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Original article

The Ilnik wolf *Canis lupus* pack: use of marine mammals and offshore sea ice

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Most wolf *Canis lupus* studies have been conducted in inland regions and comparatively little data are available for wolves inhabiting coastal areas. We monitored four members of a coastal wolf pack on the Alaska Peninsula during 2006-2008. Habitat selection ratios indicated a strong association with the coastline, and we documented pack members and other wolves feeding on several species of marine mammals in these areas. In addition, pack members were observed foraging on offshore sea ice on multiple occasions. Observed spatial use and utilization of marine mammals suggest that marine-derived subsidies may provide an important food source to coastal wolf populations. If these subsidies constitute a significant food source for coastal wolves, they likely affect wolf demographics and predator-prey relationships in these areas.

Key words: Alaska Peninsula, Canis lupus, marine mammals, scavenging, sea ice, wolves

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Wolves *Canis lupus* primarily prey on ungulates throughout their distribution and this association has led to considerable investigation concerning their ecology and feeding habits (Peterson & Ciucci 2003). As a result, wolves are among the most studied large mammal species in the world. Although wolves predominantly feed on ungulates, they are opportunistic-generalist carnivores and exhibit considerable dietary plasticity both among and within populations. Previous studies have documented extensive use of a wide variety of foods including birds (Fuller & Keith 1980), fish (Biquand et al. 1994, Kohira & Rexstad 1997, Darimont et al. 2003), large and small rodents (Pimlott et al 1969, Fuller & Keith 1980, Klein 1995, Kohira & Rexstad 1997, Darimont et al. 2004), as well as fruits (Gao 1990, Cuesta et al. 1991), intertidal organisms (Klein 1995) and human refuse (Krizan 1997, Hefner & Geffen 1999). Wolves will also scavenge and carrion may constitute an important annual or seasonal food source in some areas (Forbes & Theberge 1992). In accordance with these catholic feeding habits, the niche breadth (i.e. variance in resource use) of wolves may vary considerably in response to the distribution, abundance and seasonal availability of local food sources.

Marine-derived allochthonous inputs along coastlines increase the amount and variety of food sources available to wolves inhabiting maritime habitats. Accordingly, the niche breadth of wolves is likely to increase along coastlines or in areas where allochthonous food sources are available. If marine-derived food subsidies constitute an important component of wolf diets, these subsidies could incur population-level affects (e.g. increased pup survival and elevated densities) and may influence local predator-prey dynamics and ungulate abundance.

Although wolf diets have drawn considerable investigation throughout their distribution, reports of wolves utilizing marine mammals are relatively uncommon. Stirling & Archibald (1977) suggested five instances of wolves scavenging on seal carcasses based on tracks observed around carcasses. Darimont et al. (2004) reported the occurrence of harbor seal *Phoca vitulina* in a single wolf scat from British Columbia (Canada) and Andriashek et al. (1985) reported a single observation of a wolf feeding on a ringed seal *Phoca hispida* carcass in Labrador (Canada). Klein (1995) reported significant occurrence of harbor seal in wolf scats on Coronation Island, but only after ungulate abundance had markedly declined. However, the significance of marine mammal carcasses to wolf diets in coastal areas is currently unknown.

In this article, we report observations of wolves inhabiting a coastal environment including wolves feeding on large marine mammal carcasses and evidence of wolves hunting sea otters *Enhydra lutris*. In addition, we discuss wolf use of coastal areas and seasonally available offshore sea ice for travel and hunting. Our study complements other investigations regarding wolf use of marine-derived resources and addresses the potential ecological importance of these resources to wolf and ungulate populations inhabiting maritime habitats.

Material and methods

Study area

Our study was conducted on the Alaska Peninsula, Alaska, USA. The study area exhibits considerable topographic relief with elevations ranging from sea-level along the Bristol Bay coastal plain to an average elevation of >1,500 m and peaks > 2,500 m in the Aleutian mountain range. Local climate is primarily maritime and characterized by short cool summers and long cold winters (National Oceanic & Atmospheric Administration data 2008). Variation in the distribution of sea ice and complete freeze-up of Bristol Bay periodically trap marine mammals above the sea ice (Schneider & Faro 1975) and provide wolves in the study area the opportunity to travel and forage on offshore sea ice. Although infrequent, these conditions occurred in our study during the winters of 2006/07 and 2007/08.

Our study area is bound to the north by Bristol Bay, one of the most productive marine ecosystems in the world. As a result, the carcasses of walrus *Odobenus rosmarus divergens*, beluga *Delphinapterus leucas*, harbor seal, spotted seal *Phoca largha*, sea otter and other marine animals regularly occur along the coastline. Although less frequently, carcasses of gray whale *Eschrichtius robustus* and other large cetaceans also periodically wash ashore. Several seal *Phoca* sp. and walrus haul-out concentrations occur on tidal sandbars and beaches along the Bristol Bay coastline. Pacific salmon *Oncorhynchus* sp. are seasonally available in large numbers and are used extensively by wolves throughout the study area (D. Watts, unpubl. data). Extensive seabird colonies also are present along portions of the study area. Ungulate prey in the study area is limited to low densities of moose *Alces alces* and migratory caribou *Rangifer tarandus*.

Data collection

During 2006-2007, we darted four members of the Ilnik wolf pack from a helicopter using tiletamine-zolazepam. We fitted three wolves with standard VHF radio-collars and one wolf with an Argos GPS-collar (Telonics Inc., Mesa, Arizona, USA). Capture and sampling procedures were approved by the Alaska Department of Fish & Game Animal Care and Use Committee (Protocol Number 06-19). We programmed the GPS-collar to take one location per day and remotely downloaded these locations 1-2 times weekly using the Argos satellite system (CLS America Inc., Largo, Maryland, USA). We periodically radio-tracked collared individuals using fixed-wing aircraft during October 2006 - February 2008 and recorded location, group size, activity and feeding observations. In addition to direct observations of Ilnik wolf pack members during radio-tracking, we recorded incidental observations of wolves feeding on marine mammal carcasses along the Bristol Bay coastline.

Habitat use

We combined radio-tracking and GPS-locations for all pack members and mapped these using ArcMap 9.1. When collared wolves occurred together, we considered this to represent a single location for the pack. Furthermore, we excluded GPS-locations that occurred within 24 hours of visual locations during radio-tracking. Using the XTools Pro 5.1 extension for ArcMap (Data East LLC, Novosibirsk, Russia), we calculated a convex polygon for all terrestrial locations (i.e. excluding offshore locations) to represent the pack's territory. Because wolf spatial use is socially limited by territorial behaviours, we used the estimated territory to represent the area available to pack members for use (McClean et al. 1998). Using ArcMap 9.1 and Landsat TM satellite imagery, we categorized the territory into coastal (i.e. all habitats $\leq$ 200 m of coastline) and non-coastal habitats (i.e. tall shrub, low shrub, dwarf shrub, wet graminoid and mesic graminoid). We analysed these data using habitat selection ratios (Table 1; Manly et al. 1993) and used a G-test to compare observed and expected use values.

Table 1. Use of general habitat types by wolves inhabiting a coastal area on the Alaska Peninsula, Alaska, USA, from 2006 to 2008.

Vegetation type	Territory		% of observations	Habitat selection ratio
	Area (km^2)	% area		
Tall shrub	38.62	04.12	5.56	1.444
Low shrub	125.07	13.35	15.56	1.249
Dwarf shrub	456.82	48.76	37.78	0.830
Wet graminoid	165.26	17.64	5.56	0.337
Mesic graminoid	143.58	15.32	8.89	0.622
Coastal[a]	7.55	0.81	20.00	26.588
Offshore sea ice	NA[b]	NA	6.67	NA
Total	936.88	100.00	100.00	NA

[a] all habitats located < 200 m from the coastline.
[b] NA = not applicable.

Results

We obtained a total of 106 locations for the Ilnik pack during October 2006 - January 2008 (55 GPS-collar locations and 51 visual observations) which offered 90 locations for analyses. Estimated territory size was 937 km^2 which included approximately 36 km of coastline. Locations were biassed towards winter and early spring (i.e. 1 November - 30 April) due to weather conditions (i.e. limited radio-tracking conditions), timing of captures and mortality events. As a result, estimated territory size and annual use of areas within the territory may have been underestimated and biassed.

Ilnik wolf pack members did not use habitat types in proportion to their availability (G-test, df = 5, $P \leq 0.001$) and showed a strong association with coastal areas (see Table 1). We acknowledge that expected use of coastal habitat was < 1.0 due to the small proportion of the territory comprised by this habitat type. Of all terrestrial locations, 20% occurred within coastal habitat, an area that represented < 1% of the packs territory. In addition to the use of coastal areas, Ilnik pack members were observed travelling several miles offshore on four distinct occasions, often for multiple days. Locations on offshore sea ice comprised 6% of all locations and tracks observed in the snow indicated considerable use of offshore sea ice when appropriate conditions existed and sea otters were trapped above the sea ice (D. Watts, pers. obs.).

We obtained seven independent observations (i.e. excluding multiple observations at the same carcass) of Ilnik pack members scavenging on marine mammal carcasses. We observed pack members feeding on walrus on two occasions, beluga on three occasions, and sea otter on two occasions. Pack members were observed utilizing larger carcasses (i.e. walrus and beluga) for multiple days. We observed pack members feeding on sea otter carcasses where on both occasions tracks and blood stains on the snow indicated that the wolves had killed the sea otters near the coastline. One observation included several pack members in close proximity to each other (< 1 km) feeding on different sea otter carcasses. These observations occurred when Bristol Bay was completely frozen and sea otters were trapped above the sea ice (D. Watts, pers. obs.). In addition to direct observations of Ilnik pack members during radio-tracking flights, incidental observations of non-pack members elsewhere in the study area included wolves feeding on walrus carcasses at a haul-out near Cape Seniavin (Fig. 1) and a gray whale carcass near Port Moller.

Figure 1. Adult wolf feeding on an adult male walrus carcass at Cape Seniavin, Alaska Peninsula, Alaska, USA, in 2007.

During radio-tracking on 18 January 2008, both remaining collared individuals (1 VHF & 1 GPS collar) and concomitant pack members were observed on offshore sea ice 5.6 km from the coastline. GPS-collar locations received on 16 January 2008 indicated that the pack had spent $\geq$ 5 days on offshore sea ice prior to being observed on 18 January. Shortly after the wolves were observed, air-temperatures increased markedly and strong winds caused the remaining sea ice to drift away from the coast and break up. After 18 January, radio-tracking attempts failed to locate either radio-collared individual and no more GPS transmissions were received. Presumably, both radio-collared individuals, and five other wolves observed on the sea ice with them, drowned or died from exposure.

Discussion

Most wolf studies have been conducted in inland regions (Peterson & Ciucci 2003) and comparatively little data are available for wolves inhabiting coastal areas (Szepanski et al. 1999, Darimont & Reimchen 2002). Observations from our study expand the known diet of wolves to include several species of marine mammal. By utilizing marine mammal carcasses, the Ilnik wolf pack was able to expand its dietary niche breadth in comparison to non-coastal wolf packs in the study area which primarily feed on moose, caribou and salmon (D. Watts, unpubl. data). Because appropriate sea ice conditions are not predictable, the importance of sea otters to wolves in the study area is likely nominal. However, the carcasses of larger marine mammals regularly occur along coastlines and observations from our study indicate that these, and other marine subsidies along beaches, probably provide a significant food source for coastal wolves. In addition, few reports of wolves traveling on offshore sea ice exist and observations from this study expand our understanding of this relatively aberrant foraging strategy. Although appropriate sea ice conditions are uncommon, mortality data from our study also suggest that aberrant feeding strategies may incur severe consequences for large carnivores.

As with most large mammals, wolves would be expected to spatially orient themselves within their territories in order to maximize survival and reproductive output (Mech & Boitani 2003). Although coastal habitat represented < 1% of the total area available to pack members, the observed use within this area indicated a strong positive association with the coastline. While the coastline represents a potential travel route (Mech & Boitani 2003), feeding observations and the strong association of the pack with coastal areas suggest that marine-derived subsidies probably provided an important food source, particularly during winter when primary prey species (e.g. migratory caribou) were not available.

Marine-derived foods are known to constitute an important dietary component for wolves (Szepanski et al. 1999, Darimont & Reimchen 2002) and other large carnivore species inhabiting coastal areas (Avery et al. 1987, Hiscocks & Perrin 1987, Rose & Polis 1998, Wiesel 2006). As with most carnivore populations, wolf population demographics such as reproduction, survival, abundance and behaviour are related to the availability of prey and other important food sources (Mech et al. 1998, Fuller et al. 2003). If marine-derived subsidies constitute a significant food source for coastal wolves, these subsidies likely affect the fitness and survival of wolves in these areas and may buffer wolf populations from bottom-up effects associated with seasonal food shortages or declines in prey populations. Rose & Polis (1998) reported that coyotes *Canis latrans* inhabiting coastal areas occurred at appreciably higher densities than in neighbouring inland areas as a result of increased food availability along the coastline. If such a positive numerical response exists in coastal wolf populations, increased wolf densities along coastlines could affect terrestrial prey populations through increased predation and top-down effects (Rose & Polis 1998, Adams et al. 2009). Thus, information regarding the influence of these subsidies on population demographics would be of interest to management agencies, particularly where ungulate populations occur at low densities or are declining.

Although coastal wolves will supplement their diets with marine mammal carcasses and other foods occurring in supralittoral zones, the contributions of these foods to the annual nutritional budgets of coastal wolves are currently unknown. Due to the remoteness and weather conditions of the study area and a large-scale mortality event, sample sizes were limited in our study. As a result, our interpretations regarding the significance of marine mammals and other marine-derived subsidies to coastal wolf populations are limited. Further investigations using stable-isotope analysis and study of additional coastal packs within the study area could improve our understanding regarding the importance of marine-derived resources to coastal wolf populations and the potential population-level effects of these resources.

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