

Alopex lagopus. By Alexandra M. Audet, C. Brian Robbins, and Serge Larivière

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***Alopex* Kaup, 1829**

Canis Linnaeus, 1758:40. Type species *Canis lagopus*.
Alopex Kaup, 1829:85. Type species *C. lagopus* Linnaeus.
Vulpes Oken, 1816:1033. Type species *C. lagopus* Linnaeus.
Leucocyon Gray, 1869:521. Type species *C. lagopus* Linnaeus.

CONTEXT AND CONTENT. Order Carnivora, family Canidae, subfamily Caninae. The genus *Alopex* is monotypic. *Alopex* has been considered a subgenus of *Vulpes* (Bobrinskii 1965) and a subgenus of *Canis* (Van Gelder 1978).

***Alopex lagopus* (Linnaeus, 1758)**

Arctic Fox

Canis lagopus Linnaeus, 1758:40. Type locality “alpibus Lapponicis, Sibiria,” restricted by Thomas (1911) to “Sweden (Lapland).”
Canis fuliginosus Bechstein, 1799:270. Type locality “Island” (= Iceland).
Canis groenlandicus Bechstein, 1799:270. Type locality “Gronland” (= Greenland).
Vulpes arctica Oken, 1816:1033. Unavailable name (Hemmings 1956).
Vulpes hallensis Merriam, 1900:15. Type locality “Hall Island, Bering Sea.”
Vulpes pribilofensis Merriam, 1903:171. Type locality “St. George Island, Pribilof Islands, Bering Sea.”
Vulpes beringensis Merriam, 1903:171. Type locality “Bering Island, [Komandorskiye Islands], Bering Sea.”
Alopex lagopus Miller, 1912:319. First use of the current name combination.

CONTEXT AND CONTENT. Generic context given above. Eight subspecies are recognized (Ellerman and Morrison-Scott 1965; Hall 1981).

- A. l. beringensis* (Merriam, 1903:171), see above (*beringianus* Suworov is an incorrect subsequent spelling).
- A. l. fuliginosus* (Bechstein, 1799:270), see above.
- A. l. groenlandicus* (Bechstein, 1799:270), see above.
- A. l. hallensis* (Merriam, 1900:15), see above.
- A. l. lagopus* (Linnaeus, 1758:40), see above (*arctica* Oken, *argenteus* Billberg, *caerulea* Nilsson, *innuitus* Merriam, *kentiansis* Brass, and *typicus* Barrett-Hamilton and Bonhote are synonyms).
- A. l. pribilofensis* (Merriam, 1903:171), see above.
- A. l. spitzbergenensis* Barrett-Hamilton and Bonhote, 1898:287. Type locality “Spitzbergen” (*spitzbergenensis* Trouessart is an incorrect subsequent spelling. *A. l. spitzbergenensis* may be a synonym of *A. l. groenlandicus* [Hall 1981]).
- A. l. ungava* (Merriam, 1903:170). Type locality “Fort Chimo, Ungava” (in Quebec, Canada).

DIAGNOSIS. The Arctic fox (Fig. 1) is the only fox occupying Arctic habitats and the only Canidae to change color during winter. Where sympatric, the red fox (*V. vulpes*) can be differentiated by its larger size (>3 kg), white-tipped tail, and reddish color as opposed to bluish-brown color of Arctic foxes in summer and whitish or bluish color in winter. Arctic foxes also have proportionally smaller extremities, including shorter legs and rounder ears (Prestrud 1991).

Skull of *Alopex* (Fig. 2) is intermediate in form between that of *Canis* and *Vulpes* (Miller 1912). Occipital depth in *A. lagopus* is ca. one-third of condylobasal length, and interorbital region is more elevated than that in *Vulpes*. In contrast, dorsal profile of

forehead rises abruptly above rostrum as in *Canis* (Miller 1912). Compared with *Vulpes*, premolars of *Alopex* are higher crowned, m1 has a shorter talonid, and tubercular teeth are more reduced (Kurtén and Anderson 1980; Stroganov 1969).

GENERAL CHARACTERS. *Alopex lagopus* is a small (ca. 3–5 kg) fox with reduced limb size, short snout, short and rounded ears, thickly haired feet, and dense winter coat. Tail is bushy and accounts for one-third of total length of head and body (Prestrud 1991; Stroganov 1969).

External measurements (in cm) of Arctic foxes from Norway (Prestrud and Nilssen 1995), average \pm SE for males and females, respectively: length of head and body, 53 ± 4 ($n = 325$) and 51 ± 4 ($n = 274$); length of tail, 28 ± 5 ($n = 306$) and 27 ± 4 ($n = 254$). Southern forms are larger than northern forms (Bisaillon and DeRoth 1980; Frafjord 1992a, 1993a; Wakely and Mallory 1988).

Males are 5–20% heavier than females. Body mass (in kg) of males and females, respectively, average \pm SD: 3.2 ± 0.4 ($n = 23$) and 3.0 ± 0.5 ($n = 19$) in Churchill, Manitoba (Murray and Larivière 2002); 4.3 ± 0.6 and 3.6 ± 0.6 in Alaska (n for both sexes combined = 19—Ballard et al. 2000a); 3.6 ± 0.5 (SE, $n = 317$) and 3.0 ± 0.6 (SE, $n = 267$) in Norway (Prestrud and Nilssen 1995); and 3.8 ($n = 8$) and 3.2 ($n = 14$) in Sweden (Tannerfeldt and Angerbjörn 1996).

Skull is elongated and weak. Skull measurements (in mm), average \pm SD for 8 males and 13 females of the subspecies *A. l. lagopus* and for 8 males and 7 females of the subspecies *A. l. groenlandicus*, respectively: maximum length of skull, $128.0 \pm$



FIG. 1. Arctic fox in summer pelage. Photograph by Lyle R. Walton.

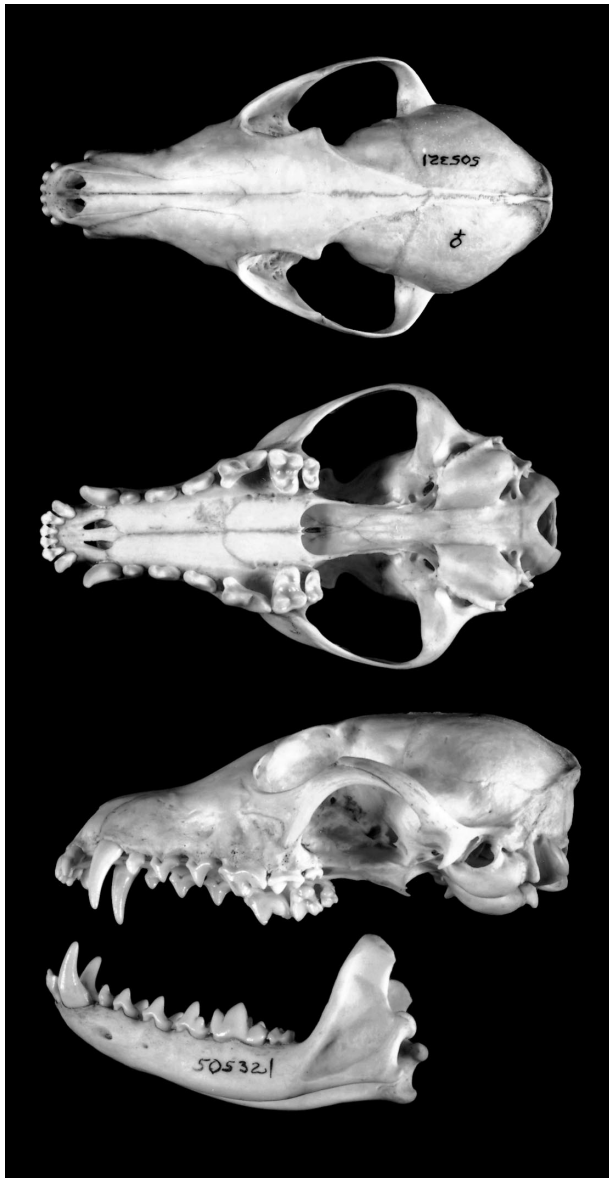


FIG. 2. Dorsal, ventral, and lateral views of skull and lateral view of mandible of female *Alopex lagopus* (USMN 505321). Condylobasal length is 120 mm. Photograph by C. Hansen.

4.54, 122.19 ± 3.88 , 124.25 ± 4.05 , 119.86 ± 3.34 ; condylobasal length, 118.19 ± 4.49 , 112.36 ± 2.93 , 115.38 ± 4.0 , 110.86 ± 2.67 ; palatal length, 60.81 ± 2.36 , 57.65 ± 1.82 , 59.25 ± 2.05 , 57.71 ± 1.60 ; nasal length, 43.31 ± 2.93 , 40.81 ± 2.0 , 41.50 ± 1.49 , 40.57 ± 1.62 ; maximum width of skull, 68.88 ± 1.89 , 65.85 ± 2.27 , 66.75 ± 1.16 , 63.93 ± 0.61 ; mastoid width, 43.75 ± 1.13 , 42.31 ± 1.03 , 42.0 ± 0.82 , 42.50 ± 1.31 (Bisaillon and DeRoth 1980).

DISTRIBUTION. *Alopex lagopus* has a circumpolar distribution that includes the Arctic and tundra zones of North America and Eurasia, parts of the alpine zones of Fennoscandia, and islands of the Arctic, North Atlantic, and North Pacific Oceans (Fig. 3). In North America, Arctic foxes also occur on several Aleutian Islands in Alaska, where they were introduced for fur farming (Bailey 1993). In Europe, the Arctic fox was omnipresent during the Pleistocene. Today, it occurs only in the tundra regions of Fennoscandia, where the populations are extremely small (Angerbjörn et al. 1995; Hersteinsson et al. 1989; Pulliainen and Ala-Kotila 1982).

FOSSIL RECORD. *Alopex lagopus* probably descended from the Middle Pleistocene alopecoid fox (Kurtén 1968). In the Arctic, fox remains have been recovered from late Rancholabrean

deposits in the Yukon (Old Crow River) and Alaska and from early Holocene sediments in Washington (Wright 1987; Youngman 1993). The Arctic fox probably originated in the Old World (Kurtén and Anderson 1980), where it ranged over most of Europe, into Spain and southern Russia. Remains of Arctic foxes occur at >80 sites, ranging from Kiev in the east to Ireland in the west (Kurtén 1968).

FORM AND FUNCTION. The Arctic fox is the smallest homeothermic carnivore that remains active in the Arctic during winter. Numerous morphological and physiological adaptations to Arctic conditions include insulating fur, compact body, foot thermoregulation, and reduced metabolism during cold weather or food shortage (Prestrud 1991; Scholander et al. 1950a, 1950b, 1950c).

The Arctic fox in winter pelage has a lower critical temperature of -40°C (Prestrud 1991). Winter fur is twice as long as summer fur, and 70% of winter fur is fine underfur (Underwood and Reynolds 1980). Vasoconstriction of arterioles in the skin and peripheral subcutaneous fat deposits further increase overall thermoregulation (Henshaw et al. 1972). Freezing of footpads is prevented by an increase in blood flow to a capillary rete in the skin pads. During storms or in unusually cold or windy weather, Arctic foxes seek shelter in a temporary den or snow burrow (Frafjord 1992b). Site-specific variations in fur length reflect surface exposure when at rest in a curled position (Follmann 1978).

Energy requirements parallel seasonal changes of available energy; energy demands are lower in winter than in summer. Energy expenditures in winter are reduced by decreasing both activity and basal metabolic rate (Fuglei and Øritsland 1999; Prestrud 1991; Underwood 1981). Energy requirements of captive Arctic foxes fed ad libitum are 275% higher in summer (220–240 kcal/kg body mass) than in winter (70–80 kcal/kg body mass), mostly because of higher metabolism. Basal metabolic rate of Arctic foxes ranges from 35 to 110 kcal/kg^{0.75} during November–February. Arctic foxes also may lower their metabolism by 40–50% when facing food shortages during winter (Prestrud 1991). Plasma glucose is resistant to change during short-term fasting (Tallas and White 1988). Fat deposits are depleted and replenished throughout winter, but in early spring fat stores are severely depleted by high-energy demands of reproduction (Prestrud and Nilssen 1992). Relative masses of major fat deposits are variable, so fatness indices that rely on one or a few depots are not an accurate reflection of total body composition (Pond et al. 1995b).

Hormones change seasonally. Concentrations of luteinizing hormone are low (ca. 3 ng/ml) during the year but peak at 28 ng/ml during estrous. In contrast, prolactin concentration remains low (ca. 2.5 ng/ml) from July to April, with increases at the end of gestation (ca. 9.7 ng/ml) and during lactation (26.7 ng/ml—Mondain-Monval et al. 1985).

Arctic foxes have relatively large feet for their mass, which yields a low footload that facilitates locomotion in snow. Footload for 52 animals from Churchill, Manitoba, averaged ($\pm SD$) $64.7 \pm 10.6 \text{ g/cm}^2$ (Murray and Larivière 2002).

The Arctic fox is the only canid with a seasonal color change (Chesemore 1970; Pocock 1912). Two color phases exist: a white color phase, in which animals turn completely white during winter, and a blue color phase, in which animals remain brownish-blue throughout the year. Both color phases are present in most populations, but the respective proportion of each color morph varies among areas. On mainland areas of North America and Europe, the white phase typically dominates, whereas blue foxes dominate populations on the Alaskan Peninsula, on numerous Alaskan islands, and in Iceland (Braestrup 1941; Chesemore 1968a; Fetherston 1947).

Dental formula is $i\ 3/3$, $c\ 1/1$, $p\ 4/4$, $m\ 2/3$, total 42. Females have 12–14 mammae. Males have a baculum ca. 59 mm in length (Burt 1960). Feet, rhinarium, and vibrissae of Arctic foxes have been described (Pocock 1914).

ONTOGENY AND REPRODUCTION. Spermatogenesis and follicle growth begin in autumn (Smith et al. 1985). Arctic foxes are monoestrous, and estrus lasts 3–5 days. Timing of estrus depends on latitude, weather, and physical condition. Mating occurs in March–April, and gestation lasts ca. 52 days. Young are born in late spring and abandon the den in late summer. Insufficient food during later stages of pregnancy may cause embryo resorption (Angerbjörn et al. 1991; Frafjord 1993b; Valtonen et al. 1985).

Families consist of male, female, and their progeny. Arctic

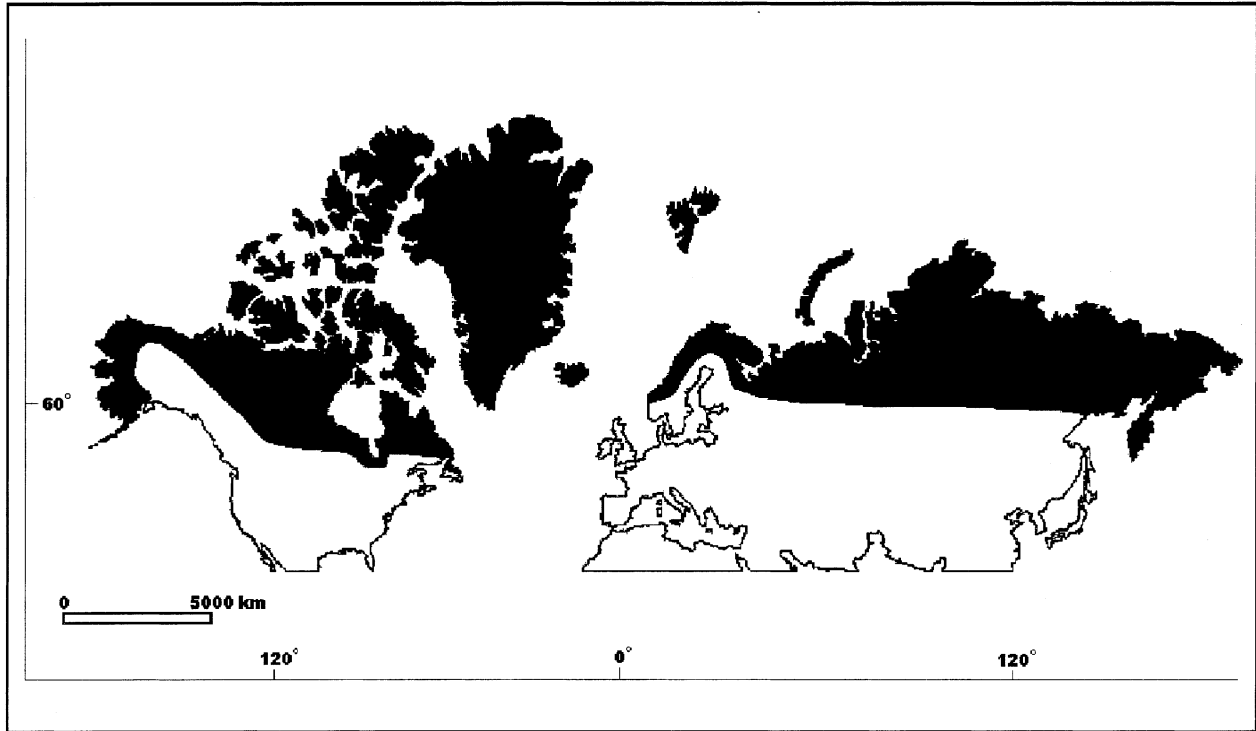


FIG. 3. Distribution of *Alopex lagopus*.

foxes are monogamous and may mate for life. Supplemental adults have been observed (Eberhardt et al. 1983a; Hersteinsson and Macdonald 1982). When helpers occur, the parents remain the only sexually active individuals and also provide more care to the young than do helpers (Korhonen and Alasuutari 1994a; Kullberg and Angerbjörn 1992; Strand et al. 2000).

Litter size varies greatly among years and regions and is strongly related to food availability (Angerbjörn et al. 1995; Strand et al. 1999; Tannerfeldt and Angerbjörn 1998). Placental scar counts are constant, indicating that offspring loss occurs through resorption of embryos or early pup mortality (Macpherson 1969). Litter size ranges from 3 to 25. Litter sizes of 6–12 young are common for inland Arctic foxes, whereas coastal fox litters more commonly average ca. 6 pups and rarely exceed 10 (Frafjord 1993b). In regions where lemmings and voles occur, litters are large but occur only during years when rodents are abundant. In areas where rodents are absent, litters are much smaller, but animals may breed annually (Frafjord 1993b; Tannerfeldt and Angerbjörn 1998).

Altricial pups weigh 60–90 g at birth. Young are born blind, and eyes and ears do not open until 14–16 days of age. Milk teeth erupt during the 3rd and 4th weeks. Replacement of milk teeth by permanent ones occurs at the end of summer (Slaughter et al. 1974). Pups emerge from the den after 3–4 weeks, are weaned at 6–7 weeks, shed the uniformly dark natal pelt at 8 weeks, and are independent at 12–14 weeks (Garrott and Eberhardt 1987; Garrott et al. 1984). Growth is rapid, and adult body size is reached at 14–28 weeks of age (Frafjord 1994; Prestrud and Nilssen 1995). Males grow larger than females by growing for a longer time (Prestrud and Nilssen 1995). Juvenile survival is related to summer food availability (Tannerfeldt et al. 1994). Sexual maturity occurs at 9–10 months (Macpherson 1969). Based on placental scars, female Arctic foxes breed in their 1st year if they are from a large cohort and in their 2nd if they are from a small cohort (Macpherson 1969). Placental scars remain visible for several months postpartum (McEwen and Scott 1957; Strand et al. 1995).

At birth, pelage varies from blue gray to sooty black. Cream-colored guard hairs begin to appear on the ventrum of 2- to 3-week-old white foxes. Color phase of pups can be easily sorted during their first molt at 4–5 weeks (Frafjord 1989; Johansson 1960).

ECOLOGY. *Alopex lagopus* inhabits a variety of coastal, inland, alpine, and marine habitats and occupies areas where food is

most abundant (Stickney 1991). Areas suitable for denning may also influence distribution of Arctic foxes within habitats (Garrott and Eberhardt 1987).

Arctic foxes are predators and scavengers that rely on small mammals such as lemming (*Dicrostonyx*, *Lemmus*) and voles (*Microtus*) throughout their distribution (Anthony et al. 2000; Elmhagen et al. 2000; Garrott et al. 1983a; Kennedy 1980). However, birds (eggs and adults), marine invertebrates, fish, and carcasses of sea mammals are important food items when rodents are rare or absent (Bantle and Alisauskas 1998; Dalerum and Angerbjörn 2000; Fay and Stephenson 1989; Prestrud 1992a; Samelius and Alisauskas 2000; Stickney 1991; Summers 1986; Underhill 1987). The distribution of many Arctic nesting birds is related to Arctic fox predation (Larson 1960; Madsen et al. 1992). Arctic foxes also kill pups of ringed seal (*Phoca hispida*) in their birth lair during winter (Smith 1976), and 1 Arctic fox was observed killing a reindeer (*Rangifer tarandus*) calf (Prestrud 1992a). Arctic foxes follow polar bears (on pack ice) or wolves (on mainland) to scavenge remains of kills (Chesemore 1968b). At mining camps and other human settlements, Arctic foxes may consume a variety of items from garbage dumps (Garrott and Eberhardt 1987). Other foods include insects, mollusks, and amphibians (Andriashek et al. 1985; Fay and Stephenson 1989; Mullen and Pitelka 1972; Murie 1959; Nielsen 1991; Schiller 1954; Shibanoff 1958). Berries that were frozen during autumn and were preserved under the snow also are consumed during winter (Kapel 1999). Adults, and especially pups, are cannibalistic on occasion (Birks and Penford 1990; Macpherson 1969; Sklepkovych 1989).

Red and Arctic foxes are direct competitors where sympatric (Frafjord et al. 1989) because they consume the same prey (Barth et al. 2000; Frafjord 2000; Smits et al. 1989). The larger red fox may kill the Arctic fox. Red foxes dominate Arctic foxes (Chirkova 1968; Korhonen et al. 1997; Rudzinski et al. 1982; Schamel and Tracy 1986; Schmidt 1985; Skrobov 1960). However, Arctic foxes generally occupy larger home ranges and seem to occupy more coastal habitats, whereas red foxes are more abundant near human dwellings (Hersteinsson and Macdonald 1982, 1992). In Norway, red foxes use dens at lower altitudes than do Arctic foxes (Linnell et al. 1999). Arctic foxes also share lemming prey with numerous other mammals, such as short-tailed weasels (*Mustela erminea*), least weasels (*M. nivalis*), and wolverines (*Gulo gulo*), and birds,

such as jaegers (*Stercorarius*) and snowy owls (*Nyctea scandiaca*—Ovsyanikov and Menyushina 1986).

When food is abundant, Arctic foxes experience higher adult survival (Angerbjörn et al. 1991), higher pregnancy rates (Angerbjörn et al. 1991), larger litters (Tannerfeldt and Angerbjörn 1998), higher juvenile survival (Eberhardt et al. 1983a; Fay and Rausch 1992; Tannerfeldt et al. 1994), and later dispersal (Frafjord 1992b). Sex ratio in the wild is typically 1:1; of 99 Arctic foxes killed in Alaska during a population reduction program, 59% were males, and 41% were females (Ballard et al. 2000a).

Abundance of Arctic foxes varies considerably among years and regions, with peaks in fox numbers generally occurring every 3–5 years (Braestrup 1941; Chesemore 1975; Chitty 1950; Tchirkova 1958). Studies of population dynamics, using age structure of harvested Arctic foxes and life table analyses, have been conducted for most Arctic regions (Braestrup 1941; Hersteinsson 1992; Hiruki and Stirling 1989; Macpherson 1969; Shibanoff 1958; Smirnov 1968; Tchirkova 1958). Variations in fox abundance often follow fluctuations in rodent abundance, but different regions may be at different stages of the cycle (Angerbjörn et al. 1995). A delayed numerical response occurs, and high fox abundance follows high rodent abundance by 1 year or less. Local fluctuations in Arctic fox numbers are caused mainly by reproduction of local animals, juvenile survival, and immigration (Angerbjörn et al. 1999; Hiruki and Stirling 1989; Wiklund et al. 1999).

Arctic foxes are territorial during summer. In Alaska, territories of adults averaged ($\pm SD$): 20.8 ± 12.5 km², whereas ranges of 5 juveniles were 3.7 ± 1.7 km² (Eberhardt et al. 1982). In the coastal Yukon-Kuskokwim Delta of western Alaska, ranges of males (10.2 ± 6.1 km²) were larger than ranges of females (4.6 ± 1.9 km²) from May to July (Anthony 1997). Summer territories were 18–24 km² in Alaskan tundra (Eberhardt et al. 1982), 8–19 km² in coastal Iceland (Hersteinsson and Macdonald 1982), 40–55 km² in Svalbard (Prestrud 1992b), 6–60 km² in Norway (Landa et al. 1998), and 4–14 km² in west Greenland (Birks and Penford 1990). Home ranges of nonbreeding animals (e.g., “floaters”) are typically larger, as are annual home ranges that often encompass areas not used during summer (Landa et al. 1998). During winter, Arctic foxes concentrate near food sources such as garbage dumps or dead whales (Chesemore 1968a; Eberhardt et al. 1983b).

Movements are grouped into 4 categories: local, sporadic, seasonal migrations, and periodic migrations. Local movements are mainly related to foraging activities, and no differences in movements exist between males and females (Anthony 1997). Sporadic movements are unpredictable movements outside the normal home range (Banfield 1954; Bannikov 1970; Cameron 1958; Northcott 1975). In Alaska, 7 of 18 ear-tagged foxes moved from 129 to 945 km from their tagging location, with a maximum average travel rate of 24 km/day (Eberhardt and Hanson 1978). In Canada, movements >1,000 km were recorded (Macpherson 1968; Wrigley and Hatch 1976). Seasonal migrations occur in late autumn–early winter or during spring (Bannikov 1970; Eberhardt et al. 1983b; Shibanoff 1958). Winter movements are poorly documented, but most Arctic foxes appear to remain near their summer range during winter (Anthony 1997; Eberhardt et al. 1983b; Landa et al. 1998). On coastal areas, Arctic foxes inhabit mainland tundra, where they breed, whereas in winter animals relocate over land and pack ice (Wrigley and Hatch 1976). Periodic migrations occur in Russia, where food shortages trigger large migrations in the fall. The severity of food shortages influences both the size and the timing of migration (Pul-liainen 1965; Shilyaeva 1968; Tchirkova 1958). Dispersal has no sex bias (Tannerfeldt and Angerbjörn 1996).

Arctic foxes harbor numerous endoparasites such as acanthocephalans (*Orynosoma hadweni* and *Polymorphus meyeri*), cestodes (*Diphyllobothrium dendriticum*, *Echinococcus multilocularis*, *Mesocestoides canislagopidis*, *M. kirbyi*, *Schistocephalus solidus*, *Taenia crassiceps*, and *T. polyacantha*), nematodes (*Capillaria aerophila*, *Crenosoma vulpis*, *Toxascaris leonina*, *Toxocara canis*, and *Uncinaria stenocephala*), protozoa (*Eimeria* and *Isospora*), and trematodes (*Brachylaemus*, *Cryptocotyle lingua*, *Maritrema afanassjewi*, *Plagiarchis elegans*, *Spelotrema*, and *Tristriata*)—Aguirre et al. 2000; Fay and Williamson 1962; Kapel et al. 1996; Skírnisson et al. 1993). Ectoparasites include mites and ticks (Bannikov 1970; Chesemore 1975).

Rabies is enzootic in most Arctic fox populations, and periodic epizootics have occurred in most mainland populations (Ballard et al. 2001; Crandell 1991; Rausch 1958; Secord et al. 1980; Syu-

zymova 1968). A relationship between lack of food, fox migrations, and the start of epizootics was noted in Russia (Dementyeff 1958; Syuzumova 1968; Tchirkova 1958). Arctic foxes also carry Aujeszky's disease (Quiroga et al. 1995). Transmission of diseases from Arctic foxes to humans (rabies, hydatid disease, diphyllobothriasis, *E. multilocularis*, brucellosis, tularemia, and trichinosis) creates a public health concern (Eberhardt et al. 1982, 1983b; Rausch 1972).

Natural predators of Arctic foxes include bald (*Haliaeetus leucocephalus*) and golden (*Aquila chrysaetos*) eagles, large hawks (*Buteo*), jaegers, snowy owls, and mammals such as dogs (*C. domesticus*), polar bears (*Ursus maritimus*), red fox, wolves (*C. lupus*), and wolverines (Chesemore 1975; Garrott and Eberhardt 1982; Tannerfeldt and Angerbjörn 1996). Trapping and shooting are important causes of mortality where humans co-occur (Anthony 1997). In Iceland, Arctic foxes are killed as pests for their depredation on domestic lambs and nests of common eiders (*Somateria mollissima*)—Hersteinsson and Macdonald 1996; Hersteinsson et al. 1989).

Starvation is a common cause of mortality in Arctic foxes and occurs mostly during migrations and in winter. In summer, adults rarely starve, but pups may starve if parents cannot find enough food, if parents prematurely abandon the den, or due to competition among siblings for food (Angerbjörn et al. 1991; Frafjord 1993; Garrott and Eberhardt 1987; Macpherson 1969).

Longevity in the wild averages 3–4 years, but may reach 9–10 years (Hiruki and Stirling 1989; Macpherson 1969). In Sweden, average longevity of 14 females and 8 males was 29 and 37 months, respectively (Tannerfeldt and Angerbjörn 1996). Captive animals may reach >12 years of age (Flower 1931).

The fur industry of the Arctic depends on the Arctic fox. Over 100,000 Arctic foxes are harvested annually throughout the circumpolar range, and the harvest appears sustainable (Chesemore 1972; Garrott and Eberhardt 1987).

Little management of the Arctic fox or its harvest occurs in North America. In Russia, however, large-scale feeding and government-sponsored research were elements of an active management program (Bannikov 1970). The Arctic fox population in Fennoscandia crashed in the 1920s, and the population remains very small despite legal protection since the 1930s (Hersteinsson et al. 1989; Strand et al. 1994). On small or moderate-sized islands in Alaska, the introduction of red foxes, toxicants, hunting, and trapping have reduced Arctic fox populations (Anthony et al. 1991; Bailey 1993).

The importance of Arctic foxes in the European fur trade has led to many studies on physiology, reproduction, nutrition, and husbandry (Ahlstrøm and Wamberg 2000; Ahola et al. 2000; Farstad 1998; Fuglei et al. 2000; Korhonen et al. 1996, 1999, 2000; Pö-lönen et al. 2000). Techniques for aging Arctic fox include characteristics of bone sutures, size of tooth pulp cavity, patterns of tooth eruption, and layers of tooth cementum (Bradley et al. 1981; Dolgov and Rossolimo 1966; Grue and Jensen 1976). Dietary patterns can be explored via stable carbon isotopes (Angerbjörn et al. 1994; Gilmour et al. 1995; Pond et al. 1995a). Arctic foxes can be immobilized with mixtures of tiletamine hydrochloride and zolazepam hydrochloride (Samelius et al., in press), ketamine and xylazine (Garrott and Eberhardt 1987), medetomidine and ketamine (Jalanka 1990), or phencyclidine and promazine (Seal and Kreeger 1987). Animals have been marked using ear tags and radio-collars (Eberhardt et al. 1982).

BEHAVIOR. Arctic foxes remain active year round. They are mainly nocturnal, but their activity patterns are flexible so they may follow those of their prey (Anthony 1997; Birks and Penford 1990; Eberhardt et al. 1982; Frafjord 1993d).

Dens are used during the breeding season for rearing young and during winter as shelter (Eberhardt et al. 1983a). In spring and early summer, the frozen ground prevents digging, so dens are generally excavated at the crests of slopes, on banks, or on mounds, on moderately rugged terrain and preferably in dry, light, sandy soil (Chesemore 1969; Eide et al. 2001). Because of soil enrichment (food remnants and fox excrements) and aeration (digging), a characteristic vegetative community develops around den sites, making dens conspicuous in aerial surveys of dry tundra communities (Chesemore 1969; Dementyeff 1958; Garrott et al. 1983b; Shibanoff 1958; Skrobov and Shirokovskaya 1968; Smith et al. 1992; Smits et al. 1988). However, dens are much less conspicuous in the wet

tundra of western Alaska (Anthony 1996) or the rocky coastal areas of western Greenland (Nielsen et al. 1994).

Arctic fox dens range from single burrows to large, complex structures, which may be used for many years (Garrott and Eberhardt 1987). A den may cover >50 m² and possess up to 100 entrances, the latter up to 34 cm in diameter (Chesemore 1969; Macpherson 1969; Nielsen et al. 1994; Prestrud 1992c). Density of dens varies between 1 den per 2,500 km² and 1 den per 12 km² and is typically low because suitable denning areas are rare and localized (Eberhardt et al. 1983a; Garrott et al. 1983b; Prestrud 1992c; Sdobnikov 1960; Smits and Slough 1993). Although den sites are scarce in some regions, based on estimates from occupancy rates, they may not limit productivity (Macpherson 1969). In developed areas, Arctic foxes may use culverts and road embankments as denning sites (Ballard et al. 2000b).

Arctic foxes have strong dominance hierarchies that relate to individual variation in aggressiveness (Fox 1969a, 1969b, 1970). Dominance among adult foxes is correlated with body size but not with body mass. Because of their larger size, males typically dominate females (Korhonen and Alasuutari 1994b, 1995; Wakely and Mallory 1988). In captivity, dominance in subadults is not related to either sex or mass.

In the wild, mates hunt and rest alone, and seldom interact (Frafjord 1991; Garrott et al. 1984; Hersteinsson and Macdonald 1982). Individuals communicate by a variety of vocalizations and body postures (Ovsyanikov et al. 1988a, 1988b).

Nuptial play between mates alternates with fights among males during the mating period. After mating, territories are established, and dens are prepared (Barabash-Nikiforov 1938; Dementyeff 1958). Arctic foxes may occasionally move their litter from one den to another. Nursing is initiated by the female calling pups out of the den or by pups nuzzling her belly. Both parents provide prey to young, but the female provides most of the food (Frafjord 1986; Garrott et al. 1984). When parents approach a den with young, a vocal cue (low chittering sound) is immediately followed by pup emergence. Pups obtain food on a first-come, first-serve basis. The parent either drops the food or lets the pups take it directly from its mouth. Adults regurgitate food to pups (Prestrud 1992b). Parents leave the den soon after feeding the pups, but occasionally stay to rest. Adults rarely play with young, and frequency of play decreases as the litter matures. Occasionally, females may share dens, leading to observations of large litters (Frafjord 1991; Strand et al. 2000).

Pups generally play (33% of the time) or rest (>50% of the time) when parents are away from the den. Play, however, is reduced during food shortages (Frafjord 1992b). Food consumption of young increases as they grow in size, but parent Arctic foxes generally return to dens less frequently as summer progresses. In compensation, young eat cached food and start hunting on their own, thus spending more time away from the den. The adult male generally abandons the family in late July or early August, whereas the female leaves a few weeks later. Dispersal of young normally occurs in autumn. When food is abundant, young may overwinter in the parental territory (Eberhardt et al. 1983a). Nonetheless, from this time until the next breeding season, the Arctic fox is highly mobile and mostly solitary.

Territorial defense is strongest during the denning season in April to August (Eberhardt et al. 1982; Korhonen and Alasuutari 1994b). Territories may overlap (Frafjord and Prestrud 1992). Territories are defended directly by chasing and mobbing and indirectly via scent-marking and vocalizations (Eberhardt et al. 1982; Hersteinsson and Macdonald 1982; Kullberg and Angerbjörn 1992). Arctic foxes scent-mark by defecating on visually conspicuous or elevated landmarks such as rocks and eskers (Gorman and Trowbridge 1989).

Caching is common when food is abundant (Samelius and Alisauskas 2000; Stickney 1991). During winter, Arctic foxes may rely on eggs cached during summer (Bantle and Alisauskas 1998; Fay and Stephenson 1989; Sklepkovych and Montevicchi 1996). Arctic foxes cache individual food items separately (scatter hoard) or several items at the same location (larder hoard). Arctic foxes may scatter hoard food to avoid cache loss to competitors (Frafjord 1993e) or may larder hoard foods where food is overly abundant or easy to defend (Frafjord 1993e; Sklepkovych and Montevicchi 1996). On Banks Island, Northwest Territories, Arctic foxes took mostly eggs when foraging among geese, and most eggs (ca. 97%) were cached. Adult geese and lemming were rarely captured, but most (83% of geese and 75% of lemmings) were consumed im-

mediately. In years of high fox abundance, Arctic foxes often moved eggs from old caches, either as a result of cache pilfering or to avoid cache pilfering (Samelius and Alisauskas 2000).

Arctic foxes are the most common predator of Arctic-nesting birds and their eggs (Larson 1960). Arctic foxes are typically more successful at stealing eggs from unattended nests or from nests of smaller birds (Samelius and Alisauskas 2001; Stickney 1991). However, predation on nesting adult birds occurs (Samelius and Lee 1998). During research activities, Arctic foxes often follow researchers and prey on eggs from nests unattended by birds because of human activity (Samelius and Lee 1998). Similarly, foxes may obtain eggs from larger birds by following larger animals that are flushing the birds (Samelius and Lee 1998). The impact of Arctic foxes can be very important because the Arctic fox may cache numerous eggs in a single day instead of immediately consuming them (Frafjord 1993e). At Icy Cape, Alaska, a single fox cached >500 eggs of common eiders (Quinlan and Lehnhausen 1982). The impact of Arctic foxes can be especially severe on islands where numerous species of colonial nesting birds, such as ducks (e.g., eiders), murrets (*Uria*), and razorbills (*Alca torda*), nest on the ground (Chesemore 1972). Arctic foxes are good swimmers and may swim for >45 min and distances >2 km (Strub 1992). The presence of Arctic foxes may prevent breeding (Spaans et al. 1998) or cause a reduction or delay (or both) in breeding effort of geese and seabirds (Bailey 1993; Birkhead and Nettleship 1995).

Arctic foxes at a large Arctic goose (*Chen caerulescens*) colony on Banks Island, Northwest Territories, took on average 900–1,570 eggs per fox per nesting season (Samelius and Alisauskas 2000). Nonetheless, the impact of Arctic fox predation on nesting geese was marginally low because Arctic foxes removed only 4–8% of all eggs available (Samelius and Alisauskas 2000). Egg remains appear in the feces of Arctic foxes even before the arrival of Arctic-nesting birds, suggesting that cached eggs are consumed long after nesting birds have left the nesting grounds (Bantle and Alisauskas 1998).

CONSERVATION STATUS. In North America and Iceland, *A. lagopus* is fairly abundant wherever it occurs, and the species is not at risk. However, populations in Fennoscandia crashed during the 1920s and are still very low despite total protection (Angerbjörn et al. 1995; Hersteinsson et al. 1989). There were as few as 40–80 Arctic foxes in Sweden in 1994 (Angerbjörn et al. 1995). Populations have been protected by law since 1928 in Sweden, 1930 in Norway, and 1940 in Finland. Hypotheses for the decline of and the failure to recover these populations include predation by red foxes, decrease in availability of large ungulate carcasses due to extermination of wolves, reduced hunting of red fox by humans, extreme cyclicity of lemming abundance, and increased incidence of new parasites and diseases such as sarcoptic mange (Hersteinsson et al. 1989; Loison et al. 2001). The distribution and abundance of Arctic foxes is likely to change with ongoing changes in global climate (Frafjord and Hufthammer 1994).

Moderate concentrations of heavy metals in organs of Arctic foxes in Svalbard suggest that anthropogenic contamination is not significant (Prestrud et al. 1994). However, high levels of PCBs may affect vital functions of the most contaminated Arctic foxes (Wang-Andersen et al. 1993).

GENETICS. The Arctic fox has $2n = 48$ –50 chromosomes. $FN = 88$ and includes 24 pairs of meta and submetacentric chromosomes. The X chromosome is medium in size and is also the smallest submetacentric (Chiarelli 1975).

Fox breeders have produced hybrids from *A. lagopus* and *V. vulpes*. However, hybrids are infertile because chromosomes of hybrids fail to pair properly to produce viable sperm or egg (Cole and Shackelford 1947; Wipf and Shackelford 1949). Phylogenetic analyses of genetic data suggest a close relationship between kit fox (*V. macrotis*), swift fox (*V. velox*), and Arctic fox (*A. lagopus*)—Mercure et al. 1993).

Historically, a single genetic locus was believed to determine color phase, with homozygous recessive individuals being white (Frafjord 1989; Nes et al. 1983). However, a number of cumulative genes contribute to the intensity of coat pigmentation in Arctic foxes (Filistowicz et al. 1997).

REMARKS. The generic name *Alopex* is from the Greek *alope* meaning a fox. The specific epithet *lagopus* is composed of two Greek words, *lago* meaning hare and *pus* meaning foot, signifying that this fox has hair on the soles of its feet (Borrer 1960;

Gotch 1979). Genetic data appear to contradict the distinction of *Alopex* from other foxes, and DNA hybridization data suggest that the Arctic fox is as similar to species of *Vulpes* as such species are to each other (Geffen et al. 1992). Most specifically, the Arctic fox and the swift fox (*V. velox*) are closely related, and mitochondrial DNA sequence divergence suggests a divergence time of 250,000 years (Geffen et al. 1992).

Other vernacular names are white fox, polar fox, and blue fox. Juveniles are commonly called pups, kits, whelps, and cubs. Other reviews of the biology of Arctic foxes include Chesemore (1975), Garrott and Eberhardt (1987), and Underwood and Mosher (1982).

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