

SPATIAL OVERLAP OF DALL SHEEP, GRIZZLY BEARS AND WOLVES IN THE RICHARDSON MOUNTAINS, CANADA

CATHERINE LAMBERT KOIZUMI^{1,2} & ANDREW E. DEROCHE¹

1. Department of Biological Sciences, University of Alberta, Edmonton AB T6G 2E9, Canada
(cathlambert@ualberta.ca)
2. Previous affiliation: Gwich'in Renewable Resource Board, PO Box 2240,
Inuvik NT X0E 0T0, Canada.

ABSTRACT

Dall sheep (*Ovis dalli dalli*) in the northern Richardson Mountains, Canada, are at the northeastern limit of the species range, and have been declining since the mid 1990s. Factors that may have contributed to the decline include: severe climate, density-dependence, interspecific competition, diseases, harvest, and predation. In this study, we investigate the indirect effects of predation by grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) on this Dall sheep population through the study of their spatial dynamics, in particular the overlap of the species composite home ranges. Between 2006 and 2009, we tracked individuals of the three species with GPS telemetry to describe their home ranges, movements and habitat use. Species composite home ranges revealed substantial overlap between areas used by all three species. The home range of wolves overlapped most of the Dall sheep range. When focusing on the core areas used by Dall sheep, however, the overlap with grizzly bears was larger. This suggests that wolves are likely encountered more often over a wider area whereas grizzly bear encounters are more likely in core areas. To refine our assessment of grizzly bear and wolf predation risk on this Dall sheep population, further analyses on individual and seasonal home range overlap, comparative habitat use, dynamics interactions, Dall sheep vigilance behaviour, predator diet and documentation of traditional ecological knowledge are required.

Keywords: *Canis lupus*, home range overlap, indirect effects, *Ovis dalli dalli*, predator-prey interactions, predation risk, spatial dynamics, thinhorn sheep, *Ursus arctos*, utilization distribution.

RESUMEN

Solapamiento espacial entre el carnero de dalli (Ovis dalli dalli), el oso pardo (Ursus arctos) y el lobo (Canis lupus) en las montañas de Richardson en Canadá

El carnero de Dall (*Ovis dalli dalli*) del norte de las Montañas de Richardson, en el Ártico canadiense, se encuentra en el límite noreste del área de distribución de la especie. Esta población

ha disminuido durante la última década. Los factores que pueden haber contribuido a este declive son el clima inhóspito, la densidad dependencia de esta especie, la caza indígena, la competencia con otros ungulados y la predación. En el presente estudio se pretende determinar el impacto del oso pardo (*Ursus arctos*) y el lobo (*Canis lupus*) sobre esta población a través de la dinámica espacial, y en concreto en el solapamiento del área de estas especies. Entre el 2006 y el 2009: (1º) hicimos un seguimiento de ejemplares de las tres especies utilizando telemetría de GPS para documentar el área de campeo, los movimientos y la dinámica espacial, comprobando que el hábitat del carnero solapa mas con el área del lobo que con el oso, sin embargo el solapamiento entre el oso y el carnero es mas duradero. Este hecho indica que aunque los lobos tienen mas posibilidades de encuentro con los carneros, sin embargo los encuentros entre el oso y los carneros son mas frecuentes al solapar el nucleo central del area de los carneros. Por ello y poder afinar mas sobre el riesgo de predación de los carneros por el oso y el lobo proponemos en el futuro analizar el solapamiento a nivel individual, comparar el uso del hábitat y la dinámica de la población, así como el comportamiento vigilante de los carneros, y la documentación de la dieta de los predadores, y documentar su conocimiento ecológico tradicional y complementar nuestros resultados.

Palabras claves: *Canis lupus*, dinámica espacial, distribución espacial, interacciones predador-presa, *Ovis dalli dalli*, riesgo de predación, solapamiento del área de campeo, *Ursus arctos*.

INTRODUCTION

Assessing the effects of predation on a declining prey population is a recurring but challenging assignment of wildlife managers and researchers (Burles & Hoefs 1984, Sawyer & Lindzey 2002, Festa-Bianchet *et al.* 2006). In remote and rugged environments, quantifying predation events (e.g., attack rates, mortality rates, functional response) necessitates financial and logistic resources unavailable to most researchers. Indirect effects of predation, in contrast, are more easily investigated and can reveal important patterns and mechanisms underlying predator-prey interactions. Indirect effects, also called non-consumptive effects, include vigilance behaviour, reduced feeding, altered activity budget, and habitat shift of prey species (Schmitz *et al.* 2004). Such indirect effects are ubiquitous (Peckarsky *et al.* 2008) and can be a major factor shaping predator-prey spatial dynamics (Iwasa *et al.* 1981, Hebblewhite *et al.* 2005, Willems and Hill 2009).

Indirect effects at the spatial level may be revealed by the examination of home range overlap. The breadth of home range overlap between individuals or populations can be helpful to explore several types of interactions and space-use patterns. For example, measures of home range overlap have been used to detect mating associations of red foxes (*Vulpes vulpes*) (Doncaster 1990), kinship among

bushbuck (*Tragelaphus scriptus*) (Wronski & Apio 2006), sexual segregation in racoons (*Procyon lotor*) (Gehrt & Fritzell 1998), Pacific tree frog (*Pseudacris regilla*) tadpole avoidance of predation by dragonflies (*Aeshna palmate*) (Hammond *et al.* 2007), temporal home range drift in grizzly bears (*Ursus arctos*) (Edwards *et al.* 2009), and wolf (*Canis lupus*) predation risk on migrant versus resident elk (*Cervus elaphus*) (Robinson *et al.* 2010). In this article, we use measures of home range overlap to assess the spatial associations and infer the potential risk of predation by grizzly bears and wolves on a declining population of Dall sheep (*Ovis dalli dalli*).

Dall sheep in the northern Richardson Mountains, Northwest Territories and Yukon Territory, Canada, are located at the northeastern limit of the species range (Valdez & Krausman 1999). Sporadic aerial surveys revealed this population was small ($N < 500$) during the 1970s (Simmons 1973), grew steadily during the 1980s (Latour 1984, Barichello *et al.* 1987) and early 1990s (Nagy & Carey 2006a), until it reached a peak in the mid 1990s ($N \sim 1,730$ in 1997) (Nagy & Carey 2006b), then declined consistently afterwards (Davison & Cooley 2006, Nagy *et al.* 2006a, 2006b). The latest abundance estimate was 704 individuals in 2006 (Davison & Cooley 2006). The principal factors hypothesized to influence the dynamics of this population include predation, density-dependence, harvest, climate, and competition with other ungulates (Lambert Koizumi *et al.* 2010). Following discussions with the local renewable resource councils, the role of predation in the recent population decline was identified as a research priority. Attempts of predation on Dall sheep by grizzly bears, wolves, wolverines (*Gulo gulo*), golden eagles (*Aquila chrysaetos*), and black bears (*Ursus americanus*) were reported by local community members, with wolves and grizzly bears being the most commonly mentioned (Shaw *et al.* 2005). Wolves in adjacent areas appear to feed mostly on moose (*Alces alces*), and seasonally on the Porcupine caribou herd (*Rangifer tarandus granti*) (Hayes & Russell 1998). Despite relying on other prey species, wolves have the potential to significantly limit mountain sheep populations (Murie 1944) and were suspected to have killed one to three radio-collared rams of four in one study (Barichello *et al.* 1987). Research in Alaska identified grizzly bears as the main predator of moose and caribou calves (Ballard & Miller 1990) and their potential as an ungulate predator seems to be higher when ungulates are only few weeks old (Zager & Beecham 2006). Grizzly

bears and wolves have both been observed repeatedly in areas near Dall sheep (in aerial surveys and Gwich'in traditional ecological knowledge (Gwich'in Elders 1997)).

STUDY AREA

The study area encompasses approximately 9,600 km² at the eastern limit of the northern Richardson Mountains (Figure 1) (approximately 67°15' - 68°24' N, 137°5' - 135°12' W) and is part of the British-Richardson Mountains ecoregion, in the Taiga Cordillera ecozone (Scudder 1997). This ecoregion is characterized by steep, V-shaped valleys in the higher range, and gentle slopes where the valleys are broader. The elevation ranges between 400 and 1,200 m. The vegetation is dominated by alpine tundra, and the treeline is located at approximately 300 m a.s.l. (Smith *et al.* 2004). Average recorded temperatures in January and July at the nearest weather station, in Aklavik NT, are respectively -28°C and 14°C; with an average of 236 mm of precipitations annually (Environment Canada 2009). Climatic records for Aklavik show a recent increase in average temperature and precipitation (Lambert Koizumi *et al.* 2010), in accordance with climate analyses that have placed northern areas amongst the most affected by climate change (Hinzman *et al.* 2005).

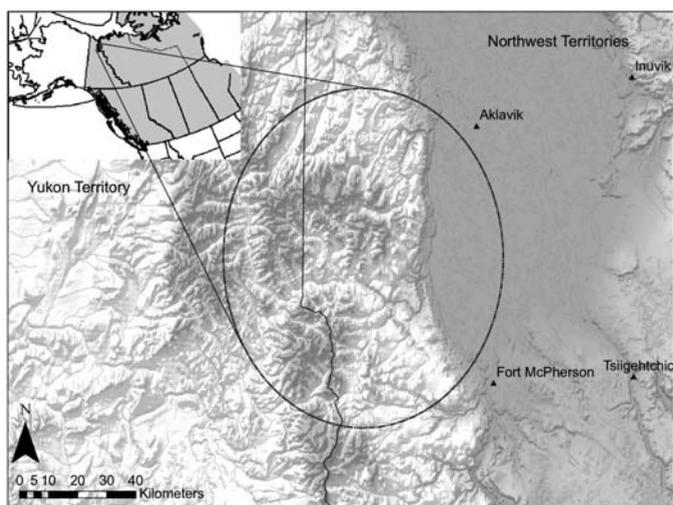


Figure 1. Location of the study area in the northern Richardson Mountains, Northwest Territories and Yukon Territory, Canada.

Aboriginal claimed lands include the Gwich'in Settlement Area, the Tetlit Gwich'in Secondary Use Area, the Inuvialuit Settlement Region, and the Vuntut Gwich'in Traditional Territory. The closest human settlements are Aklavik and Fort McPherson (each about 12 km east and southeast of the study area). Only aboriginal people can harvest this Dall sheep population and a multijurisdictional management plan is in the process of being adopted. Grizzly bear harvest is also restricted to aboriginal users and is regulated by a management agreement in the Gwich'in Settlement Area and quotas in the Inuvialuit Settlement Region. In the Yukon, in addition to aboriginal harvesters, residents and non-residents may harvest grizzly bears during the spring and fall hunting seasons. Wolves may be harvested throughout the study area, and there is no management plan for them.

MATERIAL AND METHODS

In 2006 and 2007, we conducted capture sessions to equip Dall sheep ewes, grizzly bears and wolves with GPS collars (Telonics Gen II and Gen III TGW-3580 & TGW-3680 (Mesa Arizona, USA); and Lotek 3300W (Newmarket Ontario, Canada)). Locations of Dall sheep rams monitored in the same area in 2004-05 (D. Auriat, Gwich'in Renewable Resources Board, unpub.) were also incorporated in analyses. Ewes were selected randomly in different subgroups, and we tried to collar most adult grizzly bears and at least one wolf per pack in the Dall sheep range within the study area. Animal captures were performed from helicopter (net gunning for Dall sheep and wolves; dart injection of Telazol®, a mixture of tilatamine HCl and zolazepam HCl, for grizzly bears (dosage: 8 mg/kg) and wolves when net gunning was impossible to perform (5 mg/kg)). Capture and handling protocols were approved by the Government of the Northwest Territories Wildlife Care Committee and followed the guidelines on the care and use of wildlife of the Canadian Council on Animal Care. Locations were recorded every two hours between May 15 and June 15, to get a fine resolution of spatial dynamics during the lambing season, and every four hours the rest of the year. Collars were programmed to release automatically from the animals' necks after 15-28 months of wear, and data were retrieved following collar recovery. Daily to biweekly locations were also sent through the Argos satellite system for all Telonics collars.

To standardize the time interval between animal relocations and reduce bias from temporally correlated data (Börger *et al.* 2006), only one daily location per individual was used in home range analyses. Species composite home ranges were calculated with a 50% and 95% fixed-kernel density estimates (Worton 1989). Home ranges were calculated with Hawth's Analysis Tools, version 3.27 (Beyer 2006). We used two indices to evaluate home range overlap between Dall sheep and the two potential predators. First we calculated the two-dimensional overlap between core areas (50% kernel contour) and high-use areas (95% kernel contour) of Dall sheep, grizzly bear and wolf composite home ranges (Ostfeld 1986). We quantified the overlap in core and high-use areas as the proportion of Dall sheep composite home range that is intersected by the grizzly bear and wolf core and high use areas. Second, we converted the composite kernel home ranges into utilization distributions, which provide a probabilistic measure of use, and calculated the three-dimensional overlap (volume of intersection) between the three species (Kernohan *et al.* 2001).

RESULTS

Our capture efforts resulted in the monitoring of 6 Dall sheep ewes, 15 grizzly bears (11 females and 4 males), and 9 wolves from three different packs (3 females and 6 males), in addition to 8 Dall sheep rams monitored in 2004-05. Because some collars were unavailable when conducting this analysis, the data presented here stem from the combined locations of 14 Dall sheep (N = 20,189 locations), 14 grizzly bears (N = 16,279), and 6 wolves (N = 11,918). The average time interval between locations selected for this analysis was 1.24 days per individual (SD = 3.15).

The composite 50% and 95% kernel home ranges for each population covered respectively 46 and 213 km² for Dall sheep; 252 and 1,662 km² for grizzly bears; and 434 and 3,385 km² for wolves (Figure 2). Considerable spatial overlap was observed between the monitored individuals. Most of the Dall sheep high-use areas (95% composite kernel home range) were included in the high-use areas of grizzly bears and wolves (77% and 97% overlap, respectively). Over a third (36%) of the Dall sheep core area (50% composite kernel home range) overlapped the core areas of grizzly bears, compared with an overlap of 15%

with the core areas of wolves. An examination of the animal locations indicates that six grizzly bears were in Dall sheep core areas and used these intensively, in comparison with three wolves that passed through them briefly. The volume of intersection of utilization distributions was 20% between Dall sheep and grizzly bears; and 80% between Dall sheep and wolves.

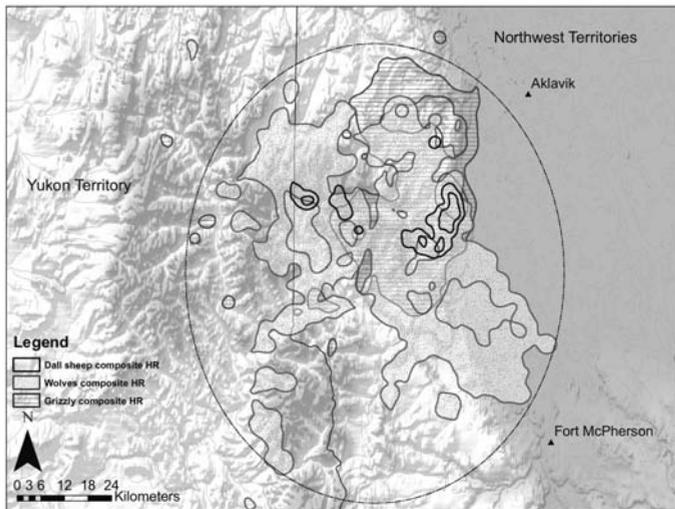


Figure 2. Composite 95% and 50% kernel home ranges of Dall sheep (N=14), grizzly bears (N=14) and wolves (N=6) monitored between 2004 and 2009 in the northern Richardson Mountains, Northwest Territories and Yukon Territory, Canada.

DISCUSSION

Our results suggest that on most of their range, Dall sheep have a higher probability of encountering wolves. Wolves have large home ranges that encompassed those of several Dall sheep and covered a larger proportion of the Dall sheep composite home range. However, when only core areas are considered, grizzly bears are more likely to be encountered. The overlap between composite home ranges of Dall sheep, grizzly bears and wolves reveal probabilities of encounter that might correspond to levels of predation risk associated with each predator population. Predation risk is a determinant of mountain sheep habitat selection (Bleich 1999) and can influence their sexual segregation and social behaviour (Frid 1997). Predation risk has been related to the degree of vigilance

exhibited by prey and predation risk can vary with group size and habitat characteristics (Frid 1997), and to the probability of occurrence of predators within the landscape (Hebblewhite *et al.* 2005, Walker *et al.* 2007, Willems and Hill 2009). In the northern Richardson Mountains, predation risk from grizzly bears appears higher in Dall sheep core areas, and wolf predation risk seems higher in other areas used by Dall sheep.

Because individual predators may specialize in their own prey niche, mortality rates from grizzly bears and wolves may be difficult to assess from this index of predation risk. The degree of carnivory of grizzly bears varies greatly among individuals (Hilderbrand *et al.* 1999) and wolves belonging to the same pack may select different food sources (Urton and Hobson 2005). As such, grizzly bears in Dall sheep core areas may vary in their predation of Dall sheep. Holders of traditional ecological knowledge have suggested that a high concentration of grizzly bears in prime Dall sheep habitat may occur because of the area's abundance in Arctic ground squirrels (*Spermophilus parryii*) and forage availability (C. Lambert Koizumi, unpub.). Similarly, other prey species present in Dall sheep high-use areas could influence the occurrence of wolves. However, as noted by Festa-Bianchet *et al.* (2006), some predators may specialize on certain prey, and few of these specialized predators may be needed to cause a population decline. In the absence of known mortality rates, a higher probability of encounter is likely to correspond to higher predation risk.

Further analyses are needed to improve our assessment of the indirect effects of predation by grizzly bears and wolves. At the spatial level, the investigation of animal locations at a finer scale (at the individual and seasonal levels), the comparison of habitat use from the utilization distributions (Marzluff *et al.* 2004), as well as the movement dynamics of paired locations have the potential to provide more detailed insights on the interactions between these three populations. We plan to pursue these analyses and combine the results with other techniques, such as observations of Dall sheep vigilance behaviour, diet analysis of grizzly bears and wolves, and documentation of traditional ecological knowledge held by elders and active land users, to better understand how these predators impact Dall sheep in the Northern Richardson Mountains.

ACKNOWLEDGEMENTS

This project would not have been possible without the generous support of the Gwich'in Renewable Resources Board (GRRB), the Polar Continental Shelf Project, EcoAction (Environment Canada), the Ehdiiat Renewable Resource Council, the Tetlit Renewable Resource Council, the Natural Sciences and Engineering Council of Canada, the Alberta Innovates Technology Futures, and the University of Alberta. We would like to thank Kristen Callaghan (GRRB) and Marsha Branigan (Inuvik Region, Environment and Natural Resources, Government of the Northwest Territories) for their logistical support; Rolland Lemieux, Jozef Carnogursky, Brian Dokum, and Ryan McLeod, for their assistance in the field. The first author is also grateful to the Department of Environment of the Regional Government of Andalusia for facilitating her participation to the 5th World Congress on Mountain Ungulates, Granada, Spain, in November 2009. Finally, we would like to thank two anonymous reviewers who helped improve this manuscript.

REFERENCES

- Ballard W.B. & Miller S.D. 1990. Effects of reducing brown bear density on moose calf survival in southcentral Alaska. *Alces*, 26: 9-13.
- Barichello N., Carey J. & Jingfors, K. 1987. *Population ecology, range use, and movement patterns of Dall sheep (Ovis dalli dalli) in the Northern Richardson Mountains*. Northern Oil and Gas Action Program (NOGAP), Project G-14. 125 pp.
- Beyer H. 2006. Hawth's Analysis Tools, version 3.27. Available from: <<http://www.spatial ecology.com/htools>> [accessed: 1 Jun. 2009].
- Bleich V.C. (1999). Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy*, 80: 283-289.
- Börger I., Franconi N., De Michele G., Gantz A., Meschi F., Manica A., Lovari S. & Coulson T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, 75: 1393-1405.
- Burles D.W. & Hoefs M. 1984. Winter mortality of Dall sheep, *Ovis dalli dalli*, in Kluane National Park, Yukon. *Canadian Field Naturalist*, 98: 479-484.
- Davison, t. And d. Cooley. (2006). *Field summary: Dall's sheep survey June 22 to 25, 2006*. Unpublished, Inuvik NT, Canada. 4 pp.
- Doncaster C.P. 1990. Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology*, 143: 431-443.
- Edwards M.A., Nagy J.A. & Derocher A.E. 2009. Low site fidelity and home range drift in a wide-ranging, large Arctic omnivore. *Animal Behaviour*, 77: 23-28.
- Festa-Bianchet M., Coulson T., Gaillard J.M., Hogg J.T. & Pelletier F. 2006. Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences*, 273: 1537-1543.

- Frid A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour*, 53: 799-808.
- Gehrt S.D. & Fritzell E.K. 1998. Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. *Animal Behaviour*, 55: 1211-1227.
- Gwich'in elders. 1997. Divii, Dall sheep. Pp: 57-62. In: *Nanh' Kak Geenjit Gwich'in Ginjik. Gwich'in words about the land*. Gwich'in Renewable Resource Board, Inuvik, Canada.
- Hammond J.L., Luttbeg B. & Sih A. 2007. Predator and prey space use: dragonflies and tadpoles in an interactive game. *Ecology*, 88: 1525-1535.
- Hayes R.D. & Russell D.E. 1998. Predation rate by wolves on the Porcupine caribou herd. *Rangifer* Special Issue No. 12: 51-58.
- Hebblewhite M.C., White A., Nietvelt C.G., Mckenzie J.A., Hurd T.E., Fryxell J.M., Bayley S.E. & Paquet P.C. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology*, 86: 2135-2144.
- Hilderbrand G.V., Schwartz C.C., Robbins C.T., Jacoby M.E., Hanley T.A., Arthur S.M. & Servheen C. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology*, 77: 132-138.
- Hinzman I.D., Bettes N.D., Bolton W.R., Chapin F.S., Dyurgerov M.B., Fastie C.L., Griffith B., Hollister R.D., Hope A., Huntington H.P. *et al.* 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, 72: 251-298.
- Iwasa Y., Higashi M. & Yamamura N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *The American Naturalist*, 117: 710.
- Kernohan B.J., Gitzen R. A. & Millspaugh J.J. 2001. Analysis of animal space use and movements. Pp. 125-166. In: J.J. Millspaugh & J.M. Marzluff (eds). *Radio tracking and animal populations*. Academic Press, Inc., San Diego, USA.
- Lambert Koizumi C., Carey J., Branigan B. & Callaghan K. 2010. *Status of Dall's sheep (Ovis dalli dalli) in the Northern Richardson Mountains*. In press, Whitehorse YT, Canada.
- Latour P. 1984. *A survey of the Mt. Goodenough Dall's sheep herd in 1983 (draft)*. N.W.T. Wildlife Service, Inuvik NT, Canada. 16 pp.
- Marzluff J.M., Millspaugh J.J., Hurvitz P. & Handcock M.S. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. *Ecology*, 85: 1411-1427.
- Murie A. 1944. *The wolves of Mount McKinley*. Fauna of the National Parks of the United States. Fauna series no. 5, U.S. Government Printing Office, Washington D.C. USA. 238 pp.

- Nagy J.A. & Carey J. 2006a. Distribution and abundance of Dall's sheep in the Richardson Mountains, August 1991. *NT Government (draft)* 26.
- Nagy J.A. & Carey J. 2006b. Distribution and abundance of Dall's sheep in the Richardson Mountains, August 1997. *NT Government (draft)* 34.
- Nagy J.A., Cooley D. & Elkin B. 2006a. Distribution and abundance of Dall's sheep in the Richardson Mountains, June 2001. *NT Government (draft)* 44.
- Nagy J.A., Cooley D. & Elkin B. 2006b. Distribution and abundance of Dall's sheep in the Richardson Mountains, August 2003. *NT Government (draft)* 26.
- Ostfeld R.S. 1986. Territoriality and mating system of California voles. *Journal of Animal Ecology*, 55: 691-706.
- Peckarsky B.L., Abrams P.A., Bolnick D.L., Dill L.M., Grabowski J.H., Luttbeg B., Orrock J.L., Peacor S.D., Preisser E.L., Schmitz O.J. & Trussell G.C. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology*, 89: 2416-2425.
- Robinson B.G., Hebblewhite M.C. & Merrill E.H. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia*, 164: 265-275.
- Sawyer H. & Lindzey F. 2002. *A review of predation on bighorn sheep (Ovis canadensis)*. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie WY, USA. 36 pp.
- Schmitz O.J., Krivan V. & Ovadia O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7: 153-163.
- Scudder G.G.E 1997. Environment of the Yukon. Pp. 13-57. In: *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa ON, Canada.
- Shaw J., Benn B. & Lambert C. 2005. *Gwich'in Renewable Resource Board Report. Dall's sheep local knowledge study*. Gwich'in Renewable Resource Board, Inuvik NT, Canada. 20 pp.
- Simmons N.M. 1973. *Dall's sheep harvest in the Richardson Mountains, Northwest Territories*. Canadian Wildlife Service, Fort Smith NT, Canada. 16 pp.
- Smith C.A., Meikle S.J.C. & Roots C.F. 2004. *Ecoregions of the Yukon Territory: Biophysical properties of Yukon landscapes*. Agriculture and Agri-Food Canada, PARC Technical Bulletin, Whitehorse YT, Canada. 313 pp.
- Urton E.J. & Hobson K.A. 2005. Intrapopulation variation in gray wolf isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) profiles: implications for the ecology of individuals. *Oecologia*, 145: 317-326.
- Valdez R. & Krausman P.R. 1999. Description, distribution, and abundance of mountain sheep in North America. Pp. 3-22. In: R. Valdez & P.R. Krausman (eds). *Mountain sheep of North America*. University of Arizona Press, Tucson AZ, USA.

- Walker A.B., Parker D.K.L., Gillingham M.P., Gustine D.D. & Lay R.J. 2007. Habitat selection by female Stone's sheep in relation to vegetation, topography, and risk of predation. *Ecoscience*, 14: 55-70.
- Willems E.P. & Hill R.A. 2009. Predator-specific landscapes of fear and resource distribution: effects on spatial range use. *Ecology*, 90: 546-555.
- Worton B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70: 164-168.
- Wronski T. & Apio A. 2006. Home-range overlap, social vicinity and agonistic interactions denoting matrilineal organisation in bushbuck, *Tragelaphus scriptus*. *Behavioral Ecology and Sociobiology*, 59: 819-828.
- Zager P. & Beecham J. 2006. The role of American black bears and brown bears as predators on ungulates in North America. *Ursus*, 17: 95-108.