

2019 Project Abstract

For the Period Ending June 30, [2023]

PROJECT TITLE: Spruce Grouse as Indicators for Boreal Forest Connectivity

PROJECT MANAGER: Julia B Ponder, DVM, MPH

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FUNDING SOURCE: Environment and Natural Resources Trust Fund

LEGAL CITATION: M.L. 2019, First Special Session, Chp. 4, Art. 2, Sec. 2, Subd. 03e

APPROPRIATION AMOUNT: \$350,000

AMOUNT SPENT: \$344,910

AMOUNT REMAINING: \$5,090

Sound bite of Project Outcomes and Results

We suggest that forest management to promote dense understory structure in boreal forest may provide climate refugia for various species of early successional forest wildlife. The landscape context should also be considered in forest planning in a changing climate to ensure that landscape connectivity is managed to meet wildlife needs.

Overall Project Outcome and Results

We completed a 4-year study (2019-2022) to examine spruce grouse (*Canachites canadensis*) occupancy of conifer forest patches, responses to timber harvest, and genetic connectivity in the boreal forest of northern Minnesota. We conducted a pellet survey of forest stands during late winter/early spring and documented the presence/absence of spruce grouse and other forest wildlife species, as it related to various landscape and forest attributes and climate variables. We examined changes in spruce grouse survival and space use in response to timber harvest with radio-marked birds. We also collected feathers from hunters and during capture efforts to examine landscape connectivity for spruce grouse using genetic methods. Our occupancy results indicated that forest management practices that promote dense vegetation structure may benefit spruce grouse, especially a dense mid-canopy layer (5.0 – 15.0 m). The mid-canopy layer was not as important for the other wildlife species we examined. Our telemetry data indicated that spruce grouse have lower survival after timber harvest, but that most harvested conifer stands were avoided prior to harvest, likely due to the sparse midstory vegetation structure in many of these mature stands. We suggest that reduced spruce grouse survival after timber harvest may be due to indirect effects of timber harvest, such as harvest-related changes in predator behavior or predator space use (e.g., edge effects, changes in predator density in nearby stands) rather than habitat loss. Finally, our genetic data indicated that spruce grouse exist as a single interconnected population in Minnesota, with coniferous forest land cover and lower average temperatures during spring dispersal being the best predictors of gene flow. Therefore, climate change could potentially threaten the persistence of the single interconnected population.

Project Results Use and Dissemination

We gave a field presentation to DNR Region 2 Assistant Wildlife Managers (August). We will present for 1) the Northeast Regional Landscape Minnesota Forest Resources Council (October), 2) The Wildlife Society Annual Meeting in November, 3) a DNR hosted Wildlife Research Webinar (December), 4) the Midwest Fish and Wildlife Conference (January), and 5) at the Minnesota Chapter of The Wildlife Society (February). A freelance reporter is writing a story on the study for release winter 2023. We submitted a manuscript on Activity 1 to *Forest Ecology and Management*. At least 2 more manuscripts will be submitted to scientific journals soon.



Environment and Natural Resources Trust Fund (ENRTF)

M.L. 2019 ENRTF Work Plan (Main Document)

Today's Date: 31 July 2023

Date of Next Status Update Report: Final Report

Date of Work Plan Approval: 5 June 2019

Project Completion Date: 30 June 2023

Does this submission include an amendment request? No

PROJECT TITLE: Spruce Grouse as Indicators for Boreal Forest Connectivity

Project Manager: Julia B Ponder, DVM, MPH

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Location: Northeast and Northwest

Total Project Budget: \$350,000

Amount Spent: \$344,910

Balance: \$5,090

Legal Citation: M.L. 2019, First Special Session, Chp. 4, Art. 2, Sec. 2, Subd. 03e

Appropriation Language: \$350,000 the first year is from the trust fund to the Board of Regents of the University of Minnesota for the Raptor Center to evaluate how to best harvest timber in the boreal forest to enable wildlife with small home ranges, such as spruce grouse, to thrive in a changing landscape. This appropriation is available until June 30, 2023, by which time the project must be completed and final products delivered.

I. PROJECT STATEMENT: Our primary objective is to study how the composition, arrangement, and size of boreal forest stands influence wildlife use of forest stands to allow incorporation of wildlife needs in forest planning. Five scientific models predict that the spruce-fir forest will shift entirely north of the US border with warmer summers and drought. As these shifts occur, maintaining habitat patches close enough to each other to allow wildlife to move successfully between patches will be important to:

- Maintain sustainable populations
- Allow colonization of new areas in a changing landscape

The recently completed Sustainable Timber Harvest Analysis conducted under Governor Dayton's direction will result in the harvest of 870,000 cords with 30,000 additional cords of ash and tamarack on lands managed by the Department of Natural Resources for the next 10 years. Our study will provide data on how close forest patches of similar composition should be to each other to accommodate even the most short-ranging wildlife.

Spruce grouse prefer black spruce, jack pine, and tamarack stands with pilot data from Northwest Minnesota indicating that they use <200 acres year round, although they are capable of moving farther. Thus, spruce grouse are short-ranging. Species most likely to be adversely impacted by landscape fragmentation and habitat loss are those with limited movement capabilities or tendencies to make short movements, and those with very specific habitat requirements. Thus, spruce grouse may serve as a sentinel of connectivity deficiencies among stands and creation of forest islands. We propose to use spruce grouse as a sentinel species for other boreal species at both local and landscape scales.

Good sentinels are easy to survey and are common, so a lot of data can be collected easily. The first annual spruce grouse survey was launched in 2018 and provides a pellet survey methodology and large scale data set on spruce grouse occupancy of forest stands. Additionally, good sentinels for forest connectivity should also be sensitive to factors that impact forest connectivity, such as timber harvest, and should have high overlap with harvested stands.

- We will conduct pellet surveys to relate spruce grouse occupancy of forest stands to site- and landscape-level characteristics.
- We will examine factors like mean patch size, stand type, patch density, and mean distance to nearest conifer patch to understand their influence on forest connectivity for spruce grouse in a Minnesota landscape.
- We will examine spruce grouse responses to timber harvest by marking spruce grouse with radio-transmitters to monitor movements and survival before and after timber harvest. We will determine whether responses to timber harvest in winter differ from responses in summer.
- Finally, to identify existing forest connectivity issues, we will collect spruce grouse fecal pellets from across northern Minnesota to obtain genetic samples. We will relate landscape features to genetic isolation and connectivity.

II. OVERALL PROJECT STATUS UPDATES:

First Update March 1, 2020

We have initiated work on all 3 activities, including hiring 2 seasonal technicians to work on Activity 1, hiring 2 seasonal technicians to work on activity 2, and sending a first round of spruce grouse pellet and feather samples to University of Minnesota Genomics Center for genetic analysis for Activity 3.

Second Update September 1, 2020

Progress on the project was heavily impacted by the COVID-19 pandemic. Governor Walz's Executive Order (EO) 20-20 and 20-33 directed state employees to stay home except to perform essential work during 28 March – 4 May 2020. This halted fieldwork by five project staff, including two seasonal technicians working on Activities 1 and 3, two temporary technicians working on Activity 2, and the Principal Investigator (PI) leading field studies on all three activities at DNR. The Governor exempted fieldwork for research and surveys on 4 May in EO 20-48, but the DNR Commissioner wanted to ensure the safe return of staff to the field and thus a gradual return to field activities was implemented. One seasonal technician was authorized to return to the field on 8 May. On 27 May, the PI and another seasonal technician were authorized to resume fieldwork. The two seasonal technicians working on Activities 1 and 3 were no longer in employment with the DNR when fieldwork resumed because their two month appointments ended during the Stay-at-Home Order (April 30), and thus they did not resume fieldwork.

The timing of the Stay-at-Home Order overlapped with critical periods for all three activities. Pellet surveys for Activities 1 and 3, which were planned to occur March – April, were truncated by 50%, with only surveys in the western portion of the survey area completed before EO 20-20 went into effect. The eastern portion of the survey area generally has higher spruce grouse densities, so we expected the majority of our genetic samples to come from the eastern region, which could not be surveyed in April as planned. Similarly, spring capture efforts to meet objectives in Activity 2 were halted (April–mid May) at the beginning of the capture season when we expected to mark the majority of the birds for the study. We also could not radio-track the 18 birds that had already been marked.

We did not budget for a spring 2021 field season on Activities 1 and 3 and had planned for spring 2020 to be our final field season. For Activity 2, we did budget for spring 2021 field season, but it was supposed to be markedly smaller than the spring 2020 field season. Later capture and marking will necessitate later radio-tracking of a newly marked birds. The missed season did not come with a saving in expenditures because we had already hired technicians. With the current budget, we have several options. We can reduce Activity 2, to pay for another field season on Activities 1 and 3, and complete those activities with a 1-year delay. This hinges on being able to hire field technicians to begin work in Mar 2021. With the current funding, we would exhaust the current funds in Oct 2021 for fieldwork on Activity 2. This would allow for only 6 months of radio-tracking of birds marked in spring 2021, which is 25-50% of the expected radio-life, and also would not include the winter 2021-2022 timber harvest season. If we had additional funds to cover Activities 1 and 3, we could continue radio-tracking birds into December 2021. Two more months of radio-tracking would still miss most of the winter 2021-2022 timber harvest season and bird responses to it. If we had additional funds to offset unanticipated costs on Activities 1, 2, and 3, then we could complete all 3 Activities as planned, but with a 1-year delay.

Amendment Request as of 12/27/2020

Due to DNR hiring restrictions related to COVID-19, we are unable to hire seasonal personnel for the field work under the DNR service contract. In order to continue project progress and complete monitoring efforts of marked grouse, we are requesting to move funding for to be hired seasonal field personnel from the DNR service contract to the University of Minnesota personnel budget. The amount we are requesting to move is \$40,064. This request has no impact on the workplan or deliverables.

Amendment Approved by LCCMR **1/13/2021**

Amendment Request as of 3/1/2021

Based on conversations with LCCMR staff after submission of the September 1, 2020 report, we are requesting a 1-year extension for Activities 1, 2, and 3 due to COVID-impacts on field activities during spring 2020. We are completely repeating the spring 2020 field season to accomplish work for Activities 1 and 3 in spring 2021. Additionally, the bulk of our capture efforts to radiomark spruce grouse for Activity 2 will be completed 1 year later than planned, so we will need time additional time to complete this activity as well.

Amendment Approved by LCCMR 3/29/2021

Third Update March 1, 2021

We have hired technicians for the March/April 2021 fecal pellet surveys that were not completed in winter 2020. Winter collection of fecal pellets for genetic analysis will occur during March/April 2021.

In fall 2020, we captured and marked 22 spruce grouse, with several more birds captured during winter, increasing our total sample numbers to 59. Throughout the year, we monitored locations of the marked birds. During hunting season, we received 101 feather submissions for genetic analysis. UMGC has reported success extracting DNA from fecal pellets, but success was higher with feather samples. We would therefore like to work with hunters again in Fall 2021 (through Jan 2022) to augment the sample of feathers, and use fecal pellet samples to fill geographic gaps in data obtained from feathers.

On the Project Budget Sheet, we show a \$19,600 overspend on in-kind contributions. The in-kind contribution was higher than expected because 1) we could not capture birds during the spring of 2020 because of the Stay-at-Home-Order and tried to recover from that unplanned interruption in field work, and 2) we could not immediately hire a full-time replacement for a departing technician because of the state-hiring freeze. Thus the co-PI worked significant extra hours to address these COVID-related project issues to attempt to mitigate failure of the project. This additional in-kind will not be recovered, but rather is an unanticipated investment (and gift) of time by the co-PI. The impact of these extra hours by the co-PI is that the project remains on track to be successful IF additional funding can be secured. If it cannot be secured, than the impact is that the project will be the best it possibly could be in the face of COVID and without additional support.

Fourth Update September 1, 2021

We secured an additional \$74,578 from the Minnesota Department of Natural Resources to complete our objectives on Activity 2. We have completed Outcome 1 for both Activity 1 and Activity 2. We continue to make progress toward the remaining outcomes on all 3 Activities, including tracking radiomarked birds and sending samples for genetic analysis to UMGC.

Fifth Update March 1, 2022

We advertised for a post-doctoral associate to assist with analysis of data collected for all 3 Activities, with intent to begin a new hire on 1 June 2022. We continue to monitor radio-marked birds for Activity 2. We completed data collection for Activity 3 Outcome 1 and sent samples to University of Minnesota Genomics Center to complete genetic analysis for Activity 3 Outcome 2.

Sixth Update September 1, 2022

Post-doctoral associate was hired and began 1 year appointment 1 July 2022. Analysis of the spruce grouse pellet survey data is underway by the post-doctoral associate. Genetics data from UMGC is still pending and analysis will begin when it is received. All tracking of radio-marked grouse supported by this grant has been completed.

Seventh Update March 1, 2023

The post-doctoral associate has drafted a manuscript for publication using the pellet survey data (objective 1). Analysis for objective 2 has been started and will continue in the next few months. We received genetic data from UMGC on 15 February 2023, which was later than anticipated. The post-doctoral associate will begin work on the genetics objective (3) now and will attempt to complete this objective for the final report in June.

Final Report between project end (June 30) and August 15, 2023

The post-doctoral associate ended his appointment with University of Minnesota -Twin Cities in mid-June 2023, upon taking another position. Prior to his end date, he submitted a manuscript for Activities 1 and drafted one for Activity 3 that will be submitted for peer-reviewed publication this summer; a third is underway on Activity 2 that will also be submitted (likely this fall). We also submitted a Final Report to the Minnesota Department of

Natural Resources, which will be made available online. The Summary of Findings for the Final Report is excerpted below:

- We completed a 4-year study (2019-2022) to examine spruce grouse occupancy of conifer forest patches, responses to timber harvest, and genetic connectivity in the boreal forest of northern Minnesota.
- Our occupancy results indicated that forest management practices that promote dense vegetation structure may benefit spruce grouse, especially a dense mid-canopy layer (5.0 – 15.0 m).
- Our telemetry data indicated that spruce grouse have lower survival after timber harvest, but that most harvested conifer stands were avoided prior to harvest, likely due to the sparse midstory vegetation structure in many of these mature stands. We suggest that reduced spruce grouse survival after timber harvest may be due to indirect effects of timber harvest, such as harvest-related changes in predator behavior or predator space use (e.g., edge effects, changes in predator density in nearby stands) rather than habitat loss.
- Our genetic data indicated that spruce grouse exist as a single interconnected population in Minnesota, with coniferous forest land cover and lower average temperatures during spring dispersal being the best predictors of gene flow. Therefore, climate change could potentially threaten the persistence of the single interconnected population.

III. PROJECT ACTIVITIES AND OUTCOMES:

ACTIVITY 1 Title: *Study wildlife use of forest stands through fecal pellet surveys*

Description: We will conduct ≥ 125 pellet surveys in conifer stands throughout northern Minnesota during winter when pellets contrast strongly against the snow. We will record the location and species type of all pellets encountered along transects. We will measure forest characteristics at the stand level including stand type, vegetation structure, and age or size class. We will also use GIS mapping software to determine mean distance between forest patches, mean patch size, patch density, patch contiguity or similar characteristics related to forest patch connectivity. These data will help understand wildlife use of forest stands that vary in size, composition, and arrangement, as well as characteristics of patches that are not used.

ACTIVITY 1 ENRTF BUDGET: \$ 67,932

Outcome	Completion Date
1. Fecal pellet surveys (125) along transects in conifer stands during winter	<i>April-2021</i>
2. Determine how wildlife use forest stands and how this is related to stand characteristics and isolation	<i>June 2023</i>
3. Make recommendations for forest planning to promote landscapes that wildlife can use after harvest or habitat loss	<i>June 2023</i>

First Update March 1, 2020

We have hired 2 seasonal technicians to conduct pellet surveys 2 March - 30 April 2020 throughout northern Minnesota.

Second Update September 1, 2020

We completed two repeat fecal pellet surveys of transects in the western portion of the survey region before EO 20-20 took effect, encompassing ~50% of the planned survey region. Importantly, our 3rd repeat survey was not completed for most of these survey transects, which is necessary for the Multi-Species Occupancy Modeling (MSOM) approach we plan to use to determine how wildlife use forest stands as it relates to stand

characteristics and isolation. This modeling approach is groundbreaking, and alternative analytical options have not yet been developed that would be able to make use of just two surveys in a detection framework. A third survey in the same field season is necessary to meet the assumptions of the MSOM analysis so that we can make recommendations for forest planning to promote landscapes that wildlife can use after harvest or habitat loss.

We plan to repeat the pellet surveys in spring 2021, if we do not face additional obstacles stemming from the pandemic and associated hiring freeze. Assuming that we are able to hire seasonal help to collect the data in spring 2021, we propose that we use funds previously planned for Activity 2 to complete Activities 1 and 3 this fiscal year. An additional season for Activity 1 (which also serves to accomplish Activity 3) will cost \$31,838, which includes additional fleet costs for staff to ride in separate vehicles to prevent the spread of COVID-19. If additional funds could be available for use in July 2021, they could be applied to Activity 2 thereafter. Under this scenario, our products for Activity 1 will be delayed by 1 year, with a revised completion date of December 2022, but we should be able to deliver the originally proposed products. If additional funds are not available, we would have to choose whether to spend available funds on Activities 1 and 3, at a cost to Activity 2, or compromise deliverables on all 3 Activities. We would prefer to realize some of our proposed deliverables, but many uncertainties make planning difficult at this stage. In particular, repeating the spring season for Activity 1 requires that the hiring freeze ends and that we are able to hire seasonal help to begin Mar 2021. As currently planned, a post-doctoral associate would work on the MSOM analysis, interpretation of wildlife use of forest stands, and recommend forest planning for wildlife after timber harvest or habitat loss. This also assumes that the hiring freeze does not preclude hiring a post-doctoral associate after the data are collected next spring.

Third Update March 1, 2021

We have hired 2 seasonal technicians to conduct pellet surveys 1 March – 29 April 2021. We need to repeat the entire spring 2020 field season due to COVID-19 impacts on the study. A second field season was not originally planned.

Fourth Update September 1, 2021

Fecal pellet surveys were completed at 290 transects throughout spruce grouse range in Minnesota during the March/April 2021 season. Fecal pellet surveys in 2021 covered the spruce grouse range more intensively than the survey in 2020, which was cut short by the Stay-at-Home Order. During spring 2021, we also measured forest characteristics at the stand level at each of 2 plots on 226 transects throughout the central and eastern part of spruce grouse range in Minnesota. This complements the 217 forest stand measurements completed at 119 survey transects in the western portion of the spruce grouse range in 2020, before the Stay-at-Home Order. Thus, forest characteristics were measured at stands throughout the spruce grouse range during the 2 year period.

Fifth Update March 1, 2022

We are advertising for a post-doctoral associate to help with analysis of data for this activity as part of Outcomes 2 and 3.

Sixth Update September 1, 2022

Post-doctoral associate has been hired and is in the process of analyzing the data collected. The summary report and recommendations for forest planning will be based on these analyses.

Seventh Update March 1, 2023

A manuscript for this objective has been completed and will be submitted to a peer-reviewed journal shortly. Outcomes 2 and 3 for this objective are addressed in this manuscript, completing all 3 outlined outcomes in preparation for the final report.

Final Report between project end (June 30) and August 15, 2023

A manuscript entitled “Forest structure mediates occupancy and extinction of early successional forest vertebrates on the training edge of the boreal forest” has been submitted for peer-review to Forest Ecology and Management. Below a summary of findings is excerpted from the MNDNR Final Report,

- Our models suggest mid-canopy density was the key stand-scale determinant of spruce grouse occupancy and persistence, which is likely related to cover from predators and thermal protection.
- Forest structure may be a stronger determinant of spruce grouse habitat selection than stand type, which may explain the widely varying descriptions of stand types used by spruce grouse in the literature.
- We also found deciduous forest cover to be a key factor limiting the range of spruce grouse.
- The strongest predictors of both occupancy and local extinction probabilities for spruce grouse were landscape-scale land-cover variables and mid-canopy density (5-15 m).
- Temperature was a predictor in the most-supported multivariate extinction model but had a small effect relative to land cover, road density, and canopy structure.
- Road densities were positively related to spruce grouse extinction probability. Road densities may be positively associated with predator density, which can affect prey species occurrence (Boan et al. 2014). Road density may also be correlated with hunter accessibility and localized harvest pressure near roads. Areas with fewer roads may promote spruce grouse persistence.
- Spruce grouse and ruffed grouse occurrence aligns with a coniferous-deciduous forest gradient with co-occurrence most probable in the mixed coniferous/deciduous transition zone. The land cover-based gradient coincides with the large-scale latitudinal transition from northern boreal forests to southern deciduous forests. This transition zone is expected to shift northward as climate warms and deciduous forests replace boreal forests (Taylor et al. 2017). Our work suggests that ruffed grouse are likely to replace spruce grouse as a result of changing habitat conditions in the study area.

ACTIVITY 2 Title: *Study spruce grouse movements after harvest of stands where they were captured*

Description: We will capture 70 spruce grouse in black spruce and jack pine stands scheduled for timber harvest and attach radiotransmitters. We will monitor movements before, during, and after timber harvest of black spruce in winter and jack pine in summer. Birds will be marked and monitored to capture responses to timber harvest during different portions of the life cycle. During winter, spruce grouse face thermoregulatory challenges, dietary constraints, and contrast strongly against the snow. During summer, spruce grouse have broods that may constrain responses of females. By monitoring spruce grouse responses during both winter and summer, we will gain a more complete understanding of how birds respond to habitat loss at different times of year, and whether loss of habitat within a substantial portion of the home range is a short-term or more chronic stressor. We will also determine if spruce grouse move to the nearest conifer forest stand, or farther, and whether there is substantial mortality risk of moving in an open landscape. We will examine movements before, during, and after timber harvest and examine areas used during these periods.

ACTIVITY 2 ENRTF BUDGET: \$ 220,531

Outcome	Completion Date
1. Capture spruce grouse (70) in stands planned for harvest and attach transmitters	Nov 2021
2. Monitor spruce grouse movements following timber harvest	April 2022
3. Recommend configuration of stands to optimize wildlife response to timber harvest	June 2023

First Update March 1, 2020

Two seasonal technicians were hired and began work 23 November 2019 to capture, radio-mark, and track spruce grouse in or near black spruce and jack pine stands planned for harvest during winters 2019-2020 and

2020-2021 and summers 2020 and 2021. We have captured 8 spruce grouse to date and expect most captures to occur in the spring as birds begin spending more time on the ground. As of February 14, we have located the birds 91 times and obtained habitat plot measurements at their locations. We also have 13 additional locations and habitat data for unmarked birds located in or near the stands. Additionally, we are searching stands planned for timber harvest for pellets to examine use of stands before harvest when birds could not be located and captured before harvest. Sixteen stands have been searched and 8 stands have been harvested. Work will continue on this activity through 2022.

Second Update September 1, 2020

As of 27 March 2020, we had captured and marked 18 spruce grouse, but all capture and tracking efforts halted during the Stay-at-Home Order, when we had hoped to capture most of the 70 planned birds. Since the resumption of fieldwork in May after the spring capture window ended, we have utilized a variety of approaches (i.e., chick calls, pointing dogs) to attempt to mark birds. To date, we have captured and radio-marked 33 birds and have obtained 538 bird locations with habitat plot measurements. Additionally, we have completed habitat measurements at 30 timber stands scheduled for harvest. Twelve stands have been harvested in the Big Falls study area and 16 in the Norris Camp study area.

We had planned to capture and radio-mark most of sample of 70 spruce grouse in March and April 2020, with a smaller capture effort in 2021 to offset birds lost due to expiration of transmitters and bird mortality. This would have given us a large sample of birds to radio-track during the summer 2020, winter 2020-2021, summer 2021, and winter 2021-2022 timber harvest seasons, with a gradual attrition of the sample and less tracking effort needed over time. This large sample would produce robust sample sizes on which to base our recommendations for stand configuration.

Because we missed the first and largest planned capture season due to COVID-19, we now plan to capture and radio-mark most of the birds next spring, when spruce grouse are most easily captured. We will deplete currently available funds to track birds in Oct 2021, so birds marked in Apr 2021 can be tracked for only 6 months (25-50% of the expected radio life) with existing funds. This potential funding lapse will occur before the winter 2021-2022 timber harvest season, cutting our planned winter tracking by a full season. To deliver the originally planned product, we will need additional funds (\$82,420) to support 2 technicians (salary, fringe) and fleet costs for the following year, after we take into account the funds diverted to hire technicians to accomplish Activities 1 and 3 in FY21 (Total Additional Request = \$82,420 for all 3 activities). Our products for Activity 2 would then have an expected completion date of December 2023. Alternatively, we could not move funds from Activity 2 to Activities 1 and 3, but this will only result in 2.5 months of additional tracking, still falling short of the winter 2021-2022 timber harvest season. The consequence of this less favored alternative would be an inability to meet deliverables for Activities 1, 2, and 3. If additional funds are not available to support Activity 2, we will likely have too small a sample to be able to come to robust conclusions for winter timber harvest. We will be able to look at responses to timber harvest in the summer of 2021, but will not fully realize the potential information that could be obtained from radios that can last >1 year. Fewer birds tracked for fewer seasons will impact our ability to make recommendations for configuration of stands for wildlife benefits.

Third Update March 1, 2021

During fall 2020, we marked 22 spruce grouse as they came to roads for grit. We also marked several chicks of collared birds when they became large enough to carry a transmitter. To date, our sample is comprised of 59 birds. We have 1,392 bird locations (3–80 locations/bird) with habitat measurements. We currently have 27 radiocollared spruce grouse that we are tracking. Mortality has been due to hunter-harvest (8) and predators (20), which is expected for gamebirds. We could not determine a cause of death for a few birds, but collected carcasses for future necropsy. We are attempting to secure additional funding so that we can continue tracking birds for the life of the transmitters. We are facing budget shortfalls due to having to repeat the spring 2020 season and deploying transmitters later than originally planned. In order to offset these issues, we are seeking

additional funds from the DNR and American Bird Conservancy. If we do not receive additional funds, we will fall short of meeting our objectives on Activity 2. We are requesting an additional \$75,000 from the DNR and an additional \$20,000 from ABC.

Fourth Update September 1, 2021

As of 3 August, we had captured and radio-marked 77 spruce grouse, meeting our goal of 70 spruce grouse for this activity. We secured \$74,578 from DNR to continue the study through the spring of 2022, which offsets additional costs due to COVID. We did not receive additional funds from ABC. We anticipate meeting our objectives for Activity 2 with this new funding. As of 3 August, we had visited 2,454 bird locations and collected forest stand measurements at these locations.

Fifth Update March 1, 2022

We captured and marked 23 additional spruce grouse since the last report and continued to track them throughout the fall and winter. Unfortunately, timber harvest has been minimal near our marked birds this winter, which will limit our conclusions about timber harvest effects on marked birds.

Sixth Update September 1, 2022

All monitoring supported by this grant has been completed. Investigators used additional funding secured from the DNR to continue monitoring this spring to increase dataset and complete objectives for this activity. Analysis of data is underway and will be completed by post-doctoral associate.

Seventh Update March 1, 2023

The post-doctoral associate has identified birds with home ranges near harvested stands in preparation for the final analysis of movements in response to timber harvest. Analysis and writing will continue on this objective for the final report.

Final Report between project end (June 30) and August 15,-2023

A manuscript is in preparation for peer-reviewed publication. A summary of findings for this activity is excerpted below from the MNDNR Final Report, which will be made available online,

- Survival of spruce grouse in and near harvested stands declined after harvest.
- Most marked spruce grouse were near harvested stands, but spruce grouse were rarely within harvested stands even before harvest.
- Spruce grouse home range overlap with harvested stands decreased after harvest.
- Avoidance of many harvested stands before harvest indicates that many of these stands were not suitable for spruce grouse before harvest. Many stands mature enough to harvest in Minnesota may lack the dense vegetation structure necessary to support spruce grouse.
- Reduced survival near harvested stands might occur indirectly through edge effects or from predator displacement from harvested stands producing greater predator densities in nearby stands used by spruce grouse.
- Timber harvest may increase spruce grouse mortality but may also be necessary at some level to promote regeneration of stands with denser vegetation structure that supports spruce grouse (i.e., to avoid over-maturation of forests). We recommend maintaining areas with dense conifer forest structure for spruce grouse near harvested stands to provide cover from predators after harvest, while also being of sufficient size and structure to meet foraging, nesting, rood-rearing, and other needs of spruce grouse throughout the year.

ACTIVITY 3 Title: *Examine large scale connectivity of the forest using genetics of spruce grouse*

Description: We will collect >300 spruce grouse pellets during winter surveys to obtain DNA and perform a

landscape-level analysis of forest connectivity in the boreal forest region of Minnesota. Genetics allow the identification of long-term barriers to movement at a regional scale. Genetic structure quickly dissipates when barriers to movement are removed and individuals mix among previously isolated areas. We will examine existing boreal forest connectivity to identify any deficiencies in connectivity that currently exist. This information can be useful in forest planning to identify areas that might be more sensitive to further reductions in connectivity and also to provide a benchmark for future comparison.

ACTIVITY 3 ENRTF BUDGET: \$ 61,538

Outcome	Completion Date
1. Collect spruce grouse fecal pellets (>300) during winter	<i>April 2021</i>
2. Laboratory analysis of spruce grouse genetic samples	<i>June-2022</i>
3. Landscape analysis of genetic samples to examine large scale connections in the forest	<i>June 2023</i>

First Update March 1, 2020

To date, we have submitted 117 fecal pellet samples and 13 feather samples to the University of Minnesota Genomic Center (UMGC) for genetic analysis. UMGc has reported successful isolation of spruce grouse DNA from the samples based on amplification with microsatellite loci designed for gallinaceous species. We anticipate collecting additional samples during the upcoming pellet survey season beginning 2 Mar 2020.

Second Update September 1, 2020

In addition to the 130 samples previously reported, we collected 37 fecal pellet samples and 5 feather samples during fieldwork in winter 2020. We have also been collecting feathers from all 33 captured birds in Activity 2, as well as 7 eggshell membranes from hatched nests and 1 unhatched chick of radio-marked birds. However, our inability to survey the eastern portion of the survey region during the pandemic, where spruce grouse densities are higher, and collect fecal pellet samples, produced a deficit of ~100 samples. We plan to repeat the survey season in spring 2021, which would serve to complete both Activities 1 and 3 as originally described. We will not be able to meet the planned deliverables without another field season. Our completion date for the originally proposed deliverables would be delayed until June 2022. Without additional funding and the ability to hire 2 technicians to begin in Mar 2021, we would either not be able to complete both Activities 1 and 3, or have to use funds dedicated to Activity 2, further compromising results for Activity 2. Another field season for Activity 3 (and Activity 1) will cost \$31,838. The hiring freeze could also affect our ability to hire a post-doctoral associate to assist with the landscape analysis of genetic samples and interpretation of large-scale connections in the forest.

Third Update March 1, 2021

UMGC has reported success with extraction of DNA from fecal pellet samples. However, the DNA quality is lower for fecal pellets than it is from feather samples. We received 101 feather submissions from hunters during fall 2020 that will be included in the genetic analysis. We hired 2 seasonal technicians to collect pellet samples during 1 March 2021– 29 April 2021. We would like to work with hunters again in fall 2021 to increase our sample size of feathers for the analysis, and then use fecal pellet samples to address deficiencies in geography among the feathers. This will produce the best results for the study and help keep costs down.

Fourth Update September 1, 2021

We sent another shipment of samples to UMGc in July 2021. This shipment included 214 feather samples and 51 offspring samples (eggshell membranes and unhatched embryos) from our radio-marked birds. These samples amplify more reliably in the laboratory than fecal pellet samples, so we are focusing on the hunter-submitted feathers from 2020 and 2021, and samples derived from radio-marked birds, to ensure that we are as cost-effective as possible with the remaining funds. We anticipate that these approved changes will enable us to meet project outcomes on Activity 3, which otherwise, would be difficult to meet.

Fifth Update March 1, 2022

We submitted 88 additional feather samples from hunter-harvested and radio-marked birds, 7 eggshell membranes, and 1 tissue sample to the University of Minnesota Genomics Center in Dec 2021. Thus, we exceeded our goal of 300 genetic samples for Activity 3 and are now working on Outcome 2. We also began advertising for a post-doctoral associate to begin analysis of sample genotypes on 1 June 2022 to complete Outcome 3.

Sixth Update September 1, 2022

Genetic analysis of samples is still underway at the University of Minnesota Genomics Center. Analysis will begin when the results are received.

Seventh Update March 1, 2023

The second outcome for this objective was completed on 15 Feb 2023, later than anticipated (15 Nov 2022). We will initiate work for outcome 3 now and hope to complete this analysis in time for the final report in June 2023.

Final Report between project end (June 30) and August 15, 2023

A manuscript is nearing submission for peer-reviewed publication. We summarize findings below in an excerpt from the MNDNR Final Report which will be made available online,

- The spruce grouse population in Minnesota currently exists as a continuous population with no distinct spatial demes. Distinct spatial demes would indicate that gene flow is restricted and that barriers to connectivity and movement exist that fragment the population into separate subpopulations.
- Gene flow was positively related to lower spring temperature during dispersal and greater coniferous forest land cover.
- Two approaches to connectivity modeling gave complementary perspectives of genetic connectivity, highlighting greater potential for gene flow in the northeast and northwest than central portions of the study area. Both indicated several partial barriers to gene flow, including Red Lake and the Mesabi Range.
- Forest management to promote gene flow through conifer forest cover may influence the connectivity of this region for spruce grouse with climate change. Our data indicate the central part of the study area may be most vulnerable to climate change impacts to gene flow. The cooler northwestern and northeastern portions of spruce grouse range in Minnesota may provide climate refugia and maintain some spruce grouse gene flow and connectivity (Huntingford and Lowe 2007; Anderson et al. 2020).
- This research highlights climate change and associated changes in conifer forest cover as important considerations for spruce grouse population connectivity at their southern range periphery.

IV. DISSEMINATION:

Description:

Our findings will be communicated with state (e.g. DNR) and federal (e.g. USFS) land managers, as well as agencies tasked with forest management and timber harvest (counties, industry). Findings will be presented at state, regional, and national meetings (e.g., SAF, TWS) as appropriate given the results. Publications will be produced for peer-reviewed journals, outreach newsletters, and annually for the DNR's Summaries of Wildlife Research Findings. Media outreach will also be pursued.

The Minnesota Environment and Natural Resources Trust Fund (ENRTF) will be acknowledged through use of the trust fund logo or attribution language on project print and electronic media, publications, signage, and other communications per the [ENRTF Acknowledgement Guidelines](#).

First Update March 1, 2020

No activity to date.

Second Update September 1, 2020

We prepared a progress report for the DNR's Wildlife Research Summaries, which should be available on the DNR website this month. Additional information about how to contribute samples for the genetics study (Activity 3) is available in the DNR Hunting Regulations book and the Grouse Hunting page on the DNR website.

Third Update March 1, 2021

The progress report for the DNR's Wildlife Research Summaries is not yet available on the DNR website due to staffing shortages related to the hiring freeze and redeployments to assist with vaccine distribution. This report will be posted, but timing is uncertain.

Fourth Update September 1, 2021

The progress report for the 2019-2020 season is now available on the DNR website with DNR's Wildlife Research Summaries at <https://files.dnr.state.mn.us/wildlife/research/summaries/2019/upland/2019upland003.pdf>. The ENRTF logo is included in the report.

We anticipate another press release this fall to provide information about how hunters can contribute to the genetics study (activity 3) by submitting feather samples from birds they harvest. Information continues to be posted on the DNR Grouse Hunting page and also in the 2021 Hunting Regulations book.

Fifth Update March 1, 2022

We issued 2 press releases to engage the participation of hunters in the study.

Sixth Update September 1, 2022

No additional dissemination was done during this period.

Seventh Update March 1, 2023

No additional dissemination was done during this period.

Final Report between project end (June 30) and August 15, 2023

- A freelance reporter requested the Final Report on the study at the end of June for a piece that will come out early next year. We provided the MNDNR Final Report that included findings for all 3 Activities.
- We will contact hunters that submitted samples for the genetic objective and share the study results with them.
- We will also present our findings to wildlife managers at regional meetings, at the Midwest Fish and Wildlife Conference in South Dakota in late January 2024, and at the Minnesota Chapter of The Wildlife Society in February 2024.
- One manuscript has been submitted (Activity 1) and at least 2 additional manuscripts will be submitted for peer-reviewed publication in scientific journals in 2023.
- Genetic connectivity results will be included in a presentation at The Wildlife Society Annual Meeting in Louisville, KY, November 2023.

V. ADDITIONAL BUDGET INFORMATION:**A. Personnel and Capital Expenditures**

Explanation of Capital Expenditures Greater Than \$5,000: NA

Explanation of Use of Classified Staff: NA

Total Number of Full-time Equivalent (FTE) Directly Funded with this ENRTF Appropriation: 1

Enter Total Estimated Personnel Hours for entire duration of project: 2,080	Divide total personnel hours by 2,080 hours in 1 yr = TOTAL FTE: 1.0
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Total Number of Full-time Equivalent (FTE) Estimated to Be Funded through Contracts with this ENRTF Appropriation:

Enter Total Estimated Contract Personnel Hours for entire duration of project: 7,800	Divide total contract hours by 2,080 hours in 1 yr = TOTAL FTE: 3.75
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VI. PROJECT PARTNERS:

A. Partners outside of project manager’s organization receiving ENRTF funding

Name	Title	Affiliation	Role
Charlotte Roy	Research Scientist	MNDNR	Oversee field studies

B. Partners outside of project manager’s organization NOT receiving ENRTF funding

Name	Title	Affiliation	Role
Various staff	Foresters, Wildlife Managers	MNDNR	Identify timber stands for inclusion in study

VII. LONG-TERM- IMPLEMENTATION AND FUNDING:

This research will provide information to improve timber harvest planning in ways that are compatible with conservation of wildlife populations. We currently lack information to manage wildlife strategically with changing forest composition and predicted loss of spruce-fir forests from Minnesota. This study will reduce that information gap. Findings and results will be communicated to foresters and wildlife staff at the Department of Natural Resources, U. S. Forest Service, and private industry through presentations at professional meetings and peer-reviewed publications.

VIII. REPORTING REQUIREMENTS:

- Project status update reports will be submitted March 1 and September 1 each year of the project
- A final report and associated products will be submitted between June 30 and August 15, 2022

IX. SEE ADDITIONAL WORK PLAN COMPONENTS:

- A. Budget Spreadsheet**
- B. Visual Component or Map**
- C. Parcel List Spreadsheet N/A**
- D. Acquisition, Easements, and Restoration Requirements N/A**
- E. Research Addendum**

Attachment A:

Environment and Natural Resources Trust Fund

M.L. 2019 Budget Spreadsheet

Legal Citation: M.L. 2019, First Special Session, Chp. 4, Art. 2, Sec. 2, Subd. 03e

Project Manager: Julia B Ponder

Project Title: Spruce Grouse: Sentinels for Boreal Forest Connectivity

Organization: University of Minnesota

Project Budget: \$350,000

Project Length and Completion Date: 3 years, 30 June 2023

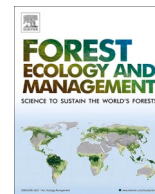
Today's Date: 31 July 2023



ENVIRONMENT AND NATURAL RESOURCES TRUST FUND BUDGET	Budget	Amount Spent	Balance
BUDGET ITEM			
Personnel (Wages and Benefits)	\$ 127,447	\$ 123,927	\$ 3,520
Project management (J Ponder) 5% effort (75% salary, 25% fringe) for 2 years; UM postdoc for 12 months *\$4000/mo. plus 22.4% fringe; seasonal field technicians \$27,324 + 31.8% fringe (\$40,064)			
Professional/Technical/Service Contracts			
DNR contract for field data collection (field technicians at \$2,782/mo.(\$85,126); fleet for 43 mos. @\$1,000/mo. (\$43,000); lodging and per diem for field crew (\$29,756); 3 telemetry flights to find missing birds @\$1,000 per flight (\$3,000); direct and necessary costs (\$25,841)	\$ 186,722	\$ 186,711	\$ 11
UMN Genomics Center: 300 samples @ \$44.88 per sample (\$13,660)	\$ 19,182	\$ 17,623	\$ 1,559
Equipment/Tools/Supplies			
Supplies to collect samples; 70 VHF transmitters @ \$200 each (\$14,000); tracking equipment (\$7,000); misc supplies (\$14,379)	\$ 16,649	\$ 16,649	\$ 0
COLUMN TOTAL	\$ 350,000	\$ 344,910	\$ 5,090

OTHER FUNDS CONTRIBUTED TO THE PROJECT	Status (secured or pending)	Budget	Spent	Balance
Non-State: Timber harvest on county lands will be conducted with existing funds and equipment		TBD	\$ -	
State: UM indirect costs at 54%		\$ 189,000	\$ 186,251	\$ 2,749
In Kind: DNR funds for additional monitoring (Activity 2)		\$ 116,035	\$ 116,035	\$ -
In kind: Matching funds for Charlotte Roy (MDNR, 0.10 FTE (9600)*2.5 years = \$10,000)		\$ 100,478	\$ 100,478	\$ -

PAST AND CURRENT ENRTF APPROPRIATIONS	Amount legally obligated but not yet spent	Budget	Spent	Balance
Current appropriation: No current appropriation		NA	\$ -	
Past appropriations: No past appropriation		NA	\$ -	



Forest structure mediates occupancy and extinction of vertebrate prey species on the trailing edge of the boreal forest

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Keywords:

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Forest structure
LiDAR
Multi-season occupancy model
Ruffed grouse
Snowshoe hare
Spruce grouse

ABSTRACT

Climate change is expected to shift the distributions of global biomes. High latitude biomes, such as the boreal forest, are among the most vulnerable and serve as a bellwether for the effects of climate change on other ecosystems. We examined patterns of occupancy, local extinction, and abundance in a guild of forest-associated vertebrate prey species on the southern margin of the boreal forest in Minnesota (USA). We used multi-season, multi-state, and multi-species occupancy modeling approaches to determine the effects of land cover, forest structural characteristics, and climatic variation on two boreal-associated species, spruce grouse (*Canachites canadensis*) and snowshoe hare (*Lepus americanus*), and a forest generalist, ruffed grouse (*Bonasa umbellus*). Occupancy, abundance, and extinction of spruce grouse was strongly associated with landscape-scale characteristics. In particular, deciduous forest cover may govern their southern range limit. Broadly, forest understory structure played a significant role in occupancy, extinction, and abundance patterns of all three species, with ruffed and spruce grouse generally associated with vegetation density in the lower and mid-canopy layer (5.00–15.00 m) and snowshoe hare associated with density in the shrub layer (1.37–5.00 m) in winter. Co-occurrence varied annually but was greatest in mixed forests during an uncharacteristically warm and snow-sparse year. Climatic variables (winter temperature and snowfall) were associated with extinction probabilities for all three species, but the effect was generally weaker than that of forest structure. Our results suggest that forest management practices that promote dense understory structure may help provide climate refugia for vertebrate prey species in boreal forest ecosystems.

1. Introduction

The center-periphery hypothesis of extinction predicts that peripheral populations are more vulnerable to extinction than central populations due to suboptimal habitat conditions, lower population densities, and greater stochasticity (Lawton, 1993). Despite greater extinction risk and generally lower genetic diversity, peripheral populations can have significant conservation value due to potential adaptation to marginal environmental conditions (Hardie and Hutchings, 2010). Deciding whether to prioritize peripheral populations for conservation has been a central focus of climate change adaptation (Lesica and Allendorf, 1995).

Climate change is causing warmer winter conditions and reduced snowfall in many regions. Therefore, habitats and wildlife species are broadly expected to shift northward and upward in elevation in the

northern hemisphere (Hickling et al., 2006). Accordingly, populations at the southern margin of species' distributions are expected to contract over the next several decades. In particular, boreal forests are expected to experience one of the most rapid shifts in distribution among the Earth's major biomes (Loarie et al., 2009). Those spatial and temporal shifts suggest conserving "trailing edge" populations (i.e., those at the low-latitude limit of a species' distribution) will be particularly challenging under changing climate conditions (Hampe and Petit, 2005). Understanding habitat and climatic requirements of boreal forest species at their southern range limits can inform climate adaptation strategies for conserving climate-sensitive wildlife species.

Climate change and land-use change are two of the strongest drivers of biodiversity loss globally (Travis, 2003; Maxwell et al., 2016). These processes can be interactive, and anthropogenic land use has the potential to harm (Jetz et al., 2007) or support (Morelli et al., 2012)

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climate-sensitive populations. Forest management can interact with climate change to either ameliorate or accelerate the negative effects of climate change on boreal forest wildlife (Virkkala, 2016). Prioritizing forest management practices that provide refugial habitat for climate-sensitive species could mitigate the effects of climate change. Despite this, most wildlife adaptation strategies have focused on large scale reserve-design planning initiatives, while local, management-relevant adaptation strategies have been largely ignored (LeDee et al., 2020).

One ecological community that appears particularly at odds with current climate mitigation priorities is early and mid-successional forest vertebrates. Climate adaptation strategies often prioritize maximizing carbon storage in managed forests, which may exacerbate the effects of climate change on wildlife dependent on early and mid-successional forest (Littlefield and D'Amato, 2022). Management strategies can improve overall adaptive capacity of forest ecosystems by acknowledging trade-offs between forest carbon storage and the need for climate refugia for early and mid-successional forest specialists.

In this study, we examined occupancy patterns of three early and mid-successional forest vertebrate prey species: spruce grouse (*Cathartes canadensis*), ruffed grouse (*Bonasa umbellus*) and snowshoe hares (*Lepus americanus*) at the southern margin of the boreal forest in northern Minnesota, USA. These three species overlap spatially in the winter, share predators, and exhibit approximately 10-year population cycles at northern latitudes (Williams et al., 2004, <https://www.adfg.alaska.gov/static/education/wns/grouse.pdf>, Pomara and Zuckerberg, 2017, although it is not yet known if trailing edge populations of spruce grouse cycle, Roy and Giudice, 2023). Population cycles have been hypothesized to be due to predator-prey interactions and delayed density dependence at northern latitudes (Williams et al., 2004), with raptors switching to ruffed grouse as snowshoe hare populations decline (Keith and Rusch, 1989). More recently, studies have found support for climate variability driving variability in demographic rates that produce population cycles at northern latitudes (Zimmerman et al., 2008, Yan et al., 2013, Pomara and Zuckerberg, 2017).

Spruce grouse ecology and distribution are closely associated with the boreal forest in North America (Schroeder et al., 2018). Although populations appear to be declining at their southern range margin (Ross et al., 2016), their ecology and status are not as well documented as many North American game birds. Furthermore, research has been focused primarily in the range of the *franklinii* subspecies, which occur within and west of the Rocky Mountains, with even less known about the *canadensis* subspecies that occurs throughout the eastern boreal forest of North America. The studies on the *franklinii* subspecies suggests spruce grouse prefer dense stands of spruce and fir trees, typically of short to intermediate height (Boag and Schroeder, 1987; Huggard, 2003). These forest characteristics may improve the survival and recruitment of young, which are important factors in population regulation (Boag et al., 1979). Recent work from the range of the *canadensis* subspecies has also documented an association with younger forests. In the Adirondack Mountains of New York, a decline in spruce grouse occupancy over thirty years was attributed to forest maturation (Ross et al., 2016). In Quebec, at the southern margin of the boreal forest, spruce grouse occupancy was associated with coniferous tree cover and deciduous shrub cover, and deciduous tree cover limited spruce grouse occupancy (Casabona et al., 2022). Because spruce grouse is likely to be affected by warming temperatures (Murray et al., 2017), we considered its niche/habitat for evaluation in the northern boreal forests of Minnesota.

The two other study species also rely on early to mid-successional forest but are more widespread and widely studied than spruce grouse. The ruffed grouse is the most widely distributed game bird in North America and uses coniferous, deciduous, and mixed coniferous/deciduous forests throughout its range (Rusch et al., 2000). Ruffed grouse require deciduous forest for forage (Svoboda and Guillon, 1972) and tend to use a mix of young and old stands due to the low cover provided by young trees and the substantial forage provided by older trees (Jones et al., 2008). Last, snowshoe hares are distributed

throughout northern North America and have several adaptations for survival in snow-covered landscapes (Wilson and Reeder, 1993). They have enlarged hind feet and stiff hairs that act like snowshoes in deep snow conditions, and they have seasonal camouflage, molting between brown (summer) and white (winter) coats to blend in with the surrounding landscape. Their reliance on seasonal camouflage for survival makes them particularly vulnerable to climate change, as temporal mismatches between seasonal molting and winter-white conditions can significantly increase predation rates (Zimova et al., 2016).

Our study area in northern Minnesota, USA (Fig. 1) encompassed two Ecoregions as defined by the Minnesota Department of Natural Resources Ecological Land Classification System: The Northern Minnesota and Ontario Peatlands and the Northern Superior Uplands. The study area occurred within the boreal-deciduous ecotone (Goldblum and Rigg, 2010), where the southern limit of the boreal forest meets the northern limit of hardwood-dominated forest. Common stand types in the study area included balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), tamarack (*Larix laricina*), white spruce (*Picea glauca*), and northern white cedar (*Thuja occidentalis*). Overall, the study area was comprised of ~73 % forested land cover including ~49 % coniferous forest (evergreen forest and wooded wetland cover types), ~15 % mixed coniferous/deciduous forest, and ~9 % deciduous forest land cover (Supplemental Table S1).

The objectives of our study were to determine the effects of land cover, climate, and forest structure characteristics on the occupancy, co-

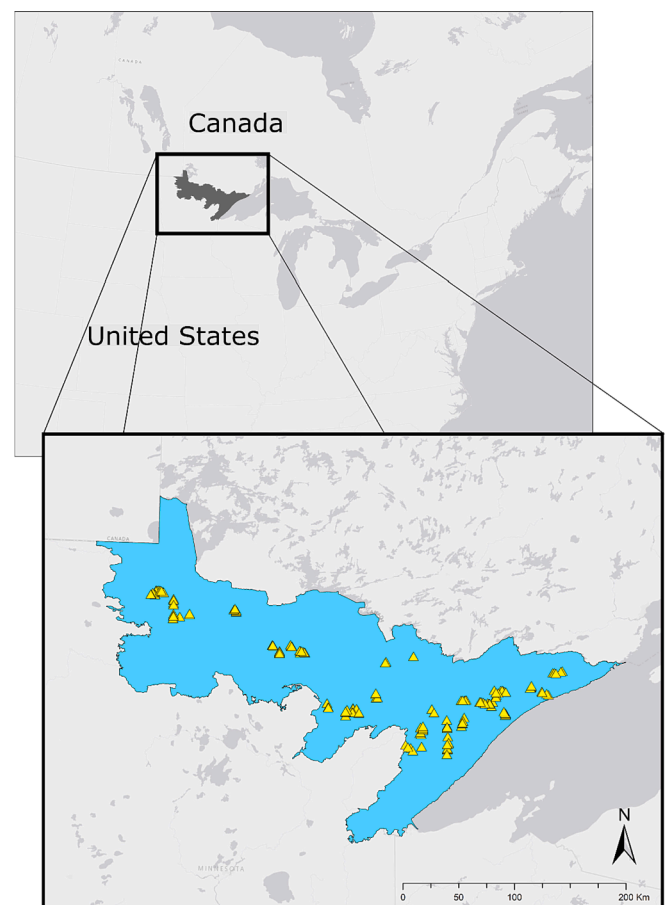


Fig. 1. Map of the study area in northern Minnesota, USA. The study area included the Northern Minnesota and Ontario Peatlands and Northern Superior Uplands Ecoregions defined by the Minnesota Department of Natural Resources Ecological Land Classification System. In the inset map, yellow triangles indicate locations of pellet survey sites for spruce grouse, ruffed grouse, and snowshoe hares (2019–2022). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

occurrence, and local extinction patterns of these three species. We were particularly interested in how peripheral populations of spruce grouse and snowshoe hare were impacted by the combined effects of climate and forest structure in comparison to the widespread ruffed grouse. We expected spruce grouse occupancy to be associated with coniferous forest at a landscape scale, black spruce and jack pine at the stand scale, and younger stands with complex forest structure in the lower- to mid-canopy (Robinson, 1969; Pietz and Tester, 1982). Additionally, we expected climate to play a significant role in local extinction of both spruce grouse and snowshoe hare, but not ruffed grouse. Although we hypothesized that ruffed grouse would exhibit weaker occupancy patterns due to more generalist habits, we expected mixed coniferous/deciduous forest to be favored because of their reliance on these forest types in winter (Pietz and Tester, 1982). Finally, given spruce grouse and snowshoe hare associations with boreal forest and ruffed grouse associations with deciduous forest, we expected co-occurrence to be greatest in areas of mixed deciduous/coniferous forest and stands of mixed tree species.

2. Materials and methods

2.1. Fecal pellet surveys

We surveyed for spruce grouse, ruffed grouse, and snowshoe hares using fecal pellet surveys as part of an annual survey coordinated by the Minnesota Department of Natural Resources (MNDNR; Roy et al., 2020). Surveys were conducted by 3 types of observers; 1) seasonal survey technicians hired specifically for this survey, 2) cooperating wildlife biologists, and 3) trained citizen volunteers. Surveys occurred throughout the northern boreal forest of Minnesota as the snowpack was dissipating each spring, usually during the months of March–May from 2019 to 2022. Surveys were organized hierarchically, such that sampling was comprised of 37 routes each with up to five transects (155 transects total). All transects were visited at least once in each of the four years. At least 1 transect per route had $\geq 30\%$ black spruce or jack pine, and all transects were located in stands with $\geq 30\%$ conifer component. We aimed for three repeat visits at each survey location, but personnel availability, particularly during the beginning of the COVID-19 pandemic in 2020, sometimes precluded completion of all three visits. Furthermore, all 2022 sites were visited a single time as the annual survey transitioned from pilot-phase examining detection covariates to a permanent format (Roy and Giudice, 2023). Following the methods outlined by Roy et al. (2020), each pellet survey was conducted along a circular transect by walking the circumference of a complete circle maintaining 100 m distance from a central road-based point. Surveyors searched 1 m on either side of the transect and recorded the number of individual fecal pellets or groups of pellets for each species. A distinct group of pellets was defined as those occurring within a 30 cm diameter circle, as this was the typical size of pellet groups formed by tree-roosting grouse and provided a repeatable metric. Spruce grouse pellets were differentiated from ruffed grouse pellets based on length, thickness, uric acid wash, and color (Roy et al., 2020). At each survey transect, we recorded survey conditions on a scale from 0 to 10 (with 0 indicating recent snow covered all pellets and 10 indicating a dissipating snowpack is exposing pellets), snow extent (complete, partial, or none), and whether the pellet was observed on snow or bare ground as possible factors influencing detection of pellets. For the vast majority of surveys, fecal pellets were on top of the snow indicating deposition during the current season. However, the possibility that pellets persisted from a previous year existed during a small number of late-spring surveys (i.e., May) when snow cover was generally lower. We handled this possibility by including snow cover and Julian date as detection parameters in our models, discussed in detail below.

2.2. Forest characteristics

Forest characteristics were derived from several sources, including forest data collected during fecal pellet surveys, stand characteristics including stand age and cover type collected during forest inventory monitoring by MNDNR, U.S. Forest Service, county forestry cooperators, remote sources including geospatial (e.g., National Land Cover Data (NLCD), MN Department of Transportation roads layers), and high-resolution aerial LiDAR data (>20 returns m^{-2}) (<https://lithub-minnesota.hub.arcgis.com>). We characterized landscape scale land cover variables as the proportion of NLCD-defined land cover types within a 5-km buffer of the site. Briefly, NLCD defines forest as areas with most trees >5 m tall and more than 20 % of vegetation cover; deciduous forest has $>75\%$ of tree species that shed foliage seasonally; evergreen forest has $>75\%$ of tree species that maintain foliage year round; mixed forest has neither deciduous nor evergreen forest as $>75\%$ of total tree cover; and wooded wetland has $>20\%$ forest or shrub cover with periodically saturated soil or substrate. We recorded three land cover categories: deciduous, mixed deciduous/coniferous, and coniferous (defined as the combination of the NLCD evergreen and wooded wetland [i.e., peatlands]) cover types. Similarly, we recorded road densities at a landscape scale as the linear extent of roads (primary, secondary, and tertiary roads, including dirt forest roads) within a 5-km buffer of the site. During fecal pellet surveys, surveyors recorded the stand type(s) (e.g., jack pine, red pine, black spruce, white cedar, balsam fir, tamarack) defined as any tree species comprising $\geq 30\%$ of the transect length. If no single species accounted for $\geq 30\%$ of the transect, it was recorded as a mixed conifer stand. We used these categorizations as stand scale forest-type predictors. Tree density (i.e., the number of trees) was measured in two circular plots of 3.6 m radius along each pellet transect. One plot was located on each side of the road, at the farthest distance from the road along the transect. We used land cover data from public sources (<https://gisdata.mn.gov/>) while recently acquired LiDAR-derived grid metrics characterizing vertical forest structure and canopy cover were obtained from MNDNR Forestry Program. In particular, canopy density (based on the proportion of LiDAR returns) in five contiguous vertical strata (0–1.37 m, 1.37–5.00 m, 5.00–10.00 m, 10.00–15.00 m, and >15.00 m) were selected considering their importance in other studies (e.g., Deo et al., 2017). Forest characteristics are summarized in Supplemental Table S2.

2.3. Multi-season occupancy modeling – detection, occupancy, and extinction

We used multi-season occupancy models to assess drivers of occupancy and local extinction (MacKenzie et al., 2003) for each species. We used survey route as a random intercept effect to account for the hierarchical sampling design. We first assessed the effects of several variables on detection probabilities – the probability of detecting a species given it is present. Next, we assessed the effects of several variables on initial occupancy probabilities (i.e., the probability a given site is occupied) while accounting for detectability by using the top detection model obtained in the previous step. Finally, we assessed the effects of several variables on extinction probabilities (i.e., the probability that an occupied site becomes unoccupied in the following year) while accounting for detectability and initial occupancy by using the top detection and occupancy models. For each of these parameters, we used a positive stepwise approach to model construction. We first assessed whether a random intercept effect for each survey route improved model performance due to the hierarchical spatial sampling design. We assessed model performance based on the Leave-One-Out Information Criterion (LOOIC), an analog of Akaike's Information Criterion (Burnham and Anderson 2002) for mixed-effects models. After determining whether the random intercept should be included, we then constructed models with a single (fixed-effect) predictor and assessed their performance based on the statistical significance of their coefficient value (see

Supplemental Table S2 for a list of predictors examined) and LOOIC. We used both 95 % confidence intervals (CI) of predictors and LOOIC as criteria for model selection because LOOIC alone is overly permissive of uninformative variables (Arnold, 2010). We discarded any candidate variables with non-significant coefficient values (i.e., 95 % CI overlapped zero) and considered the top single predictor the one with a significant coefficient and the lowest LOOIC. Next, we constructed models with two predictors; the top single predictor was included in each of these models, in addition to each predictor that had a statistically significant coefficient value. We determined the top two-predictor model based on the same criteria as above. If no two-predictor models outperformed the top single-predictor model, we accepted the single-predictor model as the top model. Finally, we constructed three-predictor models following the same process. We limited each parameter to three predictors to avoid overfitting. We modeled colonization as a constant to limit the number of predictors in models and because predictors of occupancy and extinction were our top priorities. All models were constructed in the R package ‘ubms’ using the `stan_colext` function (Kellner et al., 2021). Prior to fitting models, we used a model selection function in the ‘rfUtilities’ package in R to remove any combinations of variables exhibiting multicollinearity (Evans and Murphy, 2019).

2.4. Multi-state occupancy modeling-relative abundance and population growth

To determine whether covariates affecting abundance dynamics differed from those affecting occupancy dynamics, we used a multi-state occupancy modeling approach (MacKenzie et al., 2009). Whereas traditional occupancy modeling approaches only consider two possible occupancy states (i.e., occupied or unoccupied), multi-state occupancy modeling considers multiple types of occupancy states. For example, multi-state occupancy modeling can be used when it is important to distinguish sites with reproductive activity from those that are occupied but show no signs of breeding (McGrady et al., 2017). We selected this approach because snowshoe hare pellet counts were collected using a binned approach (e.g., 0, 1–39, or 40+ pellets) due to logistical constraints in the field. A multi-state approach allowed us to discriminate between sites with relatively fewer (1–39) and relatively greater (40+) pellet piles, as a proxy for abundance. Although continuous values of abundance may be ideal, the large number of snowshoe hare pellets at many sites posed challenges due to excessive time requirements to obtain exact counts and therefore the binned approach was adopted. To maintain consistency among species, we binned the pellet counts of spruce grouse and ruffed grouse to facilitate multi-state occupancy modeling for these species. We calculated the median pellet count values for spruce grouse and ruffed grouse and used these as the cutoffs for pellet abundance bins.

Our objective was to determine environmental predictors of variation in abundance; therefore, we used three occupancy states: 0 = unoccupied, 1 = occupied with relatively low pellet counts, and 2 = occupied with relatively high pellet counts. We focused multi-state occupancy models on predictors of state 2 (i.e., Rho, or “abundance”). We followed the same approach to model construction as in our multi-season occupancy modeling. We first determined predictors associated with the probability of detecting “abundance” (i.e., the probability of observing State 2 given that pellets are abundant at the site, or $p[22]$). Next, we determined the predictors associated with the probability of initial abundance. Finally, we determined predictors associated with transitions between the two positive occupancy states (i.e., $\Phi[12]$ = probability of observing State 2 at a site that was previously in State 1 and $\Phi[21]$ = probability of observing State 1 at a site that was previously in State 2, analogous to positive and negative population growth, respectively). We followed the same positive stepwise approach to model construction as described above and limited each parameter to a maximum of three predictors. All multi-state occupancy models were

constructed in the R package ‘unmarked’ using the `occuMS` function (Fiske and Chandler, 2011).

2.5. Multi-species occupancy modeling-species co-occurrence along environmental gradients

Finally, we constructed multi-species occupancy models to test several hypotheses of species occurrence and co-occurrence along environmental gradients. Each model compared occupancy of one of the boreal-specialist species (spruce grouse or snowshoe hare) with that of the ruffed grouse, a forest generalist. We constructed several models relating the boreal species to a boreal forest type, ruffed grouse to a deciduous forest type, and co-occurrence with an intermediate or mixed forest type. For example, at the landscape scale we constructed co-occurrence models in which spruce grouse were associated with coniferous forest land cover, ruffed grouse with deciduous forest land cover, and hypothesized that co-occurrence was associated with mixed forest land cover. Similarly, at a local scale, we hypothesized that spruce grouse would be associated with black spruce or jack pine stands, ruffed grouse with deciduous stands, and co-occurrence with mixed species composition (i.e., no single species comprising $\geq 30\%$ of the transect) or balsam fir stands (which often co-occurred with aspen). We used the top detection model (determined previously) for each species in each model and assessed models based on AICc compared to a model with no occupancy predictors and the statistical significance of coefficient values. Each model included detection predictors from each respective species’ top detection model. We constructed these models using the `occuMulti` function in ‘unmarked’. We constructed models for each of 2019, 2020, and 2021, because these years had repeat survey data, and assessed consistency of multi-species occupancy predictors across years.

3. Results

3.1. Detection probability

The top performing detection models for all species included the effect of observer type (Fig. 2; Fig. 3; Supplemental Table S3). For spruce grouse, snow extent and survey condition were also included in the top model, while survey condition and date were included in the top model for ruffed grouse. The top snowshoe hare detection model did not include additional variables. Overall detection probabilities were 0.62 (0.58–0.67) for spruce grouse, 0.69 (0.66–0.72) for ruffed grouse, and 0.96 (0.95–0.97) for snowshoe hare.

3.2. Occupancy probability

Spruce grouse occupancy was most strongly associated with land cover and forest structure. The top initial occupancy model included the effects of deciduous land cover at a landscape (5-km) scale (negative effect on occupancy) and the density of LiDAR returns at the 5.00–10.00 m (+) and 10.00–15.00 m (+) height strata (Fig. 2; Fig. 4). Additionally, coniferous land cover (+), jack pine stands (+), stand age (–), and density of LiDAR returns at >15.00 m height (–) all outperformed a null model (Supplemental Table S4).

Landscape-scale variables were not strongly associated with ruffed grouse nor snowshoe hare occupancy. Rather, local-scale variables related to forest structure and stand type were among the top predictors. The top initial occupancy model for ruffed grouse included red pine stands (–) as the only predictor (Fig. 2). Other predictors that outperformed a model with no initial occupancy predictors included deciduous forest stands (+) and LiDAR return density at the 5.00–10.00 m stratum (+; Supplemental Table S4). Tree density (+) was the only predictor that outperformed a model without initial occupancy predictors for snowshoe hare, and thus the top model included only the effect of tree density (Fig. 2).

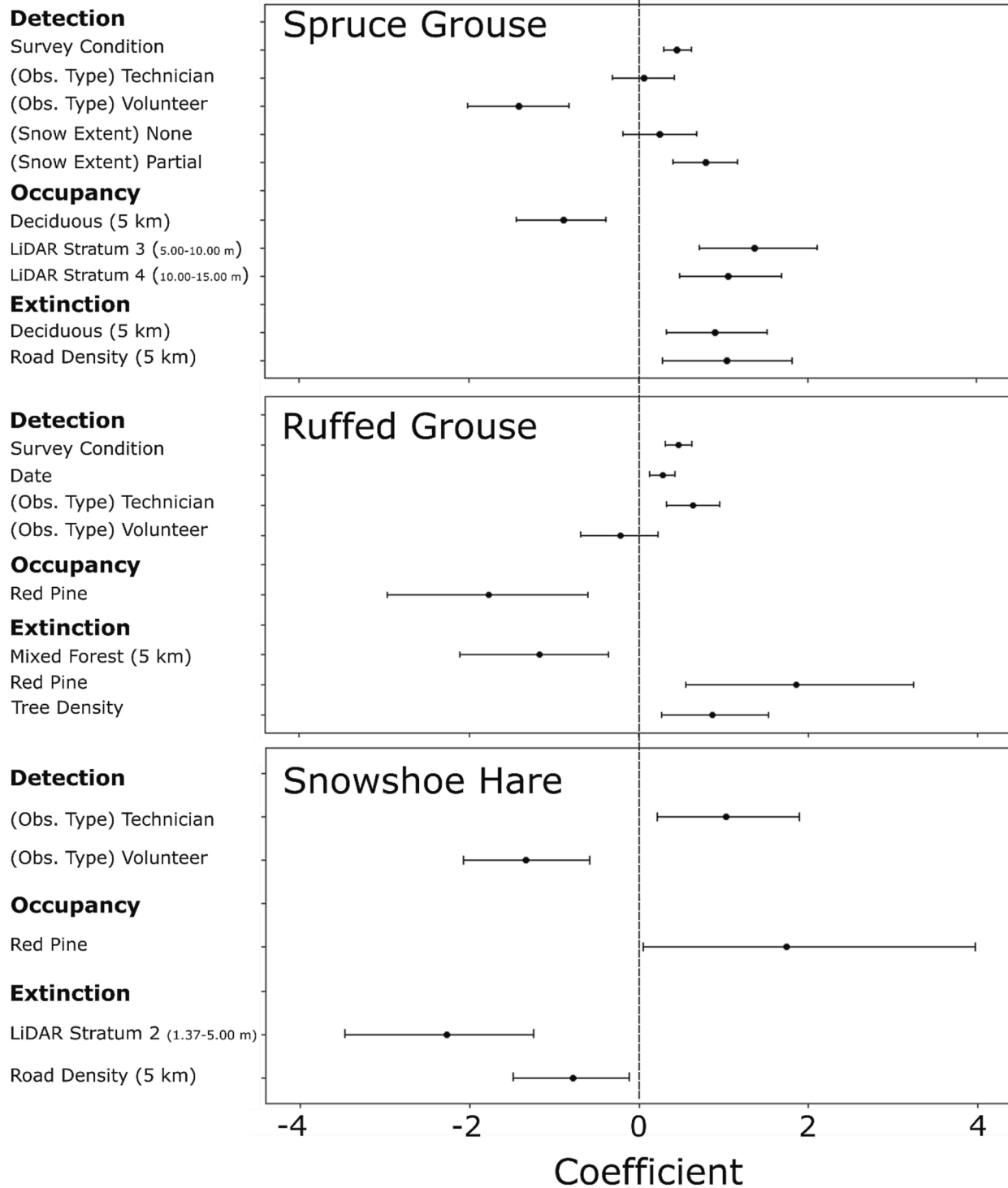


Fig. 2. Coefficients ($\pm 95\%$ confidence intervals) of detection, occupancy, and extinction predictors in top-scoring multi-season occupancy models for spruce grouse, ruffed grouse, and snowshoe hare based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Models were constructed using a positive stepwise approach with each parameter limited to a maximum of three predictors (note: some detection predictors are multi-level factors that were considered a single predictor). Full definitions of predictors are defined in [Supplemental Table S2](#).

3.3. Extinction probability

Similar to initial occupancy results, the predictors most strongly associated with spruce grouse extinction occurred at the landscape scale. The top extinction model included the effects of deciduous forest cover (+) and road density (+) at the 5-km scale (Fig. 2; Fig. 4). In single-variable models, tree density (-), structure at the 5.00–10.00 m

stratum (-), winter snowfall (-), and winter temperature (+) also outperformed a model without extinction predictors (Supplemental Table S5).

A variety of variables influenced ruffed grouse extinction probability. The top model included the effects of mixed coniferous/deciduous forest at a landscape scale (-), red pine stands (+), and tree density (+; Fig. 2). In addition, stand age (-), LiDAR density at the 1.37–5.00 m

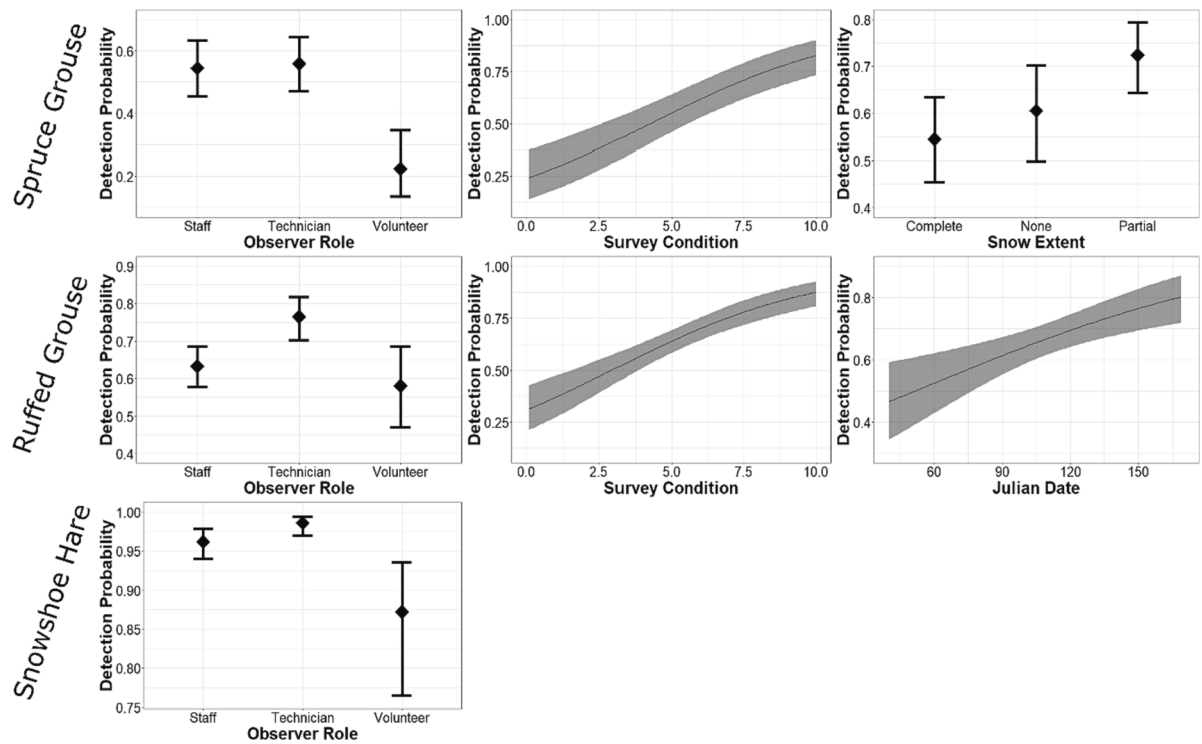


Fig. 3. Marginal effects of detection predictors in top detection models for spruce grouse, ruffed grouse, and snowshoe hares based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. For categorical variables (observer role, snow extent), error bars represent 95 % confidence intervals (CIs). For continuous variables (survey condition, Julian date), gray shaded areas represent 95 % CIs.

stratum (-), LiDAR density at the >15.00 m stratum (+), jack pine stands (+), balsam fir stands (-), deciduous stands (-), and winter snowfall (-) all outperformed a model without extinction predictors (Supplemental Table S5).

Predictors related to climate and stand-scale forest characteristics were among the top extinction predictors for snowshoe hare. The top extinction model included the effects of LiDAR density at the 1.37–5.00 m stratum (-) and winter snowfall (-; Fig. 2; Fig. 5). In addition, LiDAR density at the 5.00–10.00 m (-) and >15.00 m (+) strata, tree density (-), stands of balsam fir (-), black spruce (-), and red pine (+), and winter temperature (+) outperformed a model with no extinction predictors (Supplemental Table S5).

3.4. Multi-State occupancy probability

Multi-state occupancy models suggested that environmental drivers of occupancy and abundance (i.e., Rho) were similar for spruce grouse, but differed for both ruffed grouse and snowshoe hare. For spruce grouse, the top model for initial abundance and the top model for transitions between high and low pellet counts (e.g., Phi) included the same predictors as models for initial occupancy and extinction probability, respectively (Fig. 6). Stand types were the most important predictors of initial abundance for ruffed grouse, and forest structure characteristics were most important for snowshoe hare. The top abundance model for ruffed grouse included the effects of balsam fir (+) and deciduous (+) stands (Fig. 6; Fig. 7). Forest structure at the 1.37–5.00 m stratum (+) and mixed coniferous/deciduous forest at a landscape scale (+) also outperformed a null model (Supplemental Table S6). The top abundance model for snowshoe hare included the effects of forest structure at the 5.00–10.00 m stratum (+; Fig. 6). Stand age (-), structure at the 1.37–5.00 m (+) and >15.00 m (-) strata, tree density (+), and red pine stands (-) all outperformed a model without abundance predictors (Supplemental Table S6).

Forest structure played a significant role in abundance dynamics for

ruffed grouse and snowshoe hare. Several vertical strata were associated with year-to-year negative growth (i.e., Phi[21]). The top model describing negative growth for ruffed grouse included the effects of forest structure at the 5.00–10.00 m stratum (-), tree density (+), and jack pine stands (+). The top model describing negative growth for snowshoe hare included the effects of structure at the 1.37–5.00 m (-) and >15.00 m (+) strata. In addition, snowshoe hare were the only species in which interspecies interactions appeared to influence population dynamics. The top model for snowshoe hare also included the effect of ruffed grouse abundance on positive growth (i.e., Phi[12]), which was negative (i.e., greater ruffed grouse abundance reduced the probability of positive growth in snowshoe hares; Supplemental Fig. S1; Supplemental Table S7).

Few of our predictions of species co-occurrence across boreal-hardwood gradients were supported. However, in 2021, co-occurrence of spruce grouse-ruffed grouse and snowshoe hare-ruffed grouse was positively associated with mixed forest at a landscape scale (Supplemental Table S8). However, no co-occurrence predictors were statistically significant at the stand scale in any year or at the landscape scale in 2019 and 2020.

4. Discussion

4.1. Spruce grouse

Our results support recent work implicating deciduous forest cover as a key factor limiting the range of spruce grouse (Casabona et al., 2022). However, our results suggest that forest structure may be a stronger determinant of spruce grouse habitat selection than the particular stand type. Previous work has suggested spruce grouse occupancy is associated with black spruce and jack pine stands (Robinson, 1969; Pietz and Tester, 1982; Anich et al., 2013). Our models supported an association with jack pine, but no stand-type variables were strong enough to be included in top models. Rather, forest structure of the

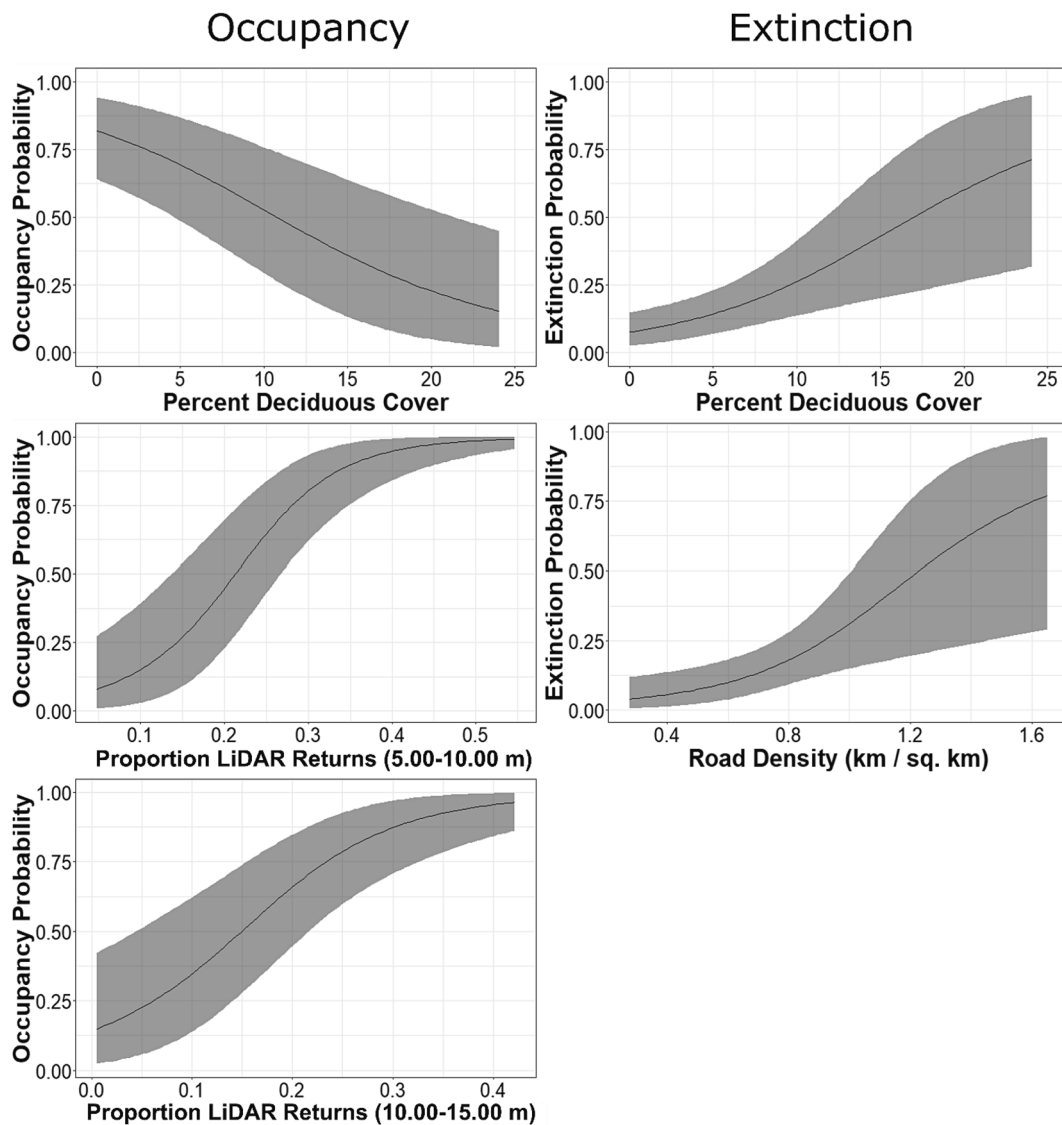


Fig. 4. Marginal effects of occupancy and extinction predictors in the top multi-season occupancy model for spruce grouse based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Gray shaded areas represent 95 % confidence intervals. Percent deciduous cover and road density were calculated within a 5-km radius of the survey site. LiDAR returns from 10 to 15 m in height, which represents the density of the mid-canopy, were calculated within a 150-m radius of the survey site.

lower and mid-canopy was the key local scale determinant of spruce grouse occupancy and persistence. Dense lower and mid-story canopy provides cover from aerial predators and provides thermal protection in winter (Thompson and Fritzell, 1988).

We expected extinction probabilities of spruce grouse to be closely associated with climatic variables given the position of the study area on their southern range margin. Lower temperatures and greater snowfall were associated with lower spruce grouse extinction probabilities, as expected, but the association was not as strong as landscape-scale land cover and road densities. Snowfall and temperature are important to maintaining a deep snowpack for subnivean roosting in winter, but spruce grouse may mitigate suboptimal snow roosting conditions by roosting in trees within a dense forest structure. Indeed, spruce grouse in Maine were observed moving into denser stands and primarily occupying trees in winter (Allan, 1985). Spruce grouse respond to inadequate snow roosting conditions by tree roosting instead, thereby moderating the effects of climate and temperature in our models. Indeed, as climate conditions are predicted to broadly shift the distribution of forest land cover types northward in our study area (Taylor et al., 2017), the effects of climate on spruce grouse occupancy and extinction may be primarily

indirect. Our results underscore the importance of managing forests for dense lower- and mid-canopy to provide climate refugia for spruce grouse at their trailing edge.

Road densities had a substantial effect on spruce grouse extinction probability. Road construction in working forests can change the predator landscape and alter community dynamics (Sirén et al., 2017). Road densities may be associated with greater densities of predators; thereby, roads can indirectly cause a decrease in the occurrence of prey species (Boan et al., 2014). In the western United States, avoidance of roads and reduced nesting success near roads was considered a potential result of fear or auditory disturbance (Pruett et al., 2009). Additionally, road density may be correlated with greater hunter and/or timber accessibility, thus, local extinction probabilities may be driven by more intense harvest. Although the link is unclear, our study suggests that road-sparse areas may promote spruce grouse persistence.

Occupancy modeling is inherently a presence/absence estimator and may not capture variation in density among occupied sites (Nielsen et al., 2005; Torres et al., 2012). Therefore, we hypothesized that models accounting for abundance may be more sensitive to associations with particular stand types. Our results suggested that the same variables

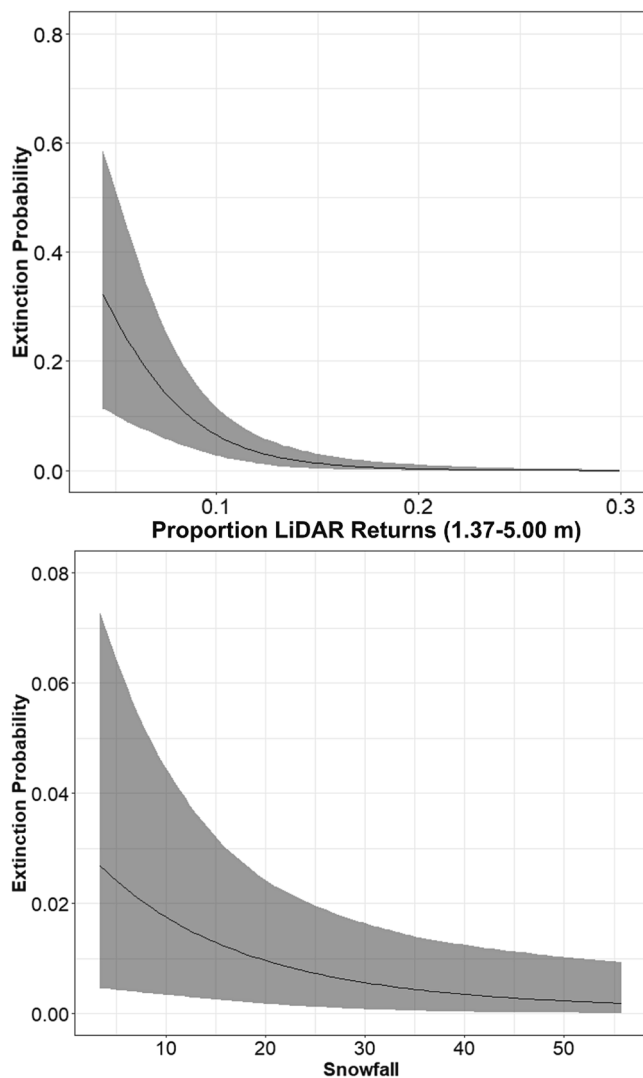


Fig. 5. Predicted extinction probability for snowshoe hares based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Gray shaded areas represent 95% confidence intervals. LiDAR returns from 1.37 to 5.00 m in height, representing the density of the shrub understory, were calculated within a 150-m radius. Snowfall was calculated at the center of the survey site using the National Gridded Snowfall Analysis from the National Oceanic and Atmospheric Administration.

governing spruce grouse occupancy – deciduous forest and vertical forest structure – were the most important predictors of relative abundance. We note that our modeling approach, multi-state occupancy modeling – may still be less sensitive to abundance patterns than a modeling approach that uses precise counts such as N-mixture modeling (Royle, 2004). Therefore, we may have had difficulty identifying some potentially important predictors (i.e., stand types). In addition, our models used an indirect estimator of abundance – the number of fecal pellet groups along a transect. Although the number of pellet groups is likely correlated with abundance (Krebs et al., 2001; Evans et al., 2007; Hanser et al., 2011), this metric could be influenced by other parameters such as use intensity and diet, which could cause variation in fecal deposition rates, and make resolution of statistical patterns more difficult.

4.2. Ruffed grouse

Ruffed grouse occupancy and extinction tended to have stronger associations with stand-level variables than landscape-scale variables, in

contrast to spruce grouse. Ruffed grouse home range sizes vary seasonally and throughout their range. Whereas some estimates from the south of their range in Missouri and Tennessee exceed 35 ha (Thompson and Fritzell, 1988; Epperson, 1988), a study conducted during spring in Minnesota found average home ranges of just 6.7 ha (Archibald, 1975). This may have contributed to the lack of landscape-scale habitat associations detected in this study.

Deciduous forests, and particularly aspen, are important sources of forage for ruffed grouse (Svoboda and Guillon, 1972). However, since deciduous forests do not provide substantial thermal cover in winter when snow roosting conditions are unfavorable, mixed deciduous/coniferous forest stands may provide some roosting habitat for ruffed grouse in the sheltered base of conifer trees. Our multi-state modeling results suggested greater ruffed grouse abundance in deciduous stands and balsam fir stands (which often co-occur with aspen in our study area), supporting the importance of mixed coniferous/deciduous stands for ruffed grouse in winter and early spring. Furthermore, mixed coniferous/deciduous forest was associated with lower extinction probability in the top extinction model, reinforcing the importance of mixed forests for providing both thermal cover and winter forage for ruffed grouse (Jones et al., 2008).

Ruffed grouse occupancy was most strongly associated with a relatively unexpected predictor. Red pine stands were strongly negatively associated with ruffed grouse occupancy and were associated with greater extinction probability in the top extinction model. One possible explanation for the negative impact of red pine is the abundance of red pine plantations in the study area. Pine plantations provide little winter food and sparse understory cover for predator avoidance (Bender et al., 1997) but can have a dense overstory that provides concealment for raptors and other forest predators (Gullion, 1967, 1970). In that regard, ruffed grouse extinction probabilities may have been associated more with forest management practices than with the red pine stand type, per se. Likewise, higher tree densities also increased the probability of ruffed grouse extinction in winter. Although greater tree densities may provide better cover from predators, higher tree densities occur in younger stands; during the winter and early spring, ruffed grouse were more likely seeking food in mature aspen forests while snow was on the ground. Moreover, ruffed grouse tend to select ground roosts when snow is present, even when snow depth is limited and potentially insufficient (Whitaker and Stauffer, 2003). Stands with greater tree densities may limit snow accumulation underneath trees, creating suboptimal ground roosting conditions. Therefore, openings in the forest may promote ruffed grouse survival by providing better snow roosting conditions. Alternatively, higher tree densities may simply be associated with young stands that lack sufficient food resources to support ruffed grouse populations (Jones et al., 2008).

4.3. Snowshoe hare

Due to their widespread occurrence in our study area, few predictors were associated with initial occupancy and abundance of snowshoe hares. Under these conditions, dynamic occupancy models can be more revealing about the environmental conditions that facilitate demographic patterns from year to year (Yackulic et al., 2015). Accordingly, we found stronger patterns in dynamic models (i.e., extinction probabilities and multi-state transition probabilities) for snowshoe hare.

We expected snowshoe hare occupancy, abundance, and survival to be associated with snowpack and structure at the shrub level (1.37–5.00 m). Understory density has been linked to snowshoe hare overwinter survival and spring population densities (Litvaitis et al., 1985). Our results strongly supported this association, as variables related to shrub-level forest structure were among the top predictors of occupancy, extinction, abundance, and transitions in abundance. Furthermore, our results suggested that greater snowfall was related to lower extinction probabilities. Our results underscore the threat of seasonal camouflage mismatch in a warming climate and highlight the increased

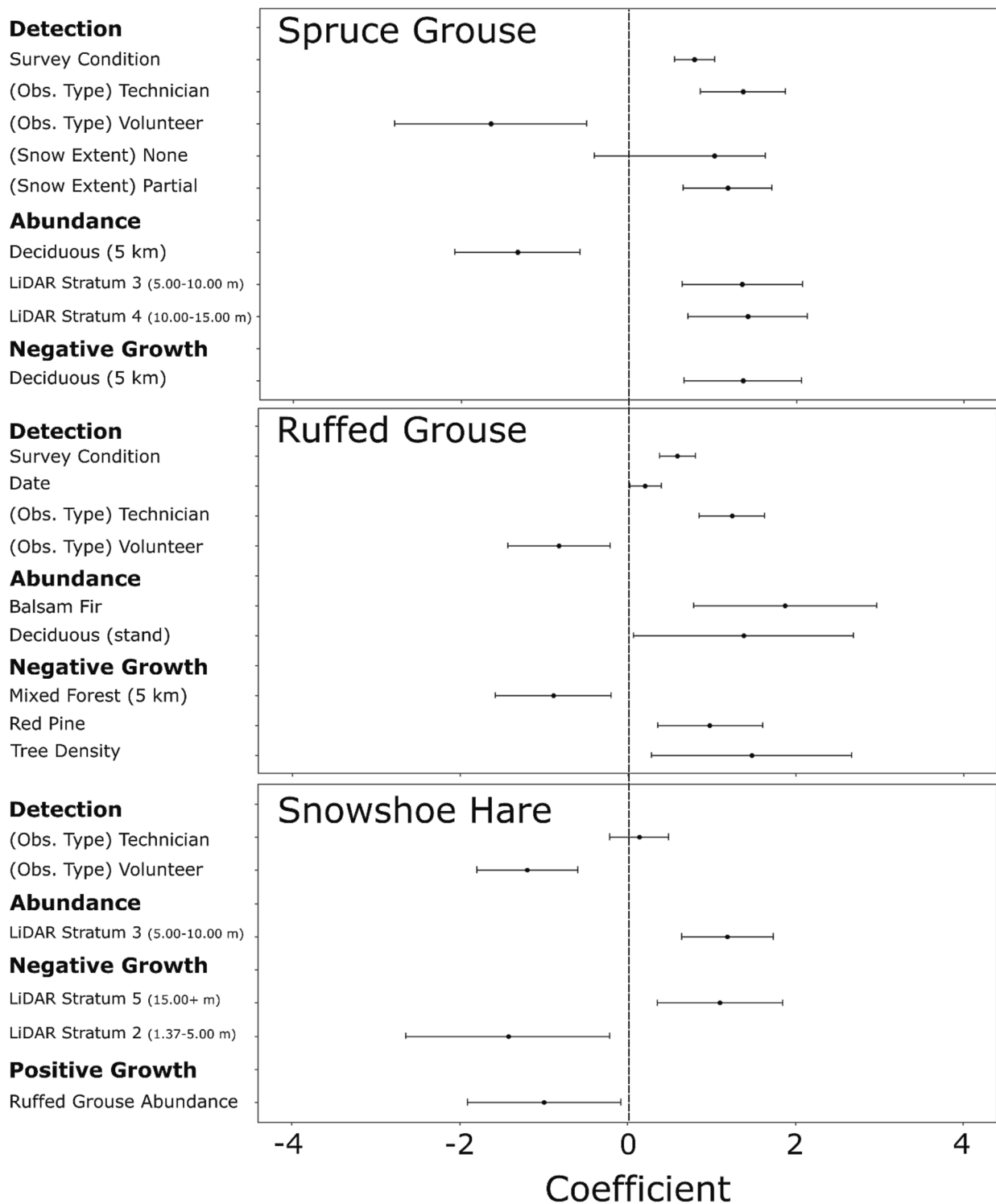


Fig. 6. Coefficients ($\pm 95\%$ confidence intervals) of detection, abundance (Rho), and growth (Phi) predictors in multi-state occupancy models for spruce grouse, ruffed grouse and snowshoe hare based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Models were constructed using a positive stepwise approach with each parameter limited to a maximum of three predictors (note: some detection predictors are multi-level factors that were considered a single predictor).

vulnerability of populations on the southern range margin (Zimova et al., 2020).

4.4. Species co-occurrence

Based on earlier studies, we expected that co-occurrence would occur along a boreal-hardwood gradient, with both spruce grouse and

snowshoe hare associated with boreal forest and ruffed grouse associated with hardwood forest. Our results were inconsistent across years and across scales, and our hypothesis was only supported at a landscape scale during one of the three years we tested. In 2021, snowfall was exceptionally low and temperatures were abnormally high (data not shown). One potential explanation of our findings is that these abnormal climate conditions forced species to be more selective in their resource

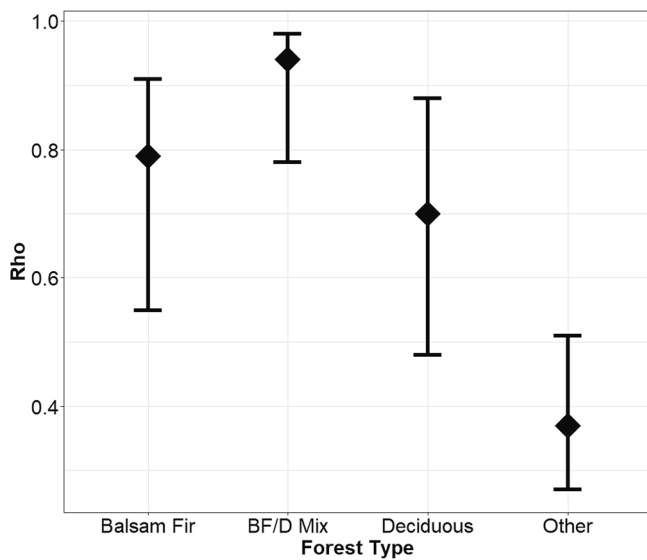


Fig. 7. Marginal effects of abundance (Rho) predictors in the top scoring multi-state occupancy model for ruffed grouse based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Error bars represent 95 % confidence intervals. BF/D Mix = stands with ≥ 30 % cover of both balsam fir and deciduous forest. Other = all stands with < 30 % balsam fir and < 30 % deciduous forest.

use, resulting in greater spatial overlap at the boreal-hardwood interface. Species co-occurrence models have previously shown the importance of elevational gradients in partitioning species distributions (Estevo et al., 2017). Similarly, the habitat gradient in our study coincides with a latitudinal transition from northern hardwood forests to northern boreal forests. As the climate warms, this transition zone is expected to shift northward as the leading edge of hardwood forests replace the trailing edge of boreal forests (Taylor et al., 2017). Our results suggest that warmer climate conditions with shallower snowpack may amplify interactions between boreal and sub-boreal species during this transition.

We sought to understand species interactions by examining changes in abundance (i.e., multi-state occupancy) in response to the occupancy state of other focal species in the study. Investigating changes in occupancy states over time can identify when interspecific interactions, such as competition, are integral to the demographic parameters of one or both species (Yackulic et al., 2014). The only significant relationship we discovered was an apparent regulating effect between ruffed grouse and snowshoe hare – (i.e., greater ruffed grouse abundance was associated with a lower probability of snowshoe hare population growth). This result corresponds with the well-documented co-cycling of ruffed grouse and snowshoe hare populations (Keith, 1963). This result may be related to a shared predator base (Hoffman, 1958). As predator populations grow and populations of one prey species shrinks due to predation pressure, predators may switch to targeting the more abundant prey species, resulting in correlated population dynamics. Our study design does not allow direct assessment of predator–prey interactions, but our results are consistent with correlated population dynamics resulting from such processes.

5. Conclusions

We examined occupancy, abundance, and local extinction patterns in a suite of forest-associated vertebrate prey species at the southern margin of the boreal forest. We found similar habitat associations of the two boreal-associated species that occur at their trailing edge in our study area. Interestingly, these species may partition niches vertically; spruce grouse were most closely associated with lower and mid-canopy

cover (5.00–15.00 m) and snowshoe hares were most closely associated with shrub-level cover (1.37–5.00 m). Snowshoe hare were the most climate-sensitive species in our study, most likely due to seasonal camouflage requirements, and spruce grouse may mitigate suboptimal climate conditions by selecting tree-roosts when lower and mid-canopy cover is sufficient. We detected a potential boreal-hardwood gradient of species co-occurrence in a year when climate conditions were suboptimal, suggesting future climate change may result in more frequent species interactions as the boreal-hardwood transition zone shifts northward. Overall, the occupancy, extinction, abundance, and population growth of all species were strongly associated with structural density of the shrub and/or lower canopy layer. This work underscores the importance of maintaining dense forest structure for this guild of forest prey species in winter. Harvest strategies that involve thinning forest stands to facilitate timber extraction may be especially harmful. Forest management practices that maintain dense vegetation in the lower canopy, mid-canopy and shrub layer of conifer forests could provide climate change refugia for boreal-associated species at the trailing edge.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

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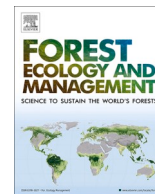
Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121568>.

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Forest structure mediates occupancy and extinction of vertebrate prey species on the trailing edge of the boreal forest

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ABSTRACT

Climate change is expected to shift the distributions of global biomes. High latitude biomes, such as the boreal forest, are among the most vulnerable and serve as a bellwether for the effects of climate change on other ecosystems. We examined patterns of occupancy, local extinction, and abundance in a guild of forest-associated vertebrate prey species on the southern margin of the boreal forest in Minnesota (USA). We used multi-season, multi-state, and multi-species occupancy modeling approaches to determine the effects of land cover, forest structural characteristics, and climatic variation on two boreal-associated species, spruce grouse (*Canachites canadensis*) and snowshoe hare (*Lepus americanus*), and a forest generalist, ruffed grouse (*Bonasa umbellus*). Occupancy, abundance, and extinction of spruce grouse was strongly associated with landscape-scale characteristics. In particular, deciduous forest cover may govern their southern range limit. Broadly, forest understory structure played a significant role in occupancy, extinction, and abundance patterns of all three species, with ruffed and spruce grouse generally associated with vegetation density in the lower and mid-canopy layer (5.00–15.00 m) and snowshoe hare associated with density in the shrub layer (1.37–5.00 m) in winter. Co-occurrence varied annually but was greatest in mixed forests during an uncharacteristically warm and snow-sparse year. Climatic variables (winter temperature and snowfall) were associated with extinction probabilities for all three species, but the effect was generally weaker than that of forest structure. Our results suggest that forest management practices that promote dense understory structure may help provide climate refugia for vertebrate prey species in boreal forest ecosystems.

1. Introduction

The center-periphery hypothesis of extinction predicts that peripheral populations are more vulnerable to extinction than central populations due to suboptimal habitat conditions, lower population densities, and greater stochasticity (Lawton, 1993). Despite greater extinction risk and generally lower genetic diversity, peripheral populations can have significant conservation value due to potential adaptation to marginal environmental conditions (Hardie and Hutchings, 2010). Deciding whether to prioritize peripheral populations for conservation has been a central focus of climate change adaptation (Lesica and Allendorf, 1995).

Climate change is causing warmer winter conditions and reduced snowfall in many regions. Therefore, habitats and wildlife species are broadly expected to shift northward and upward in elevation in the

northern hemisphere (Hickling et al., 2006). Accordingly, populations at the southern margin of species' distributions are expected to contract over the next several decades. In particular, boreal forests are expected to experience one of the most rapid shifts in distribution among the Earth's major biomes (Loarie et al., 2009). Those spatial and temporal shifts suggest conserving "trailing edge" populations (i.e., those at the low-latitude limit of a species' distribution) will be particularly challenging under changing climate conditions (Hampe and Petit, 2005). Understanding habitat and climatic requirements of boreal forest species at their southern range limits can inform climate adaptation strategies for conserving climate-sensitive wildlife species.

Climate change and land-use change are two of the strongest drivers of biodiversity loss globally (Travis, 2003; Maxwell et al., 2016). These processes can be interactive, and anthropogenic land use has the potential to harm (Jetz et al., 2007) or support (Morelli et al., 2012)

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climate-sensitive populations. Forest management can interact with climate change to either ameliorate or accelerate the negative effects of climate change on boreal forest wildlife (Virkkala, 2016). Prioritizing forest management practices that provide refugial habitat for climate-sensitive species could mitigate the effects of climate change. Despite this, most wildlife adaptation strategies have focused on large scale reserve-design planning initiatives, while local, management-relevant adaptation strategies have been largely ignored (LeDee et al., 2020).

One ecological community that appears particularly at odds with current climate mitigation priorities is early and mid-successional forest vertebrates. Climate adaptation strategies often prioritize maximizing carbon storage in managed forests, which may exacerbate the effects of climate change on wildlife dependent on early and mid-successional forest (Littlefield and D'Amato, 2022). Management strategies can improve overall adaptive capacity of forest ecosystems by acknowledging trade-offs between forest carbon storage and the need for climate refugia for early and mid-successional forest specialists.

In this study, we examined occupancy patterns of three early and mid-successional forest vertebrate prey species: spruce grouse (*Cathartes canadensis*), ruffed grouse (*Bonasa umbellus*) and snowshoe hares (*Lepus americanus*) at the southern margin of the boreal forest in northern Minnesota, USA. These three species overlap spatially in the winter, share predators, and exhibit approximately 10-year population cycles at northern latitudes (Williams et al., 2004, <https://www.adfg.alaska.gov/static/education/wns/grouse.pdf>, Pomara and Zuckerberg, 2017, although it is not yet known if trailing edge populations of spruce grouse cycle, Roy and Giudice, 2023). Population cycles have been hypothesized to be due to predator-prey interactions and delayed density dependence at northern latitudes (Williams et al., 2004), with raptors switching to ruffed grouse as snowshoe hare populations decline (Keith and Rusch, 1989). More recently, studies have found support for climate variability driving variability in demographic rates that produce population cycles at northern latitudes (Zimmerman et al., 2008, Yan et al., 2013, Pomara and Zuckerberg, 2017).

Spruce grouse ecology and distribution are closely associated with the boreal forest in North America (Schroeder et al., 2018). Although populations appear to be declining at their southern range margin (Ross et al., 2016), their ecology and status are not as well documented as many North American game birds. Furthermore, research has been focused primarily in the range of the *franklinii* subspecies, which occur within and west of the Rocky Mountains, with even less known about the *canadensis* subspecies that occurs throughout the eastern boreal forest of North America. The studies on the *franklinii* subspecies suggests spruce grouse prefer dense stands of spruce and fir trees, typically of short to intermediate height (Boag and Schroeder, 1987; Huggard, 2003). These forest characteristics may improve the survival and recruitment of young, which are important factors in population regulation (Boag et al., 1979). Recent work from the range of the *canadensis* subspecies has also documented an association with younger forests. In the Adirondack Mountains of New York, a decline in spruce grouse occupancy over thirty years was attributed to forest maturation (Ross et al., 2016). In Quebec, at the southern margin of the boreal forest, spruce grouse occupancy was associated with coniferous tree cover and deciduous shrub cover, and deciduous tree cover limited spruce grouse occupancy (Casabona et al., 2022). Because spruce grouse is likely to be affected by warming temperatures (Murray et al., 2017), we considered its niche/habitat for evaluation in the northern boreal forests of Minnesota.

The two other study species also rely on early to mid-successional forest but are more widespread and widely studied than spruce grouse. The ruffed grouse is the most widely distributed game bird in North America and uses coniferous, deciduous, and mixed coniferous/deciduous forests throughout its range (Rusch et al., 2000). Ruffed grouse require deciduous forest for forage (Svoboda and Guillon, 1972) and tend to use a mix of young and old stands due to the low cover provided by young trees and the substantial forage provided by older trees (Jones et al., 2008). Last, snowshoe hares are distributed

throughout northern North America and have several adaptations for survival in snow-covered landscapes (Wilson and Reeder, 1993). They have enlarged hind feet and stiff hairs that act like snowshoes in deep snow conditions, and they have seasonal camouflage, molting between brown (summer) and white (winter) coats to blend in with the surrounding landscape. Their reliance on seasonal camouflage for survival makes them particularly vulnerable to climate change, as temporal mismatches between seasonal molting and winter-white conditions can significantly increase predation rates (Zimova et al., 2016).

Our study area in northern Minnesota, USA (Fig. 1) encompassed two Ecoregions as defined by the Minnesota Department of Natural Resources Ecological Land Classification System: The Northern Minnesota and Ontario Peatlands and the Northern Superior Uplands. The study area occurred within the boreal-deciduous ecotone (Goldblum and Rigg, 2010), where the southern limit of the boreal forest meets the northern limit of hardwood-dominated forest. Common stand types in the study area included balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), tamarack (*Larix laricina*), white spruce (*Picea glauca*), and northern white cedar (*Thuja occidentalis*). Overall, the study area was comprised of ~73 % forested land cover including ~49 % coniferous forest (evergreen forest and wooded wetland cover types), ~15 % mixed coniferous/deciduous forest, and ~9 % deciduous forest land cover (Supplemental Table S1).

The objectives of our study were to determine the effects of land cover, climate, and forest structure characteristics on the occupancy, co-

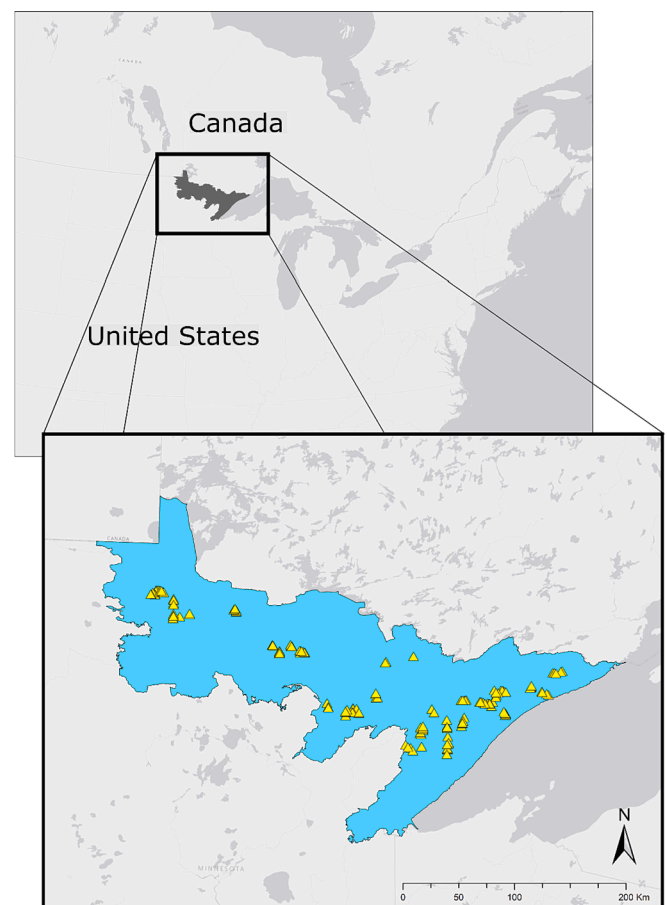


Fig. 1. Map of the study area in northern Minnesota, USA. The study area included the Northern Minnesota and Ontario Peatlands and Northern Superior Uplands Ecoregions defined by the Minnesota Department of Natural Resources Ecological Land Classification System. In the inset map, yellow triangles indicate locations of pellet survey sites for spruce grouse, ruffed grouse, and snowshoe hares (2019–2022). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

occurrence, and local extinction patterns of these three species. We were particularly interested in how peripheral populations of spruce grouse and snowshoe hare were impacted by the combined effects of climate and forest structure in comparison to the widespread ruffed grouse. We expected spruce grouse occupancy to be associated with coniferous forest at a landscape scale, black spruce and jack pine at the stand scale, and younger stands with complex forest structure in the lower- to mid-canopy (Robinson, 1969; Pietz and Tester, 1982). Additionally, we expected climate to play a significant role in local extinction of both spruce grouse and snowshoe hare, but not ruffed grouse. Although we hypothesized that ruffed grouse would exhibit weaker occupancy patterns due to more generalist habits, we expected mixed coniferous/deciduous forest to be favored because of their reliance on these forest types in winter (Pietz and Tester, 1982). Finally, given spruce grouse and snowshoe hare associations with boreal forest and ruffed grouse associations with deciduous forest, we expected co-occurrence to be greatest in areas of mixed deciduous/coniferous forest and stands of mixed tree species.

2. Materials and methods

2.1. Fecal pellet surveys

We surveyed for spruce grouse, ruffed grouse, and snowshoe hares using fecal pellet surveys as part of an annual survey coordinated by the Minnesota Department of Natural Resources (MNDNR; Roy et al., 2020). Surveys were conducted by 3 types of observers; 1) seasonal survey technicians hired specifically for this survey, 2) cooperating wildlife biologists, and 3) trained citizen volunteers. Surveys occurred throughout the northern boreal forest of Minnesota as the snowpack was dissipating each spring, usually during the months of March-May from 2019 to 2022. Surveys were organized hierarchically, such that sampling was comprised of 37 routes each with up to five transects (155 transects total). All transects were visited at least once in each of the four years. At least 1 transect per route had $\geq 30\%$ black spruce or jack pine, and all transects were located in stands with $\geq 30\%$ conifer component. We aimed for three repeat visits at each survey location, but personnel availability, particularly during the beginning of the COVID-19 pandemic in 2020, sometimes precluded completion of all three visits. Furthermore, all 2022 sites were visited a single time as the annual survey transitioned from pilot-phase examining detection covariates to a permanent format (Roy and Giudice, 2023). Following the methods outlined by Roy et al. (2020), each pellet survey was conducted along a circular transect by walking the circumference of a complete circle maintaining 100 m distance from a central road-based point. Surveyors searched 1 m on either side of the transect and recorded the number of individual fecal pellets or groups of pellets for each species. A distinct group of pellets was defined as those occurring within a 30 cm diameter circle, as this was the typical size of pellet groups formed by tree-roosting grouse and provided a repeatable metric. Spruce grouse pellets were differentiated from ruffed grouse pellets based on length, thickness, uric acid wash, and color (Roy et al., 2020). At each survey transect, we recorded survey conditions on a scale from 0 to 10 (with 0 indicating recent snow covered all pellets and 10 indicating a dissipating snowpack is exposing pellets), snow extent (complete, partial, or none), and whether the pellet was observed on snow or bare ground as possible factors influencing detection of pellets. For the vast majority of surveys, fecal pellets were on top of the snow indicating deposition during the current season. However, the possibility that pellets persisted from a previous year existed during a small number of late-spring surveys (i.e., May) when snow cover was generally lower. We handled this possibility by including snow cover and Julian date as detection parameters in our models, discussed in detail below.

2.2. Forest characteristics

Forest characteristics were derived from several sources, including forest data collected during fecal pellet surveys, stand characteristics including stand age and cover type collected during forest inventory monitoring by MNDNR, U.S. Forest Service, county forestry cooperators, remote sources including geospatial (e.g., National Land Cover Data (NLCD), MN Department of Transportation roads layers), and high-resolution aerial LiDAR data (>20 returns m^{-2}) (<https://lithub-minnesota.hub.arcgis.com>). We characterized landscape scale land cover variables as the proportion of NLCD-defined land cover types within a 5-km buffer of the site. Briefly, NLCD defines forest as areas with most trees >5 m tall and more than 20 % of vegetation cover; deciduous forest has $>75\%$ of tree species that shed foliage seasonally; evergreen forest has $>75\%$ of tree species that maintain foliage year round; mixed forest has neither deciduous nor evergreen forest as $>75\%$ of total tree cover; and wooded wetland has $>20\%$ forest or shrub cover with periodically saturated soil or substrate. We recorded three land cover categories: deciduous, mixed deciduous/coniferous, and coniferous (defined as the combination of the NLCD evergreen and wooded wetland [i.e., peatlands]) cover types. Similarly, we recorded road densities at a landscape scale as the linear extent of roads (primary, secondary, and tertiary roads, including dirt forest roads) within a 5-km buffer of the site. During fecal pellet surveys, surveyors recorded the stand type(s) (e.g., jack pine, red pine, black spruce, white cedar, balsam fir, tamarack) defined as any tree species comprising $\geq 30\%$ of the transect length. If no single species accounted for $\geq 30\%$ of the transect, it was recorded as a mixed conifer stand. We used these categorizations as stand scale forest-type predictors. Tree density (i.e., the number of trees) was measured in two circular plots of 3.6 m radius along each pellet transect. One plot was located on each side of the road, at the farthest distance from the road along the transect. We used land cover data from public sources (<https://gisdata.mn.gov/>) while recently acquired LiDAR-derived grid metrics characterizing vertical forest structure and canopy cover were obtained from MNDNR Forestry Program. In particular, canopy density (based on the proportion of LiDAR returns) in five contiguous vertical strata (0–1.37 m, 1.37–5.00 m, 5.00–10.00 m, 10.00–15.00 m, and >15.00 m) were selected considering their importance in other studies (e.g., Deo et al., 2017). Forest characteristics are summarized in Supplemental Table S2.

2.3. Multi-season occupancy modeling – detection, occupancy, and extinction

We used multi-season occupancy models to assess drivers of occupancy and local extinction (MacKenzie et al., 2003) for each species. We used survey route as a random intercept effect to account for the hierarchical sampling design. We first assessed the effects of several variables on detection probabilities – the probability of detecting a species given it is present. Next, we assessed the effects of several variables on initial occupancy probabilities (i.e., the probability a given site is occupied) while accounting for detectability by using the top detection model obtained in the previous step. Finally, we assessed the effects of several variables on extinction probabilities (i.e., the probability that an occupied site becomes unoccupied in the following year) while accounting for detectability and initial occupancy by using the top detection and occupancy models. For each of these parameters, we used a positive stepwise approach to model construction. We first assessed whether a random intercept effect for each survey route improved model performance due to the hierarchical spatial sampling design. We assessed model performance based on the Leave-One-Out Information Criterion (LOOIC), an analog of Akaike's Information Criterion (Burnham and Anderson 2002) for mixed-effects models. After determining whether the random intercept should be included, we then constructed models with a single (fixed-effect) predictor and assessed their performance based on the statistical significance of their coefficient value (see

Supplemental Table S2 for a list of predictors examined) and LOOIC. We used both 95 % confidence intervals (CI) of predictors and LOOIC as criteria for model selection because LOOIC alone is overly permissive of uninformative variables (Arnold, 2010). We discarded any candidate variables with non-significant coefficient values (i.e., 95 % CI overlapped zero) and considered the top single predictor the one with a significant coefficient and the lowest LOOIC. Next, we constructed models with two predictors; the top single predictor was included in each of these models, in addition to each predictor that had a statistically significant coefficient value. We determined the top two-predictor model based on the same criteria as above. If no two-predictor models outperformed the top single-predictor model, we accepted the single-predictor model as the top model. Finally, we constructed three-predictor models following the same process. We limited each parameter to three predictors to avoid overfitting. We modeled colonization as a constant to limit the number of predictors in models and because predictors of occupancy and extinction were our top priorities. All models were constructed in the R package ‘ubms’ using the `stan_colext` function (Kellner et al., 2021). Prior to fitting models, we used a model selection function in the ‘rfUtilities’ package in R to remove any combinations of variables exhibiting multicollinearity (Evans and Murphy, 2019).

2.4. Multi-state occupancy modeling-relative abundance and population growth

To determine whether covariates affecting abundance dynamics differed from those affecting occupancy dynamics, we used a multi-state occupancy modeling approach (MacKenzie et al., 2009). Whereas traditional occupancy modeling approaches only consider two possible occupancy states (i.e., occupied or unoccupied), multi-state occupancy modeling considers multiple types of occupancy states. For example, multi-state occupancy modeling can be used when it is important to distinguish sites with reproductive activity from those that are occupied but show no signs of breeding (McGrady et al., 2017). We selected this approach because snowshoe hare pellet counts were collected using a binned approach (e.g., 0, 1–39, or 40+ pellets) due to logistical constraints in the field. A multi-state approach allowed us to discriminate between sites with relatively fewer (1–39) and relatively greater (40+) pellet piles, as a proxy for abundance. Although continuous values of abundance may be ideal, the large number of snowshoe hare pellets at many sites posed challenges due to excessive time requirements to obtain exact counts and therefore the binned approach was adopted. To maintain consistency among species, we binned the pellet counts of spruce grouse and ruffed grouse to facilitate multi-state occupancy modeling for these species. We calculated the median pellet count values for spruce grouse and ruffed grouse and used these as the cutoffs for pellet abundance bins.

Our objective was to determine environmental predictors of variation in abundance; therefore, we used three occupancy states: 0 = unoccupied, 1 = occupied with relatively low pellet counts, and 2 = occupied with relatively high pellet counts. We focused multi-state occupancy models on predictors of state 2 (i.e., Rho, or “abundance”). We followed the same approach to model construction as in our multi-season occupancy modeling. We first determined predictors associated with the probability of detecting “abundance” (i.e., the probability of observing State 2 given that pellets are abundant at the site, or $p[22]$). Next, we determined the predictors associated with the probability of initial abundance. Finally, we determined predictors associated with transitions between the two positive occupancy states (i.e., $\Phi[12]$ = probability of observing State 2 at a site that was previously in State 1 and $\Phi[21]$ = probability of observing State 1 at a site that was previously in State 2, analogous to positive and negative population growth, respectively). We followed the same positive stepwise approach to model construction as described above and limited each parameter to a maximum of three predictors. All multi-state occupancy models were

constructed in the R package ‘unmarked’ using the `occuMS` function (Fiske and Chandler, 2011).

2.5. Multi-species occupancy modeling-species co-occurrence along environmental gradients

Finally, we constructed multi-species occupancy models to test several hypotheses of species occurrence and co-occurrence along environmental gradients. Each model compared occupancy of one of the boreal-specialist species (spruce grouse or snowshoe hare) with that of the ruffed grouse, a forest generalist. We constructed several models relating the boreal species to a boreal forest type, ruffed grouse to a deciduous forest type, and co-occurrence with an intermediate or mixed forest type. For example, at the landscape scale we constructed co-occurrence models in which spruce grouse were associated with coniferous forest land cover, ruffed grouse with deciduous forest land cover, and hypothesized that co-occurrence was associated with mixed forest land cover. Similarly, at a local scale, we hypothesized that spruce grouse would be associated with black spruce or jack pine stands, ruffed grouse with deciduous stands, and co-occurrence with mixed species composition (i.e., no single species comprising $\geq 30\%$ of the transect) or balsam fir stands (which often co-occurred with aspen). We used the top detection model (determined previously) for each species in each model and assessed models based on AICc compared to a model with no occupancy predictors and the statistical significance of coefficient values. Each model included detection predictors from each respective species’ top detection model. We constructed these models using the `occuMulti` function in ‘unmarked’. We constructed models for each of 2019, 2020, and 2021, because these years had repeat survey data, and assessed consistency of multi-species occupancy predictors across years.

3. Results

3.1. Detection probability

The top performing detection models for all species included the effect of observer type (Fig. 2; Fig. 3; Supplemental Table S3). For spruce grouse, snow extent and survey condition were also included in the top model, while survey condition and date were included in the top model for ruffed grouse. The top snowshoe hare detection model did not include additional variables. Overall detection probabilities were 0.62 (0.58–0.67) for spruce grouse, 0.69 (0.66–0.72) for ruffed grouse, and 0.96 (0.95–0.97) for snowshoe hare.

3.2. Occupancy probability

Spruce grouse occupancy was most strongly associated with land cover and forest structure. The top initial occupancy model included the effects of deciduous land cover at a landscape (5-km) scale (negative effect on occupancy) and the density of LiDAR returns at the 5.00–10.00 m (+) and 10.00–15.00 m (+) height strata (Fig. 2; Fig. 4). Additionally, coniferous land cover (+), jack pine stands (+), stand age (–), and density of LiDAR returns at >15.00 m height (–) all outperformed a null model (Supplemental Table S4).

Landscape-scale variables were not strongly associated with ruffed grouse nor snowshoe hare occupancy. Rather, local-scale variables related to forest structure and stand type were among the top predictors. The top initial occupancy model for ruffed grouse included red pine stands (–) as the only predictor (Fig. 2). Other predictors that outperformed a model with no initial occupancy predictors included deciduous forest stands (+) and LiDAR return density at the 5.00–10.00 m stratum (+; Supplemental Table S4). Tree density (+) was the only predictor that outperformed a model without initial occupancy predictors for snowshoe hare, and thus the top model included only the effect of tree density (Fig. 2).

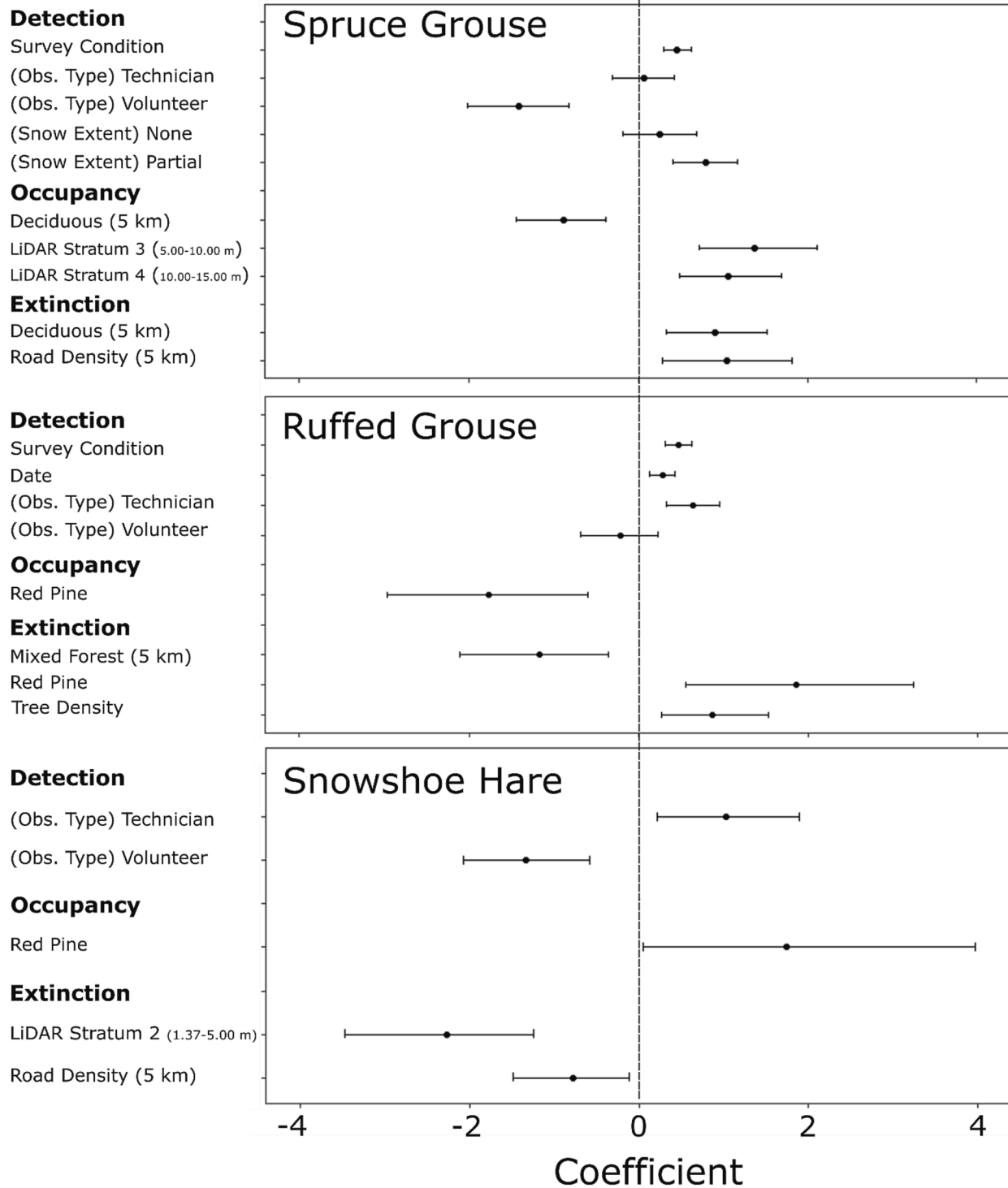


Fig. 2. Coefficients ($\pm 95\%$ confidence intervals) of detection, occupancy, and extinction predictors in top-scoring multi-season occupancy models for spruce grouse, ruffed grouse, and snowshoe hare based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Models were constructed using a positive stepwise approach with each parameter limited to a maximum of three predictors (note: some detection predictors are multi-level factors that were considered a single predictor). Full definitions of predictors are defined in [Supplemental Table S2](#).

3.3. Extinction probability

Similar to initial occupancy results, the predictors most strongly associated with spruce grouse extinction occurred at the landscape scale. The top extinction model included the effects of deciduous forest cover (+) and road density (+) at the 5-km scale (Fig. 2; Fig. 4). In single-variable models, tree density (-), structure at the 5.00–10.00 m

stratum (-), winter snowfall (-), and winter temperature (+) also outperformed a model without extinction predictors (Supplemental Table S5).

A variety of variables influenced ruffed grouse extinction probability. The top model included the effects of mixed coniferous/deciduous forest at a landscape scale (-), red pine stands (+), and tree density (+; Fig. 2). In addition, stand age (-), LiDAR density at the 1.37–5.00 m

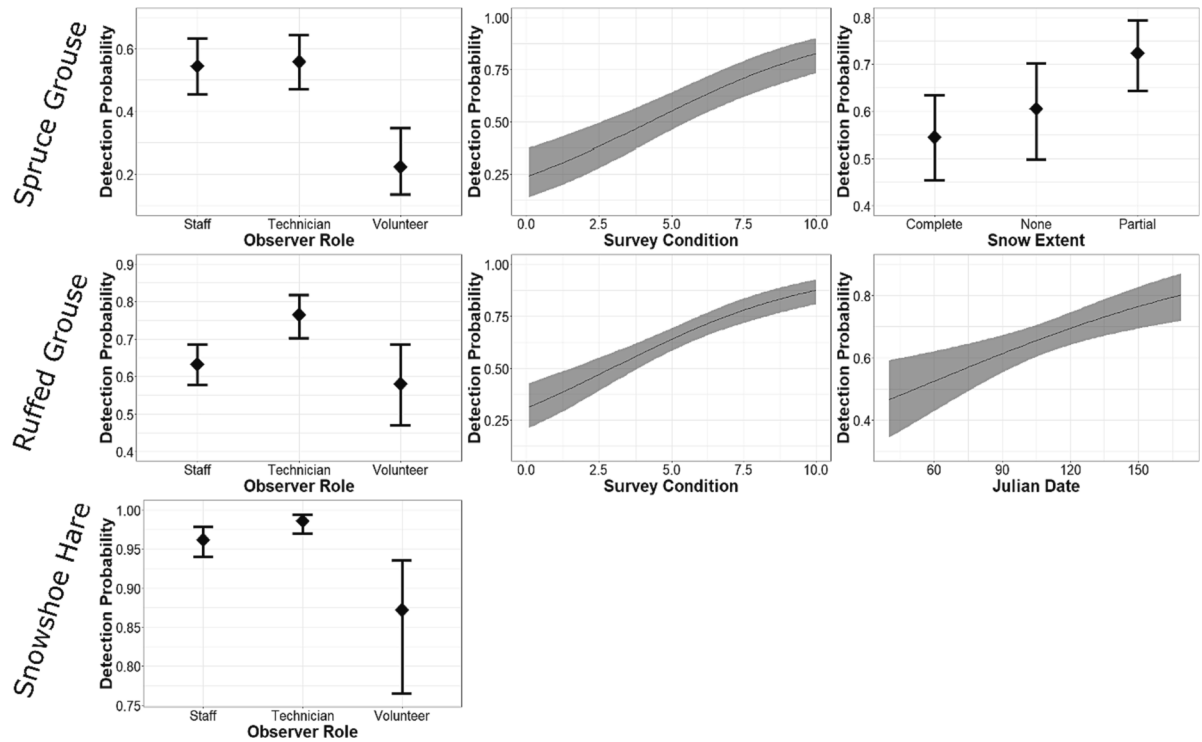


Fig. 3. Marginal effects of detection predictors in top detection models for spruce grouse, ruffed grouse, and snowshoe hares based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. For categorical variables (observer role, snow extent), error bars represent 95 % confidence intervals (CIs). For continuous variables (survey condition, Julian date), gray shaded areas represent 95 % CIs.

stratum (–), LiDAR density at the >15.00 m stratum (+), jack pine stands (+), balsam fir stands (–), deciduous stands (–), and winter snowfall (–) all outperformed a model without extinction predictors (Supplemental Table S5).

Predictors related to climate and stand-scale forest characteristics were among the top extinction predictors for snowshoe hare. The top extinction model included the effects of LiDAR density at the 1.37–5.00 m stratum (–) and winter snowfall (–; Fig. 2; Fig. 5). In addition, LiDAR density at the 5.00–10.00 m (–) and >15.00 m (+) strata, tree density (–), stands of balsam fir (–), black spruce (–), and red pine (+), and winter temperature (+) outperformed a model with no extinction predictors (Supplemental Table S5).

3.4. Multi-State occupancy probability

Multi-state occupancy models suggested that environmental drivers of occupancy and abundance (i.e., ρ) were similar for spruce grouse, but differed for both ruffed grouse and snowshoe hare. For spruce grouse, the top model for initial abundance and the top model for transitions between high and low pellet counts (e.g., ϕ) included the same predictors as models for initial occupancy and extinction probability, respectively (Fig. 6). Stand types were the most important predictors of initial abundance for ruffed grouse, and forest structure characteristics were most important for snowshoe hare. The top abundance model for ruffed grouse included the effects of balsam fir (+) and deciduous (+) stands (Fig. 6; Fig. 7). Forest structure at the 1.37–5.00 m stratum (+) and mixed coniferous/deciduous forest at a landscape scale (+) also outperformed a null model (Supplemental Table S6). The top abundance model for snowshoe hare included the effects of forest structure at the 5.00–10.00 m stratum (+; Fig. 6). Stand age (–), structure at the 1.37–5.00 m (+) and >15.00 m (–) strata, tree density (+), and red pine stands (–) all outperformed a model without abundance predictors (Supplemental Table S6).

Forest structure played a significant role in abundance dynamics for

ruffed grouse and snowshoe hare. Several vertical strata were associated with year-to-year negative growth (i.e., $\phi_{[21]}$). The top model describing negative growth for ruffed grouse included the effects of forest structure at the 5.00–10.00 m stratum (–), tree density (+), and jack pine stands (+). The top model describing negative growth for snowshoe hare included the effects of structure at the 1.37–5.00 m (–) and >15.00 m (+) strata. In addition, snowshoe hare were the only species in which interspecies interactions appeared to influence population dynamics. The top model for snowshoe hare also included the effect of ruffed grouse abundance on positive growth (i.e., $\phi_{[12]}$), which was negative (i.e., greater ruffed grouse abundance reduced the probability of positive growth in snowshoe hares; Supplemental Fig. S1; Supplemental Table S7).

Few of our predictions of species co-occurrence across boreal-hardwood gradients were supported. However, in 2021, co-occurrence of spruce grouse-ruffed grouse and snowshoe hare-ruffed grouse was positively associated with mixed forest at a landscape scale (Supplemental Table S8). However, no co-occurrence predictors were statistically significant at the stand scale in any year or at the landscape scale in 2019 and 2020.

4. Discussion

4.1. Spruce grouse

Our results support recent work implicating deciduous forest cover as a key factor limiting the range of spruce grouse (Casabona et al., 2022). However, our results suggest that forest structure may be a stronger determinant of spruce grouse habitat selection than the particular stand type. Previous work has suggested spruce grouse occupancy is associated with black spruce and jack pine stands (Robinson, 1969; Pietz and Tester, 1982; Anich et al., 2013). Our models supported an association with jack pine, but no stand-type variables were strong enough to be included in top models. Rather, forest structure of the

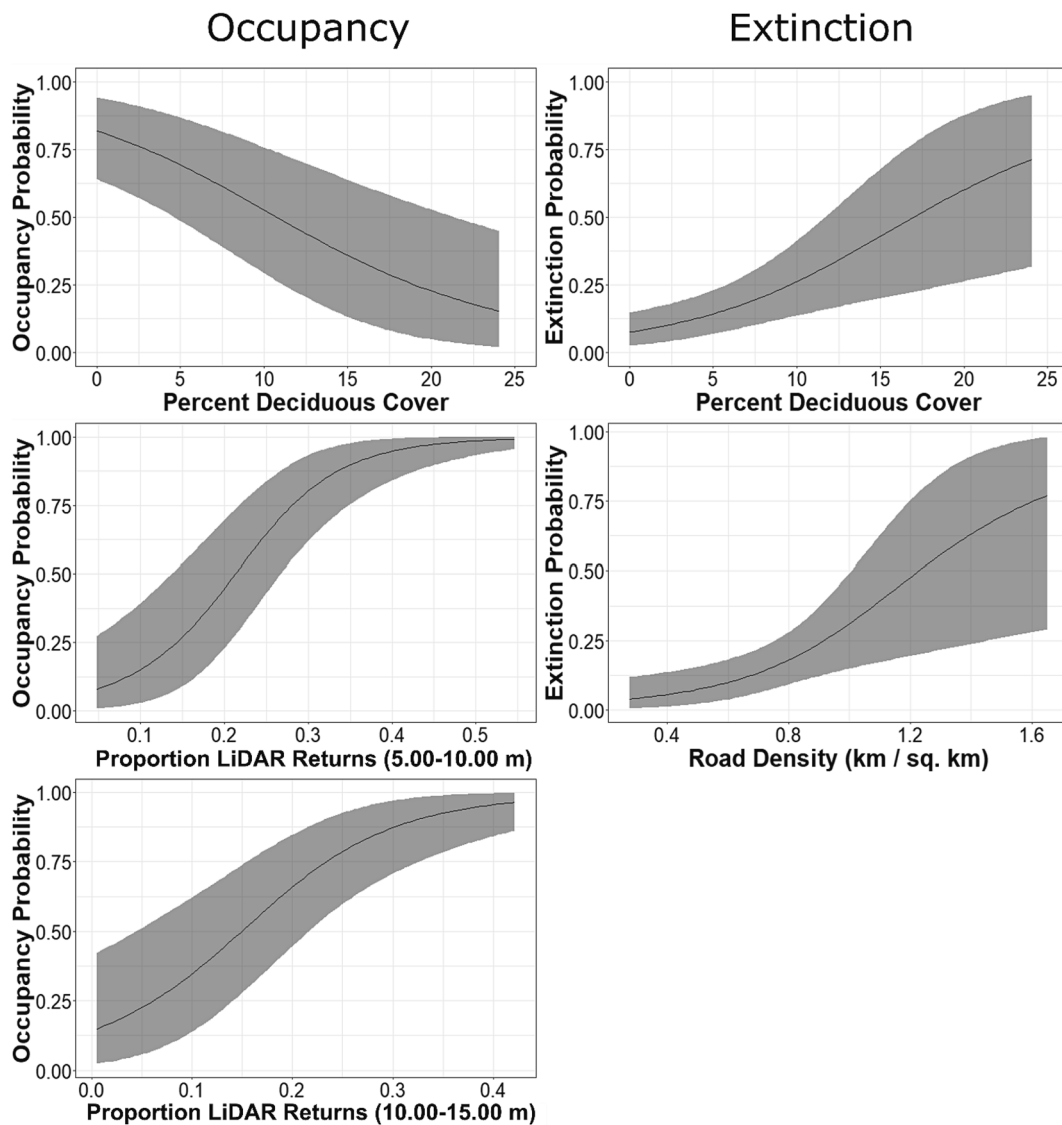


Fig. 4. Marginal effects of occupancy and extinction predictors in the top multi-season occupancy model for spruce grouse based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Gray shaded areas represent 95 % confidence intervals. Percent deciduous cover and road density were calculated within a 5-km radius of the survey site. LiDAR returns from 10 to 15 m in height, which represents the density of the mid-canopy, were calculated within a 150-m radius of the survey site.

lower and mid-canopy was the key local scale determinant of spruce grouse occupancy and persistence. Dense lower and mid-story canopy provides cover from aerial predators and provides thermal protection in winter (Thompson and Fritzell, 1988).

We expected extinction probabilities of spruce grouse to be closely associated with climatic variables given the position of the study area on their southern range margin. Lower temperatures and greater snowfall were associated with lower spruce grouse extinction probabilities, as expected, but the association was not as strong as landscape-scale land cover and road densities. Snowfall and temperature are important to maintaining a deep snowpack for subnivean roosting in winter, but spruce grouse may mitigate suboptimal snow roosting conditions by roosting in trees within a dense forest structure. Indeed, spruce grouse in Maine were observed moving into denser stands and primarily occupying trees in winter (Allan, 1985). Spruce grouse respond to inadequate snow roosting conditions by tree roosting instead, thereby moderating the effects of climate and temperature in our models. Indeed, as climate conditions are predicted to broadly shift the distribution of forest land cover types northward in our study area (Taylor et al., 2017), the effects of climate on spruce grouse occupancy and extinction may be primarily

indirect. Our results underscore the importance of managing forests for dense lower- and mid-canopy to provide climate refugia for spruce grouse at their trailing edge.

Road densities had a substantial effect on spruce grouse extinction probability. Road construction in working forests can change the predator landscape and alter community dynamics (Sirén et al., 2017). Road densities may be associated with greater densities of predators; thereby, roads can indirectly cause a decrease in the occurrence of prey species (Boan et al., 2014). In the western United States, avoidance of roads and reduced nesting success near roads was considered a potential result of fear or auditory disturbance (Pruett et al., 2009). Additionally, road density may be correlated with greater hunter and/or timber accessibility, thus, local extinction probabilities may be driven by more intense harvest. Although the link is unclear, our study suggests that road-sparse areas may promote spruce grouse persistence.

Occupancy modeling is inherently a presence/absence estimator and may not capture variation in density among occupied sites (Nielsen et al., 2005; Torres et al., 2012). Therefore, we hypothesized that models accounting for abundance may be more sensitive to associations with particular stand types. Our results suggested that the same variables

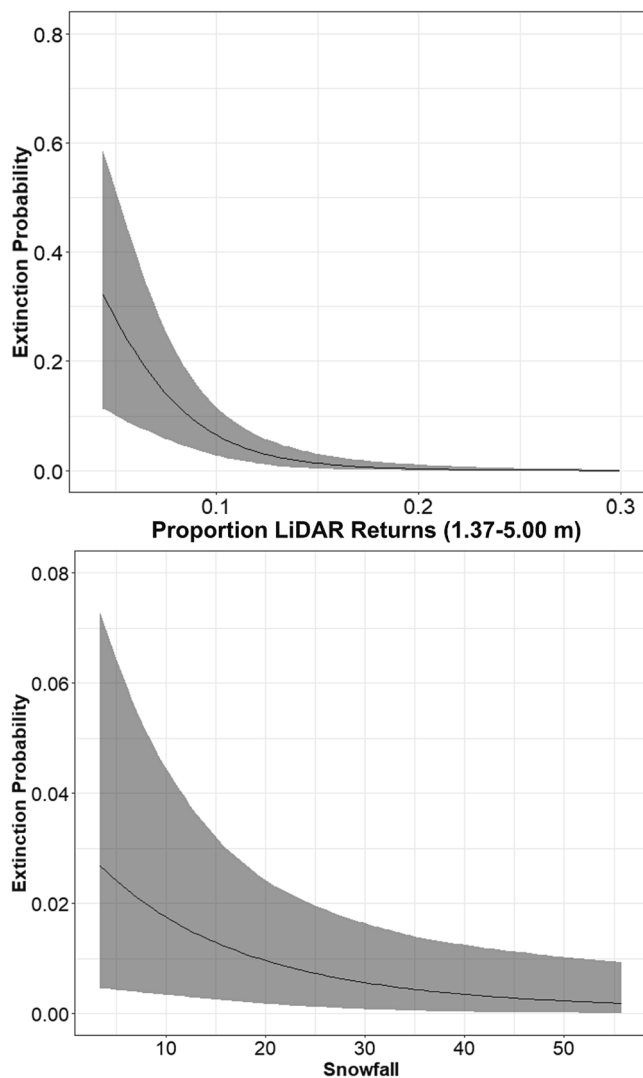


Fig. 5. Predicted extinction probability for snowshoe hares based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Gray shaded areas represent 95% confidence intervals. LiDAR returns from 1.37 to 5.00 m in height, representing the density of the shrub understory, were calculated within a 150-m radius. Snowfall was calculated at the center of the survey site using the National Gridded Snowfall Analysis from the National Oceanic and Atmospheric Administration.

governing spruce grouse occupancy – deciduous forest and vertical forest structure – were the most important predictors of relative abundance. We note that our modeling approach, multi-state occupancy modeling – may still be less sensitive to abundance patterns than a modeling approach that uses precise counts such as N-mixture modeling (Royle, 2004). Therefore, we may have had difficulty identifying some potentially important predictors (i.e., stand types). In addition, our models used an indirect estimator of abundance – the number of fecal pellet groups along a transect. Although the number of pellet groups is likely correlated with abundance (Krebs et al., 2001; Evans et al., 2007; Hanser et al., 2011), this metric could be influenced by other parameters such as use intensity and diet, which could cause variation in fecal deposition rates, and make resolution of statistical patterns more difficult.

4.2. Ruffed grouse

Ruffed grouse occupancy and extinction tended to have stronger associations with stand-level variables than landscape-scale variables, in

contrast to spruce grouse. Ruffed grouse home range sizes vary seasonally and throughout their range. Whereas some estimates from the south of their range in Missouri and Tennessee exceed 35 ha (Thompson and Fritzell, 1988; Epperson, 1988), a study conducted during spring in Minnesota found average home ranges of just 6.7 ha (Archibald, 1975). This may have contributed to the lack of landscape-scale habitat associations detected in this study.

Deciduous forests, and particularly aspen, are important sources of forage for ruffed grouse (Svoboda and Guillon, 1972). However, since deciduous forests do not provide substantial thermal cover in winter when snow roosting conditions are unfavorable, mixed deciduous/coniferous forest stands may provide some roosting habitat for ruffed grouse in the sheltered base of conifer trees. Our multi-state modeling results suggested greater ruffed grouse abundance in deciduous stands and balsam fir stands (which often co-occur with aspen in our study area), supporting the importance of mixed coniferous/deciduous stands for ruffed grouse in winter and early spring. Furthermore, mixed coniferous/deciduous forest was associated with lower extinction probability in the top extinction model, reinforcing the importance of mixed forests for providing both thermal cover and winter forage for ruffed grouse (Jones et al., 2008).

Ruffed grouse occupancy was most strongly associated with a relatively unexpected predictor. Red pine stands were strongly negatively associated with ruffed grouse occupancy and were associated with greater extinction probability in the top extinction model. One possible explanation for the negative impact of red pine is the abundance of red pine plantations in the study area. Pine plantations provide little winter food and sparse understory cover for predator avoidance (Bender et al., 1997) but can have a dense overstory that provides concealment for raptors and other forest predators (Gullion, 1967, 1970). In that regard, ruffed grouse extinction probabilities may have been associated more with forest management practices than with the red pine stand type, per se. Likewise, higher tree densities also increased the probability of ruffed grouse extinction in winter. Although greater tree densities may provide better cover from predators, higher tree densities occur in younger stands; during the winter and early spring, ruffed grouse were more likely seeking food in mature aspen forests while snow was on the ground. Moreover, ruffed grouse tend to select ground roosts when snow is present, even when snow depth is limited and potentially insufficient (Whitaker and Stauffer, 2003). Stands with greater tree densities may limit snow accumulation underneath trees, creating suboptimal ground roosting conditions. Therefore, openings in the forest may promote ruffed grouse survival by providing better snow roosting conditions. Alternatively, higher tree densities may simply be associated with young stands that lack sufficient food resources to support ruffed grouse populations (Jones et al., 2008).

4.3. Snowshoe hare

Due to their widespread occurrence in our study area, few predictors were associated with initial occupancy and abundance of snowshoe hares. Under these conditions, dynamic occupancy models can be more revealing about the environmental conditions that facilitate demographic patterns from year to year (Yackulic et al., 2015). Accordingly, we found stronger patterns in dynamic models (i.e., extinction probabilities and multi-state transition probabilities) for snowshoe hare.

We expected snowshoe hare occupancy, abundance, and survival to be associated with snowpack and structure at the shrub level (1.37–5.00 m). Understory density has been linked to snowshoe hare overwinter survival and spring population densities (Litvaitis et al., 1985). Our results strongly supported this association, as variables related to shrub-level forest structure were among the top predictors of occupancy, extinction, abundance, and transitions in abundance. Furthermore, our results suggested that greater snowfall was related to lower extinction probabilities. Our results underscore the threat of seasonal camouflage mismatch in a warming climate and highlight the increased

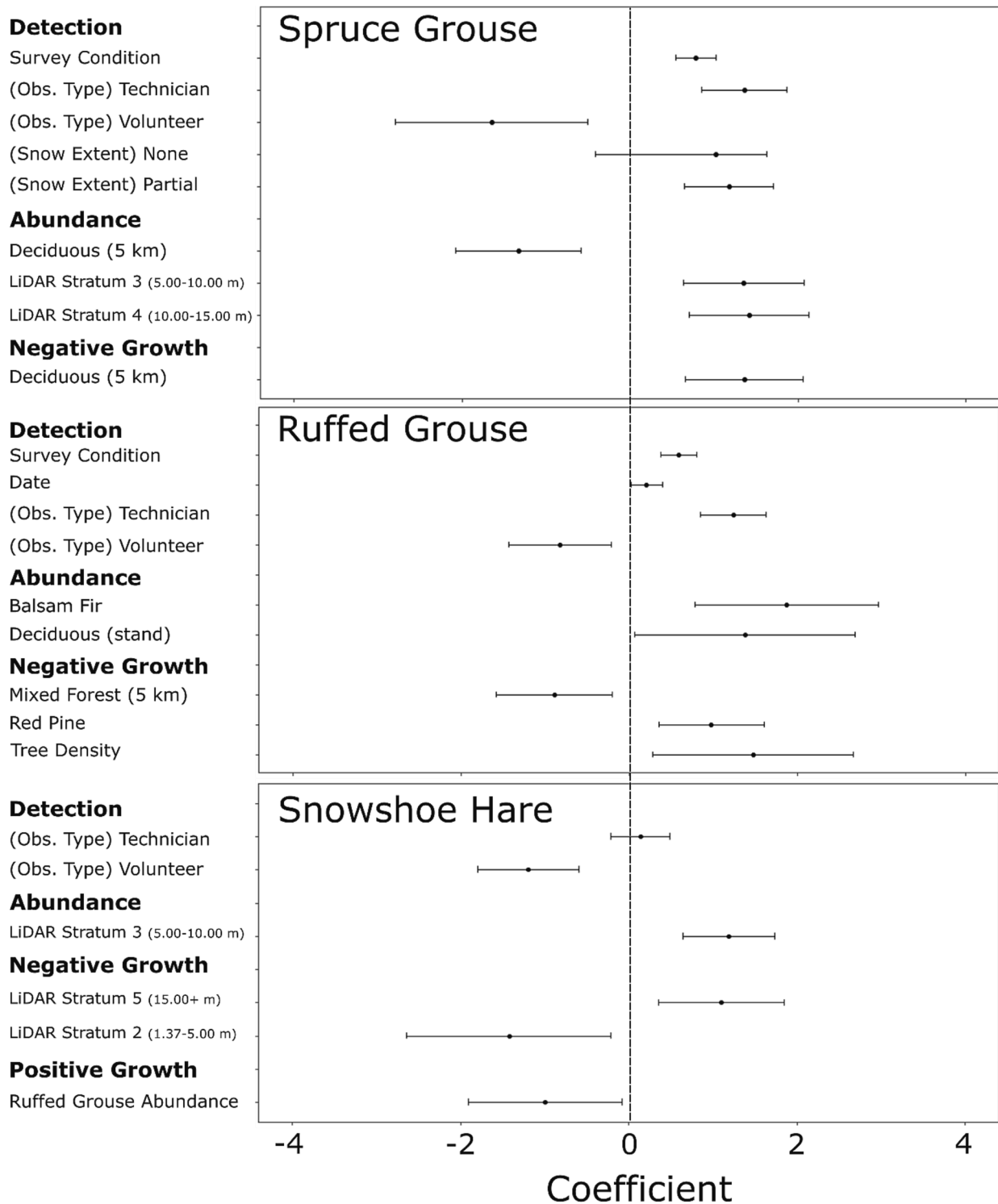


Fig. 6. Coefficients ($\pm 95\%$ confidence intervals) of detection, abundance (ρ), and growth (ϕ) predictors in multi-state occupancy models for spruce grouse, ruffed grouse and snowshoe hare based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Models were constructed using a positive stepwise approach with each parameter limited to a maximum of three predictors (note: some detection predictors are multi-level factors that were considered a single predictor).

vulnerability of populations on the southern range margin (Zimova et al., 2020).

4.4. Species co-occurrence

Based on earlier studies, we expected that co-occurrence would occur along a boreal-hardwood gradient, with both spruce grouse and

snowshoe hare associated with boreal forest and ruffed grouse associated with hardwood forest. Our results were inconsistent across years and across scales, and our hypothesis was only supported at a landscape scale during one of the three years we tested. In 2021, snowfall was exceptionally low and temperatures were abnormally high (data not shown). One potential explanation of our findings is that these abnormal climate conditions forced species to be more selective in their resource

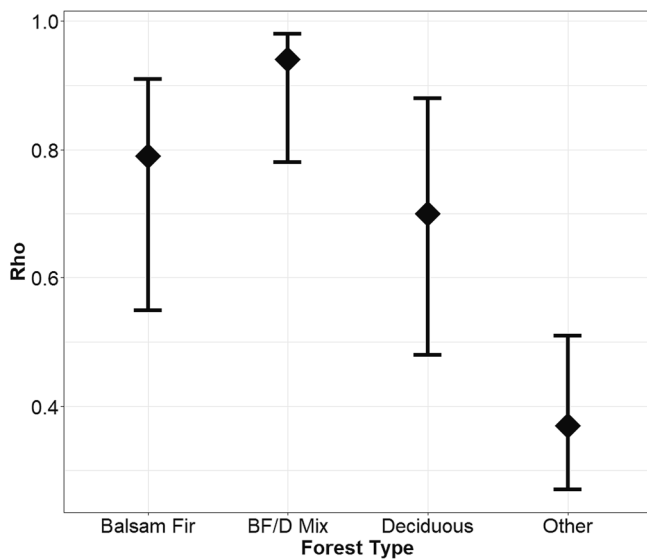


Fig. 7. Marginal effects of abundance (Rho) predictors in the top scoring multi-state occupancy model for ruffed grouse based on fecal pellet surveys in northern Minnesota (USA) from 2019 to 2022. Error bars represent 95 % confidence intervals. BF/D Mix = stands with ≥ 30 % cover of both balsam fir and deciduous forest. Other = all stands with < 30 % balsam fir and < 30 % deciduous forest.

use, resulting in greater spatial overlap at the boreal-hardwood interface. Species co-occurrence models have previously shown the importance of elevational gradients in partitioning species distributions (Estevo et al., 2017). Similarly, the habitat gradient in our study coincides with a latitudinal transition from northern hardwood forests to northern boreal forests. As the climate warms, this transition zone is expected to shift northward as the leading edge of hardwood forests replace the trailing edge of boreal forests (Taylor et al., 2017). Our results suggest that warmer climate conditions with shallower snowpack may amplify interactions between boreal and sub-boreal species during this transition.

We sought to understand species interactions by examining changes in abundance (i.e., multi-state occupancy) in response to the occupancy state of other focal species in the study. Investigating changes in occupancy states over time can identify when interspecific interactions, such as competition, are integral to the demographic parameters of one or both species (Yackulic et al., 2014). The only significant relationship we discovered was an apparent regulating effect between ruffed grouse and snowshoe hare – (i.e., greater ruffed grouse abundance was associated with a lower probability of snowshoe hare population growth). This result corresponds with the well-documented co-cycling of ruffed grouse and snowshoe hare populations (Keith, 1963). This result may be related to a shared predator base (Hoffman, 1958). As predator populations grow and populations of one prey species shrinks due to predation pressure, predators may switch to targeting the more abundant prey species, resulting in correlated population dynamics. Our study design does not allow direct assessment of predator–prey interactions, but our results are consistent with correlated population dynamics resulting from such processes.

5. Conclusions

We examined occupancy, abundance, and local extinction patterns in a suite of forest-associated vertebrate prey species at the southern margin of the boreal forest. We found similar habitat associations of the two boreal-associated species that occur at their trailing edge in our study area. Interestingly, these species may partition niches vertically; spruce grouse were most closely associated with lower and mid-canopy

cover (5.00–15.00 m) and snowshoe hares were most closely associated with shrub-level cover (1.37–5.00 m). Snowshoe hare were the most climate-sensitive species in our study, most likely due to seasonal camouflage requirements, and spruce grouse may mitigate suboptimal climate conditions by selecting tree-roosts when lower and mid-canopy cover is sufficient. We detected a potential boreal-hardwood gradient of species co-occurrence in a year when climate conditions were suboptimal, suggesting future climate change may result in more frequent species interactions as the boreal-hardwood transition zone shifts northward. Overall, the occupancy, extinction, abundance, and population growth of all species were strongly associated with structural density of the shrub and/or lower canopy layer. This work underscores the importance of maintaining dense forest structure for this guild of forest prey species in winter. Harvest strategies that involve thinning forest stands to facilitate timber extraction may be especially harmful. Forest management practices that maintain dense vegetation in the lower canopy, mid-canopy and shrub layer of conifer forests could provide climate change refugia for boreal-associated species at the trailing edge.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121568>.

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Research article

Landscape genetics of spruce grouse at the trailing edge of the boreal forest

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Populations on the periphery of a species range generally occupy marginal or less continuous habitat and can have greater extinction risk than populations in the range-center. For climate-sensitive populations on the trailing edge of a species' distribution (i.e. low latitude or low elevation), the effects of climate change are expected to compound these threats, increasing the vulnerability of these populations. The spruce grouse *Canachites canadensis* is a boreal forest specialist that is expected to experience range contraction at the trailing edge of its range due to climate change. In this study, we investigated the genetic structure, genetic diversity, and connectivity of spruce grouse in Minnesota, along the southeastern range limit in the United States. Clustering algorithms and genetic diversity indices suggested a single continuous population occurred throughout northern Minnesota. We detected no signatures of recent inbreeding or population bottlenecks. We used maximum likelihood population effects modeling and identified coniferous forest land cover and lower average spring temperatures as predictors of gene flow. We used two approaches based on circuit theory to map the potential for gene flow and identified regions of consistently high gene flow in the northwest and northeast of the study area. Omniscape, which incorporated additional parameters representing the likely origins of dispersers and the maximum dispersal distance, suggested a more continuous gene flow landscape than did Circuitscape. Our work highlights the current genetic integrity of one of the largest populations of the eastern subspecies of spruce grouse *C. c. canadensis* in the United States, identifies key landscape attributes for functional connectivity, and demonstrates complementary approaches of Circuitscape and Omniscape for gene flow mapping.

Keywords: boreal forest, *Canachites canadensis*, functional connectivity, genetic structure, landscape genetics, Omniscape



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Introduction

Populations on the margin of a species range are often subject to lower quality habitat and occur in a heterogeneous landscape of suitable habitat and non-suitable matrix (Braunisch et al. 2008). Often, peripheral populations have lower survival, densities, and genetic diversity than those in the core of a species' range (Brussard 1984). Successful dispersal and reproduction are important mechanisms to maintain genetic diversity and provide demographic connectivity (Whiteley et al. 2015, Quinn et al. 2019). Therefore, identifying landscape conditions that improve the probability of successful dispersal through the matrix can aid conservation efforts of peripheral populations (Beier and Noss 1998).

The boreal–hardwood ecotone is the region where the southern edge of the boreal forest meets the northern edge of hardwood forests in the Northern Hemisphere (Goldblum and Rigg 2010). This region represents the southern range limit of many boreal-associated species. Due to climate change, warmer conditions are expected to favor hardwoods in this region in the future, resulting in a northward shift in the ecotone. As a result, boreal-associated species are expected to experience contractions of their southern range limits (Carroll 2007). Remnant boreal forest habitat in this region is likely to become more fragmented as the range contracts; therefore, understanding conditions that facilitate connectivity for boreal-associated species can inform conservation decisions that might improve long-term persistence at southern range limits, such as the identification and protection of key movement habitat (i.e. corridors) that facilitate gene flow.

Landscape genetics provides a powerful toolset for assessing functional connectivity of landscapes by examining associations between landscape conditions and genetic dissimilarity of individuals or populations (Manel et al. 2003). Landscape genetics can provide an empirical basis for identifying gene flow corridors (Spear et al. 2015, Aylward et al. 2020). Whereas corridors are often identified using habitat suitability or occupancy modeling approaches, habitat conditions that facilitate gene flow may differ significantly from conditions required for occupancy (Mateo-Sánchez et al. 2015, Aylward et al. 2020). For example, animals may be able to disperse over suboptimal habitat types that would not support occupancy; therefore, habitat suitability models may overlook potentially important gene flow corridors due to their restrictive parameters (Mateo-Sánchez et al. 2015, Aylward et al. 2020). Landscape genetics can overcome these challenges by inferring dispersal corridors and conditions that facilitate successful dispersal based on measures of genetic connectivity.

The spruce grouse *Canachites canadensis* is a bird species strongly associated with boreal forest habitat (Schroeder et al. 2018). Spruce grouse rely on conifers to provide food; their diet in winter is comprised predominantly of short-needled conifer needles like jack pine and black spruce (MNDNR unpubl.). Conifers also provide protection from predators because spruce grouse plumage is camouflaged amongst the conifer branches. Dense conifers can also limit access by aerial predators like raptors and owls, and provide thermal cover in years where snow conditions are unsuitable for subnivean

roosting, either because the snow is not deep enough and/or it has a thin ice crust that limits diving below the snow surface.

The southern limit of spruce grouse range occurs primarily in the northern United States, including the northern Rocky Mountains in the west *C. c. franklinii*, and northern New England and the northern Great Lakes states in the east and center of their range *C. c. canadensis*. One of the largest populations of spruce grouse in the Great Lakes region occurs in northern Minnesota where minimum temperatures are colder (<https://gisgeography.com/us-temperature-map/>) and the boreal forest is more extensive. In Minnesota, spruce grouse populations are large enough to facilitate regulated harvest. Elsewhere in the region, spruce grouse are listed as threatened in Wisconsin (Wisconsin Department of Natural Resources 2021) and a fully protected Species of Special Concern in Michigan (Michigan Natural Features Inventory 2009). The population in northern Minnesota provides an opportunity to examine spruce grouse genetic diversity and connectivity in one of the most robust populations of *C. c. canadensis* in the United States. The diversity and genetic continuity of this population can be a benchmark to help understand how gene flow in climate-vulnerable systems in early stages of climate-change compare with gene flow in later stages of climate-altered systems. Understanding the genetic diversity and connectivity of spruce grouse may also help understand how climate-induced habitat fragmentation impacts populations as the climate warms and the boreal forest contracts to the north. Previous genetic work on spruce grouse is relatively limited. Genetic data have primarily been used to delimit subspecies in western North America (Barry and Tallmon 2010). Few studies have investigated subpopulation structure, diversity, and connectivity, although recent work has revealed declining mitochondrial genetic diversity at their southern range limit in New York (Kirchman et al. 2020). However, it is unclear if nuclear genetic diversity is declining at their southern range limit, and relationships between landscape variables and gene flow have not been investigated.

Our objective was to characterize the genetic diversity and connectivity of spruce grouse in northern Minnesota. We tested several hypotheses with respect to the relationship between landscape conditions and genetic connectivity. We examined the influence of coniferous forest land cover, particular stand types believed to be preferred by spruce grouse (black spruce, jack pine and tamarack, Robinson 1969, Anich et al. 2013), stand ages, human footprint (road densities), and climate, on spruce grouse genetic connectivity. Then, we used landscape genetics modeling as a basis for constructing a map of hypothesized gene flow using electric circuit theory. Our results provide an empirical basis for wildlife connectivity planning and management of a sentinel boreal forest species at its southern range margin.

Material and methods

Sample collection

We obtained feathers from hunters that harvested birds from throughout the spruce grouse range in Minnesota

(2019–2022), and also from spruce grouse that we captured as part of a pilot telemetry study (2014–2015) at Red Lake Wildlife Management Area (WMA) and during a larger radio telemetry study conducted at Red Lake WMA and a study area located north of Big Falls, MN during 2019–2022. Sampling was relatively even throughout the eastern half of the study area (i.e. the ‘Superior Uplands’), and was more clustered in the central (i.e. ‘Big Falls’) and western (i.e. ‘Red Lake WMA’) parts of the study area. We therefore categorized our samples into three putative populations: Superior Uplands, Big Falls and Red Lake WMA (Fig. 1).

Genetic data

All genetic laboratory work was conducted by the University of Minnesota Genomics Center. DNA extractions were performed using Qiagen DNEasy Blood and Tissue kits following manufacturer’s protocols. We selected microsatellite loci that had been used in spruce grouse (Barry and Tallmon 2010) and other grouse species from the literature (Piertney and Dallas 1997, Caizergues et al. 2001, Piertney and Höglund 2001, Gibson et al. 2005, Wang et al. 2012). Microsatellite PCR used the following thermal profile for all loci: 94°C for 5 min; 45 cycles of 94°C for 20 s, 56°C for 30 s, and 72°C for 60 s; and 72°C for 3 min. Replicate PCRs were conducted for a subset of samples to ensure allelic dropout was not prevalent. Amplicons were visualized on an Agilent Bioanalyzer D1000, D12000 or HS D5000. Microsatellites were then sequenced on an Illumina MiSeq v3 using 300 bp paired-end reads. To check for genotyping consistency, 92% of samples were amplified in duplicate, and two samples were chosen to be amplified four times. Read counts of each possible allele were used to score microsatellite genotypes. If only one allele had a dominant number of reads, we considered the sample homozygous; if a second allele had > 25% of the reads as the dominant allele, we considered the sample heterozygous. If multiple alleles were present in the heterozygous range of read depth, the genotype was considered undetermined. We required a read depth of at least 15 reads to consider an allele valid.

We obtained genotype data for 265 unique individuals at 16 microsatellite loci (Supporting information). Three loci were dropped from analysis due to ambiguity in allele calls and an additional 6 loci were dropped due to lack of diversity potentially associated with linkage to functional genes (Wang et al. 2012). This resulted in a data set of 7 microsatellite loci (BG15 [Wang et al. 2012], CUAAGG37 [Gibson et al. 2005], LLS2 [Piertney and Dallas 1997], TTD6 [Caizergues et al. 2001], and TUT1, TUT3, and TUT4 [Segelbacher et al. 2000]). We tested for Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using Genepop (<http://genepop.curtin.edu.au/>). Additionally, we recorded observed heterozygosity (H_o) and expected heterozygosity (H_e) using GenAEx (Peakall and Smouse 2006), and calculated allelic richness (A_r) using the R package ‘hierfstat’ (Goudet 2005) with rarefaction to the smallest population size ($n = 56$). Finally, we calculated effective population size (N_e) using NeEstimator V2.1 (Do et al. 2014).

To assess genetic structure, we first used a non-spatial method in program STRUCTURE (Pritchard et al. 2000) with the default admixture and correlated allele frequency model (Falush et al. 2003). We ran 500 000 Markov chain Monte Carlo repetitions with a 100 000 repetition burn-in period, with five unique iterations at each putative number of populations (K) ranging from $K = 1–5$. We used ‘StructureHarvester’ (Earl and vonHoldt 2012) to summarize the results and examined best-supported K values both by log likelihood scores and using the ΔK approach (Evanno et al. 2005).

Landscape genetics

To identify potential environmental drivers of genetic connectivity, we used a landscape genetics approach based on causal modeling (Cushman et al. 2006). We constructed resistance surfaces of varying strength for each of our hypothesized landscape predictors (Supporting information). All resistance surfaces were mapped at 1×1 -km spatial resolution. Resistance surfaces characterize the landscape such that

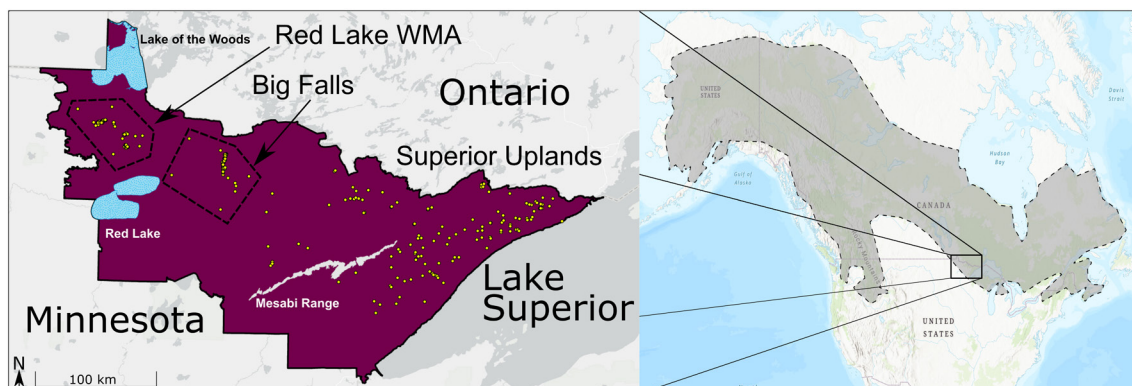


Figure 1. Study area in northern Minnesota showing individual sample locations (yellow dots) and clustered sampling in two locations (dotted lines, Red Lake Wildlife Management Area (WMA) and Big Falls). The remainder of samples were collected from a third area, the Superior Uplands. Three partial barriers to gene flow are also shown: Lake of the Woods and Red Lake (blue polygons) and the Mesabi Iron Range (light gray polygon). Spruce grouse range map (shaded gray) shows the location of the study area within the context of the species’ range.

areas that facilitate gene flow have low resistance and areas that impede gene flow have high resistance.

We tested two categorical resistance surfaces representing land cover: 1) Coniferous forest (combining the Wooded wetland and Evergreen forest categories of the National Land Cover Dataset [Dewitz and USGS 2021]) and 2) Spruce grouse preferred stand types (combining jack pine, black spruce and tamarack forest from the GAP Land Cover Dataset [USGS 2011]; [Robinson 1969, Pietz and Tester 1982, Allan 1985, Anich et al. 2013]). For each categorical resistance surface, the land cover category of interest was set to a resistance of 1 and the rest of the map area was set to a resistance of a higher value (i.e. ' R_{\max} '). We created layers with an R_{\max} of 5, 10, 50, 100 and 500 to test multiple potential hypotheses of landscape resistance.

We tested continuous resistance surfaces representing the influence of human footprint (road density), stand age, and climate variables. Road density was calculated as the linear distance of roads per square km using a Minnesota Department of Natural Resources dataset constructed from national, tribal, state, and county data (Minnesota Information Technology unpubl.). We obtained stand age from the same data set and tested two types of stand age resistance. First, we tested increasing resistance with increasing stand age; second, we tested increasing resistance with increasing deviance from 40 years of age. We selected 40 years as the age with least resistance due to previous work suggesting spruce grouse occupancy declined over time in association with forest succession, but that stands that remained occupied had a mean age of approximately 40 years (Ross et al. 2016). In the stand age data sets, any land categorized as non-forest (i.e. lacking a stand age value) was given the R_{\max} value of resistance. Finally, we created resistance surfaces for mean annual snowfall (NOAA 2023) and mean spring temperature (PRISM 2023). For mean annual snowfall, we obtained cumulative snowfall over the past five years and divided by five to obtain mean annual snowfall for each 1-km² raster cell in the study area. For mean spring temperature, we obtained the mean daily high temperature for March and April over the past 30 years (i.e. the '30-year normal' data set from PRISM) for each 1-km² raster cell in the study area. We selected March and April to coincide with the spring dispersal period prior to mating season (Herzog and Keppie 1980). Each continuous resistance surface was transformed such that the hypothesized optimal value had a resistance of 1 and values further from the optimal value increased in resistance until reaching R_{\max} (Supporting information). Similar to the categorical surfaces, we created continuous resistance surfaces with R_{\max} = 5, 10, 50, 100 and 500 for each variable. To test whether human footprint and warmer climate conditions negatively affected gene flow, we considered resistance positively related to road density and spring temperature and negatively related to snowfall. We considered two stand age resistance schemes, 1) a positive relationship between resistance and stand age, and 2) a positive relationship between resistance and the absolute value of stand age minus 40 (to create a relationship such that 40-year-old stands had the lowest resistance).

We constructed landscape genetics models using the maximum likelihood population effects (MLPE) approach (Clarke et al. 2002). The MLPE approach implements a random intercept effect for each subpopulation to account for the non-independence of samples obtained from the same sampling region. We used this approach to help account for clustered sampling in the Red Lake WMA and Big Falls areas, where inter-sample genetic distance may be lower than in the Superior Uplands simply due to denser sampling. We calculated genetic distance between individuals using the `dist_euclidean` function in the R package 'gstudio' (Dyer 2012). We calculated resistance distance between individuals for each resistance surface using Circuitscape 5 (Anantharaman et al. 2020). We then used MLPE modeling with genetic distance as the response and resistance distances as predictors to determine the environmental variables that were the strongest predictors of genetic distance.

The first step in our modeling approach was determining the best R_{\max} value for each variable. To do this, we constructed a set of models for each variable, with each model using the resistance distance obtained from one of the R_{\max} values as the single predictor of genetic distance. We used the corrected Akaike's information criterion (AICc; Burnham and Anderson 2002) to determine the R_{\max} value that resulted in the model with the strongest predictive performance for each variable. We used a 'null' model based on a uniform resistance surface where every cell had a value of 1 as a benchmark to compare other candidate models. The null model was a Circuitscape-based equivalent of an isolation-by-distance model. If none of the models for a given variable outperformed the null model, the variable was discarded from further consideration. If multiple R_{\max} values outperformed the null model, only the top-scoring R_{\max} value (based on AICc) was used for further modeling. Finally, we constructed multi-variable models by combining all subsets of landscape variables that outperformed the null model.

To select the top-scoring multi-variable model, we first removed from consideration any model with highly correlated predictors. We calculated the variance inflation factor (VIF) of predictors within each multi-variable model and removed any model with a VIF > 10 (Vittinghoff et al. 2012). Using this approach, we did not need to discard entire predictors, but instead discarded models containing highly correlated variables. Of the remaining models, we selected the model with the lowest AICc as the top-scoring multi-variable model. We then used the parameters from this model to construct a resistance surface for predicting functional connectivity across the study area. Specifically, we used the Raster Calculator tool in ArcGIS (ESRI 2011) to create a composite resistance surface raster based on the intercept and β coefficients of predictors in the top model. We multiplied the resistance surface of each landscape variable in the top model by their respective β coefficients, then summed each of these resistance surfaces and the intercept.

We then rescaled this raster from 1–100 to facilitate circuit-based connectivity mapping.

Connectivity mapping

We mapped functional connectivity using two approaches. First, we used a Circuitscape-based approach (Koen et al. 2014, Aylward et al. 2020). We buffered the study area by 300-km and placed 50 focal nodes evenly along the boundary of the buffer to reduce any biases caused by focal node attraction (Koen et al. 2014). This approach removes dependence of the results on the locations where samples were collected. Next, we assigned resistance values of 50 to each raster cell in the buffer area to allow current to flow freely from the nodes to the outer boundary of the final composite resistance surface. We ran Circuitscape in pairwise mode and clipped the resulting cumulative current map to the original study area boundary to remove the artificial buffer zone.

Our second approach to mapping functional connectivity used Omniscape (Landau et al. 2021), which has the potential to produce more biologically realistic scenarios of connectivity but is reliant on some key assumptions. Omniscape offers two key advantages over Circuitscape. First, current is emitted from a ‘source-strength’ raster layer rather than focal nodes. This allows the amount of current emitted from each raster cell on the landscape to reflect the relative abundance of potential dispersers. Second, Omniscape uses a moving-window analysis which can restrict the maximum distance a pulse of current travels on the landscape. In contrast to the Circuitscape-based approach, which allows current to travel unimpeded, the moving window parameter can be constrained to reflect a species’ maximum dispersal distance, facilitating a more biologically realistic estimate of functional connectivity. Based on the assumption that spruce grouse dispersers were most likely to originate from areas with greater proportions of coniferous forest, we created a source-strength raster from the proportion of coniferous forest cells from the National Land Cover Database data set (Dewitz et al. 2021). Based on dispersal distances observed in a study from another spruce grouse population on the southern margin of their range, in Maine (Whitcomb et al. 1996), we used a moving window size of 7-km. This number was equivalent to the 75th percentile dispersal distance observed in preliminary telemetry data from our study area (Minnesota Department of Natural Resources unpubl.). We inferred functional connectivity from Omniscape using a normalized current flow map, which compares the observed current flow to that of a null resistance surface (resistance = 1 for all cells).

Results

Allelic richness, observed and expected heterozygosity, inbreeding coefficient and effective population sizes were similar among the three sampling areas (Table 1). Expected and observed heterozygosity were between 0.66–0.73 for all populations and for the entire study area. No populations exhibited a statistically significant inbreeding coefficient. Effective population size estimates for all populations and the entire study area included infinity. One private allele was detected in LLSD2 in the Big Falls population (2% frequency) and one in TUT4 in the Superior Uplands population (1% frequency).

Structure

The number of populations (K) with the greatest log likelihood was 1 (Supporting information). Based on ΔK , which cannot be measured for $K=1$, the best supported K was 3. However, under scenarios of $K=2$ and $K=3$, the vast majority of individuals exhibited approximately equal ancestry proportions for the two or three groups and no geographic pattern of ancestry was apparent (Supporting information).

Landscape genetics

Land cover, stand age, and climate variables each had at least one model that outperformed the null model. None of the road density models outperformed the null and road density was excluded from further analysis. The optimal R_{\max} values were 100 for coniferous forest and 500 for spruce grouse stand types. Both characterizations of stand age had models that outperformed the null, so we proceeded with the characterization with the lowest AICc, which was a linear negative relationship between stand age and resistance with an R_{\max} value of 50. Optimal R_{\max} values for climate variables included 100 for temperature and 50 for snowfall (Supporting information). In general, multi-variable models that combined four or more variables were often dropped due to high VIF (Supporting information). After removal of such models, the top-scoring model included the effects of coniferous forest land cover and temperature (Table 2). The effect sizes (β coefficients) were small but statistically significant for both coniferous forest land cover ($\beta=0.004$; 95% CI 0.003–0.005) and temperature ($\beta=0.005$; 95% CI 0.004–0.006). The relationships between genetic distance and landscape resistance due to these predictors were weak ($R^2=0.052$ and 0.043, respectively), but stronger than the relationship

Table 1. Genetic diversity estimates within three sampling areas and across the entire study area. n=sample size, Ar=allelic richness rarefied to 118 allele copies, Ho=observed heterozygosity, He=expected heterozygosity, F_{IS} =inbreeding coefficient.

Population	n	Ar	Ho	He	F_{IS}
Red Lake WMA	71	7.75 (6.26–9.24)	0.66 (0.52–0.80)	0.73 (0.65–0.80)	0.06 (–0.22 to 0.33)
Big Falls	56	7.86 (6.48–9.24)	0.71 (0.58–0.85)	0.73 (0.66–0.81)	–0.01 (–0.30 to 0.28)
Superior Uplands	138	8.04 (6.45–9.63)	0.70 (0.60–0.80)	0.73 (0.66–0.80)	0.01 (–0.22 to 0.24)
Study area	265	8.09 (6.54–9.63)	0.69 (0.62–0.76)	0.73 (0.69–0.77)	0.02 (–0.12 to 0.17)

between genetic distance and landscape resistance due to geographic distance alone ($R^2 = 0.019$; Supporting information).

Connectivity modeling

Circuitscape and Omniscape produced similar maps of functional connectivity with high-intensity current generally occurring in the northwestern and northeastern parts of the study area (Fig. 2A–B). Narrow conduits of high-intensity flow generally corresponding to the concept of movement corridors were more apparent in the Circuitscape map than the Omniscape map. However, both maps emphasized black spruce, jack pine, and tamarack stands as areas of concentrated flow. The Omniscape map exhibited several areas of zero current flow, corresponding to regions that were greater than 7 km from the nearest source of current in the source-strength layer. In particular, Red Lake, a large body of water in the northwestern portion of the study area, and the Mesabi Mountain Range in the southeastern portion of the study area had low current flow in both the Circuitscape and Omniscape maps. Both maps identified particularly strong channels of current in the forest stands to the north of Red Lake. Otherwise, the region was characterized by relatively well-connected current flow, with intensity increasing in the black spruce/jack pine/tamarack stands.

Discussion

Our objectives were to assess the genetic structure and diversity of spruce grouse, determine landscape conditions

Table 2. Model comparisons of landscape genetics models using $\Delta AICc$. BJT = preferred spruce grouse stand types (black spruce, jack pine and tamarack), SNW = snowfall, STA = stand age, TMP = spring temperature, WWC = coniferous forest and wooded wetland land cover. Models with road density did not perform better than the null model so are not included here.

Model	df	logLik	AICc	$\Delta AICc$	Weight
WWC+TMP	6	-5767.68	11547.36	0.00	0.73
WWC+SNW+TMP	7	-5767.72	11549.46	2.10	0.26
WWC+STA+TMP	7	-5771.25	11556.50	9.14	0.01
WWC+BJT+TMP	7	-5774.17	11562.36	15.00	0.00
WWC+STA+SNW	7	-5785.21	11584.43	37.07	0.00
WWC+BJT+SNW	7	-5787.29	11588.58	41.22	0.00
WWC+SNW	6	-5788.60	11589.21	41.85	0.00
WWC	5	-5801.39	11612.78	65.42	0.00
SNW+TMP	6	-5800.54	11613.08	65.72	0.00
WWC+STA	6	-5801.42	11614.84	67.48	0.00
TMP	5	-5803.25	11616.50	69.14	0.00
WWC+BJT+STA	7	-5803.74	11621.48	74.12	0.00
BJT+TMP	6	-5805.27	11622.55	75.19	0.00
WWC+BJT	6	-5805.36	11622.73	75.37	0.00
STA+TMP	6	-5806.36	11624.73	77.37	0.00
BJT+SNW	6	-5817.15	11646.30	98.94	0.00
STA+SNW	6	-5824.71	11661.42	114.06	0.00
SNW	5	-5831.64	11673.29	125.93	0.00
BJT+STA	6	-5841.35	11694.70	147.34	0.00
BJT	5	-5846.06	11702.12	154.76	0.00
STA	5	-5849.97	11709.94	162.58	0.00
Null model	4	-5851.48	11710.96	163.60	0.00

associated with gene flow, and map the potential for gene flow at the trailing edge of their distribution in northern Minnesota. Our results suggest that the spruce grouse population in Minnesota represents a single continuous population with no distinct spatial demes. Gene flow was associated with temperature and coniferous forest land cover. Two approaches to connectivity modeling offered complementary perspectives of genetic connectivity; each highlighted stronger potential for gene flow in the northeastern (i.e. Superior National Forest) and northwestern (i.e. Red Lake WMA) portions of the study area relative to the central study area (e.g., east of the Big Falls area), although Omniscape suggested a more continuous gene flow landscape than Circuitscape.

Spruce grouse gene flow and forest composition

At the southern range margin in Quebec, spruce grouse occupancy was significantly reduced when coniferous forest comprised < 40% of the landscape and when deciduous forest comprised > 20% of the landscape (Casabona i Amat et al. 2022). Similarly, preliminary data suggest spruce grouse occupancy in our study area is limited by higher proportions of deciduous forest at a landscape scale (Aylward et al. 2024). These recent findings suggest that the transition from conifer-dominated landscapes in the north to deciduous-dominated landscapes in the south represents a barrier to spruce grouse occupancy, which likely governs their southern range limit. Our results extend this paradigm to the genetic connectivity of spruce grouse.

We found no support for subpopulation structure in our study area, suggesting the contiguity of the boreal coniferous forest landscape in northern Minnesota is sufficient to support a single, large, interconnected population of spruce grouse. However, the southern edge of the boreal forest is at risk of being replaced by northern hardwood forest due to climate change in the coming decades (Hickling et al. 2006). Just as previous studies imply that these effects could result in lower occupancy rates (Casabona i Amat et al. 2022, Aylward et al. 2024), our data suggest that genetic connectivity could be reduced as well. Monitoring the effects of climate change on forest composition at the boreal–hardwood ecotone (Goldblum and Rigg 2010) could have important implications for the health of spruce grouse populations in Minnesota.

Forest structure plays a significant role in spruce grouse occupancy in Minnesota (Aylward et al. 2024). Occupancy modeling work used high-resolution LiDAR data to assess the role of forest structure, but such data were not available continuously across the study area for assessment using landscape genetics modeling. Therefore, we relied on stand age data as a proxy for forest structure characteristics in this study. Our analysis suggested that stand age was a stronger predictor of gene flow than geographic distance alone but had relatively little importance compared to broad-scale coniferous forest land cover. Because stand age may not be a strong indicator of forest structure (Stevens et al. 2016), the role of

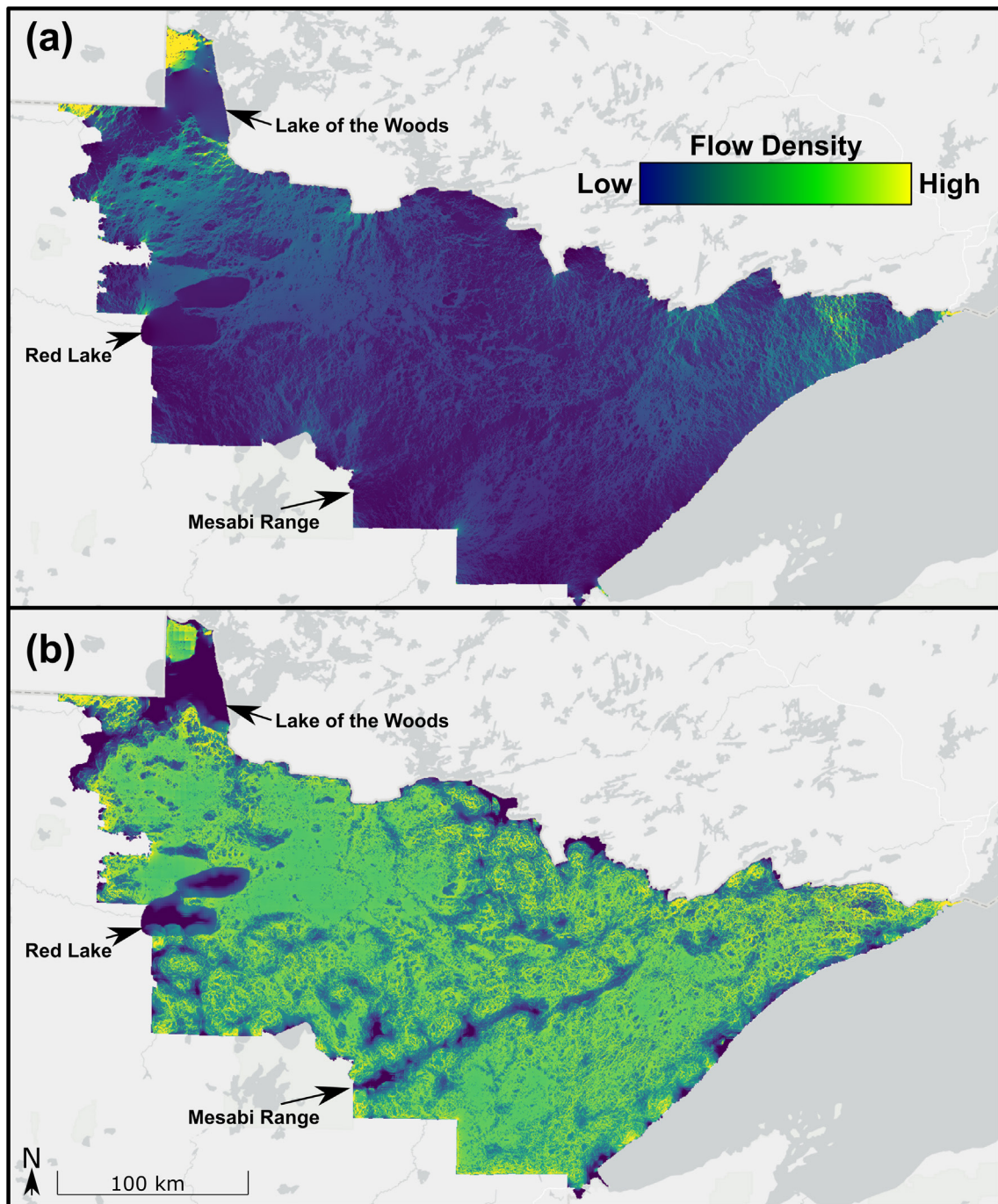


Figure 2. (a) Circuitscape prediction of cumulative current flow using a resistance surface parameterized from the top performing landscape genetics model for spruce grouse in northern Minnesota, USA. (b) Omniscape prediction of normalized current flow using the same resistance surface as (a), the proportion of coniferous forest cover within a 5-km radius as a source-strength layer, and a moving window size of 7 km. In both (a–b), yellow/light green represents greater current flow, light blue represents low current flow, and dark blue represents no current flow.

forest structure in shaping spruce grouse gene flow in our study area may have been underestimated. When continuous LiDAR data become available across the study area, future work could augment our analysis by examining the role of LiDAR-based forest structure characteristics on gene flow in a landscape genetics framework.

Mapping gene flow and connectivity

Maps of cumulative current produced in Circuitscape require nuanced interpretation. Areas of high current flow do not necessarily correlate to high gene flow, rather, they suggest greater facilitation of gene flow relative to their surroundings.

For example, a narrow channel of intermediate resistance – if adjacent to areas of very high resistance – can build up a substantial cumulative current value because all current in the area is strongly avoiding the adjacent cells. Additionally, although areas of low current flow can result from barriers to gene flow, they may alternatively arise from a vast area of uniformly low resistance that precludes current build-up in any singular location (Anderson et al. 2012, McRae et al. 2016). Interpretation of the Circuitscape-based map without considering this nuance could lead to the incorrect conclusion that the center of the study area represents a significant barrier to gene flow. Conversely, the Omniscape-based map more closely reflected genetic structure analysis suggesting a continuous deme throughout the study area. Although current flow was more heterogeneous in the center of the study area than in the northeast and northwest, no complete barriers to gene flow were evident in the Omniscape-based map.

While the Omniscape-based map suggested continuous gene flow overall, several partial barriers to gene flow were apparent. Partial barriers can attenuate gene flow but are not strong enough to cause genetic structure (Landguth et al. 2010). Partial barriers identified in our analysis did not affect spruce grouse population connectivity but could potentially create population substructure in smaller organisms with similar habitat requirements (Chambers and Garant 2010). Lake of the Woods, in the far northwestern part of the study area, represented a complete barrier to gene flow and resulted in an isolated region of high current north of the lake. However, this pattern was primarily driven by the geopolitical boundary of our study area – had our study area included parts of Canada, current would likely have circumvented Lake of the Woods and prevented the buildup of current in the part of Minnesota north of Lake of the Woods. Additionally, two conspicuous regions of low current were consistent with Red Lake, a large body of water in the northwestern part of the study area, and the Mesabi Range, a linear southwest–northeast iron range in the southern portion of the study area. The Mesabi Range is marked by mining operations and relatively little forest cover. Both features were incomplete barriers – Red Lake representing a ‘perforation’ and the Mesabi Range representing an ‘incision’ according to the framework of Jaeger (2000). Overall, despite the presence of these features, our results imply high levels of gene flow throughout the study area.

The accuracy of our Omniscape model is conditional on some key assumptions underlying our source-strength and moving-window-size parameters. Specifically, our model assumes that dispersers are more likely to originate in areas with greater proportions of coniferous forest land cover and that dispersers travel a maximum of 7 km before establishing a new home range. Indeed, previous landscape genetics work on ruffed grouse *Bonasa umbellus* revealed that expanses of unsuitable habitat beyond their typical dispersal distance (2–4 km) were important drivers of genetic distance (Jensen et al. 2019). Preliminary data from our study area suggest longer seasonal dispersals for radio-collared spruce grouse (mean = 5.1 km, max = 11.0 km; Minnesota

Department of Natural Resources unpubl.). Therefore, capturing uncertainty in model parameters is an important future step for refining spruce grouse gene flow patterns.

Expected effects of a changing climate

Resistance modeling suggested that cooler temperatures positively affected spruce grouse gene flow independent of the effect of coniferous forest land cover. During winter and spring, spruce grouse often roost under the snowpack for warmth (Schroeder et al. 2018). If snow depth is too shallow, poor roosting conditions may decrease survival and reduce the probability of successful reproduction. Similarly, freeze–thaw cycles can result in the hardening of the snowpack, which can trap spruce grouse in their roost and lead to mortality (Ménoni et al. 2010). It is possible that warmer temperatures are associated with reduced gene flow due to lower survival in warmer regions with suboptimal roosting conditions.

Climate change is predicted to increase temperatures in the study area (Taylor et al. 2017), likely resulting in a northward contraction of spruce grouse range at their trailing edge (Hickling et al. 2006). A northward range contraction could likely coincide with increasing spatial heterogeneity of spruce grouse populations in Minnesota (Hampe and Petit 2005). In other words, the ‘core’ spruce grouse habitat in northern Minnesota may become peripheral, patchy, and isolated over the next several decades. Presently, the central part of the study area is marginally warmer (~ 5°C) than the northeast and northwest parts of the study area. Continued warming could potentially create unsuitable climate conditions for spruce grouse gene flow in the center of the study area, which would threaten the persistence of genetic continuity throughout northern Minnesota. Furthermore, the distribution of coniferous forest, which also contributed to spruce grouse gene flow, is temperature dependent (Tchebakova et al. 2009, Scheffer et al. 2012, Berner and Goetz 2022). Therefore, climate change could degrade genetic connectivity of spruce grouse populations at their trailing edge through compounding direct and indirect effects.

Comparisons with other studies

Despite special status designations throughout the southern part of their range, relatively little population genetic information exists for spruce grouse. Genetic work has primarily focused on broader subspecies delineation (Gutiérrez et al. 2000, Barry and Tallmon 2010) and has identified declining mitochondrial genetic diversity in the southeastern margin of their range (Kirchman et al. 2020). Although there are biogeographical similarities between our study area and that of Kirchman et al. (2020) in the Adirondack mountains in New York – both occur in the boreal-hardwood ecotone and represent the southern limit of spruce grouse range – our results contrast in that we did not detect signatures of ongoing population fragmentation or loss of genetic diversity. Spruce grouse in New York are state-endangered ([Page 8 of 11](https://</p></div><div data-bbox=)

dec.ny.gov/nature/animals-fish-plants/spruce-grouse) in contrast to a larger, fairly contiguous, harvestable population in Minnesota that would be more likely to maintain genetic diversity. However, the use of different data types (i.e. microsatellites versus mtDNA) in these studies limits their comparability. Microsatellite analysis of spruce grouse in the core of their range in northwestern North America (Barry and Tallmon 2010) provides some context for population genetic data, although possible comparisons with our study are limited due to the use of different sets of microsatellite loci and that these studies focused on another subspecies. Observed and expected heterozygosity in our study were greater than in northwestern North America (Barry and Tallmon 2010). This result is consistent with a biogeographic history of northwestern population expansion following the retreat of ice sheets throughout the Holocene, which has been hypothesized for numerous boreal forest birds and mammals (Arbogast and Kenagy 2001, Ralston et al. 2021). However, to understand range-wide biogeographic patterns, a unified set of microsatellites should be compared throughout the species' range.

Although many boreal species have lower genetic diversity at their northern range limit as a result of their biogeographic history, several boreal species also exhibit lower genetic diversity and greater interpopulation genetic differentiation at their southern range margin due to more recent demographic instability (Browne and Ferree 2007, Kirchman and Ralston 2016, Aylward et al. 2019, Thompson et al. 2019). For example, forest clearing in the northeastern United States has caused reduced genetic diversity and connectivity in American marten *Martes americana* at their southern range limit (Aylward et al. 2019). Red-backed voles *Myodes gapperi* exhibit lower diversity and greater population structure at the southern margin of their range where they occupy boreal 'sky islands' in the Appalachian Mountains (Browne and Ferree 2007). Similarly, a historical resurvey of alpine chipmunks *Tamias alpinus* in the Sierra Nevada mountain range in California revealed an elevational contraction and associated loss of genetic continuity over the past century (Rubidge et al. 2012). Indeed, spruce grouse in the Adirondack Mountains of New York, which have experienced spatial and demographic declines (Ross et al. 2016), have lower mitochondrial genetic diversity and are genetically differentiated from a 'core' population in nearby Algonquin National Park in Ontario, Canada (Kirchman et al. 2020). In an examination of several North American boreal forest bird species, some exhibited a strong 'periphery effect' while others exhibited similar diversity and differentiation among central and peripheral populations (Ralston et al. 2021). Our results suggest the absence of a 'periphery effect' on spruce grouse population genetics in Minnesota, although expanded continuous sampling further north in Canada could improve our understanding. Between 10 000 and 20 000 spruce grouse are harvested each year without affecting the population, suggesting a very large census population size in the state (Minnesota Department of Natural Resources). Despite the climate-sensitivity of spruce grouse (Ralston and Kirchman 2013) and the location of the study area on the southern periphery of their range, our

genetic data support the persistence of a large and interconnected population that has not experienced a recent loss of genetic diversity.

This work represents the first characterization of spruce grouse nuclear genetic diversity and connectivity at their southern range periphery. Our results imply a genetically diverse and interconnected population throughout northern Minnesota at present, but also identify several warning signs that climate change could negatively impact the genetic integrity of spruce grouse at their trailing edge. Based on our maps of potential gene flow, the central part of the study area may be the most vulnerable to loss of genetic connectivity due to climate change. The cooler northwestern and northeastern portions of the study area may represent robust climate refugia for preserving spruce grouse gene flow and connectivity in climate overshoot scenarios (Huntingford and Lowe 2007, Anderson et al. 2020). Our work highlights climate change and associated changes in the distribution of boreal forest habitat as important considerations for spruce grouse population connectivity at their southern range periphery.

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Author contributions

Conceptualization and funding acquisition (CLR). Study design and methodology (CMA, CLR). Data analysis and initial manuscript writing (CMA). Manuscript revision and final approval (CMA, CLR).

Data availability statement

Genetic data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3n5tb2rp4> Location data of birds was obtained voluntarily from hunters on the condition that such information would be kept confidential, thus we are unable to publish this information.

Supporting information

The Supporting information associated with this article is available with the online version.

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