

Infrastructure and sound: oil wells and predator-prey assemblages in
the Northern prairies

By

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Abstract

Energy development is rapidly altering grassland ecosystems, but it remains unclear whether predator-prey assemblages change in response to these disturbances, and if so, whether those changes are driven primarily by physical infrastructure, associated noise, or their combined effects. Using a combination of field experiments and observational data I compared predator and prey responses to idle well infrastructure and experimental infrastructure and noise playback treatments, quantified how infrastructure influences Richardson's Ground Squirrel burrowing and landcover structure, and tested alternative trophic regulation mechanisms using piecewise structural equation modelling. Predator and prey responses were species specific and scale dependent, and the results were not consistent with a single regulatory mechanism. Across treatments, predator-prey relationships were dominated by positive associations, indicating that predators were more abundant in areas where prey were more abundant, indicating that predators concentrated in locations with higher prey density rather than reducing prey. There was limited evidence for generalized predator-shield, predator facilitation, meso-predator release, or risk-disturbance effects. Instead, habitat structure and disturbance history might be the primary drivers of community patterns. Idle well infrastructure had stronger ecological effects than did noise. Idle well sites increased ground squirrel burrowing activity, altered land cover composition and spatial configuration and created open, disturbed patches that concentrated prey. Ground squirrels act as ecosystem engineers by creating and maintaining these ecological conditions through their burrowing and soil disturbance activities, modifying landcover composition and spatial structure across the landscape. These patches

might enhance prey availability and support predators, thus connecting structural disturbances with trophic relationships. However, the noise experimental treatments did not consistently alter abundance patterns or trophic pathways but modified specific interactions in a context dependent manner, likely through effects in acoustic perception, vigilance, and foraging efficiency. Overall, the results show that oil development primarily affects grassland ecosystems through infrastructure and habitat modification. From a management perspective, it is critical to develop strategies for reclaiming structural features such as vegetation structure and persistent disturbance footprints to mitigate long term ecological impacts in grassland ecosystems.

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1. CHAPTER 1. Introduction

Worldwide grasslands continue to experience fast landscape changes due to agriculture, urban expansion, and energy development (Douglas *et al.*, 2023). In North America, those changes have reduced native habitat cover and altered the natural disturbance regimes such as fire and grazing (Hoekstra *et al.*, 2005; Wilsey *et al.*, 2019). Because of it, the prairie ecosystems now support less grassland obligate species and at the same time show declines in functional diversity (Ribic *et al.*, 2009; Rosenberg *et al.*, 2019). Canadian grasslands are also modified by energy development and its associated impacts, leading to changes in landscape structure and connectivity (Northrup and Wittemyer, 2013; Rooney *et al.*, 2012). In the Alberta's mixed-grass prairies impacts are particularly severe, with some of the highest densities of oil and gas infrastructure in North America (Riley *et al.*, 2007; Wilson and Bayne, 2019).

Energy development has the potential to alter key ecological interactions, including plant community composition and predator–prey dynamics (James 1999; Nasen *et al.*, 2011; Ripple *et al.*, 2016). Grassland predator–prey dynamics are complex and involve interactions among prey, mesopredators, and top predators. Here, I use assemblage to mean a taxonomically related group of species that co-occur in space and time, without implying that all members interact directly (Fauth *et al.*, 1996; Stroud *et al.*, 2015). To evaluate disturbance effects at multiple trophic positions, I grouped focal vertebrates in two complementary ways depending on the analysis. In taxonomic summaries, species were grouped into a rodent assemblage, a raptor



Figure 1. Grassland predator-prey assemblage species in the tall-grass prairie habitat: a) Deer Mouse, *Peromyscus maniculatus*; b) Northern Grasshopper Mouse, *Onychomys leucogaster*; c) Richardson's Ground Squirrel, *Urocitellus richardsonii*; d) Short-tailed Vole, *Microtus agrestis*; e) Red-tailed Hawk, *Buteo jamaicensis*; f) Northern Harrier, *Circus hudsonius*; g) Ferruginous Hawk, *Buteo regalis*; h) Swainson's Hawk, *Buteo swainsoni*; i) Golden Eagle, *Aquila chrysaetos*; j) Prairie Falcon, *Falco mexicanus*; k) American Badger, *Taxidea taxus*; l) Coyote, *Canis latrans*; m) Mule Deer, *Odocoileus hemionus*; n) Pronghorn, *Antilocapra americana*; o) Prairie Garter Snake, *Thamnophis radix*. (Created by JP Medina with the help of Marco Garcia 2023-2024)

assemblage, and a mammal mesopredator assemblage. In food-web focused analyses, I grouped the same species into assemblages representing co-occurring trophic components: a top-predator assemblage (Golden Eagle; Coyote), a mesopredator assemblage spanning body-size classes (large mesopredators: Ferruginous Hawk, Red-tailed Hawk; medium mesopredators: Swainson's Hawk, Prairie Falcon, American Badger; small mesopredator: Northern Harrier; and Northern Grasshopper Mouse as a small-mammal mesopredator), and a prey assemblage consisting of small to large prey (small prey: Deer Mouse; medium prey: Richardson's Ground Squirrel and lagomorphs; large prey: pronghorn and deer). These assemblages (Figure 1) describe which taxonomically related species tend to occur together within each trophic role, while predator-prey interactions link the assemblages into a broader food web in which disturbance-driven changes in habitat structure or resource availability can cascade across trophic levels and modify both prey availability and predator foraging opportunities (Miller and

Knight 1993; Bradley and Marzluff 2003; Michener 2005; Jackrel and Reinart 2009; Wiggins *et al.*, 2014; Ludlow *et al.*, 2014; Bernath-Plaisted and Koper, 2016; Lynch *et al.*, 2015).

In addition to direct habitat loss, oil development can also introduce sensory disturbances affecting animal behavior that can directly and indirectly alter wildlife distribution and ecological interactions. Noise, artificial lighting, powerlines, and traffic can potentially extend the functional footprint of oil development far beyond the physical infrastructure itself (Francis and Barber, 2013; Koper *et al.*, 2016; Shannon *et al.*, 2016). Animals sensitive to any or all of these disturbances may try to modify their movement patterns, increase vigilance, or just simply abandon the impacted habitat, leading to energetic costs and functional habitat loss despite the landscape appearing to consist of intact vegetation patches (Bayne *et al.*, 2008; Blickley and Patricelli, 2012; Antze and Koper, 2018). These effects can interfere with foraging, breeding, and predator avoidance, resulting in altered behaviors that reduce survival and reproductive success.

Oil development mainly generates sound through drilling and the extraction process. While sound is a physical property it can potentially become noise when affecting animal behavior or animal physiology (Francis and Barber, 2013; Shannon *et al.*, 2016; Jariwala *et al.*, 2017). Unlike physical infrastructure, sound can disperse across the landscape and potentially affect areas that appear otherwise undisturbed. In the Alberta's mixed-grass prairies, oil extraction and drilling emit noise that mask important acoustic signals needed for communication, predator

detection, and territory establishment (Slabbekoorn and Ripmeester, 2008; Rosa and Koper, 2018). These effects can further disrupt mating calls, reduce territory defense, and lead to lower reproductive success (Barber *et al.*, 2010; Shannon *et al.*, 2016). In prairie ecosystems where many species rely on sound to communicate and assess risk, anthropogenic noise can disrupt interactions and interfere with critical ecological processes across trophic levels, thereby playing a key role in shaping these systems (Shannon *et al.*, 2016; Proulx *et al.*, 2019).

Oil wells, roads, and powerlines can modify habitat quality, modify movement patterns, and lower reproductive success in multiple species (Nenninger and Koper, 2018; Bernath-Plaisted and Koper, 2016; Yoo and Koper, 2017), while noise from extraction and drilling can mask acoustic signals used for territorial defense, mate attraction, parental care, and predator detection (Francis *et al.*, 2012; Antze and Koper, 2020).

Infrastructure and its associated noise from conventional oil development has several specific effects on grassland wildlife because species respond differently to the direct impacts of altered soundscapes depending on their life histories, biology (e.g. hearing ranges), and the characteristics of the emitted sound (e.g. Antze and Koper, 2018; Rosa and Koper, 2021; Des Brisay *et al.*, 2023; Francis and Barber, 2013). Oil wells and its associated infrastructure like dendritic roads, power lines, and fences fragment and modify suitable native prairie habitat, change vegetation cover, and create edge conditions that can modify habitat quality for multiple taxa, including songbirds, small mammals, ungulates, and their predators (Francis and Barber, 2013; Nenninger and Koper, 2018; Daniel and Koper, 2019; Maxwell *et al.*, 2024). Oil

development associated noise can also act through interference and disturbance pathways affecting predator–prey assemblages, including masking predator and prey cues, shifting movement timing and space use, changing vigilance and foraging efficiency, and altering hunting success (Francis and Barber, 2013). These pathways can change encounter rates and foraging opportunities for raptors, mammalian mesopredators, rodents, lagomorphs, and ungulates, and the strength of those changes can vary across phases of oil extraction, when sound sources range from heavy equipment and traffic to long-term production machinery that can operate for long periods (Maxwell *et al.*, 2024; Rutherford *et al.*, 2023).

The predator–prey assemblages in tall grass prairies includes multiple species of predators that differ in mobility and sensory perception and thus, in hunting mode, respond to development in different ways (Lima and Valone, 1991; Thompson *et al.*, 1999; Pietz and Granfors, 2000; Renfrew and Ribic, 2003; Muchai and Plessis, 2005; Grant *et al.*, 2006; Klug *et al.*, 2009; Ellison *et al.*, 2013; De Gregorio *et al.*, 2014; Lyons *et al.*, 2015; Shew *et al.*, 2019). Infrastructure can increase mesopredator use by creating edges and travel corridors, which is relevant in prairie systems where declines or avoidance by top predators can concentrate predation pressure by mesopredators (Burr, 2014; Elmhagen and Rushton, 2007; Prugh *et al.*, 2009; Rodgers and Koper, 2006; Chalfoun, 2021). Noise can also shift outcomes by changing prey condition and behaviour, including reduced foraging performance and body condition in rodents under chronic exposure, and predator responses can differ, with reduced hunting success reported for some sound-dependent raptors near compressor stations (Francis *et al.*, 2012; Mason *et al.*, 2016; Shonfield and Bayne, 2017; Willems *et al.*, 2021, 2022; Bernath-Plaisted and Koper, 2016).

88

89 Even after extraction is partially complete and noise is reduced, idle wells may continue to
90 influence prairie ecosystems because their physical presence can alter ecological processes
91 despite the absence of regular human activity (Muehlenbachs, 2017). Many of these sites
92 remain unreclaimed due to regulatory delays and procedural gaps, persisting as semi-
93 permanent landscape features that contribute to long-term habitat modification
94 (Muehlenbachs, 2015; Alberta Energy Regulator, 2021). Idle wells have been shown to alter soil
95 conditions, disrupt plant succession, and shift species interactions, including reduced grazing
96 pressure that can facilitate the spread of invasive or disturbance-adapted plants (Fisher *et al.*,
97 2021; Galay and Winter, 2023). Physical remnants like fencing and vertical infrastructure can
98 also limit grazer access, enabling shrub encroachment and the establishment of forbs,
99 ultimately creating stable patches of modified habitat that persist in the landscape and reflect
100 the enduring ecological footprint of oil development (Antze *et al.*, 2020). This vegetation and
101 landcover changes can also influence how prey and predators use space by modifying
102 concealment, thermal conditions, foraging conditions, and patch edges that shape where
103 predators hunt and where prey shelter, feed or rest (Maestre and Reynolds, 2007; Fahrig, 2013;
104 Francis *et al.*, 2012; Phillips *et al.*, 2021).

105

106 One species that may respond to these changes is the Richardson's Ground Squirrel (*Urocitellus*
107 *richardsonii*), which like other burrowing species can function as an ecosystem engineer
108 (Umbanhowar Jr., 1995; Koper *et al.*, 2014). Their burrowing activity disturbs soil, reduces grass

cover, and promotes the establishment of shrubs, increasing habitat heterogeneity (Owen *et al.*, 2024). Around idle wells, these effects may become more pronounced where grazing is reduced and human activity is lower, creating favourable conditions for ground squirrel expansion (Fisher *et al.*, 2021). As they alter soil and vegetation, they can also change conditions for other species, influencing how animals use space, access resources, and interact across trophic levels (Jones *et al.*, 1994). These combined changes link small-scale soil disturbance to broader patterns in plant communities and animal behaviour, reinforcing the long-term ecological consequences of idle oil infrastructure.

Noise and infrastructure effects can also cascade indirectly through the organisms that connect trophic levels. In systems with chronic noise near energy infrastructure, shifts in the distribution or behaviour of birds and small rodents can change seed dispersal and seedling recruitment, with consequences for vegetation structure that can persist after noise is removed, altering prey habitat and predator foraging conditions (Francis *et al.*, 2012; Phillips *et al.*, 2021). In grasslands, comparable indirect pathways are possible when disturbance alters grazing patterns, plant communities, and the spatial arrangement of cover, which can shift rodent and lagomorph habitat use and change predator foraging activity across the landscape (Rutherford *et al.*, 2023; Maxwell *et al.*, 2024).

At the site scale, habitat modifications around idle oil wells can increase exposure of small prey and nests to predators, but the same mechanisms can also affect small mammal survival,

ungulate space use, and predator hunting behaviour through changes in cover, edge density, and predator detection ability (Bernath-Plaisted and Koper, 2016; Francis *et al.*, 2009; Gaynor *et al.*, 2019; Rutherford *et al.*, 2023). Noise that masks cues can reduce a predator's ability to locate prey, and it can also reduce prey ability to detect approaching predators, while disturbance responses can shift activity patterns and movements, changing overlap among predators and prey (Francis and Barber, 2013). Where burrow densities are high, Richardson's Ground Squirrel activity can interact with these habitat changes by altering vegetation height and patchiness, which can influence prey concealment and predator search efficiency across multiple trophic levels (Umbanhowar Jr., 1995; Jones *et al.*, 1994; Koper *et al.*, 2014; Owen *et al.*, 2024).

Together, these pathways show why separating infrastructure effects from noise effects is necessary for interpreting shifts in predator–prey assemblages, including changes in raptor habitat use, mammal mesopredator movement, rodent and lagomorph foraging behaviour, and ungulate space use, not only nest outcomes for grassland songbirds (Schmitz *et al.*, 2008; Gaynor *et al.*, 2019; Maxwell *et al.*, 2024; Rutherford *et al.*, 2023).

1.1 Purpose and Objectives

The overall purpose of this research was to examine how conventional oil development and its associated noise influence the predator–prey assemblages in the Alberta's mixed-grass prairies.

While oil infrastructure and noise are known to impact wildlife, their individual and combined direct effects on predator–prey assemblages and subsequent effects to the landcover and the trophic interactions in the prairies remain unclear. This thesis aims to better understand some of these effects by analyzing both direct and indirect ecological responses to infrastructure and noise at multiple trophic levels. By integrating field experimental data (See Rosa and Koper 2018) and observational data, my study contributes to a better understanding of how energy development alters ecological function in grassland ecosystems, with implications for species conservation.

1.1.1 Objectives

- Compare predator–prey assemblage abundance across distances from real oil well infrastructure and experimental playback sites to determine whether predator responses are associated with infrastructure, noise, or both. Interpret treatment and distance patterns using the Intermediate Disturbance Hypothesis as a strategic or heuristic framework, where low to moderate disturbance may create useful habitat or foraging opportunities, but stronger or unpredictable disturbance may reduce site use by increasing risk or disturbance costs. Also assess whether responses are consistent with higher predator presence under low to moderate disturbance and reduced presence under high amplitude, unpredictable noise, and assess whether patterns are consistent with the Risk Disturbance Hypothesis, where infrastructure and noise are treated as risk cues similar to predation risk; under this hypothesis, animals are expected to reduce or shift site use when disturbance becomes more intense, unpredictable, or

closer to the source because perceived risk, masking, vigilance, or foraging costs increase (Chapter 2).

- Compare Richardson's Ground Squirrel burrow densities among idle wells, control sites, and silent experimental infrastructure to assess how idle wells influence burrowing activity. Evaluate associated changes in landcover composition using vegetation diversity indices, and assess whether burrowing activity alters spatial configuration patterns such as patch shape, clustering, and dispersion, with effects expected to decline with distance from the disturbance center (Chapter 3).
- Test whether predator-prey dynamics in grasslands are regulated mainly by top-down or bottom-up mechanisms and whether the proximity to the oil wells and associated noise could shift the interaction strength. I evaluated four mechanisms: Human Shield Hypothesis (H1), where top predators avoid wells and prey increase. Predator Facilitation (H2), where top predators concentrate near wells and prey decline. Mesopredator Release (H3), where top predators decline, mesopredators increase, and prey decline; and Risk-Disturbance (H4), where all groups decline near wells, weakening local interactions. For each mechanism I also assessed whether changes in abundance and trophic overlap were driven primarily by noise or infrastructure, and whether responses could alter species interactions and shifts in community structure. (Chapter 4).

194 • Integrate findings from predator abundance, ecosystem engineering, and predator-prey
195 dynamics to identify key mechanisms driving species vulnerability and propose
196 conservation strategies aimed at mitigating the long-term impacts of energy
197 development on predator–prey assemblages (Chapter 5).

198

199

200

1.2 References Chapter 1

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CHAPTER 2. Direct impacts from infrastructure and associated noise of conventional oil extraction on predator–prey assemblages in the Northern prairies

2.1 Abstract

Assessing the impact of oil infrastructure and associated noise on predator–prey assemblages is essential for grasslands wildlife conservation. I tested whether real idle oil wells and experimentally simulated infrastructure altered the abundance of rodents, raptors, and mammalian mesopredators in mixed-grass prairie near Brooks, Alberta, Canada. Disjunct 800 × 800 m plots were randomly assigned one of six treatments: control (undisturbed grassland), infrastructure-only (silent experimental treatment), inactive well (Idle well), predictable noise (operational screw pump recordings), intermittent noise playback (randomized operational screw pump recordings), or unpredictable noise playback (drilling recordings). Predator surveys included small mammal live trapping, road-based raptor point counts, and nocturnal spotlighting for medium and large mammals. I used generalized linear mixed models to assess the effects of treatment and the distance from each site’s centre of each experimental treatment or control site. Deer Mice were less abundant near screw pumps and inactive wells but were more common near silent infrastructure. Northern Grasshopper Mice and Richardson’s ground squirrels were also more abundant near silent infrastructure, with Richardson’s ground squirrels attracted to intermittent noise. Raptors showed treatment, and species-specific responses: Swainson’s and Ferruginous Hawks were more abundant at silent and unpredictable noise sites, while Northern Harriers declined with proximity to all infrastructure types. Mammal mesopredators were more abundant at intermittent noise sites. These results are consistent with the Intermediate Disturbance Hypothesis, indicating that

predator responses depend on both the predictability and intensity of disturbance. Our findings suggest that to mitigate these impacts, managers could cluster well sites limiting mechanical noise, maintaining existing corridors or areas that have already been disturbed by previous development, rather than clearing new land, and avoiding long-term site abandonment.

2.2 Introduction

Oil and gas extraction has the potential to impact wildlife through habitat alterations, changes in resource availability, and expansion of human infrastructure (Northrup and Wittemyer 2013, Ott *et al.*, 2021). These changes impact species differently depending on their ecological traits and overall ability to tolerate disturbances (Rodgers and Koper 2017, Daniel and Koper 2019).

Anthropogenic noise is one of the many disturbances associated with oil development, amplifying existing stressors or creating new ones, with effects depending on species sensitivity to sound (Bernath-Plaisted and Koper 2016, Antze and Koper 2018). Noise pollution from energy development could impact species interactions, predator-prey dynamics, and habitat use (Hettena *et al.*, 2014, Ott *et al.*, 2021), increasing energetic costs for prey species, and interfering with essential behaviors such as foraging and communication (Frid and Dill 2002, Caro 2005, Bee and Swanson 2007, Muhly *et al.*, 2011, McLaughlin and Kunc 2013).

In grassland ecosystems, oil and gas extraction is of particular concern as grasslands are among the most threatened ecosystems worldwide (Wilsey *et al.*, 2019, Donovan *et al.*, 2024). Increased habitat loss from urbanization, agriculture, and climate change has led to significant declines in grassland obligate species (Douglas *et al.*, 2023). In North America, habitat

625 fragmentation and degradation of grasslands continue, in some degree due to energy
626 development (Augustine *et al.*, 2021, Scholtz and Twidwell 2022). Energy development,
627 including oil and gas extraction, wind farms, and solar farms, adds to this decline by causing
628 structural and functional habitat loss through land conversion (Trainor *et al.*, 2016, Dhar *et al.*,
629 2020, Nazir *et al.*, 2020, Radic and Gavrilovic 2020, Aycrigg *et al.*, 2023). North American
630 grasslands support extensive oil and gas reserves, and increasing global energy demands
631 continue to drive fossil fuel extraction (Butt *et al.*, 2013, Trainor *et al.*, 2016, Chalfoun 2021).
632 The expansion of fossil fuel infrastructure increases human disturbance, including roads,
633 industrial structures, and noise pollution (Ott *et al.*, 2021), which can significantly affect wildlife,
634 particularly species sensitive to anthropogenic activity.

635

636 The Intermediate Disturbance Hypothesis (Hanski, 1999) suggests that moderate disturbance
637 can maintain diversity by limiting competitive exclusion while keeping habitat usable. In
638 predator–prey systems, low-intensity disturbance may favour some species by changing
639 competition and predation pressure (Francis *et al.*, 2012), whereas more intense or persistent
640 disturbance can reduce habitat quality and lead to behavioural change or avoidance (Kleist *et*
641 *al.*, 2021). Support for the classic single-peaked response across disturbance gradients is mixed,
642 and outcomes depend on how disturbance is defined, measured, and sampled across space and
643 time (Moi *et al.*, 2020; Fox, 2013; Sheil and Burslem, 2013). For these reasons, I used the
644 Intermediate Disturbance Hypothesis as a strategical framework to guide predictions about how
645 predator and prey abundance might vary among disturbance contexts rather than as a strict test
646 of a unimodal pattern. To link those predictions to a mechanism that applies directly to

647 infrastructure and noise, I also draw on the Risk Disturbance Hypothesis, which treats human
648 disturbance stimuli, including sound, as analogous to predation risk and predicts stronger
649 responses when perceived risk is greater (Frid and Dill, 2002).

650

651 Under the Risk Disturbance Hypothesis, human disturbance from conventional oil extraction
652 infrastructure and sound, can function like predation because both force trade-offs between
653 avoidance and fitness-related activities such as foraging, movement, and parental care (Frid and
654 Dill, 2002). Responses are expected to track short-term changes in disturbance characteristics
655 and to be stronger when perceived risk is greater, including when disturbance occurs in areas of
656 higher natural predation risk (Frid and Dill, 2002; Peters and Otis, 2005). In this context, noise
657 from oil development can shift predator and prey space use and alter vigilance and foraging
658 trade-offs, providing a mechanism-based link between sound treatments and observed patterns
659 in predator–prey assemblages, and evidence also suggests noise can reduce attention to threats
660 and weaken risk assessment, which can change predator–prey interactions (Chan *et al.*, 2010).

661

662 Of the multiple disturbances linked to oil and gas development, anthropogenic sound presents
663 unique challenges for wildlife by altering sensory environments, disrupting essential behaviors,
664 and introducing a disturbance that can interfere with communication, predator-prey dynamics,
665 and daily activity patterns (Francis and Barber 2013, Cox *et al.* 2018, Rosa and Koper 2021).

666 Sound is a mechanical vibration transmitted through a medium like air, water, or soil, with
667 amplitude reflecting its intensity and frequency determining its sound quality, influencing if, and
668 how, it is perceived by the receiver (Pasnau 1999). Sound becomes noise when it disrupts

natural behaviors of the receiver, such as inter- or intraspecific communication, foraging, navigation, or predator avoidance (Coval and Shumway 2001, Barber *et al.*, 2010, Shannon *et al.*, 2016, Cox *et al.*, 2018). Anthropogenic noise differs from natural soundscapes in amplitude, frequency, and predictability, requiring wildlife to develop adaptive responses to mitigate its disruptive effects (Brumm 2013, Gomes *et al.*, 2021). High-amplitude noise can mask essential natural sounds, especially when it overlaps in frequency with communication signals, predator cues, or prey-detection sounds (Shannon *et al.*, 2016). Low-frequency noise can travel farther than high-frequency noise, but its ecological impact depends on amplitude, duration, and whether it overlaps with animal hearing or important acoustic cues (Duquette *et al.*, 2021). Additionally, unpredictable noise can prevent habituation, leading to prolonged stress and compounding its effects on wildlife (Francis and Barber 2013, Gill *et al.*, 2015). Diurnal raptors, although considered auditory generalists (McGee *et al.*, 2019), may still experience negative effects from noise exposure. Anthropogenic noise can interfere with prey detection and disrupt critical temporal patterns, such as sleep cycles (Francis *et al.*, 2012b). However, raptors may also take advantage of infrastructure by using it as hunting perches, benefiting from human-altered landscapes (Berry *et al.* 1998; Fleming and Bateman 2018).

Animals can behaviorally cope with noise disturbance by modifying vocalization frequency, amplitude, or timing (Brumm *et al.*, 2004, Nelson *et al.*, 2017). For example, European robins (*Erithacus rubecula*) vocalize beyond the range of anthropogenic noise or synchronize calls with quieter periods (Fuller *et al.*, 2007). A common strategy, known as the Lombard effect, involves increasing vocalization intensity to improve the signal-to-noise ratio. (Lombard 1911). However,

this strategy has limitations, especially in environments where noise overlaps with the species' vocal ranges, reducing signal transmission effectiveness (Rabin *et al.*, 2003, Ophir *et al.*, 2010, Nelson *et al.*, 2017). Similarly, prey species rely on auditory cues to assess predation risk and further adjust habitat selection (Zanette *et al.*, 2011, Emmering and Schmidt 2011, Hua *et al.*, 2013, Antze and Koper 2019). When predator auditory signals are masked by noise, prey may misinterpret risk levels, potentially leading to higher predation rates and further declines in prey (Burr 2014, Antze and Koper 2018).

Oil development can potentially restructure predator–prey assemblages by changing habitat conditions and altering risk and foraging environments for predators and prey. Predator communities in North American prairies include multiple mammal mesopredators, raptors, and reptiles (Lima and Valone 1991, Thompson *et al.*, 1999, Pietz and Granfors 2000, Renfrew and Ribic 2003, Muchai and Plessis 2005, Grant *et al.*, 2005, Klug *et al.*, 2009, Ellison *et al.*, 2013, De Gregorio *et al.*, 2014, Lyons *et al.*, 2015, Shew *et al.*, 2019). Responses to infrastructure and noise can differ among taxa. For example, mammalian mesopredators like coyotes and badgers could increase in abundance near infrastructure, likely due to habitat edges and scavenging opportunities, while some rodents like Deer Mouse may increase near noisy areas despite declines in body condition and foraging efficiency (Burr 2014; Francis *et al.*, 2012b, Willems *et al.*, 2021). Raptors that rely on acoustic cues, such as northern saw-whet owls, experience reduced hunting success near compressor stations, while diurnal raptors may be more affected by habitat fragmentation than by noise itself (Mason *et al.*, 2016, Shonfield and Bayne 2017, Bernath-Plaisted and Koper 2016). Together, these varied responses indicate that oil wells and

associated noise can shift the abundance, distribution, and trophic interactions of predator–prey assemblages in grassland ecosystems.

Here, I test whether conventional oil extraction alters the abundance and distribution of predator–prey assemblages in mixed-grass prairies. I use the Intermediate Disturbance Hypothesis as a strategical framework to guide predictions about how predator and prey abundance might vary across disturbance contexts, rather than as a strict test of a unimodal disturbance - diversity relationship (Hanski, 1999; Fox, 2013; Moi *et al.*, 2020; Sheil and Burslem, 2013). Under this framework, low to moderate disturbance may create conditions that favour higher predator presence, whereas more intense or persistent disturbance may reduce habitat quality and limit site use (Francis *et al.*, 2012a; Kleist *et al.*, 2021). To investigate this, I examined whether distance to oil wells affects abundance of predator–prey assemblages, including rodents, raptors, and mesopredator mammals, and whether patterns differ between real oil well infrastructure and experimental noise playback sites (Rosa and Koper, 2018). I evaluated whether responses were associated with oil infrastructure, predictable (chronic) noise, or unpredictable (interrupted) noise by comparing silent real idle oil wells with a replicated, landscape-scale noise playback experiment, and by contrasting noise regimes that differ in predictability and intensity (Rosa and Koper, 2018; Rosa and Koper, 2021). I also interpret patterns using the Risk Disturbance Hypothesis, in which human disturbance stimuli, including noise, function as predation risk and can reduce site use under more intense or unpredictable disturbance conditions and around disturbance sources (Frid and Dill, 2002).

I predicted that predator and prey abundance would differ among treatments and with distance from treatment centres. I expected low to moderate disturbance, like silent infrastructure or predictable noise to increase predator or prey use near treatment centres, while stronger or less predictable disturbance, such as intermittent or drilling noise, would reduce use near centres or produce weaker attraction. If responses were driven mainly by infrastructure, silent and real idle well sites would differ from controls even without noise; if responses were driven mainly by noise, the strongest responses would occur under intermittent or drilling noise treatments.

2.3 Methods

2.3.1 Study area

All sites were established in common property land used primarily for ranching, dominated by native mixed-grass prairie plant species near the southeastern region of Brooks, Alberta, Canada (49° 0' 0.004" to 50° 53' 56.475" N, 110° 0' 2.757" W to 112° 28' 44.473", at 760 m. asl) (Figure 1). The research was carried out from mid-May to early August in 2019 and 2021. This period was chosen as it corresponds to when the predator-prey assemblages are actively preying on nests of migratory songbirds (Bernath-Plaisted and Koper 2016). The predominant landscape consisted of mixed-grass prairies fragmented with oil wells, natural gas compressor stations, and the associated network of infrastructure and dendritic roads (Rosa and Koper, 2018).

756 The native vegetation included dominant grass species such as Western wheatgrass
757 (*Pascopyrum smithii*), Blue grama (*Bouteloua gracilis*), and Needle-and-thread grass
758 (*Hesperostipa comata*), mixed with Sagebrushes (*Artemisia spp.*), White beardtongue
759 (*Penstemon albidus*), Buffalo bean (*Thermopsis rhombifolia*), and Prickly pear (*Opuntia*
760 *polyacantha*) among other native forb species. Some introduced plants due habitat
761 fragmentation, farming, and cattle in the region included Crested wheatgrass (*Agropyron*
762 *cristatum*), Goat's beard (*Tragopogon dubius*), Dandelion (*Taraxacum officinale*), and Sweet
763 clover (*Melilotus officinalis*). Plant communities in the mixed-grass prairie provide essential
764 habitat and resources for a variety of vertebrates adapted to the prairie environment such as
765 Mule Deer (*Odocoileus hemionus*), White-tailed Deer (*Odocoileus virginianus*), Pronghorn
766 (*Antilocapra americana*), North American Badger (*Taxidea taxus*), Coyote (*Canis latrans*), Striped
767 Skunk (*Mephitis mephitis*), Long-tailed Weasel (*Mustela frenata*), Swift Fox (*Vulpes velox*),
768 Nuttall's cottontail Rabbit (*Sylvilagus nutalli*), Jackrabbit (*Lepus spp.*), Richardson's Ground
769 Squirrel (*Uroditellus richardsonii*), Deer Mouse (*Peromyscus maniculatus*), Northern
770 Grasshopper Mouse (*Onychomys spp.*), and Long-tailed Vole (*Microtus longicaudus*). The mixed-
771 grass prairie also supports a range of raptors like Northern Harrier (*Circus hudsonius*), Red-tailed
772 Hawk (*Buteo jamaicensis*), Ferruginous Hawk (*Buteo regalis*), Swainson's Hawk (*Buteo*
773 *swainsoni*), Prairie Falcon (*Falco mexicanus*), and Merlin (*Falco columbarius*), as well as reptiles
774 like the Common Garter Snake (*Thamnophis sirtalis*).

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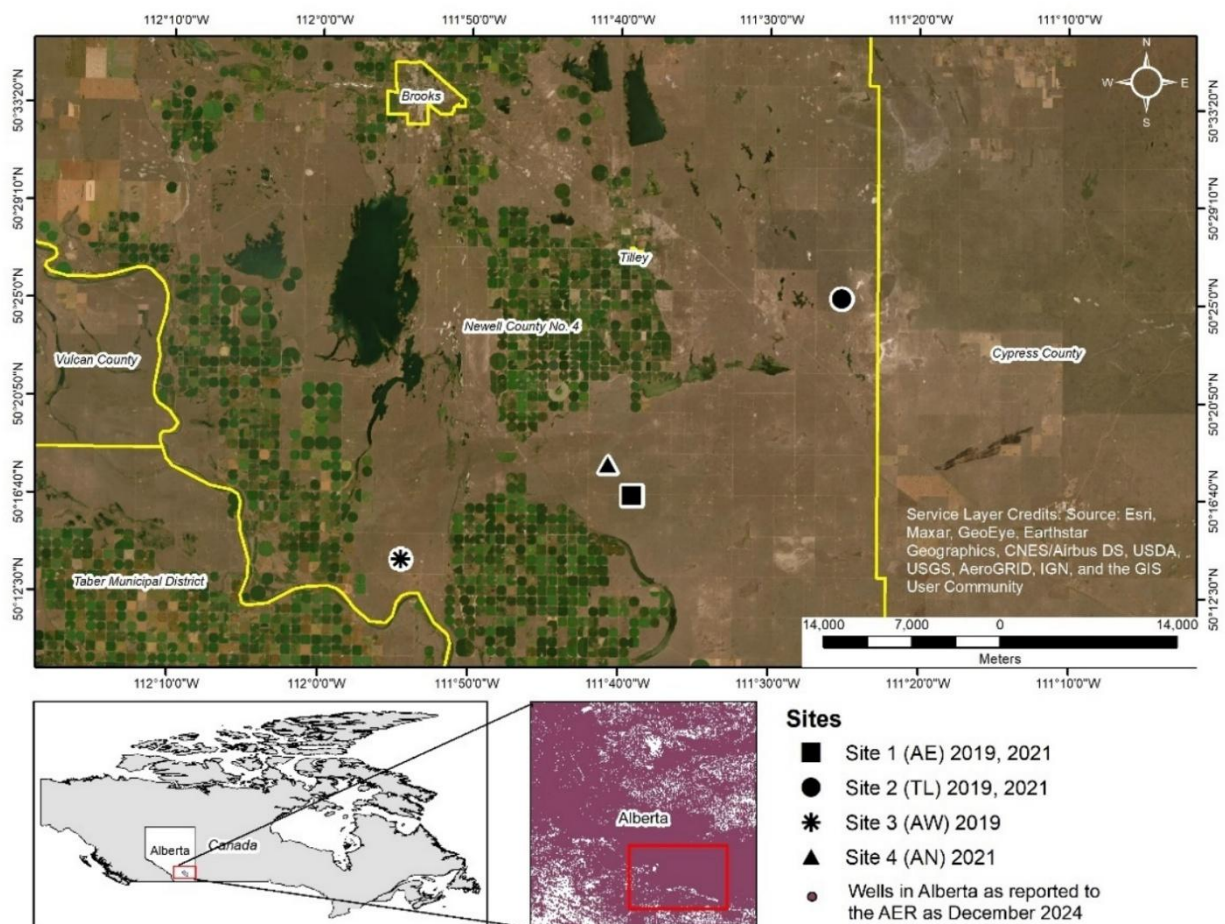


Figure 1 Macro and micro localization of study area locations around South-East of the city of Brooks in the province of Alberta, Canada. Sites and sampling years shown by dark icons. The Landscape consists of mixed-grass prairie shown surrounded by irrigated agricultural landscape.

2.3.2 Data Collection

The study was conducted at independent, disjunct 800x800 m plots with each center point situated at least 800 m apart from the center point of any other site (Figure 2). Each center point was established by control plots or experimental treatments.

786 The experimental treatments (Figure 3) included high-fidelity playback of three types of oil-
787 related noise: predictable chronic noise, intermittent noise, and unpredictable noise.

788 Predictable chronic noise was simulated using continuous playback of a progressive cavity pump
789 (PCP), also known as a screw pump, which produces a steady, mechanical sound typical of
790 operating oil wells (Devold 2013; Koper *et al.* 2015). This sound was broadcast 24 hours a day
791 throughout the 90-day grassland songbird breeding season (Screw pump, $n = 4$ sites). The
792 intermittent treatment used a randomly interrupted screw pump recording (ISP) that alternated
793 between on and off periods ranging from 15 minutes to 3 hours, maintaining a 50% duty cycle
794 over 45 days (Interrupted screw pump, $n = 3$ sites). The unpredictable treatment mimicked
795 drilling operations and included playback in three 10-day pulses with 10-day silent intervals.

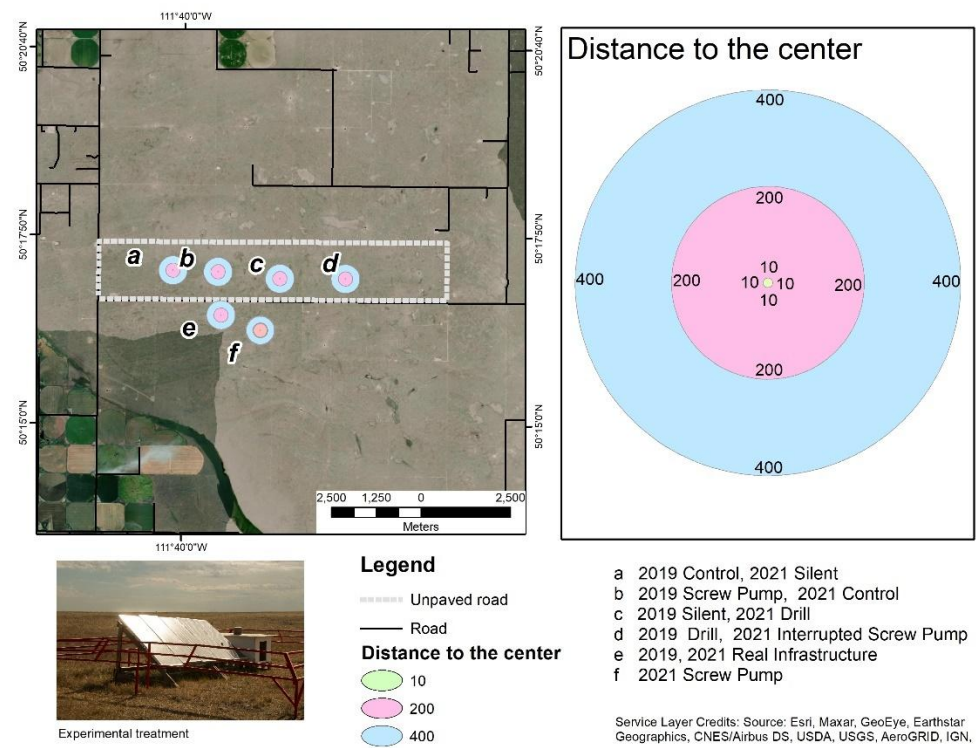
796 This noise included irregular sounds like pipe clanking, generator surges, intercom chatter, and
797 truck movement (Drill, $n = 4$ sites).

798

799 Three control conditions were also included to isolate the effects of infrastructure and noise.

800 Silent plots used mock playback equipment without sound to simulate the presence of
801 infrastructure without acoustic disturbance (Silent, $n = 4$). Control plots lacked both
802 infrastructure and sound treatments (Control, $n = 4$). In addition, I included inactive oil sites
803 where real idle well infrastructure had been present but silent for at least three years (Real
804 infrastructure, $n = 4$; Figure 2). Hereafter, treatments are referred to as *screw pump*, *interrupted*
805 *screw pump*, *drill*, *silent*, *real infrastructure*, and *control*. These treatments were designed to
806 capture key noise properties (predictability, duration, and amplitude) and test their role in
807 shaping predator responses.

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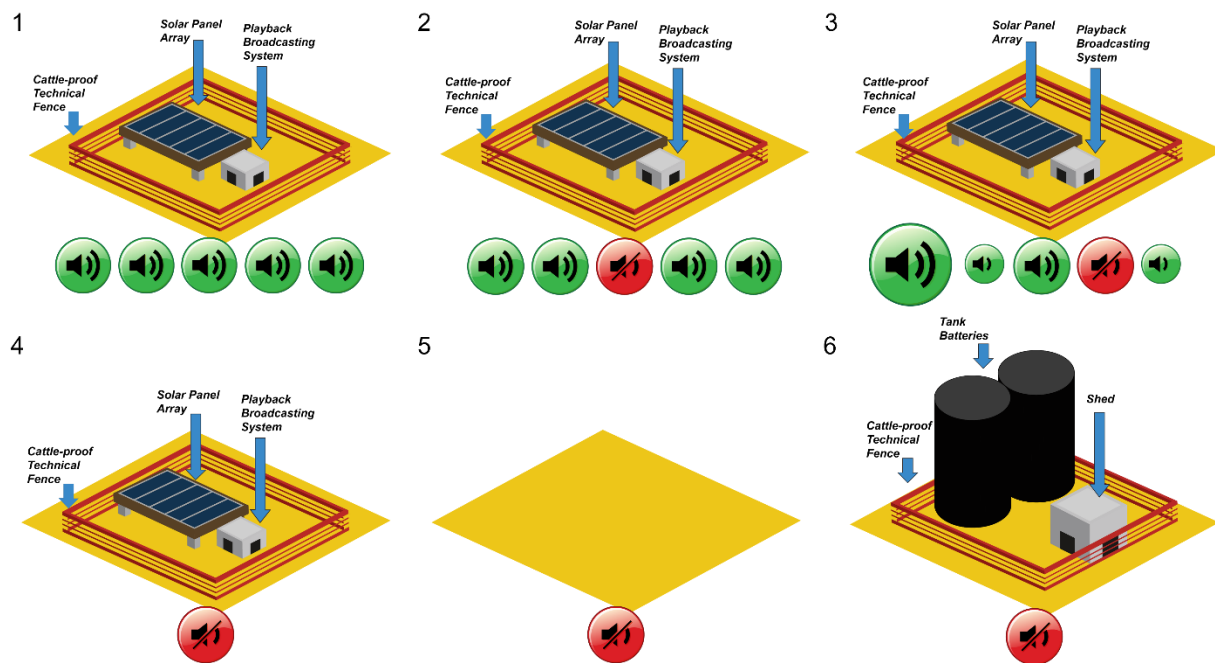
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Figure 2. Example of a site containing disjunct 800x800m treatment plots in the southeastern region near Brooks, Alberta, Canada. Each site consisted on 5 (2019) and 6 (2021) treatment plots.



820
 821 Figure 3. Experimental treatments. Mixed-grass prairie represented by yellow ground; Red
 822 circles denote the lack of anthropogenic sound emission and green circles denotes the emission
 823 of anthropic sound. The size of the green circles represents the amplitude 1.- Predictable noise
 824 (Screw pump), 2.- Intermittent noise (Interrupted Screw pump), 3.- Unpredictable noise (Drill)
 825 4.- Silent treatment (Silent), 5.-No anthropic noise with no oil infrastructure and no
 826 experimental treatment (Control), 6.- Silent, non-operational Real idle well infrastructure with
 827 tank batteries (Real). (Created by JP Medina).

828
 829 One survey was completed each month (pulse). Each predator group was sampled during each
 830 pulse (detail below) and categorized into three groups: mesopredators, raptors, and small

rodents. I used the total number of observed individuals per survey as an Index of abundance (Engeman 2005, Engeman and Whisson 2006).

2.3.1.1 Rodent Surveys

At each site, rodent abundance was quantified by using live traps at 10 m, 200 m, and 400 m from the center point at two randomly selected cardinal directions (i.e., North and West, South and East) for each pulse. Each night, field assistants and I set five medium (8 × 9 × 23 cm) Sherman folding aluminum live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) for small rodents and either two large Sherman folding aluminum live traps (10 x 11 x 38 cm) or one small (15 x 15 x 60cm) Tomahawk trap (Tomahawk live traps, Wisconsin, USA) for Ground squirrels per site in 10 meter lines running through the most uniform areas in open microhabitats (Price *et al.*, 1984). I set traps for three consecutive days each trapping session (pulses), approximately every 27 days during the sampling period at each one of the sites, each baited with approximately 5 g of moistened food, such as oats, soaked sunflower seeds, and/or with a piece of apple or carrot included as a moisture source. Defective traps, which failed to capture, had missing bait, or were damaged or absent, were either reset, replenished with bait, or replaced (Nelson and Clark 1973). To reduce the impact of residual scent on future trapping sessions, I immersed the traps in a 5% bleach solution for 20 minutes after each pulse (Mills *et al.*, 1995). Upon capturing an animal, I recorded species sex, age (categorized as juveniles, adults or unknown), and mass before marking and release. Newly captured individuals were marked using FDX-A 125KHz Biomark PIT tags (Biomark, Boise, ID, USA), and recorded prior to their release. Year one consisted of three pulse sessions and year two consisted of one. All

animals were treated in accord with guidelines and approval from the University of Manitoba Animal Care Committee (ACC 11449 F19-007/1/2) and Alberta Environment and Parks (19-384).

2.3.1.2 Raptor Surveys

Two trained observers (double-observer approach, Nichols *et al.*, 2000) employed the road transect method to monitor diurnal raptor activity using an all-animal sampling approach of unadjusted avian point-counts where I recorded individual raptors within the sites plots. This method can be considered suitable for collecting raptor data in open vegetation areas like mixed-grass prairies (Preston and Beane 1966, Meunier *et al.*, 2000, Nichols *et al.*, 2000). Data collection occurred exclusively on calm days characterized by low wind and the absence of precipitation. The survey was conducted along secondary roads associated with oil extraction and natural gas infrastructure, surrounding the 800x800 m site plots for two consecutive days for each survey session at each site every 27 days during the grassland songbird breeding season. The vehicle maintained a speed of 25-30 km/h during the survey period from 1600 to 1800 hours (Meunier *et al.*, 2000). When a raptor was observed, the truck was brought to a full stop and positioned perpendicular to the initial sighting location, allowing the identification of raptor's species, the road segment where the observation occurred, the nearest treatment site along with its UTM coordinates (Garmin GPSMAP, 60CS from Garmin International in Olathe, KS), and the distance from the road to the raptor's location to only include birds within the treatment sites. I used a Nikon Prostaff 550 range finder (Nikon Incorporated in Melville, NY) to measure the distance to the predator's first known position. This information was later used to

determine the distance of each raptor from the center point of each treatment site and to confirm that only birds within the sites were included in the survey.

2.3.1.3 Mammal mesopredator surveys

Surveys were conducted along secondary roads associated with oil and natural gas infrastructure, surrounding the 800x800 m site plots, for two consecutive nights per session at each site every 27 days throughout the grassland songbird breeding season. A heavy-duty cordless spotlight with a 1,000,000-candlepower beam was mounted on a truck, which maintained a speed of 20 km/h while driving around the site plots for two nights. Observations took place on calm nights with low wind, on clear skies with no precipitation and avoiding gibbous or full moon phases within each 8-night period.

During the surveys, two observers at the back of the truck observed both sides of the road, while the driver and co-pilot searched for potential predators on the road itself. The observers inspected the surrounding landscape to detect animals before they moved out of sight. In cases where a group of predators, such as a family group was observed, it was recorded as a single observation. Given that badgers and coyotes exhibit nocturnal and secretive behavior, frequently making use of burrows or dens when resting, I assumed that predators were actively hunting when spotted. The initial direction of my travel on the road, either north or south, was determined randomly for each observation period (i.e., each night of spotlighting). The observations started approximately 1 hour after sunset and continued until the entire site had been surveyed, which typically took 2 to 3 hours. After spotting a predator, the truck was fully

stopped to determine predator's species. Afterwards, the truck was moved parallel to the initial sighting location to determine the road segment it was observed on and the closest treatment site to its location, including UTM coordinates (Garmin GPSMAP 60CS, Garmin International, Olathe, KS), and the distance from the road to the predator's position, using a range finder. I later determined the distance of each predator to the center point for each treatment. I combined data from badgers and coyotes as I did not have sufficient sample sizes ($N = 38$) to analyse them separately.

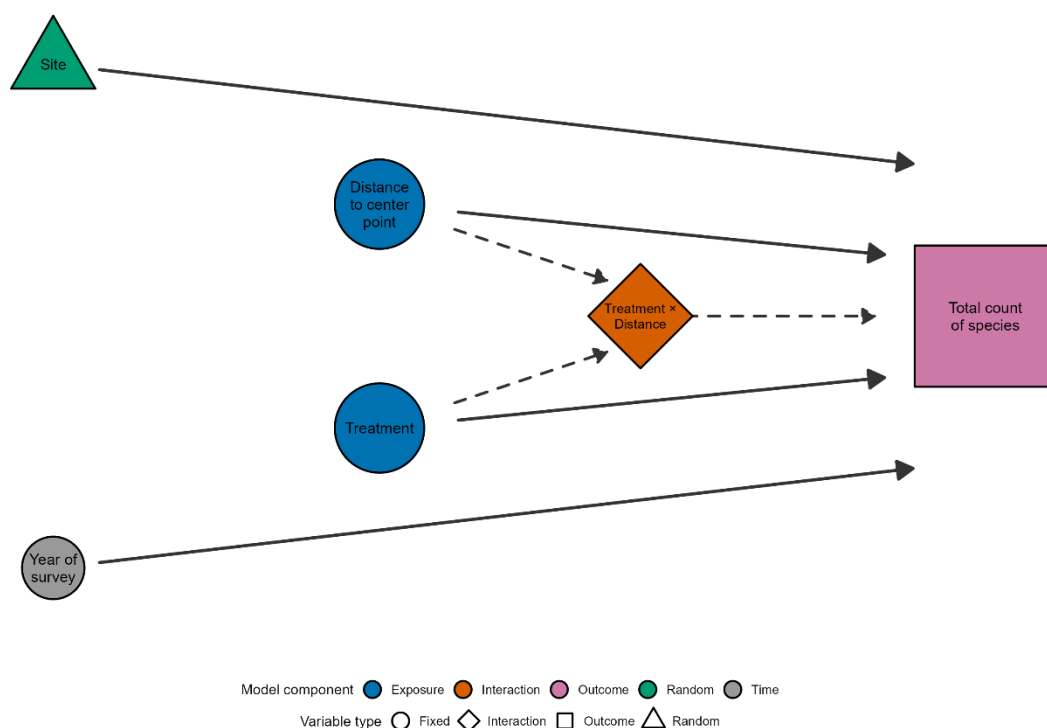
2.3.3 Data analyses

The observed individuals from each sampled group were categorized into three groups: total number of rodents, total number of raptors, and total number of mesopredators. These groups served as response variables in the analysis. Further, I also assessed the effects on the predominant individual species, within the rodent and raptor categories as response variables.

To evaluate relationships among predictors and responses, I fit a single global model specified *a priori* from ecological reasoning and an explicit causal diagram, and based inference on parameter estimates and their uncertainty rather than Information Criteria (Tredennick *et al.* 2021; Laubach *et al.* 2021; Arif and MacNeil 2022; Addicott *et al.* 2022). Hypothesis support was evaluated using effect sizes and confidence intervals for key predictors from the global model, with interpretation focused on the magnitude, direction, and uncertainty of estimates.

917 For each species and taxonomic group, I ran the global model to assess the impact of temporal
 918 factors (year) and site characteristics (as a proxy for landscape features) on species abundance.

919



920

921 Figure 4. Explicit causal diagram for the single global model. Variable type is represented by
 922 geometrical shapes that included fixed treatment and distance to the center point (blue circles),
 923 their interaction (treatment $\times$ distance; orange rhombus), year as a fixed temporal control
 924 (white circle), and site as a random intercept to account for unmeasured site-level
 925 heterogeneity (green triangle). The expected outcome is represented by the total number of
 926 each species or group (pink square).

927

928 I determined the global model by translating the study design into an explicit causal diagram
929 that identified the response and the predictors needed to represent the hypothesized pathways
930 (Figure 4). Based on this diagram and ecological reasoning, I specified a single global model a
931 priori that included treatment, distance to the center point, their interaction (treatment $\times$
932 distance), year as a fixed temporal control, and site as a random intercept to account for
933 unmeasured site-level heterogeneity. I then used generalized linear mixed models (GLMMs) in R
934 (v4.5.1; R Core Team 2021) with the glmmTMB package (Magnusson *et al.* 2017) to test whether
935 predator abundance changed with distance to oil wells and whether any distance effects
936 differed among treatments representing oil infrastructure and predictable or unpredictable
937 noise. GLMMs fit this study design because they estimate fixed effects of treatment and
938 distance while also including random effects that account for repeated sampling and site-to-site
939 differences (Venables and Ripley 2002; Bolker *et al.* 2008).

940

941 Because abundance data are counts that are often right-skewed and contain many zeros, I
942 compared count distributions and used zero-inflated forms when excess zeros were present
943 (Quinn and Keough 2002; Brooks *et al.* 2017). To select an appropriate distribution for each
944 taxon and species, I fit and compared alternative GLMM formulations, which supported using a
945 zero-inflated Poisson distribution for rodent species and a Poisson distribution for raptor species
946 and the mammal mesopredator group. This framework also allowed categorical treatments and
947 continuous distance to be evaluated within the same model while respecting constraints
948 imposed by the sampling design, such as standardized trapping effort at fixed distances from
949 the noise source (Littell *et al.* 2006). Finally, rather than using Information Criteria for model

selection, inference was based on effect sizes and their uncertainty, and hypothesis support was evaluated using confidence intervals and the magnitude, direction, and uncertainty of key parameter estimates (Tredennick *et al.* 2021; Laubach *et al.* 2021; Arif and MacNeil 2022; Addicott *et al.* 2022).

To determine appropriate distribution for each taxon and species abundance, I compared GLMMs (R statistical software, v4.5.1, R, Core Team 2021) Accordingly, I used zero-inflated Poisson distribution for rodent species, and Poisson distribution for Raptor species and the group of mammal mesopredators. Rather than using Information Criteria for model selection, inference was based on effect sizes and their uncertainty, and hypothesis support was evaluated using confidence intervals and the magnitude, direction, and uncertainty of key parameter estimates (Tredennick *et al.* 2021; Laubach *et al.* 2021; Arif and MacNeil 2022; Addicott *et al.* 2022). For each species and taxonomic group, I ran this global model to assess how abundance varied with treatment and distance while accounting for temporal variation among years and site-level characteristics as a proxy for landscape features.

Finally, to visualize each species model I generated predictions from the fitted global GLMM across the observed distance range within each treatment to describe expected abundance patterns without extrapolating beyond sampled distances. I built a treatment-specific distance grid and crossed it with all study years so predictions matched the study design and accounted for year-to-year variation. Predicted means were plotted as lines with shaded 95% intervals, overlaid on observed counts divided by each treatment to help with comparison.

2.4 Results

2.4.1 Rodent abundance

A total of 16 trapping sessions (64 trapping nights) were undertaken. I captured individuals of 6 rodent species across sampling sites. The total number of rodents captured was 485 individuals; relative abundances of species captured were: Deer Mice (59.8%), Northern Grasshopper Mice (25.25%), Richardson's Ground squirrel (8.48%), Western Harvest Mice (4.1%), Meadow vole (1.03%), and Long-tailed vole (1.24%).

2.4.1.1 Total number of Rodents

I found mixed effects on the total number of rodents (mice and voles) between treatments, with treatment specific distance effects (Figure 5). In the control treatment, the rodent abundance increased with distance from the centre point (Distance: $\beta = 0.00483$, SE = 0.00103, $p \leq 0.001$). At the centre point (Distance = 0) all treatments had higher predicted rodent abundance than the control, including predictable noise (screw pump; $\beta = 1.85$, SE = 0.42, $p \leq 0.001$), silent ($\beta = 1.77$, SE = 0.38, $p \leq 0.001$), unpredictable noise treatment (drill; $\beta = 2.58$, SE = 0.63, $p \leq 0.001$), intermittent noise (interrupted screw pump; $\beta = 2.29$, SE = 0.79, $p = 0.0038$), and idle well (real infrastructure; $\beta = 3.87$, SE = 1.60, $p = 0.0159$). Distance effects were weaker and shifted to negative in treatment sites, by negative interactions between treatment and distance to center point. For the constant and predictable noise (screw pump; $\beta = -0.00532$, SE = 0.00149, $p \leq$

0.001), silent ($\beta = -0.00807$, $SE = 0.00157$, $p \leq 0.001$), drill ($\beta = -0.01056$, $SE = 0.00284$, $p \leq 0.001$), and intermittent noise (interrupted screw pump; $\beta = -0.00678$, $SE = 0.00289$, $p = 0.019$), with a similar but weaker pattern for the idle well (real infrastructure; $\beta = -0.01431$, $SE = 0.00869$, $p = 0.10$). Rodent abundance also differed between years, with lower values in 2021 than in 2019 ($\beta = -0.714$, $SE = 0.145$, $p \leq 0.001$).

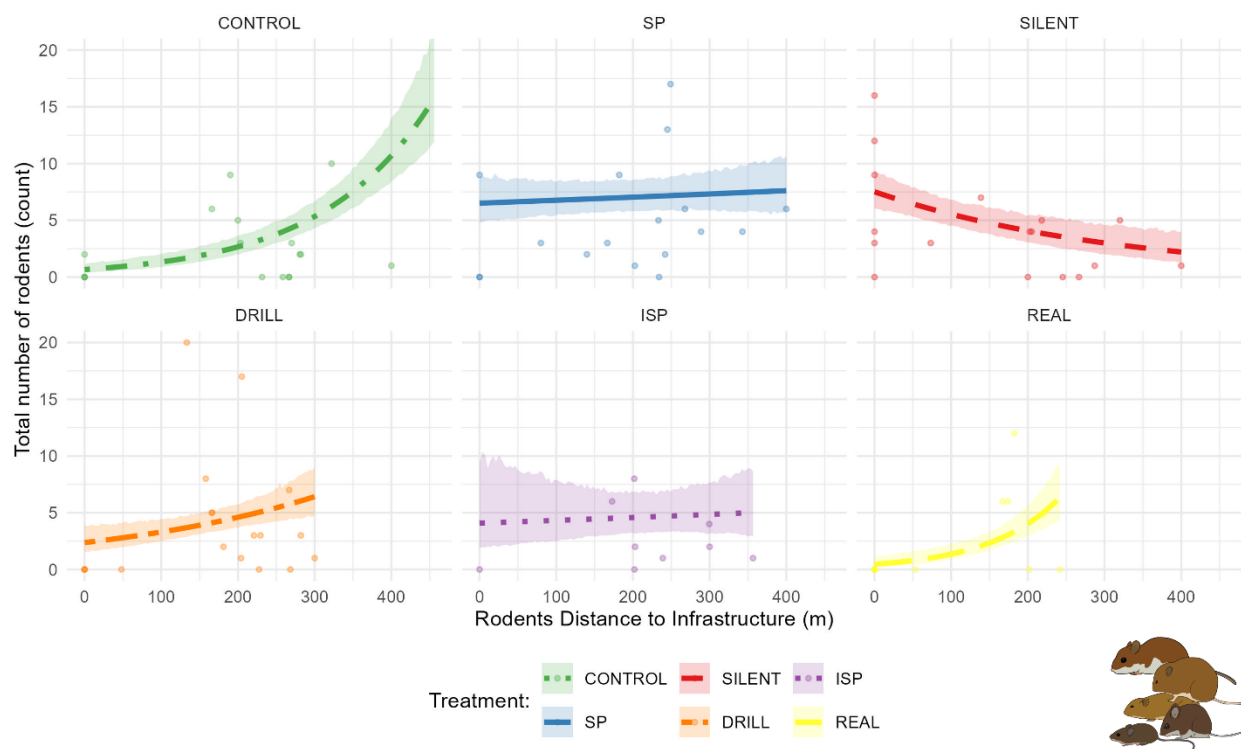


Figure 5. Total number of rodents across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

1007 2.4.1.2 Deer Mice

1008 Similar to the total number of rodents, Deer Mice abundance showed treatment specific
1009 patterns with the distance from the centre point (Figure 6). In the control treatment, Deer Mice
1010 abundance increased with distance (Distance: $\beta = 0.00451$, SE = 0.00150, $p = 0.0026$). At the
1011 centre point (Distance = 0), Deer Mice abundance was higher than the control in the silent
1012 treatment ($\beta = 1.50$, SE = 0.58, $p \leq 0.1$) and the unpredictable noise treatment (drill; $\beta = 3.96$, SE
1013 = 1.06, $p \leq 0.001$), with weaker evidence for higher abundance under constant and predictable
1014 noise (screw pump; $\beta = 1.27$, SE = 0.65, $p \leq 0.1$) and intermittent noise (interrupted screw
1015 pump; $\beta = 5.08$, SE = 2.96, $p \leq 0.1$), while the idle well was not different from the control (real
1016 infrastructure; $\beta = 1.16$, SE = 2.28, $p \geq 0.1$). Distance effects showed negative interactions
1017 between treatment and distance for silent ($\beta = -0.00739$, SE = 0.00243, $p = 0.0023$) and the
1018 unpredictable noise treatment (drill; $\beta = -0.0210$, SE = 0.00548, $p \leq 0.001$), with a weaker
1019 pattern for intermittent noise (interrupted screw pump; $\beta = -0.0247$, SE = 0.0150, $p \leq 0.1$);
1020 interactions for constant and predictable noise (screw pump) and the idle well (real
1021 infrastructure) were not different from the control ($p \geq 0.1$). Deer Mice abundance was different
1022 between years, with lower values in 2021 ($\beta = -1.00$, SE = 0.245, $p \leq 0.001$).

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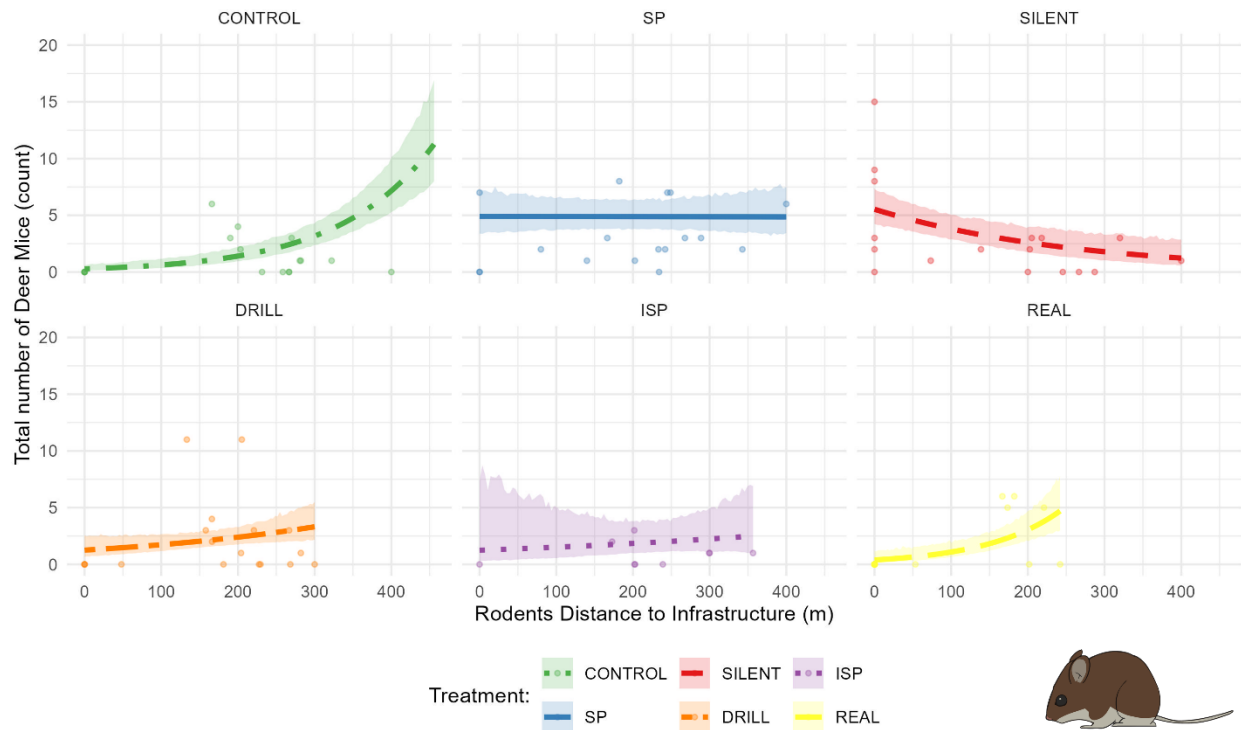


Figure 6. Total number of Deer Mice across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.4.1.3 Northern Grasshopper Mice

Northern Grasshopper Mice abundance showed weak evidence of treatment and distance effects (Figure 7). In the control treatment, abundance did not show a clear change with distance from the centre point (Distance: $\beta = 0.00234$, SE = 0.00219, $p \geq 0.1$), and abundance was not clearly different between years (YEAR: $\beta = 0.471$, SE = 0.332, $p \geq 0.1$). At the centre

point (Distance = 0), abundance was higher than the control under intermittent noise (interrupted screw pump; $\beta = 4.14$, SE = 1.81, $p = 0.022$) and showed weaker evidence of being higher under unpredictable noise (drill; $\beta = 2.17$, SE = 1.14, $p \leq 0.1$), while constant and predictable noise (screw pump) and silent treatment were not different from the control ($p \geq 0.1$). Distance effects showed a negative interaction for intermittent noise (interrupted screw pump; Distance $\times$ ISP: $\beta = -0.0176$, SE = 0.00772, $p = 0.022$) and weaker evidence of a negative interaction for drill (Distance $\times$ Drill: $\beta = -0.00884$, SE = 0.00502, $p \leq 0.1$), whereas interactions for screw pump and silent were not different from the control ($p \geq 0.1$). Estimates for the idle well (real infrastructure) were not interpretable in this model due low sample size ($n=1$).

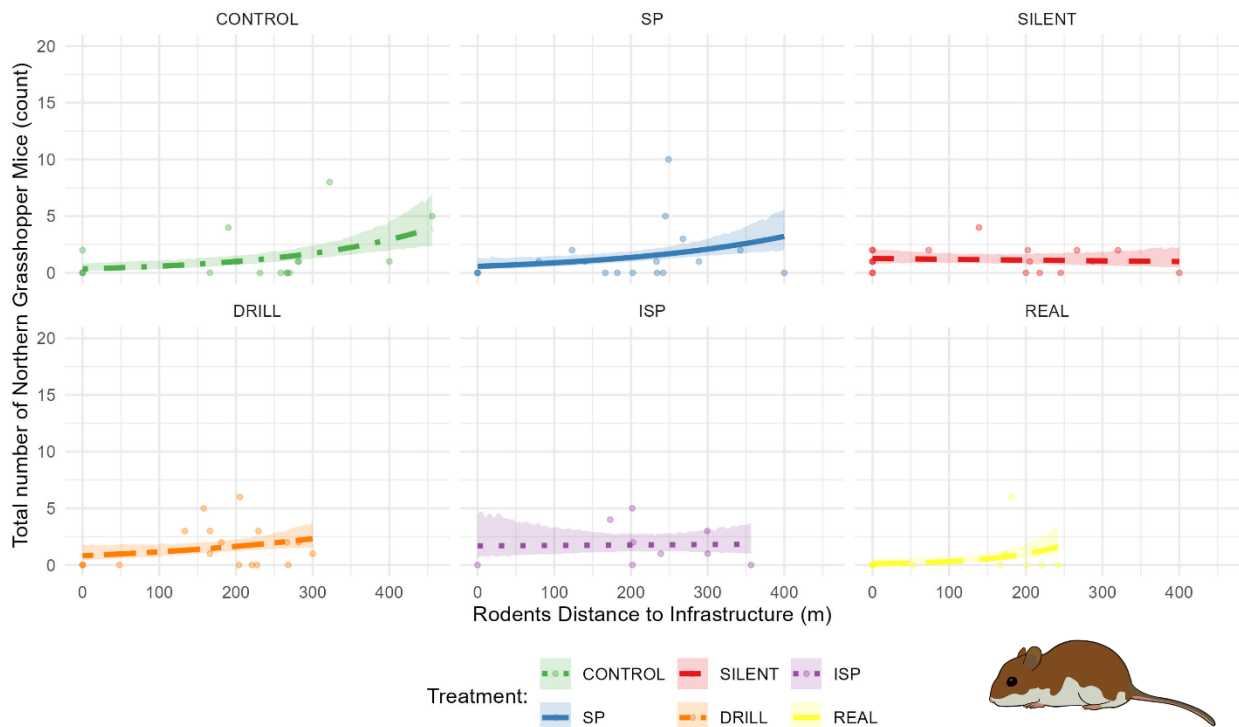


Figure 7. Total number of Northern Grasshopper Mice across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from

the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.4.1.4 Richardson's Ground squirrels

Richardson's ground squirrel abundance was not clearly different among treatments, and there was no evidence that the distance relationship depended on treatment (Figure 8). In the control sites, ground squirrel abundance showed no systematic change with distance to the infrastructure center point (RGS_DI: $\beta = 0.00165$, SE = 0.00307, $p \geq 0.1$). At the center point (Distance = 0), estimated ground squirrel abundance was not different from control in any treatment, including constant and predictable noise (screw pump; $\beta = 0.90$, SE = 0.92, $p \geq 0.1$), silent treatment ($\beta = 0.66$, SE = 0.77, $p \geq 0.1$), unpredictable noise treatment (drill; $\beta = 0.40$, SE = 0.98, $p \geq 0.1$), and idle well (real infrastructure; $\beta = 0.69$, SE = 0.91, $p \geq 0.1$). Distance-by-treatment interactions were also not different from control (all $p \geq 0.1$), indicating that treatment sites did not show stronger attraction to or avoidance of the center point than control sites across the sampled distance range.

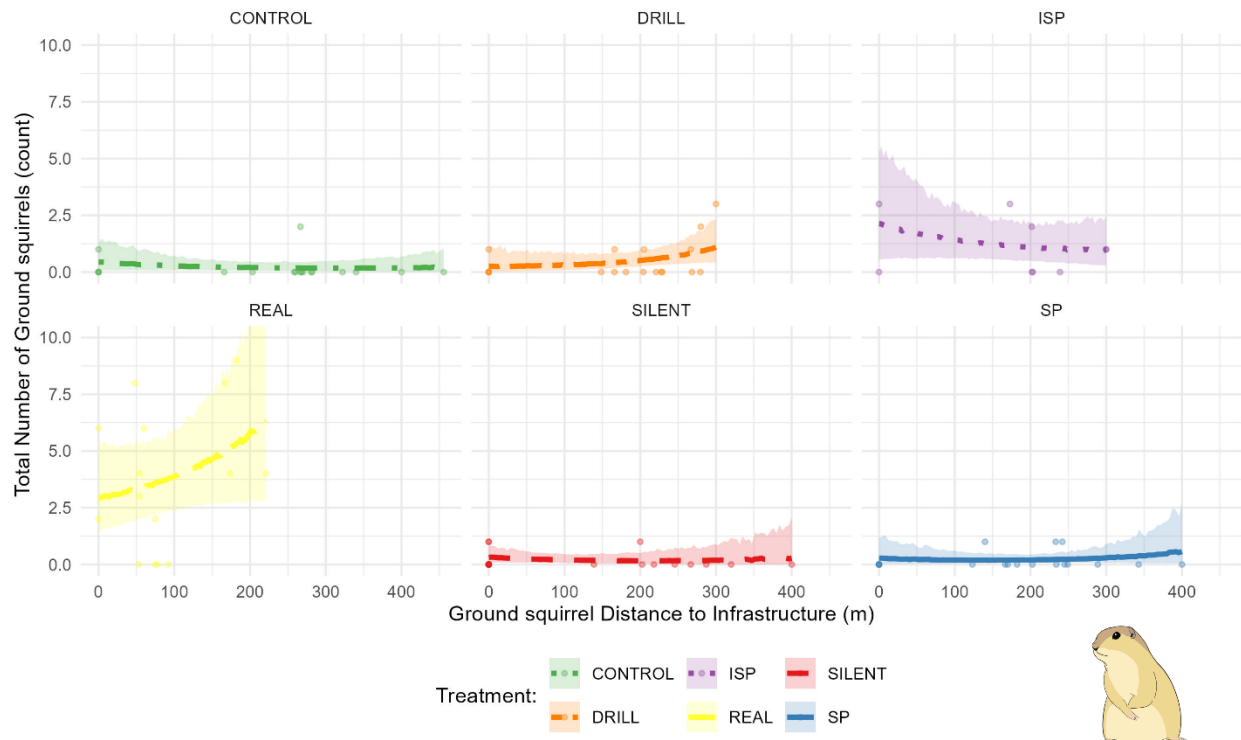


Figure 8. Total number of Richardson’s ground squirrels across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.4.2 Total number of Raptors

I observed individuals of seven raptor species across sampling sites. The total number of raptors recorded was 215 individuals; relative abundances of species observed were: Swainson’s Hawks

(56.28%), Northern Harriers (24.19%), Ferruginous Hawks (11.16%), Red-tailed Hawks (2.79%),
Prairie Falcons (2.33%), Golden Eagles (2.33%), and Merlins (0.93%).

Total raptor abundance was related to distance from infrastructure and varied between the
treatments (Figure 9). In the Control treatment, raptor abundance increased with distance
(Distance: $\beta = 0.00505$, SE = 0.00187, $p = 0.0069$). At the centre point (Distance = 0), raptor
abundance was higher than Control in the silent treatment ($\beta = 2.16$, SE = 0.73, $p = 0.0031$) and
under intermittent noise (interrupted screw pump; $\beta = 1.99$, SE = 0.91, $p = 0.0286$), with weaker
evidence for a difference under constant and predictable noise (screw pump; $\beta = 1.24$, SE =
0.72, $p = 0.0837$); drill (unpredictable noise) and idle well (real infrastructure) were not different
from control ($p \geq 0.1$). Distance - treatment interactions were not statistically significant ($p \geq$
0.1), although the silent treatment showed a weaker distance effect than control (Distance $\times$
Silent: $\beta = -0.00403$, SE = 0.00231, $p = 0.0812$). Raptor abundance was also different between
years, with lower values in 2021 ($\beta = -1.59$, SE = 0.24, $p \leq 0.001$).

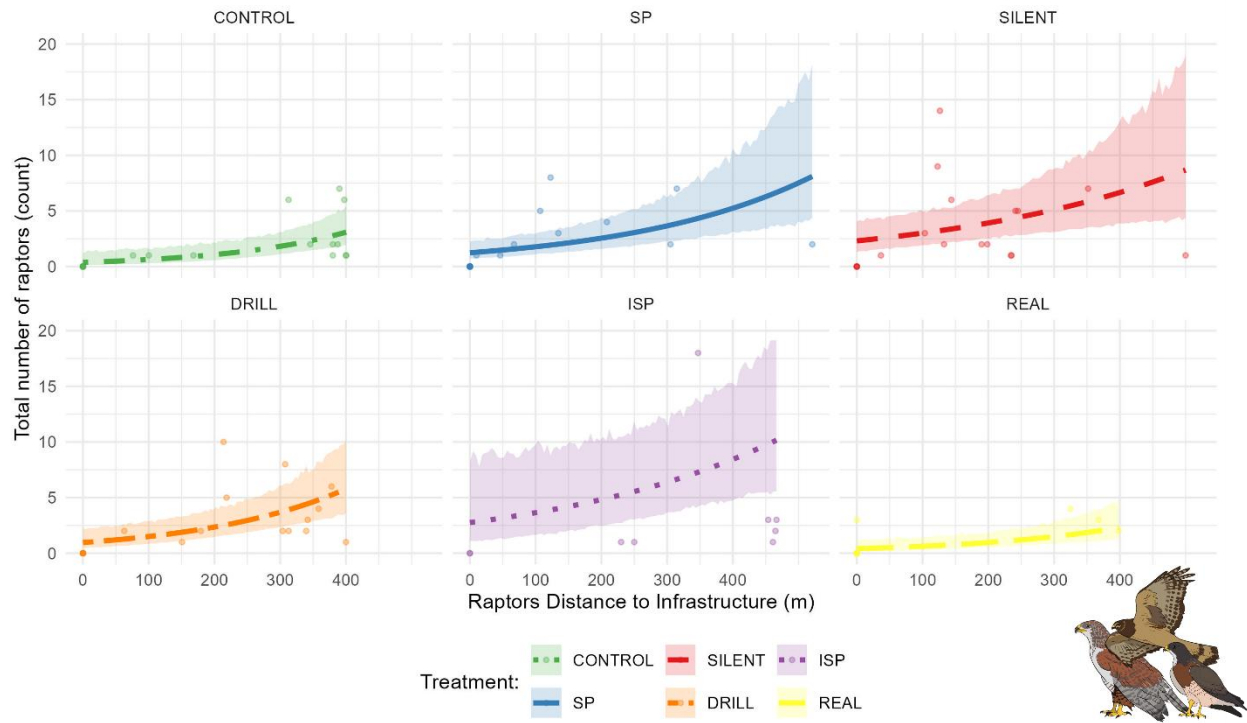


Figure 9. Total number of Raptors across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.4.2.1 Swainson's Hawk

Swainson's Hawk abundance varied with distance and year, with weaker evidence that the distance relationship changed under the silent treatment (Figure 10). In the control sites, Swainson's Hawk abundance increased with distance from the infrastructure center point (Distance: $\beta = 0.00573$, SE = 0.00270, $p = 0.0337$). At the center point (Distance = 0), predicted abundance was not different from control for constant and predictable noise (screw pump; $\beta = 1.49$, SE = 1.06, $p \geq 0.1$), unpredictable noise (drill; $\beta = 1.23$, SE = 1.14, $p \geq 0.1$), intermittent

noise (interrupted screw pump; $\beta = 2.10$, $SE = 1.67$, $p \geq 0.1$), or idle well (real infrastructure; $\beta = -1.29$, $SE = 1.85$, $p \geq 0.1$), but it was higher under the silent treatment ($\beta = 2.89$, $SE = 1.13$, $p = 0.0104$). The distance-by-treatment interaction was marginal for the silent treatment (Rapt_DI $\times$ Silent: $\beta = -0.00765$, $SE = 0.00439$, $p = 0.0817$) and was not different from control for the other treatments ($p \geq 0.1$), indicating broadly similar distance patterns across treatments. Swainson's Hawk abundance was also different between years, with lower values in 2021 ($\beta = -2.54$, $SE = 0.42$, $p \leq 0.001$).

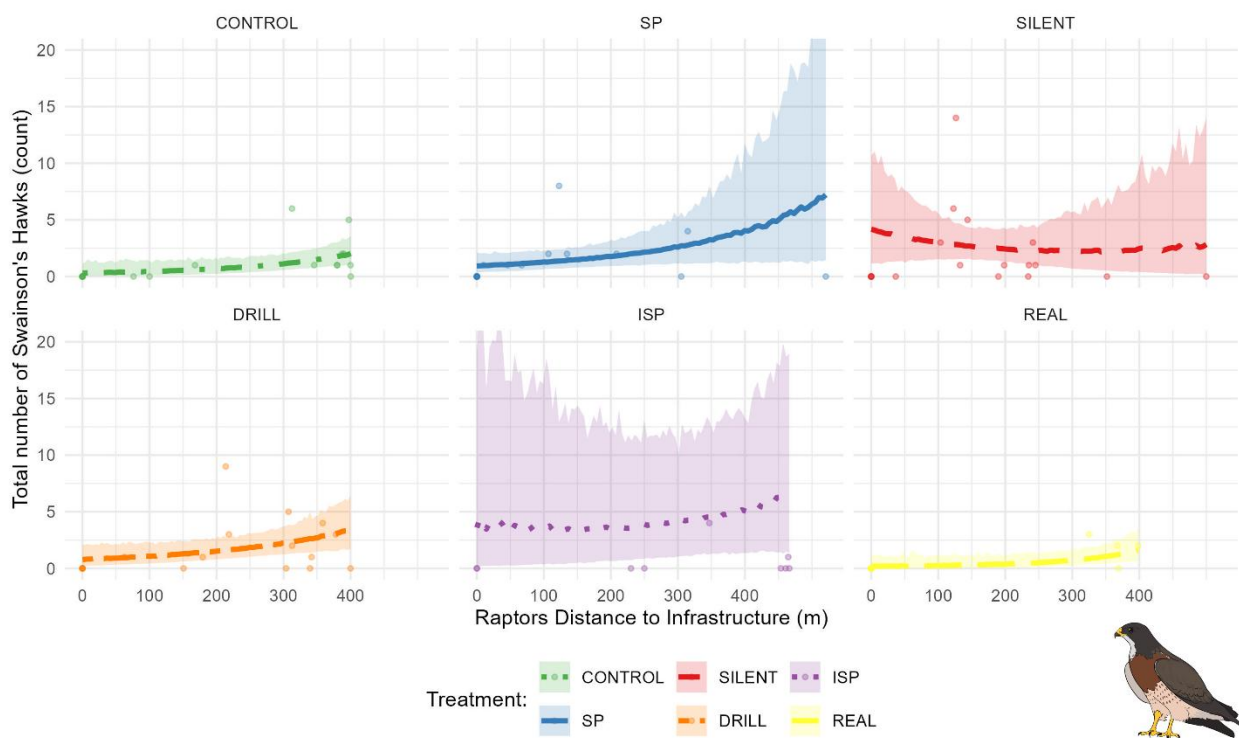


Figure 10. Total number of Swainson's Hawks across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the

predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.4.2.2 Northern Harrier

Northern Harrier abundance showed limited evidence of treatment effects and only weak evidence of a distance relationship (Figure 11). In the control treatment, harrier abundance tended to increase with distance from infrastructure, but this effect was marginal (Distance: $\beta = 0.00626$, SE = 0.00320, $p = 0.0508$). At Distance = 0, none of the treatments were different from the control (all treatment main effects $p \geq 0.28$), and none of the treatment by distance interactions were different from the control slope (all $p \geq 0.45$). Harrier abundance was different between years, with higher values in 2021 ($\beta = 1.36$, SE = 0.577, $p = 0.018$). The zero-inflation intercept was not significant ($p = 0.998$), indicating no evidence for extra zeros beyond the conditional model.

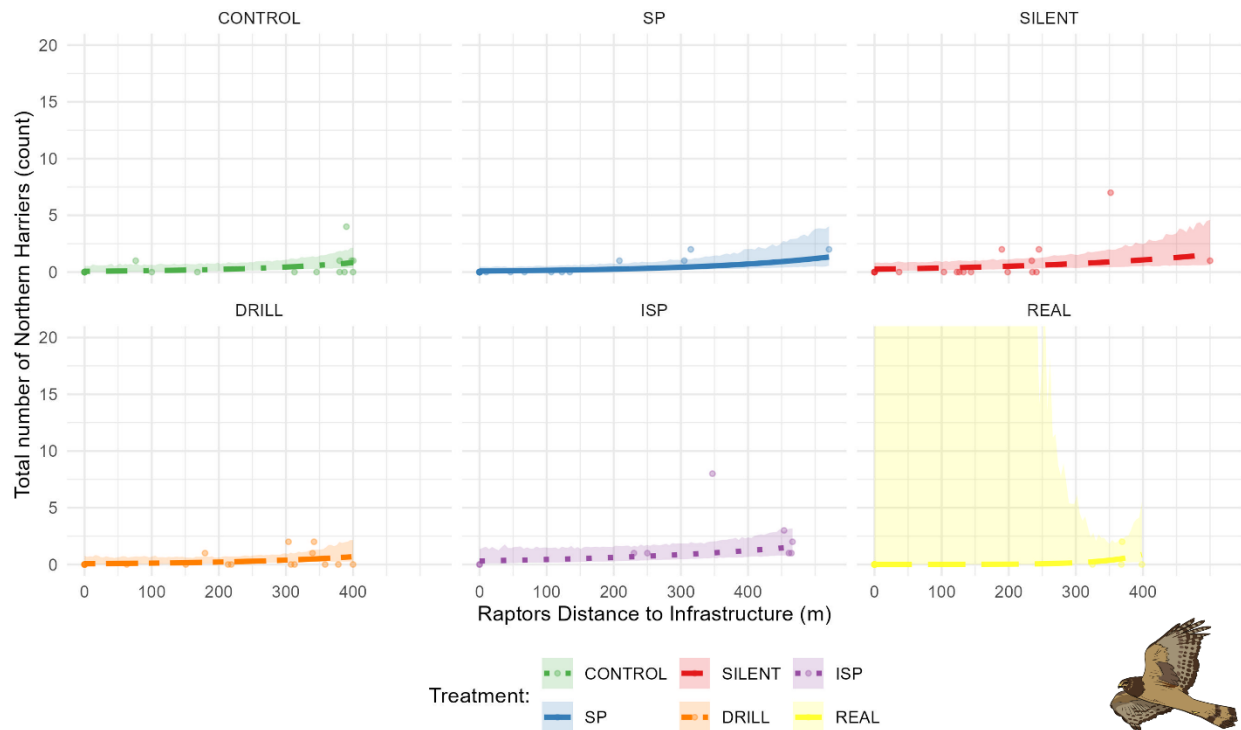
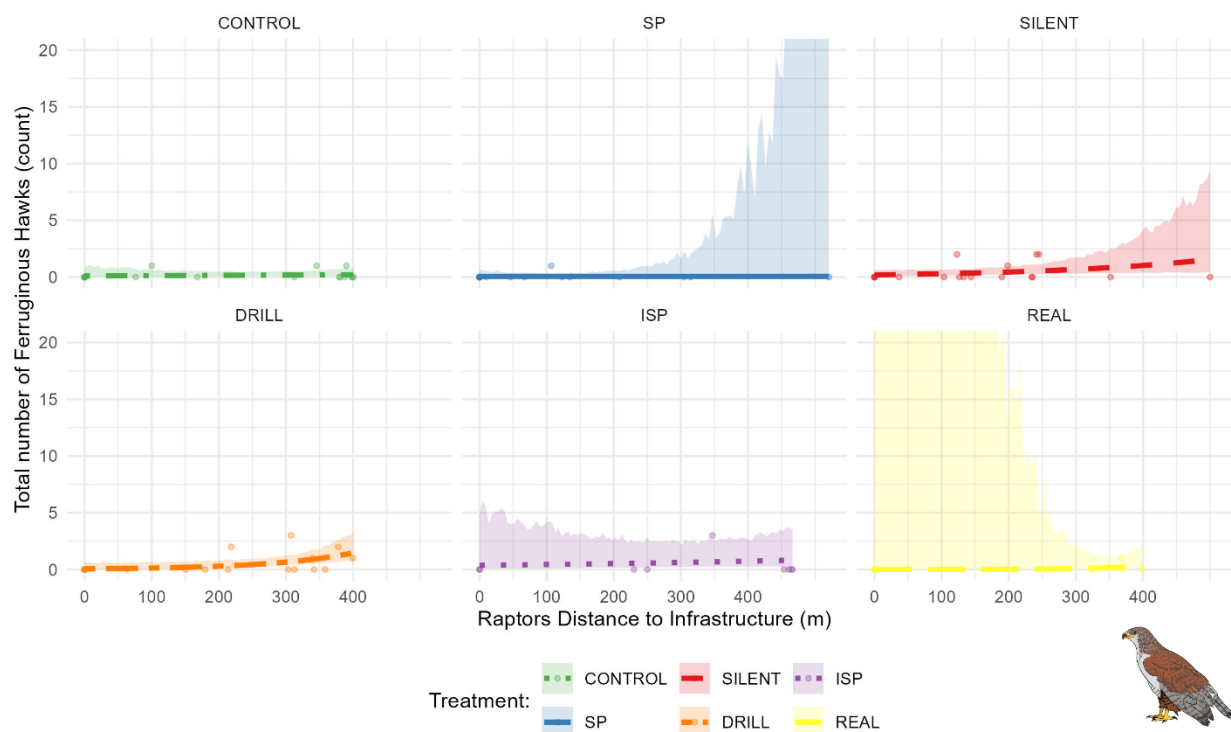


Figure 11. Total number of Northern Harriers across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.4.2.3 Ferruginous Hawk

Ferruginous Hawk abundance showed no evidence of differences between the treatments or with distance to infrastructure, with all effects showing $p \geq 0.1$. In the control treatment, Ferruginous Hawk counts did not change with distance from the centre point (Distance: $\beta =$

1146 -0.000249 , $SE = 0.00685$, $p \geq 0.1$). At the centre point (Distance = 0), Ferruginous Hawk
 1147 abundance was not different from the control under constant and predictable noise (screw
 1148 pump; $\beta = 0.612$, $SE = 2.23$, $p \geq 0.1$), silent ($\beta = 1.81$, $SE = 1.76$, $p \geq 0.1$), unpredictable noise
 1149 (drill; $\beta = 0.982$, $SE = 2.02$, $p \geq 0.1$), or the idle well (real infrastructure; $\beta = -0.818$, $SE = 3.45$, $p \geq$
 1150 0.1). Distance responses also did not differ from the control across treatments, with no
 1151 evidence for treatment by distance interactions for screw pump ($\beta = -0.00403$, $SE = 0.0108$, $p \geq$
 1152 0.1), silent ($\beta = -0.101$, $SE = 153$, $p \geq 0.1$), drill ($\beta = 0.00572$, $SE = 0.00884$, $p \geq 0.1$), or the idle
 1153 well ($\beta = 0.00742$, $SE = 0.0169$, $p \geq 0.1$).



1154
 1155 Figure 12. Total number of Ferruginous Hawks across distances from infrastructure center points
 1156 by treatment. Points show observed count data and lines show predictions from the global
 1157 GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the

predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.4.3 Mammal mesopredator abundance

I observed individuals of two mammal mesopredator species across sampling sites. The total number of mammal mesopredators recorded was 38 individuals; relative abundances of species observed were: Coyotes (65.79%) and American Badgers (34.21%).

Mammalian mesopredator abundance showed no differences between treatments or with distance to infrastructure (all treatment main effects and treatment by distance interactions: $p \geq 0.20$; Figure 13). In the control treatment, mesopredator counts did not change with distance from infrastructure (Distance: $\beta = -0.187$, $SE = 133.329$, $p = 0.999$). At the centre point (Distance = 0), mesopredator abundance was not different from the control under constant and predictable noise (screw pump; $\beta = -0.813$, $SE = 4.141$, $p = 0.844$), silent ($\beta = -0.352$, $SE = 2.562$, $p = 0.891$), unpredictable noise (drill; $\beta = -0.311$, $SE = 3.083$, $p = 0.920$), interrupted screw pump ($\beta = -2.222$, $SE = 4.171$, $p = 0.594$), or the idle well (real infrastructure; $\beta = 4.400$, $SE = 3.501$, $p = 0.209$). Distance responses were not different between the control and screw pump ($\beta = 0.188$, $SE = 133.329$, $p = 0.999$), silent ($\beta = 0.189$, $SE = 133.329$, $p = 0.999$), drill ($\beta = 0.187$, $SE = 133.329$, $p = 0.999$), interrupted screw pump ($\beta = 0.203$, $SE = 133.329$, $p = 0.999$), and the idle well ($\beta = 0.143$, $SE = 133.329$, $p = 0.999$). Only the total number of mammalian mesopredators was different between years (Year: $\beta = -2.476$, $SE = 0.981$, $p = 0.012$). The zero-inflation

component was significant (Intercept: $\beta = 1.044$, $SE = 0.233$, $p \leq 0.001$), indicating a high frequency of zero detections in the mesopredator dataset.

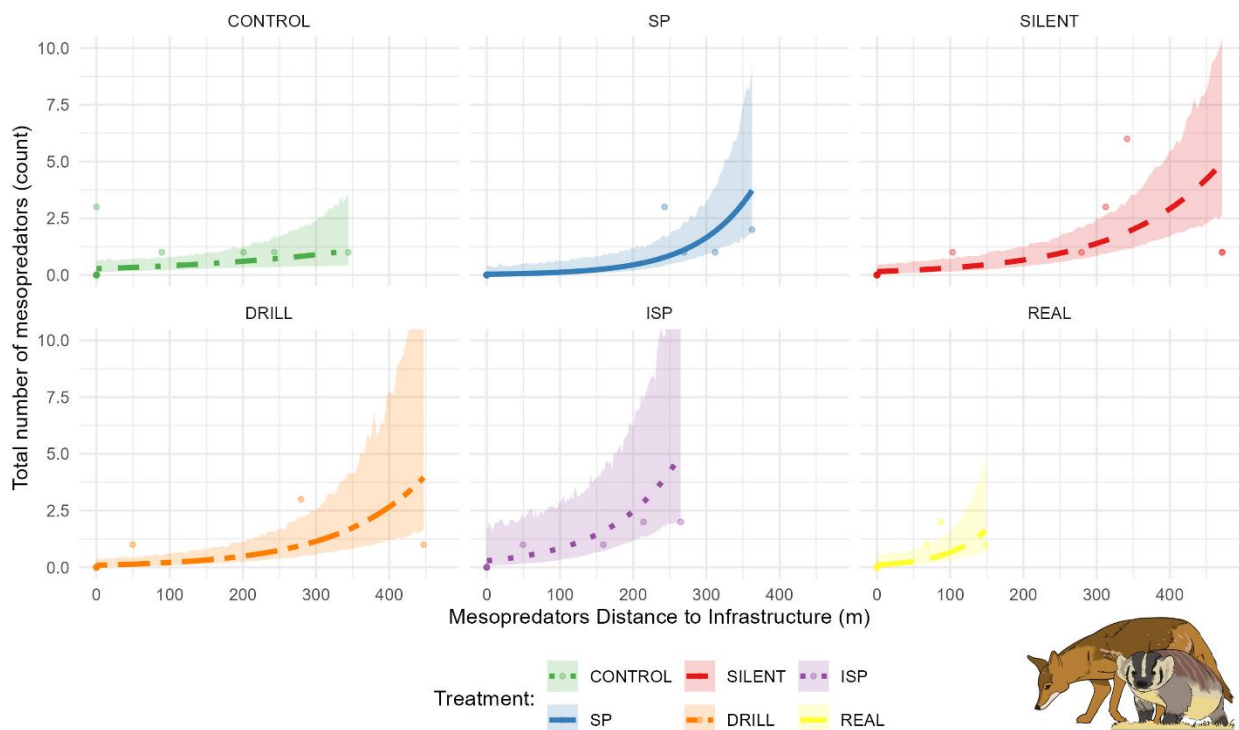


Figure 13. Total number of Mammalian mesopredators across distances from infrastructure center points by treatment. Points show observed count data and lines show predictions from the global GLMM, averaged across years. Shaded areas represent 95% confidence intervals around the predicted mean. Treatments are Control (green), Screw Pump (blue), Silent (red), Drill (orange), Interrupted Screw Pump (purple), and Real infrastructure (yellow).

2.5 Discussion

1193 I tested the hypothesis that conventional oil extraction can influence the predator–prey
1194 assemblages in the Northern prairies through changes in predator and prey abundance near the
1195 oil well infrastructure and/or its associated sound. The main disturbance sources examined
1196 were the oil infrastructure that can potentially alter habitat structure and movement, and the
1197 associated sound that varies in intensity and predictability, both of which can shift the predator
1198 and prey space use. I used the Intermediate Disturbance Hypothesis (IDH) as a strategic
1199 framework to generate predictions across disturbance contexts, without assuming a unimodal
1200 disturbance response, and I interpreted noise and infrastructure as potential risk cues under the
1201 Risk Disturbance Hypothesis (Connell, 1978; Fox, 2013; Frid and Dill, 2002; Beale and
1202 Monaghan, 2004).

1203

1204 Across the predator-prey assemblages' taxa, the main effects were scale-dependent. This
1205 pattern could fit a patch and scale framework such that the oil development's footprints can
1206 create small, independent patches different from the surrounding prairie, and species distribute
1207 themselves along the resulting short-range gradient in structure and resources by selecting
1208 microsites that best match their traits, risk perception, and foraging needs (Duflot *et al.*, 2014;
1209 Da Silveira Pontes *et al.*, 2015). These patterns may be explained by local resource
1210 concentration and edge-mediated subsidies may help explain these patterns as small disturbed
1211 footprints. Oil well centres can increase bare ground game trails (foraging or runway paths),
1212 early-successional forage, seed availability, and insect activity, creating small hotspots that are
1213 strongest near patch centres and edges (Fagan *et al.*, 1999; Kuli-Révész *et al.*, 2021).

1214 Nonetheless, the control sites also showed a positive relationship for several predator and prey
1215 assemblages with distance to the centre point.

1216

1217 Rodents tended to increase with distance from the centre point at the control sites, which may
1218 reflect random patches with specific vegetation structure and predator-prey interactions,
1219 possibly influenced by oil development associated structures in the landscape (e.g. fences, gas
1220 pipes, and signs) that were not centred on an experimental treatment (Figure 14 c), and the
1221 effects could therefore be interpreted against the control pattern in the direction and rate of
1222 change with distance, rather than assuming the control response should be flat. Compared with
1223 the control sites, the total number of rodents, was highest at the centre point across all
1224 treatment sites and then declined with distance. This disturbance attraction, suggests that local
1225 disturbances from wells can increase total rodent numbers near centre points regardless of
1226 whether the site is dominated by noise, silent experimental sites, or idle wells with real
1227 infrastructure (Figure 14 d), which is consistent with the Intermittent disturbance hypothesis
1228 based predictions, in which modified patches can concentrate activity locally while the direction
1229 and shape of the response varies with how disturbance is defined and sampled (Connell, 1978;
1230 Fox, 2013), and it also aligns with the Risk Disturbance hypothesis in that infrastructure and
1231 sound can function as disturbance cues that shift site use relative to controls and redistribute
1232 activity towards disturbance sources (Frid and Dill, 2002; Beale and Monaghan, 2004).

1233

1234 Deer Mice followed the same spatial structure as the total rodent group. Because they
1235 represented the majority of captures, their response likely had a strong influence on the total
1236 rodent pattern, but it also shows that the dominant rodent species did not avoid noisy
1237 treatment centres. Deer Mouse abundance was higher near centre points under the
1238 unpredictable noise treatment, with similar but weaker trends under predictable noise, silent
1239 infrastructure, and intermittent noise, while idle wells were no different from control.
1240 Therefore, noise did not result in clear site avoidance by Deer Mice. Instead, acoustic
1241 characteristics may modulate the perceived quality of an already attractive patch, rather than
1242 acting as the only factor determining patch suitability. This fits a risk-disturbance view, where
1243 disturbance cues shift perceived risk and foraging trade-offs rather than forcing avoidance (Frid
1244 and Dill, 2002; Beale and Monaghan, 2004). Rodents rely on hearing for risk assessment,
1245 predator detection, and social communication, but their responses to anthropogenic sound also
1246 depend on the masking risk, the predictability, and other behavioral adaptations like the
1247 availability of listening during silent windows, not only the frequency or amplitude of the sound
1248 (Dent *et al.*, 2018; Elmer *et al.*, 2021). Deer Mice, often use acoustic cues while moving and
1249 foraging at night, so masking can reduce how confidently they use open microsites even when
1250 those microsites are resource-rich (Dent *et al.*, 2018). This mechanism could help to explain why
1251 intermittent soundscapes may still leave enough quiet moments for Deer Mice to perceive key
1252 acoustic information and continue using the resources from the center point, whereas
1253 treatments with more continuous or disruptive noise and fewer silent windows may reduce the
1254 patch use.

1255

1256 Northern Grasshopper Mice did not show strong or consistent differences among all
1257 treatments. Still, their numbers tended to be higher close to the centre point at sites with
1258 intermittent and unpredictable noise. In those treatments, their abundance dropped off faster
1259 as they moved away from the centre point. This suggests their response was local and patch-
1260 based as they were using the area closest to the treatment's footprint more than the
1261 surrounding prairie. This remains consistent with their predatory and territorial behaviour.
1262 Grasshopper mice use vocal signalling and active hunting, traits that can support use of open,
1263 disturbed microsites where encounters with prey can be higher than in dense cover (Sarko *et*
1264 *al.*, 2012; Stapp, 1999; Pash *et al.*, 2017). In the intermittent noise treatment and the
1265 unpredictable noise treatment, individuals may exploit open microsites and concentrated prey
1266 access near disturbed footprints, but only over short distances, consistent with risk-sensitive
1267 patch use where benefits can outweigh perceived risk at fine scales (Frid and Dill, 2002).

1268

1269 Richardson's ground squirrel abundance showed no consistent differences among treatments or
1270 with distance to infrastructure, so the general model does not support a directional attraction
1271 or avoidance response to any treatment. A lack of detectable effect is possible given the small
1272 sample size, possibly due trapping effort combined with discrete and spatially patchy colonies.
1273 Richardson's ground squirrels are organized in colonies where space use, burrow density, and
1274 aboveground activity can strongly vary over short distances, driven by social structure rather
1275 than broad treatment differences (Yeaton, 1972). Their surface activity is also strongly shaped
1276 by predation risk, which can shift vigilance, time above ground, and use of exposed microsites
1277 without requiring a change in population size, and those behavior changes can translate into

1278 variable detectability in counts or trap-based indices (Nonacs and Blumstein, 2010), which
1279 aligns with risk-disturbance mechanisms operating through behaviour and detectability rather
1280 than abundance (Frid and Dill, 2002).

1281

1282 Raptor responses followed treatment specific distance patterns. Total raptor abundance
1283 increased with distance in control sites, while near the centre point it was higher than control
1284 under silent experimental and intermittent noise treatments, with weaker evidence under
1285 predictable noise and no detectable differences under unpredictable noise or idle wells.
1286 Treatment by distance interactions were not strong at the guild level, which suggests that
1287 raptors differed mainly in aggregation at the center point rather than in how sharply they
1288 changed across the gradient. This is consistent with an aggregative response, where predators
1289 concentrate not where prey is more abundant but where prey are easier to detect or capture
1290 (Kocina and Aagaard, 2021). Visually guided hunting and perch use can make raptors especially
1291 responsive to short-range increases in prey accessibility around modified patches (Andersson *et*
1292 *al.*, 2009). Given the large home ranges and movement capacity of grassland raptors, local
1293 clustering near a foraging patch can occur through movement decisions over kilometres, even if
1294 counts do not show a clean gradient response at the tens to hundreds of metres scale (Kocina
1295 and Aagaard, 2021; Watson, 2020). These results could mean that a prey increase near
1296 infrastructure does not guarantee a matching predator increase at the same distances.

1297



Figure 14. Rodents and Raptors use of anthropogenic features at peripheral control sites (a-d) and Swainson's Hawks using a sign (a) and a fence (b) from control sites peripheral areas. Northern Grasshopper Mouse using a fence after flushed at a control site peripheral area (c), and Deer Mice nest inside noise experimental treatment (d). (Pictures by JP Medina)

Raptors were most concentrated near the centre point when the patch was silent or had quiet windows, which suggests that the site can be suitable for hunting when acoustic conditions

1307 supported prey detection and capture, but that noisier or less predictable soundscapes
1308 especially drilling, reduced how strongly raptors concentrated there even if a perch was
1309 available, consistent with a risk-disturbance mechanism in which acoustic conditions alter
1310 hunting efficiency and perceived risk while the patch remains structurally attractive (Frid and
1311 Dill, 2002; Beale and Monaghan, 2004). Prairie raptors often hunt from relatively low natural
1312 perches such as sagebrush, boulders, and subtle landscape features, and they can switch among
1313 perch types depending on local structure and sightlines (Coates *et al.*, 2014; Parayko, 2021)
1314 (Figure 15). In open habitats, even small differences in perch height relative to surrounding
1315 vegetation can change prey visibility and hunting efficiency, which can translate into localized
1316 aggregation around patches that combine prey activity with suitable perch structures
1317 (Andersson *et al.*, 2009).

1318

1319 The silent experimental treatment produced the clearest response in Swainson's Hawks, with
1320 higher abundance recorded near silent treatment centres. This suggests that Swainson's Hawks
1321 may have used the modified infrastructure patches as hunting areas or perch sites when prey
1322 were accessible (Figure 14 a-b, 15) (Andersson *et al.*, 2009).

1323

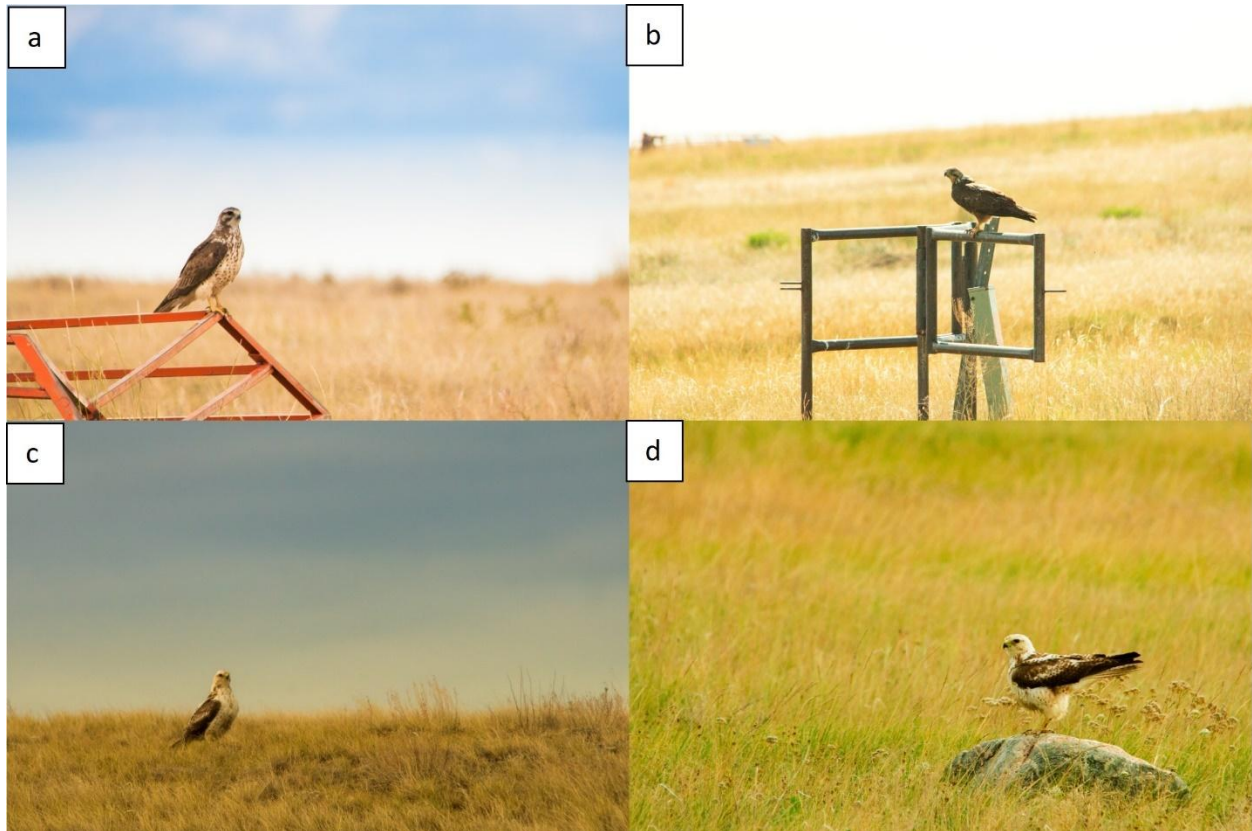


Figure 15. Swainson's Hawks using human (a and b) and natural (c and d) perches in the study location. Juvenile Swainson's Hawk (SWHA) perched on cattle fence from experimental treatments (a); Adult SWHA perched on wood pole from a short fence located near a road (b); Juvenile SWHA perched on ground near noise experimental treatment (c); Juvenile SWHA perched on a rock on a control site. (Pictures by JP Medina)

Northern Harriers and Ferruginous Hawks showed limited evidence of treatment or distance responses. This suggests that any effects were weaker than the study's ability to detect them, occurred at different spatial scales or were expressed more through behavioural responses than through consistent changes in counts along the sampled gradient. However, this does not necessarily mean they were unaffected. Their responses may depend on how each species uses

the habitat. Northern Harriers often hunt by low, coursing flight and may respond more to vegetation structure, prey movement, or acoustic masking than to the presence of a centre-point feature. As a result, disturbance effects may appear as changes in hunting behaviour, flight paths, prey detection, or a broader scale habitat use rather than as strong changes in local counts (Martin, 1987; García and Arroyo, 2005), again consistent with risk-disturbance effects expressed through behaviour and detectability (Frid and Dill, 2002).

Mammalian mesopredators showed no detectable differences among treatments and no distance response, in contrast to predictions of the mesopredator release hypothesis. However, wide-ranging mammals may respond to infrastructure at larger spatial scales than the distance gradient analysed here, or they may have behavioral responses not evaluated in this study design like changing foraging activity timing, game trail use, and microhabitat selection without increasing detections, which can still alter predator-prey encounter rates (Planillo *et al.*, 2015; Tate and Amar, 2017). Infrastructure and its associated noise may shift mesopredator space use and activity patterns rather than abundance, so predation risk could change even when counts do not, which is a key expectation under the Risk Disturbance Hypothesis (Frid and Dill, 2002; Beale and Monaghan, 2004).

An integrated community assembly perspective is useful such that (1) Oil well footprints can create small, modified patches that attract animal activity closer to the centre point, and (2) which species use those patches mostly depends on their traits and sensory constraints,

including how they forage and how they detect risk under different soundscapes. Movement among patches can concentrate individuals in the same local hotspots because animals often make habitat-use decisions around a home base or frequently used activity centre, so nearby patches get revisited whenever they offer a temporary advantage in prey access, visibility, or travel cost (Olsson and Bolin, 2014). These local increases may reflect redistribution rather than population growth: when resources are patchy, animals can repeatedly use small productive areas, creating high local abundance near treatment centres without increasing abundance across the broader landscape (Hambäck and Englund, 2005). Even in landscapes made up of many small patches, these repeated movements could produce strong clustering in the portion of patches that consistently provide more benefits, without requiring an increase in total abundance across the broader area (Fahrig, 2020). The outcome is a strong patch-scale pattern where detections accumulate near particular centres, while overall abundance across sites or years remains similar because individuals are shifting among patches rather than being added to the system (Leibold *et al.*, 2004), which matches the way Intermediate Disturbance Hypothesis is used here for generating scale-dependent predictions rather than a single expected curve (Connell, 1978; Fox, 2013).

Across taxa, the strongest effects were at a local, patch scale near the infrastructure centre point rather than a larger site-wide increases. Total rodents showed clear treatment-specific gradients: in control sites, rodent abundance increased with distance from the centre point, and treatment sites generally showed weaker or negative distance slopes relative to the control, consistent with rodents concentrating close to the centre point around footprint types rather

1379 than spreading evenly across the site. Raptors showed a narrower version of the same pattern.
1380 In control sites, total raptor abundance increased with distance, with weaker evidence under
1381 predictable screw-pump noise and no detectable centre-point increase under the unpredictable
1382 drill treatment or the idle well. Raptor species results matched those guild patterns: Swainson's
1383 Hawks increased with distance in control sites but were higher at the centre point only under
1384 the silent treatment, while Northern Harriers showed only weak evidence of a distance
1385 relationship and limited evidence of treatment differences. By contrast, Ferruginous Hawks and
1386 mammalian mesopredators showed no detectable treatment or distance effects. The positive
1387 distance patterns in control sites indicate a background spatial gradient within treatments, and
1388 one probable explanation is that small human features in the surrounding landscape, such as
1389 gas extraction pipes, signs, or fences, influenced detections more at the outer distances than at
1390 the centre point, producing a displaced concentration of activity. These results can support two
1391 predation-risk alternatives that vary among treatments. In the silent and intermittent noise
1392 treatments, rodents and raptors were both higher at the centre point than in controls, whereas
1393 in the drill and real idle well treatments rodents were higher at the centre point but raptors
1394 were not.

1395

1396 Overall, these findings suggest that even in ecosystems adapted to some degree of disturbance,
1397 the scale and intensity of human development can reshape predator-prey interactions and
1398 community structure by creating patches that reorganize local resource distribution and animal
1399 space use. Using the Intermediate Disturbance Hypothesis as a prediction guide, my results
1400 suggest that disturbance can shift local abundance patterns without following one consistent

1401 peak at intermediate disturbance, and under the Risk Disturbance Hypothesis they indicate that
1402 noise can act as a risk cue by masking acoustic information and altering hunting or foraging
1403 efficiency. (Connell, 1978; Fox, 2013; Frid and Dill, 2002; Beale and Monaghan, 2004). In this
1404 study, infrastructure likely functioned as small, predictable patches of altered structure and
1405 resources that elevated prey activity near centre points across treatments, while noise
1406 characteristics modulated how strongly species that depend on acoustic information used those
1407 patches. Raptors responded mainly through aggregation to these prey patches, whereas
1408 mesopredators showed weak responses in abundance and may respond more through
1409 behaviour than numbers. This combination can produce situations where prey concentrate near
1410 infrastructure without a proportional increase in predators at the same distances that could
1411 have direct implications for how predation pressure is distributed across the landscape,
1412 independent on the total numbers. To mitigate these impacts, land and resource managers
1413 should prioritize reducing the intensity and spatial extent of the disturbances associated with oil
1414 extraction. Clustering well sites and reusing existing infrastructure corridors could reduce
1415 cumulative habitat degradation and the density of well footprints on the landscape (Ward *et al.*,
1416 2020; Yoo and Koper, 2017). Where noise is unavoidable, managers could avoid continuous
1417 high-amplitude sources and favor technologies that produce intermittent or low noise may help
1418 keep conditions within sensory thresholds for disturbance-sensitive species (Bernath-Plaisted,
1419 2015). My results suggest that management should consider retaining native vegetation around
1420 infrastructure and minimizing new surface disturbance during breeding seasons, because intact
1421 cover may reduce edge effects and limit the formation of small activity hotspots near well
1422 footprints (Bernath-Plaisted, 2015). Regulatory frameworks should also account for the

1423 ecological value of native prairie, especially isolated patches that function as biodiversity
1424 refuges (Selwood and Zimmer, 2020). Without targeted mitigation, the northern prairies risk
1425 continued degradation of remaining grasslands, repeating patterns of weak environmental
1426 oversight despite strong governance capacity (Timoney and Lee, 2001). Management that limits
1427 cumulative footprint area while preserving grassland heterogeneity offers a practical path to
1428 conserving predator and prey communities in rapidly changing prairie landscapes.

1429

2.6 References Chapter 2

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3 CHAPTER 3. Effect of conventional Idle oil wells on landcover by influencing ecosystem engineers in the Northern mixed-grass prairies

3.1 Abstract

Idle oil wells are widespread across Alberta's mixed-grass prairies. Nonetheless, their long-term ecological effects are not fully understood. I tested whether idle wells alter the activity of Richardson's Ground Squirrels, and whether these changes influence landscape composition and configuration. Using high-resolution imagery from sUAVs, I compared ground squirrel burrow density and landcover characteristics among idle wells, control sites, and silent experimental treatments. Idle wells supported greater burrow area and higher percentages of sagebrush, alongside reduced grass cover, relative to other treatments. Diversity indices were highest near idle wells and declined with distance, suggesting localized increases in patch heterogeneity driven by ground squirrel activity. Spatial configuration also differed: Moran's I analysis showed that idle wells reduced spatial autocorrelation, producing more dispersed vegetation patterns than in control plots. These results suggest that long-term, unreclaimed infrastructure can promote structural shifts in prairie landscapes by modifying both composition and configuration. Although such changes may enhance local heterogeneity, they also reduce spatial connectivity, potentially reducing habitat quality for grassland specialists. Management should prioritize restoring grass cover and spatial continuity to mitigate the lasting ecological impacts of idle wells.

1975 **3.2 Introduction**

1976

1977 North American grasslands have been extensively modified by human activity. Once vast and
1978 continuous, major landcover changes driven by agriculture, population growth, and industrial
1979 development have changed grasslands' ecosystem dynamics (Douglas *et al.*, 2023). In Canada,
1980 these changes increased with the expansion of conventional oil extraction. Since the early 1900s
1981 energy development across the Canadian prairie landscapes has expanded significantly, with
1982 over 466,000 wells now present in Alberta alone (AER 2025). This widespread development has
1983 altered the landscape composition and configuration, reducing the habitat suitability and
1984 contributing to the ongoing wildlife declines (Preston *and* Kim, 2016; Chowdhury 2021). These
1985 changes can affect wildlife at the community, population, and species levels (Francis *et al.*, 2009;
1986 Yoo *and* Koper, 2017; Curry *et al.*, 2018). Here, I provide a test to determine if idle oil wells alter
1987 Richardson's Ground Squirrels and whether these impacts lead to changes in landscape
1988 composition and/or configuration across grassland habitat.

1989

1990 Oil infrastructure can change the spatial structure of grasslands' landscape affecting species
1991 interactions and ecological processes. Landscape structure consists of two key components:
1992 composition and configuration (Turner *et al.*, 2001). Composition refers to the types and
1993 amount of habitat present that supports biodiversity (Turner *et al.*, 2001) while configuration
1994 describes the spatial arrangement of those habitat patches that influence movement, dispersal,
1995 and interactions among species (Maestre and Reynolds, 2007; Fahrig, 2013). These two

1996 components interact but can have different effects depending on the species and spatial scale.
1997 In fragmented grasslands, configuration often plays a stronger role than composition in shaping
1998 population and community patterns (Fahrig, 2024). Nesting success in grassland songbirds is
1999 more influenced by the size, shape, and isolation of habitat patches than by the total amount of
2000 available habitat (Lockhart and Koper, 2018; McDonald and Koper, 2022). Small mammals are
2001 also sensitive to spatial structure. Even small changes in patch size or connectivity can influence
2002 rodent distribution (Heisler *et al.*, 2019). In prairie ecosystems, rodent communities respond to
2003 both the composition and configuration of habitat (Rowland-Schaefer *et al.*, 2024). Species
2004 composition in grasslands is shaped by landscape-scale connectivity and the size of individual
2005 fragments, which can influence movement and community assembly (Fischer *and* Lindenmayer,
2006 2007; Pardini *et al.*, 2010).

2007

2008 Each stage of an oil well's lifecycle may affect wildlife differently. Exploration and construction
2009 remove habitat, displace wildlife, and alter ecological processes (Bradshaw, 1997; Hobson and
2010 Van Wilgenburg 2014). Drilling introduces noise, light, and human activity, increasing the
2011 vigilance behavior, causing avoidance, and reducing the reproductive success in some species
2012 (Drolet *et al.*, 2016; Rosa *and* Koper, 2022; Rutherford *et al.*, 2023). Production stages further
2013 reduces the suitable habitat, limiting movement for grassland songbirds and small to medium-
2014 sized mammals (Francis *et al.*, 2011; Bernath-Plaisted *et al.*, 2016; Nenninger *and* Koper, 2018).
2015 Idle wells extend these effects by remaining in place without remediation, contributing to long-
2016 term habitat fragmentation and ecosystem disruption (Galay *and* Winter, 2023). Even when

2017 reclamation occurs, it often fails to fully restore ecosystems, leaving lasting impacts on
2018 biodiversity (Sylvain *et al.*, 2019).

2019

2020 Conventional wells consist of a wellbore, extraction equipment like pump jacks or screw pumps,
2021 and tank batteries. Pumps can run on either the electrical grid or on-site generators in remote
2022 areas. The tank batteries, varies in size depending on the reservoir's capacity and extraction
2023 volume, and are the largest above-ground structures in the landscape. It separates oil from
2024 impurities before storage or disposal process, contributing to habitat disturbance and
2025 fragmentation. While the ecological effects of oil wells on prairie ecosystems are well known,
2026 the differences between active and idle wells should be incorporated into management
2027 practices. Active wells extract oil, while idle wells remain unactive but potentially continue to
2028 impact habitat and disrupt ecosystems (Muehlenbachs, 2017; AER, 2018; Wisen *et al.*, 2020).
2029 Idle wells are structurally similar to active wells. However, they require little maintenance and
2030 produce no sound, and often delay reclamation indefinitely, leading to a growing number of
2031 unreclaimed sites, particularly in Alberta (Galay *and* Winter, 2023).

2032

2033 Ecosystem engineers like the Richardson's Ground Squirrels (*Urocitellus richardsonii*) can modify,
2034 maintain or even create habitats by changing the landscape structure and thus, influence
2035 resource availability (Jones *et al.*, 1994). Richardson's Ground Squirrels play this role by affecting
2036 soil properties, plant communities, and landscape structure through burrowing behavior
2037 (Umbanhowar Jr., 1995; Proulx *et al.*, 2012; Newediuk *et al.*, 2020; Fisher *et al.*, 2021). Burrows

2038 can create disturbances that maintain plant diversity and limit the spread of dominant species
2039 (Bangert *and* Slobodchikoff, 2006). However, idle wells alter Richardson's Ground Squirrel
2040 habitat selection, dispersal, and burrowing behavior, further changing the landscape structure.
2041 Edge effects introduced by idle wells could impact species composition and ecosystem dynamics
2042 (Herse *et al.*, 2020). Predators may use these areas for hunting, while prey species may avoid
2043 them, leading to shifts in predator-prey dynamics and the overall community structure (Francis
2044 *et al.*, 2011; Ramirez *and* Mosley, 2015). Habitat fragmentation and stressors associated with
2045 idle wells, might force animals to shift energy toward stress responses instead of growth and
2046 reproduction, reducing fitness and long-term population stability (Rutherford *et al.*, 2023).
2047 These disruptions can spread through food webs, changing prey availability, predator behavior,
2048 and overall ecosystem function.

2049

2050 Richardson's Ground Squirrels prefer open grassland, often in areas affected by human
2051 disturbance (Fisher *et al.*, 2021). They select tall and scattered native vegetation over cultivated
2052 fields, responding more to habitat configuration than vegetation composition (Downey *et al.*,
2053 2006; Bylo *et al.*, 2014). Their burrowing activity increases plant diversity, influencing overall
2054 landscape structure (Newediuk, 2015). However, idle wells may alter these patterns, changing
2055 habitat suitability for burrowing rodents and affecting the ecological processes they could
2056 potentially drive.

2057

2058 To test the effects of idle wells on an ecosystem engineer and the subsequent impact on
2059 landscape spatial composition and configuration, I predicted that if idle wells with larger
2060 structures and long-term presence (inactive for at least three years) influence Richardson's
2061 Ground Squirrels, the total number of burrows will differ between idle wells, control sites, and
2062 silent experimental sites (smaller, newly constructed infrastructure with less time to affect
2063 ground squirrel behavior). Second, I predicted that idle wells would have stronger cascading
2064 effects on vegetation structure than silent experimental treatments, expressed as differences in
2065 landcover proportions near treatment centres. Specifically, I expected Richardson's Ground
2066 Squirrel activity, measured as burrow density, to be associated with changes in percent cover of
2067 key landcover types, indicating that burrowing activity contributes directly to vegetation
2068 structure regardless of treatment. Third, I predicted that if idle wells influence Richardson's
2069 Ground Squirrels as ecosystem engineers, then variation in burrow abundance will be
2070 associated with vegetation structure and help explain shifts in local landscape heterogeneity.
2071 Fourth, I assessed whether idle wells influence landscape configuration by altering landcover
2072 dispersion patterns, such as spatial clustering, across treatments and whether these effects are
2073 stronger closer to idle wells. I predict that if idle wells disrupt vegetation and alter landcover
2074 structure, then sites with idle wells will exhibit changes in landscape spatial composition and
2075 configuration, and this pattern will be greater closer to the wells. Together, these predictions
2076 test whether idle wells alter landscape heterogeneity both directly through vegetation
2077 disturbance and indirectly through changes in Richardson's Ground Squirrel burrowing activity,
2078 with effects expected to be strongest near well centers.

2079

3.3 Methods

3.3.1 Study area

Three study sites were established in each of three locations to account for geographic variability ($n = 9$ sites), were randomly established within the mixed-grass prairie near Brooks, Alberta, Canada ($49^{\circ} 0' 0.004''$ to $50^{\circ} 53' 56.475''$ N, $110^{\circ} 0' 2.757''$ W to $112^{\circ} 28' 44.473''$, at 760 m. asl) (Figure 1). The research was conducted on annually grazed mixed-grass prairie managed by the Eastern Irrigation District (EID), a private landowner group that primarily uses grasslands for grazing cattle on more than 283,000 ha. The dominant native grass species included needle and thread (*Hesperostipa comata*), porcupine grass (*Hesperostipa spartea*), blue grama (*Bouteloua gracilis*), white beardtongue (*Penstemon albidus*), and western wheatgrass (*Pascopyrum smithii*). Other native plants included sagewort (*Artemisia frigida*), prickly pear cactus (*Opuntia polyacantha*), and silver sagebrush (*Artemisia cana*). The prairie also contained some non-native and invasive species introduced through habitat fragmentation, farming, and livestock grazing. These included goatsbeard (*Tragopogon dubius*), dandelion (*Taraxacum officinale*), crested wheatgrass (*Agropyron cristatum*), smooth brome (*Bromus inermis*), and sweet clover (*Melilotus officinalis*).

The research was carried out in the summer of 2021. This period was chosen as it corresponds to the peak plant growing season in the region (Jarchow *et al.*, 2020). The contrast between different types of vegetation and between vegetation and bare ground is more pronounced during late summer, enhancing the clarity and accuracy of the imagery captured by small

Unmanned Aerial Vehicle (sUAV) (Xu *et al.*, 2020). Similarly, this period also corresponds to the peak above ground activity of Richardson's ground squirrels, making it an ideal time to survey burrows and their effects on the landcover. During this season, burrow entrances are clearly visible, and consistent used by the squirrels, along with distinct vegetation patterns (Michener, 1984; Thompson and Hare, 2010).

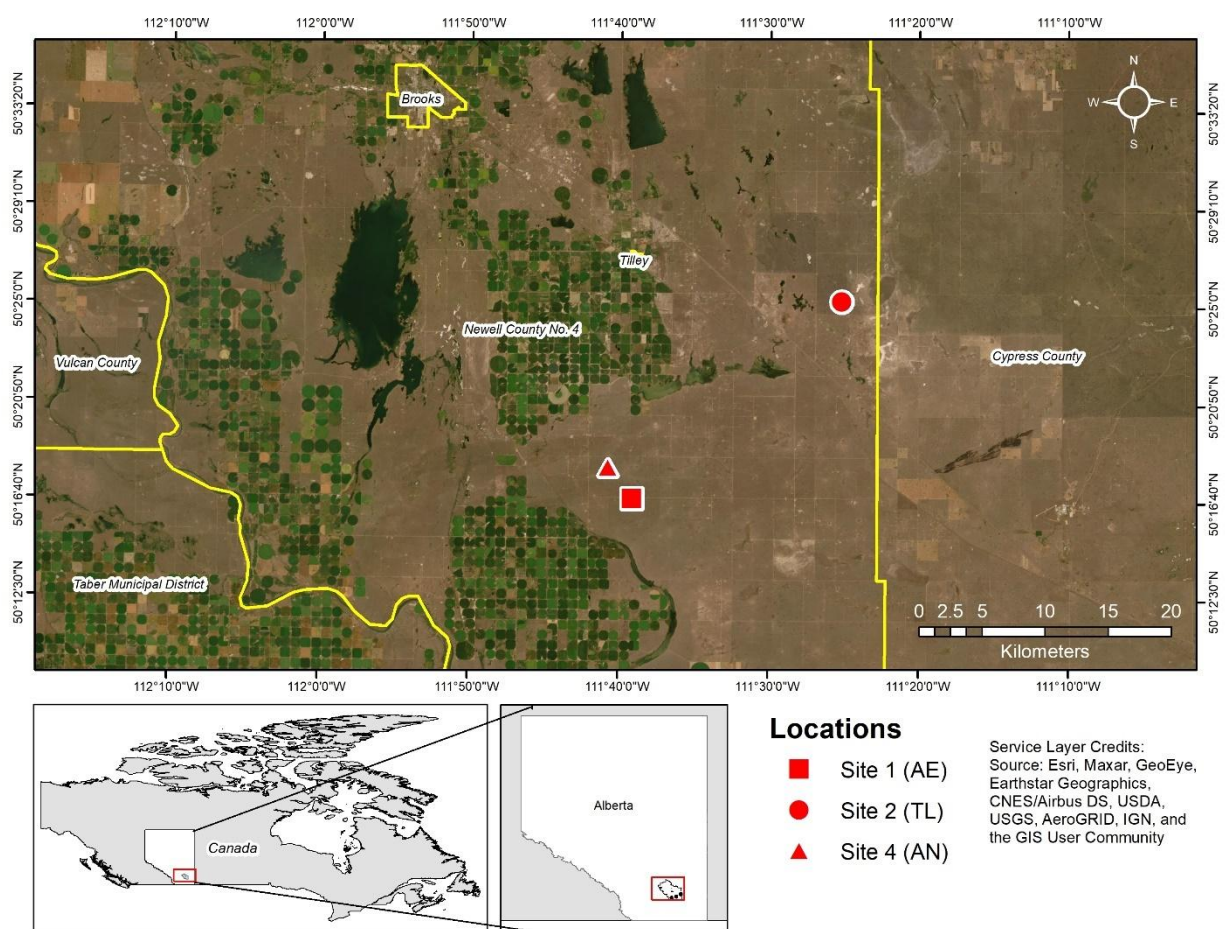
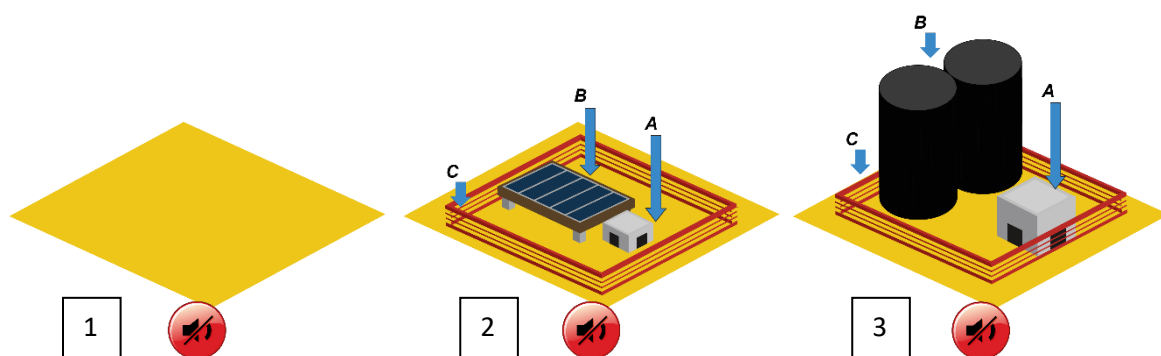


Figure 1. Study area locations. South-East of the city of Brooks Alberta, Canada shown by red polygons. Mixed-grass prairie shown contrasting with irrigated agricultural lands.

3.3.2 Data Collection

2112 Each of the nine study sites measured 800x800 meters. The center point of each site was
 2113 situated at least 800 meters apart from the center point of any other site. Each site was either:
 2114 1.- control sites (n=3), with no oil infrastructure and no experimental treatment, 2.- silent
 2115 experimental sites (n=3), small temporary structures, which contained a small shed with
 2116 inactive solar panels surrounded by Cattle-proof technical fence, similar to natural gas wells in
 2117 the region and, 3.- idle wells(n=3), large, long-term structures, consisting of non-active tank
 2118 batteries, a shed with inactive oil extraction equipment (screw pump) all surrounded by cattle-
 2119 proof technical fence used to ensure safety and prevent interference, protecting both the
 2120 infrastructure and nearby livestock (Koper *et al.*, 2014; Brown and Ruckstuhl 2012) (Figure 2).
 2121 At each site, controlled verified in the field, sUAV photographs of vegetation at 35 meters and 5
 2122 meters were captured at each of the landcover classes to later use them as supervised
 2123 classification control points combined with manual classification.

2124



2125

2126

Figure 2 Study sites diagrams used in this study. Mixed-grass prairie represented by yellow ground, red circle denotes the lack of anthropic sound emission. A) Shed, B) non-active energy source, and C) cattle-proof technical fence. 1.- control sites(n=3) with no oil infrastructure and no experimental treatment, 2.- silent sites experimental treatment (n=3) with solar panels, 3.- idle wells(n=3) with tank batteries. (Created by JP Medina, 2023)

3.3.2.1 sUAV surveys

To characterize the spatial composition and configuration of grassland ecosystems, I used small Unmanned Aircraft Vehicles (sUAVs) equipped with red, green, and blue (RGB) cameras to capture ultra-high-resolution (<5 mm) imagery of heterogeneous landscapes, providing detailed spatial data and clear orthoimages (Dronova *et al.*, 2021). This remote sensing approach is cost-effective and efficient, capturing broad datasets across various spatio-temporal scales, unlike traditional field-based measurements, which are accurate but time-intensive and costly (Ali *et al.*, 2016; Badreldin *et al.*, 2017; Olson *et al.*, 1999, Reinke and Jones 2006). Imagery was georeferenced as GeoTIFFs (Georeferenced raster image) and processed with WebODM software for accurate image classification and analysis (Mokrane, 2020). The flights followed a double transect oriented North-South and East-West, with an 80% front and side overlap at 16.1km/h (Figure 3)

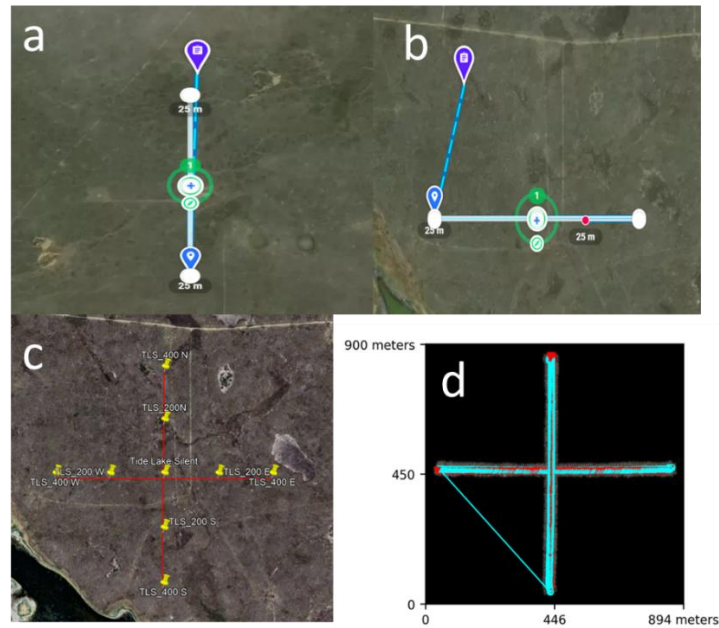


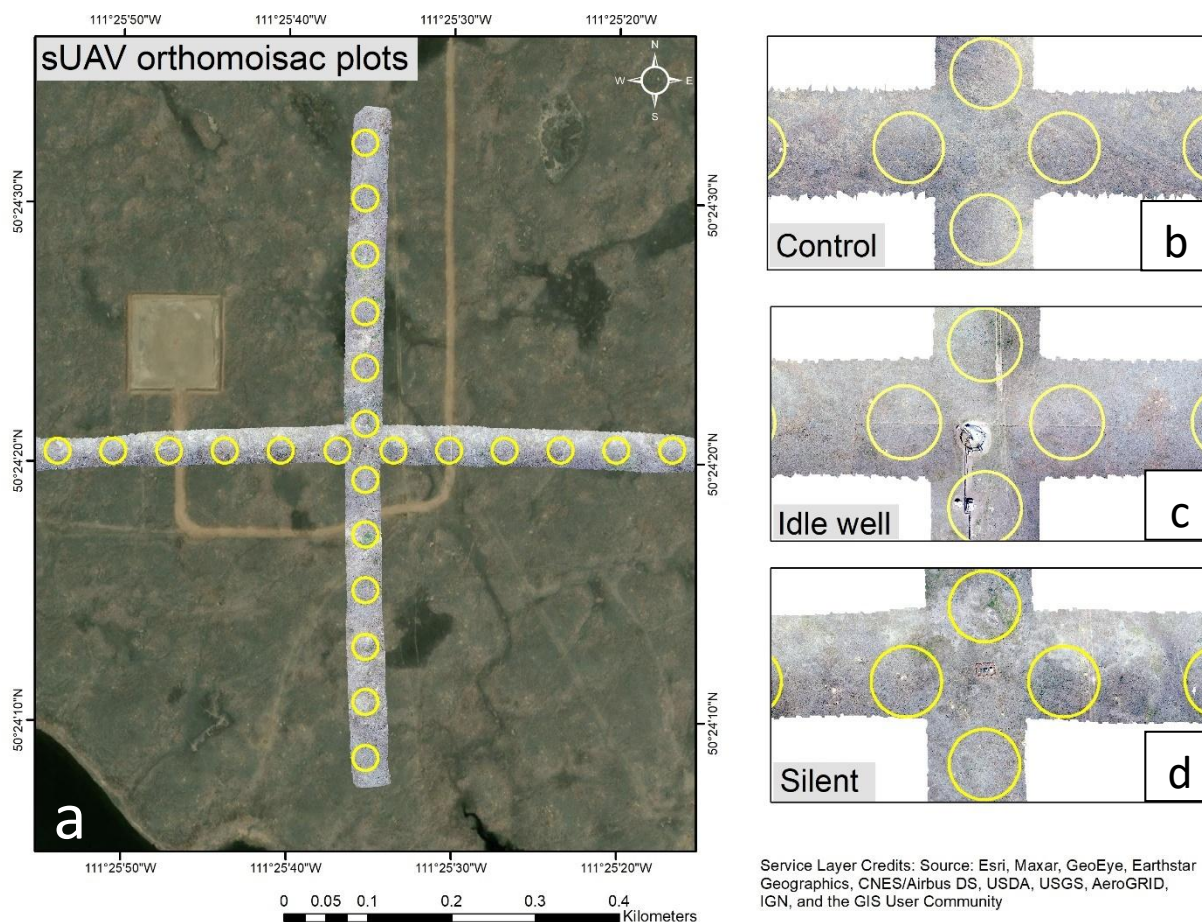
Figure 3 sUAV imaginary collection. a) Vertical, North-South and b) horizontal East-West double transect flight preplans from Dronleink Ltd, TX, showing start points and flight path. c) points set-up from Google Earth, and d) resulted fly path.

This strategy minimized the maximum positional deviation of the drone (4.127 mts) and mitigated the impact of wind gusts, which are common in prairie environments. The images were then organized and stitched together using WebODM software to create a single cross-like (N, S, E, W) high-resolution orthomosaic raster image for each study site, resulting in a total of nine orthomosaic raster images. Each raster image consisted of a cross section 800 x 800 m and 50m wide transects. However, the wind conditions resulted in a variable width alignment of the transects and only 30m were available for further analyses at all images.

These methods allowed for precise mapping of vegetation (Lopatin *et al.*, 2017; Zhang *et al.*, 2023), species-level discrimination (Laliberte *et al.*, 2011; Anderson *et al.*, 2023), and estimation of biophysical parameters such as biomass and leaf area index (LAI) (Bendig *et al.*, 2015, Liu *et al.*, 2021). High-resolution sUAV imagery is also effective in identifying landscape characteristics associated with oil development footprints in grasslands (Baynard *et al.*, 2022), making it invaluable for assessing the impacts of energy development on ecosystem structure and function.

3.3.3 Data analyses

I subdivided each raster image into six, 30m-diameter, equidistant circular plots at each direction (n=24 per site, n= 286 per treatment, N= 858 sections) for easier data rendering and processing due to hardware constraints and to enable me to obtain radial distances from the center point (Figure 4). Each raster image was trained with field control points for each landcover type (n=5 per orthomosaic) and the training samples manager based in the orthomosaic raster Geo TIFF image (100 per plot n= 2400) to later process for supervised classification using ArcGIS 10.8.2. Once the orthomosaics were obtained, and subdivided into plots, each plot of the classified raster image was vectorized to create polygons. The data were used to calculate the total area and the percentage of each landcover (Figure 5).



2179

2180 Figure 4 Geo Tiff orthomosaic raster image obtained form WebODM after fly path. a) Orthomosaic

2181 with equidistant plots at each cardinal point. Center area zoom-in of: b) Control, c) idle well, and

2182 d) silent experimental treatment.

2183

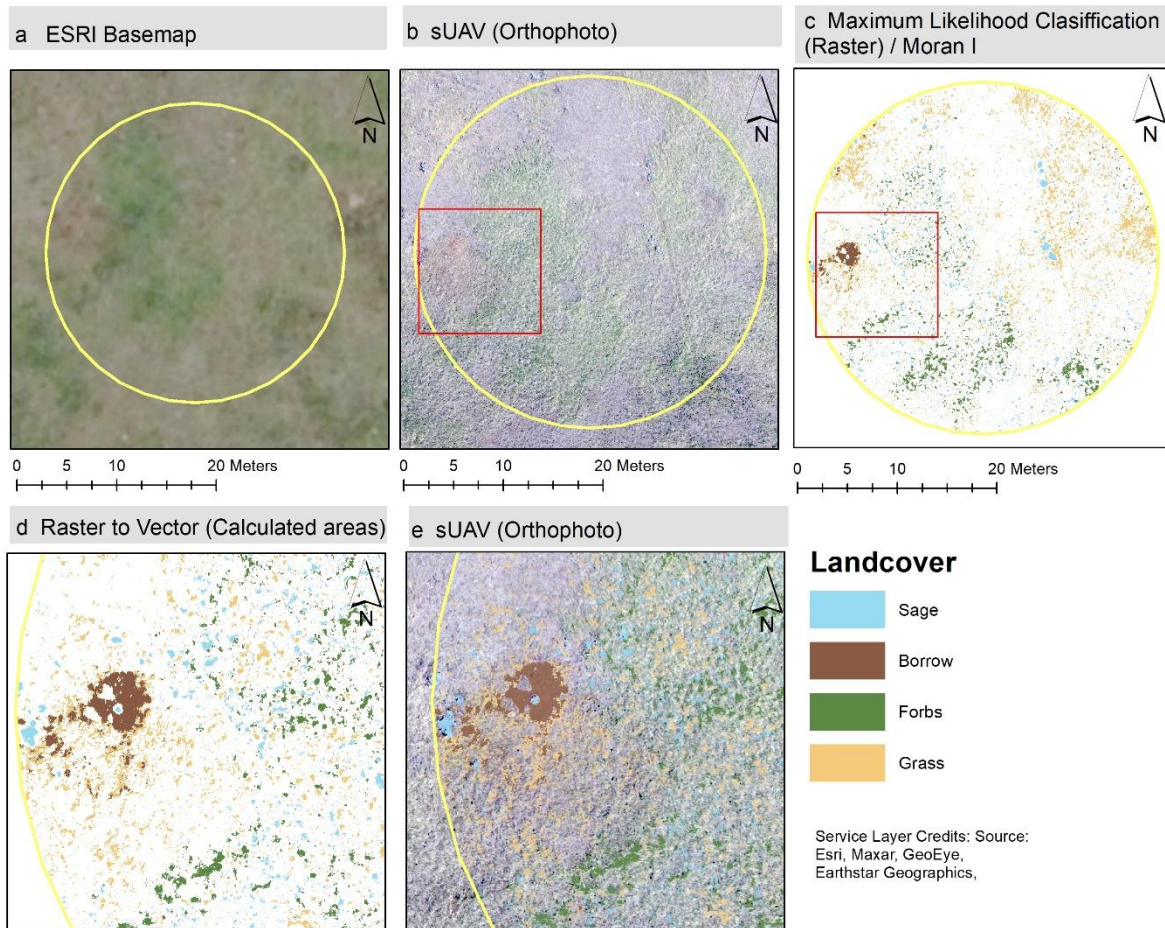


Figure 5 Close up view from a plot section. a) View from ESRI basemap similar to satellite imagineering. Unable to distinguish landforms for any classification based on RGB images. b) High-quality Geo Tiff orthomosaic basemap with distinguishable landcover used for further analyses. c) Raster (pixel) layer after Maximum Likelihood Classification (MLC) used for Moran I showing the four landcovers classification (Sages, Burrows, Forbs, and Grasses). d) Zoom-in of vectorized layer used to calculate landform areas and percentages, based on MLC Raster. e) Zoom-in of High-quality Geo Tiff orthomosaic and vectorized layer.

2194 3.3.3.1 Spatial Composition

2195 To measure relative density of ground squirrels, I determined the total burrows area at each
2196 plot by summing the areas of all vectorized polygons that belonged to the landform burrows for
2197 each site and compared it between treatments. I performed Kruskal-Wallis tests to assess the
2198 differences in the total area of burrows across treatments and across distances from the center
2199 point of each treatment. For pairwise comparisons, I used Dunn's test, adjusting for
2200 comparisons among treatments using Holm's method and applying Bonferroni correction for
2201 multiple comparisons among distances to control for Type I error (Barnett *et al.*, 2022).
2202 Statistical analyses were carried out using R software (R Core Team, 2023).

2203

2204 I calculated the percentage of each landform relative to the total area of all landforms within
2205 that plot. Statistical comparisons among plots for each of these groupings were performed
2206 using analysis of variance (ANOVA) with $\alpha = 0.05$, followed by a pairwise Tukey test adjusted
2207 with honest significant difference (HSD) ($\alpha = 0.05$) to assess potential differences in percentages
2208 of each landcover type between treatments and distances across the plots. Prior to executing
2209 the ANOVA, the data were analyzed to ensure the key assumptions of the test were met.
2210 Normality of percentages distributions within each group was evaluated using both Shapiro-
2211 Wilk tests and Q-Q plots. If non-normality was observed, data was log transformed and
2212 normality was re-assessed (Osborne, 2002). Homogeneity of variance across groups was
2213 examined using Levene's test. Statistical analyses were carried out using R software (R Core
2214 Team, 2023).

2215 I analyzed the landcover area patterns by fitting linear regression models for each landcover
2216 type, tested the effects of treatment, distance, and their interaction within each model, and
2217 summarized the model fit using adjusted R^2 . In each model the log-transformed cover area was
2218 defined as the response variable. Treatment was included as a categorical predictor and
2219 distance from the central point (meters), was modeled as a continuous predictor. An interaction
2220 between treatment and distance was included to test if the relationship between cover and
2221 distance varied among the treatments. For all the model-based regression tests I used an alpha
2222 level of 0.07 to assess evidence of effects with a safer approach sometimes used in ecology and
2223 conservation when the overall cost of missing a true impact effect could be greater than the
2224 cost of identifying a later effect that is weaker or absent (Taylor and Gerrodette 1993).

2225

2226 To assess differences in vegetation structure across treatments and distances, and to quantify
2227 the relative distribution of land among land cover types, I analyzed the percentage of each land
2228 cover type at each plot. Rather than using diversity indices, I evaluated how Richardson's
2229 Ground Squirrel activity, measured as burrow density, was associated with variation in percent
2230 cover of key land cover types. This approach allowed direct assessment of how burrowing
2231 activity relates to vegetation structure, independent of treatment. Individual linear models were
2232 used to test the influence of treatment, distance, and their interaction on land cover
2233 proportions, and to assess the relationship between burrow density and percent cover of each
2234 land cover type.

2235

2236 3.3.3.2 Spatial Configuration

2237 To evaluate the spatial configuration of the landscape at each site I used Moran's I spatial
2238 autocorrelation statistic, using the queen contiguity method based on the classified
2239 orthomosaic raster image at each plot using ArcGIS 10.8.2. (Aswi *et al.*, 2021). Moran's I values
2240 can vary from -1 to 1. Values above zero indicate spatial clustering of similar features, values
2241 below zero indicate spatial dispersion of dissimilar features, and values around zero suggest a
2242 random spatial pattern. The statistical significance of the Moran's I values was determined using
2243 the Z-score method (Mitchel 1999; Anganni *et al* 2023). Similar to previous analyses, analysing
2244 each plot facilitated comparisons across distances (D1-D6) for the four cardinal directions at
2245 each of the three sites, under each treatment. The Z-scores were later used as standardized
2246 comparative for generalized linear model (GLM) examining the effect of treatment and distance
2247 on the landscape configuration.

2248

2249 To assess whether the spatial configuration patterns are influenced by burrowing activity, and
2250 consequently by Richardson's ground squirrels, a correlation heat map was created to visualize
2251 the relationships between burrow density and other landcover types. While the heat map
2252 highlight associations, it is important to note that correlation does not imply causation, and the
2253 biological interpretation of the results was used to determine the effects.

2254

2255 To evaluate the relationship between Richardson's Ground Squirrel burrow abundance and
2256 vegetation structure, I modelled burrow abundance as a function of sagebrush cover (%) using a

2257 negative binomial regression. This analysis was conducted across all sampling units irrespective
2258 of treatment because the objective was to test the overall association between burrows and
2259 sagebrush cover. Burrow abundance was used as the response variable and sagebrush
2260 percentage as the predictor, and model fit was selected to account for overdispersion in the
2261 count data.

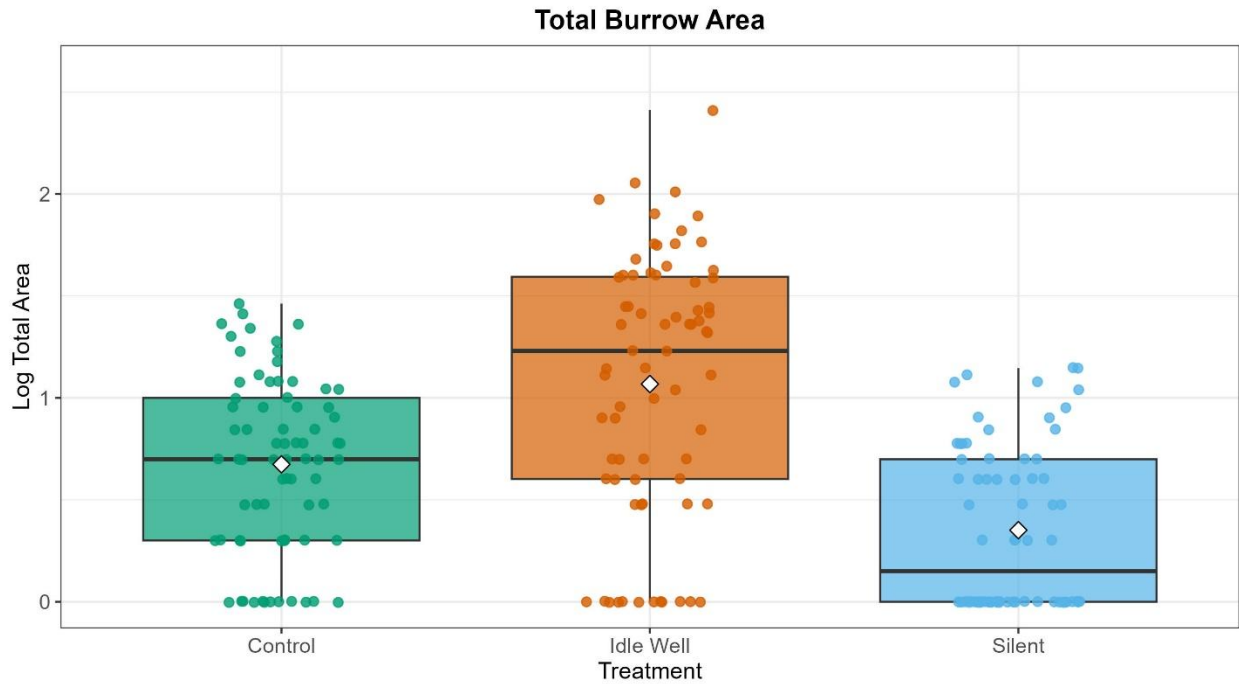
2262

2263 **3.4 Results**

2264 3.4.1 Total Burrow Area

2265 The total area of burrows was different between treatments [$F(2, 211) = 23.93, p < 0.001$].

2266 There was a greater total area of burrows in the idle wells than control ($Z = -4.404, p < 0.0001$)
2267 and silent ($Z = -6.013, p < 0.0001$) sites but no differences between silent and control ($Z = 1.639,$
2268 $p = 0.120$) (Figure 6). No differences were observed between distances at each plot either [$F(5,$
2269 $208) = 0.97, p < 0.437$], (Figure 7).



2270

2271 Figure 6 Differences in the total number of burrows between treatments. There was no significant
 2272 difference between the Control (green) and silent (blue) treatments. However, both Control and
 2273 silent treatments were significantly different from the idle wells (red).

2274

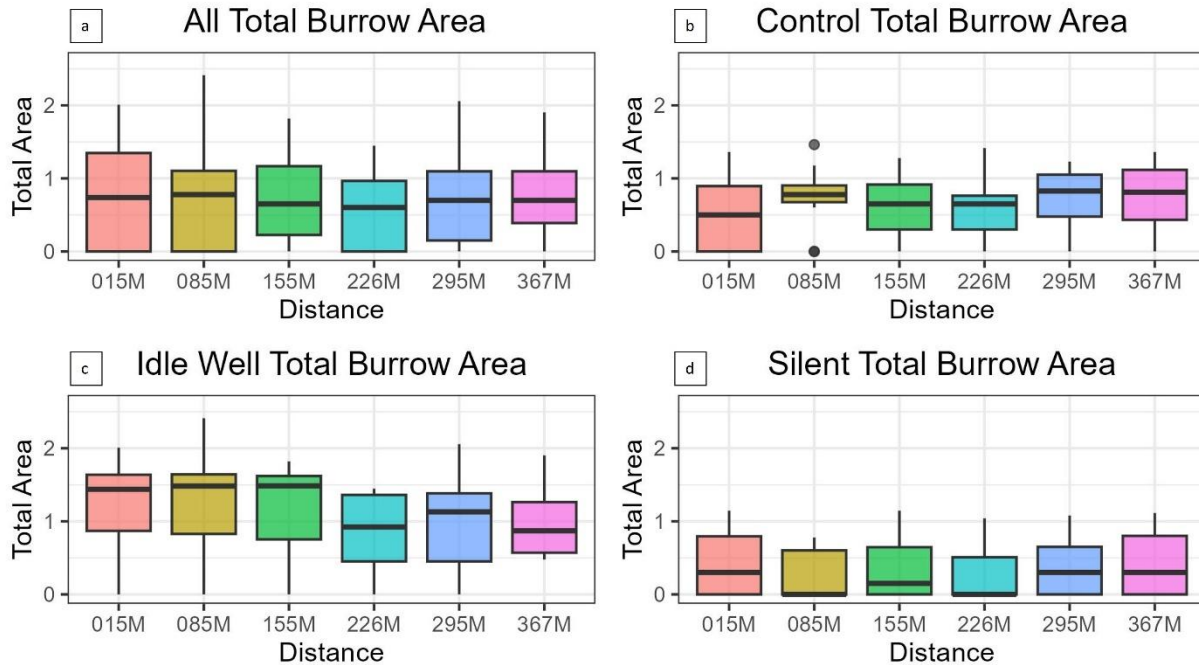


Figure 7. Total number of burrows from the center point. a) total burrow area by distance at all treatments. b) total burrow area by distance at Control site c) total burrow area by distance at idle wells, and d) total burrow area by distance at silent treatment. No differences between distances found.

3.4.2 Spatial Composition

The percentage of each landcover was different between treatments [$F(2, 211) = 23.93$, $p < 0.001$]. After adjusting for multiple comparisons using Holm's method, there was a lower percentage of burrows in the control site compared with the idle well site ($Z = -4.404$, $p < 0.00001$) but no differences between control and silent sites (Figure 8a). The percentage of sagebrush ($Z = -5.456$, $p < 0.00001$) and grasses ($Z = 7.320$, $p < 0.00001$) was also different

between control sites and idle well, with less grasses and more sagebrush at idle wells (Figure 8b and 8d, respectively) but no differences found in the percentage of forbs among treatments (Figure 8c)

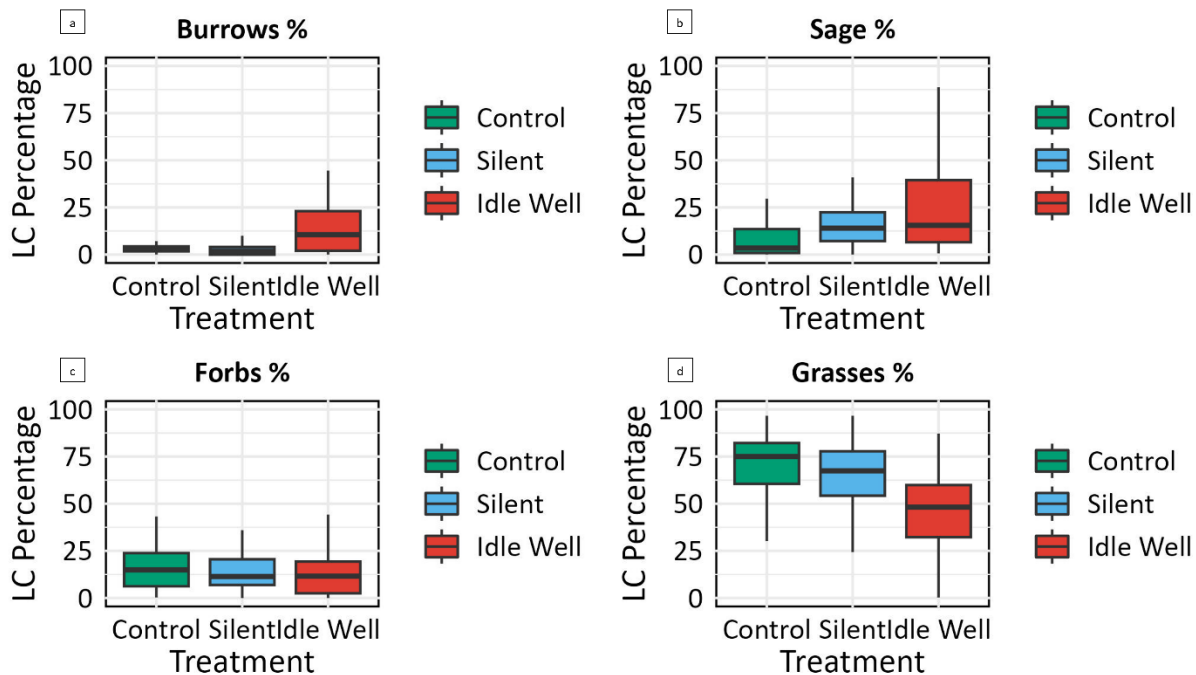


Figure 8. Percentage of Landcover forms by treatment. a) percentage of burrows by treatment. b) percentage of sagebrush by treatment c) percentage of forbs by treatment, and d) percentage of grasses by treatment. Control treatment (red), real idle Well treatment (blue), and silent, experimental treatment (green).

Distance effects were not consistent across landcover types and were generally smaller than the treatment contrasts, but two cover types showed evidence that treatment modified the distance

pattern when using an alpha level of 0.07. Model fit varied among landcover classes, with adjusted R^2 ranging from 0.059 for forbs to 0.251 for burrows (sage 0.223; grasses 0.156).

For burrows, the cover area was different among treatments. Relative to the control, burrow cover percentage was higher at real idle well treatments ($\beta = 0.396$, $p \leq 0.001$) and lower at silent sites ($\beta = -0.322$, $p \leq 0.001$). Within the control treatment, there was no evidence of a linear distance trend ($p = 0.450$), and the overall test for the treatment- distance relationships was not supported ($p = 0.149$). At the 0.07 threshold, there was evidence that the real treatment had a slightly more negative distance slope than the control ($\beta = -0.00129$, $p = 0.067$), suggesting that any distance-related change in burrow cover, if present, was most apparent under the real treatment and weaker than the main treatment differences (Figure 9a).

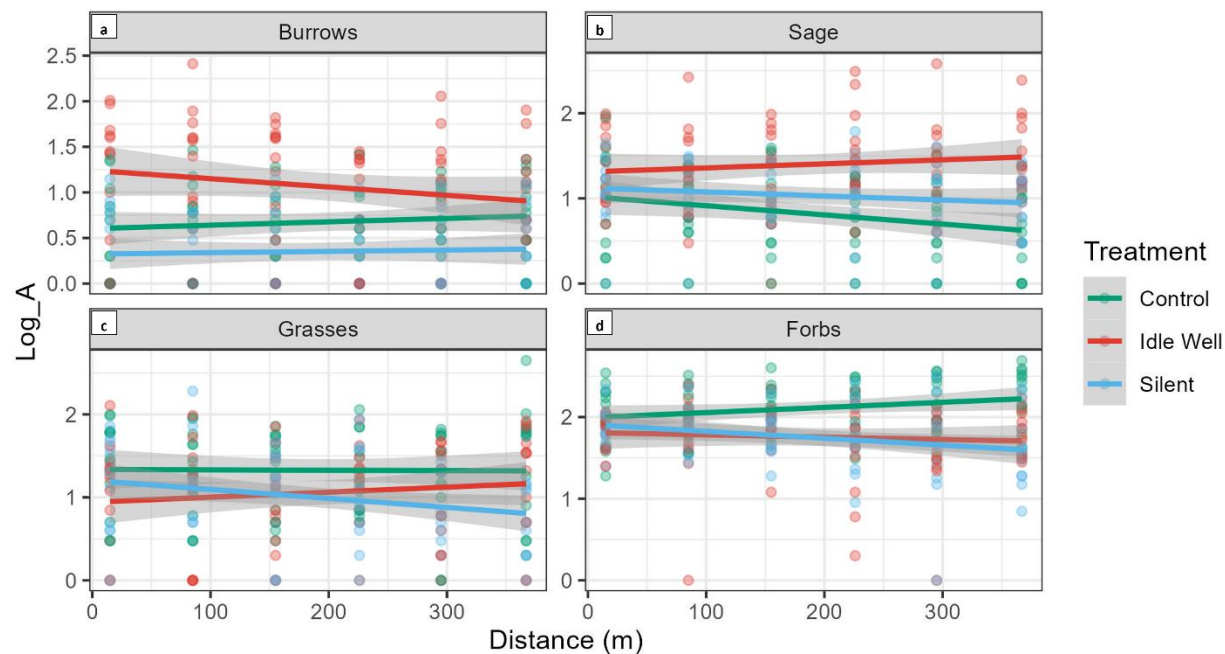


Figure 9. Percentage of a) burrows, b) sagebrush, c) grasses, and d) forbs at each distance by treatment. Percentage of burrows at control site (blue), percentage of burrows at real idle well (orange), and percentage of burrows at silent experimental treatment (green).

Sage treatment effects were strong and with evidence that cover changed with distance from the center point. Sage cover was higher at real idle well than at the control ($\beta = 0.583$, $p \leq 0.001$) and higher at experimental silent sites than at the control ($\beta = 0.216$, $p = 0.006$). Sage cover also declined with distance in the control treatment ($\beta = -0.00108$ per m, $p = 0.019$). The model found evidence that the distance-cover relationship was different among treatments (interaction test $p = 0.054$), probably driven by a difference between real and control distance slopes ($\beta = 0.00155$, $p = 0.017$). This indicates that the idle oil well treatment altered how sage cover changed with distance relative to the control (Figure 9b).

Forbes cover was lower at the idle well and the silent experimental treatment compared with the control (real: $\beta = -0.272$, $p = 0.004$; silent: $\beta = -0.328$, $p = 0.0007$). Nonetheless, there was no evidence of a linear effect on the distance ($p = 0.930$) or any treatment-specific distance patterns (interaction test $p = 0.104$). Treatment effects on forbs were consistent across the distance (Figure 9c).

2332

2333 The percentage cover for the grasses was lower at real idle oil well and silent experimental
2334 treatments than at the control (real: $\beta = -0.354$, $p \leq 0.001$; silent: $\beta = -0.361$, $p \leq 0.001$). The
2335 control treatment showed no clear linear distance effect ($p = 0.115$). However, the distance-cover
2336 relationship was different among treatments (interaction test $p = 0.0349$). This interaction was
2337 probably driven by the silent treatment, which showed a more negative distance slope than the
2338 control ($\beta = -0.00147$, $p = 0.0105$), indicating that grasses percentage cover changed with the
2339 distance under silent conditions (Figure 9d).

2340

2341 3.4.3 Spatial Configuration

2342

2343 The analysis of Moran's I Z scores (Figure 11a) for the Control, idle well, and silent treatments
2344 revealed distinct spatial autocorrelation patterns across various distances. For the Control sites
2345 (Figure 11b), the Z scores indicate moderate positive spatial autocorrelation at shorter
2346 distances, suggesting clustering. As the distance increased, the Z scores tend to decrease,
2347 reflecting weaker spatial clustering or more random spatial patterns.

2348

2349 Clustering increased with distance to idle wells (Figure 11c). This pattern of mixed positive and
2350 negative Z scores across distances suggests that the Idle well treatment creates a variable
2351 spatial structure with both clustering and dispersion influenced by specific site conditions. The

silent treatment (Figure 11d) had a diverse range of spatial autocorrelation patterns. Nonetheless, most of those ranges are closer to a random spatial pattern.

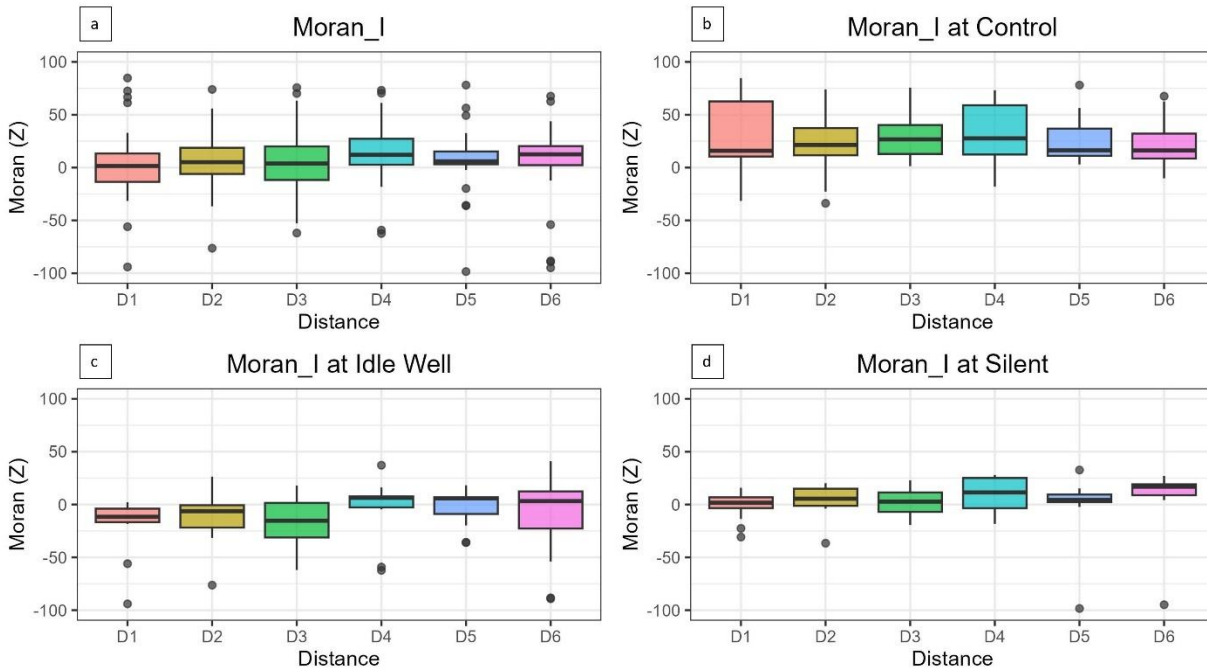


Figure 11. Z-scores of Moran I (a) All treatments (b) Control treatment, (c) idle well treatment (d) silent treatment. Distance in the X axis from closer (D1) to farther (D6) and Moran I Z-score in Y axis. Distances are differentiated by colors.

Table 1.0 Example of Moran Index results including Z-scores from each plot section. (three sites, three treatments, four cardinal points, six distances, N=216).

SITE	Northing	Treatment	Dist	Moran I	Variance	Z-score	P value
AN	N	Control	D1	1.0285	0.000147	84.7844	1E-07
AN	N	Control	D2	0.87949	0.000141	74.0017	1E-07
AN	N	Control	D3	0.87052	0.000015	70.1657	1E-07
AN	N	Control	D4	0.67243	0.000134	58.1977	1E-07
AN	N	Control	D5	0.75002	0.000092	78.0612	1E-07

AN	N	Control	D6	0.60334	0.000093	62.6506	1E-07
AN	S	Control	D1	0.66222	0.000083	72.4938	1E-07

2361

2362 The results of the generalized linear model (GLM) on the Moran's I Z scores revealed significant
2363 effects of treatment type on spatial autocorrelation. The model's intercept (25.9, $p < 0.001$)
2364 represents the baseline level of spatial autocorrelation for the control treatment at the
2365 reference distance (D1). Compared to this baseline, the idle well treatment had decreased
2366 spatial autocorrelation, with an estimate of -44.939 ($p < 0.001$), suggesting a strong dispersion
2367 effect and had reduced clustering. Similarly, the silent experimental treatment also reduced
2368 spatial autocorrelation, with an estimate of -24.167 ($p < 0.001$), these results suggest that both
2369 the idle well and the silent experimental treatment led to more dispersed spatial patterns
2370 compared with the control, with idle wells exhibiting a stronger dispersion effect than silent
2371 experimental treatment.

2372

2373 Distance alone does not significantly affect the Moran's I Z scores, as all distance coefficients (D2
2374 to D6) have p-values greater than 0.05. The lack of significant distance effects suggests that
2375 spatial autocorrelation patterns are more strongly influenced by the type of treatment rather
2376 than the distance from the central point. Overall, these findings highlight that both the idle well
2377 and silent experimental treatments significantly alter spatial patterns, reducing spatial
2378 autocorrelation and promoting dispersal, whereas the distance from the central point does not
2379 independently affect spatial autocorrelation (Figure 12).

2380

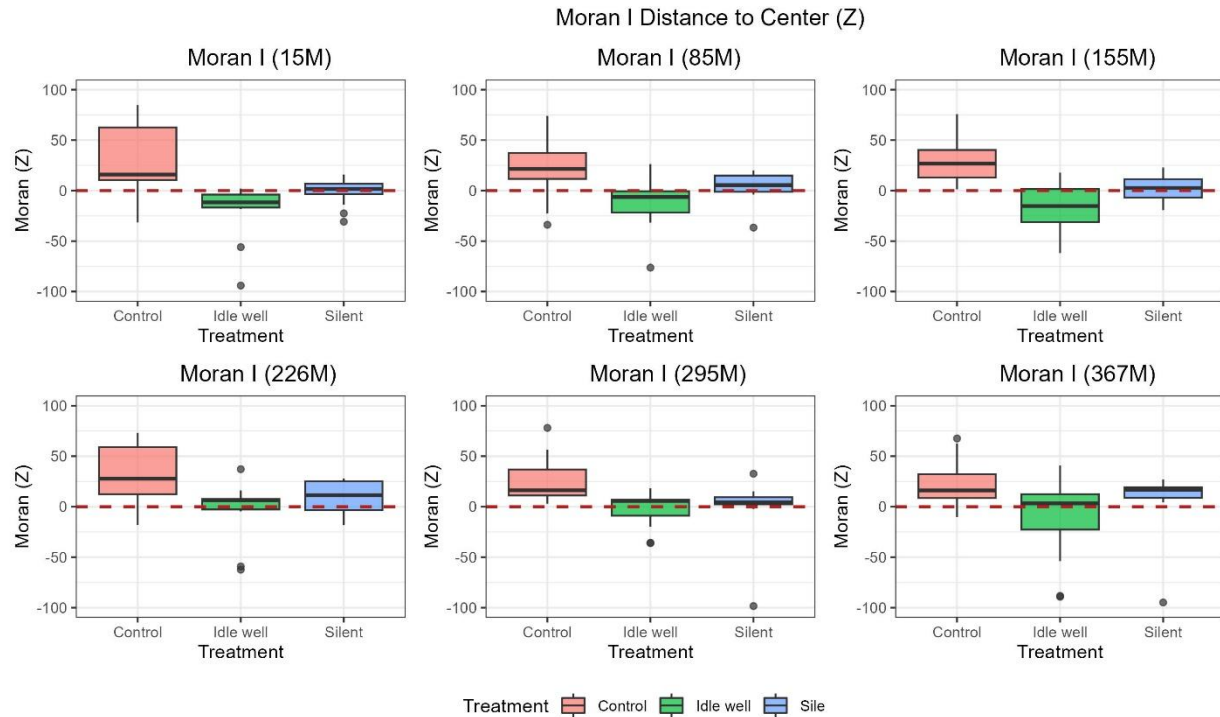
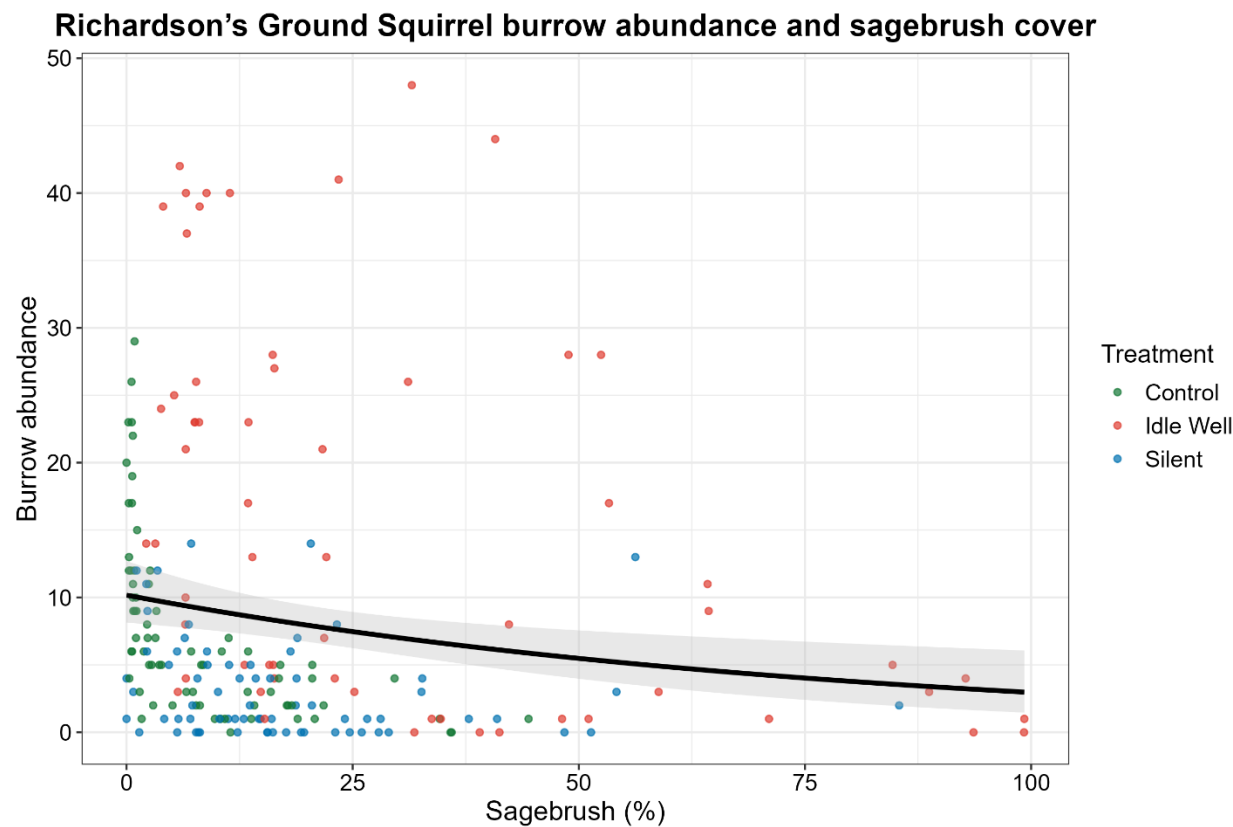


Figure 12. Z-scores of Moran I along distances. Treatments are differentiated by colors. The Z-score quantifies the degree to which the observed spatial pattern deviates from what is expected under a random spatial distribution. Red dashed line at 0 illustrates the tendency for clustered (positive Z-score), dispersed (negative Z-score), or random (Z-score near zero) landscape configuration.

Burrow abundance declined significantly with increasing sagebrush cover (Figure 13). Negative binomial regression showed a negative effect of sagebrush percentage on burrow abundance ($\beta = -0.0219$, $SE = 0.0048$, $z = -4.53$, $p < 0.001$), indicating that areas with greater sagebrush cover supported fewer Richardson's Ground Squirrel burrows.

2393



2394

2395 Figure 13. Relationship between Richardson’s Ground Squirrel burrow abundance and
2396 sagebrush cover (%). Points represent individual sampling units; Green control, red for idle well,
2397 and blue for silent. The line shows the fitted negative binomial model with 95% confidence
2398 interval.

2399

2400 **3.5 Discussion and Conclusions.**

2401

2402 Idle wells increased the total area of Richardson’s ground squirrel burrows and modify the
2403 spatial composition and configuration of mixed-grass prairie ecosystems. Supporting the first

2404 hypothesis the total burrow area was higher at the idle wells than at the control and silent sites.
2405 Silent experimental sites had shorter duration of disturbance and smaller infrastructure,
2406 resulting in a moderate burrow area. Idle wells often consist of inactive and silent screw pumps,
2407 tank batteries, and wider fenced perimeters. These sites represent some of the largest above-
2408 ground structures on the prairie landscape and have often remained inactive for over three
2409 years without reclamation (Galay and Winter 2023; AER 2018). These structural features can
2410 disturb soils, reduce vegetation recovery, and alter grazing dynamics (Muehlenbachs, 2017;
2411 Fisher *et al.*, 2021). My results indicate that infrastructure size and the length of site disturbance
2412 can shape habitat suitability and contribute to long-term ecological changes.

2413

2414 Idle wells reduce grass cover, disturb soil, and alter grazing pressure due to fencing. Such
2415 persistent site-level changes likely enhance the availability of bare ground and patchy vegetation
2416 that ground squirrels prefer (Bylo *et al.*, 2014). Although their numbers declined historically due
2417 to widespread poisoning campaigns (Proulx, 2010), current populations have increased in
2418 response to human-altered landscapes such as agriculture and energy development (Fisher *et*
2419 *al.*, 2021). Anthropogenic changes, such as agricultural fields and lawns, have also been shown
2420 to create conditions that facilitate Richardson's ground squirrel colonization (Laundré and Appel,
2421 1986; Calder, 2003). The presence of well-established infrastructure therefore appears to create
2422 favourable conditions for burrow construction, reinforcing the importance of infrastructure
2423 permanence in driving the spatial distribution of ground squirrel burrows.

2424

Richardson's Ground Squirrels can act as localized ecosystem engineers at idle well sites by creating discrete disturbance patches that alter soil structure, vegetation competition, and the spatial distribution of landcover types. Burrowing mammals can reduce compaction, modify infiltration, redistribute nutrients, and create microsites that differ from surrounding grassland, and these effects often generate patch mosaics that increase local heterogeneity rather than uniform change across space (Davidson and Lightfoot, 2008; Eldridge *et al.*, 2010; Louw *et al.*, 2019). Because Richardson's Ground Squirrels concentrate activity around burrow systems and maintain relatively discrete core areas, their effects are expected to be strongest near centres of repeated use, which is consistent with the distance patterns observed here (Michener, 1979). As ground squirrel activity is typically concentrated within 20 metres of burrows but can extend up to 150 metres (Michener and Michener, 1973), the influence of infrastructure likely extends beyond the immediate footprint, affecting habitat use at broader spatial scales. These effects suggest that long-term infrastructure reshapes both fine-scale habitat features and broader patterns of burrow distribution. Burrows were driven mainly by treatment, with some evidence of a proximity response near real idle wells. The clearest treatment contrast occurred for burrows, where real idle well sites had higher burrow cover than controls, while experimental silent sites showed lower burrow cover than controls, indicating that the burrow response was not intermediate under the experimental silent treatment. The strong burrow contrast between real idle well and experimental silent sites is consistent with differences in the magnitude or persistence of ground squirrel activity between long-standing, larger infrastructure and smaller, recently constructed experimental structures.

2447 Burrow abundance also declined with increasing sagebrush cover, suggesting that Richardson's
2448 Ground Squirrels were more abundant in sites with lower shrub cover and more open
2449 vegetation structure. This pattern supports the prediction that variation in burrow density
2450 would be associated with vegetation structure and contribute to differences in local landscape
2451 heterogeneity. Ground squirrels are known to prefer open habitats where visibility and mobility
2452 are greater, which may explain the lower burrow abundance in areas with higher sagebrush
2453 cover (Laundré and Appel, 1986; Fisher *et al.*, 2021). At the same time, this relationship may
2454 reflect ecosystem engineering feedbacks in which burrowing, soil disturbance, and vegetation
2455 clipping by squirrels help maintain open vegetation conditions, linking their activity to the
2456 compositional and configurational changes measured around the idle wells.

2457

2458 My results showed that distance effects were landcover type specific, supporting the second
2459 prediction that real idle wells can generate distinct compositional patterns compared with the
2460 experimental silent treatment and the control. In broad terms, real idle well sites were
2461 characterized by higher sagebrush cover and lower grass cover than controls, consistent with a
2462 localized shift in composition around long-standing infrastructure. Richardson's ground squirrels
2463 provide a possible pathway because burrowing disturbs soil, reduces grass competition, and can
2464 create conditions that favour shrub establishment (Platt *et al.* 2016). Distance can be
2465 interpreted as a proximity gradient around the well footprint, and the results indicate that some
2466 cover types responded more strongly to proximity than others.

2467

2468 Sagebrush differed less between real idle well and experimental silent sites because both
2469 treatments were higher relative to the control, suggesting that shrub responses can occur under
2470 both shorter and longer exposure periods and across different infrastructure size. Grasses were
2471 reduced under both real idle well and experimental silent treatments relative to controls, and
2472 proximity patterns for grasses were most apparent under the experimental silent treatment,
2473 reinforcing that proximity effects can be cover-type specific and not always strongest at real idle
2474 wells. In contrast, forbs showed a limited response, with little evidence of consistent change
2475 across treatments or distance, which aligns with observations that grasses and shrubs can be
2476 more responsive than forbs to disturbance caused by burrowing rodents (Davidson and
2477 Lightfoot 2008; Brady and Slade 2004).

2478

2479 Together, these patterns appear to fit a localized disturbance footprint where some components
2480 respond to proximity and others respond primarily to the presence of infrastructure (Westaway
2481 *et al.* 2024). A possible mechanism linking treatments to composition is the effect of ecosystem
2482 engineering by the Richardson's ground squirrels by altering soil structure and chemistry,
2483 creating patchy and localized microsites that could shift plant competition and vegetation
2484 composition, increasing patch-level heterogeneity and structural diversity across the landscape
2485 (Louw *et al.* 2019; Platt *et al.* 2016). Ground squirrels can also impose selective herbivory, which
2486 can further contribute to patchy vegetation responses rather than a smooth distance-decay
2487 pattern (Hansen and Reed 1969; Hansen and Johnson 1976; Bintz 1988).

2488

2489 These engineering effects may extend beyond vegetation. Burrows created by ecosystem
2490 engineers can function as semi-permanent refugia with distinct microclimatic conditions and
2491 can facilitate the occurrence of other organisms, meaning that increases in burrow density may
2492 restructure habitat availability for multiple taxa across the landscape (Pike and Mitchell, 2013;
2493 Machicote *et al.*, 2004). Idle wells may not only disturb the prairie vegetation directly but may
2494 also intensify indirect engineering effects by promoting Richardson's Ground Squirrel activity
2495 and the persistence of engineered patches. As a result, increases in local vegetation
2496 heterogeneity should not automatically be interpreted as evidence of healthy or intact prairie
2497 function. In disturbed landscapes, greater patch dispersion and reduced continuity of grass
2498 cover may benefit some disturbance-tolerant species while imposing costs on prairie specialists
2499 that rely on large areas of continuous grassland habitat (Davidson and Lightfoot, 2008; Louw *et*
2500 *al.*, 2019).

2501

2502 Burrow abundance declined significantly with increasing sagebrush cover, indicating that
2503 Richardson's Ground Squirrels are less common in areas dominated by shrubs. In grassland
2504 systems, higher sagebrush cover can reduce visibility, limit movement, and alter forage
2505 availability, making these areas less suitable for burrow establishment compared to more open
2506 habitats. As a result, ground squirrels concentrate in areas with lower shrub cover, where
2507 conditions favour digging, predator detection, and access to herbaceous forage (Collins *et al.*,
2508 1995; Fuhlendorf and Engle, 2001). Control and silent treatments showed lower or intermediate
2509 burrow abundance relative to sagebrush cover, whereas idle well sites, which often have
2510 reduced shrub cover and more open ground, supported higher burrow densities. Together,

2511 these results indicate that ground squirrels contribute to shaping vegetation structure in open
2512 patches, and that infrastructure effects may indirectly influence trophic interactions by
2513 modifying where these ecosystem engineers are most active.

2514

2515 Landscape configuration also changed in response to idle wells, supporting the fourth
2516 prediction. Changes in spatial configuration can influence ecological function because the
2517 arrangement of habitat can affect species mobility, foraging, and habitat connectivity. When
2518 vegetation is broken into smaller and more scattered patches for the ground squirrels, the
2519 landscape can become less connected and can work differently, even if the total amount of
2520 habitat is similar (Turner 1989; Taylor *et al.* 1993; Fahrig 2003, 2017).

2521

2522 Moran's I analysis showed strong landcover dispersion near the centres of idle wells and more
2523 clustering at greater distances. This pattern suggests that infrastructure near the idle well centre
2524 disrupts vegetation continuity, creating a more fragmented arrangement with dispersed
2525 landcover types. As distance from the well increases and the influence of infrastructure
2526 decreases, vegetation becomes more spatially aggregated, reflecting a return to the natural
2527 clustering typical of undisturbed prairie systems (Collins 2000). Control sites displayed clustering
2528 near the centre and more random patterns at greater distances, indicating relatively
2529 undisturbed vegetation, while silent sites showed weak spatial autocorrelation with Moran's I
2530 values near zero, suggesting limited change in spatial configuration. Together, these findings
2531 show that idle well infrastructure affects not only what landcover types are present but also

2532 how they are arranged across space, with potential consequences for connectivity and habitat
2533 use.

2534

2535 All four predictions were supported by my results. Idle wells increased burrow area, altered
2536 vegetation composition, raised landscape diversity near the centre, and changed the spatial
2537 configuration. Idle wells influence both vegetation composition and spatial configuration in
2538 mixed-grass prairie ecosystems. Increased vegetation diversity near idle wells suggests small-
2539 scale compositional changes driven by Richardson's ground squirrel burrowing activities.
2540 Burrowing disturbs soil, reduces grass cover, and promotes the expansion of shrubs (Bylo *et al.*,
2541 2014; Platt *et al.*, 2016; Connell *et al.*, 2019). These local disturbances can create microhabitats
2542 and increase patch diversity, potentially benefiting species that rely on a mosaic of vegetation
2543 types (Fuhlendorf and Engle, 2001; Fahrig 2020). At fine spatial scales, such changes may
2544 enhance structural heterogeneity for small rodents and support higher plant richness,
2545 contributing to some ecological processes (e.g. primary productivity, refuge availability,
2546 predator connectivity, and risk perception) (Davidson and Lightfoot, 2008; Fahrig 2020).

2547

2548 Changes in composition are also accompanied by altered configuration. Idle well sites exhibited
2549 greater spatial dispersion of vegetation types, with more scattered and less clustered landcover
2550 than control sites. Evidence from oil extraction landscapes shows that configuration can be a
2551 strong driver of animal distributions even when overall habitat loss is relatively low, so patch
2552 arrangement and edge structure can matter as much as total area disturbed. This supports

2553 treating the spatial pattern created around idle wells as a management target, not only the
2554 footprint size (Smith *et al.*, 2025). In contrast, undisturbed grasslands typically show spatial
2555 aggregation, which supports functional connectivity and more consistent resource availability
2556 (Collins 2000; Kowe *et al.*, 2019). Increased dispersion near idle wells may reduce patch
2557 continuity, limiting the movement of species that require contiguous habitat or suitable
2558 vegetation structure. While the increase in patch diversity may provide benefits at a local scale,
2559 fragmented configuration can impose costs to some species at broader spatial scales, increasing
2560 energetic demands and disrupting plant-animal interactions (Fahrig 2017).

2561

2562 Overall, my findings suggest that although composition changes near idle wells may temporarily
2563 improve some diversity metrics, the broader consequences for ecosystem integrity are likely
2564 negative. The loss of spatial connectivity and reduced grass dominance indicates declining
2565 habitat quality for many prairie specialists (Fahrig, 2017). While Richardson's ground squirrels
2566 appear to benefit from disturbed sites, other species such as grassland birds and pollinators
2567 may be negatively affected by the fragmentation of habitat and reduced structural continuity.
2568 Since idle well infrastructure persists for years without reclamation, these impacts represent
2569 lasting shifts in landcover and ecological processes.

2570

2571 To mitigate these effects, land management should address both composition and
2572 configuration. Reestablishing native grass cover and restoring spatial clustering of vegetation
2573 can enhance landscape cohesion, promote connectivity, and support a wider range of species.

2574 Restoration should consider not only biotic conditions such as species richness and vegetation
2575 structure, but also spatial patterning to align with species' movement and habitat requirements
2576 (Harlio *et al.*, 2019). Monitoring strategies must also evolve beyond traditional point-based
2577 metrics and incorporate spatial indicators such as clustering and spatial autocorrelation to
2578 better assess ecosystem responses (Aswi *et al.*, 2021). This is important because simple
2579 footprint or net-loss measures can miss strong ecological responses to configuration, and by
2580 adding metrics that reflect core area versus edge and patch disintegration, monitoring can be
2581 more sensitive to how infrastructure reshapes habitat (Smith *et al* 2025). Given the variable
2582 nature of infrastructure impacts, adaptive and spatially informed monitoring is necessary to
2583 reduce uncertainty and improve land management decisions (Haddad *et al.*, 2015;
2584 Stelzenmüller *et al.*, 2015). Reclamation planning might need to incorporate historical land use
2585 and present-day landcover structure to sustain ecosystem services and facilitate recovery in
2586 fragmented landscapes (Rae and Wong 2012).

2587

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2962

4 CHAPTER 4. How does oil development reshape predator-prey interactions in the mixed-grass prairies?

4.1 Introduction

Predator-prey interactions shape many communities, influencing prey distribution and survival (Thompson 1999, Abrams 2001). Predators alter prey behavior and habitat use by increasing both predation risk and perceived predation risk, establishing the basis of the landscape of fear framework (Laundré *et al.*, 2010). In addition to fear-mediated effects, predators regulate some communities through pathways that alter prey abundance. These mechanisms include mesopredator release, predator shield effects, and prey attraction to structures or disturbances, each of which has the potential of reshaping trophic interactions. These effects spread across trophic levels and can either regulate or disrupt population dynamics, and stabilize or destabilize ecosystems depending on the predator presence, the strength of prey responses, and environmental conditions (Schmitz 2009, Gallagher *et al.*, 2017). Impacts from energy development, and its associated noise, could affect these processes by modifying predator efficiency and thus, altering prey behavior (Francis *et al.*, 2009; Gaynor *et al.*, 2019). Thus, I tested whether oil wells and the noise associated to them, change the balance of trophic regulation by shifting the abundances of top predators, mesopredators, and prey in the directions predicted by Human Shield, Predator Facilitation, Mesopredator Release, or Risk-Disturbance, and whether any shifts were driven mainly by noise intensity and predictability or by the physical presence of infrastructure.

2986

2987 Food webs reflect interactions among prey and multiple predator guilds and trophic regulation
2988 can be expressed as consistent differences in abundance across sites. Top-down regulation
2989 occurs when predators reduce the number of organisms at lower trophic levels, so if systems
2990 are top-down regulated, higher predator abundance is expected to align with lower prey
2991 abundance (Fretwell 1987; Solomon 1949; Holling 1959). Bottom-up regulation occurs when
2992 prey availability can support higher numbers of consumers so predator and prey abundances
2993 increase together across sites (Fretwell 1987; Hury 1998, Nyström *et al.*, 2003).

2994

2995 Trophic relationships in mixed-grass prairies can reflect the habitat structure and disturbance
2996 history as vegetation communities' characteristics can determine where prey concentrates and
2997 how efficiently predators can search and hunt them (Wiens and Rotenberry 1979; Wiens and
2998 Rotenberry 1981). Natural impacts like fire, flooding, drought, grazing, and fossorial herbivores
2999 trends constantly reshape the landscape by resetting vegetation height, bare ground, litter, and
3000 burrow networks, having an effect between predator and prey dynamics across habitat patches
3001 and seasons (Noss, 2013; Meserve *et al.*, 2003; Terraube and Bretagnolle, 2018; Fronhofer *et al.*,
3002 2018). These processes can create positive predator-prey overlapping across sites because
3003 predators and prey respond to the same habitat conditions, even when predation occurs (Wiens
3004 and Rotenberry, 1979; Wiens and Rotenberry, 1981).

3005

3006 Energy development can modify this habitat through the effects of physical structures and
3007 sound impact. Conventional oil development infrastructure can alter the vegetation due to edge

3008 effects, perches, and foraging travel routes, which may change the space use for predators and
3009 prey, concentrating activity in specific patches (Houle 2010; Bernath-Plaisted and Koper 2016;
3010 Sanders and Chalfoun 2021). Anthropogenic noise may also disrupt detection and
3011 communication, affecting foraging decisions, with potential consequences for abundance
3012 patterns (Francis *et al.*, 2009; Gaynor *et al.*, 2019; Gaynor *et al.*, 2021). Because structure and
3013 sound can act together, my study evaluates whether treatments produce the abundance
3014 patterns predicted by alternative mechanisms of trophic regulation.

3015

3016 Human Shield and Predator Facilitation offer contrasting predictions about how top predators
3017 will respond to infrastructure and noise. Human Shield predicts that reduced top predator
3018 presence will occur near development, resulting in a relatively higher prey near anthropogenic
3019 infrastructure, while Predator Facilitation predicts greater top predator presence near
3020 development may result in prey suppression (Berger 2007; Kay 1998; Gaynor *et al.* 2025).
3021 However, either mechanisms might be disrupted in grasslands if large predators tolerate
3022 infrastructure or if mesopredators also increase near developed features, offsetting any refuge
3023 effect for prey (Geffroy *et al.*, 2015; Sadoul *et al.*, 2021; Granados *et al.* 2023).

3024

3025 Mesopredator release predicts that reduced top predator abundance allows mesopredators to
3026 increase and reduce prey (Crooks and Soulé 1999; Elmhagen and Rushton 2007; Prugh *et al.*
3027 2009). This mechanism can be viewed as a change in predator interactions rather than only as
3028 an increase in mesopredator abundance, because reduced top predator pressure can also alter
3029 mesopredator distribution, habitat use, and behavior (Prugh *et al.*, 2009). In North American

3030 grasslands, coyotes can function as mesopredators where wolves and grizzly bears remain, but
3031 can shift where larger carnivores have been reduced or extirpated (Gomper 2002; Chakarov and
3032 Krüger 2010, Miller 2012, Ripple *et al.*, 2013). Oil wells and noise could contribute to this
3033 pathway if they reduce the occurrence, hunting efficiency, or space use of top predators more
3034 than they reduce mesopredator activity, allowing mid-sized predators to intensify predation on
3035 rodents, songbirds, or other prey near treated sites. Under this hypothesis, treated sites would
3036 be expected to have lower abundance of top predators, higher abundance of mesopredators,
3037 and lower abundance of prey relative to control conditions. (Prugh *et al.* 2009; Rodgers and
3038 Koper 2017).

3039

3040 Risk disturbance predicts a broader response in which infrastructure and noise reduce use of
3041 treated areas by predators, mesopredators, and prey. This mechanism predicts lower local
3042 abundance and weaker trophic links because fewer animals of all guilds use the same sites
3043 (Francis *et al.*, 2009; Gaynor *et al.*, 2019; Gaynor *et al.*, 2021). If responses depend on noise
3044 produced by oil infrastructure, then predictability, intermittency, and intensity of noise may
3045 influence the strength of divergence among treatments.

3046

3047 In my study, I first evaluated a regulation-mode hypothesis (H0) that compares top-down versus
3048 bottom-up control of the grassland food web. If the web is primarily top-down regulated, then
3049 sites with higher abundance of top predators should have lower abundance of mesopredators
3050 and prey, so predator and prey abundances will be negatively associated across sites. In
3051 contrast, if the web is primarily bottom-up regulated, then sites with higher prey abundance

3052 should also have higher abundances of mesopredators and top predators, producing positive
3053 associations in abundance among all three consumer groups. I tested which pattern best
3054 described the system and whether oil wells and noise altered this balance.

3055

3056 I then tested four mechanisms that predict how wells and noise might modify regulation. Under
3057 the Human Shield hypothesis (H1), if oil development and its associated noise cause top
3058 predators to avoid wells, then top predator abundance should be lower at treatment sites than
3059 at controls. If top predators have a stronger top-down control, prey abundance should be higher
3060 at treatment sites, indicating weaker top-down regulation and relatively stronger bottom-up
3061 control near wells. In contrast, if the system is primarily bottom up regulated, lower top
3062 predator abundance may not produce detectable changes in mesopredator or prey abundance.

3063 Under the Predator Facilitation hypothesis (H2), if the web is mainly top-down regulated and oil
3064 development allows top predators to use infrastructure and/or noise as a refuge from higher-
3065 level threats, then top predator abundance should be higher and prey abundance lower at
3066 treatment sites than at controls, indicating stronger top-down regulation near wells. Under the
3067 disturbance-mediated Mesopredator Release hypothesis (H3), if top predators avoid
3068 infrastructure and noise but mesopredators use disturbed sites then, top predator abundance
3069 should be lower, mesopredator abundance higher, and prey abundance lower at treatment sites
3070 than at controls indicating that top-down regulation near wells is mainly driven by
3071 mesopredators rather than top predators. Finally, under the Risk-Disturbance hypothesis (H4), if
3072 all consumer groups perceive infrastructure and noise primarily as risky, then abundance of top
3073 predators, mesopredators, and prey should all be lower at treatment sites than at controls,

3074 indicating weakened local interactions regardless of whether the broader system is top-down or
3075 bottom-up regulated.

3076

3077 For each mechanism I also asked if there is any response, whether those responses were driven
3078 mainly by noise or by the physical presence of infrastructure. If the effects of oil infrastructure
3079 are caused by noise, then the abundance patterns predicted by H1 to H4 should be strongest at
3080 drilling-noise sites, intermediate at continuous and intermittent screw-pump noise sites, weaker
3081 or even absent at silent infrastructure and real but quiet idle wells, and weakest or absent at
3082 undisturbed controls. Under the infrastructure-driven subhypotheses (H1b, H2b, H3b, H4b), the
3083 predicted patterns should be similar across all sites with physical structures, regardless of noise
3084 treatment, and should differ most strongly between infrastructure sites and undisturbed control
3085 sites.

3086

3087 I constructed two alternative SEM structures to evaluate the regulation-mode hypothesis (H0)
3088 (Figure 4). The top-down structure tested whether variation in prey was best explained by
3089 predator-driven pathways, by modeling mesopredator guilds and prey guilds as functions of
3090 higher trophic levels and by estimating pathways that would indicate suppression cascading
3091 downward through the web. Under a strongly top-down regulated pattern, higher top predator
3092 abundance should be associated with lower mesopredator and prey abundance, either through
3093 direct negative predator to prey paths or through negative predator to mesopredator paths that
3094 translate into lower predation pressure on prey. In contrast, the bottom-up structure tested
3095 whether variation in predators was best explained by prey availability, by modeling

mesopredators and top predators as functions of prey guilds and intermediate trophic levels. Under a bottom-up regulated pattern, prey-rich sites should support higher mesopredator and top predator abundances, producing positive associations in abundance up the trophic hierarchy. Together, these paired model structures provided a formal test of whether the baseline system aligned more closely with top-down or bottom-up regulation.

3101

3102

3103 **4.2 Methods**

3104 4.2.1 Study Area

3105

My study was conducted on common property land primarily used for farming, cattle grazing, and energy development, located within the native mixed-grass prairie region near of southeastern Brooks, Alberta, Canada (49° 0' 0.004" to 50° 53' 56.475" N, 110° 0' 2.757" W to 112° 28' 44.473" W, at 760 m above sea level) (Figure 1). Research took place from mid-May to early August in 2019 and 2021, corresponding to the peak nesting season when the predator community is actively preying on grassland songbird nests (Bernath-Plaisted and Koper 2016). The landscape was dominated by native mixed-grass prairies and an expansive oil development industry composed of oil wells, natural gas compressor stations, and a dendritic network of infrastructure and access roads (Rosa and Koper 2018).

3115

The native vegetation in the study area included dominant grass species such as western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), and needle-and-thread grass

3118 (*Hesperostipa comata*), alongside sagebrush species (*Artemisia* spp.). Common forbs included
3119 white beardtongue (*Penstemon albidus*), buffalo bean (*Thermopsis rhombifolia*), and prickly
3120 pear (*Opuntia polyacantha*). Non-native plant species, such as crested wheatgrass (*Agropyron*
3121 *cristatum*), goat's beard (*Tragopogon dubius*), dandelion (*Taraxacum officinale*), and sweet
3122 clover (*Melilotus officinalis*) are also present.

3123

3124 Mammals commonly observed in the region included mule deer (*Odocoileus hemionus*), white-
3125 tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), and smaller mammals
3126 such as the North American badger (*Taxidea taxus*), coyote (*Canis latrans*), striped skunk
3127 (*Mephitis mephitis*), long-tailed weasel (*Mustela frenata*), swift fox (*Vulpes velox*), Nuttall's
3128 cottontail rabbit (*Sylvilagus nuttallii*), jackrabbits (*Lepus* spp.), Richardson's ground squirrel
3129 (*Urocitellus richardsonii*), Deer Mice (*Peromyscus maniculatus*), Northern Grasshopper Mice
3130 (*Onychomys* spp.), and Long-tailed Voles (*Microtus longicaudus*).

3131

3132 The mixed-grass prairie also supports a diverse community of avian predators, including
3133 northern harriers (*Circus hudsonius*), red-tailed hawks (*Buteo jamaicensis*), ferruginous hawks
3134 (*Buteo regalis*), Swainson's hawks (*Buteo swainsoni*), prairie falcons (*Falco mexicanus*), and
3135 Golden eagles (*Aquila chrysaetos*).

3136

3137

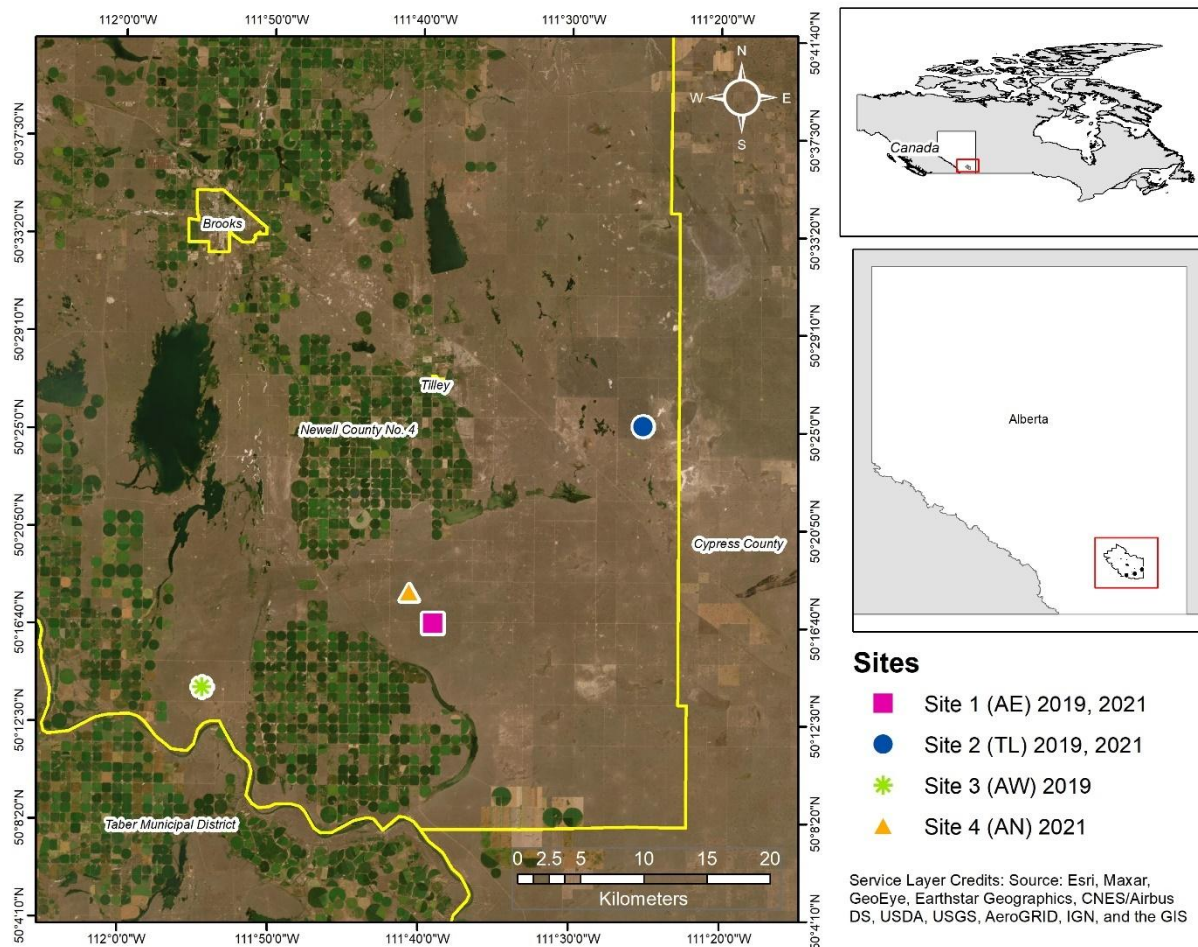


Figure 1 Study area locations in Brooks Alberta, Canada. Sites and sampling years shown by colored icons. Mixed-grass prairie shown surrounded by irrigation agricultural landscape

4.2.2 Study design and Data Collection

The study was conducted in independent 800 x 800 m plots, with each center point located at least 800 m away from the center point of any other plot to ensure spatial independence (Figure 2). Each plot was assigned to either control or experimental treatments designed to evaluate the effects of noise and infrastructure from oil development

The experimental treatments involved high-fidelity playback broadcasts of three distinct noise types: predictable chronic noise, intermittent recurrent noise, and unpredictable random noise (Figure 2). The predictable chronic noise treatment broadcasted a continuous operation of a screw pump, which is used in the extraction of deep oil reserves. This pump generates a steady, predictable noise as it forces oil from the ground into a pipe through positive displacement pressure (Devold 2013, Koper *et al.*, 2015). The playback of this sound was broadcast continuously, 24 hours a day, for approximately 90 days (n = 4 sites).

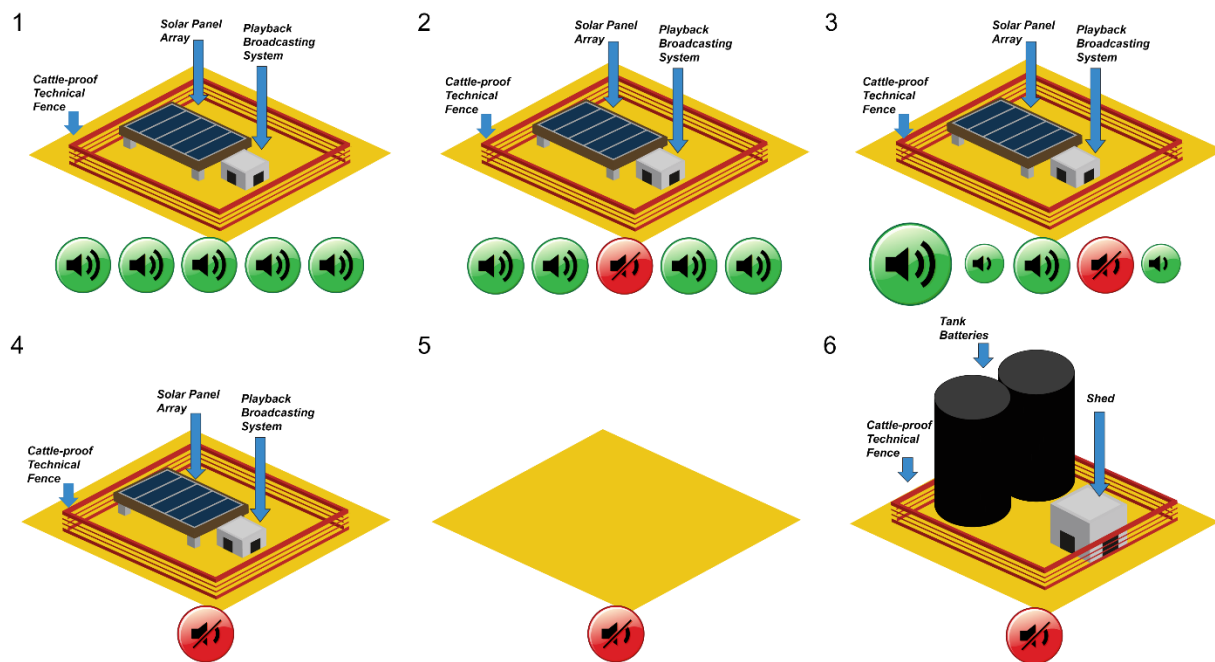


Figure 2. Experimental treatments and sound control treatments. Mixed-grass prairie represented by yellow ground, red circle denotes the lack of anthropic sound emission and

3160 green circles denotes the emission patterns of anthropogenic sound in low (small) or high
3161 (large) frequency. 1. predictable chronic noise (Screw pump), 2. intermittent recurrent noise
3162 (Interrupted Screw pump), 3. Unpredictable random noise (Drill) 4. Silent treatment (Silent), 5.
3163 No anthropic sounds and no oil infrastructure treatment (Control), and 6.- Silent, non-
3164 operational real idle well infrastructure with tank batteries (Real). (Created by JP Medina)
3165
3166
3167 The intermittent recurrent noise treatment used a recording of a screw pump with randomized
3168 on-off cycles. Noise was broadcast at random intervals ranging from 15 minutes to three hours,
3169 creating an approximately 50-50 pattern of sound and silence over a 24-hour period for 90 days
3170 (n = 3 sites). The unpredictable random noise treatment broadcasted the erratic soundscape of
3171 drilling operations, with broadcasts that included sounds such as pipe clanking, generator
3172 fluctuations, intercom chatter, and truck activity. This soundscape was played in three 10-day
3173 blocks, separated by 10-day silent intervals, to replicate the average duration and pauses typical
3174 of regional drilling activities during 90 days (n = 4 sites).
3175
3176 In addition to the noise treatments, silent plots were established to control for the visual
3177 presence of playback infrastructure (Figure 2). These plots contained identical playback
3178 structures as the noise treatment sites but did not emit any sound (n = 4). Additional control
3179 plots with no oil infrastructure or sound treatments were included as baselines (n = 4). Real idle
3180 well oil infrastructure sites that had not been operational for at least three years and produced
3181 no noise during the experiment were also included in the study design to account for potential
3182 prolonged effects of non-operational infrastructure (n = 4) (Figure 3).

3183

3184 The noise treatments were designed to understand whether the predator-prey assemblages
3185 were influenced by predictability, duration, and amplitude of energy extraction noise.

3186 Predictable chronic noise represented a continuous disturbance with consistent, high-amplitude
3187 sound levels, simulating the steady auditory environment created by active oil infrastructure.

3188 Intermittent noise introduced moderate disturbance with on-off cycles, simulating more
3189 irregular operational patterns. The unpredictable noise treatment replicated drilling operations

3190 with fluctuating amplitude, frequency, and intensity levels and abrupt bursts of high-intensity
3191 noise. These experimental treatments were contrasted with silent plots and control sites to

3192 isolate the effects of noise from those of physical infrastructure, providing a comprehensive
3193 baseline for evaluating how different noise properties influence grassland ecosystems.

3194

3195

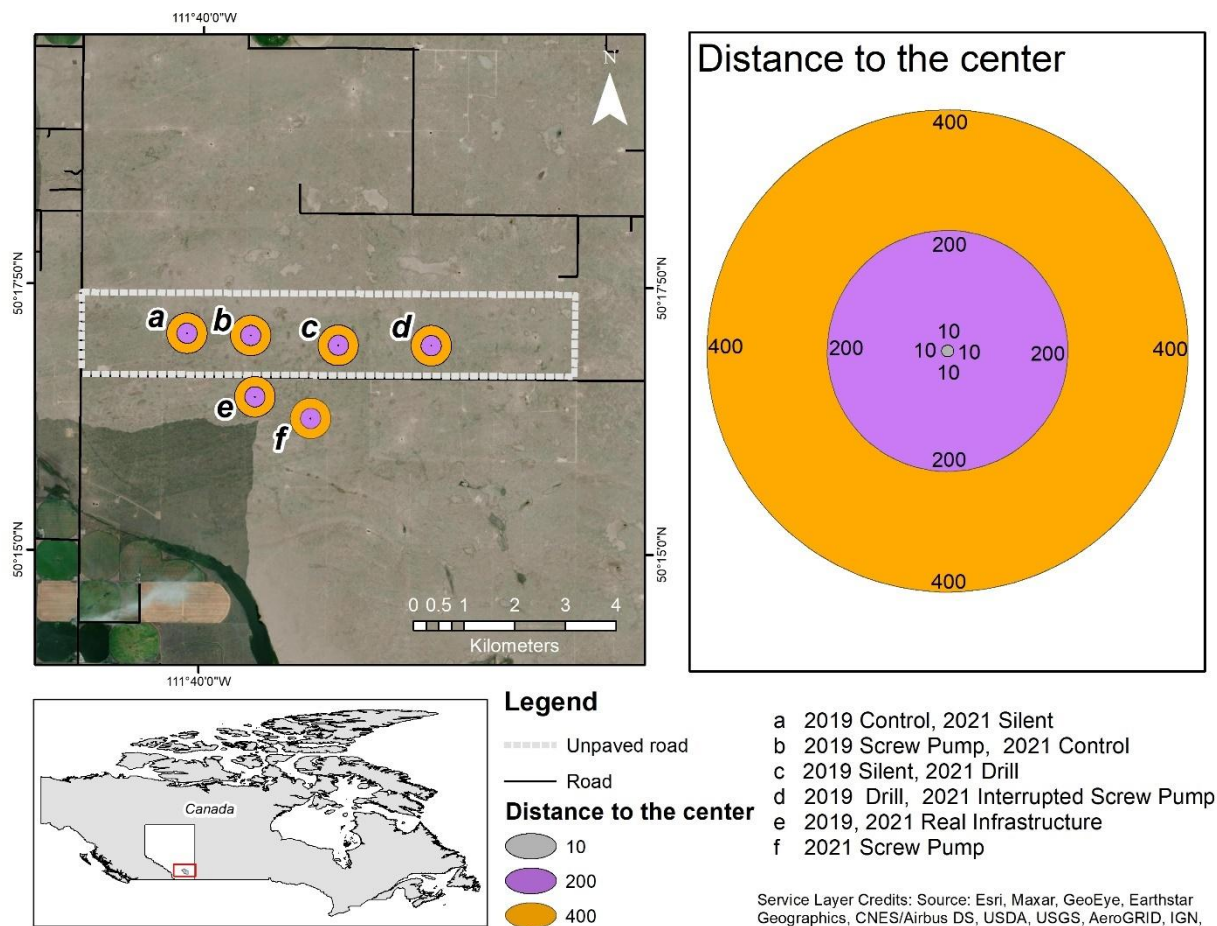


Figure 3 Example of a site containing disjunct 800x800m treatment plots in the southeastern region near Brooks, Alberta, Canada. Each site consisted on 5 (2019) and 6 (2021) treatment plots.

3201 Table 1.0. Consumers trophic level and food web roles of the predator-prey assemblages species found on the system.

<i>Species</i>	<i>Diet</i>	<i>This study</i>	<i>Authors</i>	<i>Consumer's Trophic level</i>	<i>Roles in Food web</i>
<i>Golden Eagle</i>	Lagomorphs Pronghorn Sciurids Uplandbirds Mesopredators Songbirds Raptors Reptiles Fish	Lagomorphs Richardson's GS Pronghorn Coyote Badger SWHA NOHA PEFA	Preston <i>et al</i> 2017 Bedrosian <i>et al</i> 2018 Lyly <i>et al</i> 2015? Sergio <i>et al</i> 2008 Datta 2016	Quaternary	Top predator
<i>Ferruginous Hawk</i>	Sciurids Lagomorph Rodents Uplandbirds Songbirds	Richardson's GS Lagomorph Deer Mouse Northern Grasshopper Mouse	Giovanni <i>et al</i> 2007 Ng <i>et al</i> 2020 Wiggins <i>et al</i> 2014 Datta 2016	Tertiary	Large Mesopredator
<i>Swainson's Hawk</i>	Sciurids Rodents Insects Reptiles Songbirds	Richardson's GS Deer Mouse Northern Grasshopper Mouse	Giovanni <i>et al</i> 2007 Wiggins <i>et al</i> 2014 Murphy 2010	Tertiary	Medium Mesopredator
<i>Red-tailed Hawk</i>	Lagomorph Sciurids Waterfowl Uplandbirds Rodents Songbirds	Richardson's GS	Hobbs <i>et al</i> 2006 Pauze 2001 Atuo and O'Connell 2017	Tertiary	Large Mesopredator
<i>Northern Harrier</i>	Rodents Sciurids Songbirds Uplandbirds Waterfowl	Richardson's GS Deer Mouse Northern Grasshopper Mouse	Datta 2016 Dechant <i>et al</i> 2002 Atuo and O'Connell 2017	Tertiary	Small Mesopredator
<i>Prairie Falcon</i>	Songbirds Sciurids Rodents	Richardson's GS Deer Mouse Northern Grasshopper Mouse	Squires <i>et al</i> 1989 Steenhof <i>et al</i> 1999	Tertiary	Medium Mesopredator

<i>Deer Mice</i>	Plants Insects Fungi	Sagebrush Forbs Grass	Rhea and Chalfoun 2023 Bradley and Marzluff 2003 Sanders and Chalfoun 2018	Primary	Small Prey
<i>Northern Grasshopper Mice</i>	Insects	Insects	Langley 1994,2021 Rowe and Rowe 2015	Primary/Secondary	Small Mesopredator
<i>Richardson's Ground squirrel</i>	Plants Insects	Sagebrush Forbs Grass	Newediuk <i>et al</i> 2015 Hansen 1976	Primary/Secondary	Medium Prey
<i>Badger</i>	Sciurids Insects Rodents Plants	Sciurids Rodents	Michener 2000, 2004 Thornton <i>et al</i> 2018 Proulx 2016	Secondary	Medium Mesopredator
<i>Coyote</i>	Lagomorph Sciurid Ungulates Rodents Cattle Carrion Plants Mesopredators	Lagomorph Richardson's GS Ungulates Rodents Cattle Plants Mesopredators	Bekoff and Wells 1980 Thornton <i>et al</i> 2018 Jensen <i>et al</i> 2022 Watine and Giuliano 2017 Sugden <i>et al</i> 2021	Secondary/Tertiary	Top predators
<i>Pronhorn</i>	Sagebrush Forbs Grass Sedges	Sagebrush Forbs Grass	Mitchell and Smoliak 1971 Morton <i>et al</i> 2008	Primary	Large Prey
<i>Deer</i>	Grass Forbs Woody vegetation	Sagebrush Forbs Grass	VerCauteren and Hygnstrom 1994 Collins and Urness 1983 Wickstrom <i>et al</i> 1984	Primary	Large Prey
<i>Lagomorphs</i>	Grass Forbs	Sagebrush Forbs Grass	Abercrombie 2018	Primary	Medium Prey

3203 4.2.3 Wildlife surveys

3204

3205 The total number of individuals observed per survey was used as an index of abundance
3206 (Engeman 2005; Engeman and Whisson 2006). Each species was later grouped and classified in
3207 a context of predatory behavior on their roles in a food web based on peer reviewed literature
3208 from grassland ecosystems (Table 1.0).

3209

3210 4.2.3.1 Rodent Surveys

3211 Rodent abundance was assessed at each site using live traps placed at distances of 10 m, 200 m,
3212 and 400 m from the center point along two randomly selected cardinal directions (e.g., North
3213 and West, or South and East) during each pulse. At each selected distance, five medium
3214 Sherman folding live traps (8 × 9 × 23 cm; H.B. Sherman Traps, Inc., Tallahassee, Florida) were
3215 deployed for small rodents, along with either two large Sherman traps (10 × 11 × 38 cm) or one
3216 Tomahawk trap (15 × 15 × 60 cm; Tomahawk Live Traps, Wisconsin, USA) for larger ground
3217 squirrels. The traps were set for three consecutive days at each site during each pulse, which
3218 occurred approximately every 27 days throughout the sampling period. Each trap was baited
3219 with approximately 5 g of moistened food, such as oats and soaked sunflower seeds,
3220 supplemented with a piece of apple or carrot to provide moisture. Defective traps (i.e., those
3221 missing bait, malfunctioning, or damaged) were reset, replenished with bait, or replaced as
3222 needed (Nelson and Clark 1973). To minimize residual scent effects, traps were cleaned with a
3223 5% bleach solution for 20 minutes after each pulse (Mills *et al.*, 1995).

3224

3225 Upon capture, rodents were identified to species. Newly captured individuals were marked with
3226 FDX-A 125 kHz Biomark PIT tags (Biomark, Boise, ID, USA) before release. Three monthly
3227 sessions (pulse) were conducted in 2019 and one in 2021. All animal handling protocols were
3228 approved by the University of Manitoba Animal Care Committee (ACC 11449 F19-007/1/2) and
3229 Alberta Environment and Parks (19-384).

3230

3231 *4.2.3.2 Raptor Surveys*

3232 Raptor activity was monitored using a road transect method with a double-observer approach
3233 (Nichols *et al.*, 2000). Observers conducted diurnal surveys by driving along secondary roads
3234 surrounding each 800 x 800 m site at a consistent speed of 25-30 km/h between 16:00 and
3235 18:00. Surveys were conducted exclusively on calm days with low wind and no precipitation.
3236 During each survey, individual raptors within the site plots were recorded (Gaibani and
3237 Csermely 2007).

3238

3239 When a raptor was observed, the vehicle stopped, and its position was recorded relative to the
3240 treatment site using UTM coordinates (Garmin GPSMAP 60CS, Garmin International, Olathe,
3241 Kansas). A Nikon Prostaff 550 range finder (Nikon Inc., Melville, New York) was used to measure
3242 the distance from the road to the raptor's initial sighting location to ensure that only raptors
3243 within the designated site boundaries were included. Surveys were conducted for two
3244 consecutive days per session at each site every 27 days during the grassland songbird breeding
3245 season.

3246

3247 4.2.3.3 *Mammal mesopredators, Lagomorphs and Ungulate Surveys*

3248 Surveys were conducted using nocturnal spotlight along secondary roads surrounding each site
3249 plot. The surveys took place for two consecutive nights per session at each site, approximately
3250 every 27 days during the grassland songbird breeding season. A heavy-duty cordless spotlight
3251 with a 1,000,000-candlepower beam was mounted on a truck, which was driven at 20 km/h
3252 around the perimeter of the site plots. Surveys were conducted only on calm nights with clear
3253 skies and no precipitation, avoiding full or gibbous moon phases to minimize detection bias.

3254

3255 Two observers positioned in the truck bed scanned both sides of the road, while the driver and
3256 co-pilot monitored for predators on the road itself. When a predator was sighted, the truck
3257 stopped, and the species and location were recorded. The location was identified using UTM
3258 coordinates and confirmed as within the treatment plot using a range finder (Nikon Inc.,
3259 Melville, New York). If a group of individuals (e.g., antelope family group) was observed, it was
3260 recorded as a single observation. Due to the secretive, nocturnal habits of mesopredators and
3261 prey, it was assumed that predators were actively hunting when observed and prey actively
3262 vigilant.

3263

3264 The initial survey direction (north or south) was randomly selected each night, and each site
3265 survey typically lasted 2-3 hours, beginning approximately one hour after sunset. Since sample
3266 sizes for individual species were limited, only data from badgers, coyotes, and antelopes were
3267 included in the analyses as single species. Jack rabbits and Cottontail rabbits as well as White-
3268 tailed deer and mule deer were grouped together as large prey.

3269 4.2.4. Model Construction

3270

3271 To test whether the grassland food web was regulated primarily by top-down versus bottom-up
3272 processes, and whether oil infrastructure and noise altered those relationships, I used piecewise
3273 structural equation modeling implemented in the piecewiseSEM package in R (Shipley, 2009;
3274 Lefcheck, 2016). Piecewise SEM is well suited for trophic networks because it estimates linked
3275 regression equations rather than a single covariance model, which allows different error
3276 structures, accommodates smaller sample sizes, and supports direct and indirect pathway
3277 interpretation for predator-prey systems (Sandom *et al.*, 2013; Du *et al.*, 2015; Sivy *et al.*, 2017).
3278 Observed variables represented the trophic hierarchy of the predator community and its prey,
3279 including top predators, three mesopredator guilds, and three prey size classes. Because
3280 responses were counts with many zeros, each endogenous component model was fit using
3281 generalized models with a zero-inflated Poisson distribution. For all analyses, I assessed overall
3282 model fit and verified that component models met their statistical assumptions prior to
3283 interpretation, following current guidance for piecewise structural equation modelling (Shipley,
3284 2009; Lefcheck, 2016; Mendes and Luskin, 2025).

3285

3286

3287 To evaluate whether wells and noise modified regulation in ways consistent with the
3288 mechanism hypotheses, I treated treatment as an exogenous driver of trophic abundances and
3289 compared supported pathways against the control baseline. Under the Human Shield
3290 hypothesis (H1), treatment effects were expected to reduce top predator abundance and

3291 increase prey abundance relative to controls, consistent with weakened top-down influence
3292 near development. Under Predator Facilitation (H2), treatment effects were expected to
3293 increase top predator abundance and reduce prey abundance, consistent with stronger top-
3294 down influence near development. Under disturbance-mediated Mesopredator Release (H3),
3295 treatment effects were expected to reduce top predators, increase mesopredators, and reduce
3296 prey, consistent with top-down effects operating primarily through mesopredators rather than
3297 top predators. Under Risk-Disturbance (H4), treatment effects were expected to reduce
3298 abundances across all consumer groups and prey, consistent with broad avoidance and
3299 weakened interactions near disturbance.

3300

3301 To separate noise-driven from infrastructure-driven responses, I evaluated patterns across the
3302 full treatment set, defined to match the experimental design: Control plots with no
3303 infrastructure or playback, Silent infrastructure plots with playback structures but no sound,
3304 Real idle well infrastructure plots with long-standing non-operational wells that produced no
3305 noise during the study, Predictable chronic noise plots with continuous screw-pump playback,
3306 Intermittent recurrent noise plots with screw-pump playback randomized in on-off cycles across
3307 the day, and Unpredictable random noise plots with drilling soundscapes broadcast in blocks
3308 separated by silent intervals. Under the noise-driven sub hypotheses (H1a-H4a), treatment
3309 responses were expected to be strongest under drilling noise, intermediate under intermittent
3310 and continuous screw-pump noise, weaker under silent and real idle well infrastructure, and
3311 weakest under controls. Under the infrastructure-driven sub hypotheses (H1b-H4b), responses

were expected to be similar among all treatments that included physical structures, regardless of whether sound was present, and to differ most clearly from the control plots.

Model fit and inference followed standard piecewise SEM procedures. Overall network consistency was evaluated using tests of directed separation and Fisher's C, and supported pathways were interpreted using standardized coefficients and their uncertainty (Shipley, 2009; Lefcheck, 2016). I then compared the direction and persistence of key trophic pathways across treatments to determine whether regulation mode shifted relative to control, and whether any shifts were more consistent with noise-mediated change or with the physical presence of infrastructure.

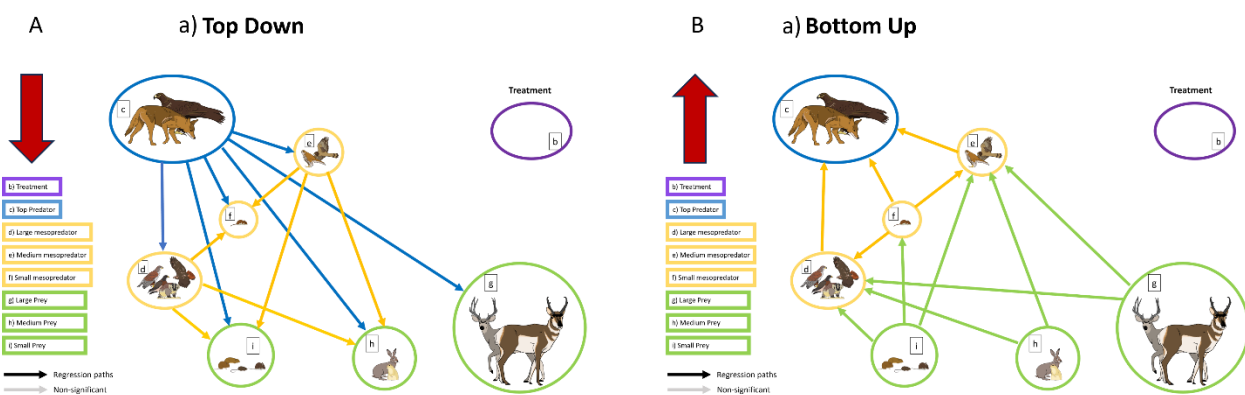


Figure 4. (A) represents the top-down model, where regulatory effects originate from top predators and cascade downward through mesopredators to prey. (B) represents the bottom-up model, where variation in prey abundance initiates changes that propagate upward through the predator hierarchy. Colors identify trophic levels: blue represent top predators, yellow represents mesopredators, green represent prey groups, and purple refers to the treatment and control effects of infrastructure and noise conditions. Arrows indicate the direction and type of

3330 hypothesized causal relationships among trophic levels, representing how changes in total
3331 number of species at one level are expected to influence others under different treatment
3332 scenarios. (Created by JP Medina with the help of Marco Garcia)

3333

3334 To complement the full guild models, I also built a more direct set of piecewise SEMs focused on
3335 the trophic pathway for which the data were most robust: avian predators versus rodents. In
3336 these models, total raptor abundance was represented by hawks and falcons pooled as a single
3337 predator response, and rodent prey were represented by Deer Mouse, Northern Grasshopper
3338 Mouse, and Richardson's Ground Squirrel as separate endogenous prey variables. I then
3339 incorporated distance to the centre of the site as an additional exogenous predictor to
3340 distinguish broad predator-prey associations among sites from local spatial responses within
3341 sites. In the bottom-up version, raptor abundance was modeled as a function of the three
3342 rodent taxa and raptor distance to centre, while each rodent taxon was modeled as a function
3343 of rodent distance to centre. In the top-down version, raptor abundance was modeled as a
3344 function of raptor distance to centre, while each rodent taxon was modeled as a function of
3345 raptor abundance and rodent distance to centre.

3346

3347

3348 **4.3 Results**

3349

3350 Neither top-down nor bottom-up hypotheses were supported in control sites. The control
3351 treatment (Figure 5A) provided a baseline that did not support a strong top-down cascade

model form. In the top-down model, only two positive links were supported: top predators were positively associated with large mesopredators with a path coefficient of 2.09, and large mesopredators were positively associated with small prey with a coefficient of 1.30. No negative paths connected predators to prey, for either top predators or mesopredators. In the bottom-up model, structure was even weaker, with only one supported consumer link, a positive association between small and medium mesopredators with a coefficient of 2.30, and no supported paths from prey guilds to higher trophic levels.

Across treatments (Figure 5B-F), top predator pathways did not shift in a consistent direction that would indicate either top predator avoidance of wells and/or noise, as predicted by the human shield hypothesis, or higher predator numbers near development, as predicted by the predator facilitation hypothesis. Relative to control (Figure 5A), the silent treatment (Figure 5E) added supported positive top predator links rather than evidence of avoidance: top predators were positively associated with large mesopredators at 0.309 and with small prey at 0.276. Under the unpredictable random noise treatment (Drill; Figure 5D), top predators were also positively associated with small prey at 0.484 and with large mesopredators at 0.194.

In the predictable chronic noise treatment (SP; Figure 5B), the top-down model did show some negative top predator links, with top predators negatively associated with small mesopredators at -2.04 and with small prey at -0.364, but this did not generalize to broader prey suppression because top predators retained positive links to large prey at 0.453 and to medium prey at

3373 0.1993, and positive associations with medium mesopredators at 0.08 and large mesopredators
3374 at 0.04, although these effect sizes were small and likely not biologically meaningful, indicating
3375 weak interactions rather than a structured trophic regulation. In the intermittent recurrent
3376 noise treatment (ISP; Figure 5C), the top-down model did not support any pathways, which is
3377 inconsistent with either H1 or H2 because neither a clear avoidance pattern nor an increase in
3378 predator pressure emerged as supported pathways. In the real idle well oil infrastructure
3379 treatment (Figure 5F), the top-down model also did not support any pathways, indicating that
3380 differences from the control baseline were not expressed as top predator-mediated prey
3381 suppression. Taken together, H1 and H2 received limited support because top predator signals
3382 were either absent or positive, and they did not align with consistent prey suppression.

3383

3384 Under mesopredator release, weaker top predator effects should result in negative
3385 mesopredator-prey relationships or increased mesopredators with lower prey. These patterns
3386 were not detected. In the control (Figure 5A), the only supported path ran in the opposite
3387 direction with large mesopredators positively associated with small prey at 1.30. The silent
3388 treatment (Figure 5E) likewise retained positive mesopredator-to-prey associations in the top-
3389 down model, with large mesopredators to small prey at 0.124 and small mesopredators to small
3390 prey at 0.234, alongside the positive top predator associations described above. Predictable
3391 chronic noise (SP; Figure 5B) further strengthened prey tracking signals by mesopredators: small
3392 mesopredators were positively associated with small prey at 0.455, large mesopredators were
3393 positively associated with small prey at 0.340 and medium prey at 0.25, and medium

3394 mesopredators were positively associated with small prey at 0.416 but with medium prey at -
3395 0.639m indicating specific responses to prey type rather than consistent prey suppression.

3396

3397 The strongest shifts in network structure appeared in the bottom-up models (Figure 5A-F,
3398 bottom-up panels), but these patterns still did not fit a classic mesopredator release. Real idle
3399 well oil infrastructure (Figure 5F) showed the strongest evidence of some prey to consumer
3400 relationship, with large prey positively associated with large mesopredators at 3.11 and small
3401 mesopredators positively associated with large mesopredators at 1.01, plus a positive
3402 association between medium mesopredators and top predators at 1.5. These relationships
3403 indicate stronger positive associations among guilds, but they do not indicate prey suppression.
3404 Intermittent recurrent noise (ISP; Figure 5C) showed contrasting responses among prey classes:
3405 large prey was positively associated with medium mesopredators at 1.46 and with large
3406 mesopredators at 2.29, and medium prey was positively associated with large mesopredators at
3407 0.449, while small prey was negatively associated with large mesopredators at -2.24 and with
3408 medium mesopredators at -1.04, and small mesopredators were negatively associated with
3409 large mesopredators at -2.16. This indicates a possible redistribution of interactions across prey
3410 guilds rather than a consistent trophic cascade.

3411

3412 Risk-Disturbance predicts that infrastructure or noise should broadly reduce trophic structure
3413 relative to the control baseline, which would appear as a widespread loss of supported links and
3414 weaker relationships among guilds. Some treatments did show some supported links in the top-

down model, but this did not translate into a consistent loss of prey-to-consumer relationships in the bottom-up model. Intermittent recurrent noise (ISP; Figure 5C) had no supported links in the top-down specification, yet the bottom-up specification retained several strong prey-to-mesopredator paths, including large prey to large mesopredators at 2.29 and large prey to medium mesopredators at 1.46. Predictable chronic noise (SP; Figure 5B) retained multiple supported positive links between mesopredators and prey, consistent with prey detection, rather than showing a broad loss of supported predator-prey associations. Unpredictable random noise (Drill; Figure 5D) also retained structure in the bottom-up specification, where small mesopredators were positively associated with large mesopredators at 0.220 and small prey was positively associated with large mesopredators at 0.151, along with the supported top predator-to-prey link in the top-down model. The persistence of these supported links is inconsistent with a broad loss of interactions across all guilds. Across treatments, effect sizes did not have a consistent reduction or increase relative to the control baseline, but instead varied in magnitude, indicating that trophic interactions were maintained and redistributed rather than uniformly weakened or strengthened by noise or infrastructure.

Comparisons to the control baseline (Figure 5A) indicate that differences among treatments were more consistent with treatment-specific shifts in prey-to-consumer relationships than with a simple increase or decrease in effects along a noise gradient. The silent treatment (Figure 5E) largely resembled control in maintaining positive associations, but it added supported positive top predator links to large mesopredators at 0.309 and to small prey at 0.276, and it retained positive mesopredator-to-small-prey links at 0.124 and 0.234, indicating that predators and prey

3437 continued to use the same areas, with predators likely tracking prey availability, even when
3438 infrastructure was present but no experimental noise was broadcast. Real idle well oil
3439 infrastructure (Figure 5F) showed the clearest strengthening of prey-to-consumer relationships,
3440 with the largest supported effect sizes in the dataset, including large prey to large
3441 mesopredators at 3.11 and small mesopredators to large mesopredators at 1.01, plus a positive
3442 link from medium mesopredators to top predators at 1.5. This pattern is most consistent with
3443 infrastructure-associated aggregation of prey and consumers, not a noise-driven breakdown of
3444 interactions.

3445

3446 Noise treatments did not produce a consistent shift away from this baseline. Predictable chronic
3447 noise (SP; Figure 5B) showed a few negative links from top predators to small mesopredators
3448 and small prey, but it simultaneously retained multiple positive predators and mesopredator
3449 links with prey, indicating that chronic predictable sound altered some lower-web associations
3450 without producing a system-wide change in regulation. Intermittent recurrent noise (ISP; Figure
3451 5C) showed the strongest redistribution across prey classes in the bottom-up model, with large
3452 prey strengthening links to mesopredators while small prey showed negative links, suggesting a
3453 reorganization among prey guilds rather than general top-down control or general avoidance.
3454 Across hypotheses, supported paths more often indicated positive co-occurrence and prey
3455 tracking than predator-driven prey suppression, and the strongest increase in prey-to-consumer
3456 relationships occurred at real idle well oil infrastructure (Figure 5F) rather than under the noise
3457 treatments.

3458

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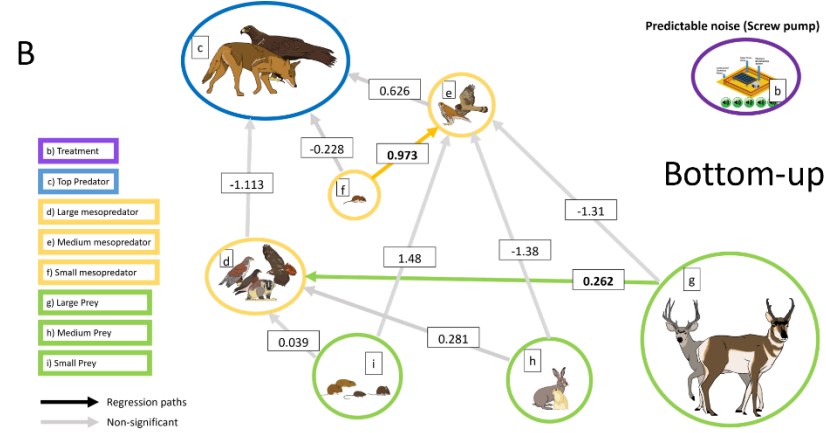
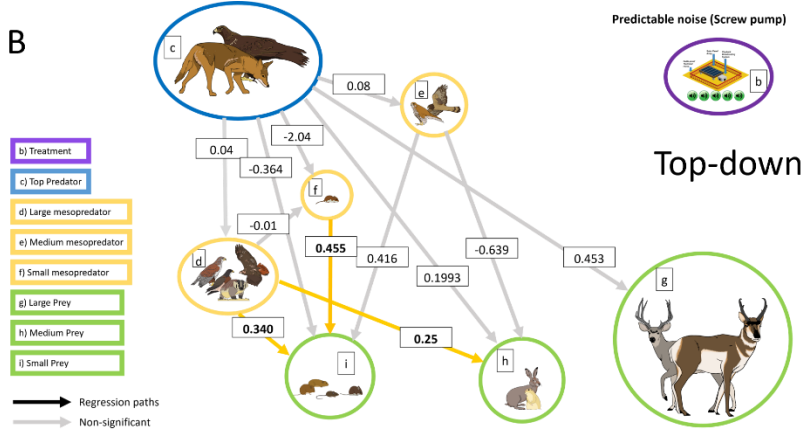
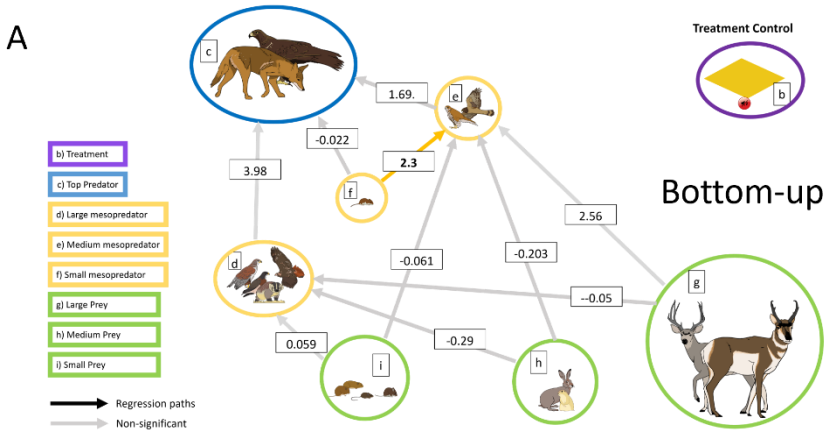
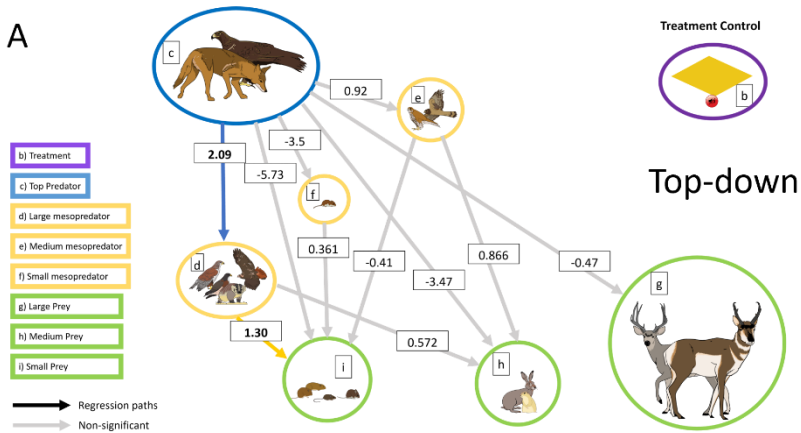
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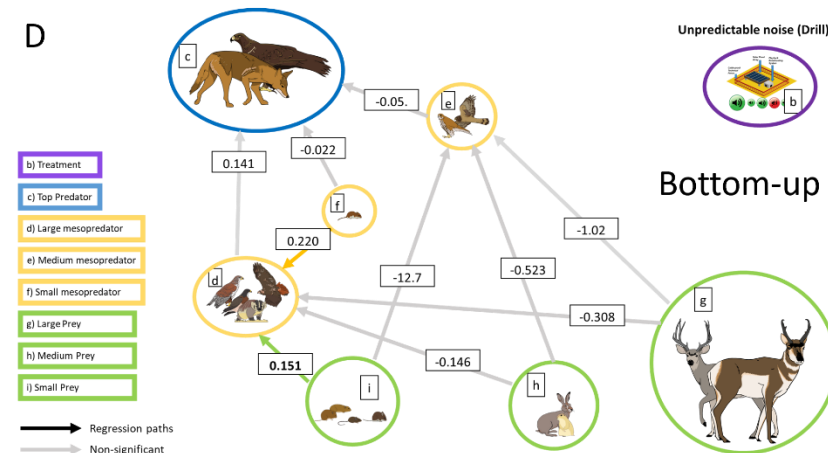
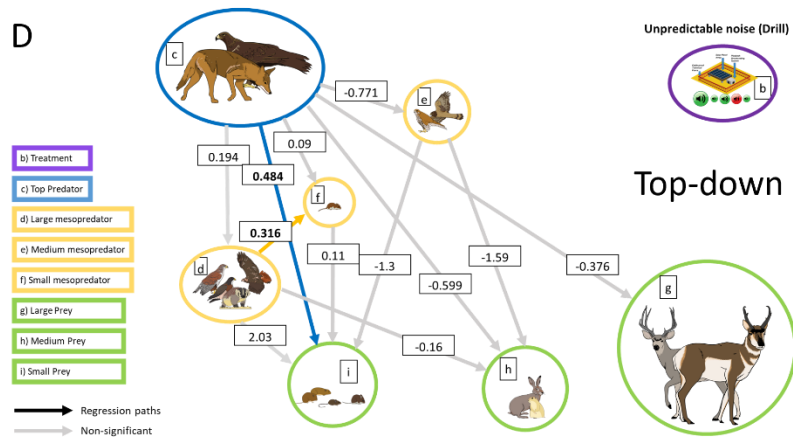
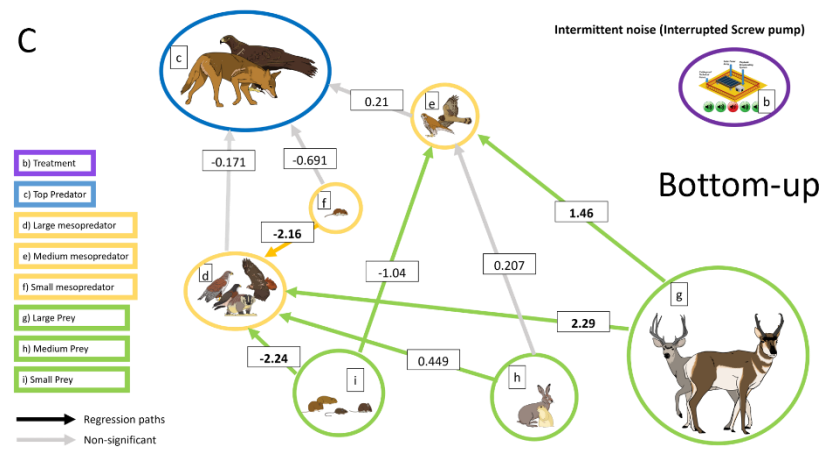
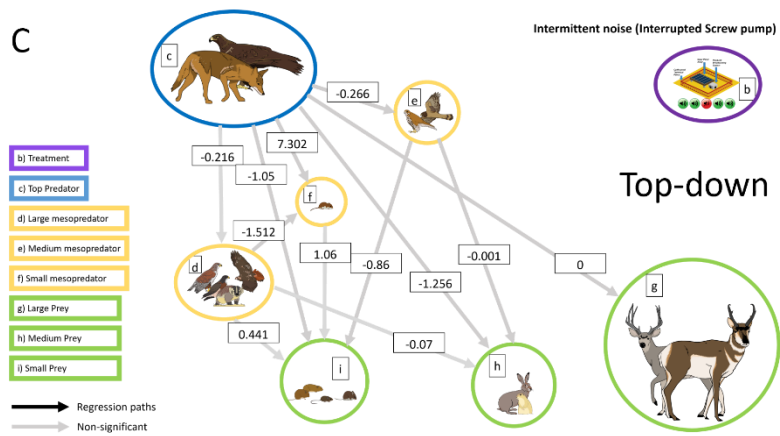
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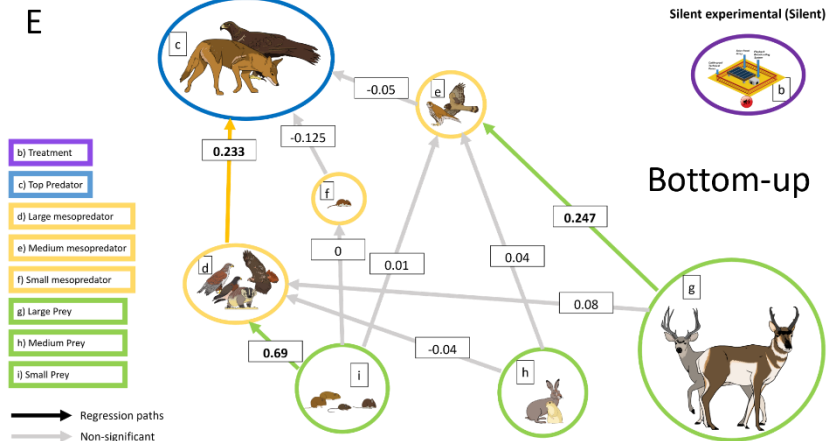
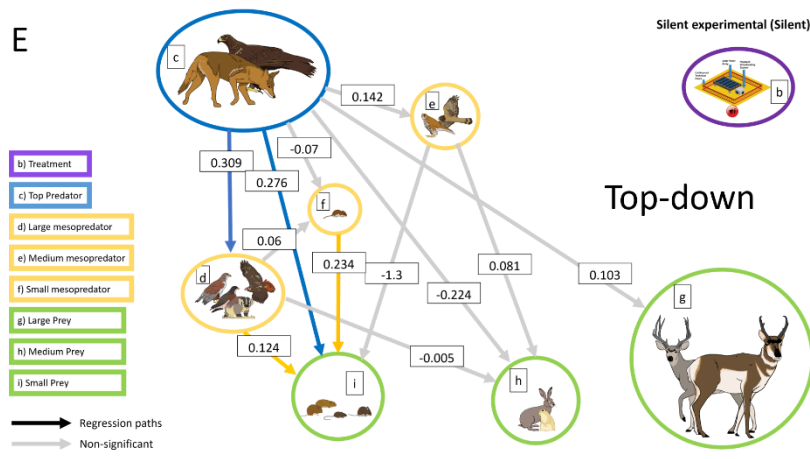
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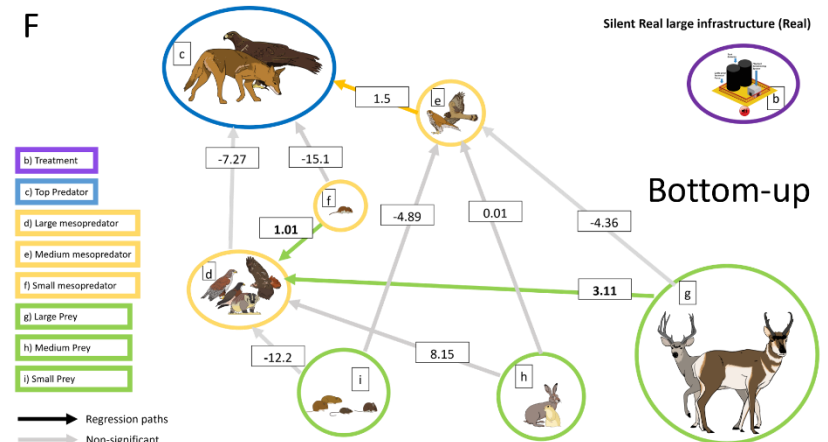
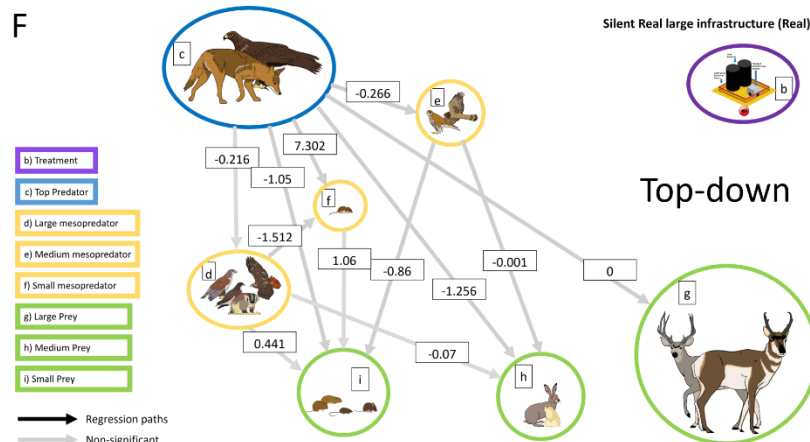


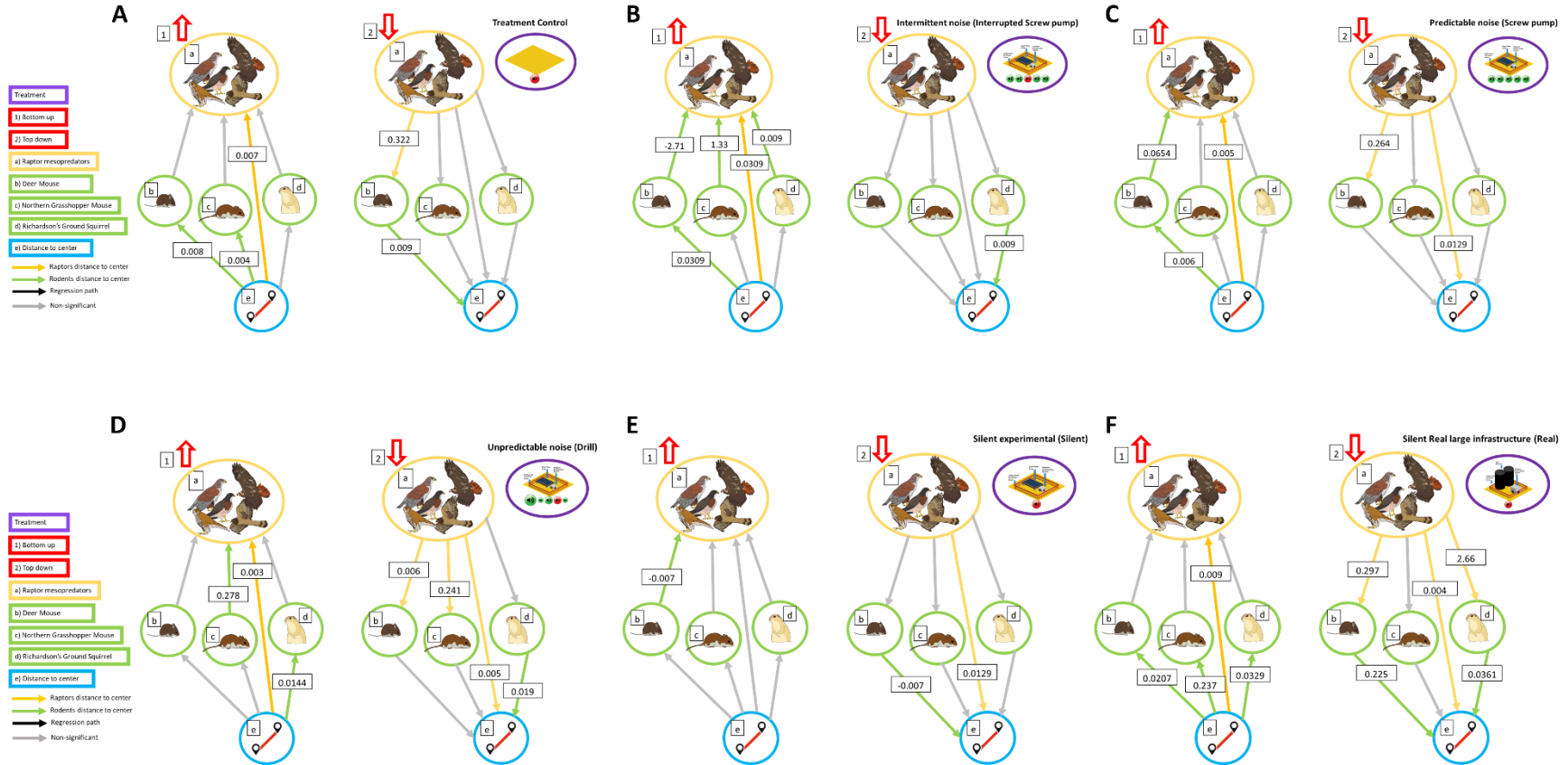
Figure 5. Structural equation piecewise model (piecewise SEM) and the different trophic levels of the predator-prey assemblages in a mixed-grass prairie system. Top-down and bottom-up proposed mechanisms. Arrows represent the regression effects between the trophic levels. Numeric values indicate estimates in the total number of individuals. Colors differentiate the food web levels (blue, top predators; yellow, mesopredators; and green, prey groups), and the treatment type (purple). Nonsignificant paths shown in grey. A, control site; B, predictable chronic noise (SP); C, Intermittent recurrent noise (ISP); D, Unpredictable random noise (Drill) treatment; E, silent treatment; F, real idle well infrastructure. (Created by JP Medina with the help of Marco Garcia 2023-2025)

3478 The direct raptor-rodent models (Figure 6) were most consistent with the regulation mode
3479 hypothesis (H0) under a bottom-up rather than a top-down pattern. In the Control (Figure 5A),
3480 Deer Mice was positively associated with raptors (0.322), which does not support top-down
3481 suppression. Relative to this baseline, the predictable chronic noise (Screw pump) (Figure 6C),
3482 Unpredictable random noise (Drill) (Figure 6D), and Real idle well infrastructure (Real) (Figure
3483 6F), treatments also retained positive rodent-raptor paths, with effect sizes that varied among
3484 treatments but did not indicate consistent prey suppression, with positive coefficients in idle
3485 well. Only intermittent recurrent noise (Interrupted Screw pump) (Figure 6B) showed a
3486 supported negative Deer Mouse-raptor path (-2.71), although Northern Grasshopper Mouse in
3487 that same treatment remained positively associated with raptors (1.33). Thus, compared with
3488 control, most treatments did not shift the system toward stronger top-down regulation, and the
3489 dominant pattern remained positive predator-prey association, consistent with prey tracking
3490 rather than predator driven suppression.

3491

3492 Human Shield hypothesis (H1) predicts lower raptor abundance and relatively higher prey near
3493 disturbance, but compared with the control, this pattern was not consistent. In Control, Deer
3494 Mouse was positively associated with raptors (0.322), Deer Mouse abundance increased with
3495 distance to the treatment centre (0.00994), and Northern Grasshopper Mouse also increased
3496 with distance to the treatment centre (0.00466). The Silent treatment (Figure 6E) showed
3497 differences from that control, with two negative prey distance coefficients (-0.007) and a
3498 positive raptor distance coefficient (0.0129), which is more consistent with a local refuge
3499 pattern, although the absence of a supported negative raptor-prey relationship could indicate

3500 this pattern is not related with a reduced predator pressure. Predator Facilitation (H2) was not
3501 supported because several treatments retained positive predator-prey associations: Deer
3502 Mouse to raptors was 0.264 in predictable chronic noise (Screw pump), Deer Mouse and
3503 Northern Grasshopper Mouse to raptors were 0.278 and 0.241 in Unpredictable random noise
3504 (Drill), and Deer Mouse, Northern Grasshopper Mouse, and Richardson's Ground Squirrel to
3505 raptors were 2.66, 0.297, and 0.237 in the silent non-operational Real idle well infrastructure
3506 (Real), indicating a co-occurrence rather than increased predation leading to prey declines.. Risk
3507 disturbance (H4) predicts weakened local interactions across treatments, but supported direct
3508 paths remained present in all treatments. Screw pump retained positive raptor and prey
3509 distance paths (0.0129, 0.006, 0.0654, 0.005), Drill retained multiple positive paths including
3510 raptors to distance (0.019) and prey to distance (0.0144, 0.006, 0.005), and Real showed the
3511 strongest positive set of direct and distance paths, including positive relationship of raptors
3512 (0.225) and prey (0.0361, 0.0329, 0.0207) to distance.



3513

3514 Figure 6. Structural equation piecewise direct raptor-rodent model (piecewise SEM) in a mixed-grass prairie system. Top-down and
 3515 bottom-up proposed mechanisms. Arrows represent the regression effects between the trophic levels. Numeric values indicate
 3516 estimates in the total number of individuals only shown when significant (p -value ≤ 0.07). Colors differentiate the food web levels
 3517 (yellow, mesopredators and green, prey groups), the distance to the center point (blue) and the treatment type (purple).
 3518 Nonsignificant paths shown in grey. A, control site; B, Intermittent recurrent noise (ISP); C, predictable chronic noise (SP); D,
 3519 Unpredictable random noise (Drill) treatment; E, silent treatment; F, real idle well infrastructure. (Created by JP Medina with the
 3520 help of Marco Garcia 2025-2026)

4.4 Discussion and Conclusions

The control results suggests that predator and prey abundances change together due the responses to the same habitat conditions rather than showing any sustained top-down or bottom-up regulation. This pattern is consistent with shared habitat responses and in some extent a weak bottom-up regulation, and my sample sizes cannot fully separate these alternatives. In a strongly top-down regulated system, higher predator abundance should align with lower prey abundance, either through direct negative predator-prey relationships or through negative mesopredator-prey pathways that transmit suppression down the web (Kay, 1998; Laundré *et al.*, 2014). That pattern did not show up and instead positive relationships among predators, mesopredators, and small prey were more frequent, which could reflect either a weak bottom-up regulation or shared responses to habitat structure, as both mechanisms can produce similar positive associations. This aligns with grassland ecology showing that vegetation structure, patch size, and patch arrangement can strongly influence where prey forage and where predators can hunt effectively producing frequent predator-prey overlap even when predation is occurring (Wiens and Rotenberry, 1979; Wiens and Rotenberry, 1981).

A possible reason these positive associations occur is that prairie communities are highly influenced by natural disturbances. Fire, flooding, draughts, grazing, and fossorial herbivores can change vegetation height, the amount of bare ground and litter as well as burrow networks,

3542 which changes the visibility, escape cover, and the movement routes for both predators and
3543 prey (Del Vallé *et al.*, 2025). These processes creates changing sections of dense covered areas
3544 and areas with open ground, and create interaction opportunities before stable trophic
3545 cascades can develop. In grasslands where fire, floods, and herbivores are central ecological
3546 forces, the population change can reflect where cover and resources are temporarily
3547 concentrated and which patches are newly opened or newly protected, rather than a stable
3548 balance of predator suppression or food limitation (Noss, 2013; Meserve *et al.*, 2003). Spatial
3549 turnover and dispersal then redistribute animals among patches, which can further weaken the
3550 appearance of consistent trophic regulation in abundance networks (Fronhofer *et al.*, 2018;
3551 Terraube and Bretagnolle, 2018).

3552

3553 The Human shield hypothesis and predator facilitation hypothesis predicted that the top
3554 predators would respond to infrastructure and noise in ways that can potentially create
3555 predictable changes in prey. Human Shield predicts reduced top predator presence near
3556 development with relatively higher prey while Predator Facilitation predicts greater top
3557 predator presence near development and prey suppression (Kay, 1998; Laundré *et al.*, 2014).
3558 Neither pattern was detected. Top predator relationships were limited and did not align with
3559 prey reductions, providing evidence against these mechanisms. The patterns that might be
3560 observed in prairie ecosystems where coyotes and some large raptors are the top predators and
3561 can tolerate human activity, adjust foraging activity and behavior depending on the prey
3562 availability (e.g. high availability of juvenile rodents), and efficiently hunt near farm edges and
3563 burrow colonies, producing localized impacts that do not propagate as a multi-link cascade

3564 across the trophic web (Schmutz and Hungle, 1989; Seamster *et al.*, 2014; Lingle *et al.*, 2022;
3565 Briggs *et al.*, 2024).

3566

3567 The landscape of fear framework emphasizes that predators can reshape prey space use,
3568 vigilance, and foraging decisions without producing uniform declines in prey abundance across
3569 the landscape (Laundré *et al.*, 2014). However, the fear concept is often complex to measure
3570 and then inferred from the space use or the abundance patterns instead of being really
3571 measured directly. Those patterns can also reflect shared habitat preferences, energetic
3572 tradeoffs, or disturbance history. The persistence of positive predator-prey associations in my
3573 study, suggests that shared habitat use is a more parsimonious explanation than fear-driven
3574 avoidance. (Gallagher *et al.*, 2017; Tulumello, 2015).

3575

3576 The evidence against predator facilitation also fits what is known about how anthropogenic
3577 features influence grassland systems. Infrastructure commonly changes vegetation structure
3578 and creates edges and travel corridors, which can increase predator-prey overlap without
3579 producing consistent prey suppression at the population scale (Wiens and Rotenberry, 1981;
3580 Terraube and Bretagnolle, 2018). In grasslands ecosystems, predation risk can potentially be
3581 mediated by the landcover as prey can coexist near predators when vegetation and burrow
3582 networks provide cover and especially when the movement among patches can allow potential
3583 recolonization (Fronhofer *et al.*, 2018; Terraube and Bretagnolle, 2018). Positive associations
3584 between predators, mesopredators, and prey can occur when the predators and prey

3585 concentrate in the same localized areas. Coexistence within predator guilds can reduce the
3586 likelihood of a single dominant cascade because predators differ in where, when, and what they
3587 hunt. This spatial, temporal, and resource partitioning (e.g. dietary) spreads predation pressure
3588 across multiple prey groups, preventing consistent suppression of any one prey guild.
3589 (Jachowski *et al.*, 2020; Barros *et al.*, 2024).

3590

3591 The real idle well infrastructure treatment is important because it illustrates how physical
3592 structure can strengthen prey-consumer relationships independent of noise. Vertical
3593 infrastructures and the altered landcover around idle wells can provide cover, concentrate food
3594 resources, and create habitat suitability that attract small mammals, increasing prey availability
3595 and then attracting predators and mesopredators that move toward areas with high prey
3596 concentrations (Dickman, 1999; Planillo *et al.*, 2015; Sanders and Chalfoun, 2018; Boucher *et*
3597 *al.*, 2022). This pattern is consistent with a bottom-up pathway in which consumer abundance
3598 increases where prey and habitat quality are higher, although the mechanism is driven by
3599 structural habitat features rather than food limitation alone. Such structural attraction can also
3600 interact with fire and grazing by changing how regrowth and edge conditions develop near
3601 infrastructure, which can further concentrate activity of both predators and prey in specific
3602 patches (Noss, 2013; Del Vallé *et al.*, 2025).

3603

3604 Mesopredator release predicts that reduced top predator influence allows mesopredators to
3605 increase and then reduce prey. This pattern was not supported. Mesopredator prey

associations, which should appear as negative mesopredator-prey relationships or a consistent pattern where higher mesopredator abundance aligns with lower prey abundance (Crooks and Soulé, 1999; Prugh *et al.*, 2009). My results do not support this hypothesis. Mesopredator-prey associations were slightly positive, which could indicate that mesopredators were most abundant where prey were most abundant. In grasslands this co-occurrence could happen when prey and mesopredators select the same features, like edge-rich patches and burrow colonies, because these features raise prey availability and improve mesopredator foraging opportunities (Wiens and Rotenberry, 1981; Meserve *et al.*, 2003). Thus, stronger negative effects would indicate increased top predator influence rather than reduced influence, and such patterns were not observed. These results are more consistent with shared habitat responses than with mesopredator release (Bernath-Plaisted and Koper, 2016; Proulx *et al.*, 2019).

Risk-Disturbance predicts weakened interactions under noise or development, but prey-consumer relationships generally persisted across treatments. This suggests continued overlap in space use, likely because vegetation structure and burrow systems buffer perceived risk and allow activity to continue even in noisy environments (Shannon *et al.*, 2016; Duquette *et al.*, 2021; Rutherford *et al.*, 2023). In open prairies if noise reduces the value of acoustic vigilance, some (or the adaptable ones) prey may rely more on visual information and refuge structure, which can still support space use near infrastructure and near soaring raptors that hunt using visual cues (Shannon *et al.*, 2016; Laundré *et al.*, 2014).

3627 Noise and physical infrastructure can therefore be treated as distinct pathways that act on a
3628 shared spatial system. Most noise treatments preserved the baseline prey-consumer
3629 relationships rather than producing a consistent shift toward either top-down dominance or
3630 bottom-up dominance, which suggests that sound alone did not restructure the community in a
3631 repeatable way. A single negative rodent-raptor relationship under intermittent recurrent noise
3632 is notable but should be discussed carefully as a treatment-specific outcome. Intermittent
3633 recurrent noise may be more difficult for predator-prey assemblages to overcome than the
3634 predictable chronic noise because it is less predictable and harder to anticipate, which can alter
3635 the vigilance, hunting, attention, detection, and encounter rates, potentially changing when and
3636 where predation risk is perceived (Clare *et al.*, 2016; Palomo-Muñoz *et al.*, 2024). In this study,
3637 this effect may be particularly relevant for Deer Mouse, which rely on rapid movement and
3638 acoustic cues in open habitats, making them more susceptible to disrupted detection under
3639 intermittent noise. This provides a mechanistic hypothesis for why intermittent noise could
3640 reduce co-occurrence in one predator-prey pair even when other relationships remain positive.

3641

3642 The most repeatable pattern across treatments is that real idle well infrastructure, and to a
3643 lesser extent unpredictable random noise, showed patterns consistent with small mammal
3644 availability supporting raptor occurrence. Bottom-up regulation predicts positive prey-consumer
3645 relationships, and persistent positive rodent-raptor associations indicate that raptors track
3646 variation in small mammal abundance across conditions (Hury, 1998). These patterns were
3647 overall strongest at idle wells, likely due to structural habitat changes that concentrate prey, and

3648 weaker under noise treatments where structure remained unaltered. Differences among raptor
3649 groups may reflect prey selectivity and foraging strategies (Huryn, 1998).

3650

3651 Raptor-rodent relationships were often positive, but their strength was variable across
3652 treatments and species. These patterns also indicate that the system was not consistently top
3653 down, as negative raptor-rodent relationships were not consistently supported. Instead, where
3654 positive associations were supported, they were more consistent with raptors concentrating in
3655 patches where rodents might be more available or more detectable, a pattern expected in
3656 grasslands where raptor occurrence can follow prey distribution and hunting conditions across
3657 habitat patches rather than produce uniform prey suppression (Elmhagen and Rushton, 2007;
3658 Giovanni *et al.*, 2007; Du *et al.*, 2015; Datta, 2016). These patterns are again consistent with
3659 both bottom-up regulation and/or shared habitat responses (Elmhagen and Rushton, 2007; Du
3660 *et al.*, 2015; Datta, 2016).

3661

3662 The positive site-level association between rodents and raptors did not translate into the same
3663 local pattern within sites. In treatments where rodents and raptors both increased away from
3664 the centre, the results are more consistent with shared responses to patch structure than with
3665 refuge use near infrastructure. By contrast, in Silent and to a lesser extent the Interrupted Screw
3666 pump, the contrast between rodent and raptor distance responses is more consistent with a
3667 local refuge effect, in which some rodents like Deer Mouse remained closer to infrastructure,
3668 while raptors used outer areas. These interpretations are based on distance coefficients

reported in the Results, where in some treatments prey and raptors responded in the same direction along the distance gradient (both increasing or both decreasing), whereas in others they showed opposite responses, with prey increasing where raptors decreased, or vice versa. Rodent taxa differ in cover use, mobility, visual cues, and dependence on burrows, while raptors depend on visibility and access to prey in open space (Langley, 1994; Rowe and Rowe, 2015; Newediuk et al., 2015; Proulx, 2016). More broadly, it also fits evidence that infrastructure can alter predator-prey overlap through physical structure, whereas noise effects are often more context dependent and can vary with how disturbance changes vigilance, perception, and space use (Francis *et al.*, 2009; Shannon *et al.*, 2016; Duquette *et al.*, 2021; Gaynor *et al.*, 2021).

A strong top-down population regulation expressed as consistent predator driven prey suppression was not supported, which limits support for these hypotheses as dominant explanations (Kay, 1998; Laundré *et al.*, 2014). Mesopredator release was not supported because mesopredator-prey relationships were typically positive, limiting support for that mechanism (Crooks and Soulé, 1999; Prugh *et al.*, 2009). Broad risk disturbance effects were not expressed as widespread loss of prey-consumer relationships, limiting support for that hypothesis (Laundré *et al.*, 2014). The clearest treatment-linked change was that real idle well infrastructure strengthened prey-consumer associations, which is consistent with structural attraction around idle wells, while noise mostly modified relationship strength in context dependent ways rather than shifting the system into a uniformly top-down or bottom-up state (Dickman, 1999; Planillo *et al.*, 2015; Sanders and Chalfoun, 2018; Boucher *et al.*, 2022; Wiens and Rotenberry, 1979; Wiens and Rotenberry, 1981; Del Vallé *et al.*, 2025).

3691

3692 Overall, rather than pointing to a single cascade that runs consistently from predators to prey,
3693 these findings suggest a consumer-influenced grassland system in which prey concentrations,
3694 habitat structure, and recurrent disturbance set the main context for predator-prey
3695 associations, while infrastructure and noise modify those associations in treatment-specific
3696 ways rather than shifting the food web into a uniformly top-down or bottom-up pathway. This
3697 interpretation is consistent with broader trophic theory showing that population growth is
3698 fundamentally constrained by resource availability but can be modified by predation and
3699 disturbance, although in this system the relative roles of bottom-up processes and shared
3700 habitat responses cannot be fully separated and with grassland theory emphasizing that many
3701 grass-dominated systems persist in an “ecosystem uncertain” space where vegetation and
3702 consumers are jointly shaped by climate, fire, and herbivory rather than by resources alone
3703 (Sinclair and Krebs, 2002; Bond 2005; Stevens *et al.*, 2022). Furthermore, large parts of the
3704 planet are consumer driven, especially where fire and herbivory keep vegetation in early
3705 successional stages (Bond, 2005), and with evidence that natural disturbance effects can
3706 reorganize ecological relationships, without producing one main response form across all
3707 systems (Moi *et al.*, 2020).

3708

3709 For management, this means noise reduction by itself is unlikely to shift predator-prey structure
3710 unless it is paired with actions that reduce the structural conditions around idle wells that can
3711 concentrate prey and improve predator foraging, like reducing edge contrast, limiting perch
3712 opportunities, and restoring vegetation structure (Dickman, 1999; Planillo *et al.*, 2015; Sanders

and Chalfoun, 2018; Boucher *et al.*, 2022). A more effective approach is to manage infrastructure footprint and post-disturbance habitat configuration together, because the strongest responses in this study were associated more clearly with structural context than with sound alone, and because long-term ecological inference in grasslands is strongest when disturbance and consumer effects are considered jointly rather than alone (Turkington, 2009; Stevens *et al.*, 2022; Bond, 2005).

4.5 References Chapter 4

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5 CHAPTER 5. Conclusions and management implications.

The thesis examines how conventional oil infrastructure and its associated noise influence the predator-prey assemblages in mixed-grass prairies, separating direct from indirect effects across trophic levels. Using a mix of field experiments and observational data, I first compared predator abundance with distance to real idle well infrastructure and to experimental noise sites to ask whether responses were driven by structure, sound, or both, and whether patterns followed an intermediate-disturbance strategical framework. I then quantified how idle wells affect Richardson's ground squirrel burrowing and, in turn, vegetation composition and spatial configuration. Finally, I tested alternative regulatory pathways with piecewise SEM, evaluating predator-shield, mesopredator-release, noise-avoidance, and prey-attraction hypotheses. The mixed results did not support a single or a simple trophic mechanism. Predators and prey showed species-specific responses to the oil infrastructure and its associated sound; idle wells increased the burrow area and reshaped the landcover. Small mammals and raptors were positively linked across treatments, with only weaken, context-dependent evidence for generalized predator shield, mesopredator release, or noise-driven prey avoidance. Overall, habitat structure and disturbance history determined where predators and prey were found and how they interacted, whereas infrastructure and noise influenced the strength and location of these interactions but did not consistently change the direction of predator-prey relationships.

4164 Altogether, predator responses to infrastructure and its associated noise were species specific
4165 and scale dependent rather than consistently explained by a single disturbance hypothesis and
4166 physical infrastructure and its persistence on the landscape were generally more important than
4167 the associated noise alone in shaping predator-prey assemblages responses. The clearest and
4168 most consistent pattern was that long-standing idle well infrastructure altered habitat structure,
4169 increased ground squirrel burrowing activity, changed landcover composition, diversity, and
4170 spatial configuration, and created conditions associated with localized prey concentration and
4171 predator use. Predator-prey associations were better explained by context dependent prey
4172 concentrations and the habitat structure than by a consistent predator-shield or mesopredator
4173 release pathway. Together, these findings show that oil development infrastructure and its
4174 associated noise do affect grassland predator-prey assemblages, but the strongest and most
4175 consistent effects were driven by long lasting changes to the habitat structure and by the
4176 indirect effects on vegetation and prey distribution, rather than by noise alone. Overall, the
4177 results show that the impacts of oil development operate through multiple pathways and across
4178 spatial scales, including direct structural disturbance, indirect changes mediated by ecosystem
4179 engineers, and trophic responses within the food web, which occur simultaneously rather than
4180 through a single top-down or bottom-up process.

4181
4182 This work was motivated by widespread population declines in grassland species and by the
4183 challenge of separating the effects of physical development from sound and from food-web
4184 interactions. Some of the North American grassland's wildlife is declining because of diverse
4185 factors related with human development. Small mammals and grassland birds are declining in

4186 number across large areas of the remaining prairies (Douglas *et al.*, 2023, Medd *et al.*, 2024).
4187 Human development in north American grasslands include oil and gas development and some
4188 of its associated impacts like access roads, anthropic sound, light pollution, and vegetation
4189 changes can reduce nesting success and shift where predators and prey spend time (Bernath-
4190 Plaisted and Koper, 2016; Proulx *et al.*, 2019; Francis and Barber, 2013; Rosa and Koper, 2021).
4191 How much either oil development infrastructure or noise alone or together affects wildlife
4192 interactions is still not fully clear due the complexities of isolating their effects. Furthermore, it
4193 is also difficult because grassland communities are linked through food webs, so noise effects
4194 can be masked or altered by wildlife interactions like predation or competition (Knight *et al.*,
4195 2012, Rosa and Koper 2021).

4196

4197

4198 Sound should be treated as a distinct form of disturbance that can influence how acoustically
4199 oriented rodents use exposed microsites. Rather than acting only through amplitude or
4200 frequency, sound may alter masking risk, predictability, and the availability of quiet windows
4201 (Dent *et al.*, 2018; Elmer *et al.*, 2021). When possible, oil development operations that preserve
4202 quiet windows and reduce disruptive acoustic patterns should be preferred. Management
4203 should also recognize that raptors were concentrated near centre points mainly in silent patches
4204 or where quiet windows occurred. This pattern is consistent with visually guided hunting and
4205 perch use responding to local prey accessibility (Andersson *et al.*, 2009), and with aggregative
4206 responses that track capture opportunity more than prey abundance (Kocina and Aagaard,

2021). It also suggests that local clustering can arise from movement decisions made across larger areas, even when the observed effects appear only at tens to hundreds of metres (Watson, 2020; Kocina and Aagaard, 2021). This implies that minimizing perch-like structures and sightline enhancements that increase hunting efficiency in sensitive areas can reduce local predator concentration, especially because prairie raptors can switch among low natural and artificial perches depending on structure and visibility, and small changes in perch height relative to vegetation can shift prey visibility and hunting efficiency (Andersson *et al.*, 2009; Coates *et al.*, 2014; Parayko, 2021). For taxa that showed weak or no distance patterns, including species that may respond through behaviour rather than counts or at broader spatial scales, management should not assume no risk, but should instead reduce persistent attractants that can alter movement routes and encounter rates (Martin, 1987; García and Arroyo, 2005; Planillo *et al.*, 2015; Tate and Amar, 2017). Finally, because repeated short-range movements can concentrate detections in the same centres without increasing total abundance (Leibold *et al.*, 2004; Hambäck and Englund, 2005; Olsson and Bolin, 2014), the most effective actions should prevent the formation of several small hotspots (Fahrig, 2020; Szangolies *et al.*, 2022), by shrinking, and rapidly recovering footprints while managing sound patterns and structural features that increase the use of small local patches.

The long-term breeding bird surveys and population trend models show a sustained negative trend for most prairie specialists, increasing the risk that management practices mistakes in prairie ecosystems will further reduce the already declining populations and make conservation efforts less effective (Smith and Edwards 2021). As bird populations decline their ability to

4229 recover from additional disturbance becomes more limited and even small changes in habitat
4230 quality or configuration can have greater effects on survival and reproduction. Work from prairie
4231 landscapes have demonstrated that energy development infrastructure and its associated
4232 impacts, can reduce nesting success and shift species occurrence by altering habitat suitability
4233 and predator-prey interactions (Bernath-Plaisted and Koper 2016; Proulx et al. 2019). These
4234 changes can increase exposure of nests to predators, modify movement patterns, and
4235 concentrate predators in areas where prey are more accessible. As a result, effective mitigation
4236 needs to address not only where infrastructure is placed, but also how it alters vegetation
4237 structure, spatial configuration, and ecological interactions after installation.

4238

4239 Chapter 3 showed that idle wells increased the total burrow area, shifted vegetation from
4240 grasses toward sagebrush, raised local diversity indices near well centres, and produced more
4241 dispersed landcover patterns. These outcomes tracked infrastructure size and duration, fencing,
4242 ground disturbance, and protracted connection to power, creating bare ground and patchy
4243 cover that ground squirrels prefer (Muehlenbachs 2017; Alboiu and Walker 2019; Utting and
4244 Heshka 2019, Tamian *et al.*, 2024). Idle wells appear to influence prairie structure not only
4245 directly through persistent disturbance but also indirectly by promoting the activity of an
4246 ecosystem engineer. Richardson's Ground Squirrels were more abundant in more open sites
4247 with lower sagebrush cover and increased burrows near idle wells was associated with shifts in
4248 landcover composition, diversity, and configuration. This suggests that part of the ecological
4249 footprint of idle wells is mediated through habitat modification driven by an ecosystem
4250 engineer, where burrowing, soil disturbance, and vegetation use (e.g. vegetation clipping) could

4251 help maintain patchy open conditions and contribute to local landscape heterogeneity. This
4252 indirect pathway is important because it extends the effect of infrastructure beyond the well
4253 itself and links physical development to broader changes in prairie habitat structure.

4254

4255 Alberta has a large amount of inactive and orphaned wells; assessments outline both risks and
4256 opportunities for remediation and stimulus programs (Utting and Heshka 2019; Bankes 2020;
4257 Kang *et al.* 2021; Nichol 2023). Pairing well site cleanup with landcover recovery and small
4258 topographic scale repair can reduce unintended attraction of small prey and the secondary
4259 concentration of predators documented at real idle well infrastructure, while also addressing
4260 potential contamination liabilities (Alboiu and Walker 2019). Because configuration changed
4261 along with composition, reclamation must target spatial pattern, not only species lists.
4262 Rebuilding clustered grass cover and reconnecting patches should improve functional
4263 connectivity and reduce concentration of prey and predators in disturbed cores. Monitoring
4264 could include spatial indicators such as patch clustering to verify movement toward reference
4265 conditions, alongside standard vegetation and species metrics (Collins 2000; Harlio *et al.* 2019;
4266 Aswi *et al.* 2021).

4267

4268 The most consistent pathway found in Chapter 4 was a positive small-mammal to raptor
4269 relationship across all treatments. Top predators and mesopredators often co-occurred with
4270 prey rather than excluding them. Since generalized predator shields were weak and
4271 mesopredator-release cascades uncommon, management should emphasize landscape

4272 structure rather than trying to engineer trophic cascades. Maintaining heterogeneous grassland
4273 mosaics with appropriate vegetation height, bare-ground availability, and intact burrow
4274 complexes can stabilize prey production that in turn organizes predator space use, with or
4275 without development (Wiens and Rotenberry 1979; Wiens and Rotenberry 1981; Crooks and
4276 Soulé 1999; Prugh *et al.* 2009). The contrast between silent and real idle well infrastructure
4277 helps separate structure from sound. Silent sites often resembled controls in pathway structure,
4278 while real idle well infrastructure, with larger and longer-standing footprints, was linked to
4279 stronger prey concentration and positive consumer links. When immediate reclamation
4280 management is not possible, reducing the footprint by reducing the pad size and unnecessary
4281 fences, and re-establishing native grasses to limit persistent prey hotspots that can draw
4282 multiple predator guilds into sensitive or endangered prey species and nesting landscapes used
4283 by grassland birds might be useful (Planillo *et al.* 2015; Sanders and Chalfoun 2018; Boucher *et*
4284 *al.* 2022).

4285

4286 Noise management in oil development should be preventive even when community wide
4287 effects appear limited. Noise can interfere with acoustic cues used by predator-prey
4288 assemblages, altering vigilance, movement, and hunting efficiency, at fine spatial or temporal
4289 scales that are not only captured by abundance data, and can still affect survival and
4290 reproduction. Predictable chronic noise and intermittent or unpredictable regimes did not
4291 consistently displace prey or reorganize trophic links but noise type sometimes altered single
4292 interactions. Implementing setback distances as buffer areas that can prevent noise from
4293 reaching habitats used by sensitive bird assemblages, avoiding high-amplitude noise events, and

4294 scheduling operations avoiding high-frequency emissions during critical breeding periods might
4295 result in better management practices. Where noise cannot be avoided, habitat management
4296 that maintain visual cover for prey and clear flight lines for raptors can be developed (Shannon
4297 *et al.* 2016; Duquette *et al.* 2021).

4298

4299 Spatial planning can incorporate the SEM findings directly by designing buffer zones that match
4300 how species actually use space. Instead of applying a single fixed setback distance, buffers
4301 should reflect the spatial extent over which small mammals are attracted to infrastructure, the
4302 foraging ranges of raptors, and the movement patterns of mesopredators. In practice, mapping
4303 ground-squirrel colonies and other areas of high prey density, avoiding as possible, the
4304 placement of new infrastructure within those areas and their surrounding zones of influence,
4305 and possibly more important, prioritizing decommissioning the orphaned infrastructure where
4306 strong prey-attraction patterns indicate increased predator activity. (Lefcheck 2016; Dyck *et al.*
4307 2025). Where active development already exists, vegetation management that reduces edge
4308 contrast and concentrates cover away from nests can lower encounter rates for nest predators
4309 (Bernath-Plaisted and Koper 2016). Building from site design to landscape tools, managers can
4310 also use natural disturbances to shape where prey and predators congregate.

4311

4312 Fire, grazing, flooding, and large herbivores reset vegetation and burrow availability. Managers
4313 can use these disturbances to manage where prey and predators congregate. Prescribed fire
4314 and bison or cattle grazing can be timed and placed to redistribute forage and cover, shaping

4315 small-mammal colonies and raptor hunting areas at scales relevant to nest success. These tools,
4316 together with well-site reclamation, could potentially help prevent prey from concentrating in
4317 legacy footprints associated with stronger prey-consumer relationships (Wiens and Rotenberry
4318 1981; Terraube and Bretagnolle 2018; Fronhofer *et al.* 2018; Del Vallé *et al.* 2025). Decision
4319 making should also be guided by monitoring that tracks the components shaping these
4320 relationships, such as small-mammal dynamics, avian predator activity, and songbird nests.

4321

4322 Policy can align with this evidence by adding biodiversity surveying to orphan-well liability
4323 frameworks. Programs that rank wells for decommissioning can include ecological criteria like
4324 proximity to priority bird habitats, demonstrated prey attraction, and nest-predator density.
4325 Targeting sites that combine environmental risk with strong predator-prey linkages can
4326 potentially maximize benefits from public funds and regulated industry contributions. Post
4327 closure monitoring should verify reductions in prey attraction and document vegetation
4328 recovery consistent with regional species conservation plans (Muehlenbachs 2017; Utting and
4329 Heshka 2019; Bankes 2020; Nichol 2023; Smith and Edwards 2021).

4330

4331 At the project scale, mitigation should reduce the chance that infrastructure creates high-
4332 resource patches for prey. Designs that minimize persistent bare ground, avoid spoil piles that
4333 mimic natural mounds, and quickly establish native cover can limit burrow expansion and
4334 rodent concentration, which Chapter 3 linked to stronger positive prey-consumer paths at real
4335 idle well infrastructure (Alboiu and Walker 2019; Proulx *et al.* 2019). Where attraction already

4336 exists, disperse prey resources through targeted habitat manipulation, and use focused predator
4337 management only where necessary and permitted, given the weak evidence for durable top-
4338 down cascades.

4339

4340 Although these conclusions are supported within this study system, several limitations should
4341 be recognized. There is a level of uncertainty due methodological constraints (e.g. spatial scales,
4342 many species with various abundances, life stages, and detectability) Most responses were
4343 measured as the total number of individuals or activity indices rather than direct demographic
4344 rates, so some mechanisms remain inferential. Species responses were also variable across
4345 guilds and scales, which means that weak effects for some taxa should not be interpreted as
4346 absence of ecological risk. In Chapter 3, the relationship between burrow abundance and
4347 landcover structure supports an ecosystem engineering pathway, and the results indicate that
4348 ground squirrel burrowing activity actively reduces vegetation and maintains open patches over
4349 time, although the observational design does not fully separate this process from initial habitat
4350 selection.

4351

4352 Future research should test whether the burrow mediated changes documented here can
4353 translate into direct demographic consequences for other prairie specialists. Longitudinal
4354 studies before and after reclamation could determine whether reducing burrow attraction and
4355 restoring grass continuity also reduce predator concentration and improve prey reproductive
4356 success. Additional work should also examine whether noise effects are more detectable

4357 through behaviour, stress, or reproductive performance than through abundance alone, and
4358 whether ecosystem engineering effects of ground squirrels persist or weaken through time as
4359 reclaimed sites recover.

4360

4361 Finally, the broader conservation picture requires integrating infrastructure policy with the
4362 grassland species recovery. The declines of some species like small mammals and songbirds
4363 documented by regional and continental trend models will not reverse without protecting large,
4364 connected grasslands, aligning energy footprints with low-conflict areas, and restoring sites that
4365 act as prey magnets (Smith and Edwards 2021; Bernath-Plaisted and Koper 2016). The results
4366 here suggest that reducing structural attraction at real idle well infrastructure, maintaining
4367 heterogeneous habitat, and addressing the pending management of idle and orphan wells are
4368 practical steps that can be implemented now, while continued monitoring with piecewise SEM
4369 provides a transparent way to test whether these actions are shifting predator and prey
4370 conditions in the desired direction (Lefcheck 2016; Dyck *et al.* 2025).

4371

4372

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