ARCTIC
VOL. 55, NO. 4 (DECEMBER 2002) P. 339–344

Feeding Patterns of Barren-Ground Grizzly Bears in the Central Canadian Arctic

ROBERT J. GAU,[1,2] RAY CASE,[1] DAVID F. PENNER[3] and PHILIP D. McLOUGHLIN[4]

(*Received 28 June 2001; accepted in revised form 26 November 2001*)

ABSTRACT. We collected 169 grizzly bear scats between 1994 and 1997 to determine the dietary habits of barren-ground grizzly bears (*Ursus arctos*) inhabiting Canada's central Arctic. From personal observations and fecal analysis, we concluded that barren-ground grizzly bears lead a predominantly carnivorous lifestyle and are effective predators of caribou (*Rangifer tarandus*). Caribou was a predominant diet item during spring, mid-summer, and fall. During early summer, grizzly bears foraged primarily on green vegetation. Berries increased in dietary importance in late summer. Declines in the caribou population of our study area or long-term absences of caribou may threaten the local grizzly bear population.

Key words: central Arctic, diet, fecal analysis, feeding patterns, grizzly bear, predation, *Ursus arctos*

RÉSUMÉ. On a prélevé 169 excréments de grizzli entre 1994 et 1997 afin de déterminer les habitudes alimentaires du grizzli de Richardson (*Ursus arctos*) qui vit dans le centre de l'Arctique canadien. En s'appuyant sur des observations personnelles et un examen coproscopique, on conclut que le grizzli de Richardson est un animal largement carnassier et qu'il est un prédateur efficace du caribou (*Rangifer tarandus*). Ce dernier constituait un aliment prédominant au printemps, au milieu de l'été et en automne. Au début de l'été, le grizzli se nourrissait surtout de végétation verte. À la fin de l'été, les baies prenaient plus d'importance dans son alimentation. Le déclin de la population du caribou dans la zone d'étude ou son absence prolongée peut constituer une menace pour la population locale de grizzlis.

Mots clés: centre de l'Arctique, régime alimentaire, examen coproscopique, comportements alimentaires, ours grizzli, prédation, *Ursus arctos*

Traduit pour la revue *Arctic* par Nésida Loyer.

INTRODUCTION

Analyzing food remains in fecal samples is one of the most common methods for determining carnivore feeding patterns (Litvaitis et al., 1994). However, using scat analysis to determine the feeding habits of grizzly bears (*Ursus arctos*) has inherent problems (O'Gara, 1986; Reynolds and Aebischer, 1991). A collection of ground-deposited scats may be biased toward collections from easily sampled areas (McLellan and Hovey, 1995). Additionally, some scats may be less cryptically concealed than others. Another problem is that consumption of foods of different digestibility produces fecal residue volumes that do not truly represent the relative quantities of the various foods consumed (Hatler, 1972; Poelker and Hartwell, 1973; Frackowiak and Gula, 1992; McLellan and Hovey, 1995; Hewitt and Robbins, 1996). Also, errors may result from the assumption that each scat contributes equally to data sets. This bias would tend to overestimate food items found in small scats and underestimate food items found in large scats (McLellan and Hovey, 1995).

Nonetheless, fecal analysis has provided insight into the feeding patterns of remote populations of grizzly bears from Alaska (Linderman, 1974), Yukon Territory (Pearson, 1975; Nagy et al., 1983a), the Mackenzie Mountains (Miller et al., 1982), and the Inuvialuit region of the Northwest Territories (Nagy et al., 1983b; Clarkson and Liepins, 1989).

Until recently, logistical problems associated with conducting research in Arctic ecosystems and low densities of grizzly bears (Case and Buckland, 1998) have precluded study of the dietary habits of bears inhabiting the central Arctic area of the Northwest Territories and Nunavut (Bromley and Buckland, 1995). However, economic activity in that area increased dramatically in the early 1990s with the discovery of diamonds. The BHP Diamonds Inc. Ekati™ diamond mine came into production in October 1998, and Diavik Diamond Mines, Inc. is constructing another mine 40 km away, expected to reach full production by early 2003. To address the effects of these developments on the grizzly populations, the Government of the Northwest Territories initiated research in collaboration with the University of Saskatchewan, Diavik, and BHP.

[1] Wildlife and Fisheries Division, Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories, #600 5102-50th Avenue, Yellowknife, Northwest Territories X1A 3S8, Canada
[2] Corresponding author: rob_gau@gov.nt.ca
[3] Penner and Associates Ltd., 3-52059 Range Road 220, Sherwood Park, Alberta T8E 1B9, Canada
[4] Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada

One study objective was to use fecal analyses to examine the food habits of this previously unstudied population of grizzly bears. However, because of the limitations of fecal analyses in accurately reflecting dietary habitats, we also present data from personal observations of grizzly bear feeding patterns.

STUDY AREA AND METHODS

From 1994 through 1997, we collected feces from grizzly bears in a study area approximately 40 000 km^2 in the central Arctic of mainland Northwest Territories and Nunavut (Fig. 1). Collection efforts were concentrated around the Lac de Gras area (64˚30′N, 110˚30′W), approximately 300 km northeast of Yellowknife, Northwest Territories.

Fecal samples were usually gathered within 48 hrs of deposition, as they were collected from areas where a bear had been observed defecating, areas where bears had been present within 24–48 hrs, or directly from the rectum of tranquilized grizzly bears. Scats were bagged, frozen in the field, and stored at -20˚C until analysis. The opportunity to collect samples from tranquilized bears and scats deposited on the ground came from other phases of our research efforts (BHP Diamonds, 1997; Gau, 1998; Penner and Associates, 1998; Gau and Case, 1999; Gau et al., 1999; McLoughlin et al., 1999, 2002; McLoughlin, 2000; Gau and Case, 2002). Personal observations were tabulated during our daily tracking flights (scheduled whenever aircraft became available) to track radio-collared grizzly bears. Ground investigations of caribou (*Rangifer tarandus*) carcasses were conducted to determine whether the death was natural or the result of predation.

Each sample bag was thawed, and water was added to moisten the scat. Individual scats were then placed in their own glass beakers. The beakers were filled with fresh water, and the scats were broken up and mixed. Food remains were placed into a convectional drying oven (Fisher Isotemp, Series 200) and dried at 100˚C for 24 hrs. Each beaker was then refilled with fresh water and returned to the oven for a second 24 hr period. Food items were then removed, spread across a paper towel, and left to air-dry further if needed.

The food remains in each scat sample were placed in enamel trays and separated according to the finest taxonomic resolution possible using laboratory reference collections. To estimate the volume and occurrence of diet items, a plastic grid was placed on top of the tray and percent cover of each item was visually estimated. The mean proportion of each food item was then calculated for each month and expressed as a percentage.

Observed changes in vegetation helped define our season parameters. Spring extended from the time bears emerged from winter dens (early to mid-May) until 15 June; most of the vegetation was in a brown pre-emergent state after snowmelt. Early summer (16 June to 6 July) had a vegetative landscape characterized by an even mixture of old brown vegetation from the year before and new growth. Midsummer (7 July to 5 August) was characterized by a fully green vegetative landscape. Late summer (6 to 31 August) coincided with the ripening of berries. Autumn extended from 1 September until bears denned (in mid to late October) and was characterized by the changing colour of the tundra shrub layer as it prepared for winter dormancy.

Fecal correction factors (Hewitt and Robbins, 1996) and other elements (e.g., importance factors; Mealey, 1980) that estimate the relative merit of different foods apparent in bear feces are useful, but can add spurious elements to the interpretation of a grizzly bear's diet (Jacoby et al., 1999). Thus, without digestibility and metabolism data for the specific foods we found, we chose not to employ correction factors to interpret feeding patterns. Also, we made no systematic attempts to determine seasonal availability of animal or plant foods during our study.

RESULTS

Undigested portions of food found in feces were visually estimated as volumes (Table 1). Birds, fish, low-volume vegetation, and microtine rodents were grouped in a miscellaneous category. Miscellaneous food items consisted of ptarmigan (*Lagopus* spp.; 4% volume, 10% frequency) and northern red-backed vole (*Clethrionomys rutilus*; 1% volume, 3% frequency) in spring; longnose sucker (*Catostomus catostomus*), unidentified fish remains (2% volume, 24% frequency) and ptarmigan (1% volume, 10% frequency) in early summer; bearberry (*Arctostaphylos alpina*; 4% volume, 7% frequency) in late summer; and bearberry (1% volume, 3% frequency) and soapberry (*Shepherdia canadensis*; 1% volume, 3% frequency) in autumn.

We excluded from the analysis items considered to have been ingested incidentally and items that had total volumes of less than 1%. These included Labrador tea (*Ledum decumbens*), dwarf birch (*Betula glandulosa*), northern pintail (*Anas acuta*), green-winged teal (*A. crecca*), arctic hare (*Lepus arcticus*), northern collared lemming (*Dicrostonyx groenlandicus*), grizzly bear hair, moss (*Lycopodium* spp.), willow (*Salix* spp.), Lapland rosebay (*Rhododendron lapponicum*), and Diptera larvae, as well as unidentifiable wasps or other insects, unidentifiable grasses, garbage, dirt, rocks, and sand.

Of the 169 scats collected, 60 were obtained from tranquilized bears. Fourteen of the 60 scats collected by induced defecation were dark red-brown in colour and liquid to tar-like in consistency, with some caribou hair present. A loose and runny scat has been reported in carnivores to be the first type deposited after a meal composed primarily of fresh meat and blood (Floyd et al., 1978; Pritchard and Robbins, 1990). When such scats were

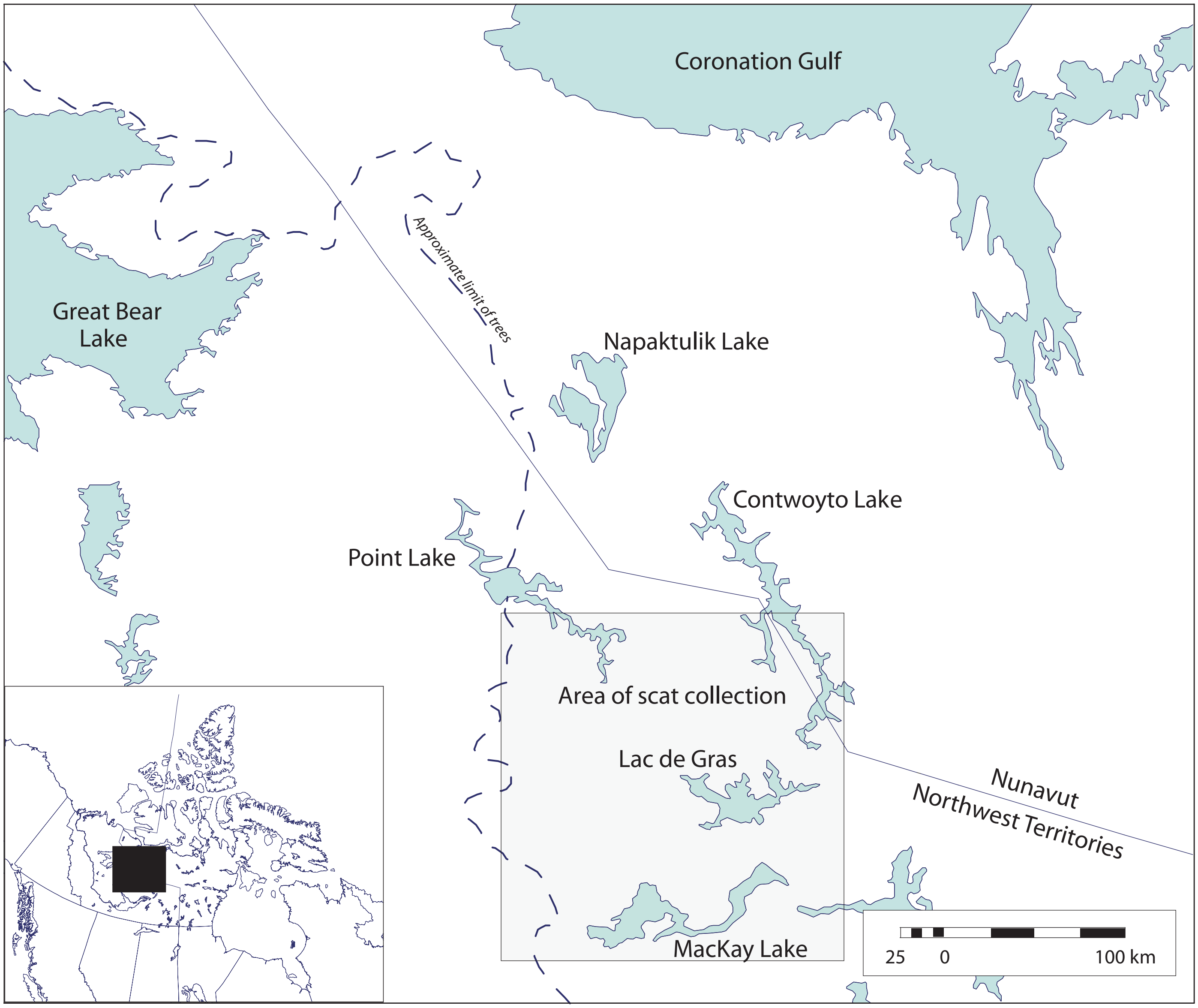

FIG. 1. The study area (shaded) where feces of barren-ground grizzly bears were collected in the central Arctic of the Northwest Territories and Nunavut between 1994 and 1997.

found at caribou carcass sites, we considered their loose consistency as evidence of a recent caribou predation event. Unfortunately, these scats were not collected because they were often partially absorbed by the ground or deposited in an area where surrounding rocks or vegetation had partially dispersed the scat.

Personal observations of barren-ground grizzly bears between 1994 and 1997 suggested that they were effective predators of caribou. During daily visual relocations of radio-collared individuals, we observed grizzlies on 136 caribou kill sites, all apparently their own, as determined by the presence of loose-consistency scats and the age of the carcass (often found within 24 hrs). Additionally, bears were observed at 13 sites where they had either usurped caribou carcasses of other predators or fed upon carrion resulting from natural deaths. We also observed bears chasing caribou on 15 occasions; however, none of these chases led to successful kills.

DISCUSSION

Upon den emergence, barren-ground grizzly bears fed on caribou of the Bathurst herd as they migrated north to their coastal calving grounds. Overwintered berries were consumed to a lesser extent in the spring. In early summer, when caribou were scarce in our study area, emergent shoots of horsetails (*Equisetum* spp.), Arctic cotton grasses (*Eriophorum* spp.), and sedges (*Carex* spp.) appeared in the diet. As mixed, post-calving herds of caribou moved south through the study area in mid-summer, caribou again became a primary staple for bears. As grizzly bears in our

TABLE 1. Percent volume and percent occurrence (in parentheses) of food items in barren-ground grizzly bear scats classified by season and collected from the central Canadian Arctic between 1994 and 1997.

Season	n	Caribou	Arctic Ground Squirrel	Horsetail	Sedge	Arctic Cotton	Crowberry	Cranberry	Blueberry	Miscellaneous
Spring	30	61 (80)	8 (30)	0	2 (10)	3 (20)	13 (60)	5 (63)	3 (30)	5 (13)
Early summer	21	8 (10)	0	37 (62)	35 (57)	16 (43)	0	1 (33)	0	3 (33)
Mid-summer	36	36 (47)	6 (14)	33 (44)	8 (14)	7 (11)	4 (22)	5 (25)	1 (17)	0
Late summer	15	39 (53)	8 (13)	0	7 (7)	0	33 (73)	1 (27)	8 (53)	4 (7)
Autumn	67	76 (93)	10 (25)	0	3 (6)	2 (6)	4 (22)	2 (25)	1 (9)	2 (6)

study area became hyperphagic in late summer (Gau, 1998), a discernible shift was noticed: more berries (crowberry, *Empetrum nigrum*; blueberry, *Vaccinium uliginosum*; cranberry, *V. vitis-idaea*; and bearberry) were consumed at that time than in all other seasons combined. However, caribou was still evident in the late summer diet. While Welch et al. (1997) noted some constraints to the importance of berries in the diet of bears, Rode and Robbins (2000) noted that consuming a mixed diet when berries ripen can be an optimal process to reduce the energy cost of maintenance. The autumn diet of grizzly bears was similar to their spring diet. Grizzly bears in autumn fed primarily on caribou during pre-rut and rutting movements near Lac de Gras and on caribou moving through the area during their migration south to the tree line for winter (Fig. 1). Additionally, Arctic ground squirrels (*Spermophilus parryii*) frequently occurred as a food item in spring, mid-summer, late summer, and autumn.

Most researchers have reported that grizzly bears in the Yukon and western Northwest Territories are predominantly herbivorous, and their predation is opportunistic (Pearson, 1975; Miller et al., 1982; Nagy et al., 1983a, b; Bromley, 1988; MacHutchon, 1996). However, a predominantly carnivorous lifestyle for certain grizzly bear populations is not unusual (Bergerud and Page, 1987; Hamilton and Bunnell, 1987; Boertje et al., 1988; Barnes, 1990; Adams et al., 1995). In fact, some researchers have detailed specific predation events by grizzly bears in the Canadian Arctic on muskox (*Ovibos moschatus*), caribou, ringed seal (*Phoca hispida*), and even young polar bears (*U. maritimus*; Gunn and Miller, 1982; Case and Stevenson, 1991; M.K. Taylor, pers. comm. 1991). Our results indicate that caribou are an important food for barren-ground grizzly bears in the central Canadian Arctic.

Additionally, the tissues of consumers occupying high trophic levels are often enriched with stable nitrogen isotopes (see reviews by DeNiro and Epstein, 1981; Peterson and Fry, 1987; Hobson, 1999; Kelly, 2000). For example, Hilderbrand et al. (1999) reported stable nitrogen isotope values from 3.2‰ to 5.8‰ for brown bears where marine dietary content was minimal and plant matter exceeded terrestrial meat in the diet. Jacoby et al. (1999) reported values from 6.8‰ to 9.1‰ for brown bears where terrestrial animals exceeded plant matter in the diet. Blood sampled from some of the same bears we investigated had a mean stable nitrogen isotope value of 7.8‰ ($n = 43$; see Gau, 1998). A value of 7.8‰ falls within the 6.8‰ to 9.1‰ range reported by Jacoby et al. (1999) where terrestrial animals exceed plant matter in the diet, and seemingly supports our findings that caribou are important to the diet of barren-ground grizzly bears. However, comparisons of isotope studies between ecosystems should be interpreted with caution (Hobson et al., 2000).

CONCLUSIONS

It is likely that the effects of human activity on caribou and grizzly bears in the central Arctic of the Northwest Territories and Nunavut will manifest themselves in many ways. However, while effects from an individual development may be relatively easy to predict, cumulative effects will be considerably more difficult to predict and measure in the central Arctic landscape. The large land area, large species ranges, many ecologically linked species, poorly understood species/habitat relationships, jurisdictional overlap, and rapidly expanding human activity (particularly the establishment of multiple diamond mines and transportation corridors) will be some basic issues regulators will have to manage. Regulatory agencies should particularly ensure that human activity in the area does not significantly alter the health or migration pathways of caribou. Declines in the caribou population, or long-term absences of caribou, could negatively affect the body size, reproductive success, and population density of the grizzly bear population within our study area (Hilderbrand et al., 1999). We recommend ongoing monitoring of grizzly bear diets, since a significant disturbance to area bears or bear habitat may cause changes in their diet. Such a monitoring program would require the long-term commitment of stakeholders across the area and must be able to control for natural variation in grizzly bear diets.

ACKNOWLEDGEMENTS

Funding for our research was supplied by the Government of the NWT Department of Resources, Wildlife, and Economic Development; the University of Saskatchewan; the West Kitikmeot/Slave Society; Indian and Northern Affairs Canada; BHP Diamonds Inc.; Rescan Environmental Services Ltd.; Diavik Diamond Mines Inc.; Monopros Limited; the Nunavut Wildlife Management Board;

the Northern Scientific Training Program; and the Polar Continental Shelf Project (no. 01298). RJG was supported by the Science Institute of the Northwest Territories James M. Harrison Bursary and the Canadian Wildlife Foundation Orville Erickson Memorial Scholarship. DFP was supported by Diavik Diamond Mines Inc. PDM was supported by two NSERC Industrial Postgraduate Scholarships in conjunction with Rescan Environmental Services Ltd. and Axys Environmental Consulting Ltd. (in partnership with Diavik Diamond Mines Inc.). Thank you to P. Hogg and J. Witteman for granting us full and unrestricted access to the archived BHP Diamonds Inc. grizzly bear data. We gratefully acknowledge the assistance in the collection of fecal samples by D. Cluff, F. Messier, N. Doctor, F. Martin, M. Svoboda, D. Panayi, D. Olesen, V. Banci, T. George, and B. Drybones. J. Obst and S. Moore assisted in analysis of fecal samples. The authors also thank the three reviewers who improved an earlier version of this manuscript.

REFERENCES

ADAMS, L.G., SINGER, F.J., and DALE, B.W. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584–594.

BARNES, V.G. 1990. The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. International Conference on Bear Research and Management 8:305–313.

BERGERUD, A.T., and PAGE, R.E. 1987. Displacement and dispersion of parturient caribou as antipredator tactics. Canadian Journal of Zoology 65:1597–1606.

BHP DIAMONDS INC. 1997. 1996 wildlife studies, BHP Diamonds Inc., Lac de Gras, NWT. Unpublished technical report prepared by V. Banci and S. Moore, Rescan Environmental Services Ltd, Yellowknife, Northwest Territories. Available from BHP Diamonds Inc., #1102, 4920 52nd Street, Yellowknife, Northwest Territories X1A 3T1, Canada. 161 p.

BOERTJE, R.D., GASAWAY, W.C., GRANGAARD, D.V., and KELLEYHOUSE, D.G. 1988. Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. Canadian Journal of Zoology 66:2492–2499.

BROMLEY, M. 1988. The status of the barren-ground grizzly bear (*Ursus arctos horribilis*) in Canada. Yellowknife, Northwest Territories: Department of Renewable Resources. 65 p.

BROMLEY, M., and BUCKLAND, L. 1995. Biological information for the Slave Geological Province. Yellowknife, Northwest Territories: Department of Renewable Resources. 39 p.

CASE, R., and BUCKLAND, L. 1998. Reproductive characteristics of grizzly bears in the Kugluktuk area, Northwest Territories, Canada. Ursus 10:41–47.

CASE, R., and STEVENSON, J. 1991. Observation of barren-ground grizzly bear predation on muskoxen in the Northwest Territories. The Canadian Field-Naturalist 105:105–106.

CLARKSON, P.L., and LIEPINS, I.S. 1989. Inuvialuit wildlife studies: Grizzly bear research progress report 1988-1989. Technical Report 8. Inuvik, Northwest Territories: Wildlife Management Advisory Council. 25 p.

DeNIRO, M.J., and EPSTEIN, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 45:341–351.

FLOYD, T.J., MECH, L.D., and JORDAN, P.A. 1978. Relating wolf scat content to prey consumed. Journal of Wildlife Management 42:528–532.

FRACKOWIAK, W., and GULA, R. 1992. The autumn and spring diet of brown bear in the Biesczady Mountains of Poland. Acta Theriologica 37:339–344.

GAU, R.J. 1998. Food habits, body condition, and habitat of the barren-ground grizzly bear. M.Sc. thesis, University of Saskatchewan, Saskatoon. 77 p.

GAU, R.J., and CASE, R. 1999. Evaluating nutritional condition of grizzly bears with select blood parameters. Journal of Wildlife Management 63:286–291.

———. 2002. Evaluating nutritional condition of grizzly bears via ^{15}N signatures and insulin-like growth factor-I. Ursus 13: 153–159.

GAU, R.J., KUTZ, S., and ELKIN, B.T. 1999. Parasites in grizzly bears (*Ursus arctos*) from the central Canadian Arctic. Journal of Wildlife Diseases 35:618–621.

GUNN, A., and MILLER, F.L. 1982. Muskox bull killed by a barren-ground grizzly bear, Thelon Game Sanctuary, N.W.T. Arctic 35:545–546.

HAMILTON, A.N., and BUNNELL, F.L. 1987. Foraging strategies of coastal grizzly bears in the Kimsquit River valley, British Columbia. International Conference on Bear Research and Management 7:187–197.

HATLER, D.F. 1972. Food habits of black bears in interior Alaska. Canadian Field-Naturalist 86:17–31.

HEWITT, D.G., and ROBBINS, C.T. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulletin 24: 547–550.

HILDERBRAND, G.V., SCHWARTZ, C.C., ROBBINS, C.T., JACOBY, M.E., HANLEY, T.A., ARTHUR, S.M., and 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.

HOBSON, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: A review. Oecologia 120:314–326.

HOBSON, K.A., McLELLAN, B.A., and WOODS, J.G. 2000. Using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. Canadian Journal of Zoology 78:1332–1339.

JACOBY, M.E., HILDERBRAND, G.V., SERVHEEN, C., SCHWARTZ, C.C., ARTHUR, S.M., HANLEY, T.A., ROBBINS, C.T., and MICHENER, R. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63:921–929.

KELLY, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1–27.

LINDERMAN, S. 1974. Ground tracking of Arctic grizzly bears. Juneau: Alaska Department of Fish and Game. 25 p.

LITVAITIS, J.A., TITIS, K., and ANDERSON, E.M. 1994. Measuring vertebrate use of terrestrial habitats and foods. In: Bookhout, T.A., ed. Research and management techniques for wildlife and habitats. 5th ed. Bethesda, Maryland: The Wildlife Society. 254–274.

MacHUTCHON, A.G. 1996. Grizzly bear habitat use study, Ivvavik National Park, Yukon: Final report. Inuvik, Northwest Territories: Western Arctic District Parks Canada. 142 p.

McLELLAN, B.N., and HOVEY, F.W. 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Canadian Journal of Zoology 73:704–712.

McLOUGHLIN, P.D. 2000. The spatial organization and habitat selection patterns of barren-ground grizzly bears in Nunavut and the Northwest Territories, Canada. Ph.D. dissertation, University of Saskatchewan, Saskatoon. 151 p.

McLOUGHLIN, P.D., CASE, R.L., GAU, R.J., FERGUSON, S., and MESSIER, F. 1999. Annual and seasonal movement patterns of barren-ground grizzly bears in the central Northwest Territories. Ursus 11:79–86.

McLOUGHLIN, P.D., CASE, R.L., GAU, R.J., CLUFF, H.D., MULDERS, R., and MESSIER, F. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. Oecologia 132:102–108.

MEALEY, S.P. 1980. The natural food habits of grizzly bears in Yellowstone National Park. International Conference on Bear Research and Management 4:281–292.

MILLER, S.J., BARICHELLO, N., and TAIT, D. 1982. The grizzly bears of the Mackenzie Mountains NWT. Completion Report No. 3. Yellowknife: Northwest Territories Wildlife Service. 118 p.

NAGY, J.A., RUSSELL, R.H., PEARSON, A.M., KINGSLEY, M.C.S., and GOSKI, B.C. 1983a. Ecological studies in the Arctic mountains, northern Yukon Territory, 1972–1975. Edmonton, Alberta: Canadian Wildlife Service. 96 p.

NAGY, J.A., RUSSELL, R.H., PEARSON, A.M., KINGSLEY, M.C.S., and LARSEN, C.B. 1983b. A study of grizzly bears on the barren-grounds of Tuktoyaktuk Peninsula and Richards Island, Northwest Territories, 1974–1978. Edmonton, Alberta: Canadian Wildlife Service. 127 p.

O'GARA, B.W. 1986. Reliability of scat analysis for determining coyote feeding on large mammals. The Murrelet 67:79–81.

PEARSON, A.M. 1975. The northern interior grizzly bear. Ottawa, Ontario: Canadian Wildlife Service. 81 p.

PENNER AND ASSOCIATES LTD. 1998. Wildlife baseline report, Diavik Diamonds Project, Lac de Gras, N.W.T. Technical report prepared for Diavik Diamond Mines Inc. and Aber Resources. Available from Penner and Associates Ltd., 3-52059 Range Road 220, Sherwood Park, Alberta T8E 1B9, Canada. 220 p.

PETERSON, B.J., and FRY, B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18: 293–320.

POELKER, R.J., and HARTWELL, H.D. 1973. Black bear of Washington. Washington State Game Department Biological Bulletin No. 14. 180 p.

PRITCHARD, G.T., and ROBBINS, C.T. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645–1651.

REYNOLDS, J.C., and AEBISCHER, N.J. 1991. Comparison and quantification of carnivore diet by faecal analysis: A critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mammal Review 21:97–122.

RODE, K.D., and ROBBINS, C.T. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78:1640–1645.

WELCH, C.A., KEAY, J., KENDALL, K.C., and ROBBINS, C.T. 1997. Constraints on frugivory by bears. Ecology 78: 1105–1119.