

The Gray Wolves, *Canis lupus*, of British Columbia's Central and North Coast: Distribution and Conservation Assessment

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The Gray Wolves (*Canis lupus*) of coastal British Columbia are a remnant group of a much larger population that once inhabited most of North America, including its west coast temperate rainforests. During summers 2000 and 2001, we surveyed 36 islands and 42 mainland watersheds on British Columbia's Central and North Coast for the presence of wolves. An extensive survey had not been conducted previously. We observed wolf sign at all locations, including islands or island groups separated by approximately 7, 8, and 12-km from other large landmasses. The distribution of wolves on islands may be dynamic, with occupancy by solitary Wolves or packs being ephemeral. The potential for an island to support a persistent population of wolves may depend on the presence and abundance of their main prey, Black-tailed Deer (*Odocoileus hemionus*), and security from exploitation by humans. These factors likely are mediated by island isolation, area, shape, topography, and extent of logging. Mounting evidence suggests that logging negatively affects Wolves in temperate rainforests by reducing carrying capacity for deer.

Key Words: Gray Wolf, *Canis lupus*, distribution, islands, British Columbia, logging, conservation.

The Gray Wolf, *Canis lupus*, is one of the most intensely studied wildlife species in North America, yet complete and recent distributional data are absent from the large and remote Central and North Coast of British Columbia (Figure 1). The equilibrium theory of island biogeography predicts that species composition on islands is a function of immigration and extinction, mediated by island area and isolation (MacArthur and Wilson 1967). The ability of a terrestrial mammal to colonize islands depends on degree of isolation, the species' swimming ability, and water conditions.

Earlier, it was postulated that the occurrence of Gray Wolves on the islands of coastal British Columbia and Alaska was a function of the presence of their main prey, Black-tailed Deer (*Odocoileus hemionus*), but limited by isolation on islands to which wolves were capable of swimming (McCabe and Cowan 1945; Klein 1965). MacDonald and Cook (1996) stated that Gray Wolves occurred in all mainland areas and on most islands of southeast Alaska, but not on small and isolated ones without adequate prey. Nagorsen (1990) described Gray Wolf range in British Columbia as comprising the "entire mainland, Vancouver Island and some adjacent islands". Our main objective herein is to describe the distribution of Gray Wolves along the Central and North Coast of British Columbia, particularly on islands. We also discuss conservation concerns relevant to wolves of coastal temperate rainforests because these factors may influence future

distribution (Person et al. 1996*; Darimont and Paquet 2000*; Person 2000). We recorded the information while conducting field studies of wolves and their prey during summers 2000 and 2001 (Darimont and Paquet 2000*; Darimont and Reimchen 2003; Darimont et al. in press).

Methods

Study Area

Boats and airplanes provide the only access to this nearly roadless and mostly unsettled region. Extensive fjords divide mainland valleys. Tidal waters separate islands that vary from < one km² to >2,200 km² (Princess Royal Island). Inter-island and mainland-island distances range from several metres to approximately 13-km. The study area was roughly delineated by the Kshwan Valley (55° 37' N, 129° 48' W) in the north to Cape Caution (51° 10' N, 127° 47' W) in the south, and oriented parallel to the coastline (Figure 1). The Coast Mountains and the Pacific Ocean bound the study area to the east and west respectively.

Most of the low elevation forest is within the Coastal Western Hemlock biogeoclimatic zone (*sensu* Krajina 1965), characterised by a wet and temperate climate. Annual precipitation exceeds 350 cm in most areas. Thirty-year average annual snowfall measured near sea level varies from 86 cm (Bella Bella) to 155 cm (Ocean Falls) (Environment Canada 1991*).

*See Documents Cited section.

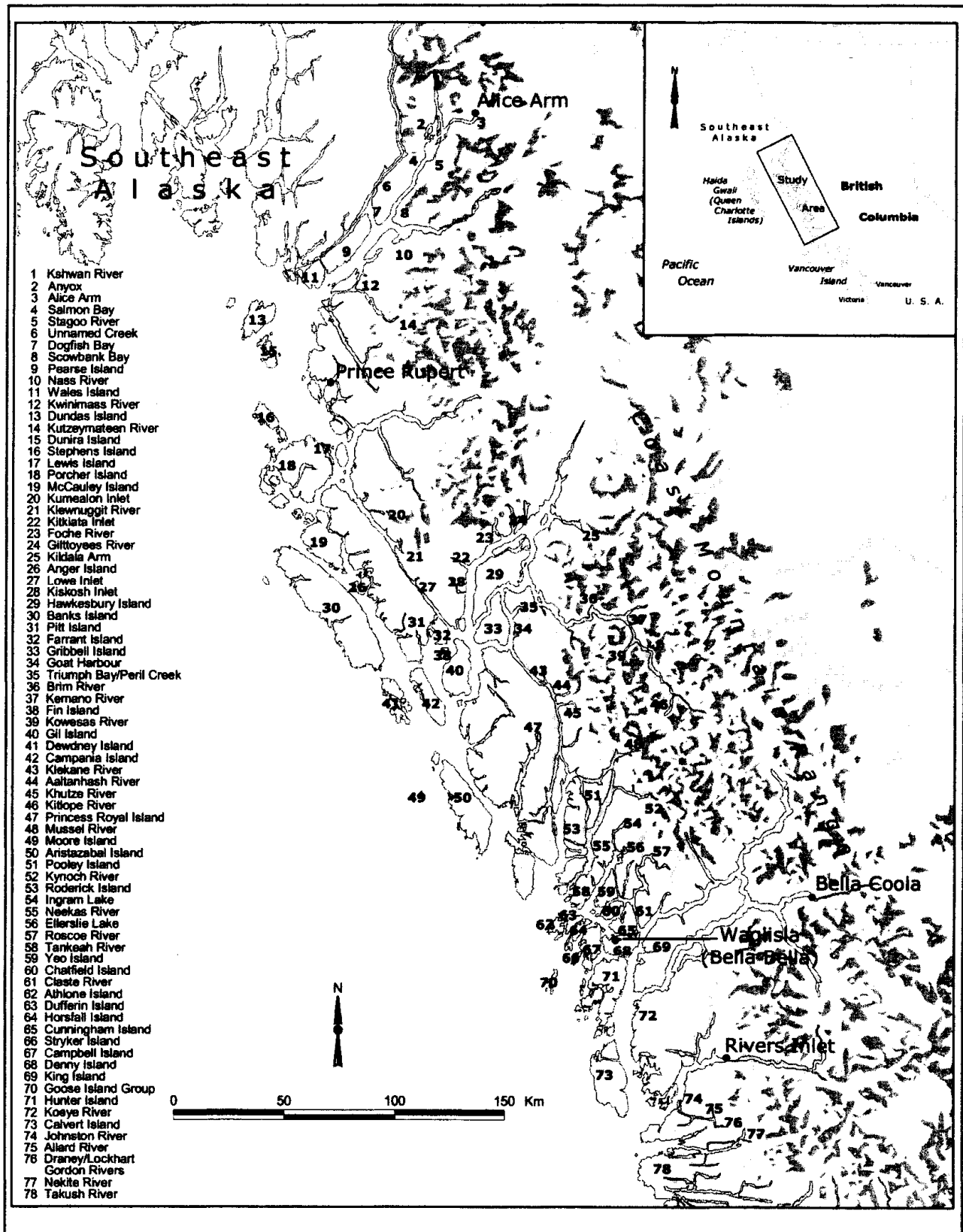


FIGURE 1. Study area, survey sites, and other notable landmarks relevant to survey for Gray Wolf distribution on British Columbia's Central and North Coasts during summers 2000 and 2001.

of the study area. Mountain Goats (*Oreamnos americanus*) are found on the mainland, but presence has been confirmed on only Pitt and Princess Royal Islands (Nagorsen and Keddie 2000). Marine foods such as spawning salmonids (Darimont and Reimchen 2002; Darimont et al. *in press*, and Paquet, unpublished) and beached marine mammals are also available. Possible competitors are Brown Bear (*Ursus arctos*) and Black Bear (*U. americanus*), Wolverine (*Gulo gulo*), Coyote (*Canis latrans*), and Cougar (*Felis concolor*).

Environmental conditions that may influence movements of wolves among landmasses vary seasonally and geographically. The following information is summarized from Thomson (1981). Mean air and water temperatures are lower during winter than summer, and average wind speed and wave height are greatest during fall and winter and in outer coastal areas. Surface currents flood primarily to the northeast and ebb to the southwest, but are consistently modified by wind, runoff, bathymetry and shoreline configuration. Typically, current velocity increases in narrow waterways. Fog is most common during summer and on the outer coast.

We used a Geographic Information System (ArcView 3.2 — Environmental Systems Research Institute Inc.) to calculate island areas from 1:20 000 forest inventory maps (Province of British Columbia) generalized to 1:250 000. Minimum shore-to-shore distances at low tides were calculated from marine charts (Canadian Hydrographic Service). We indexed isolation as the shortest island-to-mainland distance or sum of island-to-island distances (excluding distances across islands) to mainland for outer islands (Conroy et al. 1999). We also measured minimum distances to other large landmasses (> 75-km²). We used 75 km² as a threshold area because that is about the size of Coronation Island, southeast Alaska, on which some wolves among an initial introduced population of four survived in isolation for eight years (Klein 1996).

Sampling

We selected sampling sites that were well distributed throughout the study area and where we considered moorage safe. At each location, we used sandy beaches, estuaries, and forests of the beach fringe to begin our search for wolf sign. Wildlife trails, often next to watercourses, allowed travel inland. We also surveyed logging roads when encountered and often circumnavigated Beaver ponds and other wetlands. In addition, we walked forest ridgelines. Our surveys rarely extended greater than 5 km inland. Survey effort differed at each location from a few hours to several days.

We determined presence of wolves by noting tracks, scat, sightings, and carcasses. We did not systematically solicit howling but recorded all vocalizations. Wolves are the only canid known on coastal islands in the region, although Red Foxes (*Vulpes vulpes*) and Coyotes occur on the mainland

(Nagorsen 1990). Coyote tracks can be distinguished from wolf tracks based on differences in size (Rezendes 1999). Scats from Coyotes are generally smaller than scats from wolves, although there is some overlap in size (Weaver and Fritts 1979). Although the probability in this remote area is low, we may have assigned Gray Wolf presence to the tracks or scats of large feral Dogs (*Canis familiaris*).

Results

We observed recent wolf sign in all mainland watersheds (n = 42), confirming a continuous north-south distribution on the coastal mainland. Thirty-four of 36 islands had recent Gray Wolf sign. The most isolated islands on which we noted Gray Wolves were Moore Island, the Goose Group, and adjacent Dundas/Dunira Islands at 5 km, 7 km, and 12/13 km respectively from other large landmasses (Figure 1; Table 1).

We found scats and tracks at all survey locations (n = 78) except the Goose Group and Moore Island, where no tracks were observed (Table 1). We found remains of dead wolves at three island sites and observed wolves on the shoreline at several mainland rivers and on six islands (Table 1). Howling was heard at some sites (Table 1).

On the Goose Group of islands (~ 25 km²), we observed extensive sign of deer and found one old scat from a wolf. A Steller Sea Lion (*Eumetopias jubatus*) carcass showed no evidence of scavenging by large mammals. On the Moore Islands, which comprise a very small (< 5 km²) archipelago, we recorded no sign of deer. However, we found one old scat containing bird and other unidentified material. In contrast, we noted deer sign and fresh wolf tracks and scat on Dundas and Dunira Islands, which are relatively large but extremely isolated adjacent islands at least 12 km from other large (or any habitable) landmasses (Table 1).

Discussion

The current distribution of wolves in coastal British Columbia ranges from the deepest inlets of the coastal mountains to the most remote of islands (Figure 1; Table 1). The presence of wolves at all mainland survey sites concurs with earlier reports of the species' distribution along the Pacific Coast (Nagorsen 1990; MacDonald and Cook 1996).

Notably, of the 17 islands surveyed by both studies, we detected the presence of wolves on six islands that McCabe and Cowan (1945) did not. These discrepancies likely reflect an artifact of sampling effort (ours being greater and more focused), or perhaps (re)colonization. Wolf and deer sign was detected on the Goose Group, where Guignet (1953), after completing a four-month ecological inventory, reported neither species. Deer may have colonized the group since then (either naturally or assisted by humans).

TABLE I. Island areas (km²) and distances (m) from mainland and islands greater than 75 km² for island sampling sites on the Central and North Coast of British Columbia, Canada where Gray Wolves or their sign were observed. ca = carcass, ho = howling, ob(x,y) = observation (number seen at x location and at a different y location), sc = scat, tr = tracks. N/A = not applicable (i.e., island is closer to mainland than other landmasses). Sampling site codes match those in Figure 1.

Island	Sampling Site	Sign Observed	Area (km ²)	Distance to Mainland (m)	Distance to Island > 75 km ² (m)
Pearse	9	ob(3),sc,tr	226	300	N/A
Wales	11	sc,tr	97	700	350
Dundas	13	sc,tr	160	12000	N/A
Dunira	15	sc,tr	22	13050	1700
Stephens	16	sc,tr	78	3100	700
Lewis	17	ob(2),sc,tr	7	2400	100
Porcher	18	sc,tr	632	2300	1900
McCauley	19	sc,tr	273	1050	650
Anger	26	ho,ob(1),sc,tr	51	600	200
Hawkesbury	29	ca,ho,ob(2),sc,tr	322	1950	1550
Banks	30	sc,tr	1024	3250	2200
Pitt	31	ho,ob(3,1),sc,tr	1349	400	N/A
Farrant	32	ho,ob(4,1),sc,tr	50	450	50
Gribbell	33	sc,tr	207	1550	1550
Fin	38	sc,tr	13	2250	1750
Gil	40	sc,tr	238	3900	2050
Dewdney	41	sc,tr	37	6200	100
Compania	42	sc,tr	157	2450	2050
Princess Royal	47	ca,sc,tr	2295	900	50
Moore	49	sc	5	12500	8000
Aristazabal	50	sc,tr	451	4350	3450
Pooley	51	sc,tr	162	250	100
Roderick	53	sc,tr	239	350	100
Yeo	59	ob(1),sc,tr	95	250	N/A
Chatfield	60	sc,tr	48	1000	100
Athlone	62	sc,tr	40	2800	1350
Dufferin	63	sc,tr	43	2750	1300
Horsfall	64	sc,tr	32	2650	1250
Cunningham	65	sc,tr	115	850	150
Stryker	66	sc,tr	10	2800	1400
Campbell	67	ca,sc,tr	145	1450	400
Denny	68	sc,tr	127	1000	150
King	69	sc,tr	826	1750	N/A
Goose Group	70	sc	24	8700	7250
Hunter	71	ob(1),sc,tr	399	1700	700
Calvert	73	sc,tr	326	3850	3100

The presence of wolves on extremely isolated islands suggests that the potential for wolves to swim among landmasses is high. The ocean, however, likely serves as a considerable barrier to movement. Previously, Gray Wolves have been described as good swimmers, but only of short distances in fresh water (Mech 1970; Pimlott et al. 1969*; Nelson and Mech 1984; Coscia 1993). Swimming in marine environments probably carries considerably more energetic costs than travel on land, and may impose costs by elimination (e.g., drowning). Moreover, the effects of currents, which vary between landmasses, may be as important as straight-line distances in influencing movement (Cameron 1958; Williamson 1981). Finally, sightability [visibility] may affect orientation (MacArthur and Wilson 1967) and influence which

islands wolves select, especially during foggy periods of summer.

Radio-telemetry data from southeast Alaska confirm that dispersal across large water bodies is possible but infrequent. Person (2000) documented wolves swimming at least 2 km, although none of 11 dispersing animals left Prince of Wales or adjacent islands during three years of study. Although low prey density can stimulate dispersal (Peterson and Page 1988; Fuller 1989), presumably starving wolves on Coronation Island, southeast Alaska, failed to swim 900 m to a nearby island where deer were available (Klein 1996).

Due to the barrier effects of water, some populations on islands are probably independent sub-populations among which exchanges of individuals or

packs are limited. We were not able to determine if the wolf sign found on islands came from multiple or solitary animals, or whether Wolves were resident or transient. Future studies may benefit by examining the presence, movements, and demographic fates of individuals over time to examine if metapopulation theory is applicable; such frameworks for other large mammals in habitat patches have been developed (e.g., Elmhagen and Angerbjörn 2001).

Occupancy by Gray Wolves on islands likely is influenced by the presence and abundance of deer, and security from exploitation by humans. These factors might be mediated by size of island, isolation, topography, shape, and extent of logging. Because wolves are obligate predators of ungulates, islands without deer would not sustain wolves. Persistence times, however, are probably a function of the abundance and availability of deer (Fuller 1989) as well as island size and isolation. Wolves seem unable to persist indefinitely on small and isolated islands, even if deer are present. On isolated islands, they may be subject to a "minimum area effect" (*sensu* Lomolino 1986). That is, although their immigration potential is high, they can only maintain populations on the largest of isolated islands.

In the 1960s, biologists introduced four Gray Wolves to the 73 km² Coronation Island, southeast Alaska, 900 m from another landmass, to study the effects on resident deer (Klein 1996). After reaching a peak of 13 animals in four years, the wolf population, having severely reduced deer numbers, plummeted to one. Klein (1996) and Person et al. (1996*) stated that small and isolated islands, such as Coronation, are unable to support populations of wolves. Person (2000) noted that islands as large as 180 km² with deer carrying capacities greater than 2500 in southeast Alaska did not continuously support wolves between 1955 and 2000.

Lomolino (1986) argued that extinction-prone species, such as large carnivores, might be common on small islands only if their immigration rates are high relative to extinction rates. This can apply to Gray Wolf packs as a conceptual unit. The social group may be sustained if their home range includes a collection of nearby islands (Klein 1996; Person et al. 1996*; Person 2000). Including multiple landmasses would compensate for extirpation risk on individual islands. Of the four most isolated islands on which we noted sign, wolves currently were present only on Dundas and Dunira Islands (Figure 1; Table 1), and probably formed one social group. Although both are isolated from large landmasses, collectively these and smaller nearby islands total 239 km², an area within the range of home ranges calculated for wolves of southeast Alaska (Person 2000).

The viability of wolves on large but isolated islands or island groups such as Dundas and Dunira may be uncertain. For example, although the 540 km² Isle Royale has supported wolves since the late 1940s

without further immigration, the population has experienced considerable declines due to disease, demographic stochasticity, and shortage of food (Peterson and Page 1988; Vucetich et al. 1996; Peterson et al. 1998). Moreover, continued viability may be threatened by a loss of genetic diversity (Wayne et al. 1991).

In coastal British Columbia, an island's topography would interact with size and isolation in determining the abundance of deer and thus the viability of wolf populations. The complex topography of many inner coastal islands can include elevations of 1100-m or more, above which deer in adjacent southeast Alaska are not known to occur (Schoen and Kirchhoff 1985). Thus, habitat suitable for deer and wolves can be less than predicted based on area alone.

Mounting evidence suggests that carrying capacity for deer will be reduced by even age stand management in the Pacific Northwest because clearcut logging is largely incompatible with the food requirements of deer (Wallmo and Schoen 1980; Alaback 1982; Rose 1982; Alaback 1984*; Schoen et al. 1984, 1998; Van Horne et al. 1988; Hanley et al. 1989*). Most notably, closed canopies that develop 20–30 years after harvest severely limit forage for deer and persist for 140–160 years (Wallmo and Schoen 1980; Alaback 1982; Schoen et al. 1988).

Persistence on islands might also be influenced by human-caused mortality. Island wolf populations are vulnerable to over-exploitation because water bodies may slow immigration and re-colonization (Person et al. 1996*; Person 2000). Person (2000) reported that humans on Hecata Island, southeast Alaska, nearly exterminated Gray Wolves on two occasions. In our nearby roadless study area, the shape of islands may affect human-caused mortality. Coastlines are analogous to roads because travel routes of human hunters in boats and wolves converge. Because of high coastline to interior ratios, long and narrow islands provide less security than rounder islands.

Although annual human-caused mortality in the study area is only about 2 %, the human population is growing considerably and hunting regulations are liberal (Darimont and Paquet 2000*). Moreover, more road building is planned to support industrial logging (Darimont and Paquet 2000*). This is a concern, as many authors have shown the lethal impact of roads on Wolves (i.e., Thiel 1985; Jensen et al. 1986; Fuller 1989; Paquet et al. 1996*; Callaghan 2002) and other wildlife species (*review in* Trombulak and Frissell 2000).

We encourage others to invoke a broad spatial and temporal perspective when considering the distribution and conservation status of this population of Gray Wolves, regardless of their wide distribution in the study area now. Extant populations, such as those in coastal British Columbia, form remnant groups of those that first colonized North America roughly 700 000 years ago (Nowak 1979; Kurten and Anderson 1980) and historically ranged in every habitat that

supported ungulate prey. During the last few hundred years, humans have reduced Gray Wolf populations and effectively isolated them to remote areas of Canada, Minnesota, and Alaska (Mech 1970, 1995). On the West Coast, wolves were extirpated in California, Oregon, and Washington, as well as in the Lower Mainland region of British Columbia (Theberge 1991). Wolves of these coastal rainforests are now restricted to southeast Alaska and most of British Columbia. Furthermore, coastal biota, including the Gray Wolf, is thought to be at least partially isolated from continental populations by coastal mountain ranges (e.g., McCabe and Cowan 1945; Klein 1965; MacDonald and Cook 1996; Person et al. 1996*; Byun et al. 1997; Conroy et al. 1999; Darimont and Paquet 2000*; Cook and MacDonald 2001; Figure 1). Finally, wolves of coastal British Columbia should be considered a natural source population for those in nearby southeast Alaska, a population for which there is considerable conservation concern due to timber removal and associated effects (Kirchhoff 1991*; Person and Ingle 1995*; Person et al. 1996*; Person 2000)

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Documents Cited (marked * in text)

- Alaback, P. B.** 1984. Plant succession following logging in the Sitka spruce-western hemlock forests of southeast Alaska: implications for forest management. General Technical Report PNW-173. United States Department of Agriculture — Forest Service. Portland, Oregon.
- Darimont, C. T., and P. C. Paquet.** 2000. The gray wolves (*Canis lupus*) of British Columbia's coastal rainforests: Findings from Year 2000 pilot study and conservation assessment. Prepared for the Raincoast Conservation Society. Victoria, British Columbia.
- Environment Canada.** 1991. 1961–1990 weather normals for British Columbia: temperature and precipitation. Environment Canada. Atmospheric Environment Service. Ottawa, Ontario.
- Hanley, T. E., C. T. Robbins, and D. E. Spalinger.** 1989. Forest habitats and the nutritional requirements for black-tailed deer: A research synthesis with implications for forest management. General Technical Report PNW-GTR-230. United States Department of Agriculture — Forest Service. Portland, Oregon.
- Kirchhoff, M. D.** 1991. Status, biology and conservation concerns for the wolf (*Canis lupus ligoni*) in southeast Alaska. Unpublished Management Report. Alaska Department of Fish and Game. Juneau, Alaska.
- Paquet, P., J. Wierzchowski, and C. Callaghan.** 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in *A cumulative effects assessment and futures outlook for the Banff Bow Valley*. Edited by J. Green, C. Pacas, S. Bayley, and L. Cornwell. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage. Ottawa, Ontario.
- Person, D. K., and M. A. Ingle.** 1995. Ecology of the Alexander Archipelago wolf and responses to habitat change. Progress Report Number 3. Alaska Department of Fish and Game. Douglas, Alaska.
- Person, D. K., M. Kirchhoff, V. Van Ballenberghe, G. C. Iverson, and E. Grossman.** 1996. The Alexander Archipelago wolf: a conservation assessment. General Technical Report. PNW-GTR-384. United States Department of Agriculture — Forest Service. Portland, Oregon.
- Pimlott, D. H., J. A. Shannon, and G. B. Kolenosky.** 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department of Lands and Forests. Research Branch Research Report (Wildlife) 87.
- Literature Cited**
- Alaback, P. B.** 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63: 1932–1948.
- Byun, S. A., B. F. Koop, and T. E. Reimchen.** 1997. North American black bear mtDNA phylogeography: implications for morphology and the Haida Gwaii glacial refugium controversy. *Evolution* 51: 1647–1653.
- Callaghan, C. J.** 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival, and persistence in the Central Rocky Mountains, Canada. Ph.D. thesis. University of Guelph. Guelph, Ontario. 213 pages.
- Cameron, A. W.** 1958. Mammals of the islands in the Gulf of St. Lawrence. *National Museum of Canada Bulletin* 154: 1–164.
- Conroy, C. J., J. R. Demboski, and J. A. Cook.** 1999. Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. *Journal of Biogeography* 26: 343–352.
- Cook, J. A., and S. O. MacDonald.** 2001. Should edemism be a focus of conservation efforts along the North Pacific Coast of North America? *Biological Conservation* 97: 207–213.
- Coscia, E. M.** 1993. Swimming and aquatic play by timber wolf, *Canis lupus*, pups. *Canadian Field-Naturalist* 107: 361–362.
- Darimont, C. T., and T. F. Reimchen.** 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Canadian Journal of Zoology* 80: 1638–1642.
- Darimont, C. T., and T. F. Reimchen, and P. C. Paquet.** *in press*. Foraging behaviour by gray wolves on salmon streams streams in coastal British Columbia. *Canadian Journal of Zoology*.
- Elmhagen, B., and A. Angerbjörn.** 2001. The applicability of metapopulation theory to large mammals. *Oikos* 94: 89–100.

- Fuller, T. K.** 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105: 1–41.
- Guiguet, C. J.** 1953. An ecological study of Goose Island, British Columbia: with special reference to mammals and birds. Occasional papers of the British Columbia Provincial Museum Number 110. Victoria, British Columbia.
- Jensen, W. F., T. K. Fuller, and W. L. Robinson.** 1986. Wolf (*Canis lupus*) distribution on the Ontario to Michigan border near Sault Ste. Marie. *Canadian Field-Naturalist* 100: 363–366.
- Kirchhoff, M. D., and J. W. Schoen.** 1987. Forest cover and snow: implications for deer habitat in southeast Alaska. *Journal of Wildlife Management* 51: 28–33.
- Klein, D. R.** 1965. Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. *Arctic* 18: 7–20.
- Klein, D. R.** 1996. The introduction, increase, and demise of wolves on Coronation Island, Alaska. Pages 275–280 in *Ecology and conservation of wolves in a changing world*. Edited by L. N. Carbyn, S. H. Fritts, and D. R. Seip. Canadian Circumpolar Institute, University of Alberta. Edmonton, Alberta.
- Krajina, V. J.** 1965. Biogeoclimatic zones and classification of British Columbia. *Ecology of Western North America* 1: 1–17.
- Kurten, B., and E. Anderson.** 1980. Pleistocene Mammals of North America. Columbia University Press. New York, New York.
- Lomolino, M. V.** 1986. Mammalian community structure on islands: the importance of immigration, extinction and interactive effects. *Biological Journal of the Linnean Society* 28: 1–21.
- MacArthur, R. H., and E. O. Wilson.** 1967. The theory of island biogeography. Princeton University Press. Princeton, New Jersey.
- MacDonald, S. O., and J. A. Cook.** 1996. The land mammal fauna of Southeast Alaska. *Canadian Field-Naturalist* 110: 571–598.
- McCabe, T. T., and I. M. Cowan.** 1945. *Peromyscus maniculatus macrorhinus* and the problem of insularity. *Transactions of the Royal Canadian Institute* 25: 117–216.
- Mech, L. D.** 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Doubleday. New York, New York.
- Mech, L. D.** 1995. The challenge and opportunity of recovering wolf populations. *Conservation Biology* 9: 270–278.
- Nagorsen, D. W.** 1990. The mammals of British Columbia: a taxonomic catalogue. Memoir Number 4. Royal British Columbia Museum. Victoria, British Columbia.
- Nagorsen, D. W., and G. Keddie.** 2000. Late Pleistocene mountain goats (*Oreamnos americanus*) from Vancouver Island: Biogeographic implications. *Journal of Mammalogy* 81: 666–675.
- Nelson, M. E., and L. D. Mech.** 1984. Observations of a swimming wolf killing a swimming deer. *Journal of Mammalogy* 65: 143–144.
- Nowak, R.** 1979. North American Quaternary Canis. Museum of Natural History. University of Kansas. Lawrence, Kansas.
- Person, D. K.** 2000. Wolves, deer, and logging: Population vitality and predator-prey dynamics in a disturbed insular landscape. Ph.D. dissertation. University of Alaska, Fairbanks, Alaska.
- Peterson, R. O., and R. E. Page.** 1988. The rise and fall of Isle Royale wolves. *Journal of Mammalogy* 69: 89–99.
- Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite.** 1998. Population limitation and the wolves of Isle Royale. *Journal of Mammalogy* 79: 828–841.
- Rezendes, P.** 1999. Tracking and the art of seeing: How to read animal tracks and sign. Second edition. HarperCollins. New York, New York.
- Rose, C. L.** 1982. Deer responses to forest succession on Annette Island, southeast Alaska. MSc thesis. University of Alaska. Fairbanks, Alaska. 59 pages.
- Schoen, J. W., and M. D. Kirchhoff.** 1985. Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. *Journal of Wildlife Management* 49: 96–103.
- Schoen, J. W., M. D. Kirchhoff, and O. C. Wallmo.** 1984. Sitka black-tailed deer/old-growth relationships in southeast Alaska: implications for management. Pages 315–320 in *Proceedings of the symposium on fish and wildlife relationships in old growth forests (1982)*. Edited by W. R. Meacham, T. R. Merrell, and T. A. Hanley. American Institute of Fisheries Research Biologists. Juneau, Alaska.
- Schoen, J. W., M. D. Kirchhoff, and J. H. Hughes.** 1988. Wildlife and old-growth forests in southeastern Alaska. *Natural Areas Journal* 8: 138–145.
- Theberge, J. B.** 1991. Ecological classification, status and management of the Gray Wolf, *Canis lupus*, in Canada. *Canadian Field Naturalist* 105: 459–463.
- Thiel, R. P.** 1985. The relationship between road densities and wolf habitat suitability in Wisconsin. *American Midland Naturalist* 113: 404–407.
- Thomson, R. E.** 1981. Oceanography of the British Columbia Coast. Canadian Special Publication of Fisheries and Aquatic Sciences 56. Department of Fisheries and Oceans. Ocean Physics Division. Institute of Ocean Sciences. Sidney, British Columbia.
- Trombulak, S. C., and C. A. Frissell.** 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18–30.
- Van Horne, B., T. A. Hanley, R. G. Cates, J. D. McKendrick, and J. D. Horner.** 1988. Influence of seral stage and season on leaf chemistry of southeast Alaska deer forage. *Canadian Journal of Forest Research* 18: 90–99.
- Vucetich, J. A., R. O. Peterson, and T. A. Waite.** 1996. Effects of social structure and prey dynamics on extinction risk in gray wolves. *Conservation Biology* 11: 957–965.
- Wallmo, O. C., and J. W. Schoen.** 1980. Responses of deer to secondary forest succession in southeast Alaska. *Forest Science* 26: 448–462.
- Wayne, R. K., N. Lehman, D. Girman, P. J. P. Gogan, D. A. Gilbert, K. Hansen, R. O. Peterson, U. S. Seal, A. Eisenhauer, L. D. Mech, and R. D. Krumenaker.** 1991. Conservation genetics of the endangered Isle Royale gray wolf. *Conservation Biology* 5: 41–51.
- Weaver, J. L., and S. H. Fritts.** 1979. Comparison of coyote and wolf scat diameters. *Journal of Wildlife Management* 3: 786–788.
- Williamson, M. H.** 1981. Island Populations. Oxford University Press. New York, New York.

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