrate wildlife to determine the extent to which previously articulated gaps were addressed and additional patterns have emerged. I reviewed the recent literature focused on energy development and responses of birds, mammals, reptiles, and amphibians and summarized patterns (including the directionality of responses) by taxon, location, development type, development metric, response type, and habitat type. Because responses to landscape change can manifest at different scales, moreover, I investigated whether the duration of studies or number of spatial scales assessed influenced the detection of responses,

and documented evidence of threshold effects. Additionally, for species with multiple tests, I assessed the congruence in species' responses to development across contexts (locations, development metrics, and response type) to determine the consistency and predictability of responses. Finally, I discuss remaining frontiers in understanding that emerged from the review.

Approach

I conducted a literature search using the search engine Biological Abstracts for papers focused on oil and/or natural gas extraction and wildlife during the years 2014–2019. I first used the following wildlife search terms: wildlife, bird*, mammal*, avian, amphibian*, reptile*, lizard*, herp*, combined sequentially with all of the following development terms: energy development, gas and development, natural gas, oil and development, frack*, and shale gas. I then conducted a secondary search focused on the combination of energy development metrics with the response terms: occupancy, abundance, richness, diversity, habitat selection, habitat use, avoidance, reproduc*, and mortality. Results were refined taxonomically to Mammalia, Aves, Reptilia, and Amphibia.

I focused on the effects of changes to terrestrial habitats (e.g., no aquatic contaminant or oil spill studies). I did not include investigations of mining (e.g., “oil sands”) as they have very different footprints compared with energy fields. I also omitted papers exclusively focused on roads, seismic or power lines, as those landscape changes are more universal than oil and natural gas development per se. I focused on studies with empirical (field) components and omitted purely modeling papers. Papers had to focus on the current effects of development on species, not just model future impacts based on projected habitat changes, or post hoc attributions to development. No artificial nest studies or laboratory experiments were included (i.e., animals must have been studied in situ). Finally, I did not include papers in which species were pooled for analyses, with the exception of diversity and richness analyses and one paper focused on amphibian deformities throughout the USA [12].

For each study adhering to review criteria, I extracted the following information: author(s), year, journal, taxon, species, country, state or province, habitat type (forest, shrubland, grassland, wetland, mixed), development type (oil, natural gas, or both), season (spring, summer/breeding, fall, winter), study duration in years, response type(s), and development metric(s). I recorded also the number of summary scales within which development metrics were calculated, the inclusion of other habitat variables and whether they had explanatory power, tests, and presence of threshold effects, the directionality of responses, and suggestions for further study.

Development metrics included proximity to development, well density, well pad density, and surface disturbance (amount of cleared land associated with development activities). I counted tests of potential thresholds as present when explicitly articulated and/or when quadratic effects were included models in addition to linear. I binned species' responses into the following categories: occurrence/occupancy, abundance/density, fecundity metrics (e.g., clutch size, pregnancy rates, cow-calf ratios), reproductive success (e.g., nest survival, number fledged, juvenile survival), adult survival, behavioral (habitat use, habitat selection, avoidance, site fidelity), body mass and condition metrics, physiological (stress hormones, immunocompetence), disease/ecotoxicological, and richness/diversity metrics.

Each species, development type, development metric, and specific response combination was considered an individual "test." Each paper could therefore contain multiple tests. If responses were evaluated separately for different seasons or at distinct scales (e.g., home range versus within-home range), I recorded each as a separate test. Responses recorded at different times of day, however, were pooled and I recorded whether significant responses were recorded during any part of the day. I used a vote-counting approach and relied on authors' interpretation of which tests were significant or not based on their respective statistical analyses. The use of a vote-counting strategy for my review precluded the ability to calculate the overall magnitude of the effects of development across studies. Many studies did not include the requisite information with which to conduct a meta-analysis, however, which would have decreased the sample size of papers included in my review. The directionality of responses was considered negative or positive if focal metrics (e.g., abundance, survival, etc.) decreased or increased with proximity to development features, well or well pad density, or surface disturbance, respectively, and neutral if authors concluded a lack of significant effect. For multi-year studies, I recorded negative or positive responses if observed during any of the study years (e.g., year by treatment interactions). Finally, I analyzed whether study duration (number of years) or number of spatial scales examined increased the probability of detecting effects of development using binary logistic regression.

Review Summary

My literature search resulted in a sample of 465 individual tests on 102 species from 69 studies [12•, 13–15, 16•, 17–21, 22•, 23–30, 31•, 32–33, 34•, 35–40, 41•, 42–46, 47•, 48–59, 60•, 61–78, 79••]. The majority (84%) were focused on birds (44 studies, 389 tests), followed by mammals (22 studies, 67 tests), and amphibians (3 studies, 8 tests). One study focused on vertebrate diversity [13]. Of herpetofaunal studies, I located only two studies focused on anurans [12•, 14], two on salamanders [14, 15], and none on reptiles. Of the

bird studies, 18 focused on passerines, 18 on gallinaceous species, 5 on raptors, 2 on waterfowl, and 1 on a shorebird (Killdeer, *Charadrius vociferus*) [16•]. The bird species with the greatest number of tests was the greater sage-grouse (*Centrocercus urophasianus*) with 52 tests ($N = 11$ studies), followed by the chestnut-collared longspur (*Calcarius ornatus*), with 51 tests from eight studies. Of the mammal papers, the majority focused on ungulates ($N = 32$ tests from 14 studies), with three on medium-sized mammals (small canids and mustelids) [17–19], two on the deer mouse [17, 20], one on least chipmunks (*Tamias minimus*) [21], one on pygmy rabbits (*Brachylagus idahoensis*) [22•], and one on a large carnivore (grizzly bear, *Ursus arctos*) [23]. The two mammalian species that received the most study were pronghorn (*Antilocapra americana*; $N = 19$ tests from six studies) and mule deer (*Odocoileus hemionus*; $N = 13$ tests from eight studies).

Studies were located exclusively in the USA ($N = 57$ studies and 288 tests) and Canada ($N = 13$ studies, 177 tests). The US studies were conducted within 12 different states (Alaska, California, Colorado, Kansas, Oklahoma, Pennsylvania, Montana, North Dakota, Texas, Utah, West Virginia, and Wyoming). Canadian studies were located primarily in Alberta ($N = 10$), with one each in Saskatchewan and British Columbia, and one that occurred within both Alberta and Saskatchewan. Several geographic hotspots of research focused on oil and natural gas and wildlife emerged, including the forests of the Allegheny plateau in the eastern USA ($N = 7$ studies), the grasslands and arid shrublands of the western USA ($N = 41$ studies), and the grasslands of south-central Canada ($N = 10$ studies). The majority of studies occurred within shrubland ($N = 29$) and grassland ($N = 20$) habitat types, with 10 in forested landscapes, four in wetlands, and 7 in mixed habitats.

In terms of development type, studies were skewed towards natural gas ($N = 30$ studies and 240 tests), with 13 studies focused on oil ($N = 106$ tests), and 27 including a combination of both ($N = 119$ tests). Proximity to infrastructure received the most study ($N = 239$ tests; 51.4%), followed by well density ($N = 95$ tests; 20.4%), surface disturbance ($N = 63$ tests; 13.5%), well pad density ($N = 36$ tests; 7.7%), and binary (developed versus undeveloped; $N = 32$ tests; 6.9%). Response metrics were biased towards abundance and density effects ($N = 195$ tests; 41.9%). Behavioral responses, including habitat use and selection, was the second most common response type with 109 (23.4%) tests. Responses of metrics associated with fitness outcomes combined comprised 24.3% of tests ($N = 113$). Specifically, tests focused on reproductive success (e.g., nest survival) individually comprised 15.7% of tests ($N = 73$), fecundity metrics comprised 5.6% ($N = 26$), followed by adult survival with 3% of tests ($N = 14$).

The remainder of the tests examined responses categorized as occurrence or occupancy ($N = 20$ tests; 4.3%), body size or condition ($N = 9$; 1.9%), or species richness or diversity ($N = 14$; 3%). Three papers ($N = 4$ tests) fell into the category of disease and ecotoxicology, including deformities in anurans [12•], disease prevalence and ecotoxicology of pronghorn [24], and exposure to rodenticides in the fisher (*Pekania pennanti*) [18]. Finally, one test from one paper focused on fecal corticosteroids and progesterone in pronghorn [24] comprised the physiological category.

Spatiotemporal aspects, including study duration, time of year, and the number of spatial extents within which development metrics were summarized, varied across studies. Studies ranged from 1 to 40 years in duration (mean = 4.43 ± 4.05 SD). Time of year was biased heavily towards the breeding season ($N = 407$ tests or 87.5%), followed by winter ($N = 43$ tests), fall or post-breeding ($N = 6$ tests), spring ($N = 4$ tests), and year-round or multiple seasons ($N = 5$ tests). For studies examining the effects of well density, well pad density or surface disturbance ($N = 193$ tests), the number of summary spatial scales ranged from one to nine (mean = 1.68 ± 1.45 SD). Models (or model suites) of the effects of energy development often (53% of cases)

included other habitat variables. Threshold effects were examined in 122 tests (26%) and 12 studies.

Responses Across Taxa, Development Type, and Development Metrics

Overall, responses to development in 128 tests (27.5%) were negative, 260 (55.9%) were neutral, and 77 (16.6%) were positive. The prevalence of negative responses to development increased from birds to mammals and to amphibians (Fig. 1a). The number of tests revealing positive responses was higher for mammals than birds, however, and absent for amphibians (albeit with a comparatively low sample size).

The composition of the directionality of responses was remarkably similar for the three major types of energy development (Fig. 1b). The number of negative responses also was similar across response types, with the highest negative response rates for behavioral tests including habitat selection and avoidance (Fig. 1c). By contrast, species richness and diversity responses often were positive in relation to energy development. With the three fitness-related response types collapsed into one, birds displayed negative fitness outcomes in 23.5% of cases ($N = 98$ tests) compared with 33.3% in mammals ($N = 15$ tests).

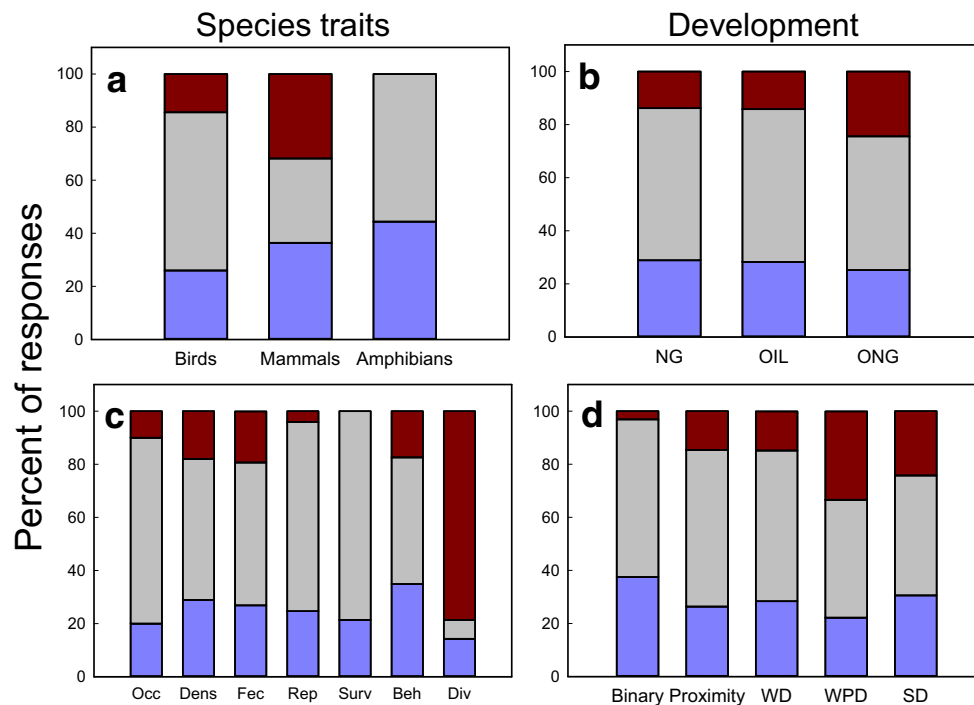


Fig. 1 Prevalence of negative (blue), neutral (grey), and positive (red) responses of wildlife to oil and natural gas development in relation to taxon (a), development type (b), species' response type (c), and development metric (d). Data extracted from a literature search spanning the period 2014–2019. For development type, NG, natural gas; Oil, oil, and ONG, oil and natural gas. For species responses, Occ, tests of occurrence or occupancy; Dens, abundance or density; Fec,

fecundity metrics such as clutch size or pregnancy rates; Rep, measures of reproductive success; Surv, adult survival; Beh, behavioral tests such as habitat use or selection; and Div, richness or diversity. Development metrics include binary (developed versus undeveloped), proximity (to development features such as wells), well density (WD), well pad density (WPD), and surface disturbance (SD).

Mammals also had a relatively high negative response rate (48.4%) for behavioral traits including habitat selection and avoidance ($N = 31$ tests). Responses related to body condition and size yielded no negative effects, but rather were neutral in 77.8% of cases ($N = 9$). For the one physiologically oriented test, pronghorn wintering in Wyoming did not have higher fecal corticosteroids or progesterone in developed versus undeveloped sites [24]. Finally, in terms of disease and ecotoxicology studies, pronghorn in Wyoming did not differ in disease prevalence or ecotoxicological measures between developed and undeveloped areas [24], and fisher exposure to rodenticides was unrelated to oil and natural gas variables [18]. The prevalence of deformities in anurans in the USA, however, increased in areas with oil and natural gas wells [12•].

Species tended to respond more negatively to binary tests of developed versus undeveloped landscapes compared with other development metrics (Fig. 1d). The percentage of negative responses ranged from 22.2% negative in relation to well pad density to 37.5% for binary tests. Birds, in particular, tended to respond negatively to binary tests of development, with 44% of tests ($N = 25$) producing negative responses compared with tests focused on mammals, which produced only 14.3% negative responses ($N = 7$; 83.7% were neutral). Mammals responded most negatively to the proximity of development (60% of tests were negative; $N = 15$) and surface disturbance (40%; $N = 25$ tests).

The habitat type within which tests were conducted did not strongly influence the directionality of responses. The percentage of negative responses to development was 24.3% in forests, 24.9% in grassland, and 33.6% in shrubland. Negative responses were most common in wetlands (83.3%) albeit with a limited sample size ($N = 6$ tests). The density of river otters (*Lontra canadensis*) was negatively associated with natural gas development in Wyoming, USA [19]. Moreover, the larval abundance of barred tiger salamanders (*Ambystoma mavortium*), boreal chorus frogs (*Pseudacris maculata*), and northern leopard frogs (*Lithobates pipiens*) in Montana and North Dakota decreased with the density of oil wells installed prior to 1982 when brines were disposed into groundwater [14].

The time of year during which tests were conducted produced some variation in the directionality of responses. There were only four tests conducted during the spring or pre-breeding season, two each on the habitat use of grizzly bears [23] and greater prairie chickens (*Tympanuchus cupido*) [25], none of which yielded negative responses. The vast majority ($N = 406$) of tests occurred within the summer and/or breeding months, for which 22.6% of responses were negative. Tests conducted in the fall period ($N = 6$) produced a negative response rate of 16.7%. Negative responses were most common during the winter months (39.5%; $N = 43$).

Spatiotemporal Effects on Responses

Thirteen studies spanned 10 years or more. The probability of detecting significant effects of energy development, in either direction, increased with study duration (logistic regression; Wald = 4.48, $df = 1$, $P = 0.03$). The mean number of years for tests producing significant effects was 4.89 ± 4.88 SD compared with 4.07 years ± 3.19 SD for non-significant results. The average study duration associated with detection of negative effects was longer, however (5.43 years ± 5.72 SD). The number of spatial scales assessed with respect to species' responses to surrounding well density, well pad density or surface disturbance ($N = 192$ tests) did not increase the probability of detecting significant effects (logistic regression; Wald = 0.25, $df = 1$, $P = 0.62$).

Threshold Effects

Of the 123 tests of potential threshold responses, 44 produced negative effects of development and 15 yielded positive effects. Of those significant results, 21 (48%) and five (33%), respectively, had associated thresholds. For example, the presence and abundance of pygmy rabbits declined sharply after approximately 2% surface disturbance associated with natural gas development [22•], and lek counts of greater sage-grouse decreased non-linearly, with an inflection point of approximately 4 wells/km² [26].

Context-Dependent Responses

Many species ($N = 59$) were the focus of more than one test, both within or across studies, which facilitated a more in-depth evaluation of the consistency of responses to energy development across contexts. Fourteen species, all avian, demonstrated similar responses (mostly neutral) to the same development metric across two or more studies with unique study areas (Table 1). This pattern was not the norm, however. In 30 other cases, species showed different directionality of response across studies. The habitat selection patterns of greater sage-grouse, for example, varied across studies in relation to the proximity to development, well density, well pad density and surface disturbance. A few grassland songbirds, including chestnut-collared longspurs, horned larks (*Eremophila alpestris*), and Savannah sparrows (*Passerculus sandwichensis*), and pronghorn demonstrated the full range of potential responses (negative, null, or positive) across contexts.

Determining whether a species tends to respond similarly to development across response types can provide insight into the cumulative effects of development. I found 22 cases in which different response types of the same species were evaluated with respect to the same development metric (Table 2). Congruence occurred for only 11 species-development metric

Table 1 Consistency in the directionality of species' responses to oil and natural gas development across studies

Species	Development metric	Response	Direction	References
Congruent responses:				
American robin	Proximity	Abundance	+	[27, 28]
Black and white warbler	Proximity	Abundance	0	[27, 28]
Chipping sparrow	Proximity	Abundance	+	[27, 28]
Clay-colored sparrow	Proximity	Abundance	0	[29, 30]
Eastern towhee	Proximity	Abundance	0	[27, 28]
Eastern wood pewee	Proximity	Abundance	+	[27, 28]
Horned lark	Proximity	Abundance	0	[29, 31•]
Ovenbird	Proximity	Abundance	–	[27, 28]
Red-eyed vireo	Proximity	Abundance	–	[27, 28]
Ferruginous hawk	Proximity	Nest success	0	[32, 33]
Greater sage-grouse	Proximity	Nest success	0	[34•, 35]
Northern bobwhite	Proximity	Habitat selection	0	[36, 37]
Baird's sparrow	Well density	Abundance	0	[29, 31•]
Sprague's pipit	Well density	Abundance	0	[29, 31•, 38]
Greater sage-grouse	Well density	Nest success	0	[34•, 35]
Greater sage-grouse	Surface disturbance	Nest success	0	[34•, 35]
Greater sage-grouse	Surface disturbance	Survival	0	[34•, 39]
Contrasting responses				
American redstart	Proximity	Abundance	+ , 0	[27, 28]
Baird's sparrow	Proximity	Abundance	– , 0	[29, 30, 31•, 40]
Black-throated-green warbler	Proximity	Abundance	– , 0	[27, 28]
Blue-headed vireo	Proximity	Abundance	– , 0	[27, 28]
Blue jay	Proximity	Abundance	– , 0	[27, 28]
Brown-headed cowbird	Proximity	Abundance	+ , 0	[27–30]
Chestnut-collared longspur	Proximity	Abundance	– , 0	[29, 30, 31•, 38]
Common yellowthroat	Proximity	Abundance	+ , 0	[27, 28]
Grasshopper sparrow	Proximity	Abundance	– , 0	[25, 30, 31•]
Indigo bunting	Proximity	Abundance	+ , 0	[27, 28]
Savannah sparrow	Proximity	Abundance	– , 0 , +	[29, 30, 38, 40, 41•]
Scarlet tanager	Proximity	Abundance	– , 0	[27, 28]
Sprague's pipit	Proximity	Abundance	– , 0	[29, 30, 31•, 38, 40]
Vesper sparrow	Proximity	Abundance	+ , 0	[29, 31•, 38, 41•]
Western meadowlark	Proximity	Abundance	+ , 0	[29, 30, 38, 40]
Chestnut-collared longspur	Proximity	Clutch size	– , 0	[38, 42, 43]
Chestnut-collared longspur	Proximity	Nest success	– , 0	[38, 41•, 42, 43]
Savannah sparrow	Proximity	Nest success	– , 0 , +	[38, 40, 41•, 42]
Vesper sparrow	Proximity	Nest success	– , 0	[38, 40, 41•]
Greater sage-grouse	Proximity	Survival	– , 0	[34•, 39]
Greater sage-grouse	Proximity	Habitat selection	– , 0	[34•, 39, 44, 45]
Pronghorn	Proximity	Habitat selection	– , 0 , +	[46, 47•, 48]
Brown-headed cowbird	Well density	Abundance	+ , 0	[29, 49]
Chestnut-collared longspur	Well density	Abundance	– , 0 , +	[29, 31•, 38]
Horned lark	Well density	Abundance	– , 0 , +	[29, 31•]
Savannah sparrow	Well density	Abundance	– , 0	[29, 31•, 38]
Greater sage-grouse	Well density	Habitat selection	– , 0	[34•, 39, 50]
Greater sage-grouse	Well pad density	Habitat selection	– , 0	[44, 45]
Brown-headed cowbird	Surface disturbance	Abundance	– , 0	[51]
Greater sage-grouse	Surface disturbance	Habitat selection	– , 0	[34•, 39]

Data derived from a literature search spanning 2014–2019. Null responses denoted with zeros, and negative and positive responses by minus and plus signs, respectively

combinations (seven species of birds, and three mammals). All were consistently neutral responses except for two cases. Pronghorn increased habitat use and had more fawns per doe closer to oil wells [46]. In contrast, both the occupancy and abundance of pygmy rabbits decreased with surface disturbance [22•]. In the majority of cases ($N = 21$), however, responses varied across response metrics for nine bird species and one mammal (deer mouse, *Peromyscus maniculatus*) (Table 2). In several cases, birds either preferred to nest (killdeer) [16•] or had higher densities of nests (northern

pintail, *Anas acuta*; vesper sparrow, *Pooecetes gramineus*) in areas that conferred lower nest survival [41•, 53].

Finally, examination of the patterns of the same species' responses to different development metrics within the same study permitted an evaluation of whether particular metrics consistently tended to yield more negative effects, while controlling for study context. Furthermore, negative responses to all assessed metrics of development could suggest an overall higher sensitivity of a species to development. The most common pairing was the inclusion of both proximity and well

Table 2 Directionality of different responses to oil and natural gas development within species and studies

Species	Dev metric	Response types	Direction	Reference
Congruent responses				
Pronghorn	Binary	Pregnancy, survival, body mass, fecal hormones, disease	0, 0, 0, 0, 0	[24]
Baird's sparrow	Proximity	Abundance, nest success, habitat use	0, 0, 0	[40]
Mule deer	Proximity	Fawn predation, adult predation	0, 0	[52]
Northern shoveler	Proximity	Nest density, nest success	0, 0	[53]
Pronghorn	Proximity	Doe/fawn ratio, habitat selection	+ +	[46]
Savannah sparrow	Proximity	Nest density, nest success	0, 0	[41•]
Sprague's pipet	Proximity	Density, nest distance, nest success	0, 0, 0	[40]
Vesper sparrow	Proximity	Density, nest distance, nest success	0, 0, 0	[40]
Chestnut-collared longspur	WD	Clutch size, nest success	0, 0	[42]
Savannah sparrow	WD	Clutch size, nest success	0, 0	[42]
Pygmy rabbit	SD	Occupancy, abundance	-, -	[22•]
Contrasting responses				
Killdeer	Binary	Nest-site selection, nest success	+ , -	[16•]
Blue-winged teal	Proximity	Nest density, nest success	+ , 0	[53]
Chestnut-collared longspur	Proximity	Clutch size, nest success	- , 0	[42]
Chestnut-collared longspur	Proximity	Abundance, clutch size, nest success	- , -, (- , 0) ^a	[38]
Greater sage-grouse	Proximity	Nest success, brood survival, adult survival, habitat selection	0, 0, -, (0, 0, -, 0, 0) ^b	[34•]
Northern pintail	Proximity	Nest density, nest success	+ , 0	[53]
Savannah sparrow	Proximity	Abundance, nest distance, nest success	+ , 0, 0	[40]
Savannah sparrow	Proximity	Abundance, clutch size, nest success	- , +, (+ , -) ^a	[38]
Savannah sparrow	Proximity	Clutch size, nest success	- , 0	[42]
Sprague's pipet	Proximity	Abundance, clutch size, nest success	- , (+ , -) ^a , 0	[38]
Vesper sparrow	Proximity	Abundance, clutch size, nest success	(+ , 0) ^a , 0, 0	[38]
Vesper sparrow	Proximity	Nest density, nest success	+ , -	[38]
Western meadowlark	Proximity	Abundance, clutch size, nest success	(+ , 0) ^a , 0, 0	[38]
Western meadowlark	Proximity	Density, nest distance, nest success	0, + , 0	[40]
Greater sage-grouse	WD	Nest success, brood survival, adult survival, habitat selection	0, 0, 0, (- , -, -, 0, -) ^b	[34•]
Savannah sparrow	WD	Abundance, clutch size, nest success	- , + , 0	[38]
Vesper sparrow	WD	Abundance, clutch size, nest success	0, 0, -	[38]
Western meadowlark	WD	Abundance, clutch size, nest success	- , 0, 0	[38]
Deer mouse	SD	Abundance, juveniles/female, survival, body condition, perceived predation risk	+ , 0, -, 0, -	[17, 20] ^c
Greater sage-grouse	SD	Nest success, brood survival, adult survival, habitat selection	0, -, 0, (0, 0, 0, -, 0) ^b	[34•]

Data derived from a literature search spanning 2014–2019. Null responses denoted with zeros, and negative and positive responses by minus and plus signs, respectively. Direction of responses parallels order of the response types

Dev metric, focal development metric; *Binary*, developed versus undeveloped comparisons; *WD*, well density; *WPD*, well pad density; *SD*, surface disturbance

^a Authors tested both natural gas and oil. First response denotes natural gas, second is oil

^b Authors tested habitat use of females during five stages: nesting, early brood-rearing, late brood-rearing, early non-brood-rearing, and late non-brood-rearing, listed in order

^c Same study area and timeframe, published in two papers

density within the same study. The directionality of different responses within studies was congruent in 28 of 57 cases (Table 3). For the majority of those ($N = 20$), responses were consistently neutral. Several open-country birds, however, responded negatively to two indices of development. Lek attendance by male greater sage-grouse decreased with both well density and surface disturbance [26]. Moreover, sage-grouse avoided areas in closer proximity to natural gas infrastructure and with higher well pad density [44]. The nest survival of chestnut-collared longspurs [38], sage thrashers (*Oreoscoptes montanus*) [55], savannah sparrows [38], and vesper sparrows [41•] all decreased with two indices of development (Table 3). In addition, one forest songbird, the Louisiana waterthrush (*Parkesia motacilla*), experienced lower nest survival in developed versus undeveloped areas and with respect to surrounding surface disturbance [54]. Finally, pronghorn increased avoidance of natural gas development over time as assayed by both binary and proximity responses [47••].

For the remaining 29 tests, species often responded negatively to one but not all indices of development (Table 3). Responses were not consistently negative more often for particular indices compared to another, although some generalities emerged. The abundance of open country birds, including greater sage-grouse and a large suite of grassland songbirds, tended to decrease more with proximity to development compared with surrounding well or well pad density (Table 3). More broadly, in studies with contrasting responses to proximity versus surrounding density tests, species were approximately equally likely to respond more negatively to the proximity of development compared with well density or well pad density.

Remaining Frontiers

Several themes emerged regarding suggested lines of future inquiry. Many authors ($N = 26$ papers) mentioned the need to better understand the mechanisms underlying species' responses to oil and natural gas development. Understanding the processes underlying observed patterns holds particular value for formulating effective mitigation measures. As a case study, sagebrush songbirds nesting within natural gas fields experienced higher nest predation rates, which was associated with increased densities of synanthropic rodents attracted to the reseeded areas around well pads and pipelines [17, 20, 21]. Reproductive success of songbirds would therefore likely benefit from the reduction of initially disturbed soils and/or reclamation practices that more closely mimic initial conditions. The extraction of fossil fuels is a temporary activity on the landscape. In theory, provided sufficient resources, and expertise, habitat could therefore be restored to resemble pre-disturbance conditions. Surprisingly, however, only two papers astutely pointed out the need to understand the responses of wildlife to post-development restoration [27, 50].

Substantial progress has been made since previous reviews in terms of the investigation of fitness outcomes of species in response to energy development. Regardless, the second most popular theme in terms of suggestions for future study was better understanding of the fitness consequences of wildlife coexisting with development ($N = 19$ papers). Moreover, in my review I characterized increased abundance as a “positive” response, yet the fitness consequences of potentially forcing more individuals into less, or poorer quality, habitat because of development remains unclear [47••]. Additionally, whereas investigation of the effects of landscape change across the full annual cycle is effort and resource-intensive, without such data the effects of habitat changes cannot be accurately extrapolated to source-sink dynamics [34•] or population-level impacts more generally [4•]. With the exception of several mammalian species and the greater sage-grouse, study of species' responses for periods outside the breeding season were extremely rare. The vast majority of North American birds, for example, are seasonal migrants. Whether habitat changes on breeding grounds associated with energy development carry over to influence survival during subsequent periods remains unclear. No studies that I reviewed focused on the effects of development on the post-fledging period for altricial birds. Moreover, whereas estimation of adult survival in relation to development was common for gallinaceous birds that can accommodate larger tracking devices, only one study estimated the annual survival and site fidelity of a migratory passerine (Louisiana waterthrush) [60•]. Finally, although a focus of previous studies and reviews [2, 10, 61], I did not locate any studies that were focused on the direct mortality of wildlife associated with development.

Long-term studies can facilitate the assessment of the population-level impacts of development, especially those that span pre- and post-development periods [47••]. Accordingly, authors of nine papers recommended more long-term studies. Indeed, the longer-term studies that I reviewed were more likely to document effects of development on wildlife, and many revealed negative effects on several high-profile species including greater sage-grouse, pronghorn, mule deer and woodland caribou (*Rangifer tarandus caribou*) [26, 47••, 69–78, 79••]. Moreover, the trend remains that very few studies of oil and natural gas development have utilized Before-After-Control-Impact (BACI) designs to account for potentially confounding factors. Accordingly, the need for more BACI analyses was suggested repeatedly ($N = 8$ papers).

The identification of thresholds, or inflection points, in species' responses to development and other forms of landscape change can be particularly informative for conservation practitioners. Whereas some authors in the current review explicitly tested for such thresholds, they were in the minority. Many authors ($N = 6$ papers) therefore encouraged future study of potential non-linear effects of development. Other suggestions ($N = 7$ papers) reflected the need for improved understanding of spatial aspects, including effects at multiple

Table 3 Species' responses to different oil and natural gas development ("Dev") metrics within the same study

Species	Response type	Dev type	Dev metrics	Responses	Reference
Congruent responses					
Baird's sparrow	Abundance	NG	Proximity, WD	0, 0	[29]
Chestnut-collared longspur	Abundance	NG	Proximity, WD	0, 0	[29]
Clay-colored sparrow	Abundance	NG	Proximity, WD	0, 0	[29]
Savannah sparrow	Abundance	NG	Proximity, WD	0, 0	[29]
Sprague's pipit	Abundance	NG	Proximity, WD	0, 0	[31•]
Savannah sparrow	Abundance	ONG	Proximity, WD	–, –	[38]
Greater sage-grouse	Abundance	ONG	WD, SD	–, –	[26]
Vesper sparrow	Clutch size	NG	Proximity, WD	0, 0	[38]
Western meadowlark	Clutch size	NG	Proximity, WD	0, 0	[38]
Chestnut-collared longspur	Nest success	NG	Proximity, WD	–, –	[38]
Greater sage-grouse	Nest success	NG	Proximity, WD, SD	0, 0, 0	[34•]
Greater sage-grouse	Nest success	NG	Proximity, WD, WPD, SD	0, 0, 0, 0	[35]
Louisiana waterthrush	Nest success	NG	Binary, SD	–, –	[54]
Sagebrush sparrow	Nest success	NG	WD, SD	0, 0	[55]
Sage thrasher	Nest success	NG	WD, SD	–, –	[55]
Savannah sparrow	Nest success	NG	Proximity, WD	0, 0	[42]
Western meadowlark	Nest success	NG	Proximity, WD	0, 0	[38]
Chestnut-collared longspur	Nest success	Oil	Binary, proximity	0, 0	[41•]
Chestnut-collared longspur	Nest success	NG	Proximity, well density	0, 0	[42]
Sprague's pipit	Nest success	Oil	Binary, proximity	0, 0	[41•]
Vesper sparrow	Nest success	Oil	Binary, proximity	–, –	[41•]
Western meadowlark	Nest success	Oil	Binary, proximity	0, 0	[41•]
Ferruginous hawk	No. fledged	ONG	Proximity, WPD	0, 0	[33]
Greater sage-grouse	Habitat selection	NG	Proximity, WPD	–, –	[44]
Greater sage-grouse	Habitat selection	ONG	Proximity, SD	0, 0	[45]
Pronghorn	Habitat selection	NG	Binary, proximity	–, –	[47••]
Pronghorn	Survival	ONG	Proximity, WD	0, 0	[56]
Fisher	Rodenticide exposure	ONG	WD, SD	0, 0	[18]
Contrasting responses					
Baird's sparrow	Abundance	NG	Proximity, WD	–, 0	[31•]
Chestnut-collared longspur	Abundance	NG	Proximity, WD	–, 0	[31•]
Grasshopper sparrow	Abundance	NG	Proximity, WD	–, 0	[31•]
Horned lark	Abundance	NG	Proximity, WD	0, +	[31•]
Horned lark	Abundance	NG	Proximity, WD	0, –	[29]
Savannah sparrow	Abundance	NG	Proximity, WD	–, 0	[31•]
Sprague's pipit	Abundance	NG	Proximity, WD	–, 0	[38]
Vesper sparrow	Abundance	NG	Proximity, WD	+, 0	[38]
Western meadowlark	Abundance	NG	Proximity, WD	+, 0	[29]
Sprague's pipit	Abundance	ONG	Proximity, WD	–, 0	[29]
Vesper sparrow	Abundance	ONG	Proximity, WD	(+, 0) ^a , 0	[38]
Western meadowlark	Abundance	ONG	Proximity, WD	(+, 0) ^a , –	[38]
Greater sage-grouse	Abundance	ONG	Proximity, WPD	–, 0	[57]
Chestnut-collared longspur	Clutch size	NG	Proximity, WD	–, 0	[42]
Chestnut-collared longspur	Clutch size	ONG	Proximity, WD	(–, –) ^a , 0	[38]
Savannah sparrow	Clutch size	NG	Proximity, WD	–, 0	[42]
Brewer's sparrow	Nest success	NG	WD, SD	0, –	[55]
Savannah sparrow	Nest success	Oil	Binary, proximity	–, 0	[41•]
Sharptail grouse	Nest success	Oil	Proximity, WD	0, +	[58]

Table 3 (continued)

Species	Response type	Dev type	Dev metrics	Responses	Reference
Vesper sparrow	Nest success	ONG	Proximity, WD	(0, 0) ^a , –	[38]
Greater sage-grouse	Brood survival	NG	Proximity, WD, SD	0, 0, –	[34•]
Ferruginous hawk	No. fledged	ONG	Proximity, WD	0, +	[32]
Mule deer	Fawn survival	NG	Binary, proximity	0, –	[59]
Greater sage-grouse	Survival	NG	Proximity, WD, SD	–, 0, 0	[34•]
Greater sage-grouse	Habitat selection	ONG	Proximity, WD, SD	0, 0, –	[39]
Greater sage-grouse	Habitat selection	NG	Proximity, WD, SD	(0, 0, –, 0, 0), (–, –, –, 0, –), (0, 0, 0, –, 0) ^b	[34•]
Greater prairie chicken	Habitat selection	Oil	Proximity, WD	(+, 0, 0, 0), (0, 0, –, –) ^c	[25]
Northern bobwhite	Habitat selection	ONG	Proximity, WPD	0, –	[37]
Pronghorn	Habitat selection	ONG	Proximity, WD	(0, –, –), (+, 0, 0, 0) ^d	[48]

Data derived from a literature search spanning 2014–2019. Null responses are denoted by zeros, and negative and positive responses are represented by minus and plus signs, respectively. Direction of responses parallels order of the development metrics assessed

NG, natural gas development; Oil, oil fields; ONG, both oil and natural gas; WD, well density; WPD, well pad density; SD, surface disturbance

^a Authors examined proximity responses in relation to both development types. First response denotes natural gas, second is oil

^b Authors tested habitat use of females during five stages: nesting, early brood-rearing, early non-brood-rearing, late brood rearing, and late non-brood-rearing, listed in order

^c Authors tested habitat use during four seasons: lekking, nesting, post-breeding, non-breeding, listed in order

^d Data are split by home-range scale in summer, patch-scale in winter, home-range in winter for proximity, followed by patch-scale in summer, home-range scale in summer, patch scale in winter, and home range in winter for well density

spatial scales, and the influence of the spatial configuration of development. Indices such as well density or well pad density in some cases may be decoupled from the actual landscape metric inducing changes, such as the amount of habitat loss [21, 55]. The use of such infrastructure metrics can therefore produce very different results even for similar species within the same system [55].

The need to better understand the additive effects and/or potential synergisms between different characteristics of energy development and other environmental stressors comprised another category of suggestions for future study ($N = 7$ papers). Moreover, the specific stimuli that elicited behavioral responses such as avoidance usually were unknown. The extraction of oil and gas resources entails a multi-step process including siting, infrastructure construction, drilling of wells, production, and completion. No study that I reviewed assessed the relative responses across these stages, which could provide inference regarding the aspects of development that elicit the strongest responses. Notable advances in the study of altered soundscapes resulting from anthropogenic activities are encouraging [80]. Disentangling the specific cues to which wildlife respond, however, remains challenging but can be accomplished via carefully designed empirical studies [41•] and field experiments [81].

Conclusions

During the period immediately preceding my review, authors lamented a paucity of evaluations of species' responses to oil

and natural gas development [2, 5, 8]. Since then, a large number of literatures have focused on how energy development influences a wide variety of wildlife responses. Whereas oil and gas reserves exist on every continent [1], unfortunately studies continue to be highly biased towards North America. The location bias is concerning because regions of high overlap between terrestrial fossil fuel reserves and biodiversity exist on other continents, especially within South America, Africa and Asia [3]. From a taxonomic standpoint, the breadth of mammalian and avian species comprising the focus of development studies has increased; however, studies focused on herpetofauna remain incredibly rare. This is concerning considering that amphibians in the studies I reviewed had the highest proportion of negative responses. Even within the other major taxa, moreover, studies have tended to focus on a relatively small group of species (for example, ungulates in Mammalia). Overall, the proportion of neutral (and even positive) responses of wildlife to development increased compared to previous summaries [1], which may be a result of the taxonomic expansion of studies to species with lower sensitivity thresholds. Negative responses, however, were universally detected (albeit with relatively low frequency) across taxa, locations, and development type, and with respect to different response types and development indices (Fig. 1). Moreover, positive responses to development by some species can have negative downstream consequences for other species, such as the case of increased rodent abundance and the nest predation rates of sagebrush songbirds [17, 20, 21].

Whereas the formulation of generalizations about the effects of energy development across species and systems would be ideal

[4•], my review revealed a continued pattern of species-specific and context-dependent effects [1]. The same species often responded differently to development across studies, and with respect to different metrics of development (Tables 1 and 3). Moreover, the directionality of species' responses often varied across response types (Table 2). Such patterns may evolve once more in-depth study has been conducted for more species. In the meantime, however, assumptions about the responses of particular species across contexts without accompanying data should be interpreted with caution. Unique responses to anthropogenic disturbance by species, moreover, may not be surprising considering that even similar species within the same system have unique evolutionary histories. Researchers should therefore think carefully about which aspects of development are most likely to influence different responses by a species and at which spatial scale, according to that species' natural and life history characteristics.

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