

Calf Survival of Woodland Caribou in a Multi-Predator Ecosystem

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ABSTRACT

The proximate role of predation in limiting caribou (*Rangifer tarandus*) populations is well documented, but the long-term effects of predation pressure on selection of calving areas and the subsequent impacts to calving success remain unclear. We examined the relationships among calf survival, predation risk, and vegetation characteristics among 3 calving areas and across spatial scales in the Besa-Prophet River drainage of northern British Columbia. Fifty woodland caribou (*R. t. caribou*) neonates were collared and monitored twice daily for the first month and once weekly during the next month of life in 2 summer field seasons (2002 and 2003). Predation risk was estimated using resource selection functions (RSFs) from Global Positioning System (GPS) locations of 15 grizzly bears (*Ursus arctos*) and 5 gray wolf (*Canis lupus*) packs. The Normalized Difference Vegetation Index (NDVI) derived from Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM) data were used to quantify large-scale characteristics of vegetation (indices of biomass and quality). We incorporated small- and large-scale characteristics (i.e., predation risk, vegetation, and movement of woodland caribou calves) of neonatal calving sites into logistic regression models to predict survival for the calving (25 May–14 Jun) and summer (15 Jun–31 Jul) seasons. Predation risk and vegetation characteristics were highly variable among calving areas and calving sites, and parturient woodland caribou responded to these characteristics at different scales. Minimizing gray wolf risk and selecting against areas of high vegetation biomass were important at large scales; areas with high biomass were likely associated with increased predation risk. Calving in areas high in vegetation quality was important across scales, as parturient woodland caribou took higher levels of predation risk to access areas of high vegetative change. Models using small-scale characteristics of calving sites to predict survival performed better in the calving season than in summer. Large-scale characteristics predicted survival of woodland caribou neonates better in summer than in the calving season, probably in part because of the unexpected role of wolverines (*Gulo gulo*) as the main predator of woodland caribou calves during calving. Gray wolves were the main cause of mortality during the summer. Movement away from calving sites corresponded to higher calf survival and appeared to be in response to increased access to forage during the peak demands of lactation and/or minimizing gray wolf risk in the summer. High variation in predation risk and vegetation attributes among calving areas and at calving sites within calving areas, with no differences in calf mortality related to that variation, illustrates the importance of behavioral plasticity as a life-history strategy for woodland caribou.

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KEY WORDS

calving, GIS, mortality, NDVI, predation risk, *Rangifer tarandus* caribou, remote sensing, scale, survival, trade-off, woodland caribou.

Sobrevivencia de Crías de Caribú de Bosque en un Ecosistema con Depredadores Multiples

RESEMEN

El papel directo de la depredación en la limitación de las poblaciones del caribú (*Rangifer tarandus*) está bien documentado, pero los efectos a largo plazo de la presión de depredación sobre la selección de las áreas de crianza y de los impactos subsecuentes sobre el éxito de la crianza son aún confusos. Hemos examinado las relaciones entre la sobrevivencia de las crías, riesgo de depredación, y características de la vegetación en 3 áreas de crianza y a diferentes escalas espaciales en la cuenca del río del Besa-Prophet, en el norte de la Columbia Británica. Cincuenta recién nacidos de caribú de bosque (*R. t. caribou*) fueron dotados de collares de telemetría y monitoreados dos veces al día en el primer mes y semanalmente durante el mes de vida siguiente en dos temporadas de campo estivales (2002 y 2003). El riesgo de depredación fue estimado a través de funciones de selección de recursos (RSFs) con coordenadas de sistema de posición global (GPS) de 15 osos grizzly (*Ursus arctos*) y 5 manadas de lobos grises (*Canis lupus*). El índice de vegetación de diferencias normalizadas (NDVI) derivado del Landsat Thematic Mapper (TM) y Enhanced Thematic Mapper (ETM) fue utilizado para cuantificar características a gran escala de la vegetación (índices de biomasa y calidad). Incorporamos características a pequeña y gran escala (o sea, riesgo de depredación, vegetación, y movimiento de las

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crías de caribú de bosque) de sitios de parto en modelos de regresión logística para predecir la sobrevivencia en las estaciones de crianza (25 de mayo a 14 de junio) y de verano (15 de junio a 31 de julio). Las características de riesgo de depredación y de vegetación fueron altamente variables entre áreas de crianza y sitios de parto, y el caribú de bosque parturiente respondió a estas características a escalas diferentes. La minimización del riesgo de lobos grises y la selección en contra de áreas con biomasa elevada fueron importantes a grandes escalas; las áreas de biomasa alta fueron probablemente asociadas con un riesgo de depredación mayor. La crianza en áreas con alta calidad de vegetación fue importante a toda escala, dado que el caribú de bosque parturiente aceptó riesgos de depredación mayores para ganar acceso a áreas de alto cambio vegetativo. Los modelos basados en características de pequeña escala de los sitios de parto dieron mejores resultados en la estación de crianza que en el verano. Las características de gran escala predijeron la sobrevivencia de los recién nacidos de caribú de bosque mejor en verano que en la estación de crianza, probablemente en parte debido al papel inesperado de los wolverines (*Gulo gulo*) como el depredador principal de las crías de caribú de bosque durante la crianza. Los lobos grises fueron la causa principal de mortalidad durante el verano. El movimiento hacia fuera de los sitios de parto correspondió a una sobrevivencia más alta de las crías y pareció ser en respuesta a mayor acceso al forraje durante las demandas máximas de la lactancia y/o a la minimización del riesgo de lobos grises en el verano. La alta variabilidad en riesgo de depredación y atributos vegetacionales entre áreas de crianza, y en sitios de parto dentro de áreas de crianza, sin diferencias en mortalidad de las crías relacionadas con esa variabilidad, ilustra la importancia de la plasticidad de comportamiento como estrategia de historia de vida para el caribú de bosque.

Survie des Nouveaux-Nés de Caribou des Bois dans un Écosystème de Plusieurs Prédateurs

RÉSUMÉ

Le rôle proximal de la prédation sur la limitation des populations du caribou (*Rangifer tarandus*) est bien documenté, mais les effets à long terme de la pression de prédation sur la sélection des aires d'élevage et les impacts subséquents pour le succès du vêlage sont moins bien connus. Nous avons examiné les relations entre la survie des jeunes caribous, le risque de prédation, et les caractéristiques de la végétation dans 3 aires d'élevage, à différentes échelles spatiales, dans le système des rivières Besa et Prophet au nord de la Colombie-Britannique. Cinquante caribous des bois (*R. t. caribou*) nouveaux-nés ont été suivis à l'aide de colliers de télémétrie deux fois par jour pour le premier mois et une fois par semaine le second mois de vie, durant 2 saisons d'été (2002 et 2003). Le risque de prédation a été estimé utilisant des fonctions de sélection de ressources (RSF) provenant des localisations basées sur le système de positionnement global (GPS) de 15 ours grizzlis (*Ursus arctos*) et 5 meutes de loups gris (*Canis lupus*). L'indice de végétation par différence normalisée (NDVI), dérivé de données provenant du Landsat Thematic Mapper (LTM) et du Enhanced Thematic Mapper (ETM), a été utilisé pour quantifier les caractéristiques de la végétation à grande échelle (indices de biomasse et de qualité de végétation). Nous avons incorporé les caractéristiques à fine et grande échelle (i.e. risque de prédation, végétation, et déplacement des jeunes caribous) des sites de mise bas des nouveaux-nés dans des modèles de régression logistiques pour prédire leur survie durant la saison du vêlage (25 Mai–14 Juin) et durant l'été (15 Juin–31 Juillet). Le risque de prédation et les caractéristiques de la végétation étaient très variables parmi les aires d'élevage et les sites de mise bas, et des caribous des bois parturients réagissent à ces caractéristiques à différentes échelles. La diminution du risque provenant du loup gris, et la sélection d'aires loin de la concentration de la biomasse, étaient importants à grande échelle; les aires avec une grande quantité de biomasse étaient associées possiblement avec une augmentation du risque de prédation. Le vêlage dans les aires avec végétation de grande qualité était important à toutes les échelles, puisque les caribous des bois parturients ont pris de plus grand risque de prédation pour avoir accès à cette végétation de grande qualité. La performance des modèles utilisant les caractéristiques à fine échelle des sites de mise bas pour prédire la survie était meilleure pour la saison du vêlage que durant l'été. Les caractéristiques à grande échelle prédisaient mieux la survie des nouveaux-nés de caribou des bois durant l'été que durant la saison de mise bas, en partie à cause du rôle des carcajous (*Gulo gulo*) comme prédateur majeur des jeunes caribou durant la saison de mise bas. Le loup gris représentait la principale cause de mortalité durant l'été. Séloigner des sites de mise bas correspondait à une meilleure survie pour les jeunes caribous et semble être en réponse à un meilleur accès aux plantes de fourrage durant les demandes accrues, due à la lactation et/ou pour minimiser le risque de prédation par le loup gris durant l'été. La grande variation dans le risque de prédation et des attributs de végétation dans les aires d'élevage et les sites de mise bas parmi les aires d'élevage, sans différences notées dans la mortalité des jeunes reliées à cette variation, illustre l'importance de la plasticité du comportement, comme stratégie de survie pour le caribou des bois.

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INTRODUCTION

Predation risk is an important component of understanding foraging strategies and habitat selection (Lima and Dill 1990, Sweitzer 1996, Rachlow and Bowyer 1998, Kie 1999, Grand 2002, Ben-David et al. 2004). For animals to maximize reproductive success, they often make trade-off decisions between predation risk and securing adequate forage to meet nutritional demands (Sweitzer 1996, Bowyer et al. 1998a, Rachlow and Bowyer 1998, White et al. 2001, Ben-David et al. 2004). Trade-offs are dependent on biological (e.g., nutritional condition, reproductive status, age; Berger and Cunningham 1988, Sweitzer 1996, Rachlow and Bowyer 1998, Barten et al. 2001, White et al. 2001, Ben-David et al. 2004), environmental (e.g., heterogeneity of vegetation on the landscape, densities and/or distribution of other prey species and predators; Bergerud et al. 1984, Seip 1991, Kie 1999, Altendorf et al. 2001), and/or social variables (e.g., group size, gregariousness, status; Lima and Dill 1990, Molvar and Bowyer 1994, Hebblewhite and Pletscher 2002, Miller 2002). Actual or perceived predation risk may alter species-specific foraging strategies (Krebs 1980, Lima and Dill 1990). Reproductive females within a species may be the most sensitive to foraging in high-risk habitats because of the susceptibility of neonates to predators (Bergerud et al. 1984, Bleich et al. 1997, Bowyer et al. 1998a, Rachlow and Bowyer 1998, Miller 2002, Ben-David et al. 2004). Both sexes of a species must ensure that body reserves are sufficient for breeding and overwinter survival, but females must also secure adequate energy and protein inputs to meet the additional demands of gestation and lactation and to minimize predation risk to themselves and their offspring.

Reproductive strategies for females are most certainly directed by ecological, behavioral, and environmental patterns within short-term, small-scale selection and long-term, larger-scale life histories. Ungulate species differ in reproductive capacities (pregnancy rates, fetal and/or twinning rates), how they spatially segregate and select rearing sites during reproductive periods, and their responses to immediate threats of predation. Moose (*Alces alces*), elk (*Cervus elaphus*), mule and black-tailed deer (*Odocoileus hemionus hemionus* and *O. h. columbianus*, respectively), and mountain sheep (*Ovis* spp.) are examples of North American ungulates representing different reproductive parameters and variable responses to characteristics of predation risk and vegetation. All of these species have high pregnancy rates (approx. 90–100%) for adult females in average to good body condition (moose, Schwartz 1997; mule deer, Andelt et al. 2004; elk, Cook et al. 2001, 2004; bighorn sheep [*Ovis canadensis*], Jorgensen 1992). Moose and deer, however, have relatively high twinning (moose, 14–75%; Pimlott 1959, Schwartz 1997, Ballard et al. 1991, Heard et al. 1997, Bertram and Vivion 2002) or fetal rates (mule deer, 1.57–1.94/female; Andelt et al. 2004) in contrast to elk and mountain sheep for which twinning is rare (elk, Henderson et al. 1998; mountain sheep, Spalding 1966, Eccles and Shackleton 1979).

The behavioral strategies that ungulates use to minimize predation risk include selection of birthing areas and/or sites in response to vegetative cover and possibly topography at both large and small spatial scales. Moose females do not congregate during calving (Bowyer et al. 1998b) and do not typically show fidelity to

specific calving areas (Hundertmark 1997). Selection of calving areas is variable among individuals and populations and may be related to landscape heterogeneity (Hundertmark 1997, Welch et al. 2000). Parturient moose calve in heavy cover, particularly willow (*Salix* spp.), and do not necessarily space away from areas of high predation risk (Bowyer et al. 1999). Variation in shrub cover with good visibility to detect predators appears to be an important feature of calving sites (Molvar and Bowyer 1994, Bowyer et al. 1999). Elk females are also solitary during and immediately after calving (Paquet and Brook 2004). During the calving period and summer, they spend most of their time in alpine and subalpine habitats or in communities associated with stream bottoms (Adams 1982). Parturient elk seek areas with good hiding cover for offspring <1 week of age (Peek et al. 1982, Skovlin 1982), but usually reassociate with other parturient and non-parturient females to form “nursery” bands a few weeks after parturition (Peek 1987, Paquet and Brook 2004). Compared to moose and elk, mule deer exhibit larger movements between wintering and fawning areas. These movements may have less to do with predation than the availability and quality of forage (Garrott et al. 1987). Depending on snow depth within an area, black-tailed deer may or may not move from wintering to fawning areas (Nicholson et al. 1997). Characteristics of fawning areas vary between deer species and populations, but hiding cover (Pierce et al. 2004) and possibly variation in that cover (Bowyer et al. 1998a) at fawning sites are important to parturient female deer. For parturient mountain sheep, lambing areas are defined by high elevations, rugged topography, steep slopes, and proximity to escape terrain (e.g., Geist 1971, Festa-Bianchet 1988, Rachlow and Bowyer 1998; Walker 2005). They may also use shrubs as hiding cover and form maternal bands (Geist 1971, Rachlow and Bowyer 1998), increasing their ability to detect potential predators earlier through collective vigilance (Dehn 1990).

The main predators of moose, elk, deer, and mountain sheep neonates are similar where the species overlap, but there are also differences. Bears (*Ursus* spp.) and wolves tend to be the primary predators of moose neonates (bears: Ballard et al. 1990, 1991; Bertram and Vivion 2002; wolves: Gasaway et al. 1983), but they also prey on elk calves and mule deer fawns as do mountain lions (*Puma concolor*) and coyotes (*C. latrans*; elk, Taber et al. 1982, Raithel et al. 2004; mule deer, White et al. 1987, Pojar and Bowden 2004). Mountain sheep lambs are typically susceptible to predation by the previously mentioned species as well as by golden eagles (*Aquila chrysaetos*; Murie 1944).

Responses to threats of immediate predation by parturient females with young also vary among ungulates. Upon detection and identification of a predator, larger body-sized moose are the most likely to defend their offspring although the cow and/or calf may also flee or hide (Bubenik 1997, Bowyer et al. 1998b). Female elk and deer may defend their young against smaller predators such as coyotes (Garner and Morrison 1980, Gese 1999), but flight is a more common response. Use of escape terrain is the primary strategy used by mountain sheep to evade predators (Geist 1971, Berger 1991).

Studies evaluating the relationships between predation risk and vegetation characteristics for reproductive females have typically been conducted at relatively small spatial scales in cervids (e.g.,

moose, Bowyer et al. 1999; mule deer, Pierce et al. 2004; black-tailed deer, Bowyer et al. 1998a) and bovids (e.g., Dall's sheep [*Ovis dalli dalli*], Rachlow and Bowyer 1998; bighorn sheep, Festa-Bianchet 1988). The costs of foraging decisions, in the form of increased predation risk, however, are likely to vary both spatially and temporally. The advent of GPS and remote-sensing technologies now offers unique opportunities to quantify predation risk and vegetation characteristics over large, diverse landscapes (Boyce and McDonald 1999, Griffith et al. 2002, Boyce et al. 2003, Nielsen et al. 2003, Johnson et al. 2004). Woodland caribou, inhabiting the northern forests, boreal and subarctic regions of North America, are an excellent species to specifically examine trade-off decisions at large scales because individuals generally have low reproductive potential, use large areas to meet stringent seasonal demands, and are demographically sensitive to predation. Caribou are also notable among ungulates in that their protein balance may be negative much of the year (Gerhart et al. 1996). This may increase the importance of access, particularly to spring forage, to meet high nitrogen demands following winters on low-protein, lichen-dominated diets. Therefore, the predation risk-foraging trade-off may be more obvious than in other species.

Woodland caribou are found across Canada, in northern Idaho-Washington, USA, and in portions of Alaska, USA. Woodland caribou stay south of the Arctic tree line during calving and either "space away" (i.e., move to alpine areas) or "space out" (disperse) from conspecifics, other ungulates, and/or predators rather than migrate to calving grounds north of the tree line (Bergerud 1992, 1996). In British Columbia, woodland caribou are further recognized as 3 ecotypes: mountain, boreal, and northern. These ecotypes represent the responses of woodland caribou herds to regional variation in snow depths, available forage, distribution of other ungulates and predators, anthropogenic disturbances, and the associated behavioral responses to these main factors during the calving season. Mountain caribou are found only in mountainous regions of southeast British Columbia at high elevations in subalpine and alpine areas (Stevenson and Hatler 1985, Johnson et al. 2004). During calving and summer seasons, they may move to lower-elevation forests (space out) or to alpine areas (space away; Seip and Cichowski 1996; E. S. Jones, University of Northern British Columbia, unpublished data). Boreal caribou are found in the lower-elevation, forested-muskeg complexes of northeastern British Columbia and their distribution extends into northern Alberta (Heard and Vagt 1998). The boreal ecotype occurs at lower densities than other ecotypes (Dzuz 2001) and has no distinct calving habitat(s). Rather, calving occurs annually in areas with relatively low densities of other caribou and ungulates (James 1999). The northern ecotype of woodland caribou is found in the mountainous portions of northern and western British Columbia (Heard and Vagt 1998), the Yukon (Farnell et al. 1998), and in central Alberta (where they are referred to as mountain caribou; Dzuz 2001). Northern caribou generally exhibit an altitudinal migration to subalpine and alpine habitats (i.e., space away) during calving and summer (Oosenbrug and Theberge 1980, Bergerud et al. 1984, Bergerud and Page 1987).

Woodland caribou have low rates of recruitment even though pregnancy rates range from 88 to 100% (Cumming 1992, Seip

and Cichowski 1996, Rettie and Messier 1998, Mahoney and Virgl 2003, McLoughlin et al. 2003, Wittmer et al. 2005). To our knowledge, twinning has not been documented for free-ranging woodland caribou and is rare in barren-ground caribou (*R. t. granti*; Dauphiné 1976). Precise estimates of parturition for woodland caribou are unavailable, but estimates for barren-ground caribou among years range from 71 to 92% ($\bar{x} = 81\%$; Griffith et al. 2002). Low recruitment rates appear to be related to high calf mortality by gray wolf predation during the early neonatal period (Gasaway et al. 1983, Bergerud and Elliot 1986, Bergerud and Page 1987, Seip 1992, Wittmer 2004), but other causes of death, such as predation from bears (Ballard 1994, Adams et al. 1995, Young and McCabe 1997, Mahoney and Virgl 2003), golden eagles (Dale et al. 1994, Adams et al. 1995, Griffith et al. 2002), and Canadian lynx (*Lynx canadensis*; Bergerud 1983), congenital defects, insect harassment, sickness or disease, malnourishment, and exposure have all been reported to play important roles in calf mortality (Seip 1991, Whitten et al. 1992, Dale et al. 1994, Bergerud 1996, Heard et al. 1996). In some populations, mortality rates through summer and winter may be as important to recruitment as mortality through the early neonatal period. Postnatal calf mortality rates in British Columbia range from 20 to 60% (Seip and Cichowski 1996).

Woodland caribou commonly move from east to west from wintering to calving areas (Bergerud 1996). Movements often occur in areas with low-elevation forested habitats that are higher in predation risk (Seip 1991, Johnson et al. 2002a). Parturient caribou may travel long distances (50–520 km) by way of indirect routes to return (within <10 km) to traditional calving areas (Bergerud et al. 1984, Brown et al. 1986, Wood 1996). This is often the longest distance that female caribou travel in their seasonal movements (Brown et al. 1986, Wood 1996). Strictly traditional migration routes are not characteristic of the northern ecotype of woodland caribou as compared to barren-ground caribou (Bergerud 1996). Selection of calving areas is likely influenced by the level of predation risk in adjacent areas (Bergerud et al. 1990, Bergerud 1996, Cumming et al. 1996, Heard et al. 1996, Barten et al. 2001). Calving areas for woodland caribou are often in rugged mountainous areas in the alpine or shrub-krummholz zones (Oosenbrug and Theberge 1980, Barten et al. 2001). Calving success can be higher for females in alpine areas, presumably due to a decreased exposure to predation (Bergerud et al. 1984, Seip 1992, Poole et al. 2000, Barten et al. 2001). Bergerud and Page (1987) proposed that calving caribou maximize distance from predators and alternate prey species regardless of vegetative phenology. The ability of calving caribou to disperse across the landscape may decrease calf mortality (Seip 1992) because dispersal by parturient females increases search time and lowers encounter rates for predators, thereby decreasing hunting efficiency (Bergerud and Page 1987, Bergerud 1992, Barten et al. 2001). Bergerud (1996:102, citing Ferguson et al. [1988]) noted that caribou will select for forage in the summer, "but only within the options provided by low-risk habitats." Calving caribou in Alaska used sites with fewer predators and a lower abundance of forage when compared to non-parturient caribou; diet quality (as measured by fecal analyses), however, was similar. This may have reflected the ability of parturient caribou to

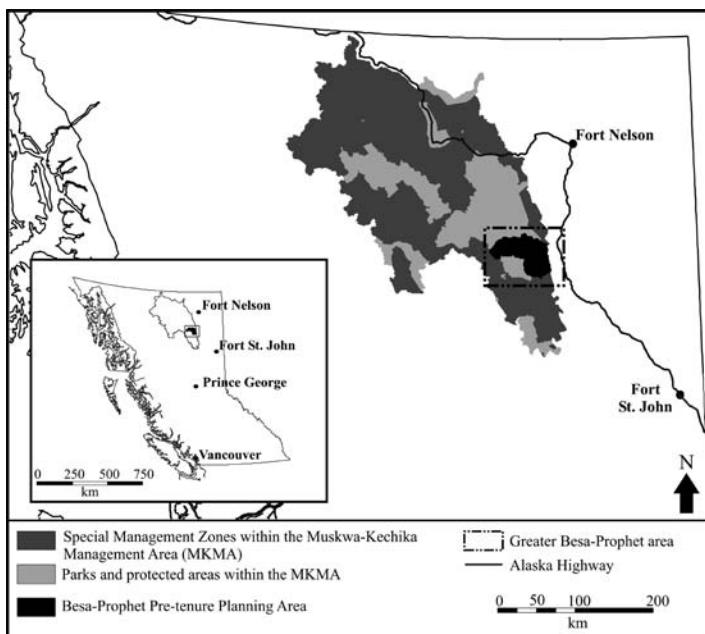


Figure 1. The Greater Besa-Prophet area of the Muskwa-Kechika Management Area in northern British Columbia, Canada, 2002–2003.

feed selectively on forages of higher quality (Barten et al. 2001:88).

Although predation risk appears to play a role in habitat selection for successful calving by woodland caribou, other factors, such as forage characteristics and snow cover at large scales, are important (Eastland et al. 1989, Barten et al. 2001, Griffith et al. 2002). Maternal condition directly impacts fetal viability and subsequent calf survival, primarily resulting from available resources (i.e., energy and protein) of the adult female towards calf production, birth mass, and mass gain (Cameron et al. 1993; Adams and Dale 1998a,b; Russell et al. 1998). Heavier (vs. lighter) calves at birth have higher rates of survival (Cameron et al. 1993), but survival also depends on maternal condition at parturition to ensure adequate milk production (Post and Klein 1999). Sex of the calf could further influence survival as male reindeer (*R. t. tarandus*) calves have been reported to be more active and engage in increased risk-taking behavior (Mathisen et al. 2003). The effect of sex on neonatal survival, however, has not been recorded in North American caribou (Adams et al. 1995). Selection of productive early summer range has direct effects on perinatal mortality (Post and Klein 1999) because physiological demands of lactation are highest during the first few weeks following calving (White and Luick 1984, Parker et al. 1990). Parturient caribou experience their lowest body condition of the year during this time (Chan-McLeod et al. 1999). The importance of forage characteristics has been documented for barren-ground caribou where the relative amount of forage available on the calving grounds, as indexed by the NDVI, was the best predictor of early calf survival (Griffith et al. 2002). A plausible explanation for widespread variation in the importance of predation and nutrition in limiting caribou populations is that the relative importance of predation risk and/or forage availability may differ between areas or herds, vary within an area or herd, or more likely, be a trade-off between the 2 factors. This trade-off

likely varies across spatial and temporal scales (Wiens 1989, Levin 1992).

Woodland caribou in mountainous environments in winter use multiple strategies to accommodate food supplies that vary with snow depth and predation risk from gray wolves (Johnson et al. 2000, 2001). Multiple strategies could be a product of a heterogeneous environment and/or a response to a dynamic predation-risk landscape, where variation in use of resources (i.e., plasticity) by caribou may make them less predictable in space and time. Behavioral plasticity among individuals and populations appears high during winter for woodland caribou in British Columbia (Johnson et al. 2002a,b, 2004). This behavioral plasticity, as in other cervids (Bowyer et al. 1999), may extend to other important times of the year (i.e., calving). In addition to spatial separation from other woodland caribou, parturient woodland caribou may use different strategies to cope with varying costs of predation risk across a diverse landscape to meet the demands of lactation that enhance calf survival (Bergerud et al. 1984, Bergerud and Page 1987, Barten et al. 2001).

The objective of this study was to compare predation risk and vegetation characteristics among and within 3 different calving areas within the Greater Besa-Prophet area (GBPA) of northern British Columbia. We examined predation risk, vegetation characteristics, and calf survival by calving area. If predation risk drives the selection of calving areas, then predation risk within each of the calving areas should be lower than predation risk on the landscape as a whole. If nutrient acquisition drives the selection of calving areas, then vegetation characteristics for all calving areas should be relatively higher than across the landscape. If trade-offs are occurring, then relative predation risk and vegetation characteristics could vary among calving areas. Within any single calving area, there may be smaller scale-dependent responses to predation risk and vegetation characteristics and/or the trade-off between them. In these cases, predation risk and vegetation characteristics at calving sites within a calving area would differ from what was generally available in that area. If predation is limiting, then calf survival should be lower in areas with higher predation risk. Alternatively, if forage is limiting, calf survival should be higher in areas with relatively higher vegetation quantity and/or quality. We assessed the roles of predation risk and forage availability at different scales in determining successful calving strategies of woodland caribou in northern British Columbia.

STUDY AREA

The GBPA encompasses 740,800 ha, the majority of which is within the 6.4-million-ha Muskwa-Kechika Management Area in northern British Columbia, Canada (Fig. 1). The GBPA is located between latitude 57°11' and 57°15'N and longitude 121°51' and 124°31'W. Elevations range from 630–3,025 m, with tree line occurring between approximately 1,450–1,600 m. Valleys and adjacent slopes in the GBPA are often covered with hybrid spruce (*Picea glauca* × *engelmanni*) and/or black spruce (*P. mariana*), quaking aspen (*Populus tremuloides*), and poorly drained willow–birch (*Salix* spp.–*Betula glandulosa*) communities with infrequent white spruce (*Picea glauca*). Mature lodgepole pine (*Pinus contorta*) is uncommon. Dominant understory species are

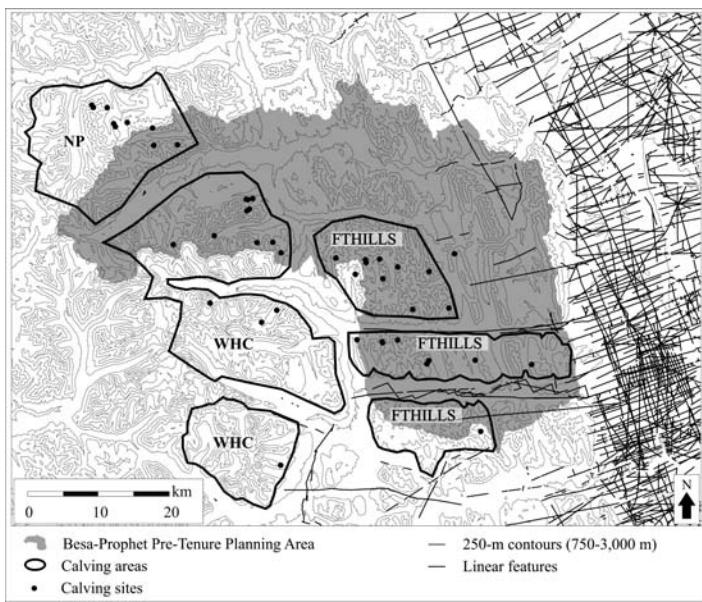


Figure 2. The Foothills (FTHILLS), North Prophet (NP), and Western High Country (WHC) calving areas and calving sites of woodland caribou and linear features of the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003.

soapberry (*Sheperdia canadensis*), Labrador tea (*Ledum groenlandicum*), sedges (*Carex* spp.), horsetails (*Equisetum* spp.), crowberry (*Empetrum nigrum*), alder (*Alnus* spp.), and various mosses with few lichens. Alpine areas consist of permanent snowfields, glaciers, barren rock with sparse or mat vegetation, and grasslands with trees in krummholz form (Demarchi 1996). Common alpine species are mountain avens (*Dryas integrifolia*), altai fescue (*Festuca altaica*), arctic white heather (*Cassiope tetragona*), moss campion (*Silene acaulis*), and a variety of terrestrial lichens and mosses.

The area is characterized by repeated east–west drainages with numerous south-facing slopes that support one of the most diverse ungulate predator–prey ecosystems in North America. Large mammals found in the GBPA are the northern ecotype of woodland caribou, elk, moose, white-tailed deer (*Odocoileus virginianus*), mule deer, Stone's sheep (*Ovis dalli stonei*), mountain goat (*Oreamnos americanus*), bison (*Bison bison*), gray wolf, grizzly bear, black bear (*U. americanus*), coyote, Canadian lynx, and wolverine.

The GBPA is currently unaffected by large-scale industrial activity, but historical and current human activities include hunting and prescribed burning. Terrestrial access is restricted, except for a low level of all-terrain vehicle–snowmobile activity in the southern portion of the study area. Moose, elk, woodland caribou, Stone's sheep, mountain goat, mule and white-tailed deer, bison, grizzly and black bear, and gray wolf hunting occurs in the area. Seismic oil exploration has been infrequent in the mountainous portions of the GBPA and common in the east (Fig. 2). The Besa-Prophet Pre-Tenure Planning Area (Fig. 2) within the GBPA is designated as a special management zone of the Muskwa-Kechika Management Area (Fig. 1). This designation allows exploration and/or extraction of natural resources if concerns for wildlife populations are addressed prior to development.

There are 3 general calving areas for woodland caribou in the GBPA as defined by differences in small- and large-scale vegetation characteristics, elevation, topography, and the distribution of adult female woodland caribou and calves during May–July 2002 and 2003 (Fig. 2). These calving areas are the Foothills, Western High Country, and North Prophet. The Foothills area on the eastern side of the Rocky Mountains, with elevations ranging from 1,000–2,100 m, is characterized by timbered valleys and steep, vegetated mountains. Vegetation types are heterogeneous, with spruce-lined valleys transitioning into shrubby subalpine and alpine associations with little non-vegetated cover and no permanent snowfields. The Western High Country area, west of the Foothills area, ranges from 1,400–3,025 m and is characterized by rugged, steep mountains with little vegetative cover and narrow valleys. Rock, permanent snowfields, and glaciers dominate this area, with vegetative cover comprising spruce-lined river bottoms, and subalpine and alpine vegetation associations in north- and south-facing hanging valleys. The North Prophet is north of the Western High Country area and northwest of the Foothills area where elevations range from 1,200–2,400 m. This area is characterized by wide valleys with no forest cover and rugged, steep mountains. Subalpine-shrub and subalpine vegetation associations in the valley bottoms grade into alpine associations on mountainsides. Permanent snowfields and talus and scree fields are common at higher elevations.

METHODS

Capture

Forty-eight female woodland caribou were captured and fitted with GPS collars (Simplex, Televilt, Lindesberg, Sweden) during the winters of 2001–2002 and 2002–2003. We took 2 10-ml blood samples to determine reproductive condition via serum progesterone concentrations (Prairie Diagnostics Services, Saskatoon, Saskatchewan, Canada; Ropstad et al. 1999). Animals were monitored from fixed-wing aircraft (Piper Super Cub 18A) twice daily to identify calving areas, onset of parturition, and parturition rates. Flights were conducted as high as possible to minimize impacts to wildlife, but varied with weather and visibility. Collared individuals were determined to be parturient or non-parturient by calf-at-heel. Once parturition began we captured calves by hand (Adams et al. 1995, Vik Stronen 2000) or by net-gun (Rongstad and McCabe 1984) with a helicopter (Bell JetRanger II-206B).

We captured 25 woodland caribou neonates during each of the summers of 2002 and 2003. Although we targeted calves from collared adult females, we captured other calves if the capture of targeted calves was not possible. A 2-person capture crew, net-gunner, and helicopter pilot searched calving areas of collared females for calves old enough for processing (>24 hr; Adams et al. 1995). To capture calves by hand, one member of the capture crew was dropped from the helicopter close to and downslope of the cow-calf pair, while the other member was dropped upslope of the pair; calves were then pursued on foot. For net-gun capture, we deployed a lightweight 3.7-m² net with 10.2-cm mesh and a tensile strength of 77.3 kg (model 5608.19; Coda Enterprises, Inc., Mesa, Arizona) via a net-gun from the helicopter.

During processing, the crew wore clean latex gloves to minimize scent transfer between humans and calves (Adams et al. 1995; T.

M. Pojar, Colorado Division of Wildlife, personal communication). Calves were sexed by the presence or absence of a vulva (Bergerud 1961). We weighed calves using a disposable cotton sling (approx. 33-cm diameter) and a 20-kg handheld spring scale. Coordination and hoof and umbilicus condition were examined to estimate age (days) from birth (Haugen and Speake 1958). General examinations included notations on presence of diarrhea and/or injuries.

Each calf was fitted with a drop-off radio-collar weighing approximately 120 g (1.3% of the average body mass of captured calves). Collars consisted of a leather-belted and elastic (1:1.5 expansion ratio) neckband with a weather- and impact-resistant motion-sensitive transmitter (Advanced Telemetry Systems, Isanti, Minnesota; as designed by T. M. Pojar, Colorado Division of Wildlife, personal communication; see Gustine 2005). The pulse rate of the transmitter increased from 60 to 90 pulses/min if stationary for >2 hr. The manufacturer-supplied collar was cut across the leather belting and reattached with 2 lengths of surgical tubing (7-mm inner and 10-mm outer diameters) approximately 57 mm long. The combination of surgical tubing and elastic ensured that the collars would accommodate calf growth. Surgical tubing is sensitive to exposure from ultraviolet radiation, and collars were expected to drop off in 4–5 months. All animals were captured and handled in accordance with the guidelines of the Canadian Council on Animal Care (2003).

For subsequent analyses, we defined the “calving site” as the site where the cow–calf pair was first observed during helicopter or fixed-wing flights. Because flights were made twice daily over the area, we assumed that this site was or was very close to the actual birthing site. The calving site was marked as a GPS location. We used a *t*-test to assess differences in birth mass (*y*) of male and female caribou calves (estimated from mass at capture [*a*] and age in days [*x*], where $y = a - 0.571x$; Parker 1989). We used analysis of variance (ANOVA) to examine birth mass among calving areas and Tukey’s honest significant difference for unequal sample sizes for multiple comparisons (Zar 1999). Annual and pooled sex ratios of captured calves were compared using chi-square (χ^2) analyses (Zar 1999).

Cause-Specific Mortality and Calf Survival

We monitored collared calves by fixed-wing aircraft twice daily (0700–1100 and 1800–2300), weather permitting, for 28 days after captures and then once weekly until the end of July per field season. To quantify monitoring frequency during 28 days postcapture, we randomly selected an animal for each year and averaged the time (hr) between relocations. Each calf represented the sample of calves for that year because all calves within a year had the same monitoring frequency. General locations of all adult female woodland caribou and calves observed during monitoring flights were documented. A “movement event” was defined as the movement of a collared calf >1 km from its calving site. In the case of movement events that occurred over >1 day, the day the calf left the calving site was defined as the day of the movement. We examined the time differences between the last date of capture efforts for each year and the date when a calf moved to determine if capture efforts in a calving area were a potential cause for movement away from the calving site. We also calculated the difference between the date each calf was captured and the age at

first movement to evaluate the effect of handling a calf on movement away from the calving site.

After detecting a mortality signal during a fixed-wing flight, the mortality site was accessed by helicopter as soon as possible (<16 hr). A GPS location was taken on the ground where the collar was found. At each mortality site, photos were taken, whole or partial carcasses recovered, and/or any evidence of predators (e.g., scat, tracks, and hairs) recorded. When possible, we conducted partial necropsies of predation mortalities. Whole carcasses were weighed and frozen for subsequent analysis. Cause-specific mortality was assigned, as outlined by Acorn and Dorrance (1998), to one of the following causes of death: (1) accident/abandonment, or predation by (2) bear, (3) eagle, (4) wolverine, (5) gray wolf, or (6) unknown predator.

Observed versus expected frequencies of cause-specific mortalities (annual, pooled over 2 yr, and by calving area) and sex ratios of calves that died were compared using χ^2 analyses. Identified predation-specific mortality among the 3 calving areas was examined using observed and expected frequencies of identified mortalities from predation per calving area. The probability of calf survival from predation for a specific time period was determined using the Kaplan–Meier estimator on an annual and pooled basis (Pollock et al. 1989). Because we were interested in survival from predation (hereafter referred to as survival), non-predation mortalities ($n = 2$) were removed from the sample at the time of death. Survival rates by age were determined in days for the first 28 days and in weeks for the next 28 days. Mortality rate from predation was estimated by week and defined as the number of animals that died by the end of week_x divided by the number of animals alive at the beginning of week_x. Survival for each calving area was calculated using pooled survival data. Survival curves across years were compared using the log-rank test with a conservative estimate of variance (Pollock et al. 1989). To increase sample size, we pooled data across years and defined 2 seasons of survival for small- and large-scale models: survival to the end of calving (25 May–14 Jun) and survival through summer (15 Jun–31 Jul). Survival was compared between these seasons and among calving areas, with a Bonferroni adjustment, using the difference in proportions test (Zar 1999). The number of animals at risk of predation at the beginning of season_x was defined as the sample size for season_x, except for the calving season when sample size was determined at the termination of capture effort ($n = 48$). Survival for season_x was equal to the Kaplan–Meier estimate of survival at the end of season_x.

Small-Scale Characteristics of Calving Sites

We collected small-scale habitat information at calving sites ($n = 50$) in the first week of July during 2002 and 2003. No cow–calf pairs being monitored were present in the areas at the time of sampling. A 100-m cloth tape was placed on the ground along a random bearing with the calving site as the center point. We noted general vegetation associations within 100 m of each calving site. The line-intercept method (Canfield 1941) was used to calculate percent intercept of trees, shrubs, and dwarf shrubs by species, and rocks–soil and cliffs (Higgins et al. 1996). If a transect extended over a cliff, the intercept value was noted and the survey was terminated ($n = 5$).

We randomly placed 5 plots (50 × 50 cm; Mosley et al. 1989) on

either side of the transect at 25-m intervals. We recorded the number of individual plants for each graminoid and forb species within the plots to estimate plant density as a relative measure of plant community dominance. We estimated percent cover by each species, which is related to potential forage abundance, and by rocks-soil visually with the aid of a laminated cardboard circle with an area approximately 1% of the plot (0.0025 m^2). Because lichens are known to be important to wintering woodland caribou (e.g., Johnson et al. 2000) and could potentially sustain parturient caribou on calving areas before greening of vegetation, we also sampled lichen biomass. We removed a $20 \times 20\text{-cm}$ sample of soil and vegetation from a randomly chosen corner of each plot (Dallmeier 1992). The first 7 transects were not sampled for biomass, as the decision to collect lichen biomass was made in the first field season after we started to collect data at calving sites. Samples of lichen biomass were air-dried in paper bags and subsequently sorted, identified to genus, and weighed to the nearest 0.001 g. We calculated the Shannon-Wiener index of diversity (H') for lichen biomass and herbaceous species at each calving site as in Krebs (1989).

We compared characteristics of vegetation by functional group (percent cover, density, and diversity for graminoids, sedges, horsetails, and forbs measured by quadrats; percent cover by line intercept for trees, shrubs, and dwarf shrubs); lichens (biomass and diversity), non-vegetated cover (percent cover by quadrats and percent cover by line intercept of rocks-soil), slope ($^\circ$), and elevation (m) of calving sites ($n = 50$) across calving areas using ANOVA and Tukey's test for unequal sample sizes for all post hoc analyses (Zar 1999). In cases of non-normality, we used the Kruskal-Wallis ANOVA of ranks and a multiple comparisons of mean ranks for post hoc analyses (Siegel 1956, Siegel and Castellan 1988). To specifically address the role of each calving site characteristic (as listed above) relative to calf survival from predation, we compared each characteristic for calves that lived and died using t -tests ($n = 48$), for both the calving and summer seasons. In cases where the data were not normally distributed (Levene's test), we used a Mann-Whitney U -test (Siegel 1956, Zar 1999).

We evaluated relationships between small-scale characteristics of calving sites and calf survival from predation ($n = 48$) to the end of the calving season and during the summer season using logistic regression. Twelve ecologically plausible models were derived from small-scale characteristics (percent graminoid-sedge-horse-tail cover, percent forb cover, percent total herbaceous cover, density of herbaceous vegetation [plants/m^2], lichen biomass [g/m^2], lichen diversity [H'], herbaceous diversity [H'], percent shrub intercept, percent dwarf shrub intercept, percent cliff intercept, and percent rocks-soil intercept) to predict calf survival. We used logistic regression with these parameters (K) to characterize differences between calves that lived and those that died. We used tolerance scores to assess model inputs for collinearity and multicollinearity which, as indications of redundancy, can inflate selection coefficients and lead to inflated error terms (Menard 2002). In both cases, if tolerance scores were <0.20 , covariates were not included in the same model (Menard 2002). We ranked the suite of models using Akaike's Information Criterion (AIC) values corrected for small sample size (AIC_c) when $n/K < 40$. The

lowest value indicated the most parsimonious ("best") model. The difference in AIC_c (Δ_i) was a relative ranking of the models. Akaike weights (w_i) provided a way to scale the Δ_i values and assisted in weighting and estimating parameters and estimates of variance (Burnham and Anderson 2002:150, 162). Evidence ratios (E_r), as relative ratios of Akaike weights, also provided relative support for fitted models (Burnham and Anderson 2002). We validated models using areas under the receiver operating characteristic (ROC) curves (Boyce et al. 2002). A ROC of >0.70 was considered to be acceptable at discriminating between small-scale characteristics of calving sites used by calves that lived and those that died (Manel et al. 2001, Boyce et al. 2002). Models were averaged if a less parsimonious model had a higher ROC value. We also calculated odds ratios (e^{β_i}), or the likelihood of a characteristic being associated with one group or the other (Zar 1999). Robust estimates of variance for the odds ratios were obtained using the Huber-White sandwich estimator (Stata Corporation, College Station, Texas). We excluded transects without lichen biomass data ($n = 7$) from analyses.

Significance for all tests was assumed at $\alpha = 0.05$. We used Statistica 6.1 (Statsoft, Inc., Tulsa, Oklahoma) for all tests; and Stata 7 and 8 (Stata Corporation) for all model development, evaluation, and validation. We use the phrase "no difference" in place of "means were similar."

Large-Scale Characteristics of Calving Sites and Calving Areas

Components of Predation Risk.—We quantified predation risk to woodland caribou using logistic regression to form RSFs that identified habitat attributes selected by grizzly bears and gray wolves in the GBPA from 14 May to 15 August in 2002 and 2003. We defined predation risk as the likelihood of being killed during a season (Lima and Dill 1990). We assumed that the components of predation risk (as in Lima and Dill 1990) were directly related to the relative selection of habitat attributes by predators as defined by RSFs, and these components of predation risk could be assessed by woodland caribou (Kats and Dill 1998). Assumptions for RSFs were as outlined in Boyce and McDonald (1999).

Locations of GPS-collared predators were determined for 15 female grizzly bears and 22 gray wolves from 5 packs that were being monitored in a concurrent study (B. Milakovic, University of Northern British Columbia, unpublished data). Numbers of collared predators were approximately 10–17% of the grizzly bear population (Poole et al. 2001) and 25–30% of the gray wolves (B. Milakovic, University of Northern British Columbia, unpublished data) within the study area. Collars had been programmed to acquire locations every 6 hr for approximately 2 years. We recovered data by remote download or by retrieving the collar. We separated grizzly bear and gray wolf data into 2 seasons: calving (14 May–14 Jun) and summer (15 Jun–15 Aug). To incorporate early and late calving events and the associated behavioral responses of predators to parturient caribou as potential prey items, the data for defining predation risk during the calving season preceded capture of the first caribou calves by 10 days. We used predator data that extended into August (2 weeks longer than the season defined for caribou) to obtain a larger sample of predator locations on the landscape to ensure robust models. For

individual grizzly bears, we divided the GPS data into season and year subsets. For gray wolves, we used pack, season, and year subsets. All but one of any duplicate gray wolf locations (i.e., same date and time) within a pack were randomly selected and removed to address issues of independence among data. We used 100% minimum convex polygons (MCPs) to define areas of resource availability for each individual grizzly bear and gray wolf pack by season and year (Mohr 1947, Hooge et al. 1998). After MCPs were identified, any GPS data that fell outside of the GBPA were excluded from analysis. We randomly selected 5 availability points per use point within each MCP for individual grizzly bears and gray wolf packs using the random point generator extension (Jenness 2003) in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California).

The resource selection models for grizzly bears and gray wolves incorporated predator GPS locations, topographical features (slope, elevation, and aspect), vegetation class as determined from Landsat ETM imagery, distance to linear features (seismic lines, roads, and pipelines), and an index of vegetation fragmentation. These covariates were 25-m-resolution raster geographic information system (GIS) data. We obtained a digital elevation model from the 1:20,000 British Columbia Terrain and Resource Inventory Management program (British Columbia Ministry of Crown Lands 1990) for elevation and used it to create the aspect and slope layers. We categorized aspect into north (316–45°), east (46–135°), south (136–225°), and west (226–315°) directions to address problems with northerly values having the same aspect but different values (0° and 360°). Pixels with slope $\leq 1^\circ$ were assigned no aspect. We identified vegetation classes using an August 2001 Landsat ETM image (Lay 2005). Fifteen vegetation classes with a minimum mapping unit of 75×75 m were combined into 9 classes (Fig. 3) to address concerns about accuracy (Table 1) and complete separation in logistic regression models while maintaining biologically important differences for gray wolves and grizzly bears. These classes were Spruce, Shrubs, Subalpine, *Carex* spp., Non-vegetated, Pine, Riparian spruce, Alpine, and Burned-disturbed.

Because linear features can be associated with higher gray wolf risk (James and Stuart-Smith 2000), we created a distance to linear features layer using existing 1997–2000 databases (G. Haines, British Columbia Oil and Gas Commission, personal communication). We did not distinguish age, level of use, and type of linear features, such as seismic line, pipeline, and road, in the resource selection models. We assessed the accuracy of linear features, however, using orthophotographs (2000) and Landsat ETM panchromatic images (2001) of the GBPA. Linear features were added, if updating was necessary, using ArcGIS 8.3 (Environmental Systems Research Institute). All linear features were rasterized and buffered by 10 m to address locational error and resolution limitations of topographical data. We generated a distance-to-linear-features surface (25-m pixel size) for the GBPA based on the perpendicular distance (km) from each pixel to the edge of linear features.

We created an index of vegetation fragmentation using Idrisi32 (Clark Labs, Worcester, Massachusetts) from the 15 satellite image-derived vegetation classes (Table 1), which were grouped according to coarse vegetation cover type (CVCT) to represent

fragmentation as open or closed cover types. Open cover types included open-water (Gravel bar and Water classes), open-rock (Rocks and Rock-crustose classes), and open-alpine (Dry and Wet alpine classes). The closed coniferous cover type incorporated Pine, Spruce, and Riparian spruce classes. The Snow-glacier, Subalpine spruce, Burned-disturbed, *Carex* spp., Shrub, and Low-productivity spruce classes were considered as separate cover types. We incorporated the raster layer of linear features into the CVCT classification as a shrub component, so contiguous vegetation polygons were bisected by these shrub-dominated linear features. This new linear shrub class was used only in the fragmentation index and not as a new class in the vegetation classification. For the index of vegetation fragmentation (F_i), we used a moving window or kernel to classify each pixel defined by the following:

$$F_i = \frac{(b - 1)}{(c - 1)},$$

where b is the number of CVCTs in a 175×175 -m kernel and c is the number of 25×25 -m pixels (49) in that kernel. F_i values ranged from 0.00 to 0.50. We categorized these values into 3 classes (low fragmentation = 0.00–0.01, medium = 0.02–0.04, and high > 0.04) based on the right-skewed frequency distribution of the data.

Analyses of Predation Risk.—We defined predation risk and distance to areas with high predation risk by grizzly bears and gray wolf packs by season and year after developing a suite of ecologically plausible RSF models with combinations of the previously mentioned components of predation risk. We used logistic regression to quantify coefficients of selection (beta coefficients, β_i) for those components and defined relative strength and direction (i.e., positive or negative) of each to differentiate between the attributes of used and available locations (Manly et al. 2002). Using the Huber–White sandwich estimator (Stata Corporation), we obtained robust estimates of variance (Boyce et al. 2002) for each coefficient. We identified the most parsimonious models using AIC or AIC_c (Burnham and Anderson 2002) and validated them using the k -fold cross-validation (Boyce et al. 2002) and an averaged Spearman's rank correlation coefficient (\bar{r}_s ; Siegel 1956). We selected the most parsimonious model(s) based on w_i , and $E_r < 2$ for grizzly bears and $E_r < 10$ for gray wolves (Burnham and Anderson 2002). The E_r criteria for averaging wolf pack models were increased from < 2 to < 10 because model performance for some packs and seasons was much lower than grizzly bear models. Models were averaged if a less parsimonious model performed better in the k -fold cross-validation or if the most parsimonious model did not perform well ($\bar{r}_s < 0.64$, $P > 0.050$). We calculated estimates of averaged coefficients and variance as outlined in Burnham and Anderson (2002:150, 162); averaged models were reevaluated with the k -fold cross-validation (Boyce et al. 2002).

We assessed all model inputs for collinearity and multi-collinearity as in analyses of calving-site characteristics unless tolerance scores were < 0.40 when collinear and multi-collinear covariates were not included. We chose a more conservative threshold than Menard's (2002) recommendation of 0.20 to minimize any unknown effects of collinearity or multi-collinearity because these model predictions for predator selection (and

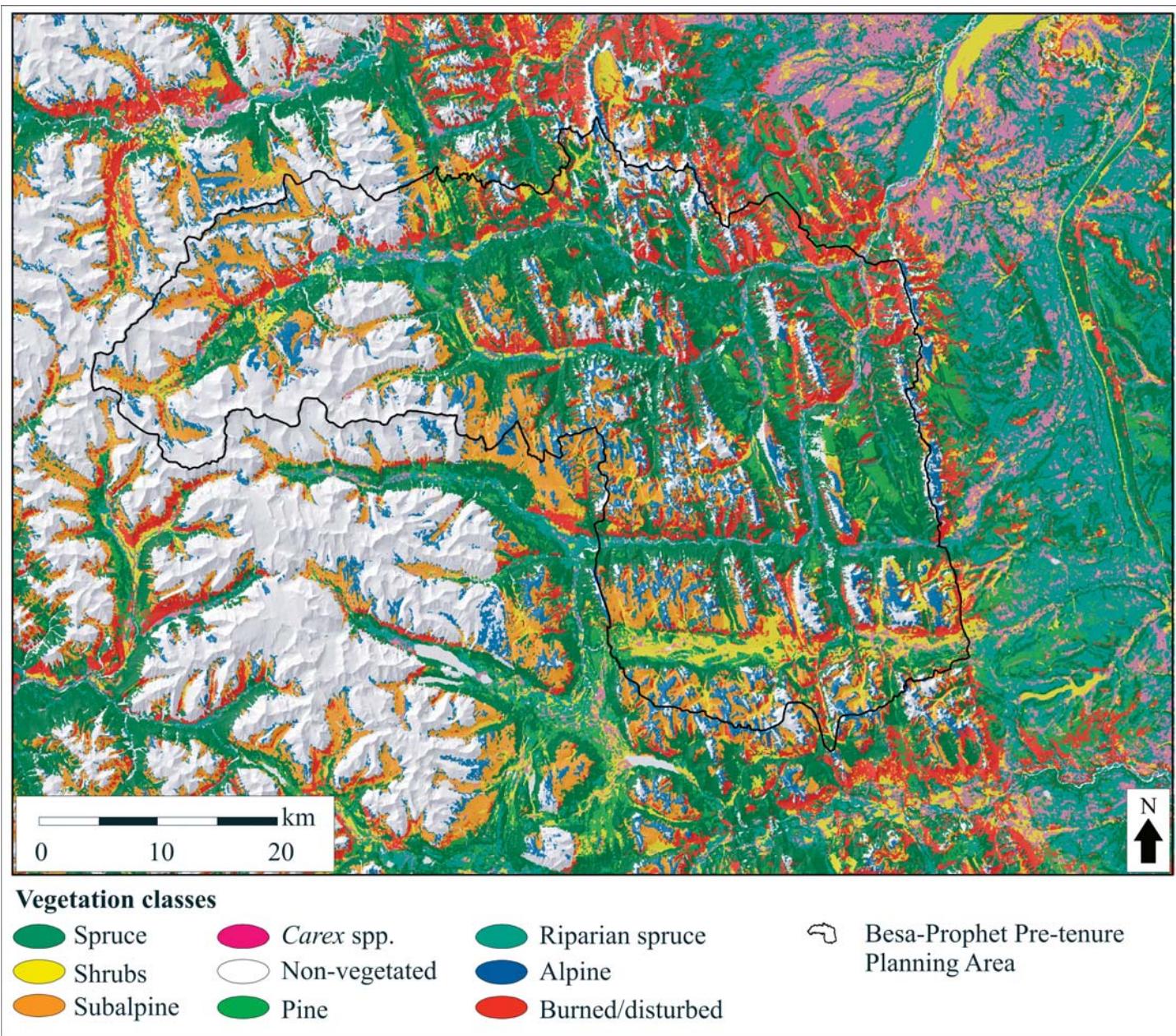


Figure 3. Nine vegetation classes, as defined using a vegetation classification from a 15 Aug 2001 Landsat Enhanced Thematic Mapper image of the Greater Besa-Prophet area, northern British Columbia, Canada.

therefore predation risk) were inputs for the woodland caribou models and subsequent analyses. Slope, distance to linear features (km), and elevation (km) were maintained as continuous variables. We entered elevation and distance to linear features as quadratic terms unless selection for these covariates was clearly linear (i.e., coefficients of both terms of the quadratic were the same sign). These variables were in kilometers to minimize model output (i.e., decimals to the fourth vs. eighth place). We did not include vegetation class and aspect categories that were rare or did not occur (i.e., near-perfect or perfect separation) in the use (GPS locations) or available data. Deviation contrasts were used to code all categorical variables (vegetation, aspect, and fragmentation; Menard 2002).

We pooled grizzly bear data by season and year because there

was little or no social exclusion of individuals and a high degree of overlap occurred among MCPs (B. Milakovic, University of Northern British Columbia, unpublished data). Consequently, 4 RSFs (2 seasons, 2 yr) defined predation risk to woodland caribou from grizzly bears (see Gustine 2005:160 for specific details). In contrast to grizzly bears, we developed RSFs for each gray wolf pack in the GBPA because gray wolf packs specifically prey on different prey items at different times of the year, and selection of habitat attributes likely varies (B. Milakovic, University of Northern British Columbia, unpublished data). Twenty-two RSFs were formed to define predation risk by gray wolf pack, season, and year (see Gustine 2005:164–170 for details per pack). Because MCPs of radio-marked gray wolf packs did not provide full coverage of the GBPA in any season or year, and because there

Table 1. Nine classes of vegetation used for analyses of resource selection by grizzly bears and gray wolves in the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003.

| Vegetation class | Users accuracy ^a (%) | Producers accuracy ^b (%) | Original 15 classes ^c | Description ^c |
|-------------------|---------------------------------|-------------------------------------|---|---|
| Spruce | 82.4 | 70.0 | Spruce and Low-productivity spruce | White and hybrid spruce-dominated communities |
| Shrubs | 50.0 | 75.0 | Shrubs | Deciduous shrubs <1,600 m dominated by birch and willow, some cinquefoil (<i>Potentilla fruticosa</i>) |
| Subalpine | 87.5 | 87.5 | Shrubs and Subalpine spruce | Deciduous shrubs >1,599 m; spruce-shrub transition zone at middle to upper elevations (white and hybrid spruce, dominated by birch and willow) |
| <i>Carex</i> spp. | 77.8 | 70.0 | <i>Carex</i> spp. | Wetland meadows dominated by sedges, typically at low elevations |
| Non-vegetated | 92.9 | 100.0 | Rocks, Rock-crustose lichens, Snow-glacier, and Water | Rock; rock with black, crustose lichens; permanent snowfields or glaciers and water bodies |
| Pine | 60.0 | 60.0 | Pine | Lodgepole pine-dominated communities |
| Riparian spruce | 78.3 | 90.0 | Riparian spruce and Gravel bar | Low-elevation wet areas with black (and hybrid) spruce; often with standing water in spring and summer; exposed gravel bars adjacent to rivers and creeks |
| Alpine | | | | Herbaceous alpine vegetation |
| Burned-disturbed | 94.1 | 80.0 | Wet and Dry alpine | Previously burned areas, graminoids, deciduous trees, or avalanche chutes |
| Burned-disturbed | 88.9 | 80.0 | Burned-disturbed | |
| Overall accuracy | 83.9 | | | |

^a Calculated by dividing the total number of correct sample units in an individual class by the total number of reference units.

^b Calculated by dividing the total number of correctly classified pixels in an individual class by the total number of sample pixels classified as that class.

^c Fifteen vegetation classes determined from remote sensing imagery (Lay 2005), which were compressed into 9 classes for this study.

was at least one other known uncollared pack in the GBPA, we used pooled RSFs to predict selection value for gray wolves for those few areas without data.

We developed the predation-risk landscapes for woodland caribou at risk from grizzly bears and gray wolves from the β_i in the logistic regression models using a raster GIS (PCI Imageworks 9.1, Richmond Hill, Ontario, Canada) and the following log-linear model (Boyce and McDonald 1999, Manly et al. 2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_i x_i),$$

where x_1, x_2, \dots, x_i are the raster data layers (e.g., elevation, slope, vegetation). This model estimated the relative selection value for a predator in each 25×25 -m pixel, based on its topographic and vegetation features, across the GBPA. The predation-risk landscapes for grizzly bears were generated from the 4 RSFs by season and year and applied across the GBPA. We combined the gray wolf RSFs from each pack's MCP for that season and year and the pooled gray wolf RSF values into one predation-risk landscape for each season and year. In areas where pack boundaries overlapped within a season and year, we assigned the lower RSF value to that pixel because of probable decreased vigilance by pack members in those areas and, subsequently, lower predation risk (Mech 1977, Rogers et al. 1980, Mech 1994). For all predation-risk layers, we created a mask for snow-glaciers (i.e., areas $>2,400$ m in rugged mountains to the west) and water (i.e., large bodies of water in the west and west-central portion of the GBPA) where the likelihood of predator use was rare, and assigned those areas RSF values of 0. We used the SCALE command in XPACE (PCI Imageworks 9.1) to scale all predation risk surfaces from 0 to 1. These scaled values for a predator were assumed to represent estimates of “actual” predation risk (Lima and Dill 1990) to woodland caribou.

We determined the distance to high-risk predation areas from each pixel in the GBPA. After smoothing the predation-risk surfaces using a 75×75 -m median filter, we binned the predation-risk values into quartiles. We defined areas of high risk as pixels with scaled RSF values greater than the 75th percentile of all values (i.e., in the top quarter of all risk values) by predator, season, and year. These high-risk areas were converted into polygons in Idrisi32 (Clark Labs). We created surfaces for each predator, season, and year of the distances from each pixel to the nearest high-risk area (polygon), which was defined as the perpendicular distance (km) to the edge of the high-risk area.

We also created GIS layers for change in gray wolf risk and change in grizzly bear risk for each season and year. Change in predation risk was equal to the summer predation-risk layer subtracted from the calving predation-risk layer.

Indices of Vegetation Biomass and Quality.—We modeled NDVI as an index of vegetation biomass and the changes in NDVI as an index of vegetation quality for the GBPA using NDVI data from partial Landsat TM and ETM images acquired on 4 June (TM), 22 July (TM), and 15 August (ETM) 2001. Our assumptions were that (1) images from 2001 were representative of the large-scale characteristics of vegetation in 2002 and 2003, (2) NDVI was correlated with aboveground net primary productivity (ANPP) and leaf area index (i.e., vegetation biomass; Tucker and Sellers 1986, Ruimy et al. 1994), (3) change in NDVI was an index of the amount of plant growth that occurred within a pixel, which is typically high in nutritional value for spring growth (Griffith et al. 2002, Oindo 2002), and (4) the timing of change important to woodland caribou was likely to occur between 4 June and 22 July (the dates of TM image data) in 2002 and 2003. We generated the NDVI models to account for areas in which some

NDVI values could not be derived from images because of cloud cover (i.e., images from 4 Jun and 22 Jul).

All images were geocorrected (root mean square error < 0.50) and raw imagery was converted to spectral radiance to address differences in sensor calibration (Chander and Markum 2003). We modeled NDVI for each image ($n = 2,062$, the number of pixels equal to 0.01% of the smallest Landsat data set) using multiple regression with slope, categorized aspect, a 15-vegetation classification, elevation, and/or incidence (the angle the sun strikes the surface of the ground at the time the image was recorded) as independent variables in a suite of models (as in Gustine 2005, Lay 2005). We assessed all model inputs for collinearity and multi-collinearity, and coded categorical variables as in analyses of calving site characteristics.

We selected models with the highest adjusted R^2 values and validated them with a resampling procedure and pixel-to-pixel rectification with the original NDVI data (Lay 2005). A new random sample without replacement ($n = 2,062$) was drawn from each set of image data for validation. We regressed predicted NDVI values from the original models on actual NDVI values from this new data set. We chose final models with the highest average adjusted R^2 values; if 2 models explained the same variation within 0.1%, we selected the more efficient model (i.e., model with fewest parameters).

We used these NDVI models to create large-scale data layers in a raster GIS (PCI Imageworks 9.1) that indexed vegetation biomass and quality across the GBPA. These layers were created using techniques identical to the predation-risk models, except that we used the coefficients of the multiple regression models as weighting factors and added those to the intercept to estimate NDVI per pixel as an index of vegetation biomass in the GBPA for that image date. To account for error in raster GIS data sets that may have influenced spatial models, we regressed actual NDVI values against a spatial representation of modeled NDVI for cloud-free areas on a pixel-to-pixel basis for a final validation of modeled data (Lay 2005).

Because of the relationships between NDVI and ANPP (Ruimy et al. 1994, Paruelo et al. 2004), the change in NDVI as the growing season progresses (Chen et al. 2000, Griffith et al. 2002), and the influence of understory on NDVI values in forested ecosystems (Hardy and Burgan 1999), we used the change in modeled NDVI values as an index of vegetation quality. This index was obtained by subtracting the 4 June image from the 22 July image. We did not calculate change for non-vegetated cover types that had negative NDVI values throughout the summer (Oindo 2002). All vegetation biomass and quality surfaces were smoothed and categorized as done for the predation-risk surfaces. Techniques for creating the distance to high-biomass and high-quality areas were also similar. We qualitatively evaluated the general trends in modeled indices by graphing estimates (\bar{x}) of vegetation biomass and quality for vegetated classes from our random sample without replacement ($n = 2,062$) for each image by vegetation class. We included modeled data from 16 September (see Lay 2005) to evaluate the ability of the models to detect senescence on the landscape.

Analyses of Large-Scale Characteristics of Calving Sites and Calving Areas.—We sampled the predation risk, vegetation biomass, and vegetation quality data for 3 scales of analyses pooled

across years to compare: (1) characteristics among the 3 calving areas and the GBPA landscape, (2) characteristics of calving sites in a calving area versus random points in that calving area, and (3) characteristics of all calving sites relative to the landscape. We set the number of random points within each calving area to be 10 times the number of calves captured within an area that were included in survival from predation analyses ($n_{\text{Foothills}} = 200$, $n_{\text{Western High Country}} = 180$, and $n_{\text{North Prophet}} = 100$), which turned out to be directly proportional to size of the calving areas. We set the number of random points on the landscape to be equal to the total number of data points across the calving areas ($n = 480$). We distributed random points using the random point generator extension (Jenness 2003) in ArcView 3.2 (Environmental Systems Research Institute). We used a raster GIS (PCI Imageworks 9.1 XPACE) to query predation risk (by season and year) and indices of vegetation biomass and quality (by season) for all random points and calving sites.

We determined the importance of predation risk, vegetation characteristics, and movement relative to the survival of calves in 2002 and 2003 using logistic regression and a biologically relevant set of models for calving and summer seasons. Grizzly bear risk, distance to areas of high grizzly bear risk, gray wolf risk, distance to areas of high gray wolf risk, vegetation biomass and quality, and calving area were covariates. We added movement (i.e., >1 km away from the calving site) a posteriori to models in the summer to evaluate the importance of movement to calf survival. Movement was not used to predict calf survival during the calving season because movement events prior to death were rare. We then developed a model set with predation-risk and vegetation characteristics, and calving area as covariates to predict movement events through the summer season and added 4 new covariates: change in gray wolf risk and change in grizzly bear risk between seasons, and distance to high vegetation biomass and distance to high-quality vegetation. We assessed model covariates for collinearity and multi-collinearity and then selected and validated models with estimates of variance as in small-scale analyses of calving site characteristics.

We used nonparametric tests for all analyses of predation risk and vegetation attributes among calving areas, the landscape, and calving sites because preliminary analyses suggested violation of the homogeneity of variances assumption (Siegel 1956). We used the Mann-Whitney U -test (Siegel 1956) to examine attributes of predation risk between years by calving area and the landscape, predation risk and vegetation characteristics (pooled across years) at calving sites versus characteristics of that calving area, predation risk and vegetation characteristics of all calving sites versus random points on the landscape, and the independent effects of predation risk and vegetation characteristics towards survival and movement. To evaluate the differences in attributes of vegetation and predation risk, slope, and elevation among calving areas and the landscape, we used Kruskal-Wallis ANOVA by ranks with multiple comparisons of mean ranks for post hoc analyses (Siegel and Castellan 1988). We evaluated changes in predation risk and vegetation characteristics (pooled across years) within calving areas and the landscape between seasons with the Wilcoxon matched pairs test (Siegel 1956).

We determined the trade-off, or cost, of foraging in areas of

Table 2. Reproductive parameters of female woodland caribou and age, mass, sex, and peak calving data from captured calves in the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003.

| Parameter | Year | \bar{x} | SE | Range | n |
|--|------|-----------|----------|---------------|----|
| Pregnancy (%) | 2002 | 91.7 | 5.8 | | 24 |
| | 2003 | 91.3 | 6.0 | | 23 |
| Parturition (%) | 2002 | 55.6 | 17.6 | | 9 |
| | 2003 | 76.9 | 12.2 | | 13 |
| Calving date ^a | 2002 | 30 May | 0.4 days | 27 May–3 Jun | 25 |
| | 2003 | 26 May | 0.2 days | 25 May–10 Jun | 25 |
| Mass of calves at capture (kg) | 2002 | 9.5 | 0.4 | 6.8–13.5 | 25 |
| | 2003 | 9.7 | 0.5 | 6.0–19.0 | 25 |
| Estimated birth mass (kg) ^b | 2002 | 7.7 | 0.2 | 5.6–10.1 | 25 |
| | 2003 | 8.1 | 0.7 | 5.1–16.1 | 25 |
| Age of calves at capture (days) | 2002 | 3.1 | 0.3 | 0.5–6.0 | 25 |
| | 2003 | 2.8 | 0.2 | 1.0–6.0 | 25 |
| Sex ratio (F:M) | 2002 | 16:9 | | | 25 |
| | 2003 | 15:10 | | | 25 |

^a Range includes observations of uncollared woodland caribou neonates.

^b Using the equation $y = a - 0.571x$, where y = estimate of birth mass (kg), a = mass of calf at capture (kg), and x = age in days at capture (from Parker 1989).

higher vegetation quality or vegetation biomass by evaluating the relationship between predation risk and vegetation characteristics with linear regression as in Bowyer et al. (1998a, 1999). We defined cost by season as the change in predator-specific risk (y) as vegetation biomass or quality (x) increased (i.e., slope of the regression). We assumed that animals experience a cost to foraging if there is a positive relationship between predation risk and vegetation characteristics (i.e., slopes > 0), whereas no cost is incurred if there is no relationship or a negative one (i.e., slopes ≤ 0 ; Bowyer et al. 1998a, 1999). We used a *t*-test with a Bonferroni adjustment to compare confidence intervals of slopes $\neq 0$ among calving areas and the landscape within and between seasons by predator (Sokal and Rohlf 1995).

RESULTS

Reproductive Characteristics

We obtained blood samples from 47 of the 48 adult female woodland caribou collared during the winters of 2001–2002 and 2002–2003. Forty-three females ($91.5 \pm 4.1\%$, $\bar{x} \pm \text{binomial SE}$) were pregnant, with similar pregnancy rates between years (Table 2). We were not able to determine parturition rates for all these animals because the GPS data loggers for 44 of the collars (22/yr) failed prior to calving. By observing animals for which the VHF (very high frequency) signals on GPS collars continued to function to calving, we determined that 15 of 22 pregnant adult females ($68.2 \pm 10.2\%$, $\bar{x} \pm \text{binomial SE}$) had their calves in the summers of 2002 and 2003. Parturition rates varied with small sample sizes and high estimates of standard error for both years (Table 2). Calving dates ranged from 25 May to 10 June, including observations of many non-collared woodland caribou, with peak calving occurring on 28 May ± 0.3 days ($\bar{x} \pm \text{SE}$).

Fifty woodland caribou calves were captured in the Foothills ($n=21$), Western High Country ($n=19$), and North Prophet ($n=10$) calving areas (Appendix A1). Only 10 calves were with collared adult females (5/yr). We captured 31 females and 19 males, with no statistical difference in sex ratios within or between years (all $P > 0.090$). Calf mass at capture was similar between years, with an average mass of $9.6 \text{ kg} \pm 0.3 \text{ SE}$ (Table 2). There was no difference

in the estimates of birth mass for males and females ($P=0.604$) or among calves captured in the 3 different calving areas ($F_{2, 49}=2.18$, $P=0.125$). Age of captured calves ranged from 0.5 to 6.0 days, with the average age at capture being 3.0 ± 0.2 days. Average handling time per calf was ≤ 2 min, not including pursuit time (in the helicopter or on foot), which was typically <5 min.

Cause-Specific Mortality and Survival in Calving Areas

We monitored woodland caribou calves during the 28 days postcapture once every 16 ± 2.3 hr ($\bar{x} \pm \text{SE}$) and 18 ± 2.2 hr in 2002 and 2003, respectively. Pooled data by year on animal movements away from calving sites peaked from 15 to 21 days of age, although movements continued to occur through 22–28 days of age in 2003 (Fig. 4a). No calves moved away from calving sites when they were <8 days of age. The earliest a calf moved from its calving site after the last day of capture efforts was 6 days in 2002 and 7 days in 2003. The earliest a calf moved after its date of capture was 8 days in both years. Therefore, it does not appear that our handling activities or helicopter flights in the calving areas caused movements by the calves. We observed peaks in mortality rate at 8–14 and 29–35 days of age (Fig. 4a).

Thirteen female and 6 male calves died in the first 2 months of life during the 2 years of the study. One calf died at 6 days of age in 2002, probably from abandonment due to handling, and another calf died at 4 days of age in 2003 from accidental drowning. The calf that was abandoned was captured <1 m from its birth site (observed afterbirth) and we did not observe this calf reunite with its mother; this dead calf was found 30 m from the capture site. The other calf was found lying in a creek. The creek cut through a snowfield, and the calf entered the creek but could not escape because of the steep and slick banks. These 2 non-predation-related mortalities were not included in survival or mortality analyses. The remainder of mortalities ($n=17$) were predator caused (Fig. 4b). There was no difference in the observed versus expected number of predation-related mortalities for males and females ($P=0.629$). There was 1 eagle- and 1 bear-caused mortality each year. In 2002 there were 3 mortalities from gray wolves and 4 mortalities from wolverines; in 2003 there were

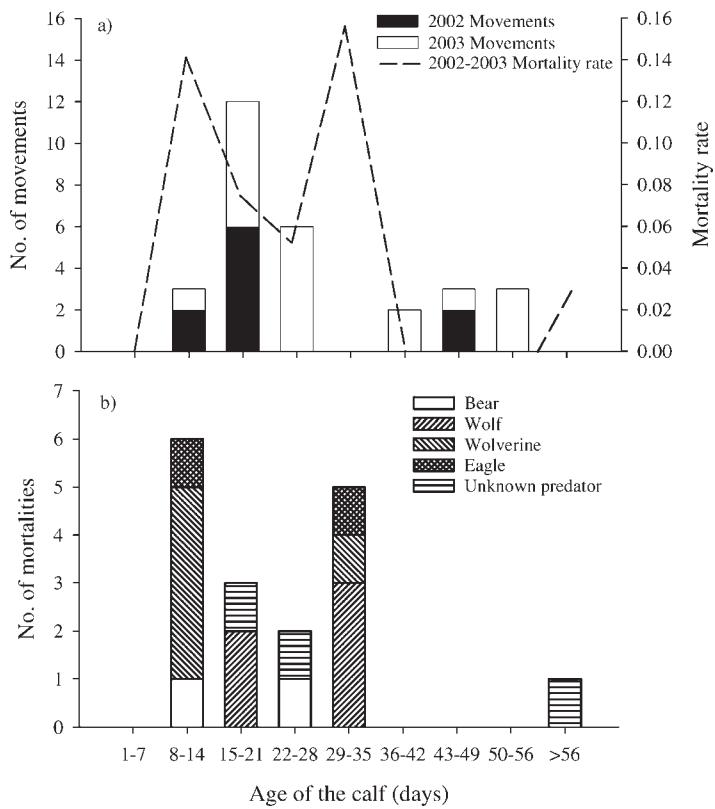


Figure 4. Age of radio-collared woodland caribou calves in relation to (a) the timing of calf movements (>1 km) away from calving sites and mortality rates (no. animals that died by the end of week_x divided by the no. of animals alive at the beginning of week_x) and (b) the timing of predation-caused mortalities in the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003.

mortalities from 1 wolverine and 2 gray wolves. We were unable to conclusively identify specific predators in 3 cases (2002: $n = 2$; 2003: $n = 1$). We also recorded mortalities of 2 uncollared woodland caribou calves, 1 by a wolverine and 1 by an eagle at approximately 1 and 2 weeks of age, respectively. Four of the 5 wolverine-caused mortalities of collared calves occurred between 9 and 15 days of age, whereas all gray wolf-caused mortalities occurred after calves were 18 days of age (Fig. 4b). There were no mortalities <14 days of age in the Foothills and no mortalities by gray wolves in the North Prophet. There were no differences in observed ($n_{\text{Foothills}} = 6$, $n_{\text{Western High Country}} = 6$, and $n_{\text{North Prophet}} = 2$) versus expected ($n = 4.67$) frequencies of causes of predation-related mortality among calving areas or using all data pooled over 2 years (all $P > 0.340$).

Survival through 56 days of life was not significantly different between 2002 and 2003 ($\bar{x} = 0.54 \pm 0.11$ SE and 0.79 ± 0.08 , respectively; $P = 0.066$). Survival was higher through the calving season (0.88 ± 0.05) than through the summer season (0.69 ± 0.07 ; $P = 0.032$). Pooled survival also was not different through 56 days of age among the Foothills (0.65 ± 0.11), Western High Country (0.61 ± 0.12), and North Prophet (0.80 ± 0.13) calving areas (all $P > 0.560$).

Small-Scale Characteristics of Calving Sites within Calving Areas in Relation to Calf Survival

There were no differences in vegetation characteristics of calving sites among calving areas, except for percent intercept of shrubs (Kruskal-Wallis ANOVA, $H_2, 48 = 8.12$; Table 3). Although not always significant, shrub cover tended to be higher at calving sites in the Foothills than in the North Prophet ($P = 0.050$) and the Western High Country ($P = 0.058$). Cover of rocks-soil ($H_2, 48 = 19.25$), slope (ANOVA, $F_{2, 47} = 8.90$), and elevation ($F_{2, 47} = 13.80$) also differed among calving areas (Table 3). Rocks-soil cover was lower at calving sites in the Foothills ($P < 0.001$) and the Western High Country ($P = 0.041$) than in the North

Table 3. Small-scale characteristics of calving sites among the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas of woodland caribou in the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003. Characteristics sharing the same letter were not significantly different, as determined by nonparametric^a and parametric analyses^b.

| Small-scale characteristic | FTHILLS | | WHC | | NP | | P |
|---------------------------------|-----------------|-----------|-----------------|-----------|-----------------|-----------|---------------------|
| | (n = 21) | SE | (n = 19) | SE | (n = 10) | SE | |
| Shrub intercept (% cover) | 29.6c | 6.0 | 15.1cd | 5.5 | 4.6d | 1.8 | 0.017 ^a |
| Rocks-soil intercept (% cover) | 5.8c | 2.7 | 18.6c | 6.0 | 51d | 10.0 | 0.001 ^a |
| Slope (°) | 27.8c | 1.6 | 16.6d | 1.9 | 22.6cd | 2.7 | <0.001 ^b |
| Elevation (m) | 1,767c | 30 | 1,783c | 38 | 2,033d | 31 | <0.001 ^b |
| Cliff intercept (% cover) | 2c | 0.4 | 3.8c | 2.6 | | | 0.473 ^a |
| Dwarf shrub intercept (% cover) | 22.5c | 5.2 | 36.4c | 6.3 | 9.4c | 7.4 | 0.132 ^b |
| Tree intercept (% cover) | 4.3c | 1.7 | 4.2c | 3.6 | | | 0.536 ^b |
| Herbaceous cover (% cover) | 21.2c | 2.4 | 17.6c | 2.6 | 11.9c | 3.5 | 0.097 ^b |
| Herbaceous diversity (H') | 1.63c | 0.1 | 1.29c | 0.1 | 1.21c | 0.2 | 0.070 ^b |
| Herbaceous density (per m^2) | 111.3c | 23.3 | 135.5c | 27.9 | 112.6c | 34.3 | 0.773 ^b |
| Graminoids (% cover) | 8.1c | 2.0 | 4.1c | 1.3 | 2.8c | 1.1 | 0.082 ^b |
| Sedges and horsetails (% cover) | 3.2c | 1.04 | 6.4c | 1.71 | 2.3c | 0.9 | 0.210 ^a |
| Forbs (% cover) | 9.9c | 1.7 | 7.1c | 1.3 | 6.8c | 1.7 | 0.300 ^b |
| Lichen biomass (g/m^2) | 44.4c | 8.9 | 28.5c | 7.5 | 31.2c | 10.7 | 0.372 ^b |
| Lichen diversity (H') | 1.28c | 0.10 | 1.09c | 0.17 | 1.29c | 0.23 | 0.582 ^b |

^a Kruskal-Wallis analysis of variance and multiple comparison of mean ranks.

^b Analysis of variance and Tukey's honest significant difference for unequal sample sizes.

Table 4. Model sets to evaluate the importance of characteristics of calving sites as predictors of calf survival for woodland caribou in the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003. Small-scale characteristics were evaluated during the calving season (25 May–14 Jun). Large-scale characteristics related to predation risk from grizzly bears and gray wolves and vegetation biomass and quality (as determined from the Normalized Difference Vegetation Index [NDVI]) were evaluated during summer (15 Jun–31 Jul).

| Model | n | LL ^{ab} | K ^{ac} | AIC _c ^{ad} | w _i ^{ae} | E _r ^{af} | ROC ^g |
|--|----|------------------|-----------------|--------------------------------|------------------------------|------------------------------|------------------|
| Small-scale characteristics (calving) | | | | | | | |
| Herbaceous cover + shrub intercept | 41 | -7.015 | 3 | 20.355 | 0.631 | 1.00 | 0.946 |
| Herbaceous cover + shrub intercept + dwarf shrub intercept | 41 | -6.762 | 4 | 22.190 | 0.262 | 2.50 | 0.953 |
| Herbaceous cover + lichen diversity | 41 | -9.358 | 3 | 25.039 | 0.026 | 10.41 | 0.845 |
| Graminoid-sedge-horsetail cover + forb cover + shrub intercept | 41 | -9.508 | 4 | 27.682 | 0.017 | 39.01 | 0.838 |
| Lichen biomass + shrub intercept | 41 | -10.783 | 3 | 27.890 | 0.015 | 43.28 | 0.791 |
| Herbaceous density + shrub intercept + dwarf shrub intercept | 41 | -10.058 | 4 | 28.783 | 0.010 | 67.64 | 0.865 |
| Rocks-soil | 41 | -12.896 | 2 | 29.898 | 0.006 | 118.10 | 0.550 |
| Lichen biomass + herbaceous density | 41 | -12.110 | 3 | 30.545 | 0.004 | 163.22 | 0.831 |
| Lichen diversity + herbaceous diversity | 41 | -12.214 | 3 | 30.753 | 0.003 | 181.09 | 0.703 |
| Rocks-soil + lichen biomass | 41 | -12.395 | 3 | 31.114 | 0.003 | 216.88 | 0.669 |
| Large-scale characteristics (summer) | | | | | | | |
| Movement | 48 | -25.835 | 2 | 55.760 | 0.335 | 1.00 | 0.740 |
| Movement + distance to wolf risk + distance to bear risk | 48 | -23.977 | 4 | 56.513 | 0.230 | 1.46 | 0.820 |
| Movement + wolf risk | 48 | -25.742 | 3 | 57.756 | 0.123 | 2.71 | 0.755 |
| Movement + quality | 48 | -25.826 | 3 | 57.924 | 0.113 | 2.95 | 0.746 |
| Movement + biomass + quality | 48 | -26.652 | 3 | 59.577 | 0.050 | 6.75 | 0.755 |
| Movement + biomass + wolf risk | 48 | -25.717 | 4 | 59.992 | 0.040 | 8.30 | 0.748 |
| Movement + quality + wolf risk | 48 | -25.727 | 4 | 60.012 | 0.040 | 8.39 | 0.742 |
| Movement + wolf risk + bear risk | 48 | -25.740 | 4 | 60.039 | 0.040 | 8.50 | 0.761 |
| Movement + biomass + quality + wolf risk | 48 | -26.634 | 4 | 61.826 | 0.016 | 20.76 | 0.751 |

^a Burnham and Anderson (2002).

^b Log-likelihood.

^c Number of parameters.

^d Akaike's Information Criterion for small samples.

^e Akaike weights.

^f Evidence ratios.

^g Area under the receiver operating characteristic (ROC; Boyce et al. 2002).

Prophet. Calving sites in the Western High Country were not as steep as the Foothills sites ($P < 0.001$). The North Prophet calving sites were at higher elevation than the Foothills ($P < 0.001$) and Western High Country ($P < 0.001$) sites. Characteristics of vegetation and lichens (quadrat data) at calving sites were highly variable (Appendix A2). Consequently, there were no differences in functional group-specific cover, density, or diversity, lichen biomass or diversity, and non-vegetative cover between the calving sites of calves that lived and those that died during the calving season or in summer within or between years.

Survival of woodland caribou calves during the calving season was best predicted by the model that incorporated both herbaceous and shrub cover (rather than functional group-specific vegetative measures) at calving sites (Table 4). Each 1% increase in herbaceous cover ($e^{\beta_i} = 0.81 \pm 0.07$ SE, $P = 0.011$) decreased the odds of survival by approximately 19%, whereas each 1% increase in shrub cover increased the odds of survival by approximately 13% ($e^{\beta_i} = 1.13 \pm 0.07$ SE, $P = 0.045$) assuming other variables were held constant. Discrimination of this model was excellent (ROC = 0.946). Models with cliff line-intercept data could not be evaluated during the calving season because no calves died at those calving sites. Survival of calves during summer was best predicted by a model using rocks-soil intercept (%), but discrimination was poor (ROC = 0.685).

Large-Scale Characteristics of Calving Sites and Calving Areas in Relation to Calf Survival

Models for predation risk performed adequately in the k -fold cross-validations (grizzly bears: all $\bar{r}_s > 0.89$, all $P < 0.001$; pooled

gray wolf models: all $\bar{r}_s > 0.87$, all $P < 0.001$; gray wolf pack models: all $\bar{r}_s > 0.66$, all $P < 0.038$). In the calving and summer seasons of both 2002 and 2003, female grizzly bears avoided areas with low fragmentation (all $\beta_i < -0.178$, all $P < 0.001$) and selected low to moderate elevations (approx. 1,100–1,350 m; all $P < 0.001$). In the calving seasons, grizzly bears selected highly fragmented areas (both $\beta_i > 0.226$, both $P < 0.001$) with some variation in the selection and avoidance of vegetation classes between years. In the summers female grizzly bears avoided Spruce, Non-vegetated areas, and the Alpine classes (all $\beta_i < -0.186$, all $P < 0.050$) and selected Shrub, Subalpine, and Burned-disturbed areas (all $\beta_i > 0.317$, all $P < 0.050$).

Variation was high in the use of resources among wolf packs. There were some similarities, however, in the pooled models estimating predation risk to woodland caribou by gray wolves between years and within seasons. In the 2002–2003 calving seasons, gray wolves avoided areas with low fragmentation (both $\beta_i < -0.368$, both $P < 0.050$) and eastern and western exposures (both $\beta_i < -0.270$, both $P < 0.050$). They selected the Shrub class (both $\beta_i > 0.659$, both $P < 0.050$) and areas with no aspect (both $\beta_i > 0.720$, both $P < 0.050$). In the 2002 and 2003 summers, wolves again selected for areas with less slope (2002: $\beta_i = -0.089$, $P < 0.001$) and no aspect (2003: $\beta_i = 0.381$, $P < 0.050$).

Few characteristics of predation risk in calving areas differed between years. Grizzly bear risk and the distance to areas of high grizzly bear risk did not change from 2002 to 2003 in any calving area or on the landscape during calving or in summer (all $P > 0.115$). Nor did the gray wolf risk and distance to areas of high

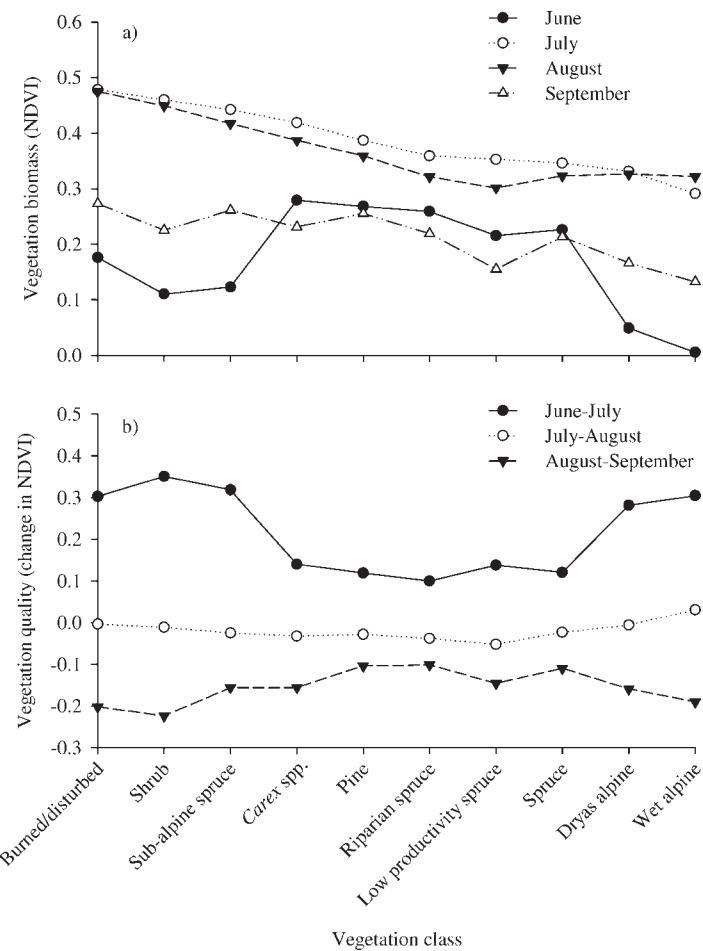


Figure 5. Mean monthly vegetation biomass and quality ($n = 2,062$, all SE < 0.004) as measured by modeled Normalized Difference Vegetation Index (NDVI) and change in modeled NDVI by vegetation class in the Greater Besa-Prophet area, northern British Columbia, Canada. (a) NDVI was obtained from 4 Landsat images (4 Jun, 22 Jul, 15 Aug, and 16 Sep 2001); (b) change in NDVI was calculated from the differences between images. Lines represent time frames for which images were acquired.

gray wolf risk differ (all $P > 0.205$), except in the Foothills. Gray wolf risk was higher in 2002 than 2003 in the Foothills, but only during the calving season ($P = 0.049$). Consequently, because predation risk appeared to change little across years within calving areas and the landscape, all predation-risk data were pooled across years to facilitate evaluating trends in risk at all scales of analyses.

Models to define the large-scale characteristics of vegetation (biomass and quality) explained the variation in NDVI adequately to exceptionally well (all $P < 0.001$) for the 4 June (adjusted $R^2 = 0.623$), 22 July ($R^2 = 0.649$), and 15 August ($R^2 = 0.850$) 2001 Landsat images. Vegetation class and elevation explained most of the variation within model sets for all images (as in Lay 2005:77). Normalized Difference Vegetation Index estimates for non-vegetated classes (Gravel bar, Rocks, Rock-crustose, and Water) were lower than all vegetated classes at their peak values in the 22 July image ($\bar{x} = 0.066 \pm 0.009$ SE; Lay 2005). All vegetative classes increased in NDVI (biomass) from June to July, remained relatively constant from July to August, and then declined in NDVI between the August and September images (Fig. 5a). During calving (4 Jun image), the coniferous and *Carex* spp.

vegetation classes had the highest vegetation biomass while the Alpine class had the lowest. In summer (22 Jul), the Burned-disturbed, Shrub, Subalpine spruce, and *Carex* spp. classes were highest in vegetation biomass and alpine areas were still the lowest (Fig. 5a). Alpine areas, however, were as high in vegetation quality because these areas experienced high vegetative change in NDVI from calving to summer (Fig. 5b). Vegetation quality changed little from July to August and then showed a decline in greening of vegetation (senescence, negative change in NDVI) from August to September.

Predation risk, vegetation, and topographical characteristics varied among calving areas in both the calving and summer seasons (all $H_{3, 958} > 27.91$, all $P < 0.001$; Table 5). The Foothills area had higher grizzly bear risk and was closer to areas of high grizzly bear risk than the overall landscape and the other calving areas (all $P < 0.001$). The North Prophet had lower grizzly bear risk than the landscape and was farthest from areas of high grizzly bear risk during calving ($P < 0.001$). In summer, trends in grizzly bear risk in the North Prophet were similar to calving, except the distance to grizzly bear risk did not differ from the Western High Country ($P = 1.000$; Table 5). Between seasons, predation risk within calving areas and the landscape did not change (all $P > 0.163$), except in the Western High Country where predation risk was lower in calving than summer ($P < 0.001$; Fig. 6). The Foothills, the North Prophet, and the landscape, however, were closer to areas of high grizzly bear risk in the summer than in calving ($P = 0.043$). At calving sites within each calving area, woodland caribou chose sites in the Foothills ($P = 0.043$) and North Prophet ($P = 0.031$) that had lower grizzly bear risk than what was available within those areas during calving; the calving sites in the Foothills also were farther than random from areas of high grizzly bear risk ($P = 0.007$). In summer, the Western High Country calving sites ($P = 0.019$) were closer to areas of high grizzly bear risk.

Relative to gray wolves, calving areas during the calving season were farther away from areas of high gray wolf risk than randomly encountered on the landscape and were lower in predation risk than the landscape (all $P < 0.001$) except for the Foothills ($P = 0.176$; Table 5). The Foothills had higher gray wolf risk and was closer to areas of high risk than other calving areas (all $P < 0.001$). Trends in predation risk and distance to high-risk areas during summer were similar to the calving season, except the Foothills no longer differed from the landscape ($P = 1.000$). Between seasons, gray wolf risk significantly increased from calving to summer within each calving area (all $P < 0.001$), although predation risk on the landscape did not change ($P = 0.807$; Fig. 6). Distance to areas of high gray wolf risk decreased within all calving areas and the landscape from calving to summer (all $P < 0.001$; Fig. 6). At calving sites, gray wolf risk was lower and sites were farther from areas of high gray wolf risk than randomly on the landscape (all $P < 0.001$). Calving sites within the Western High Country had higher gray wolf risk than that calving area during calving ($P = 0.003$) and in summer ($P = 0.008$).

During calving, calving areas had lower vegetation biomass and were farther from areas of high biomass than randomly available on the landscape ($P < 0.001$; Table 5). Among calving areas, the Foothills had the highest vegetation biomass and was closer to

Table 5. Large-scale characteristics of predation risk from grizzly bears and gray wolves, and vegetation biomass and quality (as determined from the Normalized Difference Vegetation Index [NDVI]) at random points and calving sites within the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas of woodland caribou in the Greater Besa-Prophet area (GBPA), northern British Columbia, Canada, 2002–2003. Characteristics of random points sharing the same letter were not significantly different among calving areas. Characteristics of calving sites marked with an asterisk (*) indicate significant differences ($P \leq 0.05$) from random points within that calving area.

| Season | Characteristic | FTHILLS | | WHC | | NP | | Landscape (GBPA) | |
|----------------------|---|-----------|-------|-----------|-------|-----------|-------|------------------|--------|
| | | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE |
| Random points | | | | | | | | | |
| Calving | Bear risk | 0.63a | 0.008 | 0.49bc | 0.014 | 0.47c | 0.016 | 0.52b | 0.008 |
| | Distance to areas of high bear risk (m) | 175a | 12.2 | 475b | 36.1 | 874c | 71.1 | 1,193b | 120.8 |
| | Wolf risk | 0.46a | 0.008 | 0.35b | 0.011 | 0.34b | 0.014 | 0.49a | 0.009 |
| | Distance to areas of high wolf risk (m) | 838a | 37.4 | 1,567b | 85.1 | 1,910b | 124.6 | 739c | 41.6 |
| | Biomass (NDVI) | 0.10a | 0.006 | 0.03b | 0.006 | 0.03b | 0.007 | 0.14c | 0.005 |
| | Distance to areas of high biomass (m) | 386a | 27.0 | 666b | 39.0 | 754b | 52.5 | 292c | 20.2 |
| | Bear risk | 0.61a | 0.012 | 0.43b | 0.017 | 0.46b | 0.025 | 0.53c | 0.009 |
| | Distance to areas of high bear risk (m) | 130a | 10.6 | 463b | 35.4 | 386b | 42.8 | 447b | 33.4 |
| | Wolf risk | 0.53a | 0.012 | 0.41b | 0.018 | 0.43bc | 0.022 | 0.51ac | 0.011 |
| | Distance to areas of high wolf risk (m) | 300a | 18.9 | 536b | 37.2 | 591b | 58.9 | 391a | 23.8 |
| Summer | Biomass (NDVI) | 0.34a | 0.007 | 0.16b | 0.014 | 0.20b | 0.019 | 0.31a | 0.008 |
| | Distance to areas of high biomass (m) | 123a | 10.3 | 457b | 35.5 | 421b | 45.2 | 273c | 18.2 |
| | Quality (change in NDVI) | 0.67a | 0.016 | 0.34b | 0.028 | 0.43bc | 0.039 | 0.47c | 0.014 |
| | Distance to areas of high quality (m) | 65a | 8.4 | 276b | 25.9 | 173c | 28.9 | 222bc | 14 |
| | Slope (°) | 25a | 0.7 | 26a | 0.9 | 25a | 1.0 | 19b | 0.6 |
| | Elevation (m) | 1,611a | 14.0 | 1,857b | 18.2 | 1,881b | 24.8 | 1,456c | 18.6 |
| | Bear risk | 0.57* | 0.021 | 0.54 | 0.022 | 0.38* | 0.025 | 0.52 | 0.017 |
| | Distance to areas of high bear risk (m) | 277* | 38.1 | 425 | 68.9 | 920 | 175.9 | 466 | 58.0 |
| | Wolf risk | 0.41 | 0.024 | 0.45* | 0.026 | 0.27 | 0.029 | 0.39* | 0.018 |
| | Distance to areas of high wolf risk (m) | 793 | 82.4 | 1304 | 222.7 | 2532 | 369.2 | 1347* | 149.2* |
| Calving to summer | Biomass (NDVI) | 0.04* | 0.015 | 0.07* | 0.017 | 0.001 | 0.011 | 0.04* | 0.10 |
| | Distance to areas of high biomass (m) | 494* | 56.2 | 504.1 | 109.3 | 1113* | 91.2 | 627* | 61.7 |
| | Bear risk | 0.61 | 0.039 | 0.52 | 0.053 | 0.29 | 0.028 | 0.51 | 0.031 |
| | Distance to areas of high bear risk (m) | 109 | 23.3 | 208* | 69.2 | 440 | 66.9 | 215 | 35.3 |
| | Wolf risk | 0.49 | 0.033 | 0.54* | 0.046 | 0.34 | 0.033 | 0.48 | 0.025 |
| | Distance to areas of high wolf risk (m) | 304 | 60.5 | 284 | 72.4 | 536 | 56.3 | 345 | 40.8 |
| | Biomass (NDVI) | 0.34 | 0.014 | 0.28* | 0.033 | 0.14 | 0.040 | 0.28* | 0.019 |
| | Distance to areas of high biomass (m) | 139 | 24.7 | 242 | 66.5 | 508 | 58.5 | 254 | 35.3 |
| | Quality (change in NDVI) | 0.79 | 0.026 | 0.60* | 0.062 | 0.42 | 0.104 | 0.64* | 0.039 |
| | Distance to areas of high quality (m) | 13* | 9.2 | 116* | 57.1 | 100 | 36.2 | 69* | 23.6 |
| Calving sites | Slope (°) | 28 | 1.6 | 17* | 1.9 | 23 | 2.7 | 22 | 1.3 |
| | Elevation (m) | 1,767* | 29.6 | 1,783 | 38.3 | 2,033* | 30.6 | 1,828* | 24.9 |

areas of high biomass ($P < 0.001$). Trends in summer were similar to calving except there was no difference in vegetation biomass between the Foothills and the landscape ($P = 1.000$) and the Foothills was closer to areas of high biomass than the landscape ($P < 0.001$; Table 5). Vegetation biomass increased and the distance to areas of high biomass decreased from calving to summer in all calving areas and the landscape (all $P < 0.001$; Fig. 6). All calving sites had lower vegetation biomass than encountered on the landscape ($P < 0.001$). Vegetation biomass was lower at calving sites than was available in the Foothills ($P = 0.006$), but higher in the Western High Country in the calving season ($P = 0.032$). All calving sites were farther from areas of high vegetation biomass than was available in calving areas ($P < 0.030$). In summer, all calving sites ($P = 0.003$) were lower in vegetation biomass than the landscape.

Relative to vegetation quality, the Foothills was higher in quality and closer to areas of high quality than other calving areas (all $P < 0.019$) and the landscape (all $P < 0.001$; Table 5). In contrast, the Western High Country was lower in vegetation quality than the landscape ($P = 0.002$). The North Prophet, with insignificantly

higher vegetation quality than the Western High Country ($P = 0.086$), was the next closest to areas of higher-quality vegetation. All the calving sites chosen by woodland caribou were higher in vegetation quality and closer to areas of high quality than found on the landscape (all $P < 0.001$). Western High Country calving sites were higher in vegetation quality ($P = 0.006$) and closer to areas of high quality in that calving area ($P = 0.049$; Table 5). In the Foothills, woodland caribou also selected calving sites closer to areas of higher vegetation quality than random ($P = 0.019$).

Topography varied among calving areas, the landscape, and calving sites (Table 5). Calving areas were steeper and higher than the overall landscape, and the Foothills was lower in elevation than other calving areas (all $P < 0.001$). Within calving areas, slopes at the Western High Country calving sites were not as steep as random points ($P = 0.001$). Except for the Western High Country ($P = 0.299$), calving sites compared to calving areas (Foothills: $P < 0.001$; North Prophet: $P = 0.025$) and all calving sites compared to the landscape were higher in elevation ($P < 0.001$).

Vegetation and predation-risk characteristics were positively related, with few exceptions, in all seasons for all calving areas and

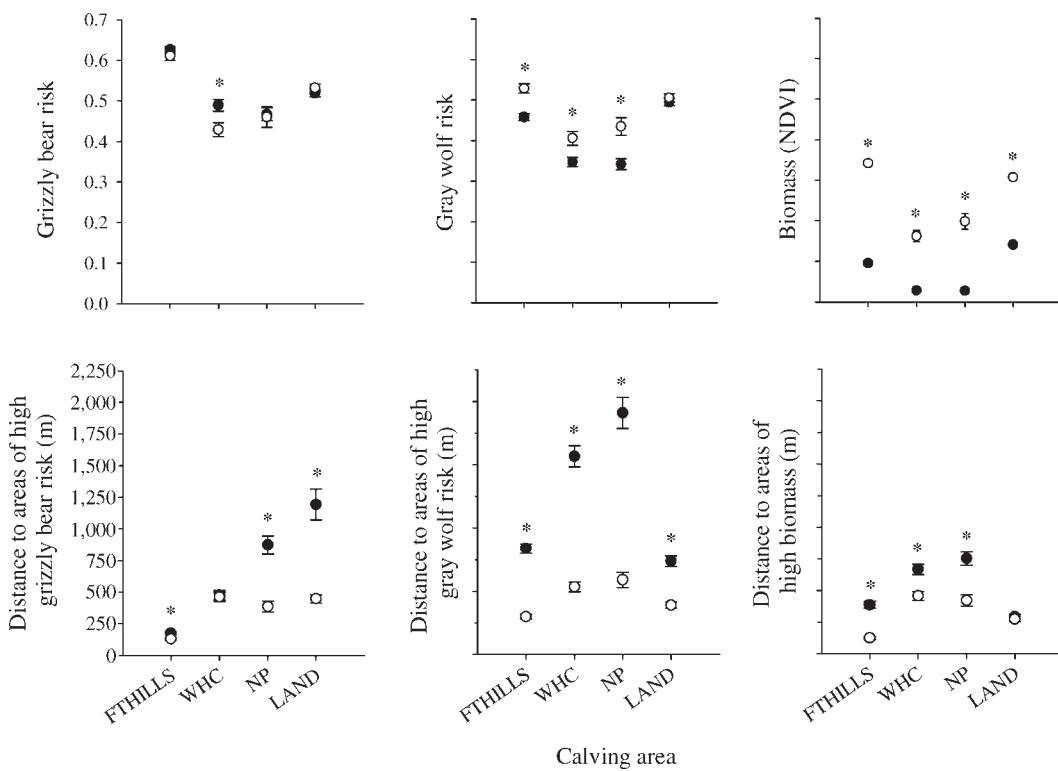


Figure 6. Changes in characteristics of predation risk by grizzly bears and gray wolves, and vegetation biomass as measured by the Normalized Difference Vegetation Index (NDVI; $\bar{x} \pm \text{SE}$) from calving (●) to summer seasons (○) for random points within the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas of woodland caribou and in the Greater Besa-Prophet landscape (LAND) of northern British Columbia, Canada, 2002–2003. Significant differences between seasons are indicated with an asterisk (*).

the landscape (all $P < 0.030$; Table 6). Exceptions were in the Foothills, where there was no relationship between vegetation quality and grizzly bear risk ($P = 0.583$) and a negative relationship between vegetation quality and gray wolf risk during calving ($P = 0.011$). Cost (i.e., change in predator-specific risk per unit of vegetation biomass or quality, measured as the slope of the relationship between predation risk and a vegetation characteristic) varied among predators, vegetation characteristics, calving areas, and seasons (Table 6). During calving, the cost in predation risk by grizzly bears and gray wolves associated with vegetation biomass was lower in the Foothills than the other 2 calving areas;

the North Prophet was the highest in cost for grizzly bear risk (all $P < 0.009$). For both calving and summer, the cost in gray wolf risk per unit biomass was higher in the Western High Country than the landscape (all $P < 0.009$). In summer, the cost in grizzly bear risk per unit biomass was higher in the Foothills than the landscape ($P < 0.009$). The cost in predation risk per unit quality usually did not differ among calving areas and the landscape during calving or summer for grizzly bears or gray wolves (Table 6). The exception was in the Foothills, where cost in gray wolf risk was lower than the other calving areas and the landscape (all $P < 0.009$). Relative to seasonal change in predation risk, cost in

Table 6. Cost (i.e., change in predator-specific risk per unit of vegetation) measured as the slope $\pm \text{SE}$ of the linear relationship between predation risk from grizzly bears and gray wolves versus vegetation biomass and quality (determined from the Normalized Difference Vegetation Index [NDVI]) for random points within the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas of woodland caribou in the Greater Besa-Prophet area (GBPA), northern British Columbia, Canada, 2002–2003. Costs sharing the same letter were not significantly different among calving areas. Costs marked by an asterisk (*) in the summer differed from the calving season.

| Season | Predation risk vs. vegetation characteristic | FTHILLS | | WHC | | NP | | Landscape (GBPA) | |
|---------|--|-----------------|------|---------|------|--------|------|------------------|------|
| | | Slope | SE | Slope | SE | Slope | SE | Slope | SE |
| Calving | Bear risk vs. biomass | 0.24a | 0.09 | 1.79 | 0.08 | 1.35b | 0.17 | 0.25a | 0.07 |
| | Wolf risk vs. biomass | 0.86a | 0.08 | 1.47 | 0.10 | 1.31ac | 0.14 | 1.05a | 0.06 |
| | Bear risk vs. quality | No relationship | | 0.30 | 0.03 | 0.24a | 0.03 | 0.28a | 0.02 |
| | Wolf risk vs. quality | -0.09a | 0.04 | 0.23 | 0.02 | 0.22b | 0.03 | 0.24b | 0.03 |
| Summer | Bear risk vs. biomass | 1.33a* | 0.07 | 1.17ab* | 0.04 | 1.21ab | 0.05 | 1.01b* | 0.03 |
| | Wolf risk vs. biomass | 1.16ab | 0.08 | 1.31b | 0.05 | 0.99 | 0.06 | 0.93a | 0.05 |
| | Bear risk vs. quality | 0.47a* | 0.04 | 0.53a* | 0.02 | 0.54a* | 0.04 | 0.55a* | 0.02 |
| | Wolf risk vs. quality | 0.33a* | 0.05 | 0.52a* | 0.03 | 0.46a* | 0.03 | 0.38a | 0.03 |

grizzly bear risk per unit biomass increased from calving to summer in the Foothills and on the landscape, and decreased in the Western High Country (all $P < 0.050$). Cost in predation risk by both grizzly bears and gray wolves per unit quality increased in every calving area (all $P < 0.050$; Table 5).

Models using large-scale characteristics (predation risk, vegetation biomass and quality) to predict survival of calves in summer showed poor discrimination (all ROC < 0.657) when movement was not included. All summer models improved, as indexed by decreased AIC_c (3.00–9.14) and increased discrimination (0.06–0.23), when movement was added as a covariate (Table 4). The most parsimonious models (i.e., $E_r < 2.00$) were Movement (ROC = 0.740) and Movement + Distance to high wolf risk + Distance to high bear risk (ROC = 0.820). These models were averaged, and the distance to gray wolf and grizzly bear risk covariates did not affect the odds of survival (i.e., e^{β_i} not different from 1.00; both $P > 0.253$). The odds ratio for woodland caribou calves that stayed at the calving site ($e^{\beta_i} = 0.34 \pm 0.12$ SE, $P = 0.002$) or moved away (2.96 ± 0.12 SE, $P = 0.002$) during the summer $\neq 1.00$. Therefore, if a calf remained at its calving site to the end of summer, with other covariates in the model held constant, the odds of survival decreased by approximately 66%. Models using large-scale characteristics to predict movement of woodland caribou calves from calving sites during the calving and summer seasons had poor discrimination (all ROC < 0.660). There were no differences in the independent effects of predation risk and vegetation characteristics on survival of calves and movement events during any season (all $P > 0.082$).

DISCUSSION

Behavioral plasticity in life-history strategies may enable animals to decrease predictability to large predators in space and time (Bowyer et al. 1999, Mitchell and Lima 2002). Calving areas of woodland caribou in the GBPA offered parturient animals a diverse landscape relative to avoiding predation risk and acquiring forage. This diversity provided options for female woodland caribou that may increase the likelihood of persistence under changing environmental and ecological conditions.

Hierarchical Scales and Trade-Offs in Predation Risk and Forage for Calving Caribou

The importance of predation risk in the selection of calving areas and calving sites by woodland caribou varied by predator and the scale of analyses. Minimizing grizzly bear risk was important in the selection of calving sites within calving areas, but not at the scale of the calving area. Woodland caribou calved in areas with grizzly bear risk that was no different or higher than available on the landscape in 2 of the 3 calving areas. The Foothills was the riskiest area in which to calve and remain during the summer, as grizzly bear risk was higher, and random locations within this area were closer to areas of high grizzly bear risk in both seasons. Within this high-risk strategy and in the North Prophet, however, calving woodland caribou minimized the predation risk by selecting low-risk, high-elevation sites that increased the distance between calving sites and areas of high grizzly bear risk (Table 5). Although grizzly bear risk to woodland caribou neonates has not been previously reported at the scale of the calving site or calving area, grizzly bears have been documented to be effective predators

of caribou neonates (Adams et al. 1995, Young and McCabe 1997).

Components of gray wolf risk, in contrast, were generally important in the selection of calving areas (Bergerud et al. 1984, Bergerud 1992), but not in selecting calving sites within those areas. Calving areas (except for the Foothills) had lower gray wolf risk than what was found on the landscape, and all calving areas were farther than random from areas of high gray wolf risk during the calving season. Again, the Foothills was the riskiest area, as it was higher in gray wolf risk and closer to areas of high gray wolf risk than the other calving areas during calving and summer. Our findings are consistent with previous research regarding the importance to woodland caribou of spacing away to minimize gray wolf risk (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1991; Bergerud 1992, 1996; Rettie and Messier 2000) and proximity to other ungulates (Bowyer et al. 1999) at larger scales. There was considerable variation, however, in gray wolf risk and distances to areas of high gray wolf risk (approx. 800–2,000 m) among calving areas (Table 5). No calving sites within any calving area maximized distance from areas of high gray wolf risk within that area.

We did not include wolverine predation as a component of predation risk in our analyses because the magnitude was totally unexpected. To our knowledge, wolverines in North America have not been documented as the main predator of caribou neonates. If we had suspected that wolverines were the primary predator of neonates <14 days of age in our study, we would have attempted to define this risk, albeit logically difficult and expensive to obtain an adequate sample (Krebs et al. 2004). Although prey species may alter foraging patterns based on the presence of predator chemical cues (Kats and Dill 1998, Herman and Valone 2000), particularly in the case of a mustelid predator, we do not believe that woodland caribou distributed themselves on the landscape to minimize the risk of wolverine predation. Rather, woodland caribou probably calved in response to the distribution of the most common predators on both adults and neonates. The calving areas happened to be in denning habitat for wolverines. Natal and weaning dens of wolverines and the associated alpine and subalpine communities likely provide protection from their predators (e.g., conspecifics and gray wolves; Persson et al. 2003, Krebs et al. 2004) while increasing access to food sources and locations for food storage (Magoun and Copeland 1998). Caribou neonates at calving sites may have been detected by wolverines with olfactory cues; we did not, however, measure prevailing winds in calving areas or at calving sites to determine if parturient woodland caribou minimized this potential. Winds generally become less predictable at smaller scales, and localized winds in rugged, mountainous areas with glacial cover and permanent snowfields are highly variable in speed and direction (Obleitner 1994). We suspect it was unlikely that caribou or wolverines were responding to predictable chemical or olfactory cues.

The importance of nutrient acquisition in the selection of calving areas by woodland caribou varied with vegetation characteristic and the scale of analyses. Avoiding areas of high vegetation biomass appeared to be most important, as also reported in other caribou studies (Barten et al. 2001, Griffith et al. 2002). Woodland caribou calved in areas that were low in

vegetation biomass and that increased their distance from areas of high biomass during calving and summer. The Foothills was the highest in vegetation biomass and closer to areas of high biomass (approx. 400 m) than the other calving areas, and in some cases much closer (e.g., North Prophet, approx. 750 m; Table 5). Within calving areas, however, response to different levels of vegetation biomass was variable. Calving sites in the high-biomass Foothills area were significantly lower in vegetation biomass, whereas sites in the low-biomass Western High Country were significantly higher in vegetation biomass. The contribution of vegetation quality to the selection of calving areas and calving sites was variable. The Foothills was higher in vegetation quality and closer to areas of high quality than the other calving areas and the landscape. Conversely, the Western High Country was lower in vegetation quality and farther away from areas of high quality than generally found on the landscape. The importance of vegetation quality was more apparent in the selection of calving sites (as in Griffith et al. 2002), which were higher in vegetation quality and closer to areas of higher quality than what was available in both low- and high-quality calving areas.

Calving woodland caribou may have used topography to minimize predation risk or increase access to forage, as evidenced by the selection of certain topographical features of calving areas and calving sites. Topography may increase separation (e.g., altitudinally) from predators or serve as a form of escape terrain (e.g., steep slopes; Bergerud et al. 1984, 1990; Bergerud and Page 1987; Barten et al. 2001). Terrain in all the calving areas of our study was steeper and higher in elevation than what was randomly available on the landscape, although elevation varied among calving areas. The high-risk Foothills area was lower (approx. 1,600 m) than the other calving areas (approx. 1,870 m; Table 5). Within the Foothills area, woodland caribou selected calving sites higher in elevation than what was available, whereas woodland caribou in areas with lower predation risk showed no selection for higher elevations. In addition, variation in topography may have provided better microsite characteristics for vegetation (Barten et al. 2001); calving woodland caribou in the Western High Country selected for gentler slopes than what was available within this area.

Variation and trends in the large-scale components of predation risk by grizzly bears and gray wolves, topographical features, and vegetation biomass and quality among calving areas and calving sites suggest that woodland caribou made trade-off decisions at several spatial scales. Avoidance of high vegetation biomass within calving areas (Whitten and Cameron 1980, Bergerud et al. 1984, Heard et al. 1996), and selection for areas and calving sites higher in vegetation quality (Bowyer et al. 1999, Barten et al. 2001), suggested that calving woodland caribou foraged selectively in an attempt to address their nutritional requirements (Whitten and Cameron 1980) and to minimize their predation risk (Barten et al. 2001, Griffith et al. 2002).

All components of predation risk and vegetation were higher in the Foothills than the other calving areas, and based on these data, we assumed animals were taking an increased cost in predation risk for access to relatively higher vegetation biomass and/or quality. Within the high-risk Foothills area, woodland caribou calved at sites low in vegetation biomass that increased the separation from areas of high biomass and this likely decreased the susceptibility of calving woodland caribou and their calves to predation, as

evidenced by cost in predation risk per unit biomass (Bowyer et al. 1998a, 1999). Calving woodland caribou that used this area did so at a higher predation risk, but not at a higher cost in predation risk per unit vegetation component. The relative cost in predation risk by both grizzly bears and gray wolves per unit biomass was lower in the high-risk Foothills area than the other calving areas during calving, and there was no cost in increased predation risk associated with foraging in areas with higher vegetation quality (Table 5). Non-parturient and male caribou and moose are known to forage in areas higher in vegetation biomass and at lower elevations than parturient caribou. Avoidance of these areas, therefore, may have been in response to the presence of conspecifics, other ungulates, and/or predators (Bergerud et al. 1984, Bergerud and Page 1987, Seip 1991, Barten et al. 2001). Parturient caribou probably foraged selectively in areas of relatively high vegetation quality to meet the nutritional requirements of lactation while avoiding areas of high vegetation biomass to minimize predation risk (Barten et al. 2001, Griffith et al. 2002). This high-risk strategy also may have increased opportunities for woodland caribou to calve in sites with access to, or that were in, areas of higher vegetation quality with no increase in predation risk per unit quality. We recorded no early predation mortalities (<14 days) in the Foothills, and our data do not support observations that caribou disperse to calve regardless of vegetative phenology (Bergerud et al. 1984, Bergerud and Page 1987).

Alternatively, in the Western High Country, calving woodland caribou selected calving sites that were relatively higher in vegetation biomass and quality in an area that had the highest cost in gray wolf risk per unit biomass. Most of this area is unsuitable (i.e., largely non-vegetated with steep and rugged terrain) for large, productive areas of vegetation. Woodland caribou calved at sites in hanging valleys, and did so at a high cost in predation risk per unit forage component within that calving area. Additionally, in the North Prophet, calving woodland caribou did not select sites lower in vegetation biomass or gray wolf risk even though cost in predation risk for biomass was high. Rather, woodland caribou selected non-vegetated, high-elevation calving sites that were low in grizzly bear risk and that increased separation from areas of high vegetation biomass. In this area, minimizing the grizzly bear risk appeared to be more important than minimizing gray wolf risk. We do not see any reason within our mortality data for this sensitivity to grizzly bear risk. This behavior may be in response to the density of grizzly bears and, subsequently, an increased encounter rate; we do not, however, have any estimates of bear density in the North Prophet.

Predictions of Calf Survival

Despite the spatial variation in predation risk, vegetation, and cost characteristics, survival of woodland caribou calves and cause-specific mortality did not differ among calving areas. There appears to be no proximate benefit(s) (i.e., higher birth mass or increased survival through summer) of calving in one area over another. Models using small- and large-scale characteristics of calving sites, however, performed well in predicting survival of calves during calving and summer, respectively.

Herbaceous and shrub cover were excellent predictors of early calf survival, with cover of shrubs increasing the odds of survival (approx. 13% per 1% increase in shrub cover) through the calving

season (Table 4). Deciduous shrubs, primarily in the form of willow and bog birch, could obscure neonates from the view of predators (Bowyer et al. 1998a, 1999; White and Berger 2001) and/or be an important spring forage for parturient woodland caribou (Boertje 1984, Ferguson et al. 1988, Crête et al. 1990a). The role of herbaceous cover in decreasing the survival of woodland caribou calves was less clear. Herbaceous and shrub cover were inversely correlated, but this relationship may have been confounded by measurements at different scales (i.e., plot vs. line-intercept data). It is possible that the influence of shrubs on calf survival was an effect of calving area because the Foothills had higher cover of shrubs than the other calving areas and only 1 mortality during the calving season (age of calf = 14 days). The model using large-scale characteristics with calving area as a covariate, however, did not perform well in predicting survival of calves for any season. Cliffs may be important refugia for calving woodland caribou from terrestrial predators, but models with cliff-intercept data could not be evaluated because no mortalities occurred at sites near (<50 m) these topographical features. The poor model performance of small-scale characteristics in predicting calf survival through summer suggested that either the importance of small-scale characteristics of calving sites to calf survival diminished during the summer and/or that other factors (e.g., movement away from calving sites) became more important for calf survival.

Large-scale characteristics of calving sites were not good predictors of woodland caribou calf survival; this is not surprising given the cause-specific mortality data. Calving areas appeared to have a high risk of wolverine predation during calving, as the first increase in mortality was caused by wolverines, with eagles and grizzly bears to a lesser extent (see Fig. 4a,b). Consequently, the influence of predation risk by grizzly bears and gray wolves was not important in our models predicting early calf survival. We underestimated the role of wolverines in the survival of woodland caribou neonates through the calving season. Although wolverines in Norway are known to feed on reindeer during the denning period (Landa et al. 1997, Vangen et al. 2001), Adams et al. (1995) observed only 1 wolverine mortality of 89 collared caribou neonates that were killed in Denali National Park, Alaska, USA. Wolverines occasionally kill adult woodland caribou (E. LoFroth, British Columbia Ministry of Environment, personal communication). The calving season for woodland caribou in our study corresponded to the time when juvenile wolverines are able to leave the natal den and begin to travel with their mothers (Magoun 1985).

Movement was an important variable in our models to predict survival of calves in the summer. Twenty-one cow-calf pairs left the calving sites when calves were 2–4 weeks of age (Fig. 4a). Movement away from calving sites significantly increased the odds of calf survival (approx. 196% when other covariates were held constant). The reasons for these movements were not clear, but the timing of movements suggested that woodland caribou may have responded to changes in vegetation, nutritional demands, and/or predation risk at smaller temporal scales than those measured in our predation-risk and vegetation models. Greening of vegetation and timing of change in vegetative phenology are important attributes of forage quality for lactating caribou

(Oosenbrug and Theberge 1980, Post and Klein 1999, Griffith et al. 2002, Post et al. 2003). The first peak of movement followed an increase in mortality (Fig. 4a,b) that corresponded with the time of high nutritional demands for lactation (White and Luick 1984) and the time when lactating females experience their worst condition of the year (Chan-McLeod et al. 1999). Although we cannot rule out insect abundance and associated harassment levels (Toupin et al. 1996) as a contributing cause for movement of woodland caribou on the landscape, our personal observations suggest that insect harassment during calving and summer was low or nonexistent within the calving areas in 2002 and 2003. Movement, therefore, was more likely in response to the changes in vegetation within calving areas.

In a mountainous environment, vegetative change is likely to vary both spatially and temporally among vegetation classes, aspects, and elevations (Reed et al. 1994). Our index of vegetation quality was based on areas of vegetation that experienced the largest amount of growth from calving to the summer season, but we can offer no estimate as to the rate or timing of onset of that growth. The relationship between the change in NDVI and vegetation quality as it references forage value at smaller temporal scales requires further in-depth study. Hardy and Burgan (1999) noted that from early to late summer, changes in the profiles of NDVI were functionally related to moisture content of understory vegetation while overstory NDVI values remained stable throughout the summer. Additionally, crude protein is positively correlated with altitude in early summer and negatively correlated in fall (Albon and Langtvn 1992). Our vegetation index of quality displayed a similar trend (Fig. 5b), in that the subalpine (Subalpine spruce) and alpine classes (Dry and Wet alpine) experienced the highest vegetative change from the calving to summer season; these are the areas where caribou calved. Based on 2 field seasons of observations and data on the timing of vegetation greening in similar systems and latitudes (Bunnell 1982), we are certain that the timing of vegetative change important to woodland caribou occurred between 4 June and 22 July (dates of Landsat imagery in 2001) in 2002 and 2003 within the GBPA. Woodland caribou, however, probably responded to the change in vegetative phenology as it happened, at a temporal scale smaller than the seasonal scale (Oosenbrug and Theberge 1980, Post and Klein 1999, Barten et al. 2001, Griffith et al. 2002, Post et al. 2003). Nonetheless, woodland caribou calved in areas (Foothills) or at sites (i.e., Foothills, Western High Country) near, or in, these areas of relatively high vegetative change between seasons.

A second extended peak in movement from calving sites (i.e., 8 cow-calf pairs) occurred during weeks 5–7 during the summer (Fig. 4a,b) following an increase in woodland caribou calf mortality. This timing appeared to coincide with the ability of gray wolves to leave the dens and, subsequently, a possible change in prey species in their diets (B. Milakovic, University of Northern British Columbia, unpublished data). Survival for woodland caribou calves was higher through calving than summer; gray wolves were responsible for 5 of the 8 identified mortalities in the summer season (Fig. 4b). The gray wolf risk increased and the distance to areas of high gray wolf risk decreased in all the calving areas from the calving to summer season. Nonetheless, calving

strategies of woodland caribou were relatively successful in minimizing losses of neonates to gray wolves during calving compared to other predators even though gray wolf risk was dynamic in the GBPA. Gray wolf predation has been identified as an important factor in survival of caribou calves, particularly for neonates (Gasaway et al. 1983, Bergerud et al. 1984, Bergerud and Elliot 1986, Bergerud and Page 1987, Seip 1992, Adams et al. 1995).

Woodland caribou started to form postcalving aggregations (approx. 20–40 cows and calves) in the Foothills and North Prophet calving areas at the end of June. This grouping behavior is contrary to observations by Poole et al. (2000), but similar to those of Bergerud et al. (1984). Concurrently, there was an increase in the cost of grizzly bear and gray wolf risk per unit of vegetation quality in all calving areas from the calving to summer season (Table 5). This suggested that grizzly bears and gray wolves could be responding to woodland caribou as a more predictable prey item (i.e., larger groups; Hebblewhite and Pletscher 2002) or were actively searching these areas of high vegetative change for other prey. Grizzly bears may be feeding on vegetation in these areas of high change (Nielsen et al. 2003), so this relationship was unclear; nevertheless, cost in grizzly bear predation risk per unit quality increased for woodland caribou using areas with higher vegetation quality. Alternatively, the gregariousness of caribou in late June could be a social response to the increased gray wolf risk within calving areas (Bøving and Post 1997, Barten et al. 2001, Hebblewhite and Pletscher 2002). A caribou with a calf could minimize predation risk by decreasing the chances of being selected from the group (Hamilton 1971), while simultaneously foraging in areas with higher vegetation biomass and/or quality (Molvar and Bowyer 1994, Bowyer et al. 1999, Kie 1999).

Implications for Understanding Successful Calving Strategies

The interpretation of our data was dependent on the spatial scale of analyses. Analyses of characteristics of all calving sites versus characteristics of random points on the landscape provided some information on large-scale processes to which woodland caribou may have responded, but often these pooled analyses collapsed important variation in predation-risk and vegetation characteristics. Conclusions from analyses at the landscape scale alone would have failed to provide insights into how animals responded to predation risk, vegetation, and topography in a hierarchical fashion at smaller spatial scales. Defining boundaries for the landscape and calving areas may have influenced our findings. We acknowledge that processes important to life-history requirements of woodland caribou and their predators are not constrained within the boundaries of the GBPA or our defined calving areas. Indeed, a few collared grizzly bears and a collared woodland caribou calf did leave the study area; collared woodland caribou, gray wolves, and grizzly bears moved among calving areas. Historical telemetry data (adult woodland caribou, gray wolves, and grizzly bears) and 2 yr of extensive observations (calving woodland caribou), however, provided good information on the distribution and social structure of animals in the GBPA, and these data were used to identify important areas for the capturing and collaring efforts.

The assumption that grizzly bear and gray wolf GPS data were

representative samples of animal locations has some limitations. Fix-rate bias in GPS data has been reported for areas with varied topography or cover types (Dussault et al. 1999, D'Eon et al. 2002, Taylor 2002) and animals with distinct diurnal behavior patterns (e.g., moose [Moen et al. 2001], grizzly bears [D. C. Heard, British Columbia Ministry of Environment, unpublished data]), particularly when fix rates are low (<90%; Frair et al. 2004). This bias may have led to an over- or underestimate in the selection of any individual resource by gray wolves and grizzly bears, which would subsequently increase Type I and/or II error rates, respectively (Frair et al. 2004). Our ability to detect whether predation risk was actually the same between years was reduced because fix rates for gray wolves and grizzly bears were <90%. The responses of calving woodland caribou to predation risk, however, were similar, with some exceptions, to what has been observed, quantified, or postulated in other studies (Bergerud et al. 1984, 1990; Bergerud and Page 1987; Bergerud 1992; Seip 1992; Barten et al. 2001). The timing of calf mortality in summer coincided with an increase in gray wolf risk in all of our calving areas. Our results suggest that modeling predation risk with RSFs is a valid technique in evaluating predator-prey interactions at large spatial scales and may become more useful as bias in GPS fix rate is identified and corrected.

The use of nonparametric tests was also a concern because these tests usually have lower power than their parametric counterparts (Siegel 1956) and may have contributed to our inability to detect potential differences among calving areas and at calving sites within calving areas. Transformation of the data was a possibility, but we wanted to avoid further manipulation of modeled data. The conservative nature of nonparametric tests (i.e., higher *P*) may have helped to address some concerns of cumulative error throughout the modeling process, although error terms for RSFs integrated with raster and vector GIS and GPS data are difficult to quantify and remain a topic for future research (Corsi et al. 2000).

Parturient woodland caribou may have responded to factors that coincided with predation risk rather than to predation risk per se. As in Johnson (2000), we can estimate animals' responses only to actual and/or perceived predation risk (Lima and Dill 1990). Furthermore, what we perceived as responses to predation risk may have been responses to the alternative prey of gray wolves and/or grizzly bears. We submit that our models of predation risk tracked relative predation risk in the GBPA at the seasonal scale, but how woodland caribou "measured" this predation risk is uncertain. We do not know if woodland caribou were actively reducing predation risk or simply experiencing a reduced predation risk (Johnson 2000). Responses to predation risk may be a product of social learning (Lima and Dill 1990, Caro 1994, Byers 1997, Miller 2002), individual experience (Lima and Dill 1990), visual and/or chemical cues (Kats and Dill 1998, Herman and Valone 2000), and/or chance. Nonetheless, the predictable fashion in how animals responded to components of predation risk within calving areas (e.g., minimized small-scale grizzly bear risk in an area with high predation risk) and on the landscape suggested calving woodland caribou were sensitive to parameters of predation risk among spatial scales.

Despite these concerns, our results confirm the importance of

predation and vegetation characteristics to the distribution of calving woodland caribou. Parturient woodland caribou generally selected for areas higher in vegetation quality (i.e., vegetated areas with high change in NDVI) and data were consistent with research that has examined the importance of forage quality at large (Griffith et al. 2002) and small scales (Barten et al. 2001). Reducing gray wolf risk and the ability of woodland caribou to space away from gray wolves was important in selection of all calving areas (Bergerud et al. 1984), although variation in the components of predation risk was high among areas. In all calving areas, woodland caribou used small-scale features (e.g., cliffs, shrub cover, steeper slopes), movement, and/or possibly gregariousness (Molvar and Bowyer 1994) to minimize predation risk and cope with the increase in gray wolf risk from calving to summer. Small-scale features and movement had prominent effects on calf survival through calving and summer, respectively. A more precise measure of movement combined with measures of predation risk and vegetation characteristics at smaller temporal scales could provide further insights into important mechanisms defining woodland caribou–gray wolf interactions in multi-predator–multi-prey systems.

Behavioral plasticity by woodland caribou was high among calving areas, and although our data showed no proximate benefits to the strategy used in any one calving area, there may be factors that maximize reproductive fitness. Characteristics of vegetation affected the level of predation risk that woodland caribou took within a calving area. The high-risk strategy in the Foothills offered woodland caribou more opportunities to forage in areas of higher quality and possibly high vegetation biomass later in the summer. These characteristics could have increased the rate of mass gain in calves through the summer and allowed the maternal female to replenish body reserves (Reimers et al. 1983, Crête et al. 1990b), which are necessary for breeding and overwinter survival. Consequently, an improved condition in autumn could have direct effects on reproductive fitness and possibly increase calf survival through winter (Dauphiné 1976; Cameron et al. 1993; Cameron and Ver Hoef 1994; Adams and Dale 1998a,b; Cook et al. 2003). Benefits of lower risk areas were less apparent, as survival did not differ from the high-risk area. The persistence of several strategies, however, suggests that different areas could become more important if ecological conditions including ungulate and/or predator distributions and densities change (Bergerud 1983; Bergerud et al. 1984; Bergerud and Elliot 1986, 1998; Dale et al. 1994).

Diversity of vegetation, topography, and large mammals in the GBPA offered woodland caribou a diversity of choices among scales. Mechanisms (e.g., social learning [Caro 1994, Byers 1997], nutritional condition [Lima 1988, Boertje 1990, Clark 1994, Sweitzer 1996]) that may or may not drive selection of a risk-averse or risk-prone calving strategy (Stephens and Krebs 1986) remain an important area for research. In particular, there is a need to define the effects of a calving strategy on physiological parameters of calving woodland caribou and their offspring as well as on calf survival through winter. Current technologies and methodologies (e.g., remotely sensed data and indices of vegetative change, GPS telemetry, RSFs, ultrasound estimates of body fat, stable isotope ecology) are likely to improve and may

assist in identifying physiological and ecological conditions that drive woodland caribou to select areas to calve and the subsequent effects on reproductive fitness.

MANAGEMENT IMPLICATIONS

Reproductive parameters for female woodland caribou in the GBPA were generally typical, but better estimates of parturition rates would be useful to assist in monitoring population condition and trends. Pregnancy rates of 91.5% in the GBPA were within previously observed estimates (88–100%) for woodland (Seip and Cichowski 1996, Dzuz 2001, Mahoney and Virgl 2003, McLoughlin et al. 2003, Culling et al. 2005) and barren-ground caribou (Griffith et al. 2002). Estimates of parturition were highly variable between years (55.6% in 2002, 76.9% in 2003) and were probably related to small sample sizes when many of the GPS collars failed prior to calving. These estimates, however, did not differ from the 81% (range = 71–92%) documented for barren-ground caribou in Alaska (Griffith et al. 2002). Low parturition rates may be an indication of poor-quality winter and/or summer range because fetal adsorption and abortion, although rare (Dauphiné 1976, Cameron and Ver Hoef 1994), can result from poor body condition (Russell et al. 1998).

Calving peaked on 28 May with observations of woodland caribou with neonates ranging from 25 May to 10 June; these estimates are similar to calving dates of other woodland caribou herds (Oosenbrug and Theberge 1980, Vik Stronen 2000). Woodland caribou possibly calved earlier and later than this range because the calving season can last up to 4 weeks (Adams et al. 1995).

Because of its relatively easier access and current lack of protection (portions of the Western High Country and North Prophet fall within either the Redfern-Keily or Northern Rocky Mountains provincial parks), the Foothills area is most susceptible to anthropogenic alteration and activity. Woodland caribou cow-calf pairs should be ensured choices in routes from calving areas to summer range within the Foothills so that they can form postcalving aggregations that may be important to calf survival. Any disturbance during times of movement or the formation of postcalving aggregations may have direct (e.g., increased predation) and/or indirect consequences (e.g., displacement to lower quality summer range) to calf survival and population productivity. *Rangifer* spp. may be especially sensitive to anthropogenic disturbance during the postcalving period (Johnson et al. 2005). Currently, areas selected by woodland caribou within the Foothills are free of anthropogenic activity during the calving and summer seasons; this attribute and the aforementioned characteristics offer woodland caribou large areas from which to select sites that maximize reproductive fitness.

Often the spatial variation in components of predation risk (Creel and Winnie 2005) and vegetation characteristics is underestimated. Subsequently, management actions or human disturbance can negatively impact other species of interest, particularly in multi-predator–multi-prey systems (Bergerud 1974). Current management actions and future industrial development may negatively affect woodland caribou in the GBPA. Prescribed burning is a common management activity in the GBPA that targets south- and west-facing slopes with

forested cover. The objective of prescribed burning is to enhance Stone's sheep populations, but it may adversely affect caribou populations throughout the year by increasing numbers of moose and elk, thereby providing a more abundant food source for wolves, bears (Gasaway et al. 1983, Bergerud and Elliot 1986, Seip 1991, Ballard et al. 2000), and possibly wolverines. Preliminary selection models suggest that moose (K. Parker and M. Gillingham, University of Northern British Columbia, unpublished data), Stone's sheep (Walker 2005), grizzly bears, and wolves (B. Milakovic, University of Northern British Columbia, unpublished data) select for Burned-disturbed areas at some times during the year in the GBPA; elk in the area also probably benefit from burns (Peck and Peek 1991). If prescribed burns increase numbers of moose and elk, wolf numbers may also increase (Gasaway et al. 1983, 1992; Ballard et al. 2000). Grizzly bears may benefit from burning because they feed on early seral vegetation typical of recent burns (Nielsen et al. 2003) and the ungulates that are attracted to these areas (B. Milakovic, University of Northern British Columbia, unpublished data). Therefore, management activities that involve land clearing and burning activities may increase predation risk for woodland caribou (James et al. 2004). Caribou in Alaska (Joly et al. 2003) and Manitoba (Schaefer and Pruitt 1991) avoided burns <50 years old. Caribou in the Beverly herd of the Northwest Territories did not use burned areas until approximately 40–60 years postburn (Thomas 1998), although fires may benefit populations in the long term (>100 yr; Klein 1982, Thomas 1998).

Wolverines and wolves were important sources of mortality for calves <14 and >18 days of age, respectively. Observations and anecdotal evidence suggest the GBPA is productive wolverine habitat. In 2002–2003 there were active traplines on the southern and northern borders of the GBPA (the Sikanni and Muskwa rivers, respectively) whereas the central portion of the GBPA was untrapped. The untrapped area includes the Foothills and Western High Country calving areas. The central portion of the GBPA may, in effect, be an untrapped "refugium" for wolverines (Krebs et al. 2004) and possibly wolves. Activating traplines in this area may decrease mortality of woodland caribou neonates from wolverines, although calf survival of 88% was relatively high during the calving season. Wolves are already regularly trapped in the Sikanni drainage, and there are few restrictions on hunting wolves in the GBPA (British Columbia Ministry of Environment 2005:81).

SUMMARY

Understanding the relationships between predation risk and forage is imperative to help direct conservation and management activities (Pierce et al. 2004). We underestimated the role of wolverine predation on woodland caribou neonates in the GBPA and suggest that mesopredators (e.g., wolverines and coyotes) in other systems as well may play as important a role in population dynamics of ungulates as the larger predators (Bergerud 1983, Prugh 2004). In the system we studied, predation risk from gray wolves had an impact on where woodland caribou calved on the landscape, and the current distribution of parturient woodland caribou within the GBPA is likely the result of selective pressure as well as individual and group responses to the spatiotemporal

variation in predation risk and the components of vegetation. Predation risk (or its surrogate) may drive the selection of calving areas because spacing away from high wolf-risk areas was consistently important across all calving areas. During calving, woodland caribou avoided areas of high vegetation biomass, which were likely associated with increased predation risk, and did not consistently select for high vegetation quality at the scale of the calving area. At the calving sites, however, there were smaller scale-dependent trade-offs between predation risk and vegetation characteristics. Even so, woodland caribou consistently selected calving sites that were high in vegetation quality. Survival and causes of mortality were not different among the calving areas, but movements away from calving sites to increase access to forage and/or minimize gray wolf risk in the summer corresponded with higher calf survival. Landscape heterogeneity (Hundertmark 1997, Welch et al. 2000, Kie et al. 2002) and diversity, therefore, may allow trade-offs between predation risk and the forage quality that is needed to meet energetic demands of lactation and neonatal growth.

Behavioral plasticity as a life-history strategy during calving and summer is likely to be successful as long as caribou have "choices" on the landscape. If woodland caribou have fewer choices at large scales, they may become more predictable in space and time for their main predators and have difficulty meeting nutritional requirements, with possible consequences to survival, reproductive success, and, ultimately, population persistence. Choices available to woodland caribou at large scales appear to have a direct impact on how animals use smaller-scale features to maximize access to forage and/or minimize predation risk (Rettie and Messier 2000; Johnson et al. 2001, 2002a,b). Sensitivity of woodland caribou to the direct and indirect effects of anthropogenic (Bradshaw et al. 1997, Stuart-Smith et al. 1997, James and Stuart-Smith 2000, Dyer et al. 2001, Weclaw and Hudson 2004) and environmental disturbances (Schaefer and Pruitt 1991, Joly et al. 2003) has been well documented. Management or industrial activities that alter the distribution of woodland caribou or their main predators during calving and summer should be avoided until they can be evaluated for possible long-term effects on population productivity. This will become increasingly important if weather patterns, which affect the availability of forage by altering the timing of spring snows or greening of vegetation (Post and Klein 1999, Lenart et al. 2002, Weladji and Holand 2003; R. Farnell, Yukon Department of Environment, personal communication), and/or the ability of calving woodland caribou to disperse from areas of high predation risk (Bergerud et al. 1984, 1990; Bergerud and Page 1987; Seip 1991) become more unpredictable. The interactions of anthropogenic and climatic factors could have both direct and indirect consequences to the survival of woodland caribou neonates.

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Appendix A1. Animal identification (ID), date of capture, sex, and estimates for the date of birth (DOB), age, and mass of newborn woodland caribou calves captured in the Foothills (FTHILLS), Western High Country (WHC), and North Prophet (NP) calving areas within the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003.

| ID | Capture date | Sex | DOB | Age (days) | Mass (kg) | Calving area |
|------|--------------|-----|-------------|------------|-----------|--------------|
| C01C | 31 May 2002 | F | 27 May 2002 | 4 | 10.5 | FTHILLS |
| C02C | 31 May 2002 | F | 29 May 2002 | 2 | 10 | FTHILLS |
| C03C | 31 May 2002 | F | 29 May 2002 | 2 | 9.5 | FTHILLS |
| C04C | 1 Jun 2002 | M | 29 May 2002 | 2.5 | 8.5 | WHC |
| C05C | 1 Jun 2002 | F | 27 May 2002 | 5 | 9.5 | NP |
| C06C | 1 Jun 2002 | F | 30 May 2002 | 2 | 6.75 | WHC |
| C07C | 2 Jun 2002 | F | 30 May 2002 | 3 | 8.5 | FTHILLS |
| C08C | 2 Jun 2002 | M | 1 Jun 2002 | 0.5 | 7.25 | FTHILLS |
| C09C | 2 Jun 2002 | M | 28 May 2002 | 4.5 | 10.75 | NP |
| C10C | 2 Jun 2002 | M | 29 May 2002 | 4 | 9.75 | NP |
| C11C | 2 Jun 2002 | F | 1 Jun 2002 | 0.5 | 6.75 | FTHILLS |
| C12C | 2 Jun 2002 | F | 1 Jun 2002 | 1 | 6.75 | FTHILLS |
| C13C | 2 Jun 2002 | F | 2 Jun 2002 | 0.5 | 7.25 | FTHILLS |
| C14C | 3 Jun 2002 | F | 31 May 2002 | 2.5 | 8.75 | WHC |
| C15C | 4 Jun 2002 | M | 29 May 2002 | 6 | 12.75 | WHC |
| C16C | 4 Jun 2002 | F | 1 Jun 2002 | 3 | 9 | WHC |
| C17C | 4 Jun 2002 | M | 1 Jun 2002 | 3 | 9 | WHC |
| C18C | 4 Jun 2002 | M | 31 May 2002 | 4 | 11.75 | FTHILLS |
| C19C | 4 Jun 2002 | F | 1 Jun 2002 | 3 | 8.75 | FTHILLS |
| C20C | 4 Jun 2002 | F | 29 May 2002 | 6 | 13 | FTHILLS |
| C21C | 4 Jun 2002 | M | 31 May 2002 | 3.5 | 8.5 | WHC |
| C22C | 4 Jun 2002 | M | 31 May 2002 | 4 | 10 | WHC |
| C23C | 4 Jun 2002 | F | 1 Jun 2002 | 2.5 | 11 | WHC |
| C24C | 4 Jun 2002 | F | 29 May 2002 | 6 | 13.5 | WHC |
| C25C | 4 Jun 2002 | F | 1 Jun 2002 | 3 | 8.75 | WHC |
| C26C | 28 May 2003 | M | 27 May 2003 | 1 | 7.25 | WHC |
| C27C | 28 May 2003 | F | 25 May 2003 | 2.5 | 8.75 | WHC |
| C28C | 28 May 2003 | F | 25 May 2003 | 2.5 | 10.5 | WHC |
| C29C | 28 May 2003 | F | 25 May 2003 | 2.5 | 8 | FTHILLS |
| C30C | 29 May 2003 | F | 25 May 2003 | 4 | 11 | FTHILLS |
| C31C | 29 May 2003 | F | 25 May 2003 | 3.5 | 8.5 | FTHILLS |
| C32C | 29 May 2003 | M | 27 May 2003 | 1.5 | 8.75 | FTHILLS |
| C33C | 29 May 2003 | F | 25 May 2003 | 3.5 | 9.75 | WHC |
| C34C | 29 May 2003 | M | 26 May 2003 | 2.5 | 9 | WHC |
| C35C | 29 May 2003 | M | 26 May 2003 | 3 | 10.25 | FTHILLS |
| C36C | 29 May 2003 | F | 26 May 2003 | 3 | 10.25 | FTHILLS |
| C37C | 29 May 2003 | M | 26 May 2003 | 3 | 13 | FTHILLS |
| C38C | 30 May 2003 | M | 28 May 2003 | 1.5 | 7 | FTHILLS |
| C39C | 30 May 2003 | F | 27 May 2003 | 2.5 | 8 | NP |
| C40C | 30 May 2003 | F | 27 May 2003 | 2.5 | 8.75 | NP |
| C41C | 30 May 2003 | F | 27 May 2003 | 2.5 | 7.5 | NP |
| C42C | 30 May 2003 | M | 28 May 2003 | 1.5 | 6 | NP |
| C43C | 30 May 2003 | F | 26 May 2003 | 3.5 | 9 | NP |
| C44C | 30 May 2003 | M | 27 May 2003 | 2.5 | 9 | NP |
| C45C | 30 May 2003 | M | 27 May 2003 | 2.5 | 8.75 | NP |
| C46C | 31 May 2003 | F | 27 May 2003 | 4 | 8.75 | WHC |
| C47C | 31 May 2003 | F | 28 May 2003 | 3 | 9 | WHC |
| C48C | 31 May 2003 | F | 29 May 2003 | 2 | 13.5 | WHC |
| C49C | 31 May 2003 | F | 27 May 2003 | 3.5 | 13.5 | FTHILLS |
| C50C | 31 May 2003 | M | 26 May 2003 | 6 | 19 | FTHILLS |

Appendix A2. Percent cover and density of vegetation by functional group and species and biomass of lichens ($\bar{x} \pm SE$) using line-intercept and plot data at calving sites of woodland caribou in the Greater Besa-Prophet area, northern British Columbia, Canada, 2002–2003.

| Functional group | Species | 2002 | | | | 2003 | | | |
|---------------------------------------|---|-----------|------|---|-------|-----------|-------|---|-------|
| | | Cover | | Density/m ² or lichen biomass (g/m ²) | | Cover | | Density/m ² or lichen biomass (g/m ²) | |
| | | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE |
| Line-intercept data | | | | | | | | | |
| Trees | <i>Abies lasiocarpa</i> (krummholz) | 0.54 | 0.54 | | | | | | |
| | Hybrid spruce | 3.71 | 2.74 | | | 0.14 | 0.11 | | |
| | Black spruce | 0.47 | 0.25 | | | 0.31 | 0.18 | | |
| Shrubs | <i>Alnus</i> spp. | | | | | 0.10 | 0.10 | | |
| | Bog birch | 10.56 | 4.21 | | | 3.10 | 1.16 | | |
| | Bog birch mix (<i>Salix</i> spp. and <i>Juniperus</i> spp.) | 0.10 | 0.10 | | | 0.97 | 0.81 | | |
| | <i>Juniperus</i> spp. | 0.06 | 0.06 | | | 0.07 | 0.05 | | |
| | Labrador tea | 0.10 | 0.10 | | | 0.30 | 0.30 | | |
| Dwarf shrubs | <i>Salix</i> spp. | 5.55 | 2.70 | | | 16.89 | 4.62 | | |
| | Arctic white heather | 1.91 | 0.71 | | | 1.02 | 0.59 | | |
| | Mountain avens | 24.44 | 5.04 | | | 15.89 | 3.97 | | |
| | Mountain avens mix (<i>Vaccinium</i> spp. and <i>Salix reticulata</i>) | 7.02 | 4.18 | | | 0.27 | 0.16 | | |
| Other Plot data | | 14.67 | 7.32 | | | 36.61 | 11.09 | | |
| Forbs | <i>Anemone</i> spp. | 0.54 | 0.30 | 3.12 | 1.32 | 0.34 | 0.16 | 1.14 | 0.53 |
| | <i>Antennaria</i> spp. | 0.52 | 0.28 | 2.49 | 1.11 | 0.12 | 0.06 | 0.63 | 0.38 |
| | <i>Astragalus alpinus</i> | 0.42 | 0.28 | 3.99 | 2.66 | 0.04 | 0.04 | 0.10 | 0.07 |
| | <i>Epilobium angustifolium</i> | 0.56 | 0.28 | 1.10 | 0.52 | 0.40 | 0.32 | 0.77 | 0.59 |
| | <i>Hedysarum</i> spp. | 0.50 | 0.38 | 0.96 | 0.59 | 1.28 | 0.68 | 1.13 | 0.45 |
| | <i>Lupinus arcticus</i> | 5.14 | 1.78 | 3.94 | 1.16 | 3.58 | 1.26 | 1.60 | 0.48 |
| | <i>Mertensia paniculata</i> | 0.76 | 0.44 | 1.78 | 0.80 | 0.16 | 0.10 | 0.43 | 0.23 |
| | <i>Oxytropis</i> spp. | 0.58 | 0.42 | 0.68 | 0.47 | 0.74 | 0.32 | 1.50 | 0.60 |
| | <i>Pedicularis</i> spp. | 0.98 | 0.28 | 9.72 | 4.16 | 1.10 | 0.42 | 4.10 | 1.44 |
| | <i>Polemonium</i> spp. | 0.54 | 0.28 | 1.63 | 0.70 | 0.46 | 0.22 | 0.80 | 0.38 |
| | <i>Potentilla</i> spp. | 1.42 | 0.62 | 4.72 | 2.23 | 0.54 | 0.24 | 1.47 | 0.60 |
| | <i>Saxifraga</i> spp. | 1.94 | 1.50 | 1.32 | 0.73 | 0.46 | 0.24 | 0.92 | 0.51 |
| | Moss campion | 1.30 | 0.54 | 1.65 | 0.59 | 1.28 | 0.68 | 0.67 | 0.20 |
| | <i>Solidago</i> spp. | 0.76 | 0.42 | 1.93 | 0.79 | 0.28 | 0.14 | 0.87 | 0.36 |
| | Other | 0.06 | 0.06 | 0.68 | 0.54 | 0.18 | 0.10 | 1.44 | 0.78 |
| Graminoids, sedges, and horsetails | Sedges | 5.56 | 1.36 | 43.72 | 13.23 | 7.30 | 2.48 | 42.93 | 14.08 |
| | Horsetails | 1.48 | 1.04 | 13.69 | 9.20 | 2.40 | 1.04 | 41.00 | 18.50 |
| | <i>Festuca</i> spp. | 12.46 | 3.56 | 5.56 | 1.07 | 7.38 | 1.98 | 4.10 | 0.92 |
| | <i>Poa</i> spp. | 1.54 | 0.94 | 3.06 | 0.94 | 0.06 | 0.04 | 0.70 | 0.44 |
| Lichens | Other | 0.01 | 0.01 | 0.07 | 0.07 | 0.58 | 0.36 | 2.30 | 1.14 |
| | <i>Cladina</i> spp. and <i>Cladonia</i> spp. | | | 0.73 | 0.14 | | | 0.43 | 0.08 |
| | Other | | | 42.20 | 4.87 | | | 30.47 | 5.43 |



A woodland caribou cow and calf are reunited after the calf was captured and collared north of the Prophet River in the Greater Besa-Prophet area (North Prophet), northern British Columbia, Canada, May 2003 (photo by Michael P. Gillingham).



A collared woodland caribou neonate is released after capture near Keily Creek in the Greater Besa-Prophet area (Western High Country), northern British Columbia, Canada, May 2002 (photo by Douglas C. Heard).