

Sharp-tailed grouse (*Tympanuchus phasianellus*) in a
resource development area at the northern edge of the
species' range

by

Joël Potié

Department of Natural Resource Sciences

McGill University, Macdonald Campus

Montréal, Québec

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1 **ABSTRACT**

2 The reproductive phenology and habitat requirements of sharp-tailed grouse (*Tympanuchus*
3 *phasianellus*) are not well understood. Northern populations of sharp-tailed grouse (STGR)
4 belonging to the *Tympanuchus phasianellus caurus* subspecies are particularly under-studied.
5 Although the *caurus* subspecies is thought to be stable, beyond anecdotal sightings, little is
6 known regarding STGR status or habitat requirements and tolerance to disturbance in the
7 northern parts of its range. The present study focuses on a STGR population located in North-
8 Central Yukon in and around the Klondike Goldfields. Female STGR were fitted with radio
9 transmitters and monitored during the reproductive period over three study years (2015-2017) to
10 quantify habitat use around identified lek sites during the nesting and brood-rearing periods,
11 analyze the habitat selection of nesting and brood-rearing hens, and assess habitat effects on
12 hatching and fledging success. Among 41 radio-collared hens, nearly all attempted to nest
13 ($96.4\% \pm 2.5$) and clutch size averaged 8.3 ± 2.1 . Overall apparent nest success for all nests was
14 $76.4\% \pm 1.9$ ($n = 39$). Nest sites were situated where a shrub layer provided vertical cover and
15 abundant bunchgrass understory provided horizontal cover. Survival was higher for early
16 hatching nests in sites with fewer hummocks than later hatch nests with many hummocks. Brood
17 rearing hens selected for habitats with mesic vegetation such as scrub birch and sedges, but also
18 showed a preference for sites classified as dry rather than wet. Brood failure occurred less often
19 within low elevation, sloping sites with abundant deadfall cover and more often within sites on
20 south and east facing slopes with less deadfall. During both the nesting and brood rearing
21 periods, hens did not select for shrub dominated sites equally; those with shrubs less than 2m in
22 height were preferred over taller shrubs and avoidance increased as the successional stage
23 progressed to maturing forest. Home range sizes (163.0 ± 52.9 ha, using 95% kernel density)
24 were larger and distances travelled from the nest site to brood rearing habitat (1119.2 ± 187.9 m)
25 were longer than previously described for STGR and other prairie grouse. Hen survival in the
26 Klondike Goldfields during the reproductive period was $64.2\% \pm 6.2$ ($n = 70$), with most
27 mortality occurring during egg laying and incubation. The current research has helped advance
28 our understanding of the phenological events, space use and habitat selection of an isolated
29 populations of a lekking bird species in a resource development region, and characterize the
30 importance, scale, and inter-relatedness of three major impacts - mining activity, fire history, and
31 predators – on STGR survival and reproductive success in the Klondike Goldfields.

RÉSUMÉ

La phénologie reproductrice et les exigences en matière d'habitat du tétras à queue fine (*Tympanuchus phasianellus*) ne sont pas bien comprises. Les populations du nord de tétras à queue fine appartenant à la sous-espèce *Tympanuchus phasianellus caurus* sont particulièrement sous-étudiées. Bien que l'on pense que la sous-espèce du *caurus* est stable, au-delà des observations anecdotiques, on connaît peu sur le statut du tétras à queue fine ou les exigences de l'habitat et la tolérance aux perturbations dans les régions plus nordiques de son aire de répartition. La présente étude porte sur une population de du tétras à queue fine située dans le centre-nord du Yukon dans et autour des champs aurifères du Klondike. Les femelles ont été équipées d'émetteurs radio et surveillées pendant la période de reproduction sur trois années d'étude (2015-2017) afin de quantifier l'utilisation de l'habitat autour des arènes identifiés pendant les périodes de nidification et d'élevage des couvées, d'analyser la sélection de l'habitat des poules pour la nidification et élevage des couvées, et évaluer les effets de l'habitat sur l'éclosion et le succès du nombre d'œuf pouvant être couvés avec succès. Parmi les 41 poules portant un émetteur radio, presque toutes ont essayé de nicher ($96.4\% \pm 2.5$) et la taille moyenne d'une couvée était de 8.9 ± 2.1 . Dans l'ensemble, le succès de nidification était $76.4\% \pm 1.8$ ($n=39$). Les sites de nidification étaient situés là où une couche d'arbuste fournissait une couverture verticale et un sous-bois abondant de graminée cespiteuses fournissait une couverture horizontale. La survie était plus élevée pour les nids d'éclosion précoce dans les sites avec moins de hummocks que les nids d'éclosion plus tard, avec de nombreux hummocks. Les poules élevant une couvées ont sélectionnées pour les habitats avec de la végétation mésique comme le bouleau broussailleux et de carex mais elles ont également montré une préférence pour les sites classés comme secs plutôt que humides. L'échec de la couvée s'est produit moins souvent dans les sites de basse altitude, en pente douce et avec une couverture abondante d'arbres morts et plus souvent dans les sites situés sur des pentes exposée au sud et à l'est avec moins d'arbres morts. Pendant les périodes de nidification et d'élevage de couvée, les poules n'ont pas choisi de sites dominés par les arbustes également; ceux avec des arbustes de moins de 2 m de hauteur ont été préférés aux arbustes plus grands et l'évitement était plus important lorsque le stade de succession a progressé à la forêt mûrissante. La taille de l'aire de répartition (163.0 ± 52.9 ha, en utilisant un noyau de densité de 95%) était plus grande et les distances parcourues entre le site de nidification et l'habitat d'élevage des couvées (1119.2 ± 187.9 m) étaient plus longues que ce qui

avait été décrit précédemment pour le tétras à queue fine et d'autres tétras des prairies. La survie des poules dans les champs aurifères du Klondike pendant la période de reproduction était de $64.2\% \pm 6.2$ ($n = 70$), la plupart de la mortalité se produisant pendant la période de ponte et l'incubation. La recherche actuelle nous a permis de mieux comprendre les événements phénologiques, l'utilisation de l'espace et la sélection de l'habitat d'une population isolée d'une espèce d'oiseau dans une région de développement des ressources, et de caractériser l'importance, l'échelle, et interdépendance de trois impacts majeurs - l'activité minière, l'histoire du feu et les prédateurs - sur la survie et le succès reproducteur du STGR dans les champs aurifères du Klondike.

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PREFACE AND CONTRIBUTION OF AUTHORS:

This is a manuscript-based thesis following McGill guidelines, and consists of two chapters prepared and formatted for publication. The candidate is the primary author on both data chapters, having developed sampling methodologies, being responsible for data collection, management, and analysis and for writing the manuscripts.

Murray M. Humphries, Michael J. Sutor, and Katie Aitken are co-authors on chapter 2 and 3. MMH was my thesis supervisor, and provided guidance and support to all stages of the process. MS contributed extensively in the field work and data collection, by providing personnel, field equipment, supervision and mentorship as I developed theories and protocols. KA provided guidance and responded to infinite number of questions, in addition to having thoroughly and diligently reviewed my thesis.

CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

Animal occurrence and abundance is a process regulated by habitat-use and selection patterns (Boyce et al. 2015). This is a dynamic spatial and temporal relationship dependent on abiotic and biotic characteristics of the animals environment such as forage availability, shelter, escape cover from predators, and breeding sites, presence or absence of conspecifics, water, soil, minerals, sunlight, climate, and will ultimately determine a population's viability within a given niche (Cody 1985). The physical and biological requirements of organisms vary according to activity, life stage, season and the spatial scale of analysis (Manly et al. 1993, Cody 1985). While some stenotopic species require specific habitats for their continued survival, others can not only withstand a certain level of habitat alterations but may thrive when habitat modifications introduce more favourable conditions.

Quantification of specific habitat needs and relating these to a species' foraging habits, predator-prey interactions, survivorship, reproduction, life history is an important area of wildlife ecology, allowing appropriate management decisions when considering alternate forms of land use (Hilden 1965). Although tagging wildlife presents inherent challenges in study design and biases in study results, radio-collaring remains the preferred technique used to document animal-habitat relationships (Kenward 2001). When quantifying the data collected from radio-collaring programs, resource selection functions (RSFs) are a commonly used tool to estimate the relative quantity and distribution of habitats used in relation to the those available (Manly et al. 2002).

The impact of northern resource development on wildlife is a major and emerging concern to local, regional and national stakeholders. And understanding of space-use patterns and of phenological events, can help provide ecologically relevant mitigation strategies, an understanding of phenological events and space-use patterns relative to specific habitat requirements is required.

This thesis investigates the reproductive habitats of sharp-tailed grouse (*Tympanuchus phasianellus*) in a northern landscape heavily influenced by past and contemporary gold mining. Specifically, the thesis focuses on sharp-tailed grouse selection of nesting and brood rearing habitats (the breeding complex) in the Klondike Goldfields located in north-central Yukon. This research aims to inform habitat suitability models and STGR habitat protection in this gold rich region and to identify some of the effects of local land use practices on this population.

Accordingly, the thesis introduction focuses first on sharp-tailed grouse and their habitat ecology, first across the entire species range then in the Yukon and Alaska in particular. The next section focuses on threats to sharp-tailed grouse, first focusing on the species in general across its range, then focusing in on the particular threats affecting grouse populations in the Klondike Goldfields. The final section of the introduction presents specific thesis objectives.

SHARP-TAILED GROUSE ECOLOGY

Reproductive phenology and habitat requirements of prairie grouse, which includes several species of lekking gallinaceous birds such as capercaillie (*Tetrao urogallus*), sage grouse (*Centrocercus urophasianus*), prairie chickens (*Tympanuchus cupido*), and sharp-tailed grouse (*Tympanuchus phasianellus*), are not well understood. For this reason, current management stipulations may be inadequate for the long-term protection and viability of prairie grouse populations. Furthermore, because habitat requirements and ecological requirements are typically specific to species, subspecies and, in many cases, geographic location, management recommendations that generalize across prairie grouse are likely inadequate. We need a better scientific understanding of prairie grouse species, subspecies and isolated populations', especially regarding their habitat needs and tolerance to disturbance.

Sharp-tailed grouse (STGR) are associated with a variety of habitats, but often occur in shrub-steppe or parkland regions, in open grassland habitats with an abundance of shrubs or treed groves. In the spring, males gather on focal points called leks, or dancing grounds, for ritualistic courtship and mating (Connelly et al, 1998, Baydack 1986). The breeding complex includes the lek, as well as adjacent nesting and brood rearing habitat (Connelly et al. 1998). Although lek habitat can vary, leks are typically located on an elevated area with sparse vegetation dominated by grasses and small shrubs (Hays et al. 1997). In Alaska and Yukon, males begin displaying on leks in early April and remain on the sites until mid May (Mossop et al. 1979, Taylor 2013). During a brief four-day window, females will arrive at lekking sites and attempt to mate with the dominant displaying males.

Nesting and brood rearing habitats are generally within 2 km of the lek (Connelly 1998). STGR are ground-nesters that most often nest in grassland areas with mixed shrubs, shrub-steppe habitats and agricultural crops, with an abundance of forbs and bunchgrasses (Hart et al. 1950, Meints 1991, Meints et al. 1992). Nests tend to be located in areas with denser cover, provided

by mixed shrubs with herbaceous growth and higher vegetation compared to unused or random locations (Giesen 1987, Manzer and Hannon 2005, Marks and Marks 1987, Meintz 1991). Residual cover from the previous growing seasons, including shrubs and woody debris from old burns, is of notable importance for nesting STGR because they begin nesting before the onset of new growth by grasses and forbs (Goddard 2007). Nests are often found under some type of overhead cover, such as grasses or forbs or near the base of a shrub (Hart et al. 1950, Giesen 1987, Marks and Marks 1987, Meints 1991, Hillman and Jackson 1973). Nests are scrapes or hollows in the ground with good vertical and horizontal cover (Goddard 2007, Roersma 2001, Baydack 1986). Females begin building nests and laying eggs shortly after copulation. They lay an average of 12 eggs, laying one per day. Once the last egg has been laid, incubation begins and continues for 21-24 days (Johnsgard 1983). STGR are known to re-nest as many as four times if a clutch is lost (Bergerud 1988).

Shortly after hatch, the precocial chicks will follow the hen to brood rearing habitat (Connelly et al. 1998). Brood rearing habitat is typically mixed shrubs, with high forb density and an abundance of insects, that is accessible from the nest site, and provides adequate concealment from predators and refugia from adverse weather (Connelly et al. 1998, Oedekoven 1985, Marks and Marks 1987, Svedarsky et al. 2003). Chicks rely on insects as their primary food source until approximately five weeks of age, when their diet shifts to forbs (Johnsgard 1983, Hays et al. 1997). Insects used as food include the orders Coleoptera, Hymenoptera, Orthoptera, and Lepidoptera (Hart et al. 1950). Brood rearing habitats are often in early successional stages, but composition varies across the range (Giesen 1987, Meints 1991). In Wisconsin, STGR broods prefer open grasslands (Hammerstrom 1963), while in the Alberta parkland they preferentially use grassland-low shrub transition zones (Moyles 1981). In Colorado, brood rearing habitat contained more than 70% shrub cover (Giesen 1987). Chicks can fly at about seven – ten days of age (Hart et al 1950), and brood break up and dispersal of juveniles may begin by mid-summer at about 35 days of age (Gratson 1988).

STGR in Yukon and Alaska

STGR present in the Yukon belong to the Alaska STGR (*Tympanuchus phasianellus caurus*) subspecies, one of six extant subspecies of STGR found in north-central North America (Connelly et al. 1998, Hanson 1953). The Alaska subspecies is found in North-central Alaska,

southern-to-north-central Yukon, north-east British Columbia, northern Alberta and northern Saskatchewan (Lake Athabasca) (Connelly et al. 1998).

Very little is known about northern subspecies of STGR, especially the Alaska subspecies, as most knowledge about STGR ecology and life history comes from southern populations occupying agricultural or grassland habitats (Connelly 1998, Johnsgard 1983, J. Staniforth, Environment Yukon, unpublished report). Limited knowledge of northern grouse suggests that northern populations may be a different ecotype, and as such, have different habitat requirements than the southern populations (Mossop et al. 1979, Raymond 2001, Taylor 2013). Ritcey (1995) described a northern forest dwelling (post-fire-sedge meadows) ecotype of the *columbianus* subspecies in British Columbia. In Alaska STGR habitat has been defined as scrubby regions at tree line, muskeg, and burns (Weeden and Ellison 1968). Mossop et al. (1979) described two STGR population types in Yukon; one occupying stable parkland habitat consisting of wet hummock meadows with extensive dwarf birch, willow and stunted black spruce (J. Staniforth, Environment Yukon, unpublished report) and the other occupying seral burns. Mossop et al. (1979) went on to postulate that stable parkland populations may serve as source populations which can colonize new seral habitats as they become available.

Although it is believed that the population of the *caurus* subspecies is stable, beyond anecdotal sightings, little is known regarding STGR status or habitat requirements in the northern parts of its range (Connelly et al. 1998, Raymond 2001, Taylor 2013, Mossop et al. 1979, J. Staniforth, Environment Yukon, unpublished report). Local knowledge has contributed the bulk of the current STGR location data for the Klondike region. Many of the historically reported leks, such as Clinton Creek, Henderson Creek, and Quartz Creek, no longer support STGR or only maintain remnant populations (Mossop et al. 1979, J. Staniforth, Environment Yukon, unpublished report; M. J. Suitor, Environment Yukon, unpublished data). In many of these situations, natural succession or anthropogenic activities have transformed the landscape to conditions that are unsuitable habitat for STGR. In spring of 2014, Environment Yukon biologists conducted flush counts to confirm the presence and estimated the approximate abundance of STGR at known leks in the Indian River and North Fork valleys (M. J. Suitor, Environment Yukon, personal communication).

Although seven species of grouse occur in the Yukon, including spruce grouse (*Falciennis canadensis*), ruffed grouse (*Bonasa umbellus*), dusky grouse (*Dendragapus*

obscurus), willow ptarmigan (*Lagopus lagopus*), rock ptarmigan (*Lagopus mutus*) and white-tailed ptarmigan (*Lagopus leucurus*), only STGR is of immediate management concern. STGR are also unique among Yukon grouse because they are the only species that exhibit lekking behavior. Northern populations of STGR are generally patchy in distribution, low in numbers, have unique habitat requirements, restricted movements, and intense social behaviour, which makes them vulnerable to disturbance (J. Staniforth, Environment Yukon, unpublished report).

Threats Across the Species Range

Historically STGR could be found in much of central and northern North America, however, recent numbers have been declining in the southern and eastern range (Connelly et al. 1998, Johnsgard 1983). The impact of human activities on prairie grouse varies by species or subspecies, geographic location, scale, intensity, cumulative impacts and habitat conditions (Brown 1978, Baydack 1986, Ritcey 1995).

STGR are hunted across their range as an upland game bird. Initially, STGR mortality from hunting was thought to be compensatory, permitting harvesting of up to 16% of the autumn population (Ritcey 1995, Hillman and Jackson 1973, Gillette 2014). More recently, many researchers caution that hunting mortality may be additive, possibly because prairie grouse today experience vastly different conditions than they did historically, therefore contribute more strongly to population declines (Ritcey 1995). Overhunting compounded by disease and habitat loss led to the modern extirpation of the heath hen (*Tympanuchus cupido cupido*) in North America (Hunter et al. 2001). Although STGR hunting is not common or widespread in the Yukon, focused hunting of small isolated populations and may have contributed to or caused some local population extirpations (Mossop 1994, J. Staniforth, Environment Yukon, unpublished report).

Predation is believed to be the greatest proximate threat to STGR reproductive success and hen survival (Ritcey 1995; Connelly et al. 1998), and higher mortality rates coincide with spring and summer reproductive periods (Svedarsky 1988). Marks and Marks (1988) reported 94% of the total annual mortality of radio-collared birds during the spring and fall dancing periods. Breeding hens, and their offspring are vulnerable to predation because of their ground-nesting habits and lekking behaviour (Bergerud and Gratson 1988). Potential predators of STGR in the Yukon include northern goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), rough legged hawks (*Buteo lagopus*), great horned owls (*Bubo virginianus*), bald eagles

(*Haliaeetus leucocephalus*), golden eagles (*Aquila chrysaetos*), ravens (*Corvus corax*), coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) (Connelly et al. 1998; J. Staniforth, Environment Yukon, unpublished report).

Weather is also important factor regulating STGR populations. Spring weather is known to be an important determinant of nest success and chick survival. Because chicks cannot thermoregulate for the first three-weeks after hatching, exposure to cold and wet weather over this period, can limit the chick's mobility and ability to feed, resulting in increased mortality (Bergerud and Gratson 1988). Spring and summer weather also effects STGR indirectly through its effects on vegetation and insect production (Goddard et al. 2009, Collins 2004) and, for northern populations, the frequency and severity of forest fires. Little is known about the impacts of snow and extreme cold on STGR in winter, but the length and severity of winter conditions may also be a limiting factor for STGR, especially near the northern range edge.

Although hunting, predation and weather can be significant causes of STGR mortality, population declines are generally attributed to direct and indirect effects of habitat loss, related to agriculture, overgrazing by livestock, oil and gas development, fire suppression and habitat fragmentation (Baydack 1986, Marks and Marks 1987, Norton 2005, Ritcey 1995, Greer 2010, Burr 2014, Goddard 2007, Williamson 2009). Conversion of native grasslands to cropland, and overgrazing are most responsible for STGR population declines (Hart et al. 1950, Giesen and Connelly 1993, Ritcey 1995). As much as 20% of the historic STGR range has been converted to agriculture (Ritcey 1995). Insecticide applications can reduce populations of insects which are important food resources for chicks and young birds (Bergerud and Gratson 1988). Overgrazing of native rangelands by domestic livestock can lead to direct trampling of nests or chicks, or a loss of nesting and brood rearing habitat (Hart et al. 1950, Manzer and Hannon 2007). Negative impacts of grazing to habitat include decreased cover needed for concealment, loss of vegetation species diversity, destruction of riparian area, and a shift in plant communities (Klott and Lindzey). Recent studies have also focused on the effects of rapidly expanding oil and gas developments on prairie grouse. Loss and fragmentation of habitat, displacement and physiological stress have been attributed to oil and gas activities (Pruett et al. 2009, Holloran 2010, Hovick 2014). Doherty et al (2006) found sage grouse (*Centrocercus urophasianus*) will avoid energy extraction activities by up to 4 km. Fire suppression has been linked to declines in STGR in some parts of its range. STGR depend on early successional habitats and fire limits

forest encroachment and maintains grassland and shrub-steppe habitats (Hamerstrom and Mattson 1952). Mossop et al. (1979) identified habitats associated with recent burns, and gravel outwashes as important habitat in Yukon and Alaska (Taylor 2013).

Secondary activities associated with industrial development, including road traffic, noise pollution, and increased predator abundance can reduce prairie grouse numbers (Braun 1986). Baydack (1986) found that females will avoid leks with physical or noise disturbances, which may result in the reproductive failure of local leks. Given STGR are a relatively short-lived species, with a life span of approximately three years, the loss of one season's hatch could potentially reduce STGR populations by 70-80% (Evans 1968). Collision with anthropogenic structures, including vehicles, fences, and powerlines, can be a serious factor influencing grouse survival in some regions (Bevanger 1995, Kociolek et al. 2011, Wolfe et al. 2077).

While reduced populations and distributions generally occur from anthropogenic activities, STGR have been found to be more tolerant of human activity than are other prairie grouse species and, in some cases, may benefit from altered habitats (Braun et al. 2002). Some agricultural crops can increase winter food supply and provide winter habitat (Ritcey 1995). Clearcut logging can mimic the effect of wildfire and can be beneficial to STGR populations (Ritcey 1995). Burr (2014) found lower meso-predator occupancy near oil and gas wells, which positively influenced nest and brood survival.

Placer Mining in the Klondike Goldfields

The Klondike Goldfields represent northern Canada's first and longest running mining development, and the long history of impact and mitigation in this region create a complex mosaic of natural and modified habitats. The goldfields are found in the unglaciated part of west-central Yukon, extending from the Klondike river south to the Indian River, and from the Yukon River east to Flat Creek, encompassing approximately 1,600 square kilometers (Lowey 2006, Willis 1997). Gold discovered on Rabbit Creek (now Bonanza Creek) in 1896, launched the famous Klondike gold rush (Willis 1997). Although the first and most famous Klondike gold rush lasted less than 10-years, ending by 1904 (Willis 1997), gold mining has been sustained in the region for more than a century, and placer mining continues to the present day. The mining sector is the main driver of economic activity in northern Canada, and the Klondike Goldfields are the richest gold producing region in the Yukon (Lowey 2006, Roy 2013).

Placer mining, the process of locating precious metals in alluvial deposits of stream beds, is the preferred method of gold extraction in the Klondike Goldfields (Brady 1984). Four distinct placer mining methods have been used in Yukon over the last century and their use has varied over time with changes in technology, the mining industry, and available placer deposits. Initially, hand mining was done by individuals or small groups who removed all vegetative cover, melted permafrost, altered water channels and created tailings piles to access the placer gravel (Brady 1984, Willis 1997). This labour-intensive method was gradually replaced by hydraulic mining and dredging (Willis 1997). Hydraulic mining uses pressurized hoses to wash away large deposits of gravel or rock, bringing large quantities of water to the hillsides and benches above the creeks. (Brady 1984). Dredging uses land-locked, multi-story floating machines that move along stream beds, while excavating and sifting for gold. Dredges operated in the Klondike Goldfields until 1966, by which time all major Klondike creek beds had been overturned at least once (Brady 1984). Dredging drastically modified the original landscape; today, the Klondike valley is marked by kilometers-long snaking mounds of river stones dredged from the river, and many of these mounds remain unvegetated today. Present-day placer mining uses heavy equipment to push gravel into sluice boxes, sometimes displacing entire valley bottoms (Brady 1984). Although the industry has improved techniques to protect water quality and fish habitats, modern placer mining operates at scales and intensities that exceed all previous mining eras, including dredges. Few studies, apart from Singleton et al. (1981) and Weir et al. (1981) have investigated the impacts of either historical or modern placer mining on wildlife in the Klondike.

There is very limited research on the impacts of mining on the habitat use and survival of STGR or other prairie grouse species. Boisvert (2002) and Collins (2004) found that populations of Columbian STGR on reclaimed mined landscapes of Colorado had higher reproductive success than those located in natural, shrub-steppe habitats. Research on sage-grouse indicated initial displacement by mining activity but found that populations returned to pre-disturbance levels once mining activity ceased (Remington and Braun 1991, Braun 1986, Scott and Zimmerman 1986). Petersen et al. (2016) observed no difference in sage grouse use of habitat in relation to a mine center. In West Virginia, surface-mined areas without canopy cover had extremely high ground temperatures on hot days, potentially decreasing survival of plant

seedlings and invertebrates and, as a consequence, reducing the survival of ruffed grouse chicks (Kimmel and Samuel 1984).

At this time, almost the entire area known to be used by STGR in the Klondike Goldfields is staked by mining claims. If the complex of breeding habitats (leks, nesting, and brood rearing habitats) extends 2 km around lek sites, many existing and planned placer mining locations are likely to overlap with the breeding habitat of STGR. This overlap has the potential to lead to land-use conflicts between placer mining and grouse habitat protection (Giesen and Connelly 1993, Raymond 2001), but there are considerable knowledge gaps regarding the breeding ecology of STGR in the Yukon and the potential impacts of placer mining on STGR population status. The data collected during this study will provide baseline ecological data contributing to evidence-based policy for wildlife conservation, land use, and impact mitigation within Yukon STGR habitat in the Klondike Goldfields.

RATIONALE AND OBJECTIVES

This study investigates STGR habitat use and selection for lekking, nesting and brood rearing (the breeding complex) in the Klondike Goldfields, and documents the impacts of habitat selection on reproductive success. The specific objectives of this research were to:

- 1. Describe habitat use of STGR around identified lek sites within the Klondike Goldfields during the nesting and brood-rearing periods;**
- 2. Analyze habitat selection of nesting and brood-rearing hens;**
- 3. Assess habitat effects on hatching and fledging success;**
- 4. Identify some of the effects of local land use practices on STGR in the Klondike Goldfields to help inform habitat suitability models and STGR habitat management requirement in this gold rich region.**

These objectives were accomplished by radio-collaring hens at lek sites, then relocating hens bi-weekly to monitor nesting/brood success, combined with sampling of vegetation and habitat at relocation site and associated random locations.

RESEARCH APPROACH AND THESIS ORGANIZATION

This thesis is organised as two stand-alone publishable papers (Chapters 2 and 3), prefaced by an introductory chapter (Chapter 1) and completed by a conclusion chapter (Chapter

486 4). Chapter 2 investigates the habitat use and selection of nesting and brood rearing hens
487 (objectives 1 and 2). Chapter 3 examines STGR reproductive success and hen survival through
488 the reproductive period as a function of habitat, anthropogenic activities and hen condition
489 (objective 3). Objective 4 is addressed in both Chapters 2 and 3 by including parameters
490 representing anthropogenic activities, which are considered further in Chapter 4 where I discuss
491 my results and the management implications of this research.

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**Chapter 2: Reproductive chronology, brood rearing success, and
hen survival in a sharp-tailed grouse population at the northern
edge of the species range.**

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Joël Potié (email: joel.potie@mail.mcgill.ca)

Natural Resource Sciences, Macdonald Campus, McGill University

21 111 Lakeshore Drive, Ste-Anne-de-Bellevue, QC, H9X 3V9, Canada

Murray M. Humphries (email: murray.humphries@mcgill.ca)

Natural Resource Sciences, Macdonald Campus, McGill University

21 111 Lakeshore Drive, Ste-Anne-de-Bellevue, QC, H9X 3V9, Canada

Michael J. Sutor, (email : mike.sutor@gov.yk.ca)

Inuvialuit and Migratory Caribou Biologist

Fish and Wildlife, Environment Yukon

PO Box 600, Dawson City, Yukon, Y0B 1G0

Kathryn E. H. Aitken (email : kaitken@yukoncollege.yk.ca)

School of Science, Yukon College,

P.O. Box 2799, 500 College Drive, Whitehorse, Yukon, Y1A 5K4

2.1 ABSTRACT

Habitat-dependent nesting and brood rearing success is well documented for prairie grouse within the core of species ranges. Compared to other prairie grouse, sharp-tailed grouse have a large home range, extending from northern prairies to boreal bogs. Studying a population of sharp-tailed grouse at the edge of the species range, we document habitat-dependent variation in reproductive chronology, brood rearing success, and hen survival. Seventy-five sharp-tailed grouse hens were radio collared and monitored during the reproductive period in the Klondike Goldfields, Yukon in 2015, 2016 and 2017. Peak female attendance at leks occurred during a 1-week interval between April 25 and April 29 during all three study years. Nearly all captured hens attempted to nest ($96.4\% \pm 2.5$), with a mean clutch size for all years and areas of 8.3 ± 2.1 ($n = 41$). Overall apparent nest success for all nests was $76.4\% \pm 1.8$, and $70.6\% \pm 40.1$ of monitored hens with broods successfully fledged at least one chick. Median nest survival estimated using the Kaplan-Meier product-limit procedure with staggered-entry design, was 29 ± 2 days for all years and areas. A series of candidate generalised linear models of logistic regression using covariates selected from a reduced set of abiotic and biotic explanatory variables indicated early hatched nests in sites with few earth hummocks survived better than later hatch nests with many hummocks. Nests below 572 m were at a greater risk of failure than higher elevation nests. The strongest predictors of brood survival were aspect and percent deadfall cover. Low sloping sites had the lowest risk of brood failure, and sites on south and east facing slopes had the highest risk of failure. Deadfall cover was positively related to brood success. Hen survival in the Klondike Goldfields during the reproductive period was $62.1\% \pm 6.2$ ($n = 58$), with greatest risk of mortality during the egg depositing and incubations stages. High reproductive success in the Klondike Goldfields, relative to southern sites, is likely the result of a relatively intact breeding complex and few mesopredators

KEY WORDS: Brood success, hen survival, Kaplan-Meier, Klondike, Mayfield estimate, nest success, radio-telemetry, reproduction, *Tympanuchus phasianellus*, Yukon

2.2 INTRODUCTION

The impacts of anthropogenic activities on wildlife depend on the timing and spatial extent of impacts relative to the timing and spatial extent of population processes (Bhakti et al. 2018, Steidl and Powell 2006). For this reason, it is important to understand the direct and indirect effects human disturbances can have at multiple spatial scales and during different life stages (Polfus et al. 2011). Identifying the spatial and temporal extent of potential and realized impacts provides critical information to decision makers in resolving emerging land-use conflicts. In particular, baseline ecological knowledge of reproductive events and annual survival is necessary for wildlife biologists to avoid anthropogenic disruption that could contribute to population declines.

Sharp-tailed grouse, (*Tympanuchus phasianellus*; STGR), have shown significant population declines across their range (Hart et al. 1950, Giesen and Connelly 1993). Impacts of human activities on prairie grouse vary by species or subspecies, geographic location, and habitat conditions (Brown 1978, Baydack 1986). Success during the breeding season is critical for species viability, and if disrupted could lead to population declines (Angelstam 1984, Bergerud 1988). Courtship display and vocalizations at leks are important factors in mate selection for prairie grouse; acoustical signals by males communicate lek location to females, while displaying activities determine a male's dominance, facilitating females' selection of mates (Sparling 1983). Variation in prairie grouse productivity may be dependent on a hen's ability to locate a mate at a lek, predator abundance, or by the habitat conditions at nesting and brood rearing sites (Hart et al. 1950, Goddard 2007, Manzer 2004, Bergerud 1988, Hoffman and Thomas 2007).

Predation is believed to be the greatest direct threat to reproductive success and hen survival (Ritcey 1995; Connelly et al. 1998). In general, adult mortality rates are higher during spring and summer, when reproduction occurs, than at other times of the year (Angelstam 1984, Svedarsky and Van Amburg 1996). Breeding hens and their offspring are vulnerable to predation because of their ground-nesting habits, large clutch sizes, and lekking behaviour (Angelstam 1984, Bergerud 1988).

Habitat quality and landscape condition are often important, albeit indirect determinants of prairie grouse reproductive success and hen survival (Bergerud 1988, Hillman and Jackson 1973). Modification of habitat that alters cover, reduces insect abundance, increases predator

abundance or degrades habitat can have dramatic impacts on STGR reproductive phenology and population viability. For example, anthropogenic structures and noise pollution can induce avoidance or displacement behaviours (Hovick et al. 2014). The loss of a single breeding season for a short-lived species such as grouse could have devastating impacts on the population (Evans 1968). Furthermore, Lyon and Anderson (2004) described reduced nest initiation rates for sage-grouse (*Centrocercus urophasianus*) in Wyoming from vehicle traffic and proximity to oil wells. Studies in Wyoming and Kansas observed lower prairie-chicken (*Tympanuchus cupido*) nest survival, and avoidance of habitats closer to wind turbines (Lebeau et al. 2014, McNew et al. 2014). Baydack (1986) observed female STGR displacement from leks in Manitoba from physical and audible disturbances. Because females only visit leks during a brief 3-4 days period, any disturbance in this attendance window may result in a lost reproductive season for local leks (Baydack 1986, Harju et al. 2010).

Upon hatching, precocial chicks follow the hen to nearby brood rearing habitat (Connelly et al. 1998). Habitat fragmentation can make brood rearing habitat physically inaccessible to newly hatched chicks, or can increase the risk of predation. Research in Finland determined that habitat fragmentation lowered grouse brood rearing success (Kurki et al. 2000). Furthermore, because chicks rely primarily on invertebrates for at least the first two-months of their life, activities that lower insect abundance can impact chick survival (Kimmel and Samuel 1984, Savory 1989).

In the northern portion of STGR range there is little quantitative information available regarding population trends and habitat selection, though based on anecdotal sightings populations are generally thought to be stable (Mossop et al. 1979). The patchy distribution and low abundance of northern populations may result in local population vulnerability to even minor disturbances (J. Staniforth, Environment Yukon, unpublished report). Manzer (2004) observed an increase of both avian and mammalian predators in the presence of anthropogenic disturbances. Habitat loss could also concentrate nesting activities in remaining habitat, increasing nest density, and increasing the risk of predator detection (Horkel et al. 1978, Niemuth and Boyce 1995). The importance of vertical and horizontal cover, and patch structure have been well documented for breeding hens and broods (Goddard 2007, Norton 2005, Roersma 2001, Holloran et al. 2005, Prose et al. 2002). Activities that reduce escape cover, or shift the vegetation community could negatively impact STGR populations. Peak female attendance and copulation at the lek vary with latitude, and are generally later in northern regions

(Kessel 1981). The reproductive phenology of northern grouse needs to balance breeding, nest initiation dates, and clutch size with adequate time for chick development, or renesting in the event of a lost clutch before inclement weather and habitat conditions degrade (Martin and Wiebe 2004). Relatively little is known about, and few data are available on, the reproductive phenology of the subspecies of STGR present in Yukon and Alaska (Leupin and Chutter 2007, Goddard 2007, Taylor 2013, Raymond 2001).

The Klondike Goldfields represent northern Canada's first and longest running mining development; experiencing a long history of impacts and mitigation measures, such as habitat recovery, resulting in a complex mosaic of natural and modified habitats (Brady 1984). Presently, almost the entire area known to be used by STGR in the Klondike Goldfields is staked by mining claims. Although the placer industry has improved techniques to manage for water quality and fish habitats, little is known in regard to the impacts of modern placer techniques on wildlife. Environmental impacts that can result from modern placer mining include noise and light pollution, dust, traffic, road and housing development, fragmentation of landscape, and loss of habitat (Willis 1997). Information on the influence of placer mining on STGR reproductive ecology is lacking and could lead to land use conflicts.

The objectives of this chapter are to provide baseline information about the reproductive ecology of a STGR population in a disturbed landscape at the northern edge of the species' range including (1) reproductive chronology (timing of lekking, peak female attendance, nest initiation, hatch date and brood break-up) (2) brood rearing success including chronological and habitat correlates of rearing success, and 3) hen survival during reproductive period, including chronological and habitat correlates of hen survival. In addition to improving knowledge of the natural history of northern grouse populations, this research provides baseline information to wildlife managers and land use planners seeking to conserve and proactively manage wildlife habitat in a region with extensive placer mining activity.

2.3 STUDY AREA

Research was conducted in the Klondike Goldfields south of Dawson City, Yukon, in the Indian River Watershed (Fig. 1). The Indian River Watershed is in the unglaciated part of west-central Yukon, encompassing approximately 2260 km² located within the Klondike Plateau Ecoregion. These valleys contain the best known STGR lek locations in the Dawson region, though other lek sites exist (M. J. Suitor, Environment Yukon, personal communication; J. Staniforth, Environment Yukon, unpublished report). The study area is in the most important gold producing region of Yukon and some of the known leks are adjacent to active mines. Within these valleys, there is a network of roads, trails, and active and decommissioned mines, firewood cutting, as well as one abandoned farm, generally concentrated close to valley bottoms on the upper tributary and stem of the Indian River Watershed.

The geology and physiography of the Klondike area reflects a largely unglaciated ecoregion during the last ice age (Vernon and Hughes 1966). The Klondike Goldfields are characterized by relatively low rounded hills with deeply dissected v shaped valleys (Smith et al. 2004). Mesic Organic Cryosols are most common in undisturbed lower slopes and valley-bottom (Smith et al. 2004). Turbic Cryosols occupy upland habitats and may form the earth hummocks typical of the region (Brady 1984). There is extensive discontinuous permafrost on north facing slopes and valley bottoms, and permafrost free soils on well-drained uplands and slopes (Brown 1978).

The Klondike Plateau Ecoregion is part of the boreal forest biome. Much of the vegetation of the Klondike has young, mid-successional communities as a result of recent natural and anthropogenic disturbances (Brady 1984, Kennedy and Smith 1999). Stunted black spruce (*Picea mariana*) and white spruce (*Picea glauca*) woodlands are common on the north-facing slopes and valleys bottoms. White spruce, trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*) mixed forests, are typical of south-facing slopes (Smith et al. 2004). On gently sloping sites, black spruce-shrub-sedge hummock communities dominate (Brady 1984). Much of the variation and landscape heterogeneity has been attributed to varying stage of post burn recovery, where small fires occur at roughly 25-year intervals (Rowe et al. 1974). Fens, swamps, bogs, marshes and shallow water occupy an important part of the Indian River Watershed (McKenna 2018).

Predators in Yukon include northern goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), rough legged hawks (*Buteo lagopus*), great horned owls (*Bubo virginianus*), bald eagles (*Haliaeetus leucocephalus*), golden eagles (*Aquila chrysaetos*), ravens (*Corvus corax*), coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) (Connelly et al. 1998, J. Staniforth, Environment Yukon, unpublished report).

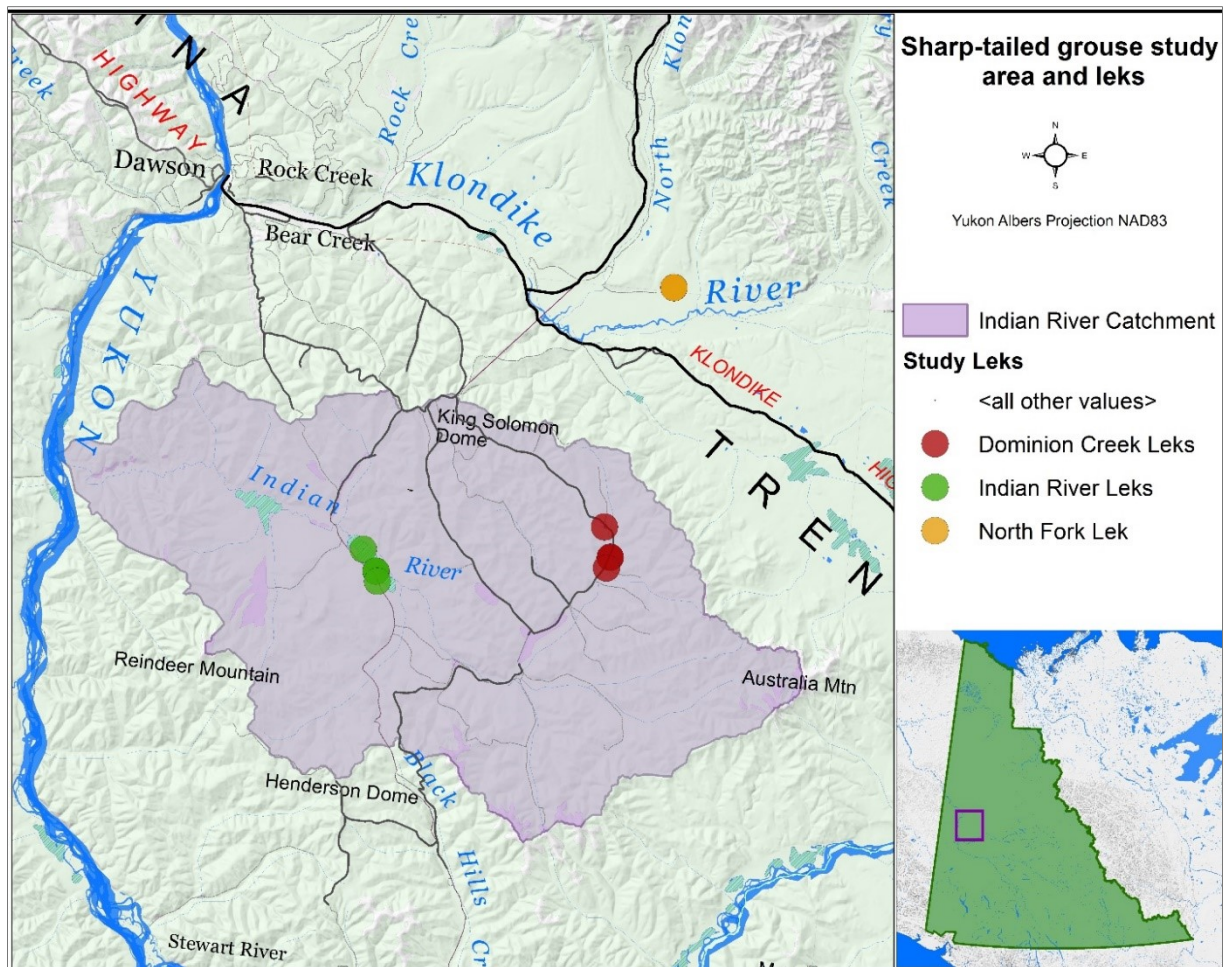


Figure 1. Study areas and associated study leks in the Klondike Goldfields, Yukon.

The Dominion Creek and Indian River leks are within the Indian River Catchment, while the North Fork leks are outside of this catchment area. This region experiences climatic extremes with long cold winters and short hot summers, with temperatures ranging from -60°C in winter

to 35°C in summer (Smith et al. 2004). Mean annual precipitation ranges from 300 – 500mm, occurring primarily in June through August (Smith et al. 2004).

2.4 METHODS

2.4.1 Field Techniques

To monitor reproductive success and identify nesting and brood rearing habitats associated with leks, STGR hens were captured and radio collared at lek sites. The communal breeding strategy of STGR on display grounds can be exploited to capture the birds. Display activity at leks begins prior to sunrise and continues until midmorning. Lek sites were located by walking transects in the goldfields and listening for STGR vocalizations; leks were approached on foot. Once active leks were identified, STGR were observed during the breeding season from ground blinds or from a distance using binoculars. During daily observations, we noted the number of birds present, sex when possible, predators, and weather, as well as general behaviour. *A priori* observation of male territories and behaviour at leks helped coordinate trap set-up to increase trapping success. A total of six leks were located and sampled within the goldfields (three in Dominion Creek drainage and three in Indian River drainage), and one farther away in an area free of any placer mining (North Fork). The number of leks trapped per year increased as new leks were discovered in the study areas. Grouse were trapped on leks between April 15 - May 7 of 2015-2017 using walk-in style funnel traps (Marks and Marks 1987, Toepfer et al. 1987, Schroeder and Braun 1991), modified from published accounts based on recommendations from previous researchers (A. Goddard, BC Ministry of Forests, Lands & Natural Resource Operations, personal communication), to include soft netting rather than chicken wire, to minimize injuries to the birds. Trapping commenced prior to the arrival of females to leks, and was terminated once females stopped visiting. The traps were strategically placed on leks in a circular, zigzag pattern to capture any birds attempting to walk in or out of the centre of the lek, toward the dominant males' territories. Leads constructed with chicken wire, 15 m in length and set up between traps guided the grouse into the funnel traps.

Three independent crews trapped grouse at the three study areas (Indian River, Dominion Creek and North Fork). Each group was responsible for a maximum of three leks, which they would monitor for captured birds at 20-minute intervals between 06:00 – 11:00 h. Traps remained open throughout the day, and were checked every 3-4 hours in the afternoon and

evening. Most birds (n = 212) were captured during the morning period of peak activity, with only 6 individuals caught after 11 h.

STGR capture and handling protocols were reviewed by an Environment Yukon Veterinarian and approved by McGill University Animal Use Committee. All captured grouse were sexed, aged, weighed and had their wing chords measured. Sex was determined by examining crown feathers, tail feathers, supraorbital combs, and presence of air sacs (Henderson et al. 1967). Weights were obtained using a 1kg Pesola scale. Based on the degree of fraying of the 9th and 10th primaries we classified birds as being in their first breeding season or their second breeding season (Ammann 1944). For each captured individual, we computed a body condition index by regressing mass against the length of the wing chord using Reduce Major Axis method (Green 2001). Additional samples taken included: buccal and uro-genital swabs, feathers, and small amounts of blood (≤ 2.0 ml) when deemed safe. Because male STGR are territorial at the leks, male by-catch was common. All captured birds were fitted with individually numbered aluminium #6 bands (Cutler Supply, Applegate, Michigan). Female grouse were fitted with a necklace-style VHF transmitter; in 2015 radio collars were provided by ATS (Advanced Telemetry Systems, G10-120 and A3950, Isanti, Minnesota) and had a 450-day transmission life and in 2016-2017 Holohil (RI-2BM, Carp, Ontario) transmitters were used with two-year expected battery life. Transmitters weighed 10 – 14 grams, representing less than 2% of the female's body mass (Carroll 1990). A small number of males were also collared, including one in 2015, two in 2016, and 14 in 2017. Radio collars were deployed opportunistically throughout study areas to ensure maximum possible deployment. Handling time of individuals that were not fit with a radio collar was <10 minutes, while those fitted with a transmitter was < 30 minutes. All birds were released at the lek of capture immediately after data collection, and were monitored for abnormal behaviours post-release.

Radio-marked grouse were located two - three times per week using portable ATS (Advanced Telemetry Systems, Isanti, Minnesota) and R1000 (Orange, California) receivers with H-element and Yagi antennas. Most relocations were conducted on the ground; however, a fixed-wing aircraft, equipped with a H-antenna attached to the struts of either wing was used to locate missing individuals. All hen locations were recorded using a Garmin handheld GPS (GPSMAP 78) with 3-5m accuracy, which also provided a measure of elevation. During the pre-nesting period, grouse were located using triangulation to avoid flushing hens and to minimize disturbance during egg laying. Once movements became localised, females were presumed to

have initiated a nest and were approached for visual confirmation. Nests were confirmed by the presence of eggs in the nest. Egg flotation was used to determine stage of incubation and predict nest initiation, incubation and hatch dates (Westerkov 1950). In 2016 and 2017, camera traps (Bushnell Trail Camera Aggressor) were deployed at all nest sites, avoiding the need to visually relocate the hens, while monitoring for predation events, predator type, extreme weather events and hatching date. After initially locating and sampling the nest, females were relocated at a distance (>50m) to monitor nesting status. Hens located near or on a nest were classified as nesting. If no transmitter signal was heard at the nest, the nest was checked to determine its fate and the camera's SDHD card was switched for a new one. A nest was considered depredated if no eggs or only eggshell fragments remained in the nest. If eggs were depredated or the hen abandoned the nest, the camera data was viewed to determine the cause (disturbance type, predator species) and date of event. We continued to monitor hens that lost or abandoned their nests for re-nesting attempts. Egg floating enabled us to predict hatching dates, and check nests two - three days prior to expected hatch date and one - two days' post hatch date. Hatch date was then confirmed using the camera trap data. Hatch date was recorded as the day prior to the hen leading the brood away from the nest. In the absence of more specific information (from trail cameras), nest failures were assumed to have occurred at the mid-point between the last day the nest was known to be active and the date the nest was found abandoned or predated. This method estimating nest mortality provided a range of mortality timing down to one – two days. Overall nesting success is expressed as the number of hens that hatched ≥ 1 chick / the number that initiated nests. A Mayfield estimate (Mayfield 1961, Mayfield 1975) was not used because all but two hens initiated a nest.

As is typical for precocial grouse, chicks quickly left the nest after hatching and followed their mother to foraging habitats. To minimize the impacts of observer disturbance on brood survival, hens were not flushed during the first seven days post hatch (when chicks are flightless and cannot thermoregulate) or during inclement weather. Hen re-locations continued until 35 days post hatch, after which time brood survival cannot be monitored by relocating hens (Goddard 2007, Gratson 1988). If broods did not flush, but the hen exhibited a broken wing display, or otherwise suggested chick presence, it was recorded as such. Total brood counts were difficult to obtain; consequently, a successful brood was defined as survival of one or more chick at 35-days post-hatch. If female mortality occurred during the first three weeks of brood rearing, broods were recorded as failed. On the other hand, if hen mortality occurred in the final week of

the brood-rearing period, those broods were censored from analyses as brood fate was impossible to confirm.

Each transmitter had an eight hour mortality sensor. Recovered transmitters were identified as dropped, predated or unknown. When possible, predator type was categorized as either avian or mammalian. Predator identification was based on examining predator sign (fecals or tracks), collar (beak or teeth marks), and carcass (plucked/masticated feathers, severed head/appendage) (Coates 2001). Hen mortalities were assumed to have occurred at the mid-point between the day the mortality signal was heard, and the last date previously known alive, resulting in a range of mortality timing of one – two days.

2.4.2 Data Analysis

Nesting Chronology and reproductive success - The date of peak lek attendance for male and female STGR grouse was estimated from weighted mean daily capture rates, with each capture day weighted by the number of birds captured per day. It is possible that individuals became trap-shy as the season progressed, peak female attendance coincided with increased lek attendance confirmed by observer lek counts.

Because there were only two re-nesting attempts over all study years, and these nests hatched within the hatch period of the first nest attempts, first and re-nesting attempts were analysed together. We initially tested whether nest initiation dates, clutch size, nest dispersal distance, nest hatch dates, apparent nest success, brood success, brood-rearing home range, distance travelled by broods and hen survival varied with year, area, female age and body condition, using a series of one-way analysis of variance tests (ANOVA). For area analysis, the three North Fork hens were removed from success and survival models due to small sample size.

Nest dispersal distances, and nest distance to active mines, historic mines, and roads were calculated using the Distance Matrix tool in QGIS (version 2.18.15). Brood rearing home ranges were estimated using the Kaplan-Meier estimator with the Animove plugin in QGIS. Only those broods with > 10 relocations were used. Centroids were projected for the home range to estimate distance traveled by broods from nest sites using the centroid and distance matrix tools in QGIS.

Hens studied in 2015 were excluded from brood rearing analyses because we did not record vegetation characteristics that year and were unable to return to those sites due to time restrictions. Another six hens were censored from brood-rearing analyses for the following

reasons: one shed collar, two failed collars, two lost hens, and one possible collar induced mortality (hen was found with leg caught in the necklace of the radio-collar in a pool of water).

Multivariate analysis and survival - Prior to multivariate analyses and model fitting, we evaluated nest and brood habitat use, using a three-step method of variable reduction to reduce potential variable interaction. The full set of variables included female physical attributes, timing of breeding, measures of the distance travelled by a nesting hen, measures of the distance travelled by a brood and habitat characteristics. We used Pearson's correlation to test for collinearity between all independent variables. If variables were correlated ($r > 0.5$), *a priori* knowledge or comparison of logistic regression using either variable was used to eliminate the weaker predictor. We found strong relationships ($p > 0.05$) for several covariates. All intervals of VOR describing nesting habitat, at all spatial extents were highly correlated. VOR2 was retained for further consideration because it has been determined that visual obstruction between 10 and 90dm is important in nest success (Apa, 1998, Collins 2004, Flake et al. 2010).

High collinearity was identified between nesting patch structure and successional stage ($r = 0.81$, $n = 378$), and for total shrub cover and low shrub cover ($r = 0.54$, $n = 378$) within brood rearing habitat. Patch structure was retained over successional stage because it was believed to a better representation of the habitat characteristics we observed in the field.

Initial vegetation categories were consistent with published terrestrial ecosystem classification techniques (B.C. Ministry of Forests and Range, and B.C. Ministry of Environment 2010). Based on priori knowledge and field observations, we concluded that not all of the distinctions and scales were clear or pertinent to grouse. For this reason, we chose to reduce patch structure (12 levels) and moisture (six levels) categorical variables into five (non-vegetated open, low shrub, high shrub, forested) and two (wet and dry) bins respectively (Table 1, Table 2). The original classifications were regrouped based on physical similarity. For example, Sparse, Herb, Agricultural field and Grassland were all attributes considered in the original factor "Patch Structure", are amalgamated in the renamed factor "Open". Patch structure and moisture were then combined into a single eight level factor, renamed habitat type (Table 2).

Of the remaining variables, using a non-parametric univariate Wilcoxon-Mann-Whitney test we further reduced variable selection to those continuous variables with a univariate difference ($p < 0.2$) between survival and non-survival (Appendix A, Appendix B). As a final step, we used a multi-factor analysis to further eliminate categorical and continuous variables).

Multiple Factor Analysis (MFA) derives an integrated picture of the observations and of the relationships between the groups of variables for mixed-data, and is an extension of principal component analysis (quantitative data) and multiple correspondence analysis (qualitative data). As determined by the MFA, five nest site variables were retained: three categorical (aspect, successional stage and microtopography) and two continuous variables (hatch day and elevation) (Table 1). These variables cumulatively explain 45.9% of the variance in nesting success. As determined by the MFA five variables explaining 27.9% of the variance in brood success were also retained: three categorical variables (aspect, habitat type and shrub type) and two continuous variables (medium height shrubs and deadfall) (Table 2).

Table 1. Comparisons (mean \pm SE) between 42 successful and 13 failed Sharp-tailed grouse nests, using two continuous variables and the relative proportion of each level of three categorical variables, after variable reduction. Variables in gray were found to be significant in top GLM models.

Continuous Variable		Successful Nests Mean \pm SE n = 40	Failed Nests Mean \pm SE n = 13
Elevation (m)		586.3 \pm 12.5	528.9 \pm 19.6
Hatch day		160.1 \pm 0.6	163.2 \pm 2.3
Categorical Variables			
Microtopography	No Hummocks	0.33	0.08
	Few Hummocks	0.49	0.54
	Many Hummocks	0.18	0.38
Aspect	North	0.29	0.15
	East	0.11	0.11
	South	0.22	0.15
	West	0.14	0.11
	None	0.24	0.03
Successional	Non-vegetated	0.00	0.00
	Pioneer seral	0.23	0.15
	Young seral	0.59	0.77
	Maturing seral	0.13	0.08
	Overmature seral	0.00	0.00
	Young climax	0.00	0.00
	Maturing climax	0.03	0.00
	Overmature	0.00	0.00
	Disclimax	0.00	0.00

Table 2. Comparisons (mean \pm SE) between 23 successful and eight failed Sharp-tailed grouse broods, using two continuous variables and the relative proportion of each level of 4 categorical variables, after variable reduction. Variables highlighted in gray were included in top GLM model.

Continuous Variable		Successful Broods n = 23	Failed Broods n = 8
Med.shrub		21.4 \pm 1.2	22.8 \pm 1.5
Deadfall		20.7 \pm 1.1	25.5 \pm 1.6
Categorical Variables			
Aspect	North	0.43	0.32
	East	0.19	0.36
	South	0.01	0.05
	West	0.02	0.01
	None	0.35	0.27
Patch structure	Non-vegetated-Dry	0	0
	Non-vegetated-Wet	0	0
	Open-Dry	0	0.01
	Open-Wet	0.01	0
	Shrub/scrub<2m-Dry	0.28	0.29
	Shrub/scrub<2m- Wet	0.17	0.15
	Shrub/scrub>2m-Dry	0.30	0.30
	Shrub/scrub>2m-Wet	0.16	0.20
	Forested-Dry	0.04	0.04
	Forested–Wet	0.05	0.01
Shrub type	None	0.01	0.01
	<i>Salix sp.</i>	0.33	0.32
	<i>Betula glandulosa</i>	0.28	0.31
	<i>Ledum palustre</i>	0.33	0.25
	<i>Rosa acicularis</i>	0.04	0.06
	<i>Populus tremuloides</i>	0	0.01
	<i>Vaccinium uliginosum</i>	0.01	0.03

We predicted nest success would be lower for nests close to anthropogenic activities due to stress related factors; however, these variables were rejected in variable reduction, and therefore not included in model construction.

From the reduced set of variables, to determine which covariates best explained patterns in variation of nest and brood success, we developed 16 candidate Generalised Linear Models (GLM) of characteristics believed to influence nest survival, and 15 GLM's describing brood survival (Table 3, Table 4). Year was included as a random effect in all candidate models. We used an information theoretic approach to estimate the support for models evaluating habitat selection patterns (Burnham and Anderson 1998). Due to small sample size, ΔQAICc along with Akaike weights (w_i) values were used to rank competing models (Akaike 1973, Burnham and Anderson 2002). Only models with $\Delta\text{QAICc} < 2$ were considered. All analyses were performed using package lme4 (Bates et al. 2008) in program R (version 1.0.136 - © 2009-2016 RStudio, Inc.).

Table 3. Candidate generalized linear models to explain nest success for 52 Sharp-tailed grouse nesting attempts, at the patch-scale, in the Klondike Goldfields, Yukon, 2015-2017.

Model	
Number	Model Structure
Model1	Succesional.Stage + Hatch Day
Model2	Succesional.Stage + Elevation
Model3	Succesional.Stage + Aspect
Model4	Succesional.Stage + Microtopography
Model5	Succesional.Stage
Model6	Hatch Day + Elevation
Model7	Hatch Day + Aspect
Model8	Hatch Day + Microtopography
Model10	Hatch Day
Model11	Microtopography + Elevation
Model13	Microtopography + Aspect
Model14	Microtopography
Model15	Aspect + Elevation
Model16	Aspect
Model17	Elevation

Table 4. Candidate generalized linear models to explain brood success for 23 Sharp-tailed grouse brood rearing attempts, at the patch-scale, in the Klondike Goldfields, Yukon., 2015-2017.

Model Number	Model Structure
Model1	Habitat type
Model2	Habitat type + Med.shrub
Model3	Habitat type + Aspect
Model4	Habitat type + Shrub type
Model5	Habitat type + Deadfall
Model6	Shrub type
Model7	Shrub type + Aspect
Model8	Shrub type + Med.shrub
Model9	Shrub type + Deadfall
Model10	Med.shrub + Aspect
Model11	Med.shrub + Deadfall
Model12	Aspect
Model13	Aspect + Med.shrub
Model14	Aspect + Deadfall
Model15	Deadfall

In addition to assessing nest and brood success, we also examined the survival time of nests, broods, and hens, using the Kaplan-Meier product-limit procedure with staggered-entry design (Kaplan & Meier 1958, Pollock et al. 1989). Nest survival was estimated from the time of nest initiation until the nest hatched or a depredation event occurred. Brood survival was estimated from the time of nest hatch to 40 days post-hatch. Hen survival was calculated over the annual reproductive period, from time of capture to brood break-up. Because the Kaplan-Meier procedure is unable to accommodate the effects of continuous covariates (Hosmer and Lemeshow 1999), I divided continuous variables, such as hatch day and elevation, into high and low bins with the mean as the division point, while ensuring there was a balanced sample size in each bin.

We evaluated hen survival by study year, study area, hen age, and hen body condition. Hens that were missing or dropped their radio-collars were censored from analyses because fate

could not be determined. Hens with data from more than one-year were considered separate individuals in analyses; in all, 64 hens had data included only from one year, six hens from two years, no hens were monitored for all three study years. All means are presented with \pm standard error.

2.5 RESULTS

2.5.1 Lek Attendance and Captures

The mean number of males attending a lek per day was 11.16 (range 2-20), with peak activity, calculated from maximum individual observation counts, across all years and areas, occurring on April 28 (Fig. 2A). Peak hen attendance, calculated from the daily number of hens captured, was also April 28 if pooled across years and sites, and ranged from April 24 to May 4 among specific year-site combinations (Fig. 2B). Peak hen attendance occurred earlier and over a shorter period in 2016 than in 2015 and 2017.

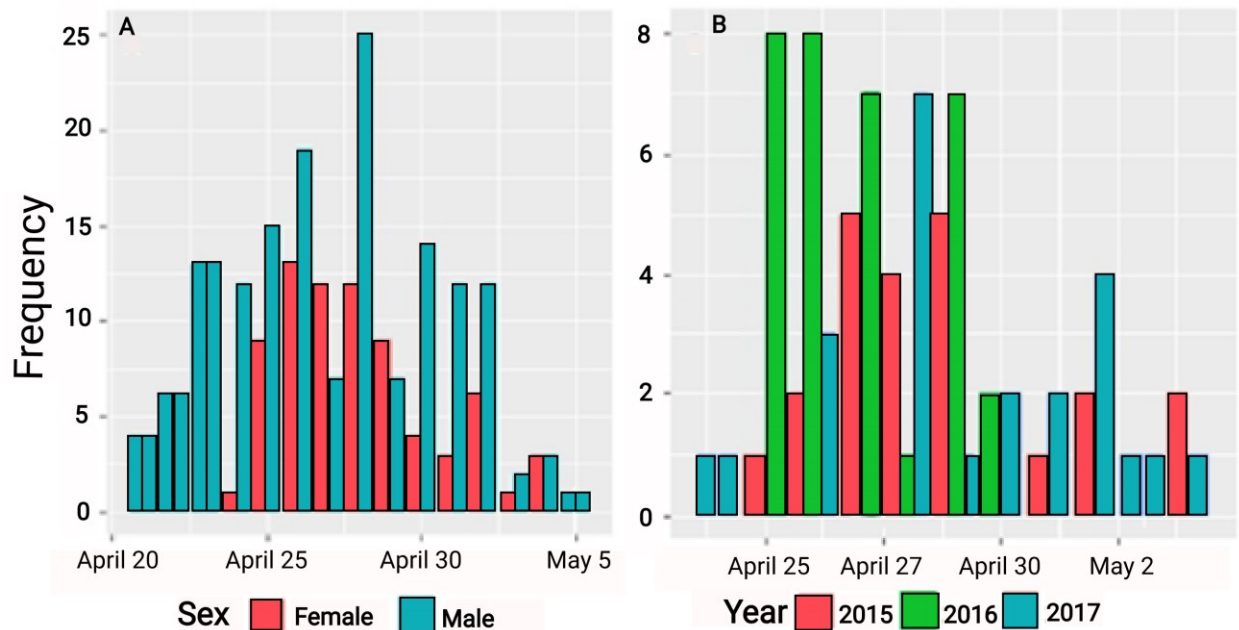


Figure 2. Daily trend in the number of (a) males observed and females captured, pooled across years, and (b) females captured in 2015, 2016, and 2017 in the Klondike Goldfields, Yukon.

Across all study years, 113 individual males were captured, and leg banded with a small subset collared; one in 2015, two in 2016, and 14 in 2017. A total of 75 hens were captured over three trapping seasons. Seventeen females were equipped with radio collars in 2015, thirty-three

females were collared in 2016, and twenty-five in 2017. Two hens in 2015 were not collared due to health concerns. At the onset of the 2016 trapping season, five females from the 2015 season still had functioning radio collars; two were captured in traps and given new transmitters, and two were captured on their nests with long handled nets in 2016 to replace 2015 radio collars. An additional two females from the 2015 capture season were not recaptured, however, their transmitters continued emitting long enough in 2016 to locate their nests, which were included in 2016 analyses. In addition, four hens' transmitters attached in 2016 were still active in the 2017 field season, but because these new transmitters had 2-year life expectancy, the hens were not recaptured. Two hens died while handling during the 2017 field season and in 2016 a northern goshawk (*Accipiter gentilis*) predated two males in traps before observers could reach them.

2.5.2 Nest Initiation

At the time of first nest location, all hens were already incubating eggs. We located a total of 15 nests, including 1 renest in 2015, 25 nests in 2016, and 15 nests, including 1 renest in 2017. Across all three study years, $96.4\% \pm 2.5$ ($n = 55$) of captured hens attempted to nest, excluding those hens that shed their collars or were lost ($n = 4$), or predated prior to nest detection ($n = 13$). Only two females during the study (1 each in 2015 and 2017) did not attempt to nest. Across two years (nest initiation dates were not assessed in 2015), average nest initiation was May 7 ($n = 38$) and incubation start date was May 15 ($n = 38$). Nest initiation was significantly earlier (5.84 , $df = 1,35$, $p = 0.02$) in 2016 ($X = 125.70 \pm 0.6$, range = 121-130) than in 2017 ($X = 127.67 \pm 0.5$, range = 123-133;)

2.5.3 Clutch Size

Mean clutch size for all years and areas was 8.3 ± 2.1 ($n = 41$). Clutches were significantly larger in 2016 ($X = 9.0 \pm 0.2$, range = 6-10) and 2017 ($X = 8.69 \pm 0.46$, range = 4-11) than in 2015 ($X = 6.6 \pm 0.8$, range = 4-10), ($F = 7.93$, $df=2,50$, $p = 0.001$) but clutch size did not differ between study areas ($F = 0.43$, $df = 2,49$, $p = 0.73$) with hen body condition ($F = 1.39$, $df = 1,48$, $p = 0.24$) or with age ($F = 0.16$, $df = 1,48$, $p = 0.69$).

2.5.4 Nest Success

Overall apparent nest success, assessed as (number of hens that hatched at least 1 chick) / (number of hens initiating a nest) was $76.4\% \pm 1.8$ ($n = 55$) for first nests. Median nest survival

was 29 ± 2 days for all years and areas (Fig. 3a). Thirteen nest failures were recorded, including five (of 15) in 2015, four (of 25) in 2016, and four (of 15) in 2017. Nest predation was the most common cause of nest failure, accounting for $53.8\% \pm 14.4$ of losses ($n = 6$), followed by hen predation ($30.7\% \pm 13.3$, $n = 4$), and abandonment ($15.4\% \pm 10.4$, $n = 2$). In most instances, nests were predated while hens managed to escape. In 2016 and 2017 cameras detected predation of STGR nests by bear ($n = 1$, black bear, *Ursus americanus*), wolf ($n = 1$, *Canis lupus*), lynx ($n = 1$, *Lynx canadensis*), and one owl (likely great horned owl, *Bubo virginianus*). Two nests were abandoned during the study, one in 2015 and one in 2017, for undetermined reasons. Although nest success tended to be higher at the Dominion study site (85.1%) than at Indian River study site (61.3%), it did not vary significantly between these sites ($F = 1.79$, $df = 3, 51$, $p = 0.16$), or with study year ($F = 0.09$, $df = 2, 52$, $p = 0.91$), hen age ($F = 0.56$, $df = 1, 50$, $p = 0.46$), or hen body condition ($F = 2.75$, $df = 1, 50$, $p = 0.10$).

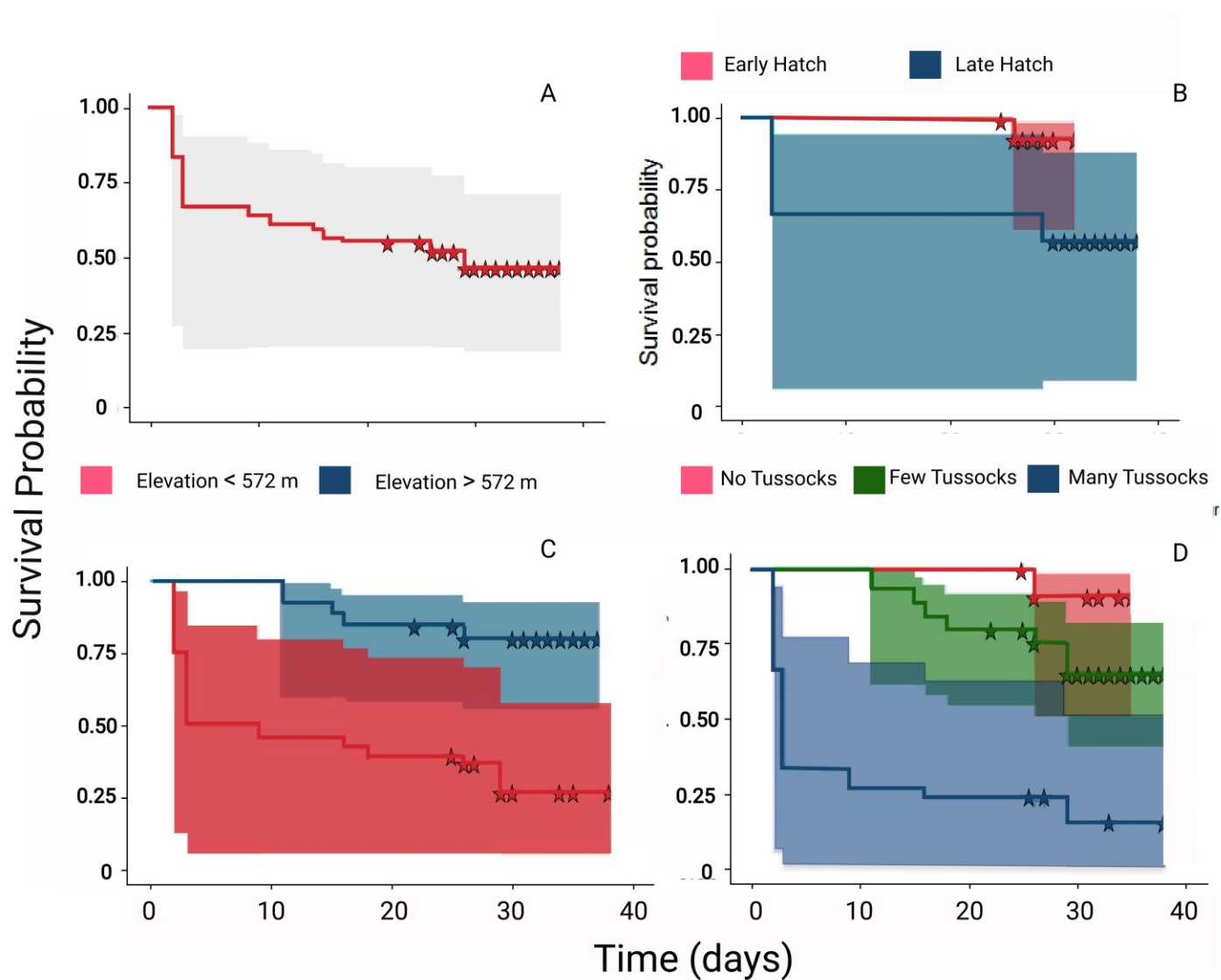


Figure 3. Kaplan-Meier survival functions and 95% confidence intervals for 55 Sharp-tailed Grouse nests in Klondike Goldfields, Yukon, a) pooled across years (2015-2017) and study areas, then separated by significant predictors including b) hatch date, c) elevation, and d) hummock abundance. Shaded bands represent the confidence intervals at each time point and plus signs represent the censored (hatched) cases at a given time point.

All nest survival models with $AIC < 2.0$ included hatch day, with late hatching nest (161-166 days after Jan 1) characterized by lower survival ($57.2\% \pm 24$) compared to early hatching nests (155-160 days after Jan 1; $92.9\% \pm 6.4$; Fig. 3b). Hatch day varied significantly by study year ($F = 46.01$, $df = 2,36$, $p = <0.01$), occurring earliest in 2016 (157), latest in 2015 (164), and at an intermediate date in 2017 (161). Hatch date also varied between study area ($F = 11.67$, $df = 2,34$, $p = <0.01$), occurring three days earlier in Dominion than Indian River, but did not vary significantly with hen age ($F = 0.05$, $df = 1,35$, $p = 0.82$) or body condition ($F = 2.26$, $df = 1,34$, $p = 0.14$). The top ranked nest survival model also included elevation, in addition to hatch day (Table 5), and had good model weight ($W_i = 0.435$). Nests below 572 m had 61.3% survival within the first 5 days of incubation, whereas those above 572 m had 86.2% survival rates (Fig. 3c). Mean nest site elevation was lower in Indian River (474.32m, range = 450–523 m) than Dominion ($X = 627.03$ m, range = 580–728 m; $F = 78.39$, $df = 2$, $p < 0.001$), but elevation was a stronger predictor of nest survival than was study area.

The third top ranked nest survival model retained hatch day but included microtopography in place of elevation as the second predictor (Table 5). Nests in habitats with many earth hummocks had a 57.9% survival compared to 77.4% for nests in habitats with few hummocks and 93.1% for nests in habitats with no hummocks (Fig. 3d). Microtopography of nest sites did not differ by year ($F = 0.03$, $df = 50$, $p = 0.99$) or study area ($F = 2.57$, $df = 49$, $p = 0.46$).

Table 5. Top 5 of 17 logistic regression models differentiating successful and failed nesting attempts by Sharp-tailed grouse in the Klondike Goldfields, Yukon, 2015-2017. Generalized linear models are described according to explanatory variables (model structure), degrees of freedom (df), Log Likelihood (Log(L)), Quasi-Akaike's Information Criterion for small sample sizes (QAICc), Δ QAICc, and Akaike weights (w_i). Strongly supported models (i.e., Δ QAICc < 2.0) are indicated in bold.

Model #	Model Structure	df	Log(L)	QAICc	Δ QAICc	W_i
6	Hatch Day + Elevation	3	-11.577	29.9	0	0.435
8	Hatch Day + Microtopography	4	-10.766	30.9	0.96	0.269
10	Hatch Day	2	-13.268	30.9	0.98	0.266
1	Successional Stage + Hatch Day	5	-12.125	36.4	6.49	0.017
7	Successional Stage + Aspect	6	-10.916	36.8	6.93	0.014

2.5.5 Brood Success

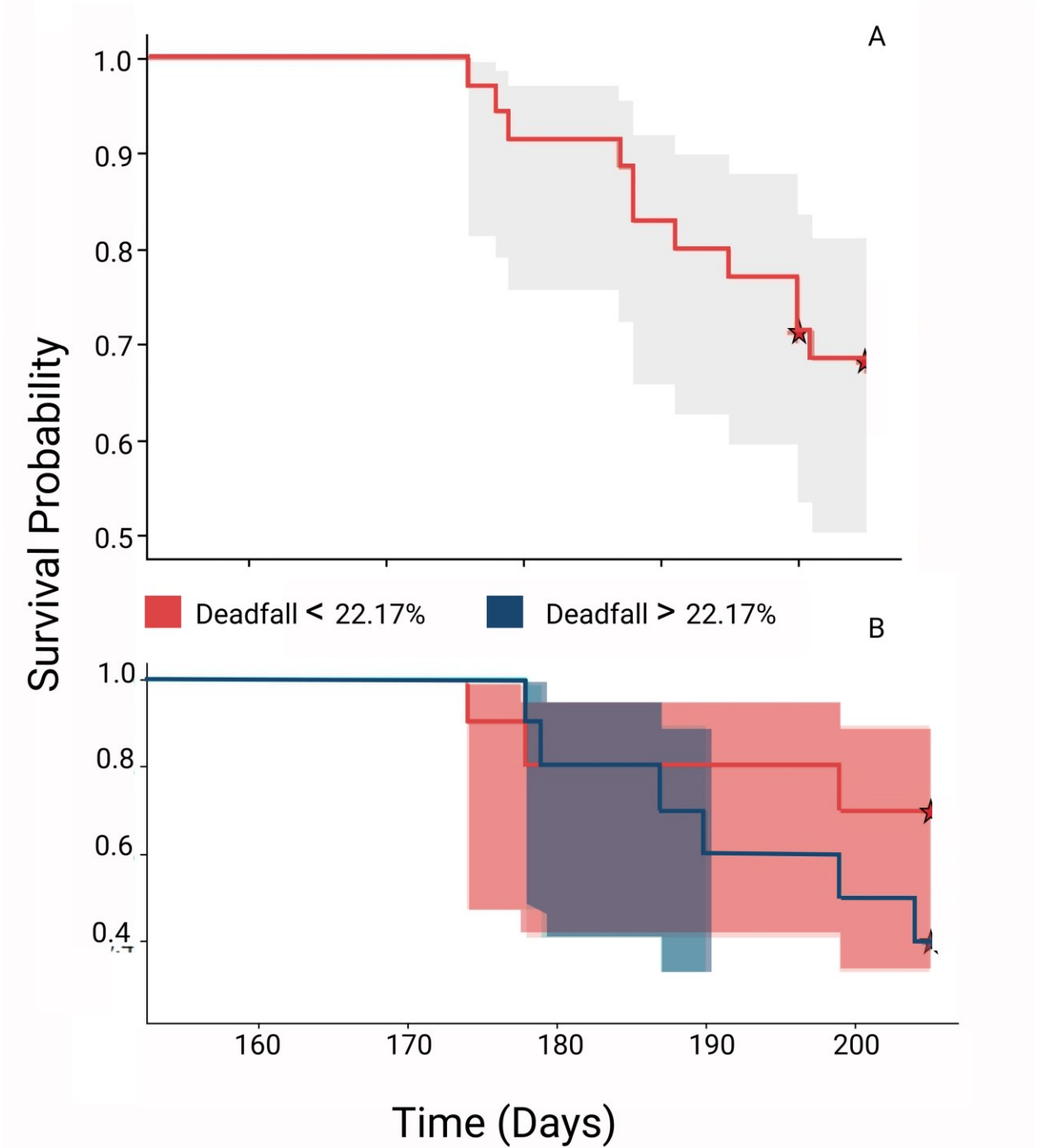
We monitored 11 hens with broods in 2015, 14 in 2016, and nine in 2017 until chicks were 35 days of age. 70.6% \pm 0.5, n = 34) monitored hens with broods successfully fledged at least one chick. Ten broods experienced total loss of chicks, including three (of 11) in 2015, five (of 14) in 2016, and 2 (of 9) in 2017. Among the ten brood failures, three resulted from hen predation and the remaining seven were from an undetermined cause (e.g., weather or predation). Brood fate did not differ significantly with study year ($\chi^2 = 3.71$, $df = 2, 31$, $p = 0.16$), study area ($\chi^2 = 2.20$, $df = 2, 31$, $p = 0.33$), hen body condition ($\chi^2 = 0.49$, $df = 1, 30$, $p = 0.48$), hen age ($\chi^2 = 0.46$, $df = 1, 29$, $p = 0.50$), brood home range ($\chi^2 = 1.62$, $df = 1, 32$, $p = 0.20$), distance traveled by broods ($\chi^2 = 0.38$, $df = 1, 31$, $p = 0.54$), or day of hatching ($\chi^2 = 0.38$, $df = 1, 31$, $p = 0.54$).

Variation in brood success was best described by a model including aspect and deadfall at the patch-scale (Table 6). Although aspect availability and use did not differ between study sites, its effects on brood survival did ($\chi^2 = 20.46$, $df = 1$, $p < 0.05$), with 100% of broods using east facing slopes in the Indian River failing, compared to only 40% in Dominion Creek. Overall, brood survival tended to be higher on east and south facing slopes than those facing west and north (Table 2). Failed broods tended to be located in sites with greater cover, including deadfall,

than successful broods (Fig. 4b), but deadfall cover varied by less than 5% between failed and successful sites (Table 2). Deadfall use and availability did not vary significantly between year ($F = 0.06$, $df = 1,326$, $p = 0.79$) or study area ($F = 1.11$, $df = 1,326$, $p = 0.29$).

Table 6. Top 5 of 15 logistic regression models differentiating successful and failed brood rearing attempts by Sharp-tailed rouse sites in the Klondike Goldfields, Yukon, 2015-2017. Generalized linear models are described according to explanatory variables (model structure), degrees of freedom (df), Log Likelihood (Log(L)), Quasi-Akaike's Information Criterion for small sample sizes (QAICc), Δ QAICc, and Akaike weights (w_i). Strongly supported models (i.e., Δ QAICc < 2.0) are indicated in bold.

Model #	Model Structure	df	Log(L)	QAICc	Δ QAICc	W_i
14	Aspect + Deadfall	6	-213.384	439	0	0.781
10	Med.shrub + Aspect	6	-215.886	444	5	0.064
13	Aspect + Med.shrub	6	-215.886	444	5	0.064
12	Aspect	5	-217.523	445.2	6.2	0.035
7	Shrub type + Aspect	11	-211.489	445.8	6.78	0.026



1167 **Figure 4.** Kaplan-Meier survival function and 95% CI for 35 Sharp-tailed Grouse broods, from
1168 day of hatch to brood break-up (35 days post hatch). Brood survival functions are shown for a)
1169 pooled across years (2016 & 2017) and study areas, then separated by the significant predictor b)
1170 deadfall. Shaded bands represent the confidence intervals at each time point and plus signs
1171 represent the censored (hatched) cases at a given time point.

2.5.6 Hen Survival

Throughout the reproductive period 12 hens were censored from survival analyses due to shedding of collar ($n = 4$), radio failure and/or missing bird ($n = 7$), and radio-collar failure resulting in hen mortality ($n = 1$). Hen survival, pooled across study years and areas, for the 12-week reproductive period from lek capture to brood dispersal was $64.2\% \pm 6.2$ ($n = 70$) (Fig. 5a). Mortality rates were highest early in the season then decreased over time, with 11 of 25 recorded hen mortalities (44%) occurring pre-incubation, eight (32%) during nesting and six (2%) during brood rearing. Hen survival was not influenced by hen age ($\chi^2 = 1.02$, $df = 1$, $p = 0.3$), or capture date ($\chi^2 = 1.37$, $df = 1$, $p = 0.24$), but did vary across years ($\chi^2 = 8.54$, $df = 2$, $p = 0.14$) with survival declining from 2015 ($92.8\% \pm 6.3$) to 2016 ($50.3\% \pm 9.8$) ($n = 16$) to 2017 ($42.5\% \pm 10.7$) ($n = 12$) (Fig. 5b). Survival was also lower in the Indian River ($50.6\% \pm 10.1$), as compared to Dominion ($70.8\% \pm 7.8$) (Fig. 5c). Body condition was found to significantly influence hen survival ($\chi^2 = 7.86$, $df = 1$, $p = <0.01$). Among 25 hen mortalities, 22 were believed to have been caused by avian predators and two by a lynx; we were unable to retrieve the remains or radio-collar for one hen that died on an active mine, resulting in an undetermined.

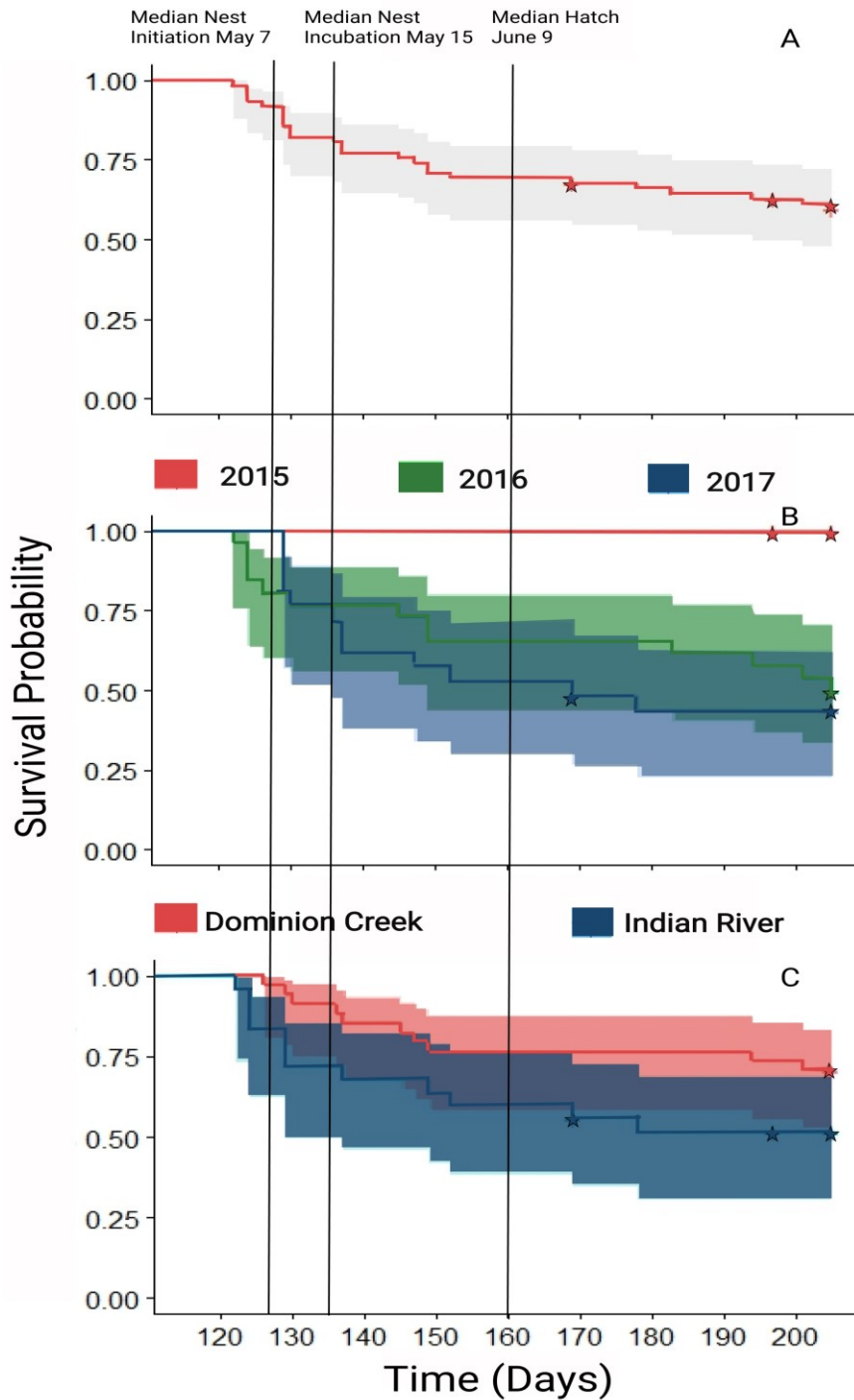


Figure 5. Kaplan-Meier survival function and 95% CI for 75 Sharp-tailed grouse hens, from time of capture to time of brood break-up (35 days post hatch) at study sites in Klondike Goldfields, Yukon. Survival functions are (a) pooled across years (2015-2017) and study areas, then separately by (b) year and (c) study area. Hen survival was significantly lower in 2017 and in the Indian River study site. Shaded bands represent the confidence intervals at each time point and plus signs represent the censored (hatched) cases at a given time point.

2.6 DISCUSSION

The phenology of lek attendance, nesting and hatching dates has been noted to vary with climate, latitude, and elevation, generally occurring later in colder climates, higher latitudes, and higher elevation regions (Connelly et al. 1998, Sadoti et al. 2016). Consistent with this general pattern, the date of peak hen attendance we documented (April 28), is very similar to Northern BC (Goddard 2007) and Alaska (Paragi et al. 2012), but one - three weeks later than more southern research sites, including the third week of April in Michigan (Drummer et al. 2011), April 21 in North Dakota Williamson (2009), April 19 in Wisconsin (Hamerstrom and Hamerstrom 1973), and April 6 in South Dakota (Norton 2005). The peak of nest initiation (May 7) and hatch dates (June 9) that we documented was also similar to other northern study sites, including Northern BC (peak nest initiation May 9, and peak hatch date, June 13, Goddard 2007) and Alaska (peak hatch date, June 5-9, Paragi et al. 2012), but was later than southern populations including South Dakota (nest initiation April 19, Norton 2005), North Dakota (peak nest initiation, April 24, and peak hatch date, June 6-10 – Williamson 2009) and Michigan (peak nest initiation, April 24, Ammann 1957). In any given year, peak dates can be delayed or advanced by climatic conditions and snow pack (Bergerud and Gratson 1988, Goddard 2007). We observed a 4-day advancement in peak dates (relative to the three-year averages presented above) in 2016 when spring thaw and green-up occurred earlier.

The mean clutch size of 8.3 we observed in this study was similar to 8.9 observed in Alaska (Paragi et al. 2012), but substantially lower than 12.3 documented in northern BC, South Dakota and Saskatchewan (Goddard 2007, Norton 2005, Pepper 1972), and 11.4-12 in North Dakota (Kirby and Grosz 1995, Kludt 2016). Collectively, these findings do not support Bergerud's (1988) expectation that northern grouse should have larger clutch size than southern grouse and Lacks (1948) observation of increasing clutch size with increasing latitude. However, they are generally consistent with the observation that smaller clutch size is associated with a shorter reproductive season and colder climates (Fiedler 2009). Furthermore, Ashmole (1963) hypothesized that clutch size is related to the seasonality of resources; In a population where size and density is regulated by resource availability during the non-reproductive periods, and where resources increase only slightly during the breeding season, then food available for chicks would be low, selecting for small clutch sizes.

The among and within year variation in reproductive timing that we observed within our study was also partially consistent with a negative correlation between laying date and clutch size. We observed the largest clutch sizes in 2016 (average 9.0, range 6 to 10), which was the year of earliest reproductive timing, and the smallest clutch sizes in 2015 (average 6.6, range 4 to 10), which was generally the year of latest timing. Within our study system, the larger clutches in 2016 agree with earlier and increased production across Yukon that year; however, 2017 had comparable clutch sizes to 2016, and was a late melt year and more similar in timing to 2015.

Re-nesting after brood loss is uncommon in North American grouse (Apa 1998) and double brooding occurs in only a few populations of a few species with exceptionally long reproductive windows (McNew and White 2012). STGR are not known to double brood but following nest loss can attempt re-nesting up to four times in a single breeding season (Bergerud and Gratson 1988, Connelly et al. 1998). In the current study, we documented no double brooding and re-nesting was attempted by only two of a possible nine hens with predated or abandoned nests. Both re-nesting hens lost their first clutches early in the nesting period (<11 days), whereas no hens that lost nests after May 19 re-nested. Research conducted in Alaska on STGR, spruce grouse, and ptarmigan also reported few re-nesting attempts (Weeden and Theberge 1972). Bergerud and Gratson (1988) suggest that by nesting early, hens have sufficient time to re-nest. This indicates that reproductive opportunities may be limited in northern latitudes by a shorter window, resulting in few re-nesting opportunities (Martin and Wiebe 2004), but other non-seasonal factors, like population density and cycle phase have also been shown to be important determinants of re-nesting rates in other systems (Bergerud 1988).

The apparent nest success observed in our study (76%) was substantially higher than the 44-72% range typically documented for STGR (Apa 1998, Goddard 2007, Williamson 2009, Manzer 2004, Norton 2005, Meints 1991). The only documentation of nest success greater than observed here, was 86% in Alaska (Paragi et al. 2012). Nesting success in excess of 60% are often associated with cyclic populations (Bergerud 1988). There is no long-term quantitative population data available for STGR in the central Yukon, and thus we do not know if populations in this region are cyclic and what cycle phase may have coincided with our study period. Furthermore, the amplitude and spatial synchrony of population cycles have been shown to deteriorate in fragmented or disturbed landscapes (Bergerud 1988). However, there are some anecdotal indications, that our study period (2015-2017) may have coincided with a 10-year peak

in the Yukon population (M. J. Sutor, Environment Yukon, personal communication) and the high rates of nesting success we observed, particularly in the first two of our three study seasons, are consistent with this possibility.

The vulnerability of ground nests to mesopredators is well documented (Manzer 2004) and is often the leading cause of nest failure for upland game birds in general (Bergerud 1988) and for STGR in particular (Burr 2014, Goddard 2007). The high nest success observed in the current study and in Alaska, may reflect the low numbers of mesopredators in these northern environments. Foxes and coyotes are present in our study site and throughout most of Yukon and Alaska, but tend to be present at low densities, likely due to the combination of a limited prey base and the presence of larger predators, including wolves and bears, that both compete with and kill mesopredators (Berger and Gese 2007, Prugh et al. 2009). Nest predation was still the most important cause of nest failures in Yukon (53.8%), but no nests were lost to mesopredators and the confirmed predators were wolves and bears. Burr (2014) recorded 81% nest failures in North Dakota were due to mammalian predators. In British Columbia, Goddard (2007) reported 86% of nest failures were predated. Nest failures due to hen mortality accounted for $30.7\% \pm 13.3$, which is greater than the 9% previously recorded in North Dakota and northern British Columbia (Burr 2014, Goddard 2007). Hens nesting later may be at a greater risk of predation due to predators improving their search image for nests as the season progresses (Dinkins et al 2013).

Previous work has found success of prairie grouse nests to be correlated with anthropogenic activities and habitat characteristics. In the present study, neither anthropogenic activities nor surface disturbances covariates were found to influence nest success. Among the landscape variables considered, nests at higher elevation were more successful than those at low elevations. However, because nests in the Indian River valley were both lower in elevation ($X = 521\text{m}$, range = 446-689m) and less successful than nests in Dominion Creek, which tended to be at higher elevation ($X = 639\text{m}$, range = 462-793m) and more successful, what we detected as an effect of elevation may reflect more generalized valley-to-valley differences, including but not limited to differences in elevation between the two valleys. Other differences between the two valleys include a more recent fire history in Dominion and therefore less early succession habitat available in the Indian River valley, as well as the presence of highly productive wetlands in the Indian River valley, which may host a greater variety of prey species that attract predatory

wildlife (Manzer 2004). Nesting success also tended to decrease with increasing hummock abundance. Sites with greater hummock abundance may lose snow later than sites with a simple microtopography, which could affect nest success (Bergerud and Gratson 1988).

Recorded brood success of 71% in this study was high, as compared to the 2-50% range recorded for STGR in southern habitats (Williamson 2009, Bousquet and Rotella 1998, Roersma 2001, Manzer 2004). STGR in northern British Columbia (75%) (Goddard 2007) and in Alaska, however, appear to be comparatively successful (50-75%) in rearing broods (Paragi et al. 2001, Goddard 2007).

Overall, brood survival in this study tended to be higher on east and south facing slopes than those facing west and north. Because chicks were not radio-marked, we were unable to determine ultimate causes of brood failure; however, because raptors that hunt visually are the primary predators to mature grouse in the study area, they presumably pose an equally great risk to chick survival. Differences in aspect and slope may influence predator detection by means of light; one slope is more shaded than another, or differences in air circulation, warmer updrafts on hills could help conceal brood from olfactory detection (Conover 2007). Aspect may also represent a shift in vegetation; north-facing slopes retain more moisture and have thicker vegetation than do south facing slopes (Conover et al. 2008). Conover (2007) found nests on south-facing slopes, in Utah, to be depredated primarily by visual predators, and nests on north-facing slopes to be depredated primarily by olfactory predators. Hovick (2014) observed that grouse reproduction is correlated with thermal heterogeneity at fine and broad scales. A structurally diverse terrain with low slopes, diversity of aspects, may be important for reproductive success and survival

Brood success and survival also tended to be lower at sites with more ground cover, including deadfall. The use of deadfall by prairie grouse has not been well documented, likely because open grassland systems generally lack significant amounts of deadfall. In Wisconsin, the presence of coarse woody debris impeded nest searching by mammalian predators (Connolly 2001). Coarse woody debris is known to increase insect abundance and different decay classes have distinctive insect communities, which could be beneficial to STGR chicks (Vanderwel et al. 2006). Although some ground cover, including woody debris, may be beneficial in offering structural complexity, thermal refuges, and increased insect abundance, too much may diminish insect productivity and interfere with predator detection and evasion. Given that we found a

negative association between woody debris and chick survival, it appears that among grouse at the northern edge of their range and living in forested and shrubby habitats, selection of sites with a minimum of woody debris and other types of ground cover may be advantageous.

Although we found no impacts of anthropogenic disturbance on brood success, reduced chick survival has been reported for greater sage-grouse (*Centrocercus urophasianus*) in areas of human development (Aldridge and Boyce 2007, Holloran et al. 2010). Proett (2017) found that there was no influence of wind turbine density on brood success, the survival of individual chicks was reduced when more than 10 turbines were present within 2.1 km of the nest. Williamson (2009) described higher chick survival of STGR within developed areas in the Little Missouri National Grasslands of North Dakota. Goddard (2007) reported brood success rates of 71% but only 35% chick survival to 35 days. Our inability to reliably record counts of chicks, compromises our ability to assess potential impacts of anthropogenic development, or other habitat drivers, on chick survival following hatching.

The $64\% \pm 6.2$ ($n = 70$) hen survival during the reproductive period observed in this study is a comparable survival estimate to other regions; 53% in Alberta and northern British Columbia (Manzer 2004, Goddard 2007), 77% in Alberta (Roersma 2001), 89% in South Dakota (Norton 2001). Predation is the greatest source of mortality for adult STGR, and the hens are particularly vulnerable during the early reproductive period (Bergerud 1988). Mortality for hens during this period is probably linked to frequent travel to and from the nest during laying and incubation, and diversion of predators from broods or nest sites. 96% of yearly hen mortalities in Alberta occurred in the breeding season (Manzer 2004), while this same period accounted for 82 % of annual hen mortalities in northern British Columbia (Goddard 2007). In most populations, mammals are the most important predator of grouse. In Alberta, Manzer (2004) attributed 39% of hen mortalities to mammals.

Goshawks have been reported as the major predator for other populations of STGR across the species' range (Paragi et al. 2012). We observed goshawks, harriers, owls and hawks frequently at leks, but only goshawks were observed successfully capturing grouse. Northern goshawks accounted for 91% of the classified hen mortalities in our system. In North Dakota, raptors preyed on 38% of collared hens, whereas mammals were responsible for 20% of the mortalities (Williamson 2009). Red grouse (*Lagopus lagopus*) numbers in Scotland were shown to be limited by raptors (Thirgood et al. 2000). Angelstam (1984) observed a sharp peak in hen

mortality to goshawks during the laying and incubation period of Black grouse (*Tetrao tetrix L*) in Sweden. In Finland, grouse constituted >40% of the goshawk's diet during the breeding season (Tornberg 2001). In Cache County, Utah, Greer (2010) attributed all hen mortalities to avian predators, particularly harriers (*Circus cyaneus*). In a study by Marks and Marks (1987), 19 of 22 collared STGR hens were predated by goshawks, but they determined the raptors were keying in to the radio collars. Despite the recent improvements to radio collars, there could still be some undetected effect of radio-collars on hen survival. Regardless of the potential bias to my survival estimates, the incidence of predation during the display period is consistent with observations made elsewhere.

The snowshoe hare (*Lepus americanus*) is a keystone species in Yukon boreal forests, characterized by a 10-year population cycle that causes many of its predators to prey switch, to grouse or squirrels, during the low phase of its cycle (Doyle 1994). The snowshoe hare cycle was at its peak during our study, but hare populations appear to have been crashing during the final study year. Declining hare populations, and associated prey switching by hare predators like goshawks and lynx are consistent with the trend of declining STGR survival observed in 2017. During a moose survey, following the final year of study, we observed very few STGR in winter ranges, indicating a possible STGR crash. Paragi et al. (2012) observed heavy goshawk predation of grouse in Alaska during a declining period of snowshoe hare cycle and found their flush counts to be much lower in the study area than during a previous study (Raymond 2001). Researchers in Colorado also indicated that annual mortality may differ considerably among years, reflecting natural decadal cycles, in part driven by goshawks (Collins 2004). Predation pressure is highest when grouse densities are lowest and can drive multiannual cycles of some grouse species (Thirgood et al. 2000, Tronberg et al 2005).

We were unable to obtain reliable estimates on yearly survival because we lost track of many of the females during the winter months and therefore cannot know if they died in the wintering range or relocated to new reproductive grounds.

2.7 MANAGEMENT IMPLICATIONS

The reproductive ecology of STGR in northern regions has not been well described. We show here that the brood rearing success and hen survival of a Yukon STGR population is equally high or higher than rates typically reported from other jurisdictions across the species'

range. Although there was some variation between study sites and years, the generally high reproductive success observed in the Klondike Goldfields could reflect some combination of the following factors: a relatively intact breeding complex, few mesopredators in this system, temporary population expansion, and/or favourable weather during the study period. Goshawks were the primary predator of breeding females, and in conjunction with limited suitable breeding habitat and short breeding season, may be limiting population abundance and distribution in the Klondike Goldfields. Caution should be used when interpreting these results, as they are limited to a specific three-year time window and the particular landscape configurations and climate conditions that prevailed during this period. The Klondike Goldfields represent a complex mix of natural and highly modified habitat, defined by the recency of fire and mining impacts, as well as the variability of successional trajectories that follow these disturbances. Given this landscape is highly dynamic and grouse are known to express lagged responses to anthropogenic activities (Harju et al. 2010) longer-term monitoring will provide additional insight regarding the viability of this northern STGR population and the major drivers of its survival and reproductive success.

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2.9 APPENDICES

Appendix A. Comparisons (mean \pm SE) of variables for 55 successful and failed STGR nest sites. Variables in bold denote variables with $p < 0.2$ from as determined by Wilcoxon-Mann-Whitney test, and that were considered in GLM candidate models.

Variable	Successful Nests Mean \pm SE n = 42	Failed Nests Mean \pm SE n = 13	p
Nest microsite			
CoverBoardGram (%)	15.1 \pm 3.1	12.8 \pm 3.6	0.97
CoverBoardforbs (%)	4.6 \pm 1.5	4.2 \pm 3.7	0.17
CoverBoardshrubs (%)	32.7 \pm 5.5	35.8 \pm 8.5	0.62
CoverBoardResidual (%)	12.2 \pm 3.5	11.8 \pm 4.0	0.29
Nest.structure	1.7 \pm 0.1	1.9 \pm 0.2	0.47
LitterQuad (%)	28.7 \pm 4.1	46.3 \pm 9.0	0.08
CryptoQuad (%)	21.9 \pm 4.4	22.9 \pm 8.2	0.99
GraminoidQuad (%)	41.4 \pm 5.5	31.3 \pm 8.7	0.44
ForbsQuad (%)	14.4 \pm 3.0	12.2 \pm 6.6	0.50
ShrubsQuad (%)	37.7 \pm 4.8	35.8 \pm 9.0	0.95
Total.cover (%)	80.8 \pm 4.1	76.5 \pm 8.9	0.88
VOR1 (%)	85.3 \pm 2.4	87.5 \pm 5.4	0.66
VOR2 (%)	61.3 \pm 3.6	69.2 \pm 8.6	0.43
VOR3 (%)	42.4 \pm 3.9	53.0 \pm 10.3	0.46
VOR4 (%)	29.4 \pm 3.7	32.5 \pm 8.5	0.97
VOR5 (%)	22.2 \pm 3.6	23.7 \pm 7.3	0.90
VORLOW (cm)	72.3 \pm 3.4	78.3 \pm 7.8	0.39
VORMAX (cm)	81.5 \pm 3.3	85.2 \pm 6.5	0.71
Nest site			
ground.shrub (%)	28.6 \pm 5.0	17.2 \pm 5.0	0.35
low.shrub (%)	24.7 \pm 3.6	19.7 \pm 5.8	0.36
Mid.shrub (%)	24.8 \pm 4.1	18.5 \pm 5.7	0.57

High.shrub (%)	17.5 ± 3.4	29.6 ± 6.8	0.05
PatchLitter (%)	31.2 ± 2.9	37.1 ± 4.7	0.33
PatchCrypto (%)	33.0 ± 4.8	28.7 ± 8.5	0.70
PatchGram (%)	23.1 ± 2.0	25.1 ± 5.8	0.91
PatchForbs (%)	15.2 ± 2.7	8.5 ± 1.9	0.21
PatchShrubs (%)	22.7 ± 2.1	25.5 ± 4.3	0.68
PatchTotCov (%)	69.2 ± 3.9	66.7 ± 7.5	0.63
PatchVOR1 (%)	74.3 ± 2.9	79.8 ± 4.0	0.46
PatchVOR2 (%)	48.4 ± 3.1	56.7 ± 5.3	0.21
PatchVOR3 (%)	36.8 ± 3.2	43.6 ± 5.2	0.35
PatchVOR4 (%)	29.0 ± 2.8	34.1 ± 4.9	0.34
PatchVOR5 (%)	23.4 ± 2.5	27.5 ± 3.9	0.29
PatchVORlow (cm)	64.7 ± 3.6	74.2 ± 5.1	0.39
PatchVORmax (cm)	71.4 ± 3.5	81.1 ± 4.2	0.71
LitterPatch (%)	36.8 ± 4.3	48.5 ± 6.5	0.12
Standing.dead (%)	69.1 ± 6.6	72.7 ± 10.3	0.54
Canopy.height (m)	6.5 ± 0.9	8.7 ± 3.0	0.74
Deadfall	14.8 ± 2.2	15.3 ± 3.7	0.72
Elevation (m)	586.3 ± 12.5	528.9 ± 19.6	0.08
Slope (%)	5.7 ± 0.9	3.6 ± 1.2	0.17
Distance to features			
Distance to edge (m)	121.9 ± 23.1	99.1 ± 33.2	0.80
Distance to Lek (m)	1394.5 ± 156.3	1042.0 ± 204.7	0.31
Active mine (m)	2364.7 ± 164.1	2554.6 ± 373.8	0.79
Roads (m)	801.7 ± 98.0	735.2 ± 115.9	0.94
Inactive mine (m)	1256.6 ± 188.8	1054.9 ± 320.6	0.50
Hen body condition and nesting chronology			
Capture day	118.1 ± 0.4	120.2 ± 2.6	0.96
Initiation day	126.6 ± 0.5	126.6 ± 1.2	0.64
Incubation day	135.2 ± 0.4	135.4 ± 0.9	0.70
Hatch day	160.1 ± 0.59	163.2 ± 2.3	<0.01

Body Index (residuals)	-0.8 ± 0.9	3.2 ± 3.3	0.25
Clutch size	8.4 ± 0.3	8.5 ± 0.5	0.91
Discrete variables			
Variable	Factor	Proportion Successful	Proportion Failed
		n = 39	n = 13
CWD Decay	Class 1	0.33	0.15
	Class 2	0.49	0.62
	Class 3	0.18	0.23
	Class 4	0.00	0.00
	Class 5	0.00	0.00
CWD Size	Small	0.46	0.62
	Medium	0.51	0.38
	Large	0.00	0.00
Microtopography	No Hummocks	0.33	0.08
	Few Hummocks	0.49	0.54
	Many		
	Hummocks	0.18	0.38
Moisture	Xeric	0.26	0.23
	Submesic	0.26	0.23
	Mesic	0.28	0.38
	Subhydric	0.10	0.08
	Hydric	0.08	0.00
	Hygic	0.00	0.00
Patch structure	Non-vegetated	0.00	0.00
	Herb	0.08	0.08
	Shrub/scrub<2m	0.44	0.46
	Shrub/scrub>2m	0.23	0.38
	Edge	0.03	0.00
	Pole sapling	0.10	0.00
	Aspen	0.08	0.08

	Mature		
	coniferous	0.00	0.00
	Mixed forest	0.03	0.00
	Agricultural		
	field	0.00	0.00
	Grassland	0.00	0.00
Successional stage	Non-vegetated	0.00	0.00
	Pioneer seral	0.23	0.15
	Young seral	0.59	0.77
	Maturing seral	0.13	0.08
	Overmature		
	seral	0.00	0.00
	Young climax	0.00	0.00
	Maturing		
	climax	0.03	0.00
	Overmature		
	climax	0.00	0.00
	Disclimax	0.00	0.00
Hen Age	Mature	0.73	0.83
	Juvenile	0.27	0.17

1666

1667 **Appendix B.** Comparisons (mean \pm SE) of variables for 23 successful and 8 failed STGR
1668 broods. Variables in bold denote variables with $p < 0.2$ as determined by Mann-Whitman test,
1669 and that were considered in GLM candidate models.

Variable	Successful Broods	Failed Broods	p
Elevation	587.5 \pm 4.5	583.8 \pm 6.4	0.49
Distance to edge	76.2 \pm 3.5	85.9 \pm 4.7	0.13
Total shrub cover	77.7 \pm 1.7	83.7 \pm 2.0	0.04
Ground shrub	13.0 \pm 0.9	11.9 \pm 0.9	0.88

Low shrub	42.9 ± 1.7	42.9 ± 2.1	0.86
Med shrub	21.4 ± 1.2	22.8 ± 1.5	0.19
High.shrub	11.9 ± 1.0	10.8 ± 0.9	0.72
Canopy.height	5.0 ± 0.3	4.4 ± 0.3	0.44
Gram.cover	42.7 ± 2.2	40.9 ± 2.6	0.53
Forb cover	16.9 ± 1.1	18.6 ± 1.3	0.11
Crypt.cover	50.2 ± 2.5	44.8 ± 3.2	0.27
Deadfall	20.7 ± 1.1	25.5 ± 1.6	0.03
Standing.dead	67.4 ± 2.2	67.7 ± 2.8	0.64
Litter	35.9 ± 1.8	36.1 ± 2.1	0.77
*Hatch day	160.1 ± 0.6	163.2 ± 2.3	<0.01
Body Index (residuals)	-0.840.9	3.2 ± 3.3	0.25
Discrete Variables			
Aspect	North	0.43	0.32
	East	0.19	0.36
	South	0.01	0.05
	West	0.02	0.01
	None	0.35	0.27
CWD Decay	Class 1	0.30	0.34
	Class 2	0.33	0.29
	Class 3	0.29	0.28
	Class 4	0.08	0.08
	Class 5	0.00	0.01
Microtopography	No Hummocks	0.23	0.18
	Few Hummocks	0.37	0.39
	Many Hummocks	0.40	0.43
Moisture	Xeric	0.20	0.25
	Submesic	0.42	0.39

	Mesic	0.24	0.23
	Subhydric	0.11	0.12
	Hydric	0.03	0.01
	Hygric	0.01	0.00
Patch structure	Non-vegetated	0.00	0.00
	sparse	0.01	0.01
	Herb	0.00	0.00
	Shrub/scrub<2m	0.44	0.49
	Shrub/scrub>2m	0.44	0.44
	Edge	0.02	0.01
	Pole sapling	0.02	0.00
	Aspen	0.02	0.04
	Mature coniferous	0.04	0.01
	Mixed forest	0.01	0.00
	Agricultural field	0.00	0.00
	Grassland	0.00	0.00
Successional stage	Non-vegetated	0.00	0.00
	Pioneer seral	0.22	0.22
	Young seral	0.68	0.72
	Maturing seral	0.03	0.02
	Overmature seral	0.01	0.01
	Young climax	0.01	0.01
	Maturing climax	0.05	0.01
	Overmature climax	0.01	0.00
	Disclimax	0.00	0.00
Hen Age	Mature	0.73	0.83
	Juvenile	0.27	0.17

1671 **LINKING STATEMENT**

1672 In chapter 2, I describe and assess habitat effects on hatching and fledging success.

1673 Chapter 3 considers the habitat use of STGR around identified lek sites during the nesting and

1674 brood-rearing periods, and analyze the habitat selection of nesting and brood-rearing hens.

Chapter 3: The habitat use and selection of nesting and brood-rearing sharp-tailed grouse in Yukon's Klondike Goldfields

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Joël Potié (email: joel.potie@mail.mcgill.ca)

Natural Resource Sciences, Macdonald Campus, McGill University

21 111 Lakeshore Drive, Ste-Anne-de-Bellevue, QC, H9X 3V9, Canada

Murray M. Humphries (email: murray.humphries@mcgill.ca)

Natural Resource Sciences, Macdonald Campus, McGill University

21 111 Lakeshore Drive, Ste-Anne-de-Bellevue, QC, H9X 3V9, Canada

Michael J. Suitor, (email : mike.suitor@gov.yk.ca)

Inuvialuit and Migratory Caribou Biologist

Fish and Wildlife, Environment Yukon

PO Box 600, Dawson City, Yukon Y0B 1G0

Kathryn E. H. Aitken (email : kaitken@yukoncollege.yk.ca)

School of Science, Yukon College,

P.O. Box 2799, 500 College Drive, Whitehorse, Yukon, Y1A 5K4, Canada

3.1 ABSTRACT

Research and conservation of lek birds, and especially lekking gallinaceous birds, often concentrates on identifying lek sites and the protection of the breeding complex that surround them. However, documenting longer-term and larger-scale space use and habitat requirements expressed during subsequent seasonal stages is also important. To document nesting and brood rearing habitat use and selection, 75 sharp-tailed grouse hens were radio collared and monitored in the Klondike Goldfields, Yukon, from 2015-2017. I examined the selection of nesting and brood rearing habitat at three scales (microsite, site and patch-scales) using resource selection functions fitted using generalised linear models and an information-theoretic approach. Overall, we found that the majority of nest sites in the Klondike Goldfields were composed of a shrub layer providing vertical cover and abundant bunchgrass understory providing horizontal cover. Brood rearing hens selected for sites with mesic vegetation such as scrub birch and sedges; However, hens with broods also showed a preference for sites classified as dry rather than wet. During both the nesting and brood rearing periods, hens did not select for shrub dominated sites equally; those with shrubs less than 2m in height were preferred over taller shrubs and avoidance increased as the successional stage progressed to maturing forest. Estimates for 95% kernel density home ranges (163.0 ± 52.8 ha) and distances travelled (1119.2 ± 187.9 m) from the nest site to brood rearing habitat are longer in the present study than have previously been recorded.

KEY WORDS: Brood-rearing, Generalised Linear Mixed Models, habitat selection, home range, habitat use, Klondike, nesting, radio-telemetry, *Tympanuchus phasianellus*, Yukon.

3.2 INTRODUCTION

Because organisms are not randomly distributed across the landscape, an important focus of wildlife managers is the assessment of the quality and quantity of habitat available to a species across a given landscape (Southwood 1977). To provide ecologically relevant conclusions, an understanding of space-use patterns relative to specific habitat requirements during seasonal stages of annual cycles is required. These habitats are used to assist in habitat restoration, promote population growth, prevent habitat degradation and facilitate species reintroduction.

Protecting habitat that wildlife use for reproduction has been a central tenet of wildlife conservation for more than a century (Fischman 2005). Birds with a lek-based mating system concentrate their breeding, nesting, and brood rearing in and around traditional lek sites, with important implications for their landscape distribution, habitat selection, and conservation requirements (Wiens et al. 1993, Kane et al. 2017). Accordingly, research and conservation of lekking birds, and especially lekking gallinaceous birds including capercaillie (*Tetrao urogallus*), sage grouse (*Centrocercus urophasianus*), prairie chickens (*Tympanuchus cupido*), and sharp-tailed grouse (*Tympanuchus phasianellus*; STGR), often concentrates on the identification and protection of lek sites and the nesting and brood rearing habitats that surround them (Fuhlendorf et al. 2002, Oja, et al. 2018, Burr et al. 2017).

Past research on STGR has documented the importance of lek sites and surrounding habitats for successful reproduction and population persistence, and many existing STGR management strategies are focused on protecting lek sites. Hamerstrom et al. (1957) and Kirsch (1974) determined that the distribution and population dynamics of STGR are dependent on the availability of suitable nesting and brood rearing habitat. Without effective habitats adjacent to leks, STGR may be unsuccessful at raising young and local populations may be impacted, depending on the magnitude and extent of change to these habitats (Giesen 1997). STGR are well adapted to ground nesting in grassland landscapes comprised of mixed shrubs, shrub-steppe, parkland and agricultural crops, with an abundance of forbs and bunchgrasses (Hart et al. 1950, Meints 1991, Meints et al. 1992, McDonald 1998, Prose et al. 2002). Nests and areas surrounding nests tend to be located in areas with denser cover and higher vegetation (e.g., provided by mixed shrubs with herbaceous understory), relative to unused or random locations across the landscape (Giesen 1987, Manzer and Hannon 2005, Marks and Marks 1987, Meintz 1991). Residual cover from the previous fall is important for nesting STGR because the hens

begin nesting before new grasses and forbs have had time for much growth (Goddard 2007). Nests are often found under some type of overhead vertical grass or forb cover or near the base of a shrub (Hart et al. 1950, Giesen 1987, Marks and Marks 1987, Meints 1991, Hillman and Jackson 1973). Brood rearing habitat must be accessible from the nest, provide adequate concealment from predators, protection from weather and have an abundance of forbs and insects for chicks to feed (Marks and Marks 1987, Svedarsky et al. 2003). Brood rearing habitat has been described as mixed shrub communities, with high forb density and an abundance of insects (Connelly et al. 1998, Oedekoven 1985), often in early successional stages, where vegetation cover is higher than random locations (Giesen 1987, Meints 1991). In Wisconsin, STGR brood rearing hens prefer open grasslands (Hammerstrom 1963) In the Alberta parkland they preferentially use grassland-low shrub transition zones (Moyles 1981). In Colorado brood rearing habitat contained more than 70% shrub cover (Giesen 1987). Goddard (2007) found STGR brood habitat selection differed between early (0-14) and late (15-49) days, as the chicks begin to thermoregulate, are more mobile, and shift their feeding habits from insects to forbs.

Although STGR have been traditionally thought of and studied as a prairie grouse that occupies the Great Plains region of North America, the species' range extends far beyond the Great Plains to include considerable montane habitat in the western portion of its range and boreal habitat in the northern portion of its range. The lekking behaviour and habitat requirements of these non-prairie populations of STGR are much less studied than populations closer to the core of the range. STGR have long been noted to frequent open habitats within boreal and mountainous regions of Alaska and Yukon (Aldrich 1963) but the lekking behaviour and reproductive habitats of these disjunct populations at the extreme northwest of the species' range are poorly documented (Connelly et al. 1998). A limited amount of investigation from Alaska and Yukon suggests that the northernmost population of STGR may have different habitat requirements than the southern populations (Mossop et al. 1979, Raymond 2001, Taylor 2013).

Seven species of grouse occur in the Yukon, but STGR is the only species that leks and the only species of immediate management concern. Although it is believed that Yukon STGR, which are generally classified within the *caurus* subspecies, are stable, beyond anecdotal sightings, little is known regarding their habitat requirements and reproductive ecology (Connelly et al. 1998, Raymond 2001, Taylor 2013, Mossop et al. 1979; J. Staniforth,

Environment Yukon, unpublished report). The general distribution of STGR in and around the Klondike Goldfields is poorly described, and the amount and distribution of suitable habitat there is unknown. In addition, nearly the entire area known to be used by STGR in the Indian River valley, Yukon, is staked by mining claims. Giesen and Connelly (1993) recommend a 2 km buffer around lek sites to protect the entire breeding complex. If such a management strategy is applied to the Yukon context, the recommended 2 km ‘no development zone’ encompassing the breeding complex would overlap existing or planned placer mining areas, leading to land use conflicts in one of the richest gold producing regions of Canada. As a result, a better understanding of STGR habitat requirements is required to better manage land use in the Klondike Goldfields and other activities in areas where this species is present.

The objectives of this study were to (1) describe the habitat use of STGR during the nesting and brood rearing periods; and (2) analyse the habitat selection of nesting and brood rearing hens in the Klondike Goldfields to help inform habitat suitability models and STGR habitat protection in this region.

3.3 STUDY AREA

Research was conducted in the Klondike Goldfields south of Dawson City, Yukon, in the Indian River Watershed, and is described in detail in Chapter 2.

3.4 METHODS

3.4.1 Field Techniques

To identify nesting and brood rearing habitats, sharp-tailed grouse hens were captured, and radio collared at lek sites. Lek sites were located by walking transects in the goldfields and listening for STGR vocalizations, and if heard, by approaching the location on foot. Once active leks were identified, sharp-tailed grouse were observed during the breeding season from ground blinds or from a distance using binoculars. During daily observations, we noted the number of birds present, genders when possible, predators, weather, as well as general behaviour. *A priori* observation of male territories and behaviour at leks helped coordinate trap set-up to increase trapping success. A total of six leks were located and sampled within the goldfields (three in Dominion Creek drainage and three in Indian River drainage), and one farther away in an area free of any placer mining (North Fork). The number of leks trapped per year increased as new leks were discovered in the study areas. Grouse were trapped on leks between April 15 - May 7 of 2015-2017 using walk-in style funnel traps (Marks and Marks 1987b; Toepfer et al. 1987; Schroeder and Braun 1991), modified from published accounts, based on recommendations from previous researchers (A. Goddard, BC Ministry of Forests, Lands & Natural Resource Operations, personal communication) to minimize injuries to the birds. Trapping commenced prior to the arrival of females on the leks, and was terminated once females stopped visiting. The traps were strategically placed on leks in a circular, zigzag pattern to capture any birds attempting to walk in or out of the centre of the lek, toward the dominant males' territories. Leads constructed with chicken wire, 15 m in length and set up between traps guided the grouse into the funnel traps.

Three independent crews trapped at the three study areas (Indian River, Dominion Creek and North Fork). Each group was responsible for a maximum of three leks, which they would monitor for captured birds at 20-minute intervals between 6:00 – 11:00. Traps remained open throughout the day, and were checked every three - four hours in the afternoon and evening.

Most birds were captured during the morning period of peak activity (6-11h, n = 212), but a few were captured after 11 h (n = 6).

STGR, and handling protocols were reviewed by an Environment Yukon Veterinarian and approved by McGill University Animal Use Committee. All captured grouse were sexed, aged, weighed and had their wing chords measured. Sex was determined by examining crown feathers, tail feathers, supraorbital combs, and presence of air sacs (Henderson et al. 1967). Weights were obtained using a 1kg Pesola scale. Birds were classified as being in their first breeding season or their second breeding season based on the degree of fraying of the 9th and 10th primaries (Ammann 1944). For each captured individual, we computed a body condition index by regressing mass against the length of the wing chord using the Reduced Major Axis method (Green 2001). Additional samples taken included: buccal and uro-genital swabs, feathers, and, in some instances, small amounts of blood (≤ 2.0 ml) when deemed safe. Because male STGR are territorial at the leks, male by-catch was common, particularly early in the trapping efforts. All captured birds were fitted with individually numbered aluminium #6 legs bands (Cutler Supply, Applegate, Michigan). Female grouse were fitted with a necklace-style VHF transmitter; in 2015 radio collars were provided by ATS (Advanced Telemetry Systems, G10-120 and A3950, Isanti, Minnesota) and had a 450-day transmission life and in 2016-2017 Holohil (RI-2BM, Carp, Ontario) transmitters were used with two-year expected battery life. Transmitters weighed 10 – 14 grams, representing less than 2% of the female's body mass (Carroll 1990). A small number of males were also collared, during all years of study. Radio collars were deployed opportunistically throughout study areas to ensure maximum possible deployment. Handling time of individuals that were not fit with a radio collar was <10 minutes, while those with a transmitter was < 30 minutes. All birds were released at the lek of capture immediately after data collection, and were monitored for abnormal behaviours post-release.

Radio-marked grouse were located two - three times per week using portable ATS (Advanced Telemetry Systems, Isanti, Minnesota) and R1000 (Orange, California) receivers with H-element and Yagi antennas. Most relocations were conducted on the ground; however, a fixed-wing aircraft, equipped with a H-antenna attached to the struts of either wing, was used to locate missing individuals. All hen locations were recorded using a Garmin handheld GPS (GPSMAP 78) with 3-5 m accuracy, which also provided a measure of elevation. During the pre-nesting period, grouse were located using triangulation to avoid flushing hens and to minimize

disturbance during egg laying. Once movements became localised, females were presumed to have initiated a nest and were approached for visual confirmation. Nests were confirmed by the presence of eggs in the nest. Egg flotation was used to determine stage of incubation and predict nest initiation, incubation, and hatch dates (Westerkov 1950). After nests hatched, hens that had successfully hatched broods were relocated every 3-4 days, until brood dispersal to record brood fate and to characterize habitat use. To reduce the risk of weather and predation to broods, hens were not flushed during the first 7-days post hatch (when chicks are flightless and cannot thermoregulate) or during inclement weather. Hen re-locations continued until 35 days post hatch (brood dispersal occurs between 30-45-days, at which time brood survival beyond this point is unreliable) (Goddard 2007, Gratson 1988). If hen mortality occurred during the first three weeks of brood rearing, broods were recorded as failed. If hen mortality occurred in the final week of the brood rearing period, those broods were censored from analyses as brood fate was impossible to confirm.

3.4.2 Vegetation and Habitat Data Collection

Characteristics of nesting habitat used by STGR were sampled from data collected from 55 nests; 15 nests in 2015, 25 nests in 2016 and 15 nests in 2017 (Fig. 3, Fig. 4). Because there were only two re-nesting attempts over all study years, and these nests hatched within the hatch period of the first nest attempts, first and re-nesting attempts were analysed together ($n = 55$).

The three North Fork hens were removed from habitat selection models due to small sample size.

We also monitored 11 hens with broods in 2015, 14 in 2016, and 11 in 2017 until chicks were 35 days of age. Hens monitored in 2015 were excluded from brood rearing habitat selection analyses because we did not record vegetation or habitat characteristics. In addition, six other hens were censored from brood rearing analyses; one shed collar, two failed, two hens were lost, and one collar induced mortality (leg caught in the necklace of the radio-collar).

The vegetative characteristics and habitats used by nesting and brood rearing grouse were documented at multiple scales, using a Robel sampling design with sampling concentrated at a focal location (nest location, brood rearing location, or random location), at four stations located at 5 m from the focal location, and at four stations located 10 m from the focal location (Fig. 1). Each sampling station consisted of a modified Robel pole, a marked vertical white pole used to estimate visual obstruction at different heights above ground, and a Daubenmire frame, used to

estimate ground and overhead cover. To determine the location of the 9 sampling locations, we identified the central focal location, then established two perpendicular 30 m line-transects, oriented north-south and east-west. Coarse habitat metrics collected were the same for nesting and brood rearing locations. We did not collect microsite vegetation characteristics, Daubenmire frames, or Robel pole stations for brood habitats.

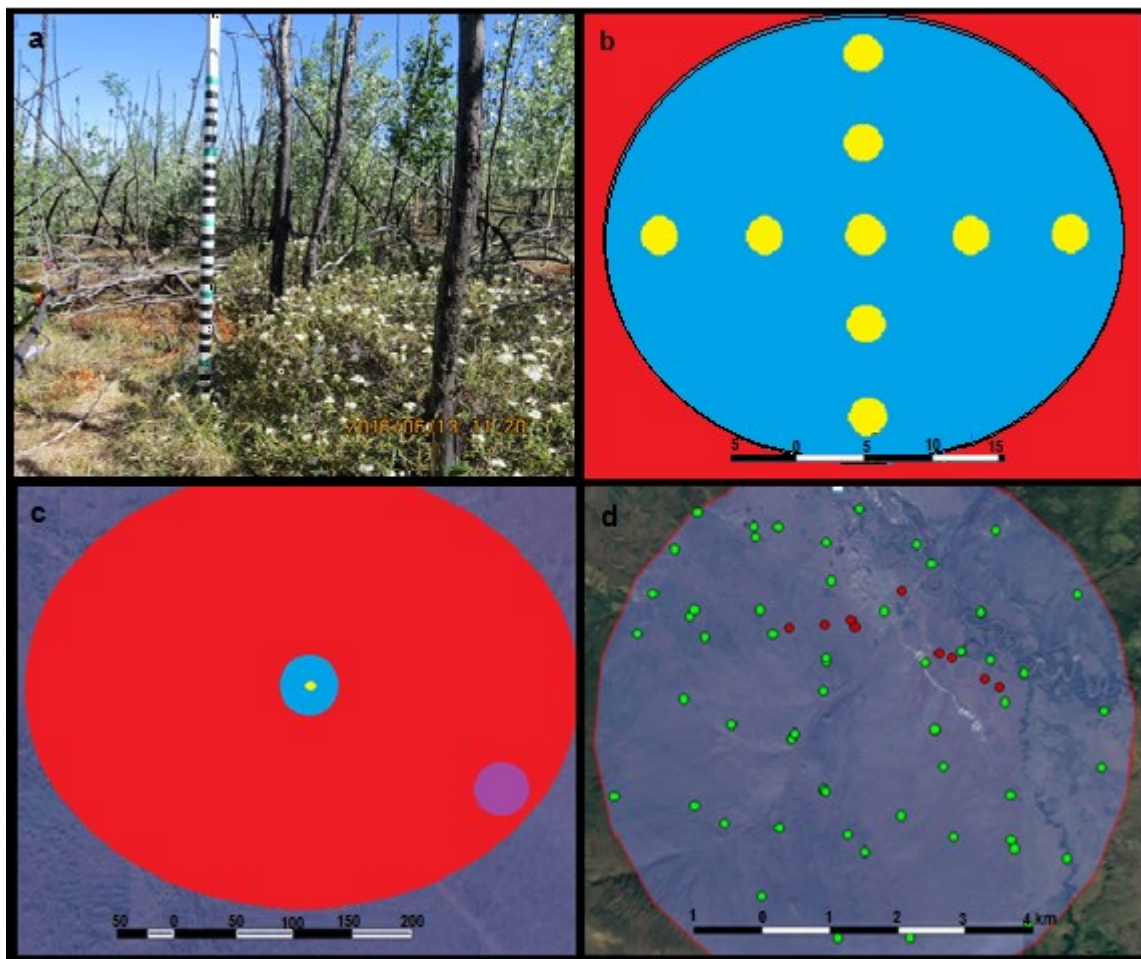


Figure 1. Vegetation and habitat sampling schematic for used and random locations. A. Photograph of a Robel pole station. B. Microsite scale illustration of a nest site (blue) with the 9 Daubenmire/Robel microsite sampling stations (yellow) centered around the nest bowl. Scale is in metres with stations separated by 7 m. C. Patch scale illustration of a nest site (blue) and a paired random location (purple). Scale is in metres, with a 250 m separation between the nest bowl and the paired random location. Diameters of blue circle is 30 m (as in panel B). D. Landscape scale illustration of nest sampling locations (red) with random patch-scale sampling sites (green) restricted within a 4 km radius area (transparent purple) centered on lek of capture.

The Robel pole visual obstruction technique was designed for open grassland habitats, and thus we modified the traditional pole and technique to facilitate observations in a shrub

dominated system (Robel et al. 1970, Payne 2013; B. Pagacz, Environmental Dynamics Inc., personal communication). Our modified Robel pole was made of 5.7 cm PVC, 122 cm tall with alternating 2.5 cm white and black increments, with every 10th increment marked with a red band. We took four visual obstruction readings of each Robel pole (VOR), one in each cardinal direction, always from 4 m away from the pole at a height of 1 m off the ground. To account for the dominant shrub layer, we chose to categorize VOR measurements into 5 incremental 25 cm sections (VOR1-VOR5). Each 25 cm section was comprised of 2.5 cm alternating white and black bands. We estimated the combined portions of intervals covered by shrub canopy and the percent, to the nearest 5%, this obstruction represented as cover at different intervals. For example, if in VOR1, bands 1-4 were obscured, 5-7 were visible, and 8-10 were obscured, we recorded VOR as 60%. We also recorded maximum understory vegetation height (VORMax) as the highest interval with any kind of vegetation visible in front of it. Low obstruction (VORLow) was recorded as the lowest band not completely obscured by vegetation (that is, the first break in VOR).

The Daubenmire frame used was 20 x 50 cm and was positioned around the base of every Robel pole station (Daubenmire 1959). Using this frame, percent cover of understory grasses, forbs, shrubs, cryptogams, litter, and tree suckers was measured. The dominant type of grass (bunchgrass, sod forming grass or sedge/rush), forb (genera), shrub (genera), tree (genera), cryptogam (genera), and litter (type) were also recorded. We measured the percentage that each quarter of the square was obscured by overhead vegetation and averaged the four cover measurements to provide an overall measure of vertical cover. Cover was recorded as a continuous variable. The estimates from each of the nine stations were used to compare nest bowl cover classes and visual obstruction to nearby microsites. The estimates from each of the nine stations were then tallied and averaged, providing a single value for each cover class and visual obstruction interval, describing the focal location.

To further describe the sampling station, we used an ocular to measure the shrub/scrub cover within a 30 m radius of the focal location center. Other coarse habitat measurements included moisture (xeric, sub mesic, mesic, sub hydric, hydric, or hygric), microtopography (no hummocks, few hummocks or many hummocks), topography (slope, aspect and elevation), percent standing dead and percent deadfall. Coarse woody debris (CWD) was classified based on decay (classes 1 – 5) and size (small, medium and large). Patch structure of the nest site was

recorded as non-vegetated, sparse/cryptogram, herb, low shrub/scrub, tall shrub/scrub, edge, pole-sapling, aspen, mature coniferous, mixed forest, agricultural field, grassland. Successional stage was described as non-vegetated, pioneer seral, maturing seral, over mature seral, young climax, maturing climax and over mature climax. Landscape type was documented as anthropogenic or natural. Distance to the nearest patch edge was measured using a digital rangefinder (Bushnell Legend 1200). Elevation was recorded using GPS, and slope using a clinometer. Aspect was categorized as north (316-45), east (46-135), south (136-225), and west (226-315) directions, and no aspect for points with a slope ≤ 1 .

To assess the habitat selection of reproducing sharp-tailed grouse hens, each used nest or brood rearing location was paired with random locations at three scales (micro-site, site and patch) (Fig. 1). At each random location we measure habitat attributes identical to those collected at used sites. Daubenmire/Robel sampling at the nest bowl (microsite) was paired with 8 Robel/Daubenmire stations, within the adjacent 30 m radius of nest, representing a ratio of 1:8 (Fig. 1, Appendix A). To record available habitat within 250 m of the nest or brood location, a random paired location was determined by moving in a predetermined direction between 30-250 m from the nest; distances and direction were obtained using a random number table in excel, and followed using a handheld GPS (ratio 1:1). Microsite vegetation characteristics were measured the day after nests hatched, or on the expected day of nest hatch, if nest was predated. Because 2015 nests were surveyed in 2016, they were assessed on the approximate date of hatch of the previous field season (Hausleitner et al. 2005). For comparison of used brood rearing and nesting sites with available habitat at the patch-scale, we collected 24 vegetation characteristics at 200 random locations, within a 4 km radius of the nearest lek (sample ratio of 1:4) (Appendix A, Appendix C). Random patch locations were determined by using random point generator in QGIS (Version 2.18.15).

3.4.3 Statistical Analyses

Habitat selection is expected to differ between coarse and fine scales, reflecting the hierarchy of factors potentially limiting a population's viability and an individual's fitness (Johnson 1980). Preliminary analysis indicated that landscape scale metrics were stronger predictors of habitat use than those quantified at the site and patch scale. Accordingly, subsequent analyses include on landscape scale metrics.

Prior to multivariate analyses and model fitting, we first used a three-step method of variable reduction for both of the nesting and brood rearing periods at each of the three spatial scales. We first chose to reduce patch structure (12 levels) and moisture (6 levels) categorical variables into, to five (bare, open, low shrub, high shrub, forested) and two (wet and dry) levels respectively. Patch structure and moisture were then combined into a single eight level factor, renamed habitat type (Table 1). We used Pearson's correlation to test for collinearity between all independent variables (Appendix A, Appendix B, Appendix C, Appendix D). If variables were correlated ($r > 0.5$), a priori knowledge or a logistic regression comparing the two variables was used to eliminate the less biologically relevant variable. During the nesting period, high collinearity was identified between nesting patch structure and successional stage ($r = 0.62$, $n = 250$), and for deadfall and litter ($r = 0.53$, $n = 250$). Nesting patch structure was retained over successional stage because it was believed to a better representation of the habitat characteristics observed in the field. Litter was retained over deadfall, because of the former's reported importance to ground nesting birds. During the brood rearing period, high collinearity was identified between patch structure and successional stage ($r = 0.71$, $n = 378$), and for total cover and low shrub ($r = 0.51$, $n = 378$). Brood rearing patch structure was retained over successional stage because it was believed to be a better description of the habitat characteristics we observed in the field. Total cover was retained because a measure of low shrub was included within the categorical variable of patch structure.

Table 1. Habitat use, availability, and Manly Selectivity Ratios for nesting sharp-tailed grouse in the Klondike Goldfields. Explanatory variables include, after variable reduction, a single continuous variable (% cover) and the relative proportion of each level of four categorical variables, with means (\pm SE) compared between 50 nests and 200 random locations, after variable reduction. Manly Selectivity Ratio (W_i) is the proportional use divided by the proportional availability of each resource, indicating a measure of habitat selection. Variables in gray were found to be significant in the top GLM model.

Continuous Variables		Used	Available	W_i^a
Total cover (%)		79.8 \pm 3.9	55.9 \pm 4.6	1.43
Categorical variables				
Microtopography	No Hummocks	0.26	0.63	0.41
	Few Hummocks	0.50	0.22	2.27
	Many Hummocks	0.24	0.15	1.60
Habitat Type	Non-vegetated–Dry	0	0.03	0.00
	Non-vegetated–Wet	0	0.05	0.00
	Open-Dry	0.06	0.01	6.00
	Open-Wet	0.02	0.04	0.50
	Shrub/scrub<2m-Dry	0.16	0.05	3.20
	Shrub/scrub<2m-Wet	0.36	0.06	6.00
	Shrub/scrub>2m-Dry	0.16	0.19	0.84
	Shrub/scrub>2m-Wet	0.1	0.15	0.67
	Forested-Dry	0.06	0.21	0.29
	Forested-Wet	0.08	0.21	0.38
Ground cover	Non-graminoid	0.00	0.09	0.00
	Bunchgrass	1.00	0.40	2.50
	Sod grasses	0.00	0.33	0.00
	Sedge/rushes	0.00	0.19	0.00
Shrub Type	None	0.00	0.16	0.00
	<i>Salix sp.</i>	0.42	0.13	3.23
	<i>Betula glandulosa</i>	0.16	0.10	1.60
	<i>Ledum palustre</i>	0.18	0.20	0.90
	<i>Rosa acicularis</i>	0.02	0.02	1.00
	<i>Chamaedaphne calyculata</i>	0.08	0.11	0.73
	<i>Shepherdia canadensis</i>	0.04	0.01	4.00
	<i>Populus tremuloides</i>	0.10	0.03	3.33
	<i>Rubus pubescens</i>	0.00	0.01	0.00
	<i>Arctostaphylos uva-ursi</i>	0.00	0.02	0.00
	<i>Vaccinium Oxyccocos</i>	0.00	0.02	0.00

Table 2. Habitat use, availability, and Manly Selectivity Ratios for brood rearing sharp-tailed grouse in the Klondike Goldfields. Explanatory variables include, after variable reduction, two continuous variables and the relative proportion of each level of 4 categorical variables, with means (\pm SE) compared between brood rearing sites ($n = 378$) and random sites ($n = 378$). Manly Selectivity Ratio (W_i) is the proportional use divided by the proportional availability of each resource, indicating a measure of habitat selection. Variables highlighted in gray were included in the top GLM model.

Continuous Variables		Used	Available	W_i
Total shrub cover		80.1 \pm 3.6	50.6 \pm 4.2	1.58
Canopy height		4.5 \pm 0.5	6.5 \pm 0.8	0.69
Categorical variables				
Microtopography	No Hummocks	0.22	0.68	0.32
	Few Hummocks	0.38	0.18	2.11
	Many Hummocks	0.40	0.13	3.08
Habitat type	Non-vegetated-Dry	0.00	0.05	0
	Non-vegetated-Wet	0.00	0.04	0
	Open-Dry	0.01	0.02	0.5
	Open-Wet	0.00	0.03	0
	Shrub/scrub<2m-Dry	0.31	0.05	6.2
	Shrub/scrub<2m-Wet	0.17	0.09	1.89
	Shrub/scrub>2m-Dry	0.28	0.16	1.75
	Shrub/scrub>2m-Wet	0.16	0.14	1.14
	Forested-Dry	0.04	0.26	0.15
	Forested-Wet	0.04	0.17	0.24
Ground cover	Non-graminoid	0.02	0.21	0.10
	Bunchgrass	0.35	0.48	0.73
	Sod grasses	0.24	0.22	1.09
	Sedges/rushes	0.39	0.09	4.33
Shrub type	None	0.01	0.11	0.10
	<i>Salix sp.</i>	0.33	0.26	1.27
	<i>Betula glandulosa</i>	0.29	0.06	4.83
	<i>Ledum palustre</i>	0.30	0.26	1.15
	<i>Rosa acicularis</i>	0.05	0.02	2.5
	<i>Chamaedaphne calyculata</i>	0.00	0.05	0
	<i>Shepherdia canadensis</i>	0.00	0.02	0
	<i>Populus tremuloides</i>	0.01	0.04	0.25
	<i>Rubus pubescens</i>	0.00	0.00	0
	<i>Arctostaphylos uva-ursi</i>	0.00	0.05	0
	<i>Vaccinium Oxycoccos</i>	0.00	0.00	0
	<i>Scrub Picea mariana</i>	0.00	0.01	0
	<i>Alnus sp.</i>	0.00	0.00	0
	<i>Betula nana</i>	0.00	0.08	0
	<i>Vaccinium uliginosum</i>	0.02	0.03	0.67

Using a non-parametric univariate Wilcoxon-Mann-Whitney (WMW) test, we further reduced variable selection to those continuous variables with a univariate difference ($p < 0.2$) between used and available (Appendix A, Appendix C). As a final step, we used a multi-factor analysis (MFA) to further eliminate categorical and continuous variables. An MFA is an extension of principal component analysis, where several sets of variables (quantitative and/or qualitative) collected from the same or different sets of observations are aggregated into a structured table and given a factor score, providing a summary of variable contribution to the variability in the dataset. As determined by the MFA, five nest site variables were retained: four categorical (patch structure, shrub type, gram type and microtopography) and one continuous (total cover). These variables cumulatively explain 29.3% of the variation of the nesting dataset. The MFA determined six variables explained 27.4% of the variance in the brood rearing site dataset and were retained; these included four categorical (habitat type, shrub type, ground cover and microtopography) and two continuous variables (total cover and canopy height) (Table 2).

We developed candidate Generalised Linear Mixed Models of logistic regression using a priori knowledge and the reduced set of variables for both nest sites and brood sites at the patch-scale (Table 3, Table 4) (Boyce et al. 2002, Manly et al. 2002). We included year and area as random effects in the nesting binomial models; however, because the variance estimates of year and area equaled zero, they were removed and generalized linear models were used instead of generalized mixed models for nest models. Brood rearing mixed effect models also initially included year and area in addition to Hen ID as random effects. Similarly, to the previously discussed nesting models, year and area were unable to explain any variance and were subsequently removed. Hen ID, however, was retained.

2021 **Table 3.** Candidate generalized linear models explaining nest site selection for 52 sharp-tailed
 2022 grouse nesting attempts, at the landscape-scale, in the Klondike Goldfields, Yukon, 2015-2017.

Model Number	Model Structure
1	Microtopography
2	Standing dead + Microtopography
3	Habitat type + Microtopography
4	Ground cover + Microtopography
5	Shrub type + Microtopography
6	Habitat type
7	Habitat type + Ground cover
8	Habitat type +Shrub type
9	Habitat type + Standing
10	Standing,dead + Ground cover
11	Standing,dead + Shrub type
12	Standing,dead
13	Ground cover

2023

Table 4. Candidate generalized linear models explaining brood rearing site selection for 33 sharp-tailed grouse, at the landscape-scale, in the Klondike Goldfields, Yukon, 2016-2017.

Model Number	Model Structure
Model1	Microtopography
Model2	Canopy height + Microtopography
Model3	Habitat type + Microtopography
Model4	Ground cover + Microtopography
Model5	Shrub type + Microtopography
Model6	Total cover + Microtopography
Model7	Habitat type
Model8	Habitat type + Ground cover
Model9	Habitat type + Shrub type
Model10	Habitat type + Total cover
Model11	Habitat type + Canopy height
Model12	Total cover + Ground cover
Model13	Total cover + Shrub type
Model14	Total cover + Canopy height
Model14	Canopy height + Shrub type
Model14	Canopy height + Ground cover
Model15	Total cover
Model16	Ground cover
Model17	Ground cover + Shrub type
Model18	Shrub type
Model19	Habitat type

We used an information theoretic approach to estimate the support for models evaluating habitat selection patterns (Burnham and Anderson 2002). Due to small sample size, ΔQAICc along with Akaike weights (w_i) values were used to rank competing models and select the best approximating model from the group of candidate models given the data (Burnham and Anderson 2002). Only models with $\Delta\text{QAICc} < 2.0$ were considered. All analyses were performed using package lme4 (Bates et al. 2008) in program R (Version 1.0.136 - © 2009-2016 RStudio, Inc.). Manly's standardized habitat selection index was then used to compare habitat selection

for the discrete landscape variables deemed significant (Manly et al. 2002). The index is based on the selection ratio, which is the proportional use divided by the proportional availability of each resource.

Nest dispersal distances were calculated using the Distance Matrix tool in QGIS (Version 2.18.15 – Las Palmas ©). Brood rearing home ranges were estimated using the Kernel density home range estimator with the Animove plugin in QGIS. Only those broods with > 10 relocations were used. Centroids were projected for the home range to estimate distance traveled b broods from nest sites using the centroid and distance matrix tools in QGIS

3.5 RESULTS

3.5.1 Nest Site Habitat Use

The distance between lek and nesting site averaged 1337 ± 177.4 m (range 214.02 – 3654.96 m) (Fig. 4) and did not differ between years ($F = 0.17$, $df = 1$, $p = 0.68$), lek ($F = 1.54$, $df = 3$, $p = 0.23$), hen age ($F = 1.09$, $df = 1$, $p = 0.31$) or body condition ($F = 0.01$, $df = 1$, $p = 0.91$) and was not predictive of clutch size ($F = 0.05$, $df = 1$, $p = 0.83$).

Overall, STGR nested in habitat patches where vegetative cover was relatively homogenous within 250 m of the nest bowl (Appendix A, Appendix B). In the present study nesting sites were in dry, low sloping (<5 degrees) areas, with early successional vegetation that were either open or dominated by low shrubs. With few exceptions, nests were in regions that had been burned within the previous 20 years (Fig. 2, Fig. 3).



Figure 2. Typical nest locations for STGR in Klondike Goldfields (a) at the base of a shrub or tree with an abundance of bunchgrasses and shrub/scrub, (b) in mesic habitats, and (c) in open-dry habitats. Nest bowls are indicated by red circle.

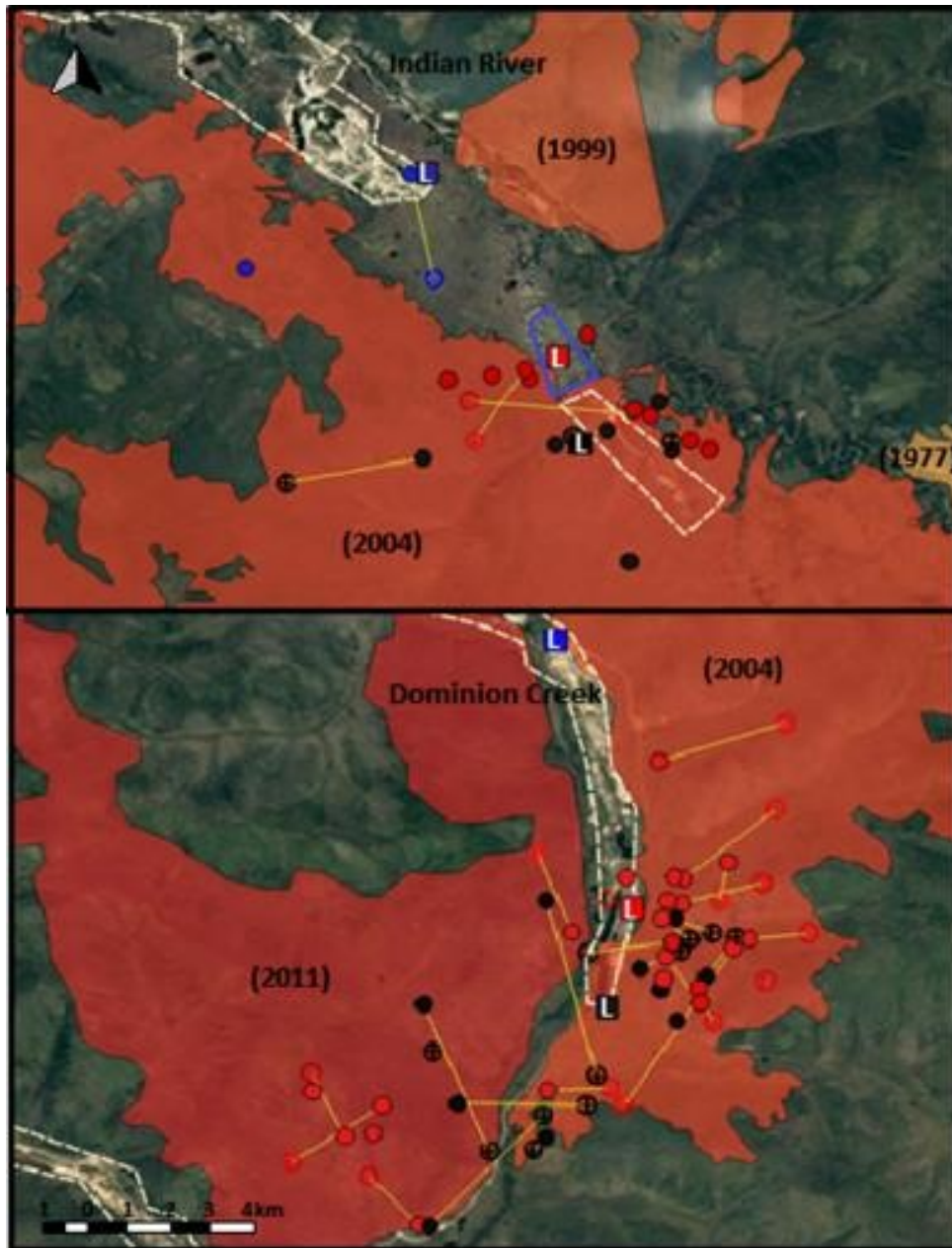


Figure 4. Leks, nest sites, and brood rearing centroids for 33 brood rearing sharp-tailed grouse in the Klondike Goldfields, Yukon, 2015-2017. Leks are identified by squares and the letter “L”, nest sites are circles, and brood rearing centroids (derived from kernel density home range estimations) are circles with a “+” in the center. Each lek in the two study areas, and associated hens and broods, have a unique color (blue, red or black). Yellow lines connect an individual hens’ nesting site with its brood rearing centroid. Recency of burn is indicated by color intensity with year of fire indicated in brackets on the fire polygons. Placer mines are contoured with dashed white lines, and the abandoned farm by a blue line.

Used sites had greater amounts of standing dead vegetation ($71.9\% \pm 5.6$) than available sites, both within 250m of the nest ($58.7\% \pm 5.5$) and within the breeding complex (51.1 ± 6.3);

however, mean canopy height, including standing dead, was lower at nest sites ($6.8\% \pm 1.0\text{m}$) than at available sites. Used sites were characterized by more vegetative cover, but less forbs and graminoids, than available sites. However, the area immediately around nest bowls had more graminoid cover than adjacent available sites. Visual obstruction was higher at used sites than available sites and tended to be highest around the nest bowl (Appendix A), with nests often located at the base of a shrub or small tree, or underneath deadfall (Fig. 2).

The top ranked model included ground cover (graminoid type) and habitat type (representing the merging of variables patch structure and moisture). Of the 13 models, only this one had a $\Delta \text{AIC} < 2$, and had excellent support (W_i 0.859) (Table 5). Bunchgrass was dominant at 100% of used sites but only 40% of available sites ($W_i = 2.50$). Bunchgrass distribution was significantly greater in 2017 ($X = 14.77$, $df = 2$, $p = >0.001$) than in other study years but did not vary between study areas ($X = 4.51$, $df = 1$, $p = 0.05$).

Table 5. Top 5 logistic regression models among 13 candidates assessing the habitat selection of nesting sharp-tailed grouse by comparing nest sites ($n = 52$) and random sites ($n = 208$) at the patch-scale in the Klondike Goldfields, Yukon, 2015-2017. Quasi-Akaike's Information Criterion for small sample sizes, degrees of freedom (df), Log Likelihood (Log(L)), (QAICc), ΔQAICc , and Akaike weights (w_i) are presented for each generalized linear model.

Model #	Model Structure	df	Log(L)	QAICc	ΔQAICc	w_i
fit7	Habitat type + Ground cover	12	-71.582	168.6	0	0.859
fit4	Ground cover + Microtopography	5	-81.099	172.5	3.91	0.122
fit13	Ground cover	3	-87.578	181.3	12.71	0.001
fit10	Standing dead + Ground cover	4	-87.027	182.2	13.68	0.001
fit3	Habitat type + Microtopography	12	-90.344	206.1	37.52	0

During nesting, hens displayed selection for open-dry habitat ($W_i = 6$) and sites dominated by shrub/scrub less than 2 m in height in both wet ($W_i = 6.00$) and dry landscape conditions ($W_i = 3.20$) (Table 1). Habitat selection did not differ significantly with study area ($X = 0.59$, $df = 1$, $p = 0.44$) or study year ($X = 2.18$, $df = 2$, $p = 0.34$). STGR predominately nest in patches with shrub/scrub comprised of soapberry, aspen, willow, scrub birch and rose, in declining order of preference.

3.5.2 Brood Habitat Use

The distance between nest site and brood rearing centroid averaged 1119.20 ± 187.9 m ($n = 33$ hens, Fig. 4) and did not differ by year ($F = 0.08$, $df = 2$, $p = 0.92$), lek ($F = 1.00$, $df = 2$, $p = 0.38$), hen age ($F = 0.620$, $df = 1$, $p = 0.44$), or hen body condition ($F = 1.28$, $df = 1$, $p = 0.27$). This distance between nest site and brood rearing centroid was also unrelated to brood rearing home range size ($F = 1.55$, $df = 1$, $p = 0.23$). Hens with broods remained within 2.2 km of their nest site and within 4 km of their lek throughout the brood rearing period (Fig. 4).

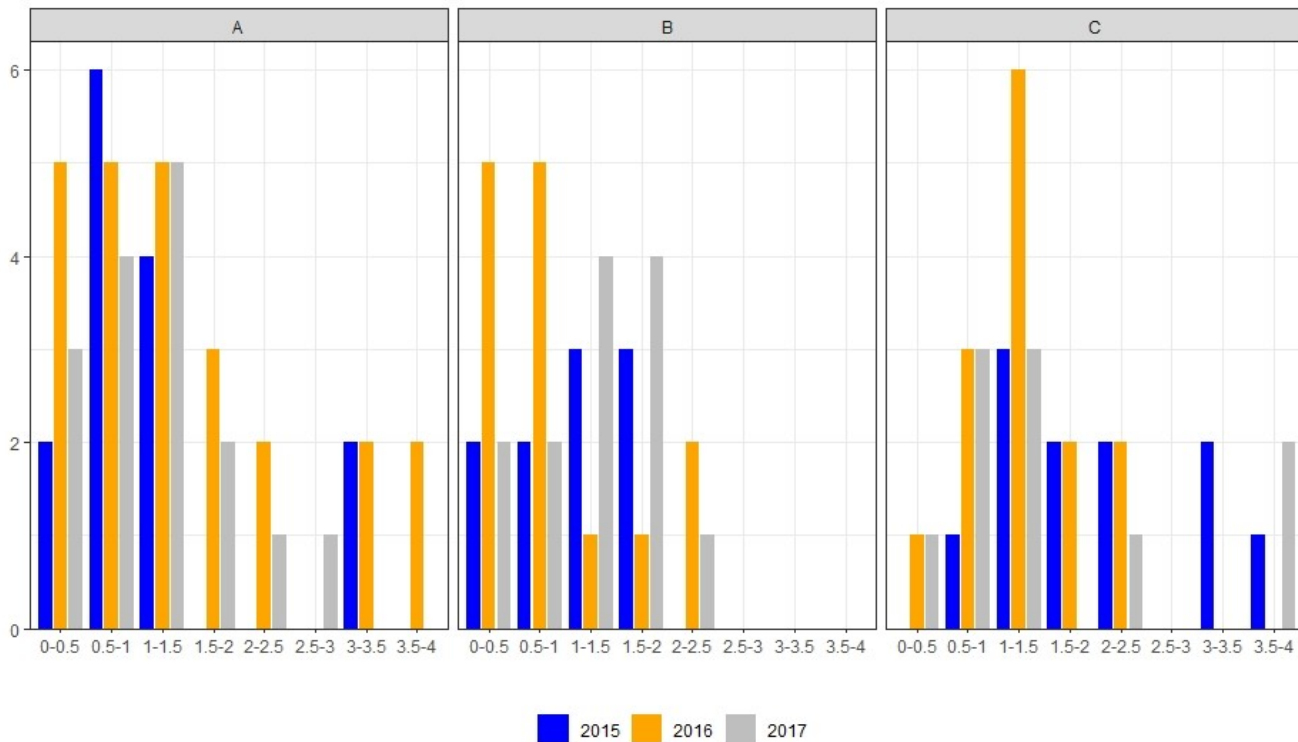


Figure 5. Histogram indicating distance (km) of (a) 52 sharp-tailed grouse nests to the lek of capture, (b) 33 brood rearing centroids to nest sites, and (inset) brood rearing centroids to lek sites, coloured by study year (2015-2017).

Broods were frequently located in recently burned areas of early seral successional stage and shrub/scrub patch structure. Brood rearing locations had 66.8 ± 4.3 standing dead vegetation (fire kill) compared to $30.4\% \pm 5.9$ at available locations in the breeding complex. Brood sites were often located in mesic-sub hydric locations described as low shrub-sedge meadows and, relative to nesting sites, had greater microtopography complexity in the form of earth hummocks. There was little variation between used brood rearing locations and available sites up to 250m, with the exception of marginally greater shrub cover and graminoid cover at used sites. 19 candidate

models were developed using combination of two habitat variables and the reduced form of each of the 6 retained variables. A single model, which included habitat type and total shrub cover, had an $\Delta\text{QAICc} < 2$. There was substantial variation between sites used by broods and sites available to them; overall there was greater habitat complexity and cover at used sites (Appendix C, Appendix D); Hens displayed strong selection for shrub-scrub, and avoidance of non-vegetated, and forest type habitats (Table 2).

Table 6. Top 5 logistic regression models from 19 candidates assessing the habitat selection of 33 brood rearing sharp-tailed grouse by comparing brood rearing sites ($n = 378$) with random sites ($n = 378$) at the landscape-scale in the Klondike Goldfields, Yukon, 2015-2017. Quasi-Akaike's Information Criterion for small sample sizes degrees of freedom (df), Log Likelihood (Log(L)), (QAICc), ΔQAICc , Akaike weights (w_i) are presented for each generalized linear model.

Model #	Model Structure	df	logLik	QAICc	ΔQAICc	w_i
10	Habitat type + Total shrub cover	4	-84.074	176.3	0	1
9	Habitat type + Shrub type	25	-374.226	800	623.7	0
3	Habitat type + Microtopography	16	-399.306	831.3	654.94	0
5	Shrub type + Microtopography	18	-403.048	842.9	666.6	0
17	Ground cover + Shrub type	17	-408.492	851.7	675.4	0

Brood rearing hens selected for shrub sites with greater total shrub cover (80.1 ± 3.6) than available (50.6 ± 4.2) on the landscape. Total shrub cover did not differ between area ($F = 0.02$, $df = 1$, $p = 0.89$) or year ($F = 2.04$, $df = 1$, $p = 0.89$). Within the shrub dominated habitats, those with shrubs less than 2m in height in a dry (xeric-sub mesic) moisture condition were strongly preferred ($W_i = 6.2$; Table 6). Low (38.4 ± 3.7) and medium height shrubs (24.7 ± 3.2) contributed most to total shrub cover at brood rearing sites, while ground (12.4 ± 1.8) tall shrubs (14.3 ± 1.9) were marginally selected against (Appendix C, Appendix D). Broods also demonstrated disproportionate use (29%) of scrub birch and sedge (39%) as compared to their availability (6% and 9% respectively) on the landscape. *Salix* spp. and *Ledum palustre* were also used approximately 30% of the time, but were used proportionally to their availability on the landscape (Table 2).

3.6 DISCUSSION

STGR hens in the present study occupied adjacent, and occasionally overlapping habitats for nesting and brood rearing. The habitat and vegetation characteristics although similar for the two reproductive periods, differed on several key features, exemplifying the importance of a mosaic of habitat types within the breeding complex.

Hens used a variety of sites for nesting, ranging from dry, open uplands to wet or dry shrub/scrub lowlands (Table 1). However, open, dry habitats were rare in this system, representing only 1% of the available habitat and typically in the form of reclaimed mining or agricultural areas.

Overall, we found that the majority of nests in the Klondike Goldfields were composed of a shrub layer providing vertical cover and abundant bunchgrass understory providing horizontal cover (Table 1). The graminoid understory was particularly dense immediately around the nest bowl, as compared to the surrounding habitat. Bunchgrasses have been described as an important habitat component across the STGR range, providing greater habitat complexity than sod forming grasses (Hart et al. 1950, Klott and Lindzey 1989, Meints 1991, Stonehouse et al. 2015). Structurally diverse habitats have been noted to offer greater visual and olfactory concealment from predators while still permitting prey animals to detect an incoming predatory threat (Bergerud and Gratson 1988, Conover 2007). Bunchgrass are also a source of residual cover for nesting prior to the emergence of new, spring vegetation (Bergerud and Gratson (1988), Hart et al. 1952, Prose et al. 2002). The combined importance of vertical and horizontal cover for nesting is supported by research across STGR's range (Roersma 2001, Gratson 1988, Marks and Marks 1987, Giesen 1987), including in northern B.C. where STGR hens nested in shrub-steppe habitats when grasslands were limiting (Goddard 2007). A lack of residual grass cover has been identified as a major contributor to poor nesting success (Meints 1991, Prose et al. 2002). Leupin and Chutter (2007) suggested that STGR declines in British Columbia were, in part, due to a decrease in bunchgrass cover.

Nesting STGR in the Klondike Goldfields did not select for all shrub dominated habitat types equally; those with shrubs less than 2m in height were preferred over taller shrubs and avoidance increased as the successional stage progressed to maturing forest (Table 1) (Raymond 2001, Goddard 2007). Dense stands of tall shrubs provide perches for raptors while limiting a hens' ability to see them (Manzer 2004). Low and medium height shrubs, in addition to serving

as adequate cover, also provide forage for hens, including species such as soapberry (*Shepherdia canadensis*), scrub birch (*Betula glandulosa*), willow (*Salix spp.*) and prickly rose (*Rosa acicularis*) (Table 1) (Paragi et al. 2012). The summer crop contents of necropsied STGR in Alaska were comprised of 50% lowbush cranberry, 14% rose hips, 7% birch leaves and 7% birch catkins (W. B. Sidle, USDA Forest Service, unpublished report). Within the Klondike Goldfields, nesting STGR also preferred low shrubs in wet areas, even though low shrubs in dry areas were equally available STGR in Wisconsin and prairie chickens in Texas nest in wet sites, despite the risk of flooding, possibly because of the reduced number of perches for avian predators and less abundant alternate prey (Svedarsky 1988, Manzer 2004). Potts (1998) observed greater harrier abundance on dry wetland sites than on wet sites. Brady (1984) found mesic sites in the Klondike Goldfields have greater plant species richness and provide greater cover.

Upon hatching STGR hens lead the precocial chicks to nearby brood rearing habitats. The data suggested that brood rearing STGR hens in the Klondike Goldfields selected relatively homogenous patches (up to 250 m). The brood rearing sites had an abundance of shrub cover, and exhibited particular preference for sites with low- and medium-height shrubs and avoidance of bare-ground and tall shrubs. An abundance of tall shrubs, or cover that is too dense, has been shown to reduce the ability of grouse to detect predators (Erikstad and Spidso 1982). Low shrub sites were uncommon in the landscape, representing only 14% of available habitat (Table 2). The use of shrub habitats by brood rearing sharp-tailed grouse differs from findings in northern British Columbia, where broods used habitats dominated by grasses and forbs (Goddard 2007, Klott and Lindzey 1990, Klebenow 1969, Oedekoven 1985), but is similar to results in Alaska, Nebraska and Colorado where STGR brood habitats are characterized by an abundance of shrubs (Raymond 2001, Sisson 1976, Giesen 1987).

While brood rearing hens in this study showed selection for mesic vegetation such as scrub birch and sedges (Table 2), hens with broods also showed a preference for sites classified as dry rather than wet. Selecting this combination of mesic and xeric features may offer the best combination of insect abundance, cover, and thermal comfort (Aldridge and Brigham 2002, Goddard 2007). (Aldridge and Brigham 2002). Brady (1984) found that Mesic sites in the Klondike Goldfields generally had greater plant species richness and higher cover values than dry uplands (Brady 1984) and the higher forb diversity associated with mesic sites has been

shown to positively influence insect abundance and brood occupancy ((Connelly et al. 1998, Giesen and Connelly 1993, Norton 2005, Svedarsky et al. 2003, Aldridge and Brigham 2002, Wachob 1997). Hanson (1953) found that muskeg habitats around James Bay offered an abundance of food for STGR. Moreover, Svedarsky (1988), suggested STGR in Wisconsin used wetlands as a predator avoidance strategy, because of the reduced number of perches for avian predators, and fewer alternate prey inhabiting these habitats. Ammann (1957) suggested that prairie chickens roost in marshes and bogs for protection from foxes, which avoid the moisture, provided that hens can find dry spots within these mesic habitats. Another possible benefit associated with mesic sites is that some sedges, such as cotton grass, form hummocks, which are ideal for concealing chicks without impeding travel. The microhabitats provided by hummocks could be important in providing thermal refugia, cover from predators, and optimal feeding sites (Peach and Zedler 2006, Flake et al. 2010, Norton 2005, Jones 1963).

The distance traveled from lek to nest site or from nest site to brood rearing habitat and home range size during nesting and/or brood rearing have been used as indicators of habitat quality or availability for lekking gallinaceous birds (Giesen 1997). Movement of recently hatched chicks from nest sites to brood rearing habitat is common in gallinaceous birds (Erikstad and Spidso 1982) and chick survival has been shown to decline as distance travelled increases (Goddard 2007), presumably because travelling reduces time spent foraging and increases risk of predation (Goddard 2007, Erikstad and Spidso 1982). Average movements from nest sites to brood rearing areas were reported by Meints (1991) and Boisvert et al. (2005) as 0.6 km and 0.4 km, respectively. Collins (2004) found an average distance travelled by broods of 0.8 km; however, he reported some unusually long movements (>3.5 km) to brood rearing sites, possibly due to drought conditions. The distances travelled by hens with broods in the current study (1119.2 ± 187.9 m) are longer than previously reported. Because females select nest sites within or immediately adjacent to suitable brood rearing habitat (Goddard 2007), brood rearing and nesting habitat may be limiting in this system. Furthermore, anthropogenic structures that fragment the landscape could isolate or increase the mortality rate of chicks travelling to brood rearing habitats (Aldridge and Brigham 2002). Reproductive home ranges were recorded as 69 ha in Alberta (Roersma 2001), 100 ha in Colorado (Giesen 1987), and 190 ha in Idaho (Marks and Marks 1987). Our estimate of $163.0\% \pm 52.8$ ha 95 kernel density home ranges was for the brood rearing period only, whereas the aforementioned studies included both nest sites and brood

rearing locations. The larger home ranges observed in our study could be a further indication of subprime or limited amount of habitat. Ryan et al. (1998) demonstrated that prairie chicken broods have smaller home ranges and higher survival in large contiguous grasslands than in a prairie–mosaic landscape.

Although topographic features such as slope, elevation and aspect were not shown to be selected for nesting or brood rearing STGR in this study, they are often inter-related with successional stage and habitat types. Goddard (2007) determined there was regional variation in selection for elevation dependent on availability of suitable habitat. In the Klondike Goldfields, forested habitat is more common at low elevations and shrub/scrub is more common at higher elevations. In some upland habitats, scrub birch may represent a climax community. Kojima and Brooke (1986) reported that scrub birch is common on moderately to well-drained habitats near and above treeline, but is gradually replaced by *Salix* spp. in more moist habitats near the base of slopes or valley bottoms, where willow may completely dominate the vegetation.

3.7 MANAGEMENT IMPLICATIONS

Reproducing STGR hens in Yukon use open, dry habitat when available, but also readily use a mosaic of shrub-bunchgrass and shrub-sedge meadows. Open habitats are rare in this study area. Such habitats may occur temporarily in the wake of a forest fire. Disturbances, such as fire, are important in preventing forest encroachment, and creating and maintaining suitable STGR habitat (Connelly et al. 1998). Although disturbances may be important in maintaining STGR habitat, Gratson (1988) found hens did not nest in areas until four years after a fire had passed. As the successional stage progresses the local population may increase in abundance, until conditions are no longer favourable to STGR, as high shrubs begin to dominate, and forest encroachment occurs. The regular and relatively short fire interval of the Klondike Goldfields may create the ideal open habitat or shrub dominated conditions for temporary population expansions (Oswald and Brown 1990, Rowe et al. 1974). For the northernmost populations of STGR, wet shrub meadows may provide long-term seral habitat alternatives to the grasslands, parklands and shrub-steppe habitat critical to southern populations of reproducing STGR (McKenna 2018). Shrub-sedge meadow complexes have been identified as STGR habitat in northern B.C., northern Ontario and Yukon (Hanson 1953, Mossop et al. 1979, Ritcey 1995). I

hypothesize that wet shrub meadows are attractive breeding areas for STGR in Yukon provided there is an abundance of dry sites dispersed amongst the biologically productive moist sites. Moisture regimes can be influenced by topography, hydrology and vegetation. Naturally occurring (fire, succession, flooding, changes in hydrology, climate change) or anthropogenic disturbances (trenching, regrading, drainage alteration, vegetation disturbance, vehicles) could alter the hydrology of the region (McKenna 2018). The low shrub wet meadows may provide long-term habitat alternatives to burns, and provide source populations for the temporary expansion into recently disturbed areas.

Non-vegetated sites in this study were mostly anthropogenically disturbed sites. Revegetated tailings piles or agricultural fields were the primary lekking grounds in this study region. STGR may be attracted to these open habitats but may also be disturbed by human activity that occurs there. However, there was strong avoidance by nesting and brood rearing hens of sites bare of vegetation, such as placer tailings, regardless of time since disturbance (Table 1, Table 2). While studying reclamation techniques in the Klondike Goldfields, Brady (1984) found that land disturbed by mining is initially sterile, devoid of seed and vegetative material, and is slow to recover. Although several brooding hens used gravel road ditches, and others crossed roads, only one hen successfully crossed an active mining site with a brood. Without proper reclamation techniques, mined sites may take much longer to revegetate to a stage suitable for breeding STGR than rates of succession following natural disturbance. In addition to eliminating available habitat for reproducing STGR, placer mining may be increasing habitat fragmentation and reducing habitat connectivity in this landscape.

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3.9 APPENDICES

Appendix A. Comparisons (mean \pm SE) between continuous variables collected at 52 nest sites and paired random locations collected at three scales. Variables in gray denote variables with correlation $r > 0.5$. Continuous variables with WMW p-values < 0.2 for the patch-scale were retained for further consideration in multi-factor analysis.

Variables	Used nest bowl (microsite) n = 52	Available microsite n = 416	Used Site 30 m radius around lek n = 52	Available site 30-250 m of nest bowl n = 52	Available patch 4 km radius of lek n = 208	p
Dist. to edge (m)	na	na	115.8 \pm 19.6	80.1 \pm 12.1	119.3 \pm 15.6	0.374
Elevation (m)	na	na	570.7 \pm 11.4	575.0 \pm 11.8	698.2 \pm 6	0.068
Slope (%)	na	na	4.9 \pm 0.7	4.0 \pm 0.6	6.5 \pm 0.9	0.051*
Patch VOR1 (%)	83.9 \pm 2.6	65.7 \pm 4.0	75.1 \pm 2.4	69.6 \pm 3.4	na	na
Patch VOR2 (%)	59.3 \pm 3.6	38.3 \pm 4.0	49.5 \pm 2.7	41.5 \pm 3.4	na	na
Patch VOR3 (%)	41.2 \pm 3.7	26.6 \pm 4.0	37.4 \pm 2.7	30.2 \pm 3.2	na	na
Patch VOR4 (%)	27.9 \pm 3.4	21.4 \pm 4.0	29.4 \pm 2.4	23.4 \pm 2.7	na	na
Patch VOR5 (%)	21.3 \pm 3.2	17.3 \pm 3.0	24.0 \pm 2.1	19.2 \pm 2.4	na	na
VOR low (%)	28.2 \pm 1.3	21.8 \pm 1.7	25.9 \pm 1.2	22.5 \pm 1.4	na	na
VOR max (%)	31.6 \pm 1.3	23.4 \pm 1.7	28.6 \pm 1.2	25.5 \pm 1.5	na	na
Ground shrub (%)	na	na	23.7 \pm 3.9	23.0 \pm 3.7	24.5 \pm 3.9	0.301
Low shrub (%)	na	na	23.8 \pm 3.1	25.1 \pm 3.6	24.7 \pm 3.8	0.091*
Mid shrub (%)	na	na	24.1 \pm 3.5	22.9 \pm 3.2	14.7 \pm 2.7	0.860
High shrub (%)	na	na	21.0 \pm 3.2	18.5 \pm 2.9	18.7 \pm 3.7	0.199*
Gram (%)	40.7 \pm 4.5	27.90 \pm 4.02	23.8 \pm 2.1	25.0 \pm 2.6	39.2 \pm 5.3	<0.001*
Forbs (%)	10.1 \pm 2.0	12.23 \pm 1.84	12.3 \pm 1.8	11.1 \pm 1.5	20.5 \pm 3.7	0.380
Total cover (%)	82.7 \pm 3.5	64.13 \pm 4.88	79.8 \pm 3.9	61.2 \pm 5.1	56.0 \pm 4.6	<0.001*
Litter (%)	29.6 \pm 3.6	29.02 \pm 4.23	39.3 \pm 3.7	30.4 \pm 3.4	27.7 \pm 3.2	<0.001*
Deadfall (%)	na	na	14.7 \pm 1.9	12.3 \pm 1.7	18.2 \pm 2.9	0.255
Standing dead (%)	na	na	71.9 \pm 5.6	58.7 \pm 5.5	51.1 \pm 6.3	<0.001*
Canopy height (m)	na	na	6.8 \pm 1.0	8.7 \pm 1.7	9.1 \pm 1.0	0.528

Appendix B. Relative proportion of the full set of used and available categorical variables collected at 52 nest sites and random locations at the site and patch scales. Variables in gray denote variables with correlation $r > 0.5$. All categorical variables were retained for further consideration in multi-factor analysis.

	Variable	Proportion	Site Proportion	Patch Proportion
Microtopography	No hummocks	0.26	0.26	0.63
	Few hummocks	0.50	0.44	0.22
	Many hummocks	0.24	0.30	0.15
Moisture	Xeric	0.24	0.20	0.15
	Submesic	0.24	0.16	0.32
	Mesic	0.36	0.32	0.32
	Subhydric	0.10	0.20	0.05
	Hydric	0.06	0.08	0.06
	Hygric	0.00	0.04	0.10
CWD	Class 1	0.30	0.26	0.46
	Class 2	0.50	0.40	0.29
	Class 3	0.20	0.30	0.14
	Class 4	0.00	0.04	0.09
	Class 5	0.00	0.00	0.02
CWD Size	Small	0.50	0.02*	0.57
	Medium	0.50	0.60*	0.38
	Large	0.00	0.38*	0.05
Patch Structure <i>Factor</i>	Non-vegetated	0.00	0.04	0.09
	sparse	0.00	0.02	0.00
	Herb	0.08	0.06	0.03
	Shrub/scrub<2m	0.50	0.46	0.09
	Shrub/scrub>2m	0.28	0.16	0.34
	Edge	0.02	0.04	0.03
	Pole sapling	0.04	0.10	0.13
	Aspen	0.06	0.04	0.09
	Mature coniferous	0.00	0.02	0.06

	Mixed forest	0.02	0.04	0.14
	Agricultural field	0.00	0.02	0.00
	Grassland	0.00	0.00	0.02
Successional stage	Non-vegetated	0.00	0.04	0.09
	Pioneer seral	0.22	0.14	0.26
	Young seral	0.66	0.68	0.28
	Maturing seral	0.10	0.12	0.06
	Overmature seral	0.00	0.00	0.14
	Young climax	0.00	0.00	0.07
	Maturing climax	0.02	0.02	0.09
	Overmature climax	0.00	0.00	0.01
	Disclimax	0.00	0.00	0.00
Aspect	North	0.22	0.16*	0.15
	East	0.10	0.08*	0.15
	South	0.22	0.30*	0.12
	West	0.14	0.12*	0.10
	None	0.32	0.34*	0.47
Gram Type	None	0.00	0.00	0.09
	Bunchgrass	1.00	0.700	0.66
	Sod grasses	0.00	0.10	0.32
	Sedge/rushes	0.00	0.20	0.19
Shrub Type	None	0.00	0.00	0.16
	<i>Salix sp.</i>	0.42	0.47	0.13
	<i>Betula glandulosa</i>	0.16	0.14	0.10
	<i>Ledum palustre</i>	0.18	0.16	0.20
	<i>Rosa acicularis</i>	0.02	0.03	0.02
	<i>Chamaedaphne</i>	0.08	0.08	0.11
	<i>Shepherdia canadensis</i>	0.04	0.02	0.01
	<i>Populus tremuloides</i>	0.10	0.08	0.03
	<i>Rubus pubescens</i>	0.00	0.00	0.01
	<i>Arctostaphylos</i>	0.00	0.00	0.02
	<i>Vaccinium uliginosum</i>	0.00	0.00	0.02

Appendix C. Comparisons (mean \pm SE) between 15 continuous variables collected at 378 brood rearing locations and 378 random locations at the patch-scale. Variables in gray denote variables with correlation $r > 0.5$. Continuous variables with WMW p-values < 0.2 .

Variables	Used Site 30m radius around lek n = 36	Site Available <250m of nest Mean \pm SE n = 36	Patch Available 4 km radius of lek n = 36	p
Elevation	598.1 \pm 8.7	573.0 \pm 15.0	570.6 \pm 10.0	< 0.001*
Slope	4.9 \pm 0.6	6.6 \pm 0.7	3.7 \pm 0.7	0.121*
Dist.edge	85.5 \pm 8.8	73.9 \pm 7.3	85.4 \pm 15.0	0.001*
Tot.shrub.cover	80.1 \pm 3.6	76.6 \pm 4.4	50.6 \pm 4.2	< 0.001
Ground.shrub	12.4 \pm 1.8	13.3 \pm 2.0	17.9 \pm 2.6	0.194*
Low.shrub	38.4 \pm 3.7	34.2 \pm 4.1	16.0 \pm 2.5	< 0.001
Med.shrub	24.7 \pm 3.2	18.4 \pm 2.2	16.5 \pm 3.3	0.0419*
High.shrub	14.0 \pm 1.9	7.8 \pm 1.1	21.5 \pm 3.8	< 0.001*
Canopy.height	4.5 \pm 0.5	4.7 \pm 0.5	6.5 \pm 0.8	< 0.001*
Gram.cover	42.0 \pm 4.3	35.8 \pm 4.6	41.0 \pm 4.0	0.0741*
Forb.cover	14.3 \pm 1.7	16.0 \pm 2.1	22.4 \pm 3.0	0.883
Crypt.cover	55.4 \pm 5.5	51.9 \pm 5.5	33.7 \pm 5.8	0.085*
Deadfall	21.8 \pm 2.4	19.7 \pm 2.6	15.6 \pm 3.4	< 0.001*
standing.dead	66.8 \pm 4.3	64.8 \pm 5.2	30.4 \pm 5.9	< 0.001*
Litter	29.7 \pm 3.8	36.5 \pm 4.3	42.3 \pm 4.6	0.057*

Appendix D. Relative proportion of each level for 8 categorical variables collected at 378 brood rearing locations and 378 random locations at the landscape-scale. Variables in gray denote variables with correlation $r > 0.5$. All categorical variables at the patch-scale were retained for further consideration in multi-factor analysis.

Variable		Site Used n = 378	Site Available	Patch Available
Microtopography	No Hummocks	0.22	0.22	0.68
	Few Hummocks	0.38	0.37	0.18
	Many Hummocks	0.40	0.41	0.13
Moisture	Xeric	0.22	0.21	0.18
	Submesic	0.41	0.33	0.37
	Mesic	0.23	0.29	0.26
	Subhydric	0.11	0.13	0.04
	Hydric	0.02	0.00	0.06
	Hygric	0.01	0.00	0.09
CWD	Class 1	0.34	0.30	0.52
	Class 2	0.30	0.31	0.22
	Class 3	0.27	0.30	0.15
	Class 4	0.08	0.09	0.09
	Class 5	0.00	0.00	0.01
Patch Structure	Non-vegetated	0.00	0.00	0.09
	sparse	0.01	0.01	0.00
	Herb	0.00	0.00	0.01
	Shrub/scrub<2m	0.46	0.52	0.10
	Shrub/scrub>2m	0.44	0.42	0.30
	Edge	0.02	0.01	0.04
	Pole sapling	0.01	0.01	0.11
	Aspen	0.03	0.01	0.13
	Mature coniferous	0.03	0.02	0.10
	Mixed forest	0.01	0.01	0.08
	Agricultural field	0.00	0.00	0.00
	Grassland	0.00	0.00	0.03
Successional stage	Non-vegetated	0.00	0.00	0.09
	Pioneer seral	0.22	0.22	0.23
	Young seral	0.68	0.72	0.26
	Maturing seral	0.03	0.03	0.14
	Overmature seral	0.01	0.01	0.05

	Young climax	0.01	0.01	0.06
	Maturing climax	0.03	0.02	0.16
	Overmature climax	0.01	0.00	0.01
	Disclimax	0.00	0.00	0.00
Aspect	North	0.37	0.18	0.12
	East	0.28	0.18	0.16
	South	0.03	0.03	0.12
	West	0.02	0.08	0.12
	None	0.31	0.53	0.48
Gram Type	None	0.02	0.01	0.21
	Bunchgrass	0.35	0.34	0.48
	Sod grasses	0.24	0.25	0.22
	Sedge/rushes	0.39	0.41	0.09
Shrub Type	None	0.01	0.01	0.11
	<i>Salix sp.</i>	0.33	0.29	0.26
	<i>Betula glandulosa</i>	0.29	0.30	0.06
	<i>Ledum palustre</i>	0.30	0.27	0.26
	<i>Rosa acicularis</i>	0.05	0.13	0.02
	<i>Chamaedaphne</i>	0.00	0.00	0.05
	<i>Shepherdia canadensis</i>	0.00	0.00	0.02
	<i>Populus tremuloides</i>	0.01	0.01	0.04
	<i>Rubus pubescens</i>	0.00	0.00	0.00
	<i>Arctostaphylos uva-ursi</i>	0.00	0.00	0.05
	<i>Vaccinium Oxycoccos</i>	0.00	0.00	0.00
	<i>Scrub Picea mariana</i>	0.00	0.00	0.01
	<i>Alnus sp.</i>	0.00	0.00	0.00
	<i>Betula nana</i>	0.00	0.00	0.08
	<i>Vaccinium uliginosum</i>	0.02	0.01	0.03

CHAPTER 4. GENERAL CONCLUSIONS

The goal of this thesis research was to describe the nesting and brood rearing ecology of a northern population of Sharp-tailed Grouse (STGR), and to examine patterns and sources of variation in their habitat use including the impacts of mining and fire history. My findings support previous research that identified the adaptability of STGR to exploit a variety of habitats across its range (Hanson 1953). While results suggest STGR in this region currently have high rates of survival and reproductive success, identifying the form and extent of habitat protection needed to ensure the future viability of STGR in this region remains challenging. The current research has helped to characterize the importance, scale, and inter-relatedness of three major impacts-mining activity, fire history, and predators – on STGR survival and reproductive success in the Klondike Goldfields.

STGR can tolerate a moderate degree of habitat disturbance and have, in some systems, been observed using and benefiting from anthropogenic habitats (Connelly et al. 1998, Stinson and Schroeder 2012). In most cases, however, anthropogenic activities have had negative impacts, including reduced survival rates, avoidance of noise and infrastructure, increased collisions, and reduced lek attendance (Hovick 2015, Harju et al. 2010, Hagen et al. 2011).

Bare-ground habitats that characterize active placer mining sites are avoided by nesting and brood rearing STGR, but their survival and breeding success did not vary with distance from current or past placer mining disturbance (Chapter 3). Because most mining disturbances occurred prior to the study period, variation in survival and reproductive success resulting from anthropogenic activities may have occurred prior to the onset of this study. Avoidance of bare-ground may force STGR into marginal habitats where their reproduction and survival may be compromised (Connolly 2001, Hagen 2010), suggesting that scale, cumulative impacts, and configuration could reach a threshold at which population collapse occurs. Although, surface mining displaces STGR in the short-term, appropriate reclamation techniques could result in habitats that are highly attractive to STGR in the long-term (Boisvert 2002, Collins 2004). While studying reclamation techniques in the Klondike Goldfields, Brady (1984) found that land disturbed by mining is initially sterile, devoid of seed and vegetative material, and is slow to recover. Although, surface mining displaces STGR in the short to medium-term, eventual vegetation succession on disturbed sites may create early succession habitats that are highly suitable for successful STGR reproduction (Boisvert 2002, Collins 2004). However, long

latencies between disturbance and vegetation establishment combined with breeding site fidelity of STGR, may limit the capacity of STGR to successfully exploit these windows of opportunity, especially if, following initial growth of vegetation, successional proceeds more rapidly.

Fire history and patterns of post-fire vegetation succession are important drivers of STGR habitat use and reproductive success in the Klondike Goldfields. The regular occurrence of small wildfires (roughly 25-year intervals) in the Klondike Goldfields, as compared to surrounding regions, has resulted in a mosaic of habitat types, and ideal early successional habitats for STGR reproductive range. The commonality of fire created habitats through this region may permit temporary population expansions from sedge-meadow habitats into neighbouring, recently burned areas (Connolly 2001, Mossop et al. 1979).

The dynamic relationship between fire followed by succession suggests that these small populations require large tracts of relatively undisturbed land to transition to novel areas when old areas become inadequate (Bergerud 1988, Johnsgard 1983). These natural dynamics of disturbance and succession may cause prime breeding habitat to move around the landscape. Prime lek locations may also move around the landscape as males attempt to intercept females next to the highest quality nesting and brood-rearing habitat (Akçakaya et al. 2004). Due to the dynamic relationship between fire history and breeding habitat, it is likely that the area required for successful STGR reproduction has been underestimated (Hovick et al. 2015). Further investigation of the temporal dynamics with which STGR colonize, occupy, and abandon fire impacted habitats according to their successional stage is required for northern landscapes.

These results suggest that STGR cannot persist on small, isolated tracts of native habitat. The protection and, if necessary, the production of large scale early successional habitat in heterogenous landscapes should be a priority. Management should focus on identifying low sloping, moist shrub/scrub meadows, which provide habitat for long term-viable populations of STGR, while maintaining heterogenous hydrology and microtopography.

Modification of habitat that alters cover, reduces insect abundance, increases predator abundance or degrades habitat could have dramatic impacts on STGR reproductive phenology and population viability. Activities within nesting habitat should be avoided until incubation has reached the estimated mid-point to reduce the risk of nest abandonment. Connectivity between brood and nesting habitats should be maintained; specifically, having the entire known lekking complex bisected with developments is likely to impede brood mobility and impact survival.

Artificial augmentation of predator densities can be avoided or minimized by reducing wildlife attractants, such as garbage and artificial perches (dredges, powerlines, tall buildings), particularly those that may attract corvids and generalist mammalian predators such as bears, foxes and coyotes. In some cases, prescribed burning might be considered as a management tool that could help to avoid or mitigate the negative impacts of active or planned anthropogenic activities on STGR (Hovick 2015). Sufficient habitat should be managed to permit population home ranges to shift in response to the successional stage of the landscape. Such an approach would ensure there are source populations available for temporary expansion when suitable habitat becomes available. Re-seeding native herbaceous understory should be a priority; bunchgrasses should be favored over sod-forming grasses in xeric-sub mesic sites, and sedge grasses in mesic sites.

Resource extraction in the Klondike Goldfields is a major economic driver for the Yukon Territory that has the potential to negatively impact wildlife and wildlife habitat, which are also highly valued by Yukoners. Accordingly, placer mining creates land use trade-offs and challenges to local, regional and territorial stakeholders. The study findings presented here advance our understanding of the phenological events, space use and habitat selection of an isolated populations of a lekking bird species in a resource development region. Better scientific understanding of STGR in the Yukon, including their habitat needs and tolerance to disturbance; will enable wildlife managers and land-use planners to implement evidence-based conservation and mitigation strategies. Nevertheless, these findings are restricted to a particular spatial, temporal and methodological extent, and long-term protection and viability of prairie-grouse in the north requires continued research on community dynamics, particularly in the face of climate change. Management planning and implementation need to occur at ecologically meaningful scales, and the necessary scale can vary over time, from region to region, and among different ecological processes.

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