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Linking Wolf Diet to Changes in Marine and Terrestrial Prey Abundance

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ABSTRACT. Since most wolf (*Canis lupus*) diet studies have been conducted in inland ecosystems, comparatively few data are available on diets of wolves in coastal systems. We investigated the diet of wolves in Glacier Bay, Alaska, from 12 May to 28 June in both 2010 and 2011. Although we identified 12 different prey species, including birds and small to medium-sized mammals, in wolf scats, moose (*Alces alces*) was the most frequent food item, observed in 80% of all scats. In contrast, a study conducted in 1993 in an area 37 km away found harbor seal (*Phoca vitulina richardii*) in 41% of wolf scats. Although we cannot account for differences in sampling design between the two studies, wolf diets may have changed between the two time periods.

Key words: wolves, *Canis lupus*, diet, Glacier Bay, Alaska

RÉSUMÉ. Puisque la plupart des études sur le régime alimentaire des loups (*Canis lupus*) ont été réalisées dans des écosystèmes situés à l'intérieur des terres, relativement peu de données existent sur le régime alimentaire des loups évoluant dans les environnements côtiers. Nous avons étudié l'alimentation des loups de Glacier Bay, en Alaska, du 12 mai au 28 juin 2010 et 2011. Bien que nous ayons retrouvé 12 proies différentes, y compris des espèces aviaires et des mammifères de taille petite ou de taille moyenne dans les déjections de loups, l'aliment le plus fréquemment rencontré, dans une mesure de 80 %, a été l'orignal, aussi appelé élan (*Alces alces*). Par contraste, une étude effectuée en 1993 dans une zone située à 37 kilomètres de distance a permis de découvrir du phoque commun (*Phoca vitulina richardii*) dans 41 % des déjections de loups. Bien que nous ne soyons pas en mesure de prendre en compte les différences d'échantillonnage entre les deux études, il est possible que le régime alimentaire des loups ait changé entre ces deux périodes.

Mots clés : loups, *Canis lupus*, régime alimentaire, Glacier Bay, Alaska

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Тезис. Большинство исследований рациона волка (*Canis lupus*) проводилось на внутриматериковых территориях, в то время как имеется сравнительно небольшое количество данных по рациону волка в прибрежных экосистемах. Ежегодно с 12 мая по 28 июня 2010-2011 гг. нашей группой проводились исследования рациона волков в бухте Глейшер-Бей, Аляска. Несмотря на то, что нами было определено 12 различных видов, используемых волками в качестве добычи, включая птиц, а также мелких и средних млекопитающих, останки лося (*Alces alces*) встречались в 80% экскрементов волков, указывая на то, что данный вид является наиболее частым пищевым объектом волка.

В отличие от данных результатов, эксперимент, проведенный в 1993 г. на участке, удаленном от нашего на 37 км, обнаружил наличие останков тюленя (*Phoca vitulina richardii*) в 41% экскрементов волков. Несмотря на то, что мы не можем объяснить различия в выборке по каждому из исследований, их результаты указывают на то, что в период между двумя исследованиями в рационе волков могли произойти изменения.

Ключевые слова: Волки, *Canis lupus*, изменение рациона, Глейшер-Бей, Аляска

INTRODUCTION

Throughout much of their North American range, wolves (*Canis lupus*) are considered predominantly ungulate predators (Peterson and Ciucci, 2003). As opportunistic carnivores, however, wolves are known to consume a diverse

assemblage of prey species (Carnes, 2004). For example, studies from Alaska and coastal British Columbia have demonstrated that wolves may augment their diets with non-ungulate prey, such as seasonally abundant salmon (*Onchorynchus* spp.) (Szepanski et al., 1999; Darimont et al., 2008; Adams et al., 2010), whereas other studies have

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shown that carrion from various terrestrial and marine species may serve as an important component of wolf diets (Forbes and Theberge, 1992; Wilmers et al., 2003; Watts et al., 2010). Consequently, the diet of wolves may vary spatially and temporally across the landscape in response to variation in the distribution, density, and seasonal availability of local food resources.

Since the late 1800s, wolves have been documented in Glacier Bay, Alaska (Muir, 1915), but little information is available on the food habits of wolves in this region. Continuous landscape change in Glacier Bay due to glacial retreat and primary succession of nearly 1500 km² of newly emergent coastal land (Hall et al., 1995) has influenced the distribution, abundance, and diversity of potential wolf prey species. For example, moose (*Alces alces*) colonized this coastal landscape in the mid-1960s (Streveler and Smith, 1978; Dinneford, 1990), and moose abundance has since increased markedly (White et al., 2006). Salmon also have colonized recently deglaciated watersheds in Glacier Bay (Milner et al., 2007). In addition, the spatial distribution of harbor seals (*Phoca vitulina richardii*) has changed over the past two decades, and the number of harbor seals in Glacier Bay has decreased substantially since 1992 (Mathews and Pendleton, 2006; Womble et al., 2010). Thus, the potential terrestrial and marine prey base of wolves in Glacier Bay has changed considerably over the past several decades.

Our objective was to evaluate the late spring–early summer diet of wolves in Glacier Bay, an area where wolves inhabit the marine-terrestrial interface. Specifically, we sought to determine whether moose had become an important component of wolf diets in this region. As few data are available on the diet of wolves in Glacier Bay, we contrast our results with the findings presented in an unpublished report by Meiklejohn (1994) that described the diet of wolves in southeastern Glacier Bay. We interpret these results in the context of changing prey abundance in this rapidly deglaciating coastal ecosystem.

METHODS

We investigated wolf diet in the Glacier Bay area of Alaska (58°27' N, 135°43' W) from 12 May to 28 June in 2010 and 2011 (Fig. 1). The 600 km² study area included the southeastern portion of Glacier Bay National Park and Preserve (hereafter, Glacier Bay) and the coastal community of Gustavus (population 442; U.S. Census Bureau, 2013). Field observations, aerial surveys, camera trap imagery, and GPS-collar data indicate that at least one pack of 8–12 wolves and one solitary female wolf occupied the study area (N. Barten, Alaska Department of Fish and Game [ADFG], pers. comm. 2010). The territory of this wolf pack encompassed the East Arm of Glacier Bay, which included more than 320 km of shoreline (Fig. 1). We overlaid a 900 × 900 m grid across the study area using a geographic information system and then each year obtained wolf scats by searching 50 randomly selected grid cells. We searched each cell for

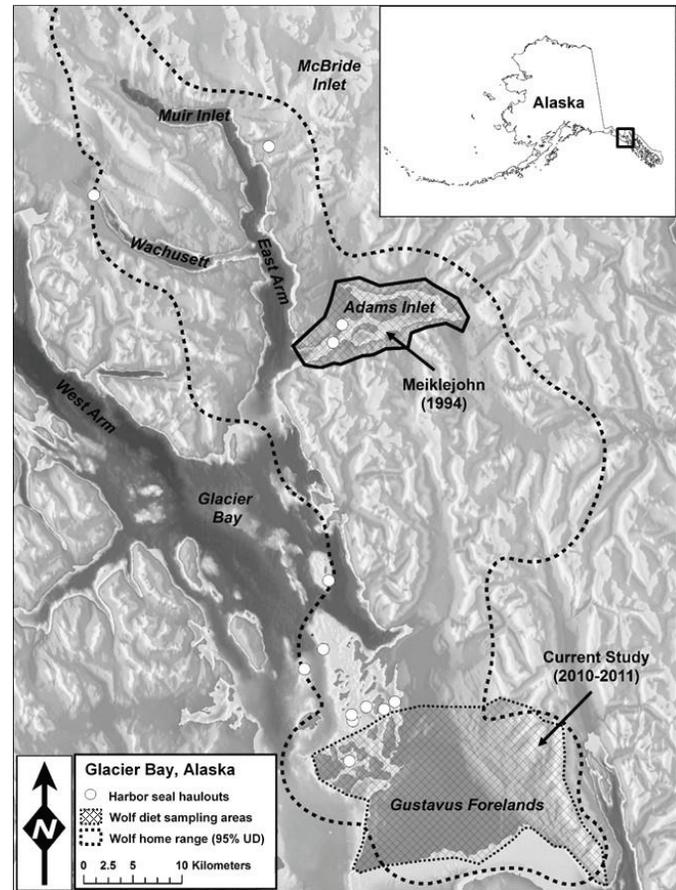


FIG. 1. Study areas where wolf diets were examined in southeastern Glacier Bay, Alaska, during the current study (2010–11) and in 1993 (Meiklejohn, 1994). The wolf home range (95% fixed kernel utilization distribution) is from a GPS-collared adult female wolf tracked during 2010–11 (N. Barten, ADFG, unpubl. data). Current harbor seal haulout site locations occupied during summer within the wolf home range are from Womble and Gende (2013).

one hour and collected all fresh wolf scats. Each fresh scat was identified by its moisture and by insect activity, which decreases markedly after about 10 days (D. Person, ADFG, pers. comm. 2010). We also collected all fresh wolf scats we found while traveling throughout the study area, including those we observed while searching previously identified wolf travel routes leading to and along the Gustavus beach. Scats smaller than 30 mm in diameter were excluded to avoid including coyote (*C. latrans*) scats in analyses (Weaver and Fritts, 1979). We used standard methods to collect, prepare, and identify prey items (Carnes, 2004). Whole scats were placed in 0.95 L plastic bags labeled with date and location and frozen until completion of fieldwork each year. Scats were then transferred to nylon bags and washed by hand or in a clothes washing machine to remove fecal debris (Carnes, 2004). We air dried undigested prey remains (e.g., bone, teeth, and hair) and identified each to the lowest taxonomic level possible using a reference collection and dichotomous keys (e.g., Moore et al., 1974). To describe wolf diets, we calculated percent frequency of occurrence (FO) ($100 \times \text{no. of occurrences of a food item} / \text{total no. of occurrences of all food items}$) for each food item

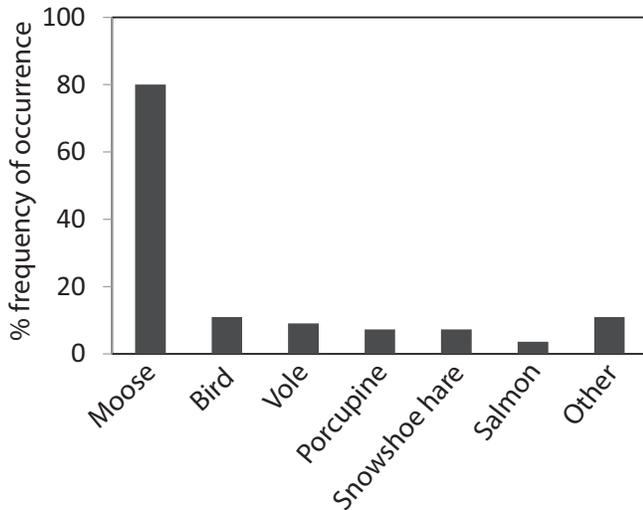


FIG. 2. Percent frequency of occurrence of food items identified in 55 wolf scats from southeastern Glacier Bay, Alaska, in May and June of 2010 and 2011. Food items observed only once were combined in the “Other” category.

identified in wolf scats (Carnes, 2004). Food items identified only once were combined in the category “other.”

RESULTS

We collected 55 wolf scats (47 in 2010 and 8 in 2011), of which 24 were located within the randomly selected grid cells. We identified 71 food items (Fig. 2). In 11 cases, we could identify food items only to genus (e.g., *Microtus*) or class (e.g., Aves, hereafter bird); thus, the number of identified food items is conservative. Scats contained 1–3 different food items (mean = 1.3 ± 0.7 standard deviation). Moose was the most common food item (80% FO), followed by bird (11% FO), vole (*Microtus* spp., 9% FO), porcupine (*Erethizon dorsatum*, 7% FO), snowshoe hare (*Lepus americanus*, 7% FO), and Pacific salmon (4% FO). Beaver (*Castor canadensis*), river otter (*Lontra canadensis*), red squirrel (*Tamiasciurus hudsonicus*), coyote, three-spined stickleback (*Casterosteus aculeatus*), and harbor seal were observed once each. Strawberry (*Fragaria chiloensis*) was the only plant matter identified in wolf scats. Too few samples were collected during 2011 to compare scat contents between sampling years; however, moose was the most frequently observed food item in both years.

DISCUSSION

Our data suggest that since moose colonized southeastern Glacier Bay in the mid-1960s, moose has become an important component of the diet of wolves whose territory includes the Gustavus forelands. Although moose density has varied since colonization (Fig. 3), this high-density moose population will likely continue to serve as an important food source for wolves. Moose calves, for

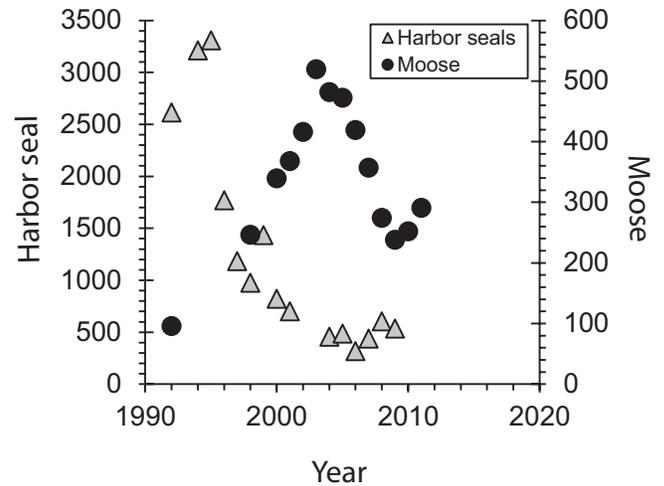


FIG. 3. Moose and harbor seal population trends in Glacier Bay, Alaska, from 1992 to 2011. Estimates of harbor seal population (non-pups only) are derived from data collected at terrestrial haulout sites (see Mathews and Pendleton, 2006; Womble et al., 2010). Moose population estimates were derived from data collected on the Gustavus forelands winter range. The value for 1993 is based on unpublished observations (Glacier Bay National Park and Alaska Department of Fish and Game files). Values for 1998–2011 are from moose data collected during aerial surveys; estimates were adjusted on the basis of sighting probabilities derived from mark-resight data (K. White, ADFG, unpubl. data).

example, are most vulnerable to predation during the first several weeks of life (Ballard et al., 1981), which coincided with our sampling period. Adult moose with calves also suffer greater mortality than those without calves (Testa, 2004). Furthermore, at the high density observed during the sampling years of this study (i.e., ~ 2.5 – 3.1 moose/km² on moose winter range), the Gustavus moose population exhibited poor body condition attributed to nutritional constraints imposed by habitat carrying capacity and intraspecific competition (White et al., 2006). This poor condition may have resulted in greater overwinter mortality due to malnutrition. Thus, expanding moose populations not only provide increased predation opportunities, but also may result in increased carrion biomass through non-predatory mechanisms. Therefore, it is not surprising that moose has become an important component of the late spring–early summer (May–June) diet of wolves in southeastern Glacier Bay.

In contrast to our study, a study conducted in 1993 that evaluated the diet of wolves in Adams Inlet, an area 37 km north of our study area, showed that moose occurred in less than 3% of wolf scats classified as moderate age (i.e., representing late spring–early summer wolf diets; $n = 68$), whereas harbor seal was observed in 41% of wolf scats (Meiklejohn, 1994). The high frequency of occurrence of harbor seal in wolf scats coincided with a period before dramatic declines were observed in harbor seals. After the grounding of Muir Glacier in the East Arm of Glacier Bay around 1993 (Hall et al., 1995), the glacier no longer produced icebergs that seals could use as resting sites (Mathews, 1995). Before the grounding of the glacier, more than 1300 seals were documented in Muir Inlet (Streveler,

1979). More recently, however, substantially fewer seals have been counted in the East Arm of Glacier Bay, with the primary haulout areas for seals restricted to Adams Inlet, McBride Inlet, and Wachusett Inlet (Womble et al., 2010). From 1992 to 2011, harbor seals at terrestrial sites in Glacier Bay declined at a rate of 9.3% per year (Fig. 3) (Mathews and Pendleton, 2006; Womble et al., 2010; J.N. Womble, unpubl. data).

Harbor seals occur in Glacier Bay throughout the year (Womble and Gende, 2013); however, their numbers increase substantially during the May-June pupping season (Mathews and Pendleton, 2006; Womble et al., 2010), when young seals are most vulnerable to terrestrial predators. Young harbor seals likely are vulnerable when hauled out at terrestrial sites where wolves can access them. Meiklejohn (1994) reported that the small claws of harbor seal pups were common in wolf scats collected in Adams Inlet, a well-known terrestrial haulout site used by harbor seals. Carnes (2004) and Klein (1995) also reported the presence of harbor seal in summer diets of wolves in northern and southern Southeast Alaska, respectively. Thus, naïve harbor seal pups hauled out at terrestrial sites may have been an important seasonal prey for wolves before the recent harbor seal population decline in Glacier Bay.

Differences in sampling methods and potential differences in local prey assemblages between sampling locations do not allow for a direct comparison of our study with Meiklejohn's (1994) study. However, existing data suggest that during Meiklejohn's study, moose were present at moderate density in Adams Inlet (Robus, 1996) and had not yet irrupted on the Gustavus forelands (White et al., 2006). Harbor seal haulout sites have been found in the Beardslee Islands in our study area (Mathews and Pendleton, 2006; Womble et al., 2010), and observations from our ground surveys confirmed that harbor seals were present in 2010–11. These records and diet data demonstrate that both moose and harbor seal were present in each study area at the time of that study. Although differences in the frequency of occurrence of moose and harbor seal in the diet of wolves in these two studies may be due to differences in local prey availability, they may also be a consequence of changes in primary prey densities through time, resulting in prey switching behavior by wolves (Murdoch, 1969).

Because of rapid landscape change in Glacier Bay (Hall et al., 1995), coastal wolves likely will exhibit a dietary response to continuing changes in prey populations. For instance, as salmon continue to colonize streams in Glacier Bay (Milner et al., 2007), they may become an important seasonal food for wolves, as demonstrated in coastal British Columbia (Darimont et al., 2008), other areas of Southeast Alaska (Szepanski et al., 1999), and interior Alaska (Adams et al., 2010). In our study, it is likely that scat analysis resulted in an underrepresentation of salmon in wolf diets not only because these fish are highly digestible (Hilderbrand et al., 1999), but also because scat collection occurred before the peak of spawning season. Thus, wolf use of salmon may have been greater than suggested by our results.

Recent dramatic increases in sea otters (*Enhydra lutris*) (Esslinger and Bodkin, 2009), Steller sea lions (*Eumetopias jubatus*) (Mathews et al., 2011), and humpback whales (*Megaptera novaeangliae*) (Hendrix et al., 2012) in the Glacier Bay region may also provide subsidies to wolves via increased scavenging opportunities. In 2010, for example, we observed wolves in western Glacier Bay scavenging a humpback whale carcass over several months, as well as members of a wolf pack scavenging the remains of a male Steller sea lion on Lester Island. Increasing marine mammal subsidies through predation or scavenging may influence the survival and fitness of wolves in Glacier Bay and buffer this coastal wolf population from seasonal fluctuations in preferred prey availability (Watts et al., 2010). Given ongoing climate change and glacial retreat, as well as continued shifts in potential primary prey abundance and the importance of wolves to predator-prey dynamics in this system, continued monitoring of wolf diets in Glacier Bay appears warranted.

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REFERENCES

- Adams, L.G., Farley, S.D., Stricker, C.A., Demma, D.J., Roffler, G.H., Miller, D.C., and Rye, R.O. 2010. Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? *Ecological Applications* 20(1):251–262. <http://dx.doi.org/10.1890/08-1437.1>
- Ballard, W.B., Spraker, T.H., and Taylor, K.P. 1981. Causes of neonatal moose calf mortality in South Central Alaska. *Journal of Wildlife Management* 45(2):335–342. <http://dx.doi.org/10.2307/3807916>

- Carnes, J.C. 2004. Wolf ecology on the Copper and Bering River deltas. PhD dissertation, University of Idaho, Moscow, Idaho.
- Darimont, C.T., Paquet, P.C., and Reimchen, T.E. 2008. Spawning salmon disrupt tight trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecology* 8:14. <http://dx.doi.org/10.1186/1472-6785-8-14>
- Dinneford, B. 1990. Moose colonization of post-glacial sites in southeastern Alaska. In: Milner, A.M., and Wood, J.D., eds. *Proceedings of the Second Glacier Bay Science Symposium, 19–22 September 1988, Glacier Bay National Park and Preserve*. Vol. 2:83–85.
- Esslinger, G.G., and Bodkin, J.L. 2009. Status and trends of sea otter populations in Southeast Alaska, 1969–2003. *Scientific Investigations Report 2009-5045*, Anchorage: U.S. Geological Survey.
- Forbes, G.J., and Theberge, J.B. 1996. Response by wolves to prey variation in central Ontario. *Canadian Journal of Zoology* 74(8):1511–1520. <http://dx.doi.org/10.1139/z96-165>
- Hall, D.K., Benson, C.S., and Field, W.O. 1995. Changes of glaciers in Glacier Bay, Alaska, using ground and satellite measurements. *Physical Geography* 16(1):27–41. <http://dx.doi.org/10.1080/02723646.1995.10642541>
- Hendrix, A.N., Straley, J., Gabriele, C.M., and Gende, S.M. 2012. Bayesian estimation of humpback whale (*Megaptera novaeangliae*) population abundance and movement patterns in southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 69(11):1783–1797. <http://dx.doi.org/10.1139/f2012-101>
- 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(1):132–138. <http://dx.doi.org/10.1139/z98-195>
- Klein, D.R. 1995. The introduction, increase, and demise of wolves on Coronation Island, Alaska. In: Carbyn, L.N., Fritts, S.H., and Seip, D.R., eds. *Ecology and conservation of wolves in a changing world*. Edmonton: Canadian Circumpolar Institute, University of Alberta. 275–280.
- Mathews, E.A. 1995. Long-term trends in abundance of harbor seals (*Phoca vitulina richardii*) and development of monitoring methods in Glacier Bay National Park, Southeast Alaska. In: Engstrom, D.R., ed. *Proceedings of the Third Glacier Bay Science Symposium, 15–18 September 1993, Glacier Bay National Park and Preserve*. Vol. 3:254–263.
- Mathews, E.A., and Pendleton, G.W. 2006. Declines in harbor seal (*Phoca vitulina*) numbers in Glacier Bay National Park, Alaska, 1992–2002. *Marine Mammal Science* 22(1):167–189. <http://dx.doi.org/10.1111/j.1748-7692.2006.00011.x>
- Mathews, E.A., Womble, J.N., Pendleton, G.W., Jemison, L.A., Maniscalco, J.M., and Strevler, G. 2011. Population growth and colonization of Steller sea lions in the Glacier Bay region of southeastern Alaska: 1970s–2009. *Marine Mammal Science* 27(4):852–880. <http://dx.doi.org/10.1111/j.1748-7692.2010.00455.x>
- Meiklejohn, B.A. 1994. Ecology and sensitivity to human disturbance of a wolf pack at Glacier Bay National Park and Preserve, Alaska. Unpubl. report. Available at Glacier Bay National Park, Bartlett Cove, Alaska 99826, USA.
- Milner, A.M., Fastie, C.L., Chapin, F.S., III, Engstrom, D.R., and Sharman, L.C. 2007. Interactions and linkages among ecosystems during landscape evolution. *Bioscience* 57(3):237–247. <http://dx.doi.org/10.1641/B570307>
- Moore, T.D., Spence, L.E., and Dugnolle, C.E. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. *Bulletin* 14. Cheyenne: Wyoming Game and Fish Department.
- Muir, J. 1915. *Travels in Alaska*. Boston and New York: Houghton Mifflin. <http://dx.doi.org/10.5962/bhl.title.1874>
- Murdoch, W.W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39(4):335–354. <http://dx.doi.org/10.2307/1942352>
- Peterson, R.O., and Ciucci, P. 2003. The wolf as a carnivore. In: Mech, D., and Boitani, L., eds. *Wolves: Behavior, ecology, and conservation*. Chicago: University of Chicago Press. 104–130.
- Robus, M. 1996. Moose management report. Unpubl. ms. Available at Alaska Department of Fish and Game, Juneau, Alaska 99811, USA.
- Strevler, G.P. 1979. Distribution, population ecology, and impact susceptibility of the harbor seal in Glacier Bay, Alaska. Report to Glacier Bay National Park. Available at Glacier Bay National Park, Bartlett Cove, Alaska 99826, USA.
- Strevler, G.P., and Smith, L. 1978. Endicott Gap large mammal survey. *Wildlife Research Report*. Unpubl. ms. Available at Glacier Bay National Park, Bartlett Cove, Alaska 99826, USA.
- Szepanski, M.M., Ben-David, M., and Van Ballenberghe, V. 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* 120(3):327–335. <http://dx.doi.org/10.1007/s004420050866>
- Testa, J.W. 2004. Population dynamics and life history trade-offs of moose (*Alces alces*) in south-central Alaska. *Ecology* 85(5):1439–1452.
- U.S. Census Bureau. 2013. 2010 demographic profile, Gustavus, Alaska. <https://www.census.gov/popfinder>
- Watts, D.E., Butler, L.G., Dale, B.W., and Cox, R.D. 2010. The Ilnik wolf *Canis lupus* pack: Use of marine mammals and offshore sea ice. *Wildlife Biology* 16(2):144–149.
- Weaver, J.L., and Fritts, S.H. 1979. Comparison of coyote and wolf scat diameters. *Journal of Wildlife Management* 43(3):786–788.
- White, K.S., Barten, N., and Crouse, J. 2006. Ecology of moose on the Gustavus forelands: Population irruption, nutritional limitation, and conservation implications. In: Piatt, J.F., and Gende, S.M., eds. *Proceedings of the Fourth Glacier Bay Science Symposium, 26–28 October 2004, Juneau, Alaska*. *Scientific Investigations Report 2007–5047*. 25–28.

Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W., and Getz, W.M. 2003. Resource dispersion and consumer dominance: Scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters* 6(11):996–1003.

<http://dx.doi.org/10.1046/j.1461-0248.2003.00522.x>

Womble, J.N., and Gende, S.M. 2013. Post-breeding season migrations of a top predator, the harbor seal (*Phoca vitulina richardii*), from a marine protected area in Alaska. *PLoS ONE* 8(2): e55386.

<http://dx.doi.org/10.1371/journal.pone.0055386>

Womble, J.N., Pendleton, G.W., Mathews, E.A., Blundell, G.M., Bool, N.M., and Gende, S.M. 2010. Harbor seal (*Phoca vitulina richardii*) decline continues in the rapidly changing landscape of Glacier Bay National Park, Alaska 1992–2008. *Marine Mammal Science* 26(3):686–697.

<http://dx.doi.org/10.1111/j.1748-7692.2009.00360.x>